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**How to verify fossil tracks: the first record of dinosaurs from Palestine**

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# How to verify fossil tracks: the first record of dinosaurs from Palestine

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## ABSTRACT

The identification of presumed tetrapod tracks is not always unequivocal. Other sedimentary structures have been repeatedly mistaken for tracks, including other trace fossils such as arthropod tracks, burrows and fish feeding traces; erosional features; and human-made traces. We here review instances of difficult, ambiguous, or controversial cases that have been discussed in the literature. We then discuss four main criteria for the verification of tetrapod tracks: (1) preservation of regular trackway morphology, (2) preservation of track morphology, (3) deformation structures (best seen in cross-section) and (4) the temporal or environmental context. Of these criteria, criterion 1 is the most unambiguous and has rarely been challenged. We apply these criteria to a new site located within the city of Al-Bireh, Palestine, which belongs to the Lower Cretaceous (Albian) Soreq Formation. The site preserves a surface with many indistinct depressions that lack anatomical detail. Two unequivocal trackways are identified per criterion 1, demonstrating the first known occurrence of dinosaur fossils in Palestine. The tracksite is part of the late Lower Cretaceous carbonate platform of the eastern Levant, demonstrating temporal emergence of the platform above sea level and a connection to the mainland.

## ARTICLE HISTORY

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## KEYWORDS

Fossil footprints; ichnology; recognition; verification; identification

## Introduction

Distinguishing tetrapod tracks from other sedimentary structures can be challenging. When indistinct in shape, or when exposed in cross section, tracks are often only recognised by specialists (e.g. Meyer and Thüring 2003; Bennett and Morse 2014). Conversely, other structures may be misinterpreted as tetrapod tracks, including arthropod trackways, burrows, impressions of other objects such as coprolites, fish feeding traces, sedimentary structures such as concretions, weathering pits and traces of anthropogenic origin, amongst others (see review below). One example of dinosaur tracks whose identification may not be immediately evident is described and discussed herein. This tracksite, located in carbonate platform deposits in the Al-Irsal area of Al-Bireh, Palestine, is the first record of dinosaurs in the country. Dinosaur remains are rare in the Middle East region. A number of tracksites, however, have been reported in recent years from Yemen (Schulp et al. 2008; Schulp and Al-Wosabi 2012; Al-Wosabi and Al-Aydrus 2015), Lebanon (Gèze et al. 2016), Jordan (Klein et al. 2020) and Jerusalem (Avnimelech 1962a, 1962b). The new tracksite presents new information on the palaeogeography of the region.

The purpose of the present contribution is twofold. First, we provide a review of the main criteria for the recognition of structures as tetrapod tracks as well as of controversial cases discussed in the literature, and discuss the potential pitfalls that may arise. Second, we apply these criteria to the Al-Irsal tracksite to demonstrate an unequivocal occurrence of dinosaur tracks – addressing previous doubt put forward by Palestinian scholars.

## Materials and methods

The tracksite is located in the Al-Irsal area of Al-Bireh, Ramallah and Al-Bireh Governorate, Palestine (Figure 1); (31°55'43.7" N, 35°12'27.2" E). The area exposes carbonate rocks of the Albian Soreq Formation, a 60–120 m thick succession that mainly comprises dolomites and marls with chert nodules in some horizons (Shachnai 2006). The Soreq Formation is part of the late Early Cretaceous carbonate platform of the eastern Levant (Figure 1) (Sass and Bein 1982; Bachmann and Hirsch 2006). This carbonate platform extends from southern Lebanon to northern Egypt and was part of the southern margin of the Tethys (Sass and Bein 1982; Bachmann and Hirsch 2006). The Al-Irsal tracksite is, to our knowledge, only the second dinosaur tracksite found on the carbonate platform. The first such record (Avnimelech 1962a, 1962b) stems from the village of Beit Zait, west of Jerusalem, in Israel, and is also part of the Soreq Formation (Sass and Bein 1982). The Beit Zait tracksite is around 17 km from the Al-Irsal tracksite. The carbonates of the Al-Irsal tracksite contain abundant black intraclasts.

The Al-Irsal tracksite was discovered by one of us (Owais) in 2019, and tracks were confirmed to be of dinosaurian origin by two of us (Lallensack and Sander) based on presented photographs. A preliminary report was published by Owais (2020). Collection of additional data of the tracksite, including a more complete photographic documentation for photogrammetry (Matthews and Breithaupt 2001; Matthews et al. 2006, 2016; Falkingham 2012), was conducted by Owais in fall 2020. The tracksite is located within an



**Figure 1.** Location of the Al-Irsal tracksite in the city of Al-Bireh, Palestine (red star). The tracksite is located within the carbonate platform of the eastern Levant (grey areas, after Sass and Bein 1982).

urban area and has partly been destroyed by building activity; cement was applied to parts of the surface. The site may be threatened by further destruction if no protective measures are taken.

Photographs for photogrammetry were collected using a cell phone camera (Samsung Galaxy A51), and the digital model was built using Agisoft Metashape (agisoft.com). Despite limited resolution and quality of the photographs, the resolution of the resulting model is sufficient to allow for evaluation and verification of the trackways. The 3D model was automatically fitted to the horizontal plane using Meshlab (meshlab.net) to allow for a precise top view in orthographic projection. Visualisations, including an orthophoto and a surface inclination plot (enhancing the slopes of topographic features), were exported from ParaView (paraview.org); see Lallensack et al. (2022a) for a detailed discussion of this methodology.

## Results and discussion

### Recognising tracks from photographs

Because single photographs are inherently two-dimensional, they cannot completely convey a three-dimensional structure such as a track. Consequently, such photographs may be highly misleading. For example, a photograph presented by González et al. (2006, fig. 2G) shows what appears to be a convincing human track including separate toe impressions. However, this ‘footprint’ is in fact a set of anthropogenic tool marks, and lost all track-like features when visualised as depth-colour map based on a 3D model (Morse et al. 2010, fig. 3L). 3D models may overcome the limitations of simple photographs and can be easily and cost-effectively created based on multiple photographs of the track or tracksite using photogrammetry (e.g. Matthews et al. 2016). A basic photogrammetric model can be calculated based on as few as two photographs that show the same surface at slightly different angles,

although more photographs are preferred. The resulting 3D models can be oriented in a precise top view and visualised without perspective distortion (see Lallensack et al. 2022a for methodology). 3D models may allow for an independent evaluation of reported tracks even when physical access to the specimens is not possible and should be publicly provided (Falkingham et al. 2018). Unfortunately, 3D models of many of the controversial tracks reviewed below are not yet available.

When discovered by locals, an initial assessment of a potential tracksite often has to be done from afar based on presented photographs, which are often shot at angles to the surface and under suboptimal light conditions. In some cases, and especially when the tracks are larger and preserved as natural moulds, naturally-occurring colour distinctions can help with recognising depressions. The floor of depressions may trap organic matter or enable algae growth due to increased moisture (Kuban 1989b), and evaporation of infilling water may leave concentric rings that are equivalent to rough contour lines (Figure 2). In the case of the Palestine tracks, trapped organic matter and white and black contours greatly helped with the initial identification (Figure 2).

### Previous misinterpretations and controversial cases

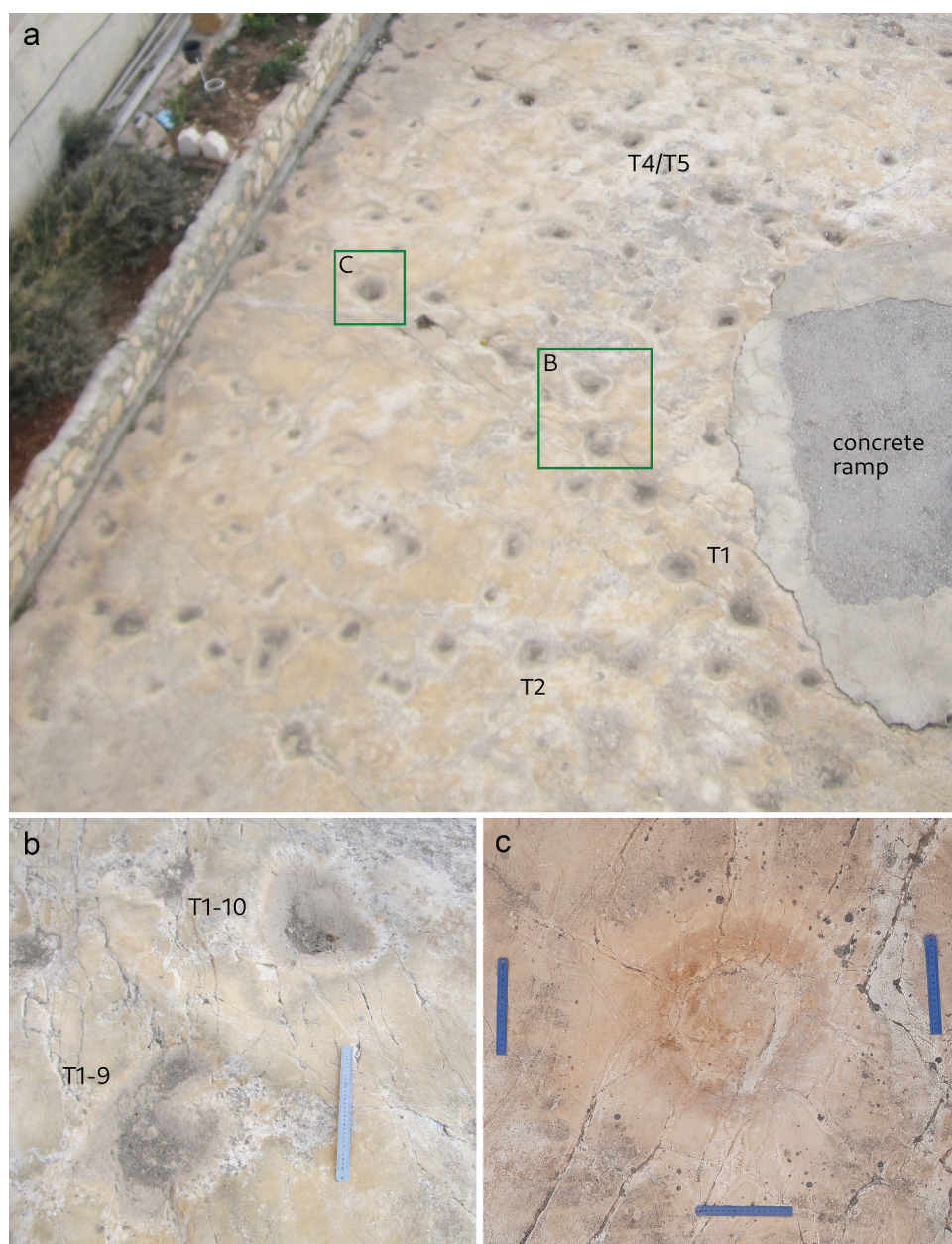
In the past, other sedimentary structures had been repeatedly confused with tetrapod tracks. We here review cases discussed in the literature in which tracks have either been misidentified or their verification has proven difficult. Our goal is not to call out specific work as being wrong, but to highlight how difficult it can be to ascertain the nature of track-like structures. We also do not necessarily agree with the reinterpretations in all cases. We restrict ourselves to published cases, but note that the majority of previous misidentifications remain unpublished.

