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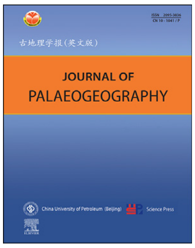

Research article

Early Pleistocene vertebrate tracks impressed on Oligocene beds from the southernmost Iberian Peninsula: Palaeogeographic implications

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Abstract The southern of the Iberian Peninsula preserves a diverse ichnological record of vertebrates from the late Neogene—Quaternary. While the ages of several tracksites, such as those from the Miocene—Pliocene transition and the middle-late Pleistocene, are well-established, others remain undated or have unknown ages. This paper reports the discovery of the southernmost tracksite in the Iberian Peninsula and continental Europe on the Island of Tarifa (Cádiz). The tracksite contains over 600 vertebrate footprints from the early Pleistocene that are grouped in four morphotypes. Morphotypes 1, 2 and 3 (M1, M2 and M3) are predominantly didactyl-shaped, rounded to ovoid and elongated, and associated with tracks left by artiodactyls. Morphotype 4 (M4), suboval to subcircular in outline, is the largest and is probably related to the imprint left by proboscideans.

We also document the progressive transition from morphotype 2 with isolated, rounded footprints to morphotype 3 with elongated tracks formed by overlapping two tracks of the same animal which is observed. The consistency of the substrate, together with the trackmaker limb dynamics, conditioned the final morphology of the tracks, which were produced in a very soft clay-rich substrate of late Oligocene, that was folded and tilted in the latest Pliocene. This relief configuration gave rise to a narrow, partially or totally flooded corridor through which the trackmaker animals passed continuously, simultaneously, and in opposite ways. This discovery from the southernmost tip of continental Europe is the first one from the early Pleistocene in the Iberian Peninsula and a rare example from the Mediterranean region.

Keywords Ichnology, Artiodactyls, Proboscideans, Footprint overlapping, Tarifa (Spain)

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1. Introduction

In recent years, southern Iberia has become a key location for understanding the late Neogene—Quaternary vertebrate ichnological record of the Mediterranean region. Specifically, middle and upper Pleistocene tracksites related to coastal deposits have been found in the south of Portugal and the west of Andalusia, yielding a very diverse fauna: hominins, proboscideans, cervids, bovids, ursids, canids, lagomorphs and birds (e.g., Neto de Carvalho, 2009; Neto de Carvalho *et al.*, 2016, 2020a, b, 2022, 2023; Muñiz *et al.*, 2019; Neto de Carvalho and Belo, 2022; Mayoral *et al.*, 2021, 2022). Moreover, the Iberian Peninsula also preserves, tracks of ursids, proboscideans, equids, artiodactyls, canids and birds from the late Neogene (Miocene—Pliocene transition) (Lancis and Estévez, 1992; Doyle *et al.*, 2000; Fierro Bandera *et al.*, 2014; McCann *et al.*, 2018). However, until today, the vertebrate ichnological record between the late Pliocene and early Pleistocene is unknown.

Recently, a new locality with hundreds of vertebrate tracks has been found in the southernmost part of the Iberian Peninsula on the Atlantic coast of Cadiz, Tarifa Island Beach (Figs. 1—8). The tracks formed during a regression that occurred at the end of the late Pliocene, and transgressive pulses that occurred during the Pleistocene in this area (González Lastra *et al.*, 1990; Lario, 1996; Zazo *et al.*, 1999; Gracia *et al.*, 2004). Surprisingly, the tracks are atop of tilted and eroded Oligocene turbidites, making the discovery even more peculiar (Fig. 1). The discovery of this tracksite, the southernmost in continental Europe, allows us to discuss vertebrate faunas of a coastal setting in the early Pleistocene. The tracksite formed over a much older folded substrate that emerged previous to the formation of the tracks.

The objectives of this work are: i) to describe and compare this new ichnological record; ii) to designate tracks taxonomically; iii) to analyse the formation and preservation of the different morphotypes; and iv) to discuss the age of tracks and landscape evolution of the tracksite.

2. Geographical and geological setting

The tracksite is in the current intertidal zone of the beach of the Tarifa Island, province of Cadiz, also known as Isla de las Palomas. This island is currently connected to land by a road (Figs. 1 and 2A), located south of the town of Tarifa and whose south edge, the Punta de Tarifa, represents the southernmost point of the Iberian Peninsula. Technically an island, its proximity to the mainland (150 m), the continuity of geological structures and the development of beaches on both sides of the link road mean that it can be considered the southernmost point of continental Europe. (coordinates 36°00′10″N, 5°36′36″W).

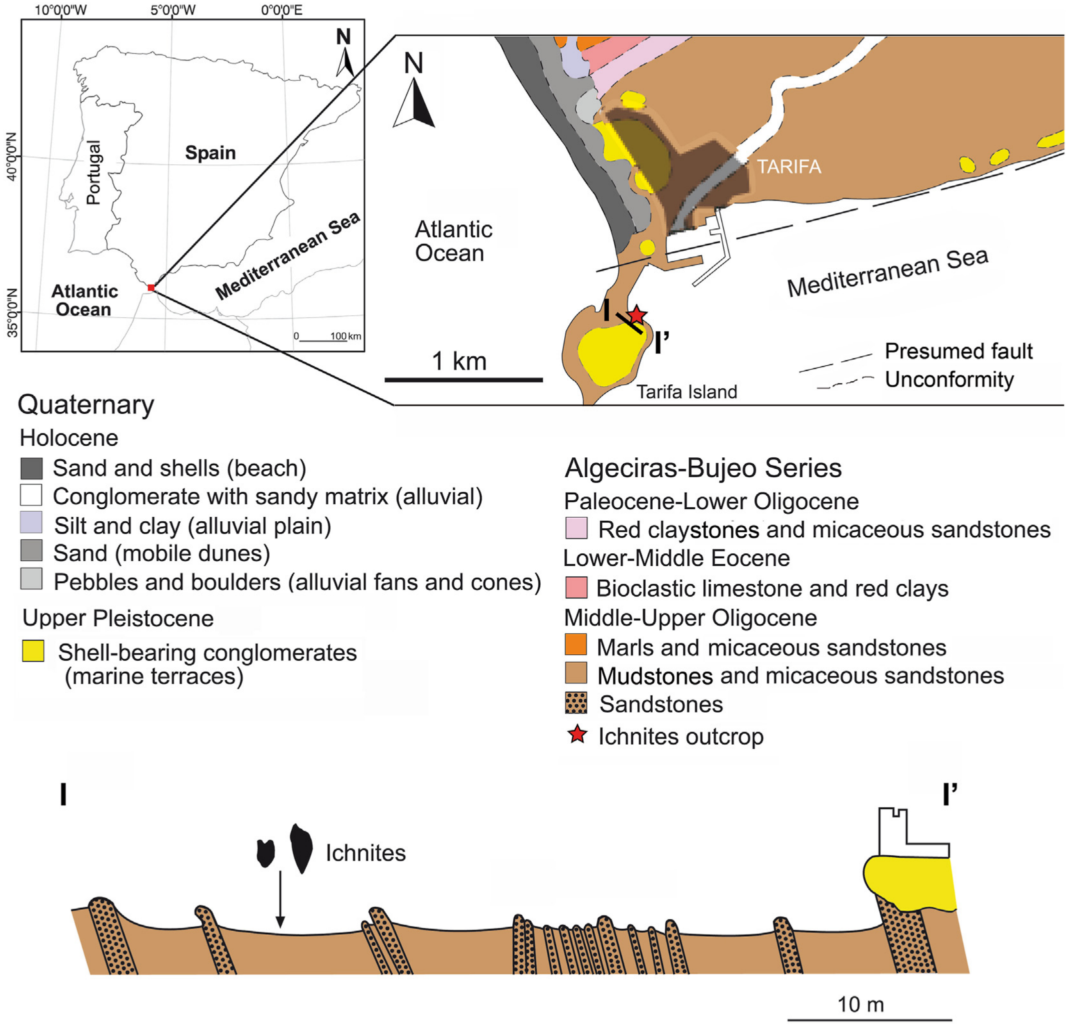

Fig. 1 Geographical and geological location of the footprint site.

The vertebrate tracks are preserved on a grey-bluish mudstone-dominated unit of about 8 m in thickness (Figs. 1—8). It corresponds to a succession of micaceous sandy-turbidite deposited on a shelf margin. These fine-grained rocks are part of the Algeciras-Bujeo Series (Fig. 1), containing a rich association of nannoflora of middle-late Oligocene age (zones NP 24; NP 25 from Martini, 1971; González Lastra *et al.*, 1990).

