



New dinosaur, crocodylomorph and swim tracks from the Late Jurassic of the Lusitanian Basin: implications for ichnodiversity

DIEGO CASTANERA , ELISABETE MALAFAIA , BRUNO C. SILVA , VANDA F. SANTOS  AND MATTEO BELVEDERE 

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New dinosaur (theropod and sauropod), crocodylomorph and swim tracks from Upper Jurassic units of the Lusitanian Basin, housed at the Sociedade de História Natural in Torres Vedras, are here described. They were collected from three different geological formations, the Praia da Amoreira-Porto Novo (upper Kimmeridgian) and the Alcobaca (Kimmeridgian-lower Tithonian) formations in the Consolação Sub-basin and the Freixial Fm. (middle-upper Tithonian) in the Turcifal Sub-basin. Four different theropod morphotypes are identified as follows: cf. *Jurabrontes* isp., *Megalosauripus* cf. *transjuranicus*, Grallatoridae indet. and an indeterminate morphotype (Theropoda indet.) that have affinities with other *Therangospodus*-like tracks described in Europe. An indeterminate sauropod track is also identified. These five morphotypes suggest high saurischian dinosaur ichnodiversity, similar to that seen in other European Late Jurassic areas (e.g. the Swiss Jura Mountains), but represent just a portion of the higher diversity exhibited by the osteological record in the Lusitanian Basin. Further, one crocodylomorph pes track identified as *Crocodylopodus* isp. and swim tracks assigned to *Characichnos* isp., possibly also produced by crocodylomorphs, are also identified. The newly identified ichnotaxa, together with the older and other recent identifications, indicate ichnodiversity comparable with the richest coeval Upper Jurassic units. □ Theropod, sauropod, crocodylomorph, footprints, Kimmeridgian, Tithonian, Portugal.

Diego Castanera  [diego.castanera@icp.cat], Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, c/ Escola Industrial 2308201, Sabadell, Barcelona, Spain; Elisabete Malafaia [emalafaia@gmail.com], Vanda F. Santos [vafsantos@fc.ul.pt], Instituto Dom Luiz (IDL), Faculdade de Ciências, Universidade de Lisboa, Campo Grande 1749-016 Lisboa, Portugal; Elisabete Malafaia [emalafaia@gmail.com], Grupo de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional de Educación a Distancia, C/ Senda del Rey, 928040, Madrid, Spain; Elisabete Malafaia [emalafaia@gmail.com], Bruno C. Silva [laboratorio@alt-shn.org], Laboratório de Paleontologia e Paleoecologia, Sociedade de História Natural, Travessa Florêncio Augusto Chagas, n° 8B, R/C2560-230, Torres Vedras, Portugal; Bruno C. Silva [laboratorio@alt-shn.org], European Centre of Paleontology, Institute of Biology, Laboratory of Paleobiology, University of Opole, ul. Oleska 4845-052, Opole, Poland; Vanda F. Santos [vafsantos@fc.ul.pt], Departamento de Geologia, Faculdade de Ciências da Universidade de Lisboa, Edifício C6, Piso 3, Campo Grande 1749-016, Lisboa, Portugal; Matteo Belvedere [matteo.belvedere@hotmail.com], Dipartimento di Scienze della Terra, Università degli Studi di Firenze, via G. La Pira, 4, 50121, Firenze, Italy; Matteo Belvedere [matteo.belvedere@hotmail.com], Institute for Studies in Landscape and Human Evolution, Faculty of Science and Technology, Bournemouth University, Talbot Campus, Fern Barrow Poole BH12 5BB, UK; manuscript received on 13/05/2020; manuscript accepted on 6/08/2020.

Late Jurassic deposits of the Lusitanian Basin have yielded a large number of dinosaur tracksites. Many tracksites found in different localities and geological formations have been described across different areas of the basin, since the first description of theropod tracks in Cabo Mondego more than 100 years ago (Gomes 1916). The Late Jurassic sauropod tracksites are the most significant in terms of number of footprints and were the subject of the first references in the late 1970s and the 1980s (Antunes 1976, 1981,

1990). In the following years, tracks assigned to *Parabrontopodus* isp. and *Brontopodus* isp. were identified at the Avelino and Pedra da Mua tracksites, respectively (Lockley & Santos 1993; Meyer *et al.* 1994; Lockley *et al.* 1994a, b; Castanera *et al.* 2014). Other tridactyl tracks were subsequently identified, such as the ornithopod ichnotaxon *Dinehichnus socialis* (Lockley *et al.* 1998), *Therangospodus*-like tracks (Lockley *et al.* 2000a) and indeterminate tridactyl dinosaur tracks (Antunes & Mateus 2003).

More recent research has shown considerable dinosaur ichnodiversity in the Upper Jurassic deposits of the Lusitanian Basin. For instance, various morphotypes have been described in the Lourinhã area, such as a giant ornithopod track (Mateus & Milàn 2008), plus tracks of medium- to large-sized sauropods, stegosaurs (*Deltapodus*) and medium- to large-sized theropods (Mateus & Milàn 2010a; Mateus *et al.* 2011). New research is providing data about the ichnotaxonomic relationships among some of the tracks described, as well as new findings (Belvedere *et al.* 2019; Castanera *et al.* 2020). The former authors reported in the Lusitanian Basin the same dichotomy seen in other European and North African areas, where large, gracile (*Megalosauripus transjuranicus*-like) together with giant, robust (*Jurabrontes*-like) theropod morphotypes have been distinguished. The latter authors reported new ornithopod tracks assigned to three different ornithopod morphotypes (Iguanodontipodidae indet., *Dinehichnus* isp. and *Anomoepus?* isp.). Tracks assigned to other vertebrates are scarcer, and only a few pterosaur and crocodylomorph tracks have been reported (Mateus & Milàn 2010b).

The dinosaur osteological record reported in the Lusitanian Basin is markedly high compared with the footprint record. Dinosaurs from different groups have been identified throughout the basin, including theropods (Malafaia *et al.* 2017a), ornithopods (Rotatori *et al.* 2020), sauropods (Mocho *et al.* 2017) and thyreophorans (Costa and Mateus 2019). The crocodylomorph record has recently been shown to be remarkably rich, with at least six taxa reported (Guillaume *et al.* 2020). This high diversity is particularly notable in comparison with the rather low ichnodiversity identified so far.

The Sociedade de História Natural (SHN) in Torres Vedras houses a significant collection of ichnites. Although a large collection of ornithopod tracks has recently been described (Castanera *et al.* 2020), there are still several specimens that call for detailed description. The aim of this paper was to describe the most interesting specimens, emphasizing their implications for the ichnodiversity recognized within the Lusitanian Basin in Late Jurassic times.

Geographical and geological setting

The footprints under study were found in various localities situated along the central-west coastline of Portugal. The outcrops where the specimens were discovered belong to the municipalities of Alcobaça (Praia da Fraga-São Martinho do Porto), Caldas da Rainha (Salir do Porto), Peniche (São Bernardino),

Lourinhã (Porto Dinheiro and Ribamar), Torres Vedras (Pedra da Ulsa) and Mafra (Porto Barril) (see Fig. 1, Table S1).

Like the locations studied by Castanera *et al.* (2020), the sites are located in the central sector of the Lusitanian Basin, which is situated in the western region of the Iberian Peninsula. The basin is subdivided into several sub-basins, and the outcrops in question are situated in the Consolação and Turcifal sub-basins (Kullberg *et al.* 2013; Taylor *et al.* 2014). As in Castanera *et al.* (2020), we here follow the lithostratigraphical scheme of Manuppella *et al.* (1999) (see Fig. 1). The specimens were collected from three different geological formations: the Alcobaça and Praia da Amoreira-Porto Novo formations in the Consolação Sub-basin; and the Freixial Formation in the Turcifal Sub-basin. The Alcobaça Formation was deposited in a shallow carbonate platform with frequent siliciclastic inputs and mainly comprises an alternation of sandy marls and calcareous limestones with marls and sandstones. It is primarily Kimmeridgian and possibly early Tithonian in age according to different authors (Manuppella *et al.* 1999; Schneider *et al.* 2009; Kullberg *et al.* 2013). The Praia da Amoreira-Porto Novo Formation is siliciclastic in nature, with a lower section mainly composed of sandstones and mudstones deposited in alluvial fans or meandering river systems (Praia da Amoreira Member; Hill 1989; Taylor *et al.* 2014) and an upper section (Porto Novo Member; Hill 1989) composed of sandstone channel bodies, mudstones and calcrete palaeosoils deposited in fluvial meander systems grading laterally to tide-influenced deltaic deposits (Mateus *et al.* 2013). The age of this formation is late Kimmeridgian (Manuppella *et al.* 1999). The Freixial Formation was deposited in a shallow ramp and is composed of an alternation of limestones, marls and siliciclastic material. It is middle-late Tithonian in age (Schneider *et al.* 2009; Kullberg *et al.* 2013).

