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Late Jurassic globetrotters compared: A closer look at large and giant theropod tracks of North Africa and Europe

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ABSTRACT

Late Jurassic theropod tracks are very common both in North Africa and Europe. Two recently described ichnotaxa *Megalosauripus transjuranicus* and *Jurabrontes curtedulensis* from the Kimmeridgian of Switzerland show the coexistence of two apex predators in the same palaeoenvironment. Similar tracks can be found in tracksites from the Iberian Peninsula and from Morocco. Here, we further explore the similarities among the Swiss ichnotaxa and the other tracks from Germany (Kimmeridgian), Spain (Tithonian-Berriasian), Portugal (Oxfordian-Tithonian) and Morocco (Kimmeridgian) through novel three-dimensional data comparisons. Specimens were grouped in two morphotypes: 1) large and gracile (30 < Foot Length < 50 cm) and 2) giant and robust (FL > 50 cm). The analyses show a great morphological overlap among these two morphotypes and the Swiss ichnotaxa (*Megalosauripus transjuranicus* and *Jurabrontes curtedulensis*, respectively), even despite the differences in sedimentary environment and age. This suggests a widespread occurrence of similar ichnotaxa along the western margin of Tethys during the Late Jurassic. The new data support the hypothesis of a Gondwana-Laurasia faunal exchange during the Middle or early Late Jurassic, and the presence of migratory routes around the Tethys.

1. Introduction

Late Jurassic dinosaur tracksites are common and offer an abundance of fossils from localities all around the world (Fig. 1). In Europe, Late Jurassic dinosaur tracks are found in Switzerland (e.g., Meyer, 1993; Meyer and Lockley, 1996; Meyer and Thüring, 2003; Marty et al., 2003; Razzolini et al., 2017; Marty et al., 2018), France (Mazin et al., 1997, 2016; 2017; Moreau et al., 2017), Spain (Canudo et al., 2005; Castanera et al., 2013; Alcalá et al., 2014; Cobos et al., 2014; Piñuela, 2015), Portugal (e.g., Lockley et al., 1994a, 1994b; Meyer et al., 1994; Antunes and Mateus, 2003; Santos, 2008; Mateus and Milàn, 2010), Poland (Gierliński and Niedźwiedzki, 2002; Gierliński et al., 2009), Italy (Conti et al., 2005), Croatia (Mezga et al., 2007, 2017), whereas in North Africa the only occurrence of Late Jurassic dinosaur tracks is from Morocco (e.g., Dutuit and Ouazzou, 1980; Ishigaki, 1985b, 1985a; Belvedere, 2008; Boutakiout et al., 2009; Belvedere et al., 2010; Marty et al., 2010; Nouri et al., 2011), probably due to sampling bias.

In some cases, e.g., in Portugal (Mateus et al., 2006; Mateus and Milàn, 2010), Spain (Cobos et al., 2014; Rauhut et al., 2018), Germany (Lallensack et al., 2015) skeletal sites and tracksites are in close geological proximity allowing a more precise trackmaker identification. This should allow to extrapolate the dinosaur faunal composition by

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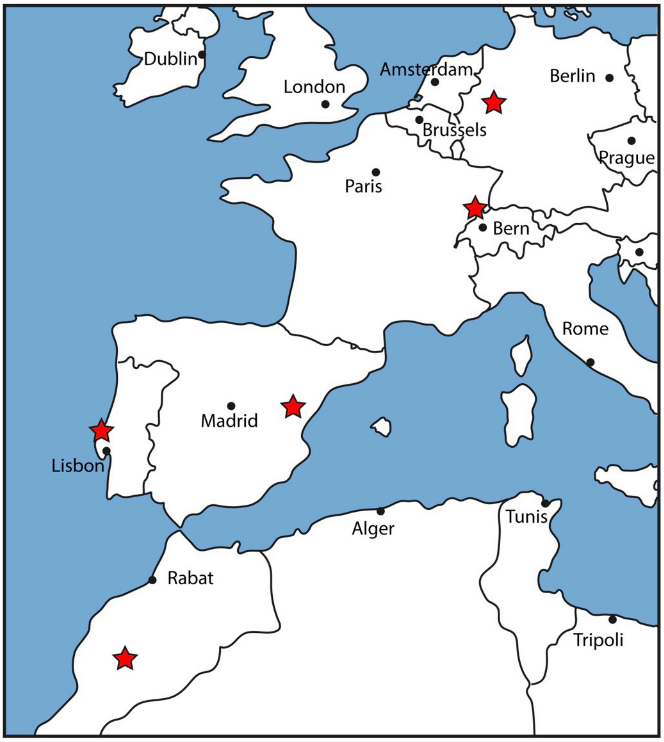

Fig. 1. Location of the Late Jurassic tracksites of this study, indicated by stars.

comparing the tracks. Nonetheless, this correlation is not possible due to the general scarcity of complete feet skeletons in those areas.

Dinosaur footprints have proved to be a valuable tool for palaeoecological analyses and reconstructions of faunal associations (e.g., Lockley, 1986; Belvedere et al., 2013). Despite the uncertainty of trackmaker identification, ichnotaxonomy would be a good tool to pursue these purposes, at least to determine which groups of animals where present in a certain environment. Unfortunately, ichnotaxonomy suffers from the issue of too subjective criteria for erecting new ichnotaxa, often based on too poorly-preserved material, and on the availability of the type material for revisions. A classical controversy is that of the large theropod ichnotaxa *Megalosauripus-Megalosauropus* (Lockley et al., 1996, 2000; Thulborn, 2001), which is based on comparatively specimens with low morphological quality (Marchetti et al., 2019), not good enough for reliable comparisons, rather than on objective morphology-related issues. Recent research has demonstrated the presence of two distinctive large theropod track morphotypes in different areas in Europe during the Late Jurassic (Cobos et al., 2014; Razzolini et al., 2017; Marty et al., 2018; Rauhut et al., 2018). The main differences of these two morphotypes are the robustness, mesaxony and the size (large vs. giant).