The turbidites are tilted in NNW-SSE compression in the late Oligocene and later further deformed by extension in the late Miocene (Tortonian—Messinian) (González Lastra *et al.*, 1990). Post-tectonic sedimentation events are represented by transgressive deposits consisting of yellow sandstones with some carbonates that formed in a coastal marine setting in the early Pliocene.

Overall, the differential erosion of prominent sandstone beds and the less resistant mudstones between them generates a large-scale, shallow trough-like topography, with the sandstones forming the walls and the mudstones constituting the floor of the trough (Figs. 1, 2 and 4).

3. Material and methods

The Tarifa Island Beach tracksite was discovered by Miguel Cano Molina in September 2021. Since the outcrop is in the intertidal zone, it can only be studied during low tide, which limits the time for data collection, photography, and surface scanning. Field work was performed in 2021 and the entire surface was digitalised using a Leica BLK2GO Handheld Laser

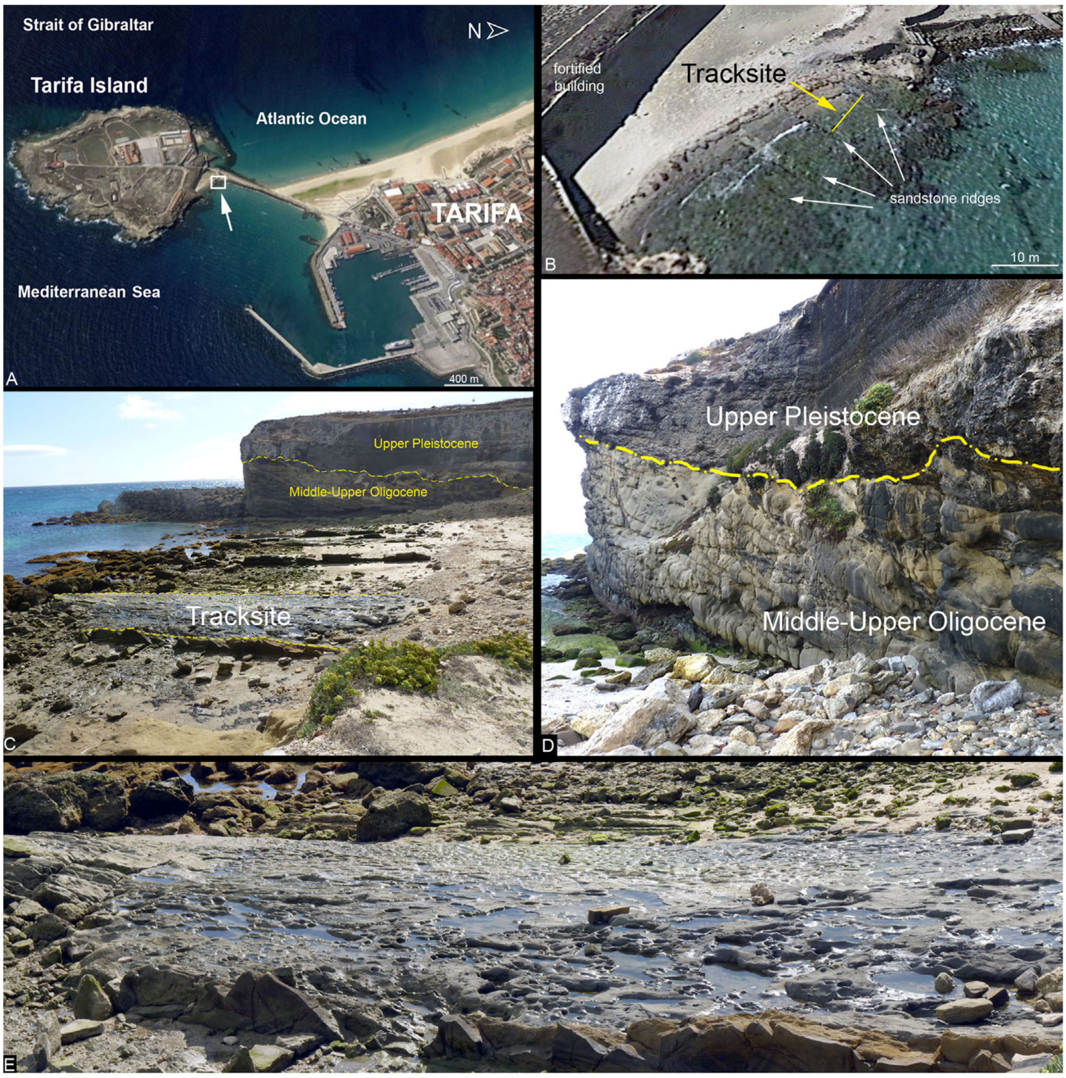

Fig. 2 Outcrop views. **A)** General view (Source Google Earth). White box (arrow): location of the outcrop; **B)** Detail view; **C)** View of the tilted Oligocene succession and its contact with Quaternary marine conglomerates; **D)** Detail view of the angular unconformity (dashed yellow line); **E)** Site detail with the trampled surface of the Oligocene bluish-grey mudstones.

Scanner. Canon EOS 77D coupled with a macro lens Canon 100 mm f/2.8 L was used to prepare detailed 3D photogrammetric models following the general methodology of Mallison and Wings (2014) and Falkingham *et al.* (2018). The photogrammetric 3D models were processed in Agisoft Metashape Professional version 1.1.4. software (https://www.agisoft.com/) and converted to occlusion images in the same software and colour depth maps in the open-source software Paraview 4.4.0 version (http://www.paraview.org/).

The identification of tracks, as well as their dimensional parameters and abundance percentages have been obtained from field observations and the orthomosaic images generated from laser scanning (Fig. 3). In order to proceed with the study and subsequent orientation of the tracks, the surface was divided into 16 grid squares (Fig. 3) and documented in a 2D cartography (Fig. 4). The preservation quality of the tracks is determined following the proposal of Marchetti *et al.* (2019). To clarify the terminology used, it is considered that the sediment surface on which the trackmaker walked is referred to as the “tracking surface” (Fornós *et al.*, 2002), while the imprint left on that surface is called a “true track” (Lockley, 1991). In the didactyl tracks, the length and width were measured based on the general works (see Díaz-Martínez *et al.*, 2020). In the poorly preserved tracks, the longest axis is considered as length, and its perpendicular axis is the width. Considering that there are no clearly preserved individual trackways, the

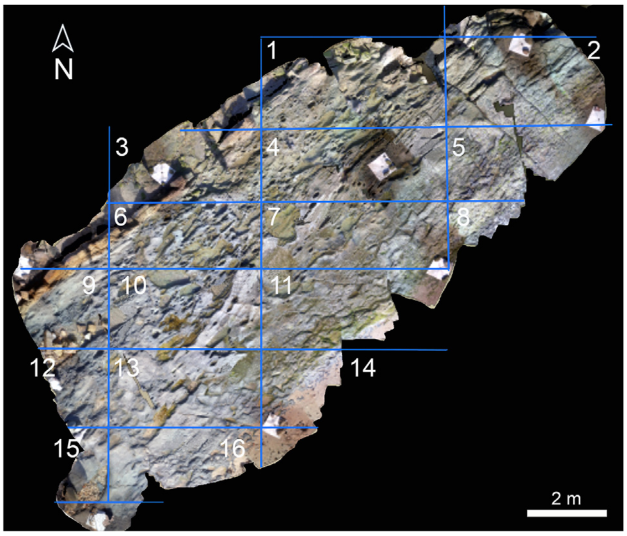

Fig. 3 Orthomosaic of the trampled surface with the grids established for the footprint study.

orientation patterns were examined by plotting Stereonet online (https://app.visiblegeology.com/stereonet.html) in a rose diagram, with the information of individual tracks (Fig. 4). The track orientation is measured as the angle between the track axis and the magnetic north thus it shows the orientation of movement, but not its direction represented as a line with values between 0° and 180° (see Díaz-Martínez *et al.*, 2020).

4. Results

4.1. *Ichnological descriptions*

A total of 635 tracks have been identified in the Tarifa Island Beach tracksite (Fig. 4; Table 1). The surface has an approximate area of 100 m^2 and is moderately trampled (sensu the bioturbation index of Lockley and Conrad, 1989), hampering the identification of individual trackways. There is no evidence of layering inside the tracks that would suggest the presence of underprints or overtracks in the studied surface. Moreover, the tracks present variable depth and extrusion rims, suggesting that all the tracks are probably true tracks on a tracking surface (see above).

