The abundance and diversity of penetrative tracks: a critical re-evaluation of theropod ichnotaxa

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Abstract

Tetrapod ichnotaxonomy aims to classify tracks based on features that reflect trackmaker anatomy. Consequently, distinct ichnotaxa are assumed to represent distinct (though often unidentified) biological taxa. However, track shape is not only determined by trackmaker anatomy, but also by the properties of the substrate, the movements of the foot, the level of exposure, and any post-formational alteration. Because of these multiple sources of variation, determining if, and to what degree, a particular feature conveys anatomical information remains a major challenge. A major source of confusion has been penetrative tracks, which form when the foot sinks deeply into soft sediment, causing sediment to flow around the foot to seal its path. Penetrative tracks of long-toed, tridactyl trackmakers often show conspicuous features that appear to reflect foot anatomy but do in fact reflect the penetrative nature of the tracks. We studied dozens of tracksites in the Middle Jurassic of El Mers, Morocco and the Early Cretaceous Cameros Basin, Spain, showing that penetrative tracks are much more diverse and common than previously thought. We discuss formational mechanisms that explain the variation of several features commonly used to define ichnotaxa. We conclude that the type ichnospecies of *Saurexallopus*, *Magnoavipes*, *Theroplantigrada*, *Ordexallopus*, and *Archaeornithipus* are probably based on penetrative tracks and therefore *nomina dubia*.

Introduction

The majority of dinosaur tracks convey only limited information on the anatomy of the trackmaker. Many tracks are shallow and vaguely defined, and have traditionally been categorized as transmitted undertracks, i.e., tracks transmitted though the sediment onto a subsurface layer without direct foot contact. Thulborn (1990 p. 27) suspected that many of the described dinosaur tracks were in fact transmitted undertracks. On the other hand, tracks that were not considered to be transmitted undertracks have often been accepted as copies of the trackmaker's feet, with "modifications" called extramorphological features (i.e., features that do not relate to the trackmaker's anatomy). These conceptions have been challenged only recently. Transmitted undertracks are now understood to have been relatively rare (e.g., Marty et al., 2009), and a different mode of preservation, that of penetrative tracks, has been recognised as a major source of confusion (Falkingham et al., 2020; Gatesy & Falkingham, 2020; Lallensack, Farlow, et al., 2022). Penetrative tracks have been studied through experiments, computer simulations, and examinations of fossil material from particular sites, especially from the Lower Jurassic Connecticut Valley. However, their abundance and diversity has not yet been assessed using a broad range of tracksites, and the many misinterpretations of what we can now identify as penetrative tracks have only begun to be rectified (e.g., Lallensack, Farlow, et al., 2022). The present contribution aims to fill this gap.

Penetrative tracks of tridactyl non-avian theropods can show thin, widely splayed digit impressions and a posteromedially directed hallux impression, and may therefore more closely resemble the tracks of modern birds than shallow theropod tracks. A number of ichnotaxa with such "bird-like" morphologies have been erected, including, amongst others, *Magnoavipes* and *Saurexallopus*, the latter containing several ichnospecies. In the following, we discuss penetrative tracks of multiple tracksites from the Middle Jurassic of El Mers, Morocco and the Early Cretaceous of La Rioja, Spain, and assess their diversity and abundance. We then describe formational mechanisms that may result in shape features that have often been misinterpreted as anatomical features. Finally, we discuss established theropod ichnotaxa that have been defined on such features.

Material and Methods

The tracksites described herein were studied in the field during the spring of 2023. The field work in the Cameros Basin of La Rioja, Spain, was conducted by two of us (Félix Pérez-Lorente and Jens N. Lallensack) under permit E-298616 and included a total of 22 tracksites. The field work in the El Mers I and II formations, Morocco, was conducted by a team led by Mustapha Amzil and Mostafa Oukassou. In all cases, the tracksites were carefully cleaned before photogrammetric documentation. Photogrammetry was performed using a handheld Olympus TG-5 digital camera held approximately perpendicular to the track surface. Models were created using Metashape Professional (agisoft.com), and post-processed following the methodology of Lallensack et al. (2022) and in line with standard protocols outlined by Falkingham et al. (2018). We selected appropriate color scales that optimise visibility of the tracks in the height maps; the optimal scale may differ between models. In some cases, the vertical range of the color scale was restricted to the interval of interest so that subtle differences in elevation remain visible.

All the tracksites discussed herein have been reported on elsewhere. The El Mers Centre site was first studied by one of us (Christian Meyer) in 2004 (Meyer & Thüring, 2004), and then discussed in greater detail by Hadri and Pérez-Lorente (2012), as well as by Amzil et al. (2024) based on the 2023 field work. Inzar O'Founass was discovered during the 2023 field work and reported in Amzil et al. (2024). The tracksites from La Rioja, Spain, have been described in multiple, often Spanish-language works (see Pérez-Lorente, 2015 and references therein). The El Mers Centre sitemap is an updated version of Amzil et al. (Amzil et al., 2024 fig. 5); only the lowermost surface (surface 1) is shown. The La Rioja sitemaps are new interpretations based on the obtained photogrammetric models. We attempted to correlate all trackways with previously published sitemaps (Pérez-Lorente, 2015), and use the published trackway nomenclature instead of creating new labels. However, our trackway interpretations differ from the original interpretations in the assignments of tracks to the individual trackways. Also note that our maps of the Era del Peladillo, El Villar-Poyales, and La Pellejera tracksites do not cover the entire exposed surface. Photogrammetric models of the El Mers tracksites are available from https://doi.org/10.6084/m9.figshare.25330354 Photogrammetric models of La Rioja are available from https://doi.org/10.6084/m9.figshare.28015949, including all 22 tracksites.

Terminology follows that of Lallensack et al. (2025). We distinguish three types of deep tracks (tracks formed by deep sinking of the foot into soft sediment) that depend on the flowability of the sediment (a function of cohesion, friction, and viscosity depending on substrate). In a cohesive and frictional or viscous sediment, an open track may form; such tracks are commonly preserved as natural casts. In more flowable sediments, the track walls may collapse above the descending foot, or at some point after the tracks were withdrawn, creating a collapsed track in which the paths of the digits are sealed. If flowability is further increased, sediment may flow around the descending digits, sealing their paths and creating a penetrative track as defined by Gatesy and Falkingham (2020). In practice, however, collapsed tracks and penetrative tracks sensu Gatesy and Falkingham may be difficult to distinguish, and both types are here termed "penetrative tracks" (Lallensack et al., 2025).

Results and Discussion

Preservation and abundance of penetrative tracks

Intravolumetric variation

The El Mers Centre tracksite in Morocco exposes finely laminated sandy marls in the bed of the El Mers river (Amzil et al., 2024; Hadri & Pérez-Lorente, 2012). The site is situated near the base of the El Mers I Formation and therefore is early Bathonian in age (Khaffou et al., 2023). The site consists of three surfaces, the most extensive of which is the lowest (henceforth “main surface”). A broad river scour extends northwards from the centre of the riverbed into this surface (Fig. 1). The lowest tracks within the scour are on a level 12 cm deeper than the higher tracks on the less eroded parts of the surface. At least two trackways (T5 and T9) can be followed over this entire vertical range (Fig. 1). Track shape changes from the lowest to the highest areas of the surface. The tracks in the lowest area tend to be small and short, with short to absent outer digit impressions (Fig. 2E–F). Tracks tend to be most clearly defined on the middle areas, where long metatarsal marks with hallux traces are seen (Fig. 2A–C, Fig. 3A–C, G–H). Many of these tracks show a regular theropod-like track morphology. In contrast, the tracks on the highest areas – on both sides of the river scour – tend to be more indistinct. This is best seen in trackways T1 and T2; these tracks are well-defined in the middle area of the surface but become more indistinct towards the higher areas (Fig. 1, Fig. 3D). This succession resembles that seen in a simulated penetrative track (Falkingham et al., 2020), in which the track on the highest level is indistinct while the tracks on the uppermost subsurface layers show hallux and metatarsal marks. However, further down, the simulated track shows increasingly elongate outer digits that are sub-parallel to each other, different from the short and broad tracks seen within the river scour at El Mers (Fig. 2D–F). The short and broad shape of the river scour tracks might be the result of a much steeper trajectory of the foot.

At the La Senoba tracksite, La Rioja (Lower Enciso Group, Upper Barremian–Aptian), probably three, and possibly five, trackways are crossing three different surfaces over a vertical distance of up to 9 cm (Fig. 4). Penetrative tracks with narrow, slit-like digits are most common on the highest surface, while tracks on the lowest surface tend to show broader digit impressions. However, the highest surface also shows tracks with broad digit impressions, in close proximity to the slit-like tracks, suggesting that these types were produced at different times at different substrate consistencies. It is possible that there was only a single tracking surface, either the highest preserved surface or an even higher, now eroded surface. In this case, all tracks on the lower surface would be penetrative undertracks. However, some tracks on the highest surface show elongated digit impressions II and IV that are relatively straight, with their tips curved outwards, and with a U-shaped track rear. These shapes closely match the second-lowest level in a “fossil volume” specimen and a simulated track volume (Falkingham et al., 2020 fig. 4), raising the possibility that these tracks are penetrative undertracks from the lower parts of the track volume. If this is the case, the presumed associated trackways LS8 and LS13, which traverse both the lowest and highest surface, would be accidental, and multiple tracking surfaces would have been present.

Shrinking tracks

The northern part of the Era del Peladillo tracksite (Middle Enciso Group, Aptian) preserves a single surface, but the relatively long trackways show striking changes in morphology (Fig. 5). Trackway 2PL162 (Fig. 6A–D) includes both typical theropod tracks with broad digits (Fig. 6A–B) and tracks in which the digit impressions are collapsed to narrow slits (Fig. 6C–D). When such collapse occurs, the posterior part of the track is generally much deeper than the digit impressions (Fig. 6D, H). Trackway 2PL166 (Fig. 6E–H) preserves some very robust and broad theropod tracks in its proximal portion that resemble *Jurabrontes* in shape, although merely measuring 38 cm in length (Fig. 6E). More distally, the same trackway includes clear penetrative tracks with slit-like, curved digit impressions as well as metatarsal and hallux impressions (Fig. 6F–H). Curiously, the slit-like tracks are foreshortened compared to other tracks of the trackway – in one case (Fig. 6H), track length (excluding the metatarsal mark) is just 67% of that of a robust track from the proximal portion of the trackway (Fig. 6E). Although both tracks were made by the same individual, the first one imitates a massive theropodan trackmaker, and the second one imitates a much smaller trackmaker with thin, widely splayed digits. Superimposition of the tracks suggests that this apparent “shrinking” is the result of a distal shortening of the digit impressions and an anteriorly displaced rear margin of the track. This effect also creates a significant gap between the central depression and the hallux trace. In extreme cases, this shrinking effect can result in tracks in which the impression of the hallux is longer than those of the functional digits (e.g., Razzolini et al., 2014 fig. 5A).

