

1 **Late Jurassic globetrotters compared: a closer look at large and giant theropod tracks of North**
2 **Africa and Europe**

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27 **Abstract**

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

42

43 **Keywords:** vertebrate tracks, digital ichnology, Late Jurassic, theropod, ichnotaxonomy,
44 palaeobiogeography

45

46 **Highlights**

- 47 • Digital ichnology allowed 3D comparison of tracks from different tracksites and
48 palaeoenvironments

49 • Analyses shows that there were two types of apex predators in those palaeoenvironments

50 • Ichnotaxonomical reviews will profit of digital ichnology

51 • Faunal exchanges between Gondwana and Laurasia are likely, but routes are not evident

52

53 **1 Introduction**

54

55 Late Jurassic dinosaur tracksites are common and offer an abundance of fossils from localities all
56 around the world (Fig. 1). In Europe, Late Jurassic theropod tracks are found in Switzerland (e.g.,
57 Meyer, 1993; Meyer and Lockley, 1996; Meyer and Thüring, 2003; Marty et al., 2003; Razzolini et
58 al., 2017; Marty et al., 2018), France (Mazin et al., 1997, 2016, 2017; Moreau et al., 2017), Spain
59 (Canudo et al., 2005; Castanera et al., 2013; Alcalá et al., 2014; Cobos et al., 2014; Piñuela, 2015),
60 Portugal (e.g., Lockley et al., 1994a, 1994b; Meyer et al., 1994; Antunes and Mateus, 2003; Santos,
61 2008; Mateus and Milàn, 2010), Poland (Gierliński and Niedźwiedzki, 2002; Gierliński et al., 2009),
62 Italy (Conti et al., 2005), Croatia (Mezga et al., 2007, 2017), whereas in North Africa the only
63 occurrence of Late Jurassic dinosaur tracks is from Morocco (e.g., Dutuit and Ouazzou, 1980;
64 Ishigaki, 1985b, 1985a; Belvedere, 2008; Boutakiout et al., 2009; Belvedere et al., 2010; Marty et al.,
65 2010; Nouri et al., 2011), probably due to sampling bias.

66 In some cases, e.g., in Portugal (Mateus et al., 2006; Mateus and Milàn, 2010), Spain (Cobos et al.,
67 2014; Rauhut et al., 2018), Germany (Lallensack et al., 2015) skeletal sites and tracksites are in close
68 geological proximity allowing a more precise trackmaker identification. This should allow to
69 extrapolate the dinosaur faunal composition by comparing the tracks. Nonetheless, this correlation
70 is not possible due to the general scarcity of complete feet skeletons in those areas.

71 Dinosaur footprints have proved to be a valuable tool for palaeoecological analyses and
72 reconstructions of faunal associations (e.g., Lockley, 1986; Belvedere et al., 2013). Despite the
73 uncertainty of trackmaker identification, ichnotaxonomy would be a good tool to pursue these
74 purposes, at least to determine which groups of animals were present in a certain environment.
75 Unfortunately, ichnotaxonomy suffers from the issue of too subjective criteria for erecting new
76 ichnotaxa, often based on too poorly-preserved material, and on the availability of the type material

77 for revisions. A classical controversy is that of the large theropod ichnotaxa *Megalosauripus-*
78 *Megalosauropus* (Lockley et al., 1996, 2000; Thulborn, 2001), which is based on comparatively
79 specimens with low morphological quality (Marchetti et al., 2019), not good enough for reliable
80 comparisons, rather than on objective morphology-related issues. Recent research has
81 demonstrated the presence of two distinctive large theropod track morphotypes in different areas
82 in Europe during the Late Jurassic (Cobos et al., 2014; Razzolini et al., 2017; Marty et al., 2018;
83 Rauhut et al., 2018). The main differences of these two morphotypes are the robustness, mesaxony
84 and the size (large vs. giant).

