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New vertebrate tracksites from the Last Interglacial dune deposits of coastal Murcia (southeastern Spain): ecological corridors for elephants in Iberia?

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ABSTRACT

Analysis of new vertebrate tracksites from the Last Interglacial (Marine Isotope Stage 5e) dune deposits along the southeastern coast of the Iberian Peninsula, specifically in Murcia, Spain, enabled to identify the likely presence of a medium-sized mustelid, wolf, large artiodactyls, an equid and the straight-tusked elephant *Palaeoloxodon antiquus*. These eolianite successions offer valuable ichnological evidence beyond the traditional body fossil record, illuminating the presence and behaviors of several Pleistocene mammals in coastal dune and beach environments. Detailed fieldwork, geological mapping, digital photogrammetry, paleoenvironmental reconstruction and morphometric analyses provided ichnotaxonomic and behavioral ecology data from vertebrate tracks preserved in the oolitic dune systems at Calblanque (Cartagena) and Torre de Cope (Águilas). The mammalian ichnoassemblages reflect the proximity of a Last Interglacial mixed forest ecosystem on the coast of southeastern Iberia, with forest-adapted species thriving near coastal dunes stabilized by shrub vegetation. The presence of the track-inferred producers highlights a mosaic of habitats influenced by climate shifts toward more oceanic conditions during MIS 5. The straight-tusked elephant tracks suggest an episodic presence in the coast, possibly related to seasonal congregation or transit. Obtained evidence has been compared with other Pleistocene sites with straight-tusked elephants in Iberian Peninsula, pointing to the use of beaches and dune systems as travel corridors for this species during interglacials, likely associated to main Neanderthal site distribution.

1. Introduction

Ichnology plays a vital role in the study of Pleistocene coastal successions. It provides insights into communities' past life behaviors and interactions with dynamic coastal processes related to climate changes, which are preserved as the result of dynamic relations between organisms and substrates like bromalites, bioerosions, burrows, trails and tracks. Trace fossils provide direct evidence of behavioral patterns and ecological interactions at spatial and temporal scales that are not typically provided by the body fossil record (e.g., Hatala et al., 2023; Neto de

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Carvalho et al., 2023b). These traces can be used to infer paleoenvironmental conditions (e.g., Bromley, 1996; Wetzel and Rodríguez-Tovar, 2021), such as sedimentation characteristics, development of rocky shores, wave and tidal influences, by analyzing their type, distribution, morphology and preservation. For instance, tracks might indicate specific substrate consistencies or the amplitude of the tides (Donovan, 2025). Additionally, ichnological studies can help reconstruct ancient shorelines and sea level shifts in coastal ecosystems due to climate fluctuations during the Pleistocene (Burns et al., 2022). Such insights are invaluable for understanding how past environmental changes impacted coastal life and can inform predictions about future changes in similar settings. By establishing possible producers and comparing with present behaviors, tracks can also be used to reconstitute trophic ecology and social behaviors (Falkingham, 2014; Neto de Carvalho et al., 2021, 2022; Hatala et al., 2023).

Vertebrate ichnological studies from the Pleistocene of the Iberian Peninsula have illuminated the interactions and environmental adaptations of ancient fauna. This region's diverse geological settings have preserved numerous trace fossils, predominantly in fluvial and coastal deposits, offering a window into the activities of large mammals and other vertebrates. Key sites such as the ones found in eolianites from the southwest coast of Portugal (Neto de Carvalho et al., 2003, 2016, 2023a; Neto de Carvalho, 2009, 2011, 2014), and other coastal deposits in the Iberian Peninsula, such as in El Asperillo cliff (Matalascañas Trampled Surface), Huelva Province (Neto de Carvalho et al., 2020a, 2020b, 2020b, 2020c; Neto de Carvalho et al., 2020a,c, 2021, 2022, 2023b; Muñiz et al., 2025), Cape Trafalgar, Cádiz Province (Neto de Carvalho et al., 2022), Gibraltar (Muñiz et al., 2019), and the Balearic Islands (Fornós and Pons-Moya, 1982; Quintana, 1993; Fornós et al., 2002) have been pivotal in these studies, revealing a range of trackways and tracks that shed light on the behaviors, habitats, and ecological dynamics of the time they were produced.

At the southwestern Portugal, Matalascañas Trampled Surface, Cape Trafalgar and Gibraltar, researchers have uncovered trackways attributed to Pleistocene megafauna, including proboscideans and large predators (Neto de Carvalho, 2009, 2011; Muñiz et al., 2019; Neto de Carvalho et al., 2020a,b, 2021, 2022; Gómez-Gutiérrez et al., 2023). These trace fossils suggest the presence of varied ecosystems capable of sustaining large herbivores and their predators, including Neanderthals (Neto de Carvalho et al., 2023a; Muñiz et al., 2025). The orientation, quality of preservation and depth of tracks provide insights into the landscape's topography and the animals' movement patterns, indicating proximity to resources like water and food (Neto de Carvalho, 2009; Neto de Carvalho et al., 2021, 2022). Such ichnites are crucial for reconstructing the paleoecological frameworks that governed these ancient communities.

The significance of these ichnological findings extends to understanding the broader impacts of Pleistocene climatic oscillations on vertebrate fauna. Analysis of track size, stride length, and depth allows for estimations of animal size and behavior, contributing to reconstructions of faunal diversity and distribution (Burns et al., 2022; Hatala et al., 2023). As the Iberian Peninsula served as a refugium during glacial periods (Gómez and Lunt, 2006; Abellán and Svenning, 2014), these records are vital for studying the resilience and adaptation of vertebrates in the face of environmental changes. Recent studies continue to refine our understanding of these dynamics (Neto de Carvalho et al., 2020a; b, 2022; 2023a), emphasizing the role of the Iberian Peninsula as a critical region for Pleistocene vertebrate research (e.g., Piñero et al., 2022; Fernández-García et al., 2024; García-Morato et al., 2024).

The ongoing research project that is mapping and describing new Pleistocene vertebrate tracksites in the coastal successions of southern Iberian Peninsula led our team to find two new tracksites in the region of Murcia (SE Spain). Eolianite successions regarded as Late Pleistocene in age provide evidence for the presence of large and small mammals in the littoral sandy coasts between Cape Cope and Cape Palos (Fig. 1), that otherwise would be unknown in the region from the body fossil record alone. In this study we describe one ichnosite at Torre de Cope (municipality of Águilas) and three ichnosites in Calblanque, Monte de las Cenizas and Peña del Águila Regional Nature Park (municipality of Cartagena) and discuss their ecological implications within the Last Interglacial.

In the region of Murcia, the only tracksites known until now in Cenozoic formations are Hoya de la Sima and Sierra de las Cabras, both of late Miocene age, and located a few kilometers distant of each other in the Prebetic ranges near the town of Jumilla. The Hoya de la Sima site provided diverse mammal tracks, including an undetermined ungulate, camelid, equid, carnivores, ursid and possible elephant tracks (Perez-Lorente et al., 1997; 1999). Sierra de las Cabras contains abundant vertebrate ichnofauna produced by mammals such as horse, rhinocerotid, canid, big felid, ursid, zapodid and possible suid, as well as wetland avifauna, preserved in carbonate facies that were deposited in a semi-arid wetland system with shallow ponds and marshes (Herrero et al., 2022a,b, 2023). Our study introduces the first Quaternary tracksites found in southeastern Iberian Peninsula and discuss the ecological implications for the perennial presence of megafauna, especially the large proboscidean *Palaeoloxodon antiquus* Falconer & Cautley, in coastal environments.

2. Geological and stratigraphic setting

The Neogene and Quaternary sedimentation in Murcia-Cartagena-Aguillas-Almeria region is highly controlled by the morphostructural framework of the eastern Betic Cordillera (in the southeastern portion of Spain), which is linked with the tectonic processes related to the Africa-Iberia collision, culminating in the genesis of the Betic-Rif Arc (or Gibraltar Arc) (e.g. Silva et al., 1993; Zazo et al., 2003, 2013; Daudet et al., 2020).

The eastern Betics tectonics is conditioned by the indentation of the Aguilas arc, and consequent lateral spread, which generates E-W trending morphostructural reliefs and basins resulting from transpressional-transtensional tectonics (Montenat et al., 1987; Silva et al., 1993). As an outcome of this process, the Cartagena mountain range developed (extending between Aguillas and Cape Palos; Fig. 1A). This is composed of successive overthrusted metamorphic complexes that conform the Internal Zones of the Betic Cordillera (from the lower to the upper unit, Nevado-Filábride, Alpujárride-Sebtide and Maláguide Complexes; Fig. 1A), separating the Campo de Cartagena-Mar Menor Basin, to the north, from the Mediterranean Sea Basin, to the south (Silva et al., 1993; Bardají et al., 1995a). The Aguilas arc inner basins opened during the early Pliocene in response to the differential uplift of the main thrust-sheets previously mentioned (Bardají et al., 2015).

To the south of the Cartagena range where Calblanque and Torre de Cope study areas are located (Fig. 1B and C, respectively), the Quaternary succession highly controlled by morphostructural framework and tectonic uplift (Bardají et al., 2015), shows significant environmental lateral variations, from continental (alluvial fan and fluvial) deposits, to coastal dune and beach deposits (Zazo et al., 2003, 2013; Bardají et al., 2009, 2015).

Along the Mediterranean coast of Spain, Last Interglacial sea-level proxies have been preserved mostly as beach-dune complexes or tidal deposits, containing remnants of the so-called Senegalese faunal complex. This fauna, easily identified by the presence of *Persististrombus latus* (De Torres et al., 2010), has been used widely to mark the Mediterranean warming during Marine Isotope Stage (MIS) 7 and MIS 5. While some sites preserved fossil specimens of the coral *Cladocora* sp., dated to MIS 5e with U-series (e.g., Muhs et al., 2015), several other sites, in Almeria, Murcia, Alicante and Mallorca, rely on chronological constraints given by amino acid racemization on bivalve shells (e.g. Hearty et al., 1986), U-series on mollusk shells, corals and rodoliths (e.g., Hillaire-Marcel et al., 1986; Goy et al., 1986, 1993; Causse et al., 1993; Zazo, 1999; Zazo et al., 2003), electron spin resonance (e.g., Brückner,

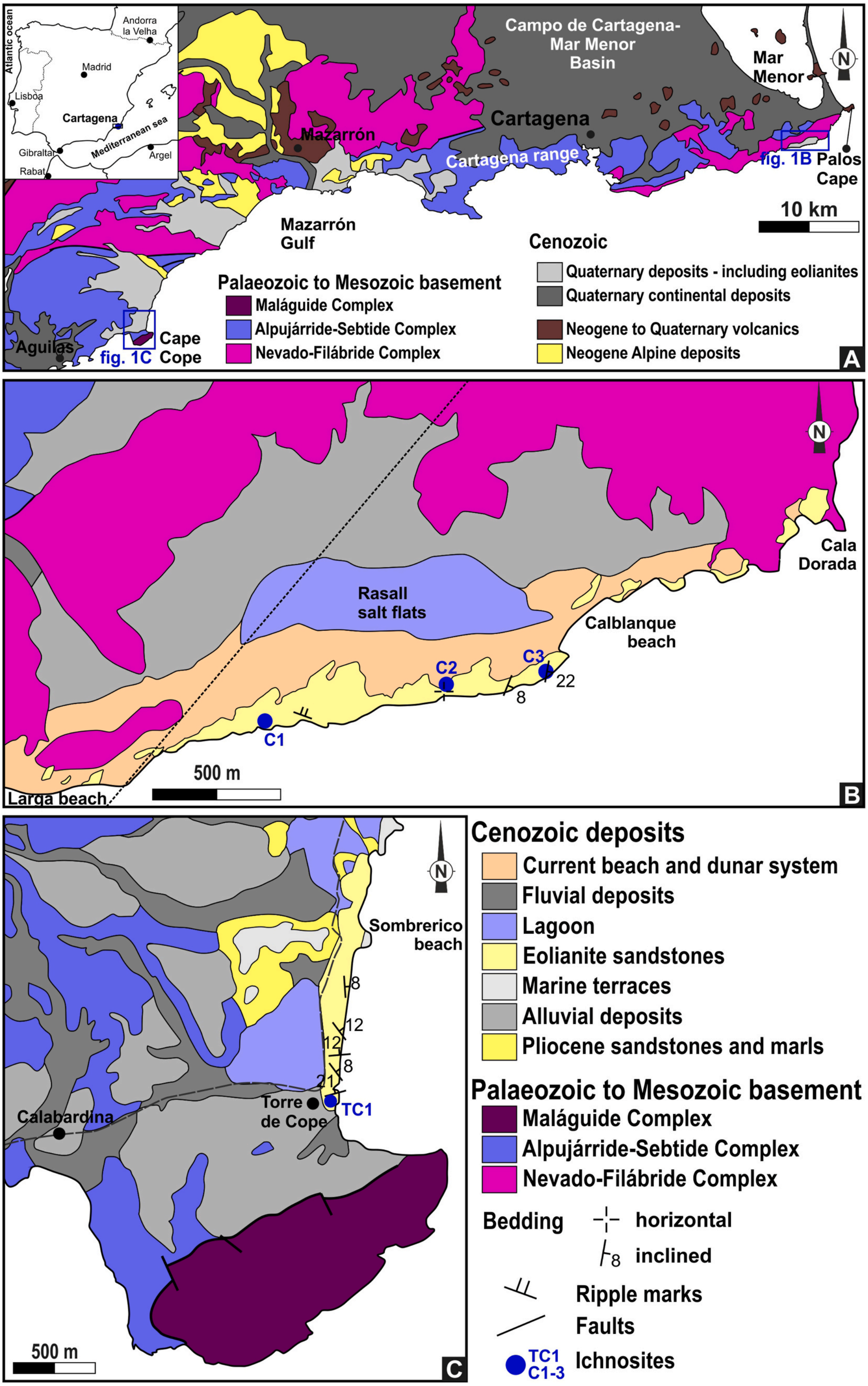

Fig. 1. Geological framework of the study area: (A) Simplified geological map of southeastern Iberia (adapted from Rodriguez Fernandez and Oliveira, 2015), locating both Calblanque and Torre de Cope study areas; (B) Geological map of Calblanque area (adapted from Garcia-Tortosa et al., 2004a); (C) Geological map of Cape Cope area (adapted from Garcia-Tortosa et al., 2004b).