Tracks with “wrinkle structures”

A key feature of penetrative tracks is the down-bending of layers caused by the sinking foot (Falkingham et al., 2020; Gatesy & Falkingham, 2020). Layers gradually become more inclined towards the central axis of the digit impression until they are oriented vertically. Modern erosion may remove the less inclined parts of these layers while the vertical parts within the impressions, which sit deeper, remain preserved with their broken-off edges exposed. This creates a “false bottom” of the track that seals the path of the foot, which would have descended much deeper than the false bottom suggests (Falkingham et al., 2020; Gatesy & Falkingham, 2020). False bottoms may be obscured by subsequent infill, or may not be evident due to a lack of layering in the track-bearing substrate. These structures are, however, exquisitly preserved at the El Mers Centre tracksite.

At the El Mers Centre site, the down-bended laminae, which are exposed in cross-section by river erosion, form intricate patterns within and around the tracks. Deep penetrative undertracks, such as those exposed inside the river scour, often show thick packages vertically oriented layers that can be thicker than the visible digit impressions themselves (Fig. 2E–F). These packages are often exposed in positive relief. In well-defined tracks on the middle levels, the packages tend to sit within the digit impressions (Fig. 2A, C). Broken-off layers are also seen in-between the digit impressions II to IV, where they are less steeply inclined (Fig. 2A). It is logical to assume that digit impressions that preserve packages of down-bent laminae can only represent the entry traces of the digits, formed by sediment flow around the descending digits or subsequent sediment collapse. If the digits had followed the same path out of the sediment, one would expect these laminae to be disturbed. However, some of the metatarsal marks also show packages of down-bent layers (Fig. 2B), and in this case the metatarsus must have moved back through these laminae as the foot was withdrawn. It is therefore possible that the sediment collapse was not immediate, but occurred after the foot was withdrawn.

Broken-off, down-bent layers within and around tracks have sometimes been referred to as “wrinkle structures” in the literature (Lallensack et al., 2025), and have repeatedly caused confusion. Hadri and Pérez-Lorente (2012), in their original description of the El Mers tracksite, correctly identified these structures as the edges of laminae that were bent downwards by the foot and were subsequently eroded by the river. Martin et al. (2012, 2014) described similar structures in bird-like tracks from Australia as “pressure-release structures”, while Carvalho (2004) and Carvalho and Lindoso (2024) interpreted examples from Brazil as “fluidisation structures”. Similar structures have been described by Lockley et al. (2022) and Deiques et al.

(2025), who correctly described them as deformation structures in undertracks. We argue that in all these cases, the described structures can probably be identified as the broken laminae of penetrative tracks.

Penetrative undertracks or swimming tracks?

The Inzar O'Founass tracksite (El Mers I Formation, Early–Middle Bathonian; Figs. 7–8) consists of two long and narrow exposures on the left and right bank of the Taghzout valley, El Mers (Amzil et al., 2024). On both surfaces, many tracks are clearly penetrative, including examples with elongated metatarsal marks (Fig. 8A–B). Regular tracks are also preserved, though digital pad impressions are generally absent, and digit impressions are often at least partially collapsed. In such cases, it is possible that only some of the digit impressions are penetrative, and possibly only their distal portions. Both surfaces also preserve numerous scratch marks of various lengths, which are often narrow anteriorly with a broader and deeper proximal end that is sometimes associated with a pronounced posterior mud rim (Fig. 8D–E). Where all three functional digits (II–IV) left a scratch mark, they are sub-parallel and extend posteriorly to similar degrees, resulting in a rectangular posterior margin of the track (Fig. 8D).

There are two possible explanations for the numerous scratch marks encountered on both surfaces: They could either represent deep penetrative undertracks or swimming tracks. Penetrative tracks are expected to be found on any subsurface layer that the foot penetrated, including the deepest layers, which may only show scratch marks, as seen in the "fossil volume" specimens of Hitchcock (1858) (see Falkingham et al., 2020). Swimming tracks, on the other hand, are produced by punting (buoyant) trackmakers pushing against the ground for propulsion, or by swimming individuals that accidentally touched the ground. Some tracks found on surface 2 have a U-shaped rear and outer digit impressions that curve outwards (Figs. 7D, 8B), and resemble simulated penetrative tracks from the lower part of the track volume in which digits were dragged through the substrate (Falkingham et al., 2020 fig. 4). The track shown in Fig. 7D includes a sediment mound posterior to digit impression III. If this track were a swimming track, the sediment mound would have been piled up the digits as they were scratching backwards. If this track is a penetrative undertrack, the sediment mound might be a raised exit trace (cf. Falkingham et al., 2020).

There is unequivocal evidence that some of the Inzar O'Founass tracks are surface tracks formed by swimming trackmakers. Four tracks can be assigned to the ichnogenus *Hatcherichnus*, which is a possible crocodylomorph trace. These scratch marks differ from the dinosaur tracks in being short and broad, with three curved digit marks (Fig. 7C). A pronounced sediment mound is located to the posterior of the tracks, and all examples preserve striations produced by scales as the foot moved backwards (Fig. 7C). These striations demonstrate that the surface must have been a tracking surface. Similar well-defined sediment mounds are associated with the posterior ends of many of the dinosaur scratch marks, especially those that only consist of a single digit impression (Fig. 8C–E), suggesting that these are also surface tracks left by a buoyant trackmaker. Inzar O'Founass therefore preserves both swimming tracks and penetrative surface tracks, and possibly penetrative undertracks, on the same surface.

Tracksites are often time-averaged, i.e., tracks could have been accumulated over extended periods of time, possibly while environmental conditions were changing. At Inzar O'Founass, the occurrence of both regular tracks and swimming tracks, evidently left by trackmakers of about the same size, implies a change in water depth over time. In at least two instances on surface 1, isolated scratch marks are overprinting regular tridactyl tracks (Fig. 8E), suggesting that scratches did generally form after the regular tridactyl tracks. Therefore, the regular tridactyl tracks and the penetrative tracks probably formed first, when water levels where rather low. After the water level increased, the scratch marks were produced by buoyant trackmakers. It cannot be excluded, however, that buoyant trackmakers were responsible for some of the penetrative tracks. When the swimming tracks formed, the water depth can be estimated at around 120–180 cm, considering that track lengths of 30–45 cm suggest hip heights of roughly 120 to 180 cm (Henderson, 2003).

A similar combination of penetrative tracks and swimming tracks can be seen at the El Villar-Poyales site in La Rioja (Fig. 9). The site includes regular tridactyl tracks and unequivocal penetrative tracks with long metatarsal marks and hallux impressions, such as the *Theroplantigrada* holotype trackway (EVP1) that will be discussed below. The surface also preserves numerous well-defined but isolated scratch marks of single digits. Trackway EVP12 starts with regular tridactyl tracks that then turn into scratch marks, with the last two tracks showing very pronounced mud rims immediately posterior to the scratches (Fig. 9). It is possible that the water level increased along the course of this trackway; the trackmaker would have been buoyant when leaving the scratches, and might have lost ground contact afterwards as the trackway cannot be followed further.

Penetrative tracks of quadrupedal ornithopods

The majority of identified penetrative tracks belong to bipedal trackways that were probably left by tridactyl theropods. Some examples of penetrative quadrupedal trackways can also be attributed to small ornithischians (Dalman & Weems, 2013; Lockley et al., 2009), but clear examples of quadrupedal ornithopods leaving penetrative tracks have, to our knowledge, not yet been identified. Pérez-Lorente (2015 p.285) reported ornithopod tracks with manus tracks and metatarsal marks from the La Pellejera tracksite (Upper Enciso Group, Lower Albian), which we examine here.

Trackway 1LP15 consists of at least sixteen pes tracks and is curved towards the right, with the greatest change in direction occurring in its proximal part (Fig. 11). Four unequivocal manus tracks are preserved (in front of the first, second, eighth, and twelfth track), and rounded impressions in front of tracks four and five might also represent manus tracks. The manus tracks are generally about twice as wide as long and have a straight posterior margin and a rounded anterior margin. The second manus track is reduced to a narrow, curved slit, a morphology also often seen in sauropods and that is probably the result of deformation by the pes (e.g., Lallensack et al., 2019). The manus tracks are slightly to strongly outwards rotated and match the morphology, position, and orientation typical for ornithopods (Lockley & Wright, 2001). The pes tracks are highly variable in shape, ranging from oval to triangular, and of very low anatomical fidelity. A clear tridactyl morphology is absent, but there is often a short anterior extension that corresponds with digit impression III. At least eleven of the tracks show narrow to broad metatarsal marks.

The trackway can be confidently identified as that of an ornithopod. Theropod trackways generally lack manus impressions except very rarely at stopping points (Weems, 2006) or in resting traces, and in such cases are expected to face laterally due to the semi-supinated forelimb posture (Bonnan, 2003; Milner et al., 2009), not anterolaterally as seen in the described trackway. Furthermore, inward rotation is generally less pronounced in theropods (see below). Sauropod trackways, on the other hand, are generally much broader, although extremely narrow-gauged sauropod trackways have been described by Lallensack et al. (2019). Sauropod trackways also show a pronounced outward rotation of the pes tracks rather than an inward rotation, and an entaxonic foot in which digit I is the longest rather than a central digit as seen in the described tracks. Sauropod tracks also lack metatarsal marks since the metatarsus is supported by the extensive plantar pads and the rest of the limb is columnar. It is unlikely that the posterior marks are drag marks created by the large digit I of a sauropod because the marks are laterally offset (see below) while digit I is the medial digit. The trackway is crossing a second ornithopod trackway (1LP14) that includes clear tridactyl ornithopod pes morphologies and metatarsal marks (Fig. 11), and at least one other ornithopod trackway on the surface also preserves manus impressions (Pérez-Lorente, 2015).

