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The dinosaur tracksite from the lower Barremian of Areia do Mastro Formation (Cabo Espichel, Portugal): implications for dinosaur behavior

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A B S T R A C T

We described a dinosaur tracksite found in the uppermost part of the Areia do Mastro Formation (lowermost Barremian, Lower Cretaceous), located at 1.5 km north of Cabo Espichel (Sesimbra, Portugal). The studied tracks are distributed in a heavily trampled limestone bed which crops out alongside the rocky beach. The studied trampled surface is highly dinoturbated, 541 tracks assigned to sauropods, ornithopods and theropods were identified. The majority of footprints (336) were produced by the herbivores. The dinoturbated level is a micritic nodular limestone, deposited in a very shallow subtidal to intertidal lagoon environment. Due to the intense bioturbation and limited exposed area, it is difficult to clearly define trackways, but the tracks can provide information about the producers and their behaviours. It is inferred that dinosaurs crossed this area at different times; the herbivores (sauropods and ornithopods) may possibly used the coastal area as passage between feeding spots, while carnivores frequented the area to hunt in groups or individually.

1. Introduction

Dinosaur tracks are globally found in Mesozoic successions and the fossil record of dinosaurs in the Lower Cretaceous of Europe is very abundant. During the Early Cretaceous, theropods and three groups of quadrupedal dinosaurs (sauropods, ankylosaurs and ornithopods) inhabited Europe, including the Iberian Peninsula (e.g., Antunes, 1976; Madeira and Dias, 1983; Upchurch et al., 2004; Vickaryous et al., 2004; Ortega et al., 2006; Santos, 2008; Buffetaut and Nori, 2012; Santos et al., 2013, 2015; Díaz-Martínez et al., 2015; Figueiredo et al., 2015, 2017, 2021).

Palaeontological investigations at Cabo Espichel began in the late 19th century (Sauvage, 1897). Since then, skeletal remains of crocodiles, turtles, pterosaurs, fishes and dinosaurs were reported from the Papo-Seco Formation (Lapparent and Zbyszewski, 1957; Buffetaut, 2007; Figueiredo, 2010; Mateus et al., 2011; Figueiredo et al., 2015, 2016). Regarding dinosaur remains, theropods have

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been reported: *Megalosaurus* (Lapparent and Zbyszewski, 1957) and *Baryonyx* (Buffetaut, 2007; Mateus et al., 2011; Figueiredo et al., 2015); sauropods, including *Astrodon valdensis* (Lapparent and Zbyszewski, 1957) and Sauropoda indet. (Figueiredo et al., 2015); and ornithopods such as *Iguanodon* (Lapparent and Zbyszewski, 1957), *Mantellisaurus* sp. and Ornithopoda indet. (Figueiredo, 2010; Figueiredo et al., 2015, 2016).

In the Cabo Espichel area, several Mesozoic dinosaurian tracksites have been described: at Praia do Guincho (Papo-Seco Formation, Barremian), a natural cast of an ornithopod dinosaur track was reported (Figueiredo et al., 2017); at Boca do Chapim and Praia do Areia do Mastro, tracks and natural casts were reported (Areia do Mastro Formation; lowermost Barremian) (Figueiredo et al., 2021; Figueiredo et al., 2022); Praia do Cavalo (Upper Jurassic) presents theropod tracks (Santos, 2003, 2008); at Pedreira do Avelino Natural Monument (Upper Jurassic) a trackway of a large sauropod (Santos, 2003, 2008) and a few pterosaur tracks (Mateus and Milàn, 2010) were reported; at Pedra da Mua (Upper Jurassic), trackways of sauropods and theropods have been reported, including evidence of gregarious behaviour based on seven parallel sauropod trackways (Lockley et al., 1994a; Santos, 2003, 2008); the Lagosteiros site (Hauterivian, Lower Cretaceous) shows trackways and tracks of theropods and ornithopods (Antunes, 1976, 1990; Carvalho and Santos, 1993; Mateus and Antunes, 2003; Figueiredo, 2004, 2008, 2014). In 1997, Pedreira do Avelino, Pedra da Mua and Lagosteiros were protected as Natural Monuments.

In the Lower Cretaceous of Portugal others tracksites are known. From the Algarve Basin, ornithopod trackways have been described from Praia da Santa and Praia de Salema, at Vila do Bispo (Santos, 2008; Santos et al., 2013). At the last site, rare sauropod and abundant small theropod tracks and trackways can also be found (Santos et al., 2013). From the Lusitanian Basin, besides the tracksites of the Espichel area, others tracksites with ornithopod, theropod and sauropod tracks were described: Praia Grande, at Sintra; Olhos de Água, at Óbidos; and Praia da Parede, at Cascais (Madeira and Dias, 1983; Mateus and Antunes, 2003; Santos et al., 2015). In total, nine tracksites are known in the Lower Cretaceous of Portugal.

The study of dinosaur tracks has contributed significantly to a better understanding of dinosaur behaviour, because they record their daily activities in environments in which the trackmakers lived. Dinosaur herding or other behaviours such as locomotion gaits and speed have been inferred from several tracksites worldwide (e.g., Ostrom, 1972; Lockley et al., 1994a,b; Myers and Fiorillo, 2009; Castanera et al., 2011). Several parallel trackways and bone beds evidence have suggested gregarious behaviour for several dinosaur taxa, including ceratopsids, ornithopods, theropods, and sauropods (Gillette and Lockley, 1989; Lockley, 1991; Myers and Fiorillo, 2009). However, the ichnological record provides most of the firm evidence of social behaviours, with many tracksites exhibiting evidence of gregarious behaviour (Lockley et al., 1994a,b; Lockley et al., 2002; Myers and Fiorillo, 2009). The origin and preservation of a track is related to many distinct environmental factors, concerning especially the substrate cohesiveness, plasticity, grain size, texture and water content. Then, the sedimentation and diagenesis processes play a role that enhances the origin and quality of the tracks and their preservation (see Carvalho and Leonardi, 2020 and references therein).

In 2019, in the scope of the palaeontological investigations carried out by the Centro Português de Geo-História e Pré-História (CPGP), three new sets of dinosaur footprints were found in three limestone beds (Barremian, Lower Cretaceous), between Boca do Chapim and Praia do Areia do Mastro, from the top of the Areia do Mastro Formation (Figueiredo et al., 2021). The purpose of this paper is to describe one of this newly-discovered dinosaur tracksites from Cabo Espichel (western central mainland Portugal). The

