ARTICLE IN PRESS
PGEOLA-01069; No of Pages 23
Proceedings of the Geologists' Association xxx (xxxx)
Contents lists available at ScienceDirect
Proceedings of the Geologists' Association
journal homepage: www.elsevier.com/locate/pgeola

New dinosaur tracks from the Middle Jurassic red beds of the Middle Atlas (Morocco): Application of photogrammetry to ichnology and conservation of geological heritage

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A R T I C L E I N F O

Article history:
Received 11 March 2024
Received in revised form 14 June 2024
Accepted 16 June 2024
Available online xxxx

Keywords:
Digital photogrammetry
Dinosaur footprints
Geotourism
Bathonian
El Mers
Morocco

A B S T R A C T

The El Mers I and II formations (Middle Jurassic, Bathonian) are geological units outcropping in the folded Middle Atlas of Morocco rich in body and trace fossils of dinosaurs. The numerous tracksites of these units have been little studied and are severely affected by ongoing erosion (*e.g.*, seasonal flooding) and, to a lesser degree, human activities (*e.g.*, urbanisation). The aim of this project is to fully document and interpret the dinosaur tracks of two historic sites and four new sites discovered in the El Mers area using digital photogrammetry. The ichnofauna comprises abundant tracks and trackways of theropod and sauropod dinosaurs as well as of probable crocodylomorph tracks. The theropod tracks include several footprints of high anatomical fidelity, but the majority of the discovered tracks are identified to be penetrative tracks, with one site preserving abundant swim tracks. The sites preserve both small and enormous sauropod tracks. The enormous sauropod tracks are among the largest known worldwide, with a pes track length of up to 130 cm. The obtained 3D models are compared with site maps created by analogue mapping performed more than 15 years ago of the historical sites, revealing how erosion has both destructed surfaces and exposed new ones. The application of photogrammetry allows for the rapid collection of accurate high-resolution data with sustainable costs. The resulting 3D models can be used in research to digitally conserve threatened sites, and as a basis for knowledge transfer to the public. The present contribution encourages the intellectual, logistical, and social involvement of the local population to collaborate with scientists for the conservation of the rich geological heritage. Furthermore, scientific investigations in this area could shift from academic-only research to research focused on conservation and geotourism initiatives that involve local communities.

1. Introduction

Middle–Late Jurassic continental deposits of the Moroccan Atlas domain (High Atlas and Middle Atlas) in North Africa are abundant sources of tetrapod footprint assemblages, including well-preserved trackways of crocodylomorphs, pterosaurs and dinosaurs (*e.g.*, Monbaron, 1979; Dutuit and Ouazzou, 1980; Jenny et al., 1981; Ishigaki, 1985; Boutakiout et al., 2008, 2009, 2020; Gierliński et al., 2009, 2017; Belvedere and Mietto, 2010, Belvedere et al., 2011; Marty et al., 2010; Hadri and Pérez-Lorente, 2012; Klein et al., 2018, 2023; Lallensack et al., 2019; Oukassou et al., 2019, 2023; Masrour et al., 2020, 2023; Oussou et al., 2023). Dinosaur ichnoassemblages with different compositions occur on extensive surfaces with theropod, sauropod, and possible crocodylomorph (*Hatcherichnus*) tracks. Several localities, such as Demnat, Iouaridène, Imilchil, and others..., became important references for Jurassic dinosaur tracksites comparable to those from Europe, North America, and East Asia. Recently, the Middle Atlas region became a Moroccan hotspot for the study of Mesozoic vertebrates, especially the Boulemane-El Mers area, which is rich in diverse dinosaur bones, eggs, and footprints. Dinosaur body fossils have been described from several Middle Jurassic sites in this area (Termier et al.,

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https://doi.org/10.1016/j.pgeola.2024.06.004
0016-7878/

Please cite this article as: M. Amzil, M. Oukassou, J.N. Lallensack, et al., New dinosaur tracks from the Middle Jurassic red beds of the Middle Atlas (Morocco): Application of ..., Proceedings of the Geologists' Association, https://doi.org/10.1016/j.pgeola.2024.06.004

1940; de Lapparent, 1955; Du Dresnay, 1963; Charroud and Fedan, 1992; Maidment et al., 2020, 2021; Zafaty et al., 2024), but the documentation of dinosaur tracks is still in its infancy.

The El Mers region contains several Middle Jurassic (Bathonian–?Callovian) tracksites that have been mentioned since the 1930s (Termier, 1936; Jenny et al., 1981) but not described until the early 2000s (Meyer and Thüring, 2004, 2005; Hadri and Pérez-Lorente, 2012). In addition to the Middle Jurassic tracks, the study region also yielded a few isolated tracks comprising a sauropod manus–pes set and a small stegosaur pes imprint (*cf. Stegopodus*) from the ?Late Jurassic–?Early Cretaceous Oued Atchane Formation at the Boulahfa locality near Boulemane (Oukassou et al., 2023).

In this paper, we studied the dinosaur tracks and trackways of two historic sites (Meyer and Thüring, 2004, 2005; Hadri and Pérez-Lorente, 2012) and four new localities in the El Mers area (Middle Atlas, Morocco) using digital photogrammetry and generating 3D models of the surfaces. The dinosaur track assemblages pertain to the Bathonian red beds of the El Mers I and II formations, which are composed of abundant theropod and sauropod tracks and trackways.

The objectives of this contribution are: (i) to produce the 3D data of traces and tracksites for visualisation and analysis for ichnotaxonomic studies, (ii) to exploit these data for digital conservation and dissemination of knowledge to specialists and the general public, and (iii) to encourage collaboration between the scientific community and local associations and organisations that will raise awareness of the conservation and enhancement of this valuable heritage.

2. Geological setting

The Middle Atlas is a northeast–southwest trending mountain range extending between the western Central Moroccan Meseta in the West and the High Moulouya and High Plateaus in the East (Fig. 1A–B). The Middle Atlas belongs to the Atlas system of intracontinental belts formed by the Alpine inversion of the Triassic–Early Jurassic rifts at the northern margin of the African plate (Frizon de Lamotte et al., 2008). The belt is characterised by NE–SW trending faults inherited from the major structures of the Variscan basement (Charrière, 1990). The Northern Middle Atlas Fault (NMAF) separates the faulted tabular Middle Atlas in the NW and the folded Middle Atlas in the SE (Fig. 1A–B) (Choubert, 1956; Martin, 1973, 1981; Hollard et al., 1985). The latter consists of four narrow anticlinal ridges (*e.g.*, Tichoukt ridge) associated with longitudinal faults and extrusions of Triassic tholeiitic basalts and evaporites (Ouarhache et al., 2012; Escosa et al., 2021), which are separated by wide and open synclines (*e.g.*, Skoura, El Mers, Marmoucha) (Colo, 1961). These synclines expose marine formations ranging from the Early to Middle Jurassic (Du Dresnay, 1963, 1969; Choubert and Faure-Muret, 1967; Benshili, 1989; Charrière, 1990; Fedan, 1993).

Marine deposits are followed by a thick Middle Jurassic regressive sequence represented in the axis of the different synclines by the El Mers Group, which is dated as Bathonian–? Callovian (Charrière and Haddoumi, 2016). It is divided into three formations known as El Mers I, II, and III: i) The El Mers I formation, which is the equivalent of the "*Couches d'El Mers*" (Termier, 1936), and the two formations (El Mers Fm. and Kitane Fm.) (Fedan, 1993; Soufiani and Fedan, 2002). The El Mers I Fm. exhibits the following succession: basal member (Mb 1) (few metres) grey–blue limestones, fine sandstones and highly indurated platy black marls; middle member (Mb 2) represented by a thick series (50–100 m) of purplish-red marls that become increasingly rich in limestone coquina beds at the top; and upper member (Mb 3) (one to a few tens of metres) made up of massive bedded black limestones. It is an essential lagoon and deltaic set recording some marine incursions. In the Skoura syncline, the base of this formation is dated to the Early Bathonian on the basis of dinoflagellate cysts (Khaffou et al., 2023). Laterally, in the El Mers syncline, the middle part of this formation is dated as Middle Bathonian based on the occurrence of one ammonite in the interbedded marine interval (Fedan, 1993). ii) The El Mers II formation, which is equivalent to the '*série marno-gréseuse*' (Fedan, 1993) or Tizi Issoultane Fm. (Soufiani and Fedan, 2002) in the El Mers syncline. Unconformably deposited on the northeastern termination of the Tichoukt ridge, this formation is several hundred metres thick and consists of many multi-decametric sequences of grey and red marls interbedded with thick biocalcarenite and sandstone beds. These margino-deltaic sequences are attributed to the Bathonian–?Callovian (Charrière, 1990). iii) The El Mers III formation consists of dark marls and evaporitic deposits and is a thick lagoonal series that marks the latest term of the Middle Jurassic regression.

The dinosaur footprints presented in this paper were found at several localities situated in the eastern part of the El Mers syncline. The latter is located in the central part of the folded Middle Atlas, between the Tichoukt anticline ridge in the west and the Marmoucha ridge in the east (Fig. 1B). At the southwestern termination of the syncline (southeast of Boulemane, Boulhfa sector), the three formations of the El Mers Group are represented by reduced decametric thicknesses. In this sector, the El Mers III formation has recently yielded bone remains of thyreophoran dinosaurs (Maidment et al., 2020, 2021; Zafaty et al., 2024). In the central and northeastern parts of the syncline, only the El Mers I and El Mers II formations are represented, but they have thicknesses of several hundred metres. Near the El Mers village, several sites stratigraphically positioned 55–60 m from the base of the El Mers I formation have yielded a rich vertebrate fauna (fishes, crocodilians, and dinosaurs), including the first large Moroccan sauropod dinosaur (Termier, 1936; de Lapparent, 1955). At the El Mers historical site, the base of the series yielded a moderately diverse dinosaur ichnofauna that consists of theropod and sauropod footprints (Jenny et al., 1981; Meyer and Thüring, 2004, 2005; Hadri and Pérez-Lorente, 2012). The tracksites with theropod, and sauropod dinosaur footprints reported here were found at several localities in the eastern part of the El Mers syncline and occur at different levels, from the base to the upper part of the El Mers I and II formations (Early–? Late Bathonian) (Figs. 1C and 2).

3. Materials and methods

The present material comprises 433 tracks, some isolated and others linked to 29 trackways of sauropods, and theropods from several localities situated in the northeastern part of the El Mers syncline. All tracks are *in situ*, and most are preserved as negative epireliefs, whilst some are preserved as positive endichnia. Field work was conducted in early May 2023, and standard ichnological and sedimentological field methods were applied (Fig. 3). An earlier campaign took place in April 2004 by one of the co-authors (Ch. M); at that time, photogrammetry was still in its infancy, and only analogue methods were used. The fossiliferous surfaces were cleaned by dry-brushing and samples were studied using a hand lens. Furthermore, thin sections were subsequently made for detailed microfacies analysis (Fig. 3C–F). Ichnological analyses were performed during fieldwork with outline drawings on transparent plastic sheets, photographs and direct measurements of the tracks and trackways. Photographs were taken under natural light conditions. Track and trackway measurements (including stride and pace length; track rotation; trackway orientation; track length and width; interdigital angles; and, for tridactyl tracks, digit III projection) were taken following the standard ichnological methodology (*e.g.*, Leonardi, 1987; Thulborn, 1990; Romano et al., 2007; Marty, 2008; Marchetti et al., 2019; Lallensack et al., 2022a).

3.1. Study sites

There are at least six tracksites located in the El Mers area (Fig. 1C and Table 1). **Site I** (***El Mers Center***), at the bottom of the river SW of the administrative post; this is the historical site with a surface of ~300 m^2 in laminated black silts with a dense distribution of theropod trackways; footprints were noted in three horizons associated with numerous invertebrate traces (*Arenicolites*, *Rhizocorallium* and

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Fig. 1. A. Moroccan geographical map showing the location of the Middle Atlas range. B. Structural map of the folded Middle Atlas and location of the study area (El Mers syncline). C. Simplified map of the El Mers area with the studied dinosaur tracksites.

Thalassinoides). **Site IIa** (***Tasra***) is located approximately 6 km east of the village El Mers on the right bank of the Tamghilt river close to an ancient mill (Moulay Said locality); two large surfaces on two distinct horizons have been identified, the first consisting of a blue limestone with mud cracks and ripple marks containing only two specific theropod trackways and a relatively dense assemblage of sauropod tracks; the second track-bearing surface, 2.8 m above the first level, contains isolated large theropod tracks and one sauropod trackway including two consecutive manus–pes sets. **Site IIb** (***Tasra Westbank***) lies south, 330 m further downstream on the west bank of the river but was completely destroyed by a massive flood event in 2014. The surface is a blue micritic limestone and can be correlated with the main level of site IIa. The track-bearing horizon has a size of 100 m^2 and yields 4 trackways of very large sauropods (FL ~ 110 cm) and six theropod trackways of small- to medium-sized animals among many isolated footprints. Sites I and II are located at the base of the El Mers I Formation.