The metatarsal marks are laterally displaced with respect to the digital portion of the track, as is evident especially in tracks 8 to 11 (Fig. 11, bottom). The marks are sub-parallel to the trackway midline, but the impression of digit III, where visible, is oriented towards the trackway midline (Pérez-Lorente, 2015). Both features probably reflect the pronounced inward rotation typical for ornithopod tracks. Pérez-Lorente (2015) and Ishigaki et al. (2019) independently proposed that inward rotation evolved in short-legged bipeds as a way to bring the feet closer to the trackway midline (and thus, the centre of mass). The described tracks demonstrate that the rotation took place in the ankle of the foot (Pérez-Lorente, 1993).

Abundance

During field work in Morocco and La Rioja/Soria, we visited a total of 34 tracksites, 18 of which are large (50+ tracks) (Supplementary Material S1). Although penetrative tracks were not the original objective of this fieldwork, they were strikingly abundant: 8 of the large tracksites are clearly dominated by penetrative tracks, while an additional 5 large sites show at least some penetrative tracks. Only 5 of the large sites do not show clear evidence for penetrative tracks. Of the smaller tracksites, 13 sites show no clear evidence for penetrative tracks, while one site preserves penetrative tracks. These figures (Supplementary Material S1) highlight that penetrative tracks are more than mere curiosities that are unlikely to be encountered in the field – they can in fact make up the bulk of the fossil track record, at least locally.

There are several reasons that may explain this abundance of penetrative tracks. First, as penetrative tracks extend through multiple layers, they are more likely to be exposed and discovered. Second, penetrative undertracks are less likely to be eroded before they can lithify, because they are covered by sediment from the start. This increases their chances of preservation especially in dunes and tidal flats (e.g., Campos-Soto et al., 2025). Last but not least, penetrative tracks are also more likely to survive modern erosion, as demonstrated by the El Mers Centre site where penetrative tracks occur on erosional surfaces and within a river scour.

Mechanisms: Morphological features explained by substrate flow

A number of ichnotaxa, including *Saurexallopus*, are characterised by narrow-toed, widely splayed digit impressions and elongated, retroverted hallux impressions. Such ichnogenera and ichnospecies are typically distinguished based on variations in those features, the absence of some of them, or additional features such as metatarsal marks and putative interdigital webs. In the following, we describe how these features and their variations can be explained by a combination of mechanisms that occur as the foot deeply penetrates a soft substrate.

Narrow vs. wide digit impressions

A key consequence of sediment collapse or substrate flow is the reduction of digit impressions to narrow slits with V-shaped cross sections (Gatesy & Falkingham, 2020). Such tracks can often be identified as penetrative tracks, although scratch marks may show similar morphologies.

However, in the field, digit impression width in penetrative tracks ranges from narrow to wide. Wide impressions result from breakage of the sediment that sealed the path of the digit, creating a flat track floor that Gatesy and Falkingham (2020) termed a "false bottom" as it suggests a shallow track even when the foot penetrated much deeper. In laminated sediments, broken laminae stuck within the digit impressions may cause longitudinal striations (see section "Tracks with wrinkle structures"). Consequently, while narrow digit impression widths generally indicate penetrative tracks, wider digit impressions do not preclude this possibility.

Increase of interdigital angles

Interdigital angles in penetrative tracks can be much larger than those of the trackmaker's feet as a result of differential substrate flow (Gatesy & Falkingham, 2020). This is especially the case in the upper part of the track volume (cf. Falkingham et al., 2020; Turner et al., 2020). In extreme cases, digit impressions II and IV form a right angle relative to digit impression III at their bases before gradually curving anteriorly. Interdigital angles and digit impression curvature are highly variable, and change throughout the track volume (Falkingham et al., 2020). At the lower parts of the volume, the digits may be dragged backwards to form scratch marks. In such cases, the digit impressions can be straight, or with their tips curving outwards (away from digit impression III).

Presence and length of metatarsal mark

Because the metatarsus in tridactyl dinosaurian trackmakers is inclined rather than vertical, it may leave a mark if the foot sinks deeply into soft sediment. Variation in the presence and length of metatarsal marks can be explained by multiple factors including trackmaker anatomy and foot posture. Another important factor are foot movements: Because the metatarsus is elevated with respect ot the digits, it touches the substrate at a later point in time (Lallensack, Farlow, et al., 2022). If the foot moved anteriorly while descending into the substrate, the metatarsal mark will be shortened accordingly. If the rotation of the metatarsus into a vertical position occurs early, the metatarsal mark may also be shortened or absent.

Relative elongation of hallux impression

In penetrative tracks, the hallux impression often appears elongated in proportion to and can even be longer than digit impressions II and IV. Such proportions are often the result of drastic foreshortening of digits II to IV due to sediment collapse or substrate flow, leading to a "shrinking" of the digital portion of the track. The hallux impression does not seem to be affected by such foreshortening because the hallux enters the sediment at a steep angle.

Position of hallux impression

The anteroposterior position of the hallux impression varies greatly in penetrative tracks. The impression may be directly attached to the origin of digit impressions II–IV as a putative "fourth functional digit", resulting in the typical "tetradactyl" tracks commonly referred to as *Saurexallopus* (see below). The hallux impression may also be separated from digit impressions II–IV by a substantial gap. We observe that such a gap often occurs together with a long metatarsal mark, while a more anterior position occurs when the metatarsal mark is short or absent. This variation can be partly explained by the degree of anterior movement of the foot as it sinks into the sediment. If the foot sinks vertically (no anterior movement), a larger gap may be expected due to shrinking of digit impressions II–IV. If the foot moves anteriorly while sinking, the hallux impression will be displaced anteriorly by the same degree, as it touches the substrate at a later point in time than digits II–IV. The same effect may lead to a shorter metatarsal mark.

Retroversion of hallux impression

In most non-avian dinosaurs, the hallux is anteromedially oriented. Perplexingly, many tracks instead show a posteromedially directed hallux impression, which has been repeatedly interpreted as evidence for a retroverted hallux as found in birds. However, such tracks are common even in the Upper Triassic and Lower Jurassic, where no known theropod shows a retroverted hallux (Gatesy et al., 1999). In our sample from El Mers and La Rioja, hallux impressions were either medially or posteromedially directed.

Gatesy et al. (1999) suggested that a retroverted hallux impression can be produced by an anteromedially directed hallux. This can be the case if the foot moves anteriorly while sinking into the substrate and if the hallux was slightly abducted and more vertical than the trajectory of the foot. In this case, the distal end of the hallux would enter the substrate first. As the foot sinks further, more and more of the hallux would be immersed in the substrate, extending the hallux impression medially towards the metatarsal mark, and connecting to the latter once the hallux is entirely submerged. Because the foot moves anteriorly while sinking, the hallux impression would also extend anteriorly. This creates an anteriomedially elongated hallux mark as observed in the tracks.

The ichnotaxonomy of penetrative tracks

Saurexallopus – "four-toed" theropod tracks

One perplexing type of dinosaur track was described by Harris et al. (1996) and named *Exallopus lovei*, later amended to *Saurexallopus lovei* as the original name was preoccupied (Harris, 1997). These tracks, discovered in the Maastrichtian Harebell Formation of Wyoming, US, show four narrow and widely splayed digit impressions that radiate directly from a central, rounded impression in a "stellate pattern" (Harris et al., 1996). This central impression, originally identified as a metapodial impression, is deeper (3.8 cm) than the digit impressions (2.4 cm on average). Anatomical details such as phalangeal pad demarcations are absent, and the area in-between digits II and IV is depressed. The trackmaker of *Saurexallopus* proved to be a "conundrum" (Harris et al., 1996). Theropods are the most obvious candidates, but, as noted by Harris et al. (1996), the hallux in theropods is sitting high on the metatarsus, while in the tracks it is evidently impressed along its entire length and connected to the supposed metapodial impression, indicating that it must be the trace of a functional digit. Many more *Saurexallopus* tracks have been identified since, including two additional ichnospecies, yet their producer remained elusive (Lockley et al., 2004; Lockley, Gierlinski, et al., 2018; Lockley, Helm, et al., 2022; Lockley, Hirschfeld, et al., 2018). Gierlinski and Lockley (2013) identified caenagnathids such as *Chirostenotes* as probable trackmakers, which do indeed show a proportionally long hallux. However, even in these trackmakers, the hallux originates from an elevated position – the caenagnathid hypothesis therefore cannot explain the observation of Harris et al. (2013) that the hallux appears to be impressed along its entire length in the type material of *S. lovei*. Harris et al. (1996) did discuss the possibility that their tracks might have formed when the feet sank deeply into soft sediment, which could have brought the hallux in full contact with the substrate. They concluded that this "clearly cannot be the case", as this requires that the "tracks would be extremely deep". However, Harris et al. (1996) did not consider the possibility that their tracks were penetrative and could have sunk in much more deeply than is evident from the impressions that are exposed today.

A number of unequivocal penetrative tracks, often left by the same theropod trackmakers that produce conventional theropod tracks, are very similar to the *Saurexallopus lovei* tracks (Fig. 2A). Their formation can be explained by two key insights – the “shrinking” of digit impressions II–IV, which results in a proportionally large hallux impression; and the anterior movement of the foot while sinking, which leads to an anteriorly displaced, posteromedially directed hallux impression (see section “Mechanisms: Morphological features explained by substrate flow” above). The central, rounded depression noted by Harris et al. (1996) likely represents the exit trace of the digits, which would have been drawn together and oriented vertically to facilitate extraction from the sediment.

An instructive example of how misleading penetrative tracks can be is track 3 of trackway T3 of the El Mers site (Fig. 2A). This track is of the *Saurexallopus* morphotype but is unequivocally penetrative, as the down-bent layers are still stuck in the digit impressions, demonstrating that the digit impressions are merely entry traces and that the digits must have been extracted from the “heel” area posterior to the digits. Despite being penetrative, the digit impressions appear relatively broad, and there is only a short metatarsal mark. The hallux impression is proportionally very large due to substantial shrinking of the digital part of the track anterior to it. Curiously, the hallux impression is also separated from the track as if only its distal portion was impressed. In fact, however, the proximal portion of the impression might simply have collapsed.