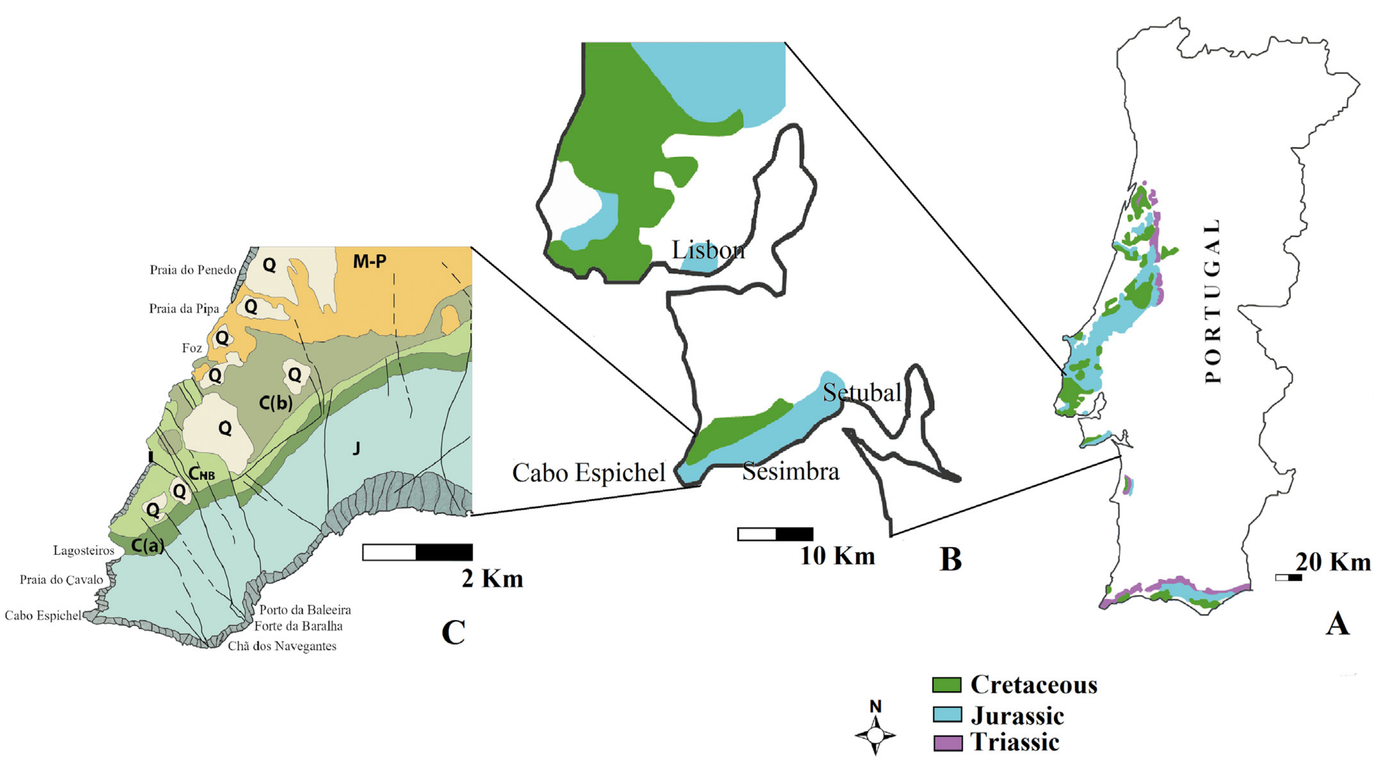

Fig. 1. Location of the Boca do Chapim and Praia do Areia do Mastro ichnosites, Cabo Espichel, south of Lisbon. (J – Jurassic; C – Cretaceous; C(a) – lower Berriasian to lower Hauterivian; Chb – lower Hauterivian to lower Barremian; C (b) – upper Barremian to Aptian; M–P – Miocene to lower Pleistocene; Q – middle to upper Pleistocene and Holocene).

producers and behaviour are analysed and an interpretation of the palaeoenvironmental context of these footprints is provided.

2. Geological and stratigraphical settings

The area where the heavily trampled limestone was found is located between Boca do Chapim and Praia do Areia do Mastro sites. Those localities are at the coastal cliffs, about 2 km to the north of Cabo Espichel (between 38°26′02″N/9°12′43″W and 38°26′14″N/9°12′33″W), in the municipality of Sesimbra (SW of Setúbal peninsula), about 40 km south of Lisbon (Fig. 1).

The sedimentary succession exposed at the beach and cliff includes limestones, marls, sandstones and thin gravel levels,

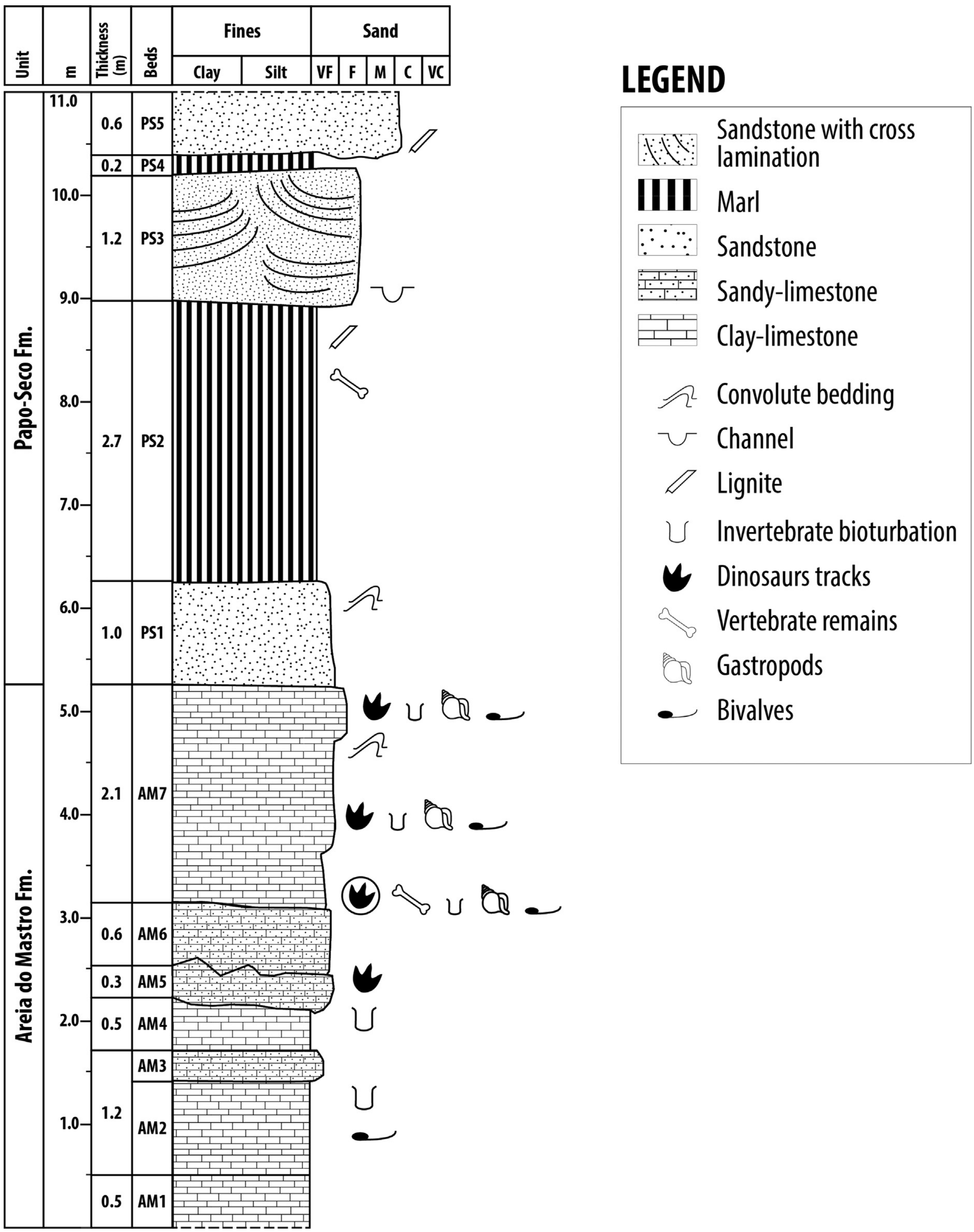

Fig. 2. Stratigraphic column of the transition from the upper beds of the Areia do Mastro Formation to the first (lower) beds of the Papo-Seco Formation. The footprint symbol inside the circle indicates the track-bearing bed studied in this work.

deposited in shallow marine, lagoon and estuary environments. This succession comprises three Lower Cretaceous lithostratigraphic units (from the bottom to top; formal stratigraphy according to Rey, 1992) (Figs. 1 and 2): the sequence of the biostratigraphy units at the Areia do Mastro Formation is attributed, in the Geological Map of Setúbal (CGP, 1:50000, fh. 38-B) to the uppermost Hauterivian to lowermost Barremian (the lowermost Barremian is on the top, where the dinosaur tracks are located); the Papo-Seco Formation is considered to be lower Barremian; and the Boca do Chapim Formation to be middle Barremian (e.g., Rey, 1972; Manupella et al., 1999; Aillud, 2001; Dinis et al., 2008; Figueiredo et al., 2020).

The succession now studied in detail locally dips 8° west and comprises the last seven strata of the Areia do Mastro Formation and the first five levels of the Papo-Seco Formation (Fig. 2).

The exposed Areia do Mastro Formation beds mainly consist of bluish-grey clay-limestones dominated by micrite, 0.5–2.1 m thick, intercalated with sandy (quartz-rich) micritic limestone beds, 0.3–0.6 m thick. Most of the beds show a nodular texture due to intense invertebrate bioturbation (mainly *Thalassinoides suevicus*), typical of an intertidal to subtidal lagoon environment (Neto de Carvalho et al., 2007, Figueiredo et al., 2021). Some beds also yield bivalves (AM2, AM4, AM5, AM6 and AM7) (Fig. 2); bed AM6 (Fig. 2) also includes fish teeth and turtle shell remains. Levels with dinosaur footprints were found at the top surfaces of the beds AM5 and AM6 (Fig. 2), characterized in detail in the present work and in several stratigraphic positions in bed AM7 (Fig. 2). The bed AM7 (Fig. 2) also contains internal moulds of gastropods and rare fragments of turtle shell. The observed beds of the Areia do Mastro Formation are interpreted as recording a carbonate subtidal to intertidal lagoon environment according to the bioturbation and body fossils (Figueiredo et al., 2021).

