Tracking Late Jurassic ornithopods in the Lusitanian Basin of Portugal: Ichnotaxonomic implications

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The Sociedade de História Natural in Torres Vedras, Portugal houses an extensive collection of as yet undescribed dinosaur tracks with ornithopod affinities. They have been collected from different Late Jurassic (Kimmeridgian–Tithonian) geological formations (Praia de Amoreira-Porto Novo, Alcobaça, Sobral, and Freixial) that outcrop along the Portuguese coast, and belong to two different sub-basins of the Lusitanian Basin (the Consolação and Turcifal sub-basins). Three main morphotypes can be distinguished on the basis of size, mesaxony and the morphology of the metatarsophalangeal pad impression. The minute to small-sized morphotype is similar to the Anomoepus-like tracks identified in other Late Jurassic areas. The small to medium-sized morphotype resembles the Late Jurassic–Early Cretaceous ichnotaxon Dineichnus, already known in the Lusitanian Basin. Interestingly, these two morphotypes can be distinguished qualitatively (slightly different size, metatarsophalangeal pad impression and digit morphology) but are nevertheless difficult to discriminate by quantitatively analysing their length-width ratio and mesaxony. The third morphotype is considered a large ornithopod footprint belonging to the ichnofamily Iguanodontipodidae. This ichnofamily is typical for Cretaceous tracksites but the new material suggests that it might also be present in the Late Jurassic. The three morphotypes show a negative correlation between size and mesaxony, so the smaller tracks show the stronger mesaxony, and the larger ones weaker mesaxony. The Upper Jurassic ornithopod record from the Lusitanian Basin has yielded both small and medium-sized ornithopod remains, mainly iguanodontians such as dryosaurids and ankylopollaxians, which are the main candidates to be the trackmakers.

Key words: Iguanodontipodidae, Dineichnus, Anomoepus-like, Kimmeridgian, Tithonian, Europe.

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Introduction

Small to medium-sized tridactyl tracks assigned to ornithopods are scarce in the Late Jurassic European record compared with other types of tridactyl dinosaur footprints such as those of theropods, which are quite abundant in areas such as the Jura platform (Marty et al. 2018; Mazin et al. 2017; Castanera et al. 2018), the Lusitanian Basin (Lockley and Santos 1993; Lockley et al. 1994; Mateus and Milàn 2010) or the Asturian Basin (Lockley et al. 2008; Piñuela...
This scarcity of ornithopod tracks is a consequence of an abundance of sauropod- and theropod-dominated ichnofaunas preserved in carbonate facies in the so-called Brontopodus ichnofacies, which are characterized by a rather low ichnodiversity (Hunt and Lucas 2007). On the other hand, siliciclastic units have provided higher ichnodiversity, and two or possibly three different types of ornithopod tracks have been described in the Late Jurassic of the Morrison Formation in the USA and the Asturian Basin (Spain), respectively (Lockley et al. 2008). Furthermore, in the last few years new ornithopod tracks have been described in several Late Jurassic units belonging to the Maestrazgo and Asturian basins in Spain (e.g., Castanera et al. 2013b; Alcalá et al. 2014; Piñuela et al. 2016). Another factor that may explain the apparent scarcity of ornithopod tracks in the Late Jurassic is the similarity in footprint morphology of theropod and ornithopod tracks in Late Jurassic times (e.g., Lockley et al. 2008; Castanera et al. 2013b).

The classic ornithopod ichnotaxon during the Late Jurassic is Dineichnus Lockley, dos Santos, Meyer, and Hunt, 1998, which has been described in North America, Europe, Africa, and possibly Asia (Lockley et al. 1998; Gierliński et al. 2009; Belvedere et al. 2010; Xing et al. 2014). This ichnotaxon has also been identified in the Lower Cretaceous in Europe (Lockley et al. 1998; Hornung and Reich 2012). In addition, Anomoepus-like tracks have been identified in the Late Jurassic (Lockley et al. 2008). However, large ornithopod tracks (generally those with a footprint length > 25 cm, Thulborn 1990; see also Moreno et al. 2012 and Díaz-Martínez et al. 2015 for a wider definition) from the Late Jurassic are rare, and only a few examples have been described (Mateus and Milàn 2008; Diedrich 2011; Schulp and Al-Wosabi 2012; Piñuela et al. 2016). It is noteworthy that some of these examples come from the Iberian Peninsula.