### Arthropod tracks

Extant limulids (horseshoe crabs) have four pairs of walking legs with bifid feet and one posterior pair of ‘pusher’ legs, which leaves prints of variable morphology with elongate ‘digit impressions’ that may resemble tracks of birds or lizards (Shibata and Varricchio 2020). Size is of limited use as a criterion to recognise such tracks; e.g. Gaillard (2011) described a giant trackway pertaining to a limulid approximately 38 cm wide and 80 cm long. In the 19th and early 20th centuries, limulid tracks were widely believed to be the produced by tetrapods, until Caster established their true identity in a series of papers (Caster 1938, 1939, 1940, 1941). Limulid tracks from the Upper Jurassic Solnhofen limestone of Germany have been misinterpreted as the tracks of pterosaurs, *Archaeopteryx*, and the dinosaurs *Compsognathus* or *Ornitholestes* (see Caster 1941 and references therein). Although key features of these tracks – the pronounced heteropody and the side-by-side (rather than alternating) placement of the prints – have been noted, they were interpreted as evidence that the animal must have impressed its wing (or hand) while using a hopping gait (e.g. Abel 1935). Other limulid tracks from the Devonian to the Palaeogene had originally been ascribed to birds or dinosaurs (Abel 1926, 1935; Caster 1939); amphibians (Aldrich and Jones 1930; Willard 1935; Caster 1938; King et al. 2019); and lizards (Young 1979; Lockley and Matsukawa 2009; Xing et al. 2012). Other arthropod walking traces, such as *Diplichnites*, may be difficult to distinguish from tetrapod tracks (Lockley 1993) and have been repeatedly mistaken for such (e.g. Sarjeant 1976; Lockley and Hunt 1995; Lucas and Lerner 2001; Gouramanis et al. 2003).

In the Devonian fossil record, the distinction between tetrapod trackways and those of arthropods remains a controversial issue. The most widely accepted Devonian tetrapod trackways are from the





**Figure 2.** The Al-Irsal tracksite. (a) Overview, showing trackways T1, T2 and the partly overlapping T4/T5. Detritus accumulating in depressions highlight individual footprints on photographs. Note the heavy destruction by urban development. Green rectangles indicate the position of tracks shown in (b) and (c). (b) Detail of footprint 9 and 10 of trackway T2. Note the whitish outlines contouring the impressions. (c) Detail of unidentified footprint.

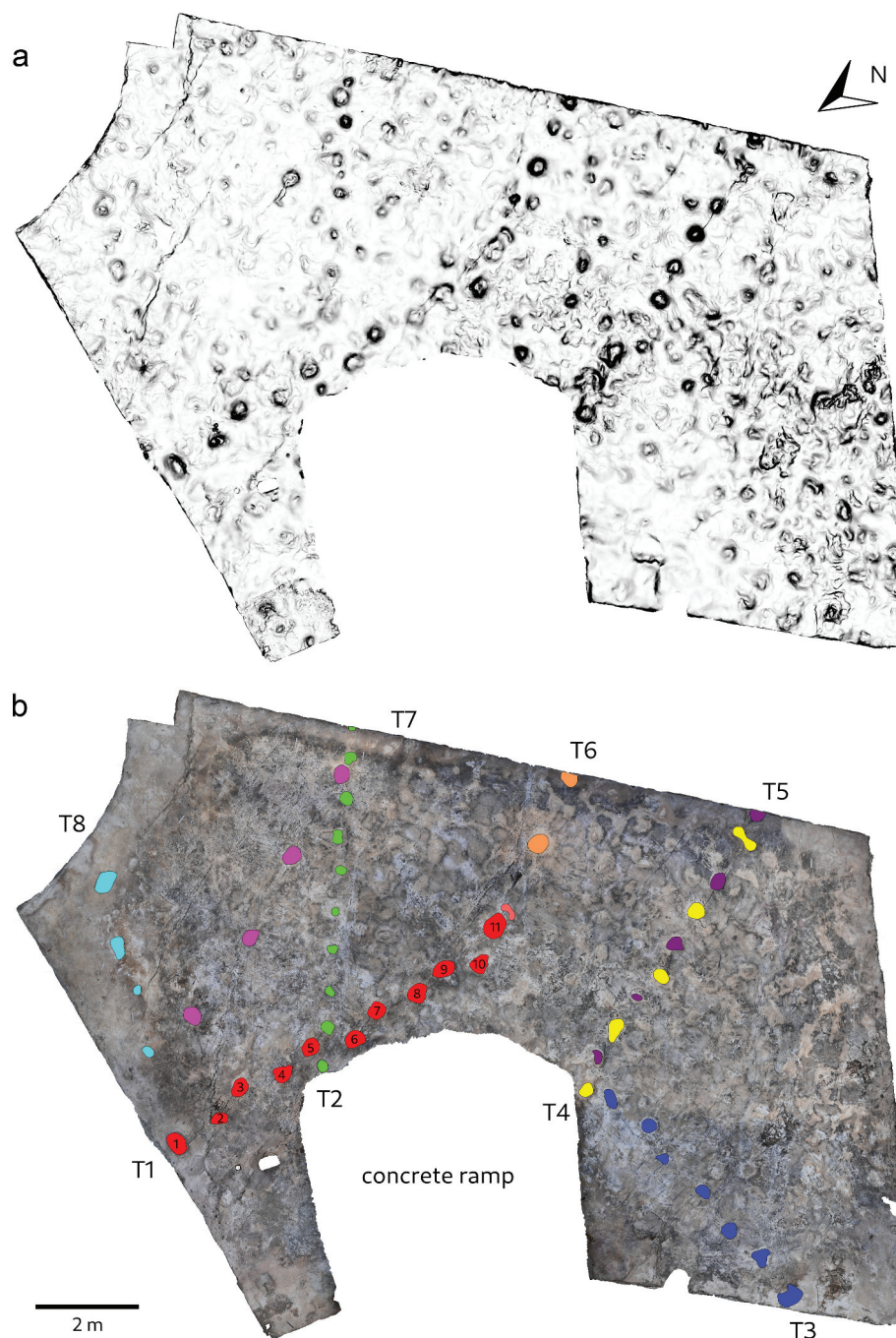
Genoa River Beds, Australia (trackway 1, Warren and Wakefield 1972) as well as from Valentia Island, Ireland (Stössel 1995). Both trackways show an alternating (zigzag) footprint arrangement as well as consistent size differences in the pes and manus tracks that support their identification; both features are not expected in arthropod trackways (e.g. Clack 1997; Lucas 2015; Stössel et al. 2016). In contrast, a possible tetrapod origin of two long trackways from eastern Greenland (Friend et al. 1976) is generally dismissed because of the lack of an alternating pattern, overstepping, and size differentiation that could be related to pes and manus (Clack 1997; Lucas 2015). Other trackways are more equivocal. A short trackway with an alternating pattern from North Scotland was accepted as a tetrapod trackway by recent reviews (Rogers 1990; Clack 1997; Lucas 2015), though an arthropod origin could not be fully discarded (Rogers 1990; Clack 1997). A trackway from the Grampians Group, Australia, was described as the earliest tetrapod trackway (Warren

et al. 1986), but lacks both an alternating pattern and any size differentiation between manus and pes and was therefore questioned (Clack 1997) or entirely dismissed (Lucas 2015). Clack (2012) notes that this trackway could have been produced by a large invertebrate or, if formed under water, by the forelimbs of a placoderm fish such as *Bothriolepis*. A single, short trackway from the Tumblagooda Sandstone, Western Australia, with very short steps and markings reminiscent of scratch marks, was interpreted as evidence for tetrapods as early as the Early–mid Silurian (McNamara 2014); yet again, this identification was subsequently questioned (Ahlberg 2018).