Moreover, until very recently (Castanera et al., 2015; Hornung et al., 2016; Lallensack et al., 2016; Belvedere et al., 2018), comparison methods mostly relied on qualitative descriptions of the morphology of the tracks. Here we are using latest comparison methods (Belvedere et al., 2018) to analyse Late Jurassic theropod tracks from different European and North African tracksites, which exhibit a morphological similarity. Our goal was the quantification of similarities and investigating if thresholds can be drawn for comparing these footprints. This approach would allow to draw a more reliable comparison among different tracksites and set a threshold for future quantitative comparisons. Thus, the aim of this paper is trying to understand whether this dichotomy between the two morphotypes 1) giant and robust (FL > 50 cm) and 2) large and gracile (30 < FL < 50 cm, Marty, 2008) persists by analysing tracks from various tracksites from Germany, Switzerland, Spain, Portugal and Morocco (Fig. 1). In most of these tracksites, both these morphotypes are present, with the large and slender being more abundant than the giant and robust tracks. Finally, we also discuss palaeoecological and palaeobiogeographical aspects.

2. Material

The standard for comparisons is type material from the Late Jurassic of the Swiss Jura Mountains, notably the mediotype (Belvedere et al., 2018) of the recently established *Megalosauripus transjuranicus* Razzolini et al., (2017) and *Jurabrontes curtedulensis* Marty et al., (2018) (Fig. 2A and B). Apart from their size, the two ichnotaxa also differ regarding their robustness, mesaxony and FL/FW ratio (Fig. 3). The two ichnotaxa come from the same stratigraphic levels and from several different tracksites located about 6 km to the west of Porrentruy (Ajoie district, Canton Jura, NW Switzerland), which all belong to the Kimmeridgian (Jank et al., 2006a, 2006b; Comment et al., 2011, 2015) Reuchenette Formation (Thalmann, 1966; Gygi, 2000). These tracks have been chosen as reference also because they were rapidly excavated after the discovery and are now stored indoor, not suffering from recent weathering that affects all the other *in situ* tracks.

Other tracks examined in this paper come from different Late Jurassic tracksites from Morocco, Germany and the Iberian Peninsula. All this material is published and we refer to the original papers for detailed descriptions. References and geological data for each track are listed in Supplementary Table 1.

Morocco: The tracksites around Demnat from the Iouaridène Formation are Late Jurassic in age, probably Kimmeridgian (Charriére et al., 2005), and are known since the early eighties (Dutuit and Ouazzou, 1980; Ishigaki, 1985a, 1985b). They have provided a series of new discoveries in the last decade (e.g., Boutakiout et al., 2008, 2009; Belvedere and Mietto, 2010; Belvedere et al., 2010; Marty et al., 2010; Nouri et al., 2011). Large *Megalosauripus*-like and giant theropod tracks have been recorded on this area (Boutakiout et al., 2009; Belvedere et al., 2010), and the most significative specimens were photographed for photogrammetry in 2009. Three key specimens were selected for this study: DEIO CXXVIII/16 and DEIO XLII, as labelled by Belvedere et al. (2010) and 23IGR1.7 as labelled by Boutakiout et al. (2009) and originally-illustrated in Ishigaki (1985b).

Spain: Deposits of the Iberian Range (Maestrazgo basin) have yielded a large amount of dinosaur footprints. The most representative tracksites are located in the middle–upper part of the Villar del Arzobispo Fm (*sensu* Campos-Soto et al., 2017, 2019). Aguilar del Alfambra Fm (*sensu* Aurell et al., 2016; Bádenas et al., 2018) in the Peñagolosa and Galve subbasins. Regardless of the name of the unit, the different authors propose a Tithonian vs. late Tithonian-middle Berriasian age for these deposits. Three footprints have been selected from 2 different tracksites. 1AB-1-7, comes from Ababuj tracksite (Ababuj village, Galve subbasin, Teruel province, Alcalá et al., 2012). 1CB1.4 and 2CA1.1 comes from two different levels (CA–upper level and CB–lower level) of the El Castellar tracksite (El Castellar village, Peñagolosa subbasin, Teruel province, Alcalá et al., 2014). 1CB1.4 is the holotype of *Iberosauripus grandis* (Cobos et al., 2014).

Portugal: The Late Jurassic deposits from the Lusitanian basin have yielded a large amount of tracksites located in different geological formations and localities (Lockley et al., 1992, 1994a, 1994b, 1996, 2000; Lockley and Santos, 1993; Meyer et al., 1994; Antunes and Mateus, 2003; Santos, 2008; Mateus and Milàn, 2010; Castanera et al., 2016, 2017). At Cabo Mondego (Figueira da Foz), tetradactyl footprints were identified in 1884 and this tracksite was the first to be described within the Lusitanian basin (Gomes, 1916). These tracks were attributed to *Eutynichnium lusitanicum* by Nopcsa (1923) but without a proper description. Later, Lockley et al. (2000) redescribed the material and amended *Eutynichnium lusitanicum*. The footprints, preserved as natural casts, that were recovered from the Cabo Mondego tracksite at the end of the XIX century, are now stored at the Museu Nacional de História Natural e da Ciência – Universidade de Lisboa (MNHNUL.ICN1,