Although significant Late Jurassic tracksites have been described in the Lusitanian Basin, few ornithopod tracks have been identified so far (Lockley et al. 1998; Antunes and Mateus 2003; Santos 2008; Mateus and Milàn 2008). Of all these records, only a slab from Sào Martinho do Porto has yielded tracks assigned to Dineichnus (Lockley et al. 1998), but this is now lost because of the erosion of the cliff. By contrast, the Late Jurassic ornithopod bone record from the Lusitanian Basin has yielded a sizeable, rich ornithopod fauna (Galton 1980; Rauhut 2001; Mateus and Antunes 2001; Antunes and Mateus 2003; Escaso et al. 2014; Rotatorì et al. 2020).

The Sociedade de História Natural in Torres Vedras, Portugal houses an extensive collection of as yet undescribed tridactyl ornithopod-like dinosaur tracks, which considerably extend our knowledge of the morphological features of ornithopod tracks in the Late Jurassic. The aim of this paper is to describe this new material and discuss the tracks’ ichnotaxonomic affinities, emphasizing the implications for the ornithopod ichnodiversity during the Late Jurassic and discussing the morphological variations among the morphotypes.
plus floodplain mudstone deposits and well-developed levels of calcite palaeosols. These sediments were deposited in fluvial meander systems grading laterally to upper deltaic deposits (Mateus et al. 2013). The Sobral Formation (upper Kimmeridgian–lower Tithonian; Manuppella et al. 1999; Schneider et al. 2009) is mainly composed of siliclastic deposits, silt or sandy marl, siltstone or sandstone, plus some calcareous levels. This formation was deposited in a deltaic estuarine system (Schneider et al. 2009; Kullberg et al. 2013). The Alcobaça Formation (mostly Kimmeridgian, but some authors suggest that it may extend to the lower Tithonian; Manuppella et al. 1999; Schneider et al. 2009; Kullberg et al. 2013) is composed of an alternation of sandy marl and calcareous limestone, marl and sandstone, deposited in a shallow carbonate platform with frequent siliciclastic inputs (Manuppella et al. 1999; Schneider et al. 2009; Kullberg et al. 2013). It is interesting to note that these three formations are partially equivalent in age although they outcrop in different areas of the Consolação sub-basin. The Praia da Amoreira-Porto Novo Formation is overlapped by the Sobral Formation, and both outcrop in the littoral region from Santa Cruz to Salir do Porto whereas the Alcobaça Formation outcrops in the Alcobaça-Caldas da Rainha region (see Fig. 1). Within the Turcifal sub-basin the specimens belong to the Sobral Formation (upper Kimmeridgian–lower Tithonian) and the overlapping Freixial Formation. The Freixial Formation is composed of an alternation of limestones, marls and siliciclastic material deposited in a shallow ramp. The age of this formation is middle–upper Tithonian (Schneider et al. 2009; Kullberg et al. 2013).

Material and methods

The tracks (SOM: table S1) are housed in the collection of the Sociedade de História Natural in Torres Vedras. The tracks are labelled as: SHN.(JJS).ICNO.#, # being the entry number in the collection. Some tracks have the same
number, so a letter has been added to distinguish them (e.g., SHN.(JJS).ICNO.03, SHN.(JJS).ICNO.48). Additionally, m and p refer to manus and pes, respectively. For the sake of simplicity we have used the acronym ICNO.# throughout some parts of the text.

