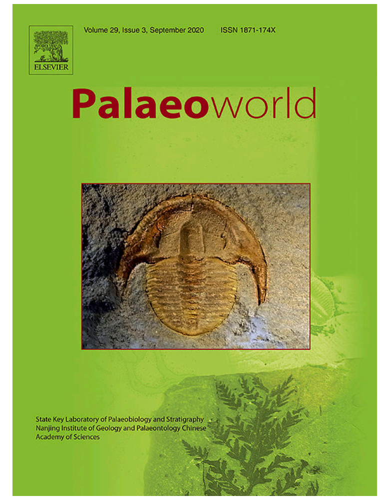
Journal Pre-proofs



Dinoturbation in Upper Jurassic siliciclastic levels at Cabo Mondego (Lusitanian Basin, Portugal): evidences in a fluvial-dominated deltaic succession

Ismar de Souza Carvalho, Pedro Proença Cunha, Silvério M.D. Figueiredo

PII: S1871-174X(21)00070-6
DOI: https://doi.org/10.1016/j.palwor.2021.09.001
Reference: PALWOR 645

To appear in: *Palaeoworld*

Received Date: 22 January 2021
Revised Date: 13 August 2021
Accepted Date: 3 September 2021

Please cite this article as: I.d. Souza Carvalho, P.P. Cunha, S.M.D. Figueiredo, Dinoturbation in Upper Jurassic siliciclastic levels at Cabo Mondego (Lusitanian Basin, Portugal): evidences in a fluvial-dominated deltaic succession, *Palaeoworld* (2021), doi: https://doi.org/10.1016/j.palwor.2021.09.001

Dinoturbation in Upper Jurassic siliciclastic levels at Cabo Mondego (Lusitanian Basin, Portugal): evidences in a fluvial-dominated deltaic succession

Ismar de Souza Carvalho [a, b] *, Pedro Proença Cunha [c], Silvério M. D. Figueiredo [b, d, e]

[a] Departamento de Geologia, CCMN/IGEO, Universidade Federal do Rio de Janeiro, 21.910-200 Cidade Universitária, Ilha do Fundão, Rio de Janeiro, Brazil

[b] Centro de Geociências, Universidade de Coimbra, Rua Sílvio Lima, 3030-790 Coimbra, Portugal

[c] Department of Earth Sciences, Marine and Environmental Sciences Centre, University of Coimbra, Rua Sílvio Lima, 3030-790 Coimbra, Portugal

[d] Centro Português de Geo-História e Pré-História, Largo de São Caetano, 2150-265 Golegã, Portugal

[e] Instituto Politécnico de Tomar, Quinta do Contador, Estrada da Serra, 2300-313 Tomar, Portugal

* Corresponding author.

E-mail addresses: ismar@geologia.ufrj.br (Carvalho); pcunha@dct.uc.pt (Cunha); silverio.figueiredo@ipt.pt (Figueiredo)

Abstract

At Cabo Mondego (western central Portugal), the Upper Jurassic marine to coastal succession contains several stratigraphic levels preserving dinosaur footprints on the surface bedding plane, as well as convolute bedding and soft sediment injection structures interpreted as dinoturbation structures. At least nineteen new three-dimensional structures observed in cross-sections are interpreted as produced by dinosaur trampling. The identification of three-dimensional structures of dinosaur footprints provides an important complement to the information obtained from footprints preserved on single bedding surfaces, such as the substrate consistency, potential trackmaker identification, and the possibility to enhance the distinction of sauropods and tridactyl dinosaurs, and paleoenvironmental interpretations. In the lower part of the Arenitos da Boa Viagem Formation, eight levels of probable lowermost Kimmeridgian age (ca. 157–156 Ma), displaying the above-mentioned deformational structures, were analyzed in detail. They support interpretations concerning the relationship between the footprints and the substrate consistency at the time of their formation. Three distinct cohesiveness patterns, defined by the penetration of the feet from the paleosurface, are the result of different degrees of substrate cohesiveness. Identifying the trackmakers of levels belonging to the middle Oxfordian–lower Kimmeridgian has important implications for Late Jurassic ecosystem reconstructions, as the footprints observed in Cabo Mondego indicate a change in the morphotypes throughout the Upper Jurassic succession.

Keywords: Dinoturbation; dinosaur footprints; Cabo Mondego; Upper Jurassic; Lusitanian Basin

1. Introduction

Many dinosaur footprints are features transmitted to the sedimentary bed and do not represent 'true' depositional surface footprints, which are produced only at the contact between the foot and an exposed sedimentary surface (e.g., Milàn and Bromley, 2006). A true track is produced on the surface that was in direct contact with the foot (Leonardi, 1987), just after the passage of the trackmaker. It can also be observed as a cross-section cast produced due to the sink of track maker's foot within the sediment. They are distinct from transmitted footprints, which are the deformations in the lower sedimentary levels induced by the step pressure on the surface (Thulborn, 2012). An undertrack is a transmitted print, or ghost print, formed in (bio-) laminated and plastic substrate when the foot does not penetrate the sediment but compresses it in a way that creates a miniature stratigraphic sequence or stack of transmitted prints (Thulborn, 1990; Lockley, 1991; Marty, 2008). The substrate properties and the animal's behavior allow a wide range of track morphologies. The main types of footprint preservation can be in this way evaluated as the relationship between the substrate and lower surface of the autopodia. Footprints can also occur as pillar-like or barrel-like morphologies (Difley and Ekdale, 2002) made by a trackmaker sinking the foot deeply into soft mud (Gatesy, 2003) or high water-content sand. In a track cross-section, track penetration depth is the maximum depth (measured from the tracked surface) where undertracks or deformation of the sediment are still discernable (Marty, 2008).

The preservational aspects of footprints can be related to the substrate cohesiveness, plasticity, grain size, texture and water content (Lockley et al., 1989).

The footprints can present well-defined morphologies or without a clear morphological identity with the trackmaker. Those with impressions of claws, nails and soft tissue such as the sole and phalangeal pads are considered to be produced in mud sediments with high plasticity and low water content. In subaqueous environments, there is a decrease in the morphological details of the footprints losing aspects such as nails, claws, pads and sole marks (Lockley and Conrad, 1989; Carvalho and Leonardi, 2021). Then, the geotechnical substrate properties and the animal's behavior allow for a wide range of track morphologies to be produced (e.g., Manning, 2011; Falkingham et al., 2018). From observations of recent environments, Laporte and Behrensmeyer (1980) found that there is a narrow range of sediment textures and moisture content, which will allow preservation of the footprints in the geological record. Footprints are best preserved in a relatively narrow zone of deltas, estuaries/lagunes, lakes, fluvial plains and tidal flats where moist, vegetation-free sands and silts are buried (protected) after trampling.

Footprints may present a low preservation potential, since surface impressions in soft sediments are readily partially destroyed or eroded just before the succeeding bed is deposited. After short periods of subaerial exposure or an absence of strong hydrodynamic action, footprints may be preserved (Tucker and Burchette, 1977). After the footprint formation, there is a fast degradation of the exposed footprints and the low preservation potential is related to many destructive processes that include early bioturbation, weathering, erosion, deformation and reworking during the successive later depositional events (e.g., Nadon, 2001; Marty et al., 2009). The degree to which the track morphology matches that of the foot (Belvedere and Farlow, 2016; Gatesy and Falkingham, 2017; Marchetti et al., 2019, 2020) generally has a direct relationship with the substrate consistency at the time of its genesis.

Little difference is observed between the deformation produced on and in the ground by the weight and movement of an animal's autopodium and the deformation produced by environmental processes (e.g., Nadon, 2001; Abrahams et al., 2020, in press; Carvalho and Leonardi, 2021). Footprints represent sedimentary distortions that potentially provide anatomical, functional, and behavioral insights into trackmaker biology, affecting sediments continuously from the surface to its maximum penetration depth. They only record the final sediment conformation at the end of its developmental sequence (Falkingham and Gatesy, 2014; Gatesy and Falkingham, 2017).

Dinoturbation, defined as the dinosaur trampling that extensively affected Mesozoic substrates or soils (Lockley, 1991), footprints in the substrate surface or as cross-sections, is a well-documented feature in Mesozoic deposits (e.g., Lockley, 1991; Avanzini et al., 1997; Gatesy et al., 1999; Milàn et al., 2004; Carvalho et al., 2013; Abrahams et al., 2020, in press,; Christofoletti et al., 2021). Sometimes dinoturbation structures preserved in cross-section are misinterpreted as non-biogenic features, e.g., load structures produced by sedimentary processes (Powell, 2010; Carvalho et al., 2021). However, unlike non-biogenic structures, footprints present more regular, uniform or aligned undulations with less relief. Furthermore, the bases of the footprint casts are frequently flat or rounded (convex down), with coarsely crinkled and irregular surfaces, and often bear polygonal pressure imprints. Other criteria to distinguish true footprints from non-biogenic structures are vertical to subvertical striae that often appear on the margins (outside surfaces) of some track structures (Difley and Ekdale, 2002). Otherwise, dinosaur footprints include: dish-shaped structures (which resulted from repeated trampling); deformed track casts grading into undulating, globular, or highly irregular sandstone forms; deformed ball structures, which may graduate into dish-like, lunate, or trough structures with laminated fill.

In the Lusitanian Basin (Portugal, western Iberian Peninsula; Fig. 1), Middle and Upper Jurassic sedimentary successions preserve a great number of ichnosites, which include dinosaur footprints and dinoturbation structures, e.g., Pedreira do Avelino and Pedreira da Ribeira do Cavalo, in Zambujal (Sesimbra); Praia do Cavalo and Pedra da Mua, in Cabo Espichel; Pedreira do Vale de Meios and Pedreira do Galinha, in Serra de Aires e Candeeiros; Praia de Amoreira-Porto Novo, Alcobaça, Sobral, and Freixial; Pedras Negras (Caldas da Rainha) and São Martinho do Porto (Alcobaça) (e.g., Antunes, 1976; Figueiredo, 2002, 2004; Santos, 2003, 2008; Santos et al., 2008; Mateus and Milàn, 2010; D'Orazi Porchetti et al., 2016; Razzolini et al., 2016; Santos et al., 2016; Castanera et al., 2017, 2019, 2020a, 2020b; Belvedere et al., 2019). At Cabo Mondego, a cape which mainly consists of resistant Jurassic rocks and is located immediately north of the Figueira da Foz town (western central Portugal; Fig. 1), the base of the Upper Jurassic (locally represented by the Complexo Carbonoso lithostratigraphic unit; middle Oxfordian; Fig. 2) also includes dinosaur footprints and dinoturbation structures (e.g., Gomes, 1915–1916; Nopcsa, 1923;

Lapparent et al., 1951; Lessertisseur, 1955; Lapparent and Zybszewski, 1957; Santos, 2008).

At Cabo Mondego (Figueira da Foz), four tracksites are here considered: Pedra da Nau (Fig. 2, PN), Laje do Costado (Fig. 2, LC), Calcários Hidráulicos (Fig. 2, CH) and Arenitos da Boa Viagem (Fig. 2, ABV). The previous descriptions on these tracksites (Gomes, 1915–1916; Nopcsa, 1923; Lapparent et al., 1951; Lessertisseur, 1955; Lapparent and Zybszewski, 1957; Lockley et al., 1996, 1998; Antunes, 1999; Santos, 2008, 2017; Santos and Neto de Carvalho, 2016) recognized over 67 footprints attributed to theropods in Oxfordian strata of Pedra da Nau and Laje do Costado tracksites. In the coastal cliffs of this cape, at the base of the Complexo Carbonoso, a limestone surface with striking fossil footprints was discovered in 1884 at Pedra da Nau tracksite (Fig. 2, PN), but the study was only published later (Gomes, 1915–1916). All the exposed footprints were excavated and stored at Museu Mineralógico e Geológico da Escola Politécnica (nowadays the Museu Nacional de História Natural e da Ciência), in Lisbon. These tracks were recognized as large theropod tetradactyl footprints attributed to megalosaur dinosaurs. Since then, the studies that analyzed these footprints (Nopcsa, 1923; Lapparent et al., 1951; Lessertisseur, 1955; Lapparent and Zybszewski, 1957; Lockley et al., 1996, 1998; Antunes, 1999; Santos, 2008, 2017; Santos and Neto de Carvalho, 2016) presented a review of the ichnotaxonomy and recognized as valid names the ichnospecies *Eutynichnium lusitanicum* (first described by Nopcsa, 1923) and the ichnogenus *Megalosauripus* isp., both related to megalosaur theropods. Belvedere et al. (2019), in the revision of Late Jurassic large theropod footprints from North of Africa and Europe, considered that there are great similarities between *Megalosauripus transjuranicus* and *Eutynichnium lusitanicum*, supporting the attribution of the two taxa to the same ichnofamily (Eubrontidae).

By 1951, about 50 footprints attributed to Theropoda were found in three successive beds of Oxfordian dark marly limestones, at a tracksite called Laje do Costado (Fig. 2, LC) (Lapparent and Zbyszewski, 1957), located ~50 m stratigrafically above the Pedra da Nau ichnosite (Fig. 2, PN). Most of the footprints were excavated and moved to the Museum of Geologic Survey (presently the Museu Geológico) in Lisbon.

Santos (2003, 2008) summarized eight stratigraphic levels with theropod footprints in the unit locally called as Complexo Carbonoso (middle Oxfordian; Fig.

2). The oldest level is the one described by Gomes (1915–1916) at the cliff, at the Pedra da Nau tracksite (Fig. 2, PN), stratigraphically located near the base of Complexo Carbonoso. Another level with a well-known theropod footprint, also located at Pedra da Nau tracksite, was described by Santos (2003, 2008). The following successive three beds with referred footprints were the ones previously described at the Laje do Costado tracksite (Fig. 2, LC) by Lapparent and Zbyszewski (1957). The other three levels with footprints, referred to by Santos (2008), also belong to the Complexo Carbonoso, but the precise stratigraphic position was not indicated.

In the present study we analyze the Arenitos da Boa Viagem tracksite, which comprises eight distinct track-bearing strata with true footprints on the trampled surface, including at least nineteen three-dimensional structures observed in cross-sections, and transmitted relief of dinosaur footprints. The cohesiveness patterns of the substrate is also evaluated based on these footprints.

2. Geological setting

During the Late Jurassic, Europe was an assemblage of numerous islands of various sizes, separated by shallow epicontinental seas in the Tethys realm, with many isolated areas of continental, coastal plain and shelf deposition (Yilmaz et al., 1996). There are a great number of Middle and Late Jurassic footprints from the surrounding margins of Tethys Ocean. Theropod and sauropod footprints are found in carbonate successions of tidal-flat deposits of carbonate platforms, such as those from Great Britain (e.g., Romano and Whyte, 2003; Powell, 2010), France (e.g., Mazin et al., 2017), Germany (e.g., Diedrich, 2011), Poland (e.g., Gierlinski et al., 2009), Italy (e.g., Avanzini et al., 1997), Switzerland (e.g., Marty et al., 2007, 2018; Marty, 2008; Razzolini et al., 2017; Castanera et al., 2018), Croatia (e.g., Solt et al., 2020), Moroccan High-Atlas (e.g., Belvedere, 2008; Belvedere et al., 2010), Spain (e.g., García-Ramos et al., 2006; Canudo et al., 2009; Piñuela Suárez, 2015; Campos-Soto et al., 2017; Rauhut et al., 2018) and in many localities of Portugal (e.g., Lapparent et al., 1951; Lapparent and Zbyszewski, 1957; Lockley et al., 1994, 1996, 2000a, 2000b; Henriques et al., 1998; Mateus and Milàn, 2008, 2010; Santos et al., 2009; Rocha et al., 2014; Henriques and Pena dos Reis, 2015; Razzolini et al., 2016; Santos, 2016).

The Kimmeridgian–lowermost Berriasian clastic succession of the Arenitos da Boa Viagem Formation, preserved at Cabo Mondego, was deposited in a fluvial-dominated delta environment (Manuppella et al., 1976; Pena dos Reis et al., 1996, 2000). In the early Kimmeridgian delta plain, dinosaur footprints were mainly produced and preserved within interdistributary bay, floodplain and crevasse splay environments. Areas with low hydrodynamics and wet sedimentary surfaces allowed the preservation of dinoturbation events. This context is observed in other tracksites, such as the ones in Brazil (Sousa Basin), Spain (Ibero-Armorican domain), Morocco (High Atlas) and western USA, described by Carvalho (1995, 2000a, 2020b, 2004), Leonardi (1989, 1994), Lockley and Conrad (1989), Carvalho and Leonardi (1992), Belvedere et al. (2010), Carvalho et al. (2013), and Pérez-Lorente (2017). Therefore, a very similar paleoenvironmental context of the dinosaur footprints in Arenitos da Boa Viagem Formation is found in Villar del Arzobispo Formation (Kimmeridgian–Tithonian, Spain). This lithostratigraphic unit is a succession with many depositional environments (carbonate platform, tidal and shallow marine carbonate platform), indicating an inner carbonate platform, which episodically underwent subaerial exposure and siliciclastic inputs. This environment evolved upward into a siliciclastic coastal and alluvial plain affected by periodic floods, where abundant, diverse, and well preserved (mainly as infillings or natural casts) dinosaur footprints are found (Campos-Soto et al., 2017).