Several other tracks that have since been assigned to *Saurexallopus* also appear to be penetrative in origin. The most obvious examples are tracks from the Meetinghouse Canyon locality, Blackhawk Formation, Utah (Lockley, Gierlinski, et al., 2018 fig. 2A), as well as tracks from the Gething Formation of British Columbia (Lockley, Helm, et al., 2022) – both cases include tracks in which the hallux is even longer than the impressions of any of the principal digits. However, other examples from different sites might be non-penetrative and anatomically fidelitous. Particularly convincing are two consecutive tracks from the Upper Cretaceous Lance Formation named *Saurexallopus zerbsti* (Lockley et al., 2004), which do not show indications of a possible penetrative origin and might indeed have been left by a large tridactyl trackmaker with a retroverted hallux. In any case, the possibility that tracks referred to *Saurexallopus* are penetrative in origin has not been considered before, and a careful re-examination of the original tracksites is required to exclude or confirm this possibility.

Besides the three *Saurexallopus* ichnospecies, a number of other “four-toed” ichnogenera have been named that are distinguished by features such as the size and orientation of the hallux mark, their interdigital angle, and the widths of the digit impressions. Lockley et al. (2018) described the new ichnotaxon *Ordexallopus zhanglifui* based on three trackways of large tetradactyl tracks from a single surface in the Jingchuan Formation of Inner Mongolia, China. Although similar to *Saurexallopus* in their wide splay and the size and orientation of the hallux, *Ordexallopus* differs in its larger size and its much wider digit impressions, leading Lockley et al. to conclude that it was a “larger, more robust, or fleshy form” (Lockley, Li, et al., 2018, p. 163). However, two of these tracks show long metatarsal marks, demonstrating that at least these tracks are penetrative tracks.

Magnoavipes and other “large bird” tracks

The ichnogenus *Magnoavipes* was named by Lee (1997) from tracks in the Cenomanian Woodbine Formation, Texas. The tracks are distinctly bird-like, being wider than long with widely splayed and extremely narrow digit impressions, leading Lee to conclude that they must have been produced by a bird. Perplexingly, the tracks are large – 19 to 21 cm in length – and therefore three times longer than the largest Mesozoic bird track recognized at that time, a fact that is reflected in the genus name (*Magnoavipes* – "large bird foot") (Lee, 1997). Lee noted more unusual features, including a short metatarsal mark; a distinct curvature in digit impressions II and IV creating a U-shape; and an unusually long stride length. The long stride length led Lee to conclude that *Magnoavipes* was a large wading bird with long legs.

However, before a hypothetical giant bird can be invoked as probable trackmaker, a much simpler explanation must be considered: the tracks could have been formed by a non-avian theropod dinosaur, with the bird-like features merely being the result of deep sinking of the foot. A penetrative origin appears very likely, given the extremely narrow digits (which, in the holotype track, become as narrow as 3% of the width of the track) as well as the strong curvature of the digit impressions. Indeed, Lockley et al. (2001) questioned the identification as a bird track and attributed the slenderness of the tracks to "collapse and inflow of sediment into the digit impressions". Lockley et al. (2021), however, accepted the bird-like morphology as genuine and suggested that the large size of the tracks could be due to "the presence of convergent groups that represent clades not represented in the skeletal record". Three more ichnospecies of *Magnoavipes* have since been named, and *Magnoavipes* tracks have been attributed to either large birds (Fiorillo et al., 2011; Lee, 1997) or slender-toed, non-avian dinosaurs (Lockley et al., 2001; Matsukawa et al., 2014; McCrea et al., 2014). As is the case with *Saurexallopus*, this material should be re-examined to exclude the possibility of a penetrative origin. A similar bird ichnotaxon from La Rioja, *Archaeornithipus* (Fuentes Vidarte, 1996), has recently been questioned, as the avian-like morphology may be due to sediment collapse (Castanera et al., 2016); we agree that at least the type material of *Archaeornithipus* is probably penetrative in origin.

Theroplantigrada – theropods with "webbed feet"

One perplexing track morphology whose interpretation has caused considerable difficulty is the *Theroplantigrada* tracks at the El Villar-Poyales site (Middle Enciso Group, Aptian). The steeply inclined surface preserves at least 19 trackways (Fig. 9), including regular tridactyl tracks, penetrative tracks, and swim tracks (see section "Penetrative undertracks or swimming tracks?"). The holotype, and only known, trackway of *Theroplantigrada*, EVP1, is markedly larger than the others (Fig. 10). This trackway is highly irregular, with a strong variation in step length and trackway width. These tracks have indistinct, irregular shapes, but an elongated metatarsal mark, a hallux mark, and the three functional digits are clearly visible. The digit impressions tend to be V-shaped in cross-section. These V-shaped grooves unite in the centre of the impression, which is the deepest point. The areas in-between the digit impressions are recessed. Curiously, the area between the hallux impression and digit impression II is recessed, while the area between the hallux impression and the metatarsal mark is not, creating a distinct step separating the metatarsal mark from the digital portion of the track (Fig. 10). This morphology led Casanovas et al. (Casanovas et al., 1993) to conclude that the recessed areas were impressed by interdigital webs (Fig. 10B). Since the hallux is included in the web, the foot would have been totipalmate – a morphology observed in some modern birds such as cormorants and pelicans. Casanovas et al. argued that the presence of a metatarsal mark requires that the animal moved with a plantigrade posture, supposedly to enhance stability on a difficult substrate, an idea that had been advocated by Kuban (1989) for elongate dinosaur tracks from the Paluxy River in Texas. Casanovas Cladellas et al. (Casanovas et al., 1993) consequently named the ichnotaxon *Theroplantigrada encisensis* ("plantigrade theropod from Enciso") based on the presence of interdigital webs, formally referring it to Tyrannosauroidea (we note, however, that the referral to this group is invalid as ichnotaxa must not be formally assigned to biological taxa according to the rules of the ICZN).

Conti et al. (2005) argued that the supposed webbing is likely an extramorphological feature resulting from the downward bending of layers close to the foot, yet retained *Theroplantigrada* as a valid ichnotaxon produced by plantigrade trackmakers. Pérez-Lorente (2015) discussed the possibility of an extramorphological feature, taking into account recent work that suggests that most supposed webs in the fossil track record may simply be the result of sediment displacement during track formation (Falkingham et al., 2009; Manning, 2004), and correctly inferred that many of the other tracks at the site are the result of deep sinking of the foot rather than plantigrade postures. However, Pérez-Lorente (2015) argued that there must have been an interdigital web, as it can otherwise not be explained that the area between digits I and II is depressed while that between digit I and the metatarsal mark is not. This riddle can be solved by recognising these tracks as penetrative tracks. As there probably was substantial foreshortening of the digit impressions, the track probably appears smaller than the foot that made it. In fact, the putative web between digit impressions I and II might have corresponded to the medial margin of the foot, either when the foot sank in or when it was withdrawn.

Conclusions

Penetrative tracks of long-toed tridactyl trackmakers often show morphological features that have commonly been assumed to reflect the actual anatomy of the trackmaker, even though these tracks bear little resemblance to the feet that made them. These features include the width of the digit impressions; digit impression curvature; interdigital angles; the presence, length, orientation, and position of the hallux impression; and the presence and length of the metatarsal mark. Variation in these features in penetrative tracks can be partly explained by the trajectory of the foot when moving through the sediment, and by the level of the track volume that is exposed. The type species of the ichnotaxa *Saurexallopus*, *Magnoavipes*, *Theroplantigrada*, *Ordexallopus*, and *Archaeornithipus* have been defined on typical features of penetrative tracks, and are here considered to be *nomina dubia*. Given the ubiquity of penetrative tracks, this possible mode of formation has to be carefully evaluated when describing fossil tridactyl tracks, and should be the null hypothesis that needs to be disproven before any paleobiological or ichnotaxonomical conclusions can be made.

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Data availability statement

The 3D models of the Moroccan sites are available at https://doi.org/10.6084/m9.figshare.25330354.v1 (2.7 GB). The 3D models of the Spanish sites are available at https://doi.org/10.6084/m9.figshare.28015949.v1 (9.52 GB) Full-resolution sitemaps and figures are available at https://10.6084/m9.figshare.30465713 (not yet activated; temporary private link: https://figshare.com/s/397b0d28ff752d247f26) (173 MB). All licenced under CC BY 4.0.

Supplementary Material

* Supplementary Material S1: Table of analysed tracksites including semi-quantitative estimates on the abundance of penetrative tracks

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Figure captions

Fig. 1. The El Mers Centre site, Morocco. Stratigraphic profile based on two sections taken directly south (section part I) and north (section part II) of the track surfaces in 2004. A single sauropod track was exposed above the three surfaces that comprise the El Mers Centre site. The hight map and interpretive site map show the lowermost (main) track surface. Note the central river scour (green/blue depression of the lowermost surface seen in the heightmap). Blue marks the deepest areas, and purple marks the highest.

Fig. 2. Penetrative tracks of the El Mers Centre site. A: *Saurexallopus*-like track (T3-3), showing a posteromedially directed hallux impression as well as broken-off down-bent laminae within the digit impressions. Total depth of height map: 5.6 cm. B: Elongate track with long metatarsal mark and five toes, probably due to superimposition of two tracks (T1-5). C. Elongate track with pronounced hallux impression and long metatarsal mark (T4-2). Total depth of height map: 9.1 cm. D. Short and wide track, bordered anteriorly by packages of down-bent laminae . E–F: Tracks from within the river scour, showing strongly foreshortened digital parts and thick packages of down-bent laminae (T12-1; T12-3; T12-2).

Fig. 3. Trackways and tracks of the El Mers Centre site. A: Trackways with metatarsal marks (T1, T2). Compare with respective tracks illustrated in Fig. 2B and 2D. Total depth: 8.4 cm. B: Trackway showing long metatarsal marks in the first two tracks that are absent in the subsequent two tracks (T3). Note the *Saurexallopus*-like shape of the third track (compare with detail in Fig. 2A). Total depth: 6.3 cm. C: Trackway with medium-sized metatarsal marks and hallux impressions (T7). Total depth: 8.1 cm. D: The distal sections of trackways T1 and T2 in the higher areas of the surface. The tracks are somewhat less defined than those on the lower areas. Total depth: 8.9 cm. E: Track of trackway T2 with scratch marks indicating a substantial backward-motion of the foot. Note the thick package of down-bent laminae within the right digit impression. F: Intricate pattern of down-bent laminae, probably as a result of superimposition of two tracks (T2-4). G–H: Elongate tracks with long metararsal marks and hallux impressions (T1-4; T3-2).

Fig. 4. The La Senoba tracksite, La Rioja, height map (top) and site map (bottom). Trackways can be seen crossing different layers.

