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Vertebrate tracksites from the Mid–Late Pleistocene eolianites of Portugal: the first record of elephant tracks in Europe

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This study describes the palaeoichnology of the Malhão Dune Field (Pleistocene), the first report of vertebrate tracksites from all the Cenozoic from Portugal. At least 14 stratigraphic horizons with mammal and bird footprints and trackways occur, including those of elephants. Concave epirelief footprints produced by elephants show four feet with four toes imprints on each foot and heteropody in a narrow gauge. The presence of three possibly parallel trackways points to gregarious behavior of sub-adults/females of *Elephas antiquus*. The ichnospecies *Proboscipeda panfamilia*, found in the Malhão and Pessegueiro sectors, represents possibly the first Pleistocene elephant trackways, and record one of the latest occurrences of *E. antiquus* in Europe. The new ichnogenus and ichnospecies *Leporidichnites malhaoi* igen. et isp. nov., interpreted as lagomorph tracks, are also described.

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INTRODUCTION

The preservational potential of Pleistocene eolian carbonate sandstones for tracks and burrows is rather low (e.g., Scrivner and Bottjer, 1986) because of: their young geological age; the general homogenous character of the sediments; the changing sedimentary-erosional dynamics of dunes; high rates of pedogenesis and lithification; and limited sizes of outcrops scattered along the shore. Nevertheless, the increasing interest in these low-stand systems in recent years allowed the discovery of several sites with vertebrate (mostly mammal) trace fossils in the Atlantic and Mediterranean coasts (e.g., Flor, 1989; Fornós *et al*., 2002; Fanelli *et al*., 2007; Roberts *et al.*, 2008), which contributed to understanding the ecology and behavior of these extinct terrestrial communities. Pleistocene carbonate eolianites occur in Portugal parallel to its N–S trending coastline, and crop out as a narrow belt of cliff-front (echodunes and sand ramps) and fossilized dune fields cut by Holocene river incision and neotectonic movements. These eolianites also extend beyond Portugal, for more than 1000 km and largely between latitudes 41°54'N and 37°7'N, occurring in: the Madeira Autonomic Region (off the Morocco coast): in the main island at S. Lourenço cape; in Porto Santo Island; and in the small Selvagens archipelago, halfway between Madeira and Canary islands (Fig. 1). The most extensive and continuous outcrops occur between south of Ericeira and western Cascais (33 km), near Lisbon, and south of Sines to the Armação de Pera Beach (165 km). The majority of the latter area constitutes a part of the SW Alentejano e Costa Vicentina Natural Park. Most of the studies developed in these fossil dune formations regarded geomorphology and stratigraphy, or the palaeontology (taxonomy) of land snails and birds (e.g., Ramos Pereira, 1990; Goodfriend *et al*., 1996; Ramos Pereira and Angelucci, 2004). Fossils are usually scarce, consisting mostly of rhizoliths, dune snails, rare marine mollusk associations, and bird remains, as well as macroscopic plant remains and pollen in rare turf deposits (Diniz, 1986; Goodfriend *et al*., 1996). Since 2002, a systematic palaeoichnological survey of Pleistocene eolianite carbonates in Portugal has been developed, leading to the identification of at least 14 stratigraphic horizons with mammal and bird footprints and trackways, reported preliminarily by Neto de Carvalho *et al.* (2003). All finds come from the Malhão Dune Field, in SW Alentejo, the largest eolianite outcrop in Portugal. In this paper, the ichnological content of the Malhão Dune Field is assessed, as well as the behavioral traits of trackways and footprints made by *Elephas antiquus*, *Cervus elaphus*, hare, fox, and possibly wolf, as well as avian tracks produced

Fig. 1. Location of carbonate eolianites in Portugal (green) and tracksites studied (red dots)

A — trackways from the Mid Pleistocene Malhão section (from north to south, Malhão Beach and Angra da Vaca sections); **B** — distribution of trackways found in the Late Pleistocene Pessegueiro Islet section (Aivados eolianite); images from Google Earth and Google Maps

by storks or cranes. The presence of smaller-mammal trackways is quite unusual for an eolianite environment. The find of Pleistocene elephant trackways is probably the first in Europe; these elephants would represent one of latest *E. antiquus* that may have crossed Malhão Dune Field, less than 40 000 years ago.