In general, the shape of the tracks is variable, commonly including didactyl, rounded to ovoid and elongate forms. Four morphotypes have been identified based on the overall morphology of the tracks.

4.1.1. Morphotype 1 (M1) (Fig. 5A—F)

They are didactyl, showing two symmetrical and parallel-arranged digit imprints, and have a well-defined outline. The tracks present separated digit traces, that have been individually measured (Fig. 5A—E). Generally, they are large and are always longer than wide (10.8 cm long, 4.8 cm wide on

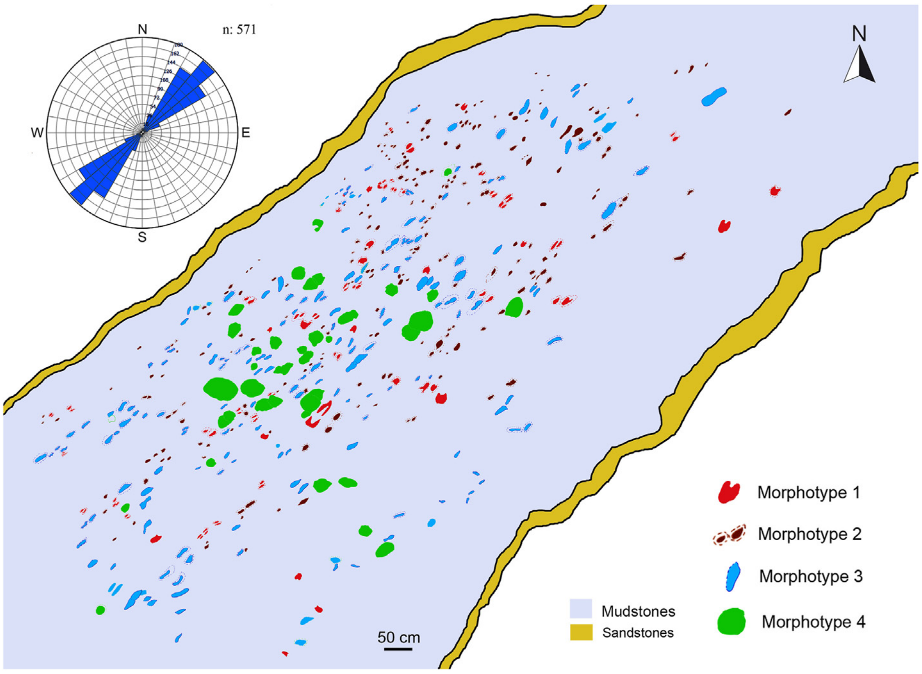

Fig. 4 Spatial distribution of the four track morphotypes along the muddy corridor between the two sandstone ridges and NE-SW orientation of the footprints shown in a rose diagram.

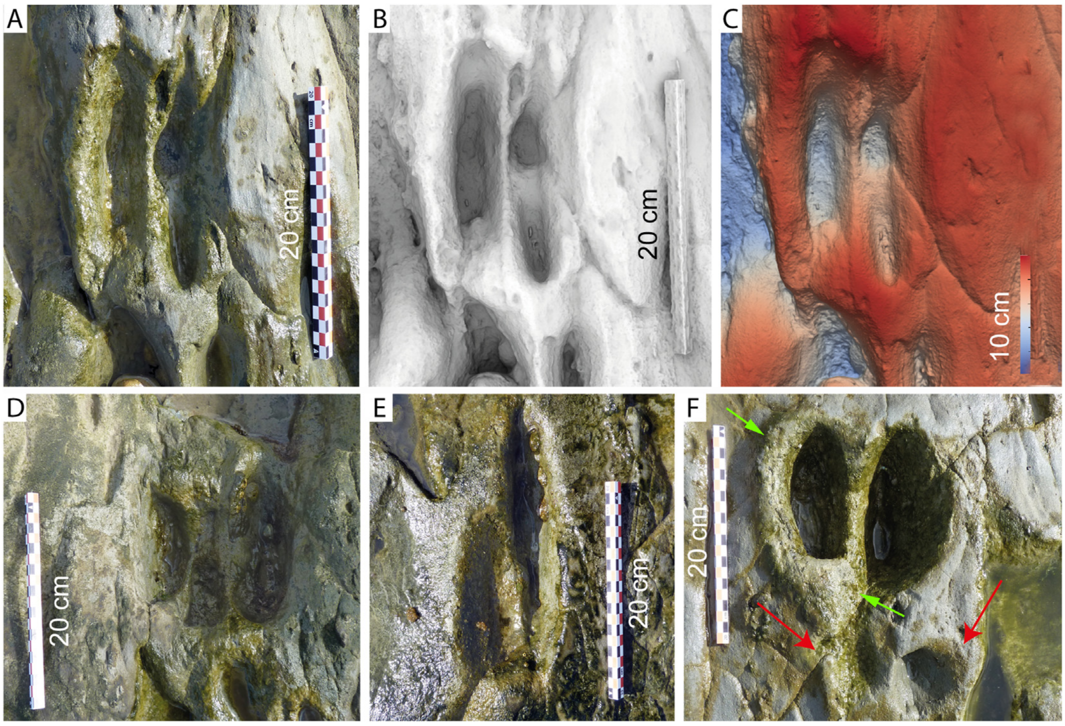

Fig. 5 Examples of morphotype 1 tracks. **A), B), and C)** are images of the same track, where A) is an orthophoto, B) is an occlusion image, and C) is a color depth map. **D—F)** Orthophotos of other morphotype 1 tracks. Red arrows in F indicate digit impressions of a poorly preserved track. The green arrows in F) point to the expulsion rims.

average, Table 1; Supplementary Table S1). It is difficult to differentiate between the impressions of the anterior and posterior surfaces of the foot because the imprints are semi-symmetrical and rounded. Elongated digit impressions have also been identified as associated with the tracks related to the degree of autopod slippage (Fig. 5A—E). They lack lateral (crew) digit impressions even in the depth tracks.

Most footprints have sharply defined expulsion rims, measuring 1—5 cm in width and 2—5 cm in depth. This characteristic makes the footprints well-marked. These tracks are equivalent to grade 1—1.5 of Marchetti *et al.* (2019), which suggests that they provide good information about the trackmaker and can be related to a previously defined ichnogenus. This morphotype is not very abundant (110 tracks) and represents 17% of the total (Table 1), being intermediate in size between the other morphotypes.

4.1.2. Morphotype 2 (M2) (Fig. 6A—L)

Tracks with a subrounded to subovate contour, more or less elongated, smaller in size than morphotype 1 (between 6.2 cm in average length and 2.9 cm width, Table 1; Supplementary Table S2), which may appear isolated (Fig. 6A—J, L) or in groups of two individualised tracks, one behind the other or one next to the other (Fig. 6D—G). When they are preserved in pairs of two, usually one track is significantly larger than the other (Fig. 6D—G). Moreover, some of them have didactyl shapes with very poorly preserved digit impressions (Fig. 6A). The depth of the tracks varies 4—10 cm, and the tracks preserve well-developed expulsion rims. The tracks of this morphotype are equivalent to the grade 1 of Marchetti *et al.* (2019). This morphotype is one of the most abundant at the Tarifa Island tracksite (231 tracks, 35%, Table 1).