Site III (***Inzar O'Founass***), approximately 20 m above the base of the El Mers I formation, following the canyon of the Thaghzout river approximately 1 km SW of Site II; it consists of two superposed horizons of sandy limestone with theropod tracks: the first one shows a theropod

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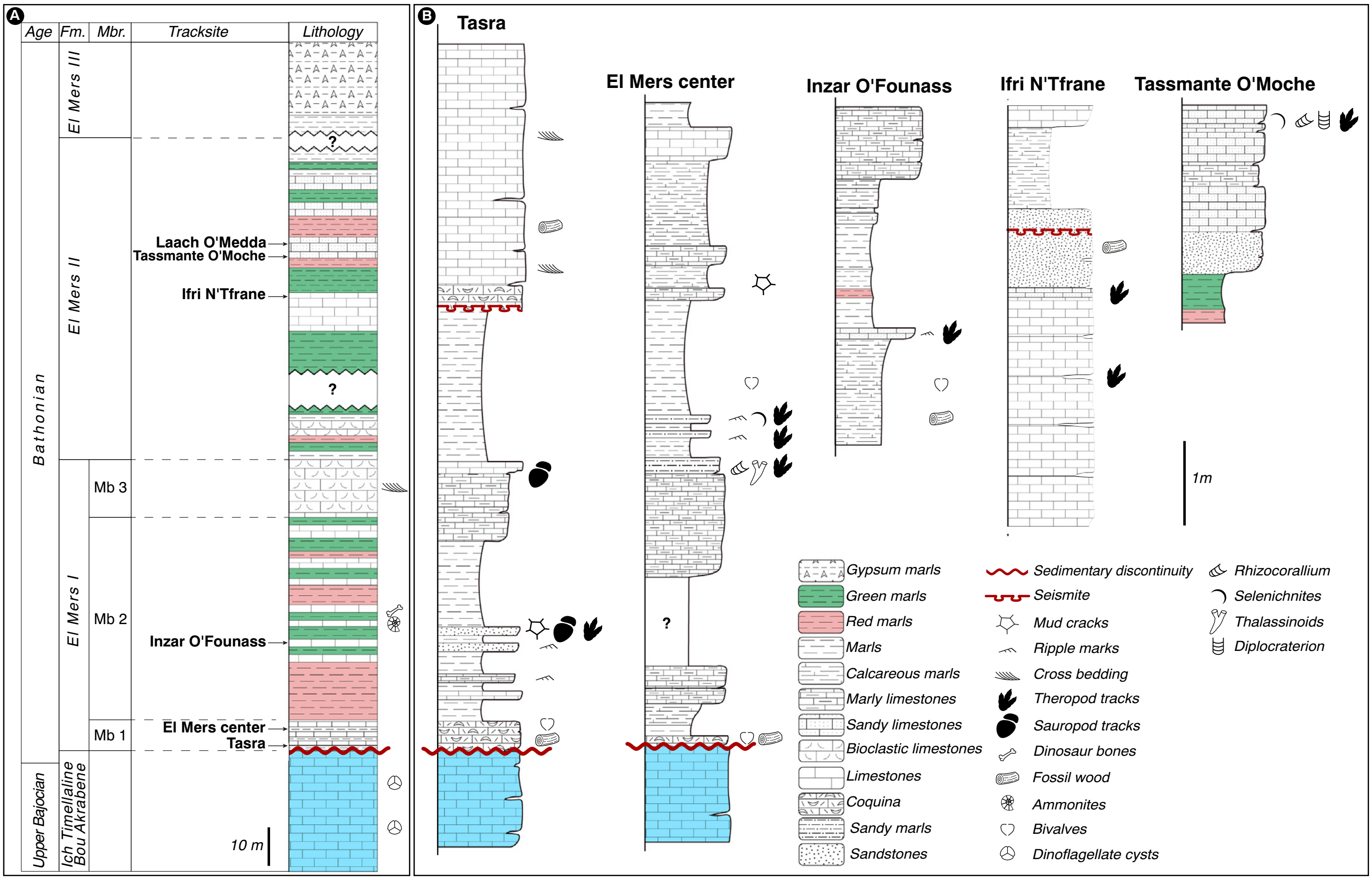

Fig. 2. Stratigraphical subdivision of Bathonian deposits in the El Mers area with the positions of the studied track-bearing levels and a detailed stratigraphical log of each tracksite.

trackway at the bottom of the river, and the second one, which is exposed on both sides of the river, shows multiple theropod and possible crocodylomorph tracks. **Site IV** (***Ifri N'Tfrane***) and **Site V** (***Laach O'Medda***) are near the Mausoleum of Sidi Lahcen Amkhchoune, along the El Mers river; Site IV shows numerous isolated theropod tracks and a theropod trackway on two superposed levels of bioclastic limestone; and Site V is a detached slab (~3 m^2) with isolated small theropod tracks. **Site VI** (***Tassmante O'Moche***) at Ait Makhchoune village; this is a sandstone bar in the middle part of a hillside north of the village that has at least three different theropod tracks associated with invertebrate traces (*Diplocraterion*, *Rhizocorallium*, and *Selenichnites*). Sites IV, V and VI are located at different levels of the El Mers II formation.

3.2. Photogrammetry

Photogrammetry was performed using an Olympus TG-5 digital camera held by hand approximately perpendicular to the track surface (Fig. 3). To avoid gaps in the models, each surface was systematically photographed at least two times: first, photographs were obtained row-wise by walking equally spaced, parallel paths; this process was then repeated by following parallel paths perpendicular to the previous ones. In addition to the surface coverage, detail shots were taken from individual tracks. Additional photographs were obtained using Canon Eos 6D Mark II and Sony alpha 580 cameras.

A DJI Mavic 2 Pro drone equipped with a Hasselblad L1D-20c camera (4000 × 3000 pixels) provided additional coverage of the Tasra and Inzar O'Founass sites (Fig. 3). This drone coverage was helpful to produce overview models, placing the track surfaces in the context of the local geomorphology. The resulting models were scaled based on metre sticks.

Photogrammetric models were obtained with 4995, 4717, 3065, 483, 494, and 666 photographs from Sites I to VI, respectively, and were generated using Agisoft Metashape Professional (agisoft.com). The meshes were built based on depth maps without calculating dense clouds, with depth filtering set to "aggressive". Processing was done using the cloud computing service of Agisoft. The horizontal plane of the model was automatically determined using Meshlab (meshlab.net). Orthographic depth-colour maps were generated using Paraview (paraview.org); see Lallensack et al. (2022a) for a detailed discussion of this methodology. Photogrammetric models, orthophotos, and depth-colour maps were used to obtain measurements. All models and maps (https://doi.org/10.6084/m9.figshare.25330354), as well as photographs for photogrammetry (https://doi.org/10.6084/m9.figshare.25914010, https://doi.org/10.6084/m9.figshare.25914007, https://doi.org/10.6084/m9.figshare.25912537), are openly accessible in Figshare, following the standard protocol of Falkingham et al., 2018.

Institutional abbreviations

HIIUC = Hassan II University of Casablanca, Casablanca, Morocco.

4. Results and discussion

4.1. Site I (El Mers Center)

4.1.1. Description

The El Mers Center site, originally published by Meyer and Thüring (2004, 2005) and subsequently described by Hadri and Pérez-Lorente (2012), exposes numerous theropod tracks on four subsequent bedding planes. The highest density of tracks is found on the lowest of these bedding planes (surface 1), including at least 9 trackways (Figs. 4 and 5). The surface is highly eroded by the El Mers river, yet the tracks appear clear with well-preserved deformation structures. All tracks are

Fig. 3. Fieldwork in the El Mers area and 3D data acquisition. A–B. Panoramic view of the studied outcrops at the El Mers Center and Tasra sites, respectively. C–F. Cleaning of the fossiliferous surface for study and 3D data acquisition at the Tasra and Tassmante O'Moche sites, respectively. D–G. Photograph acquisition for terrestrial photogrammetry at the Tasra and Laach O'Medda sites, respectively. E. Geotagged aerial imagery by the unmanned aerial vehicle DJI Mavic 2 Pro.

unequivocal penetrative tracks that record deep sinking into soft sediment (Gatesy and Falkingham, 2020; Falkingham et al., 2020); see discussion below.

A total of 14 trackways was recorded. We consider only unequivocal trackways that consist of at least three tracks, and whilst more trackways are probably present, their identification is more ambiguous.

Table 1
El Mers (Middle Atlas, Morocco) dinosaur tracksites and locality data.

Id. site	Tracksite	GPS coordinates	Institutional code	Formation	Age	Dinosaur track assemblage
Site I	El Mers Center	33°26′40,2″ N/4°27′01,8″ W	HIIUC-EM-01	El Mers I	Early Bathonian	Theropod tracks
Site IIa	Tasra	33°26′37,6″ N/4°23′28,8″ W	HIIUC-EM-02	El Mers I	Early Bathonian	Theropod and sauropod tracks
Site IIb	Tasra Westbank	33°26′25,7″ N/4°23′29,3″ W	–	El Mers I	Early Bathonian	Theropod and sauropod tracks
Site III	Inzar O'Founass	33°26′19,1″ N/4°23′47,2″ W	HIIUC-EM-03	EL Mers I	Early–Middle Bathonian	Theropod tracks
Site IV	Ifri N'Tfrane	33°27′40,0″ N/4°24′40,2″ W	HIIUC-EM-04	El Mers II	Late Bathonian?	Theropod tracks
Site V	Laach O'Medda	33°27′46,4″ N/4°24′21,7″ W	HIIUC-EM-05	El Mers II	Late Bathonian?	Theropod tracks
Site VI	Tassmante O'Moche	33°27′54,0″ N/4°23′33,1″ W	HIIUC-EM-06	El Mers II	Late Bathonian?	Theropod tracks

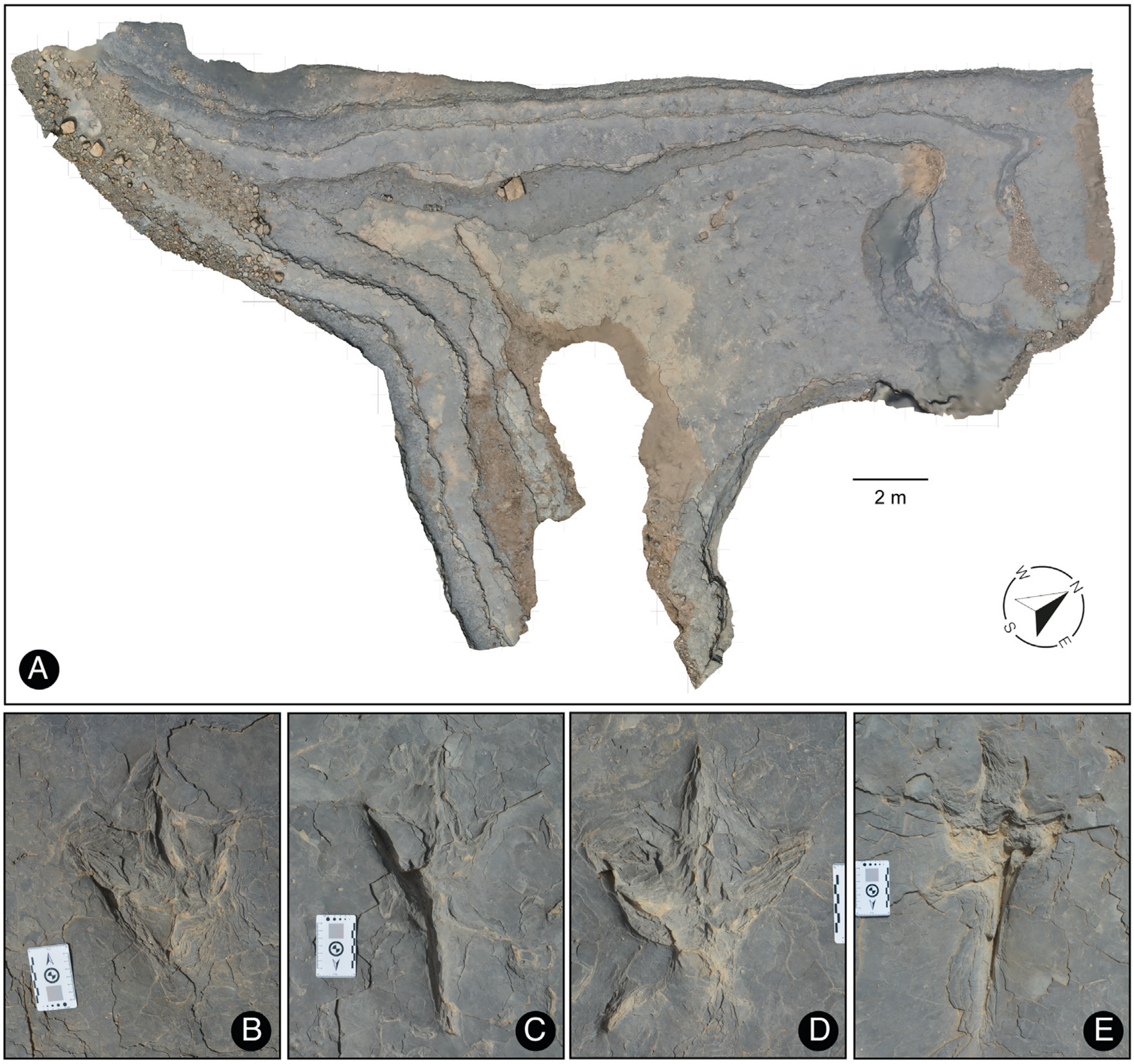

Fig. 4. El Mers Center site (HIIUC-EM-01) from the El Mers I Formation (Middle Atlas, Morocco). A. Orthophoto. B–E. Details of different types of theropod tracks from the site.

One additional trackway is probably present just southwest of trackway T7, but since this region contains several tracks of different individuals, and stride lengths are not consistent, this potential trackway is ambiguous. The trackways are generally straight with regular stride lengths. An exception is trackway T3, which appears to start with a short step, followed by two longer steps. This change in speed might have been caused by differences in substrate properties, as the first two tracks show elongated metatarsal impressions which are absent in the following two tracks, possibly indicating different sinking depths. However, other trackways with elongated metatarsal impressions at the site show relatively long strides, an observation that is consistent with similar tracksites (Lallensack et al., 2022b).

The two longest, and most salient trackways are trackways 1 and 2, which each consists of 9 tracks of which one is eroded. These trackways run sub-parallel towards the north-east, with their tracks curiously placed besides each other in their distal half. They are also very similar in size, stride length, preservation, and general appearance, including long metatarsal marks and hallux impressions. These two trackways first converge and, at their distal end, partly overlap; therefore, there is no evidence that these individuals might have travelled together. The second-last pair, which is partly overlapping, might suggest that T2 crossed the surface after T1.

The size distribution of the trackmakers is difficult to estimate because of the penetrative nature of the tracks that can lead to strong foreshortening (in case of undertracks) or elongation (when foot movement within the sediment is involved and/or a metatarsal mark is present). Therefore, track width can be a more reliable estimator of relative sizes than track length, and we measured this parameter in all trackways (maximum value) and isolated tracks where it is possible ($n = 69$). However, it has to be cautioned that track width is only a very rough proxy for size because it can be heavily influenced by the interdigital angle. For example, in trackway T3, track width increased from 19 to 24 cm from one step to the next due to the increased interdigital angle. Track width ranges between 13 and 43 cm, with a mean of 22 cm and a standard deviation of 4.8 cm. The majority of the trackways and isolated tracks fall within the size bin between 15 and 20 cm, with larger tracks becoming increasingly rare. Orientations were measured for trackways and isolated tracks ($n = 123$); assuming that each isolated track represents one individual. As indicated by the rose diagrams, there is no pronounced preference of travel directions but a slight tendency towards east–northeast and south–southwest, especially on surface 1.