1986), paleomagnetic data (Montenat et al., 1987; Coppier et al., 1989; Goy et al., 1989) and biostratigraphy, as in the case of Cope Basin (e.g., Bardají et al., 2015). The association of oolitic facies and *P. latus* has been correlated with the first peak of the Last Interglacial MIS 5e (Goy et al., 1993; Zazo et al., 2003). Therefore, the Torre de Cope and Calblanque sections described in this paper are dated from the Last Interglacial (MIS 5e: between ca. 128 ka and 116 ka *sensu* Stirling et al., 1998) by correlation with similar well dated oolitic-rich deposits found in Almeria to the southwest, and in other areas of Murcia and Alicante to the North (Zazo et al., 2003; Bardají et al., 2009; see Bardají et al., 1995a, 2015 for the Cope Basin).

2.1. Cope Basin

Strike-slip oblique faults (N60° and more recent N120°) were responsible for the opening of the Cope Basin during the early Pliocene (Bardají et al., 1999; Silva et al., 2003; Bardají et al., 2015). This last set of faults has controlled relief development and sedimentation during the Middle-Late Pleistocene (Bardají et al., 2010), and also the spatial and altitudinal distribution of Pleistocene marine and terrestrial units (Bardají et al., 2015). To the north of Cape Cope, several terraces attributed to different interglacials were detailed by studies in the late 1980s/1990s (Dabrio et al., 1991; Bardají et al., 1986, 1987, 1995a,b, 1999). The sites were later re-described by Zazo et al. (2003, 2013), who clarified that paleomagnetic data and chronostratigraphic correlations with other sites in Almería and Alicante were used for providing an age to these deposits. Within the sites in the so-called Cope Basin, the most complete in terms of stratigraphic descriptions and ages was reported from a location called Casa de Renco, where marine conglomerates outcrop up to 5.2 m above the present mean sea level (a.m.s.l.). The Quaternary deposits overlie the yellow calcarenite subtidal facies from the Late Pliocene (Bardají et al., 1995a), or in an angular unconformity developed over the Alpujárride Complex (Fig. 2A) and are considered one of the most complete Quaternary marine sequences of the Betics. Bardají et al. (2015) described the sedimentological main units along the Cope Basin, constituted by up to 10 highstand marine units composed of coarsening-upward conglomerates and beach deposits, separated by lowstand reddish alluvial fan deposits and paleosols, or erosional surfaces. The two most recent oolite-dominated units (MIS 7 and MIS 5) are exposed along the coast, oriented N-S, suggesting a prevailing strong and persistent wind direction from east and warmer surface currents (Bardají et al., 2009). They are developed as an oolite shoal on top of a former wave-cut platform carved in the Pliocene yellow calcarenites and disposed in a staircase into the older sequence of Pleistocene marine terraces (Bardají et al., 2015). In particular, Bardají et al. (2015) assigned the shell-rich sandstones interpreted as barrier-island facies and associated oolitic dune (Unit 9) where the newly found track-bearing level is located, to the climate optimum MIS 5e, identifying different sea-level oscillations within it (Fig. 2B). The reworked dune can be related with the previous development of an oolitic beach-dune system during an early stage of MIS 5e or even MIS 7, from which foreshore/shoreface sandstones of units 8 to 10 still remain (Fig. 2C). In its southernmost end, the oolitic eolianite, developed as a ramp over the northern slope of Cape Cope, covers colluvial deposits and paleosols with cobbles of Alpujárride and Maláguide basement origins, as well as land snails. The authors do not rule out a possible MIS 5c or 5a age for the uppermost quartz-rich Unit 10 overlapping the oolite dune in the Sombrerico beach, as its age attribution is based solely on the presence of *P. latus* and other warm-water faunas that can be found in units 8 to 10 (Fig. 2D). It is worth noting that, in a short stretch of coast (2.5 km), the MIS 5 shoreline appears deformed by tectonics, raising from ~+2 to ~+12 m a.m.s.l., with sedimentary liquefaction and other evidences likely produced by paleoseismic activity (Bardají et al., 2015).

2.2. Calblanque coastal deposits

In the Calblanque Regional Park (we reduced the name of the park to the area that is important for this work), the oolitic dune system forming a succession of ridges in the present landscape is considered among the best-preserved examples in the Mediterranean Spanish littoral (Fig. 3A). They are developed between the west-southwestern Larga and east-northeastern Cala Dorada beaches. The eolianites were deposited unconformably over the mentioned metamorphic complexes (Nevado-Filábride Complex) of the Internal Zones of the Betic Cordillera. Up to four different units have been distinguished (Baena et al., 1981; Somoza, 1993; Bardají et al., 2011). The top of the succession reaches 23 m a.m.s.

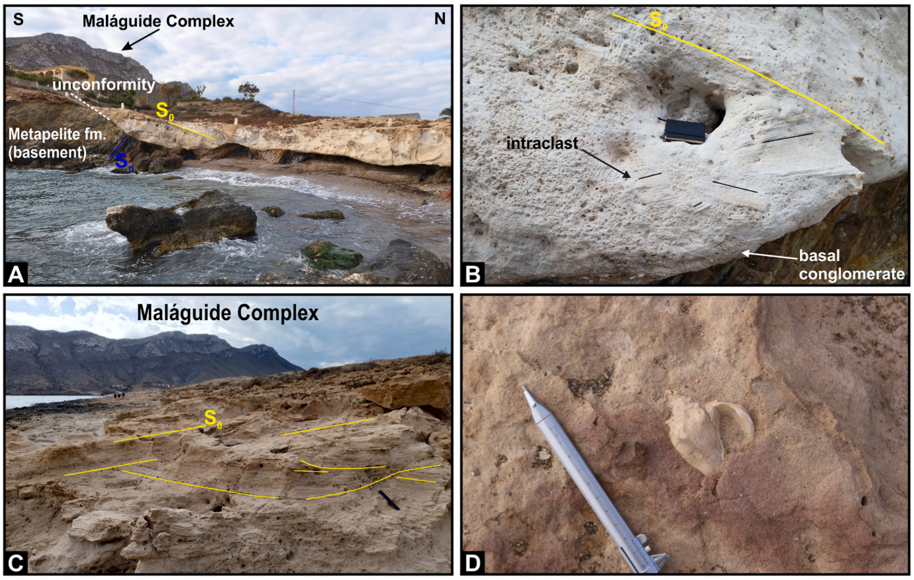

Fig. 2. Stratigraphic features of the Torre de Cope section. A – The dune system where the proboscidean track-bearing level was found, in its southernmost end, unconformably overlying the Metapelite formation of the Alpujárride Complex. B – The dune includes a basal quartz-rich conglomerate and fragments of a pre-existent oolitic dune (MIS 7(?) or early MIS 5e(?)); scale is 150 mm. C – Unit 9 large-scale, low-angle cross bedding in shoreface facies indicating offlap and coastal progradation; the Maláguide up-thrust of Cape Cope as background; scale is 150 mm. D – *Persististrombus latus* in the MIS 5e sandy beach sequence of the Unit 9, according to Bardají et al. (2015).

Fig. 3. Stratigraphic features of the Calblanque eolianites. A – Distribution of the dune landforms in Calblanque showing successive cordons developed by predominantly south-westerly winds. B – Coarse-grained bioclastic and oolitic sandstone from the basal unit of Calblanque indicating the transition to beach sands deposited below the present sea level. C – Ripple-marks produced by south-westerly winds. D – Raindrop prints. E – Yellow siliciclastic dune onlapping the interdune oolite sandstones. F – Foredune sets in the onlapped dune dipping east. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

l. In the lower part of the dune, coarse-grained bioclastic (bivalves, echinoderms, algae) and oolitic sandstone (Fig. 3B) defines the transition from beach facies to the dune system. They were produced by active southern winds (Fig. 3A–C). Raindrop impressions may indicate moistened sediments favorable to the formation and preservation of tracks (Fig. 3D). Rhizoturbation is locally intense (Cala Arturo) and mostly horizontal, as well as horizontal traces made by insects (possibly coleoptera as in Muñiz et al., 2019) in the oolite eolian lithofacies (Fig. 4). These oolitic dune system was attributed close to the peak of MIS 5e highstand by morphosedimentary correlation with other dated beach-dune deposits found in the region (Bardají et al., 2011, 2015). The three track-bearing levels were found in foredune and interdune laminae of the oolite dune system. A more recent highstand is defined by the onlapping of a yellow quartz-rich dune (Fig. 3E) attributed to a later stage of the MIS 5e, or MIS 5c/MIS 5a (Bardají et al., 2011), showing intense horizontal and vertical rhizoturbation and a different source of sediment, mainly siliciclastic, accumulated by the same prevailing winds (Fig. 3E and F) and indicating either a change in oceanographic or climatic conditions (Bardají et al., 2009).

3. Methods

The geological mapping of both study areas in Murcia was updated from published sheets of the Geological Map of Spain at 1:50.000 scale, published from IGME (Geological Surveys of Spain) (Garcia-Tortosa et al., 2004a, 2004b), by including new data from field campaigns. In the Calblanque area, the published geological map was refined using the open access satellite images of Google Maps, well defining the outcropping areas of Pleistocene eolianites, not differentiating either oolitic and siliciclastic eolianites, and either present beach and dune systems. The footprints were found as true tracks on the top of oolite eolianite laminae and in vertical cross sections. Besides the vertebrate tracks, small invertebrate burrows are also present in the succession, including horizontal backfilled burrows *Taenidum* in Torre de Cope section (shoreface facies) and coleopteran-like burrows in the Calblanque section (oolite eolianite), but they are not the focus of the present study. Ichnological descriptive and morphometric procedures follow standard approaches (see Falkingham et al., 2018; Bennett and Reynolds, 2021). The images taken in the field with a digital camera

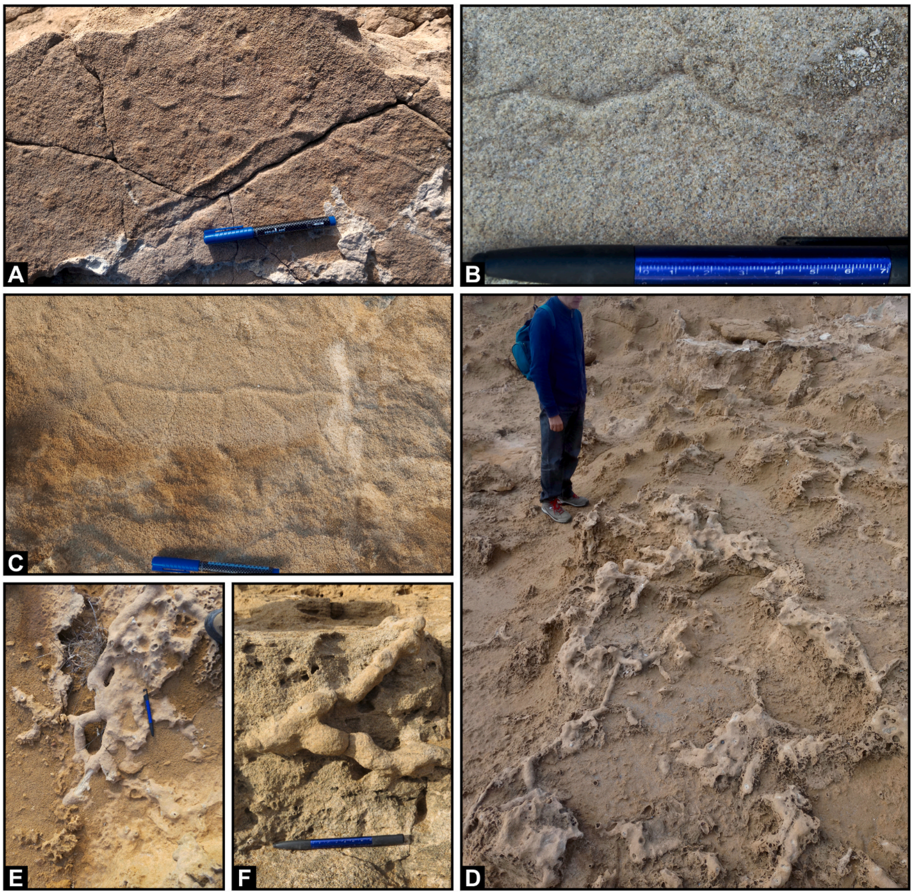

Fig. 4. Insect burrows and rhizoliths from Calblanque eolianites. A to C – Coleopteran-like insect burrows in the oolite eolianite unit. D – Mainly horizontal rhizoturbation in the lower oolite eolianite unit. E and F – Examples of rhizoliths from the upper siliciclastic eolianite unit. Pen with ruler as scale (cm). Length of the pen is 140 mm.