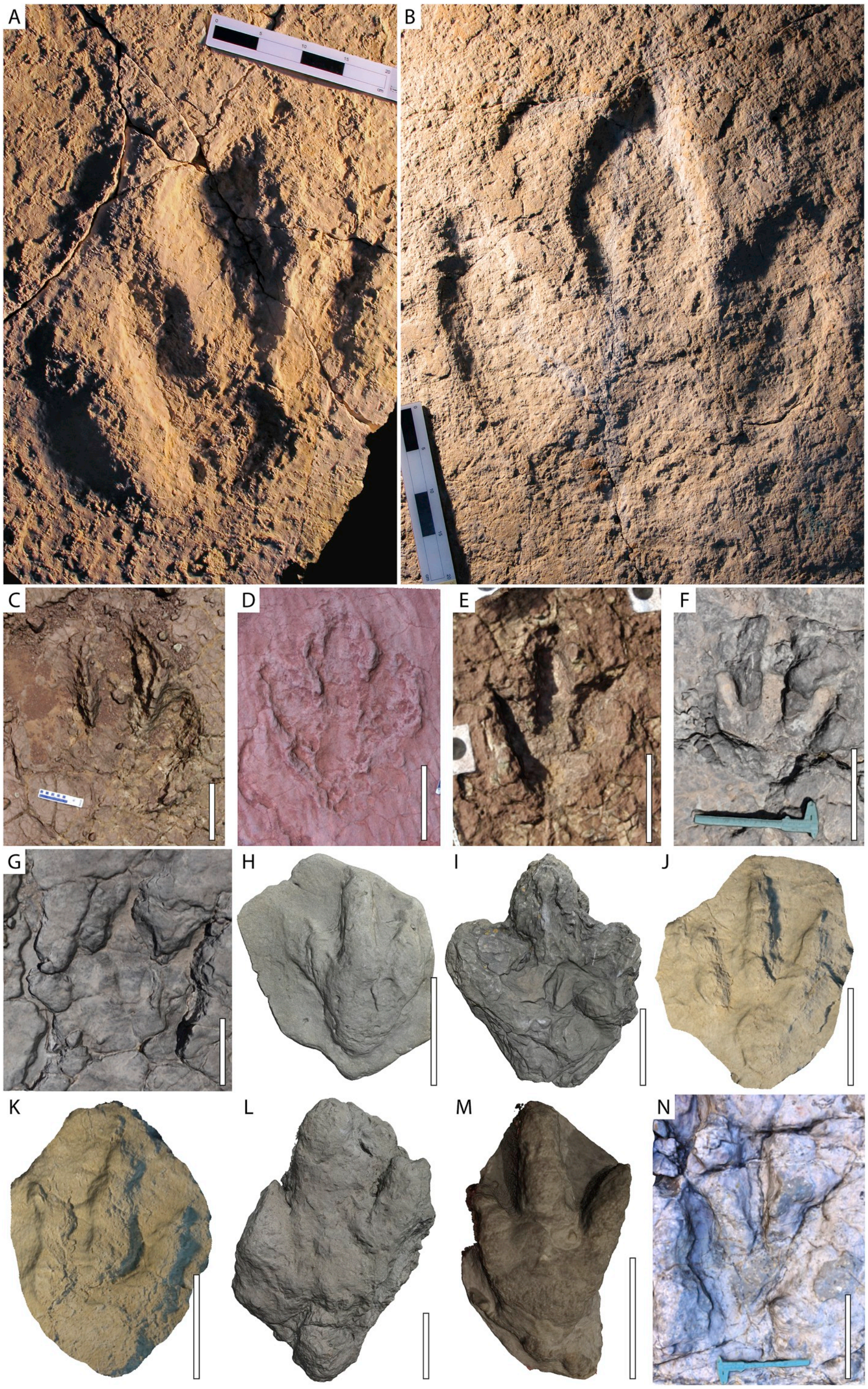

Fig. 2. Photograph of the holotypes of the ichnotaxa used as references for the analyses. **A.** Holotype of *Megalosauripus transjuranicus* (Razzolini et al., 2017). **B.** Holotype of *Jurabrontes transjuranicus* (Marty et al., 2018). **C.** 23IGR1.7 coloured mesh; scale 20 cm. **D.** DEIO XLII coloured mesh; scale 20 cm. **E.** DEIO CXXVIII/16 coloured mesh; scale 20 cm. **F.** 2CA1.1 coloured mesh; scale 20 cm. **G.** 1CB1.4 (*Iberosauripus grandis*) coloured mesh; scale 20 cm. **H.** ML1875 coloured mesh; scale 20 cm. **I.** ML2366 coloured mesh; scale 20 cm. **J.** SHN.(JJS).ICNO.001E coloured mesh; scale 20 cm. **K.** SHN.(JJS).ICNO.001F coloured mesh; scale 20 cm. **L.** ML2035 coloured mesh; scale 20 cm. **M.** MNHNUL.ICN1 (*Eutynichnium lusitanicum*) coloured mesh; scale 20 cm. **N.** 1AB-1-7 coloured mesh; scale 20 cm.

MNHNUL.ICN2, MNHNUL.ICN3, MNHNUL.ICN4 replace the former acronyms MNHN-MG-P261, MNHN-MG-P262, MNHN-MG-P263, and MNHN-MG-P264 respectively, published in Lockley et al., 1996, 2000). The holotype of *E. lusitanicum* (MNHNUL.ICN1) has been selected for the analyses of this study. The Cabo Mondego tracksite belongs to the Cabaços Formation and is Oxfordian in age (Azerêdo et al., 2002, 2010). The overall preservation is suboptimal for a modern erection of a new taxon, but it preserves clearly distinctive morphological features, notably the occurrence of digit I, that allow to preserve its taxonomical status. For a correct comparison, since this is the only tetradactyl analysed ichnotaxon, digit I (the hallux) has been digitally eliminated from the 3D models (and derived images) so that the track appears tridactyl for the comparisons. Three more theropod tracks (gigantic: ML2035, ML2366; large: ML1875) from Porto Dinheiro locality (Lourinhã municipality) and currently stored in the Museu da Lourinhã collection (Mateus and Milàn, 2010) have been included in this study. Both tracks are from the Late Kimmeridgian – Early Tithonian of the Lourinhã Formation.

Finally, we have selected the theropod tracks, SHN.(JJS).ICNO.001F and SHN.(JJS).ICNO.001E housed at the Sociedade de História Natural de Torres Vedras (Castanera et al., 2017). They come from Praia de Porto Barril, near the Assenta village (Mafra municipality), and belong

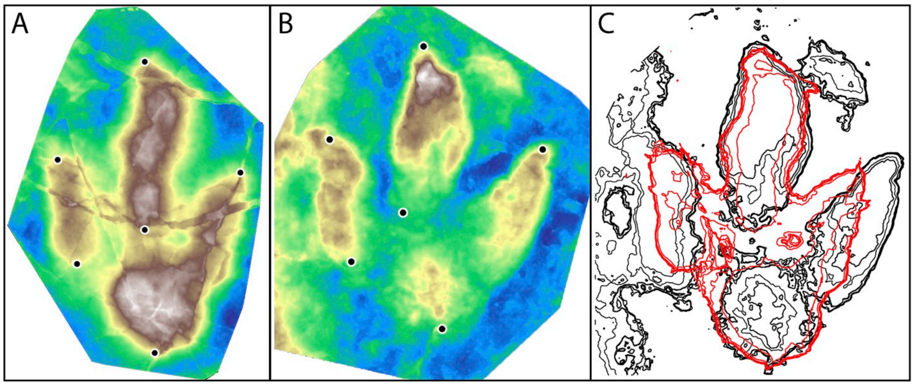

Fig. 3. Comparison between the mediotypes of *M. transjuranicus* and *J. curtedulensis*. **A.** False-colour depth map of *M. transjuranicus* mediotype with indicated the landmarks used for track registration. **B.** False-colour depth map of *J. curtedulensis* mediotype with indicated the landmarks used for track registration. **C.** Registered overlap of *M. transjuranicus* (red) and *J. curtedulensis* (black) mediotypes. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

to the Tithonian Freixial Formation.