The studied Upper Jurassic sedimentary succession at Cabo Mondego belongs to the Lusitanian Basin, located on the Western Portuguese Margin and extending onshore from Aveiro to Sines (Fig. 1). The sedimentary infill ranges from the Upper Triassic to Holocene, recording rifting, passive margin and compressive tectonic-sedimentary stages; the successive tectonic phases are recorded by sedimentary discordances, that separate allostratigrapic units (Wilson et al., 1989; Cunha, 1992; Azerêdo et al., 2003; Pena dos Reis and Henriques, 2018). The Mesozoic allostratigraphic units are: UBS (unconformity-bounded sequence) 1 (Upper Triassic to middle Calovian; UBS2 (middle Oxfordian to lower Berriasian); UBS3 (upper Berriasian to lower Aptian); UBS4 (upper Aptian to lower Campanian); UBS5 (middle Campanian to Maastrichtian).

The basin underwent a major rifting phase during the late Oxfordian to earliest Kimmeridgian, with fault and fault-related diapiric activity creating several sub-basins (depocenters). These included the Bombarral–Alcobaça, Arruda, and Turcifal sub-basins (e.g., Pena dos Reis et al., 1996, 2000; Leinfelder and Wilson, 1998; Alves et al., 2003). This tectonic activity is reflected in the sedimentary infill by faults displacing the Lower and Middle Jurassic and by diapiric structures affecting the Lower Jurassic marly and evaporitic Dagorda Formation.

In the UBS2 of the central sector of the Lusitanian Basin, several lithostratigraphic units were defined (see synthesis by Mateus et al., 2017): Cabaços Formation – up to 400 m thick (micritic limestones, with organic matter), Montejunto Formation – up to 1200 m thick (mainly bioclastic limestones; marine environments), Alcobaça Formation – up to 200 m thick (alternation of marls and limestones; shallow-marine to brackish environments) and Lourinhã Formation – up to 400 m thick (siliciclastic deposits; deltaic, fluvial and alluvial fan environments).

The Lourinhã and Alcobaça formations contain the most vertebrate remains in the Lusitanian Basin (Lapparent and Zbyszewski, 1957; Dantas, 1990; Mateus, 1998; Antunes and Mateus, 2000; Crespo, 2001; Mateus et al., 2006; Ortega et al., 2006, 2009; Figueiredo, 2008, 2014; Escaso et al., 2014; Mocho et al., 2014, 2016a, 2016b, 2017a, 2017b, 2017c, 2017d, 2019; Pérez-García, 2015), including dinosaurs (theropods, sauropods, stegosaurs, ankylosaurs and ornithopods), pterosaurs, crocodilians, mammals, turtles, basal diapsids and amphibians, with fauna and flora assemblages being somewhat similar to those of the Morrison Formation in North America, but with coastal influence and some European-related faunal input (Crespo, 2001; Mateus et al., 2006; Escaso et al., 2007; Malafaia et al., 2010). The occurrence of the genera *Allosaurus* and *Stegosaurus* in Late Jurassic of Portugal (Dantas et al., 1999; Escaso et al., 2007) represents a relevant example of this similar faunal assemblage between the Lusitanian Basin and the Morrison Formation (Mateus, 2006; Mateus et al., 2006, 2017; Escaso et al., 2007; Ortega et al., 2009).

The studied coastal area at Cabo Mondego was located at the NNE margin of the basin during the Late Jurassic, and the successive lithostratigraphic units that comprise the allostratigraphic unit UBS2 document more marginal facies (described below from the base to the top; e.g., Wilson, 1979; Bernardes, 1992; Pena dos Reis et al., 1996, 2000; Fig. 2):

– The Vale Verde Formation (middle Oxfordian) overlays, by disconformity, the Callovian upper levels of the marine Brenha Formation. It is ~150 m thick and includes two local units: (i) the Complexo Carbonoso (Carbonaceous Complex) unit (~75 m), which can be differentiated in a lower division of predominant lignites and sandstones (12 m; coastal siliciclastics), a middle division of limestones (~30 m; lagoon), and an upper division of sandstones, limestones and siltites (~35 m;

distributary channels, bays and marshes); and (ii) the Calcários Hidráulicos (Cement Limestones) unit, which comprises ~30 m of marginal brackish-freshwater algal marsh limestones followed by ~60 m of evaporitic lagoon limestones.

– The *Pholodomya protei* Formation is ~100 m thick and mainly comprises biomicritic limestones rich in bivalves (*Ostrea pulligera* Gold, *Mytilus beirensis* Sharpe, *Pinna* sp., *Perna* sp. and *Pholodomya protei*); it records a shallow marine environment of late Oxfordian age.

– The Arenitos da Boa Viagem Formation (Boa Viagem Sandstones Formation) is ~600 m thick and of Kimmeridgian to early Berriasian age (a lateral equivalent of the Alcobaça and Lourinhã formations). This fluvial-prevailed deltaic succession is dominated by sandstone units that usually show fining upward sequences, in which coarse- and medium-grained cross-bedded sandstones are replaced by red fine to very fine sandstones and siltstones, the latter sometimes culminating in the development of caliche horizons (fossil carbonate soils) (Wilson, 1979; Bernardes, 1992). A large number of marine shales, marl and sandstone horizons occur in the succession, recording marine incursions.

The studied dinosaur dinoturbation are located in stratigraphic levels included in the Complexo Carbonoso (e.g., Gomes, 1915–1916; Lapparent and Zbyszewski, 1957; Santos, 2003, 2008; Rocha et al., 2014). The new structures referred in the present work occur at the lower division of the Calcários Hidráulicos (CH tracksite; subunit d; freshwater lakes to brackish environments – carbonate restricted lagoon) and at the lower part of the Arenitos da Boa Viagem Formation (ABV tracksite; shallow marine, brackish and freshwater environments of a siliciclastic fluvial-dominated deltaic succession) (Fig. 2). The present analysis will focus on eight siliciclastic levels, at the lower part of the Arenitos da Boa Viagem Formation and examine the paleoenvironmental context where the fossil footprints occur.

3. Results

In the Upper Jurassic deposits of the Cabo Mondego, many dinosaur footprints preserved as superficial impressions and cross-section structures are found. The older ones are preserved in middle Oxfordian brackish levels of the Complexo Carbonoso unit, on the palaeosurfaces of cyclic succession of limestones and marls or in sandstones. These footprints are tetradactyl preserved as isolated tracks or short trackways, attributed to megalosaurids (Nopcsa, 1923; Lapparent et al., 1951;

Lessertisseur, 1955; Lapparent and Zybszewski, 1957; Lockley et al., 1996, 1998; Santos and Neto de Carvalho, 2016). Based on them, Nopcsa (1923) designated the ichnogenus *Eutynichnium* that presents many similarities with *Megalosauripus*. Although being tetradactyl it is properly defined as a different ichnotaxon (Belvedere et al., 2019). There are also some surfaces in which these footprints are associated with large rounded deformations presenting extrusion rims, interpreted as sauropod footprints. The lower portion of the Calcários Hidráulicos (Fig. 2), mainly consisting of freshwater limestones, also preserves footprints on the bedding surface and as cross-section structures (Fig. 3) in at least four distinct levels. They are here interpreted as large tetradactyl footprints of slender large Theropoda (Fig. 2).

In this study we analyzed in detail eight distinct track-bearing strata of fine to coarse-grained sandstones, with some thin levels of mudstones, siltstones and shelly sandstones, recognized at the lower part of the Arenitos da Boa Viagem Formation (Fig. 2), at Cabo Mondego. The tracks are preserved as true footprints on the trampled surface, cross-section casts and transmitted relief of the dinosaur footprints.

The footprints from the ABV level 1, are five three-dimensional casts observed in cross-section and they are distributed within the same bedding interval, deforming up to 35 cm from the bedding surface (Fig. 4). The casts were preserved in a 40 cm layer of laminated mudstones, siltstones and fine sandstones and the molds are infilled with fine-grained sandstone from the upper sediment level. The cross-sections range from 15 cm to 20 cm width and 25 cm to 35 cm depth, presenting a V-shaped geometry, with sediment crenulations on the lateral borders. These are vertical and near the upper margins there are straight platforms. Two footprints can be observed on the bedding surface related to these cross-sections. They are tridactyl, mesaxonic, with pointed digits indicating large functionally three-toed theropod. The posterior margins are broken. They range from 15 cm to 23 cm width (Fig. 4D) and 10 cm to 15 cm length. In one of these footprints (Fig. 4), it is possible to observe in a cross-section (Fig. 4A, B) the internal deformational features (Fig. 4C) and the footprint surface (Fig. 4D); in the direction of the lower bedding plane there is the narrowing of the deformation, developing a tubular structure with ~30 cm in length, 8 cm wide and 15 cm deep. The lower extremity of this tube progressively narrows to a pointed extremity, similarly to the feature produced by digit III drag during the theropod foot movement (Gatesy et al., 1999; Carvalho et al., 2021). There are also fine crenulations surrounding the footprints margins and digits as fluidization structures (Fig. 4C).

The footprints from the ABV level 2 (Fig. 5) are two cross-sections and at least nine casts on the surface of a fallen sandstone block. The cross-section footprints present slight concave bottom and steep borders. They are 25 cm to 45 cm width and 20 cm to 30 cm depth filled with successive fine-laminated laminae; the upper edges of these depressions are high and probably correspond to displacement rims (Fig. 5A). Nine tridactyl footprint casts, one large and eight smaller footprints are preserved on the surface of the fallen block (Fig. 5B, E). The tracks have pointed digits without digital or plant pads and generally digit III is the longest one. The largest track is mesaxonic, has a 45 cm width and 50 cm length, preserves three digits and has a rounded posterior margin. The smaller footprints are mesaxonic, range from 12 cm to 20 cm width and 15 cm to 25 cm length (Fig. 5C, E). All of them are preserved as convex hyporeliefs and are filled with fine reddish sandstones from the upper strata. Also preserved on the block is a rounded mound, 35 cm and 25 cm axes, showing fluidization structures and irregular interior division (Fig. 5D).

The tracks in the ABV level 3 are preserved as natural casts beneath ceiling overhangs and as a cast on a fallen sandstone block (Fig. 6). In the ceiling overhangs it is possible to recognize three complete footprints (~9 cm width and ~12 cm length) and two partial ones (only individual digits are preserved, ~10 cm length). These footprints are tridactyl, mesaxonic and present sharp borders. A peculiar aspect is the geometry presented by the complete footprints, denoting tapering limits of the digits' edges, which lends a pyramidal aspect to the digits (Fig. 6A). The isolated digit impressions are long tubular structures (~10 cm length), folded in the middle (Fig. 6B). On the surface of a fallen block (Fig. 6C) there is a tridactyl footprint with pointed digits. It is mesaxonic, 23 cm width and 26 cm length, without digital or plant pads. Digit III is the longest one (13 cm length) and digits II and IV are ~5 cm length. The footprints are filled with coarse sandstones.

The dinoturbation in the ABV level 4 are two depressions observed in cross-section, in a 1 m interval of fine to coarse sandstones, interspersed with mudstones, lumachelle and shelly sandstones (Fig. 7). They are two footprints in the lower portion of level 4 in mudstones; they are large concave deformations (Fig. 7A), ranging from 50–60 cm in width and 30–45 cm in depth, filled with coarse and shelly sandstones. There are steep borders and the upper edges of these depressions are slightly high and probably correspond to displacement rims. The sandstone laminae sometimes are deformed, showing an irregular geometry inside the footprints, with a prominent pointed central V-shaped deformation, which probably corresponds to digit III and shows the maximum penetration depth; it is also curved, and lamination follows the path of the digit (Fig. 7B). This curved and pointed projection in the direction of the lower portion of the track is similar in some aspects to the sagittal section of a simulated track presented by Falkingham et al. (2020). These aspects are typical of penetrative footprints.

On the surface of the fine sandstone of the ABV level 5 (Fig. 8A) there are at least six isolated large footprint impressions, with or without fluidization structures. They are tridactyl and mesaxonic, ranging from 35–40 cm in width and 35–40 cm in length. The digits are pointed and digit III is the biggest one. Their posterior borders are concave. The footprints without any kind of fluidization show a massive sandstone fill, that presents a slight, distinct grain size from the surrounding matrix, highlighting it in the surface of level 5 (Fig. 8B). There are also footprints filled with fluidized sandstones; these deformations are restricted to the interior of the footprints. The footprints are filled with the same sandstone of the surrounding surface, and fluidization follows the contour of the digits and posterior border of footprints (Fig. 8C).

The surface of the ABV level 6 presents three isolated digit impressions (Fig. 8D) and two shallow footprints casts. The digit impressions are molds of curved pointed digits, larger in the lower portion and very narrow in the distal extremity. They range from 10 cm to 12 cm in length. There are also two shallow casts of tridactyl, mesaxonic footprints, filled with coarse sandstones. They have a width of ~8 cm and a length of ~12 cm. The digit impressions and footprints are randomly distributed on the surface of level 6 and they are probably related to theropods.

The track-bearing ABV level 7 is highly deformed. Four footprints are observed in cross-section in reddish sandstones as large contorted bulges of sandstones that penetrate at least 35 cm from the strata surface. These concave features present a larger upper portion (40–50 cm width) that progressively becomes narrower in the lower surface. They are V-shaped or slightly concave, filled with the same coarser sandstone from the upper strata. There are also some pointed tubular structures that reach 30 cm in length, projecting from the lower portion of these rounded deformed bulges; they probably correspond to the mold of a big-sized digit

III (Fig. 9A). These features are very similar to the sagittal section of tridactyl footprints simulated by Falkingham et al. (2020). There are highly complex structures beneath the original surface, with folds and faults of interbedded laminations following the paths of the toes. The sagittal section shows highly complex structures beneath the original surface, which are characteristic of penetrative footprints.

The lower portion of the ABV level 8, a coarse sandstone bed, shows a large amount of dinoturbation structures that reworked the strata completely. There are six curved conical projections ranging from 10 cm to 20 cm in length that can be grouped as structures of different sizes. The larger superior border and the narrow lower portion result to an acute V-shaped morphology. They are filled with the same coarse sandstone of the surrounding matrix and do not present a regular pattern of distribution (Fig. 9B). Another kind of structure from this level is some long ridges and grooves of various widths that can reach 50 cm in length (Fig. 9C). In both cases, no preferential direction was observed on the lower surface. There are also some concave deformations, which reach 40 cm in width and 15 cm in depth, filled with a succession of distinct laminae that follow a concave pattern. They can be superimposed and produce deformation in the lower structures.

4. Discussion

4.1. The dinoturbation and substrate consistency

Fossil footprints are volumetric structures, which extend beneath the surface. Footprint morphology, which can range from similar to the trackmaker's feet to indistinguishable impressions, is determined by biological factors (including the trackmaker's locomotion) and substrate properties. Deep footprints rarely look like the trackmaker's feet and the foot motion heavily disturbs the subsurface sediments (Sarjeant and Leonardi, 1987; Avanzini, 1998; Gatesy et al., 1999; Gatesy, 2003; Manning, 2004, 2008, 2011; Milàn, 2006; Milàn and Bromley, 2006; Falkingham et al., 2011; Avanzini et al., 2012; Falkingham and Gatesy, 2014; Falkingham et al., 2014, 2016; Citton et al., 2015; Lockley and Xing, 2015; Gatesy and Falkingham, 2017). During the trackmaker movement and load, all particles of the substrate are physically displaced. Sedimentological analyses underline the influence of the substrate on the final track morphology and length (e.g., Lockley, 1991; Milàn et al., 2004; Milàn and Bromley, 2006; Thulborn, 2012; Razzolini et al., 2014; Razzolini, 2016). Substrate consistency and cohesion (a function of moisture content) are the most important factors controlling track formation, morphology and preservation (e.g., Marty et al., 2006).

During the formation of a footprint, the energy (related to the trackmaker's weight) is transmitted downwards and outwards through the substrate generating indirect structures (also known as transmitted or ghost prints) which, unlike true tracks, do not preserve the direct contact between the trackmaker's feet and substrate. If observed in cross-section, they are the underlying deformations below the original contact surface of the animals. Indirect structures have a close relationship with sediment properties during or after track formation, and they are the most common record of fossil footprints (Gatesy, 2003; Gatesy and Falkingham, 2017; Carvalho and Leonardi, 2021). Most dinosaur footprints recognized in the eight levels of Arenitos da Boa Viagem Formation are indirect structures.

The dynamic interaction between the trackmaker and the substrate enables a wide variety of preservational states and morphologies (García-Ramos et al., 2009). This can be observed in the experiments performed by Milàn (2006) in Emu (*Dromaius novaehollandiae*) track morphology. These experiments show that the main cause of variation is substrate consistency. The deformations observed in the Arenitos da Boa Viagem Formation are not liquefaction distortions resulted from environmental processes. They are the result of the interaction between an animal autopodium and a substrate that was disrupted, deformed, resulting in dinoturbation structures.