#### **Fish feeding traces/nests**

Numerous depressions from the Middle Devonian of the Holy Cross Mountains, Poland, were interpreted as the earliest known tetrapod tracks based on trackway patterns and footprint morphology (Niedźwiedzki et al. 2010; Qvarnström et al. 2018). The





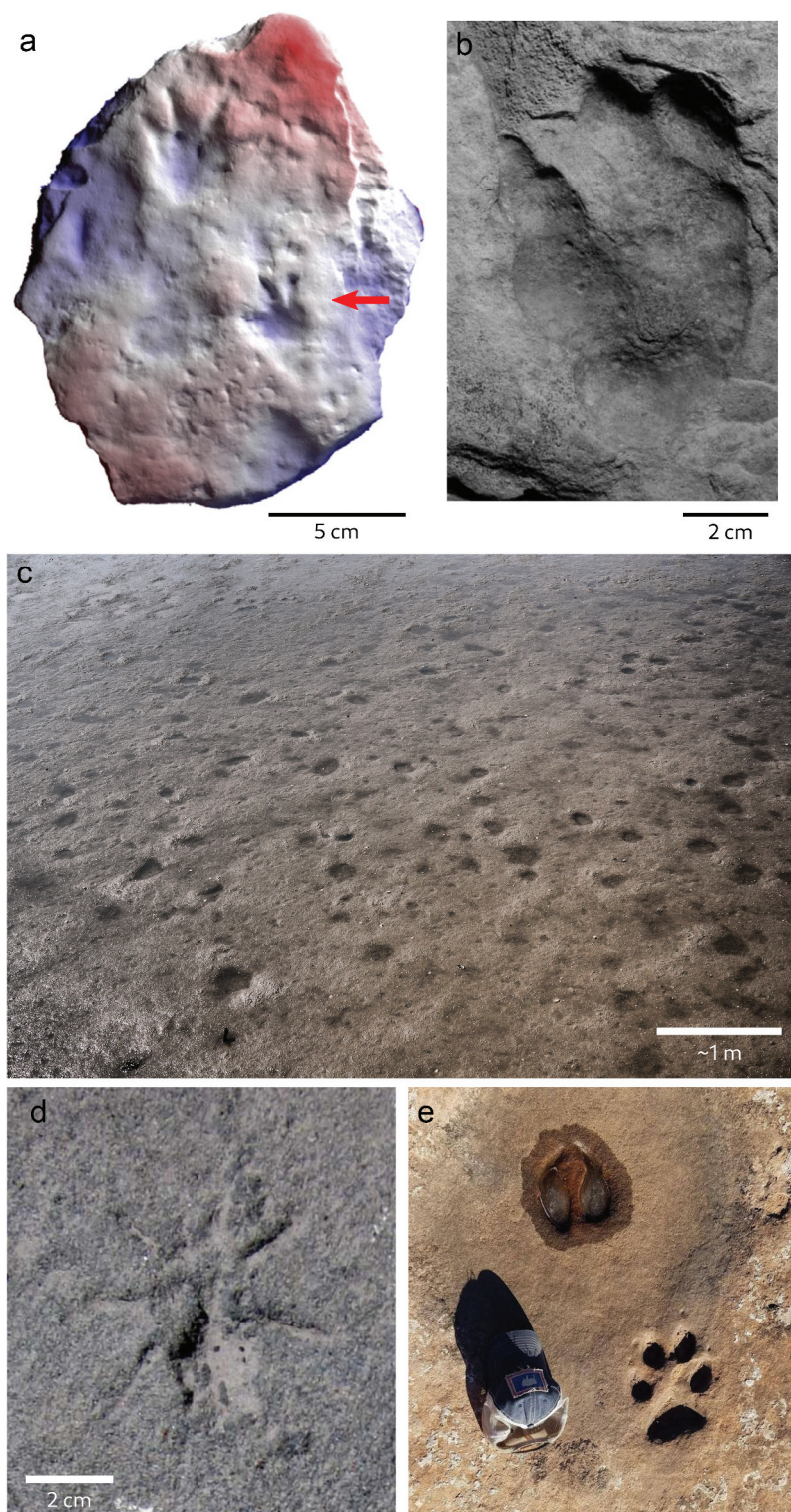
**Figure 3.** Photogrammetric model and site map of the Al-Irsal tracksite. (a) Surface inclination plot (normal plot) of the photogrammetric model. Darker shades of grey indicate more inclined areas, while white shades indicate less inclined areas, thus outlining the slopes of tracks and other topographic features. (b) Photogrammetric orthophoto with superimposed sitemap, showing trackways T1–T8. Note the clear and predictable trackway pattern in T1.

interpretation of both the trackway patterns and the apparent anatomical detail has been refuted in detail by Lucas (2015), who favours an interpretation as fish feeding or fish nest traces. Lucas argued that only one of the trackways shows a clear alternating pattern; this trackway is short, differs from the other presumed trackways, and is not completely regular. A consistent alignment in double-rows, as was interpreted by Niedźwiedzki et al. (2010) for a number of trackways, would, however, be inconsistent with an interpretation as fish feeding traces/nests. A cross-section appears to show deformation structures including downward bending of layers (Niedźwiedzki et al. 2010, supp. fig. 19), which, again, is not expected in a fish-feeding trace where

sediment is removed rather than pushed down. Several isolated impressions show what Niedźwiedzki et al. (2010) interpreted as digit impressions, while Lucas (2015) compared them with broken-up faecal matter of fish (Pearson et al. 2007, fig. 7A). We note that the alternative possibility, that some of the trackways were produced by arthropods, has not been sufficiently discussed and may require attention.

Fish feeding traces (Figure 4C) can easily be mistaken for tetrapod tracks (Martinell et al. 2001; Belvedere et al. 2011; Lucas 2015). These are generally round or oval impressions that are otherwise featureless, although impressions of parts of the fish, such as the barbels, may occur on one side; these can





**Figure 4.** Examples of potential pitfalls in the identification of tetrapod tracks. (a) Two apparent tracks from the Late Triassic of Wales (Larkin et al. 2020). The lower impression (arrowed) is an erosional artefact caused by shell fragments still visible within the 'digit impressions'. modified from Larkin et al. 2020. (b) The impression *Thinopus* Marsh (1896), originally identified as the oldest record of a limbed vertebrate, but now thought to represent the impressions of fish coprolites (Abel 1935; Lucas 2015). Modified from Lucas (2015). (c) Modern fish feeding traces on a tidal flat in Conwy, North Wales. (d) Invertebrate trace fossil (*Asterichnites octoradiatus*, Early Cretaceous, Mowry Shale, Wyoming) that may be confused with tetrapod tracks especially when incomplete. Photo courtesy of Susan Susan Bednarczyk. (e) Carved bison and mountain lion 'tracks' in Pennsylvanian/Permian sandstone (Casper Formation, southeastern Wyoming). Photo courtesy of David B. Peel.

resemble impressions of digits (Pearson et al. 2007, fig. 2; Lucas 2015). The distribution of the impressions can be moderately regular (Martinell et al. 2001) to very regular (Belvedere et al. 2011), but they may occasionally be aligned in short, irregular

rows (Lucas 2015). Importantly, fish feeding traces generally do not overlap, because fish tends to feed in areas that have not been probed for foot before (Martinell et al. 2001); in tracksites with a higher density of tracks, overprinting is common.

### Erosional features

Holes that may resemble tracks can be produced by weathering and erosion. Conversely, highly weathered tracks may be difficult to identify as such. Erosional features include scour marks, which are generally oriented to local flow of water or wind (Lallensack et al. 2022b). Erosion may remove chunks of rock from the walls of existing depressions that, when smoothed by subsequent weathering, can result in an undulating margin that may resemble digit impressions (Falkingham et al. 2021). A slab from the Late Triassic of Gloucestershire, England, shows two apparent reptile footprints, but Larkin et al. (2020) demonstrated with macro photography that one of these impressions is an complex erosional trace initiated by broken bivalve shells that are still visible within the 'digit impressions' (Figure 4A).

Seiler and Chan (2008) described a site from the Navajo Sandstone of Arizona as a trampled surface with multiple track types attributed to dinosaurs, which were subsequently demonstrated to be weathering pits (Breithaupt et al. 2021). These depressions are circular, oval, or irregular in shape, and, in some cases, are arranged in clusters that show superficial resemblance to tridactyl tracks (Seiler and Chan 2008, fig. 5D) and pes-manus sets (Seiler and Chan 2008, fig. 5C,E,G) of dinosaurs. Narrow extensions leading out of the impressions resemble digit drag marks (Seiler and Chan 2008, fig. 5A,I). Strikingly, some of these pseudofossils show distinctive rims that resemble the displacement rims of tracks (Seiler and Chan 2008, fig. 5F). The exact formational mechanism of these rims is unknown; they may be the result of differential weathering (Breithaupt et al. 2021). Trackway patterns, consistent track morphology, or correspondence of shape features to known trackmaker anatomy is absent (Breithaupt et al. 2021). Most convincingly, there is no evidence for sediment deformation, as seen in cross-sections of the depressions.

Seemingly, randomly distributed pits were reported from the Late Triassic Caturrita Formation of Brazil and attributed to basal sauropodomorph dinosaurs (Da Silva et al. 2007). Circular depressions of highly variable sizes are more or less randomly distributed over a surface; few tracks show three prominent 'finger-like' structures resembling digit impressions, but without correspondence to known trackmaker anatomy. Breithaupt et al. (2021) questioned their interpretation as tracks due to the absence of footprint and trackway morphology. Ashton et al. (2014) interpreted a pitted surface from the Early Pleistocene of Happisburgh, UK, as a trampled ground containing numerous human footprints. Although footprint size is variable and toe impressions could only be identified on a single footprint, these authors based their interpretation on the consistent shape of these impressions (Ashton et al. 2014).