GEOLOGICAL SETTING OF THE MALHÃO DUNE FIELD

The Malhão Dune Field on the SW Alentejo coast crops out between S. Torpes and Pedra de D. Rodrigo, within an onshore area of 28 km^2 that is 3 km wide (Ramos Pereira, 1990). The structure of Pessegueiro and other islets shows that the dune field extended far beyond the present coastline. It is composed mainly of variably cemented (by pedogenic processes) carbonate bioclastic sandstone. Two depositional-pedogenetic cycles developed during the Mid and Late Pleistocene, i.e., between Marine Isotope Stages MIS6? and MIS3-2? (Ramos Pereira and Angelucci, 2004; Fig. 2). A marine regression formed the oldest Malhão eolianites, producing an erosive unconformity covered by the younger Aivados eolianite. A few remnants of these marine sediments (Monte Figueira Formation) contain a rocky shore shells, consisting of *Patella vulgata*, *Littorina littorea*, and *Mytilus edulis* (Ramos Pereira, 1990) together with *Monodonta striata*, *Stramonita haemastoma*, *Gibbula* sp., balanomorphs, serpulids and ostreids. Such a fauna is characteristic of a high energy, nearshore/foreshore environment. An unconsolidated and active Holocene dune field overlaps and is "fed" by both eolianite successions.

The Malhão section (Fig. 1A), representing the oldest eolianite, is composed of three medium to coarse-grained, moderately sorted, bioclastic sandstone units, as much as 20 m thick (Fig. 3A). This sequence lies unconformably on the Xistos de S. Luis Formation, dated to the Late Devonian (Carvalho, 1976). The lowermost unit, as much as 12 m thick, is formed by bedsets 2 m thick with large-scale trough cross-laminae dipping at more than 30°. The next unit, as much as 10 m thick, shows large-scale planar cross-lamination on a metre-scale; clusters of dense vertical rhizoliths are also in these beds (Fig. 3B). This unit was formed by dune foreset progradation. The uppermost unit, showing a different foreset orientations in comparison to previous ones, is much thinner (<3 m) and bedsets are less visible due to dense vertical rhizoturbation. Pedogenic processes led to dissolution of abundant shelly calciclasts and to diagenetic carbonate cementation. Measurements of eolian cross-bedding show dominant wind directions from the N and the WSW. Trackways and footprints are found mainly in two sections of the Malhão section: Malhão Beach and Angra da Vaca, and mostly in the lowermost unit.

The Aivados eolianite is well developed in the Pessegueiro Islet section (Fig. 1B), where it forms up to 18 m thick sandstone bodies (Fig. 3C). This islet, located 250 m away from the coast, is 340 m long and 235 m wide. This succession can be followed also at the Forte da Ilha de Dentro cliff, which is as much as 10 m thick, where it discordantly covers the Vermelha Formation. The eolianite is strongly fractured and composed of three calcarenite units exposed in the cliff WNW from the small fort. The units are separated by reactivation surfaces. The lowermost unit is built of a medium to coarse-grained sandstone with planar cross-stratification, over 4 m thick. Foresets 1–1.2 m thick show dips of up to 34°. Individual laminae are less than 2 cm thick and may show asymmetrical wind ripples, showing long and parallel crests of low amplitude. Rhizoturbation is intense but irregularly distributed, having formed protosols. The size, orientation, and ichnofabric distribution of rhizoliths allowed for the interpretation of herbaceous bushes vegetation with occasional trees that covered dunes parallel to slipfaces (Neto de Carvalho *et al.*, 2003). The second unit is as much as 11 m thick, with a planar erosional bottom, and shows a similar grain size to the previous