Reworking of sedimentary substrates by terrestrial vertebrates is important in disturbing the primary grain fabric and sedimentary structures, and there is a narrow range of sediment textures and moisture content that will allow the preservation of footprints in the geological record (Laporte and Behrensmeyer, 1980; Sanz et al., 2016). Generally, only the outline of the footprint is preserved, produced by the stirring of the substrate at the contact zone with the autopodium (Lockley, 1991; Lockley and Meyer, 2000), and, as stressed by Marty et al. (2018), foot morphology responds to sedimentological substrate aspects, more flattening against firm substrates and less against soft ones. The preservation potential of footprints depends both on taphonomic processes and weathering after exhumation (Laporte and Behrensmeyer, 1980; Falkingham and Gatesy, 2014; Gatesy and Falkingham, 2017).

In the studied ABV levels 3, 5 and 6 of the Arenitos da Boa Viagem Formation, footprints are observed on the palaeosurfaces as true footprints (ABV level 5) and natural casts (ABV levels 3 and 6). The true footprints are shallow impressions, and the natural casts filled with coarse-grained sandstones exhibit few morphological details. In both cases, it is possible to observe deformation structures on the surrounding matrix (Figs. 6C, 8C), although the casts generally present a more defined outline of the digits and rear portion of the track.

The identification of true footprints on vertical sections was performed by Cariou et al. (2014) by determining the most deformed surface and by track infilling analysis. Similar features were already described in Jurassic deposits by Romano and Whyte (2003, 2012), Powel (2010), Piñuela (2012), and Cretaceous deposits in China, USA, Brazil and Portugal as presented by Difley and Ekdale (2002), Xing et al. (2015), Carvalho et al. (2021), and Figueiredo et al. (2021). The morphology of true track cross-sections is generally induced by distinct degrees of the substrate deformation. In ABV level 1 of Arenitos da Boa Viagem Formation, they are usually 15 cm from the palaeosurface, reaching up 35 cm. The track margins and digits are surrounded by fine crenulations showing the fluidization of the sediments (Fig. 4D). In ABV level 2, the cross-section preservation is slight concave deformations reaching 45 cm long and 30 cm deep (Fig. 5A). There are also large concave deformations (Fig. 7), ranging from 50–60 cm wide and 30–45 cm deep in ABV level 4. The margins of the concave deformations of ABV level 2 and ABV level 4 are limited by higher convex edges, probably extrusion rims. In ABV levels 7 and 8 (Fig. 9), it is possible to observe large contorted bulges of sandstones, indicating a high degree of substrate deformation. In all these cross-section footprints, there are pointed tubular projections on their lower portions, interpreted as digit casts.

Although the footprint morphology is generally unclear, there are typical aspects of theropod tracks such as the pronounced V-shaped impression of digit III. To distinguish the trackmakers, we used the analysis by Milàn et al. (2004), which observed sequential slices through theropod footprints, producing a schematic section through theropod cross-section footprints. We have then analyzed the structures described by Milàn et al. (2006) on the material of Lavini di Marco (Hettangian, Rovereto, Italy). Other analyses, such as the observational data on experimental ichnology (Falkingham et al., 2020) and sectioned views of fossil footprints (Avanzini, 1998), allow us to explain the dynamics of particle movement and the internal geometry in deep footprints. The sagittal and transverse cross-sections show deformed laminations where the foot has passed, with complex structures beneath the original surface.

The degree of substrate deformation can reveal some aspects concerning the plasticity and water content of the sediment reworked by the trackmaker's movement (Milàn, 2006; Graversen et al., 2007). The abundance of vertebrate bioturbation depends upon rates of trampling, burial, and varies from single, isolated footprints to bioturbated sedimentary layers (Lockley, 1986; Romano and Whyte, 2003). The depth of the depression depends both on the animal's weight and the plasticity of the sediment, and the deformation can reach one meter with the transmitted effect (e.g., Milàn, 2003, 2006; Falkingham et al., 2010; Carvalho et al., 2021). The superficial shallow footprints preserved as concave epirelief (or its molds as convex hyporelief) on the ABV levels 3, 5 and 6 are generally produced on sandy substrates that show a low possibility of deformation, whereas deeper footprints, that reach 45 cm in depth when observed in cross-section, are related to soft substrates (Marty et al., 2006). However, in all levels there are shreds of evidence of fluidization structures, indicative of the high water content in the pores of the unconsolidated sands.

Dinoturbation can disturb a single bed or successively alternate beds, and there is a wide variety of track patterns according to the deformation, especially when observed as cross-section footprints. The penetration of the foot in the substrate can be an indication of the substrate's original consistency. Marty et al. (2010) observed in the Iouaridène Formation (Late Jurassic, Morocco) that the low penetration of footprints (15 cm), even for the largest dinosaurs, was an indicator of a cohesive sediment. In ABV level 1 of Arenitos da Boa Viagem Formation, the penetration ranges from 15–35 cm from the paleosurface, thus it can be considered, compared with the Iouaridène footprints and with the other levels of Arenitos da Boa Viagem Formation, the most cohesive substrate in this succession. In ABV level 2, the cross-sections are 30 cm deep, and in ABV level 4, 30–45 cm deep. These two levels demonstrate a different degree of substrate cohesiveness, enabling greater penetration of the feet in the substrate. There is another distinctive aspect on ABV levels 2 and 4; the upper borders of the concave deformations show higher convex edges, probably extrusion rims, a sign of higher substrate plasticity. The large contorted sandstone bulges in ABV levels 7 and 8 indicate a higher degree of substrate deformation. The distinct aspects of the deformational structures could be related to the observation on sagittal (ABV level 7) or transverse (ABV level 8) sections of the footprints.

When the footprints are observed as cross-section casts in the substrate, they are designated as three-dimensional dinoturbation structures. They record the three-dimensional foot cast and the locomotion pattern of the trackmakers, providing an important complement to the information obtained from footprints preserved on single-bedding surfaces (Xing et al., 2015). Another term is "4D footprints", defined by Cobos et al. (2016) for the Villar del Arzobispo Formation (Late Jurassic, Spain), as footprints that are preserved as natural casts revealing the trajectory of the tracksmaker's foot within the sediment and can reveal how the dinosaur moved (Campos-Soto et al., 2017). The track casts of level 8 of Arenitos da Boa Viagem Formation could also be considered as an example of "4D footprints". The regular ridge and groove casts (Fig. 9C) are probably drag marks, observed on a transverse section, produced by the digits during the penetration of the foot on the substrate.

The substrate consistencies at the different levels are linked to the footprint preservation aspects. In the ABV levels 1 and 5, some tracks show the borders and digits associated with fluidization features, indicating a high water content in the sediments and liquefaction events after the load of the feet on the tracking surface. In ABV levels 2 and 4, the cross-sections are large concave deformations, limited by extrusion rims, showing a more cohesive sediment with high plasticity. The footprints in ABV level 3 are casts with well-defined borders, representing a very cohesive substrate. A similar interpretation can be considered to ABV level 6 where isolated digit impressions are found. The large contorted bulges of sandstones found in ABV levels 7 and 8, point toward a high water content and plasticity in the substrate, allowing the disturbance in high depth.

4.2. Paleoenvironmental context of the dinoturbation

Dinosaur footprints are common in fluvial settings (e.g., Sciscio et al., 2016; Díaz-Martínez et al., 2018), shallow lacustrine facies (e.g., Xing et al., 2015), fluvial-dominated delta depositional systems (e.g., Niedzwiedzki and Pieńkowski, 2004), shallow marine platforms which underwent episodic subaerial exposure (e.g., Kvale et al., 2001), and in tidal flats (e.g., Carvalho and Pedrão, 1998; Figueiredo et al., 2021).

According to Laporte and Behrensmeyer (1980), the amount of time between footprint formation and burial affects their preservation potential. Therefore, in part, the sedimentation processes determine whether a footprint will be preserved or not. Other factors, such as microbial mats, also play a crucial role during and after track formation. The presence of biolaminites and microbial mats leads to early lithification, rapid covering by sediment and overgrowth by microbial mats, favoring the preservation of footprints (Chafetz and Buczynski, 1992; Noffke et al., 2001; Dupraz et al., 2004; Marty et al., 2009). During periods of drought, footprints quickly consolidate, thus resisting to trampling or erosion (Carvalho et al., 2013). The surfaces of levels 3, 5 and 6, in which there are tracks preserved as shallow impressions or natural casts of these impressions, could be under this environmental scenario. Exposed sand bars of the fluvial channels allowed for footprint preservation due to the more cohesive surface on the contact zone of the foot. Therefore, the underlying sediments are relatively water-satured, leading to the partial fluidization of these footprints. This preservational condition is also observed in fluvial deposits from the Lower Cretaceous of Sousa Basin (Brazil; Leonardi, 1994; Carvalho, 2000a, 2000b, 2004) and Cameros Basin (Spain; Pérez-Lorente, 2015).

4.3. The trackmakers from the Upper Jurassic of Cabo Mondego

The identification of the trackmakers of Arenitos da Boa Viagem Formation has important palaeoecological implications for the Upper Jurassic dinosaur community and Late Jurassic ecosystem reconstructions. If the footprints are seen in cross-section, as in the case described herein, it is very difficult to classify them and to identify the trackmaker. In the theropod footprints, it is possible to observe the vertical to oblique walls of the footprint. In the middle point, there is generally a pointed, triangular sharp section that deepens down to the bottom layer. It is interpreted as the impression of digit III, deeper than the others. Digit III sustains the weight of the trackmaker, allowing for greater evidence of the toe print as found in ABV levels 4 and 7 (Figs. 7B, 9A). Another possibility is that it (in section) represents a scratch mark made by the claw of digit III throughout the footprint, as observed in Lower Cretaceous footprints in Brazil (Carvalho et al., 2021; Leonardi and Carvalho, 2021). When they are observed on the surface of the bedding plane, such as the footprints of ABV levels 3 and 5, they are tridactyl, mesaxonic and show pointed digits indicating the presence of claws (Figs. 6C, 8C).

Other aspects of theropod footprints observed in cross-sections and track-bearing paleosurfaces (Figs. 4, 7) are pointed projections, in distinct penetration depths, that could correspond to the transverse view (normal to the orientation of the toes) of the footprints. A similar aspect is observed in the experimental data of

Falkingham et al. (2020). The laminations that are drawn downwards produce tightly nested V-shapes, and there are other, more deformed levels, as particles are pushed aside by the rising foot. Another possibility is a prominent pointed central deformation (Fig. 7B), which probably corresponds to digit III of large or robust theropod footprints in a low cohesive substrate.

It is very difficult to pinpoint the identity of the theropod trackmaker based on footprints (Rauhut et al., 2018). Theropod footprints are generally attributed to large theropods with "megalosaurian affinity", although the giant theropod trackmakers known from the Late Jurassic of the Iberian Peninsula probably include members of the ceratosaurid, allosaurid, and megalosaurid dinosaurs (Holtz et al., 2004; Tykoski and Rowe, 2004; Carrano et al., 2012; Marty et al., 2018; Rauhut et al., 2018). Some osteological remains from the Late Jurassic of Lusitanian Basin are also attributed to these groups (Mateus, 1998; Mateus et al., 1998; Pérez-Moreno et al., 1999; Mateus and Antunes, 2000; Mateus et al., 2006; Malafaia et al., 2010, 2015, 2016, 2017a, 2017b, 2019; Mateus and Milàn, 2010; Hendrickx and Mateus, 2014).

A simple division of the theropod footprints into two ichno-groups is based on their sizes (Cobos et al., 2014). Ichno-group 1 is composed of slender, large theropod footprints of Allosauridae theropods (such as *Bueckeburgichnus*, *Hispanosauropu*s, *Megalosauripus*), while ichno-group 2 is made up of robust morphotypes, produced by giant Megalosauridae theropods (e.g., *Eutynichnium*, *Iberosauripus*, *Jurabrontes*). Rauhut et al. (2018) considered that the slender large footprints might have been made by a wide variety of basal tetanurans; in addition to allosaurids, there were also metriocanthosaurids, afrovenatorine megalosaurids and exceptionally large ceratosaurs. Also, Razzolini et al. (2017), Marty et al. (2018), and Belvedere et al. (2019) made some revisions of *Megalosauripus* footprints. The division of theropod footprints can be based on the foot length (FL) following Belvedere et al. (2019): large and gracile (30 < FL< 50 cm); and giant and robust (FL > 50 cm). Another possibility is the classification based on ichnotaxonomy (ichnogenus and ichnospecies) as proposed by Castanera et al. (2020a, 2020b).

The footprints observed at Cabo Mondego indicate a change in the morphotypes of Cobos et al. (2014) throughout the Upper Jurassic succession. There is a dominance of ichno-group 1 in the Arenitos da Boa Viagem Formation, with slender large theropod footprints, and few that may be attributed to ichno-group 2, composed of robust morphotypes. The same occurs at the levels found in the lower division of the Calcários Hidráulicos. This contrasts with the older succession at the Complexo Carbonoso unit, where palaeosurfaces of limestones and marls present a clear dominance of footprints of the ichno-group 2, more robust footprints attributed to megalosaurids (Nopsca, 1923; Lapparent et al., 1951; Lessertisseur, 1955; Lapparent and Zybszewski, 1957; Lockley et al., 1996, 1998).

Two interpretations can be proposed concerning this ichnofauna change in the Upper Jurassic succession of Cabo Mondego. The first possibility is environmental control in the distribution of dinosaur track makers. The Complexo Carbonoso is interpreted as deposited with brackish to freshwater carbonate and siliciclastic coastal environments, and the footprints were produced in the exposed sedimentary beds. Here, in the preferred environments for megalosaurids, possibly in search of suitable food (Razzolini et al., 2016), robust footprints interpreted as megalosaurid trackmakers prevail. In the lower division of Calcários Hidráulicos (footprints produced in exposed freshwater limestones) and in the lower part of the Arenitos da Boa Viagem Formation (footprints produced in exposed sand bars and crevasses of a deltaic plain), theropod footprints are slender and less robust, probably related to allosaurid morphotypes. However, it is also possible to consider that this represents a faunistic succession through time. The robust footprints end at the top of the Complexo Carbonoso unit and the next unit (lower division of the Calcários Hidráulicos), both of middle Oxfordian age, only contains footprints of slender large Theropoda. The studied sandstone levels of the lower part of the Arenitos da Boa Viagem Formation (lowermost Kimeridgian), deposited in a deltaic setting, also only contains footprints of slender large Theropoda. In addition to representing a new ecological space, they are also in a later time span (early Kimmeridgian) in the succession of Cabo Mondego. So the morphotype changes could be related to new environmental scenarios in a distinct time, with new trackmakers. Such changes over the Jurassic–Cretaceous are also observed in other dinosaur footprints, like the sauropod footprints of the Cameros Basin, in Spain (Moratalla, 2009; Moratalla and Hernán, 2010).

In the Lusitanian Basin, large theropods such as *Megalosaurus*, *Lourinhanosaurus*, *Allosaurus*, *Torvosaurus*, *Lusovenator*, for the Late Jurassic, and *Megalosaurus* and *Baryonyx* for the Lower Cretaceous (Lapparent and Zbyszewski, 1957; Dantas et al., 1999; Antunes and Mateus, 2003; Ortega et al., 2006; Buffetaut, 2007; Figueiredo, 2008, 2014; Mateus et al., 2011; Hendrickx and Mateus, 2014;

Figueiredo et al., 2015; Belvedere et al., 2019; Malafaia et al., 2019, 2020; Castanera et al., 2020a, 2020b) have been identified. The analysis of the Cabo Mondego footprints is relevant as good evidence of a distinct theropod fauna throughout the Late Jurassic in the Lusitanian Basin (Fig. 10). This evaluation could enable a better understanding of the faunal exchange corridors between further south (Iberian Massif – Massif Central and North Africa, Morocco) and further north (Rhenish Massif – London-Brabant Massif), as proposed by many authors (e.g., Meyer, 1993; Marty et al., 2018; Rauhut et al., 2018). The footprints in Cabo Mondego play an important role in the assessment of such faunal exchanges during sea level lowstands, and the paleoenvironmental control on the distribution of distinct trackmakers in lagoon and deltaic settings throughout the Late Jurassic.

5. Conclusions

In the Lusitanian Basin, there are a great number of Middle and Upper Jurassic sedimentary successions with dinosaur footprints and dinoturbation structures. This study analyzes the stratigraphic distribution of dinoturbation structures from the Upper Jurassic of Cabo Mondego (western central Portugal). These structures are good evidence of the diverse theropod fauna in the Lusitanian Basin throughout the Late Jurassic.

Besides paleobiological insights into trackmakers, footprints also provide information about the substrate stepped on by the dinosaurs. The affected substrate trampled from the surface to its whole deformable thickness enables the interpretation of the substrate consistency when the track was formed. In the lower part of the Arenitos da Boa Viagem Formation, the studied dinosaur footprints are distributed over eight levels, generally in siltstones and fine- to medium-grained sandstones. They are preserved as true footprints on the sedimentary bedding surface, natural cast infillings, or as cross-section casts. There are also transmitted prints, originated by the load induced after stepping on the surface. Dinoturbation may disturb a single bed or successively alternate beds, and there is a wide variety of track patterns due to the deformation, especially when observed as cross-section footprints.