The studied levels of the Papo-Seco Formation comprise dark yellow fine sandstones, 1.0–1.2 m thick, intercalated with some light grey and green marls, up to 2.7 m thick. The sandstones show sedimentary structures related to hydrodynamics (currents along tidal channels); lignite remains and dolomitic concretions also occur. These Papo-Seco Formation beds indicate a depositional environment comprising a marly subtidal to intertidal lagoon adjacent to a sandy littoral barrier. The convolute bedding present at the top part of beds AM7 and PS1 is interpreted as probable palaeoseismites, which could be related with seismic events located in the NW-SE trending strike-slip faults that cross the study area or in the WSW-ENE Arrábida thrust fault (Kullberg et al., 2000) (Fig. 1).

3. Materials and methods

This study deals with the analysis of a large number of dinosaur tracks found in a limestone bed located at the topmost part of the Areia do Mastro Formation. Most of the work was performed in the field, comprising the measurements (width and length) and photographic documentation and codification of each footprint. The geographic location and orientation of each track was also recorded.

A database was erected with information regarding each dinosaur footprint: code, coordinates x and y from the centre point of dinosaur tracks, orientation and dinosaur morphotype. From the field tables containing the coordinates, it was produced a geographical thematic map that allowed the spatial distribution and visualization in the geographic information system (GIS). Each dinosaur track was represented by a colour (yellow for sauropods; blue for ornithopods and red for theropods) and the orientation of each track was represented by an arrow (Figs. 4 and 5). Other detailed observations of sediment samples, analysis of the data collected in the field and the interpretation of the distribution in GIS were done in the laboratory.

Institutional abbreviations:

CPGP, Centro Português de Geo-História e Pré-História, Lisbon/Golegã, Portugal.

Abbreviations:

GIS, Geographic Information System

CGP – Carta Geológica de Portugal (Geologic Map of Portugal)

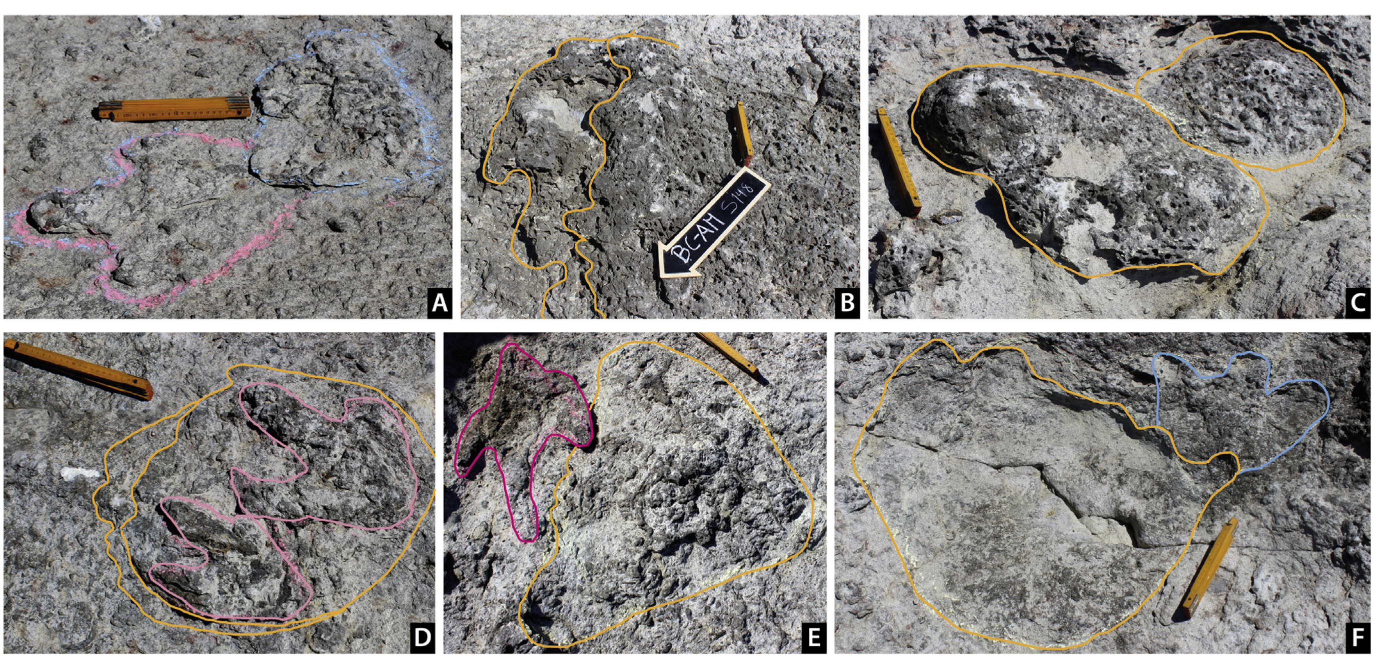

Fig. 3. Some examples of footprint overlapping. A – theropod (red)/ornithopod (blue); B and C – sauropod/sauropod (the yellow line delimits the footprints); D – sauropod/sauropod (yellow)/theropod (red); E – theropod (red)/sauropod (yellow); F – sauropod (yellow)/ornithopod (blue). Scale bar is 20 cm. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

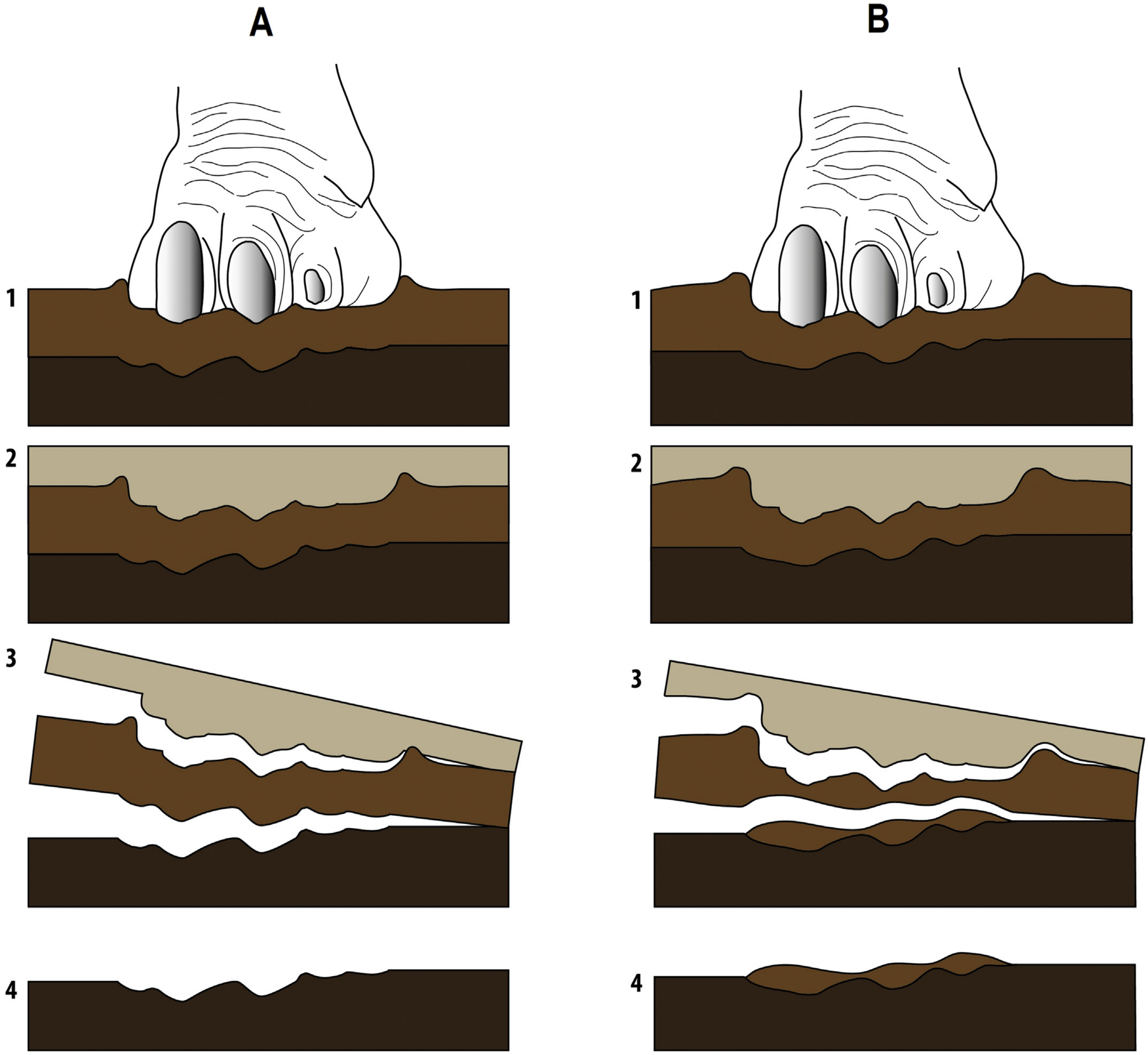

Fig. 4. Schematic representation of the formation of the tracks and the identified types of preservation: A (type 1); B (type 2). In A, the track is imprinted in a sandy-limestone layer; the weight of the animal causes the formation of undertracks in the layers subjacent to the foot. B (type 2) – present day erosion level has exposed the track as a limestone plug; the clay-limestone layers around the sandy-limestone cast seem to form a bowl-shaped structure filling the sandy-limestone cast (Art by Fernanda Sousa).