Most of the tracks are preserved as natural casts (convex hyporelief, H) although some true tracks (concave epirelief, E) are also present (see SOM: table S1). Analysis of track morphology was performed independently for each track, by evaluating the morphological preservation (MP) according to the scale of Marchetti et al. (2019). A total of 57 individual tracks were analysed (SOM: table S1), but only those tracks that have an MP grade of 2 or higher (n = 18, see SOM: tables S1, S2) were used for proper systematic assignments (see Marchetti et al. 2019). The outlines of only these tracks are drawn and figured in the present paper. Those with a grade of less than 2 (n = 39, see SOM: table S3) are described but the systematic assignment is only an attempt to link these track morphologies to a putative ornithopod trackmaker. Open nomenclature follows the recommendations of Bengston (1998). Several parameters such as the footprint length (FL), footprint width (FW), the length and width of digits II (LII, WII), III (LIII, WIII), and IV (LIV, WIV), the “heel” (metatarsophalangeal area) (HA), and the divarication angles (II–III, III–IV) were measured (see SOM: fig. S1, tables S2, S3). Subsequently, the FL/FW ratio and the mesaxony (AT) were calculated. The latter was calculated on the basis of the anterior triangle length (ATl)/width of digits II (LII, WII), III (LIII, WIII), and IV (LIV, WIV), the “heel” (metatarsophalangeal area) (HA), and the divarication angles (II–III, III–IV) were measured (see SOM: fig. S1, tables S2, S3). Subsequently, the FL/FW ratio and the mesaxony (AT) were calculated. The latter was calculated on the basis of the anterior triangle length (ATl)/width of digits II (LII, WII), III (LIII, WIII), and IV (LIV, WIV), the “heel” (metatarsophalangeal area) (HA), and the divarication angles (II–III, III–IV) being slightly greater than interdigital angle II–III being slightly greater than interdigital angle II–III being slightly greater than interdigital angle II–III being slightly greater than interdigital angle II–III.

Description.—Medium to large-sized (pes length 28–32.5 cm) tridactyl tracks (Fig. 2 and SOM: table S2), generally slightly wider than long or almost as wide as long (length/width ratio 0.82–1.03) with low mesaxony (AT ratio 0.32–0.42). The tracks are relatively symmetrical, with a lateral and medial notch and a rounded to quadrangular metatarsophalangeal pad impression. The medial notch looks slightly more developed in some specimens (ICNO.03, ICNO.75), so these tracks are slightly asymmetric. The digits are considerably robust. Digit III is longer than digits II and IV, digit IV being slightly longer than digit II. The hypices are fairly symmetrical. No discrete phalangeal pad impressions can be discerned, possibly suggesting one pad impression in each digit. The distal end of the digit impressions is rounded, possibly indicating blunt claw marks. Only ICNO.03 shows evidence of blunt but acuminate claw marks. The interdigital angle II–IV is medium (65–85°), interdigital angle II–III being slightly greater than interdigital angle III–IV.

Remarks.—Large ornithopod tracks, i.e., those larger than 25 cm and generally assigned to iguanodontians, are not very common during the Late Jurassic, although they are frequent subsequently during the Cretaceous (Lockley and Wright 2001; Lockley et al. 2014; Diaz-Martinez et al. 2015). On the basis of the metatarsophalangeal pad and digit impressions, the latter authors identified three main groups of large ornithopod tracks, which belong to the ichnogenera Iguanodontipodidae and are related to the ichnifamily Iguanodontopodidae and Caririchnium, and Hadrosauropodus. Interestingly, this ichnifamily is so far mainly restricted to the Cretaceous. The authors include some tracks from the literature in their so-called Group 1; these were included in Iguanodontipus. This ichnaxon has been considered monospecific (I. burreyi), being characterized by a small,
rounded metatarsophalangeal pad and elongate, narrow digit impressions (see also Castanera et al. 2013a), and its distribution is limited to the Berriasian–Valanginian of Europe. Recently, Piñuela et al. (2016) described medium to large-sized (28–30 cm) ornithopod tracks in the Late Jurassic of Asturias (Spain) and suggested that the tracks “are quite different from known ichnogenera, but they are not sufficiently well preserved to propose a new one”. Moreover, the authors questioned the validity of Iguanodontipus because of the preservation of the material and even called into question the ornithopod origin of the possible trackmaker. The tracks from the Lusitanian Basin studied here share some features with the tracks from Group 1 defined by Díaz-Martínez et al. (2015). Nonetheless, there are some features described in the diagnosis of I. burreyi (Sarjeant et al. 1998) that they do not share, such as the similar digit length in the three digits. Given the current status of the type material of Iguanodontipus burreyi, the poor preservation of whose holotype has been pointed out by several authors (Piñuela et al. 2016 and references therein), its distribution apparently limited to the Berriasian–Valanginian (Díaz-Martínez et al. 2015) and the possible presence of a different ornithopod ichnotaxon in the Late Jurassic (Piñuela et al. 2016), the tracks studied here are tentatively assigned to Iguanodontipodidae indet. because they perfectly fit the diagnosis proposed for the ichnofamily by Díaz-Martínez et al. (2015). These new specimens expand the record of the ichnofamily Iguanodontipodidae to the Late Jurassic.