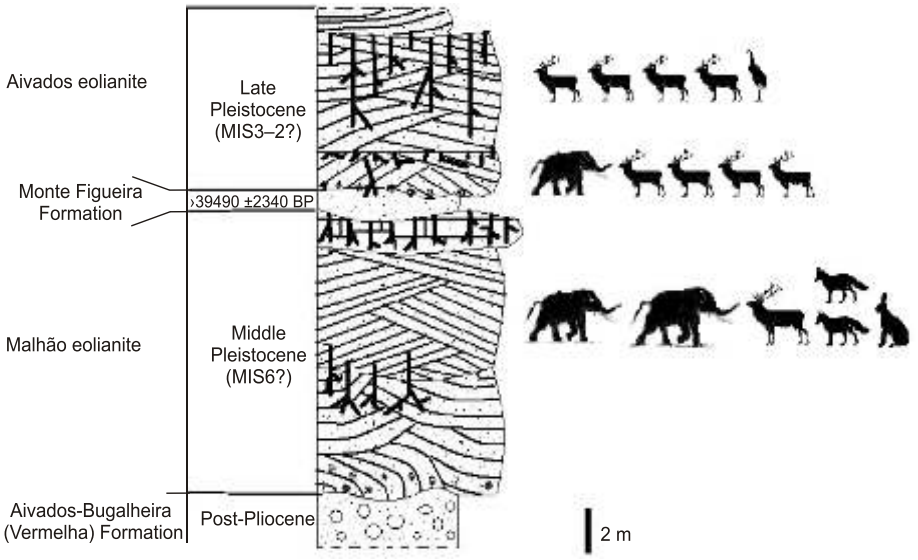

Fig. 2. Stratigraphy of the Malhão Dune Field with location of vertebrate tracks

Data compiled from Malhão Beach and Pessegueiro Islet sections; formations from Ramos Pereira (1990); Marine Isotope Stages from Ramos Pereira and Angelucci (2004)

one. Cross-stratification dips at less than 20° and wind ripples are more common. The lateral persistence of low-angle cross-stratification reflects deposition on broad and stable interdune areas (Roberts *et al*., 2008). Rhizoturbation is denser and mainly composed of deep vertical structures, indicating that bush-size plants covered the dunes (Neto de Carvalho *et al.*, 2003). The last unit is over 1.5 m thick and built of gently dipping, trough cross bedding. Rhizoturbation is sparse and characterized by small horizontal structures, indicating that the floral coverage changed to herbal vegetation over mobile dunes. The dune-forming winds blew mainly from the NW and the SW, producing parallel dune belts and parabolic dunes (Fig. 3D), oriented WSW–ENE and SW–NE (Ramos Pereira, 1990). The dunes are also well exposed between Sitava Campsite and Malhão Beach. Vertebrate tracks are commonly found in the two lower units. The age of the Aivados eolianite is younger than the 39 490 ±2 340 BP^{14}C years datum found by Schröeder-Lanz (1971) in a tuff deposit below the eolianite at S. Torpes.

PALAEOICHNOLOGICAL ANALYSIS OF THE TRACKSITES

Almost all of the 14 stratigraphic horizons with mammal and bird footprints and trackways were found in the bottom of 15–20 m high sea cliffs, within a scree of fallen calcarenite blocks. Exceptions are large, elephant-made, downward bulges and deep bifid footprints overlying a protosol at Forte da Ilha de Dentro, which was differentially eroded, as well as a deer footprint on a sand lamina exposed by wave erosion. The homogenous succession of eolianite, cemented by pedogenic processes, makes tracks almost impossible to find on the bedding planes. Only in sections less homogenized by secondary carbonate cement can one can see tracks preserved as epirelief and hyporelief on fallen blocks broken along laminae. Usually dune sands, moistened by rain or dew, have cohesiveness sufficient for preserving anatomical details of footprints, even of the smaller footprints (Roberts *et al*., 2008). Windblown sand can fill footprints by processes of grainflow and sand collapse. Fast burial and rapid calcification by groundwaters and root physiological activities allowed preservation of the tracks.