Material and methods

A review of the footprint collection of the SHN was recently carried out, and the ornithopod tracks were the subject of the first publication output (Castanera *et al.* 2020). Here, we follow a similar methodology to that in the previous study. The tracks are labelled as: SHN.(JJS).ICNO.#, # being the entry number in the collection. Some tracks have the same number because they were considered to come from the same stratum or to belong to the same trackway; in these cases, a letter was thus added to distinguish them (e.g. SHN.(JJS).ICNO.64A, SHN.(JJS).ICNO.64B).

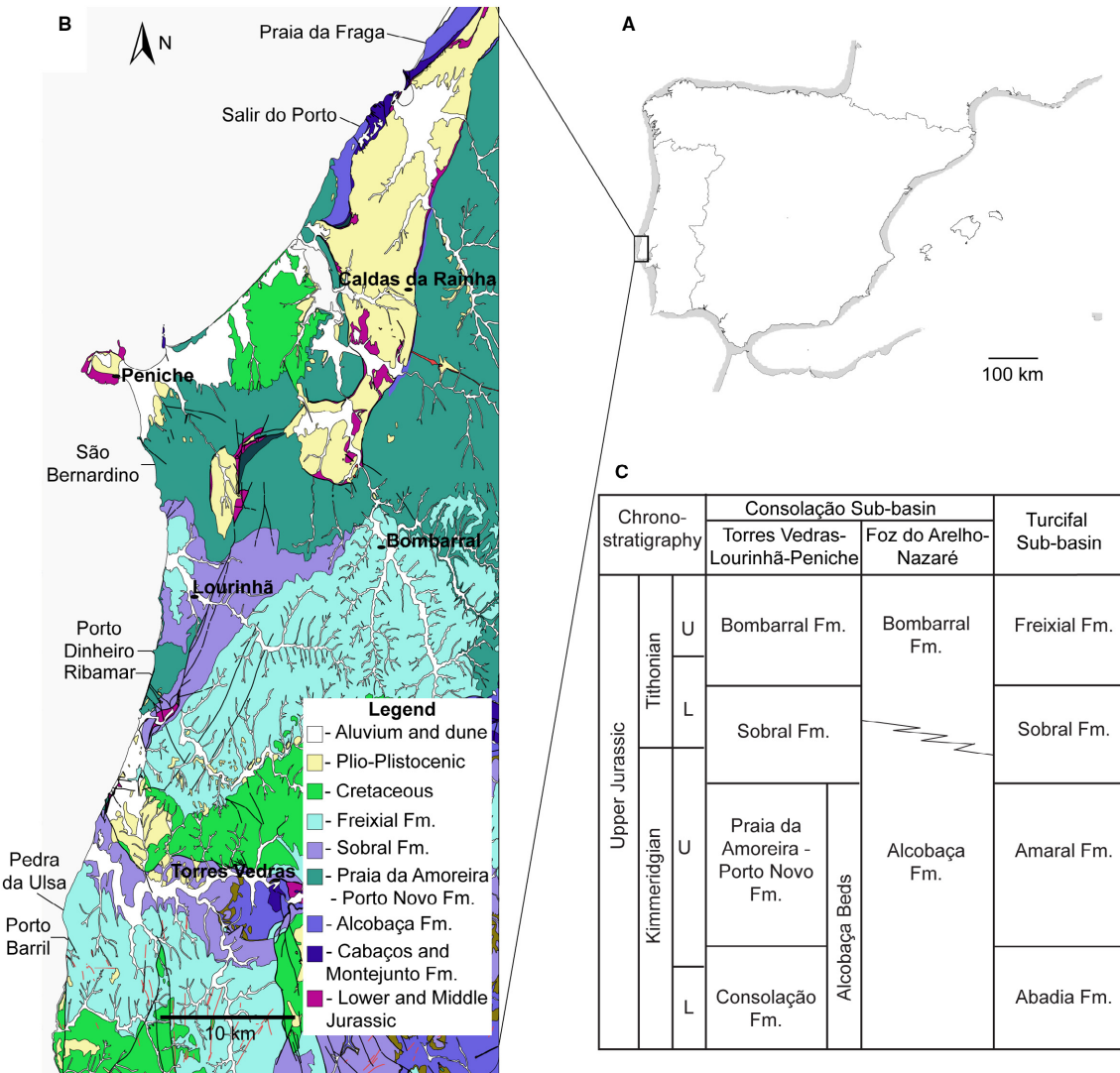


Fig. 1. Geographical and geological setting of the localities where the specimens were collected. A, map of the Iberian Peninsula showing the location of the studied sector within the Lusitanian Basin. B, geological map of the western and central sector of the Lusitanian Basin (after Oertel *et al.* 1960; Oliveira *et al.* 1992) showing the localities where the footprints were found. C, stratigraphical correlation of Upper Jurassic units of the Consolação and Turcifal sub-basins. [Colour figure can be viewed at wileyonlinelibrary.com]

For the sake of simplicity, we use the acronym ICNO.# through some parts of the text.

All the tracks are preserved as natural casts (convex hyporelief) in different lithologies (Table S1). A total of 14 individual tracks were analysed (Table S1). Morphological preservation (MP) was evaluated according to the numerical scale (Table S1) of Marchetti *et al.* (2019). Only four tracks have a MP of 2 or higher (good to exceptional preservation) and are thus suitable for proper ichnotaxonomic assignment; nonetheless, specimens with lower MP values (0–1, very poor to poor preservation) show interesting features as regards ichnodiversity, although their

ichnotaxonomic status should be regarded with caution, and open nomenclature (following Bengtson 1988) is accordingly used.

Several parameters (Table S2) were measured, such as the footprint length (FL), footprint width (FW), length and width of digits II (LII, WII), III (LIII, WIII) and IV (LIV, WIV), length of the claw marks (CLI, CLII, CLIII) and the divarication angles (I[∧]II; II[∧]III; III[∧]IV). The FL/FW ratio and the mesaxony (AT) were also calculated. The latter was calculated on the basis of the anterior triangle length (ATL)/(ATw) ratio in accordance with Lockley (2009). The dinosaur tracks were classified according

to different size classes (Marty 2008; Marty *et al.* 2018) on the basis of pes length (FL) as: (1) minute, $FL < 10$ cm; (2) small, $10 \text{ cm} < FL < 20$ cm; (3) medium, $20 \text{ cm} < FL < 30$ cm; (4) large, $30 \text{ cm} < FL < 50$ cm; (5) giant, $FL > 50$ cm. The large and giant theropod tracks have been considered either gracile or robust following Belvedere *et al.* (2019).

All the measurements were taken from the false-colour depth maps exported from the 3D-photogrammetric models, using the software ImageJ. 3D models were generated from pictures taken with a Sony Alpha 5100, by means of Agisoft Photoscan (v. 1.3.2). The scaled meshes were processed in CloudCompare (v.2.7.0) to obtain the false-colour depth maps. All the photogrammetric meshes employed in this study are available for download in the Supporting Information, and the outlines of the tracks were drawn and figured (following the recommendations of Falkingham *et al.* 2018). In addition, the proportions of the studied tracks were compared in a bivariate plot (length/width ratio vs. mesaxony) with Late Jurassic theropod tracks from Asturias in Spain and the Swiss Jura Mountains, such as *Grallator* isp. (Castanera *et al.* 2016a), *Jurabrontes curtedulensis* (the holotype in Marty *et al.* 2018), *Megalosauripus transjuranicus* (holotype and paratypes in Razzolini *et al.* 2017), cf. *Kalohipus* isp., cf. *Therangospodus* isp. and ? *Therangospodus* isp. (Castanera *et al.* 2018), plus other key theropod ichnotaxa, for example *Grallator*, *Anchisauripus* and *Eubrontes* (data taken from Lockley 2009), *Iberosauripus* (data taken from Cobos *et al.* 2014), *Jialingpus* (data taken from Xing *et al.* 2014) and *Kalohipus* (data taken from Castanera *et al.* 2015, 2016a).

Results

Giant and robust tridactyl tracks

The collection contains three tridactyl specimens (ICNO.38, ICNO.52 and ICNO.65) characterized by their very large to giant size (Fig 2A–C). These tracks are also characterized by weak mesaxony (0.32–0.36), a low FL/FW ratio (1.01–1.05) and asymmetry. The digits are very robust (digit width greater than 7.5 cm), digit III being the most robust in two specimens (ICNO.38, ICNO.65), whereas in ICNO.52, digit II is the most robust. Nonetheless, this might be an extramorphological feature. Digit III is clearly the longest, whereas digit II is slightly longer than, or equal in length to, digit IV. The digit divarication angle II–IV is low (58° – 71°), the angles II–III and III–IV varying among the three specimens. The digital pads are not well preserved, nor are the claw marks. Only ICNO.38 shows some evidence of claw marks in digits II and III.