Canon EOS100D + EF-S 18–55 mm f/3.5–5.6 IS STM + EF 40 mm f/2.8 STM were processed with Adobe Photoshop software. The dimension and orientation data were measured directly on the outcrop (taken in mm) and compared with the scaled 3D images obtained by photogrammetry according to procedures described by Lallensack et al. (2016).

Close-range photogrammetry as one of the most coherent and realistic 3D digital methods, economical and with relatively simple logistics. It is nowadays one of the most widely used technique for recording ichnological sites (e.g. Amzil et al., 2024), but also to help carry out increasingly specific analyses and interpretations of ichnites (e.g. Adams et al., 2025; Belvedere et al., 2025). In this work, digital photogrammetry was used to record and subsequently analyze the tracks and trackways studied, as a way of obtaining reliable 3D records in geometry and radiometry, which could support subsequent visualization assisted by algorithms that allow highlighting morphological details and carrying out precise measurements in the office (2D and 3D). The methodology used followed guidelines addressed by Mallison and Wiings (2014), Matthews et al. (2016), Falkingham et al. (2018), and Lallensack et al. (2022). The equipment used to carry out the photographic surveys was a Samsung NX500 camera with a 16–50 mm lens, a Vanguard Alta Series 70 tripod and an 8 m extendable pole, the latter used to survey trackways and larger bioturbated areas, on a smaller scale. Photogrammetric processing was performed using RealityCapture© software (Now RealityScan 2.0; Epic Games, 2025) and post-processing, which includes visual, qualitative, quantitative analysis and metrics collection, based on the 3D models and 2D data obtained, was performed using the freeware Cloud Compare (GPL License; CloudCompare, 2025), MeshLab© (GPL License; Cignoni et al., 2008) and QGIS (GPL License).

In this paper, a trackway is considered as a sequence of three or more tracks of the same animal left by locomotion (Thulborn, 1990). Measurements of the morphometric features of tracks and trackways, and the nomenclature system follow previous works. In the description of tracks and surface features, terms from Thulborn (1990), Allen (1997), Fornós et al. (2002) and Falkingham et al. (2018) are used. The track length (Tl) is measured on the longitudinal axis of the track; the width (Tw) is measured perpendicular to the longitudinal axis; the pace (P) of is the distance between consecutive, alternating tracks (i.e., right-left or left-right pes or manus) (Lockley, 1991). Stride length (Sl) is defined as the distance between corresponding points in successive prints from the same limb (Thulborn, 1990). These measurements are taken between the anterior tips of the tracks. The gauge was obtained from the track ratio that is calculated using the formula of Romano et al. (2007), where the side width (Sw) of the trackway, or the width measured perpendicular to the trackway midline is related to the overall width (Ow) (the width measured from the outermost edges of subsequent right and left impressions perpendicular to the trackway midline). Track and trackway measurements were used to determine the estimated hip height (H) of the trackmakers. The most commonly first-approach used to estimate hip height correlates Tl with H through a scaling factor (Alexander, 1976).

Belvedere and Farlow (2016) proposed a four-point scale (0-1-2-3) for quantifying the preservation quality of vertebrate tracks. In general, tracks in eolianites do not show outstanding preservation (see Helm et al., 2021). Tracks in dune facies (and coarse beach sand) usually do not rise above level 2 on this scale. This means that morphological details like digit and especially claw impressions may not be present due to grain size. However, track size and shape can usually still be determined, especially when displacement rims are identified (Marchetti et al., 2019).

4. Description of the ichnosites

4.1. Calblanque section

4.1.1. Ichnosite 1

Ichnogenus *Mustelipeda* Kordós 1985.

Type ichnospecies: *Mustelipeda punctata* Kordos (1983).

Diagnosis: A small, circular track with the imprints of five closely attached toes; the sole does not penetrate the ground, only its outline can be followed (Kordos, 1985).

Ichnospecies Mustelipeda aff. *punctata* Kordos (1983)

Description: A single trackway approximately 1500 mm long was found at the ichnosite 1. This trackway is composed of 10 tracks with a quality of preservation between 1 and 2 in the scale of Belvedere and Farlow (2016) (Fig. 5A). In fact, the sediment from the upper layer that sometimes fills the tracks or is present in their surrounding area makes them difficult to read. The tracks are grouped in pairs. The pairs of printed tracks are slightly laterally distant from their axis (Fig. 5B). The pairs of tracks are at a regular distance from each other that varies approximately between 330 and 350 mm, which corresponds approximately to the P. The Sl is approximately 660–680 mm. As for the shape and size of the various tracks, these are relatively variable due to their state of preservation. The shape is subcircular, oval, triangular or elongated, almost always wider than long. Taking measurements show some patterns and concordances between tracks as can be seen in Table 1. The mean Tl (n = 10) is 46.3 mm and Tw is 69.6 mm.

The Tw/Tl^3 index presented a mean value of 0.096, varying between a minimum of 0.025 and a maximum of 0.183. This index is relatively variable (Standard Deviation or SD = 0.061) due to the high variability

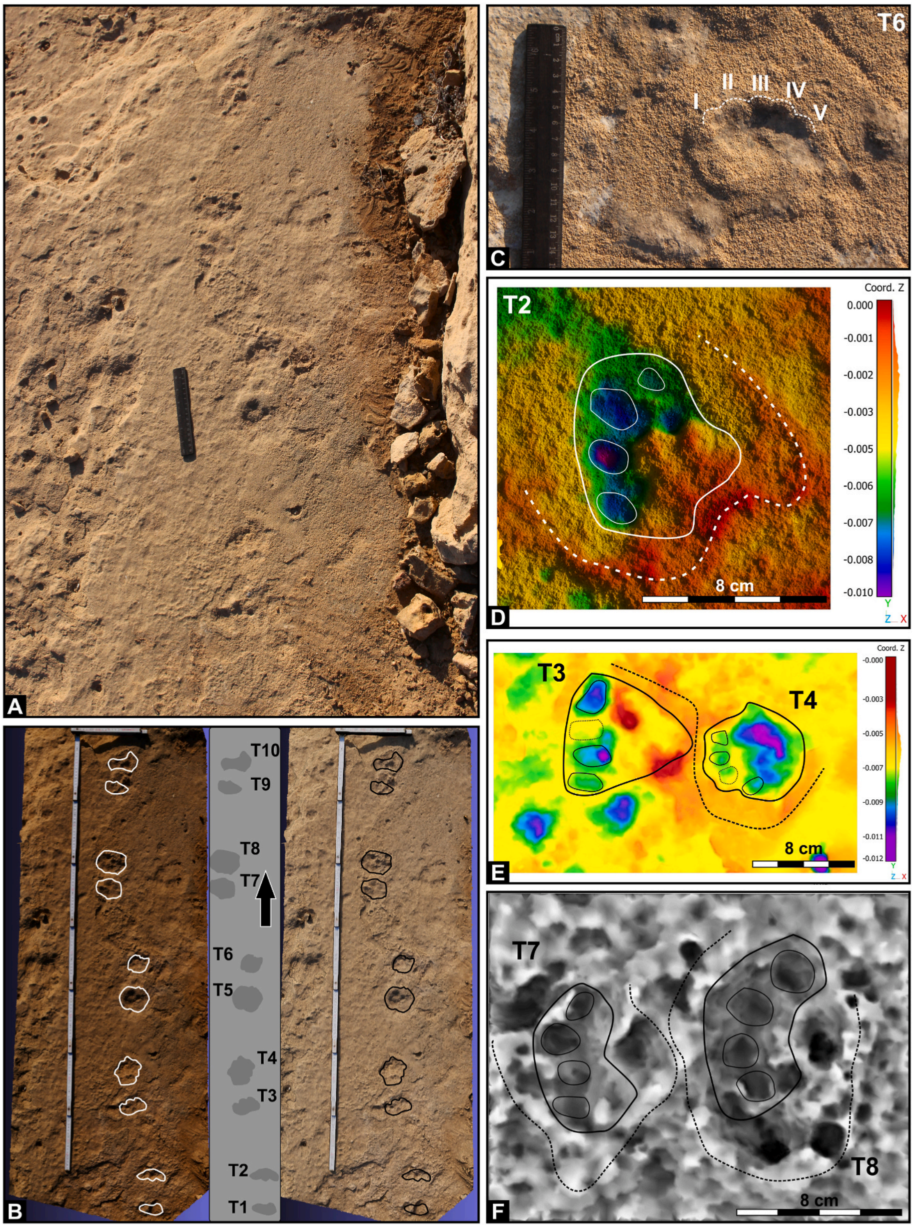

Fig. 5. *Mustelipeda* aff. *punctata* Kordos. A – General aspect of the trackway (pair T1-T2 not seen). B – Interpretation of the trackways, over the shadowed real colors 3D models, shows a paired tracks gait. C – Oblique view of T6 showing the presence of 5-digit prints. D – T2, false color depth map scale (m). E – Interpretation of the tracks T3-T4 over the false color DSM model (m). F – Interpretation of tracks T7-T8 on the false color, shadowed ambient occlusion 3D model. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 1
– Measurements of the individual tracks in the trackway from Ichnosite 1.

Tracks	Tl (mm)	Tw (mm)	Tw/Tl	Tw/Tl^3
T1	32.6	63.3	0.51	0.183
T2	40.6	67.2	0.60	0.1
T3	36.0	70.8	0.51	0.152
T4	35.7	77.3	0.46	0.17
T5	48.5	75.8	0.64	0.066
T6	36.1	65.5	0.55	0.139
T7	58.3	75.6	0.77	0.038
T8	52.1	76.7	0.68	0.054
T9	60.2	62.1	0.97	0.028
T10	62.8	62.1	1.01	0.025
Mean	46.29	69.64	0.67	0.096
Max	62.8	77.3	1.01	0.183
Min	32.6	62.1	0.46	0.025
SD	6.763	3.721	0.11	0.061

in the shape and size of the analyzed tracks, derived from their state of preservation. The Tw/Tl ratio presents a mean value of 0.67, varying between a minimum of 0.46 (digitigrade) and a maximum of 1.01 (semi-plantigrade). A well-preserved track T6 shows the evidence of five-digit prints (Fig. 5C), but tracks commonly preserve only four or even three digits.