### Other cases of ambiguous track morphology

Impressions from the late Miocene of Crete have been interpreted as possible hominin footprints (Gierliński et al. 2017). However, both their interpretation as footprints and their interpretation as hominin footprints was subsequently questioned by Meldrum and Sarmiento (2018). The possible prints are variable in size (Meldrum and Sarmiento 2018) but show some repetitive shape features such as an elongate shape, a rounded heel, and a broad and asymmetrical distal margin with indentations interpreted as digit impressions (Gierliński et al. 2017). Identified trackways are equivocal (Gierliński et al. 2017). We argue that the described morphological features and their consistency in separate tracks are difficult to explain by any of the alternative formation mechanisms considered herein. Therefore, the identification of at least some of these structures as mammalian tracks, possibly hominin (Gierliński et al. 2017) or rock hyrax (Meldrum and Sarmiento 2018), is likely.

Hirschfeld and Simmons (2021) interpreted sub-circular depressions from the Late Cretaceous of Colorado as non-dinosaurian tetrapod tracks occurring together with unequivocal dinosaur tracks. Alternative explanations that were discussed include clam escape burrows (*Fugichnia*), ray feeding traces, fish nests, load casts, and fossil gas domes. These structures had been described as features of uncertain origin by Lockley et al. 2018.

Most problematic are isolated tracks showing an apparent track morphology that does not closely correspond with the anatomy of known trackmaker candidates. Marsh (1896) described an apparent footprint, *Thinopus antiquus*, from the Late Devonian that appears to show digit impressions with well-defined phalangeal pad impressions. This specimen was later interpreted as the impressions of fish coprolites (Abel 1935; Lucas 2015). Another isolated Devonian specimen, a possible isolated footprint with four digit impressions, was originally described by Leonardi (1983) as *Notopus petri*, now *Allophylichnus* (Van Bakel et al. 2003). Roček and Rage (1994) considered this specimen to be a starfish or ophiuroid trace. A fossil from the Orkney Islands was considered to be a tetrapod trackway (Westoll 1937) but possibly is a plant fossil (Lucas 2015). The digit-like impressions of the possible cephalopod trace *Asterichnites octoradiatus* (Figure 4d), (e.g. Connely 2019) have been repeatedly misidentified as tetrapod tracks (Vokes 1941; Burford 1985). Dickas (2018, p. 249) misidentified three aligned *Diplocraterion* burrows from the Red Gulch Dinosaur Tracksite as a theropod track because of their coincidently tridactyl arrangement. Horseshoe-shaped invertebrate burrows attributable to the *Rhizocorallium* have been repeatedly confused with tetrapod tracks (Hitchcock 1858; Gabunia et al. 1988; Lockley et al. 1994). Sedimentary structures such as sand crescents (Lockley et al. 1994) and eroded gypsum nodules (Falkingham et al. 2021) may potentially be confused with tracks in some cases.

### Anthropogenic traces

Last but not least, artificial anthropogenic structures are occasionally confused with tracks. Markings in volcanic ash of the Valsequillo Basin, Mexico, have been interpreted as human footprints by González et al. (2006), despite a lack of convincing trackways. The identification as human tracks was quickly questioned because refined dating revealed an unlikely age of 1.3 Ma (Renne et al. 2005; Feinberg et al. 2009). Morse et al. (2010) identified the artefacts as tool marks left by quarry workers (see discussion below). Panarello et al. (2018) described a similar case from Carangi, Italy, where markings resembling human-like footprints were found near the Ciampate del Diavolo site that contains actual human footprints. The isolated markings were interpreted as tool marks smoothed by transit of humans, animals, and vehicles as well as by weathering (Panarello et al. 2018).

A special case of anthropogenic structures are frauds (Figure 4E). Because footprints are simple surface relief features that do not involve materials other than the host rock, they are principally easy to forge (Seilacher 2007). Some of the most infamous cases of forgery are purported human tracks from dinosaur tracksites in the bed of the Paluxy River, Texas (Kuban 1989a). Such chiselworks are inspired by actual elongate dinosaur tracks found locally that show a superficial human-like appearance (Farlow et al. 2012; Lallensack et al. 2022b). A single track from the Eocene of Washington referred to a bird similar to *Diatryma* had been considered a fraud, but was later found to be probably genuine (Patterson and Lockley 2004). Frauds may be deceiving especially when subsequently weathered, or when genuine tracks are 'improved' by chiselling, as was documented for some dinosaur track casts from coal mines of Utah (Lockley and Hunt 1995, p. 226). As with erosional features, study of the



purported tracks in cross section may reject or support their veracity – while rock can easily be chiselled away, it cannot be bent to imitate sub-surface deformations such as undertracks.

### Criteria for the recognition of tetrapod tracks

We here distinguish four main criteria that may be used to recognise tetrapod tracks:

- (1) Regular trackway morphology
  1. Alternating foot placement
  2. Differentiation into pes and manus
- (2) Track morphology
  1. Correspondence with known anatomy
  2. Consistency in multiple tracks
- (3) Deformation structures
- (4) Temporal and environmental context

### Regular trackway morphology

The majority of trackways are straight and with minimal variation in stride lengths (and thus, locomotion speed). Therefore, a series of impressions in a geometric pattern with consistent distances and angles between footprints and predictable footprint positions can be considered the strongest evidence for an identification as tracks (but not necessarily tetrapod tracks, see below). Clear trackway patterns have rarely been disputed in the literature, and therefore can be regarded as the most objective and unambiguous evidence. An exception is a specimen from the Devonian of Poland that was interpreted as an unambiguous trackway consisting of nine tracks (Niedzwiedzki et al. 2010), but was questioned by Lucas (2015), who argued that it is more irregular than expected.

A high density of impressions at a tracksite can increase uncertainty, especially when the trackway segment is short and/or irregular. However, size, shape and depth of tracks within a trackway tend to be less variable than between other tracks. Ideally, the shape of the individual footprints, as well as markings that were potentially formed by digits, will align with the direction of the recognised trackway, corroborating its interpretation. It has to be noted that the absence of recognisable trackways does not necessarily preclude an identification as tracks, and extensive surfaces with many tracks but no clear trackways are not uncommon (e.g. Meyer and Thüring 2003; Ashton et al. 2014; Falkingham et al. 2021).

Quadrupedal tetrapod trackways have often been confused with those of arthropods. Arthropod trackways, however, are expected to show a 'ladder-like' arrangement of tracks, where tracks are placed one next to another rather than in the alternating zigzag arrangement diagnostic for tetrapod tracks (Clack 1997; Lucas 2015). Tetrapods may produce a 'ladder' arrangement only if the combination between stride length and gleno-acetabular distance is such that the pes-manus distance is equal to half a stride length. Tetrapod tracks may furthermore show a size differentiation of the pes and manus tracks, i.e. heteropody (e.g. Lucas 2015). However, heteropody is also found in limulid tracks (Shibata and Varricchio 2020), while manus and pes may be similar in size in tetrapods. The absence of heteropody in a trackway may be due to a lack of anatomical fidelity of the tracks.

### Track morphology

Tracks may be reliably identified as such when they show unequivocal track characteristics, most importantly anatomical detail. The question as to what constitutes such characteristics, however, has proved to be highly controversial and subjective in many cases (see review above). The great diversity of anatomy-related features that

can possibly be observed in tracks, in combination with the incalculable diversity of alternative processes that may potentially produce such features, has repeatedly resulted in misinterpretations even when the features in question are clearly defined (e.g. Figure 4B). We consequently define two additional criteria that, especially when used in combination, may greatly strengthen an interpretation as tracks: (1) correspondence with known track-maker anatomy (Lucas 2015) and (2) consistency of these features in separate tracks.

These criteria may be illustrated using the purported human tracks from the Valsequillo Basin, Mexico (González et al. 2006), which have subsequently been questioned (Lockley et al. 2007) and were later demonstrated to be quarrying tool marks (Morse et al. 2010). González et al. (2006) based their interpretation on six criteria that are all based on expected morphology of human tracks, such as a large, protruding hallux mark and deeply impressed ball and heel areas, while the track is shallower at mid-length. However, these features are not consistent even in the figured example tracks. Morse et al. (2010) demonstrated that the markings are, on average, deepest at mid-length, which is incompatible with the known anatomy of human feet. The contradicting observation of González et al. (2006) may therefore be based on a sampling bias. A sampling bias can be difficult to avoid when only a fraction of the tracks show sufficient anatomical detail, as is common with fossil tetrapod tracksites (Lockley and Hunt 1995). It is crucial to select potential tracks using objective criteria devoid of *a priori* assumptions about anatomy. Statistical methods may be suitable to test for the presence of particular features in a quantitative and objective way (Morse et al. 2010), although these may blur or average out details that occur in only some tracks.

It has to be stressed that the shape of a track is not only determined by anatomy but also by foot kinematics and substrate properties (especially the water content), post-formational alteration, and the mode of preservation (e.g. transmitted undertrack vs. true track) (Falkingham 2014). For example, collapse of track walls may not only erase such detail but greatly shrink an impression and even lead to unexpected shapes (Falkingham et al. 2020; Gatesy and Falkingham 2020; Lallensack et al. 2022b). In many cases, rounded holes are identified as tracks purely based on their unequivocal arrangement in a trackway (e.g. Xing et al. 2013). On some trampled surfaces, only a single isolated track bears sufficient anatomical detail that allows for their interpretation (e.g. Ashton et al. 2014; Falkingham et al. 2021). Therefore, the absence of track morphology does not necessarily falsify an interpretation as tracks. Furthermore, the criterion of consistency may be more useful in some cases than in others.