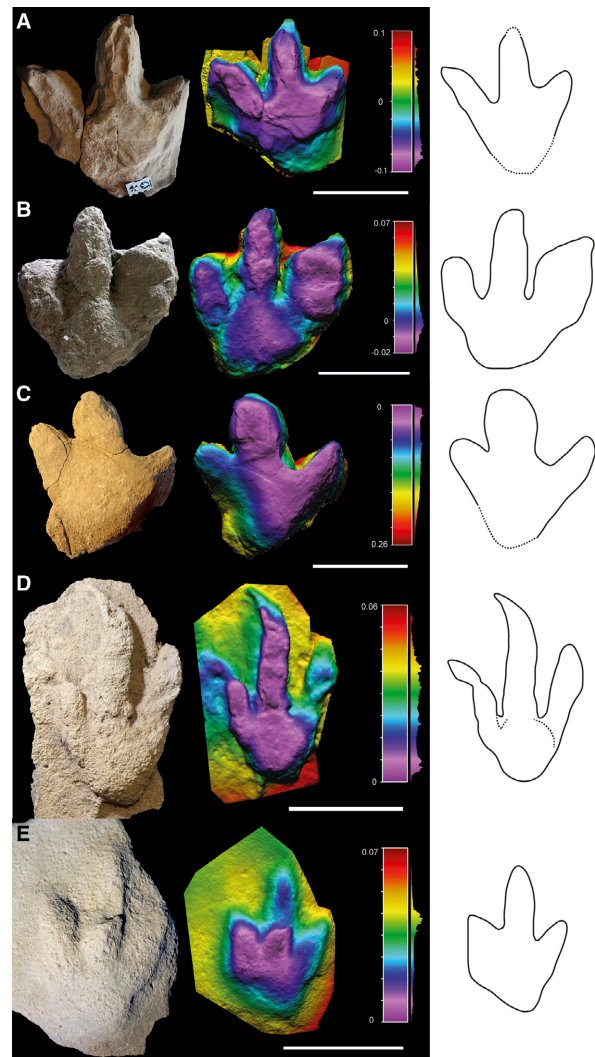


Fig. 2. Pictures, false-colour depth maps and outline drawings of the large and giant theropod tracks. A, SHN.(JJS).ICNO.38, cf. *Jurabrontes* isp. (Praia da Amoreira-Porto Novo Fm.). B, SHN.(JJS).ICNO.52, cf. *Jurabrontes* isp. (Praia da Amoreira-Porto Novo Fm.). C, SHN.(JJS).ICNO.65, cf. *Jurabrontes* isp. (Praia da Amoreira-Porto Novo Fm.). D, SHN.(JJS).ICNO.119, *Megalosauripus* cf. *transjuranicus* (Praia da Amoreira-Porto Novo Fm.). E, SHN.(JJS).ICNO.98, *Megalosauripus* cf. *transjuranicus* (Freixial Fm.). Note that the specimen also shows an isolated digit overprinting in the central part of the footprint. Scale bar = 35 cm (A, C), 25 cm (B, E), 20 cm (D). False-colour depth scale in metres. [Colour figure can be viewed at wileyonlinelibrary.com]

Large and gracile theropod tracks

Two specimens (Fig. 2D, E) are large-sized (ICNO.98, ICNO.119) ($FL = 31.5$ – 34 cm), the tracks being quite gracile with a generally medium FL/FW ratio (1.38–1.5) and medium mesaxony ($AT = 0.43$ – 0.5). They are tridactyl and asymmetrical. The digits are slender (generally < 5 cm in width), with slight variation between the digits in the two specimens. Digit III is the longest in the two specimens, digits II

and IV being equal in length in ICNO.119, whereas digit II is shorter than digit IV in ICNO.98. The digit divarication angle II-IV is quite low in both

specimens (50°–52°). Digital pads are not preserved but at least in ICNO.119 some constrictions can be discerned, so this might be a preservational feature. This specimen also shows clear, large claw impressions in digits II and III, which are oriented antero-medially.

Medium-sized theropod tracks

Four specimens (ICNO.04, ICNO.23, ICNO.41 and ICNO.42) with five footprints can be included within this category (Fig. 3A–D). They are all tridactyl and medium-sized, but some of them are close to the large-sized category (FL = 24–29.5 cm). The specimens within this size category show quite variable features and parameters, suggesting that they might include several morphotypes. Indeed, some of them show features and parameters similar to those of the large, gracile theropod tracks described in the previous section. For instance, ICNO.04 is almost large-sized (FL = 29 cm), has medium values for its FL/FW ratio (1.6) and mesaxony (0.56) and a very low digital divarication angle (44°). ICNO.23 has two footprints that are also almost large in size (FL = 26.5, 29 cm), with what seem to be low values for FL/FW (1.26 in ICNO.23A although digit IV is poorly preserved and FW is an approximation) and medium mesaxony (0.53). The digits are robust, and the digital divarication angle is medium (64°). ICNO.42 is almost large in size (FL = 29.5 cm). It shows the lowest values of FL/FW (1.15), medium mesaxony (0.54) and the divarication angle is the highest (72°) in the whole sample. The digits are relatively robust and the footprint is quite asymmetrical, with a rounded (but broken) ‘heel’ pad impression. ICNO.41 is medium-sized (FL = 24 cm), showing a medium FL/FW ratio (1.5) and medium-high mesaxony (0.64). It exhibits low digital divarication angles (54°). The digits are notably thin, the footprint being quite gracile.

Small-sized theropod tracks

ICNO.64A and ICNO.64B (Fig. 3E, F) are tiny tridactyl tracks with a FL < 10 cm. The tracks are very gracile with a very high FL/FW ratio (1.58–1.8) and

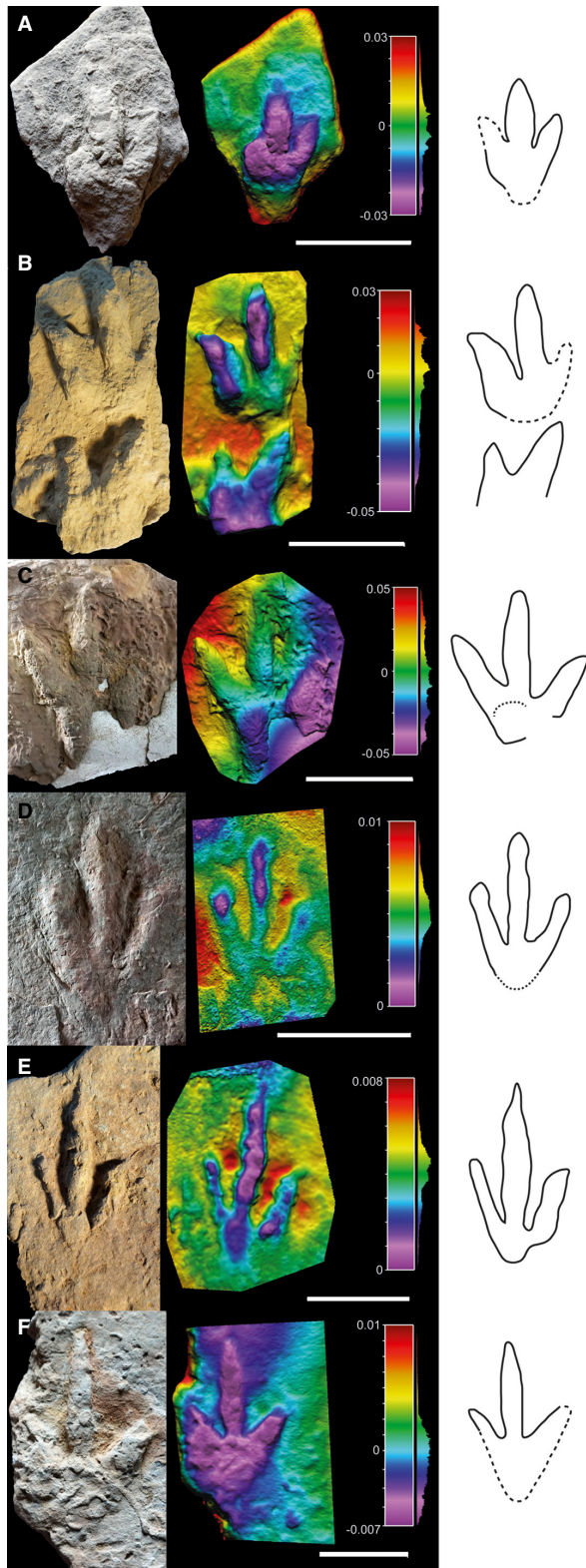


Fig. 3. Pictures, false-colour depth maps and outline drawings of the small and medium-sized theropod tracks. A, SHN.(JJS).ICNO.04, *Megalosauripus* cf. *transjuranicus* (Freixial Fm.). B, SHN.(JJS).ICNO.23, Theropoda indet. (Alcobaça Fm.). C, SHN.(JJS).ICNO.42, Theropoda indet. (Alcobaça Fm.). D, SHN.(JJS).ICNO.41, Gallatoridae indet. (Freixial Fm.). E, SHN.(JJS).ICNO.64A, Gallatoridae indet. (Alcobaça Fm.). F, SHN.(JJS).ICNO.64B, Gallatoridae indet. (Alcobaça Fm.). Scale bar = 25 cm (A, B), 20 cm (C, D), 5 cm (E, F). False-colour depth scale in metres. [Colour figure can be viewed at wileyonlinelibrary.com]

very strong mesaxony ($AT = 0.81\text{--}0.9$) and are asymmetrical. The digits are very thin (<1.3 cm), digit III being the thickest and the longest. Digit II is slightly longer than digit IV, while their widths vary between the two specimens. The distal ends of the digits are sharp. ICNO.64A shows constrictions in digits II and III and evidence of claw marks. The digit divarication angle II-IV is low ($51^\circ\text{--}53^\circ$). ICNO.64A shows a small subcircular 'heel' pad.