Track T8 appears to be one of the best preserved (Fig. 5F). It is approximately 52 mm long, 76 mm wide and has a Tw/Tl^3 index of 0.054. Almost all around the track, there is a ridge of sediment expulsion produced by pressure exerted directly on the substrate. Near the inner edge of the most distal part, there is an impression of four digits, without claw marks. T8 is digitigrade like most other tracks, with toe impresions pointing forward. It is difficult to see the sole (impression of the pad, lobes), with the toes being well marked, which means that the apparent Sl of may be shorter than the real one. The pair of T8, T7 is 58.3 mm long, 75.6 mm wide and has a Tw/Tl^3 index of 0.038 (Fig. 5F). It has a subcircular shape, sediment expulsion ridges and three to four probable toe marks. T2 has a subcircular to oval shape, is approximately 41 mm long, 67 mm wide and has a Tw/Tl^3 index of 0.025. It has a slight partial sediment expulsion ridge and a mark of three to four oval digits. T9 is poorly imprinted and is partially covered with sediment from the upper layer, which makes its interpretation difficult, but it still has two-to-three-digit prints. It is 60.2 mm long by 62.1 mm wide and has a Tw/Tl^3index of 0.028. Its pair T10 is subcircular in shape, 62.8 mm long by 62.1 mm wide and has a Tw/Tl^3index of 38.99. There is sediment of the upper layer embedded in the track or present in areas surrounding it, which does not allow to observe fully. T3 is complex and appears to be wider than it actually is (Fig. 5D). It has a triangular subcircular shape measuring 36 mm long by 70 mm wide and a Tw/Tl^3index of 0.152. T4 has a circular to subcircular shape. It does not have well-defined digits, but it does have a slight ridge of partial sediment expulsion around it. It is 35.7 mm long, 77.3 mm wide and has a Tw/Tl^3 index of 0.17 (Fig. 5E).

Comments: Mustelid ichnospecies presently recognized are *Mustelipeda punctata* Kordos (1983), *Mustelidichnum enigmaticum* Aramayo and Manera de Bianco (1987), *M. vallecitoensis* Remeika (2001), *Phacelpus therates* Sarjeant and Langston (1994) and *Carnivoripeda nogradensis* (Kordos, 1985). *Mustelipeda punctata* was described by Kordos (1983, 1985) from the Lower Miocene Ipolytarnóc ichnosite (Hungary). The tracks are commonly preserved only as digit or claw imprints, so mainly digitigrade. When complete, the tracks show small circular, slightly compressed proximo-distally sole prints with equal spacing five-digit, oval to rhombic prints attached to it or discontinuously. In these cases, the claw prints are present only occasionally (Kordos, 1985). *M. punctata* was attributed to a medium-sized mustelid, but further studies are needed according to Botfalvai et al. (2023).

Mustelidichnum enigmaticum and *M. vallecitoensis* were designated by Aramayo and Manera de Bianco (1987) and Remeika (2001) for a questionable aquatic webbed-mustelid and otter tracks, respectively from the Late Pleistocene ichnosite of Pehuén Co and from the Pliocene of California. *Mustelidichnum enigmaticum* shows mainly plantigrade to digitigrade, heteropodial, pentadactyl tracks; the tracks are roundish, slightly wider than long, with the pes webbed between the central digits; the toe prints are circular to oval and sharply clawed, with the outer digits I and V separated slightly from central digits; the interdigital pad imprint is sub-quadrangular, deeply lobed, fused and continuous (Aramayo and Manera de Bianco, 1987). Morphologically, *M. vallecitoensis* designated by Remeika (2001) is similar to *M. enigmaticum*, being tracks only larger. While *M. enigmaticum* was attributed to a species of the family Mustelidae “like *Lutra platensis* but smaller” (Aramayo and Manera de Bianco, 1987), *M. vallecitoensis* from the early Pleistocene of Virginia was compared by Weems (2018) to the river otter *Lutra canadensis*.

The ichnogenus *Mustelidichnum* differs from *Phacelopus* in having very short and straight digits and sub-quadrangular palmar and plantar impressions (Sarjeant and Langston, 1994). Besides, *Phacelopus therates* from Late Eocene of Texas is a mainly plantigrade to semi-plantigrade track, with manus somewhat smaller than pes and the digits and claws curving inwards.

Carnivoripeda nogradensis exhibits the closest resemblance to *Phacelopus therates*. A notable difference is the position of digit I which is situated in a lateral position in the case of the Ipolytarnóc traces, as opposed to *P. therates* where digit I is directed forward, in a similar way to the other digits. Furthermore, the length of the digital imprints of *P. therates* are proportionally longer than that of *C. nogradensis* and the shape of the palm print is also different (Botfalvai et al., 2023). A wolverine-sized mustelid like *Ischyrictis* or *Hoplictis* could have produced *C. nogradensis* (Botfalvai et al., 2023).

Mustelipeda aff. *punctata* from the Late Pleistocene of Calblanque is mostly digitigrade, with tracks wider than long under the size range of the Ipolytarnóc tracks (Kordos, 1985), without clear evidence for a palm impression; when this is preserved it appears to be sub-circular to trapezoidal in shape (Fig. 5C–E). The digit prints displaced in an arch do not show evidence for claws and are not webbed, neither curve inwards. They point forward and the outer digits may show a small divarication angle. There may be heteropody according to the Tw/Tl^3 index but it was not possible to differentiate manus from pes.

Given the arrangement and regularity of the tracks of the trackway in ichnosite 1, they should correspond to a regular walking pattern at a relatively slow pace. Considering the layout of the tracks on the trackway, their arrangement in pairs, the regular equidistance between the pairs of tracks and their lateral deviation in relation to the axis, as well as the metrics presented, they fit well with a medium-sized mustelid, such as the stone marten, *Martes foina*, which is present nowadays in the Calblanque area. The distribution of the tracks in pairs at regular distances of 330–350 mm on the trackway is similar to the present species. The paired prints gait interpreted from the Calblanque trackway is characteristic of this species (Bang and Dahlstrom, 2001). The marten’s tracks have a length that varies between 50 and 60 mm and a width between 45 and 60 mm (Brown et al., 1992) However, as a rule the marten leaves thin claw marks that are not visible in the model and images obtained. As for the length of Calblanque tracks, this is relatively shorter than of *Martes foina*. On the contrary, in relation to the width, the Calblanque tracks are relatively larger with a mean width of 69.6 mm. However, these margins of error can be considered acceptable when dealing with loose substrates (Bang and Dahlstrom, 2001). Besides, compound manus-pes tracks may account for the variations in width recorded for the tracks in Table 1. Martens show five toes of each foot, but digit I barely leaves prints. This may be the case for the fossil trackway. Although T6 shows five-digit impressions, this could result in theory from a tetradactyl pes track on a tetradactyl manus track. All the toe impressions present have a diameter greater than or equal to 10 mm, which can be considered relatively large for a mustelid, again not considering a loose substrate. In all the tracks that present toes, these form an arch, but the palm impression is barely visible. The outlines of the pine marten print appear more indistinct, due to the covering of hair on the sole between the pads (Bang and Dahlstrom, 2001). The otter *Lutra lutra* is also present nowadays at Calblanque. However, the tracks of this species are larger, especially the pes, than the ones in the ichnosite 1 (Bang and Dahlstrom, 2001). They also present large palm pads or prints of the entire sole, not visible in the mainly digitigrade fossil tracks.

The relatively large size of the tracks, wider than long, composed mainly of 4 toe impressions arranged in an arch and without claw marks, could suggest, on the other hand, that they were made by a small, medium-sized feline. In this case, it could fit a sub-adult male lynx or a medium-sized female (Neto de Carvalho, 2014), in a species that shows sexual dimorphism. According to Brown et al. (1992), *Felis lynx* tracks have a length that varies between 70 and 80 mm, a width that varies between 85 and 95 mm and a W/L^3 index that varies between 0.019 and 0.024. In this sense, the overall dimension of lynx tracks is greater than the ones in Calblanque, in addition to the fact that they are not usually arranged in pairs on the trackway. The W/L^3 index obtained for the tracks of Calblanque is much higher than the expected for lynx tracks, and more comparable to *Martes foina*.

4.1.2. Ichnosite 2

Ichnogenus *Canipeda* Panin and Avram 1962.

Type ichnospecies: *Canipeda longigriffa* Panin and Avram (1962).

Diagnosis: Digitigrade to semidigitigrade, tetradactyl, paraxonic, longer than wide footprints; arranged in quadrupedal and homopodial trackways. Elliptic, similar-sized and clawed digital pads form an arc in front of, and are well separated from, a large metapodial pad; this is rounded to triangular or trapezoidal in shape (after Melchor et al., 2018).

Ichnospecies *Canipeda* isp.

Description: It corresponds to an isolated track, deeply printed in coarse-grained sediments of a lamina that dips north about 10°. It is a true track because it preserves a ridge of sediment expulsion in the inner and posterior sides (resulting from footfall in a sloped surface) of the track (Fig. 6A). The track has an approximate size of 100 × 80 mm (Tl x Tw). It shows a typical canine morphology of four teardrop-shaped, elongated toe prints surrounding a medial pad that extends almost up to the middle digits (Fig. 6B). The rear edge of the central pad curves inward, making it bilobed. The two middle digit prints slightly splay, and the divarication angles of digits II and V are very low. It appears to have better defined claw marks (3) than the print of the digital pads; they are thick and in continuation of those due to the deep impression of the track.

Comments: There are presently three ichnospecies of *Canipeda* considered valid (Melchor et al., 2018). According to the emended diagnosis of Melchor et al. (2018), *Canipeda gracilis* from the Late

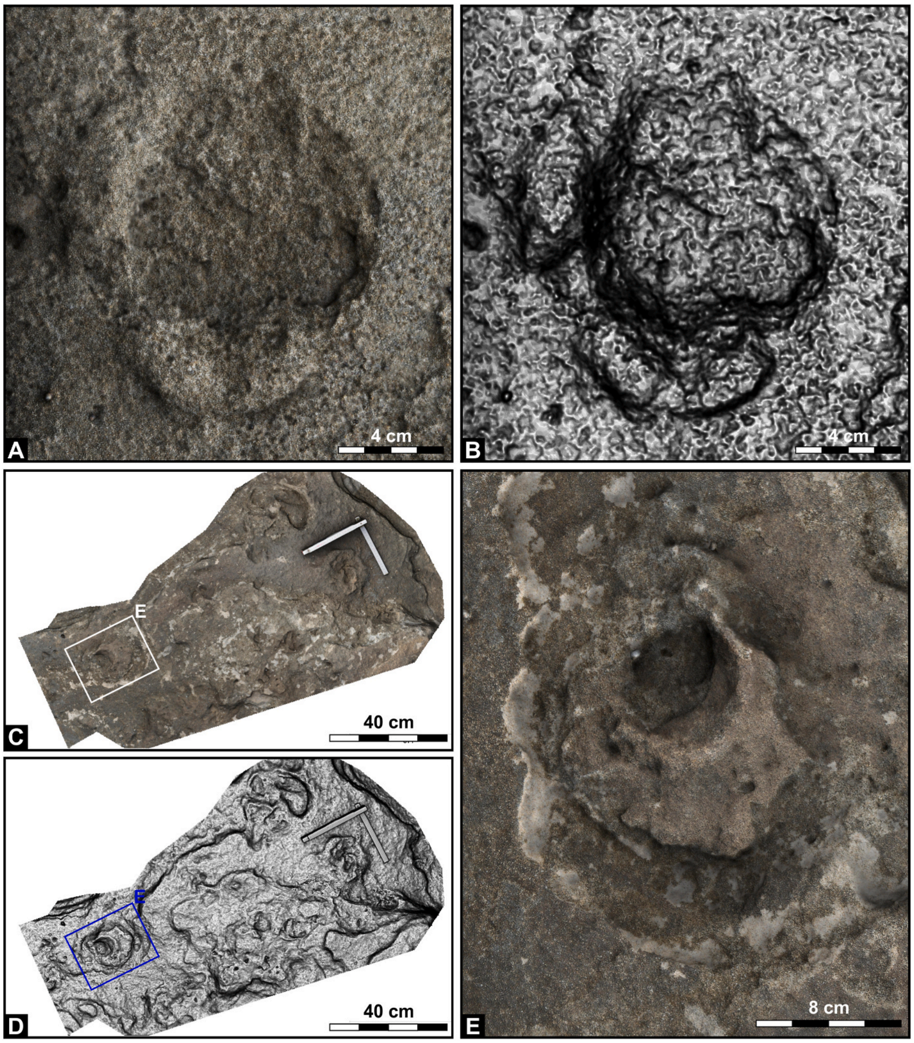

Fig. 6. Tracks found in the ichnosite 2. A – *Canipeda* isp. B –Shadowed ambient occlusion 3D model showing morphological details, including four digits extended by the claw prints (in digits III to V) and forming an arch around the trapezoidal metapodial pad. C – Pair of apparently artiodactyl-like bifid tracks. The size of the tracks and the distance between them could represent the Sl of an adult. D - Shadowed ambient occlusion 3D model perpendicular view. E – Detail of the best-preserved artiodactyl-like track showing differential cementation of the deformed sediment facing present erosion.