Ichnofamily uncertain
Ichnogenus Dinehichnus Lockley, dos Santos, Meyer, and Hunt, 1998

Type ichnospecies: Dinehichnus socialis Lockley, dos Santos, Meyer, and Hunt, 1998, Boundary Butte, San Juan County, Utah; Salt Wash Member of the Morrison Formation (Upper Jurassic, Kimmeridgian)

Diagnosis.—“Trackway of small- to medium-sized biped with footprints about as wide as long. Tracks quadripartite, symmetric and tridactyl with distinctive circular heel pad impression. Digit impressions consisting of single elongate oval impressions sometimes with tapered claw impression. Digit divarication (II–IV) averaging about 90°. Trackway narrow with pace angulation of about 155°. Negative (inward) rotation of digit III about 10–15° from trackway midline. Step length averaging a little more than three times foot length” (Lockley et al. 1998).

Dinehichnus isp.

Material.—SHN.(JJS).ICNO.03, Valmitão Norte. Note that the track still preserves part of the infill. B. SHN.(JJS).ICNO.54, Valmitão Sul. C. SHN.(JJS).ICNO.48, Praia Azul. D. SHN.(JJS).ICNO.75, Foz Do Rio Sizandro. Note that the track has been painted and the real morphology is not exactly the same as the drawing. E. SHN.(JJS).ICNO.110, Foz Do Rio Sizandro. Scale bars E, 15 cm; A–C, 20 cm; D, 25 cm.

Fig. 3. Photographs, false-colour depth maps, and outline drawing of the tracks of high morphological quality (MP = 2) that belong to the Iguanodontipodidae indet. morphotype. Portugal, Praia de Amoreira-Porto Novo Formation, upper Kimmeridgian (A, B) and Sobral Formation, upper Kimmeridgian–lower Tithonian (C–E). A. SHN.(JJS).ICNO.03, Valmitão Norte. Note that the track still preserves part of the infill. B. SHN.(JJS).ICNO.54, Valmitão Sul. C. SHN.(JJS).ICNO.48, Praia Azul. D. SHN.(JJS).ICNO.75, Foz Do Rio Sizandro. Note that the track has been painted and the real morphology is not exactly the same as the drawing. E. SHN.(JJS).ICNO.110, Foz Do Rio Sizandro. Scale bars E, 15 cm; A–C, 20 cm; D, 25 cm.
located more proximally in some specimens. The distal end of the digit impressions is acuminated, showing slender and pointed claw marks in some specimens. The interdigital angle II–IV is medium (66–78°), interdigital angle II–III being generally greater than interdigital angle III–IV in the majority of the specimens.

Remarks.---Dineichnus is the main formally named Late Jurassic ichnogenus assigned to medium-sized ornithopods. It has been described in several places in Europe (including the Lusitanian Basin), the USA, Africa and possibly Asia (Lockley et al. 1998, 2008; Lockley 2009; Gierliński et al. 2009; Belvedere et al. 2010; Xing et al. 2014). Dineichnus has also been identified in Early Cretaceous deposits in Europe (e.g., Lockley et al. 1998; Hornung and Reich 2012).

The assignment of the studied tracks to this ichnotaxon is justified by the fact that the tracks have many of the features described in the diagnosis such as digit divarication, symmetry and especially the distinctive circular pad impression. The reason for not including the tracks in the type ichnospecies D. socialis is the fact that in our sample the quadripartite morphology described in the diagnosis of the ichnospecies is not clearly recognized.

Ichnofamily uncertain
Anomoepus isp.
Figs. 4, 5.

Material.—SHN.(JJS).ICNO.18, SHN.(JJS).ICNO.29, SHN.(JJS).ICNO.34, SHN.(JJS).ICNO.37, SHN.(JJS).ICNO.56, SHN.(JJS).ICNO.74, SHN.(JJS).ICNO.103, SHN.(JJS).ICNO.105C. From Serra do Bouro, Boavista do Bouro, Santa Rita, Foz Velha, Cambelas Sul, Praia da Corva; Alcobaça (Kimmeridgian–lower Tithonian) and Sobral (upper Kimmeridgian–lower Tithonian) formations (for details see SOM: table S1).