Sauropod track

ICNO.35 (Fig. 4A) is interpreted as the anterior part of a sauropod pes track. The specimen shows the first three digits (I-II-III) and a possible partial digit IV. All the digits are oriented laterally; it thus being a partial right pes. The FL is more than 45 cm and the FW is 51 cm, making this a very large specimen. Digits I and III are of similar length (measured to the hypex), and digit II is slightly longer. Digits I and II are very wide and thick, digit III being less robust. The distal end of the digits is notably sharp, suggesting the presence of claw marks that are especially marked and large in digits I and II. The footprint shows some tubercle-like structures covering parts of the three digits; these are of variable dimensions (1–3 cm), with a morphology that might represent poorly preserved scale marks although the classical polygonal pattern cannot be discerned.

Crocodylomorph track

ICNO.62 (Fig. 4B) is interpreted as a left pes of a crocodylomorph. It is tetradactyl and slightly wider (8.5 cm) than long (7.5 cm; FL/FW ratio = 0.88). Digit

II is the longest but is similar to DIII, which has a poorly preserved tip. In general, the digit lengths show a small variation, ranging from 6 cm of the shortest (DI) to 7.5 cm of the longest (DII), following the order: digit II > digit III > digit IV > digit I. The digits are very gracile with widths of <1 cm, which also show small variations in the following order: digit II > digit I > digit III > digit IV. The digit divarication angles increase as follows from digit I to digit IV: $I\wedge II$ (20°), $II\wedge III$ (32°) and $III\wedge IV$ (34°). The medial part of the footprint (DI and DII) is deeper than the lateral (DIII and DIV). Digit IV is the shallowest and not all of it is well impressed. DI and DII show clear claw impressions. The orientation of the digits varies from antero-medial (DI) to anterior (DII and DIII) and anterolateral (DIV). The 'heel' mark is also shallow and poorly preserved, but shows a subtriangular morphology.

Swim tracks

ICNO.118 (Fig. 5) is a slab composed of several slender, straight to sinusoidal, parallel scratch marks (striations), which are posteriorly curved, arranged in tetradactyl, tridactyl and didactyl traces of similar dimension, show regular spacing and orientation and have been preserved as a natural cast (convex hyporeliefs). Some invertebrate traces cross the tracks, making interpretation more difficult (Fig. 5). Four main sets of scratches are identified (A-D), plus a possible fifth (E) in the upper part of the specimen. ICNO.118A is tetradactyl and is formed by three clear subparallel ridges, plus a fourth shallower parallel mark. It is the largest and the widest track with a total length of more than 25 cm and a total width of 7.5 cm. It is quite symmetrical in its anterior part and sinuous in its posterior part, especially in the

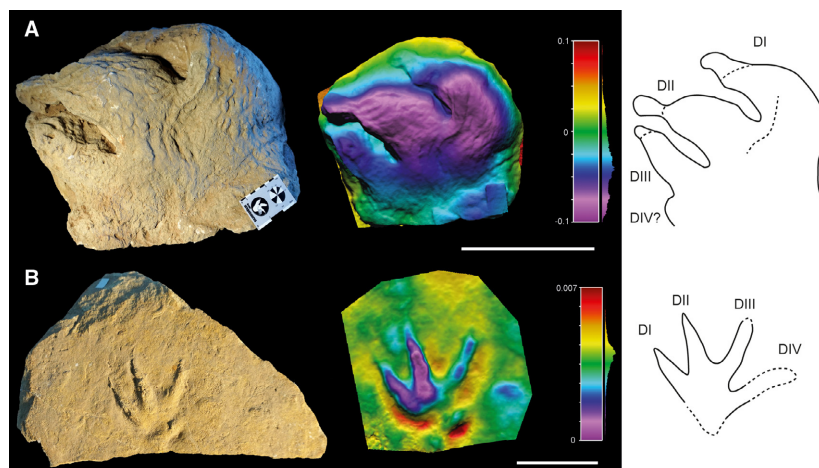


Fig. 4. Pictures, false-colour depth maps and outline drawings of the sauropod and crocodylomorph track. A, SHN.(JJS).ICNO.35, Sauropoda indet. (Freixial Fm.). B, SHN.(JJS).ICNO.62, *Crocodylopus* isp. (Alcobaça Fm.). Scale bar = 35 cm (A), 5 cm (B). False-colour depth scale in metres. [Colour figure can be viewed at wileyonlinelibrary.com]

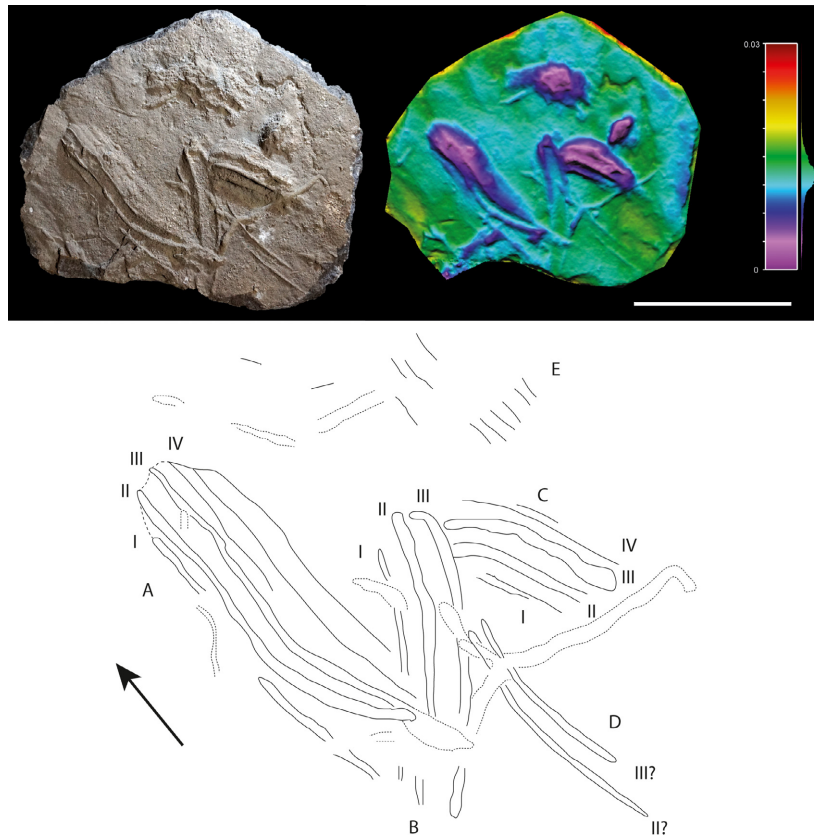


Fig. 5. Picture, false-colour depth map and outline drawing of the swim tracks in the specimen SHN.(JJS).ICNO.118, *Characichnos* isp. (Praia da Amoreira-Porto Novo Fm.). Note that the identification of the digits is an interpretation as specified in the description. Scale bar = 25 cm. False-colour depth scale in metres. [Colour figure can be viewed at wileyonlinelibrary.com]

central digits, which are subparallel. Three thin (about 1cm-wide) ridges can be distinguished, plus an interdigital area that is wider (1.5–2 cm) than the digits and might represent some kind of webbing or some extramorphological character related to the contact of the autopods with the substrate during the paddling movement (Falkingham *et al.* 2009) or both. The central digit traces (II–III?) are the longest; both show sharp distal ends. The medial/lateral digit traces (I and IV?) are slightly shorter; DI is posteriorly located and has a sharp distal end, whereas DIV is in a more anterior position and has a flat distal end. ICNO.118B is tridactyl, formed by three subparallel symmetrical ridges with a slightly sinuous trajectory. It has a total length of 20 cm and a total width of 5.5 cm. The central and lateral? digit traces (II–III?) are the longest (20 cm) and of similar length, and the medial? digit trace (I?) is slightly shorter (16 cm). The digit traces are thin with a similar width (0.7–0.9 cm) and an interdigital width of about 1–1.7 cm. The three-digit traces are subparallel and show a curved trajectory. ICNO.118C is tetradactyl, comprising three clear ridges plus another shallower and flatter ridge formed by the fourth digit. The total length is 13 cm, with a total width of 6.3 cm. The

two central digit traces (II–III?) are longer at 13 cm than the lateral? (DIV, 11 cm) and medial? (DI, 8.5 cm) ones. Digits I, II and IV are very thin (0.5–0.8 cm), with an interdigital area of 1–1.1 cm. The trace of digit III? is thicker, with a width of 1.1 cm and an interdigital area of 0.7 cm. The trajectory is slightly curved, with the anterior part more robust and deeper, becoming shallower posteriorly. ICNO.118D is didactyl, formed by two subparallel, symmetrical ridges probably produced by the central digit traces (DII–DIII?). One of the digits is slightly longer than the other (17 and 15 cm) in the posterior part. The digits are thin (0.4–0.8 cm) and the interdigital width is 1.2 cm. The trajectory is more sinuous. ICNO.118E is a tridactyl mark located in the upper part of the specimen although it is poorly preserved. Three subparallel, symmetrical marks can be distinguished. The total swim track length (anterior part of ICNO.118A to posterior part of ICNO.118D) would be at least 41 cm, and the total swim track width 28 cm (ICNO.118A to ICNO.118E). The maximum swim track depth is seen in the central digits of the tracks. In general, the scratches suggest that the digits are similar in length (with just a few variations between central and medial/lateral digits),

parallel and all close together, dragging along the sediment surface. No clear posterior overhangs or reflectures (retraction marks) can be distinguished.

