Dinosaur tracks from the Early Cretaceous (Albian) of Parede (Cascais, Portugal): new contributions for the sauropod palaeobiology of the Iberian Peninsula

V.F. Santos¹,²*, P.M. Callapez²,³, D. Castanera⁴, F. Barroso-Barcenilla⁵,⁶, N.P.C. Rodrigues¹, C.A. Cupeto⁷

¹Museu Nacional de História Natural e da Ciência, Rua da Escola Politécnica 58, 1250-102 Lisboa, Portugal
²Centro de Investigação da Terra e do Espaço da UC – CITEUC, Avenida Dr. Dias da Silva, 3000-134 Coimbra, Portugal
³Departamento de Ciências da Terra da Universidade de Coimbra, Largo Marquês de Pombal, 3001-401 Coimbra, Portugal
⁴Grupo Aragosaurus-IUCA, Paleontología, Facultad de Ciencias, Universidad de Zaragoza, Calle Pedro Curbuna 12, 50009 Zaragoza, Spain
⁵Departamento de Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, 28040 Madrid, Spain
⁶Grupo de Investigación IberCreta, Universidad de Alcalá de Henares, 28871 Alcalá de Henares, Spain
⁷Departamento de Geociências da Universidade de Évora, Rua Romão Ramalho 59, 7000-671 Évora, Portugal

e-mail addresses: vsantos@museus.ul.pt (V.F.S., *corresponding author); callapez@dct.uc.pt (P.M.C.); dcastanera@unizar.es (D.C.); fbarroso@geo.ucm.es (F.B.B.); nunopcrodrigues@museus.ul.pt (N.P.C.R.); cupeto@uevora.pt (C.A.C.)

Received: 17 January 2014 / Accepted: 18 December 2014 / Available online: 25 March 2015

Abstract

A recently discovered Early Cretaceous (early late Albian) dinosaur tracksite at Parede beach (Cascais, Portugal) reveals evidence of dinoturbation and at least two sauropod trackways. One of these trackways can be classified as narrow-gauge, which represents unique evidence in the Albian of the Iberian Peninsula and provides for the improvement of knowledge of this kind of trackway and its probable trackmaker, in an age when the sauropod record is scarce. These dinosaur tracks are preserved on the upper surface of a marly limestone bed that belongs to the Galé Formation (Água Doce Member, middle to lower upper Albian). The study of thin-sections of the beds C22/24 and C26 in the Parede section has revealed a microfacies composed of foraminifers, radiolarians, ostracods, corals, bivalves, gastropods, and echinoids in a mainly wackestone texture with biomicritic matrix. These assemblages match with the lithofacies, marine molluscs, echi- nids, and ichnofossils sampled from the section and indicate a shallow marine, inner shelf palaeoenvironment with a shallowing-upward trend. The biofacies and the sequence analysis are compatible with the early late Albian age attributed to the tracksite. These tracks and the moderate dinoturbation index indicate sauropod activity in this palaeoenvironment. Titanosaurs can be dismissed as possible trackmakers on the basis of the narrow-gauge trackway, and probably by the kidney-shaped manus morphology and the pes-dominated configuration of the trackway. Narrow-gauge sauropod trackways have been positively associated with coastal palaeoenvironments, and the Parede tracksite supports this interpretation. In addition, this tracksite adds new data about the presence of sauropod pes-dominated trackways in cohesive substrates. As the Portuguese Cretaceous sauropod osteological remains are very scarce, the Parede tracksites yields new and relevant evidence of these dinosaurs. Furthermore, the Parede tracksite is the youngest evidence of sauropods in the Portuguese record and some of the rare evidence of sauropods in Europe during the Albian. This discovery enhances the palaeobiological data for the Early Cretaceous Sauropoda of the Iberian Peninsula, where the osteological remains of these dinosaurs are relatively scarce in this region of southwestern Europe. Therefore, this occurrence is also of overall interest due to its impact on Cretaceous Sauropoda palaeobiogeography.