Penetration of the foot in the substrate can be an indication of the substrate's original consistency. Three distinct cohesiveness patterns have been observed, defined by the penetration of the foot from the paleosurface. The most cohesive substrate considered to Arenitos da Boa Viagem succession, was when penetration reaches up to 15 cm from the palaeosurface. The cross-sections that are 30–45 cm deep demonstrate a different degree of substrate cohesiveness, which allowed for greater penetration of the foot in the substrate. In this case, there is another distinctive aspect: the upper borders of the concave deformations present higher convex edges. These are probably extrusion rims, a sign of greater substrate plasticity. The large contorted sandstone bulges indicate a higher degree of substrate deformation.

Identifying the trackmakers of the Cabo Mondego Upper Jurassic has important implications for ecosystem reconstructions. The footprints indicate a change in the morphotypes throughout the Upper Jurassic succession. There is a clear dominance of robust morphotypes in the Complexo Carbonoso (middle Oxfordian), while in the younger, lower division of Calcários Hidráulicos (middle Oxfordian) and in the lower part of Arenitos da Boa Viagem Formation (lowermost Kimmeridgian), almost only slender large theropod footprints are present.

Acknowledgments

The authors thank Matteo Belvedere (Office de la Culture, Switzerland), Miengah Abrahams (University of Cape Town, South Africa), Novella L. Razzolini (Institut Català de Paleontologia Miquel Crusafont, Carrer de l'Escola Industrial), Min Zhu (Associate Editor of Palaeoworld) for their careful revisions. The support of Giuseppe Leonardi (Istituto Cavanis, Italy), Marco Avanzini (Lavini di Marco, Museo Tridentino di Scienze Naturali, Italy), Félix Perez-Lorente (Cameros Basin, Universidad de la Rioja, Spain), Laura Piñuela and José Carlos García-Ramos (Asturia, Museo del Jurásico de Asturias, Spain) were very important for the discussion on dinosaur footprints and dinoturbation, which helped us to interpret the dinoturbation structures from the Jurassic of Cabo Mondego. We thank Joel Loureiro Carvalho, Jaime Joaquim Dias and Deverson Silva (Pepi) for the final drawing of the figures and reconstruction scenario. This research was supported by Conselho Nacional de Desenvolvimento Científico e Tecnológico and Fundação Carlos Chagas Filho de Amparo à Pesquisa do Estado do Rio de Janeiro (E-26/202.910/2017). This work was also funded by the Fundação para a Ciência e Tecnologia (FCT), through national funds, by the projects UIDB/MAR/04292/2020 (Marine and Environmental Sciences Center) and UID/Multi/00073/2020 (Centro de Geociências, Universidade de Coimbra).

References

Abrahams, M., Sciscio, L., Reid, M., Haupt, T., Bordy, E.M., 2020. Large tridactyl dinosaur tracks from the Early Jurassic of southern Gondwana — uppermost Elliot Formation, Upper Moyeni, Lesotho. Annales Societatis Geologorum Poloniae 90, 1–26.

Abrahams, M., Bordy, E.M., Knoll, F., in press. Hidden for one hundred years: a diverse theropod ichnoassemblage and cross-sectional tracks from the historic Early Jurassic Tsikoane ichnosite (Clarens Formation, northern Lesotho, Southern Africa). Historical Biology, doi: 10.1080/08912963.2020.1810681.

Alves, T.M., Manuppella, G., Gawthorpe, R.L., Hunt, D.W., Monteiro, J.H., 2003. The depositional evolution of diapir-and fault-bounded rift basins: examples from the Lusitanian Basin of West Iberia. Sedimentary Geology 162 (3–4), 273–303.

Antunes, M.T., 1976. Dinossáurios Eocretácicos de Lagosteiros. Ciências da Terra 1, 1–35.

Antunes, M.T., 1999. Dinossauros e Portugal. Dois casos menos conhecidos. Ciências da Terra 13, 59–69.

Antunes, M.T., Mateus, O., 2003. Dinosaurs of Portugal. Comptes Rendus Palevol 2, 77–95.

Avanzini, M., 1998. Anatomy of a footprint: Bioturbation as a key to understanding dinosaur walk dynamics. Ichnos 6, 129–139.

Avanzini, M., Frisia, S., Van den Driessche, K., Keppens, E., 1997. A dinosaur tracksite in an early Liassic tidal flat in northern Italy: Palaeonvironmental reconstruction from sedimentology and geochemistry. Palaios 12, 538–551.

Avanzini, M., Piñuela, L., García-Ramos, J.C., 2012. Late Jurassic footprints reveal walking kinematics of theropod dinosaurs. Lethaia 45, 238–252.

Azerêdo, A.C., Duarte, L.V., Henriques, M.H., Manuppella, G., 2003. Da dinâmica continental no Triásico aos mares do Jurássico Inferior e Médio. Cadernos de Geologia de Portugal. Instituto Geológico e Mineiro, Lisboa, 43 pp.

Belvedere, M., 2008. Ichnological researches on the Upper Jurassic dinosaur tracks in the Iouaridène area (Demnat, Central High-Atlas, Morocco). PhD Thesis, Università degli Studi di Padova, Padova, 121 pp.

Belvedere, M., Farlow, J.O., 2016. A numerical scale for quantifying the quality of preservation of vertebrate tracks. In: Falkingham, P.L., Marty, D., Richter, A.

(Eds.), Dinosaur Tracks: The Next Steps. Indiana University Press, Bloomington and Indianapolis, pp. 92–99.

Belvedere, M., Mietto, P., Ishigaki, S., 2010. A Late Jurassic diverse ichnocoenosis from the siliciclastic Iouaridène Formation (Central High Atlas, Morocco). Geological Quaterly 54 (3), 367–380.

Belvedere, M., Castanera, D., Meyer, C.A., Marty, D., Mateus, O., Silva, B.C., Santos, V.F., Cobos, A., 2019. Late Jurassic globetrotters compared: A closer look at large and giant theropod tracks of North Africa and Europe. Journal of African Earth Sciences 158, 103547.

Bernardes, C., 1992. A sedimentação durante o Jurássico Superior entre o Cabo Mondego e o Baleal (Bacia Lusitana): Modelos deposicionais e arquitecturasequencial. PhD Thesis, University of Aveiro, Aveiro, 261 pp.

Buffetaut, E., 2007. The spinosaurid dinosaur *Baryonyx* (Saurischia, Theropoda) in the Early Cretaceous of Portugal. Geological Magazine 144, 1021–1025.

Campos-Soto, S., Cobos, A., Caus, E., Benito, M.I., Fernández-Labrador, L., Suarez-Gonzalez, P., Quijada, I.E., Mas, R., Royo-Torres, R., Alcalá, L., 2017. Jurassic Coastal Park: A great diversity of palaeoenvironments for the dinosaurs of the Villar del Arzobispo Formation (Teruel, eastern Spain). Palaeogeography, Palaeoclimatology, Palaeoecology 485, 154–177.

Canudo, J.I., Barco, J.L., Pereda Suberbiola, X., Ruiz-Omeñaca, J.I., Salgado, L., Torcida, F., Gasulla, J.M., 2009. What Iberian dinosaurs reveal about the bridge said to exist between Gondwana and Laurasia in the Early Cretaceous. Bulletin de la Societé Géologique de France 180 (1), 5–11.

Cariou, E., Olivier, N., Pittet, B., Mazin, J.-M., Hantzpergue, P., 2014. Dinosaur track record on a shallow carbonate-dominated ramp (Loulle section, Late Jurassic, French Jura). Facies 60, 229–253.

Carrano, M.T., Benson, R.B.J., Sampson, S.D., 2012. The phylogeny of Tetanurae (Dinosauria: Theropoda). Journal of Systematic Palaeontology 10 (2), 211–300.

Carvalho, I.S., 1995. As pistas de dinossauros da Ponta da Guia (Bacia de São Luís, Cretáceo Superior–Maranhão, Brasil). Anais da Academia Brasileira de Ciências 67, 413–431.

Carvalho, I.S., 2000a. Geological environments of dinosaur footprints in the intracratonic basins from Northeast Brazil during the South Atlantic opening (Early Cretaceous). Cretaceous Research 21, 255–267.

Carvalho, I.S., 2000b. Huellas de saurópodos de la Formación Antenor Navarro (Cretácico temprano de la Cuenca de Sousa), Serrote do Letreiro, Paraíba, Brasil. Ameghiniana 37, 353–362.

Carvalho, I.S., 2004. Dinosaur footprints from northeastern Brazil: Taphonomy and environmental setting. Ichnos 11, 311–321.

Carvalho, I.S., Leonardi, G., 1992. Geologia das bacias de Pombal, Sousa, Uiraúna-Brejo das Freiras e Vertentes (Nordeste do Brasil). Anais da Academia Brasileira de Ciências 64, 231–252.

Carvalho, I.S., Leonardi, G., 2021. Fossil footprints as biosedimentary structures for paleoenvironmental interpretation: Examples from Gondwana. Journal of South American Earth Sciences 106, 102936.

Carvalho, I.S., Pedrão, E., 1998. Brazilian theropods from the Equatorial Atlantic margin: behavior and environmental setting. Gaia 15, 369–378.

Carvalho, I.S., Borghi, L., Leonardi, G., 2013. Preservation of dinosaur tracks induced by microbial mats in the Sousa Basin (Lower Cretaceous), Brazil. Cretaceous Research 44, 112–121.

Carvalho, I.S., Leonardi, G., Rios-Netto, A.M., Borghi, L., Paula Freitas, A., Andrade, J.A., Freitas, I.F., 2021. Dinosaur trampling from the Aptian of Araripe Basin, NE Brazil, as tools for paleoenvironmental interpretation. Cretaceous Research 117, 104626.

Castanera, D., Belvedere, M., Silva, B., Marty, D., Razzolini, N., Meyer, C., Santos, V.F., 2017. New megalosauripus tracks in the Late Jurassic of Portugal. 15th Annual Meeting of the European Association of Vertebrate Palaeontologists, Munich, Germany, 1–3 August 2017. Zitteliana 91, 27–28.

Castanera, D., Belvedere, M., Marty, D., Paratte, G., Lapaire-Cattin, M., Lovis, C., Meyer, C.A., 2018. A walk in the maze: variation in Late Jurassic tridactyl dinosaur tracks from the Swiss Jura Mountains (NW Switzerland). PeerJ 6, e4579, doi: 10.7717/peerj.4579.

Castanera, D., Silva, B.C., Santos, V.F., Malafaia, E., Belvedere, M., 2019. The Late Jurassic vertebrate footprint collection of the Sociedade de História Natural in Torres Vedras (Portugal). In: Buchwitz, M., Falk, D., Klein, H., Wings, O. (Eds.), 3rd International Conference of Continental Ichnology, Abstract Volume & Field Trip Guide. Hallesches Jahrbuch für Geowissenschaften/Beiheft 46, 6.

Castanera, D., Malafaia, E., Silva, B.C., Santos, V.F., Belvedere, M., 2020a. New dinosaur, crocodylomorph and swim tracks from the Late Jurassic of the Lusitanian Basin: implications for ichnodiversity. Lethaia 54, 271–287.

Castanera, D., Silva, B.C., Santos, V.F., Malafaia, E., Belvedere, M., 2020b. Tracking Late Jurassic ornithopods in the Lusitanian Basin of Portugal: Ichnotaxonomic implications. Acta Palaeontologica Polonica 65 (2), 399–412.

Chafetz, H.S., Buczynski, C., 1992. Bacterially induced lithification of microbial mats. Palaios 7, 277–293.

Christofoletti, B., Peixoto, B.C.P.M., Warren, L.V., Inglez, L., Fernandes, M.A., Alessandretti, L., Perinotto, A.J.A., Simões, M.G., Assine, M.L., 2021. Dinos among the dunes: Dinoturbation in the Pirambóia formation (Paraná basin), São Paulo State and comments on cross-section tracks. Journal of South American Earth Sciences 109, 103252.

Citton, P., Nicosia, U., Nicolosi, I., Carluccio, R., Romano, M., 2015. Elongated theropod tracks from the cretaceous Apenninic carbonate platform of southern Latium (central Italy). Palaeontologia Electronica 18, Article number 18.3.49A, doi: 10.26879/578.

Cobos, A., Lockley, M.G., Gascó, F., Royo-Torres, R., Alcalá, L., 2014. Megatheropods as apex predators in the typically Jurassic ecosystems of the Villar del Arzobispo Formation (Iberian Range, Spain). Palaeogeography, Palaeoclimatology, Palaeoecology 399, 31–41.

Cobos, A., Gascó, F., Royo-Torres, R., Lockley, M.G., 2016. Dinosaur tracks as “four dimensional phenomena” reveal how different species moved. In: Falkingham, P.L., Marty, D., Richter, A. (Eds.), Dinosaur Tracks: The Next Steps. Indiana University Press, Bloomington and Indianapolis, pp. 244–256.

Crespo, E.G., 2001. Paleo-Herpetofauna de Portugal. Museu Bocage, Museu Nacional de História Natural, Lisboa, 186 pp.

Cunha, P.P., 1992. Estratigrafia e sedimentologia dos depósitos do Cretácico Superior e Terciário de Portugal Central, a leste de Coimbra [Stratigraphy and sedimentology of the Upper Cretaceous and Tertiary of central Portugal, east of Coimbra]. PhD Thesis, University of Coimbra, Coimbra, 262 pp. (in Portuguese, with English abstract).

Dantas, P., 1990. Dinossáurios de Portugal. Gaia 2, 17–26.

Dantas, P., Pérez-Moreno, B.P., Chure, D.J., da Silva, C.M., Santos, V.F., Povoas, L., Cachão, M., Sanz, J.L., Pires, C., Bruno, G., Ramalheiro, G., Galopim de Carvalho, A.M., 1999. O dinossáurio carnívoro *Allosaurus fragilis* no Jurássico português. Al-Madam 8, 23–28.

Díaz-Martínez, I., Cónsole-Gonella, C., de Valais, S., Salgado, L., 2018. Vertebrate tracks from the Paso Córdoba fossiliferous site (Anacleto and Allen formations, Upper Cretaceous), Northern Patagonia, Argentina: Preservational, environmental and palaeobiological implications. Cretaceous Research 83, 207–220.

Diedrich, C., 2011. Upper Jurassic tidal flat megatracksites of Germany — coastal dinosaur migration highways between European islands, and a review of the dinosaur footprints. Palaeobiology and Palaeoenvironments 91 (2), 129–155.

Difley, R.L., Ekdale, A.A., 2002. Footprints of Utah's last dinosaurs: track beds in the Upper Cretaceous (Maastrichtian) North Horn Formation of the Wasatch Plateau, Central Utah. Palaios 17, 327–346.

D'Orazi Porchetti, S., Bernardi, M., Cinquegranelli, A., Santos, V.F., Marty, D., Petti, F.M., Caetano, P.S., Wagensommer, A., 2016. A review of the dinosaur track record from Jurassic and Cretaceous shallow marine carbonate depositional environments. In: Falkingham, P.L., Marty, D., Richter, A. (Eds.), Dinosaur Tracks: The Next Steps. Indiana University Press, Bloomington and Indianapolis, pp. 380–392.

Dupraz, C., Visscher, P.T., Baumgartner, L.K., Reid, R.P., 2004. Microbe-mineral interactions: early carbonate precipitation in a hypersaline lake (Eleuthera Island, Bahamas). Sedimentology 51, 745–765.

Escaso, F., Ortega, F., Dantas, P., Malafaia, E., Pimentel, N.L., Pereda-Suberbiola, X., Sanz, J.L., Kullberg, J.C., Kullberg, M.C., Fernando Barriga, F., 2007. New evidence of shared dinosaur across Upper Jurassic Proto-North Atlantic: *Stegosaurus* from Portugal. Naturwissenschaften 94, 367–374.

Escaso, F., Ortega, F., Dantas, P., Malafaia, E., Silva, B., Gasulla, J.M., Mocho, P., Narváez, I., Sanz, J.L., 2014. A new dryosaurid ornithopod (Dinosauria, Ornithischia) from the Late Jurassic of Portugal. Journal of Vertebrate Paleontology 34 (5), 1102–1112.

Falkingham, P.L., Gatesy, S.M., 2014. The birth of a dinosaur footprint: Subsurface 3D motion reconstruction and discrete element simulation reveal track ontogeny. Proceedings of the National Academy of Sciences of the United States of America 111 (51), 18279–18284.

Falkingham, P.L., Margetts, L., Manning, P.L., 2010. Fossil vertebrate tracks as paleopenetrometers: confounding effects of foot morphology. Palaios 25, 356–360.

Falkingham, P.L., Bates, K.T., Margetts, L., Manning, P.L., 2011. The 'Goldilocks' effect: preservation bias in vertebrate track assemblages. Journal of the Royal Society Interface 8 (61), 1142–1154.

Falkingham, P.L., Hage, J., Bäker, M., 2014. Mitigating the Goldilocks effect: the effects of different substrate models on track formation potential. Royal Society Open Science 1, 140225–140225.

Falkingham, P.L., Marty, D., Richter, A. (Eds.), 2016. Dinosaur Tracks: The Next Steps. Indiana University Press, Bloomington and Indianapolis, 413 pp.