Discussion

Ichnotaxonomic affinities and candidate trackmakers for the dinosaur tracks

Regarding the giant, robust, tridactyl tracks (ICNO.38, ICNO.52 and ICNO.65), it is not easy to discern their ichnotaxonomic affinities or even their trackmaker. Some of the features, such as their giant size, weak mesaxony or the robustness of the digits, have been described in Late Jurassic giant theropod tracks such as *Jurabrontes curtedulensis* (Marty et al. 2018; Belvedere et al. 2019), *Iberosauripus grandis* (Cobos et al. 2014) and *Megalosauripus teutonicus* (Lockley et al. 2000b; Belvedere et al. 2019), as well as other, similar *Megalosauripus* tracks described in the Asturian Basin (Rauhut et al. 2018). With respect to *Jurabrontes curtedulensis*, the specimens in question have some features described in the diagnosis such as ‘narrow and slightly asymmetric interdigital divarication angles ($II^{\wedge}III < III^{\wedge}IV$); small anterior triangle and weak mesaxony, [...] or the massive digits with a blunt aspect and lack of a hallux impression’ (Marty et al. 2018). Other characters, such the clear phalangeal pads, the pointed claw marks or the asymmetrical ‘heel’ region, cannot be properly seen in the studied specimens, possibly as a result of preservation factors. One notable difference is that the Portuguese specimens are not clearly longer than wide, showing a lower FL/FW ratio (1.01–1.05). As far as *Iberosauripus grandis* is concerned, the studied specimens also show some of the features considered to be autapomorphies of this ichnotaxon by Cobos et al. (2014), such as an obtuse anterior triangle with low values of mesaxony, the fact that digit III is proportionally long in relation to the total track length and a low interdigital angle. On the other hand, they do not show equidistance of the distal impressions of digits II and IV from the digit III midline and they also have a lower FL/FW ratio. The tracks also show some features shared with *Megalosauripus teutonicus* (Lockley et al. 2000b), but this ichnotaxon has recently been considered a *nomen dubium* due to its poor morphological quality (Belvedere et al. 2019), so comparison with this ichnotaxon is not recommended. Furthermore, the features of the three specimens also recall the giant ornithopod track described by Mateus & Milàn (2008) in the Upper Jurassic of the Lusitanian Basin, which is also characterized by its giant size, weak mesaxony, robust digits and a

similar length–width ratio. Nonetheless, the ornithopod track is considerably larger in size, is more symmetrical, the divarication angle is clearly higher (90°), and it shows short, blunt claws. In summary, the studied specimens show more features described in various giant theropod tracks than in the single giant ornithopod track from Lourinhã, so we consider these specimens to be giant theropod tracks. They cannot be ascribed with confidence to either of the aforementioned ichnotaxa (*Jurabrontes curtedulensis* or *Iberosauripus grandis*) on the basis of qualitative features, because of the absence of some of the diagnostic features due to the poor morphological preservation of the studied specimens. It is interesting to note that on the basis of quantitative features (Fig. 6) such as mesaxony and the FL/FW ratio, the specimens under study are slightly closer to *Jurabrontes* than to *Iberosauripus*. Thus, we classify the tracks as cf. *Jurabrontes* isp.

With regard to the large, gracile theropod tracks, they show features of the ichnogenus *Megalosauripus* (Lockley et al. 2000b; Fanti et al. 2013; Razzolini et al. 2016, 2017). Concretely, ICNO.119 shows many of the features described in the diagnosis of the ichnospecies *Megalosauripus transjuranicus* from the Kimmeridgian of the Jura Mountains in Switzerland (Razzolini et al. 2017). These features include the length/width ratio, similar size, asymmetry, moderate mesaxony, slender digits, well-marked and elongated claws, digit IV as the shallowest digit, and especially the characteristic circular (rounded) shape of the ‘heel’ pad impression, which is around twice the width of digit IV. On the other hand, ICNO.119 does not show a well-developed posteromedial notch and the phalangeal pads are not well preserved, so the phalangeal formula cannot be known, and the mesaxony is slightly lower than in the Swiss samples. ICNO.98 also shares some of the features described in *Megalosauripus transjuranicus*, such as the length/width ratio, similar size, asymmetry and moderate mesaxony. Recently, Belvedere et al. (2019) described two specimens from the Freixial Formation in the Lusitanian Basin that were assigned to *Megalosauripus* cf. *transjuranicus*. Both studied specimens ICNO.119 and ICNO.98 could also be classified under this label as *Megalosauripus* cf. *transjuranicus*, since quantitatively the FL/FW ratio and mesaxony fall within (or close to) the range of the type ichnospecies. Specimen ICNO.04 could also be classified as *Megalosauripus* cf. *transjuranicus*, since it bears some similarities with this morphotype and quantitatively (Fig. 6) falls within the range of this ichnospecies. Thus, these new identifications provide further evidence for the presence of *Megalosauripus* tracks in the Freixial Fm. and also represent a new

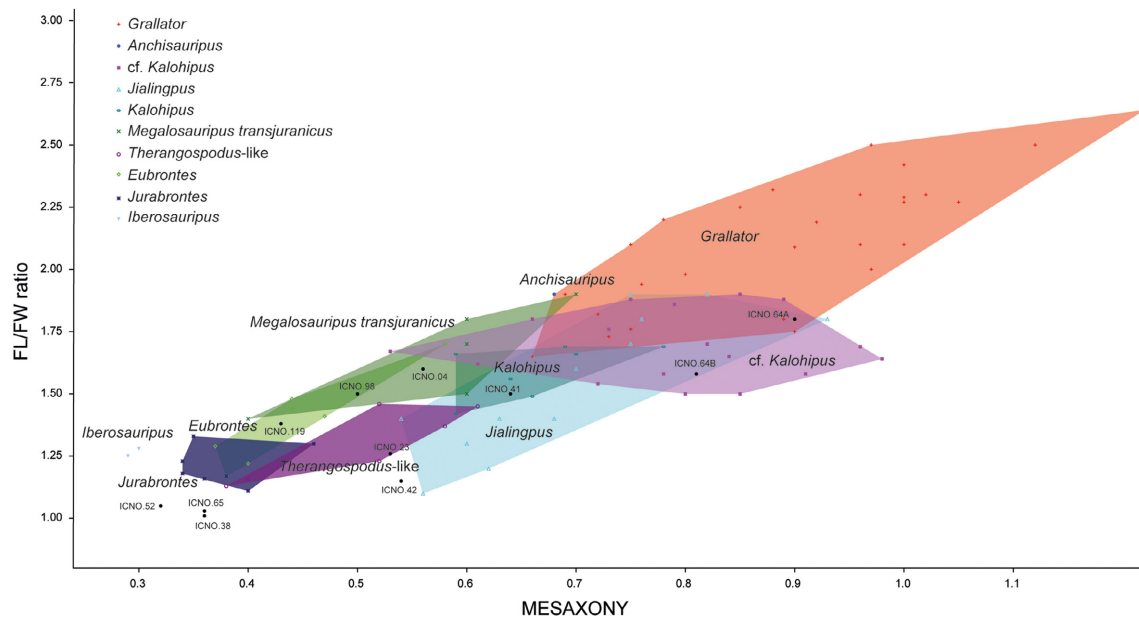


Fig. 6. Bivariate graph plotting the footprint length/footprint width ratio against the mesaxony of the studied tracks with some of the main tridactyl theropod ichnotaxa mentioned in the text. [Colour figure can be viewed at wileyonlinelibrary.com]

identification of *Megalosauripus* cf. *transjuranicus* in older sediments (Amoreira-Porto Novo Formation, Kimmeridgian).