Keywords: Sauropod tracks, intertidal palaeoenvironment, Lower Cretaceous, upper Albian, Lusitanian Basin, Portugal

Resumen

El reciente descubrimiento de huellas de dinosaurios del Cretácico Inferior (início do Albiense tardio) en la playa de Parede (Cascais, Portugal) ha revelado evidencias de dinoturbación y al menos dos rastros de saurápolodas. Uno de ellos puede clasificarse como estrecho y representa la única evidencia de este tipo de rastros en el Albiense de la Península Ibérica. Estos nuevos datos permiten mejorar el conocimiento tanto de este tipo de rastros como de su posible productor, en una edad en la que el registro de saurápolodas es escaso. Las huellas de dinosaurios se localizan en un nivel de caliza margosa perteneciente a la Formación Galé (Miembro Água Doce, Albiense medio-base del
The sauropod track record from Portugal is well known in the ichnological literature, with significant sites from the Middle Jurassic (Santos et al., 1994, 2009) and the Late Jurassic (Lockley and Santos, 1993; Lockley et al., 1994; Mateus and Milân, 2005, 2010). However, the Praia Grande tracksite (Sintra, near Lisboa), which is early Aptian in age, has been so far the only record of sauropod tracks in the Cretaceous of Portugal (Santos et al., 2013a). The occurrence of sauropod tracks at Praia Grande has been noted by several authors (e.g. Lockley et al., 1994; Lockley and Meyer, 2000) and the detailed description of the site can be found in the unpublished PhD Thesis of Santos (2003). In the same way, the Spanish sauropod ichnological record has well-known tracksites from the Late Jurassic (Lockley et al., 2007), the Jurassic-Cretaceous (Tithonian-Berriasian) transition (Sanz et al., 1997; Castanera et al., 2010a, 2010b, 2011, 2012; Pascual-Aribas and Hernández-Medrano, 2011; Alcalá et al., 2012; 2014), the Early Cretaceous (mainly pre-Albian: Moratalla et al., 2003; Pérez-Lorente, 2003; Moratalla, 2009; Castanera et al., 2013), and the Late Cretaceous (Vila et al., 2005, 2008, 2013). The Spanish tracksites from Monte Grande (Albian, near Bilbao) and Yecla (Albian, Murcia) are the only ones from the “Mid Cretaceous” (Moratalla et al., 1994; Pérez-Lorente et al., 2006) in the entire Iberian Peninsula.

According to the classification of sauropod trackways into narrow and wide-gauge categories (Farlow, 1992; Lockley et al., 1994), the former have been considered as common during the Jurassic and scarce during the Cretaceous (Lockley et al., 1994; Wilson and Carrano, 1999; Wright, 2005; Mannon and Upchurch, 2010). Several works have associated the narrow-gauge trackways with diplodocids or non-titanosauriform sauropods, and the wide-gauge trackways with titanosaur/titanosauriform sauropods (Lockley et al., 1994; Wilson and Carrano, 1999; Wright, 2005; Mannon and Upchurch, 2010). Furthermore, Mannon and Upchurch (2010) registered a positive correlation of narrow-gauge trackways with coastal environments, and of wide-gauge trackways with inland environments. Significant Albian sauropod tracksites have been described in North America (Farlow et al., 1989, 2012; Pittman and Gillette, 1989; Pittman and Lockley, 1994), in Asia (Lim et al., 1989; Lee et al., 2000; Lee and Lee, 2006; Lockley et al., 2006), and in Europe (Moratalla et al., 1994; Dalla Vecchia and Tarlao, 2000; Pérez-Lorente et al., 2006). All of them have been classified into the wide-gauge (or intermediate category), with the exception of the sauropod trackway reported by Lee and Lee (2006) from Jag-eun Guhakpo, Korea (Mannon and Upchurch, 2010).

The Portuguese Cretaceous sauropod osteological record is reduced to some material from the Barremian marginal-marine beds of Boca do Chapim (north of Cabo Espichel, Sesimbra) described by Sauvage (1896, 1897-1898) and Lapparent and Zbyszewski (1957), and assigned to “Pleurocoelus valdensis” (Antunes and Mateus, 2003). The presence of this sauropod was also recognized in Spain, among other Early Cretaceous sauropods (for an overview on dinosaurs, especially sauropod remains, from the Iberian Peninsula, see: Ruiz-Omeñaca et al., 2004; Ortega et al., 2006; FCP-TD, 2009; Royo-Torres, 2009; Castanera and Canudo, 2011). Despite the fact that thyreophorans have been described in