4.1.2. Discussion

All tracks from the El Mers Center site can be identified as penetrative tracks, although in at last one example on surface 4 the sediment collapse seems to have been restricted to the digit impressions. The strong erosion of the lower surface that created some relief cutting several smaller layers suggests that most, if not all, of the lower surface

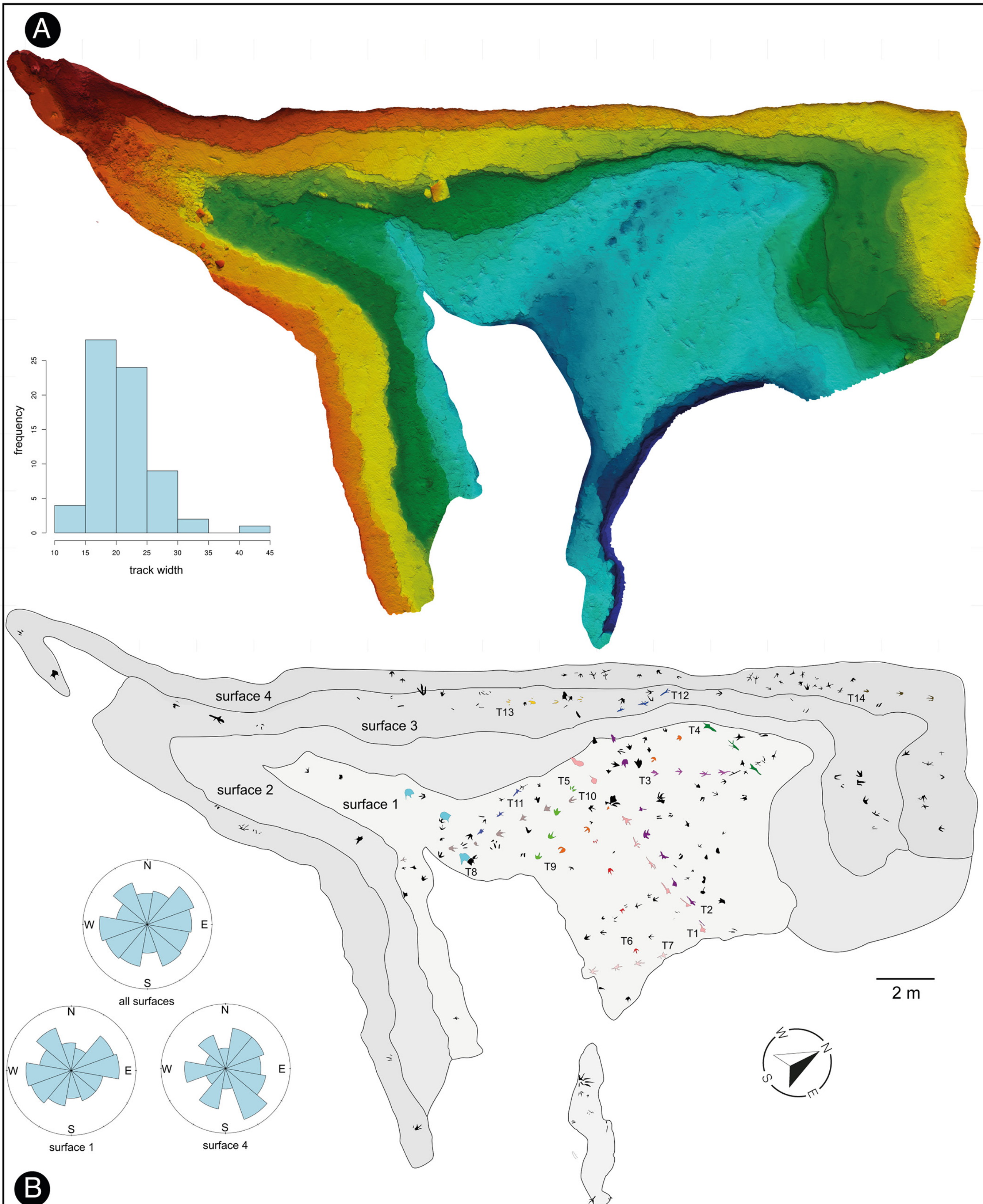

Fig. 5. El Mers site (HIIUC-EM-01) in the El Mers I formation (Middle Atlas, Morocco). A. False-colour depth map. B. Schematic sketch of the trampled surfaces with tracks size histogram and orientation rose diagrams of tracks and trackways.

tracks are penetrative undertracks (*i.e.*, the upper parts of the track volumes have been eroded by the El Mers river). Typical features of penetrative tracks can be seen, including the digit impressions that often collapse to narrow slits, are distinctly curved, and have high divarication angles at their bases. In contrast, anatomical details such as phalangeal pads are absent. Many of the tracks also show a hallux impression, and 7 of the 11 unequivocal trackways show an elongated metatarsal impression. Such "elongate tracks" form when the foot sinks deeply into a soft substrate — deep enough for the metatarsus to make contact with the substrate (Lallensack et al., 2022b). Some trackways (T5, T6, T8, T9, T10, T13, T14) and many isolated tracks do not show elongated metatarsal marks but show the edges of the down-bended laminae. The absence of metatarsal marks in these tracks is best explained either by a lower sinking depth (*i.e.*, the metatarsus did not make sufficient contact with the ground) or by the exposure of the track at a deeper subsurface level (*i.e.*, the upper part of the track volume containing the metatarsal mark has been eroded, leaving only a distal penetrative undertrack).

The trackmakers seem to be exclusively theropodan. Track morphologies range from typical tridactyl theropod tracks to elongate tracks with metatarsal mark to bird-like tracks with high interdigital angles and narrow digits. These different morphologies can be explained by their preservation as penetrative tracks (see Gatesy and Falkingham, 2020), and there is no evidence for the presence of more than one trackmaker taxon. This interpretation is corroborated by the unimodal distribution of track sizes (using track width as size proxy). The different track morphologies indicate that the tracks of each surface accumulated over an extended period of time (time averaging), and this period would have been even longer when considering the distribution of the tracks on different track surfaces.

4.2. Site IIa (Tasra)

4.2.1. Description

This site, located in the bed of the Tamghilt valley, was originally published by Meyer and Thüring (2004, 2005) and subsequently described by Hadri and Pérez-Lorente (2012). They illustrated two theropod trackways consisting of three and five tracks, respectively. Extensive cleaning of the surface from river debris during our 2023 field work revealed numerous sauropod tracks south of these trackways, including at least five trackways; some of these tracks had already been mapped and illustrated by Meyer and Thüring (2004, 2005). The excavated part of the surface measures 17.5 by 11.5 m, but the surface continues southwards towards the centre of the riverbed under an increasingly thick layer of debris, with tracks becoming more indistinct. In addition, we discovered a second surface with theropod and sauropod trackways on a higher level adjacent to the first surface, which measures approximately 24 by 9 m.

The detection of trackways on both surfaces is complicated due to river erosion and a high degree of trampling. Our identification and tracking of individual tracks are mostly based on displacement rims, which are absent from erosional features such as river scour marks. Notably, the inner margins of the displacement rims may be partly eroded, resulting in a slightly larger appearance of the tracks. The track-bearing surface is finely laminated, and these laminae are bent around the track as they were pushed downwards by the foot and upwards by the raising displacement rims during track formation. When eroded, the bent laminae appear as concentric rings around tracks, which also aid in tracing the tracks. Trackways were identified by looking for repetitive patterns such as a sequence of tracks of similar shape, size, depth, and orientation that were arranged at equal distances, as is the case with the left pes tracks of trackway S3, following the methodology of Lallensack et al. (2019). Additional tracks of the trackway were then found by scrutinising their expected locations based on the known trackway pattern. Whilst the identification of trackways is relatively unequivocal, the assignment of individual tracks is often uncertain.

4.2.2. Surface 1

The main surface consists of two theropod and five sauropod trackways. Both theropod trackways, especially trackway T1, show broad displacement rims, indicating a soft substrate at the time of track formation. These tracks are therefore of low anatomical fidelity. The track length is 38 cm in T1, whilst T2 is slightly larger at 41 cm; both trackways are of equal size when claw marks are excluded from the measurements, as these appear to be more pronounced in T2. The stride lengths are 213 cm for T1 and 283 cm for T2, suggesting that T2 was moving faster. Several isolated tracks that can probably be referred to theropods can be found elsewhere on surface 1, but these tracks are poorly defined (Fig. 6).

A single, giant, sauropod trackway (S1; pes length 95–100 cm) is heading towards the southeast. Only the pes tracks were confidently identified. These tracks are suboval, with a broad anterior edge, a narrower and rounded posterior end, a curved lateral margin, and a straighter medial margin with an indentation at the mid-length of the tracks. The anterior edge has broad and triangular indentations. Such indentations can easily form when rock chunks are eroded from displacement rims. However, the described indentations are consistent in at least three of the tracks and are aligned with the track midline in both the left and right tracks. They therefore possibly represent claw marks, even though the outward deflection typical for sauropods (Hall et al., 2016) is not evident. The stride length between the two most unequivocal tracks is 221 cm. The WAP/PL ratio (width of the pes pace angulation / pes length) is 0.76, indicating a narrow-gauge trackway; however, the trackway appears to become wider distally where the WAP/PL ratio cannot be measured. Pes tracks are rotated outwards by 20°, as is typical for sauropods.

Trackways S2 to S5 are parallel to each other and head towards the west. Trackways S2 and S3 can be followed across most of the surface, whilst S4 and S5 are shorter sections; it is possible that S4 is the continuation of S5. The tracks of trackways S2 to S5 are much smaller than those of trackway S1, with confident tracks ranging from 46 to 57 cm in length. The best-preserved tracks are relatively narrow and triangular. Manus tracks are often reduced to narrow slits due to the pes stepping immediately behind. S4 shows manus tracks with no signs of such deformation. These tracks are wider (30 cm) than long (20 cm), with a rounded anterior edge and a convex posterior edge. Some of the tracks are subdivided into two oval impressions that are separated by a posterior bulge of sediment extending into the track and by a smaller anterior bulge. A similar morphology has been described from the sauropod trackways at Tafaytour, Morocco (Lallensack et al., 2019).

The median stride lengths are similar for trackways S3 to S5 (152 to 165 cm), whilst the strides are longer in S2 (195 cm). It is unclear whether the longer strides of S2 reflect a higher absolute speed of locomotion, as this trackway is probably somewhat larger in terms of both pes length and apparent gleno-acetabular distance. However, the track length in this trackway is variable, and the identification of manus tracks is uncertain, preventing accurate comparisons of sizes and therefore of speeds.

For comparison, we added the surface map that was made in 2004 (Fig. 7) because it shows the degree of erosion that occurred during the flood event in 2014 that resulted in the loss of a large portion of the south-eastern section of the site, including the first segment of TR1 (TR L.I–TR.LIV), whilst exposing additional sauropod tracks in the western portion of the surface. At that time, the surface showed more details, especially in T1 and T2 theropod trackways. They show bulges that are consistently higher on the inner side of the trackway (Figs. 7 and 8C). This might be explained by a special substrate consistency, although tracks of TR 1 have the same morphology but no asymmetric bulges. The overall morphology and the well-distinct pads point to the ichnotaxon *Megalosauripus*.

4.2.3. Surface 2

Surface 2 preserves two theropod trackways, T3 (four tracks) and T4 (two tracks), but only T3 is unambiguous. The most fidelitous track of T3

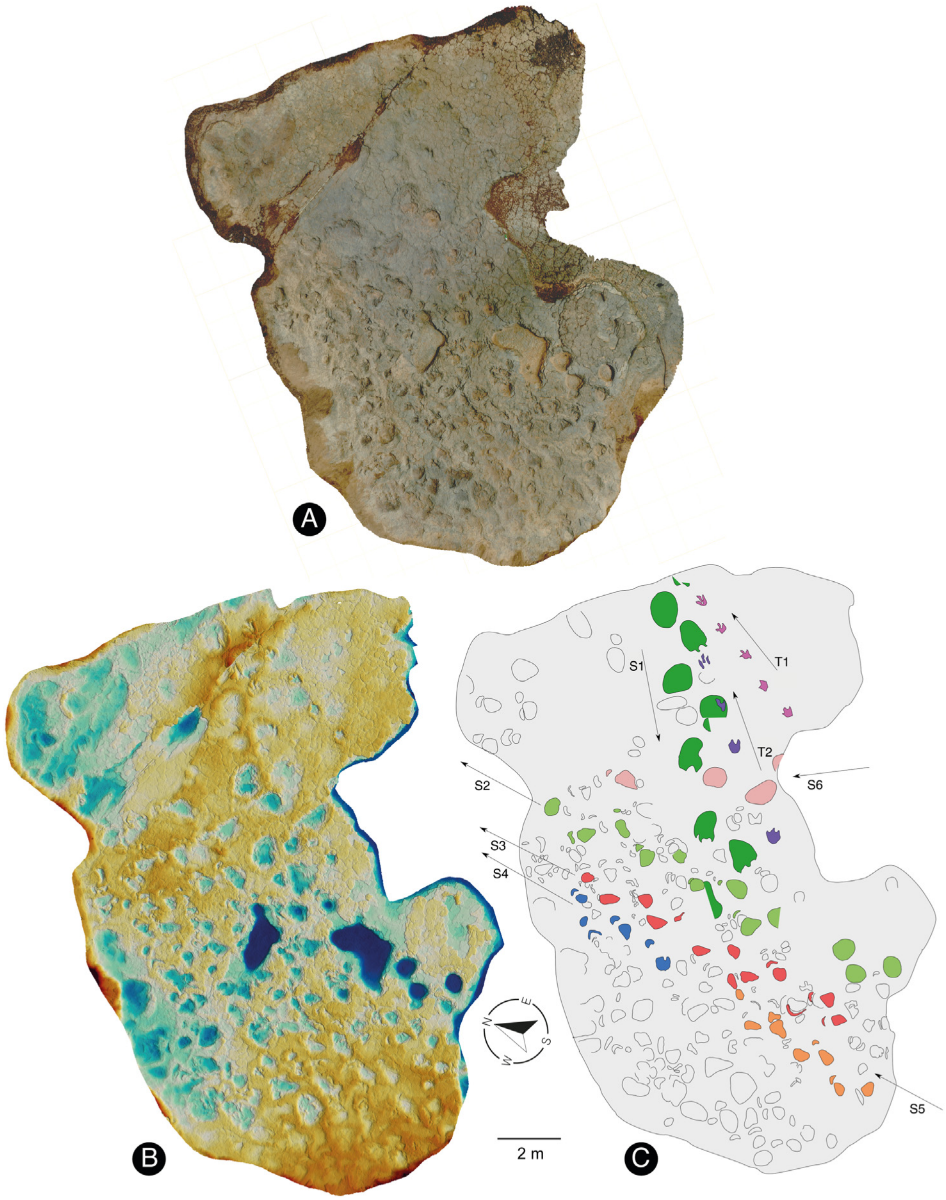

Fig. 6. Tasra site (surface 1) (HIIUC-EM-02) in El Mers I formation (Middle Atlas, Morocco). A. Orthophoto. B. False-colour depth map. C. Schematic sketch of the trampled surface.

is 47 cm in length, which is slightly larger than the theropod tracks of surface 1. The stride length cannot be measured directly because the third track is eroded but can be approximated at 257 cm based on the position of the first and last tracks of the trackway (Fig. 9).

