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Dinosaur footprints from the Lower Cretaceous of the Algarve Basin (Portugal): New data on the ornithopod palaeoecology and palaeobiogeography of the Iberian Peninsula

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ABSTRACT

Fieldwork carried out during the past few years in the Algarve region (Portugal) has allowed the description of dinosaur tracks for the first time in the Mesozoic Algarve Basin. Five track levels of Early Barremian age have been described from the Santa and Salema tracksites situated near Vila do Bispo (southwest Algarve). These comprise theropod and iguanodontian footprints (*Iguanodontipus* isp. was identified at the Santa tracksite). A sequence of subcircular and tridactyl impressions with a characteristic morphology of ornithopod footprints with a high pace angulation value made it possible to determine how erosion changes the print morphology and to understand the sequences of subcircular impressions with a high value of pace angulation in the track record. These dinosaur footprints are preserved in marginal-marine carbonate sediments of a large inner shelf palaeoenvironment with shoals and tidal-flat areas that were periodically exposed. The warm and dry climate favoured extensive growth of algal mats and the deposition of dolomitic sediments. The discovery of these track levels has also enabled the palaeobiogeographical data available for the Early Cretaceous Iguanodontia of the Iberian Peninsula and southwestern Europe to be refined.

1. Introduction

The presence of vertebrates in the Mesozoic Algarve Basin (Portugal) was first reported by Palain (1975, 1976) followed by Russell and Russell (1977). They mentioned the existence of fish, primitive amphibians and unknown reptiles in at least five levels of the Triassic "Grés de Silves" Formation. Recently, Kasprak et al. (2010) have recognized terrestrial vertebrate material, including remains of large stereospondyl temnospondyls, close to the Triassic/Jurassic boundary. Dinosaur osteological remains were first identified by Pedro Terrinha at Porto de Mós beach (Lagos) in 1992 (Santos et al., 2000a). Here, in an Aptian layer (Clansayesian–Gargasian according to Rey, 1983), dinosaur teeth and longitudinal sections of vertebrae were recognized. An analysis based on visible morphological aspects in section allowed its assignation to theropods (Santos et al., 2000a). Dinosaur tracksites are still scarce in Mesozoic rocks of the Algarve Basin when compared with the well-documented dinosaur track record from the Mesozoic Lusitanian Basin (Fig. 1), which has been yielding significant palaeobiological and palaeoecological information from abundant tracks and trackways (e.g., Madeira and Dias, 1983; Santos et al., 1992, 1994, 2009a, b; Lockley and Santos, 1993; Lockley et al., 1994b, 1998; Meyer et al., 1994).

Five Cretaceous dinosaur tracksites have been described from the Lusitanian Basin (Fig. 1, Table 1). These contain sauropod, theropod and ornithopod tracks. Among the best evidence of this fossil record are two track levels (Lagosteiros A) in a Berriasian clastic sequence that overlies the Upper Jurassic (Tithonian) limestones in Lagosteiros Bay, north of Cabo Espichel (Sesimbra), which were discovered by José Luís d'Orey in 1996. Here, dinoturbation and bipedal dinosaur tracks of probable theropod origin were identified (Santos, 2003). In the north cliff of Lagosteiros Bay, theropod footprints and a probable ornithopod trackway were documented in a single track level (Lagosteiros B) of Hauterivian age (e.g., Antunes, 1976; Santos et al., 1992; Meyer et al., 1994; Santos, 2003). An Early Aptian tracksite at Praia Grande (Sintra) consists of an upper level with sauropod, theropod and ornithopod

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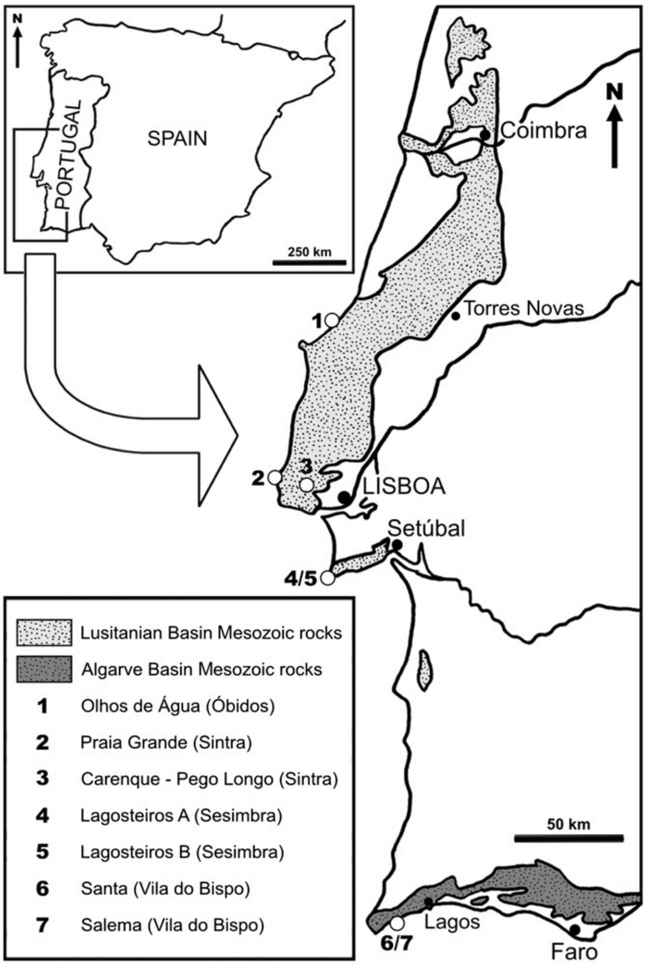

Fig. 1. Cretaceous dinosaur tracksites in the Mesozoic Lusitanian and Algarve basins (Portugal).

tracks, and a lower level with dinoturbation (Madeira and Dias, 1983; Lockley et al., 1994a; Santos, 2003). At the Olhos de Água tracksite (Óbidos), theropod and ornithopod trackways of Aptian–Albian age were described by Mateus and Antunes (2003).

Table 1
Cretaceous dinosaur tracksites known in Portugal.

Tracksite	Age	Trackmakers	References
Carenque–Pego Longo	Cenomanian	Theropoda and ?Ornithopoda	Santos et al. (1991, 1992)
Olhos de Água	Aptian–Albian	Theropoda and Ornithopoda	Mateus and Antunes (2003)
Praia Grande	Early Aptian	Sauropoda, Theropoda and Ornithopoda	Madeira and Dias (1983); Lockley et al. (1994a); Santos (2003)
Santa	Early Barremian	Ornithopoda (Iguanodontia)	Santos et al. (2000a, b); Santos (2003)
Salema	Early Barremian	Theropoda and Ornithopoda (Iguanodontia)	Santos et al. (2000a, b); Santos (2003)
Lagosteiros B	Hauterivian	Theropoda and ?Ornithopoda	Antunes (1976); Santos et al. (1992); Meyer et al. (1994); Santos (2003)
Lagosteiros A	Berriasian	?Theropoda	Santos (2003)

It is also worth mentioning the Cenomanian Carenque–Pego Longo tracksite, situated near Sintra, which is the only Late Cretaceous dinosaur tracksite known in Portugal. This tracksite consists of a long bipedal dinosaur trackway. It was the world's longest dinosaur trackway (127 m) when first described (Santos et al., 1991, 1992). It comprises a sequence of subcircular tracks that is reinterpreted herein on the basis of additional ichnological evidence resulting from a better understanding of its particular preservational features.