Falkingham, P.L., Bates, K.T., Avanzini, M., Bennett, M., Bordy, E.M., Breithaupt, B.H., Castanera, D., Citton, P., Díaz-Martínez, I., Farlow, J., Fiorillo, A.R., Gatesy, S.M., Getty, P., Hatala, K.G., Hornung, J.J., Hyatt, J.A., Klein, H., Lallensack, J.N., Martin, A.J., Marty, D., Matthews, N.A., Meyer, C.A., Milàn, J., Minter, N.J., Razzolini, N.L., Romilio, A., Salisbury, S.W., Sciscio, L., Tanaka, I., Wiseman, A.L.A., Xing, L.D., Belvedere, M., 2018. A standard protocol for documenting modern and fossil ichnological data. Palaeontology 61, 469–480.

Falkingham, P.L., Turner, M.L., Gatesy, S.M., 2020. Constructing and testing hypotheses of dinosaur foot motions from fossil tracks using digitization and simulation. Palaeontology 63 (6), 865–880.

Figueiredo, S.D., 2002. Os dinossauros da Arrábida. Revista Evolução 1, 5–8.

Figueiredo, S.D., 2004. Os dinossauros do Cabo Espichel. Techne 9, 285–290.

Figueiredo, S.D., 2008. Dinossauros de Portugal. Edições Cosmos, Chamusca, 152 pp.

Figueiredo, S.D., 2014. Os Dinossáurios em Território Português: as espécies, as jazidas e os fósseis. Chiado Editora, Lisboa, 232 pp.

Figueiredo, S.D., Rosina, P., Figuti, L., 2015. Dinosaurs and other vertebrates from the Papo-Seco Formation (Lower Cretaceous) of southern Portugal. Journal of Iberian Geology 41, 301–314.

Figueiredo, S.D., Neto de Carvalho, C., Cunha, P.P., Carvalho, I.S., 2021. New dinosaur tracks from the lower Barremian of Portugal (Areia do Mastro Formation, Cape Espichel). Journal of Geoscience and Environment Protection 9, 84–96.

García-Ramos, J.C., Piñuela, L., Lires, J.L., 2006. Atlas del Jurásico de Asturias. Ediciones Nobel, Oviedo, 228 pp.

García-Ramos, J.C., Piñuela, L., Avanzini, M., Ruiz-Omeñaca, J.I., 2009. Deep theropod undertracks look like ornithopod tracks. A conclusion from a three-dimensional study of dinosaur-footprints. In: Buscalioni, A.D., Martinéz, M.F. (Eds.), 10th International Symposium on Mesozoic Terrestrial Ecosystems and Biota, 2009. Proceeding, Universidad Autónoma de Madrid, Teruel, pp. 279–281.

Gatesy, S.M., 2003. Direct and indirect tracks features: what sediment did a dinosaur touch? Ichnos 10, 91–98.

Gatesy, S.M., Falkingham, P.L., 2017. Neither bones nor feet: track morphological variation and 'preservation quality'. Journal of Vertebrate Paleontology 37, e1314298.

Gatesy, S.M., Middleton, K.M., Jenkins Jr., F.A., Shubin, N.H., 1999. Three-dimensional preservation of foot movements in Triassic theropod dinosaurs. Nature 399 (6732), 141–144.

Gierliński, G., Niedzwiedzki, G., Nowacki, P., 2009. Small theropod and ornithopod footprints in the Late Jurassic of Poland. Acta Geologica Polonica 59, 221–234.

Gomes, J.P., 1915–1916. Descoberta de rastos de sáurios gigantescos no Jurássico do Cabo Mondego. Comunicações dos Serviços Geológicos de Portugal 11, 132–134.

Graversen, O., Milán, J., Loope, D.B., 2007. Dinosaur tectonics: A structural analysis of theropod undertracks with a reconstruction of theropod walking dynamics. The Journal of Geology 115, 641–654.

Hendrickx, C., Mateus, O., 2014. *Torvosaurus gurneyi* n. sp., the largest terrestrial predator from Europe, and a proposed terminology of the maxilla anatomy in nonavian theropods. PLoS ONE 9 (3), e88905, doi: 10.1371/journal.pone.0088905.

Henriques, M.H.P., Pena dos Reis, R., 2015. Framing the palaeontological heritage within the geological heritage: An integrative vision. Geoheritage 7, 249–259.

Henriques, M.H., Pena dos Reis, R., Duarte, L.V., 1998. Locais com interesse geológico da orla costeira portuguesa entre o Cabo Mondego e a Nazaré. Comunicações do Instituto Geológico e Mineiro 84, 6–9.

Holtz, T.R., Molnar, R.E., Currie, P.J., 2004. Basal Tetanurae. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), The Dinosauria (2nd Edition). University of California Press, Berkley, pp. 71–110.

Kvale, E.P., Johnson, A.D., Mickelson, D.L., Keller, K., Furer, L.C., Archer, A.W., 2001. Middle Jurassic (Bajocian and Bathonian) dinosaur megatracksite, Bighorn Basin, Wyoming, USA. Palaios 16, 233–254.

Laporte, L.F., Behrensmeyer, A.K., 1980. Tracks and substrate reworking by terrestrial vertebrates in Quaternary sediments of Kenya. Journal Sedimentary Petrology 50, 337–346.

Lapparent, A.F., Zybszewski, G., 1957. Les Dinosauriens du Portugal. Memória dos Serviços Geológicos de Portugal 2, 1–63.

Lapparent, A.F., Zybszewski, G., Moitinho de Almeida, F., Viega Ferreira, O., 1951. Impreintes de pas de dinosaurienes dans le Jurassique du Cap Mondego (Portugal). Compte Rendu Sommaire de Sceances de la Societè Géologique de France 14, 252–252.

Leinfelder, R.R., Wilson, R.C., 1998. Third-order sequences in an Upper Jurassic rift-related second-order sequence, central Lusitanian Basin, Portugal. Mesozoic and Cenozoic Sequence Stratigraphy of European Basins. Society for Sedimentary Geology, Special Publication 60, 507–525.

Leonardi, G., 1987. Glossary and manual of tetrapod footprint palaeoichnology. Departamento Nacional da Produção Mineral Brasil, Brasília, 117 pp.

Leonardi, G., 1989. Inventory and statistics of the South American dinosaurian ichnofauna and its paleobiological interpretation. In: Gillette, D.D., Lockley, M.G. (Eds.), Dinosaur Tracks and Traces. Cambridge University Press, Cambridge, pp. 165–178.

Leonardi, G., 1994. Annotated Atlas of South America Tetrapod Footprints (Devonian to Holocene) with an Appendix on Mexico and Central America. Companhia de Pesquisa de Recursos Minerais, Brasil, Brasília, 248 pp.

Leonardi, G., Carvalho, I.S., 2021. Dinosaur Tracks from Brazil: A Lost World of Gondwana. Indiana University Press, Bloomington, 445 pp.

Lessertisseur, J., 1955. Traces fossiles d'activite animale et leur signification paleobiologique. Memoires de la Societe Geologique de France 74, 1–150.

Lockley, M.G., 1986. The paleobiological and paleoenvironmental importance of dinosaur footprints. Palaios 1, 37–47.

Lockley, M.G., 1991. Tracking Dinosaurs: A New Look at an Ancient World. Cambridge University Press, Cambridge, 238 pp.

Lockley, M., Conrad, K., 1989. The paleoenvironmental context, preservation and paleoecological significance of dinosaur tracksites in the Western USA. In: Gillette, D.D., Lockley, M.G. (Eds.), Dinosaur Tracks and Traces. Cambridge University Press, Cambridge, pp. 121–134.

Lockley, M.G., Meyer, C., 2000. Dinosaur Tracks and Other Fossil Footprints of Europe. Columbia University Press, New York, 323 pp.

Lockley, M.G., Xing, L.D., 2015. Flattened fossil footprints: implications for paleobiology. Palaeogeography, Palaeoclimatology, Palaeoecology 426, 85–94.

Lockley, M.G., Matsukawa, M., Obata, I., 1989. Dinosaur tracks and radial cracks: unusual footprint features. Bulletin of the National Science Museum, Tokyo, Series C 15, 151–160.

Lockley, M.G., Meyer, C.A., Santos, V.F., 1994. Trackway evidence of a herd of juvenil sauropods from the Late Jurassic of Portugal. Gaia 10, 27–35.

Lockley, M.G., Meyer, C.A., Santos, V.F., 1996. *Megalosauripus*, *Megalosauropus* and the concept of megalosaur footprints. In: Morales, M. (Ed.), The Continental Jurassic. Museum of Northern Arizona Bulletin 60, 113–118.

Lockley, M.G., Meyer, C.A., Santos, V.F., 1998. *Megalosauripus* and the problematic concept of megalosaur footprints. Gaia 15, 313–337.

Lockley, M.G., Meyer, C.A., Moratalla, J.J., 2000a. *Therangospodus*: trackway evidence for the widespread distribution of a Late Jurassic theropod with well-padded feet. Gaia 15, 339–353.

Lockley, M.G., Meyer, C.A., Santos, V.F., 2000b. *Megalosauripus* and the problematic concept of megalosaur footprints. Gaia 15, 313–337.

Malafaia, E., Ortega, F., Escaso, F., Dantas, P., Pimentel, N., Gasulla, J.M., Ribeiro, B., Barriga, F., Sanz, J.L., 2010. Vertebrate fauna at the *Allosaurus* fossil-site of Andrés (Upper Jurassic), Pombal, Portugal. Journal of Iberian Geology 36 (2), 193–204.

Malafaia, E., Ortega, F., Escaso, F., Silva, B., 2015. New evidence of *Ceratosaurus* (Dinosauria: Theropoda) from the Late Jurassic of the Lusitanian Basin, Portugal. Historical Biology 27, 938–946.

Malafaia, E., Mocho, P., Escaso, F., Ortega, F., 2016. A juvenile allosauroid theropod (Dinosauria, Saurischia) from the Upper Jurassic of Portugal. Historical Biology 29, 654–676.

Malafaia, E., Mocho, P., Escaso, F., Ortega, F., 2017a. New data on the anatomy of *Torvosaurus* and other remains of megalosauroid (Dinosauria Theropoda) from the Upper Jurassic of Portugal. Journal of Iberian Geology 43, 33–59.

Malafaia, E., Escaso, F., Mocho, P., Serrano-Martínez, A., Torices, A., Cachão, M., Ortega, F., 2017b. Analysis of diversity, stratigraphic and geographical distribution of isolated theropod teeth from the Upper Jurassic of the Lusitanian Basin, Portugal. Journal of Iberian Geology 43, 257–291.

Malafaia, E., Mocho, P., Escaso, F., Dantas, P., Ortega, F., 2019. Carcharodontosaurian remains (Dinosauria, Theropoda) from the Upper Jurassic of Portugal. Journal of Paleontology 93 (1), 157–172.

Malafaia, E., Mocho, P., Escaso, F., Ortega, F., 2020. A new carcharodontosaurian theropod from the Lusitanian Basin: evidence of allosauroid sympatry in the European Late Jurassic. Journal of Vertebrate Paleontology 40, e1768106.

Manning, P.L., 2004. A new approach to the analysis and interpretation of tracks: examples from the dinosauria. Geological Society, London, Special Publications 228, 93–123.

Manning, P.L., 2008. *T. rex* speed trap. In: Carpenter, K., Larson, P.L. (Eds.), *Tyrannosaurus rex*, The Tyrant King. Indiana University Press, Bloomington, pp. 204–231.

Manning, P., 2011. 3-dimensional dinosaur tracks: the hidden depths and geometry of vertebrate traces. In: Richter, A., Reich, M. (Eds.), Abstract Volume and Field Guide to Excursions of Dinosaur Tracks 2011. Obernkirchen Dinosaur Track Symposium, Obernkirchen, April 14–17, 2011, p. 36.

Manuppella, G., Rocha, R.B., Soares, A.F., 1976. Notícia Explicativa da Folha 19-C – Figueira da Foz. Carta Geológica de Portugal na escala de 1/50 000. Serviços Geológicos de Portugal, Lisboa, 126 pp.

Marchetti, L., Belvedere, M., Voigt, S., Klein, H., Castanera, D., Díaz-Martínez, I., Marty, D., Xing, L.D., Feola, F., Melchor, R.N., Farlow, J.O., 2019. Defining the morphological quality of fossil footprints. Problems and principles of preservation in tetrapod ichnology with examples from the Palaeozoic to the presente. Earth-Science Reviews 193, 109–145.

Marchetti, L., Francischini, H., Lucas, S.G., Voigt, S., Hunt, A.P., Santucci, V.L., 2020. Chapter 9. Paleozoic vertebrate ichnology of Grand Canyon National Park. In: Santucci, V.L., Tweet, J.S. (Eds.), Grand Canyon National Park: Centennial Paleontological Resource Inventory (non-sensitive version). Natural Resource Report NPS/GRCA/NRR — 2020/2103. National Park Service, Fort Collins, pp. 333–379.

Marty, D., 2008. Sedimentology, taphonomy, and ichnology of Late Jurassic dinosaur tracks from the Jura carbonate platform (Chenevez–Combe Ronde tracksite, NW Switzerland): insights into the tidal-flat paleoenvironment and dinosaur diversity, locomotion and palaeoecology. GeoFocus 21, 1–278.

Marty, D., Meyer, C.A., Billon-Bruyat, J.-P., 2006. Sauropod trackway patterns expression of special behaviour related to substrate consistency? An example from the Late Jurassic of northwestern Switzerland. Hantekeniana 5, 38–41.

Marty, D., Ayer, J., Becker, D., Berger, J., Billon-Bruyat, J., Braillard, L., Hug, W., Meyer, C.A., 2007. Late Jurassic dinosaur tracksites of the Transjurane highway (Canton Jura, NW Switzerland): overview and measures for their protection and valorisation. Bulletin für Angewandte Geologie 12, 75–89.

Marty, D., Strasser, A., Meyer, C.A., 2009. Formation and taphonomy of human footprints in microbial mats of present-day tidal-flat environments: Implications for the study of fossil footprints. Ichnos 16, 127–142.

Marty, D., Belvedere, M., Meyer, C.A., Mietto, P., Paratte, G., Lovis, C., Thüring, B., 2010. Comparative analysis of Late Jurassic sauropod trackways from the Jura Mountains (NW Switzerland) and the central High Atlas Mountains (Morocco): implications for sauropod ichnotaxonomy. Historical Biology 22 (1), 109–133.

Marty, D., Belvedere, M., Razzolini, N.L., Lockley, M.G., Paratte, G., Cattin, M., Lovis, C., Meyer, C.A., 2018. The tracks of giant theropods (*Jurabrontes curtedulensis* ichnogen. & ichnosp. nov.) from the Late Jurassic of NW Switzerland: palaeoecological & palaeogeographical implications. Historical Biology 30, 928–956.

Mateus, I., Mateus, H., Antunes, M.T., Mateus, O., Taquet, P., Ribeiro, V., Manuppella, G., 1998. Upper Jurassic theropod dinosaur embryos from Lourinhã (Portugal). Memórias da Academia de Ciências 37, 101–110.

Mateus, O., 1998. *Lourinhanosaurus antunesi*, a new upper Jurassic allosauroid (Dinosauria: Theropoda) from Lourinhã, Portugal. Memórias da Academia de Ciências de Lisboa 37, 111–124.

Mateus, O., 2006. Late Jurassic dinosaurs from the Morrison Formation (USA), the Lourinhã and Alcobaça formations (Portugal), and the Tendaguru beds (Tanzania): a comparison. In: Foster, J.R., Lucas, S.G. (Eds.), Paleontology and Geology of the Upper Jurassic Morrison Formation. New Mexico Museum of Natural History and Science Bulletin 36, 223–231.

Mateus, O., Antunes, M.T., 2000. *Ceratosaurus* sp. (Dinosauria: Theropoda) in the Late Jurassic of Portugal. Abstracts of 31st International Geological Congress, Rio de Janeiro, Brazil (CD-ROM).

Mateus, O., Milàn, J., 2008. Ichnological evidence for giant ornithopod dinosaurs in the Upper Jurassic Lourinhã Formation, Portugal. Oryctos 8, 47–52.

Mateus, O., Milàn, J., 2010. A diverse Upper Jurassic dinosaur ichnofauna from central-west Portugal. Lethaia 43, 245–257.

Mateus, O., Walen, A., Telles Antunes, M., 2006. The large theropod fauna of the Lourinhã Formation (Portugal) and its similarity to that of the Morrison Formation, with a description of a new species of *Allosaurus*. In: Foster, J.R., Lucas, S.G. (Eds.), Paleontology and Geology of the Upper Jurassic Morrison Formation. New Mexico Museum of Natural History and Science Bulletin 36, 123–129.

Mateus, O., Araújo, R., Natário, C., Castanhinha, R., 2011. A new specimen of the theropod dinosaur *Baryonyx* from the early Cretaceous of Portugal and taxonomic validity of *Suchosaurus*. Zootaxa 2827, 54–68.

Mateus, O., Dinis, J., Cunha, P.P., 2017. The Lourinhã Formation: the Upper Jurassic to lowermost Cretaceous of the Lusitanian Basin, Portugal — landscapes where dinosaurs walked. Ciências da Terra 19 (1), 75–97.