There is no conventional order in presenting vertebrate fossil tracks. For our purposes, we describe mammal ichnotaxa from the largest to the smallest producers. The bird trampling tracksite is described at the end.

SYSTEMATIC ICHNOLOGY

Ichnogenus *Proboscipeda*
Proboscipeda panfamilia Mc Neil, Hills, Tolman and Kooyman (2007)
(Fig. 4A, B, H)

D e s c r i p t i o n. — A remarkable proboscidean tracksite composed of 14 almost circular and overstepping footprints organized at 3 narrow-gauge trackways occur in a bedset with oblique thick laminations dipping 30° at Malhão Beach section (Fig. 4A). These tracks occur as large bulges in convex hyporelief preservation, frequently bordered by displacement rims and microfaults. Footprints are 38–55 cm long. The deepest part of the footprint is deviated to the front part and opposite of dip, which are accompanied by dragging-foot marks, indicating the animal's direction of locomotion. Measured stride lengths vary from 1.5–2.4 m. Concave epirelief footprints show 4-digit imprints and heteropody, where the smaller hindprints (pes impressions) oversteps the larger foreprints (manus impressions) (Fig. 4B). Two other elephantine track horizons were found in the Angra da Vaca section and from the Late Pleistocene of the Forte da Ilha de Dentro section (Fig. 4H).

Fig. 3. Stratigraphic features and tracksites

A — Malhão section, scale bar = 10 m; **B** — cluster of large vertical rhizoliths penetrating the underlying unit, scale bar = 2 m; **C** — Pessegueiro section, scale bar = 10 m; **D** — eroded parabolic dune at Pessegueiro section, scale bar = 3 m; **E** — trampled horizon with cloven-hoof and tridactyl bird footprints (Pessegueiro section), scale bar = 50 cm; **F** — detail of the trampled horizon, scale bar = 20 cm; **G** — large exposure with several fox tracks (Angra da Vaca section), scale bar = 50 cm; **H** — track of half footprints left possibly by wolf (Malhão Beach section), scale bar = 50 cm; 1, 2, 3 — numbers in A and C indicate units described in the text

R e m a r k s. — Panin and Avram (1962) proposed a new ichnogenus *Proboscipeda* for proboscidean tracks from the Miocene of Romania. Lucas *et al.* (2007) described mammoth trackways and trampled grounds from the Late Pleistocene of Tularosa Basin, New Mexico. These researchers also revised the few reported occurrences of *Proboscipeda*, including the new ichnospecies *P. panfamilia* erected by McNeil *et al.* (2007) for the the St. Mary Reservoir mammoth tracks (Alberta, Canada). Pleistocene elephant tracks from the Malhão Dune Field match the diagnosis of this ichnospecies. *Elephas (P.) antiquus* body fossil remains have been reported from near Malhão (*vide* Antunes and Cardoso, 1992), and in the Middle? Pleistocene from Santa Cruz (Santiago do Cacém). Some of the latest *E. antiquus* in Europe 33 600 ±500 BP old were found in the Central Portugal Tejo River Basin and only one report of *Mammuthus primigenius* dated at 14 170 ±330 BP may indicate its later presence at this latitude (Cardoso, 1996). The three parallel trackways indicate the same direction of movement, with two footprint sizes and calculated shoulder heights of 1.5 and 2.4 m. We propose that these footprints are evidence of gregarious behavior of three sub-adults/females of the straight-tusked elephant, slowly climbing a 20 m high dune belt at speeds of >1.7 to <3 km/h. Walking at slow speeds would be expected in soft sand dunes; toe-impressions and drag marks indicate walking up a gentle slope. Proboscidean tracksites are rare and only a few have been described from North America, Argentina, Africa, the Balkans, Abu Dhabi and Japan (Lucas *et al.*, 2007). To the present author's knowledge, this find may be the first record of Pleistocene elephant trackways in Europe, and the only one known that is possibly related with *E. antiquus.*

Ichnogenus *Bifidipes* Dematheiu, Ginsburg, Guérin and Truc (1984)
Bifidipes isp.
(Figs. 3E, F and 4C, D, F)

Bifidipes aeolis Fornós, Bromley, Clemmensen and Rodríguez-Perea, 2002; Neto de Carvalho *et al.* (2003), figs. 1–2.