4.1.3. Morphotype 3 (M3) (Fig. 7A—J)

It is characterized by having an elongated shape (12.7 cm length on average, Table 1), simple (Fig. 7C—H, J) or divided into two parts (Fig. 7A and B; I and J). The footprints apparently lack anatomical features, but based on detailed observations of the 3D models, they sometimes show the impression of two elongated digits or claw traces (Fig. 7A, B, I). It is even observed that the elongate shape of this morphotype is formed by the superposition of two consecutive tracks

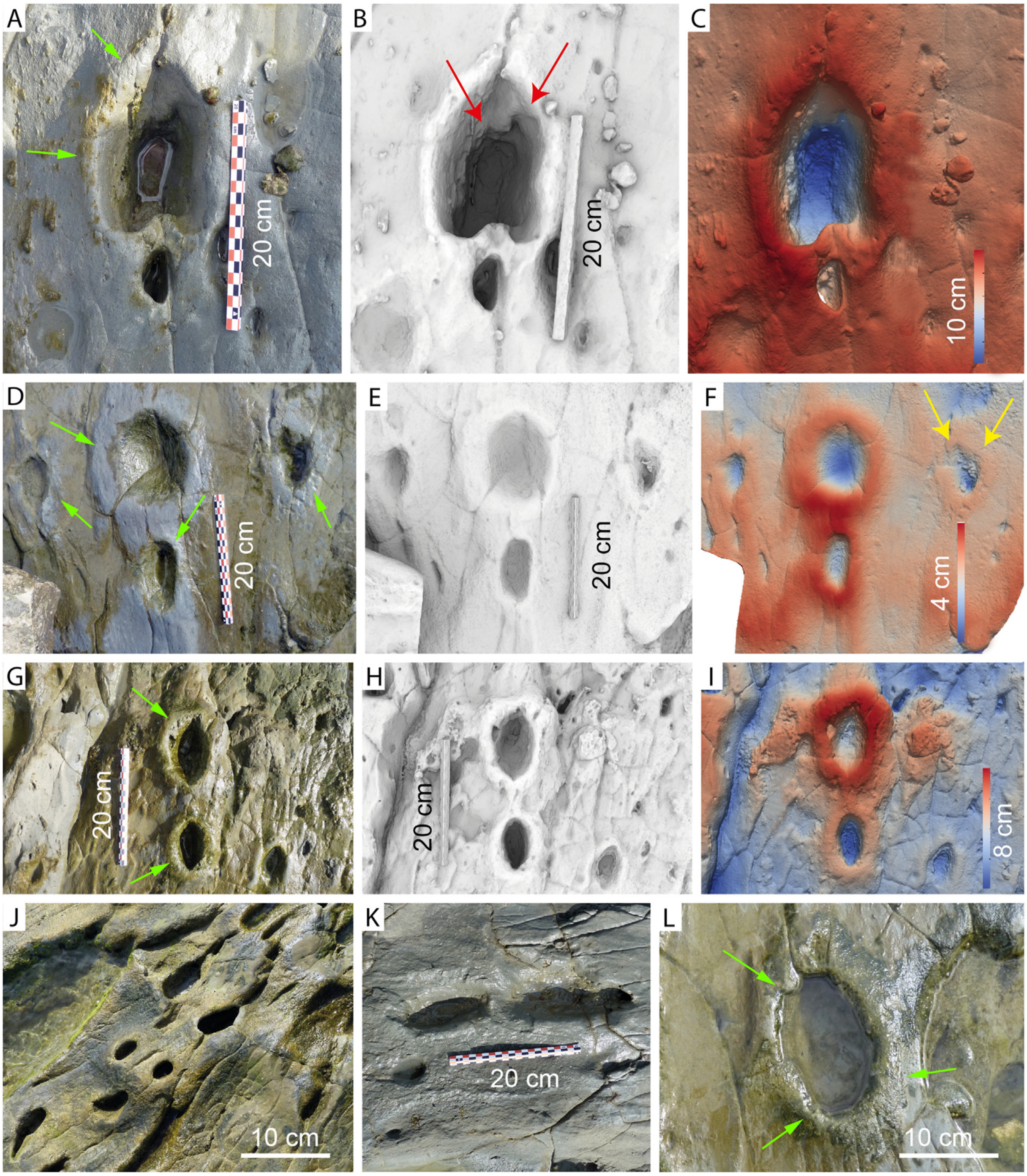

Fig. 6 Examples of morphotype 2 tracks. **A), B) and C)** are images of the same track, where A) is an orthophoto, B) is an occlusion image, and C) is a blue to red color depth map; **D), E) and F)** Same images from another track; **D)** Orthophoto; **E)** Occlusion image; **F)** Blue to red color depth map where yellow arrows indicated morphotype 1 track. **G, H**, and **I** another track; **G)** Orthophoto; **H)** Occlusion image; **I)** Blue to red color depth map; **J)** Series of different tracks; **K)** Elongated track; **L)** Detail of another track. The green arrows in D, A, G, and L point to the expulsion rims.

(manus and pes) which can be up to 6 cm deep. The tracks are poorly preserved, equivalent to the grade 0–1 of Marchetti *et al.* (2019). They are the most numerous footprints (257 tracks, 40%, Table 1; Supplementary Table S3).

4.1.4. Morphotype 4 (M4) (Fig. 8)

These are the largest tracks, generally subovate or subcircular in shape, with an average length and width of 19.1 × 15.8 cm (Table 1), though the

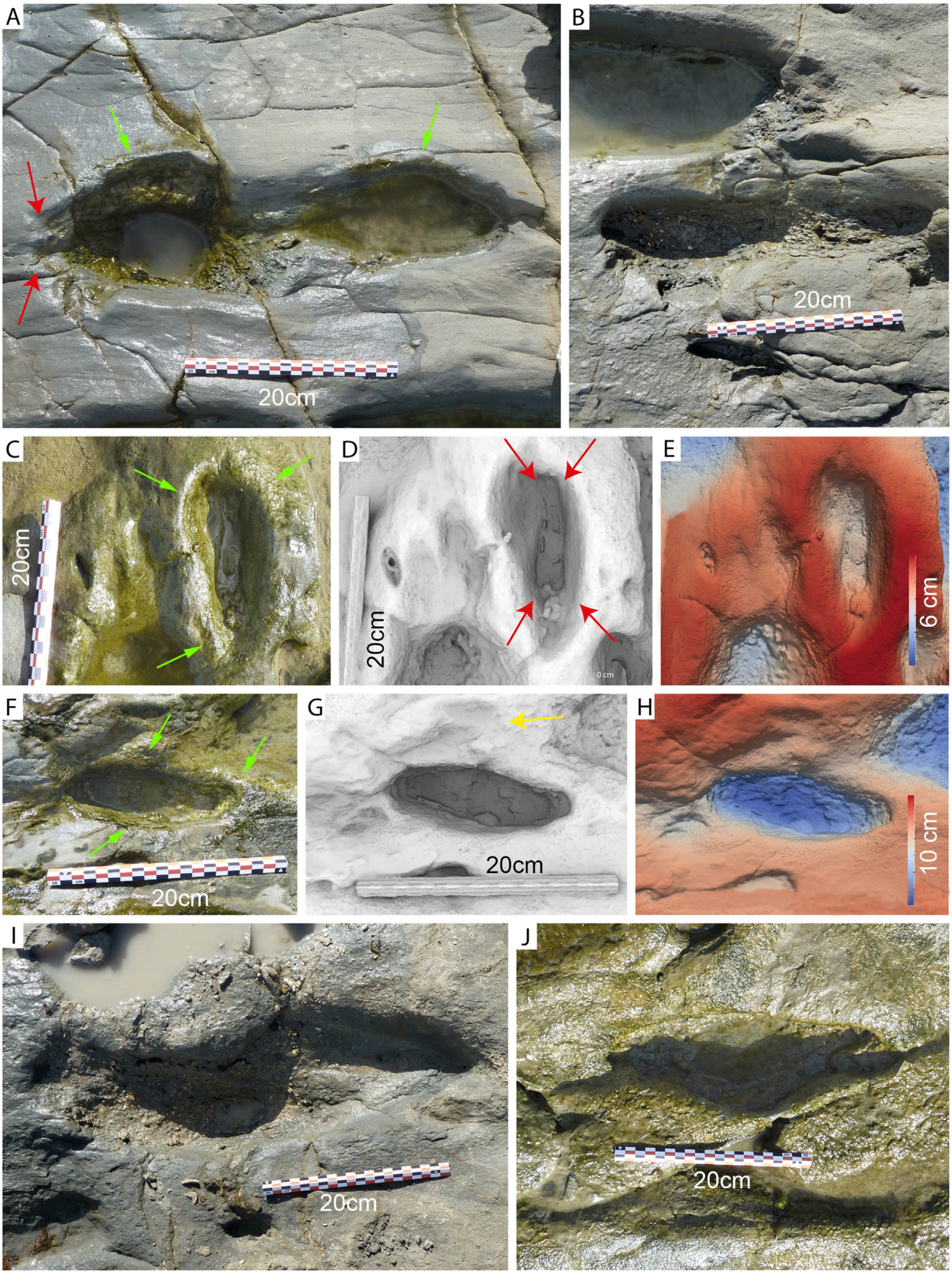

Fig. 7 Examples of morphotype 3 tracks. **A) and B)** Orthophotos of different tracks; **C), D) and E)** are images of the same track, where C is an orthophoto, B is an occlusion image with red arrows indicated digit and E is a blue to red color depth map; **F) to H)** Another track where F) is an orthophoto, G is an occlusion image with yellow arrow indicating morphotype 1 track and H) is a blue to red color depth map; **I) and J)** Different views of another tracks. The green arrows in A, C), and F point to the expulsion rims.