Pleistocene of Pehuén Co (Argentina) and attributed to a small fox shows manus larger than pes imprints, track length between 35 and 65 mm, track length/width ratio between 1.0 and 1.3, divarication of outer digits (II and V) from 30 to 70°, divarication of inner digits (III-IV) from 10 to 20°, metapodial pad impression triangular in the manus and subrounded to elliptical in the pes. *Canipeda longigriffa* first described in the Lower Miocene of Romania by Panin and Avram (1962) has a larger track length/width ratio (1.6–1.9), rather different from the track of Calblanque, but a smaller divarication of outer digits (II-V less than 30) similar to the track under study. *Canipeda sanguinolenta* designated by Vialov (1965) from the Lower Miocene locality of Dobrotov in western Ucrania is larger than the other valid ichnospecies of *Canipeda* (Tl of 75–85 mm), but still much smaller than the Calblanque track, and exhibits arcuate metapodial pads with strongly bilobed rear end somewhat similar to the specimen under the present study, although more sub-triangular in shape. Since we found only one track it is not enough to define a new ichnospecies of *Canipeda*.

The occurrence of *Canipeda* in the late Miocene of La Hoya de la Sima (Murcia, Spain) by Pérez-Lorente et al. (1999) was considered doubtful by Melchor et al. (2018). Furthermore, the presence of *?Canipeda* indicated by Doyle et al. (2000) based on previous reports in the Late Miocene Sorbas Member of the Sorbas Basin, Almería Province, was not supported by descriptions or illustrations. Therefore, this isolated print may be the only occurrence of *Canipeda* presently known in SE Spain.

According to the size and shape of the track, it was probably made by an adult wolf (considering that the dimensions of wolf tracks vary approximately between 100 and 110 mm in length and 80–95 mm in width; Brown et al., 1992). The Tw/Tl index of the track is 0.8, while for wolves the index varies between 0.75 and 1.045. Although we are only analyzing a single track, which is statistically very poor, the index obtained for this specimen corroborates the possibility that it is from a wolf. Moreover, the deepest part of the track, corresponding to the paw pad, is consistent with the delineation proposed for the canine track (Melchor et al., 2018), and specifically wolf (Bang and Dahlstrom, 2001). The fact that it corresponds to an isolated track does not allow us to extract much information, other than the likely presence of the wolf in Calblanque, in that coastal habitat, at that chronology. Similar tracks in both morphology and size were reported in the Middle Pleistocene of Matalascañas Trampled Surface, Huelva (SW Spain) by Neto de Carvalho et al. (2020c) attributed to wolf, and in Middle Holocene coastal deposits at Formby (NE England) by Roberts (2009), attributed to dog or wolf.

4.1.2.1. Artiodactyl tracks. The interdune laminae overlying the track described before show a small surface that presents two structures corresponding to bioturbation, but poorly preserved. The tracks are located approximately 900 mm apart (Fig. 6C–D). They are apparently true tracks with displacement rims, the shape is crudely bifid and therefore would represent hoofprints with sharp tips, although differential erosion of the sediment does not allow to define detailed morphological characteristics. The Tl in Fig. 6E is 100 mm and the Tw in the widest point of the track is 70 mm. Given the distance between the structures, their general shape, orientation and estimated size, seem to be produced by a single animal. Position of pes print relative to manus print is dependent on gait: the pes is placed progressively further forward as speed increases. The size and elongated shape of the hoofprint in Fig. 6E match with the stag's fore print of an adult red deer (*Cervus elaphus*).

4.1.3. Ichnosite 3

4.1.3.1. Artiodactyls tracks. Description: the interdune deposits of Calblanque in this ichnosite show in perpendicular sections several large indentations which intersect and deform the primary sedimentary laminae producing pressure curved faults and displacement folds (Allen, 1997), similar to the plastic deformation and microtectonic rupture of sediment produced by hoofprints (Fig. 7A–C, E) described in eolianites by Loope (1986), Fornós et al. (2002), Fanelli et al. (2007) and Neto de Carvalho et al. (2016). However, they never result in trample grounds assuming low bioturbation indices along time. The large sizes of the tracks point to large artiodactyls, such as large cervids, as producers, without discarding the possibility of the presence of bovids such as aurochs (Fig. 7D), if the apparent track does not result from a combination of the pes falling shortly behind manus, which is the typical gait for walking or steady trotting artiodactyls (e.g., Bang and Dahlstrom, 2001; Fornós et al., 2002).

Ichnogenus *Hippipeda* Vialov 1966.

Type ichnospecies: *Hippipeda aurelianis* Vialov (1966).

Diagnosis: Tracks of functionally single-digit hooved herbivores, having a hemi-ellipsoidal to hemispherical or hemiovoidal hoof wall, with or without traces of a "frog". One or two lateral digits (II and IV) may also be impressed in trackways during a fast gait, but these are much smaller than the central impression of digit III. Trackway narrow; stride and pace long (Sarjeant and Reynolds, 1999; McNeil et al., 2007).

Ichnospecies *Hippipeda* isp.

Description: It corresponds to a single track of moderate size, moderate to poorly preserved due to intense, small-diameter rhizoturbation and consequent differential erosion. The track is a single pad impression with a subcircular shape, approximately 100 mm long by 120 mm wide, although tapering to the anterior edge. It corresponds to a true track, with a notable ridge of sediment expulsion along its most distal part of the broad hoof wall, around 10 mm in thickness (Fig. 7F). Inside, along the edge of the depressed wall, there is a set of small pits related to present erosion; a "frog" is recognized at the posterior part as a raised v-shaped indentation (Fig. 7G).

Comments: The length of a horse's track, specifically the solar length of the hoof, varies according to the different breeds and age groups but generally ranges in adults from 115 to 131.5 mm (Stachurska et al., 2008; Kawareti et al., 2017). That means that the *Hippipeda* isp. was produced possibly by a sub-adult *Equus* or by an adult of a smaller species. Distinguishing equid species based on tracks is difficult, especially if they are preserved in coarse sediments and in isolated tracks. During the Last Interglacial period in Iberia, both *Equus ferus* (wild horse) and the smaller *Equus hydruntinus* (European wild ass) were present (Sanz-Royo et al., 2020). These wild equids thrived in the warmer, interglacial climates before eventually declining and becoming extinct by the Late Pleistocene or early Holocene (Bernáldez-Sánchez et al., 2024).

The tracks of Equoidea previously described in southern Spain include representatives from the upper Miocene of Hoya de la Sima and Sierra de las Cabras tracksites in Murcia (Perez-Lorente et al., 1999; Herrero et al., 2022a,b), and the lower Pliocene in Sierra del Colmenar, Alicante (Lancis and Estévez, 1992). The track from Calblanque is the most recent one attributed to a horse in the stratigraphic record from SE Spain.

A single track in a limited exposure does not bring much information about gaits. In the diversity of gaits assumed by the Equidae along their evolution (Vincelette, 2021), the preservation of manus-pes couples at short distance or partial overprints is the most common occurrence. More or less isolated tracks may be associated to galloping, slow pace and canter gaits (sensu Vincelette, 2021).

4.2. Torre de cope section

Ichnogenus *Proboscipeda* Panin and Avram, 1962.

Type ichnospecies: *Proboscipeda enigmatica* Panin and Avram (1962).

Diagnosis: Large oval to subcircular tracks, large and flat sole/palm impression surface either ornamented or smooth, three to five short and blunt digit impressions pointing anteriorly, deep tracks with a noticeable marginal ridge (after emended by Aramayo et al., 2015).

Comments: Both *Stegomastodonichnum* Aramayo and Manera de Bianco 1987; *Mammuthichnum* Remeika 2001 have the same

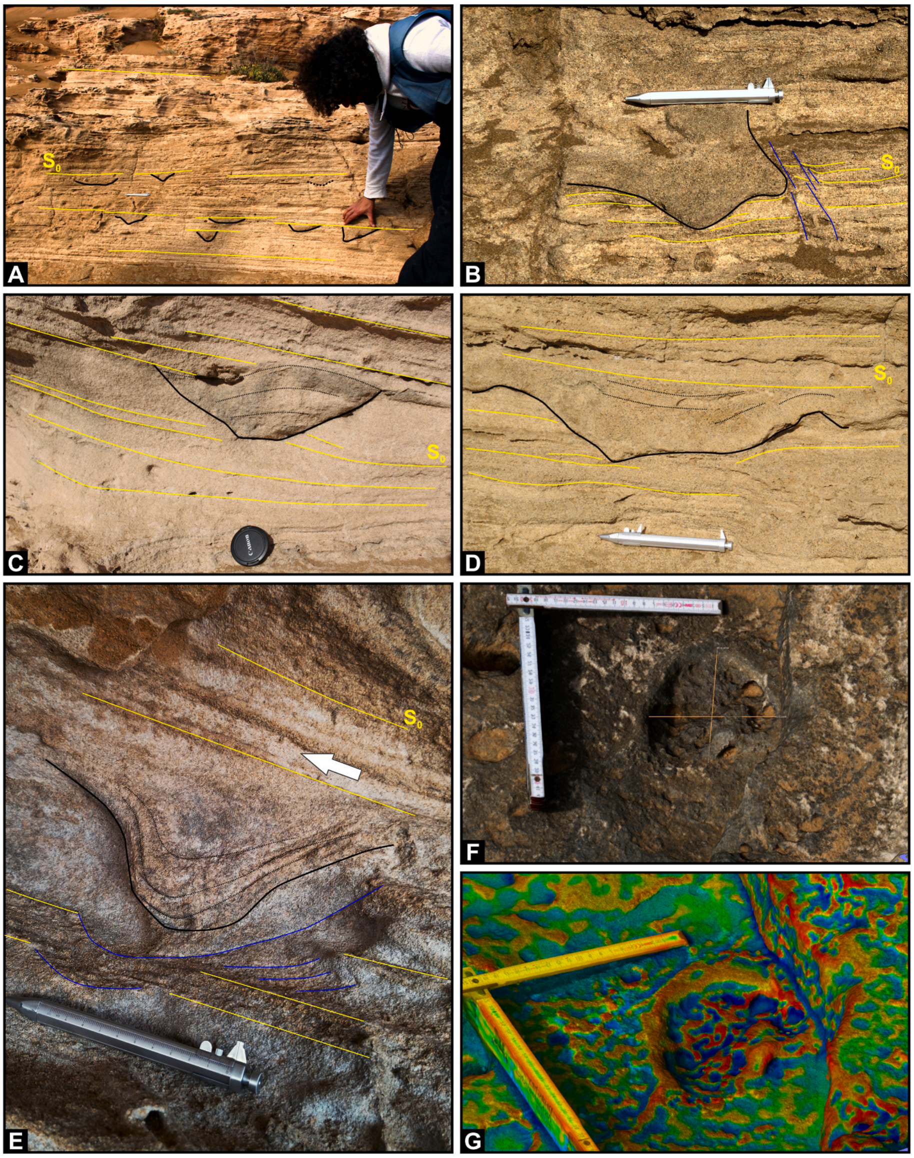

Fig. 7. True tracks and track cross sections in the ichnosite 3 of Calblanque. S$_0$ yellow lines represents sedimentary laminae; black lines show the sectioned track; blue lines indicate deformation of the sediment; black dots indicate sediment laminae passively filling the track. A – Interdune laminae intersected by different generations of artiodactyl hoofprints. B – Detail of one of these cross sections of hoofprints deforming the surrounding sediment by applied propulsive pressure of the foot. The path of the withdrawal of the limb to the left of the photo turned almost parallel with lamination, producing a drag trace sensu Fornós et al. (2002). C – Another example intersecting foredune laminae; scale is 58 mm. D- Large cross section showing marginal ridges, which apparently indicates a single track of a very large artiodactyl, instead of a manus-pes couple. The deepest part of the track displaced towards the steep face shows that the sharp hoof withdrawn was made to the left of the photo (west). E—the same reasoning is applied to this section of a hoofprint, together with the deformation of the sediment around the anterior most part of the print, indicating the direction of movement towards the left of the photo (west). F – *Hippipeda* isp. with the partial definition of the "frog" in the posterior edge of the track; real colors 3D model perpendicular view. G - Curvature map presents information on the microtopography of the track and surrounding surface in false colors: green colors correspond to flattened areas, reddish colors to convex areas and bluish colors to concave areas. Scale of B, D, E-G is 150 mm. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

morphology of *Proboscipeda* so that Lucas et al. (2007) had considered the first two ichnogenera as junior synonyms of *Proboscipeda*.

Ichnospecies *Proboscipeda panfamilia* McNeil et al. (2007).

Diagnosis: Large-size impressions of the *Proboscipeda* type. Only pes prints typically visible, as the manus impressions are overprinted by the pes in typical locomotion. Impressions are circular to oval in outline, with the width being the greatest dimension. Three to five short wide toe impressions visible on the anterior portion of the impression (after McNeil et al., 2007).