Mazin, J., Hantzpergue, P., Olivier, N., 2017. The dinosaur tracksite of Plagne (early Tithonian, Late Jurassic; Jura Mountains, France): the longest known sauropod trackway. Geobios 50 (4), 279–301.

Meyer, C.A., 1993. A sauropod dinosaur megatracksite from the Late Jurassic of northern Switzerland. Ichnos 3, 29–38.

Milàn, J., 2003. Experimental Ichnology — experiments with track and undertrack formation using emu tracks in sediments of different consistencies, with comparisons to fossil dinosaur tracks. PhD Thesis, Geological Institute, University of Copenhagen, Copenhagen, 91 pp.

Milàn, J., 2006. Variations in the morphology of Emu (*Dromaius novaehollandiae*) tracks reflecting differences in walking pattern and substrate consistency: Ichnotaxonomic implications. Palaeontology 49 (2), 405–420.

Milàn, J., Bromley, R.G., 2006. True tracks, undertracks and eroded tracks, experimental work with tetrapod tracks in laboratory and field. Palaeogeography, Palaeoclimatology, Palaeoecology 231, 253–264.

Milàn, J., Clemmensen, L.B., Bonde, N., 2004. Vertical sections through dinosaur tracks (Late Triassic lake deposits, East Greenland) — undertracks and other subsurface deformation structures revealed. Lethaia 37, 285–296.

Milàn, J., Avanzini, M., Clemmensen, L.B., García-Ramos, J.C., Piñuela, L., 2006. Theropod foot movement recorded by Late Triassic, Early Jurassic and Late Jurassic fóssil footprints. New Mexico Museum of Natural History and Science Bulletins 37, 352–364.

Mocho, P., Royo-Torres, R., Ortega, F., 2014. Phylogenetic reassessment of *Lourinhasaurus alenquerensis*, a basal Macronaria (Sauropoda) from the Upper Jurassic of Portugal. Zoological Journal of the Linnean Society 170, 875–916.

Mocho, P., Royo-Torres, R., Malafaia, E., Escaso, F., Silva, B., Ortega, F., 2016a. *Turiasauria*-like teeth from the Upper Jurassic of the Lusitanian Basin, Portugal. Historical Biology 28, 861–880.

Mocho, P., Royo-Torres, R., Malafaia, E., Escaso, F., Ortega, F., 2016b. Systematic review of Late Jurassic sauropods from the Museu Geológico collections (Lisboa, Portugal). Journal of Iberian Geology 42 (2), 227–250.

Mocho, P., Royo-Torres, R., Malafaia, E., Escaso, F., Ortega, F., 2017a. First occurrences of non-neosauropod eusauropod procoelous caudal vertebrae in the Portuguese Upper Jurassic record. Geobios 50 (1), 23–36.

Mocho, P., Royo-Torres, R., Malafaia, E., Escaso, F., Narváez, I., Ortega, F., 2017b. New data on Late Jurassic sauropods of central and northern sectors of the

Bombarral Sub-basin (Lusitanian Basin, Portugal). Historical Biology 29 (2), 151–169.

Mocho, P., Royo-Torres, R., Escaso, F., Malafaia, E., de Miguel Chaves, C., Narváez, I., Pérez-García, A., Pimentel, N., Silva, B.C., Ortega, F., 2017c. Upper Jurassic sauropod record in the Lusitanian Basin (Portugal): Geographical and lithostratigraphical distribution. Palaeontologia Electronica 20, Article number 20.2.27A, doi: 10.26879/662.

Mocho, P., Royo-Torres, R., Ortega, F., 2017d. New data of the Portuguese brachiosaurid *Lusotitan atalaiensis* (Sobral Formation, Upper Jurassic). Historical Biology 29 (6), 789–817.

Mocho, P., Royo-Torres, R., Ortega, F., 2019. A new macronarian sauropod from the Upper Jurassic of Portugal. Journal of Vertebrate Paleontology 39, e1578782.

Moratalla, J.J., 2009. Sauropod tracks of the Cameros Basin (Spain): Identification, trackway patterns and changes over the Jurassic–Cretaceous. Geobios 42, 797–811.

Moratalla, J.J., Hernán, J., 2010. Probable palaeogeographic influences of the Lower Cretaceous Iberian rifting phase in the Eastern Cameros Basin (Spain) on dinosaur trackway orientations. Palaeogeography, Palaeoclimatology, Palaeoecology 295, 116–130.

Nadon, G.C., 2001. The impact of sedimentology on vertebrate track studies. In: Currie, P.J., Tanke, D.H., Carpenter, K., Skrepnick, M.W. (Eds.), Mesozoic Vertebrate Life. Indiana University Press, Bloomington, pp. 395–407.

Niedzwiedzki, G., Pieńkowski, G., 2004. A dinosaur track association from the Early Jurassic deltaic deposits of Podole near Opatów, Poland. Geological Quarterly 48 (4), 333–338.

Noffke, N., Gerdes, G., Klenke, T., Krumbein, W.E., 2001. Microbially induced sedimentary structures: a new category within the classification of primary sedimentary structures. Journal of Sedimentary Research 71, 649–656.

Nopcsa, F. von, 1923. Die familien der reptilien. Fortschritte der Geologie und Paläontologie 2, 1–210.

Oliveira, J.T., Pereira, E., Ramalho, M.M., Antunes, M.T., Monteiro, J.H. (Coords.), 1992. Carta Geológica de Portugal, Escala 1:500,000. Serviços Geológicos de Portugal, Lisboa.

Ortega, F., Escaso, F., Gasulla, J.M., Dantas, P., Sanz, J.L., 2006. Dinosaurios de la Península Ibérica. Estudios Geológicos 62 (1), 219–240.

Ortega, F., Malafaia, E., Escaso, F., García, A.P., Dantas, P., 2009. Faunas de répteis do Jurássico Superior de Portugal. Paleolusitana 1, 44–45.

Pena dos Reis, R., Henriques, M.H., 2018. Geoheritage and advanced training for the oil industry: The Lusitanian Basin case study (Portugal). American Association of Petroleum Geologists Bulletin 102 (8), 1413–1428.

Pena dos Reis, R., Dinis, J., Cunha, P.P., Trincão, P., 1996. Upper Jurassic sedimentary infill and tectonics of the Lusitanian Basin (Western Portugal). In: Riccardi, A.C. (Ed.), Jurassic Research. GeoResearch Forum, Transtec Publications, Zurich 1–2, 377–386.

Pena dos Reis, R., Cunha, P.P., Dinis, J.L., Trincão, P.R., 2000. Geologic evolution of the Lusitanian Basin (Portugal) during the Late Jurassic. GeoResearch Forum, Transtec Publications, Zurich 6, 345–356.

Pérez-García, A., 2015. Revision of the British record of *Tropidemys* (Testudines, Plesiochelyidae) and recognition of its presence in the Late Jurassic of Portugal. Journal of Iberian Geology 41 (1), 11–20.

Pérez-Lorente, F., 2015. Dinosaur Footprints & Trackways of La Rioja. Indiana University Press, Bloomington, 363 pp.

Pérez-Lorente, F., 2017. Developments and contributions in the study of La Rioja dinosaur footprints (Spain). Spanish Journal of Palaeontology 32 (1), 171–184.

Pérez-Moreno, B.P., Chure, D.J., Pires, C., Marques Da Silva, C., Santos, V., Dantas, P., Povoas, L., Cachao, M., Sanz, J.L., Galopim de Carvalho, A.M., 1999. On the presence of *Allosaurus fragilis* (Theropoda: Carnosauria) in the Upper Jurassic of Portugal: first evidence of an intercontinental dinosaur species. Journal of the Geological Society, London 156, 449–452.

Piñuela, L., 2012. Dinosaur true tracks and undertracks. Recognition criteria and nomenclature problems. The Asturian case (Spain). In: Xing, L.D., Lockley, M.G. (Eds.), Qijiang International Dinosaur Tracks Symposium, Chongqing, 2012. Abstract Book, pp. 91–95.

Piñuela Suárez, L., 2015. Huellas de dinosaurios y de otros reptiles del Jurásico Superior de Asturias. PhD Thesis, Universidad de Oviedo, Oviedo, 366 pp.

Powell, J.H., 2010. Jurassic sedimentation in the Cleveland Basin: a review. Proceedings of the Yorkshire Geological Society 58 (1), 21–72.

Rauhut, O.W.M., Piñuela, L., Castanera, D., García-Ramos, J.C., Cela, I.S., 2018. The largest European theropod dinosaurs: remains of a gigantic megalosaurid and giant theropod tracks from the Kimmeridgian of Asturias, Spain. PeerJ 6, e4963, doi: 10.7717/peerj.4963.

Razzolini, N., 2016. Morphological variation and ichnotaxonomy of dinosaur tracks: linking footprint shapes to substrate and trackmaker's anatomy and locomotion. PhD Thesis, Universitat Autonoma de Barcelona, Barcelona, 188 pp.

Razzolini, N.L., Vila, B., Castanera, D., Falkingham, P.L., Barco, J.L., Canudo, J.I., Manning, P.L., Galobart, A., 2014. Intra-trackway morphological variations due to substrate consistency: The El Frontal dinosaur tracksite (Lower Cretaceous, Spain). PLoS ONE 9 (4), e93708, doi:10.1371/journal.pone.0093708.

Razzolini, N.L., Oms, O., Castanera, D., Vila, B., Santos, V.F., Galobart, À., 2016. Ichnological evidence of Megalosaurid dinosaurs crossing Middle Jurassic tidal flats. Scientific Reports 6, Article number 31494, doi: 10.1038/srep31494.

Razzolini, N.L., Belvedere, M., Marty, D., Paratte, G., Lovis, C., Cattin, M., Meyer, C.A., 2017. *Megalosauripus transjuranicus* ichnosp. nov. A new Late Jurassic theropod ichnotaxon from NW Switzerland and implications for tridactyl dinosaur ichnology and ichnotaxomy. PLoS ONE 12 (7), e0180289, doi: 10.1371/journal.pone.0180289.

Rocha, J., Brilha, J., Henriques, M.H., 2014. Assessment of the geological heritage of Cape Mondego Natural Monument (Central Portugal). Proceedings of the Geologists' Association 125, 107–113.

Romano, M., Whyte, M.A., 2003. Jurassic dinosaur tracks and trackways of the Cleveland Basin, Yorkshire: preservation, diversity and distribution. Proceedings of the Yorkshire Geological Society 54, 185–215.

Romano, M., Whyte, M.A., 2012. Information on the foot morphology, pedal skin texture and limb dynamics of sauropods: evidence from the ichnological record of the Middle Jurassic of the Cleveland Basin, Yorkshire, UK. Zubia 30, 45–92.

Santos, V.F., 2003. Pistas de dinossáurio no Jurássico–Cretácico de Portugal. Considerações paleobiológicas e paleoecológicas. PhD Thesis, Facultad de Ciencias, Universidad Autónoma de Madrid, Madrid, 365 pp.

Santos, V.F., 2008. Pegadas de Dinossáurios de Portugal. Museu Nacional de História Natural, Lisboa, 124 pp.

Santos, V.F., 2016. Dinosaur tracksites in the Middle Jurassic of Maciço Calcário Estremenho (west-central Portugal): a geoheritage to be enhanced. Comunicações Geológicas 103, 55–58.

Santos, V.F., 2017. Museu Nacional de História Natural e da Ciência: one hundred years of dinosaur ichnology in Portugal. Bollettino della Società Paleontologica Italiana 56 (2), 97–107.

Santos, V.F., Neto de Carvalho, C., 2016. Gomes (1915–1916) to Ichnia 2016 — one hundred years of vertebratye Ichnology in Portugal. 4th International Congress on Ichnology. Idanha-a-Nova, UNESCO Naturtejo Global Geopark. Ichnia Abstract Book, p. 284.

Santos, V.F., Silva, C.M., Rodrigues, L.A., 2008. Dinosaur track sites from Portugal: Scientific and cultural significance. Oryctos 8, 77–88.

Santos, V.F., Moratalla, J.J., Royo-Torres, R., 2009. New sauropod trackways from the Middle Jurassic of Portugal. Acta Palaeontologica Polonica 54 (3), 409–422.

Santos, V.F., Caetano, P., Pólvora, A., 2016. Sesimbra Geocircuit and dinosaur tracksites. Comunicações Geológicas 103, 153–158.

Sanz, E., Arcos, A., Pascual, C., Pidal, I.M., 2016. Three-dimensional elasto-plastic soil modelling and analysis of sauropod tracks. Acta Palaeontologica Polonica 61 (2), 387–402.

Sarjeant, W.A.S., Leonardi, G., 1987. Substrate and footprints. In: Leonardi, G. (Ed.), Glossary and Manual of Tetrapod Footprint Palaeoichnology. Departamento Nacional da Produção Mineral Brasil, Brasília, 1–117.

Sciscio, L., Bordy, E.M., Reid, M., Abrahams, M., 2016. Sedimentology and ichnology of the Mafube dinosaur tracksite (Lower Jurassic, eastern Free State, South Africa): a report on footprint preservation and palaeoenvironment. PeerJ 4, e2285, doi: 10.7717/peerj.2285.

Solt, P., Szuromi-Korecz, A., Ösi, A., 2020. New Late Cretaceous (Coniacian) sauropod tracks from Hvar Island, Croatia. Central European Geology 63 (1), 19–26.

Thulborn, T., 1990. Dinosaur Tracks. Chapman & Hall, London, 410 pp.

Thulborn, T., 2012. Impact of sauropod dinosaurs on lagoonal substrates in the Broome Sandstone (Lower Cretaceous), Western Australia. PLoS ONE 7 (5), e36208, doi: 10.1371/journal.pone.0036208.

Tucker, M.E., Burchette, T.P., 1977. Triassic dinosaur footprints from South Wales: their context and preservation. Palaeogeography, Palaeoclimatology, Palaeoecology 22 (3), 195–208.

Tykoski, R.S., Rowe, T., 2004. Ceratosauria. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), The Dinosauria (2nd Edition). University of California Press, Berkley, pp. 47–70.

Wilson, R.C., 1979. A reconnaissance study of Upper Jurassic sediments of the Lusitanian Basin. Ciências da Terra 5, 53–84.

Wilson, R.C.L., Hiscott, R.N., Willis, M.G., Gradstein, F.M., 1989. The Lusitanian Basin of west-central Portugal: Mesozoic and Tertiary tectonic, stratigraphy, and subsidence history. Memoir of American Association Petroleum Geologists 46, 341–361.

Xing, L.D., Li, D.Q., Lockley, M.G., Marty, D., Zhang, J.P., Persons IV, W.S., You, H.L., Peng, C., Kümmell, S.B., 2015. Dinosaur natural track casts from the Lower Cretaceous Hekou Group in the Lanzhou-Minhe Basin, Gansu, Northwest China: Ichnology, track formation, and distribution. Cretaceous Research 52, 194–205.

Yilmaz, P.O., Norton, I.O., Leary, D., Chuchla, R.J., 1996. Tectonic evolution and paleogeography of Europe. In: Ziegler, P.A., Horvàth, F. (Eds.), Peri-Tethys Memoir 2: Structure and Prospects of Alpine Basins and Forelands. Mémoires du Museum National d'histoire Naturelle 170, 15–45.

Figures captions

Fig. 1. Geological map, showing the location of the Cabo Mondego with dinoturbation in the Upper Jurassic Arenitos da Boa Viagem Formation (Lusitanian Basin, Portugal). Adapted from the Geological Map of Portugal, 1:500,000 (Oliveira et al., 1992).

Fig. 2. Synthetic stratigraphic column of the Upper Jurassic strata preserved at Cabo Mondego (adapted from Bernardes, 1992), showing the distribution of dinoturbation levels.

Fig. 3. Deformation structure related to the footprints found in the Calcários Hidráulicos lower division, mainly consisting of freshwater limestones. A digit cross-section can be seen in the lower portion of a bed, pointing downward. The V-shaped deformation is considered related to digit III, which sustains the weight of the trackmaker, allowing a greater evidence of the III digit print. The arrow points to the lower extremity of the V-shaped feature.

Fig. 4. ABV level 1 of the Arenitos da Boa Viagem Formation preserves three-dimensional casts in cross-section. They are distributed within the same bedding interval, deforming up to 35 cm from the bedding surface. (A) A tridactyl footprint in the bedding-plane (indicated by an arrow) and in cross-section; the dashed line follows the contour of the footprint in the upper bedding plane. (B) A tubular structure (indicated by an arrow) connected to the lower portion of the footprint cross-section. (C) A cross-section footprint presenting a pronounced V-shaped geometry, interpreted as produced by a theropod. (D) A detail of the footprint illustrated in (C) in which a digit is surrounded by fine crenulations (indicated by an arrow); this was interpreted as the fluidization of the sediments related to the load induced by the foot. Scale bar is 10 cm.