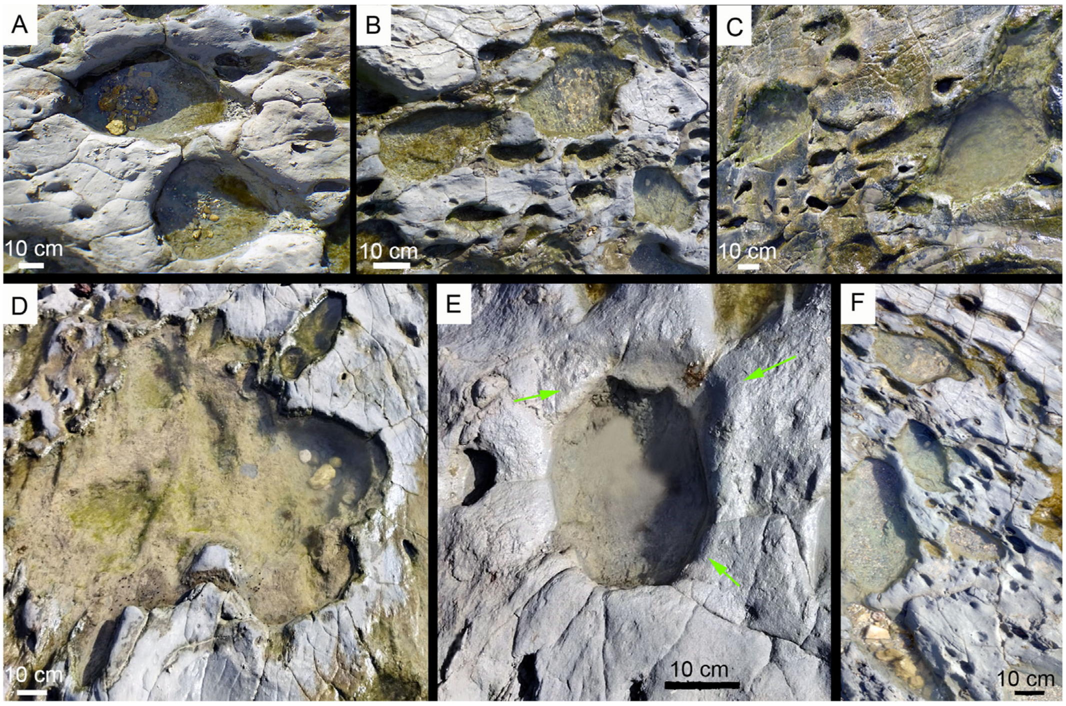

Fig. 8 Examples of morphotype 4 tracks. **A), B) and C)** Orthophotos of different pairs of tracks; **D)** View of at least, two amalgamated and eroded tracks; **E)** Isolated track; **F)** Different tracks and sizes. The green arrows in E point to the expulsion rims.

Table 1 Dimensional parameters and percentage of morphotypes. All values in cm.

Morphotype	Number of tracks	Percentage	Length (cm)			Width (cm)		
			Min.	Max.	Mean	Min.	Max.	Mean
M1	110	17%	1.6	31.3	10.8	0.4	22.0	4.8
M2	231	36%	1.5	18.6	6.2	0.8	12.4	2.9
M3	257	40%	1.7	43.2	12.7	1.0	18.2	4.6
M4	39	7%	5.9	39.3	19.1	4.8	34.0	15.8

contours are sometimes very irregular. Erosion has created depressions up to 19 cm deep, complicating accurate observation of the tracks. These tracks are equivalent to the grade 0—0.5 of Marchetti *et al.* (2019). These footprints are the least frequent (39 tracks, 7%, Table 1; Supplementary Table S4) and are preferentially located in the central area of the corridor.

4.2. Orientation patterns

The tracks are restricted to one of the sections of the turbidite series and bounded by two micaceous sandstone ridges (Figs. 1—4). All tracks have a clear SW-NE orientation (Figs. 3 and 4) parallel to the protruding sandstone layers, which bound the tracksite (Figs. 1, 2 and 4). In some cases, well-defined tracks that show a particular polarity can be distinguished, with tracks that can be oriented in opposite directions, back and forth. It is impossible to differentiate whether any general orientation is linked to a particular morphotype track, so it is deduced that they all occurred in the same direction and probably at successive moments, although probably, not necessarily at the same time.

5. Discussion

5.1. Track formation and preservation

In coastal rock exposures, pits and depressions can form from non-biological marine processes driven by tides and waves, which weather eroded, and shaped the rocks. (see Helm *et al.*, 2019). When resembling vertebrate tracks, these non-biological structures are referred to as pseudo-tracks (Panarello *et al.*, 2017, 2018). Fortunately, this site exhibits several features that indicate their biological origin, as true vertebrate tracks. On the one hand, many of them have very distinctive shapes that correlate with artiodactyl tracks (i.e., impressions of two parallel digits, elongated digits longer than they are wide, see Abbassi *et al.*, 2016). On the other hand, and most importantly, over 90% of these tracks display a characteristic mud rim produced by an element exerting force on the substrate (Allen, 1997), thus ruling out a current erosive agent. Moreover, the aforementioned characteristics are repeated throughout the outcrop, leading us to consider that the depressions studied here are, with high probability, vertebrate tracks.

Four main factors influence the formation and preservation of vertebrate tracks: autopod anatomy, substrate features, limb dynamics and taphonomic modifications (see Falkingham, 2014 and references therein), excluding, the mass of the animal since the more significant the mass, the greater the weight and the greater the depth of the footprint. The shape of the four morphotypes in the Tarifa Island Beach tracksite is the result from the variation of these factors. For instance, morphotypes 1, 2 and 3 were produced by didactyl trackmakers of different size, resulting in very similar correlation coefficients and length-frequency histograms (Figs. 9 and 10), whereas morphotype 4 trackmaker has large and rounded autopods. Moreover, no mud cracks have been found along the entire surface, so, it can be inferred that the sediment was sufficiently wet to prevent drying (see Schanz *et al.*, 2016). The tracks show associated expulsion rims implying that the sediment was cohesive and plastic when the trackmaker traversed it (Allen, 1997). On the other hand, the tracks have different depths. This variability may initially relate to the autopod shape—wide autopods penetrate less than narrow ones—and the type of substrate, where finer grain size and greater moisture produce deeper tracks (Allen, 1997; Manning, 2004; Jackson *et al.*, 2009, 2010; Falk *et al.*, 2017). The variations in track depth are randomly distributed both across the tracksite and within each morphotype. The depth range in M1 varies from 1 to 4 cm, in M2 from 0.5 to 6 cm, in M3 from 1.5 to 7 cm, and in M4 from 4 to 13 cm. Therefore, based on the absence of variations in grain size across the tracking surface (based on observations of hand samples in the field), it can be inferred that alterations in moisture content have occurred. These changes can happen simultaneously because the same substrate may behave differently based on specific characteristics, such as its proximity to areas that are more ponded or more depressed. These factors could lead to lateral variations in moisture within the substrate. Additionally, the tracks might have been created at different times, resulting in differences in moisture levels or water depth. Unfortunately, there are no clear cross-cutting relationships either between the tracks to help reconstruct the order of the events. Moisture influences track morphology, with well-preserved tracks (e.g., morphotype 1) typically forming in moist but not saturated substrates, which commonly lead to deeper, oval-shaped tracks with or without autopod drag marks (e.g., morphotypes 2 and 3) (e.g., Scrivner and Bottjer, 1986; Díaz-Martínez *et al.*, 2020; Abbassi *et al.*, 2016). This tracksite probably presents a brief preservational window (sensu

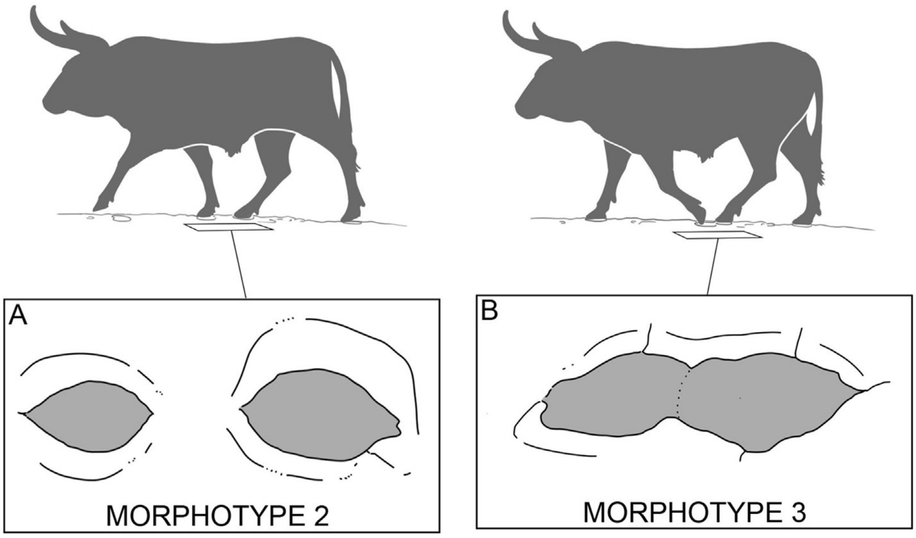

Fig. 9 Illustration showing the formation of tracks at the transition between morphotypes 2 and 3. **A)** Isolated, subrounded to subovate tracks; **B)** Elongated track formed by the superposition of two consecutive tracks (manus and pes).