Description: Track size 400–500 mm (longest diameter measured); depth of impressions 50–100 mm. Total number of tracks measured: 4. Abundance: Only one narrow gauge trackway, possibly two isolated tracks. In this case, as in many others, the three-dimensional modelling and digital microtopographic enhancement techniques used allowed to validate the presence of a proboscidean trackway. It became much more easily visualized and interpretable in a digital environment, according to the three-dimensional modelling techniques applied (Fig. 8). The trackway is preserved on a foreset lamina gently dipping north, in a succession showing strong rhizoturbation and affected by present sea erosion threatening the preservation of the ichnosite. The trackway is linear and is approximately 2.75 m long. It consists of four variably preserved but visible and well-marked tracks (Fig. 8A–C), although finer morphological characteristics, such as nail marks (digits), are not apparently noticeable, except in ml1 which shows the best preservation

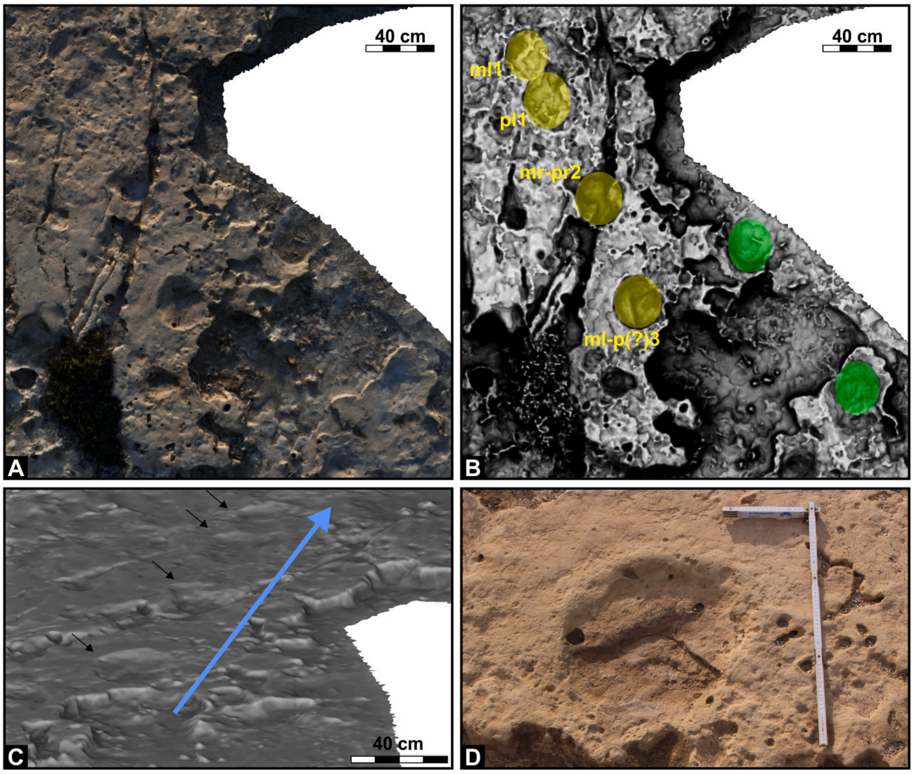

Fig. 8. *Proboscipeda panfamilia* McNeil et al., (2007) from Torre de Cope, southern coast of Murcia. A – Narrow gauge trackway. Real colors 3D model perpendicular view of the trackway. B – Shadowed ambient occlusion 3d model perpendicular view with the interpretation of the tracks/trackway. Manus (m) and pes (p) numbered by inversed stepping order; *r* and *l* indicate right and left, respectively; the tracks identified in yellow correspond to the interpreted trackway and those identified in green to the probable isolated tracks. C – Oblique view of the trackway allows to visualize the displacement rims more prominent in the anterior border of the tracks (pointed with black arrows) which results from the pressure exerted for forward foot off and indicates direction of movement (blue arrow). D – The best preserved track ml1 with evidence for at least three nail prints on the anterior side deforming the thick displacement rim; rhizoliths intersect the track; vertical ruler is 60 cm. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

(Fig. 8D). It is certain that all four depressions analyzed correspond to true tracks since all the tracks present clear ridges of sediment expulsion (Fig. 8C). The four rounded to oval outlined tracks or track couples are aligned, with three of them at a regular distance of approximately 900–1000 mm (P). The pl1 track is partially superimposed on the ml1. The other tracks may represent couples with pes overprinting manus. The tracks have a regular diameter that varies between 400 and 500 mm in the longer axis, with slightly concave walls and sole impressions. The presence of nail prints and expulsion rims (Fig. 8C and D) allowed to determine the direction of movement landwards (towards SE).

Comments: The Torre de Cope trackway is direct register in quadrupedal locomotion, as a result of the large animal placing both the front and hind feet in the same track, which is the typical gait of a proboscidean. The narrow Sw is characteristic of proboscideans with the limbs tending to swing below the body (Hutchinson et al., 2003). The tracks described herein are broadly similar to *P. panfamilia* as described by McNeil et al. (2007). The tracks of *P. panfamilia* are always wider than long, *P. enigmatica* (Panin and Avram, 1962) are longer than wide, and in *P. australis* the largest dimension can be either the width or the length of the track (Aramayo et al., 2015). *Proboscipeda* indistinct tracks with a larger antero-posterior axis could be interpreted as two tracks that are partially overlapped or adjacent, producing a single relatively long or ovoid shape (Lucas et al., 2007; Neto de Carvalho, 2009, 2011). However, present African loxodonts and Asian elephants both show manus round and pes broadly oval (Stuart and Stuart, 1994). *P. australis* does not show any indication of overlapping tracks and manus and pes can be distinguished. The sole impression surface in *P. panfamilia* is relatively featureless (McNeil et al., 2007), while *P. australis* shows pockmarks (Aramayo et al., 2015). In the case of Torre de Cope, the quality of preservation of the sole impression surfaces do not allow to take solid conclusions. Commonly it shows short 3-to-5-digit imprints in the anterior margin of the sole print, sometimes appearing as slight undulations on the anterior margin (Neto de Carvalho, 2009; Neto de Carvalho et al., 2021), with their long axis tangential to the margin of the track, as in the case of Torre de Cope. However, when made in non-cohesive substrates, or when the quality of preservation is poor, digit impressions may not be reliably registered or preserved (Neto de Carvalho et al., 2016; Helm et al., 2021). Also, at least well-defined toe prints are not expected in older animals since nails are worn out during life (Stuart and Stuart, 1994; McNeil et al., 2007; Pasenko, 2017).

While *P. australis* was attributed to a smaller proboscidean, notably *Notiomastodon ornatus* (Aramayo et al., 2015), and *P. enigmatica* to a deinothere (Panin and Avram, 1962), *P. panfamilia* was originally attributed to mammoths (*Mammuthus primigenius*) by McNeil et al. (2007) and related species (Pillola and Zoboli, 2017; Zoboli and Pillola, 2018). It was later attributed also to *Palaeoloxodon* species (Neto de Carvalho, 2009, 2011; Neto de Carvalho et al., 2016, 2021; Pillola et al., 2020; Altamura and Serangeli, 2023). For southern Iberian Peninsula, all proboscidean tracks found in SW Portugal and SW Spain/Gibraltar were likely attributed to the straight-tusked elephant *Palaeoloxodon antiquus* by the general absence of other possible producers at these latitudes, especially during the Last Interglacial (Neto de Carvalho, 2009, 2011; Neto de Carvalho et al., 2016, 2020a, 2021; Muñiz et al., 2020).

The size of proboscidean tracks correlates well with shoulder height and has been used to study demography of both present (e.g., Western et al., 1983; Lee and Moss, 1995) and Pleistocene (McNeil et al., 2005; Neto de Carvalho et al., 2021) populations. We chose ml1 track as the most reliable to obtain the age of the trackway producer. Forelimb tracks are ideal to calculate hip height in straight-tusked elephants (Larramendi, 2016; Larramendi et al., 2017). For a 370 mm size track, the height obtained from the linear relation of Western et al. (1983) was 2300 mm and the age estimated for the *P. antiquus* producer from the growth curve obtained by the same authors of >30 years old, therefore indicating the presence of a sub-adult or early mature individual. Body mass from shoulder height was calculated using the equation of Larramendi et al. (2017) for Young-Grade I individuals, estimating 2.6 tons for the Torre de Cope *P. antiquus* trackmaker.

5. Discussion

5.1. A new faunal snapshot of the Last Interglacial in Southern Iberia

The Late Pleistocene, MIS 5-related vertebrate ichnosites from coastal Murcia included isolated tracks as well as trackways attributed to *Mustelipeda* aff. *punctata*, *Canipeda* isp., large artiodactyls, *Hippipeda* isp. (Calblanque) and *Proboscipeda panfamilia* (Torre de Cope). By the morphology and size of the tracks, and taking into account the variable preservation conditions in coarse-grained eolianites that prevented a more accurate identification, they were compared respectively to the carnivores stone marten and wolf, as well as to the herbivores red deer, aurochs(?), equids and straight-tusked elephant. These mostly forest-adapted mammal communities, also revealing the proximity of the eastern Betic Mountains to the coast, reflect the expansion of the closed Mediterranean forests in SE Iberia during the Last Interglacial (Sanchez Goñi et al., 1999; Camuera et al., 2019, Fig. 9A). During the Eemian period, southern Spain likely had a mixed forest ecosystem, with a shift from Mediterranean to oceanic vegetation (Carrión et al., 2024a). Specifically, it transitioned from a Mediterranean vegetation to broader Eurosiberian forests, indicating a shift from a Mediterranean climate to a more oceanic one (Sanchez Goñi et al., 2005), and including the higher presence of humid climate species such as *Fraxinus*, *Betula*, *Abies* and even *Carpinus*, nowadays missing from southern Iberia (Camuera et al., 2019). The intensity of rhizoturbation in some of the ichnosites at Calblanque and Torre de Cope, as well as the diameter of the rhizoliths, show the colonization and stabilization of the dunefields by vegetation cover composed mainly by shrubs.

The trackway likely attributed to stone marten is particularly interesting since it is the first time that mustelid tracks are described in the Iberian Peninsula fossil record. Stone martens are found in Calblanque nowadays. They are adaptable and can thrive in a variety of habitats, including woodlands and grasslands, but preferring environments near water and with an abundance of small prey (Virgós and García, 2002). The stone marten is mainly a crepuscular and nocturnal animal, which may have favored the substrate conditions (rain or dew increasing sediment cohesiveness) for the preservation of the trackway in the coastal backdune of Calblanque.

The Iberian grey wolf *Canis lupus* primarily favors areas with rough and wooded landscapes, including forests, mountains, and plains (Iglesias Izquierdo et al., 2017). During the MIS 5 wolf (*Canis lupus*) remains have been identified in coastal Mediterranean settings as in the Cova del Rinoceront (NE Iberian Peninsula) (Daura et al., 2015). The last wolf sights in the region of Murcia were in the 1930s. Nevertheless, wolf tracks are seldom identified in the fossil record of coastal deposits. Rare tracks were identified in the Middle Pleistocene Matalascañas Trampled Surface (MTS), SW Spain (Neto de Carvalho et al., 2020c). The partially preserved trackway described by Neto de Carvalho (2009, 2011) in the Late Pleistocene eolianites from Praia do Malhão ichnosite, SW Portugal, and attributed to wolf cannot be supported by morphological evidence. In Holocene contexts it is hard to distinguish tracks of wolf from domestic dog, especially in sandy substrates where hominin footprints and other remains are preserved in the same layers (Roberts, 2009).