4. Results

4.1. Ichnological description of the site

The dinosaur footprints are distributed in a limestone that crops out alongside the rocky beach, adjacent to a cliff about 60 m high; two other limestone beds (90 and 160 m from the site here described) containing dinosaur tracks were also found, but they are not described here (Figueiredo et al., 2021). During the palaeontological field work performed in 2019, a long and narrow surface, with 265 m long, of a strata with dinosaur footprints, located at the base of the cliff (Fig. 2), was identified between Boca do Chapim and Praia do Areia do Mastro. During the year 2020, field work was done to survey these tracks on this highly dinoturbated stratigraphic surface. A total of 541 footprints were identified in an area of ~1,600 m^2 (Fig. 3). The taphonomic issues allowed that, in the same surface, occur impressions and casts (Figs. 3 and 5). There are several overlapping footprints (Fig. 3), evidencing the passage of different animals at different times. Overlapping footprints were identified not only among the same group of dinosaurs, but also between distinct dinosaur groups such as sauropods, ornithopods and theropods.

The dinosaur tracks were produced by different groups of dinosaurs (theropod, ornithopod and sauropod) and have different morphologies: theropods and ornithopods tracks are digitigrade, while the sauropods tracks are plantigrade. Some are tridactyl, mesaxonic, with the impression of digit III considerably larger than either digit II or IV; digits divergent. We attributed these tracks to theropod dinosaurs. Other footprints are also tridactyl but with rounded, short and more blunt digits and tend to be

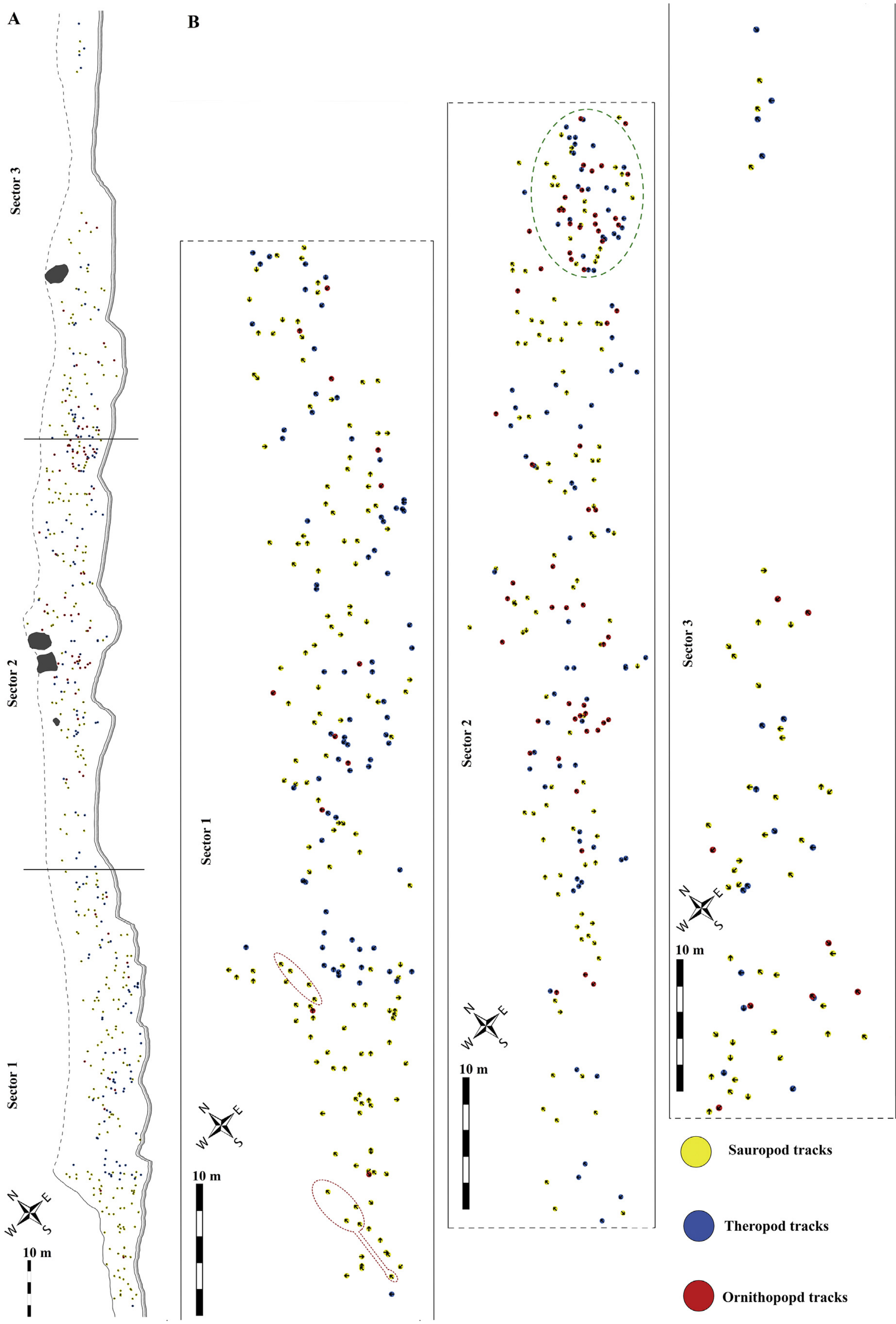

Fig. 5. A: distribution of tracks on the trampled surface. The dark spots represent fallen blocks of rock. The top end is dashed, because, although the slab is continuing, the area beyond the dashed area is very eroded by the sea, and it is not possible to identify sharp tracks in this area. Scale bar is 10 m; B: enlargement of the image that resulted from the GIS

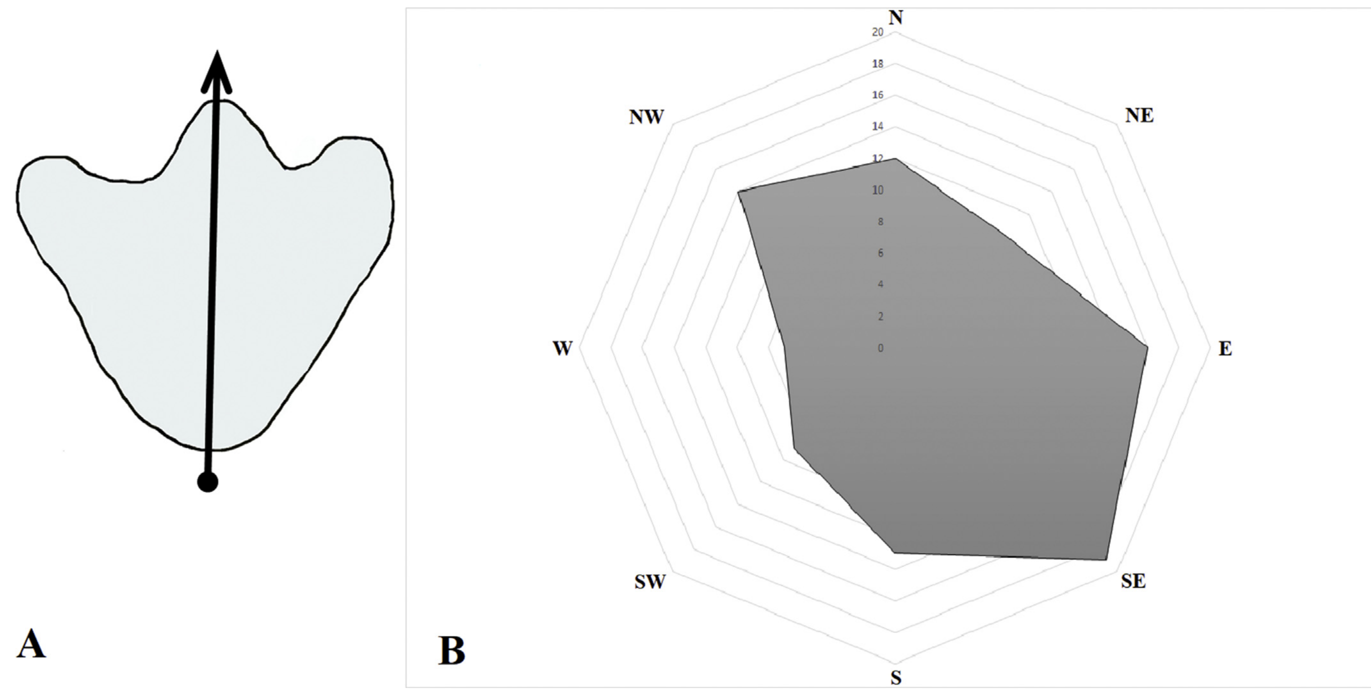

Fig. 6. A: orientation of the tracks, according to an axis heel – fingers (arrow); B: a rose diagram that shows the orientation preferences of the tracks, according to the cardinal points.