Germany: Two main tracksites (Barkhausen and Langenberg quarry) have been described from the Late Jurassic of Germany (Diedrich, 2011; Lallensack et al., 2015). Historically, it is noteworthy that the ichnotaxon *Megalosauripus teutonicus* (Keaver and Lapparent, 1974; Lockley et al., 2000), comes from the Barkhausen tracksite (Bad Essen municipality, Lower Saxony). Despite being a reference trackway, the track is rather poorly-preserved and it is just of grade 1 (*sensu* Belvedere and Farlow, 2016). We do agree with Lallensack et al. (2015) that the resemblance of *M. teutonicus* with *Megalosauripus* as defined in Lockley et al. (2000) is rather poor. This is the reason why we have selected track number 3 from trackway B (here referred to as B.3) as figured and labelled by Diedrich (2011) to be included in the morphological comparisons.

3. Methods

Analyses in this paper are based on classical qualitative comparisons and on more innovative analyses based on three-dimensional models. For the comparison, two groups have been defined, based on robustness, size and mesaxony of the tracks (see Material). Description of tracks are based on standard ichnological terminology (as used, e.g., in Razzolini et al., 2017). The term "heel" is not used in the morphological sense, but it is intended as the posterior end of the track (Leonardi, 1987), while the term mesaxony is used *sensu* Lockley (2009) to indicate digit III protrusion with respect to the medial and lateral digits. Phalangeal pads are numbered from proximal to distal for each digit, thus, e.g., the acronym PIV1 indicates the first (most proximal) pad of digit IV, and PIV3 indicated the third (more distal) pad of digit IV. Synthetic information of the tracks and tracksites used for this analysis, the comparison error table and all models and point clouds used in this project are available for download at doi:10.6084/m9.figshare.7477772, following the guidelines of Falkingham et al. (2018).

3.1. 3D models

3D models are generated through Agisoft PhotoScan Professional (v.1.4.2–1.4.4), following Mallison and Wings (2014) and Matthews et al. (2016) to obtain more accurate models. For this specific project, we have gathered photogrammetric data collected by different people and different cameras in a quite wide time span (e.g., photos of Moroccan tracks were taken in 2009). For the purposes of this work, we considered a scaling error < 0.5 mm as reliable.

3.2. 3D comparisons

3D comparisons have been carried out with the freeware DigTrace (Budka et al., 2016). This software uses the idea of 'whole-track' analysis, introduced by Crompton et al. (2012) and serves as a base for the introduction of mediotypes and stat-tracks (Belvedere et al., 2018), which provide the core sample for this study. Since we want to address the morphological differences among the tracks, the 'Rigid transformation' function was used. It allows a lower degree of shape variation during the registration of landmarks and therefore it highlights shape and size properties, but it doesn't allow to compare tracks of different sizes. therefore, all the tracks were scaled to the same size, assuming for all tracks an arbitrary foot length (from the tip of digit III to the tip of the "heel") of 1 m. In this way, the rigid comparison is provided, and morphological similarities and differences are highlighted. From an ichnotaxonomical point of view, since the size should not be a diagnostic feature (Bertling et al., 2006), having the tracks scaled at the same length removes the size bias.

Six landmarks were used to register the tracks. They were chosen as they are clearly recognizable in all studied tracks, therefore increasing the precision of the registration, and trying to avoid those landmarks that are subjected to a too great variability (e.g., hypeces, Belvedere, 2008; Castanera et al., 2015; Lallensack et al., 2016). Hence the six points chosen are the tips of the digits, the "heel", and the proximal part of pad impressions PII1 and PIII1 (Fig. 3A and B).

DigTrace provides an error as root mean squared distance among all the landmarks, which, given an accurate landmark placing, can be considered as an indicator of the quality of the match between different tracks. Theoretically, the same footprint with perfectly placed landmarks should give an error = 0. At the current stage of the use of this method there are no fixes thresholds dividing different ichnotaxa, but the lower the comparison error, the more similar are the specimens (values of the comparisons are provided in Supplementary Table 2).

4. Results

4.1. Large theropod tracks

As reference tracks we have used the mediotype of *Megalosauripus transjuranicus* (Razzolini et al., 2017), as the ichnotaxon is based on a large number of specimens with very good preservation of morphological quality (Figs. 2A, 3A and 4A and B).

M. transjuranicus vs. Deio CXXVIII/16 (Fig. 4C and D): the two specimens show a good overlap and the same proportions, including the diagnostic large PIV1 impression. Differences are located in the marked dragging of the claw of digit II and on a less pronounced PIV1 pad of the Moroccan track, but the digital pad configuration, the bending of digit III and the overall morphology of the two tracks match very well. The Moroccan tracks were classified as *Megalosauripus* isp. By Belvedere et al. (2010) but can now confidently be assigned to *Megalosauripus* cf. *transjuranicus*.

M. transjuranicus vs. 1AB-1-7 (Fig. 4E and F): the overall morphology of the Ababuj track is coherent with that of *M. transjuranicus* (i.e., asymmetric, with sigmoidal dIII), but the lack of internal details does not allow a clear assignment. Therefore, we suggest interpreting this track as *Megalosauripus* isp.