Fig. 5. Fine reddish sandstones with footprints from ABV level 2 of Arenitos da Boa Viagem Formation. (A) The dashed line is the level with footprints and the arrow indicates one footprint in cross-section. (B) A fallen block found directly beneath the track-bearing level 2 where natural casts are found. (C) Rounded mound showing fluidization and irregular interior division. (D) A small tridactyl, mesaxonic footprint (indicated by an arrow) on the bedding surface with crenulations filled with fine sandstone. (E) Distribution map of tridactyl footprints and also a rounded fluidized mound on the surface of an isolated block from the level 2 (illustrated in (B)) of the Arenitos da Boa Viagem Formation.

Fig. 6. ABV level 3 of the Arenitos da Boa Viagem Formation. (A) Track surface in a lower sandstone-bedding plane (observed from the bottom); the footprints are molds filled with coarse sandstone and present sharpened edges. (B) Isolated finger with a tubular shape and more rounded extremity. (C) A cast of a tridactyl, mesaxonic

footprint filled with coarse-grained sandstone; deformation of the surrounding matrix around digit III; scale bar in cm.

Fig. 7. Cross-section footprints observed in ABV level 4 of the Arenitos da Boa Viagem Formation showing the high deformation of the substrate. (A) A cross-section dinoturbation as a large concave deformed bulge of sandstone; the dashed line is the lower limits of the deformation. (B) A cross-section footprint presenting an inclined V-shaped structure (indicated by an arrow) that is interpreted as the impression of digit III.

Fig. 8. Surface of ABV level 5 of the Arenitos da Boa Viagem Formation (A) presenting theropod footprints filled with massive (B) and fluidized sandstones. (C) Isolated theropod track with fluidization structures. (D) The surface of ABV level 6 of the Arenitos da Boa Viagem Formation preserves isolated digit impressions filled with a coarse sandstone; arrows indicate the digit impressions on this level.

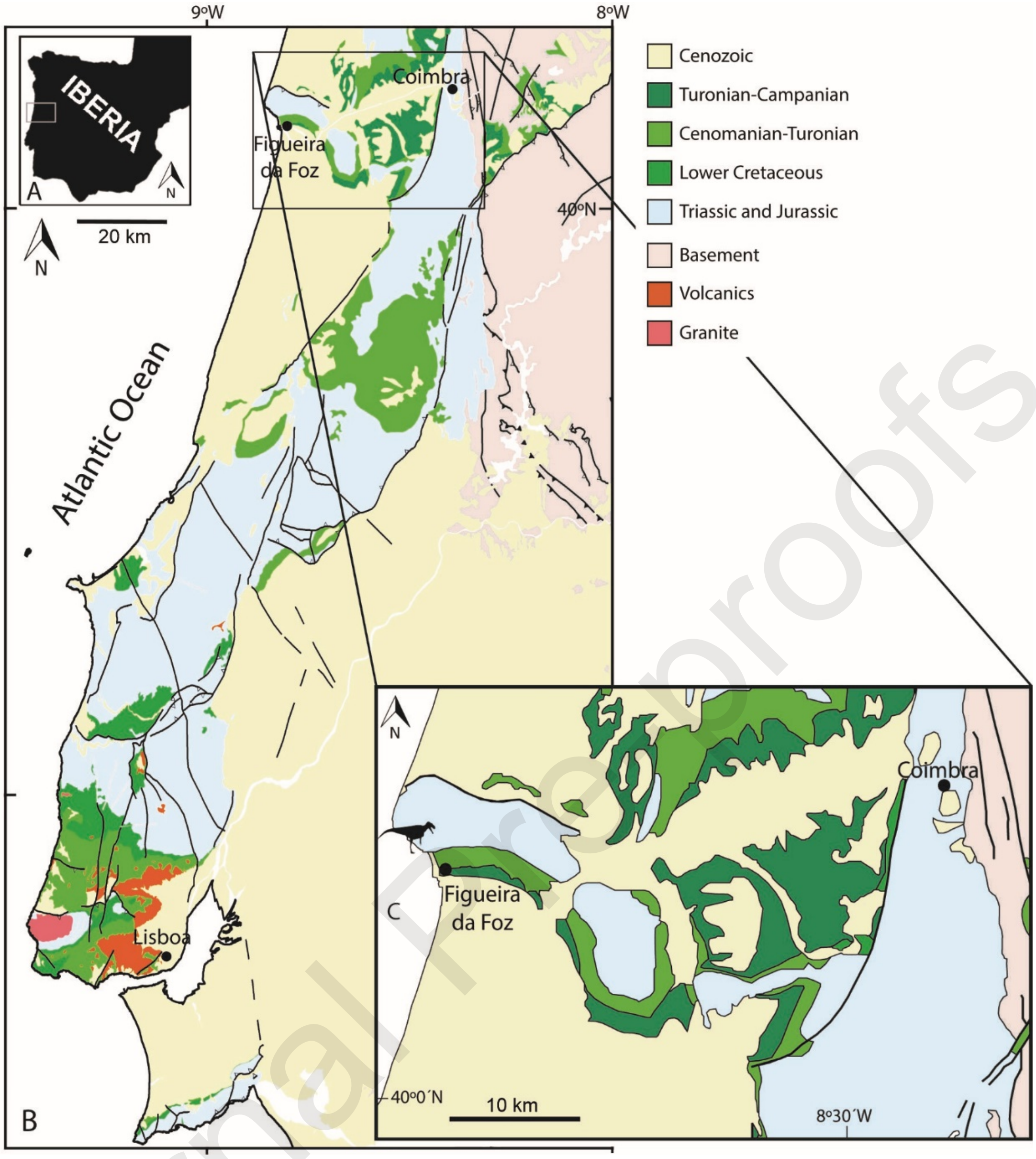
Fig. 9. (A) Deformations of ABV level 7 of the Arenitos da Boa Viagem Formation, in which it is possible to observe large contorted bulges of sandstones; the arrow indicates a pointed tubular projection, probably related to a digit mold. (B) Dinoturbation of ABV level 8 of the Arenitos da Boa Viagem Formation in which superimposed conical projections (indicated by arrows) in the lower surface of ABV level 8, are interpreted as three-dimensional digit molds. (C) The highly reworked ABV level 8 of Arenitos da Boa Viagem Formation shows ridge and groove impressions (indicated by an arrow), interpreted as drag marks produced by the foot movement.

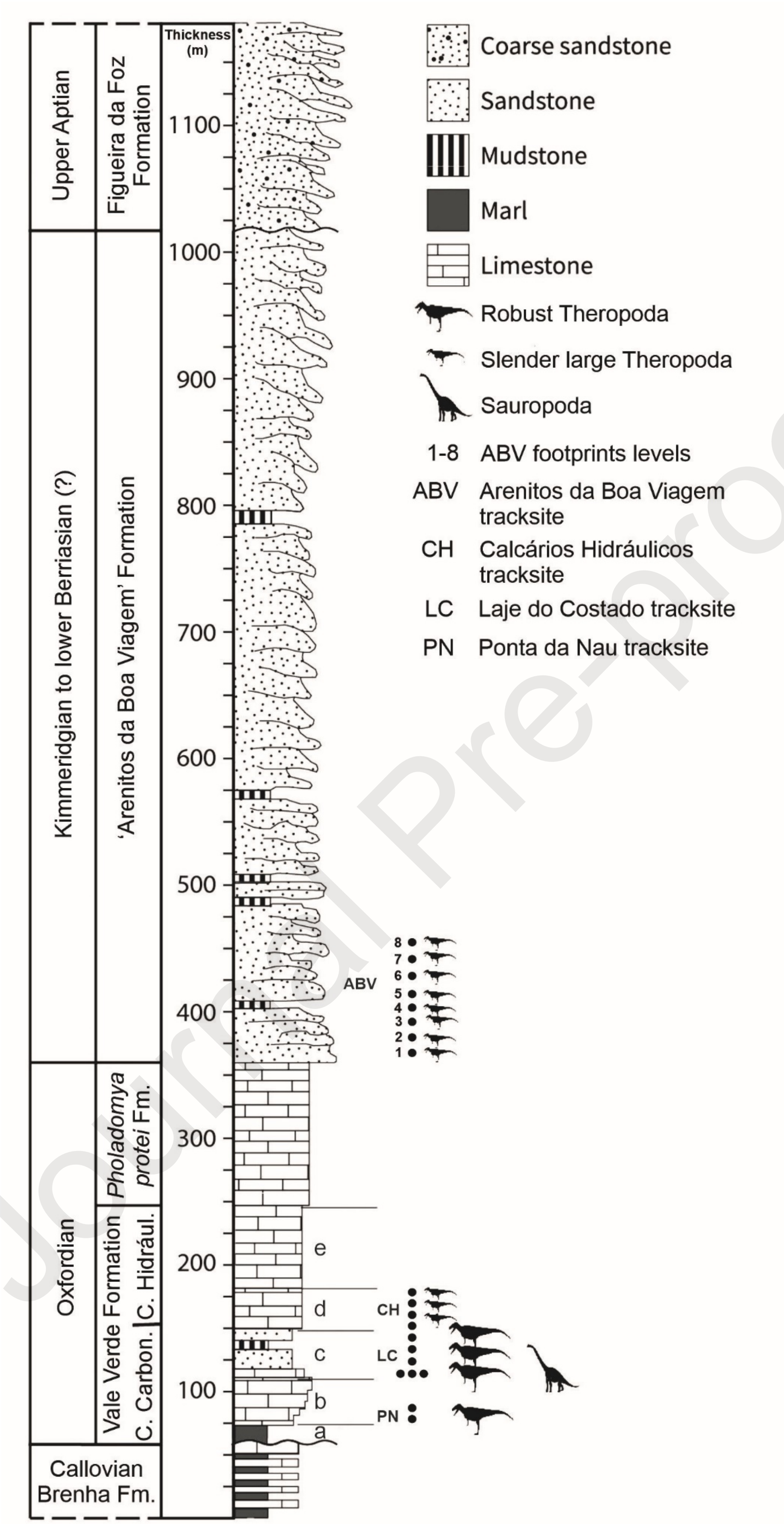
Fig. 10. Palaeoenvironmental reconstruction of Cabo Mondego area, with dinoturbation in the early Kimmeridgian siliciclastic levels of the Arenitos da Boa Viagem Formation (art by Pepi).

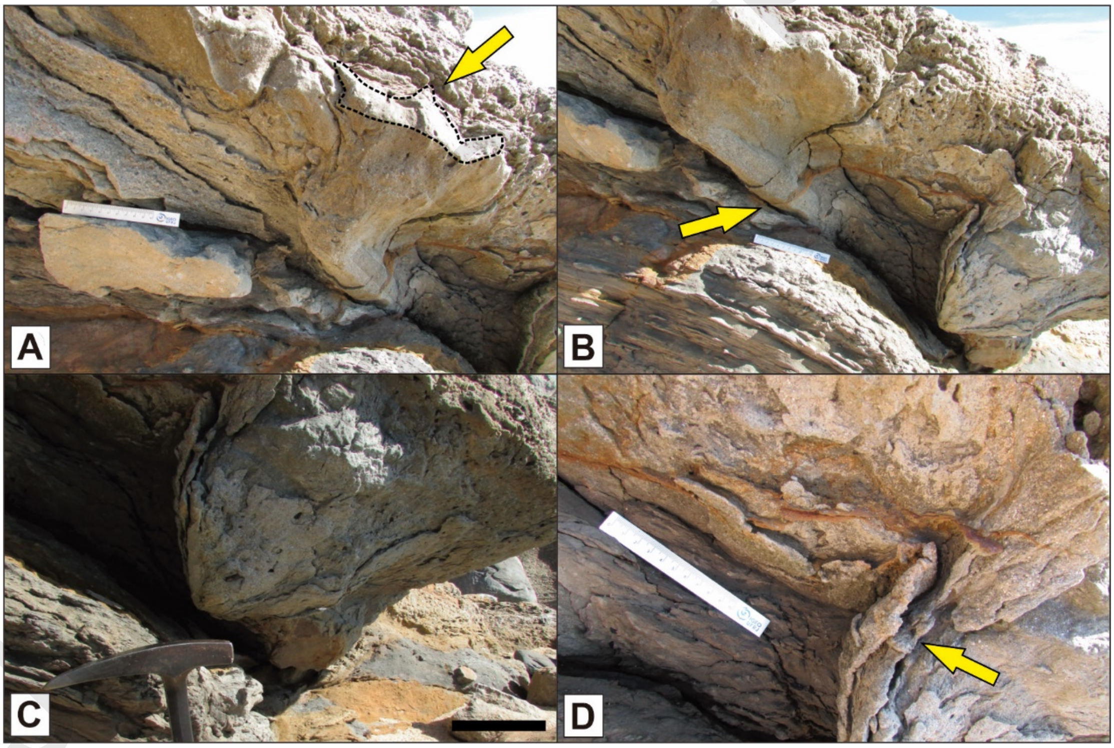
Abstract

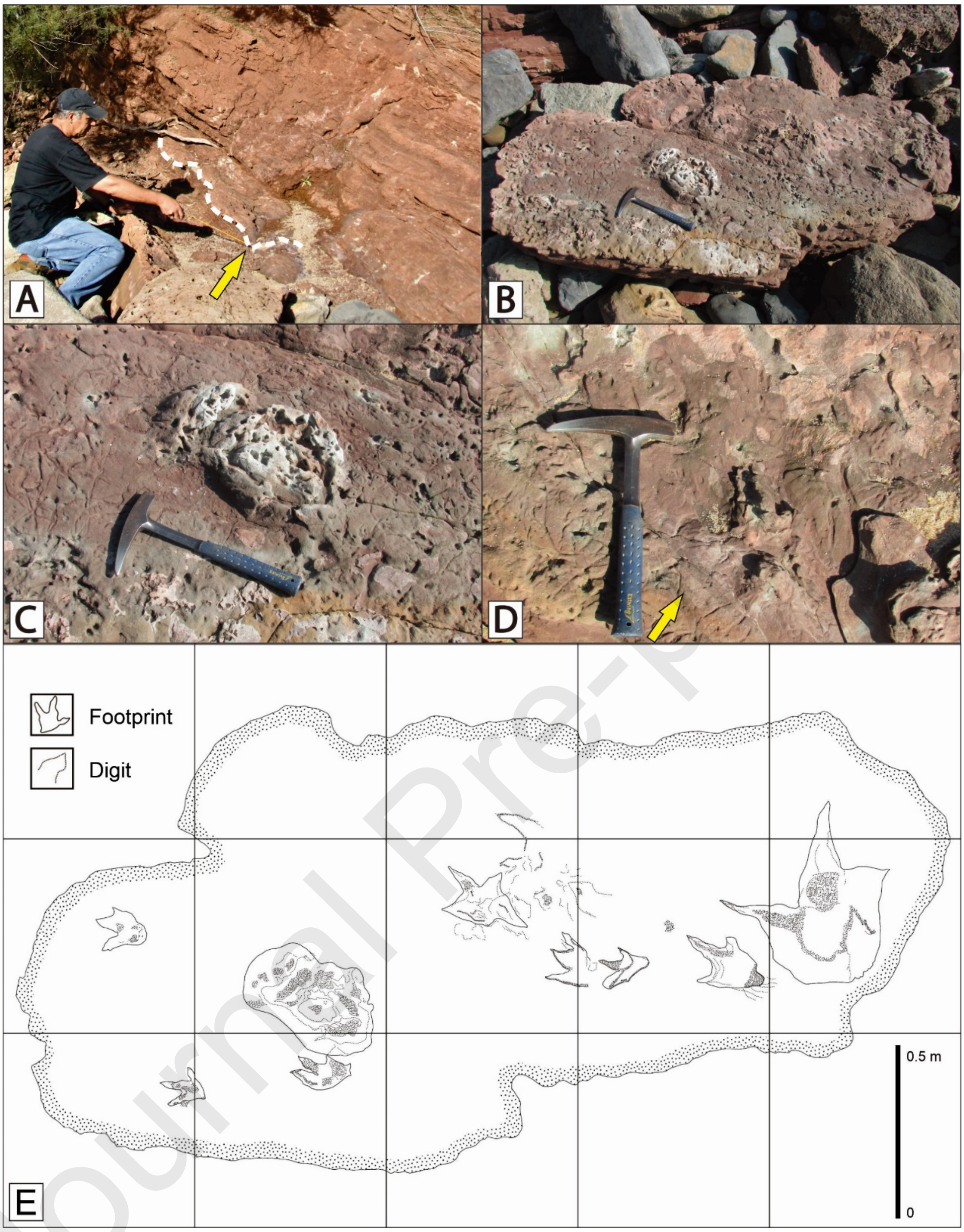
At Cabo Mondego (western central Portugal), the Upper Jurassic marine to coastal succession contains several stratigraphic levels preserving dinosaur footprints