The surface also preserves a second giant sauropod trackway (S7), which is potentially from an even larger individual than S1 from the main surface, with a median pes track length of 112 cm. As this trackway also includes two manus tracks, the gleno-acetabular distance may be estimated at approximately 350 cm when assuming a limb phase of 35 %, as has been calculated from giant sauropod trackways from the Cretaceous (see Lallensack and Falkingham, 2022). The stride length is also larger (median of 289 cm) than that in S1, possibly reflecting both a slightly larger size and a higher speed of locomotion. The pes tracks are oval and less distinct in shape than those of S1. The manus tracks are rounded at their anterior edge and concave at their posterior edge. The heteropody (*i.e.*, pes size index/manus size index) is 1.7.

Several other clearly defined sauropod tracks are present on the surface but cannot be associated with a trackway. These tracks generally seem to be of sizes comparable to those of S7 (Fig. 9).

4.2.4. Discussion

Both surfaces probably represent time-averaged assemblages of tracks, *i.e.*, the tracks have been recorded over an extended amount of time, as indicated by the high degree of trampling and variations in track preservation. The two theropod trackways of surface 1, although spatially close to each other and showing similar travel directions, probably traversed the surface independently from each other. This is indicated by their trackway midlines being at an angle of 15° to each other and by the differences in speed of locomotion. Trackway T2 overprints a pes track of sauropod trackway S1, indicating that at least this theropod passed through the surface after the giant sauropod. Likewise, the first track of theropod T3 on surface 2 disrupts the displacement rims of one large sauropod pes track, again suggesting that the theropod appeared after at least one of the sauropods.

The tracks in the strongly trampled area in the southern portion of the studied surface appear relatively homogeneous in terms of clarity and depth of impression, with no apparent tracks that could be regarded as "background trampling". It is therefore possible that they were made during a relatively short interval of time. The four (or three) recognised smaller sauropod trackways are parallel to each other and head in the

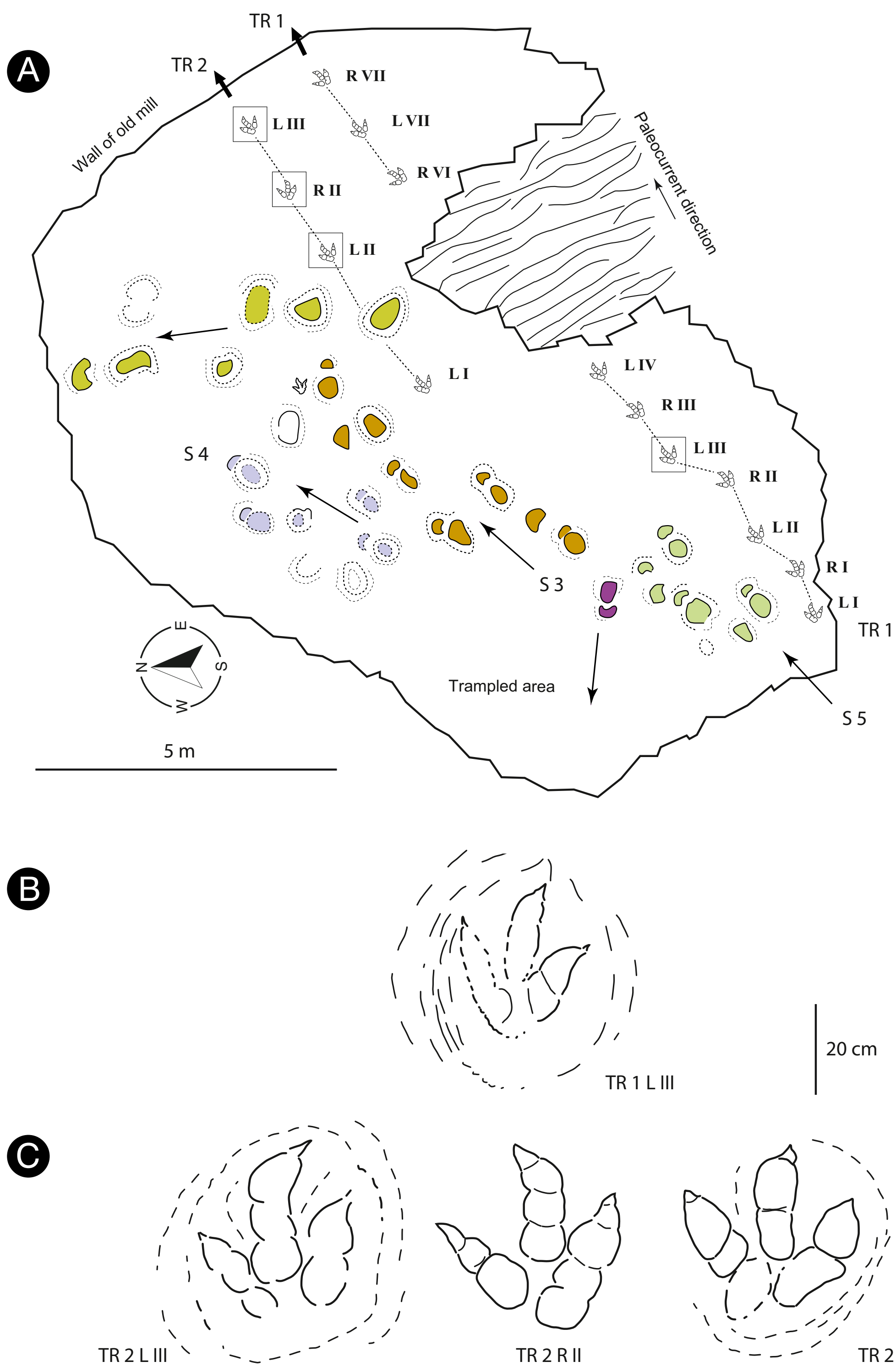

Fig. 7. Tasra site (surface 1) (HIIUC-EM-02) in El Mers I formation (Middle Atlas, Morocco). A. Schematic sketch of the trampled surface (in 2004). B. Interpretive drawing of left theropod track from *Megalosauripus* trackway TR1. C. Interpretive drawings of theropod tracks from *Megalosauripus* trackway TR2.

same direction, raising the possibility that these individuals traversed the surface as a group, adding to the evidence for gregarious behaviour in sauropods. Although one of these trackways (S2) appears to be somewhat larger, the speeds of locomotion of all four trackways, roughly estimated here at 0.68 to 0.78 m/s using Alexander's formula (Alexander, 1976), are similar and therefore do not contradict the possibility of herding. However, whilst some of the isolated tracks and manus–pes sets indicate a direction of travel similar to that of trackways S2–S5, others show a variety of different orientations.

4.3. Site IIb (Tasra Westbank)

This site, originally published by Meyer and Thüring (2004, 2005), is located in the bed of the Tamghilt valley, on the west bank of the river,

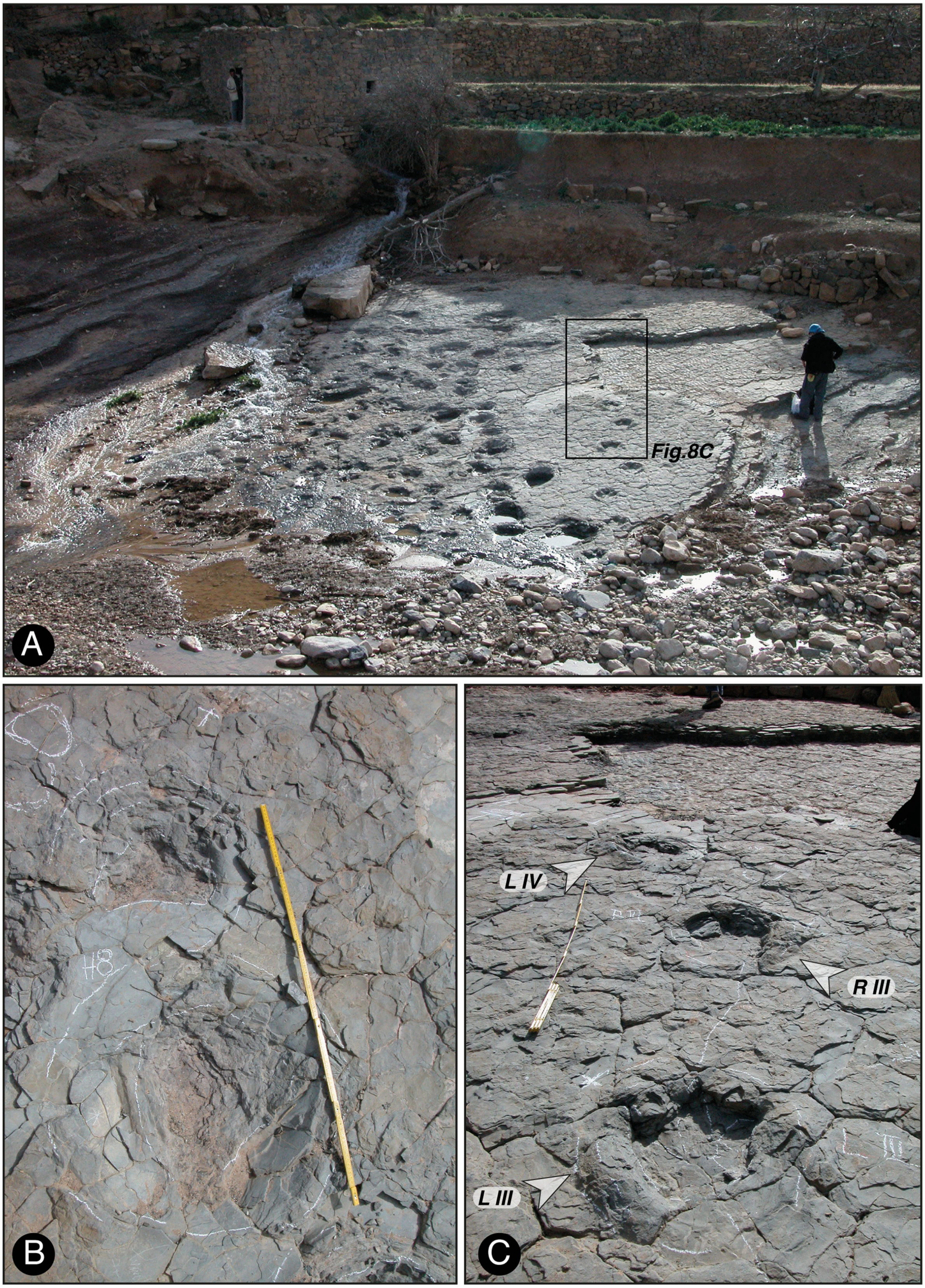

Fig. 8. A. Panoramic view of the Tasra site (surface 1) (HIIUC-EM-02) in El Mers I formation (Middle Atlas, Morocco). B. Photograph of sauropod pes–manus set. C. Close-up of theropod trackway (*Megalosauripus* isp.).

approximately 400 m downstream. This main level can be correlated with level 2 of the Tasra site (F_2 in Fig. 10). It is a surface that is approximately 50 m^2 in size and contains 39 theropod and 33 sauropod tracks arranged in 10 different trackways (Figs. 11 and 12). The tracks are preserved as negative epichnia and show faint ripples and mud cracks. The sauropod prints show an oval to rounded pes and a classical horse-shoe