So far only two Early Cretaceous dinosaur tracksites are known in the Algarve Basin. These are near Vila do Bispo, 17 km to the west of Lagos (Fig. 1, Table 1). In 1995, dinosaur footprints were discovered for the first time in this onshore area by Carlos Coke during a geological fieldtrip (Santos et al., 2000a). At that time, seven small tridactyl and mesaxonic footprints were identified in the eastern sector of Salema beach. Subsequent discoveries at this beach include an ornithopod trackway identified by high-school children during a fieldtrip organized by Celestino Coutinho in 1996. In 1997, ornithopod trackways were found at Santa beach by Sebastião Pernes (Santos et al., 2000a).

In this paper we discuss the palaeobiological significance of the *Iguanodontipus* tracks and their association with specific marginal-marine depositional environments. At the same time, as a result of their location and age, these new findings also have implications for the palaeobiogeographical distribution presently assumed for the Early Cretaceous Iguanodontia of the Iberian Peninsula and southwestern Europe.

2. Material and methods

Non-metrical and metrical ichnological parameters were considered to characterize tridactyl tracks and trackways. The first provides indirect evidence of anatomical manus and foot features such as marks of pads and interdigital webs, heel shape and the shape of distal claws (rounded or sharp). The metrical parameters are: L, total footprint length; W, footprint width; λ, stride; S, step; TW, trackway width; γ, pace angulation. Two angular parameters are also considered: α, angle measured between the axis of digits II and III; β, angle measured between the axis of digits III and IV (e.g., Leonardi, 1987; Moratalla et al., 1988; Thulborn, 1990; Lockley, 1991; Moratalla, 1993).

The measurements were made on each of the ornithopod tracks and trackways at the Santa and Salema tracksites using these parameters. The Salema tracksite initially yielded eight ornithopod footprints, but recent studies have led to the accumulation of new data and the description of at least 13 very lined-up footprints. Six footprints are clearly tridactyl and mesaxonic. The others have an almost subcircular shape and do not reveal any morphological features. At the Santa tracksite there is one main level with at least four trackways and also some isolated footprints in a total of 16 tracks.

It was considered important to make a cast of the best footprint assigned to the *Iguanodontipus* isp. discovered at the Santa tracksite, because this outcrop is being continually damaged by marine coastal erosion. This cast is part of the collections of the Museu Nacional de História Natural e da Ciência (Universidade de Lisboa), reference MNHN.UL.II 513.

3. Geographical and geological settings

The two Early Cretaceous dinosaur tracksites in the Algarve Basin (Santos et al., 2000a, b) are present in coastal exposures of the western sector, near the village of Salema (Vila do Bispo, southwest Algarve). They consist of two track levels preserved on the beach together with a set of three others at Santa beach, a small bay 2 km to the west (Fig. 2).

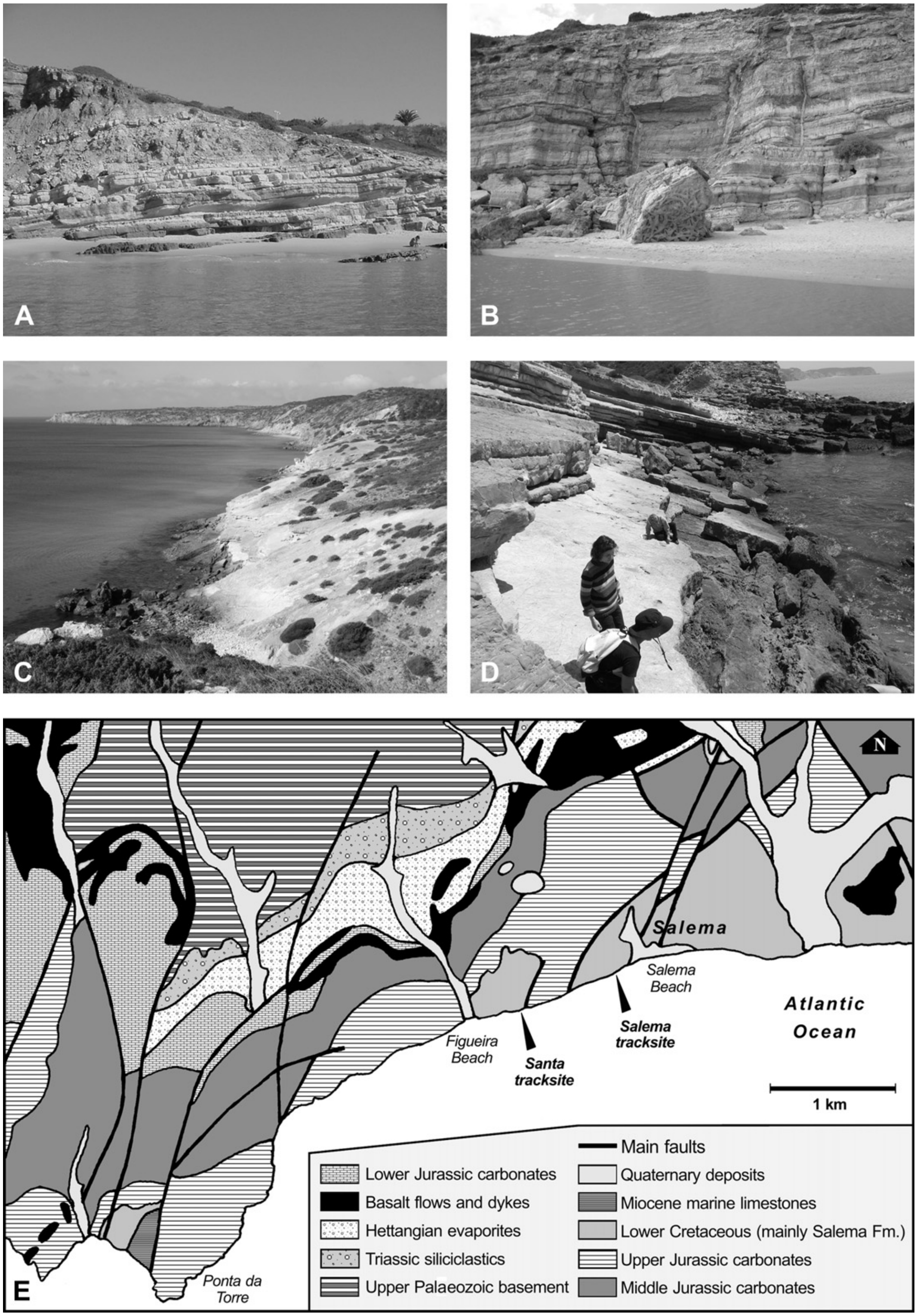

Fig. 2. General aspects of the dinosaur tracksites studied. A, B, succession of nodular limestones and marls with shallow marine benthic fauna, regressive beds with *Ophiomorpha* pavements, and thick dolomitic strata and algal-laminated layers from the west sector of the Salema beach (Vila do Bispo, southwest Algarve). C, succession of thick massive or laminated dolomitic beds at Santa beach (west of Salema beach), correlative to the regressive upper half of the sequence S2 with ornithopod tracks. D, Santa tracksite heavily weathered by tidal erosion. E, simplified geological sketch of the Mesozoic border of the western Algarve showing the sector of the Salema beach and the location of the dinosaur tracksites described in the text; adapted from the Map 52-A (Portimão) of the Geological Map of Portugal, scale 1:50000, of the Serviços Geológicos de Portugal (Rocha et al., 1983).

These areas with steep sea cliffs of limestone and massive dolomitic beds are at the western end of a nearly 15 km of continuous coastal exposures of Lower Cretaceous formations (Fig. 2). This succession is bounded to the east by Lower and Middle Miocene biocalcarenitic units (Lagos area), and by Middle and Upper Jurassic carbonates in the opposite direction (Sagres area).