Description.—Minute to small-sized (pes length 9–15 cm) tridactyl tracks (Figs. 4, 5 and SOM: table S2), slightly longer than wide (pes length/width ratio 0.85–1.22) with medium mesaxony (AT ratio 0.36–0.61). The tracks are gracile and slightly asymmetrical. The metatarsophalangeal pad impression is subtriangular. One specimen (ICNO.56) shows a constriction in the digits, suggesting possible phalangeal pads. Digit III is the longest, digit IV being slightly longer than II. The digits are considerably thin. The hypices are almost symmetrical. The distal end of the digit impressions is acuminated, showing tapered claw mark impressions in some specimens. The interdigital angle II–IV is medium to high (ranging from 68–102°); the interdigital angles II–III and III–IV are quite similar, with variations between the specimens. Specimen ICNO.18 probably shows the evidence of a manus mark, being oval in morphology, but no digits can be recognized.

Remarks.---Anomoepus-like tracks have been known ever since the earliest days of dinosaur ichnology, thanks to the descriptions by Hitchcock (1848, 1863). The ichnofamily Anomoepodidae was defined by Lull (1904, 1953), and subsequently Gierliński (1991) emended the diagnosis. Anomoepus-like tracks are well known from Early Jurassic deposits all around the world (Díaz-Martínez et al. 2017 and references therein). Nonetheless, there are different views about how many ichnospecies should be considered valid (Olsen and Rainforth 2003; Lockley and Gierliński 2006). As suggested by Lockley et al. (2009), Anomoepus is hard to identify “unless both manus and pes tracks are found”, and in many cases hallux impressions may not be present when the trackmaker was progressing bipedally. The latter authors also pointed out the difficulties of distinguishing Anomoepus-like tracks from other tridactyl or tetradactyl dinosaur footprints, and suggested that trackway configuration may help in drawing this distinction.
However, the absence of complete trackways in the studied sample precludes the use of trackway configuration to resolve the issue. Although notably abundant in Early Jurassic deposits, Anomoepus-like tracks are much scarcer in the context of younger deposits from the Late Jurassic. Lockley et al. (2009) suggested that “there is a significant gap in the distribution of Anomoepodidae between the early Jurassic and the early Cretaceous”. However, Anomoepus-like tracks have been described from the Late Jurassic of Asturias, Spain and the USA (Foster and Lockley 2006; Lockley et al. 2008; Piñuela Suarez 2015) and subsequently at the beginning of the Cretaceous with Neoanomoepus (Lockley et al. 2009). The studied tracks differ considerably with respect to the diagnosis of Neoanomoepus in that the pes is tridactyl instead of tetradactyl. The relation of the studied tracks to the ichnofamily Anomoepodidae should be taken with caution as they do not comply with one of the main features of the diagnosis, namely “pedal digits II, III, and IV tend to be subequal in length”. Nonetheless, we consider that the studied tracks resemble the group of tracks classified as Anomoepus found in Late Jurassic deposits from several areas, and this is why we have classified them with open nomenclature (see also discussion). It should be highlighted that there are some differences in digit width among the specimens. Notably, ICNO.56 (Fig. 4B) and ICNO.18B (Fig. 5D) look more gracile, with lower digit widths. These might just be extramorphological differences, as seen in the differences in the values of morphological quality (M-Preservation; Marchetti et al. 2019).

Fig. 4. Photographs, false-colour depth maps and outline drawing of the tracks of high morphological quality (MP = 2) that belong to the Anomoepus? isp. morphotype, Portugal, Alcobaça Formation, Kimmeridgian—lower Tithonian (A, B), Praia de Amoreira-Porto Novo Formation, upper Kimmeridgian (C), and Freixial Formation, middle—upper Tithonian (D). A. SHN.(JJS).ICNO.29, Serra do Bouro. Note the possible manus track. B. SHN.(JJS).ICNO.56, Boavista do Bouro. C. SHN.(JJS).ICNO.103, Santa Rita, Foz Velha. D. SHN.(JJS).ICNO.74, Cambelas Sul. Scale bars 10 cm.