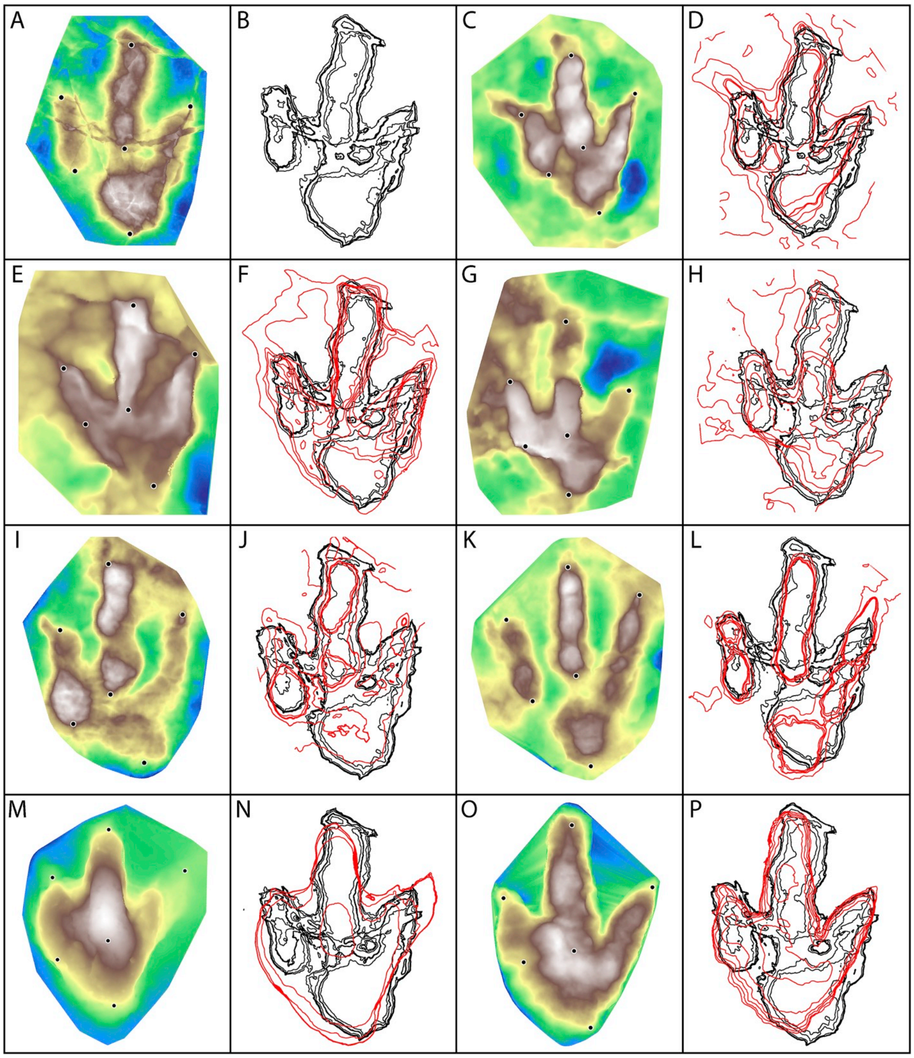

Fig. 4. Depth maps and registration overlap of large theropod tracks. For comparison reasons, all tracks are illustrated as right tracks. Depth gradient goes from dark blue (highest point) to white (deepest point). Normals of the 3D models of tracks preserved as natural cast (positive epirelief) were inverted to make the model appear in negative hyporelief. Black points indicate the landmarks used for registration. *M. transjuranicus* mediotype is outlined in black. **A.** False-colour depth map of the mediotype of *M. transjuranicus*. **B.** Contours of *M. transjuranicus* mediotype as created by DigTrace for registration. **C.** False-colour depth map of DEIOCXXVIII/16. **D.** Registered overlap of DEIOCXXVIII/16 with *M. transjuranicus* mediotype. **E.** False-colour depth map of 1AB-1-7. **F.** Registered overlap of 1AB-1-7 with *M. transjuranicus* mediotype. **G.** False-colour depth map of 2CA1.1. **H.** Registered overlap of 2CA1.1 with *M. transjuranicus* mediotype. **I.** False-colour depth map of SHN.(JJS).ICNO.001F. **J.** Registered overlap of SHN.(JJS).ICNO.001F with *M. transjuranicus* mediotype. **K.** False-colour depth map of SHN.(JJS).ICNO.001E. **L.** Registered overlap of SHN.(JJS).ICNO.001Ewith *M. transjuranicus* mediotype. **M.** False-colour depth map of ML1875. **N.** Registered overlap of ML1875 with *M. transjuranicus* mediotype. **O.** False-colour depth map of *Eutynichnium lusitanicum* (MNHNUL.ICN1). **P.** Registered overlap of *E. lusitanicum* (MNHNUL.ICN1) with *M. transjuranicus* mediotype. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

M. transjuranicus vs. 2CA1.1 (Fig. 4G and H): the track from El Castellar shows an overall similitude with *M. transjuranicus*. It presents a slightly less-developed digital pad PIV1, and a more pronounced notch on the "heel". Despite the lack of internal morphologies, the shape and configuration of the track very much resemble that of Deio CXXXVIII/16 (Fig. 4C and D), and therefore we assign this track to *M.* cf. *transjuranicus*.

M. transjuranicus vs. SHN.(JJS).ICNO.001F (Fig. 4I and J): this track presents strong similarities (asymmetry, sigmoidal dIII, similar pad configuration for dII and dIII, occurrence of a PIV1 larger than other pad impressions) with *M. transjuranicus* and differences are located mostly in the slightly less pronounced PIV1 pad impression and thus a less rounded "heel". Therefore, we assign this track to *M.* cf. *transjuranicus*.

M. transjuranicus vs. SHN.(JJS).ICNO.001E (Fig. 4K and L): like the other track from Praia de Porto Barril described above, this track presents strong similarities with *M. transjuranicus* (asymmetry, sigmoidal dIII, similar 2-3-4 pad configuration, occurrence of a PIV1 larger than other pad impressions). This track is also shallower than the *M. transjuranicus* mediotype or SHN.(JJS).ICNO.001F, and this is reflected in a slightly different morphology. It differs for the straighter digit III impression and for a relatively longer digit IV impression, although a certain degree of toe dragging to explain this shape cannot be excluded. It has a neat PIV1 pad impression and well-defined phalangeal pad and claw marks in all digits. We assign this track to *M.* cf. *transjuranicus*.

M. transjuranicus vs. ML1875 (Fig. 4M and N): this comparison is biased by the preservation of the track. The track outline was quite vague because of the variable depth of the track and the lack of internal details. We decided to place the landmark in the external part of the track, roughly at the same depth. The comparison shows a generic overlap of the two tracks. It is worth noticing that the extension of digit IV is probably driven by the preservation of the track, which records more locomotion-related extramorphologies than if it was preserved as concave epirelief and at the same time prevents accurate landmark placing. Given this, we attribute ML1875 only a *Megalosauripus*-like affinity.