### Deformation structures

Tracks are the result of the interaction of the foot with the substrate, and consequently involve deformation of the latter. Tracks, therefore, extend into the subsurface to varying degrees, either transmitting deformation (transmitted undertracks) or penetrating through the original surface (penetrative undertracks) (Gatesy and Falkingham 2020). In contrast, depressions resulting from ancient or modern erosion (Breithaupt et al. 2021), or even human activity such as tool marks or frauds, are topographic features which will cut through subsurface layers without deflecting them downwards. Evidence for an extension of the track volume into the subsurface, seen in cross-section, may therefore exclude such possibilities. It is, however, not always easy to distinguish tracks seen in cross section from features related to local subsidence or soft-sediment deformation (Bennett and Morse 2014). Deformation may be difficult to detect when layering is absent. In many cases, cross sections may



not be available unless destructive methods are applied, and subsurface deformation cannot be directly studied in cases where only the natural casts are preserved.

Surface relief features, such as well-developed, asymmetrical displacement rims, may indicate deformation (e.g. Falkingham et al. 2021). However, rims surrounding depressions may alternatively be caused by differential weathering (Breithaupt et al. 2021) or burrowing or foraging activity of other animals (cf. Pearson et al. 2007), or even eroded gypsum nodules, amongst others.

### Context

Potential tracks may not always fit into their presumed context, which has repeatedly been used as an argument to question their identity. For example, purported human tracks from Valsequillo, Mexico, have been rejected as such due to their old age (Renne et al. 2005; Feinberg et al. 2009). In many cases, such a mismatch may not necessarily be due to a misinterpretation of the tracks, but could possibly be due to a misconception of the context, or incomplete knowledge about the spatial and temporal distribution of trackmakers. Because of their different preservation potential, tracks predate the body fossil record in many cases (e.g. Brusatte et al. 2011). The possible identity of tetrapod tracks from the Devonian of Poland (Niedzwiedzki et al. 2010) was questioned partly based on their assumed marine environment (Niedzwiedzki et al. 2010; Lucas 2015), although a subsequent study argued for a non-marine environment (Qvarnström et al. 2018). Tracks are often the only unequivocal evidence for a temporal emergence of surfaces above sea level (e.g. Shuler 1917; Avnimelech 1962a; Benton 1986; Dalla Vecchia 1994, 2005; Breithaupt et al. 2004, 2006; Mezga et al. 2007; Marty 2008; Petti et al. 2011; Lallensack et al. 2015). Tracks as well as bones are frequently found on carbonate platforms, sometimes a hundred kilometres from the predicted mainland, which indicates short-term terrestrialisation including lush vegetation that was necessary to sustain dinosaur populations (Dalla Vecchia 1998; Mezga et al. 2007).

In some cases, the identification of potential tracks as erosional features has been rejected based on the lack of similar depressions on other surfaces found nearby (e.g. Ashton et al. 2014). However, Breithaupt et al. (2021) noted that weathering pits in the Navajo Sandstone are found on particular exposed surface but not others. Conversely, the proximity of potential tracks to unequivocal tracks does not necessarily support their identity (Panarello et al. 2018; Breithaupt et al. 2021).

### Interpretation of the Al-Irsal site

The Al-Irsal tracksite contains numerous depressions, most of which are indistinct, and details that may relate to the anatomy of a trackmaker are not obvious. A moderate displacement rim, however, can be observed in the southernmost footprint of trackway 5. Most convincingly, the identification as vertebrate tracks is demonstrated by the clear trackway pattern of trackway 1 (T1), which comprises 11 consecutive impressions arranged in a zigzag pattern with consistent pace, stride and pace angulation values. This consistent zigzag pattern over a relatively long distance rules out an interpretation of the impressions as fish feeding traces or weathering pits. The footprints of T1 tend to be somewhat elongated, with their long axes parallel to the trackway midline. They also are distinctly larger and deeper than most impressions that are located nearby; the possibility that the observed trackway configuration is simply coincidence can thus be discarded as unlikely. More difficult to reject, however, is the possibility that some individual footprints are not part of the trackway. Particularly ambiguous are the first

footprint of the trackway, which greatly differs in shape, and the last footprint, whose referral to the trackway indicates a smaller pace angulation than seen elsewhere in the trackway.

A second unequivocal trackway is trackway 2 (T2), which consists of 10 tracks. Compared to trackway 1, the tracks of trackway 2 are much smaller, and the trackway is straight without a zigzag-pattern. The pace and stride lengths, pace angulation values, and footprint sizes are consistent within the trackway. Other trackways are more equivocal. Trackway 3 (T3) consists of seven tracks arranged in a subtle zigzag pattern, with consistent pace, stride and pace angulation values. However, the individual tracks are more indistinct and variable in size, and their distinction from nearby prints is less obvious. Finally, trackways 4 and 5 (T4, T5) consist of a row of distinct impressions, which are, however, very variable in size and shape and do not match a regular trackway pattern. These tracks are here interpreted as two separate trackways, with T4 arranged in a subtle zigzag pattern and T5 arranged in a relatively straight line. Additional, but more equivocal trackways can be identified on the surface (Figure 3B).

The variation in pace angulation between trackways, resulting in both straight and zigzag patterns, is known from other Lower Cretaceous theropod track sites (e.g. Lallensack et al. 2016). The described tracks vary greatly in size. The track walls are gently sloping so that the innermost footprint outline is often only a fraction of the area of the outer footprint outline. These features may indicate a soft substrate into which the feet penetrated deeply, with sediment partly collapsing during or after track formation. It is possible that the feet penetrated the sediment more deeply than apparent from the track surface, and therefore are penetrative (Gatesy and Falkingham 2020; Turner et al. 2020). A preservation as transmitted undertracks is inconsistent with the high relief of some of the smaller tracks, such as footprint 2 of T1.

T1 and T2 show similar stride lengths (mean: 152 and 148 cm, respectively), although the tracks of T2 are consistently smaller (maximum footprint length: 55 cm in T1; 30 cm in T2) and pace angulation values are larger (mean: 145° in T1; 175° in T2). This indicates that at least two trackmaker taxa were probably present at the site, although it cannot be excluded that the trackmaker of trackway 2 was a juvenile of the trackmaker taxon responsible for T1. The very narrow gauge of T2 indicates a theropod trackmaker (Thulborn 1990), although its direction of travel is difficult to reconstruct. The possible trackmaker and direction of travel of T1 is equivocal. Owais (2020) interpreted subtle indentations of footprint 10 of T1 as the broad digit impressions of an ornithopod trackmaker. This would indicate a walking direction of T1 towards the east, and a strong outward rotation of footprint 10. However, unequivocal ornithopod trackways typically show a marked inward rotation instead (Thulborn 1990). Rotation of the remaining tracks of T1 is difficult to discern due to their indistinct shape. Three tracks (4, 8 and 9) are tapering towards the east, which could possibly be interpreted as the impression or drag mark of digit III. Assuming a direction of travel towards the west, it is alternatively possible that these tapering ends represent metatarsal marks of the deeply penetrating feet (Gatesy et al. 1999). A dumbbell-shaped impression in front of the last footprint of T1 (footprint 11) resembles the manus impression of a sauropod trackmaker. This opens the possibility that T1 is in fact a very narrow-gauged, pes-only sauropod trackway. However, the long strides, and in particular the high pace angulation values (maximum: 161°) speak against this interpretation (Lallensack et al. 2019). We here tentatively interpret T1 as the trackway of a theropod or ornithopod dinosaur that leads towards the east.

## Significance of the site

Together with the Beit Zait tracksite in Israel, the present tracksite demonstrates an at least local and temporary emergence of the carbonate platform of the eastern Levant above sea level, as well as a connection to the main land that allowed for the migration of the dinosaurs. Furthermore, the dinosaur tracks might indicate the presence of vegetation and, consequently, soil formation, as has been inferred for other Jurassic to Cretaceous carbonate platforms of the Tethys (Dalla Vecchia 2003; Waite et al. 2013). Dinosaur tracks, especially when showing little anatomical detail, can easily remain unnoticed when occurring in unexpected locations (e.g. Meyer and Thüning 2003). Their first recognition in Palestine, therefore, is hoped to increase awareness, which may possibly lead to the discovery of additional sites in the future.

While significant for the palaeogeography of the region, the indistinct appearance and low anatomical fidelity of the individual tracks revealed limited information about the dinosaurs themselves. However, discarding these tracks as ‘badly preserved’ (e.g. Marchetti et al. 2019) disregards their nature as sedimentary structures, as it implies degradation from an original state that was better preserved, which is not necessarily the case (Gatesy and Falkingham 2017; Falkingham and Gatesy 2020).

## Conclusions

Distinguishing tetrapod tracks from other structures can be challenging. We discuss four main criteria to verify tracks. The first – the presence of regular trackway morphology – is argued to be the most convincing and unequivocal criterion. Additional criteria are needed to distinguish tetrapod from arthropod trackways, including an alternating arrangement of tracks as well as size differentiation of pes and manus tracks. The second criterion – the presence of track morphology – is the most obvious but proved to be ambiguous in many controversial cases discussed in the literature. Again, two additional criteria may strengthen an identification as tracks, namely the correspondence with known trackmaker anatomy and consistency of discussed features in multiple tracks. The third criterion, the presence of deformation structures that are part of the track, is particularly useful when cross-sections are available. The fourth criterion is the temporal or environmental context the supposed tracks are found in, although assumptions about the context often come with uncertainties.

Conspicuous surface depressions in the Al-Irsal site in Al-Bireh, Palestine, are demonstrated to represent unequivocal dinosaur tracks based on our criterion 1. The site likely records at least two different trackmaker taxa. A larger trackmaker walked with a zigzag pattern, while a smaller, bipedal trackmaker set one foot directly in front of the other. This narrow gauge of the smaller trackmaker indicates a theropod dinosaur. The identification of the larger trackmaker is ambiguous, and although a larger biped, possibly a theropod or ornithomimid, seems likely, the possibility of a sauropod trackmaker could not be fully discounted. The new tracksite is part of the carbonate platform of the eastern Levant, demonstrating temporal emergence above sea level and a connection to the main land.