D e s c r i p t i o n. — Isolated or small sets of 2–6 didactyl symmetrical cloven-hoofed prints (Fig. 4C), usually preserved as concave epirelief and rarely as convex hyporelief (Fig. 4F). Individual prints are rounded to elliptical, deeply imprinted (>5 cm deep; Fig. 4F) or as shallow undertracks, and partially bordered by displacement rims with radial large cracks (*sensu* Fornós *et al.*, 2002). Locally, faint circular pits of dew claws can be seen (Fig. 4D). No size differences between foreprints (manus impressions) and hindprints (pes impressions) were identified, but footprint sizes can vary from 5–15 cm, depending also on substrate conditions. Pace length varies from 0–82 cm and external track width may vary from 19–44 cm; stride length may reach 139 cm (Neto de Carvalho *et al.*, 2003 for track measurements).

R e m a r k s. — In the Pessegueiro Islet and Forte da Ilha de Dentro sections (Late Pleistocene), 9 stratigraphic horizons with big cloven-hoofed prints and small trackways assigned to *Bifidipes* isp. were found. Only one isolated footprint was found in the Middle Pleistocene at the Malhão section. Previously, Neto de Carvalho *et al.* (2003) attributed the Late Pleistocene forms to the ichnospecies *Bifidipes aeolis.* According to the diagnosis of Fornós *et al.* (2002), *Bifidipes aeolis* is the same as the type ichnospecies *B. velox* (Demathieu *et al.*, 1984) but is associated with disturbances of eolian sediments, including microfolding and microfaulting. These deformation features vary with substrate cohesiveness, grain size, and water content, furthermore, they depend on whether these are "true" footprints or undertracks. Moreover, *B. aeolis* is attributed to the behavior of *Myotragus balearicus.* Considering this very different artiodactyl producer, interpreted for *Bifidipes* from the Malhão Dune Field, and the longevity of this ichnogenus since Oligocene, it is reasonable to leave *Bifidipes* in open nomenclature until more detailed taxonomic revisions are made.

The small trackways show different pace lengths and angulations, but footprint morphology is congruent with a single producer species. The morphology and size of these didactyl footprints, the anterior opening of the digits produced by locomotion on soft sediment, the internal width, the glenoacetabular size inferred by stride (Neto de Carvalho *et al.*, 2003) and palaeoenvironmental setting are compatible with large-sized cervids, especially red-deer juveniles, females and large males. In the Pleistocene of Portugal, large cervids known from body fossils are *Cervus elaphus* and *Dama dama* (Cardoso, 1996). Nevertheless, *Dama dama* adult footprints are usually smaller, narrow and straight, with almost parallel digit in their most forward portion (MacDonald and Barrett, 1993). *Cervus elaphus* footprints are broader, with cloven hoofprints as symmetrical arcs opening forwards (Fig. 4F), and are thus closer to *Bifidipes* isp. from the Ilha do Pessegueiro and Forte da Ilha de Dentro sections. Measured gaits vary from sub-stacionary to trotting and galloping, with increasing stride length and decreasing trackway width.

Ichnogenus *Canipeda* Vialov, 1983
Canipeda isp.
(Fig. 3G, H)

D e s c r i p t i o n. — Faint digitigrade quadruped tracks composed of symmetrical footprints with four well-developed toe pads and a large central pad. Two stratigraphic horizons found in the Malhão sector show tracks with the same gait pattern but different sizes. Type 1 occurs as at least three trackways cross-cutting in a vertical block surface of 6 m^2, which was difficult to measure (Fig. 3G). Concave epirelief footprints are rounded and 5 cm long. Mean stride length is 20 cm and pace width is <10 cm. The central pad is quite large. Type 2 is a single track of 11 large half-footprints, 8 cm long, preserved as concave epirelief (Fig. 3H). Mean stride length is 68 cm and pace width is 6–12 cm.