Salema beach is a large sandy beach with easy access to the carbonate beds that crop out on the nearby slopes. The track levels are found on both sides of the beach, with emphasis on the ornithopod trackway set, which lies on massive beds on the western side near the wooden stairs used to access the cliff base. The succession exposed in this part of the section dips slightly towards the seashore and yields *Choffatella*-rich levels in the lower strata. At Santa beach there is a correlative succession of limestone and dolomitic beds that are steeply dipping towards the sea, allowing clear observation of bedding surfaces, some of which are bioturbated. Here, three dinosaur track levels were identified.

Both Salema and Santa beach successions containing the tracksites studied belong to the upper part of the Salema Formation (Rey, 1986, 2006a, 2010), an uppermost Hauterivian–Lower Barremian unit that correlates with the lower half of a thicker dolomitic succession of Barremian age, previously named "Margas, dolomias e calcários com *Choffatella decipiens*" Formation (Rey and Ramalho, 1973–1974; Rey, 1983). This designation was also used in the geological map of the area: Map 52-A (Portimão) of the Geological Map of Portugal, scale 1:50000, of the Serviços Geológicos de Portugal (Rocha et al., 1983). The lithology and micropalaeontological assemblages of this unit show many analogies with the "Calcários e margas com *Choffatella*" Formation known from the Upper Hauterivian–Lower Barremian of Cabo Espichel, Cascais and Ericeira, on the southern onshore part of the Lusitanian Basin (Rey, 1972, 2006b, 2010; Rey and Ramalho, 1973–1974).

From a sequence stratigraphical point of view, the Salema Formation records a regressive trend on the local and regional sedimentary settings. The succession begins with inner platform marine carbonates with diverse benthic microfauna, and gradually changes upwards to marginal-marine, inner-shelf carbonates with dolomitic beds, and mixed nearshore carbonate-siliciclastic lithofacies with a scarce brackish fauna of medium to low salinity biomarkers such as *Glauconia* and cerithoid gastropods. The dinosaur track levels occur in the upper half of this second-order sequence (Rey, 1986) as part of a succession of massive or ripple-laminated thick strata compatible with an Early Barremian tidal-flat environment. The upper boundary of this unit is a basin-wide unconformity with a low angular discordance related to an intra-Barremian tectono-sedimentary event that deformed earlier units of the active margin (Rey et al., 2006; Rey, 2010).

Besides this unconformity it is also relevant to note that the overall Cretaceous onshore record in the Algarve Basin, especially on its central and western sides, is comparatively more incomplete than the correlative succession of the adjacent Lusitanian Basin (Rey, 2006b, 2009, 2010; Dinis et al., 2008). The regional stratigraphical setting is almost restricted to the Berriasian–Aptian interval (Rey and Ramalho, 1973–1974; Rey, 1983), and marked by a scarcity of suitable biostratigraphical markers and several basin-wide lacunas, including an extensive Upper Valanginian–Lower Hauterivian sedimentary gap (Rey, 1983). This rather incomplete stratigraphical succession dominated by shallow water facies clearly suggests a very marginal onshore record, as well as a basin history where tectonic events often masked the eustatic signature.

Fig. 3 illustrates a detailed section of the Salema cliffs (western side) in order to indicate precisely the stratigraphical and palaeo environmental settings of the ornithopod track level. The lower part of the succession with *Chofatella* concentrations is partly masked by modern beach sands, but the remaining fraction consists of 34 m of well-exposed beds organized in several parasequences and third-order sequences (S1–S4), showing an overall regressive trend. S1 consists of nodular limestones and marls with a shallow-water benthic fauna and regressive beds with *Ophiomorpha* pavements in the upper part of the sequence (Figs. 2A, B, 3). S2 is dominated by thick dolomitic beds, sometimes intercalated with algal-laminated layers. The main ornithopod track level lies at the top of bed 50. Dolomitic strata also prevail within the S3 sequence, but the thick beds of massive dolomite are less frequent and there is a small fauna of brackish molluscs. S4 also shows a transition to laminated marly strata with laminated algal layers and small molluscs that seem to indicate less restricted environmental conditions.

Finally, the succession exposed at Santa beach is reduced to several metres of thick massive or laminated dolomitic beds, which correlate with the regressive upper half of the S2 sequence where ornithopod footprints were identified at the Salema tracksite. There are also several beds with *Ophiomorpha* and bioturbation. Along this sedimentary sequence, dinosaur tracks were identified in three main track levels constituting the Santa tracksite described here, as well as at other levels showing scattered ornithopod footprints, isolated or in sets.

4. Description of the Early Cretaceous ornithopod tracks

4.1. Salema tracksite

In the western sector of Salema beach at the surface (Fig. 2A), there is a horizontal track level situated below the local school (Escola Básica do 1° Ciclo de Salema) where a sequence of subcircular and tridactyl marks (SAL1-T1) was documented (Santos et al., 2000a, b; Santos, 2003). It is a trackway with at least 13 very lined-up footprints (the inner width of the trackway is almost zero) with a pace angulation value of about 170° (Fig. 4). Although these impressions are quite degraded because of the constant marine erosion, we recognize six of them as clearly tridactyl and mesaxonic footprints. They are as long (38 cm) as wide (37 cm) and present short toes with rounded distal ends and symmetrical heel marks, like those attributed to ornithopod dinosaurs. The interdigital angles range from 30 to 40°. The other footprints are almost subcircular in shape and do not reveal any morphological features. Step values were measured on this trackway and it is notable that the step shortens. This is more obvious when the stride length is measured between the most distal points of digits III. The average step and stride values are about 70 cm and 1.4 m respectively.

Other track levels with theropod footprints are exposed along the cliff at Salema beach (Santos et al., 2000a; Santos, 2003), but their description is beyond the scope of this paper.

4.2. Santa tracksite

This tracksite, located at Santa beach, was discovered by Sebastião Pernes in 1997, and at that time two track levels were identified (Santos et al., 2000a, b). New discoveries were made during further fieldwork. Beatriz Oliveira identified a third track level 50 cm above the main one. More recently, to the east of this tracksite (Fig. 2C, D) Sebastião Pernes identified and photographed some new, isolated and paired, ornithopod footprints exposed at three other levels in the same sedimentary succession with *Ophiomorpha* burrows. Track level 1 at the Santa tracksite (SAN1) has an extensive intertidal exposure where the footprints are extremely eroded and all that exists today is evidence of dinoturbation and one isolated tridactyl track. It is longer (75 cm) than wide (65 cm). Toe prints II and III have a sharp distal end whereas toe print IV has a rounded distal end (Fig. 5A). Toe print III is slightly bent. The poorly preserved morphology of this track does not allow us to describe it better.