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

98

99 **2 Material**

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

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

114 *Morocco*: The tracksites around Demnat from the Iouaridène Formation are Late Jurassic in age,
115 probably Kimmeridgian (Charrière et al., 2005), and are known since the early eighties (Dutuit and
116 Ouazzou, 1980; Ishigaki, 1985a, 1985b). They have provided a series of new discoveries in the last
117 decade (e.g., Boutakiout et al., 2008, 2009; Belvedere and Mietto, 2010; Belvedere et al., 2010;
118 Marty et al., 2010; Nouri et al., 2011). Large *Megalosauripus*-like and giant theropod tracks have
119 been recorded on this area (Boutakiout et al., 2009; Belvedere et al., 2010), and the most
120 significant specimens were photographed for photogrammetry in 2009. Three key specimens were
121 selected for this study: DEIO CXXVIII/16 and DEIO XLII, as labelled by Belvedere et al. (2010) and
122 23IGR1.7 as labelled by Boutakiout et al. (2009) and originally-illustrated in Ishigaki (1985b).

123 *Spain*: Deposits of the Iberian Range (Maestrazgo basin) have yielded a large amount of dinosaur
124 footprints. The most representative tracksites are located in the middle–upper part of the Villar del
125 Arzobispo Fm. (*sensu* Campos-Soto et al., 2017; 2019) / Aguilar del Alfambra Fm (*sensu* Aurell et al.
126 2016; Bádenas et al., 2018) in the Peñagolosa and Galve subbasins. Regardless of the name of the
127 unit, the different authors propose a Tithonian vs. late Tithonian-middle Berriasian age for these
128 deposits. Three footprints have been selected from 2 different tracksites. 1AB-1-7, comes from
129 Ababuj tracksite (Ababuj village, Galve subbasin, Teruel province, Alcalá et al., 2012). 1CB1.4 and
130 2CA1.1 comes from two different levels (CA–upper level and CB–lower level) of the El Castellar
131 tracksite (El Castellar village, Peñagolosa subbasin, Teruel province, Alcalá et al., 2014). 1CB1.4 is the
132 holotype of *Iberosauripus grandis* (Cobos et al., 2014).

133 *Portugal*: The Late Jurassic deposits from the Lusitanian basin have yielded a large amount of
134 tracksites located in different geological formations and localities (Lockley et al., 1992, 1994a,
135 1994b, 1996, 2000; Lockley and Santos, 1993; Meyer et al., 1994; Antunes and Mateus, 2003; Santos,
136 2008; Mateus and Milàn, 2010; Castanera et al. 2016, 2017). At Cabo Mondego (Figueira da Foz),
137 tetradactyl footprints were identified in 1884 and this tracksite was the first to be described within
138 the Lusitanian basin (Gomes, 1916). These tracks were attributed to *Eutynichnium lusitanicum* by
139 Nopcsa (1923) but without a proper description. Later, Lockley et al. (2000) redescribed the material
140 and amended *Eutynichnium lusitanicum*. The footprints, preserved as natural casts, that were
141 recovered from the Cabo Mondego tracksite at the end of the XIX century, are now stored at the
142 Museu Nacional de História Natural e da Ciência – Universidade de Lisboa (MNHNUL.ICN1,
143 MNHNUL.ICN2, MNHNUL.ICN3, MNHNUL.ICN4 replace the former acronyms MNHN-MG-P261,
144 MNHN-MG-P262, MNHN-MG-P263, and MNHN-MG-P264 respectively, published in Lockley et al.,
145 1996, 2000). The holotype of *E. lusitanicum* (MNHNUL.ICN1) has been selected for the analyses of
146 this study. The Cabo Mondego tracksite belongs to the Cabaços Formation and is Oxfordian in age

147 (Azerêdo et al., 2002, 2010). The overall preservation is suboptimal for a modern erection of a new
148 taxon, but it preserves clearly distinctive morphological features, notably the occurrence of digit I,
149 that allow to preserve its taxonomical status. For a correct comparison, since this is the only
150 tetradactyl ichnotaxon, digit I (the hallux) has been digitally eliminated from the 3D models (and
151 derived images) so that the track appears tridactyl for the comparisons. Three more theropod tracks
152 (gigantic: ML2035, ML2366; large: ML454) from Porto Dinheiro locality (Lourinhã municipality) and
153 currently stored in the Museu da Lourinhã collection (Mateus and Milàn, 2010) have been included
154 in this study. Both tracks are from the Late Kimmeridgian – Early Tithonian of the Lourinhã
155 Formation.