---

1. Introduction

The sauropod track record from Portugal is well known in the ichnological literature, with significant sites from the Middle Jurassic (Santos et al., 1994, 2009) and the Late Jurassic (Lockley and Santos, 1993; Lockley et al., 1994; Mateus and Milân, 2005, 2010). However, the Praia Grande tracksite (Sintra, near Lisboa), which is early Aptian in age, has been so far the only record of sauropod tracks in the Cretaceous of Portugal (Santos et al., 2013a). The occurrence of sauropod tracks at Praia Grande has been noted by several authors (e.g. Lockley et al., 1994; Lockley and Meyer, 2000) and the detailed description of the site can be found in the unpublished PhD Thesis of Santos (2003). In the same way, the Spanish sauropod ichnological record has well-known tracksites from the Late Jurassic (Lockley et al., 2007), the Jurassic-Cretaceous (Tithonian-Berriasian) transition (Sanz et al., 1997; Castanera et al., 2010a, 2010b, 2011, 2012; Pascual-Aribas and Hernández-Medrano, 2011; Alcalá et al., 2012; 2014), the Early Cretaceous (mainly pre-Albian: Moratalla et al., 2003; Pérez-Lorente, 2003; Moratalla, 2009; Castanera et al., 2013), and the Late Cretaceous (Vila et al., 2005, 2008, 2013). The Spanish tracksites from Monte Grande (Albian, near Bilbao) and Yecla (Albian, Murcia) are the only ones from the “Mid Cretaceous” (Moratalla et al., 1994; Pérez-Lorente et al., 2006) in the entire Iberian Peninsula.

According to the classification of sauropod trackways into narrow and wide-gauge categories (Farlow, 1992; Lockley et al., 1994), the former have been considered as common during the Jurassic and scarce during the Cretaceous (Lockley et al., 1994; Wilson and Carrano, 1999; Wright, 2005; Mannon and Upchurch, 2010). Several works have associated the narrow-gauge trackways with diplodocids or non-titanosauriform sauropods, and the wide-gauge trackways with titanosaur/titanosauriform sauropods (Lockley et al., 1994; Wilson and Carrano, 1999; Wright, 2005; Mannon and Upchurch, 2010). Furthermore, Mannon and Upchurch (2010) registered a positive correlation of narrow-gauge trackways with coastal environments, and of wide-gauge trackways with inland environments. Significant Albian sauropod tracksites have been described in North America (Farlow et al., 1989, 2012; Pittman and Gillette, 1989; Pittman and Lockley, 1994), in Asia (Lim et al., 1989; Lee et al., 2000; Lee and Lee, 2006; Lockley et al., 2006), and in Europe (Moratalla et al., 1994; Dalla Vecchia and Tarlao, 2000; Pérez-Lorente et al., 2006). All of them have been classified into the wide-gauge (or intermediate category), with the exception of the sauropod trackway reported by Lee and Lee (2006) from Jag-eun Guhakpo, Korea (Mannon and Upchurch, 2010).

The Portuguese Cretaceous sauropod osteological record is reduced to some material from the Barremian marginal-marine beds of Boca do Chapim (north of Cabo Espichel, Sesimbra) described by Sauvage (1896, 1897-1898) and Lapparent and Zbyszewski (1957), and assigned to “Pleurocoelus valdensis” (Antunes and Mateus, 2003). The presence of this sauropod was also recognized in Spain, among other Early Cretaceous sauropods (for an overview on dinosaurs, especially sauropod remains, from the Iberian Peninsula, see: Ruiz-Omeñaca et al., 2004; Ortega et al., 2006; FCP-TD, 2009; Royo-Torres, 2009; Castanera and Canudo, 2011). Despite the fact that thyreophorans have been described in
Spain (Pereda-Suberbiola, 2006), no other quadrupedal dinosaurs, apart from sauropods, have been identified in the late Early Cretaceous of the Iberian Peninsula.

Here we describe a new Early Cretaceous (early late Albian) sauropod tracksite that has recently been discovered at the beach at Parede (Santos et al., 2012, 2013b), near Lisbon and Cascais, in west-central Portugal (Fig. 1). Apart from its scientific importance, the Parede tracksite has important educational and cultural value, since dinosaur tracksites have been considered as crucial places for the non-formal teaching and learning of geology, in general, and palaeontology, in particular.