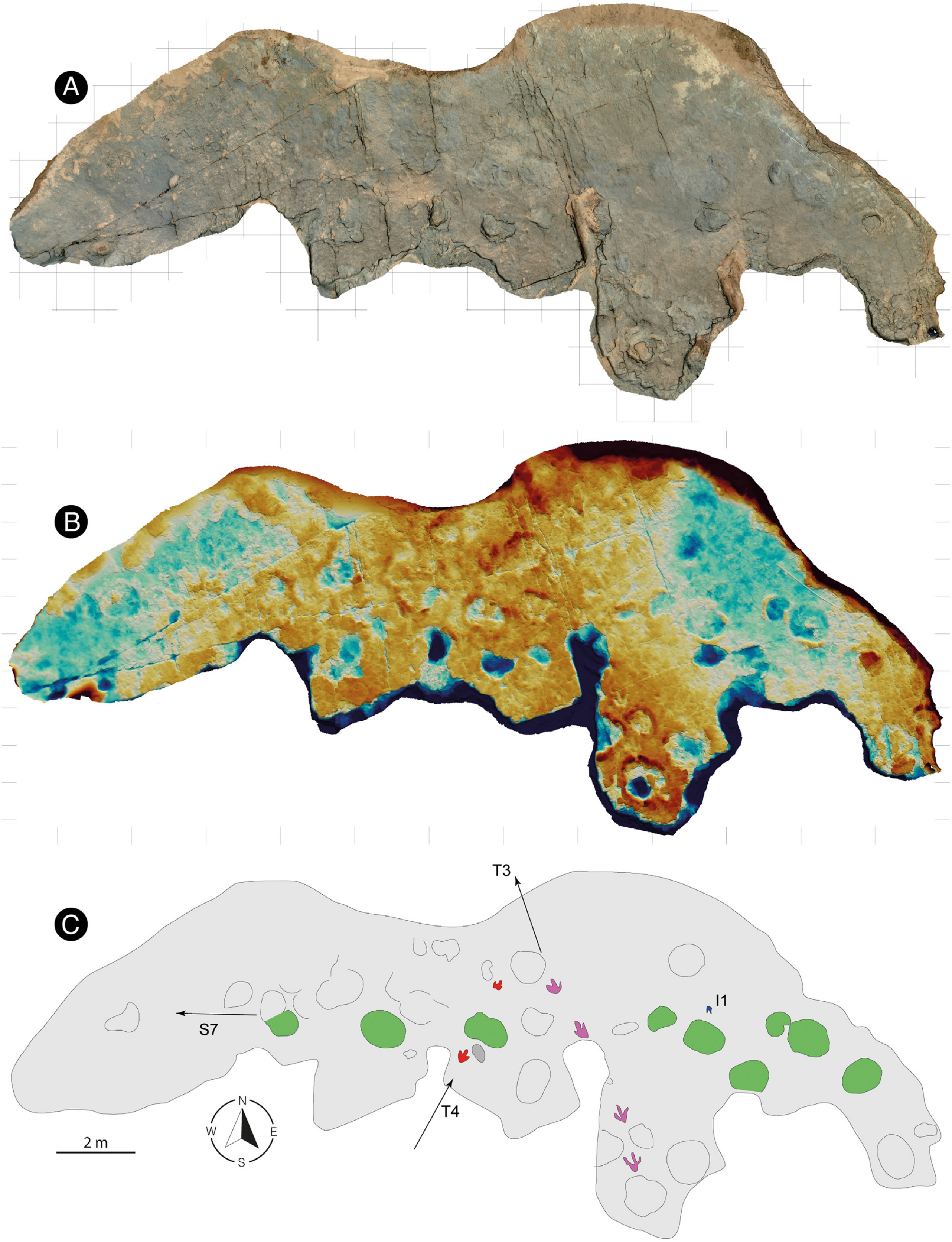

Fig. 9. Tasra site (surface 2) (HIIUC-EM-02) in El Mers I formation (Middle Atlas, Morocco). A. Orthophoto. B. False-colour depth map. C. Schematic sketch of trampled surface.

shaped manus and trackway show a narrow-gauge pattern. The most striking feature is their enormous size. The few measurable pes lengths vary from 123 to 130 cm, whereas their widths range from 100 to 124 cm; the step length is extremely short (270 cm). Assuming a hip height of 4 times footprint length, this would mean that the animal had a hip height of approximately 5.2 m (Fig. 11B).

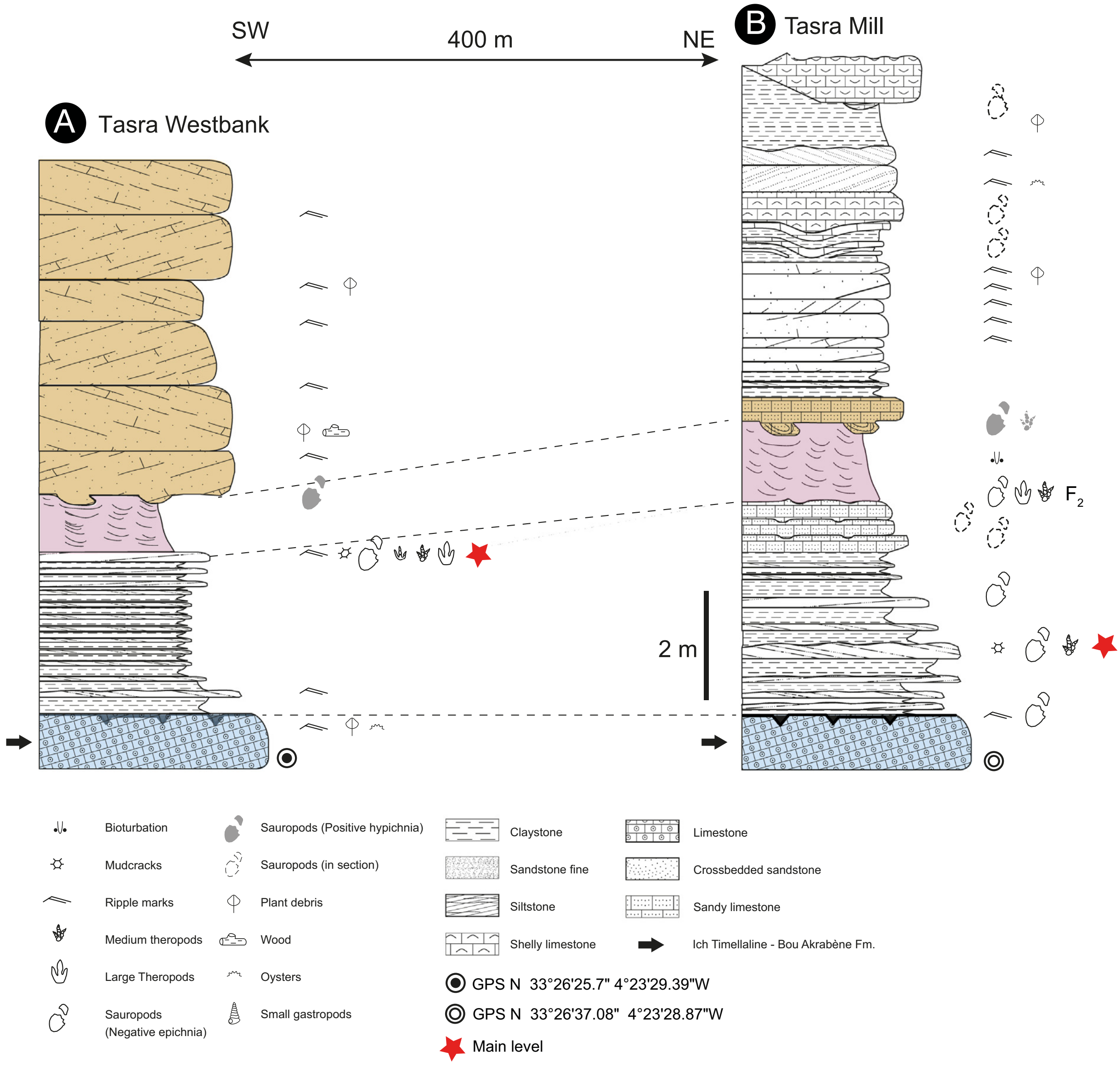

Fig. 10. Detailed stratigraphical log of Tasra and Tasra Westbank sites in the El Mers I formation (Middle Atlas, Morocco) with positions of the studied track-bearing surfaces.

The smaller theropod tracks range between 16 and 18 cm in pes length, and their width varies between 15 and 17 cm, respectively; they show slender and pointed digits; as there are no distinct step cycles, stride length cannot be determined (Fig. 11B). The medium-sized theropods are 29 to 41 in length and 21 to 29 in width, and the stride length is 1.2 m. The medium-sized theropods are very similar to those from the main level at the Tasra IIa site, have distinct fleshy pads and ichnotaxonomically can be attributed to *Megalosauripus* (Fig. 11C).

4.4. Site III (Inzar O'Founass)

4.4.1. Description

Inzar O'Founass consists of three surfaces (labelled surfaces 1–3) on the left and right banks of the Taghzout valley that form a canyon with a width of *ca.*, 9.5 m (Fig. 13). Surface 1 is the southeastern exposure located on the right bank of the wadi; it is the stratigraphically highest surface. With its western margin eroded by the river, it forms a narrow, sinuous exposure that is 25 m in length (when measured along the exposure) but only 0.8 to 1.7 m in width. This surface contains the highest density of tracks at the site, with 59 clearly defined tridactyl dinosaur tracks most probably those of theropods along with various scratch marks.

Surface 2 is on the left bank of the wadi, located northeast of surface 1. It is 23.5 m along the exposure and 0.25 to 2.3 m in width and positioned *ca.*, 0.3 m below surface 1. Surface 2 contains 23 clearly defined tridactyl dinosaur tracks, an even higher number of dinosaur scratch marks, and at least four crocodylomorph *Hatcherichnus* scratch marks. The top layer of this surface is partially eroded, exposing the layer below that occasionally shows clear tracks and scratch marks, as well as many indistinct marks which partly could represent tracks as well. On the southern end of the exposure, this lower layer shows ripple marks. Surface 3 is 65 cm below surface 2 and extends into the wadi bed; it preserves a single tridactyl dinosaur trackway of four poorly defined tracks on a ripple-marked surface. An *ex-situ Hatcherichnus* track was collected a few metres above the track horizons.

4.4.2. Tridactyl dinosaur tracks

The dinosaur tracks at the site are highly variable, including fully impressed, regular tridactyl tracks, long and subparallel scratch marks, and short scratch marks of individual digits. The fully impressed tracks are often well preserved (*i.e.*, are little affected by erosion and

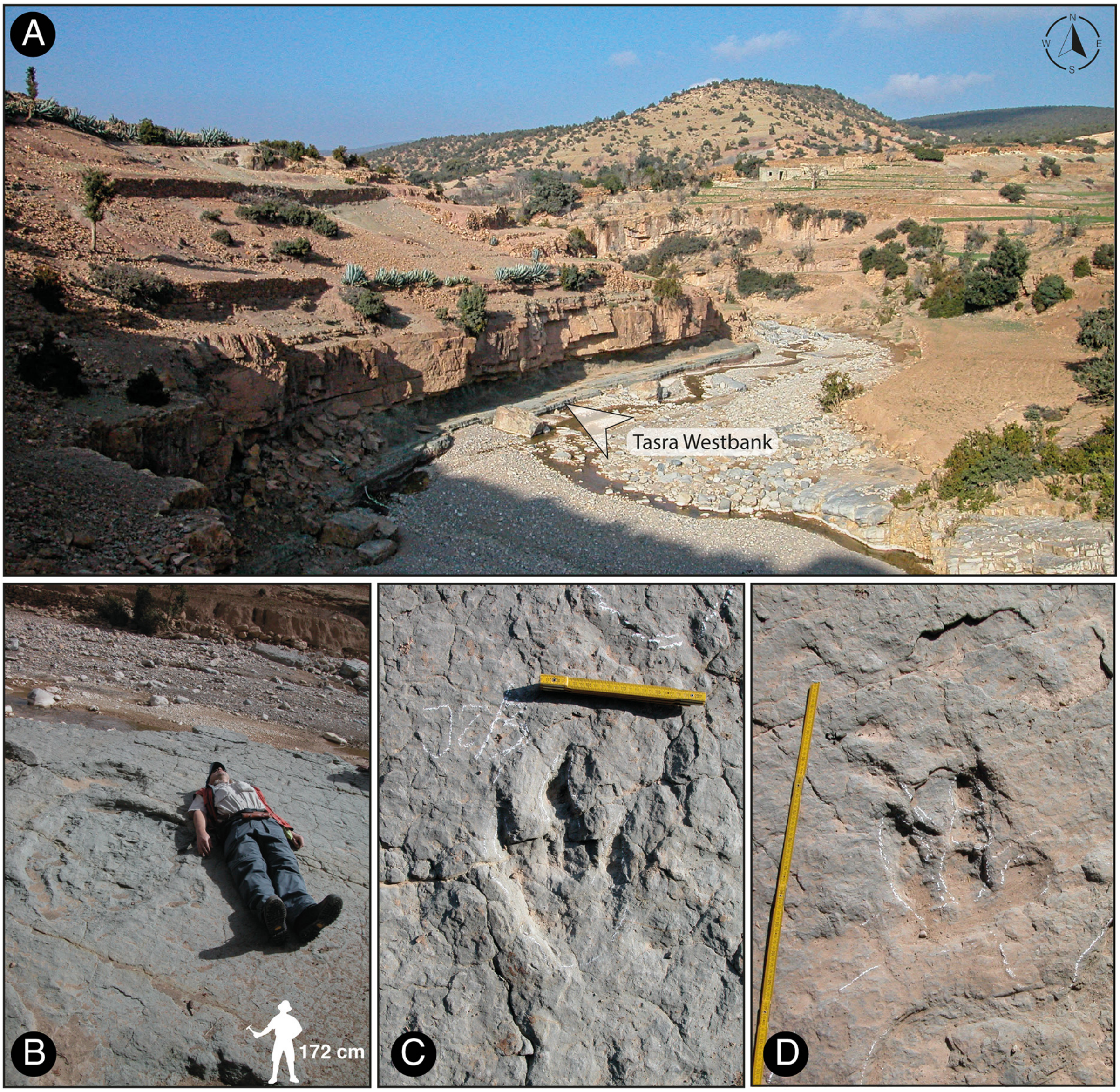

Fig. 11. A. Panoramic view of the Tasra Westbank site in the El Mers I formation (Middle Atlas, Morocco). B. Photograph of sauropod pes–manus set (co-author CM for scale = 1.72 m). C–D. Close-up of medium size theropod tracks.

weathering), especially on surface 1, but in all cases lack anatomical details such as phalangeal pad impressions and are therefore of low anatomical fidelity. Whilst some of the tracks are clearly penetrative (*i.e.*, formed when the foot sank deeply into soft sediment), most tracks and scratch marks appear to be surface traces, and it is likely that the exposed surfaces represent the original tracking surface. The length, parallel arrangement, and associated sediment mounds of the scratch marks, as well as the associated *Hatcherichnus* tracks (see below), indicate that these tracks were left by both walking and punting ('swimming') trackmakers, implying that this site records changes in water level over time. The tracks are generally between 30 and 45 cm in length, indicating mid- to large-sized trackmakers. Based on this restricted size range, it is probable that only a single tridactyl trackmaker species was present, even though the presence of multiple species cannot be excluded.