Fig. 5. The northern part of the Era del Peladillo tracksite; height map (top) and site map (bottom). Two longer trackways (2PL162 and 2PL166) show striking variation in track morphology (see Fig. 6).

Fig. 6. Within-trackway variation in penetrative tracks. A–D: Tracks of the trackway 2PL162 from the northern part of Era del Peladillo. E–H: Tracks from trackway 2PL166 of the same site (see Fig. 5). Note the shrinking effect of the tracks (compare E and H). Depths of areas shown: A: 6.1 cm; B: 5.6 cm; C: 8.2 cm; D: 7.2 cm; E: 6.4 cm; F: 6.6 cm; G: 7.1 cm; H: 8.3 cm.

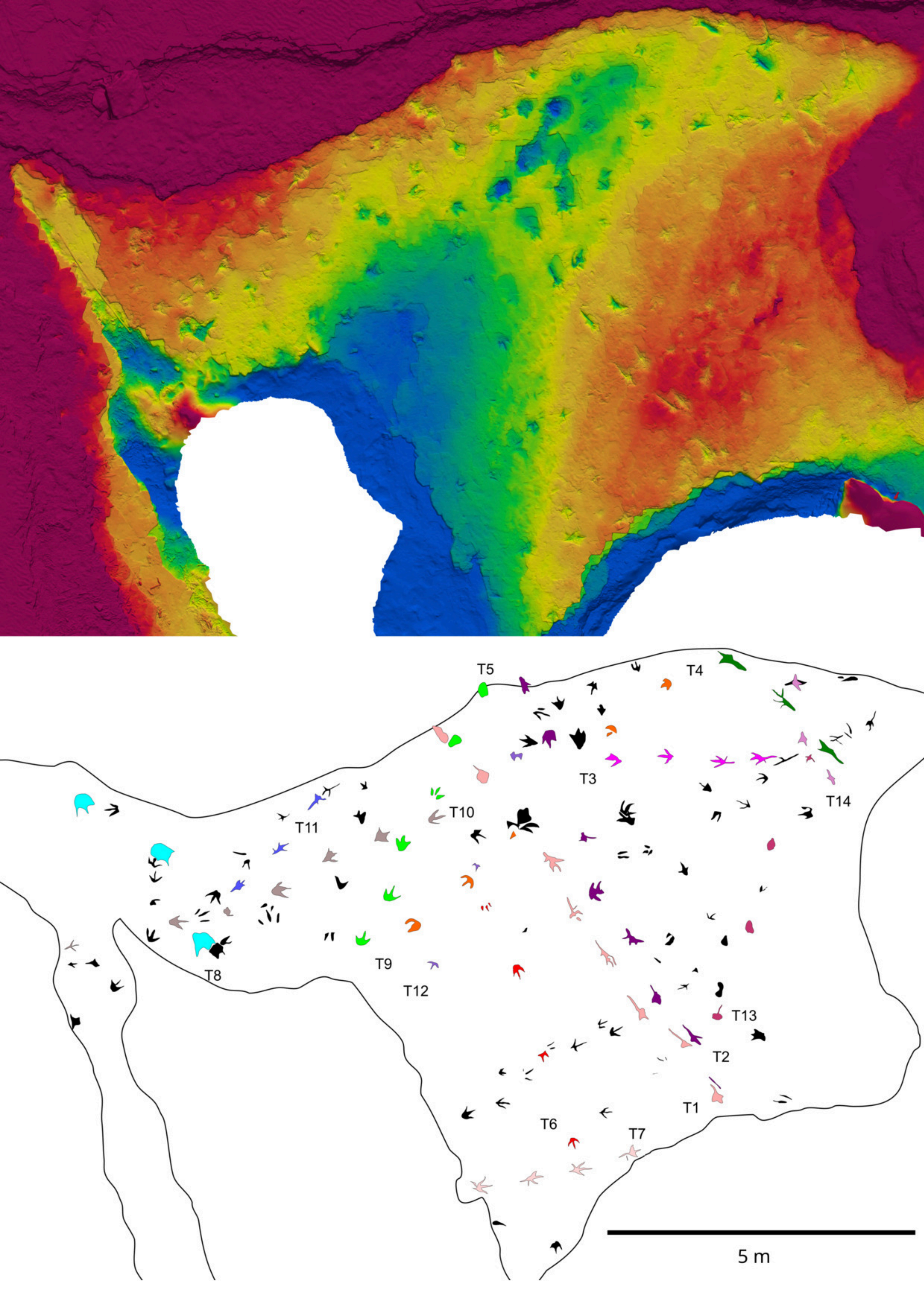
Fig. 7. The Inzar O'Founass tracksite, Morocco. A: Details from surface 1 (right bank), including a regular tridactyl track (middle); a clear penetrative track (top), and isolated scratch marks (middle right). B: Part of surface 2 as exosed in the canyon. C: *Hatcherichnus* track from surface 1 (left bank). Note the sediment mound and the striations. D: Penetrative tracks from surface 1.

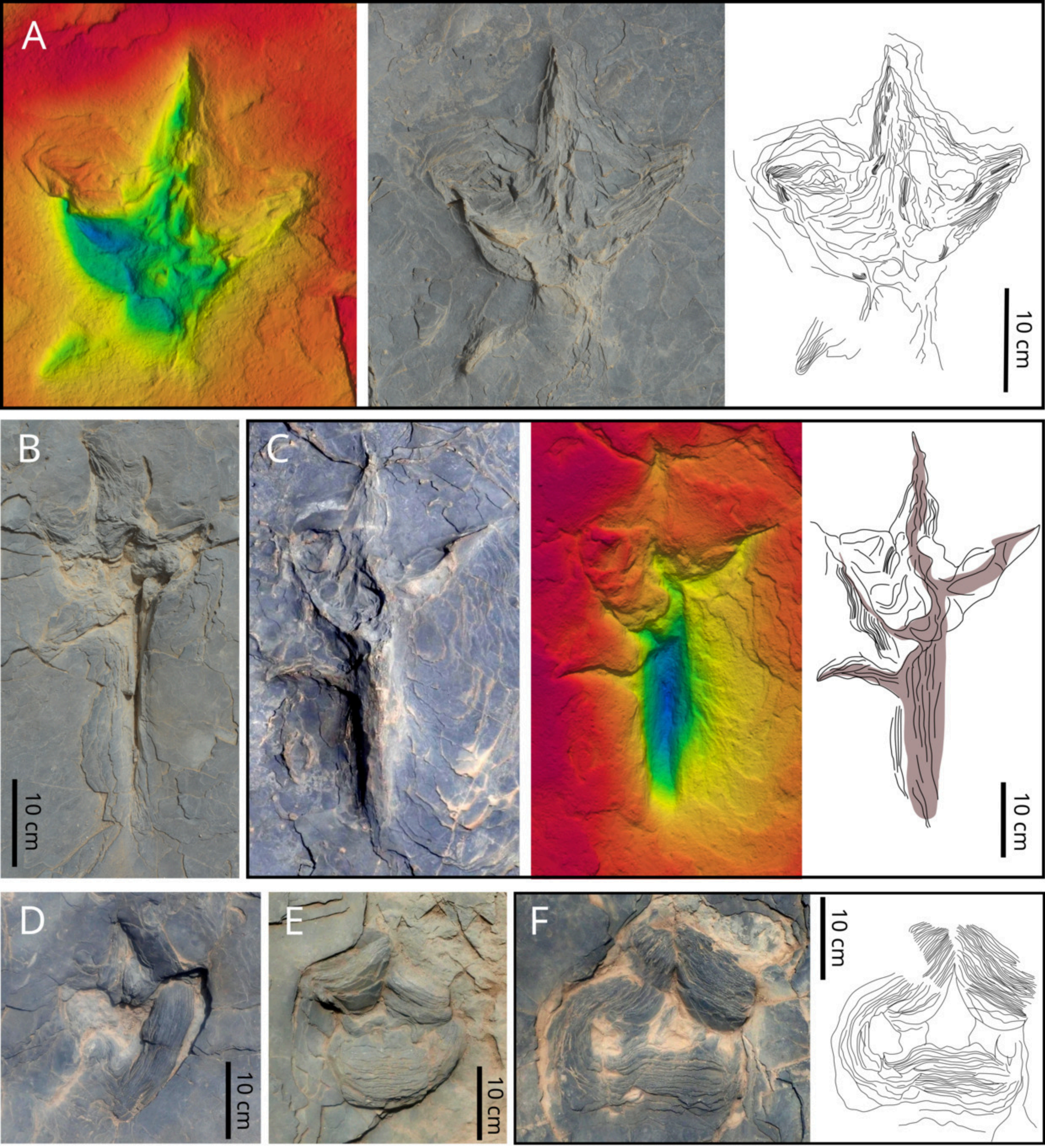
Fig. 8. Penetrative tracks and swim tracks at Inzar O'Founass. A: Penetrative track from surface 2, showing a very wide splay and strongly curved outer digit impressions. B: Penetrative track from surface 2, showing slit-like digit impressions and a U-shaped rear. C: An isolated digit impression from surface 1, possibly a scratch mark. D–E: Height maps of parts of surface 1, showing regular tracks and many isolated scratch marks (arrowed). Maximum of track surface: 12.4 cm.