The main goal of this paper is to provide a detailed description of the youngest sauropod tracks from the Cretaceous of Portugal, discussing their assignment within Sauropoda and emphasizing their importance due to the scarcity of narrow-gauge trackways during the Cretaceous. Their overall significance and implications for the Cretaceous dinosaur ichnological/osteological record is also discussed herein, as well as their contribution to the knowledge of the palaeobiology and palaeobiogeography for the Early Cretaceous Sauropoda of the Iberian Peninsula, and of the entire southwestern Europe, in a period of time where sauropod remains are relatively scarce in this region.

2. Geographical and geological settings

The studied tracksite is exposed on the Atlantic rocky shore of Parede beach, within a small embayment of the Cascais-Estoril coast located in front of the village of Parede (Fig. 2), about 20 km west of the centre of Lisbon. This coastal area has several sandy beaches and a nearly continuous shoreline of vertical cliffs and rock falls cut in Lower Cretaceous carbonate units of the Lusitanian Basin (Ramalho et al., 1999).

The local seashore comprises a 150 m long sandy cover surrounded by cliff areas, with Cretaceous limestone pavements slightly dipping to the east and mostly uncovered at low tide. Specifically, the Lower Cretaceous strata consist of a 15.5 m thick succession of massive limestone and nodular marly limestone beds interbedded with marly interstrata (Fig. 3). These beds are part of an incompletely-exposed middle to lower upper Albian carbonate platform sequence that represents the Água Doce Member of the Galé Formation (Rey, 1992, 2006) and its upper boundary with the rudist-rich Ponta da Galé Member (Dinis et al., 2002). These levels are cut in several points of the outcrop by vertical dykes of weathered basaltic rocks related to the Upper Cretaceous “Volcanic Complex of Lisbon” (Pais et al., 2006). At the
Sensible at low tide and exposed in front of the “Terrace Bar cur (Exogyra Neithia) and gryphaeid bivalves a dominance of pectinid (The invertebrate macrofauna is of moderate diversity, with burrows. There is also a dense concentration of and a few of them are densely bioturbated by produced by tidal dynamics. been recently recognized after a massive sand removal in-

The invertebrate macrofauna is of moderate diversity, with burrows. There is also a dense concentration of and a few of them are densely bioturbated by produced by tidal dynamics.

Most nodular limestone beds have a rich fossil content and a few of them are densely bioturbated by Thalassinoides burrows. There is also a dense concentration of Diplocraterion in the strata immediately below the dinoturbated bed. The invertebrate macrofauna is of moderate diversity, with a dominance of pectinid (Neithia) and gryphaeid bivalves (Exogyra and Ceratostreon), and moulds of heterodontid bivalves tentatively assigned to Anisocardia, Protocardia, Fimbria, and Proveniella. Rudists are found above the dinoturbated bed of the sequence “AL8” defined by Dinis et al. (2002) and Rey (2006) for the Cascais region. This means that the local stratigraphic section is above the middle-upper Albian transition, where the Knemiceras uhligi bed of the sequence “AL7” records a basal Upper Albian maximal flooding surface, followed by a regressive system tract on the overall carbonate platform. The sauropod trackways are preserved on the sedimentary tract of the subsequent transgressive phase (“AL8”), when several parasequences of inner shelf and tidal flat carbonates accumulated. The limestone bed with Polyconites clusters lying on the top of the Parede beach section indicates the growth of small rudist buildups on the carbonate platform. This record is correlative of the upper part of “AL8” (Dinis et al., 2002) and also represents the lower boundary of the rudist-rich Ponta da Galé Member of the Galé Formation (Rey, 1992).