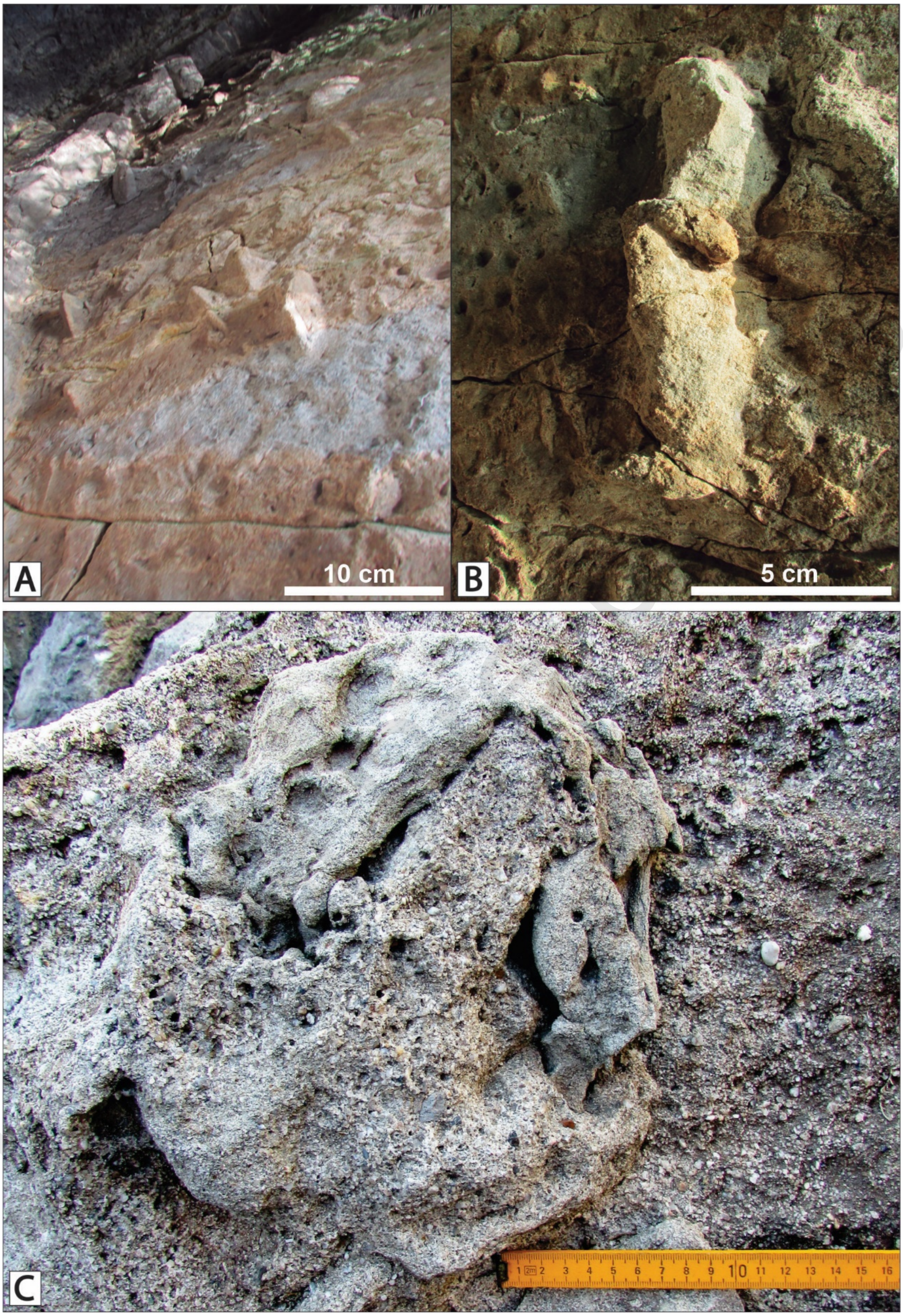
on the surface bedding plane, as well as convolute bedding and soft sediment injection structures interpreted as dinoturbation structures. At least nineteen new three-dimensional structures observed in cross-sections are interpreted as produced by dinosaur trampling. The identification of three-dimensional structures of dinosaur footprints provides an important complement to the information obtained from footprints preserved on single bedding surfaces, such as the substrate consistency, potential trackmaker identification, and the possibility to enhance the distinction of sauropods and tridactyl dinosaurs, and paleoenvironmental interpretations. In the lower part of the Arenitos da Boa Viagem Formation, eight levels of probable lowermost Kimmeridgian age (c. 157-156 mya), displaying the above-mentioned deformational structures, were analyzed in detail. They support interpretations concerning the relationship between the footprints and the substrate consistency at the time of their formation. Three distinct cohesiveness patterns, defined by the penetration of the feet from the paleosurface, are the result of different degrees of substrate cohesiveness. Identifying the trackmakers of levels belonging to the middle Oxfordian-lower Kimmeridgian has important implications for Late Jurassic ecosystem reconstructions, as the footprints observed in Cabo Mondego indicate a change in the morphotypes throughout the Upper Jurassic succession.

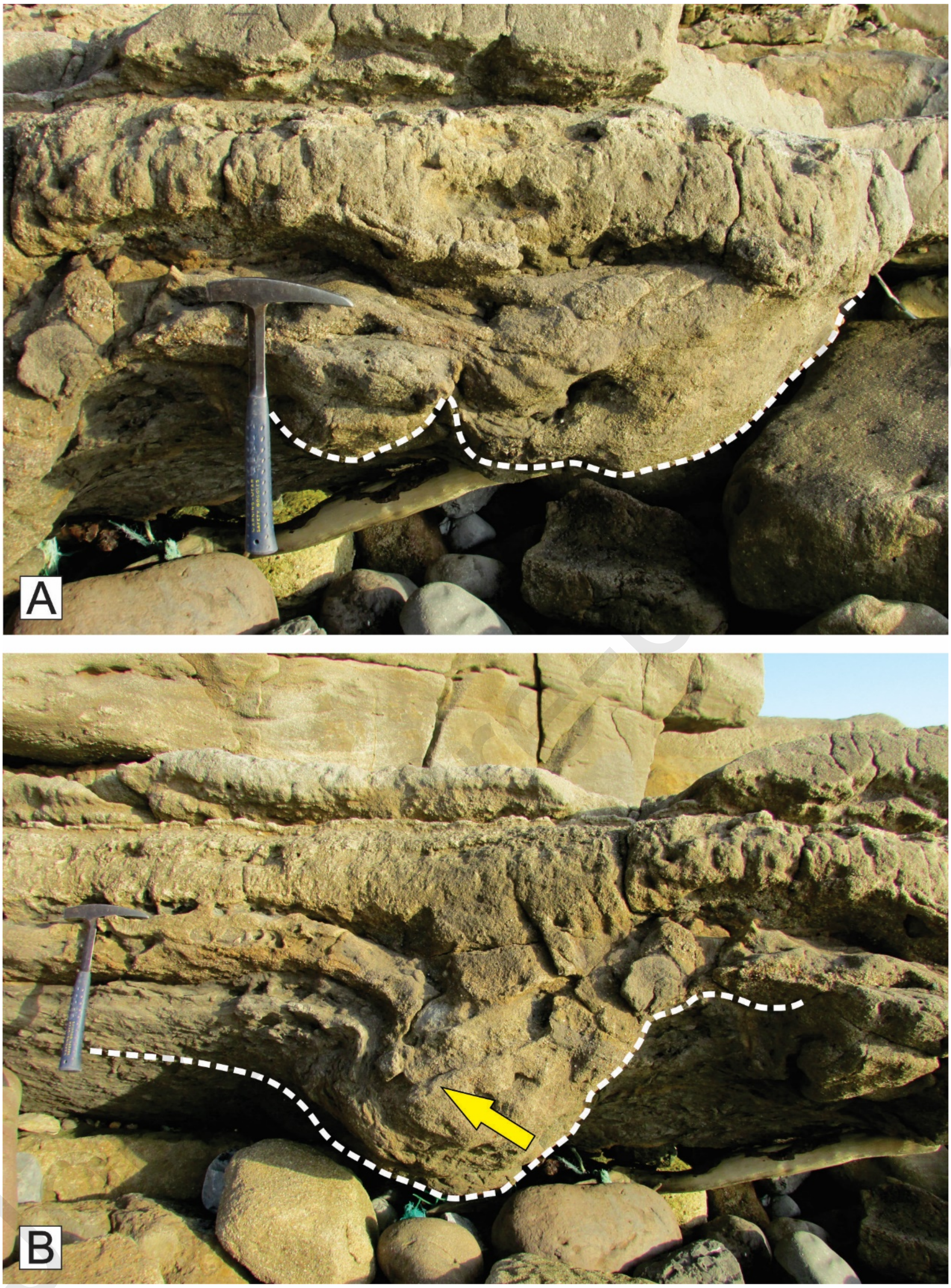

9ºW
8ºW
IBERIA
A
N
20 km
N
Coimbra
Figueira da Foz
40ºN
Atlantic Ocean
Lisboa
B
Cenozoic
Turonian-Campanian
Cenomanian-Turonian
Lower Cretaceous
Triassic and Jurassic
Basement
Volcanics
Granite
N
Coimbra
Figueira da Foz
C
40º0´N
10 km
8º30´W

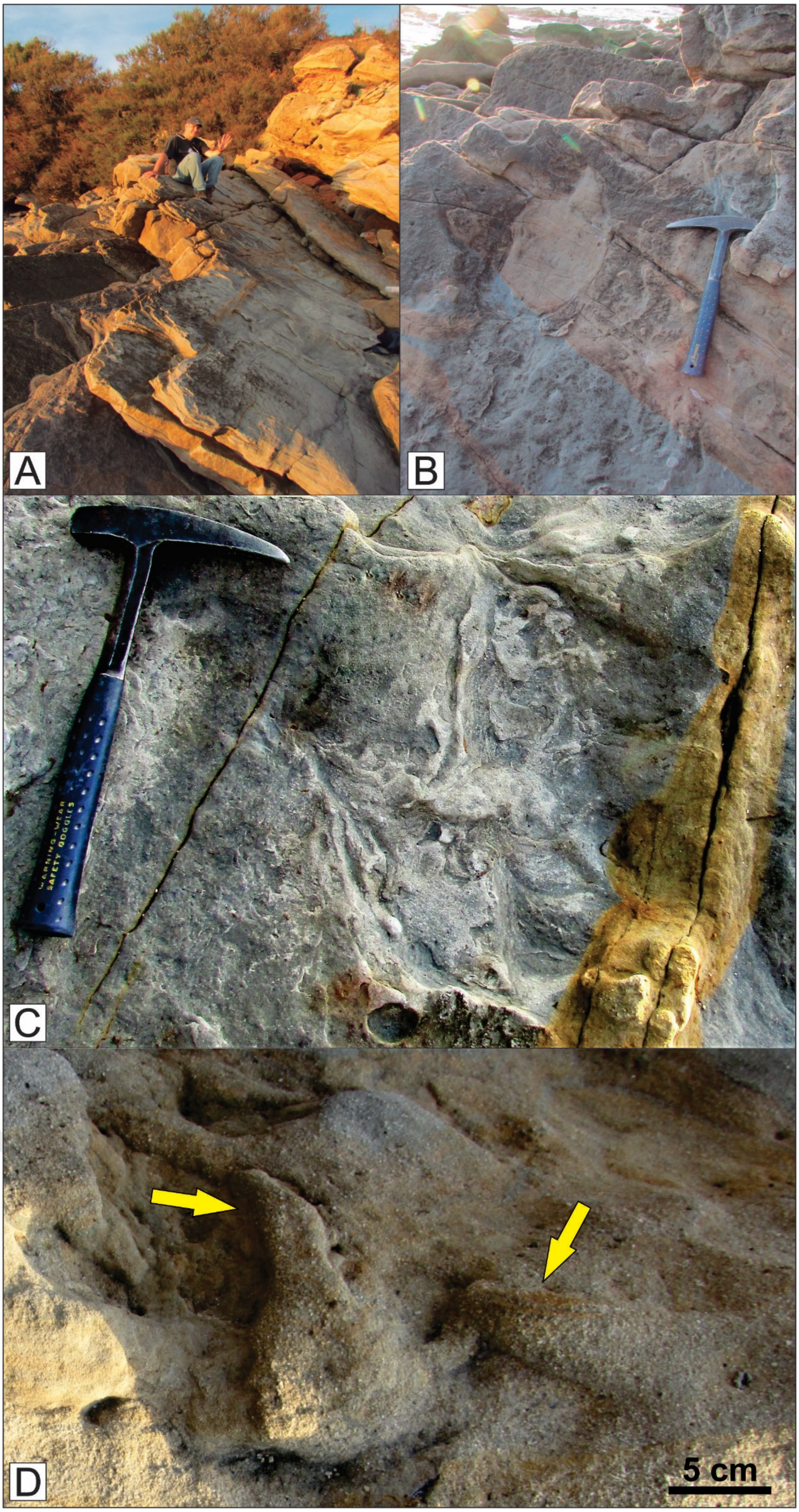

Upper Aptian
Figueira da Foz Formation
Kimmeridgian to lower Berriasian (?)
'Arenitos da Boa Viagem' Formation
Oxfordian
Pholadomya protei Fm.
Vale Verde Formation
C. Hidrául.
C. Carbon.
Callovian
Brenha Fm.
Thickness (m)
1100
1000
900
800
700
600
500
400
300
200
100
a
b
c
d
e
ABV
CH
LC
PN
1
2
3
4
5
6
7
8
Coarse sandstone
Sandstone
Mudstone
Marl
Limestone
Robust Theropoda
Slender large Theropoda
Sauropoda
1-8 ABV footprints levels
ABV Arenitos da Boa Viagem tracksite
CH Calcários Hidráulicos tracksite
LC Laje do Costado tracksite
PN Ponta da Nau tracksite

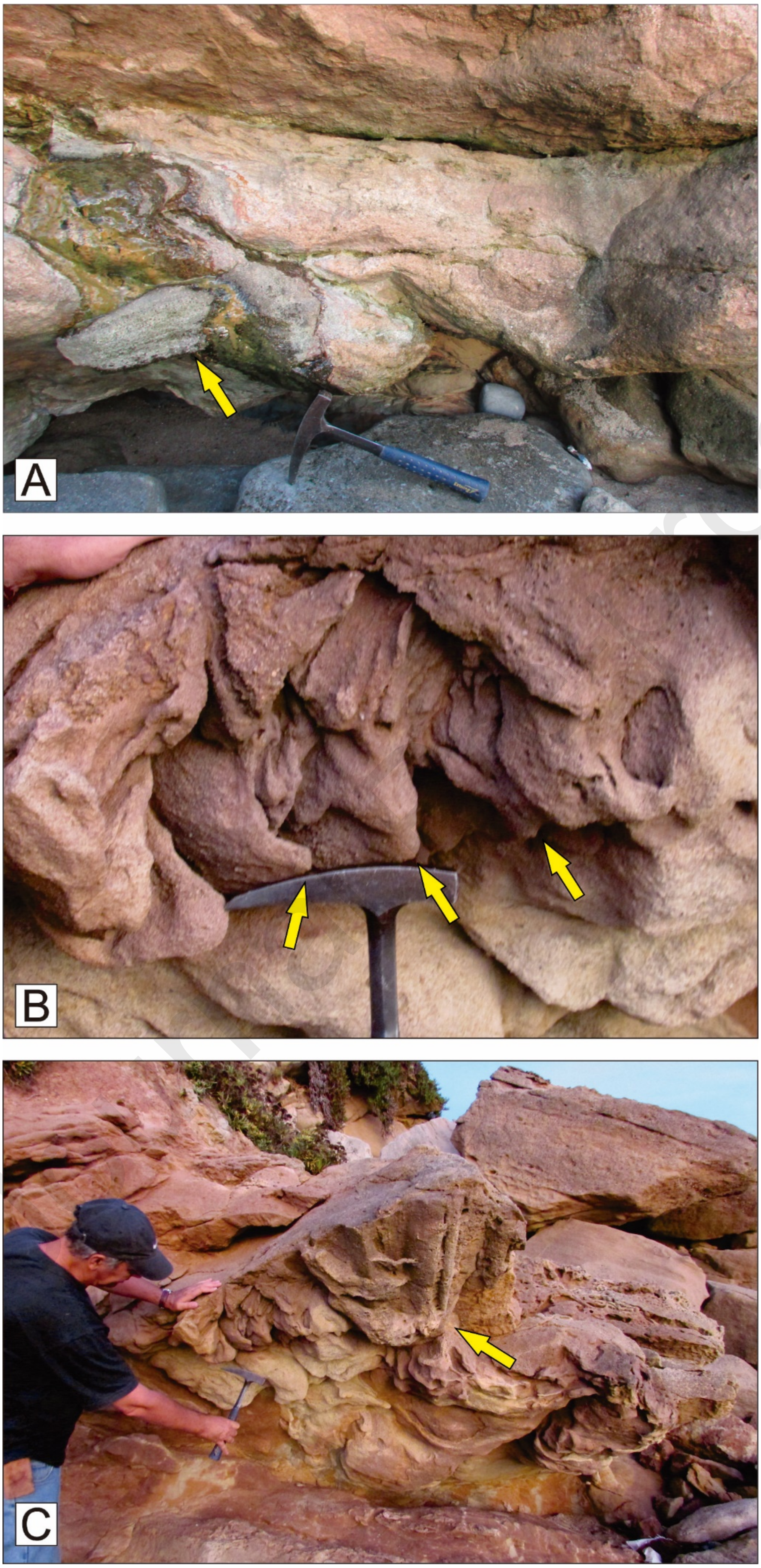

A
B
C
D


A
B
C
D
E
Footprint
Digit
0.5 m
0


A
10 cm
B
5 cm
C


A
B


A
B
C
D
5 cm


A
B
C