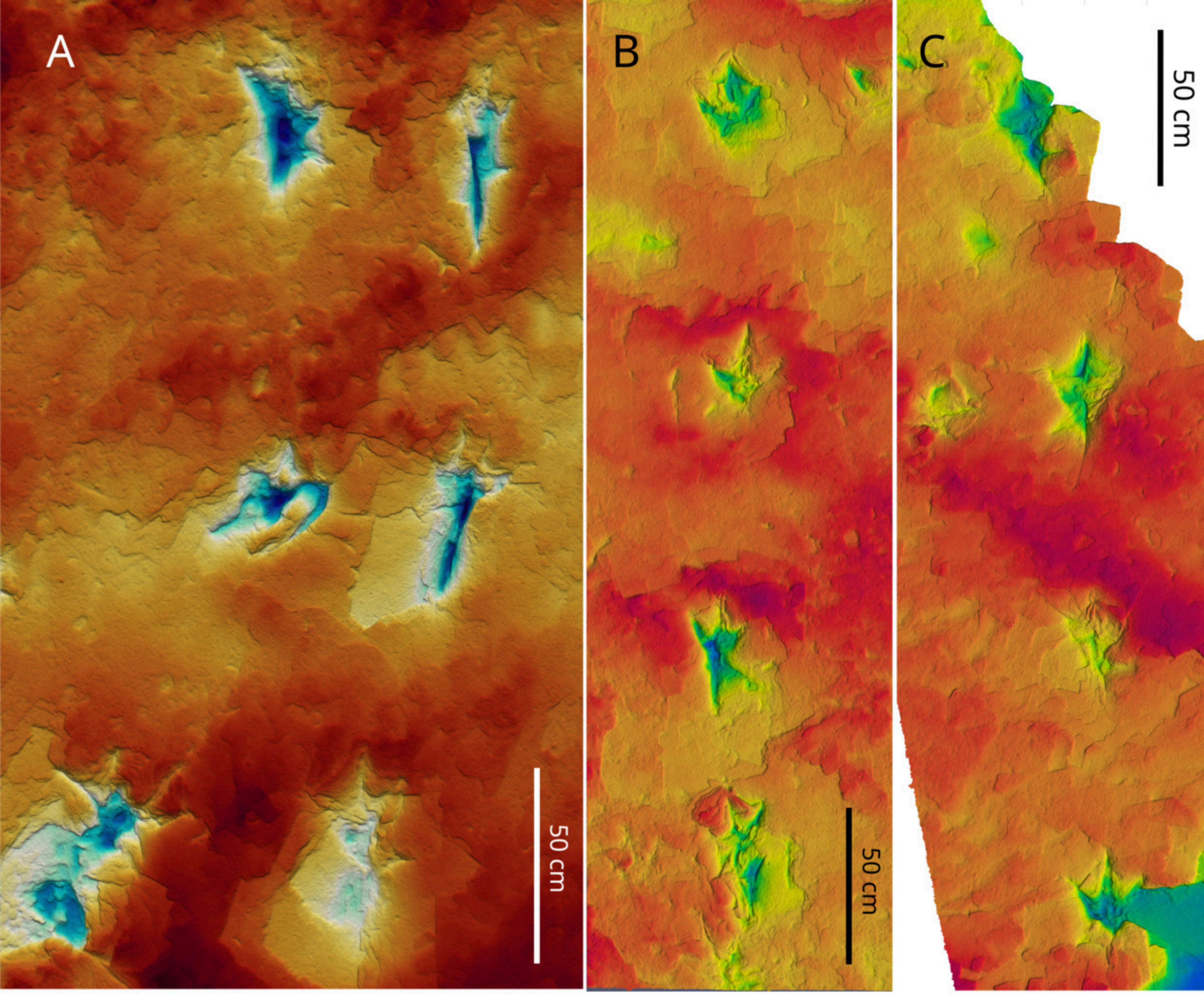
Fig. 9. The El Villar-Poyales site, La Rioja, height map (top) and site map (bottom). The *Theroplantigrada* type trackway (EVP1) is marked in red. Note the swim tracks, especially those of EVP12 (purple).

Fig. 10. Detail of the *Theroplantigrada* holotype track. A: Height map (total depth: 7.1 cm), B: Original interpretation as a plantigrade track with interdigital webs (re-drawn after Casanovas et al., 1993).

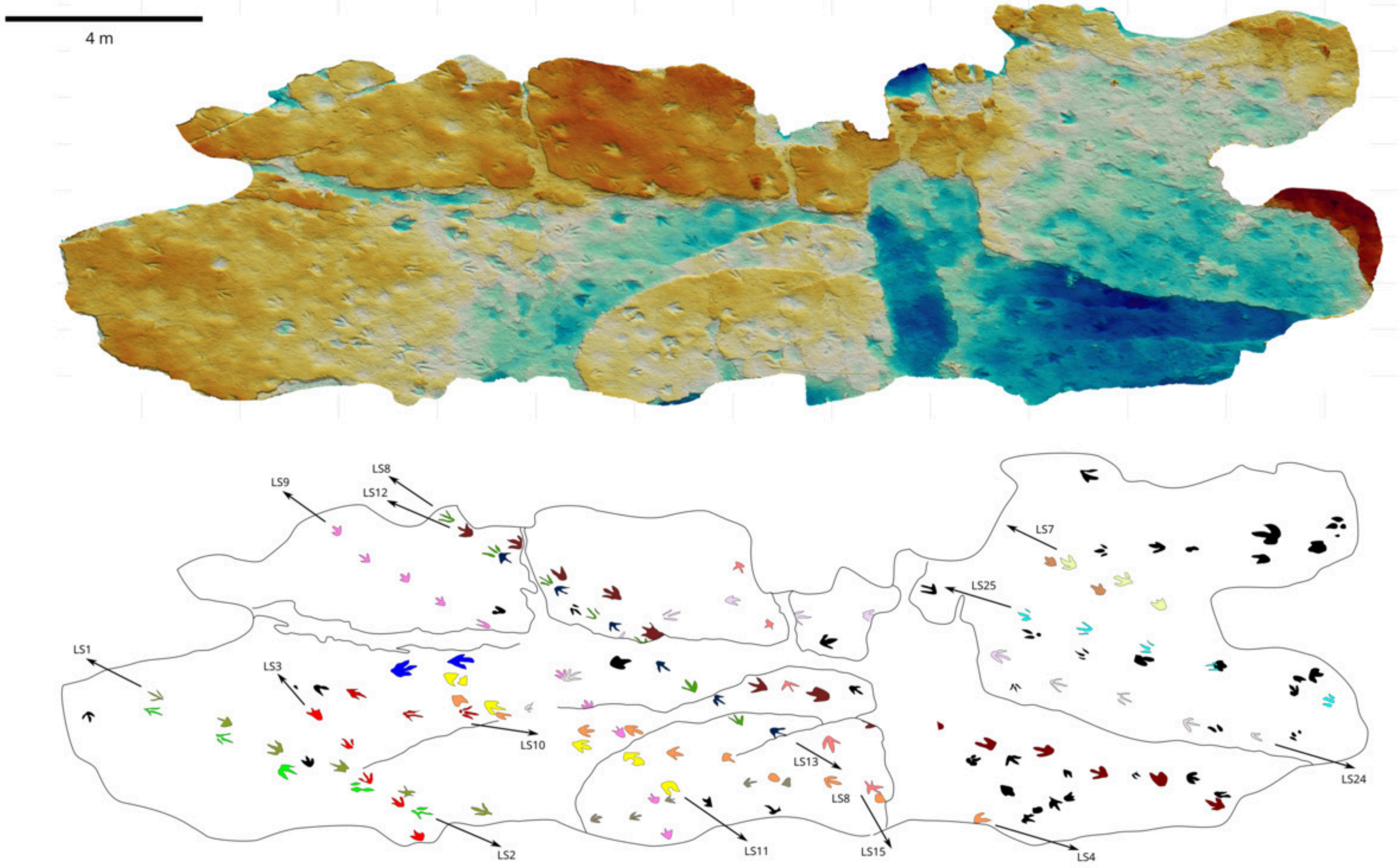
Fig. 11. The La Pellejera tracksite, La Rioja, height map and site map. Trackway 1LP15 (red) can be assigned to an ornithopod trackmaker, is penetrative, and includes manus impressions.