3. Material and methods

The track level at Parede beach corresponds to an extensive intertidal exposure with moderate dinosaur trampling, considering the dinoturbation index proposed by Lockley and Conrad (1989). Despite the slight erosion of these tracks, at least two quadruped trackways can be identified. The main trackway (PT1) is a sequence of at least eight subtriangular impressions (pes) and one kidney shaped impression (manus), which is crossed subperpendicularly by a poorly preserved quadruped trackway with one clear kidney-shaped impression (PT2).
The description of the Parede trackways follows standard procedures and ichnological terminology (e.g., Leonardi, 1987; Thulborn, 1990; Lockley, 1991; Moratalla, 1993; Romano et al., 2007): track length, width, and depth, stride length, pace length, inner trackway width, total trackway width, pace angulation and footprint rotation. Heteropody was calculated using the formula \[(\text{manus length x manus width})/(\text{pes length x pes width}) \times 100\] proposed by Moratalla (1993). We have taken the heteropody index of the one manus-pes set that best represents the manus-pes dimensions of the main trackway (PT1). We used the formulas of Alexander (1976) to estimate hip height. Due to the poor preservation of the tracks, we have used the general morphology of the pes and manus prints as the only non-metric ichnological parameters. Due to the outcrop conditions, it was not possible to estimate some parameters such as the pes trackway ratio (Romano et al., 2007) and the width of the angulation pattern/pace length ratio (Marty et al., 2010).

The local stratigraphic section of Parede beach was also studied in order to interpret the depositional environment and the palaeogeographical setting. Accordingly, the lithofacies and sequence analyses were followed by the determination of the invertebrate taxa found in each bed, and by a microfacies overview of the strata close to the dinoturbated surface (beds C22/24 and C26).

### 4. Dinosaur tracks description and facies analysis

An overview of the nearly horizontal track level (C21) situated at the Parede beach reveals a first sequence of quadruped footprints (PT1) (Fig. 5). This trackway is crossed and distorted by a second one (PT2) that is partially preserved, making it difficult to obtain measurements of the parameters. This ichnological occurrence becomes more evident whenever sand removal induced by tidal dynamics occurs.

The dinosaur tracks at Parede are preserved in bioclastic coarse sediment not favourable for the preservation of any anatomical features in manus and pes prints. This absence of details could be merely a consequence of the substrate conditions or the depth of preservation of the tracks. It is difficult to interpret whether the track level is the original tracking surface, so we accept that when the trackmakers passed in this area they could go through C22 sediment layer leaving their undertracks \textit{(sensu} Marty et al., 2010) on the top of C21, the sedimentary layer below.

The main trackway (PT1) is a sequence of at least eight subtriangular impressions and one kidney-shaped to semicircular impression (Fig. 5B). As a result, the trackway configuration is that of a pes-dominated trackway (Marty, 2008). One additional print may belong to this trackway but there is some uncertainty (see question mark in Fig. 5B). Track depth
Fig. 5.- The main sauropod trackway (PT1) at Parede (early late Albian, Galé Formation, Cascais, Portugal) is crossed by another trackway (PT2), which is partially preserved and crosses and disrupts the footprint sequence of PT1. A, Photographic overview of the slab with dinosaur tracks. B, trackways PT1 and PT2; *, manus print from PT2; C, the best preserved manus-pes set of trackway PT1.

is about 2 cm, but due to the effects of erosion, this may not be accurate. One manus-pes print set in the main trackway (PT1) indicates movement of the animal to the present-day south. The pes prints are longer than wide (55 cm long by 50 cm wide) and subtriangular in shape, though no morphological details such as digit or claw impressions can be discerned. It is supposed that some indentations on the outer wall of the pes prints from PT1 are due to mud collapse (Fig. 5C). At the time these sauropods crossed the sediment interface, the substrate was not sufficiently firm and cohesive, allowing the walls of a footprint to slump inwards as the track-maker pulled out its foot. The preserved manus print is wider than long (25 cm long by 30 cm wide, TL/TW = 0.83) and kidney-shaped to semicircular. The centre of the manus print is closer to the trackway midline than the centre of the pes print. The pace length is variable and ranges from 95 cm to 110 cm. Both the manus and pes prints show positive rotation of about 50° relatively to the trackway midline. The inner width is no more than a few centimetres and the pes prints are close to the midline, suggesting a narrow-gauge trackway. The heteropody index is intermediate (1:3) and the pace angulation is about 90-100°. The hip height estimation is about 220 cm. The glenoacetabular distance and the outer trackway width could not be estimated. This trackway is crossed by a poorly preserved quadruped trackway (PT2) represented by one clear kidney-shaped impression far from the main track-
way (Fig. 5B). There are other isolated tracks but it is not possible to associate them to either trackways PT1 and PT2. The record of dinosaur trackways preserved in stratal surfaces from shallow, low-energy, tidal-controlled sedimentary palaeoenvironments, is well documented in the Iberian Cretaceous (Santos et al., 2013a). From these other occurrences, many of the reported finds are known from marginal marine contexts close to carbonate platforms, and are often associated with transgressive episodes during the sequential evolution of some basins (e.g. Lockley and Santos, 1993; Lockley et al., 1994; Lockley and Meyer, 2000; Santos, 2003; Santos et al., 2009). The Parede section is a noteworthy example of this kind of depositional setting developed within the inner sectors of a carbonate platform (Fig. 6). Its local succession of shallow marine carbonate facies is part of a transgressive-system tract deposited when a sea-level rise created new accommodation space for coastal sedimentation (Rey, 2006).