Wolves are known to prey on red deer, and red deer is often the main prey species for wolves in some areas. Artiodactyl tracks possibly

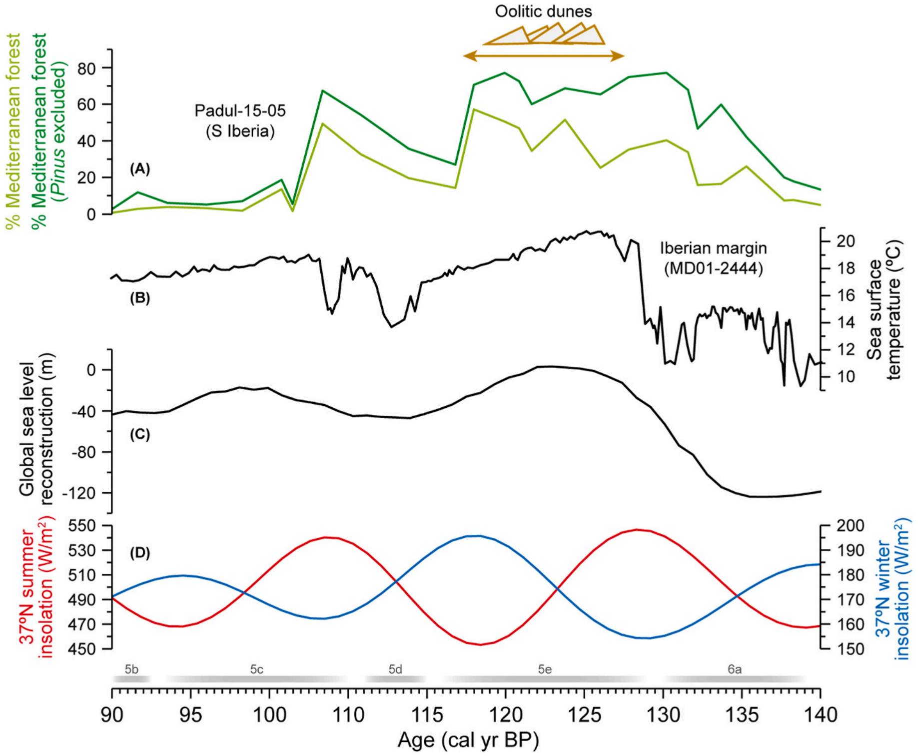

Fig. 9. Age range of oolitic dunes (top) together with other paleoclimate and insolation records between 140 and 90 ka BP. A - Mediterranean forest (%) from Padul-15-05 record (Camuera et al., 2019); B - Sea surface temperature from the MD01-2444 marine record (Iberian Margin) (Martrat et al., 2007); C - Global Sea level reconstruction (Spratt and Lisiecki, 2016) and (D) summer and winter insolation at 37°N (Laskar et al., 2004). The Marine Isotope Stages (from MIS 6a to MIS 5b) are shown at the bottom.

attributed to red deer are relatively common at Calblanque, especially at the ichnosite 3. They are generally considered a woodland species but have adapted to living on exposed moorland and in other open areas. Red deer prefer areas with a mix of woodland and open spaces, including grasslands, meadows, and river valleys. On the Doñana National Park (SW Spain) the red deer is found in all different habitat types, showing a slight preference for the shrub and dunes areas, especially during late autumn to spring (Braza and Álvarez, 1987). Tracks probably attributed to deers are common in Quaternary coastal deposits, including eolianites, worldwide (e.g., Aramayo and Manera de Bianco, 1987; Allen, 1997; Neto de Carvalho et al., 2003; Fanelli et al., 2007; Roberts, 2009; Matsukawa and Shibata, 2015; Aramayo et al., 2015; Burns et al., 2022). Large didactyl tracks attributed to red deers were described in the Middle-to-Late Pleistocene eolianites of SW Portugal (Neto de Carvalho et al., 2003, 2016; Neto de Carvalho, 2009, 2011), SW Spain (Neto de Carvalho et al., 2020c, 2022) and the Middle Pleistocene of Gibraltar (Muñiz et al., 2019). The presence of aurochs by the track record is not certain in Calblanque. Although there are tracks attributed to aurochs in the coastal deposits of Matalascañas and Cape Trafalgar (Neto de Carvalho et al., 2022), SW Spain, during the late Middle to Late Pleistocene and they are commonly recognized in the early-to-middle Holocene coastal deposits from Great Britain (e.g., Roberts, 2009; Burns et al., 2022), no clear individual tracks with bovid morphology were found at Calblanque. Aurochs preferred temperate forests and areas with a mix of open grasslands and forests. They were particularly drawn to wetter environments like river valleys, deltas, and bogs. During the Late Pleistocene epoch, either *Equus ferus* (the wild horse) and *Equus hydruntinus* (the European wild ass) inhabited a wide range of habitats, including steppes, open grasslands, and even areas with temperate forests, though they generally preferred open environments (Boulbes and Van Asperen, 2019; Strani and DeMiguel, 2023). Therefore, Cartagena coastal lowlands and dune fields may have provided favorable habitats for Last Interglacial equids. *Equus ferus* is known from the Middle Palaeolithic site of Cueva Antón, 65 km from the Murcia coast and about 300 a.m.s.l., dated to MIS 5a (Sanz et al., 2019).

The proboscidean tracks from Torre de Cope are the first identified in SE Spain and according to the age attributed to the eolianite where they were found they can be safely attributed to *Palaeoloxodon antiquus* (Neto de Carvalho et al., 2020a). *P. antiquus* had a wide distribution in Europe during the Middle and Late Pleistocene (Larramendi et al., 2020). The earliest occurrence of the straight-tusked elephant in Europe is documented around 850 ka in SE Spain (Lister, 2015). The Middle Pleistocene (ca. 600 ka) Atella site in the northern Basilicata, Italy, includes large tracks found in sections that were attributed to *Palaeoloxodon antiquus* by Fabiano (2000) and Fabiano and Zucchelli (2003), due to their size and the presence of osteological remains of this species. Without details of pad morphology, if other possible producers can be discarded in the area during this period, then these could be the first proboscidean tracks described in the Pleistocene of Europe, and possibly the oldest of *P. antiquus*. Remains of *P. antiquus* in the Mediterranean coast of Spain, mainly skeletal material found in archeological contexts, are known in the Bolomor Cave (MIS 9-5), Valencia, Muscle Cave (MIS 5), Barcelona and Cau del Duc (Middle to Late Pleistocene), Girona (Rosell and Blasco, 2021).

5.2. *Beaches as coastal corridors for elephants in Iberia?*

Elephants have been deeply studied by paleoanthropology because they strong interaction with humans along most part of the Prehistory (Konidaris et al., 2021). This relationship is so relevant that water, elephants and stone has been called the “Paleolithic Holy Trinity” (Finkel and Barkai, 2024).

Evidence of elephant butchery by hominins in Southern Iberia dates back more than 1 Ma (Yravedra et al., 2024). The record of Middle-to-Late Pleistocene *P. antiquus* in Southeastern Spain pertains to the Guadix-Baza Basin (Granada province) by the Solana de Zamborino outcrop (Martín-Penela, 1988) and to the eastern Guadalquivir Basin (Jaén Province) by the Cuadros outcrop (Reolid et al., 2021). If we focus in the MIS 5e, the presence of *P. antiquus* has been described in the coastal Bolomor Cave (Valencia), (~300 km north to the studied site, with one absolute date of ~121 ka) (Blasco et al., 2008; Blasco and Fernández Peris, 2010). Therefore, the Cape Cope track record allows to confirm and extend the biogeography of the straight-tusked elephant to the Mediterranean coasts of SE Spain during the Last Interglacial. However, coastal dunes are not usually expected to be the preferred habitat for elephants. Indeed, current potential distribution (interglacial conditions) indicate that entire Murcia region has very low probability of occurrence for the *P. antiquus* (Gaiser et al., 2025). So, how to explain the presence of P. *antiquus* at Torre de Cope?

During Middle and Late Pleistocene, *P. antiquus* showed a broad ecological adaptation, and has been reported from moderate, humid and warm climates (e.g., Stuart, 1991; Konidaris et al., 2018); this species lived mainly in forested areas, or mixed habitats, where they fed on leaves, branches and soft grass (e.g., Garutt, 1986; Lister, 2004). The straight-tusked elephant is primarily associated with temperate and Mediterranean-type forest and woodland habitats, as opposed to the colder open steppe environments inhabited by contemporary mammoths (Braun and Palombo, 2012), though the species is also known to have inhabited open grasslands, and is thought to have been tolerant of a range of environmental conditions (Fisher, 2018; Roditi et al., 2024). The distribution along Europe during interglacial periods confirm *P. antiquus* broad distribution, with a preference for the Mediterranean region (Gaiser et al., 2025). During warm periods the isotopic signals and microwear patterns point to a prevalent browser/intermediate type diet, relatively rich in herbaceous plants, in quite arid Mediterranean environments (Palombo et al., 2005; Rivals et al., 2012). Moreover, if we focus in the Iberian Peninsula or the Mediterranean region (Italian Peninsula and Levantine region) we can observe that the overwhelming majority of the sites with body or trace fossils attributed to *P. antiquus* are located near (<10 km) to present day coast (Fig. 10).

The Torre de Cope trackway is an isolated example so far identified and may be interpreted better as likely resulting from transit, instead of the trampled grounds produced by a stationary social group (McNeil et al., 2007). Indeed, the existence of proboscidean trampled grounds in Middle-to-Late Pleistocene coastal deposits from Iberian Peninsula has been extensively described. Neto de Carvalho (2009, 2011) and Neto de Carvalho et al. (2016, 2020a) identified a Middle Pleistocene (ca. 200 ka) trampled ground at Praia da Ilha ichnosite (SW Portugal). The base of a well-cemented eolianite unit (Aivados formation) shows a high concentration of poorly-preserved, proboscidean-sized tracks, some of the undertracks reaching 800 mm in diameter but many of them revealing much smaller sizes. In the same bedding plane associated to interdune deposition, parallel trackways attributed to adult elephants moving simultaneously can be found. Paralleled trackways were also observed in the nearby ichnosite of Praia do Malhão, revealing the near simultaneous slow walking of at least three sub-adult *P. antiquus* during MIS 5e (Neto de Carvalho, 2009, 2011; Neto de Carvalho et al., 2016). These occurrences in SW Portugal were interpreted as resulting from trophic migrations of social groups of straight-tusked elephants along the coast, which is bordered by a rough, hilly terrain across over 50 km between main river systems.

A different explanation was provided for the MTS in the Huelva Coast, SW Spain. The elephant tracks found on the MTS are numerous; while most of them are isolated tracks, there are at least eight trackways made by single individuals. Also attributed to the straight-tusked elephant *P. antiquus*, the tracks range in size from 96 to 545 mm (Neto de Carvalho et al., 2021); tracks of newborns, juveniles (2–7 years old) and adolescents (8–15 years old) are predominant, while those of adults (both male and female) are fewer, indicating that the interpreted coastal wetland environment was a major environmental resource for elephant herds, a place where they gave birth to and reared their young (Neto de Carvalho et al., 2021). Another proboscidean trampled ground was

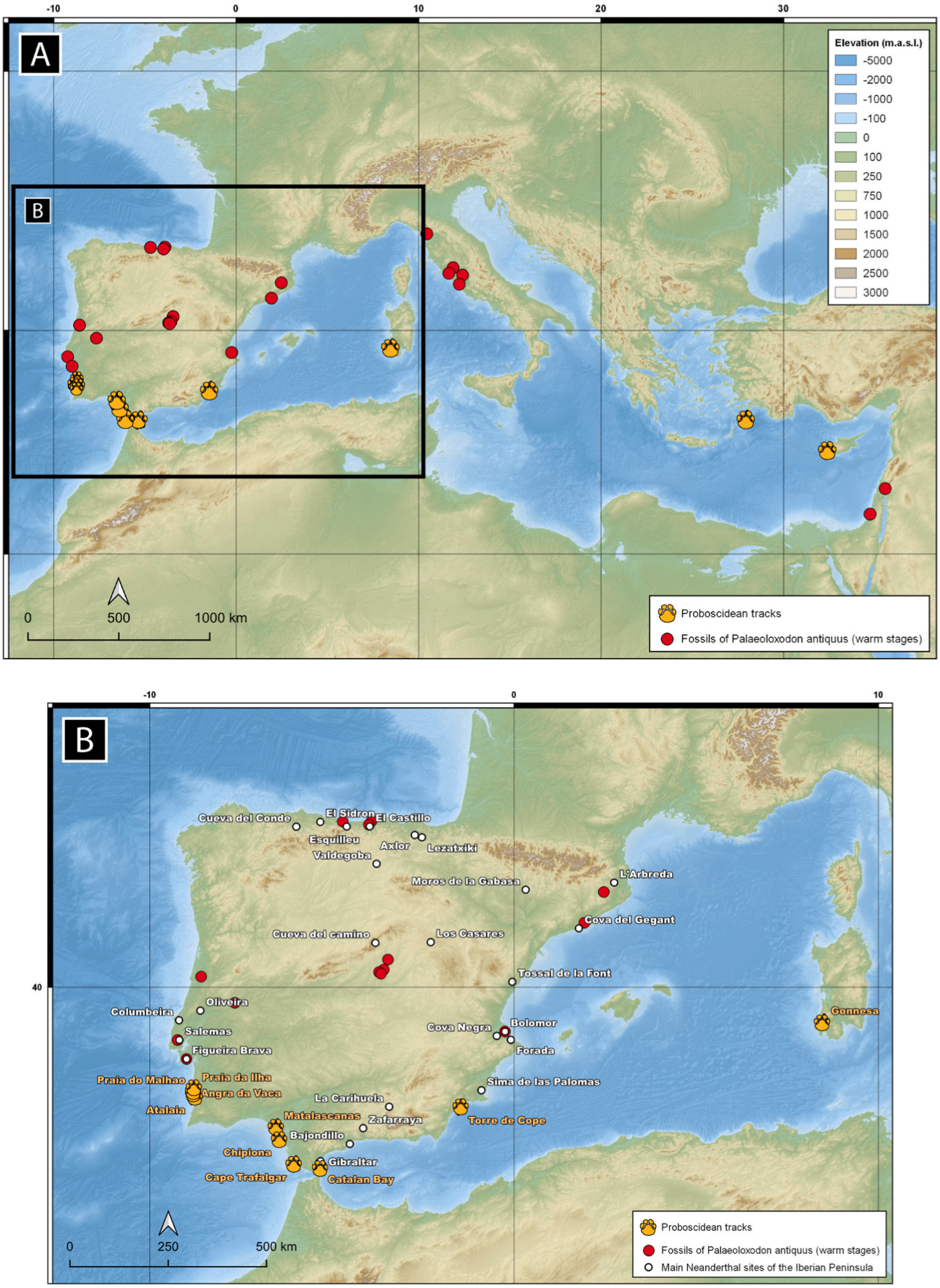

Fig. 10. A – Coastal sites in the Mediterranean with *P. antiquus* body fossils during warm stages (red dots; Gaiser et al., 2025) and proboscidean trace fossils (this study). B - Sites in the Iberian Peninsula with *P. antiquus* body and trace fossils during warm stages (modified from Gaiser et al., 2025; Rosell and Blasco, 2021), and main Neanderthal sites modified from Arsuaga et al. (2012). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

found in SW Spain at Chipiona beach (Cádiz province), but until the present only preliminarily described by Gomez Gutiérrez et al. (2023) due to the special temporary exposure conditions of the tracksite. Isolated large tracks in sections of *P. antiquus* were described in Cape Trafalgar and dated from MIS 5c (Neto de Carvalho et al., 2022: supplementary material). Rare tracks and a body impression attributed to *P. antiquus* were also described in the late Middle Pleistocene Catalan Bay eolianite, Gibraltar (Muñiz et al., 2020).