Fig. 5. Photographs, false-colour depth maps and outline drawing of the tracks of high morphological quality (MP = 2) that belong to the Anomoepus? isp. morphotype, Portugal, Alcobaça Formation, Kimmeridgian—lower Tithonian (A–C) and Praia de Amoreira-Porto Novo Formation, upper Kimmeridgian (D). A. SHN.(JJS).ICNO.34A (left) considered Anomoepus? isp. and SHN.(JJS).ICNO.34B, (right) considered Ornithopoda indet., Boavista do Bouro. B. SHN.(JJS).ICNO.37, Boavista do Bouro. C. SHN.(JJS).ICNO.105C, Serra do Bouro. D. SHN.(JJS).ICNO.18A (top) and SHN.(JJS).ICNO.18B (bottom), Praia da Corva. Scale bars 10 cm.
Ornithopoda indet. tracks

Figs. 6, 7.


Remarks.—Within the collection there are a large number of footprints (n = 39) where the morphological quality is lower than 2, and whose ichnotaxonomic affinities should thus be regarded with caution (Marchetti et al. 2019). These specimens show ornithopod features, in that they are characterized by a low length/width ratio, low mesaxony, symmetry, broad digits, etc., which in many cases resemble the morphotypes described above. For instance, some specimens (ICNO.21, ICNO.53, ICNO.87, ICNO.89, ICNO.97, ICNO.99, ICNO.112) are medium to large-sized (pes length 23–38.5 cm) tridactyl tracks (Figs. 6, 7 and SOM: table S3) with a low length/width ratio (0.84–1.21) and low mesaxony (0.29–0.54). These specimens generally resemble in many features the tracks classified as Iguanodontipodidae indet. in the previous section. In addition, there are a large number (Figs. 6, 7 and SOM: table S3) of minute and small-sized specimens (pes length 9–21.5 cm), with a low to medium length/width ratio (0.79–1.35), low to medium mesaxony (0.3–0.86), broad digits, relatively high interdigital angle and quite symmetrical shape. These parameters generally fit with those described in the previous section for the tracks classified either as Dineichnus isp. or Anomoepus? isp. Some specimens even show a rounded circular pad impression (e.g., ICNO.78E, ICNO.94, ICNO.100) similar to that described in Dineichnus isp. Nonetheless, given the low morphological quality of these tracks, and in the absence of other morphological features typical of the described ichnotaxa, these tracks are considered simply to be indeterminate ornithopod tracks.

Discussion

Despite the difficulties of distinguishing between theropod and ornithopod tracks in the Late Jurassic and Early Cretaceous (e.g., Lockley et al. 2008; Schulp and Al-Wosabi 2012; Castanera et al. 2013a, b; Hübner 2016), the features of the three morphotypes described herein fit well with the characters typical of small, medium to large-sized ornithopod tracks, namely: short, U-shaped digits, the absence of sharp claw impressions with generally blunt and rounded morphology of the digit tips, low length-width ratios, medium to high divarication, symmetry, and similar width among the digits (Thulborn 1990; Lockley et al. 2008). Hübner (2016) proposed that weak mesaxony and broad digits can be interpreted as diagnostic features of ornithischian tracks. Recently, Lallensack et al. (2019) proposed that for small-sized tridactyl tracks the interdigital angle and the projection of digit III are the best features for discriminating between theropods and ornithischians, the former having smaller interdigital angles and a larger projection of digit III. Here, we propose ornithopods, a group of ornithischians, as the best candidates to be the trackmakers according to the osteological record found in the Lusitanian Basin (see below). This is also consistent with the identification of gracile ornithopod tracks from the Late Jurassic in other sites of the Iberian Peninsula (Santisteban et al. 2003; Lockley et al. 2008; Castanera et al. 2013b; Alcalá et al. 2014).

The three morphotypes described in the present paper have been assigned to three different ornithischian ichnotaxa, named Iguanodontipodidae indet., Dineichnus isp. and Anomoepus? isp. These three ichnotaxa have generally been associated with iguanodontians such as dryosaurs and ankylopollaxians and with basal ornithischians as candidate trackmakers (Lockley et al. 1998; Lockley and Gierliński 2011). Moreover, given that the majority of the specimens are preserved as natural casts, possible morphological variations due to undertrack preservation should be kept in mind, as some theropod tracks might look ornithopod in origin when preserved as undertracks (Avanzini et al. 2012). Accordingly, we cannot confidently assert that all the studied specimens (especially those of low morphological quality) were produced by ornithopods, even though the parameters and the features (length-width ratio, mesaxony, interdigital angle, symmetry, broad digits) do indeed suggest an ornithopod origin.