We have also seen poorly preserved crescent-shaped marks, which could be sauropod manus impressions. However, a problem arises here because the track level area is too confined to permit us to find a trackway. The tracks cannot be reliably attributed to sauropods because of the poor print morphology. Some marks are quite similar to sauropod manus prints, but erosion can produce

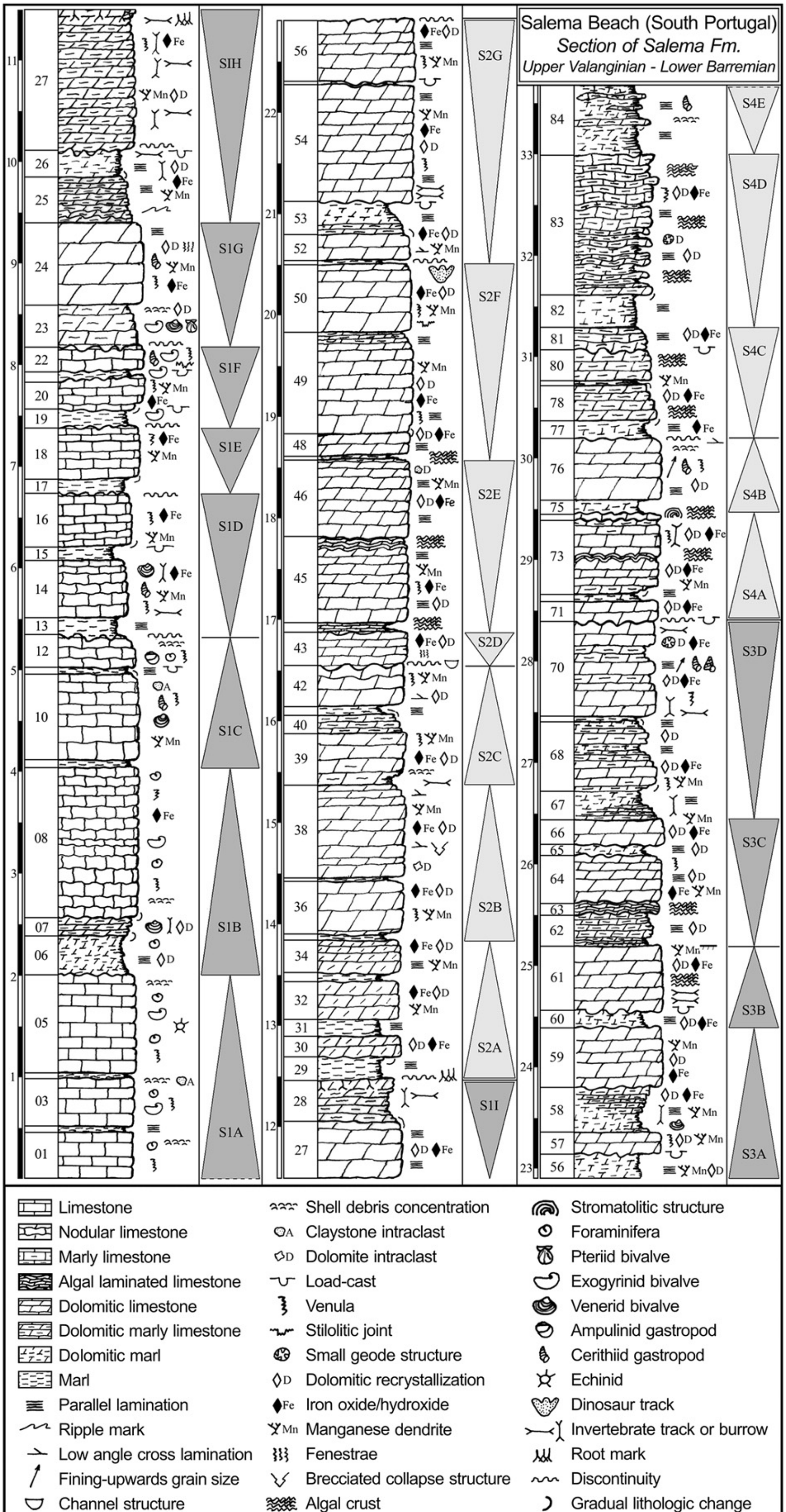

Fig. 3. Detailed section of the cliffs in the western side of the Salema beach (Vila do Bispo, southwest Algarve), with precise stratigraphical and palaeoenvironmental settings of the ornithopod track level.

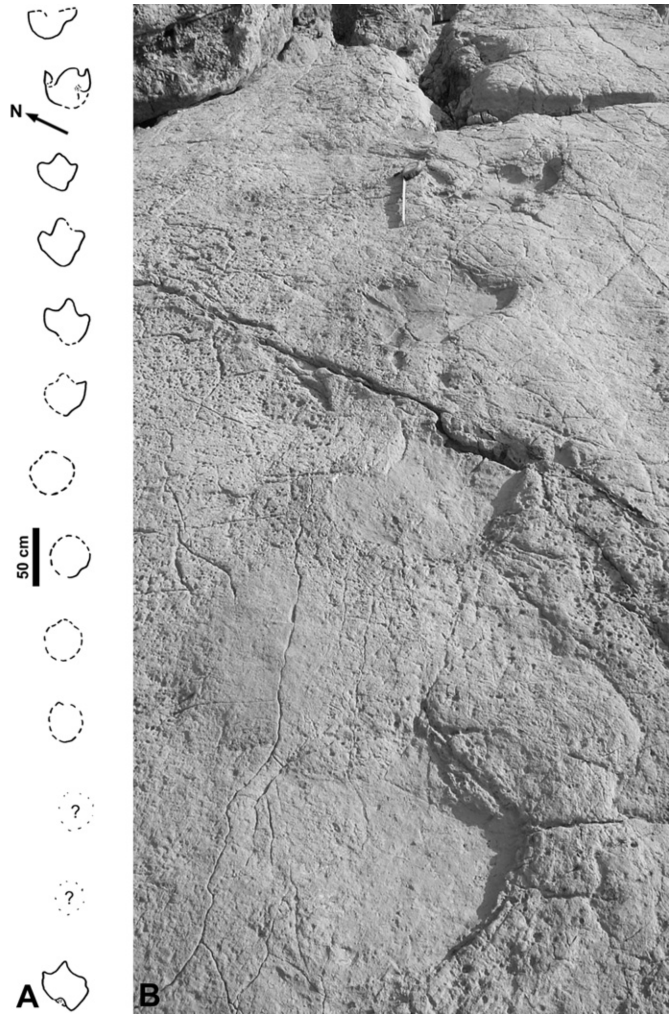

Fig. 4. Trackway of an ornithopod dinosaur at the Salema tracksite (Vila do Bispo, southwest Algarve). A, very lined-up sequence of tridactyl and subcircular impressions (SAL1-T1). B, photograph of a trackway segment.

strange morphologies. It is not prudent, therefore, to suggest the presence of these dinosaurs in the Algarve Basin during the Early Cretaceous based only on these marks. It is also possible to find circular marks defined by a groove, similar to a wrinkle, without a particular distribution pattern. We think that these may be atypical undertracks.

One metre above this dinoturbated level lies track level 2 (SAN2), which comprises at least four trackways and some isolated footprints. SAN2-1 is an isolated tridactyl and mesaxonic footprint, 30 cm long by 30 cm wide (Fig. 5B). It has a symmetrical and U-shaped heel mark and toe impressions with rounded distal ends.

Trackway 1 (SAN2-T1) is at the edge of this level and consists of four tridactyl and mesaxonic footprints, three of which are incompletely preserved (Fig. 5C). These footprints, 32 cm long by 26 cm wide, are rotated inward, have oval toe prints with rounded distal ends, and the last in the sequence has a symmetrical heel mark with two indentations. The interdigital angle values in these footprints are: α, about 20°; β, about 30°. The step and stride values are about 89 cm and 1.7 m, respectively. The pace angulation value is about 140–150°.