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

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

169

170 **3 Methods**

171 Analyses in this paper are based on classical qualitative comparisons and on more innovative
172 analyses based on three-dimensional models. For the comparison, two groups have been defined,
173 based on robustness, size and mesaxony of the tracks (see Material). Description of tracks are based
174 on standard ichnological terminology (as used, e.g., in Razzolini et al., 2017). The term “heel” is not
175 used in the morphological sense, but it is intended as the posterior end of the track (Leonardi, 1987),
176 while the term mesaxony is used *sensu* Lockley (2009) to indicate digit III protrusion with respect to
177 the medial and lateral digits. Phalangeal pads are numbered from proximal to distal for each digit,
178 thus, e.g., the acronym PIV1 indicates the first (most proximal) pad of digit IV, and PIV3 indicated
179 the third (more distal) pad of digit IV. Synthetic information of the tracks and tracksites used for this
180 analysis, the comparison error table and all models and point clouds used in this project are available
181 for download at <https://figshare.com/s/6b0ec7c4dd8d0ffbdcce> (10.6084/m9.figshare.7477772),
182 following the guidelines of Falkingham et al. (2018).

183

184 **3.1 3D models**

185 3D models are generated through Agisoft PhotoScan Professional (v.1.4.2 – 1.4.4), following
186 Mallison and Wings (2014) and Matthews et al. (2016) to obtain more accurate models. For this
187 specific project, we have gathered photogrammetric data collected by different people and different
188 cameras in a quite wide time span (e.g., photos of Moroccan tracks were taken in 2009). For the
189 purposes of this work, we considered a scaling error < 0.5 mm as reliable.

190 **3.2 3D comparisons**

191 3D comparisons have been carried out with the freeware DigTrace (Budka et al., 2016). This software
192 uses the idea of ‘whole-track’ analysis, introduced by Crompton et al. (2012) and serves as a base
193 for the introduction of mediotypes and stat-tracks (Belvedere et al., 2018), which provide the core
194 sample for this study. Since we want to address the morphological differences among the tracks,

195 the 'Rigid transformation' function was used. It allows a lower degree of shape variation during the
196 registration of landmarks and therefore it highlights shape and size properties, but it doesn't allow
197 to compare tracks of different sizes. therefore, all the tracks were scaled to the same size, assuming
198 for all tracks an arbitrary foot length (from the tip of digit III to the tip of the "heel") of 1 m. In this
199 way, the rigid comparison is provided, and morphological similarities and differences are
200 highlighted. From an ichnotaxonomical point of view, since the size should not be a diagnostic
201 feature (Bertling et al., 2006), having the tracks scaled at the same length removes the size bias.
202 Six landmarks were used to register the tracks. They were chosen as they are clearly recognizable in
203 all studied tracks, therefore increasing the precision of the registration, and trying to avoid those
204 landmarks that are subjected to a too great variability (e.g., hypoces, Belvedere, 2008; Castanera et
205 al., 2015; Lallensack et al., 2016). Hence the six points chosen are the tips of the digits, the "heel",
206 and the proximal part of pad impressions PII1 and PIII1 (Fig. 3A and B).
207 DigTrace provides an error as root mean squared distance among all the landmarks, which, given an
208 accurate landmark placing, can be considered as an indicator of the quality of the match between
209 different tracks. Theoretically, the same footprint with perfectly placed landmarks should give an
210 error = 0. At the current stage of the use of this method there are no fixes thresholds dividing
211 different ichnotaxa, but the lower the comparison error, the more similar are the specimens (values
212 of the comparisons are provided in Supplementary Table 2).

213

214 **4 Results**

215 **4.1 Large theropod tracks**

216 As reference tracks we have used the mediotype of *Megalosauripus transjuranicus* (Razzolini et al.,
217 2017), as the ichnotaxon is based on a large number of specimens with very good preservation of
218 morphological quality (Figs. 2A, 3A, 4A and B).