The other small- and medium-sized theropod tracks are more difficult to classify because of the poor preservation of some of the studied specimens and the complexity of classifying small- and medium-sized theropod ichnotaxa, either by their complex ichnotaxonomy and the possible variations due to ontogeny and substrate-foot interactions (Razzolini *et al.* 2014; Castanera *et al.* 2018). The main small- to medium-sized theropod ichnotaxa identified in the Late Jurassic of Europe (see fig. 7 in Castanera *et al.* 2018) are grallatorid tracks, including *Grallator* in Spain (Castanera *et al.* 2016a), cf. *Kalohipus* isp. in Switzerland (Castanera *et al.* 2018) and cf. *Jialingpus* in Poland (Gierliński *et al.* 2009). In addition, other ichnotaxa identified are *Eubrontes* in France (Mazin *et al.* 2000), *Wildeichnus* in Poland (Gierliński *et al.* 2009), *Carmelopodus*-like tracks in France and Italy (Conti *et al.* 2005; Mazin *et al.* 2016) and *Therangospodus*-like tracks in Portugal, Italy and Switzerland (Lockley *et al.* 2000a; Conti *et al.* 2005; Castanera *et al.* 2018). The latter authors bring to light a dichotomy seen in medium-sized tridactyl tracks from the Swiss Jura Mountains, distinguishing between a gracile morphotype (cf. *Kalohipus* isp.) and a robust one (*Therangospodus*-like). ICNO.23 and ICNO.42 share more similarities with the robust morphotype from the Swiss Jura

Mountains than with any other of the aforementioned ichnotaxa. Indeed, both specimens fall within or close to the *Therangospodus*-like morphotype described in the Swiss Jura Mountains. These tracks also show similarities with *Therangospodus*-like tracks described in the Late Jurassic of Portugal (Lockley *et al.* 2000b). Nonetheless, the low MP values of the studied specimens, the uncertainties around the diagnostic features of *Therangospodus*-like tracks and the fact that they do not follow the diagnosis of the type ichnospecies *T. pandemicus* (see Lockley *et al.* 2000b; Fanti *et al.* 2013; Castanera *et al.* 2013, 2018; Razzolini *et al.* 2017) prevent us from classifying these tracks in the above ichnotaxa; they are thus considered Theropoda indet.

Specimens ICNO.41, ICNO.64A, ICNO.64B recall the general morphology of the grallatorid footprints identified in other Upper Jurassic units (Castanera *et al.* 2016a, 2018 and references therein). Shared features include the very high footprint length/width ratio, very strong mesaxony, slender digits with digits II and IV of similar length, low divarication angles and the oval/subrounded 'heel'. All these features can be clearly seen in specimen ICNO.64A, and some of them in ICNO.41 and ICNO.64B. Castanera *et al.* (2018) used mesaxony and the FL/FW ratio to distinguish between different grallatorid ichnotaxa such as *Grallator*, *Kalohipus* and *Jialingpus*. The values of both parameters in the studied specimens, especially in ICNO.64A (which has the highest MP value), are

similar (Fig. 6) to those for the tracks assigned to *Grallator* isp. from the Late Jurassic of Asturias, characterized by high values of both mesaxony and the FL/FW ratio, but they also fall within the range of variation for the tracks classified as cf. *Kalohipus* isp. from the Swiss Jura Mountains and *Jialingpus* from the Late Jurassic of China (Xing et al. 2014). ICNO.41 and ICNO.64B have lower MP values and fall within the range of *Kalohipus*, cf. *Kalohipus* isp and *Jialingpus*. Since there are only three specimens and the variation seen in other areas is very high, we classify these tracks to the ichnofamily level as Grallatoridae indet. (Lull 1904; Melchor et al. 2019); thus, the possibility that there are different grallatorid ichnotaxa in the Lusitanian Basin remains open.

The theropod osteological record of the Upper Jurassic (Kimmeridgian-Tithonian) deposits of the Lusitanian Basin reveals the diversity of theropod taxa to be exceedingly high (compared with just the at least four identified morphotypes in the ichnological record). For instance, seven different taxa of medium- to large-sized theropods have been identified, such as ceratosaurs, including *Ceratosauros* (Mateus et al. 2006; Malafaia et al. 2015, 2017a), as well as various allosauroid theropods; this is the most diverse group, with remains assigned to *Allosaurus*, *Lourinhanosaurus*, and a more derived allosauroid related with the clade Carcharodontosauria such as *Lusovenator* (Mateus 1998; Mateus et al. 2006; Malafaia et al. 2016, 2017a, 2019, 2020). Moreover, cranial and post-cranial material assigned to megalosaurid theropods, including *Torvosaurus*, has been described, as well as a non-megalosaurid megalosauroid (Hendrickx & Mateus 2014a; Malafaia et al. 2017a, 2017b). The Upper Jurassic fossil record of theropods from the Lusitanian Basin also includes some isolated teeth assigned to abelisaurids (Hendrickx and Mateus 2014b). Small-sized and more derived theropods (six more taxa) have also been described, such as Tyrannosauroida (Rauhut 2000) and a great diversity of maniraptoran coelurosaur, mostly identified on the basis of isolated teeth, including Dromaeosauridae, *Richardoestesia*, velociraptorine dromaeosaurids, compsognathids, and troodontids (Zinke 1998; Hendrickx and Mateus 2014b; Malafaia et al. 2017a).

Although there are both good osteological and ichnological records, it is difficult to establish any correlation between them given our current state of knowledge. The task of assigning the described morphotypes to a known clade is almost impossible due to the absence of osteological remains that have preserved complete feet for many of the aforementioned clades. This is a common situation in dinosaur ichnology and prevents a synapomorphy-based

correlation between the footprint and the osteological record (Carrano & Wilson 2001) in the Lusitanian Basin. This is especially true for the small- to medium-sized theropod footprints. The giant, robust tracks (cf. *Jurabrontes* isp.) and the large, gracile tracks (*Megalosauripus* cf. *transjuranicus*) once again show the dichotomy recently identified in Swiss tracksites (Razzolini et al. 2017; Marty et al. 2018) and in several areas of Europe, including the Lusitanian Basin, as well as in Morocco (Belvedere et al. 2019). The giant tracks are probably the only ones that fit well with the notable robustness of the megalosaurine megalosaurids specified by Rauhut et al. (2018) and Belvedere et al. (2019), remains of which (e.g. *Torvosaurus*) have been described in the same geological formation (Praia da Amoreira-Porto Novo Fm.: Hendrickx & Mateus 2014a; Malafaia et al. 2017a, 2017b). Smaller theropods such as allosauroids or ceratosaurs might be the trackmakers of *Megalosauripus* cf. *transjuranicus* (Razzolini et al. 2017; Rauhut et al. 2018). It should be also noted that the recently described carcharodontosaurian theropod *Lusovenator* have preserved an almost complete foot collected in the Freixial Formation (Malafaia et al. 2019, 2020) which size and morphology would be compatible with *Megalosauripus* cf. *transjuranicus* tracks collected in the same formation. Interestingly, although no more detailed assignments can be undertaken, the differences seen in the studied specimens show a scenario of relatively high ichnodiversity, with at least four theropod morphotypes (cf. *Jurabrontes* isp.; *Megalosauripus* cf. *transjuranicus*; Grallatoridae indet., Theropoda indet.), plus the possibility of a variety of grallatorid ichnotaxa and the fact that the tracks classified as Theropoda indet. might also represent various morphotypes. This high theropod ichnodiversity is similar to that in other coeval areas (e.g. Lockley et al. 2008; Belvedere et al. 2010), but it only partially reflects the high theropod diversity identified at species level for the Late Jurassic of the Lusitanian Basin on the basis of the osteological fossil record.

Regarding the sauropod specimen ICNO.35, an ichnotaxonomic assignment is not possible since it is just a partial track, and generally, the type of trackway and the manus morphology are also important in sauropod ichnotaxonomy (Lockley et al. 1994b; Santos et al. 2009; Castanera et al. 2016b). Nonetheless, the specimen has some features that are worthy of mention, namely the orientation of the digits and claw marks. Several examples of sauropod pes prints have been described in the Late Jurassic and Early Cretaceous of the Iberian Peninsula, including the Lusitanian Basin (Mateus & Milàn 2010a; Castanera et al. 2016b), being characterized by claw marks

oriented anterolaterally for digits I-III. In the case of ICNO.35, the orientation of the three digits, including digit I, is more lateral than anterolateral. Another feature that draws our attention is the fact that digit II is not smaller in size with respect to digit I, although the morphology of the digits and the claws might be influenced by the motion of the foot. These features might represent some kind of plantar flexion as described by Hall *et al.* (2016), which would have produced the extramorphological features and the more lateral orientation of the claw marks.

The Lusitanian Basin also has a rich sauropod osteological record, with several taxa identified in the Freixial Formation in localities close to ICNO.35, in the Cambelas area (Mocho *et al.* 2017). At least two different taxa have been identified, with material that shares similarities with camarasaurids and other material with diplodocids. Furthermore, within the Turcifal Sub-basin other groups such as non-neosauropod eusauropods and other macronarian members within Titanosauriformes have also been identified in Upper Jurassic deposits (Mocho *et al.* 2017). Accordingly, several sauropod groups are candidate trackmakers for the studied specimen.