M. transjuranicus vs. *E. lusitanicum* (Fig. 4O and P): this comparison was carried out to verify the *Megalosauripus* affinities inferred for *E. lusitanicum* (Lockley et al., 1996, 2000; Thulborn, 2001). Contra Thulborn (2001) we agree that *E. lusitanicum* is distinct from *Megalosauripus* as it is a clearly tetradactyl ichnotaxon. This analysis, however, highlighted that excluding digit I from the analysis, the two ichnotaxa have a very similar outline and, as for the previous tracks, without the occurrence of the diagnostic anteriorly-oriented digit I impression the specimen could be classified as a *Megalosauripus*-like track.

4.2. Giant theropod tracks

For the same reason as above, we have used the mediotype of *Jurabrontes curtedulensis* (Marty et al., 2018), as reference material for the giant theropod tracks (Figs. 2B, 3B and 5A and B).

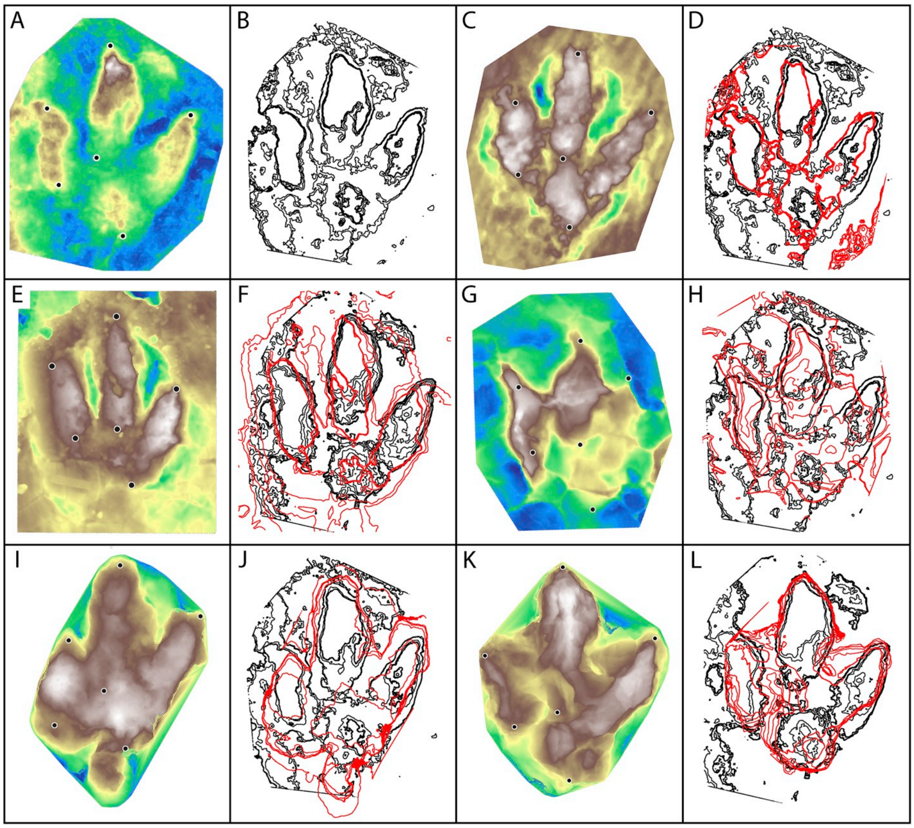

Fig. 5. Depth maps and registration overlap of giant theropod tracks. All tracks are illustrated as right tracks. Depth gradient goes from dark blue (highest point) to white (deepest point). Normals of the 3D models of tracks preserved as natural cast (positive epirelief) were inverted thus to make the model a negative hyporeliefs. Black points indicate the landmarks used for registration. *J. curtedulensis* mediotype is outlined in black. **A.** False-colour depth map of the mediotype of *J. curtedulensis*. **B.** Contours of *J. curtedulensis* mediotype as created by DigTrace for registration. **C.** False-colour depth map of DEIO XLII. **D.** Registered overlap of DEIO XLII with *J. curtedulensis* mediotype. **E.** False-colour depth map of 23IGR1.7. **F.** Registered overlap of 23IGR1.7 with *J. curtedulensis* mediotype. **G.** False-colour depth map of the holotype of *Iberosauripus grandis* (1CB1.4). **H.** Registered overlap of *I. grandis* (1CB1.4) with *J. curtedulensis* mediotype. **I.** False-colour depth map of ML2035. **J.** Registered overlap of ML2035 with *J. curtedulensis* mediotype. **K.** False-colour depth map of ML2366. **L.** Registered overlap of ML2366 with *J. curtedulensis* mediotype. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

J. curtedulensis vs. Deio XLII (Fig. 5C and D): the two specimens show a very high overlap, with the only differences located in the width of the digits (broader in the Swiss specimen). The Moroccan specimen shows most of the diagnostic features of *J. curtedulensis* (broad and massive digits with a blunt aspect, sub-triangular, pointed claw marks present on the tips of all three, slightly asymmetric interdigital divarication angles, small anterior triangle and weak mesaxony, isolated position of the impression of PIII). The slightly detached and internally shifted PIII1 pad impression defining *J. curtedulensis* is also present, although this feature is less-marked in DEIOXLII. For these reasons we assign the specimen to *Jurabrontes* cf. *curtedulensis*.

J. curtedulensis vs. 23IGR1.7 (Fig. 5E and F): the rather poor preservation of this track, despite being from the same formation as the previous, does not allow a very detailed comparison. The overlap shows very similar proportions in the digits but the lack of internal details prevents any classification more detailed than *Jurabrontes* isp.

J. curtedulensis vs. *I. grandis* (Fig. 5G and H): the comparison with *Iberosauripus grandis* is important as it may define the occurrence, in different palaeoenvironments, of two main types of apex predators in the Late Jurassic. Despite having similar size, the outlines of the two ichnotaxa do not match, with the two tracks having different digits proportions (especially dIII, shorter in *Iberosauripus* than in *Jurabrontes*); the differences could be related to the different preservation and weathering, but at the current stage of research we believe that *Jurabrontes* and *Iberosauripus* should be considered as two separate ichnogenera.