wider than long and with a rounded heel impression. We attributed these footprints to ornithopod pes. There are a few oval to sub-oval footprints, with the long axis oriented anteromedially, but no clearly differentiated digit impressions. These tracks were attributed to ornithopod manus. The last footprints morphology that was attributed to sauropods are oval and large, with the impressions of five/four rounded digits with a distinctive front edge, the boundaries between digits are often indistinct, making it difficult to differentiate between four or five digits present on certain prints (those footprints correspond to sauropod pes). There are few handprints of sauropod manus with a typical crescent shape, posteriorly concave, the digits are not preserved in these footprints. The footprints, which we interpret as being underprints, are casts and depressed impressions and they have different dimensions. The depressions have various depths: between 4 and 12 cm; the casts footprints have thicknesses between 3 and 8 cm.

The tracks show two distinct types of preservation:

Type 1. They are preserved as concave epireliefs (Fig. 4A). This morphology can either be the result of a true track exposed to erosion which includes pressure pads surrounding the imprint, or an undertrack originally formed on a subjacent horizon, due to the pressure of the dinosaur's foot being transferred down into the subjacent layers of sediment (Lockley, 1991).

Type 2. Preserved as isolated limestone plug as full relief (Fig. 4B). These footprints are preserved as a combination of both undertrack origin and erosion (Fig. 4B).

4.2. *Distribution of dinosaur tracks and interpretation of possible trackways*

Due to the intense dinoturbation and the limited exposed area, no clear dinosaur trackways were identified, but the distribution of the dinosaur footprints in the trampled bed shows that most of them appear randomly in the bedding surface and present distinct orientations (Fig. 5). However, two sets of sauropod footprints are probably two parallel trackways (Fig. 5B, Sector 1), as they present similar dimensions and the same orientation. In the analysis of the dispersion of the tracks, after handling the tracks survey data in GIS, it was possible to identify several footprints of the same dinosaur group, with the same orientation, and same sequence, and, although spaced between each other, some sets of footprints could indicate trackways. More detailed studies on these tracks and their survey and treatment in 3D are needed to clarify whether they are really trackways. An important aspect of the distribution of the tracks on this surface is the large concentration of tracks in a portion of the extensively dinoturbated bedding plane (Fig. 5B, Sector 2).

The orientation of each track was recorded according to the azimuth of a vector that begins at the heel and ends at the fingers (Fig. 6A). The projection in a rose diagram, of the data obtained in the identification of each track's orientation, indicates a predominance of orientation of the tracks to Southeast. There is also a considerable relevance in the azimuths to East and West (Fig. 6B).

4.3. *The trackmakers*

The total distribution of dinosaur tracks is the following: theropods – 81 (15%), sauropods – 291 (55%), and ornithopods – 169 (30%). Sauropods and some species of ornithopods were quadrupedal animals, so they left twice as many tracks (pes and manus) than the bipedal animals. The theropods are represented only by bipedal species. In the dinosaur trampled bed both pes and manus impressions of sauropods and ornithopods were found. So, to make the percentages of each dinosaur group and the percentages between herbivores and carnivores, we only considered the pes

study of the distribution of the footprints (A). In Sector 1, the red dashed line indicates two possible sauropod trackways, and in Sector 2, the green-dashed line indicates an area with a high concentration of tracks (scale bar: 10 m). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

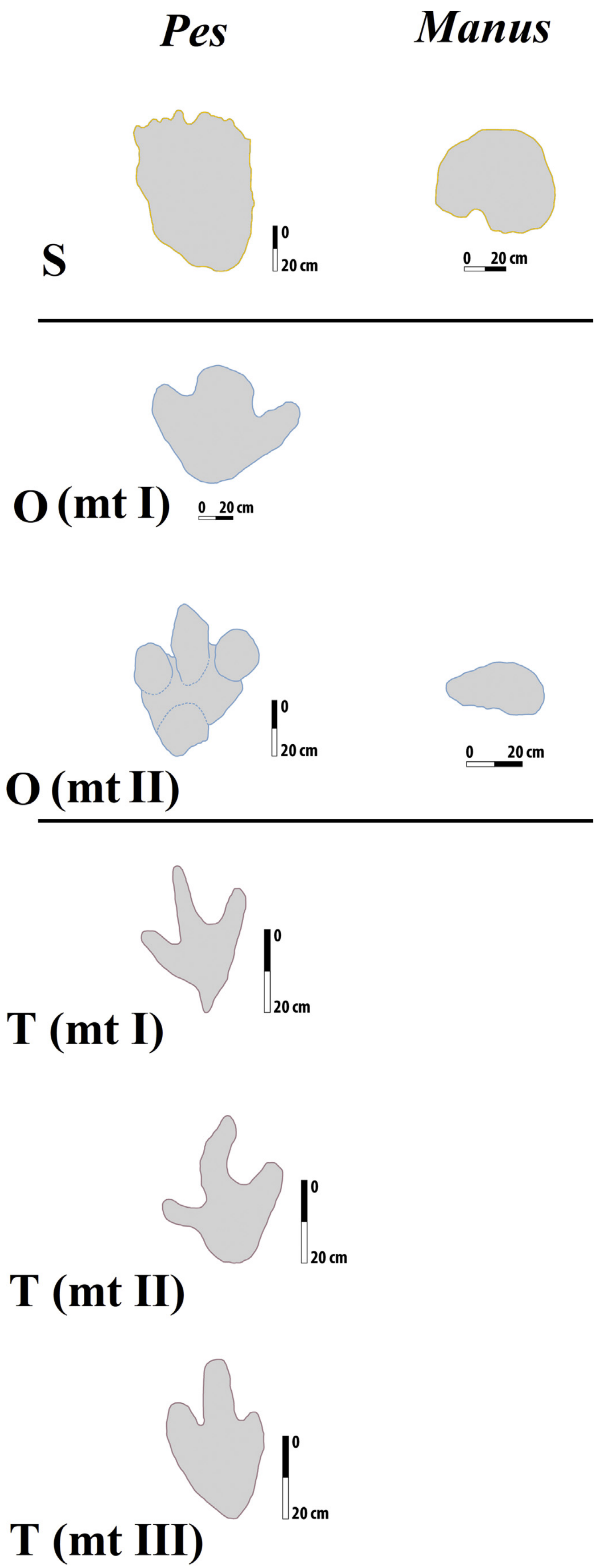

Fig. 7. The track morphotypes identified in the studied tracks: S – sauropod morphotype; O(mI) – ornithopod morphotype I; O(mI) – ornithopod morphotype II; T(mI) – theropod morphotype I; T(mII) – theropod morphotype II; theropod morphotype III. Scale bar: 20 cm.

tracks. Therefore, the percentage of pes impressions of each dinosaur group is the following: theropods - 19% (81 tracks); sauropods - 46% (189 tracks) and ornithopods - 35% (147 tracks). The carnivore's tracks are 19%, while herbivores tracks are 81%. The size of the tracks is variable and the morphological differences between some tracks of the same group of dinosaurs suggest that they were produced by individuals of different species and different ages. Moreover, it cannot be ruled out that part of the observed morphological variability is due to preservational biases.

In the sauropod tracks, both pes and manus impressions have been found. They are similar to Brontopodus-like tracks, which are related to titanosauriforms (Lockley et al., 1994b, 2002; Wilson and Carrano, 1999; Wright, 2005; Marty et al., 2010). Pes impressions are entaxonic and always longer than wide, with a shape that is variable from slightly elliptical to bell shaped, having a narrow "heel" and a wider anterior area. The phalangeal area is generally the deepest part of the track. Manus impressions are wider than long, and they are horseshoe-shaped, with two lobes corresponding to digits I and V. No claw impressions are present.