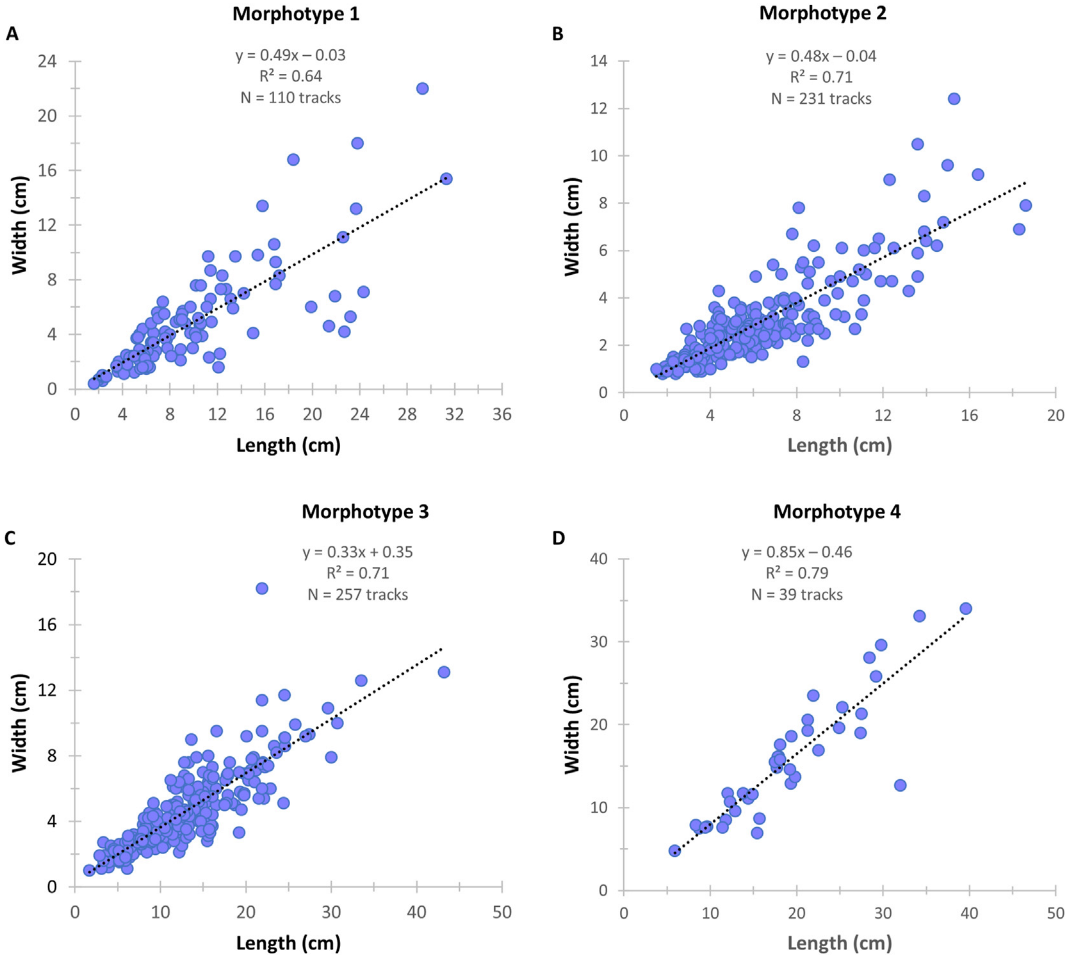

Fig. 10 Regression lines and correlation coefficients. **A)** Morphotype 1 (M1); **B)** Morphotype 2 (M2); **C)** Morphotype 3 (M3); **D)** Morphotype 4 (M4).

Díaz-Martínez *et al.*, 2021) with a relatively short time between track formation and their burial due to the absence of desiccation cracks and post-formational taphonomic signals (see Scrivner and Bottjer, 1986).

Despite the surface has a moderate degree of bioturbation, many of the tracks are isolated (morphotypes 1, 2 and 4). In any case, in some of them, the original shape of the track is modified by a subsequently imprinted track (morphotype 3). Overlapping can occur on the same tracking surface before burial or when younger tracks imprint over older tracks in underlying unconsolidated beds that deform the underlying levels (post-burial). Track interference can also occur between different trackways or within the same trackway (self-overlapping) (see Díaz-Martínez *et al.*, 2009 for further explanations). In this case, the overlapping is pre-burial. Although there is undoubtedly overlap due to the interference of different trackways, it is common to find pairs of tracks stacked very close, even with different degrees of overlap. Thus, it is possible to see a progressive transition between morphotype 2 with isolated and rounded tracks (Fig. 9A) to morphotype 3 with elongated tracks formed by the superposition of two tracks from the same type of animal (Fig. 9B). The transition between morphotypes 2 and 3 can be clarified through the concepts of 'overprinting' and 'underprinting,' which are phenomena observed in contemporary artiodactyls and perissodactyls, particularly in equids (Van den Heever *et al.*, 2017). These phenomena are linked to the speed of the trackmaker. Underprinting occurs when the manus track is laid down before the pes track, typically at slower gaits. At a normal walking pace, the pes track directly overlaps the manus track. As the gait accelerates, progressive overprinting takes place, with the pes track appearing ahead of the manus track. Therefore, it is likely that these footprints were created by trackmakers moving at varying speeds. This transition is also reflected in the scatter plots of morphotypes M1 to M3, especially in M2 and M3, which have almost the same correlation coefficient (r^2) of 0.7085 and 0.7127, respectively

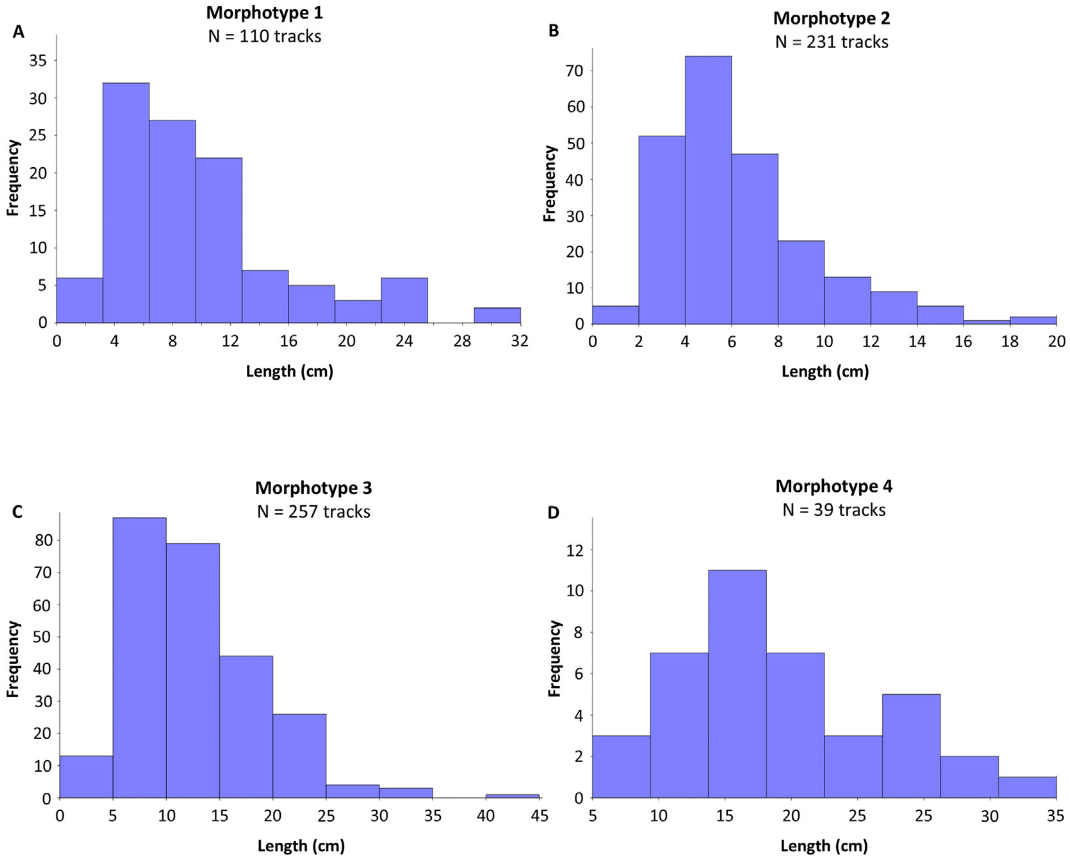

Fig. 11 Length-frequency histograms. **A)** Morphotype 1 (M1); **B)** Morphotype 2 (M2); **C)** Morphotype 3 (M3); **D)** Morphotype 4 (M4).