R e m a r k s. — In soft grounds, such as loose sand, canids place their hind feet exactly in the forefoot print while trotting, and usually keep their body the straight in the direction of movement. Judging by the mean size of the footprints and stride length, type 1 tracks were probably made by one adult fox; type 2 was produced by a larger canid, perhaps a sub-adult wolf that trotted parallel to the slipface of the dune, leaving a track of half-prints.

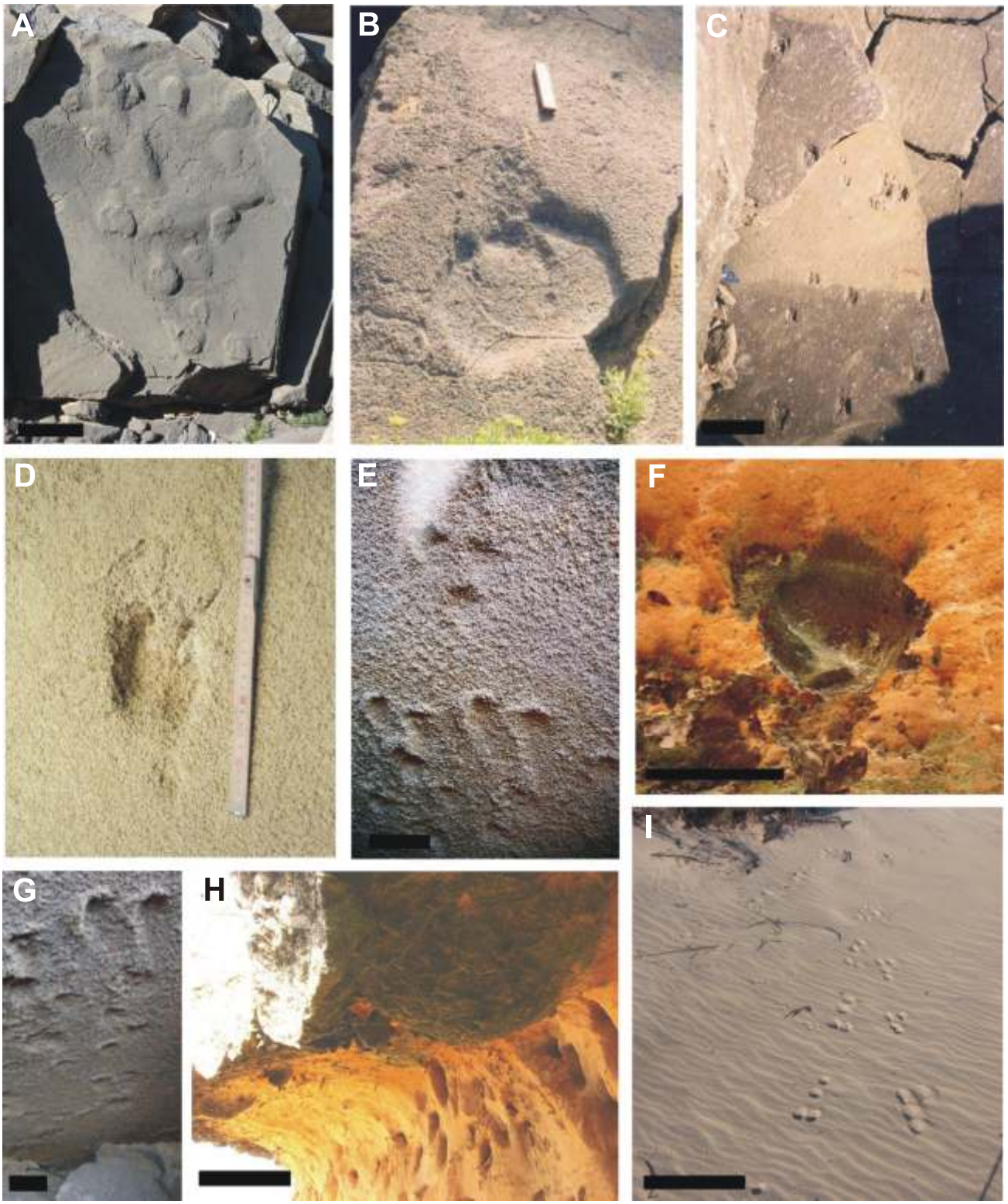

Fig. 4. Trackways and footprints produced by large and smaller mammals

A — main stratigraphic horizon with *Proboscipeda panfamilia* (Malhão Beach section), scale bar = 1 m; **B** — compound print records fore- and hindlimb overstepping and showing anteriorly-directed toe impressions (same stratigraphic level as the previous), scale = 20 cm; **C** — *Bifidipes* isp. — the same tracks occur in two different stratigraphic levels separated by 7 cm: upper level shows enlarged footprints on wind ripples, partially filled by grainflow and grainfall sand. Bifid shape typical of *Bifidipes* — true size more discernible on the lower, more cohesive level (Pessegueiro section), scale bar = 30 cm; **D** — footprint with the faint pit of right dew claw print (Pessegueiro section); **E**–**G** — the curious 5-print set, with 3 fore prints, very common in the parallel tracks of the Malhão section, scale bar = 10 cm; F — deep V-shape forward opening of cloven hoof imprints (Forte da Ilha de Dentro section), scale bar = 10 cm; G — *Leporidichnites malhaoi* tracks on the top of the overturned block (for the bottom track record see Figure 4A), scale bar = 10 cm; **H** — undertrack with large bulges and deer footprints differentially preserved under root influence (Late Pleistocene from Forte da Ilha de Dentro section), scale bar = 20 cm; **I** — hare tracks common in the present active dune field of Malhão showing the typical leaping pattern, scale bar = 50 cm

Ichnogenus *Leporidichnites* igen. nov.