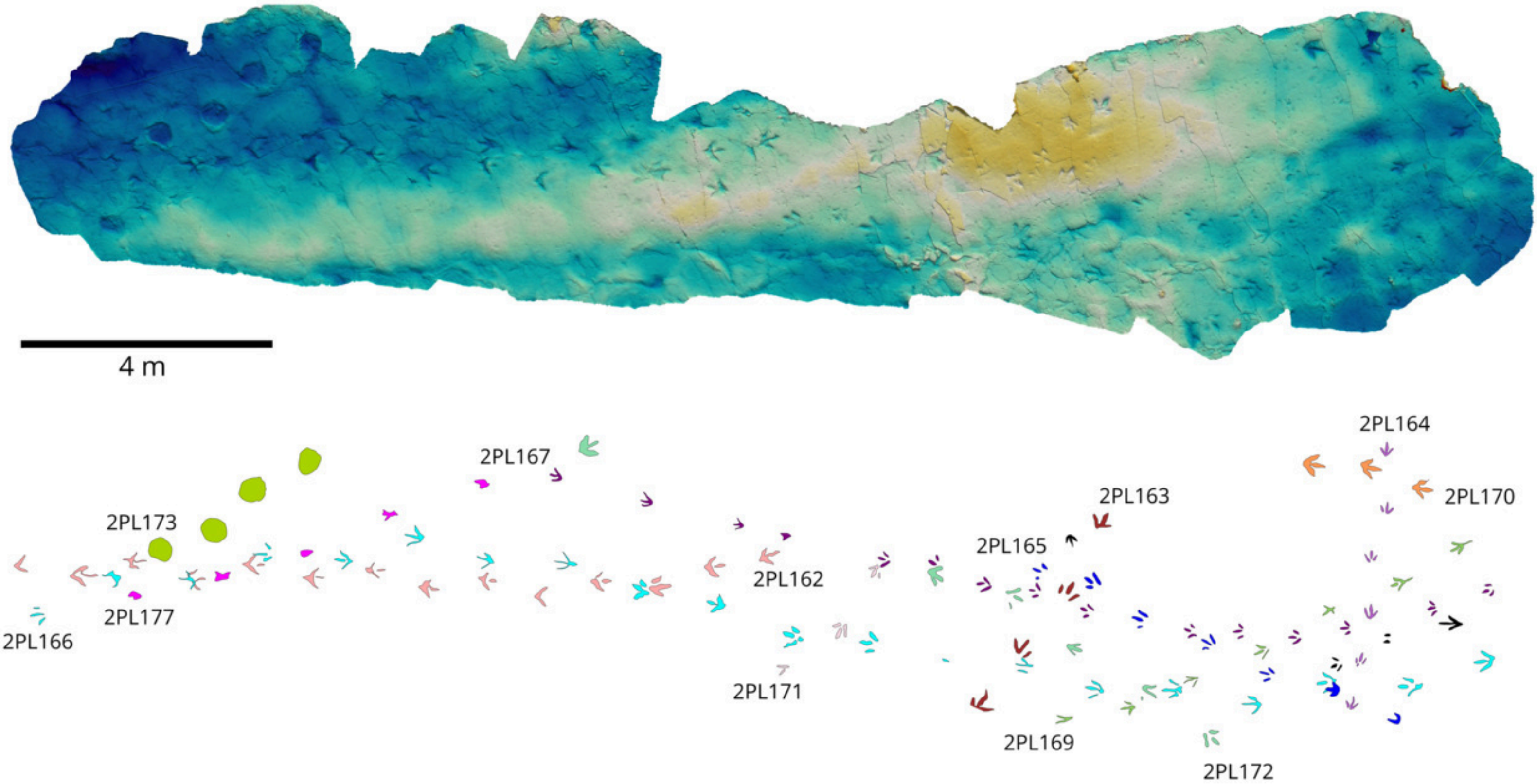

T5
T4
T3
T14
T10
T11
T8
T9
T12
T13
T2
T1
T6
T7
5 m

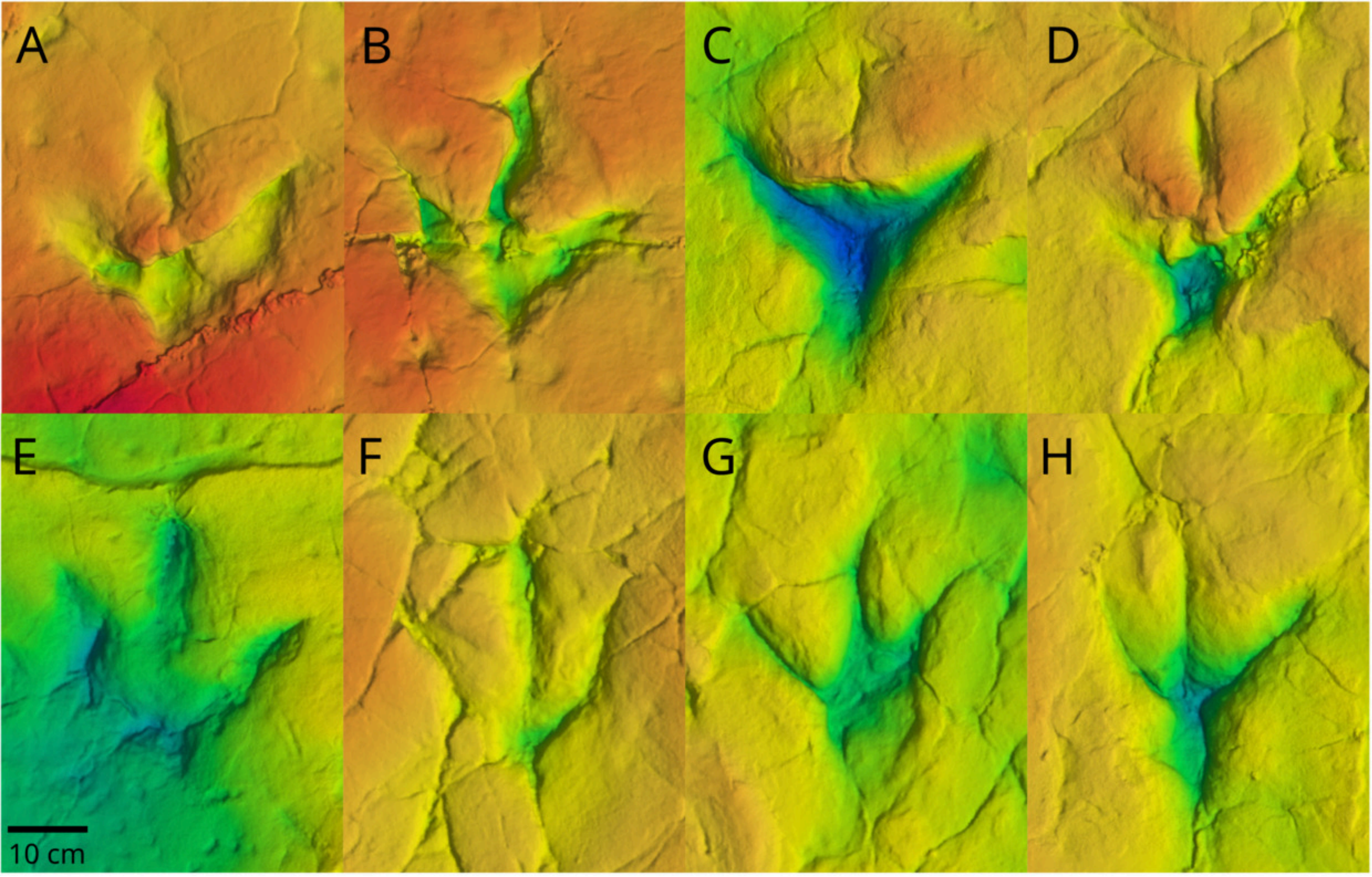

A
10 cm
B
10 cm
C
10 cm
D
10 cm
E
10 cm
F
10 cm



A
50 cm
B
50 cm
C
50 cm

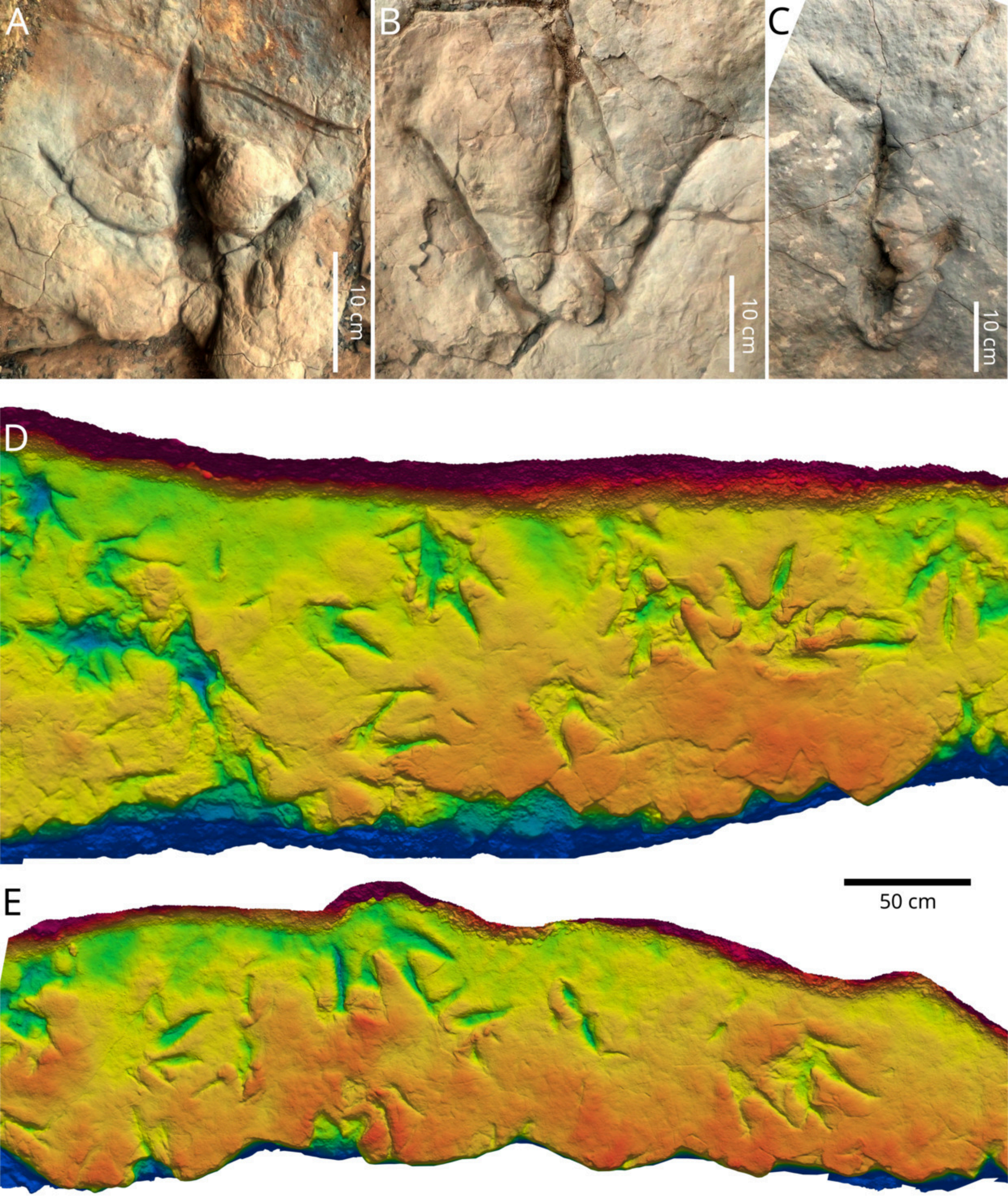

4 m
LS9
LS8
LS12
LS7
LS25
LS1
LS3
LS10
LS13
LS8
LS24
LS2
LS11
LS15
LS4

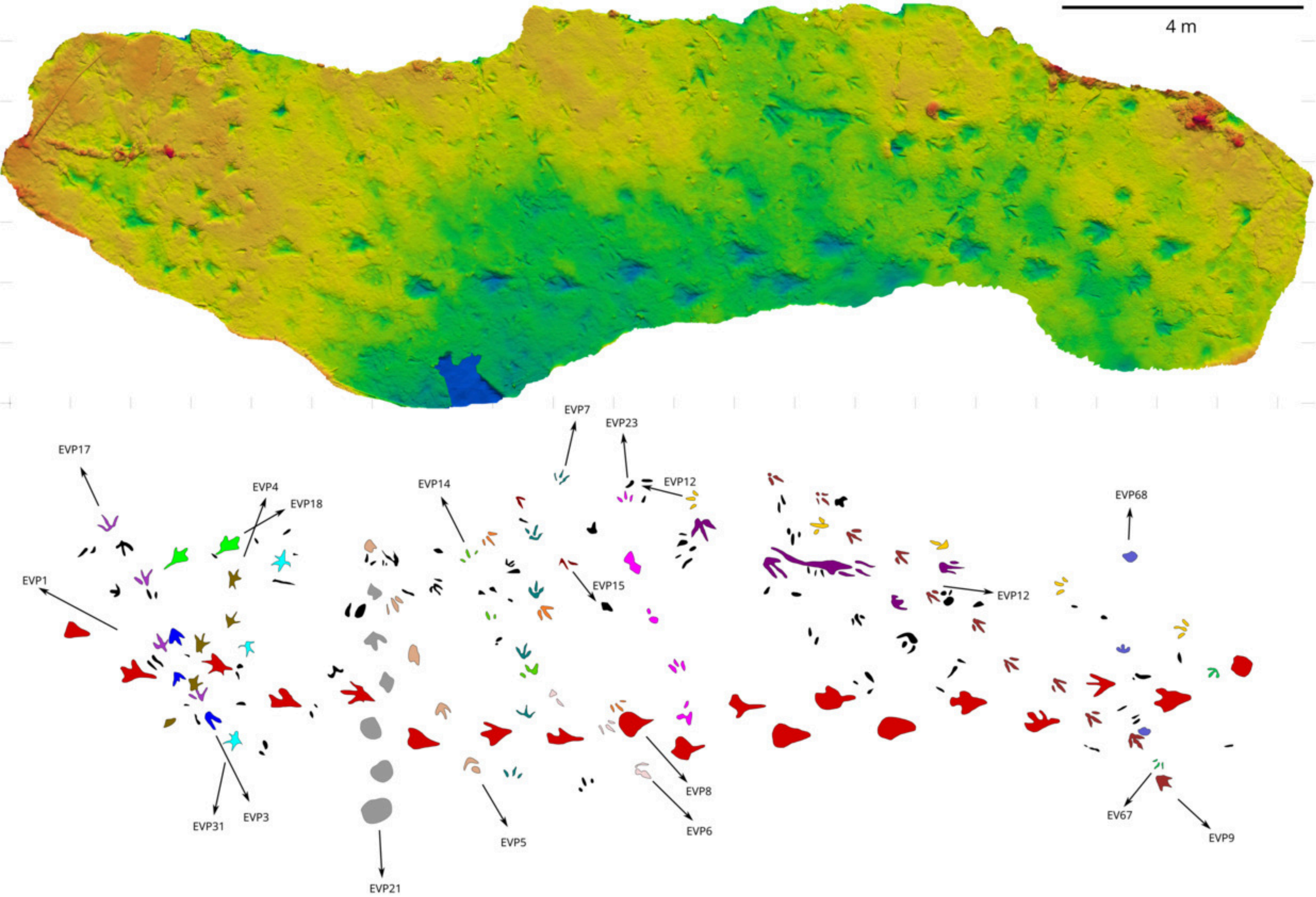

4 m
2PL164