219 *M. transjuranicus* vs. Deio CXXVIII/16 (Fig. 4C and D): the two specimens show a good overlap and
220 the same proportions, including the diagnostic large PIV1 impression. Differences are located in the
221 marked dragging of the claw of digit II and on a less pronounced PIV1 pad of the Moroccan track,
222 but the digital pad configuration, the bending of digit III and the overall morphology of the two tracks
223 match very well. The Moroccan tracks were classified as *Megalosauripus* isp. By Belvedere et al.
224 (2010) but can now confidently be assigned to *Megalosauripus* cf. *transjuranicus*.

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

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

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

239 *M. transjuranicus* vs. SHN.(JJS).ICNO.001E (Fig. 4K and L): like the other track from Praia de Porto
240 Barril described above, this track presents strong similarities with *M. transjuranicus* (asymmetry,
241 sigmoidal dIII, similar 2-3-4 pad configuration, occurrence of a PIV1 larger than other pad
242 impressions). This track is also shallower than the *M. transjuranicus* mediotype or

243 SHN.(JJS).ICNO.001F, and this is reflected in a slightly different morphology. It differs for the
244 straighter digit III impression and for a relatively longer digit IV impression, although a certain degree
245 of toe dragging to explain this shape cannot be excluded. It has a neat PIV1 pad impression and well-
246 defined phalangeal pad and claw marks in all digits. We assign this track to *M. cf. transjuranicus*.

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

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

262

263 **4.2 Giant theropod tracks**

264 For the same reason as above, we have used the mediotype of *Jurabrontes curtedulensis* (Marty et
265 al., 2017), as reference material for the giant theropod tracks (Figs. 2B, 3B, 5A and B).

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

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

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

285 *J. curtedulensis* vs. ML2035 (Fig. 5I and J): the comparison with this huge theropod track shows very
286 few similarities, i.e., in the length and width of digit III. This is due to the poorer quality of the
287 Portuguese track, but also of the preservation that, as for ML1875, due to the less defined track
288 margins, doesn't allow the proper placing of landmarks. Notably, the angle between digit II and III is
289 extremely narrow, and, while this can be due to morphological features, it is more probable that it

290 is the result of the locomotion influence. Also, the “heel” of ML2035 is elongated presenting a
291 possible impression of the distal metatarsus. For these reasons, we cannot find any taxonomical
292 correlation with ML2035.

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

297 **4.3 The *Megalosauripus teutonicus* case**

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

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

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

311

312 **5. Discussion**

313

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

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

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

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

334 It is also worth noticing the morphological similarities between *Megalosauripus transjuranicus* and
335 *Eutynichnium lusitanicum*, when the digit I impression is not considered. Although not an
336 ichnotaxonomically correct approach, the exclusion of dI from the whole-track analysis has
337 highlighted the similarities between *Megalosauripus* and *Eutynichnium*. This overlapping in the track

338 morphology is important when it comes to trackmaker identification, as *E. lusitanicum* possesses
339 more data (four digits) for the comparison of the tracks with the pedal skeletal remains of coeval
340 theropods. In fact, an almost complete theropod pes with a prominent digit I have recently been
341 described in the Freixial Fm. (Malafaia et al., 2018) showing a good develop of digit I.

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

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

354 Identification of the producer of the giant tracks is not easier, but the extremely large size somehow
355 narrows the possibilities to the largest Late Jurassic theropods known, as suggested in Marty et al.
356 (2018). Candidates could be an allosaurid theropod of the size of *Saurophaganax* (Chure, 1995), an
357 exceptionally large *Allosaurus*, or a large megalosaurid theropod such as *Torvosaurus* (Galton and
358 Jensen, 1979; Mateus et al., 2006). The potential trackmaker for the giant tracks in the Late Jurassic
359 of Portugal is *Torvosaurus gurneyi* Hendrickx and Mateus, 2014, taking in consideration the
360 morphology and synchronous and coeval occurrences of bones and tracks in the Lusitanian basin
361 (Hendrickx and Mateus, 2014; Malafaia et al., 2017).