Trackway 2 (SAN2-T2) is a sequence of six footprints, but only the first four are represented (Fig. 6A, B). The fifth print is underneath a block of rock that lies over track level 2 and has the same morphology as the others that are behind it. The last footprint is deformed, probably by the passage of another dinosaur whose trackway is not completely preserved. The first impression is partially preserved and represented by the dotted line in Fig. 6. In general, these footprints are slightly rotated inwards, with a form as long (41 cm) as wide (39 cm), and have a symmetrical heel mark with two indentations and oval toe prints with rounded distal ends. In the best-preserved footprint both interdigital angles are about 30°. The step and stride values are about 1 and 1.9 m, respectively. The pace angulation value is about 130–140°.

There are at least two other trackways (SAN2-T3 and SAN2-T4) with a similar footprint morphology and the same trackway pattern as SAN2-T2 (Fig. 6C). The step and stride values are about 1.2 and 2.3 m, respectively. The pace angulation value is about 140–147°.

At this tracksite it is possible to recognize the characteristic morphology of ornithopod footprints in trackways 1 (Fig. 5C), 2 (Fig. 6A, B), 3 and 4 (Fig. 6C).

Other poorly preserved subcircular and crescent-shaped impressions can be recognized on this track level, but they do not have morphological characteristics that support trackmaker identifications and we cannot find a revealing trackway pattern.

About 50 cm above the main track level is another surface (SAN3) with dinosaur tracks. This third track surface is barely visible. Through a small space left by differential erosion of the marly bed 15 cm thick that overlies it, it is possible to identify a sequence of apparently rounded impressions and one isolated small tridactyl and mesaxonic footprint impression (12 cm long by almost 10 cm wide and slender toe prints) of an undetermined biped dinosaur.

5. Discussion

There are several aspects of the Santa tracksite to be pondered. According to the dinoturbation index proposed by Lockley and Conrad (1989) and Lockley (1991), we consider that track level 1 (SAN1) is an area of moderate dinosaur trampling. The long exposure to tidal erosion has left only one footprint with a poorly preserved morphology (Fig. 5A). This morphology might suggest a theropod trackmaker if a close look is taken at the sharp distal ends of toes II and III and the slightly bent toe print III. However, owing to its poor preservation, there are insufficient characters to distinguish it as either a theropod or an ornithopod footprint. Thus, we prefer to assign this track to an undetermined biped dinosaur.

Track level 2 (SAN2) consists of footprints with inward rotation that are characterized by being almost as long as wide, and in having a symmetrical U-shaped heel mark with two indentations, and short and wide toe marks (oval shaped) with rounded distal ends (Fig. 6B). The morphological and stratigraphical resemblance of these footprints to those of the ichnogenus *Iguanodontipus* from the Berriasian of Dorset (southern England) and defined by Sarjeant et al. (1998) is remarkable, so we attribute them to the same ichnogenus.

There are some Early Cretaceous tracksites in the Iberian Peninsula from which ornithopod tracks have been described. Footprints most similar to those of the Santa beach track record were described by Moratalla and Hernán (2008) at the Los Cayos tracksite (Cornago, La Rioja, Spain) of Barremian–Early Aptian age, and Pascual-Arribas et al. (2009) at the Las Cuestas I tracksite (Santa Cruz de Yanguas, Soria, Spain) of Berriasian age. Both were assigned to the ichnogenus *Iguanodontipus*. Trackway STC-1 (Pascual-Arribas et al., 2009, fig. 4) specially resembles trackway 2 (SAN2-T2) of the main level at the Santa tracksite, here attributed to *Iguanodontipus* isp.

There are other European Early Cretaceous tracksites with ornithopod footprints attributed to *Iguanodontipus* isp. with a widespread temporal distribution throughout the Early

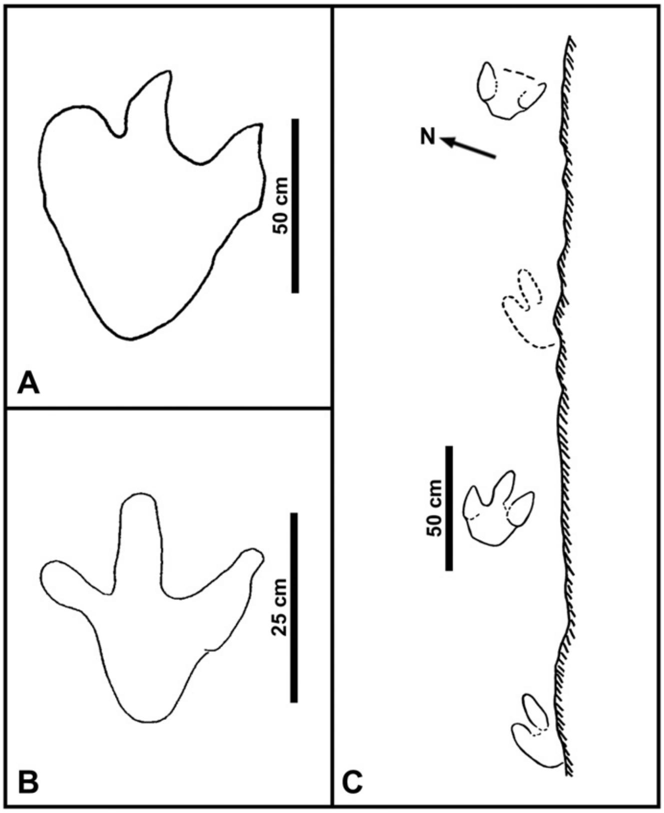

Fig. 5. Tridactyl tracks from the Santa tracksite (Vila do Bispo, southwest Algarve). A, left footprint of an undetermined biped dinosaur (SAN1-1) recognized in track level 1 with dinoturbation. B, a possible ornithopod isolated footprint at the main track level (SAN2-1). C, trackway 1 (SAN2-T1) with one well-preserved tridactyl footprint from the main track level (modified from Santos, 2003).

Cretaceous, i.e., from Berriasian to Late Aptian (Table 2). Wings et al. (2005) reported the existence of five trackways in the Berriasian of Münchehagen (northern Germany) and assigned them to *Iguanodontipus*. This ichnogenus was also identified in Wealden strata at

Table 2
Early Cretaceous European dinosaur tracksites (except the Portuguese ones) with the ichnogenus *Iguanodontipus*. **Iguanodontipus* holotypes.

Tracksite	Age	Location	References
Risleten quarry	Late Aptian*	Switzerland	Meyer and Thüring (2003)
Los Cayos	Barremian–Early Aptian	Spain	Moratalla and Hernán (2008)
Lee Ness, Cooden and Hanover Point	Valanginian–Early Aptian	England	Goldring et al. (2005)
Münchehagen	Berriasian	Germany	Lockley et al. (2004)
Münchehagen	Berriasian	Germany	Wings et al. (2005)
Obernkirchen	Berriasian	Germany	Diedrich (2004)
Las Cuestas I	Berriasian	Spain	Pascual-Arribas et al. (2009)
Dorset	Berriasian*	England	Sarjeant et al. (1998)

Lee Ness and Cooden in south-east England and Hanover Point on the Isle of Wight (Valanginian–Lower Aptian) by Goldring et al. (2005). Other ornithopod trackways with a general morphology that resembles the Santa beach track record were described by Diedrich (2004) from the Obernkirchen tracksite in the Berriasian of northwest Germany. Meyer and Thüring (2003) also reported ornithopod tracks of Late Aptian age from the Schrattenkalk Formation of the Swiss Central Alps, in Risleten quarry, and attributed them to iguanodontids. However, these differ in the general morphology from the Santa beach track record. The ornithopod footprints at Santa beach resemble some of the Berriasian ornithopod tracks at Dinosaurier Freilichtmuseum Münchehagen (Germany), which occur as natural casts and were described by Lockley et al. (2004), who thought they might be referred to *Iguanodontipus*.