2PL167
2PL163
2PL170
2PL173
2PL165
2PL162
2PL177
2PL166
2PL171
2PL169
2PL172



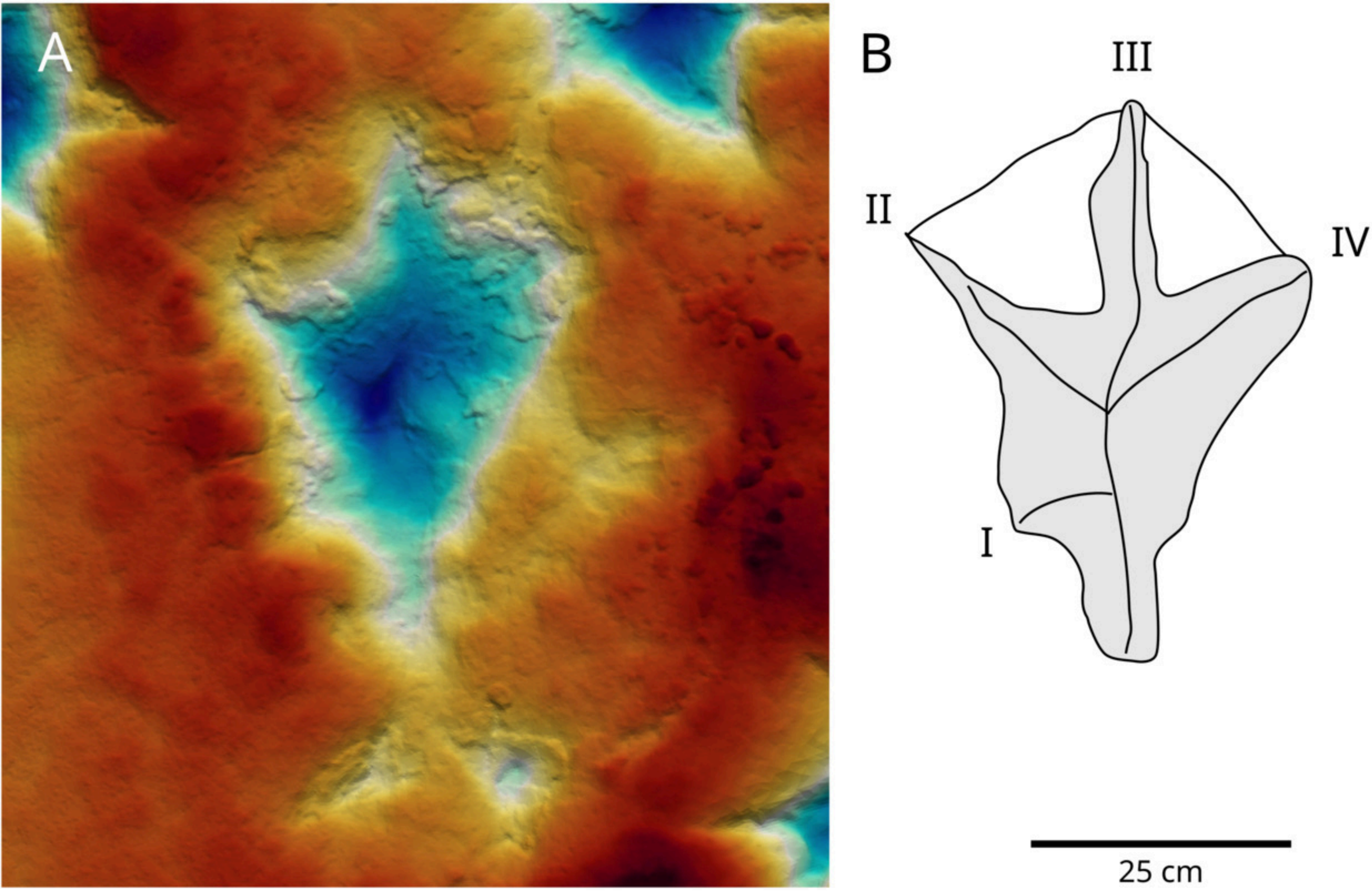
A
B
C
D
E
F
G
H
10 cm

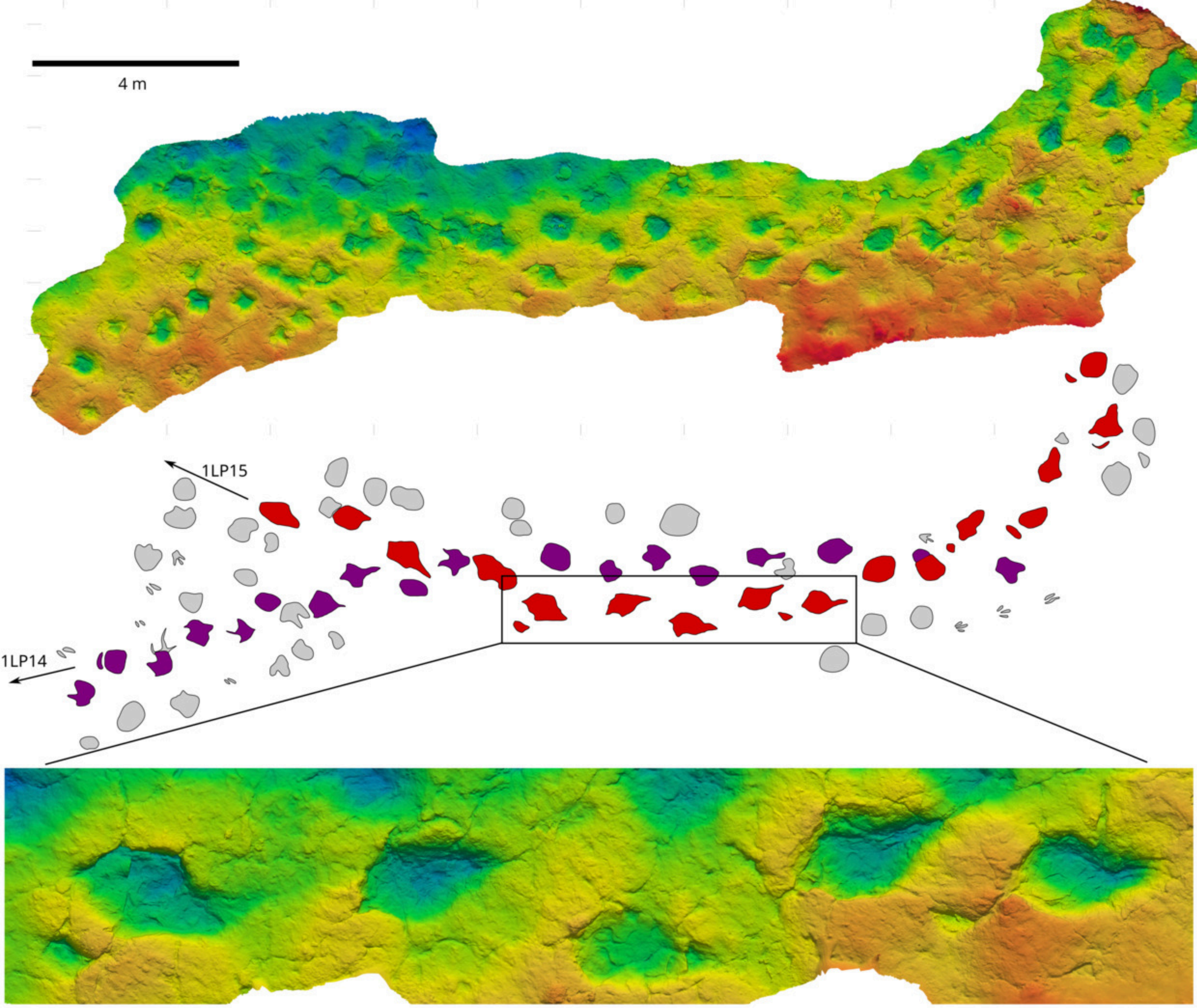

A
B
C
D


A
10 cm
B
10 cm
C
10 cm
D
E
50 cm



4 m
EVP17
EVP4
EVP18
EVP1
EVP14
EVP7
EVP23
EVP12
EVP15
EVP68
EVP12
EVP31
EVP3
EVP21
EVP5
EVP8
EVP6
EV67
EVP9


A
B
III
II
IV
I
25 cm


4 m
1LP15
1LP14