D e r i v a t i o n o m i n i s. — *Leporidichnites* is a compound word coming from the Greek and means fossilized track, trace or footstep of a hare-form, recalling Leporid (hares and rabbits) long-limb footprints and the characteristic bounding gait.

Type ichnospecies: *Leporidichnites malhaoi* isp. nov.

D i a g n o s i s. — Sets of four separate footprints: two short forelimb prints (manus impressions) rounded and aligned one behind the other; two longer and narrow hindlimb prints (pes impressions) with a distinctively pointed shape, side by side (fully in phase). Footprints distributed in a leaping pattern, half-bounding gait.

R e m a r k s. — Although very common in present dune fields (Fig. 4I) and other (including technogenic) substrates, the leporid fossil tracks record is very poorly represented and ambiguously defined in existing literature. The small size of the footprints results in little information in sandy substrates. However, strong heteropody and the characteristic half-bounding gait (hindlimbs moving fully in phase) allow for assigning the trackway to *Leporidichnites*. In soft ground, hare and rabbit tracks can be recognized by very regular gait patterns typical of jumping or galloping animals. Rabbit tracks can be differentiated from hare by the smaller size of the footprint and much smaller stride lengths.

Leporidichnites malhaoi isp. nov.
(Fig. 4E, G)

D e r i v a t i o n o m i n i s. — *malhaoi* after Malhão type locality and horizon (see below).

H o l o t y p e. — In the field (in Natural Park), but the cast CCR 424CNC is stored in the Geological collections of Centro Cultural Raiano, Idanha-a-Nova in Portugal.

D i a g n o s i s. — The same as for the ichnogenus.

M a t e r i a l. — One huge, overturned block of eolianite sandstone with *Leporidichnites malhaoi* tracks, reached by waves during the high tide, which makes the access difficult. So far, this is the only known occurrence of this trace fossil. The track-bearing block is protected within a natural park and the cast has been taken and secured in the Geological Collections of the Centro Cultural Raiano (holotype CCR 424CNC).