In the Late Jurassic track record of Europe there are some iguanodontid-like footprints of uncertain affinity, such as those from Portugal (Mateus and Milàn, 2005, 2008), Spain (Piñuela Suárez, 2000; García-Ramos et al., 2002) and Germany (Diedrich, 2011). As these tracks do not have morphological characteristics that allow their confident assignation to *Iguanodontipus*, and because it is also possible that they were not made by an

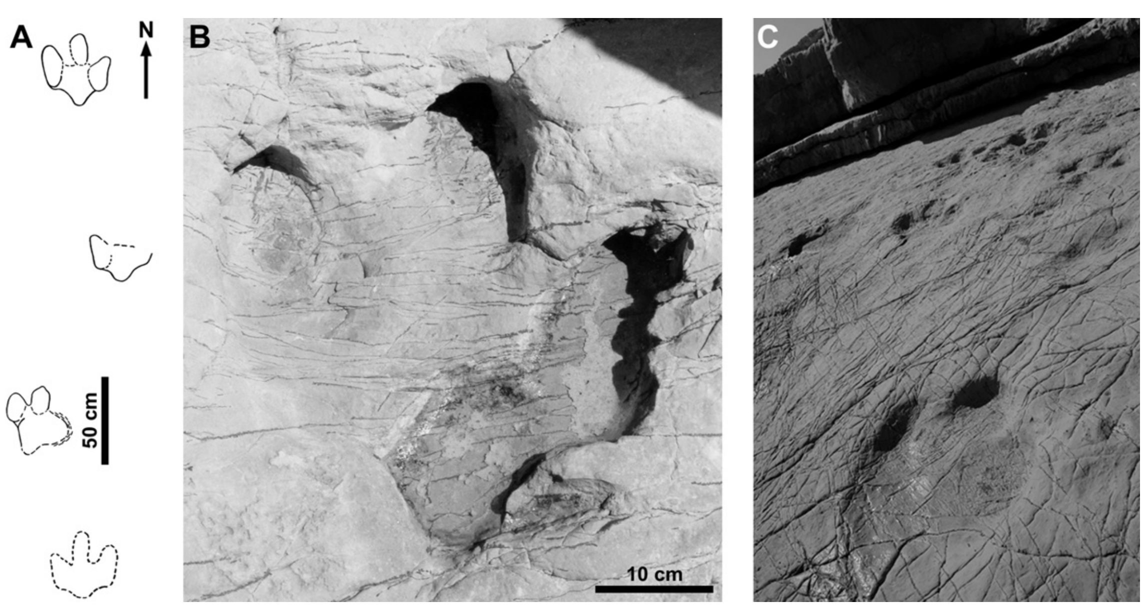

Fig. 6. Ornithopod footprints (*Iguanodontipus* isp.) at the main level of the Santa tracksite (Vila do Bispo, southwest Algarve). A, sketch of trackway 2 (SAN2-T2) with four of six footprints (modified from Santos, 2003). B, footprint 4 from trackway 2 (SAN2-T2). C, ornithopod trackways SAN2-T3 and SAN2-T4 from the main track level of the Santa tracksite (photograph by Luís Quinta).

iguanodontian dinosaur, we consider that they differ from the track record of the Santa tracksite attributed to this ichnogenus.

The morphological features of the footprints from the Santa tracksite (Figs. 5B, C, 6) allow its attribution to *Iguanodontipus* and suggest iguanodontian dinosaur trackmakers (Iguanodontia). These dinosaurs would have had posterior limbs with a hip height of about 1.8 to 2.4 m and moved at speeds ranging between 3.1 and 4.4 km/h, based on the equations of Alexander (1976).

The study of the European Early Cretaceous basal iguanodonts is in continuous review and quite a few osteological remains assigned to *Iguanodon* have been reassigned to new genera (e.g., Norman, 2002, 2004, 2010; Norman and Barrett, 2002; Paul, 2006, 2008; Naish and Martill, 2008; Galton, 2009; Carpenter and Ishida, 2010; McDonald et al., 2010; McDonald, 2012).

Ornithopod remains have been known in Portugal since the nineteenth century in the coastal cliffs of Boca do Chapim, to the north of Cabo Espichel, near Sesimbra (see Rodrigues et al., 2008 for a historical review of the vertebrate fauna of this site). These earliest discoveries were reported by Sauvage (1896, 1897–1898, 1898). *Iguanodon mantelli* Meyer, 1832 was recognized by this author and its presence was later confirmed by de Lapparent and Zbyszewski (1957). Galton (1994) provided a new description of these ornithopod remains and assigned them to *Iguanodon* sp. Since then, a few publications about the dinosaurs of Boca do Chapim have appeared in which their taxonomy is reviewed. For example, Ruiz-Omeñaca and Canudo (2003, 2004) confirmed that the ornithopod remains at this site belong to *Iguanodon* sp. and Antunes and Mateus (2003) supported this assignation.

In Spain, ornithopod osteological remains from several provinces were attributed traditionally to the genus *Iguanodon* and to Iguanodontidae indet. or Iguanodontoidea indet. (e.g., Ruiz-Omeñaca et al., 1998, 2004, 2009; Ruiz-Omeñaca and Canudo, 2003, 2004; Torcida Fernández-Baldor et al., 2006; Contreras-Izquierdo et al., 2009; Ruiz-Omeñaca, 2011). Recent studies have led to the description and assignation of these ornithopod remains to the clade Iguanodontoidea non-Hadrosauridae (sensu Norman, 2002, 2004). Ruiz-Omeñaca and Canudo (2003) presented a comprehensive synthesis of the ornithischian dinosaurs from the Lower Cretaceous (Hauterivian–Aptian) of the Iberian Peninsula, referring to the existence of remains of hypsilophodontids, dryosaurids, iguanodontids, possible heterodontosaurids and ?hadrosauroids. *Iguanodon bernissartensis* Boulenger, 1881 and *Delapparentia turolensis* Ruiz-Omeñaca, 2011 from the Spanish Lower Cretaceous dinosaur osteological record are accepted as Iguanodontoidea species (e.g., Sanz et al., 1982; Gasulla et al., 2009; Ruiz-Omeñaca, 2011). The synthesis presented by Ortega et al. (2006) considered that ornithopods like hypsilophodontids, dryosaurids and iguanodontids (*Iguanodon*) are represented in the Lower Cretaceous of the Iberian Peninsula and that *Iguanodon*, represented by *Iguanodon bernissartensis*, was probably the most common dinosaur in Barremian and Aptian times. Recently, Norman (2010) presented a review of the history, anatomy and taxonomy of the Hauterivian–Early Aptian iguanodontian dinosaurs from southern England and concluded that the Upper Wealden Group (Hauterivian–Lower Aptian) contains evidence of *Iguanodon bernissartensis* and *Mantellisaurus atherfieldensis*. Therefore, according to these data, dinosaurs like *Iguanodon* and *Delapparentia* or other taxa that can be determined based on classic or new material, are possible trackmakers of the ichnogenus *Iguanodontipus*. Thus, we conclude that the footprints at the Santa tracksite, assigned to *Iguanodontipus*, were quite possibly made by one of these ornithopod dinosaurs.

Santa beach track level 3 (SAN3) shows dinoturbation and there is evidence of a small undetermined bipedal dinosaur, but we cannot discard the possibility of an ornithopod or theropod affinity.