The distribution (Fig. 10A) and described paleoecological meaning of these occurrences in coastal areas of the Mediterranean indicate that they could acted as megafaunal corridors, as described in this region for humans (Bailey et al., 2008) and in other regions for the same period (Helm et al., 2021). In fact, Helm et al. (2023) identified 35 elephant tracksites dated from MIS 11 to MIS 3, which supports the existence of a migration corridor for *Loxodonta* in the Paleo-Agulhas Plain, as suggested by Marean et al. (2020), which is not obvious from the body fossil record (Helm et al., 2024). Previous studies already indicate that the Iberian Peninsula could be just a corridor instead a cul-de-sac base in the lack of barrier and the use of coastal corridors (O'Regan, 2008). Even during glacial periods, the lying coastal regions of Iberia have provided refugia for thermophilous trees (Carrión et al., 1999, Carrión et al., 2024a, 2024b). Nowadays, African elephants seasonally shift their ranges between different vegetation types, for example, by selecting open woodlands, shrublands, and grassland in the wet season and woody vegetation in the dry season (Loarie et al., 2009; Helm et al., 2023). In the Mediterranean climate realm large mammals are concentrated in places rich in water, such as river mouths and coastal lagoons (e.g., Doñana National Park). Elephants are obligate drinkers, consuming up to ~200 l daily (Wall et al., 2013), and possess a spatial memory that allow them, along same paths ~50 km long, reach nearest water holes (Wato et al., 2018). They are great wanderers and beaches may have provided easy corridors for the straight-tusked elephant, similarly to what was described in other regions and coeval period for *L. africana* under Mediterranean climate conditions as South Africa (Helm et al., 2021, 2023).

Proposed Iberian faunal coastal corridors also could explain the preferential distribution of Neanderthal major sites along the coast in the Atlantic and Mediterranean regions (Finlayson, 2008; Jennings et al., 2011; Arsuaga et al., 2012, Fig. 10B). Despite marine and shellfish resources by Neanderthal in Southern Iberia started ~150 ka (Cortés-Sánchez et al., 2011; Brown et al., 2011), the only Neanderthal shell midden (mainly consisting of mollusc shells) described to date also contain high amount of mammals and even *P. antiquus* fragments (Zilhão et al., 2020). These Neanderthal coastal sites were hunting grounds for large mammals such as red deer, horses, aurochs and wild goat, as well as territories for elephant procurement (Blasco et al., 2008; Cortés et al., 2011; Blasco and Fernandéz Pélis, 2021; Neto de Carvalho et al., 2025). The relevance of this coastal mammal migration routes remains relevant in Europe even during the Mesolithic when large stonewalls was constructed to manipulate the movement and hunting migrational herds (Geersen et al., 2024).

5.3. A global comparison between proboscidean track records in paleodune systems

In similar coastal eolian contexts, Pillola and Zoboli (2017) described isolated *Proboscipeda panfamilia* manus-pes couples from the Middle-Late Pleistocene eolianites of Gonnesa (SW Sardinia). Furthermore, proboscidean tracks are clearly visible in transverse sections in the field. The track size and the occurrence of body fossils in the same deposits indicate that the trackmaker in this case was likely the Sardinian dwarf mammoth *Mammuthus lamarmorai*. The purported latest record of proboscidean activity known in Europe on the basis of tracks was found in the SW coast of the island of Rhodes (Greece) by Milàn et al. (2007). The Kattavia eolianite recorded poorly-preserved tracks from Late Pleistocene-to-Early Holocene age. The age of the oolite eolianite is considered speculative due to the lack of geochronological constraints. The largest undertracks were attributed by these authors to the insular dwarfed species *Palaeoloxodon tiliensis*. Another dwarf elephant, *Elephas cypriotes* was considered the possible trackmaker of the poorly preserved tracks found in undated eolianites cropping out in the coast of western Cyprus (Milàn et al., 2015). The paleoecological meaning of these occurrences in coastal areas of the Mediterranean islands was not discussed.

Phreatomagmatic eruptions of Mt. Songak in Jeju Island (South Korea) produced pyroclastic surge deposits known as the Songaksan Tuff. In Songaksan Tuff and Hamori Formation, Kim et al. (2009) presented an account of the track-bearing strata, including 505 hominin, >1000 artiodactyl (deer), 8 proboscidean, 5 carnivore, 85 bird (of 8 different types), and 2 fish tracks and trackways. No ichnotaxonomical or paleoecological studies were made. Two of the track-bearing levels contain eight large circular or irregularly shaped tracks that were attributed to woolly mammoths (*Mammuthus primigenius*). The presence of these elephant tracks would be indicative of a Pleistocene age, at least for these stratigraphic levels. However, the dating of the track-bearing horizons is still a matter of dispute.

Many proboscidean tracksites were described in Plio-Pleistocene formations from Japan. Matsukawa and Shibata (2015) provide a good account of the distribution of ichnosites, including some associated to coastal lowland environments, namely in the Kwanto Plain (west Tokyo). The proboscidean tracks were assigned to cf. *Proboscipeda* and produced most likely by *S. protoaurorae* in the Early Pleistocene Terada Formation, and *S. aurorae* and *Palaeoloxodon neumanni* in the upper formations, due to the stratigraphic range of the three species. Once again, no paleoecological conclusions from the presence of these proboscidean tracks and trackways were taken.

Proboscipeda australis was first described from two trackways by Aramayo and Manera de Bianco (1987) in the Late Pleistocene coastal deposits of Pehuen Co, Argentina. They were attributed to the small *Notiomastodon* by Aramayo et al. (2015). These authors interpreted Pehuen Co as a congregation site around ephemeral lakes and ponds.

In the very extensive Pleistocene coastal deposits from South African, elephant tracks have been documented (Roberts et al., 2008; Helm et al., 2021, 2023). For example, in Still Bay, on the west-southern coast, Roberts et al.'s (2008) main focus was on tracks of the Cape's elephant (*Loxodonta africana africana*). A date range of 140 ± 8 ka – 91 ± 5 ka (mostly 5e to 5b) was established for this track record through optically stimulated luminescence and amino acid racemization. The explanation provided for the presence of elephant trampled grounds in the dune deposits was the closer proximity of woodland during MIS 5 in the area, or a nearby source of water which may have been provided by an interdune wetland, similar to what was described for the MTS in SW Spain (Neto de Carvalho et al., 2021).

From the above examples, we can conclude that elephant and mammoth tracks can be commonly found in coastal eolian-related paleoenvironments worldwide, associated or not to wetlands expected to congregate these and other animals. The reasons for this can be either ecological, ethological and taphonomic (Altamura and Serangeli, 2023). On the one hand, *P. antiquus* tracks may likely indicate the proximity of woodland resulting from higher rainfall regime during interglacial stages and sub-stages, as other mammal tracks found in Calblanque suggest for coetaneous similar depositional conditions. Besides, proboscideans explore vast territories looking for food and water, and these resources vary seasonally either in quantity and quality; besides, coastal areas with favorable conditions may be used on occasions for activities as diverse as migration corridors or reproductive habitats. On the other hand, high-rate sedimentary environments positioned between seasonally dry and submerged areas, or cyclically moistened by dew or rain, favor substrate cohesiveness and therefore track formation and preservation, especially very large prints produced by heavy and highly mobile animals.

6. Conclusions

This study introduces the first Quaternary vertebrate tracksites found in the SE Iberian Peninsula, specifically in the Murcia region. New tracksites were identified at Torre de Cope and three ichnosites at Calblanque Regional Nature Park. These sites provide evidence of large and small mammals living along the littoral sandy coasts between Cape Cope and Cape Palos during the Last Interglacial (MIS 5) period. The identified tracks include those possibly attributed to mustelids (*Mustelipeda* aff. *punctata*), canids (*Canipeda* isp.), large artiodactyls (hoofed mammals including red deer and possibly aurochs), equids (*Hippipeda* isp.), and proboscideans (*Proboscipeda panfamilia*, attributed to the straight-tusked elephant *Palaeoloxodon antiquus*). This diversity reflects a mixed forest ecosystem with both carnivores and herbivores, suggesting the proximity of forested areas in the eastern Betic mountains to the coast. The ichnological evidence reflects the expansion of closed evergreen forests and a shift from Mediterranean to broader Eurosiberian forest types in SE Iberia during the Last Interglacial.

The trackway *Mustelipeda* aff. *punctata* represents the first fossil mustelid-like tracks described in the Iberian Peninsula. The morphology and gait patterns closely match those of the extant stone marten, indicating habitat continuity and adaptation to coastal backdune environments. Tracks attributable possibly to wolves and red deer may indicate the presence of these species in coastal habitats of SE Iberia during MIS 5. The wolf-like track is notable due to rarity in the fossil record and suggests a wooded and rough landscape habitat in the proximities, while red deer-like tracks are common and consistent with woodland and dune environments still found nowadays in southern Spain. The very large tracks attributed to *P. antiquus* may extend the known biogeographic range of this species to the Iberian Mediterranean coast during the Last Interglacial. Although coastal dunes are not typically preferred elephant habitats, the presence of these tracks may indicate transient use of coastal corridors or access to resources such as water or food in the nearby forests. This is in agreement with ecological flexibility and seasonal habitat shifts known for proboscideans.

The study situates the Murcia tracksites within a broader context of Pleistocene vertebrate ichnology in the Iberian Peninsula and worldwide, noting similarities with tracksites in SW Portugal, SW Spain, Gibraltar, and Mediterranean islands, as well as global occurrences from South Africa, Japan, Argentina and South Korea. These comparisons underline the common use of coastal dune environments by large mammals, including proboscideans, during Middle-to-Late Pleistocene interglacial and glacial stages. Comparison between main Neanderthal sites in the Iberian Peninsula and straight-tusked elephants body and trace fossil evidences compilation allow us to propose a link between Neanderthals and coastal mammal migration routes.

Author's contributions

Conceptualization: CNC, FJE; Methodology: CNC, FJE, NM, JB, JC; Validation: CNC, FJE, FM, JC, MCS; Formal analysis: CNC,FJE, NM, JB, JC; Investigation: CNC, FJE, NM, FM, JB, JC, JGM, LMC; Resources: CNC, FJE, NM, JB, JC, LMC; Data Curation: CNC, FJE, NM, JB, JC; Writing - Original Draft: CNC, FJE, NM, FM, JB, JC; Writing - Review & Editing: CNC, FJE, NM, FM, JB, JGM, JC, MSC, LMC; Visualization: CNC, FJE, NM, JB, JC; Supervision: CNC, FJE, NM, FM, JB, MSC, LMC; Project administration: CNC, FJE; Funding acquisition: FJE, LMC. All authors have approved the final version of the manuscript.

Declaration of generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used Grammarly and ChatGPT in order to refine grammar and style. After using these tools, the authors reviewed and edited the content as needed and take full responsibility for the content of the publication.

Declaration of competing interest

The authors declare that they have no conflict of interest.

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Data availability

All data and/or code is contained within the submission.

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