(Fig. 10A—C). A similar trend is shown in the frequency histograms, especially between morphotypes M2 and M3 (Fig. 11B and C).

In this sense, we hypothesize that changes in the dynamics of the trackmaker limbs mediate in their relative spatial position (see examples in Castanera *et al.*, 2012; D'Orazi Porchetti *et al.*, 2017; Razzolini and Klein, 2018), and, therefore, in its degree of overlap.

5.2. *Ichnotaxonomy and trackmaker identity*

The best-preserved tracks of morphotypes 1, 2, and 3 have didactyl impressions, which are traditionally related to artiodactyl trackmakers. Morphotype 1 with a preservation quality of 1—1.5 provides good information about the trackmaker and can be related to a previously defined ichnogenus. Morphotypes 2 and 3 present a preservation quality of 0—1, so they indicate only the presence of trackmakers in the area (sensu Marchetti *et al.*, 2019). Considering the morphological and size differences among these morphotypes, one might expect the tracks to have been left by different species of artiodactyls, but different individuals of the same species could also impress tracks quite differently (see Díaz-Martínez *et al.*, 2020). It is uncertain whether the tracks were made by the same animals or at the same time. The morphotype 1 presents two-digit impressions separated throughout the tracks. This feature allows to differ between different ichnotaxa (e.g., *Entelodontipus* Casanovas-Cladellas and Santafe-Llopis, 1982 or *Cervipus* Matsukawa *et al.*, 2007 have separated digit imprints; *Bifidipes* Demathieu *et al.*, 1984 or *Lamaichnum* Aramayo and Manera de Bianco, 1987 presented joined digit impressions). Nevertheless, the ichnotaxonomy of artiodactyl tracks is a complicated task because a very general morphology (i.e., didactyl track) is classified within more than 30 ichnotaxa (see Abbassi *et al.*, 2016). We prefer to classify these ichnites as indeterminate artiodactyl tracks, because they are not well preserved and it is sometimes very difficult to know the producer autopod anatomy. Nevertheless, the morphotype 1 tracks have similarities with the ichnogenus *Bovinichnus* Neto de Carvalho *et al.* (2022) in the size and overall shape. This ichnogenus has been identified in other middle-upper Pleistocene tracksites of the Iberian Peninsula and is attributed to bovines (Neto de Carvalho *et al.*, 2022). The footprints also exhibit a notable similarity to those of giraffes described by Helm *et al.* (2018) from the Lower Pleistocene of South Africa. Giraffid remains have been reported in the Lower Pleistocene of the Iberian Peninsula (Van der Made and Morales, 2011). In this context, it is important to consider these animals as potential producers of the footprints, even though giraffid footprints have not been documented in the European Pleistocene. While it is highly probable that the tracks were made by multiple taxa, we cannot entirely dismiss the hypothesis that they were produced by individuals of varying sizes or ages within the same taxon.

In the Iberian Peninsula, the late Neogene—Pleistocene artiodactyl ichnological record is in its southern region. The upper Miocene-lower Pliocene beds of Sorbas present artiodactyl tracks, which were classified as *Pecoripeda* (*Gazellipeda*) *gazella* Vialov (1961) and related to gazelles (McCann *et al.*, 2018). The late Pliocene-early Pleistocene record is only composed of the tracks studied herein, whereas the middle-late Pleistocene specimens were attributed to goats, cervids, wild boars and aurochs (see Neto de Carvalho *et al.*, 2003, 2020b; c, 2022). The middle Pleistocene tracks are located at the Matalascañas tracksite (age sensu Mayoral *et al.*, 2022). There, the suid ichnospecies *Suidichnus galani* Neto de Carvalho *et al.* (2020c) is described, and the ichnogenera *Bifidipes* and *Bovinichnus*, produced by cervids and aurochs respectively, are also identified. On the other hand, almost all the artiodactyl tracks from upper Pleistocene beds are classified within the ichnogenus *Bifidipes*. They were found in Pessegueiro, Fort of Ilha de Dentro, Aivados Beach and Gibraltar, and they were related to cervids and caprinae trackmakers (see Neto de Carvalho *et al.*, 2016; Muñiz *et al.*, 2019). Moreover, the auroch ichnospecies *Bovinichnus uripeda* is defined in the Trafalgar tracksite (Neto de Carvalho *et al.*, 2022).

Morphotype 4 is composed of subovate tracks of large size (19.1 cm average length). Although coastal erosion could modify its contour, the shape, the distribution and the presence of more tracks on the same surface coincide with what is expected from a track of a large vertebrate. Based on the shape and size, these tracks could be related to proboscideans (cf. Altamura and Serangeli, 2023). There are other records of this kind of track in the lower Pleistocene of the Iberian Peninsula. In the upper Miocene—lower Pliocene beds of Alicante, several mastodont tracks have been recognized (Fierro Bandera *et al.*, 2014?). The middle Pleistocene record has been identified in the Matalascañas tracksite (Neto de Carvalho *et al.*, 2020a), while the late Pleistocene tracks are located in Praia do Malhâo, Praia da Ilha, Angra da Vaca and Gibraltar (Neto de Carvalho, 2009; Neto de Carvalho *et al.*, 2016, 2020a; Muñiz *et al.*, 2019). Almost all the above-cited proboscideans tracks have been related to the ichnogenus *Proboscipeda* Panin and Avram, 1962 (see Neto de Carvalho *et al.*, 2020a). Other similar tracks have been reported in the lower Pleistocene of Kenya, Japan and Arizona (Thrasher, 2007; Matsukawa and Shibata, 2015; Roach *et al.*, 2016). Unfortunately, the Tarifa Island Beach tracks are poorly preserved, and we classified them preliminarily as undetermined proboscidean tracks.

The southern Iberian Peninsula is key for assessing the latest Pliocene-Pleistocene ichnodiversity in the Mediterranean region. While middle and upper Pleistocene tracks are well-represented, the Tarifa Island Beach site is the only known locality from the upper Pliocene—upper Pleistocene transition. Elsewhere in the Mediterranean, only two lower Pleistocene vertebrate track sites have been identified, both in Italy: one in Sardinia, featuring artiodactyl tracks attributed to *Bifidipes* aff. *B. aeolis* likely left by a small endemic bovid, and the other in Tuscany with proboscidean tracks (see Pillola *et al.*, 2020 and references therein).

5.3. *When were the tracks formed?*

The tracks are imprinted on the surface of a substrate that is tilted as a consequence of the last tectonic phases that occurred at the end of the Alpine orogeny during the late Miocene (Tortonian-Messinian). In this scenario, one possibility is that these tracks may have formed immediately after these tectonic phases during the Pliocene. However, during the early Pliocene, this part of the Cádiz coastline was submerged due to a transgression at the beginning of the Pliocene, and it was only during the late Pliocene that a generalized regression began along the entire coast. Nevertheless, at some points, the sea continued to occupy extensive gulfs, which generally coincide with the large valleys that can be seen today in the coastal area (Zazo and Goy, in González Lastra *et al.*, 1990). For this reason, and given that the vertebrate tracks are fossilized within the oyster conglomerates that form the late Pleistocene marine terrace (Figs. 1 and 2), the most plausible hypothesis is that the tracks were produced in the interval between the end of the late Pliocene regression and this last Quaternary transgression (Fig. 12).