The most interesting ichnological feature in the western sector of Salema beach is the trackway SAL1-T1 with at least six tridactyl footprints, as long as wide, plus four subcircular impressions without toe marks (Fig. 4). Although they have been tridactyl tracks, like the others, marine erosion has degraded them. The

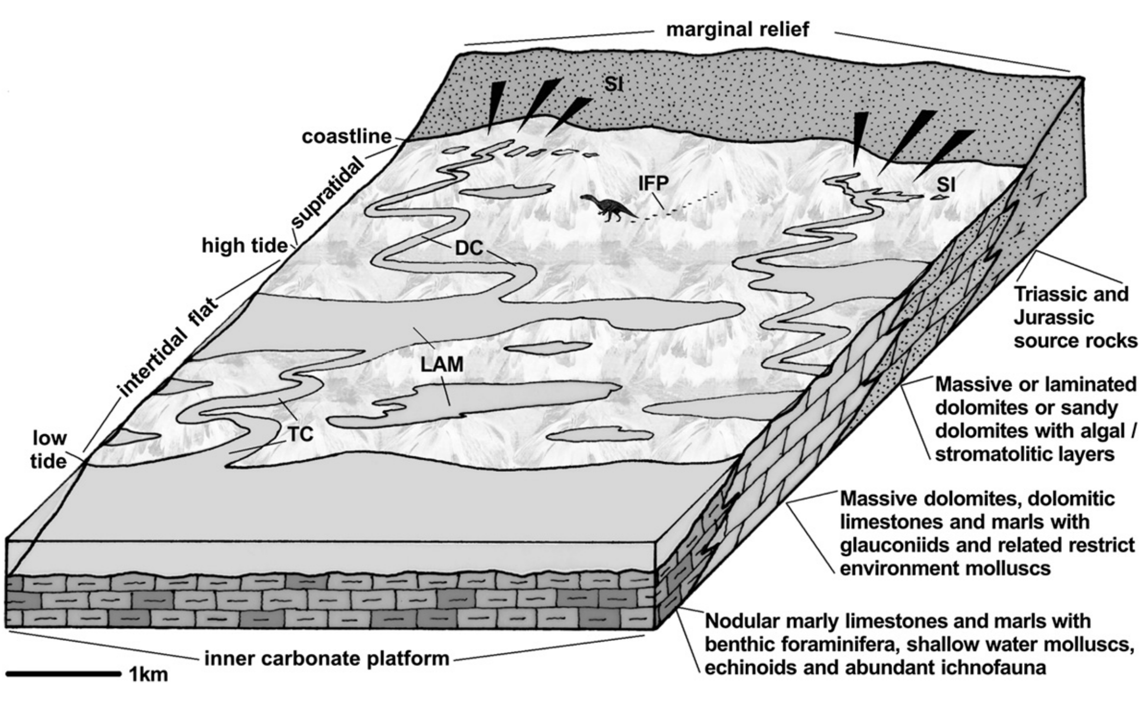

Fig. 7. Schematic palaeoenvironmental reconstruction for the Lower Barremian carbonate platform of the Mesozoic Algarve Basin showing an idealized tidal-flat model with combined onlap and offlap features for the sector of Salema beach (Vila do Bispo, southwest Algarve) and a trackway of an iguanodontian dinosaur. The marginal reliefs are interpreted as uplifted Triassic redbeds and Jurassic limestones and siliciclastics from the western sector of the Mesozoic Algarve Margin. IFP, iguanodontian footprints; SI, siliciclastic influx; DC, distributary channels; LAM, laminated algal mats and restricted lagoons; TC, tidal channels with seawater influx.

morphology of the best-preserved tridactyl impressions allows us to attribute them to an ornithopod, possibly an iguanodontian dinosaur with a hip height of about 2.2 m that could have been moving at 1.7 km/h, based on Alexander's (1976) equations. This trackway was the first evidence of well-preserved ornithopod dinosaur footprints in Portugal (Santos et al., 2000b).

The variation in footprint morphology observed along this trackway demonstrates that characteristic ornithopod footprints can be transformed into subcircular impressions when exposed to erosion or if they are not preserved as true tracks (sensu Lockley, 1991). Therefore, this particular trackway shows how erosion changes track morphology and allows the attribution of subcircular impressions at least to ornithopod footprints. Where preservation state does not change the value of pace angulation and the high pace angulation value indicates bipedal trackways (e.g., Santos et al., 1992), we can conclude that a sequence of subcircular tracks having a pace angulation of high value can almost certainly be assigned to an ornithopod trackmaker.

Several authors have brought to light new data from controlled laboratory track simulations in order to understand better the effects of erosion on the size and morphology of dinosaur tracks, as well as to evaluate how the shape of the footprint deteriorates with depth in different substrates (e.g., Gatesy et al., 1999; Gatesy, 2003; Milàn et al., 2004; Henderson, 2006; Milàn, 2006; Milàn and Bromley, 2006; Manning, 2008; Jackson et al., 2009; Marty et al., 2009). The variation in footprint morphology along the trackway at the Santa tracksite reveals how an ornithopod footprint can become a rounded track. With this example it is clear that footprints attributed to iguanodontians can be subcircular in shape since they were originally as wide as long. The ornithopod trackway at the Salema tracksite with subcircular and tridactyl impressions is important for understanding sequences of subcircular impressions with a high pace angulation value in the track record, such as those at the Carenque–Pego Longo (Sintra) and Lagosteiros (Cabo Espichel, Sesimbra) tracksites (Santos et al., 1992). Thus, the ornithopod track record from the onshore southwest Algarve Basin also supports the interpretation that the main trackways at these sites were very likely to have been made by bipedal ornithopods, such as iguanodontian dinosaurs. Therefore, taking into account information presented in these earlier publications, iguanodontians were probably one of the commonest dinosaurs in the Iberian Peninsula during the Barremian–Aptian period.

From a palaeoecological point of view, the composition of the facies suggests that the dinosaur tracks in the southwest Algarve Basin were produced in a marginal-marine environment (Fig. 7) where a large tidal flat associated with the inner shelf of a nearby carbonate platform was periodically exposed (Shinn, 1983). The warm and dry local climate also favoured the deposition of