Trackway 1 on surface 3 comprises shallow tracks that do not show evidence of sediment collapse, suggesting a different mode of formation. Although the tracks are indistinct with very low anatomical fidelity, their length (37–40 cm) is consistent with that of the tracks at surfaces 1 and 2. The tracks form a slight zig-zag pattern and are rotated inward. The stride lengths are 224 and 227 cm, and the pace lengths are 108, 117, and 111 cm. As these tracks interrupt the ripple pattern of the surface, with no ripples evident within the track, they probably formed when the ripples were already in place. A second trackway (trackway 2) is very indistinct and was only discovered in the photogrammetric 3D models. These tracks lack definition but appear to be tridactyl theropod tracks; their presence is betrayed by slight displacement rims in two of them and the overprinting of the ripple pattern of the surface. However, they can be confidently interpreted as tracks due to their very regular arrangement (Lallensack et al., 2022a), with pace lengths varying between 89 and 91 cm, and the slight zig-zag arrangement being consistent. Several scratch or drag marks and other very indistinct tracks are probably present but are difficult to identify with confidence.

4.4.3. *Hatcherichnus* tracks

Surface 2 preserves at least four distinctive scratch marks, each consisting of three short and sub-parallel to slightly diverging digit traces (Fig. 14A4, A7). These traces are relatively consistent in size and are always shorter than wide (6 by 11 cm; 8 by 12; 6 by 10; and 9 by 11 cm in the best-defined examples, respectively). The digit traces are distinctly curved, although they are straighter in one specimen. There is a high sediment mound immediately behind the digit traces. The digit traces are typically parabol-shaped when seen in longitudinal cross-section, being deepest at mid-length (although this is variable, and in one specimen, they reach their deepest point more posteriorly). At their posterior end, they are almost vertical, extending into the anterior surface of the sediment mound; the latter therefore appears to have been actively pushed up by the digits. There are conspicuous scale striations within the digit traces and in specimen 3 (Fig. 14A7) between the digit traces; this demonstrates that these traces are scratch marks that record the backward motion of the autopodium. Specimen 1 (Fig. 14A4) shows at least four broad striations within the central digit trace that are *ca.*, 2.5 mm in width, with some much finer striations further up the wall of the digit trace. The striations between the digit traces in specimen 3 (Fig. 14A7) are *ca.*, 5 mm apart but are itself covered by several finer striations with the same orientation.

The features of these tracks, their consistent smaller size, their shortness, the parabol-shaped digit traces that extend onto the anterior side of the sediment mound, and the distinct striations are different from any known tridactyl dinosaur tracks. Consequently, these tracks were probably left by a different, possibly non-dinosaurian, trackmaker species. The tracks do in fact closely resemble tracks described from the Late Jurassic of Utah, which were named *Hatcherichnus* and have been attributed to a crocodylomorph trackmaker (Foster and Lockley, 1997). *Hatcherichnus* tracks have since been reported from around the world, including the mid-Cretaceous Mibladen locality in Morocco (Klein et al., 2018) and from Early–mid-Cretaceous deposits of Algeria (Bouchemla et al., 2023). In particular, the latter material shows some similarities with the Inzar O'Founass tracks. However, note that Bouchemla et al. (2023) also discuss swimming pterosaurs as potential producers of *Hatcherichnus* tracks from Algeria. The possible crocodylomorph trackmaker at Inzar O'Founass might have been either punting or bottom walking.

4.5. Site IV (Ifri N'Tfrane)

The Ifri N'Tfrane site, located in the El Mers riverbed, preserves several strongly eroded theropod tracks as well as an intriguing trackway of three complete and two partial tracks (Fig. 15). This trackway was initially thought to represent an ornithischian (ornithopod or thyreophoran) trackmaker, based on its broad, semicircular digit impressions and a digit impression III that only slightly projects beyond the impressions of digits II and IV. These features resemble Cretaceous hadrosaurid tracks named *Ornithopodichnus* that were attributed to short-toed forms such as *Gilmoreosaurus* and *Gobihadros*. However, ornithopod tracks are rare in the Jurassic, and the occurrence of hadrosaurids in the Middle Jurassic seems less probable. Given the significance of extending their stratigraphical range, such claims must be supported by solid evidence.

The tracks are 36 cm in length on average and longer than they are wide. Track width cannot be measured precisely because digit II appears to be shortened due to sediment collapse; the maximum measured width is 29 cm. The digit impressions are very broad and hoof-like (11 cm in digit impression IV of track 2). The "heel" region in track 2 is elongated, broad and rectangular, separated from digit IV by an embayment, and distinctly angled against digit impression III (Fig. 15C). In the other tracks, the "heel" region is also elongated but more indistinct. The projection of digit impression III beyond other digits is very low (19 % of the total track length in track 2). In track 3, there is a subtle medial extension that resembles a hallux impression. At least one of the tracks (track 3) is rotated inwards by 5°, although no rotation is obvious for

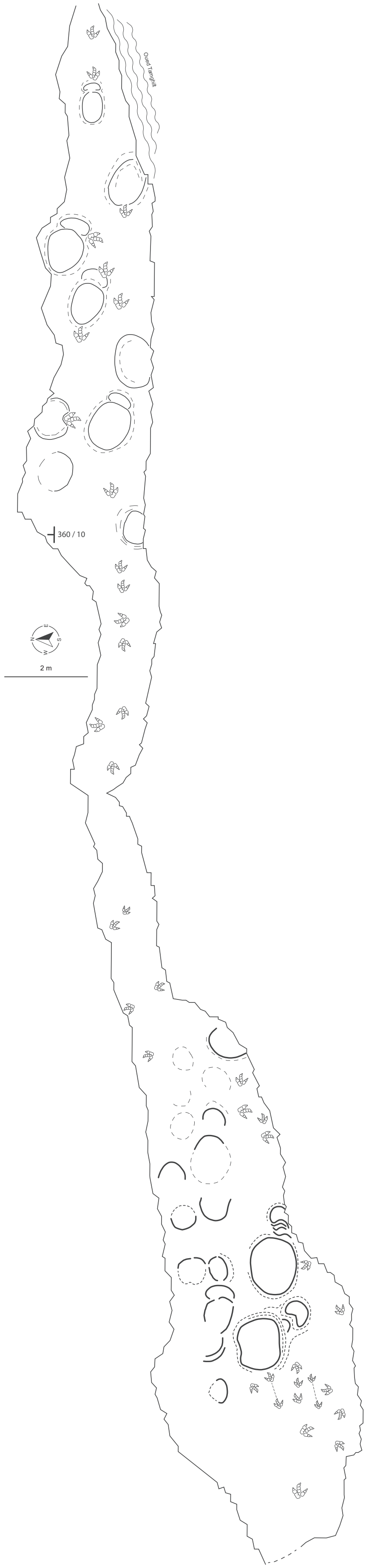

Fig. 12. Schematic sketch of trampled surface at the Tasra Westbank site; solid line: external outline of the footprint; dotted line: displacement rim.

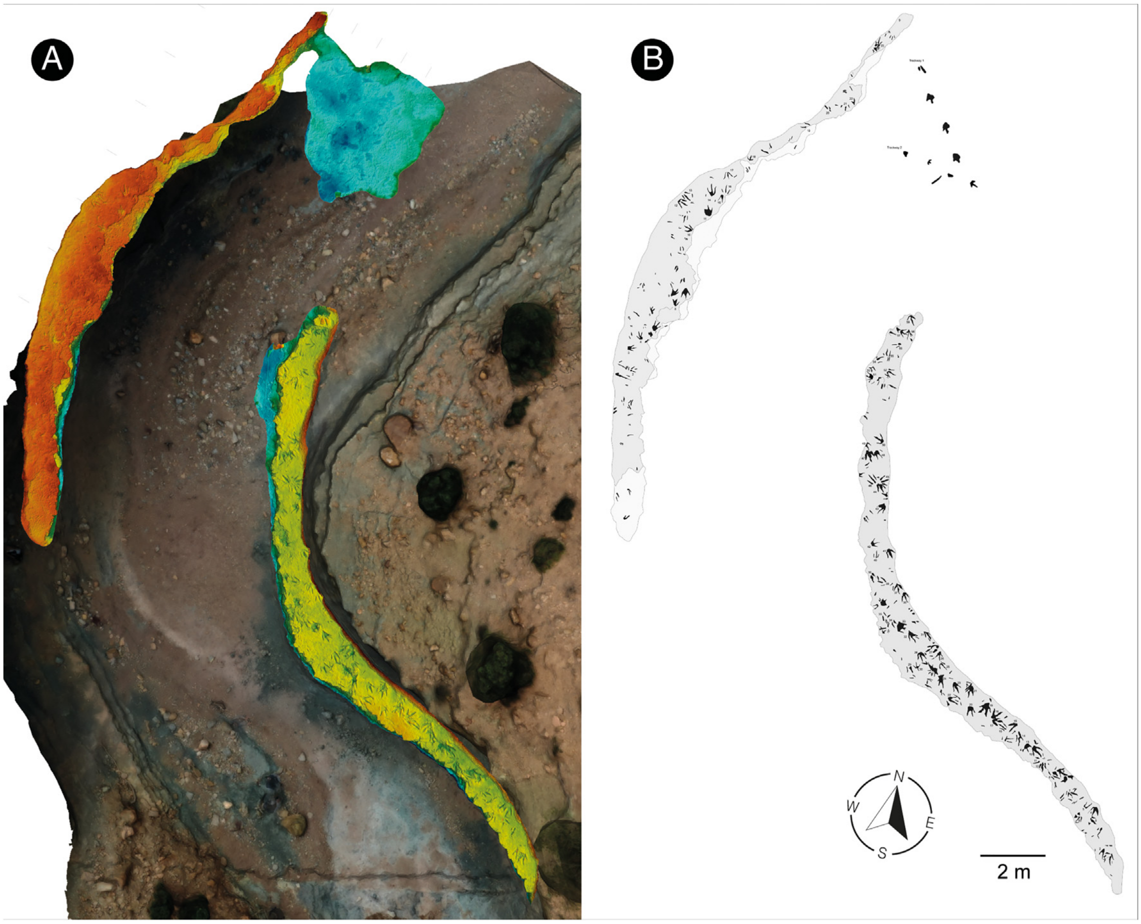

Fig. 13. Inzar O'Founass site (HIIUC-EM-03) in the El Mers I formation (Middle Atlas, Morocco). A. Overlap of a textured 3D model of both banks of the Taghzout river and a false-colour depth map of the tracksite. B. Schematic sketch of the trampled surface.

track 2. The measured stride lengths are 180 and 184 cm, and the measured pace angulations are 171° and 179°, documenting a very narrow trackway pattern and gait. The tracks are also surrounded by swallow but broad (~20 cm) displacement rims. Irregular, radial ridges are visible on the left side of the tracks, both within and outside of the impressions. The track surface is heavily eroded by the El Mers river, as indicated by scour marks that, in the case of track 2, extent into the track.

The listed features match the thyreophoran ichnogenus *Deltapodus* well known from the Middle and Late Jurassic. However, *Deltapodus* trackways or *Deltapodus*-like plantigrade versions of *Stegopodus* belong to quadrupeds, whereas the **Ifri N'Tfrane** trackway was left by a bipedal animal. Thus, a possible theropod affinity of this trackway cannot be ruled out. Moreover, a theropod affinity is also supported by the trackway pattern, which is very narrow with relatively long steps, and the footprints are directed forwardly. Assuming a theropod producer would imply that the observed morphologies are not matching the anatomy of the trackmaker but are instead are result of foot dynamics and interaction with a soft substrate, where the tracks penetrated more deeply into the substrate than is obvious from the relatively shallow tracks.

The trackway configuration and the temporal context also argue against an ornithischian trackmaker. Jurassic ornithischian ichnotaxa, such as *Anomoepus*, *Moyenisauropus*, *Shenmuichnus*, or *Dinehichnus*, differ in their much narrower digit impressions and in their typically shorter strides and lower pace angulation values (Gierliński, 1991; Lockley et al., 2009). The same characteristics can be observed in other typical thyreophoran trackways (Le Lœuff et al., 1999; Lockley et al., 2018). The inward rotation of pes imprints in the **Ifri N'Tfrane** trackway is consistent with that of both ornithischian and theropod trackmakers (Pérez-Lorente, 2015; Masrour et al., 2023). We therefore conclude that the affinity of this trackway is ambiguous, and that further analysis is needed.

Eight isolated theropod tracks at the Ifri N'Tfrane are exposed on a small (1 × 3 m) surface (Fig. 16). These tracks fall into two size classes: moderately large tracks (32 cm length of track 2) and small, *Grallator*-sized tracks (14 cm length of track 8). The large tracks (tracks 1–4) are probably true tracks and not penetrative, as evidenced by clearly discernible phalangeal pad impressions. One of these tracks (track 2) is of particularly high anatomical fidelity, showing the configuration of two phalangeal pad impressions in digit II and three phalangeal pad impressions in digit III (Fig. 16C–D); furthermore, a well-defined metatarsophalangeal pad that is slightly offset to the right, resulting in a weak asymmetry of the metatarsophalangeal region the so-called 'heel' region. This asymmetry is slightly weaker than in the *Eubrontes* type material (see Olsen et al., 1998). However, the metatarsophalangeal region is slightly larger than that of *Eubrontes*, smaller than that of *Megalosauripus sensu* Lockley et al. (1998b) and similar in size to the wide morphological variants of *Hispanosauropus* and *Changpeipus* tracks (see Foster, 2015; Xing et al., 2014; Klein et al., 2023). Track 2 also shows evidence of a metatarsophalangeal pad of digit II, which is characteristically well exhibited in the *Eubrontes* type material but also seen in *Hispanosauropus* from Utah and in the *Changpeipus* type. This track shows the same discrepancy in the projections of digits II and IV seen in the Tassmante O'Moche theropod tracks and clearly demonstrates that this is the result of the claw being impressed to different depths as a result of foot kinematics; the digits project equally when measured to the claw tips.