Both microfacies analysis of beds C22/24 and C26 and the palaeoecological requirements of the invertebrate taxa collected from several levels of the section suggest that the dinoturbation occurred in a low-energy tidal flat palaeoenvironment, close to an inner shelf opened to fully marine conditions. However, fragments of dasycladacean algae found in the carbonated microfacies indicate the relative proximity of shallow lagoons with restricted conditions.

The presence of echinoids and the abundance of articulated infaunal bivalves and *Thalassinoides* burrows in the lower beds of the section also indicate fully marine conditions at the palaeoenvironment, with euhaline salinity and relatively stable and oxygenated soft substrates. This fossil association changes in the uppermost beds of the section, where exogyrynid bivalves become more common and clusters of small rudists appear. The sauropod trackway occurs above a bed with dense *Diplacreratium* burrows, suggesting a typical tidal flat episode on the transgressive sedimentary process.

All these data match well with the ecostratigraphic and palaeogeographical models described by Rey and Cugny (1977) and Rey et al. (1977) for the Albian of the Sintra-Cascais-Lisboa carbonate platform.

5. Discussion

During the late Early Cretaceous two main groups of quadruped dinosaurs (sauropods and ankylosaurs) inhabited Europe, including the Iberian Peninsula, though the osteological record is scarce (Martin et al., 1993; Upchurch et al., 2004; Vickaryous et al., 2004; Buffetaut and Nori, 2012; Kirkland et al., 2013). Sauropod tracks are generally distributed over the entire world during the Mesozoic, with some significant tracks in the “mid” Cretaceous in Korea and North America (Thulborn, 1990; Lockley et al., 1994; Wright, 2005; Mannion and Upchurch, 2010). By contrast, ankylosaur tracks are less well known in the ichnological literature and are restricted to the Cretaceous. They have been described in several localities from different continents, mainly in North America (McCrea et al., 2001; Lockley et al., 2006) and South America (Meyer et al., 2001).
et al., 2001) but also in Europe (see Petti et al., 2010; Hornung and Reich, 2014 and references therein). As concerns ankylosaur tracks morphology, the manus presents five digits arranged in a semicircular or radiating pattern and pes with four digits and a wide and elongated heel (Thulborn, 1990; McCrea et al., 2001; Petti et al., 2010). Other quadrupedal dinosaurs like stegosaurs (Galton and Upchurch, 2004) or ceratopsians (Dodson et al., 2004) have not been described yet (neither by osteological or ichnological remains) from the Aptian-Turonian of Europe, so we assume that these dinosaurs are not candidates to be the trackmakers of Parede.

As happened with sauropod and thyreophoran tracks (such as those of ankylosaurs), the distinction between them is not obvious when dealing with tracks that do not preserve anatomical characters, such as digit marks. Sacchi et al. (2009) distinguished between sauropod and ankylosaur tracks from the Aptian of Italy on the basis of heteropody and footprint rotation. Thus, according to the interpretation of these authors and of McCrea et al. (2001) and Petti et al. (2010), ankylosaur tracks have low heteropody and lower footprint rotation than the great majority of sauropod trackways (Thulborn, 1990; Wright, 2005).

Due to the arrangement of the tracks with clear outward rotation and intermediate heteropody (1/3) along the trackway PT1 at Parede, we can assume that these features are more sauropod-like than ankylosaur-like. Furthermore, the general morphology of the tracks (subtriangular pes impressions and kidney-shaped to semicircular manus impressions) is more consistent with the interpretation of a sauropod origin than an ankylosaur one. The kidney-shaped manus and the subtriangular pes morphologies have been described in other sauropod trackways that do not show digit impressions (Thulborn, 1990; Wright, 2005). The ankylosaur tracks described by Petti et al. (2010) have kidney-shaped manus tracks, though clear digit impressions are discerned. The absence of digit impressions in sauropod manus tracks is not uncommon, even in well-preserved trackways where digit impressions have been preserved in pes prints (Marty, 2008; Santos et al., 2009; Marty et al., 2010; Castanera et al., 2011, 2012, in press). As such, this absence is not a limitation to assign the footprints to Sauropoda. In fact, it could reinforce this idea.