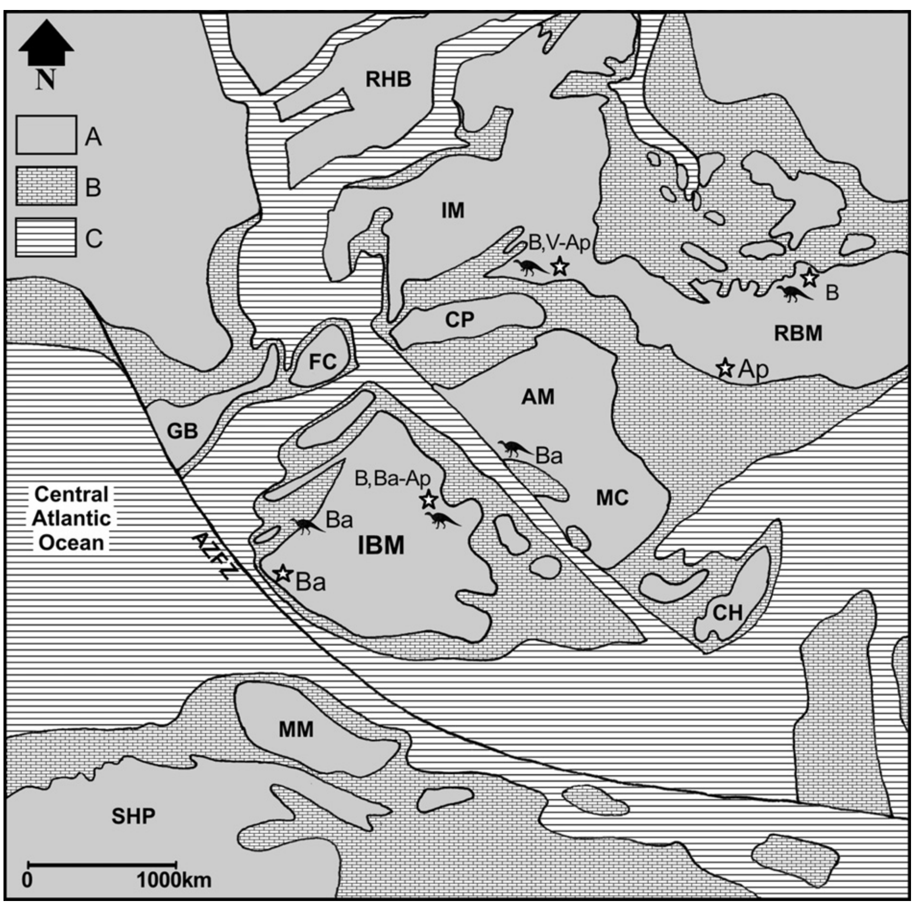

Fig. 8. Simplified palaeobiogeography of Southern and Central Europe and adjacent areas during the Berriasian–Aptian interval, with the known occurrences of *Iguanodontipus* tracksites (white stars) and iguanodontian fossil sites (dinosaur silhouettes). Main shallow and emerged areas: A, emerged massifs; B, shallow platforms; C, adjacent marine and oceanic domains; AM, Armorican Massif; CH, Corsica-Sardinia High; CP, Cornish Platform; FC, Flemish Cap; GB, Grand Banks; IBM, Iberian Massif; IM, Irish Massif; MC, Massif Central; MM, Morocco Meseta; RBM, Rhenish-Bohemian Massif; RHB, Rockall and Hatton banks; SHP, Sahara Platform. Other area: AZFZ, Azores fault zone (adapted from Ziegler, 1988). Ages of *Iguanodontipus* tracksites: B, Berriasian; V, Valanginian; Ba, Barremian; Ap, Aptian. Dinosaur data from Sarjeant et al. (1998), Santos et al. (2000a, b), Antunes and Mateus (2003), Meyer and Thüring (2003), Ruiz-Omeñaca and Canudo (2003, 2004), Santos (2003), Diedrich (2004, 2011), Lockley et al. (2004), Goldring et al. (2005), Wings et al. (2005), Moratalla and Hernán (2008), Pascual-Arribas et al. (2009).

intertidal and upper infralittoral dolomitic sediments, much as in modern sabkha environments (McKee and Ward, 1983). The abundance of algal-laminated layers interbedded with massive levels of dolomite can also be related to the existence of algal mats in channels and ponds within the tidal flat.

The occurrence of iguanodontian dinosaur footprints in the Algarve Basin also indicates that these ornithopod dinosaurs had an Early Barremian biogeographical range that extended to the south of the Iberian Massif (Fig. 8). Nevertheless, there are previous records of *Iguanodontipus* tracks in the north of Spain at least from the Berriasian (Pascual-Arribas et al., 2009; Castanera et al., 2012), suggesting that this group of dinosaurs appeared no later than the beginning of the Cretaceous Period in the Iberian Massif as a result of coastal migration across the nearby European islands of the Armorican, Central, Irish and Rhenish-Bohemian massifs, where iguanodontian dinosaurs and footprints of this age have also been recorded (Diedrich, 2004; Lockley et al., 2004; Goldring et al., 2005; Wings et al., 2005). These coastal routes that allowed the interchange of land species between emerged areas of the Central Europe and those from the Tethyan branch of the Southern Europe were mainly open during intervals of eustatic low stands, when a general progradation of landward sedimentary systems led to large intertidal-flat domains, sometimes acting as episodic bridges (Diedrich, 2011). The growing number of new finds confirms that these land bridges would have existed periodically depending on local geotectonic evolution, despite the more or less extensive submerged areas that separated the European massifs during the Early Cretaceous (Dalla Vecchia, 2002; Meyer and Thüring, 2003; Gheerbrant and Rage, 2006).

The possibility of an additional intercontinental land bridge between southern Iberia and the North African domains of Gondwana seems unlikely before the Late Barremian–Early Aptian because of the divergent geotectonic settings for most of the "Neocomian" and different dinosaur faunas in these two continental areas (Canudo et al., 2009). The tidal-flat and carbonate inner-shelf domains reported for the Algarve Basin were, therefore, directly connected to the open ocean and did not allow any land-vertebrate migrations. Nevertheless, several authors have supported the possibility of the existence of a route across the Apulian Plate (Nicosia et al., 2007; Petti et al. 2008; Sacchi et al., 2009; Torcida Fernández-Baldor et al., 2011) at least since the Late Barremian and during the Aptian (Canudo et al., 2009), when shallow carbonate shelves were widespread between this area and North Africa. A better understanding of European ornithopod palaeo biogeography is needed to determine whether or not this interpretation can be substantiated.

6. Conclusions

Fieldwork in the southwest Algarve Basin has led to the first dinosaur track discoveries in this area. Well-preserved iguanodontian footprints have been described for the first time in Portugal and *Iguanodontipus* isp. was identified at the Santa tracksite. The existence of several track levels along the sedimentary sequence described here with ornithopod tracks suggests that this dinosaur group was well-represented in the Iberian Peninsula and southwestern Europe during the Early Cretaceous. We regard this as compelling evidence of the frequent occurrence of *Iguanodon* in Portugal, thus supporting the recovery of isolated and fragmentary remains of this dinosaur (five isolated teeth and few caudal vertebrae) from Boca do Chapim.

The trackways of the Santa tracksite reveal the presence of iguanodontian dinosaurs having posterior limbs with a hip height of 1.8–2.4 m that moved at speeds ranging from 3.1 to 4.4 km/h. *Iguanodon*, *Delapparentia* or other still unidentified or undescribed taxa from the Iberian Peninsula are the possible trackmakers of the footprints assigned to the ichnogenus *Iguanodontipus* and in this case the footprints from the Santa tracksite.

A single trackway at the Salema tracksite that comprises subcircular and tridactyl impressions attributed to an ornithopod, a possible iguandontian dinosaur, shows that ornithopod footprints, being as long as wide tridactyl impressions, result in subcircular impressions when they are eroded. Since it is known that a biped dinosaur trackway is characterized by having a high pace angulation value, we conclude that a sequence of subcircular footprints having a high value of pace angulation can almost certainly be assigned to an ornithopod trackmaker. This is a very significant record regarding trackmaker identification, when very lined-up sequences of subcircular footprints are found, such as those of the Carenque–Pego Longo and Lagosteiros tracksites in the Lusitanian Basin.

These dinosaur trackways are preserved in marginal-marine carbonate sediments of a large inner-shelf environment with shoals and intertidal-flat areas with algal mats, tidal channels and ponds, somewhat restricted brackish conditions, and dolomitic sedimentation related to a warm and dry climate.

The occurrence of this iguanodontian evidence also has implications for the palaeobiogeography of the group, because it shows that the Southern European range of these ornithopod dinosaurs reached the south of the Iberian Massif during the Early Barremian. This became possible after one or more earlier migratory events took place after the Berriasian, which are well-documented by records of *Iguanodontipus* tracks in the north of Spain. The successful opening of coastal bridges between Iberia and the nearby European emerged massifs was thus possible, but the hypothesis of an intercontinental route between Iberia and North Africa seems very unlikely, at least during the "Neocomian".

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