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## Disclosure statement

No potential conflict of interest was reported by the author(s).

## Additional information

High-resolution versions of figures, site maps, and 3D models of the described tracks are provided at figshare ([10.6084/m9.figshare.19196099](https://doi.org/10.6084/m9.figshare.19196099)).

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## References

- Abel O. 1926. *Amerikafahrt: Eindrücke, Beobachtungen und Studien eines Naturforschers auf einer Reise nach Nordamerika und Westindien*. Jena: Gustav Fischer Verlag.
- Abel O. 1935. *Vorzeitliche Lebensspuren*. Jena: Gustav Fischer Verlag.
- Ahlberg PE. 2018. Follow the footprints and mind the gaps: a new look at the origin of tetrapods. *Earth Environ Sci Trans R Soc Edinburgh*. 109(1–2):115–137. doi:[10.1017/S1755691018000695](https://doi.org/10.1017/S1755691018000695).
- Al-Wosabi M, Al-Aydrus AA. 2015. Dinosaur footprint sites in Arhab area: an aspiring geopark in Yemen. In: Errami E, Brocx M, Semeniuk V, editors. *From Geoheritage to Geoparks: Case Studies from Africa and Beyond*. Cham: Springer International Publishing; p. 167–182. doi:[10.1007/978-3-319-10708-0\\_12](https://doi.org/10.1007/978-3-319-10708-0_12)
- Aldrich TH, Jones WB. 1930. Footprints from the coal measures of Alabama. *Alabama Museum of Natural History, Museum Paper*. 9:13–62.
- Ashton N, Lewis SG, Groote ID, Duffy SM, Bates M, Bates R, Hoare P, Lewis M, Parfitt SA, Peglar S, et al. 2014. Hominin footprints from Early Pleistocene deposits at Happisburgh, UK. *PLOS ONE*. 9(2):e88329. doi:[10.1371/journal.pone.0088329](https://doi.org/10.1371/journal.pone.0088329).
- Avnimelech M. 1962a. Dinosaur tracks in the lower Cenomanian of Jerusalem. *Nature*. 196(4851):264. doi:[10.1038/196264a0](https://doi.org/10.1038/196264a0).
- Avnimelech M. 1962b. Découverte d’empreintes de pas de Dinosaures dans le Cénomanien inférieur des environs de Jérusalem (Note préliminaire). *CRAS Geol*. 8:233–235.
- Bachmann M, Hirsch F. 2006. Lower Cretaceous carbonate platform of the eastern Levant (Galilee and the Golan Heights): stratigraphy and second-order sea-level change. *Cretaceous Research*. 27(4):487–512. doi:[10.1016/j.cretres.2005.09.003](https://doi.org/10.1016/j.cretres.2005.09.003).
- Belvedere M, Franceschi M, Morsilli M, Zoccarato PL, Mietto P. 2011. Fish feeding traces from middle Eocene limestones (Gargano Promontory, Apulia, southern Italy). *Palaio*. 26(11):693–699. doi:[10.2110/palo.2010.p10-136r](https://doi.org/10.2110/palo.2010.p10-136r).
- Bennett MR, Morse SA. 2014. Human footprints: fossilised locomotion? Cham: Springer.
- Benton MJ. 1986. Ichnology: sedimentological use of dinosaurs. *Nature*. 321(6072):732. doi:[10.1038/321732a0](https://doi.org/10.1038/321732a0).
- Breithaupt BH, Chan MA, Seiler WM, Matthews NA. 2021. Weathering pits versus trample marks: a reinterpretation of the “dinosaur dance floor”: a Jurassic Navajo Sandstone surface in the Vermilion Cliffs National Monument, Arizona. *Palaio*. 36(11):331–338. doi:[10.2110/palo.2020.077](https://doi.org/10.2110/palo.2020.077).
- Breithaupt BH, Matthews NA, Noble TA. 2004. An integrated approach to three-dimensional data collection at dinosaur tracksites in the Rocky Mountain West. *Ichnos*. 11(1–2):11–26. doi:[10.1080/10420940490442296](https://doi.org/10.1080/10420940490442296).
- Breithaupt BH, Southwell EH, Adams TL, Matthews NA. 2006. Myths, fables, and theropod community dynamics of the Sundance vertebrate ichnofauna province interpretations of middle Jurassic tracksites in the Bighorn Basin, Wyoming. *Ninth International Symposium on Mesozoic Terrestrial Ecosystems and Biota*, 2006, Manchester, UK Barrett, P.M., Evans, S.E. London: Natural History Museum, 1–4.