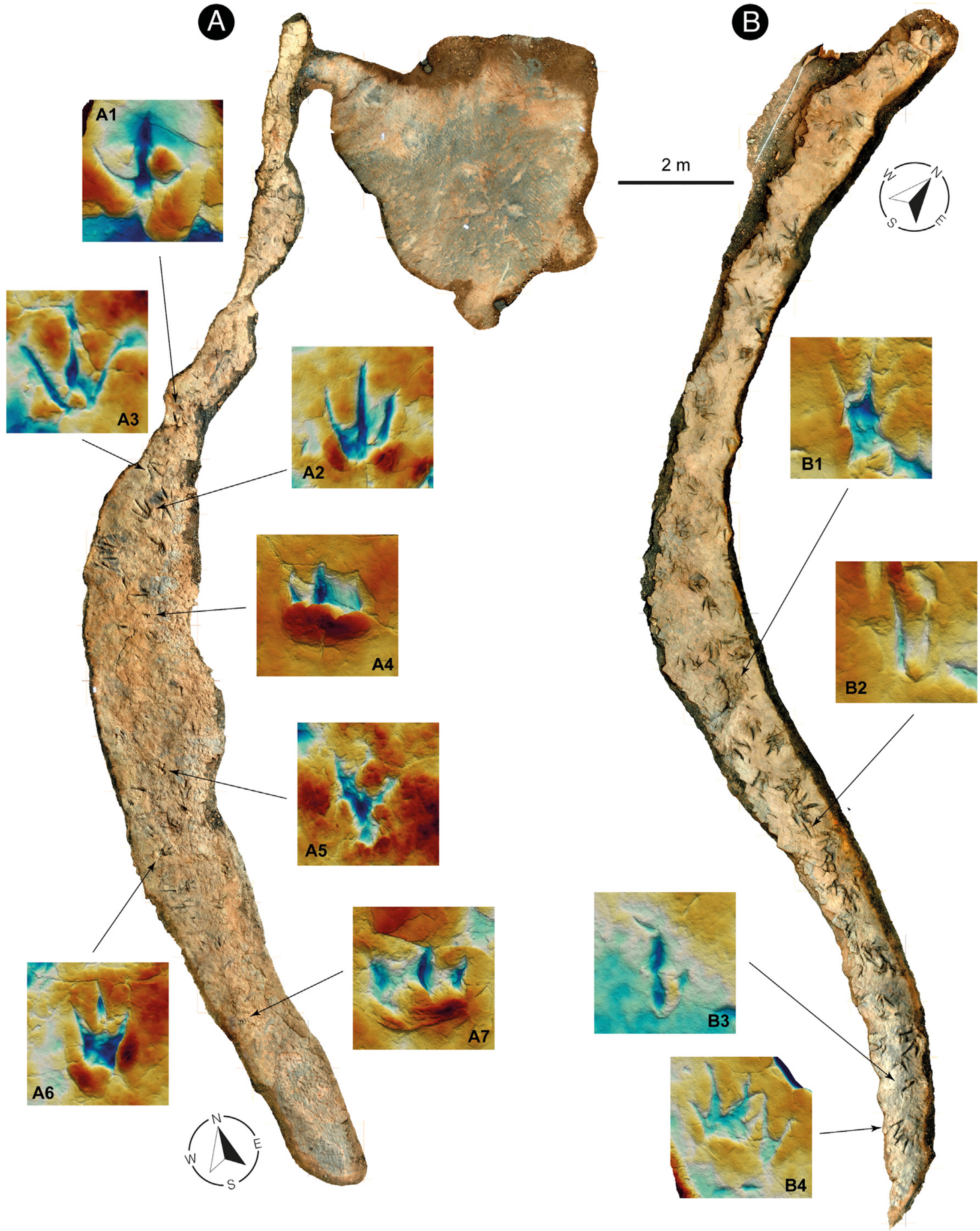

Fig. 14. Inzar O'Founass site (HIIUC-EM-03) in the El Mers I formation (Middle Atlas, Morocco). A–B. Orthophoto of both banks of the Taghzout river and close-up of different tridactyl dinosaurs and *Hatcherichnus* tracks in depth colour.

The small theropod tracks (tracks 5–8) are not very well preserved and lack unambiguous phalangeal pad impressions. In two examples (tracks 6 and 8), the digit impressions are either collapsed into narrow, and probably abbreviated slits. In another example (track 5), digit impression III is not continuous and is separated from the rear of the track by a sediment rim. These observations indicate that these tracks are partly penetrative; at least the digits would have penetrated deeper into the substrate than is evident from the surface tracks. Such preservation makes their ichnotaxonomic comparison definitely unreliable.

4.6. Site V (Laach O'Medda)

The Laach O'Medda site consists of a fallen block below a cliff face. It consists of three clear but low fidelity theropod tracks approximately 18 cm in length; a number of incomplete or indistinct additional tracks are discernible (Fig. 17). A second fallen block was found adjacent to the first that shows additional yet very poorly defined tracks.

The tracks appear more robust, broader, and with a greater splay of digits II and IV than the fidelitous large theropod tracks of Ifri

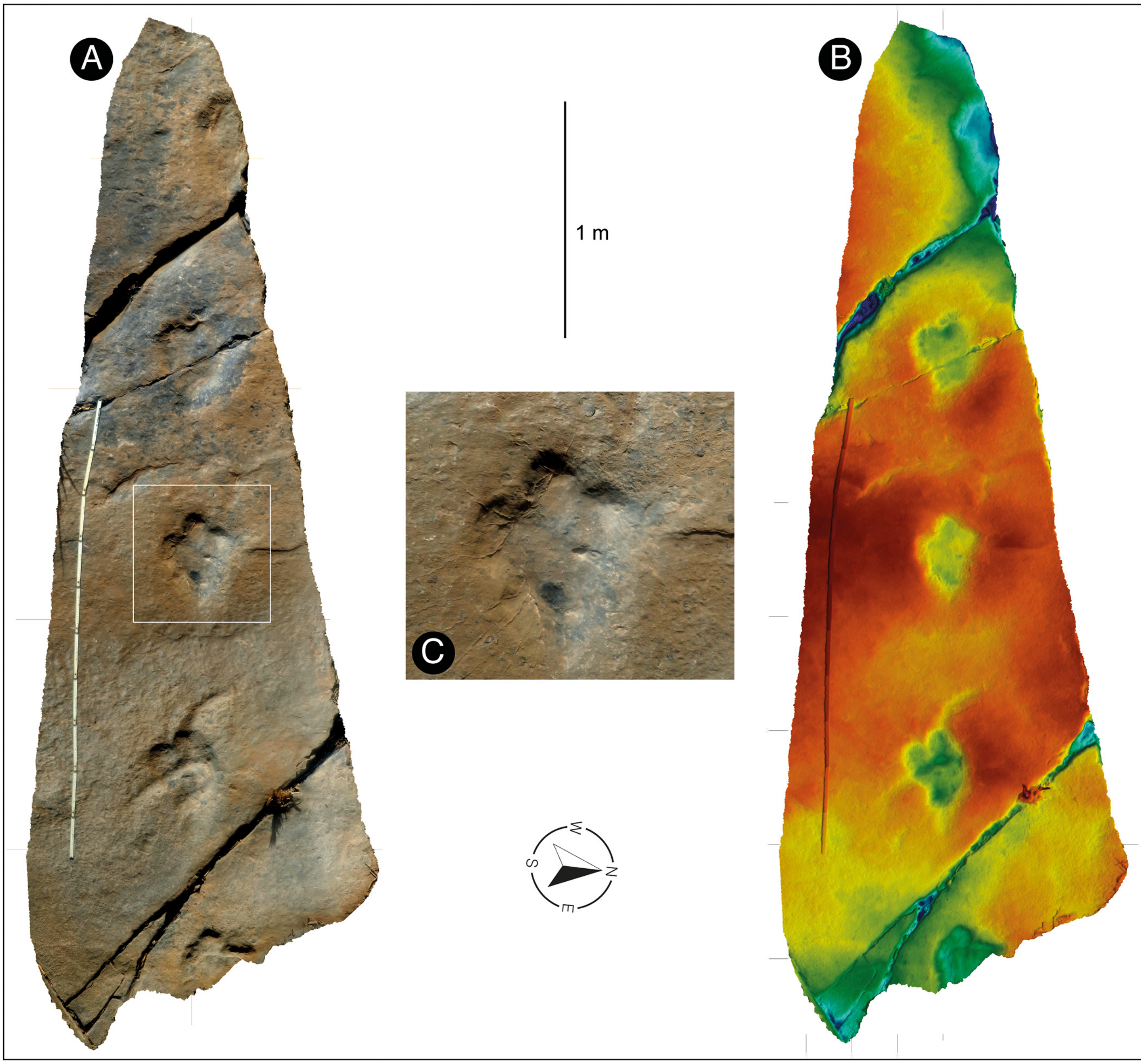

Fig. 15. Ifri N'Tfrane site (HIIUC-EM-04) in the El Mers II formation (Middle Atlas, Morocco). A–B. Orthophoto and false-colour depth map of the trackway with three complete and two partial tracks. C. Details of track.

N'Tfrane and Tassmante O'Moche. These differences, however, might be due to deeper sinking into soft sediment rather than anatomical differences. It is therefore prudent to leave these tracks without ichnotaxonomic designation.

4.7. Site VI (Tassmante O'Moche)

Tassmante O'Moche is a small site exposed on a cliff edge and is composed of at least three different surfaces spanning a vertical range of 6.6 cm. The site preserves at least four isolated theropod tracks, two of which show a reasonably high degree of anatomical fidelity (Fig. 18). These two tracks can be interpreted as either true tracks or shallow undertracks, as evidenced by a clear set of phalangeal pad impressions. The larger track measures 27 cm in length, whilst the smaller track measures 16 cm in length. The larger track is fully impressed with a clearly asymmetrical 'heel' region, indicating that it is the track of the left foot (Fig. 18D–E). In the smaller track, the metatarsophalangeal pad of digit IV was not impressed (Fig. 18B–C). In the larger track, digit impression IV appears to be much longer than digit impression II. However, the termination of digit II is broadly rounded rather than acute as that of digit IV, indicating that the claw mark is not visible in digit II but contributed to digit IV. The length discrepancy might therefore be a result of foot kinematics during track formation rather than an anatomical feature. In the smaller track, the right digit (digit II?) also appears to be shorter than the left digit, but a shallow extension, which can be interpreted as the claw mark, is clearly visible. As expected for its larger size (Lallensack et al., 2020), the larger track has a lower projection of the digit impression III and is more robust overall with a large metatarsophalangeal region.

The smaller track matches the key feature of *Carmelopodus* because of the lack of a "heel" region, being more digitigrade (see Lockley et al., 1998a). In contrast, the larger track matches the main concept of

Please cite this article as: M. Amzil, M. Oukassou, J.N. Lallensack, et al., New dinosaur tracks from the Middle Jurassic red beds of the Middle Atlas (Morocco): Application of ..., Proceedings of the Geologists' Association, https://doi.org/10.1016/j.pgeola.2024.06.004

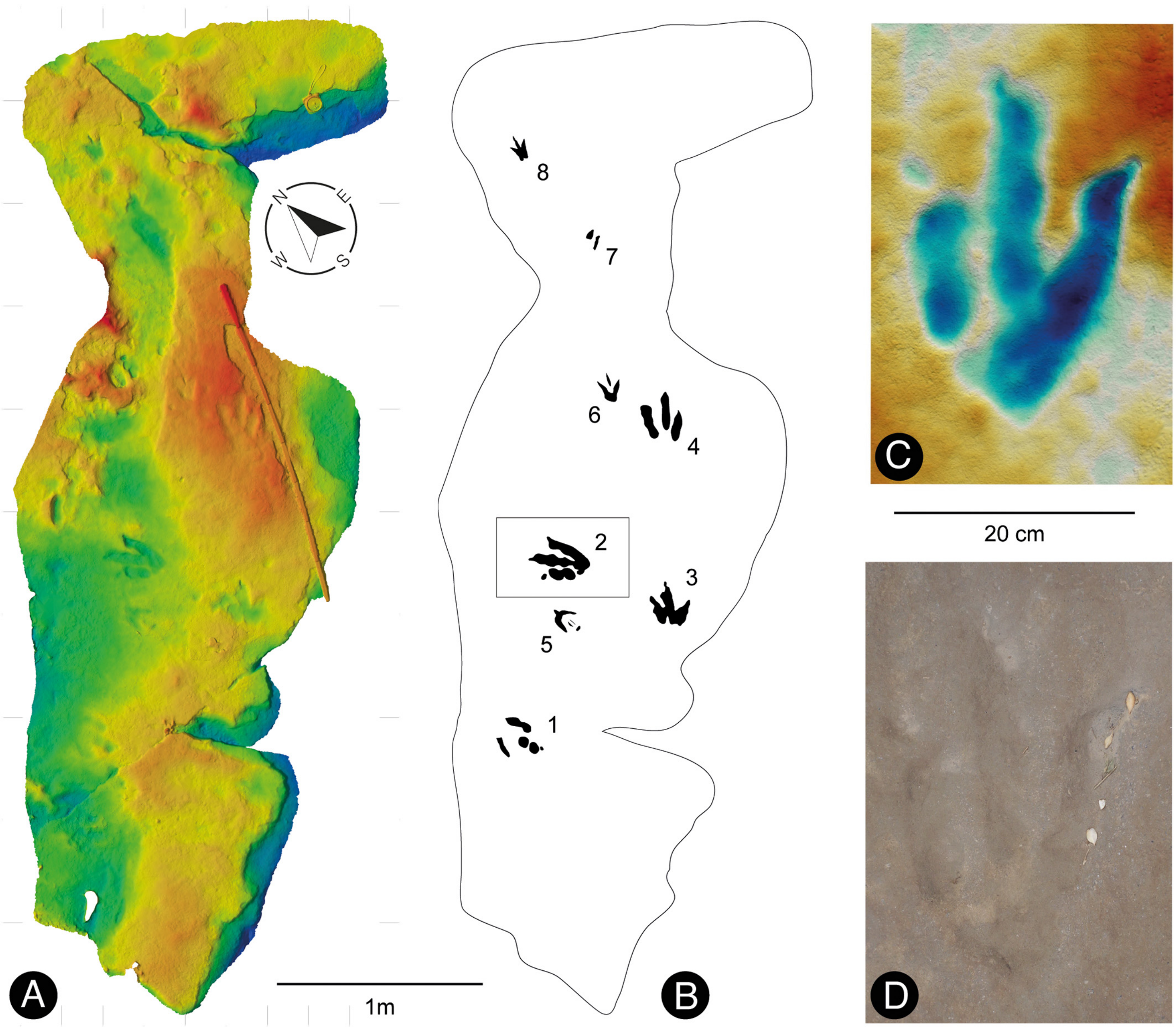

Fig. 16. Ifri N'Tfrane site (HIIUC-EM-04) in the El Mers II formation (Middle Atlas, Morocco). A. False-colour depth map of the site with isolated theropod tracks. B. Schematic sketch of trampled surface. C–D. Close-up of large isolated theropod track, false-colour depth map and photograph.