Concerning the ornithopods, tracks attributed to this group have two distinct morphologies: Morphotype O1: pes tracks. Tridactyl, subsymmetrical and mesaxonic tracks, longer than wide, with large and rounded heel and three short, wide digits; pad and claw impressions are lacking. These tracks can be assigned to "Group 1" as defined by Díaz-Martínez et al. (2015) and attributed to Iguanodontipus; Morphotype O2: large pes prints. Tridactyl subsymmetrical and mesaxonic tracks, with a pad impression in the heel, and short, wide digits. The tracks have one rounded pad impression in the heel, and a short and wide pad impression in each digit. These footprints can be assigned to "Group 2" as defined by Díaz-Martínez et al. (2015) and attributed to Caririchnium, originally described by Leonardi for tracks discovered in Paríba, Brazil (Leornardi, 1979). Some small and elliptical manus prints are also known. Because of their morphology, they agree with the Caririchnium manus prints.

In the case of the theropods, three different morphotypes have been identified: Morphotype T1: of this morphotype we only have one footprint, that is tridactyl narrow and mesaxonic with the possible impression of the digit I. This footprint is longer than wide, with a long digit III. Morphotype T2 is comprised of tridactyl impressions, relatively narrow and mesaxonic footprints with a U-shaped heel. The digits II and IV are short, and digit III is very long. Morphotype T3 has tridactyl, relatively wide and mesaxonic impressions, with digit III curved. Although they are distinct morphotypes, these theropod tracks may belong to Megalosauripus as this ichnogenus is one of the most common theropod ichnotaxa in the Upper Jurassic and Lower Cretaceous. It has been described from several localities in Europe, America and Asia (Castanera et al., 2017) (see Fig. 7).

4.4. Fauna and paleoenvironmental interpretation

The dinosaur trampled bed consists of bluish-grey limestones showing a nodular texture due to a high invertebrate bioturbation (mainly Thalassinoides suevicus) which is typical of a shallow subtidal to intertidal lagoon, suggesting that the dinosaurs crossed that environment (Figueiredo et al., 2017, 2020, 2021).

Vertebrates bones and teeth have been found together with the tracks (Fig. 8): sea turtle shell fragments (Fig. 8A–E); a pterosaur tooth (Fig. 8F) and two fish teeth cf. Lepidotes sp. (Osteichthyes, Actinopterygii, Lepisosteiformes; Fig. 8G). The correspondence between body fossils and tracks makes this site a Type 2b deposit (sensu Lockley 1991), where the fossil track record dominates and bone evidence is inconsistent with the track fauna. Regarding macroinvertebrates, internal moulds of medium-sized (6–13 cm) gastropods of the genus cf. Ampullina sp. have been identified (Fig. 9E–G). These internal moulds feature an ovoid shell, with a low, slightly convex turns and a deep suture sling. The last lap is large, which corresponds to a large opening.

Invertebrate body fossils and ichnofossils were also found. The genus Ampullina (Fig. 9E–G) is associated with shallow marine (infratidal) to aquatic transition environments (Ayoub-Hanna and Fürsich, 2011), which corresponds to the depositional environments of the identified facies. Ampullina fossils are relatively abundant and appear scattered over the entire surface. It was found that most of the shells are oriented in the W-E direction to the present north, and a substantial part in the opposite direction (Fig. 9), which is consistent with dispersion in an intertidal area. According to Suguio (2003) conical bioclastic remains, such as the shells of gastropods, have the thinnest end directed against the current that transport them. Thus, the orientation of the gastropods identified in the trampled surface indicate that the tidal currents have oriented the gastropod shells mostly in the W-E direction, at the time of the tide flow and in the E-W direction, at the time of the tide ebb. Such orientation of the tidal currents is in accordance with the palaeogeographic reconstructions of the coastal area in this sector of the Lusitanian basin, showing a N-S orientation according to present magnetic pole (Rey, 1972; Rey and Caetano, 2017). This may also be evidence for the transport of the gastropods by tidal currents to a shallower intertidal environment.

The invertebrate bioturbation is intense and provides a nodular texture to the trampled bed. On the bedding plane linear to slightly winding large burrows are present (Fig. 9C-D), with no burrow lining and filling represented by limestone which is less bioclastic than the surrounding sediment (Fig. 9B, D). The Y-shaped branching of these mostly horizontal burrows is typical of Thalassinoides suevicus (Fig. 9A). The absence of lining and the elliptical cross section of the burrows, with the long axis parallel to the bedding plane, suggest their development in a soft-to stiff-ground. Thalassinoides is a common trace fossil in intertidal to shallow subtidal carbonate lagoon environments (Fürsich, 1974; Myrow, 1995, and references therein).

4.5. Interpretation of the dinosaur behaviour from the palaeoichnological record

The heavy dinoturbation from the Areia do Mastro Formation was produced in a low energy carbonate intertidal to tidal depositional environment (Fig. 10). The large number of tracks, their

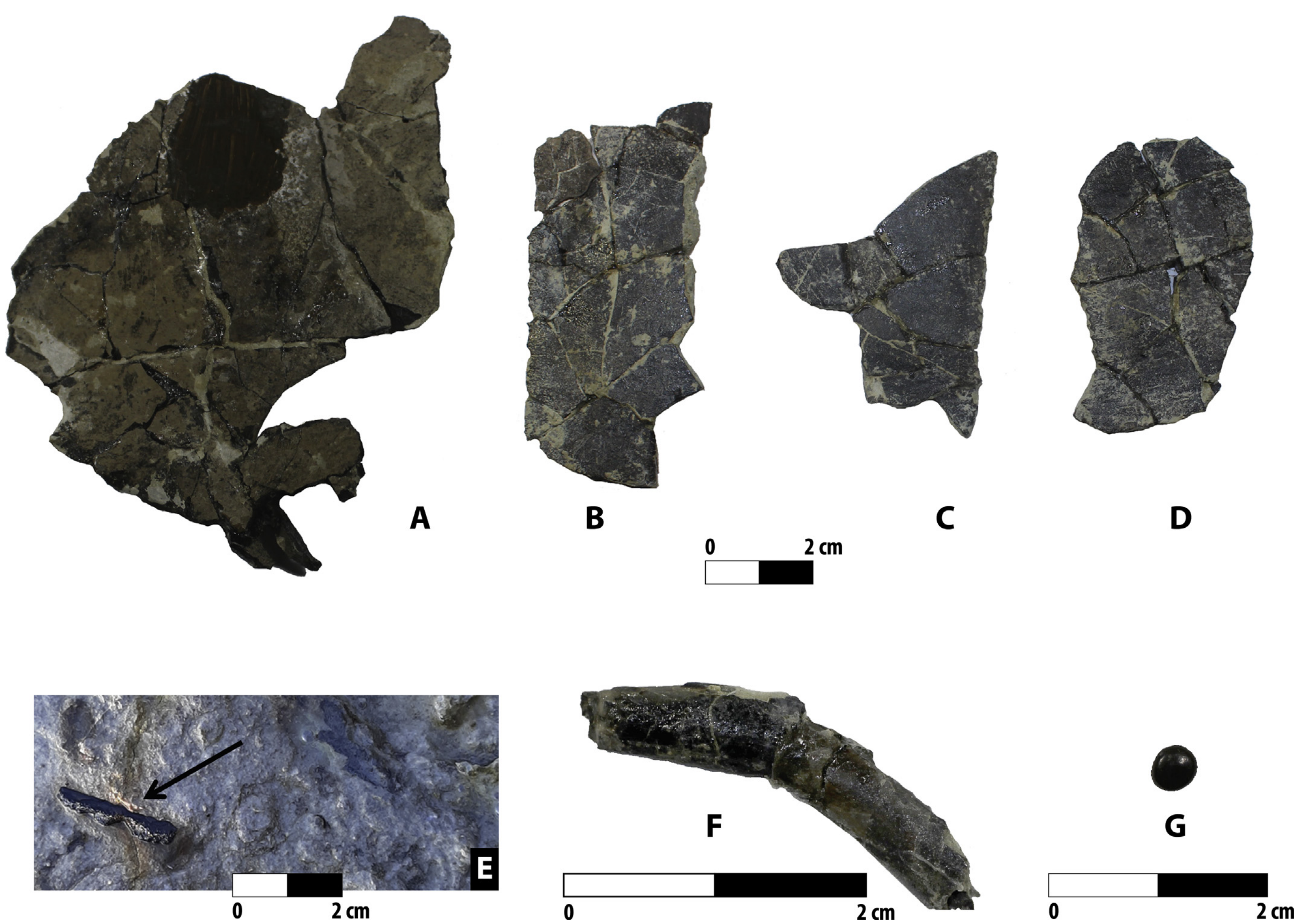

Fig. 8. Vertebrate skeletal fossils found in the trampled surface: A to E: turtle shell remains (in E a fragment de turtle shell, still embedded in the rock; F – Pterosaur tooth; G – cf. *Lepidotes* tooth.