- Brusatte SL, Niedźwiedzki G, Butler RJ. 2011. Footprints pull origin and diversification of dinosaur stem lineage deep into Early Triassic. *Proceedings of the Royal Society B*. 278(1708):1107–1113. doi:10.1098/rspb.2010.1746.
- Burford AE. 1985. Reptilian markings on the upper Mowry shale Emigrant Gap area, Natrona County, Wyoming. In: *The Cretaceous Geology of Wyoming*, Wyoming Geological Association 36th Annual Field Conference Guidebook. Casper, Wyoming: Wyoming Geological Association; p. 157–158.
- Caster KE. 1938. A restudy of the tracks of *Paramphibius*. *J Paleontol*. 12(1):3–60.
- Caster KE. 1939. Were *Micrichnus scotti* Abel and *Artiodactylus sinclairi* Abel of the Newark series (Triassic) made by vertebrates or limuloids? *Am J Sci*. 237(11):786–797. doi:10.2475/ajs.237.11.786.
- Caster KE. 1940. Die sogenannten „Wirbeltierspuren“ und die Limulus-Fährten der Solnhofener Plattenkalke. *Paläontologische Zeitschrift*. 22(1):12–29. doi:10.1007/BF03042256.
- Caster KE. 1941. Trails of *Limulus* and supposed vertebrates from Solnhofen lithographic limestone. *Pan-American Geologist*. 76:241–258.
- Clack JA. 1997. Devonian tetrapod trackways and trackmakers; a review of the fossils and footprints. *Palaeogeogr Palaeoclimatol Palaeoecol*. 130(1):227–250. doi:10.1016/S0031-0182(96)00142-3.
- Clack JA. 2012. Gaining ground: the origin and evolution of tetrapods. 2nd ed. Bloomfield (IN): Indianapolis: Indiana University Press.
- Connelly MV. 2019. Vertebrate trace fossils in the Mowry Shale (Lower Cretaceous) of Wyoming, USA. *Paludicola*. 12(2):68–82.
- Da Silva RC, Carvalho IDS, Schwanke C. 2007. Vertebrate dinoturbation from the Caturrita Formation (Late Triassic, Paraná Basin), Rio Grande do Sul State, Brazil. *Gondwana Research*. 11(3):303–310. doi:10.1016/j.gr.2006.05.011.
- Dalla Vecchia FM. 1994. Jurassic and Cretaceous sauropod evidence in the Mesozoic carbonate platforms of the southern Alps and Dinarids. *Gaia*. 10:65–73.
- Dalla Vecchia FM. 1998. Remains of Sauropoda (Reptilia, Saurischia) in the Lower Cretaceous (upper Hauterivian/lower Barremian) limestones of SW Istria (Croatia). *Geologia Croatica*. 51(2):105–134.
- Dalla Vecchia FM. 2003. Observations on the presence of plant-eating dinosaurs in an oceanic carbonate platform. *Natura Nascosta*. 27(1):14–27.
- Dalla Vecchia FM. 2005. Between Gondwana and Laurasia: Cretaceous sauropods in an intraoceanic carbonate platform. In: Tidwell V, Carpenter K, editors. *Thunder-lizards: the sauropodomorph dinosaurs*. Bloomington: Indiana University Press; p. 395–429.
- Dickas AB. 2018. 101 American fossil sites you've gotta see. Missoula: Mountain Press Publishing Company.
- Falkingham PL. 2012. Acquisition of high resolution three-dimensional models using free, open-source, photogrammetric software. *Palaeontologia Electronica*. 15(1):1–15.
- Falkingham PL. 2014. Interpreting ecology and behaviour from the vertebrate fossil track record. *J Zool*. 292(4):222–228. doi:10.1111/jzo.12110.
- Falkingham PL, Bates KT, Avanzini M, Bennett M, Bordy EM, Breithaupt BH, Castanera D, Citton P, Diaz-Martinez J, Farlow JO, et al. 2018. A standard protocol for documenting modern and fossil ichnological data. *Palaeontology*. 61(4):469–480. doi:10.1111/pala.12373.
- Falkingham PL, Gatesy SM. 2020. Discussion: Defining the morphological quality of fossil footprints. Problems and principles of preservation in tetrapod ichnology with examples from the palaeozoic to the present by Lorenzo Marchetti et al. *Earth Science Reviews*. 208:103320. doi:10.1016/j.earscirev.2020.103320
- Falkingham PL, Maidment SCR, Lallensack JN, Martin JE, Suan G, Cherns L, Howells C, Barrett PM. 2021. Late Triassic dinosaur tracks from Penarth, South Wales. *Geological Magazine*. 1–12. doi:10.1017/S0016756821001308
- Falkingham PL, Turner ML, Gatesy SM. 2020. Constructing and testing hypotheses of dinosaur foot motions from fossil tracks using digitization and simulation. *Palaeontology*. 63(6):865–880. doi:10.1111/pala.12502.
- Farlow JO, O'Brien M, Kuban GJ, Dattilo BF, Bates KT, Falkingham PL, Piñuela L. 2012. Dinosaur tracksites of the Paluxy River valley (Glen Rose Formation, Lower Cretaceous), Dinosaur Valley State Park, Somervell County, Texas. *Actas de V Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno Salas de los Infantes*. Burgos:41–69.
- Feinberg JM, Renne PR, Arroyo-Cabrales J, Waters MR, Ochoco-Castillo P, Perez-Campa M. 2009. Age constraints on alleged “footprints” preserved in the Xalnene Tuff near Puebla, Mexico. *Geology*. 37(3):267–270. doi:10.1130/G24913A.1.
- Friend PF, Alexander-Marrak PD, Nicholson J, Yeats AK. 1976. Devonian sediments of east Greenland II: sedimentary structures and fossils. *Meddelelser om Grønland*. 206(2):1–91.
- Gabunia LK, Kurbatov VV, Sennikov AG. 1988. Hoof-like footprints from the Cretaceous of southwest Gissar. *Izvestija Akademii Nauk SSSR/Seriya Biologiceskaja*. 14:189–197.
- Gaillard C. 2011. A giant limulid trackway (*Kouphichnium lithographicum*) from the lithographic limestones of Cerin (Late Kimmeridgian, France): ethological and environmental implications. *Swiss Journal of Geosciences*. 104(1):57–72. doi:10.1007/s00015-010-0032-2.
- Gatesy SM, Falkingham PL. 2017. Neither bones nor feet: track morphological variation and ‘preservation quality’. *J Vertebr Paleontol*. 37(3):e1314298. doi:10.1080/02724634.2017.1314298.
- Gatesy SM, Falkingham P. 2020. Hitchcock's Leptodactyli, penetrative tracks, and dinosaur footprint diversity. *J Vertebr Paleontol*. 40(3):e1781142. doi:10.1080/02724634.2020.1781142.
- Gatesy SM, Middleton KM, Faj J, Shubin NH. 1999. Three-dimensional preservation of foot movements in Triassic theropod dinosaurs. *Nature*. 399(6732):141–144. doi:10.1038/20167.
- Gèze R, Veltz I, Paicheler J-C, Granier B, Habchi R, Azar D, Maksoud S. 2016. Preliminary report on a dinosaur tracksite from Lower Cretaceous strata in Mount Lebanon. *Arabian Journal of Geosciences*. 9(19):730. doi:10.1007/s12517-016-2759-1.
- Gierliński GD, Niedźwiedzki G, Lockley MG, Athanassiou A, Fassoulas C, Dubicka Z, Boczarowski A, Bennett MR, Ahlberg PE. 2017. Possible hominin footprints from the late Miocene (c. 5.7 ma) of Crete? *Proceedings of the Geologists' Association*. 128(5):697–710. doi:10.1016/j.pgeola.2017.07.006.
- González S, Huddart D, Bennett MR, González-Huesca A. 2006. Human footprints in Central Mexico older than 40,000 years. *Quat Sci Rev*. 25(3):201–222. doi:10.1016/j.quascirev.2005.10.004.
- Gouramanis C, Webb JA, Warren AA. 2003. Fluviodeltaic sedimentology and ichnology of part of the Silurian Grampians Group, western Victoria. *Aust J Earth Sci*. 50(5):811–825. doi:10.1111/j.1440-0952.2003.01028.x.
- Hirschfeld SE, Simmons B. 2021. The non-dinosaur tracks at the Late Cretaceous Cherryvale tracksite, Colorado. *Fossil Record 7*. New Mexico Museum of Natural History and Science Bulletin. 82:121–140.
- Hitchcock E. 1858. Ichnology of new england: a report on the sandstone of the Connecticut Valley, especially its fossil footmarks, made to the government of the Commonwealth of Massachusetts. Boston: William White.
- King OA, Stimson MR, Lucas SG. 2019. The ichnogenus *Kouphichnium* and related xiphosuran traces from the Steven c. Minkin Paleozoic footprint site (Union Chapel Mine), Alabama, USA: ichnotaxonomic and paleoenvironmental implications. *Ichnos*. 26(4):266–302. doi:10.1080/10420940.2018.1561447.
- Klein H, Gierliński G, Lallensack JN, Hamad AA, Al-Mashakbeh H, Alhejoj I, Konopka M, Błoński M. 2020. First Upper Cretaceous dinosaur track assemblage from Jordan (Middle East) – preliminary results. *Annales Societatis Geologorum Poloniae*. 90(3):331–342. doi:10.14241/asgp.2020.10.
- Kuban GJ. 1989a. Elongate dinosaur tracks. In: Gillette DD, Lockley GM, editors. *Dinosaur tracks and traces*. Cambridge: Cambridge University Press; p. 57–72.
- Kuban GJ. 1989b. Color distinctions and other curious features of dinosaur tracks near Glen Rose, Texas. In: Gillette DD, Lockley GM, editors. *Dinosaur tracks and traces*. Cambridge: Cambridge University Press; p. 427–440.
- Lallensack JN, Buchwitz M, Romilio A. 2022a. Photogrammetry in ichnology: 3D model generation, visualisation, and data extraction. *Journal of Paleontological Techniques*. doi:10.31223/X5J30D
- Lallensack JN, Farlow JO, Falkingham PL. 2022b. A new solution to an old riddle: elongate dinosaur tracks explained as deep penetration of the foot, not plantigrade locomotion. *Palaeontology*. 65(1):e12584. doi:10.1111/pala.12584.
- Lallensack JN, Ishigaki S, Lagnaoui A, Buchwitz M, Wings O. 2019. Forelimb orientation and locomotion of sauropod dinosaurs: insights from the Middle Jurassic Tafaytour tracksite (Argana Basin, Morocco). *J Vertebr Paleontol*. 5(38):1–18. doi:10.1080/02724634.2018.1512501.
- Lallensack JN, Sander PM, Knötschke N, Wings O. 2015. Dinosaur tracks from the Langenberg quarry (Late Jurassic, Germany) reconstructed with historical photogrammetry: evidence for large theropods soon after insular dwarfism. *Palaeontologia Electronica*. 18(2.24A):1–34. doi:10.26879/529.
- Lallensack JN, Wings O, van HAH. 2016. Geometric morphometric analysis of intratrackway variability: a case study on theropod and ornithomimid dinosaur trackways from Münchshagen (Lower Cretaceous, Germany). *PeerJ*. 4:e2059. doi:10.7717/PEERJ.2059
- Larkin NR, Duffin CJ, Dey S, Stukins S, Falkingham P. 2020. The first tetrapod track recorded from the Rhaetian in the British Isles. *Proceedings of the Geologists' Association*. 131(6):722–729.
- Leonardi G. 1983. *Notopus petri* nov. gen., nov. sp.: une empreinte d'amphibien du Devonien au Parana (Bresil). *Geobios*. 16(2):233–239. doi:10.1016/S0016-6995(83)80021-7.
- Lockley MG. 1993. Ichnotopia – the paleontology society short course on trace fossils. *Ichnos*. 2(4):337–342. doi:10.1080/10420949309380107.
- Lockley MG, Hirschfeld SE, Simmons B. 2018. A new dinosaur track locality in the Late Cretaceous (Maastrichtian) Laramie Formation of Colorado. *Fossil Record 6*. New Mexico Museum of Natural History and Science Bulletin. 79:395–406.