Distinguishing between ornithopod morphotypes is not an easy task. In fact, Hornung et al. (2016) have recently pointed out the difficulties of discriminating in qualitative and quantitative terms between several ornithopod tracks from the Berrissian of Germany. In this regard, it is interesting to note that in our sample the three described morphotypes can be distinguished qualitatively and also by size, whereas quantitative discrimination analyzing mesaxony (AT) and length/width ratio is not significant (Fig. 8), especially between the smaller (Anomoepus? isp.) and the medium-sized
Fig. 7. Photographs, false-colour depth maps of the tracks of low morphological quality (MP < 2) of Ornithopoda indet. tracks, Portugal, Sobral Formation, upper Kimmeridgian–lower Tithonian (A–D), Freixial Formation, middle–upper Tithonian (E–K), and Alcobaça Formation, Kimmeridgian–lower Tithonian (L).

A. SHN.(JJS).ICNO.21, Praia Azul.
B. SHN.(JJS).ICNO.87, Praia Azul.
C. SHN.(JJS).ICNO.97, Praia Azul.
E. SHN.(JJS).ICNO.71, Porto Chão, Cambelas.
F. SHN.(JJS).ICNO.78C, Porto Chão, Cambelas.
G. SHN.(JJS).ICNO.78E, Porto Chão, Cambelas.
H. SHN.(JJS).ICNO.80, Cambelas sul.
I. SHN.(JJS).ICNO.99, Cambelas.
L. SHN.(JJS).ICNO.121, Boavista do Bouro.

Scale bars D–H, J, 10 cm; I, K, 15 cm; A–C, L, 20 cm.
(Dineichnus isp.) morphotypes. This raises the question of how similar to one another or different from one another the three different morphotypes are. The fact that the footprints come from different locations and different geological formations rules out possible ontogenetic variations as the only reason for the size differences among the three morphotypes, so diversity and taxonomy are likely to have played a role in this distinction. Whatever the case, we cannot exclude the possibility that ontogeny may play a role in distinguishing some of the tracks included in the different morphotypes, and that the morphometric differences might be a consequence of differential allometric growth between small and large individuals (e.g., Olsen et al. 1998). Nonetheless, little is known about the influence of ontogenetic changes on the feet of ornithopod dinosaurs and thus possible footprint shape variations, so this assumption would be more a matter of speculation than a scientific fact based on currently available data.

It is noteworthy that the length/width ratio is very similar among the three different morphotypes in the studied sample, the main differences being in the mesaxony (Fig. 8). The studied sample shows the tendency noted by Lockley (2009) for smaller ornithopod tracks to be more elongated (stronger mesaxony) than large ornithopod tracks. In fact, some of the smaller tracks (Anomoepus? isp.) show the strongest mesaxony whereas tracks assigned to Iguanodontipodidae indet. display the weakest mesaxony. Nonetheless, there is some overlap between the three morphotypes. In this respect, Anomoepus? isp. and Iguanodontipodidae indet. can mainly be distinguished quantitatively, but the intermediate morphotype (Dineichnus isp.) shows intermediate values. This raises the question whether the three morphotypes should be classified as three different ichnotaxa or not. For instance, some authors have suggested that Dineichnus should be synonymized with Anomoepus at the ichnogenetic level (Dalman and Weems 2013; Piñuela Suarez 2015). Other authors (Gierliński et al. 2009) have also noted the similarities but emphasized the differences, stating that “Anomoepus footprints are often narrower, with less divergent and thinner digits, which usually show well defined phalangeal pads”. In our sample, Anomoepus? isp. tracks do not show clear phalangeal pads (with the possible exception of ICNO.56, Fig. 4B), although the digits are considerably thinner and some specimens show higher divarication angles than in the Dineichnus isp. morphotype. Lockley et al. (2008) studied Anomoepus-like tracks from the Late Jurassic of Asturias and suggested that “these tracks are enigmatic because they are unlike any previously described from the Upper Jurassic”. The authors pointed out the similarities with Anomoepus but added that “this label is tentative at best” and concluded that “very little is known of the morphology and spatial and temporal distribution of Anomoepus-like tracks”. According to Lockley et al. (2009), Anomoepus ichnospecies generally vary in size from 5 to 15 cm (without metatarsus impressions), so although size should not be taken into account in classifying footprints (Bertling et al. 2006), this threshold value of 15 cm is also a good criterion for distinguishing between the smaller (Anomoepus? isp.) and the intermediate (Dineichnus isp.) morphotypes. Another issue of note is that these Anomoepus-like tracks from the Late Jurassic do not properly comply with the diag-
nosis of the ichnofamily Anomoepodidae because digit III is clearly the longest whereas in the emended diagnosis proposed by Gierliński (1991) “the pedal digits II, III, and IV tend to be subequal in length”. Thus, further work is needed in order to understand how these Late Jurassic Anomoepus-like tracks fit within Anomoepodidae, as well as whether *Dineichnus* tracks might also fit within this ichnofamily.