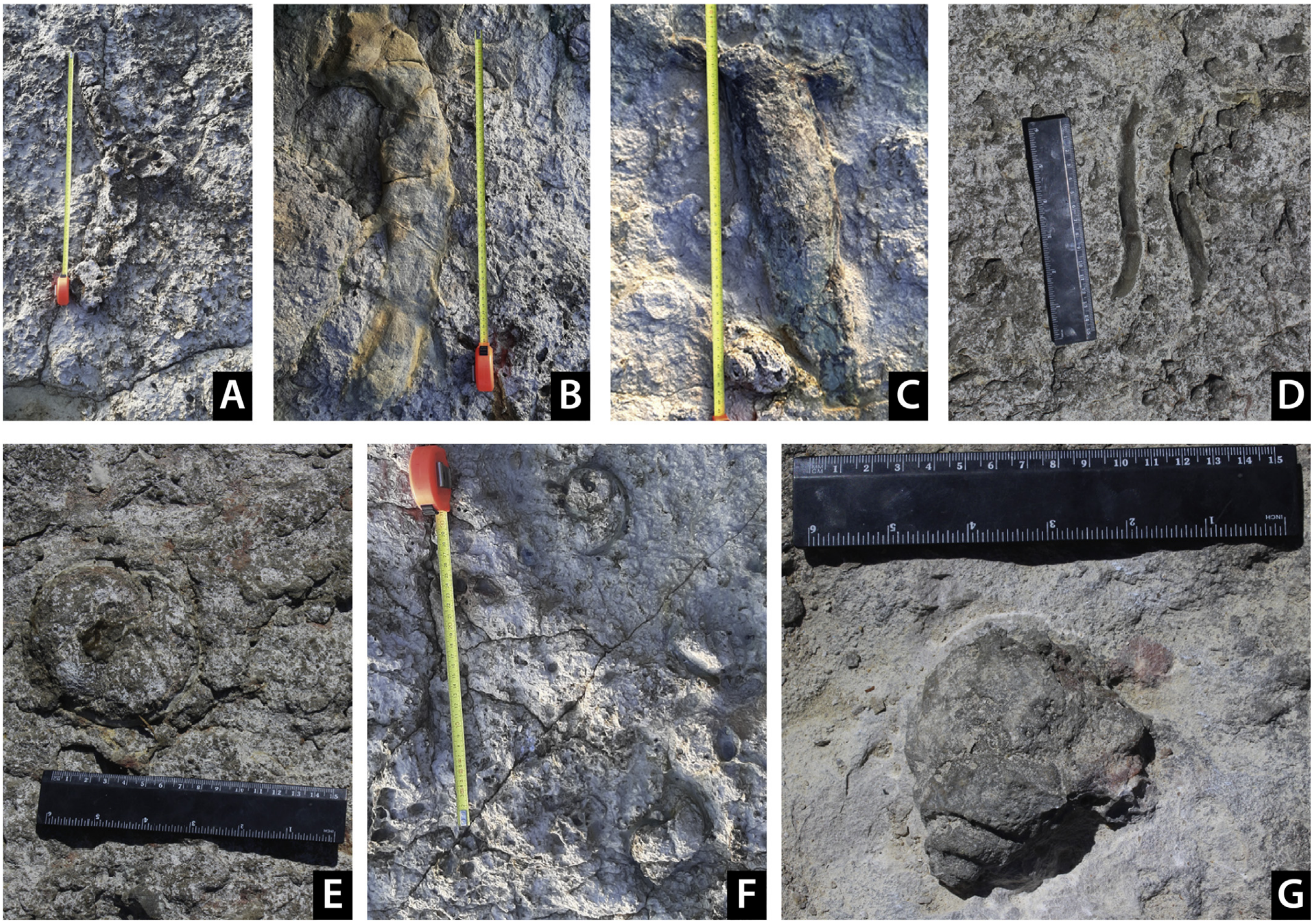

Fig. 9. Invertebrates body fossils and ichnofossils (A–D) *Thalassinoides* burrows and internal moulds of the gastropod cf. *Ampullina* (E–G).

orientation and the diversity of dinosaur groups suggest the existence of a coastal area intensely crossed by different dinosaur species, mainly herbivores that probably used the area as a passageway between feeding zones in the nearby alluvial plain. Parallel or any trackways were not identified. Parallel or any trackways were not identified. The large number of dinosaurs tracks identified led to the interpretation that the area was very frequented by many solitary individuals. Also, as the tracks show similar depth and orientation, mainly of sauropods, suggest the presence of herds. The common track overlapping indicates successive crossing moments. The smaller number of carnivore tracks suggests the presence of few theropod individuals. According to the inferred frequency, it seems that the large theropods (few tracks identified) may have been solitary hunters with exclusive territorial behaviour, while the small theropods, which left a greater number of tracks there, may have hunted in groups, or maybe were just more common on the landscape than big theropods. It is, however, difficult to relate observed tracks/trackways to gregarious behaviour of carnivores. Indeed, the analysed tracks do not display typical patterns of gregariousness such as those observed for herds of herbivorous dinosaurs (Lockley et al., 1994a,b; Lockley and Hunt, 1995; Myers and Fiorillo, 2009; Castanera et al., 2011; Moreno et al., 2012) (see Fig. 11).

5. Discussion

The presence of dinosaurs, especially ornithopods, sauropods and theropods is documented in the fossil record, not only in the ichnofossil record of Lagosteiros (with two track levels with dinosaur footprints from Berriasian and Hauterivian), but with specific regard to the occurrence of dinosaurs in the Barremian, skeletal remains of ornithopods, sauropods and theropods have been found in the Papo-Seco Formation, especially in basal beds of this formation, that are in stratigraphic continuity with the trampled surface presented in this work (Figueiredo et al., 2021).

Odum (1988) states that animal behaviour is an important component of compensation for environmental factors (limiting and regulatory) and ecotypic development. Organisms regulate their internal environments and external microenvironments by physiology and conduct. Animal behaviour plays a key role in the adaptations of biological functions. It represents the extension of an organism through which it interacts with the environment (Snowdon, 1999). The behaviours are grouped into functional categories, such as postural reflexes, patterns of locomotion and eating, sexual, parental care, and communication behaviours, among others (Baptistar et al., 2017). Animal behaviour from the point of view of evolutionary biology presents characteristics that,