D e s c r i p t i o n. — A series of 4–5 footprints in at least two parallel tracks, preserved in concave epirelief (Fig. 4G) 3 m above the main *Proboscipeda* track level, in the Malhão section; 2–3 sets of footprints are reported for both tracks. Foreprints are rounded with 4 cm defining the vertices of an equilateral triangle. Hindprints are 12 cm long and 5 cm wide, sub-parallel and juxtaposed. Toe imprints are not visible. Expulsion rims attest for the direction of locomotion. Pace length is 24–34 cm and mean stride length is 45 cm. External trackway width is 12.5 cm.

R e m a r k s. — The leaping gait and large, similar sizes is characteristic of both parallel tracks that may have been produced by a single hare. Remarkably, the presence of three forelimbs prints can be noticed in almost all sets (Fig. 4E). Behavioral explanation of this feature remains unclear. Maybe the animal was limping from the right forelimb, because the typical front-back aligned forelimb prints are impressed deeper than the lateral “exotic” print, located at a distance of a half manus pace length between them.

T y p e l o c a l i t y. — Malhão Beach section, Vila Nova de Milfontes, Portugal. The area is protected as a natural park.

T y p e h o r i z o n. — Malhão eolianite, Malhão Dune Field, Middle Pleistocene.

Ichnogenus *Avipeda* Vialov, 1965
Avipeda isp.
(Fig. 3G, H)

D e s c r i p t i o n. — Numerous large tridactyl footprints and tracks composed of forward-directed digits with interdigital wide open angles. Digit I only rarely occurs and were visible is seen as a faint pit. The middle toeprint is 6–8 cm long and slightly longer than the outer toes. Clawprints are common. They occur in a trampling stratigraphic horizon with *Bifidifes* tracks preserved in convex hyporelief in the Pessegueiro section (Fig. 3G). Visible tracks show a mean pace length of 10 cm.

R e m a r k s. — Large footprints with long and slender front toeprints and an almost non-existent rear toeprints such as these (Fig. 3H) are typical of waders, storks, and cranes that nowadays nest along coastal environments and usually look for food in the coastal inlets and beaches. Waders and cranes have long, thin toes that are widely splayed and thus adapted for walking on soft ground without sinking. The gait of rarely discernible tracks is compatible with birds walking in the interdune area.

DISCUSSION

The Mid to Late Pleistocene (<40 000 BP) Malhão Dune Field eolianites contain 14 stratigraphic levels with a moderately diverse ichnofauna composed of vestiges made by straight-tusked elephants, red deer, foxes, hares, and wolves, as well as a trampled horizon made by wader/stork/crane large birds (Fig. 5). Most of these animals can be also found nowadays in active dune fields. Smaller mammal tracks are usually uncommon in eolianite sequences, but *Leporidichnites malhaoi* igen. and isp. nov., assigned to the locomotion behavior of hares, is described herein from the Malhão eolianite.

Sedimentary aggradation, dune migration and stabilization, and water-table changes were the major factors of plant colonization and pedogenesis. Red deer and *E. antiquus* are regarded as forest dwellers in humid temperate conditions (Cardoso, 1996). Incursion (even if episodic) of these animals into the seemingly much less hospitable environment of an active dune field may be related to the local geography of that time. The Cercal mountain range borders the Malhão Dune Field like a giant wall, more than 300 m high, and deeply incised by a dense network of streams.

Fig. 5. Picture of the dune landscape during the Mid to Late Pleistocene at the Malhão Dune Field and vertebrate community interpreted from the track fossil record (drawing by Andrea Baucon)

During the Pleistocene it would have been densely covered by forest along the steep slopes and highs. For the 2–3.5 ton straight-tusked sub-adult/female elephants, the dune field could have provided an easier migration path for crossing the area located between lush flatlands and the main sources of water (Sado alluvial plain and Mira River). This is the first record of Pleistocene elephantine trackways in Europe and possibly the first record of *Elephas antiquus* behavior. It is also one of the latest occurrences of *E. antiquus* in Europe, when compared with the revision of this species by Stuart (2005). These trace fossils tend to support the previous idea of Iberia as a biotope refuge during Pleistocene glacial/interglacial stages for fauna already extinct over the main part of Europe.

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