The ornithopod record from the Lusitanian Basin is quite rich compared with that of other Late Jurassic areas in Europe (e.g., Campos-Soto et al. 2019), where fossils from this group are relatively scarce. The ornithopod fauna is mainly composed of medium-sized ornithopods: members of Ankylopollexia (Galton 1980; Mateus and Antunes 2001; Ortega et al. 2009; Rotatori et al. 2020) such as *Draconyx loureiroi* (Bombarral Formation, Tithonian), but also smaller forms such as dryosaurids (e.g., Rotatori et al. 2020), including *Eousdrysaurus nanohallucis* (Praia da Amoreira-Porto Novo Formation, Kimmeridgian, Escaso et al. 2014), and some materials assigned to possible “hypsilophodontids” (Galton 1980; Rauhut 2001; Antunes and Mateus 2003). None of the tracks has preserved hallux marks, which may suggest a “camptosaur” affinity rather than a dryosaurid one (Gierliński et al. 2009) for some of the morphotypes. These authors estimated 26 cm for the length of the track that *Camptosaurus dispar* would have produced, so this estimate would fit within the range of the tracks here classified as Iguanodontipodidae indet. Bakker (1996) proposed that small ornithopod dinosaurs such as *Drinker* or *Othnielia* would have been good candidates for producing *Anomoepus*-like tracks. Assigning the described morphotypes to a specific group of ornithopods is difficult since a synapomorph-based technique (Carrano and Wilson 2001) cannot be applied with confidence, making it impossible to positively identify the best ornithopod group to be the candidate trackmaker. Nonetheless, it is interesting to note that considering their size and in the light of the previous discussion, ankylopollexians are the best candidates for having produced Iguanodontipodidae indet., whereas both dryosaurids and the possible “hypsilophodontids” are better candidates to be the producers of the *Dineichnus* isp. and *Anomoepus?* isp. morphotypes.

**Conclusions**

Ornithopod footprints collected from different areas along the Portuguese coast within the Lusitanian Basin (Consolação and Turcifal sub-basins) are described for the first time. The footprints come from different geological formations (Praia de Amoreira-Porto Novo, Alcobaça, Sobral, and Freixial) that are Late Jurassic in age (Kimmeridgian–Tithonian). Three different morphotypes are identified: *Anomoepus?* isp., *Dineichnus* isp., and Iguanodontipodidae indet. This new study highlights the difficulties of quantitatively distinguishing between ornithopod footprints although they can be differentiated qualitatively by morphological differences (robustness of the digits, metatarsophalangeal pad impression morphology and size). The tracks included in the largest morphotype (Iguanodontipodidae indet.) represent one of the oldest records of this ichnofamily. The descriptions of the smallest (*Anomoepus?* isp.) and the medium-sized (*Dineichnus* isp.) morphotypes provide new data for identifying gracile ornithopod tracks in the Late Jurassic, although the ichnotaxonomic status of the former and the relationships of both within the ichnofamily Anomoepodidae cannot be completely resolved with the studied material. Thus, the study also highlights the great need for a systematic review to clarify the ichnotaxonomy of small to medium-sized ornithopod tracks in general, and help to ascertain the similarities/differences between Early Jurassic and Late Jurassic ichnotaxa. The new material adds to the ornithopod record of the Lusitanian Basin, where osteological remains have already been described but few ornithopod tracks had been identified. Although no direct correlations can be drawn between the ichnological and osteological records, the described footprints are consistent with the main ornithopod groups described so far (dryosaurids, ankylopollexians, and “hypsilophodontids”), which are excellent candidates to be the trackmakers.

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