Other interesting feature of the main trackway (PT1) is its narrower inner width. Despite the fact that some ankylosaur trackways are also narrow-gauge (Petti et al., 2010), these trackways, with intermediate to high heteropody, have been described from elsewhere and assigned to sauropod ichnotaxa like Parabrontopodus and Breviparopus (Lockley et al., 1994; Marty et al., 2010). In fact, Moratalla (2009) described narrow-gauge sauropod trackways in the lower Aptian (Enciso, Spain) from the Iberian Peninsula.

The narrower width of the trackway may also have some taxonomic implications. Wide-gauge sauropod trackways are usually assigned to titanosaur species or titanosauriforms, while narrow-gauge sauropod trackways are usually assigned to diplodocoids (Farlow, 1992; Lockley et al., 1994; Wilson and Carrano, 1999; Day et al., 2002; Wright, 2005). This distinction fits well with the global distribution of sauropod remains and the type of trackway due to the abundance of wide-gauge trackways and titanosaurians in the Cretaceous and narrow-gauge trackways and diplodocoids in the Jurassic (Lockley et al., 1994; Wilson and Carrano, 1999; Day et al., 2004; Wright, 2005). Despite the fact that the inner width (and then the type) of the trackways can change along the same trackway (Romano et al., 2007; Castanera et al., 2012), this characteristic may have a clear taxonomical implication in narrow-gauge trackways that presumably could not have been produced by titanosaurians. If the tracks of Parede are preserved as undertracks, then the inner width can also change with the depth of preservation (Jackson et al., 2009; Falkingham et al., 2010; Castanera et al., 2012), such that the trackway would have been preserved as if it were narrower. Even considering this option, the narrow width of the trackway of Parede probably would not represent a truly wide-gauge trackway.

Another significant character that distinguishes sauropod groups is the presence/absence and the morphology of the manus digit I claw mark (pollex). Generally, the presence of pollex marks is a feature that is not found in advanced titanosaurians (Dalla Vecchia and Tarlao, 2000; Day et al., 2004; Castanera et al., in press). The manus of the trackway PT1 apparently do not show any sign of the pollex mark, although this absence may also be a preservational consequence (Wright, 2005; Castanera et al., in press). Wright (2005) also suggested that, according to the metacarpal arrangement, neo-sauropods might be considered as potential trackmakers of the kidney-shaped manus impressions. In the review of the sauropod tracks of the Iberian Peninsula made by Castanera et al. (in press), it is suggested that during the “mid” and Late Cretaceous, sauropod tracks with titanosaur affinities would potentially have manus tracks with a horseshoe morphology that would show the metacarpal arrangement of an arc of 270º of the derived sauropods like titanosaurians (Wright, 2005). The scarce material of manus footprints do not provide a clear conclusion about their original morphology; nonetheless, the TL/TW ratio of 0.83 is quite high. Thus, on the basis of the inner width and perhaps the manus morphology, we also can discard titanosaurians as the potential trackmakers of Parede.

The sauropod record from the Iberian Peninsula in the Albian is very scarce, based mostly on taxonomically-unidentifiable material (Canudo et al., 2004a, 2004b). To associate the trackway PT1 with a specific group of sauropods is not really prudent. Nonetheless, discarding titanosaurians, the other main group of sauropods that inhabited Europe during the late Early Cretaceous were the rebbachisaurids (Mannion et al., 2011; Torcida Fernández-Baldor et al., 2011). The morphology of rebbachisaurid tracks so far is not well understood. Apesteguía et al. (2010) associated sauropod tracks from Campanian-Turonian beds of the Candeleros Formation in Northern Patagonia (Argentina) to these dinosaurs, on the basis of low heteropody due to the presence of osteologi-
cal remains in the same unit. Neither it is well-known about the type of trackway (narrow or wide gauge) that would have produced a rebbachisaurid, but considering their diplodocoid affinities, they could be considered as potentially trackmakers of the narrow-gauge trackways of the Cretaceous. Nevertheless, this hypothesis, proposed by Moratalla (2009) who suggested that rebbachisaurids might have produced narrow-gauge trackways in the lower Aptian of Cameros (Spain), should be tested on the basis of osteological and ichnological remains.