J. curtedulensis vs. ML2035 (Fig. 5I and J): the comparison with this huge theropod track shows very few similarities, i.e., in the length and width of digit III. This is due to the poorer quality of the Portuguese track, but also of the preservation that, as for ML1875, due to the less defined track margins, doesn't allow the proper placing of landmarks. Notably, the angle between digit II and III is extremely narrow, and, while this can be due to morphological features, it is more probable that it is the result of the locomotion influence. Also, the “heel” of ML2035 is elongated presenting a possible impression of the distal metatarsus. For these reasons, we cannot find any taxonomical correlation with ML2035.

J. curtedulensis vs. ML2366 (Fig. 5K and L): the two tracks show a good overall overlap, and also the impressions of digit II and IV coincide fairly well. The poorer morphological quality compared to the Swiss specimen, especially the lack of the diagnostic pad configurations, bias an accurate taxonomical attribution, but we are inclined to assign this large theropod track to *Jurabrontes* isp.

4.3. The *Megalosauripus teutonicus* case

If selected on the basis of size and robustness, *Megalosauripus teutonicus* had to be compared with the larger *Jurabrontes* specimen. However, since the German ichnotaxon supposedly is a sister taxon of *M. transjuranicus*, it was compared with both of the Swiss reference taxa (Fig. 6).

The comparison with *M. transjuranicus* clearly shows the difference in width and robustness of the tracks, with *M. transjuranicus* being slenderer and more gracile than the *M. teutonicus*. The comparison with *Jurabrontes*, however, shows a very good overall overlap of the outlines of the two ichnotaxa, although *M. teutonicus* shows a shorter dIV length and a less asymmetric and more linear shape of the “heel”. However, apart from this overall resemblance, no diagnostic features can be found due to the poor morphological quality of the German specimen.

It is outside the purposes of this study to review the taxonomical position of *M. teutonicus*, despite the long-lasting controversy on *Megalosauripus*-like tracks, but, because of the poor quality of the type material, and the lack of clear diagnostic features, we suggest that *Megalosauripus teutonicus* should be considered as a *nomen dubium*, if not a *nomen nudum*.

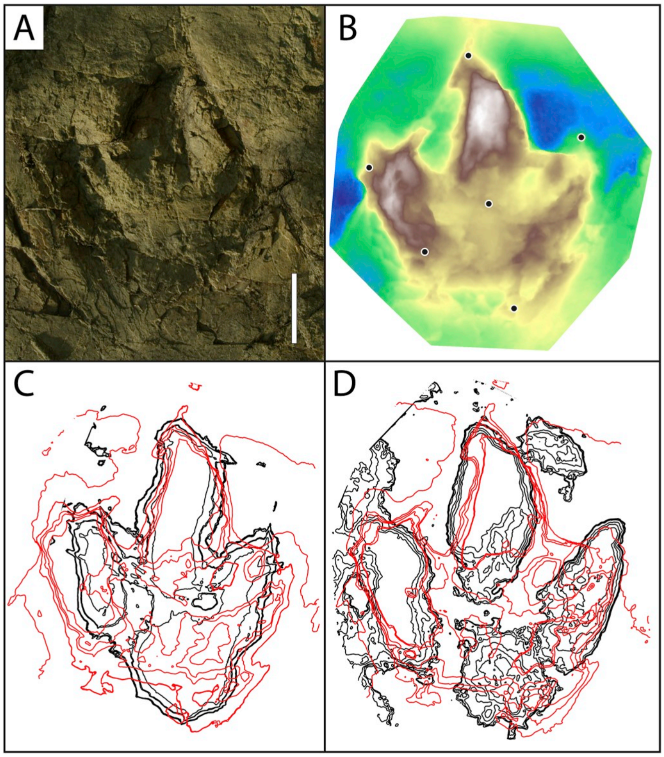

Fig. 6. *M. teutonicus* comparisons with *M. transjuranicus* and *J. curtedulensis*. **A.** coloured mesh; scale 20 cm. **B.** False-colour depth map of *M. teutonicus* (track B.3) **C.** Registered overlap of *M. teutonicus* (red) with *M. transjuranicus* mediotype (black). **D.** Registered overlap of *M. teutonicus* (red) with *J. curtedulensis* mediotype (black). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

5. Discussion

The analysed tracks perfectly exhibit the two categories of theropod tracks as described from the Late Jurassic of Spain by Cobos et al. (2014) (but see also Rauhut et al., 2018). They are mainly distinguished on the basis of their robustness/gracility and the low/high mesaxony plus size (giant/large).

It is worth noticing that both morphotypes are found in carbonate tidal flat environments as well as in siliciclastic alluvial plains and transitional environments, and that morphology and morphological quality of the footprints are related more to rheological features of the substrate than to the mineralogical/sedimentological composition of the substrate, although recent weathering can influence carbonate and siliciclastic rocks and tracks preserved within in different ways.

All samples used show a great degree of similarity with the ichnotaxa they are compared to *(M. transjuranicus* and *J. curtedulensis*), much higher than when determined from the qualitative morphological analysis alone. The similarities are significant among all the tracks, especially those with a higher preservation grade/morphological quality, that is the morphology of the pes is very similar in all the cases.

Deciphering whether the tracks are similar because they were made by similar trackmakers (same genus, or family) or because of the conservative form of the theropod pes (Farlow et al., 2000) is beyond the purpose of this paper and would need a much larger sample. However, as discussed in Razzolini et al. (2017) and Marty et al. (2018), the morphological differences (dIII extension, digit shape, interdigital angles, pad impression configuration) between *M. transjuranicus* and *J. curtedulensis* are such that we strongly support the first hypothesis.

It is also worth noticing the morphological similarities between *Megalosauripus transjuranicus* and *Eutynichnium lusitanicum*, when the digit I impression is not considered. Although not an ichnotaxonomically correct approach, the exclusion of dI from the whole-track analysis has highlighted the similarities between *Megalosauripus* and *Eutynichnium*. This overlapping in the track morphology is important when it comes to trackmaker identification, as *E. lusitanicum* possesses more data (four digits) for the comparison of the tracks with the pedal skeletal remains of coeval theropods. In fact, an almost complete theropod pes with a prominent digit I have recently been described in the Freixial Fm (Malafaia et al., 2018).