Ichnotaxonomic affinities and candidate trackmakers for the crocodylomorph track

Specimen ICNO.62 has been interpreted as a left pes of a crocodylomorph. During the Mesozoic, three main crocodylomorph ichnotaxa have been described: *Batrachopus* (Early Jurassic-Cretaceous), *Hatcherichnus* (Late Jurassic-Cretaceous) and *Crocodylopodus* (Late Jurassic-Cretaceous) (Lockley & Meyer 2004; Lockley *et al.* 2020; Kim *et al.* 2020 and references therein). In addition, Mateus *et al.* (2017) described *Angolaichnus adamanticus* from the Early Cretaceous of Angola. ICNO.62 differs from *Batrachopus* (Olsen & Padian 1986; Lockley & Meyer 2004; Kim *et al.* 2020) in the digit proportions, the orientation of the digits and especially in the digital divarication (higher in ICNO.62). With respect to *Hatcherichnus sanjuanensis* from the Late Jurassic of the United States (Foster & Lockley 1997), ICNO.62 differs in the length of the digits, since digit III is the longest in *Hatcherichnus sanjuanensis* whereas in ICNO.62 it is digit II (although DII is almost subequal to DIII), but especially in that digits I and II are not recurved laterally and the total divarication is higher in ICNO.62. Generally, tracks assigned to *Hatcherichnus* are wider and shorter than ICNO.62 and in many cases represent crocodylomorph 'swim tracks' (Kukihara *et al.* 2010; Milner & Lockley 2016). *Hatcherichnus*-like tracks have also been described in other Late Jurassic areas in the

Iberian Peninsula (Avanzini *et al.* 2010a). As far as *Angolaichnus adamanticus* is concerned (Mateus *et al.* 2017), this has only been described in the type locality so far, and it differs in the fact that its digit IV is the shortest whereas in ICNO.62 digit I is the shortest; there is also greater digital divarication in ICNO.62. The greatest similarities with the aforementioned ichnotaxa are with *Crocodylopodus meijidei* from the Early Cretaceous of Spain (Fuentes Vidarte & Meijide Calvo 2001), since in both cases the central digits (II-III) are the longest and digit I is the shortest. There is a slight variation in digit lengths, since in ICNO.62 digit II is the longest whereas in *Crocodylopodus meijidei* it is digit III (although the tip of digit III is poorly preserved and might be similar). Fuentes Vidarte & Meijide Calvo (2001) suggest that digit III is not 'excessively' long with respect to digit II and IV, as is the case with ICNO.62. There are also considerable differences in digit divarication, this being higher in ICNO.62. The specimen also shows similarities with other tracks assigned to *Crocodylopodus* identified in other areas, such as the Late Jurassic of Spain (Avanzini *et al.* 2007, 2010b), plus the Middle Jurassic of Iran (Abbassi *et al.* 2015), the Middle-?Late Jurassic of Morocco (Klein *et al.* 2018) and the Lower Cretaceous of Korea (Lockley *et al.* 2020). Since we cannot compare manus morphology and the trackway parameters, the slight differences described above and the variability seen in the tracks assigned to *Crocodylopodus* suggest that we should classify ICNO.62 as *Crocodylopodus* isp.

Ichnotaxonomic affinities and candidate trackmakers for the swim tracks

Generally, swim tracks are represented by parallel to subparallel, elongated scratch marks produced by the distal phalangeal digit and/or claw marks and characterized by similar dimensions, regular spacing, similar orientation, posterior projections or overhangs, and reflectures/retraction marks of the digits and striations. Ideally, the footmarks record the number of functional digits on each limb but generally not the morphology of the autopod. Further, if they form part of a trackway ('traceway'), they show high variability in pace angulation, variable lengths compared to the widths, unequal representation of manus and pes and unexpected configurations (McAllister 1989; Romano & Whyte 2010; Milner and Lockley 2016). Lockley *et al.* (2010) noted that the definition of swim tracks is 'rather vague, inherently ambiguous and in need of more precise definition' since it implies some contact of the limbs with a subaqueous substrate. Indeed, Farlow *et al.* (2018)

suggested that ‘many or most trackways interpreted as having made by ‘swimming’ animals can more accurately be described as having been made by bottom-walkers, and in some instances by reptiles that were punting as they moved along the bottom’. ICNO.118 shows many of the abovementioned features and is thus here referred to as swim tracks although this does not necessarily mean that the trackmaker was literally swimming. McAllister (1989) pointed out that there may be a variety of traces produced by a paddling animal depending on the degree of foot-sediment contact. In the case of ICNO.118, the didactyl to tetradactyl scratch marks suggest that the trackmaker just touched the ground with different digits that varied with the tracks, but the central digits (DII and DIII) touched the ground in all five tracks (ICNO.118A-E). This kind of mark is what McAllister (1989) suggested for traces produced when the digits ‘barely touch the substrate’ and ‘the foot would not encounter much resistance’. Moreover, the trackmaker did not produce prints in the same place, suggesting discontinuous propulsion in which the direction of movement is probably towards the upper left part of the specimen (Fig. 5); however, the size of the slab is too small to determine these aspects beyond any doubt. The marks were probably produced by just the distal part of the digits, mainly the claws, as seen by the ridges plus the dragging of the digits when the trackmaker was paddling. The differences in footprint length between the traces suggest that some of them, especially ICNO.118A, were produced by a considerable dragging of the digits through the substrate.

Two main ichnotaxa are represented by swim tracks. *Characichnos* (Whyte & Romano 2001) has been applied to swim tracks produced by various tetrapods (see Milner & Lockley 2016 and references therein). The other ichnotaxon is the aforementioned *Hatcherichnos*, generally applied to crocodylomorph swim tracks (Foster & Lockley 1997; Lockley et al. 2010). Specimen ICNO.118 fits perfectly with the diagnosis of the ichnogenus *Characichnos*, but it does not conform to the diagnosis of the type ichnospecies *Characichnos tridactylus* (Whyte & Romano 2001), which is tridactyl. ICNO.118A and ICNO.118C show a tetradactyl configuration, suggesting a tetradactyl condition in the trackmaker, although there are also tridactyl and didactyl marks such as ICNO.118B, ICNO.118D and ICNO.118E. Milner & Lockley (2016) warned about the possibility that tetradactyl trackmakers could produce ‘tridactyl tracks resembling or practically indistinguishable from *Characichnos* in strictly morphological terms’, and proposed that ‘the label *Characichnos* (implying *C. tridactylus*) may not be applied to swim tracks, which display

four or more digit traces, as in the case of many examples of *Hatcherichnos*’. Morphologically, ICNO.118 does not conform to the diagnosis of *Hatcherichnos* and is not similar to many of the described swim tracks assigned to this ichnogenus, whose traces are generally shorter and wider (Foster & Lockley 1997; Lockley et al. 2010; Avanzini et al. 2010a). Thus, we consider that ICNO.118 should be classified as *Characichnos* isp.

It should be noted that the interpretation of swim tracks is often problematic because they do not usually display regular trackway patterns and, as suggested by Milner & Lockley (2016), ‘are sometimes incomplete and are often found to have irregular and confusing configurations’. Identification of the trackmaker and even the distinction between manus and pes tracks is therefore often difficult. During the Mesozoic, the main producers of swim tracks are generally dinosaurs, crocodylomorphs, pterosaurs and chelonians (Lockley et al. 2014; Milner & Lockley 2016 and references therein). These authors emphasized that among the four groups ‘tracks may only be recognized in some cases, notably, where tracks are relatively complete and/or well preserved’ and they proposed a series of tips for distinguishing between them. Among candidate trackmakers for ICNO.118, we can rule out dinosaurs, since the majority of dinosaur swim tracks were produced by tridactyl dinosaurs (mainly theropods), giving rise to tridactyl tracks in which digit III trace is longer than those of digits II and IV (Milner & Lockley 2016 and references therein). Although chelonians can produce didactyl to tetradactyl traces, they generally produce shorter and proportionally wider tracks with well-developed webbing and wide trackways, as exemplified by several cases described in Mesozoic deposits (e.g. Avanzini et al. 2005; Lockley et al. 2014, 2018; Klein et al. 2018). Having ruled out dinosaurs and chelonians, pterosaurs and crocodylomorphs are the best candidate trackmakers. In fact, both groups show a tetradactyl condition in the hind feet whereas the manus is pentadactyl in crocodylomorphs and tridactyl in pterosaurs. Ichnological distinction between the two groups has been a matter of intense discussion for walking trackways (e.g. Lockley et al. 1995; Kubo 2008 and references therein), so for swim tracks distinguishing the two groups might be even harder. Several papers have proposed a diagnostic pes digit length ratio of $II = III > I = IV$ for pterosaur swim tracks (Lockley et al. 2014; Lockley & Schumacher 2014; Milner & Lockley 2016). Thus, digits II and III are equal in length and slightly longer than the traces of digits I and IV, forming four long, parallel striations ‘many times the length of normally registered pes tracks, which show narrow

heel traces'. Lockley & Wright (2003) suggested that since the two middle digit traces (II and III) are longer than the outer ones (I-IV), it would be expected for them to leave a deeper impression. Thus, pterosaur swim tracks are generally long parallel striations that represent incomplete pes tracks produced by the pes touching the substrate. Besides, the webbing traces (when preserved) are located in the distal ends of the digit traces (Lockley *et al.* 2014). On the other hand, crocodylomorph swim tracks would have a tetradactyl pes where digits I-III are robust with strong claws and digit IV is more slender, with a diagnostic digit length ratio of $III > II = IV > I$ (Lockley *et al.* 2014; Lockley & Schumacher 2014; Milner & Lockley 2016). The manus are pentadactyl, with digits II-IV longer than I and V, with a digit length ratio of $III > II$ and $IV > I$ and V. Some traces also present a conspicuous posterior 'heel' trace. Further, crocodylomorph traces do not show well-developed webbing, and webbing is generally seen in the proximal part (in the hypices).