5.4. *Pleistocene vertebrates modified Oligocene deposits*

Regarding their particular preservation, the Tarifa Island Beach tracks are found on tilted Oligocene

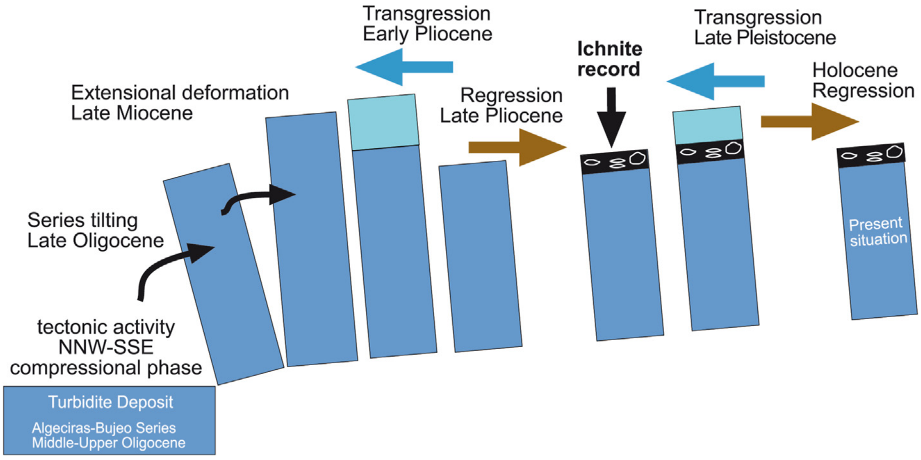

Fig. 12 Sketch illustrating the tectonic evolution of the substrate and the formation of ichnites during the transgressive and regressive pulses in late Neogene—Quaternary.

turbidites, although, as indicated earlier, they were imprinted between the late Pliocene and early Pleistocene. The tracks could not have been produced in the mudstone during the Oligocene because they were formed after these turbidites were folded in successive orogenic events. This is evident from the tracks' current position on the tracking surface, a horizontal surface in a mudstone that is perpendicular to their bedding plane.

In ichnology, it is quite common that a producer modifies a substrate older than the time of trace production. For example, in bioerosion traces, it is very frequent, as in the case of the boring structures of Cenozoic or Quaternary organisms on Mesozoic rocks that were ancient palaeocliffs (Martinell *et al.*, 2008; Santos *et al.*, 2008, 2010, 2015; Cachão *et al.*, 2009; Johnson *et al.*, 2011). In invertebrates' traces (Pemberton *et al.*, 1976), and some vertebrates burrows (Smith, 1987; Doody *et al.*, 2015), the concept of tiering itself (substrate zoning in depth, Bromley, 1996), already implies a degree of penetration (e.g. current crabs that dig several meters in a much older substrate). However, in locomotion traces of vertebrates, except that the producers can modify several older layers when stepping, we have not found another similar example where tectonically deformed rocks were later weathered to the extreme to preserve millions of years younger tracks. In our case, the folding and subsequent erosion of the turbidites resulted in the formation of mudstone corridors bounded by sandstone ridges. These corridors would have remained totally or partially flooded and, due to their fine grain size, would have constituted soft substrates on which the tracks were imprinted, in some cases even reaching several centimetres in depth.

5.5. *Palaeogeographical implications*

On the coast of the Gulf of Cádiz, there is only one palaeogeographic reconstruction for the Bay of Cádiz (Gutiérrez Mas *et al.*, 1991), located about 80 km NW of the study area. This reconstruction ranges from the early Pliocene to the early Quaternary. However, the Tarifa sector is not represented and the configuration of the coast is practically the same as it is today. For this reason, the existence of this tracksite is of great interest, as it can provide relevant additional data for understanding the configuration of the coast in this sector and its relationship with the known reliefs of the nearby mountain ranges.

In the vicinity of the Tarifa area, only two levels of old hanging glacis are known, which drained to the SW during the early Pleistocene (Gracia *et al.*, 2004). The upper glacis is of lower Pleistocene age (Rose and Rosenbaum, 1991) and is located at an elevation of +50—60 m, while the lower one is located at +19.5 m and would connect with the marine terrace of Isla de las Palomas and Tarifa.

In comparison, in the southern part of the Sierra de Enmedio, some 12 km northwest of Tarifa, another glacis of similar elevation has been identified (Gracia *et al.*, 2004).

Collectively, this evidence seems to indicate that there must have been a direct relationship between the sectors attached to the foot of the higher reliefs (hills) and their more distal areas towards the coast. These distal areas were likely broad coastal plains, where mudstone-floored, sandstone-walled, and partially waterlogged corridors preserved the passage of vertebrates in different directions (Fig. 13).

This coastal configuration could have preceded other coastal plains identified in the Gulf of Cádiz. In

Fig. 13 Reconstruction of artiodactyl and proboscidean migration through the Oligocene corridor on a coastal plain that would link up with the glacis deposits of the nearby mountain ranges. Drawing by Adri Blázquez Riola.

the Chipiona sector, about 100 km NW, Rodríguez-Ramírez *et al.* (2024) defined an extensive late Pleistocene coastal plain corresponding to the high Marine isotope stage (MIS) 5e2). Moreover, in the same gulf, but on the coast of Huelva (Doñana sector), Zazo *et al.* (1999, 2005) and Roquero *et al.* (2013) also recognized a coastal plain of the same chronology (MIS5), while Mayoral *et al.* (2022) assigned it to the transition between MIS9 and MIS8 (mid-Pleistocene).

In short, this deposit suggests that the coastal plains in the Gulf of Cádiz may have formed since the beginning of the Pleistocene, with the oldest records in the Tarifa area and the newest in Cádiz and Huelva. Additionally, this ichnological record is unique, representing the only evidence of ?artiodactyls and ?proboscideans during a period with no other palaeontological records from the region.

The track preservation quality is not particularly remarkable, which is typical for most tracks globally. This is the case of morphotypes M3 and M4, which have Marchetti grades between 0 and 1, but this does not diminish the importance of their discovery, because their presence is a significant heritage and holds great palaeobiological and palaeo-biogeographical significance.

6. Conclusions

The southern part of the Iberian Peninsula has a rich collection of vertebrate footprints from the late Neogene to Quaternary. While some time periods, like the transition from the Miocene to Pliocene and the middle to late Pleistocene, are well documented, others are still not fully understood. This paper highlights the discovery of the southernmost tracksite in both the Iberian Peninsula and continental Europe, located on the Island of Tarifa in Cádiz (Spain).

This tracksite features over 600 vertebrate footprints from the early Pleistocene, categorized into four different types. The first three morphotypes (M1 to M3) are mainly didactyl in shape, ranging from rounded to oval and elongated, and are linked to tracks made by artiodactyls. The fourth morphotype, which is larger and has a suboval to subcircular shape, is likely associated with footprints from proboscideans.

We also observed a gradual change from morphotype 2, which has isolated rounded footprints, to morphotype 3, characterized by elongated tracks created by overlapping footprints from the same animal. The type of ground and the movement of the animals' limbs influenced the final shape of the tracks. These footprints were made in a soft, clay-rich substrate from the late Oligocene, which was later folded and tilted during the late Pliocene. This unique landscape created a narrow corridor that was constantly flooded, allowing the animals to move through it in different directions.

This finding from the southernmost point of continental Europe represents the first early Pleistocene discovery in the Iberian Peninsula and is a rare example from the Mediterranean region.

CRediT authorship contribution statement

Eduardo Mayoral: Writing — review & editing, Writing — original draft, Supervision, Methodology, Investigation, Conceptualization. **Antonio Rodríguez Ramírez:** Writing — review & editing, Methodology, Investigation, Formal analysis. **Jérémy Duveau:** Writing — review & editing, Visualization, Methodology, Formal analysis, Conceptualization. **Ricardo Díaz-Delgado:** Writing — review & editing, Software, Methodology, Formal analysis. **Juan Antonio Morales:** Writing — review & editing, Supervision, Methodology, Investigation, Formal analysis. **Eloísa Bernáldez Sánchez:** Writing — review & editing, Supervision, Investigation. **Esteban García-Viñas:** Writing — review & editing, Supervision, Investigation. **Ana Santos:** Writing — review & editing, Supervision, Methodology, Formal analysis, Conceptualization. **Mili Jiménez Melero:** Visualization, Validation, Supervision. **Milagros Alzaga:** Visualization, Validation, Supervision. **Ignacio Díaz-Martínez:** Writing — review & editing, Supervision, Methodology, Investigation, Formal analysis.

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Declaration of competing interest

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jop.2025.01.004.