- Lockley MG, Hunt AP. 1995. Dinosaur tracks and other fossil footprints of the western United States. New York: Columbia University Press.
- Lockley MG, Kim JY, Roberts G. 2007. The ichnos project: a re-evaluation of the hominid track record. *Cenozoic Vertebrate Tracks and Traces: Bulletin*. 42:79–89.
- Lockley MG, Matsukawa M. 2009. A review of vertebrate track distributions in east and southeast Asia. *J Paleontol Soc Korea*. 25(1):17–42.
- Lockley MG, Novikov V, Dos Santos VF, Nessov LA, Forney G. 1994. “pegadas de mula”: an explanation for the occurrence of Mesozoic traces that resemble mule tracks. *Ichnos*. 3(2):125–133. doi:10.1080/10420949409386380.
- Lucas SG. 2015. *Thinopus* and a critical review of Devonian tetrapod footprints. *Ichnos*. 22(3–4):136–154. doi:10.1080/10420940.2015.1063491.
- Lucas SG, Lerner AJ. 2001. Reappraisal of *Oklahomaichnus*, a supposed amphibian trackway from the Pennsylvanian of Oklahoma, USA. *Ichnos*. 8(3–4):251–253. doi:10.1080/10420940109380192.
- Marchetti L, Belvedere M, Voigt S, Klein H, Castanera D, Díaz-Martínez I, Marty D, Xing L, Feola S, Melchor RN. 2019. Defining the morphological quality of fossil footprints. Problems and principles of preservation in tetrapod ichnology with examples from the Palaeozoic to the present. *Earth-Science Reviews*. 193:109–145. doi:10.1016/j.earscirev.2019.04.008.
- Marsh OC. 1896. Amphibian footprints from the Devonian. *Am J Sci*. 2(11):374. doi:10.2475/ajs.s4-2.11.374.
- Martinell J, De Gibert JM, Domènech R, Ekdale AA, Steen PP. 2001. Cretaceous ray traces?: an alternative interpretation for the alleged dinosaur tracks of La Posa, Isona, NE Spain. *Palaaios*. 16(4):409–416. doi:10.1669/0883-1351(2001)016<0409:CRTAAL>2.0.CO;2.
- Marty D. 2008. Sedimentology, taphonomy, and ichnology of late Jurassic dinosaur tracks from the Jura carbonate platform (Chevenez-Combe Ronde tracksite, NW Switzerland): insights into the tidal-flat palaeoenvironment and dinosaur diversity, locomotion, and palaeoecology. *GeoFocus*. 21:1–278.
- Matthews NA, Breithaupt BH. 2001. Close-range photogrammetric experiments at Dinosaur Ridge. *Mt Geol*. 38(3):147–153.
- Matthews NA, Noble T, Breithaupt BH. 2006. The application of photogrammetry, remote sensing and geographic information systems (GIS) to fossil resource management. *Americas antiquities: 100 years of managing fossils on federal lands. Bulletin*. 34. 34:119.
- Matthews NA, Noble T, Breithaupt BH. 2016. Close-range photogrammetry for 3-d ichnology: the basics of photogrammetric ichnology. In: Falkingham PL, Marty D, Richter A, editors. *Dinosaur tracks: the next steps*. Bloomington: Indiana University Press; p. 28–55.
- McNamara KJ. 2014. Early Palaeozoic colonisation of the land—evidence from the Tumblagooda Sandstone, southern Carnarvon Basin, Western Australia. *J R Soc West Aust*. 97:111–132.
- Meldrum J, Sarmiento E. 2018. Comments on possible Miocene hominin footprints. *Proceedings of the Geologists' Association*. 129(4):577–580. doi:10.1016/j.pgeola.2018.05.006.
- Meyer CA, Thüring B. 2003. Dinosaurs of Switzerland. *Comptes Rendus Palevol*. 2(1):103–117. doi:10.1016/S1631-0683(03)00005-8.
- Mezga A, Tešović BC, Bajraktarević Z. 2007. First record of dinosaurs in the Late Jurassic of the Adriatic-Dinaridic carbonate platform (Croatia). *Palaaios*. 22(2):188–199. doi:10.2110/palo.2006.p06-043r.
- Morse SA, Bennett MR, González S, Huddart D. 2010. Techniques for verifying human footprints: reappraisal of pre-Clovis footprints in Central Mexico. *Quat Sci Rev*. 29(19):2571–2578. doi:10.1016/j.quascirev.2010.03.012.
- Niedzwiedzki G, Szrek P, Narkiewicz K, Narkiewicz M, Ahlberg PE. 2010. Tetrapod trackways from the early Middle Devonian period of Poland. *Nature*. 463(7277):43–48. doi:10.1038/nature08623.
- Owais A. 2020. Discover the first evidence of “herbivorous” dinosaurs ornithopod tracks in Palestine. *The Comprehensive Multi-Knowledge Electronic Journal for Publishing Scientific and Educational Research (MECSJ)*. 27:27.
- Panarello A, Santello L, Belvedere M, Mietto P. 2018. Is it human? Discriminating between real tracks and track-like structures. *Ichnos*. 25(1):66–75. doi:10.1080/10420940.2017.1337010.
- Patterson J, Lockley MG. 2004. A probable *Diatryma* track from the Eocene of Washington: an intriguing case of controversy and skepticism. *Ichnos*. 11(3–4):341–347. doi:10.1080/10420940490442278.
- Pearson NJ, Gingras MK, Armitage IA, Pemberton SG. 2007. Significance of Atlantic sturgeon feeding excavations. Mary's Point, Bay of Fundy, New Brunswick, Canada *Palaaios*. 22(5):457–464.
- Petti FM, Bernardi M, Todesco R, Avanzini M. 2011. Dinosaur footprints as ultimate evidence for a terrestrial environment in the late Sinemurian Trento carbonate platform. *Palaaios*. 26(10):601–606. doi:10.2110/palo.2011.p11-003r.
- Qvarnström M, Szrek P, Ahlberg PE, Niedzwiedzki G. 2018. Non-marine palaeoenvironment associated to the earliest tetrapod tracks. *Sci Rep*. 8(1):1074. doi:10.1038/s41598-018-19220-5.
- Renne PR, Feinberg JM, Waters MR, Arroyo-Cabrales J, Ochoa-Castillo P, Perez-Campa M, Knight KB. 2005. Age of Mexican ash with alleged ‘footprints’. *Nature*. 438(7068):E7–E8. doi:10.1038/nature04425.
- Roček Z, Rage J-C. 1994. The presumed amphibian footprint *Notopus petri* from the Devonian: a probable starfish trace fossil. *Lethaia*. 27(3):241–244. doi:10.1111/j.1502-3931.1994.tb01417.x.
- Rogers DA. 1990. Probable tetrapod tracks rediscovered in the Devonian of N Scotland. *J Geol Soc London*. 147(5):746–748. doi:10.1144/gsjgs.147.5.0746.
- Sarjeant WAS. 1976. Track of a small amphibian from the Pennsylvanian of Oklahoma. *Texas J Sci*. 27:107–112.
- Sass E, Bein A. 1982. The Cretaceous carbonate platform in Israel. *Cretac Res*. 3(1–2):135–144. doi:10.1016/0195-6671(82)90014-3.
- Schulp AS, Al-Wosabi M. 2012. Telling apart ornithopod and theropod trackways: a closer look at a large, Late Jurassic tridactyl dinosaur trackway at Serwah, Republic of Yemen. *Ichnos*. 19(4):194–198. doi:10.1080/10420940.2012.710672.
- Schulp AS, Al-Wosabi M, Stevens NJ. 2008. First dinosaur tracks from the Arabian Peninsula. *PLoS One*. 3(5):e2243. doi:10.1371/journal.pone.0002243.
- Seilacher A. 2007. *Trace fossil analysis*. Heidelberg: Springer.
- Seiler WM, Chan MA. 2008. A wet interdune dinosaur trampled surface in the Jurassic Navajo Sandstone, Coyote Buttes, Arizona: rare preservation of multiple track types and tail traces. *Palaaios*. 23(10):700–710. doi:10.2110/palo.2007.p07-082r.
- Shachnai E. 2006. Geological map of Israel 1:50,000, Ramallah (sheet 8–IV). Jerusalem: Geological Survey Israel.
- Shibata I, Varricchio DJ. 2020. Horseshoe crab trace fossils from the Upper Cretaceous Two Medicine Formation of Montana, USA, and a brief review of the xiphosurid ichnological record. *J Paleontol*. 94(5):887–905. doi:10.1017/jpa.2020.16.
- Shuler EW. 1917. Dinosaur tracks in the Glen Rose Limestone near Glen Rose, Texas. *Am J Sci*. 262(262):294–298. doi:10.2475/ajs.s4-44.262.294.
- Stössel I. 1995. The discovery of a new Devonian tetrapod trackway in SW Ireland. *J Geol Soc London*. 152(2):407–413. doi:10.1144/gsjgs.152.2.0407.
- Stössel I, Williams EA, Higgs KT. 2016. Ichnology and depositional environment of the middle Devonian Valentia Island tetrapod trackways, south-west Ireland. *Palaeogeogr Palaeoclimatol Palaeoecol*. 462:16–40. doi:10.1016/j.palaeo.2016.08.033.
- Thulborn RA. 1990. *Dinosaur tracks*. London (New York): Chapman and Hall.
- Turner ML, Falkingham PL, Gatesy SM. 2020. It's in the loop: shared sub-surface foot kinematics in birds and other dinosaurs shed light on a new dimension of fossil track diversity. *Biol Lett*. 16(7):20200309. doi:10.1098/rsbl.2020.0309.
- Van Bakel BW, Jagt JWM, Fraaije RHB. 2003. An interesting case of homonymy: *Notopus* de Haan, 1841 (Crustacea, Raninidae; Recent) and *Notopus* Leonardi, 1983 (ichnofossil; Devonian). *Contrib Zool*. 72(2–3):83–84. doi:10.1163/18759866-0720203002.
- Vokes HE. 1941. Fossil imprints of unknown origin. *Am J Sci*. 239(6):451–453. doi:10.2475/ajs.239.6.451.
- Waite R, Marty D, Strasser A, Wetzel A. 2013. The lost paleosols: masked evidence for emergence and soil formation on the Kimmeridgian Jura platform (NW Switzerland). *Palaeogeogr Palaeoclimatol Palaeoecol*. 376:73–90. doi:10.1016/j.palaeo.2013.02.020.
- Warren A, Jupp R, Bolton B. 1986. Earliest tetrapod trackway. *Alcheringa: Australas J Paleontol*. 10(3):183–186. doi:10.1080/03115518608619153.
- Warren JW, Wakefield NA. 1972. Trackways of tetrapod vertebrates from the Upper Devonian of Victoria, Australia. *Nature*. 238(5365):469–470. doi:10.1038/238469a0.
- Westoll TS. 1937. The Old Red Sandstone fishes of the north of Scotland, particularly of Orkney and Shetland. *Proc Geol Assoc*. 48(1):13–45. doi:10.1016/S0016-7878(37)80021-8.
- Willard B. 1935. Chemung tracks and trails from Pennsylvania. *J Paleontol*. 9(1):43–56.
- Xing L, Lockley MG, He Q, Matsukawa M, Persons IVWS, Xiao Y-W, Zhang J-P. 2012. Forgotten Paleogene limulid tracks: *Xishuangbanania* from Yunnan, China. *Palaeoworld*. 21(3–4):217–221. doi:10.1016/j.palwor.2012.09.003.
- Xing L, Peng G, Marty D, Ye Y, Klein H, Li J, Gierliński GD, Shu C. 2013. An unusual trackway of a possibly bipedal archosaur from the Late Triassic of the Sichuan Basin, China. *ACPP*. 59(4):863–871. doi:10.4202/app.2012.0087.
- Young CC. 1979. Footprints from Jinghong, Yunnan. *Vert PalAs*. 17(2):114–120.