In the light of these data, it is difficult to interpret specimen ICNO.118, since a formula is not easy to calculate among the scratches. In their anterior part, the four main traces show central digits (digits II and III) that reached a similar level, both of them showing deeper impressions than the other digits, especially in ICNO.118A and ICNO.118C. The first three digits are also seen to be deeper than the fourth, and the ridges are much more clearly marked than that of digit IV, which might be because of the claw marks in the first three digits and the absence of a claw mark in the fourth, as seen in the crocodylomorph pes, or due to kinematic effects during the paddling movement (e.g. the angle of the limbs when they contact the sediment). The formula thus seems more similar to the one proposed by Milner and Lockley (2016) for crocodylomorphs, although it would be $III = II > IV > I$. Vila *et al.* (2015) also noted the similarities between pterosaur and crocodylomorph traces and suggested that the digit orientation may be somewhat different. In this regard, ICNO.118A shows a lateral digit trace (IV?) that is placed more anteriorly than the medial one (I?), which would fit better with a rather asymmetrical pes like those of crocodylomorphs than with the more symmetrical pes characteristic of pterosaurs. It is true that the close spacing between the digits might be more consistent with the configuration of pterosaur feet, but the traces are not completely parallel scratch marks like those assigned to pterosaur swim tracks (Lockley & Wright 2003; Lockley *et al.* 2014; Milner & Lockley 2016). However, this could be a consequence of different limb movements during locomotion. On the other hand, swim tracks assigned to

crocodylomorphs are in general shorter and wider, as in *Hatcherichnus*. Milner & Lockley (2016) also proposed that size may be useful in discriminating between candidate trackmakers. Generally speaking, Late Jurassic pterosaur tracks are smaller in size (Lockley *et al.* 1995; Lockley *et al.* 2008; Elgh *et al.* 2019), but there is one report from the Late Jurassic of Asturias that might also fit with ICNO.118 in terms of size (Lockley *et al.* 2008). The track width of the traces of ICNO.118 (5.5–7.5 cm) might fit with the track width (8.5 cm) of specimen ICNO.62 assigned to *Crocodylopodus* sp. or with the crocodylomorph track (4.9 cm in width) described by Mateus & Milàn (2010b). The low variation in digital divarication suggests that such a pes configuration might have also produced relatively symmetrical swim tracks like ICNO.118. Other possible scenarios should be taken into account too. One such scenario is that different crocodylomorphs produced different types of swim tracks, which means that (at least some) *Hatcherichnus*-like swim tracks may have been produced by more robust crocodylomorphs than the specimen described here. Another is that different locomotor patterns, speeds, behaviours or degrees of buoyancy (McAllister 1989; Lockley & Schumacher 2014; Lockley *et al.* 2014; Farlow *et al.* 2018) associated either with crocodylomorphs or with pterosaurs resulted in morphologically different swim tracks. Thus, *Hatcherichnus*-like swim tracks might represent a different state of subaqueous locomotion (Farlow *et al.* 2018) from specimen ICNO.118.

Analysis of the osteological record reveals that crocodylomorphs were diverse in the Late Jurassic ecosystems of the Lusitanian Basin, with six different taxa reported so far (Krebs & Schwarz 2000; Puértolas-Pascual & Mateus 2020; Guillaume *et al.* 2020). The latter authors recently reported five different clades (*Lusitanisuchus*, Atoposauridae, Goniopholididae, Bernissartiidae and an undetermined mesoeucrocodylian) in the same formation (Praia da Amoreira-Porto Novo Fm.) where ICNO.118 was found. By contrast, the pterosaur record in the Late Jurassic of the Lusitanian Basin is quite sparse (Ortega *et al.* 2009). Finally, the palaeoecology of both groups should be analysed. Many of the crocodylomorphs identified in the formation are freshwater crocodylomorphs that would have been well adapted to an aquatic lifestyle (Guillaume *et al.* 2020; Wilberg *et al.* 2020). By contrast, although pterosaurs lived close to marine and freshwater habitats, there are doubts about how they could have produced the traces since they would have been partially constrained to remain at the surface of the water (Hone & Henderson 2014). In this scenario, the authors propose that pterosaurs could have been

‘vulnerable to drowning’ and that they ‘did not regularly rest on the surface of the water and if immersed would need to take off again rapidly’. The authors note that their posture when floating in the water would be high on the waterline and that their feet were ‘lowermost in the water column,’ giving them the potential to leave swim traces with the pedes (not the manus). They conclude that their floating postures were ‘not inconsistent with the ichnological record for pterosaurs that are suggested to have been swimming or at least partially supported in the water column’.

In summary, given the current state of knowledge, it is difficult to discriminate between pterosaurs and crocodylomorphs as candidate trackmakers for specimen ICNO.118. Nonetheless, there are several lines of evidence that would probably point more to a crocodylomorph than to a pterosaur trackmaker. These include the robustness of the tracks (though gracile for a crocodylomorph), the digit lengths closer to the diagnostic formula proposed for crocodylomorphs (Lockley *et al.* 2014; Lockley & Schumacher 2014; Milner & Lockley 2016), the osteological record itself, which is more diverse but also with larger trackmakers, plus palaeoecological and biomechanical constraints.

Conclusions

The new archosaur footprint record identified in the palaeontological collection of the SHN provides new evidence of dinosaur ichnotaxa already identified (or closely related specimens) in the Lusitanian Basin (e.g. cf. *Jurabrontes* sp., *Megalosauripus* cf. *transjuranicus*), but also represents the first identification of gallatorid theropod tracks (the Gallatoridae indet. morphotype). Furthermore, it yields the first identification of *Crocodylopodus* sp. tracks and swim tracks assigned to *Characichnos* sp. within the basin. In conjunction with the recently identified ornithischian (ornithopod: *Anomoepus*? sp.; *Dinehichnus* sp. and Iguanodontipodidae, Castanera *et al.* 2020; stegosaur: *Deltapodus* sp., Mateus *et al.* 2011) and sauropod (*Brontopodus* sp. and *Parabrontopodus* sp., e.g. Castanera *et al.* 2014) ichnofauna, the identified ichnodiversity is comparable to that of other coeval Late Jurassic areas, as in the western United States (Morrison Formation) and in Asturias, Spain (Vega, Tereñes and Lastres formations) (Lockley *et al.* 2008) and Morocco (Belvedere *et al.* 2010; Belvedere & Mietto 2010; Marty *et al.* 2010). Although the described specimens come from different lithostratigraphical units,

such ichnodiversity provides an outstanding window onto the Late Jurassic ecosystems of the Lusitanian Basin. The Late Jurassic units where the specimens come from can be categorized as those where tracks and bones co-occur but footprints represent a small portion of the available evidence (category 4 of Lockley 1991). Besides, the footprint record would not be consistent with known osteological remains since more taxa than footprint morphotypes have been identified so far although both records show a similar faunal story with theropods showing higher diversity and ichnodiversity than the other groups. This paper also provides further evidence for the identification of the *Megalosauripus transjuranicus*-like/*Jurabrontes*-like ichnoassociation in Late Jurassic deposits, but highlights (once again) the difficulties of identifying small- to medium-sized theropod tracks (whether gallatorid or tracks with *Therangospodus*-like affinities). It also highlights the difficulties in interpreting and identifying so-called swim tracks, especially when it comes to identifying the trackmaker (whether crocodylomorph or pterosaur).

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Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

3D models of the studied specimens from the SHN.

Table S1. List of the studied specimens from the SHN showing their location, formation, lithology, morphological preservation quality (MP), ichnotaxon and figure. LNH = Lourinhã; PEN = Peniche; ALC = Alcobaça; CDR = Caldas da Rainha; MFR = Mafra; TVD- Torres Vedras.

Table S2. Measurements of the parameters in the studied specimens: (FL), footprint length; (FW), footprint width; (FL/FW), footprint length/footprint width ratio; (LI, LII, LIII), digit length; (WI, WII, WIII), digit width; (CLI, CLII, CLIII), claw length; (HA), 'heel' (metatarsophalangeal) area; (I^{II}, II^{III} and III^{IV}), divarication angles; mesaxony (ATw, anterior triangle width; ATI, anterior triangle length; AT, anterior triangle ratio). The * in specimen ICNO.118 denotes that the two width measurements indicate digit trace width and interdigital width.