The presence of two morphotypes in areas located in considerable distance from each other and preserved in different palaeoenvironments indicate high adaptation capabilities in both types of trackmakers. Both the large and giant morphotypes have been distinguished in the same area, in the same geological interval (e.g.: Switzerland, Spain and Morocco), and even on single track levels/palaeosurface (e.g.: Switzerland).

Trackmaker identification is difficult, especially for the large tridactyl tracks (i.e., those similar to *Megalosauripus transjuranicus*), as several theropod groups such as “allosaurids, metriocanthosaurids or afrovenatorine megalosaurids, or even exceptionally large ceratosaurs” (see Rauhut et al., 2018 and references therein) are possible candidates. Other possible trackmakers could be other allosauroids such as carcharodontosaurid theropods, as this group has been recently described from skeletal remains from the same formation/locality of some of the Portuguese tracks (Malafaia et al., 2018).

Identification of the producer of the giant tracks is not easier, but the extremely large size somehow narrows the possibilities to the largest Late Jurassic theropods known, as suggested in Marty et al. (2018). Candidates could be an allosaurid theropod of the size of *Saurophaganax* (Chure, 1995), an exceptionally large *Allosaurus*, or a large megalosaurid theropod such as *Torvosaurus* (Galton and Jensen, 1979; Mateus et al., 2006). The potential trackmaker for the giant tracks in the Late Jurassic of Portugal is *Torvosaurus gurneyi* Hendrickx and Mateus (2014), taking in consideration the morphology and synchronous and coeval occurrences of bones and tracks in the Lusitanian basin (Hendrickx and Mateus, 2014; Malafaia et al., 2017).

The occurrence of these two morphotypes, but especially of the *Jurabrontes*-like, during the Kimmeridgian–Tithonian both in Gondwana and Laurasia implies a faunal exchange during the early Late Jurassic. Canudo et al. (2009) concludes that an Early Cretaceous faunal interchange between Africa and Europe through an Iberian corridor was improbable before the Barremian-Aptian. In the Late Jurassic, the southern margin of Iberia and the Northern of Africa were already separated by a deep sea as indicated by oceanic floor (Olóriz, 2002) and by pelagic sediments in the Betic Cordillera (Olóriz et al., 2002). Although short time emergence of parts of this area due to eustatic sea level changes cannot be ruled out, the complete formation of a land bridge between Iberia and northern Africa in the Late Jurassic seems unlikely. Similarities in the ichnofauna could be explained by the conservative shape of theropod tracks (Farlow, 2001), although in our case the match among the Moroccan giant track and the Swiss *Jurabrontes* is surprisingly high, although preservation differences prevent to assign them to the same ichnotaxon. The presence of two different large to giant theropods in the Late Jurassic advanced by Rauhut et al. (2018) and supported by our analyses, suggests that at least two different related groups might have inhabited Europe and North Africa, alongside with other regional (ichno)taxa.

Therefore, alternative dispersal routes for the interval between late Middle to early Late Jurassic have to be considered. One path could go through North America into western Europe and might explain the faunal similarities noticed by Mateus et al. (2006); the other could lead through the carbonate platforms of Northern Africa, southern Italy and the Balkans. Late Jurassic tracks sites are rare in those areas (Conti et al., 2005; Citton et al., 2015), but they support a connection between the Panormide carbonate Platform and the African continent in the Late Jurassic-Early Cretaceous period (Zarcone et al., 2010). A migration route through Northern Africa and Asia could also be considered as, at least, *Megalosauripus* (i.e., *Megalosauripus uzbekistanikus*) has been often found in Asian Late Jurassic tracksite (e.g., Lockley et al., 2000; Fanti et al., 2013). Further research and new data are however needed to test these hypotheses.

6. Conclusions

- *Megalosauripus transjuranicus* and *Jurabrontes curtedulensis* are different ichnotaxa with differences that go beyond the intra-taxonomical variation.
- Similarities between M. *transjuranicus* and *E. lusitanicum* support the attribution of the two taxa to the same ichnofamily (Eubrontidae, Lull, 1904). Morphological details are, however, enough to keep the two ichnotaxa separate.
- Identification of *Jurabrontes* cf. *curtedulensis* and *Megalosauripus* cf. *transjuranicus* in the Kimmeridgian siliciclastic Iouaridène Formation (Morocco).
- First identification of *M.* cf. *transjuranicus* in the Freixial Formation (Portugal), and co-occurrence of *Jurabrontes* isp. and *Megalosauripus*-like tracks in the Lourinhã Formation (Portugal). Occurrence of *I. grandis* and *M.* cf. *transjuranicus* in two different levels of the El Castellar tracksite (Spain).
- *J. curtedulensis* and *Iberosauripus grandis* are considered as two different ichnotaxa. This implies the occurrence of different types of apex predators.
- *Megalosauripus teutonicus* should be considered as a *nomen dubium* (or even *nudum*) due to the poor quality of the holotype material. Our comparison shows more morphological similarities with the ichnogenus *Jurabrontes* rather than with *Megalosauripus*, although there is a bias due to the poor preservation of *M. teutonicus.*
- Occurrence of similar tracks in different palaeenvironments demonstrate a high adaptability of Late Jurassic apex predators.
- Occurrence of *Jurabrontes* isp. and *Megalosauripus* cf. *transjuranicus* in Morocco, and of *M.* cf. *transjuranicus* and giant theropod tracks similar to *Jurabrontes* in the Iberian Peninsula, suggest the existence of faunal exchange routes between Gondwana and Laurasia through North Africa and/or North America and/or Asia between the Middle to early Late Jurassic.
- Comparing tracks preserved as epireliefs and hyporeliefs is feasible but they often preserve different morphological features in different ways, with the natural casts exhibiting more extramorphological features, e.g. due to locomotion. Therefore, such comparisons have to be made with care using all the available material: physical and digital, bi- and tridimensional.
- The potential trackmaker for the giant robust tracks in the Late Jurassic of Portugal is *Torvosaurus gurneyi*, taking into consideration the morphology, synchronous and coeval occurrences of bones and tracks in the area. The trackmaker of the other giant and even more of the large gracile tracks is more complex to define, and will need more ichnological and osteological data.

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Appendix A. Supplementary data

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