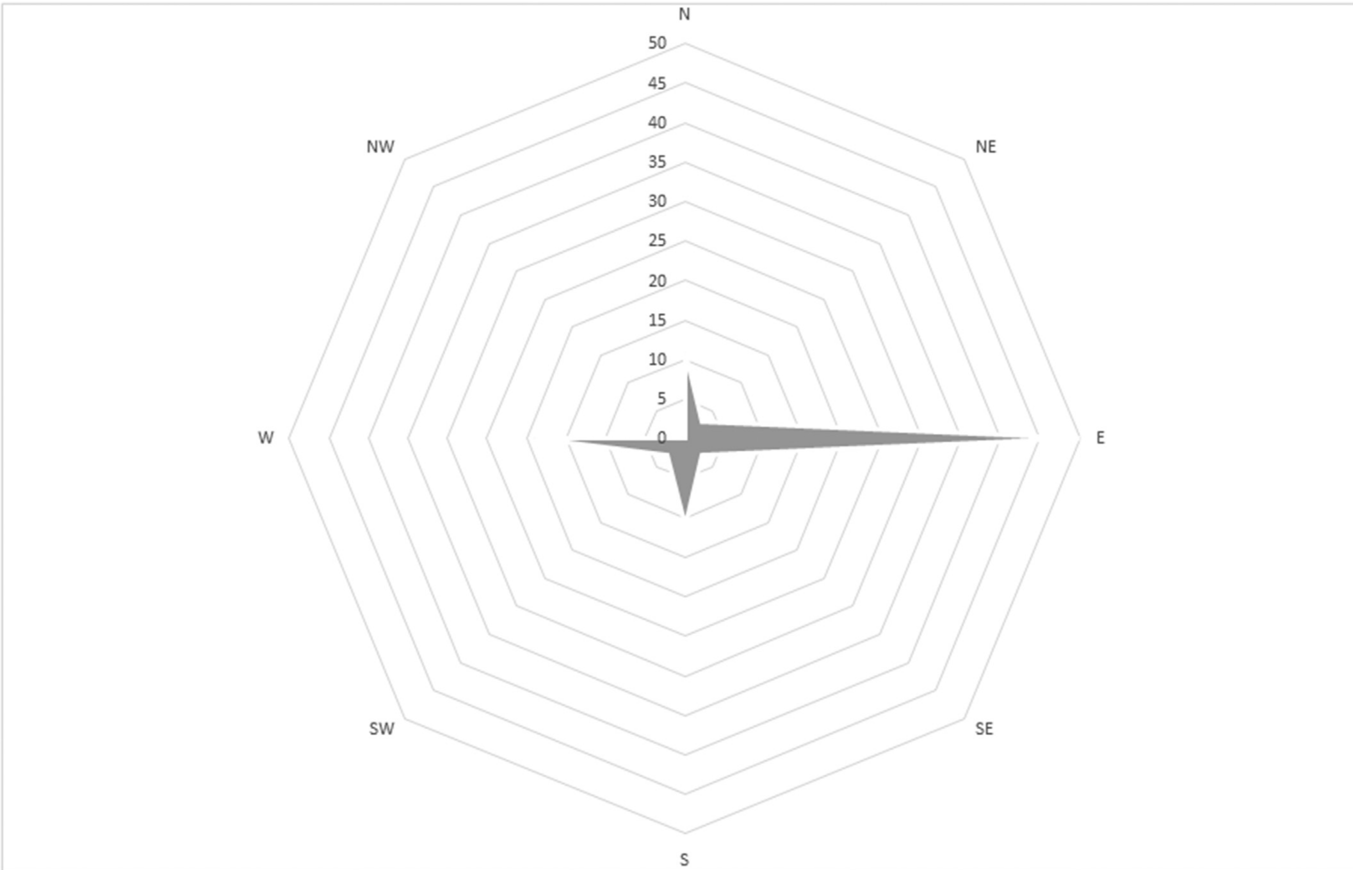

Fig. 10. Rose diagram with the percentage of the orientation of the gastropods on trampled with reference to the present magnetic north location.

like any other class of characters, can exhibit genetic and non-genetic variations, differences between populations and species and these are subject to evolution by natural selection. This evolutionary process is related to the change in behavioural traits within the species as instinct, resulting in behaviours that appear in a completely functional form the first time they are executed (Alcock, 2011), and learning modifications of behaviour in response to specific experiences. However, they are factors that result in behavioural differences in several situations (Del-Claro, 2004). However, they are factors that result in behavioural differences in several situations (Del-Claro, 2004). Sauropods could be segregated in small herds, according to age: the juveniles could live in groups, and adults may have chosen to live alone (i. e. Lockley et al., 1986, 1994a, 2018; Myers and Fiorillo, 2009; Xing et al., 2019). The set of tracks described in this work shows that most of the sauropod tracks belong to adult individuals. Further studies could clarify if that the sauropods have crossed the surface at the same time, since it is already clear by overlapping tracks and their repetition in the stratigraphic succession that they have crossed the area at different moments. Gregarious behaviour based on ichnological evidence has been described in several parts of the world and in different ages. Several dinosaur tracksites, especially containing sauropod tracks, indicate that those animals often formed social groups (i. e. Lockley et al., 1994a,b; Castanera et al., 2011). On the other hand, some accumulations of dinosaur skeletons with numerous individuals of the same species suggest the existence of very large herds or group gathering (Moreno et al., 2012).

Sea level oscillations in a low hydrodynamic intertidal carbonate environment, recorded by the dinoturbated stratigraphic surfaces at the upper portion of the Areia do Mastro Formation, likely facilitated the preservation of the dinosaur tracks as a reflection of a preferential habitat for these animals, although of short term, were those animals crossing the area, as they moved from one feeding ground to another. In other Portuguese ichnosites with occurrence of dinosaur tracks/trackways, sediments were deposited in very shallow marine, estuarine or deltaic environments (Santos, 2003, 2015; Santos, 2008; Figueiredo et al., 2017).

Trackways are the closest approximation of motion pictures of the behaviour of fossil animals (Paul, 2010). Tracks, especially when they occur in large numbers, can also give indications about behaviour of fossil vertebrates and can provide useful complementary constraints on the problem of population density and behaviour of large predators (e.g., Lockley and Hunt, 1995) and other groups of dinosaurs. Dinosaur trackways have shown that some groups of dinosaurs travelled in herds. Such social behaviour has been described from the study of sauropod tracks: in Oxfordshire (England), from the Middle Jurassic (Day et al., 2004); at Pedra da Mua (Sesimbra region, Portugal), from the Upper Jurassic (Lockley et al., 1994a); and Las Cerradicas (Teruel province, Spain), from the Lower Cretaceous (Castanera et al., 2011); from ornithopod tracks at Tereñes (Asturias, Spain), from the Upper Jurassic (Piñuela et al., 2016); from hadrosaurid dinosaur tracks at Denali National Park (Alaska), from the Upper Cretaceous (Fiorillo et al., 2014). Some tracksites have also revealed that in some cases herds protected their young by keeping them in the centres of migrating groups (i.e., Thulborn and Wade, 1989; Malkani, 2007; Diedrich, 2010; Romano et al., 2018). The study of trackways can estimate dinosaur's gait and speed and provide information about the way of locomotion of dinosaurs, by measuring the pace and stride, or determine the gregarious behaviour (e.g., Ostrom, 1972;

Fig. 11. Reconstruction of the coastal environment and the different dinosaurs identified by the skeletal and trace fossil record during the lowermost Barremian (Areia do Mastro Formation) in the Cabo Espichel area (Art by Fernanda Sousa).

Lockley et al., 2002; Santos, 2008). In the case of the new tracksite described in this study, trackways have not yet been clearly identified, and it is not possible to measure the distance between eventual parallel trackways in order to estimate the speed at which the individual animals were moving as a group. Therefore, at the moment, there is not enough information to have specific conclusions about the types of gregarious behaviour for the dinosaurs that produced these tracks.

6. Conclusions

Despite the palaeontological sites of Boca do Chapim and Areia do Mastro yielded significant vertebrates remains, including skeletal fossils of dinosaurs, these paleontological remains come from the Papo-Seco Formation, from the Areia do Mastro Formations, the footprints described in this work are the first dinosaur fossil record described in there. These newly found trampled surface shows hundreds of tracks attributed to sauropods, ornithopods and theropods and, by the high number of identified tracks, is the largest tracksite hitherto known from the Lower Cretaceous of Portugal. The dinosaur footprints of the Barremian Areia do Mastro Formation constitute an important patrimonial element of Portuguese paleontology and relevant from the scientific point of view, because it represents an important contribution to the knowledge of the dinosaurs from the Lower Cretaceous not only of Portugal, but also of the Iberian Peninsula.

The sauropods are the most representative group of dinosaurs, with the larger number of tracks. It was found both pes and manus impressions of sauropod tracks, similar to Brontopodus-like tracks, which are related to titanosauriforms. The ornithopod footprints also preserve both pes and manus impressions and have two distinct morphologies that can be attributed to Iguanodontipus and to Caririchnium. In the case of the theropods, three different morphotypes have been identified. The last morphotype (T3) may belong to Megalosauripus isp. Most of the contemporaneous sauropod tracks belong to adults. High number of sauropod and ornithopod tracks in shallow subtidal to lower intertidal environments, found at three different beds, allow us to consider that these herbivores used the coastal flats to move between destinations, possibly related to nearby alluvial plains, contributing for trampling the muddy ground, possibly for a long time. Also, the relatively small theropod tracks outnumber the larger tracks of the same group, enabling identification of the predominance of small carnivores in the recorded early Barremian carbonate tidal flat, giving as a working hypothesis, a possible chasing of prey in groups. The beds where these footprints are located are composed of micritical limestone deposited in an intertidal context in a lagoon environment, under a tropical climate. The beds have a large bioturbation index, essentially resulting from the intense trampling produced by the dinosaurs that passed there. It is interpreted that those footprints were produced at various times, because overprinted footprints and because herbivores used this coastal area as they were crossing the surface as they moved from one location to another, while the carnivores frequented the area to hunt.

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