Megalosauripus by showing the typical large 'heel' region (see Lockley et al., 1998b). However, a number of other theropod ichnotaxa found in strata younger than the Early Jurassic have similar shapes.

5. Geoheritage and conservation

El Mers represents an 'integrity' heritage area and, as such, contains a valuable finite ichnological resource. The majority of the tracksites are located on riverbeds and therefore at risk of erosion due to the seasonal flooding. One of the previously reported sites has since been entirely lost to river erosion, and parts of the El Mers and Tasra surfaces have disappeared since they have been first described. In addition, the seasonal flooding also results in surfaces being covered by gravel to variable extends, especially at the Tasra and El Mers Center sites, which can limit their attractiveness for visitors. On the other hand, the same erosional processes are constantly exposing additional tracks and tracksites. Therefore, whilst the life expectancy of individual tracks and sites may be limited, the El Mers area as a whole has a large long-term value for geoheritage. A similar area with transient riverbed sites is the Paluxy River near Glen Rose, Texas, US, where the famous Dinosaur Valley State Park was established (Farlow et al., 2015).

Additionally, the scarce documentation of the tracksites has limited their impact on the scientific community. To address both these issues and evaluate the wider application of photogrammetry technique, an integrated UAV and terrestrial photogrammetry of the sites was performed.

The data collected in the course of this study were sufficient to construct 3D models of varying resolutions that document the ichnological resources in the El Mers area. The 3D models generated have clear advantages over traditional documentation techniques and can potentially be used as a key element in ichnotaxonomy. Footprint relative depth patterns, when appropriately compared with other tracks and skeletal remains, refine the correlation of tracks with their potential trackmakers. False colour depth maps also help to unravel the formation and superimposition of structures that can mask footprints. Such structures may result from the locomotion of the same (or other)

Please cite this article as: M. Amzil, M. Oukassou, J.N. Lallensack, et al., New dinosaur tracks from the Middle Jurassic red beds of the Middle Atlas (Morocco): Application of ..., Proceedings of the Geologists' Association, https://doi.org/10.1016/j.pgeola.2024.06.004

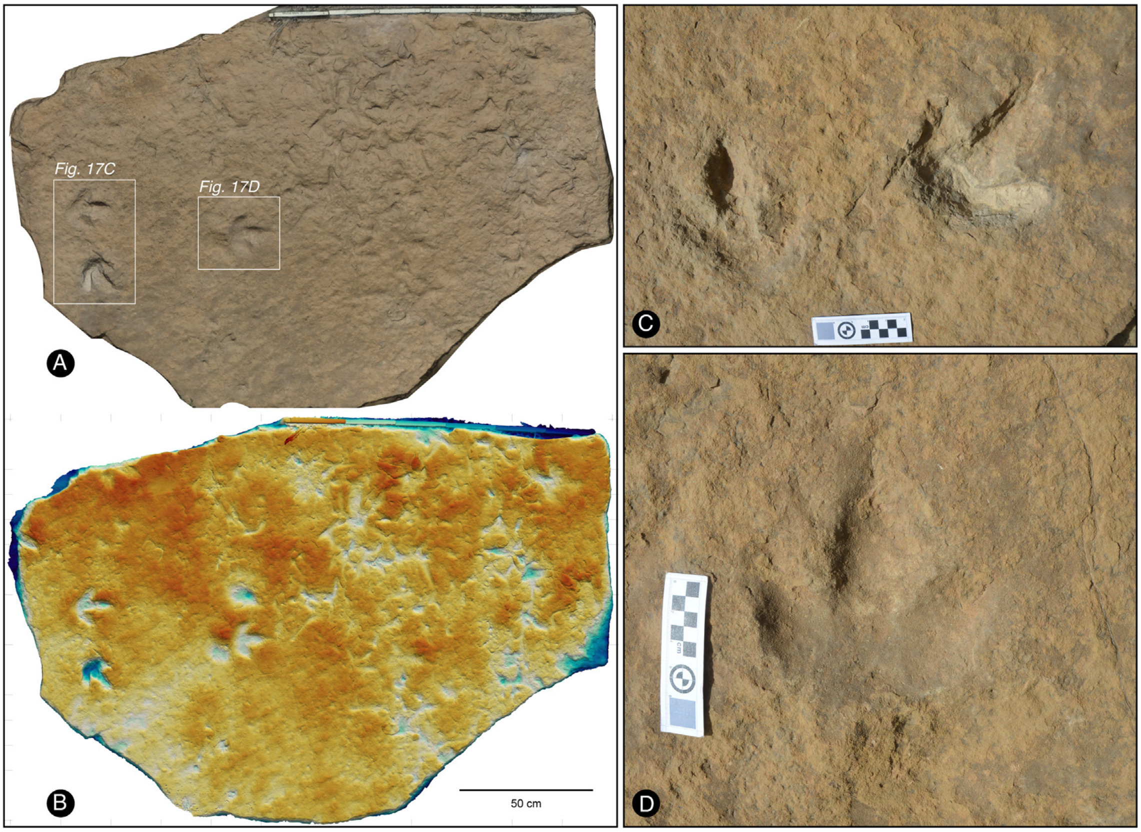

Fig. 17. Laach O'Medda site (HIIUC-EM-05) in the El Mers II formation (Middle Atlas, Morocco). A–B. Orthophoto and false-colour depth map with isolated theropod tracks. C–D. Photographs of small theropod tracks.

trackmakers and from sedimentary processes (*e.g.*, ripples, substrate collapse on inclined palaeosurfaces), as well as from weathering. Photo-textured 3D models constitute a powerful visualisation tool, particularly when viewed in an immersive 3D environment (virtual visit).

The data can be communicated through digital media, increasing the ease of scientific communication *via* the Internet. By allowing workers to construct high-resolution photorealistic 3D models, an integrated UAV and terrestrial photogrammetry may provide the means to produce an inventory of geological heritage sites. This approach provides a unique level of accessibility and can assist land managers in making decisions for the potential development of geotourism and geoeducation projects. Furthermore, 3D models serve as a suitable solution for preserving ichnological records, especially when original specimens cannot be collected and thus are subjected to disappearance. It is important to conduct such surveys regularly in order to document new tracks and tracksites exposed by river erosion.

The dinosaur tracksites in the El Mers region offer excellent opportunities for cultural and geotourism development. All data from this study will be made available to local associations and authorities for use in a geotourism development project planned for the region. These will be used to create a database that will support a planned geotourism trail (Dinosaur Trail) in collaboration with the local sustainable development association (*e.g.*, Anejdi Group/www.anejdi.com) (Fig. 19). It should be noted that the El Mers region is part of a major ongoing project to create a Middle Atlas Geopark, which will contribute to the socio-economic and cultural development of the region.

6. Conclusion

The Middle Jurassic continental deposits of the El Mers area in the Middle Atlas of Morocco preserve a diverse palaeontological and ichnological record particularly relevant for dinosaur evolution studies and palaeobiogeographic reconstructions as well as for the popular scientific divulgation and geoheritage promotion. The rich dinosaur ichnoassemblage in this area with different associations (theropod, sauropod and ornithischian tracks) occurring on extensive surfaces has been little studied and is facing destruction due to erosion and human activities. This paper presents an ichnological study of several dinosaur tracksites using UAV and terrestrial photogrammetry. The application of this technique allows for the rapid collection of high-resolution data with sustainable costs that can be used both by specialists and as a means of a conservation survey and as a basis for knowledge transfer to the public. This contribution will encourage the intellectual, logistical and social involvement of the local population to collaborate with scientists for the conservation of valuable geoheritage.

The institution of new dinosaur tracksites referred to in the evidence here presented could represent an auspicious opportunity for cultural and geotouristic development. The next steps are more field work and the promotion of geosites, in collaboration with local mountain tourism associations in an area that has already revealed a large and significant palaeontological and ichnological record.

CRediT authorship contribution statement

Mustapha Amzil: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Resources, Software, Writing – original draft. **Mostafa Oukassou:** Conceptualization, Data curation, Investigation, Methodology, Project administration, Supervision, Writing – original draft. **Jens N. Lallensack:** Data curation, Formal analysis, Investigation, Methodology, Software, Writing – original draft. **Hendrik Klein:** Data curation, Investigation, Validation, Writing – review & editing. **Omar Zafaty:** Data curation, Investigation, Resources, Writing

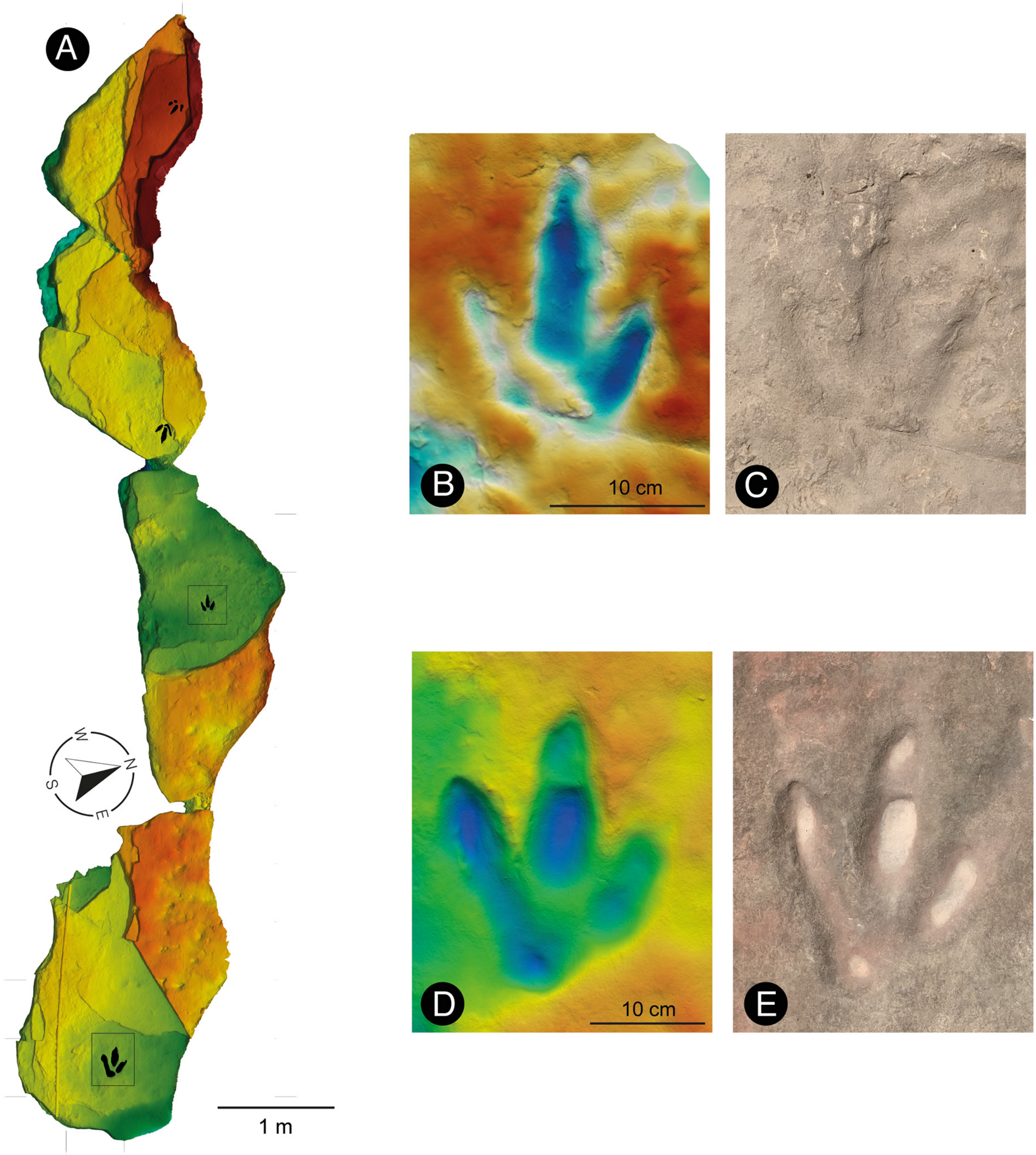

Fig. 18. Tassmante O'Moche site (HIIUC-EM-06) in the El Mers II formation (Middle Atlas, Morocco). A. False-colour depth map of the Tassmante O'Moche site with isolated theropod tracks. B–C. False-colour depth map and photograph of small isolated theropod track (*cf.*, *Carmelopodus*). D–E. False-colour depth map and photograph of a large isolated left theropod track (*cf.*, *Megalosauripus*).

– review & editing. **Hafid Saber:** Data curation, Investigation, Validation, Writing – review & editing. **André Charrière:** Data curation, Validation, Writing – review & editing. **Christian Meyer:** Data curation, Investigation, Resources, Validation, Writing – review & editing. **Gerard D. Gierliński:** Validation, Writing – review & editing.

Data availability

All data (photogrammetric 3D models and site maps) are available from https://doi.org/10.6084/m9.figshare.25330354.

Photographs for photogrammetry are available from https://doi.org/10.6084/m9.figshare.25914010, https://doi.org/10.6084/m9.figshare.25914007, and https://doi.org/10.6084/m9.figshare.25912537.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank the editor and reviewers for their positive and constructive comments, which improved the manuscript. We would like to thank Haj Moulay Lahsen Inirz for the hospitality and valuable assistance in the fieldtrip. The Faculty of Sciences Ben M'sick of Hassan II University of Casablanca, and the Faculty of Sciences of Chouaïb Doukkali

Fig. 19. Proposed panel of tracksite and 'Dinosaur Trail' in the El Mers area.

University, El Jadida, kindly provided logistical support during the field trip. Field campaign of Ch.M. in 2004 was financed by the "Lehre und Forschung" trust of the Natural History Museum Basel. This paper is dedicated to the memory of Martin G. Lockley (1950–2023), the prime mover of vertebrate footprint studies.

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Please cite this article as: M. Amzil, M. Oukassou, J.N. Lallensack, et al., New dinosaur tracks from the Middle Jurassic red beds of the Middle Atlas (Morocco): Application of ..., Proceedings of the Geologists' Association, https://doi.org/10.1016/j.pgeola.2024.06.004