Additionally, the trackway PT1 adds new data to the sauropod pes-dominated trackways in the Cretaceous. Pes-dominated trackways are those in which the forelimbs leave no (or faint) impressions, whereas the hindlimbs are well marked (Marty, 2008; Falkingham et al., 2012). The pes-dominated trackways are generally produced when the manus do not deform the substrate or by overstepping of the manus by the pes. These kinds of trackways are more likely to be produced by sauropods with a center of mass (CM) posteriorly located (Falkingham et al., 2011, 2012). Although no predictions of the CM position have been made for rebbachisaurids or derived titanosaurs, sauropods like diplodocoids would have had a CM located more posteriorly than titanosauriforms like Brachiosaurus (Henderson, 2006; Falkingham et al., 2012). This would be another argument pointing to a non-titanosauriform as the candidate trackmaker of Parede. Furthermore, Falkingham et al. (2012) suggested that the Cretaceous pes-dominated tracks are associated with non-cohesive substrates. As this bias is not recorded in the Jurassic, these authors interpreted that it might be related to a different sauropod bauplan and niche partitioning among sauropods as a consequence of the rise and diversification of the titanosaurians during the Cretaceous. The trackway PT1 is preserved in a cohesive substrate (marly limestone), so it does not fit with this interpretation. Nonetheless, the preservation of the tracks in a coastal environment fits with the association proposed by Mannion and Upchurch (2010), of narrow-gauge trackways with coastal environments, suggesting that non-titanosaur sauropods preferred these environments. Again, a non-titanosaur origin for the trackway PT1 could be the explanation for the presence of a pes-dominated trackway in a cohesive substrate of a coastal environment.

6. Conclusions

The ichnological record of the Parede tracksite presented herein is the only clear evidence for sauropods during the Early Cretaceous of Portugal. The micro- and biofacies from the Parede section in conjunction with a sequence stratigraphic correlation indicates a relative age slightly above the middle-late Albian transition. The Parede tracksite is the first occurrence of dinosaur tracks within the Galé Formation and one of the few occurrences of sauropod tracks in the Albian of the Iberian Peninsula. Moreover, it reveals the youngest evidence of sauropods in the Portuguese dinosaur record. The footprints were made by a medium-sized narrow-gauge sauropod dinosaur with probable non-titanosaur affinity that was walking on an exposed surface of a shallow marine palaeoenvironment. The Parede section is also a source of palaeobiological, palaeoecological and palaeogeographical information about this group of vertebrates from the Early to Late Cretaceous transition in the Iberian Peninsula, which will improve knowledge of the dinosaurs in the European context.

Acknowledgements

The authors acknowledge collaboration with António Carvalho and Mário Lisboa from the Câmara Municipal de Cascais. Our gratitude goes to Prof. Dr. Julio Rodríguez-Lázaro of the Universidade del País Vasco/Euskal Herriko Unibertsitatea (Spain) for the micropalaeontological study. Fieldwork was partly supported by the Centro de Investigación da Terra e do Espaço, Universidade de Coimbra, Portugal (Fundação para a Ciência e a Tecnologia) and by the research projects CGL2011-25894 and CGL2012-35199 of the Ministerio de Ciencia e Innovación (Spain). Diego Castanera also acknowledges the support of a grant from the Europa Cai-DGA program (CB 5/11). We wish to thank Ignacio Díaz-Martínez for their constructive comments on an earlier draft of the paper, and to Christian A. Meyer and David B. Weishampel for comments that improved the text editing. Technical help from Diamantino Tojo from the “Terrace Bar Xana” is gratefully acknowledged.

References


Berthou, P.Y. (1984b): Résumé synthétique de la stratigraphie et de la paléogéographie du Crétacé moyen et supérieur du bassin occidental


Rey, J. (1972): Recherches géologiques sur le Crétacé inférieur de l’Estremadura (Portugal). Memórias dos Serviços Geológicos de Por-