362

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

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

386 in Asian Late Jurassic tracksite (e.g., Lockley et al. 2000, Fanti et al., 2013). Further research and new
387 data are however needed to test these hypotheses.

388

389 **6. Conclusions**

390 • *Megalosauripus transjuranicus* and *Jurabrontes curtedulensis* are different ichnotaxa with
391 differences that go beyond the intra-taxonomical variation.

392 • Similarities between *M. transjuranicus* and *E. lusitanicum* support the attribution of the two taxa
393 to the same ichnofamily (Eubrontidae, Lull, 1904). Morphological details are, however, enough
394 to keep the two ichnotaxa separate.

395 • Identification of *Jurabrontes* cf. *curtedulensis* and *Megalosauripus* cf. *transjuranicus* in the
396 Kimmeridgian siliciclastic Iouaridène Formation (Morocco).

397 • First identification of *M.* cf. *transjuranicus* in the Freixial Formation (Portugal), and co-
398 occurrence of *Jurabrontes* isp. and *Megalosauripus*-like tracks in the Lourinhã Formation
399 (Portugal). Occurrence of *I. grandis* and *M.* cf. *transjuranicus* in two different levels of the El
400 Castellar tracksite (Spain).

401 • *J. curtedulensis* and *Iberosauripus grandis* are considered as two different ichnotaxa. This implies
402 the occurrence of different types of apex predators.

403 • *Megalosauripus teutonicus* should be considered as a *nomen nudum* (or even *dubium*) due to
404 the poor quality of the holotype material. Our comparison shows more morphological
405 similarities with the ichnogenus *Jurabrontes* rather than with *Megalosauripus*, although there is
406 a bias due to the poor preservation of *M. teutonicus*.

407 • Occurrence of similar tracks in different palaeoenvironments demonstrate a high adaptability of
408 Late Jurassic apex predators.

- 409 • Occurrence of *Jurabrontes* isp. and *Megalosauripus* cf. *transjuranicus* in Morocco, and of *M.* cf.
410 *transjuranicus* and giant theropod tracks similar to *Jurabrontes* in the Iberian Peninsula, suggest
411 the existence of faunal exchange routes between Gondwana and Laurasia through North Africa
412 and/or North America and/or Asia between the Middle to early Late.
- 413 • Comparing tracks preserved as epireliefs and hyporeliefs is feasible but they often preserve
414 different morphological features in different ways, with the natural casts exhibiting more
415 extramorphological features, e.g. due to locomotion. Therefore, such comparisons have to be
416 made with care using all the available material: physical and digital, bi- and tridimensional.
- 417 • The potential trackmaker for the giant robust tracks in the Late Jurassic of Portugal is
418 *Torvosaurus gurneyi*, taking into consideration the morphology, synchronous and coeval
419 occurrences of bones and tracks in the area. The trackmaker of the other giant and even more
420 of the large gracile tracks is more complex to define, and will need more ichnological and
421 osteological data.

422

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438

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703
704

705 **FIGURE CAPTIONS**

706
707 **Figure 1.** Location of the Late Jurassic tracksites of this study, indicated by asterisks.

708
709 **Figure 2.** Photograph of the holotypes of the ichnotaxa used as references for the analyses. **A.**
710 Holotype of *Megalosauripus transjuranicus* (Razzolini et al., 2017). **B.** Holotype of *Jurabrontes*
711 *transjuranicus* (Marty et al., 2018). **C.** 23IGR1.7 coloured mesh; scale 20 cm. **D.** DEIO XLII coloured
712 mesh; scale 20 cm. **E.** DEIO CXXVIII/16 coloured mesh; scale 20 cm. **F.** 2CA1.1 coloured mesh; scale
713 20 cm. **G.** 1CB1.4 (*Iberosauripus grandis*) coloured mesh; scale 20 cm. **H.** ML1875 coloured mesh;
714 scale 20 cm. **I.** ML2366 coloured mesh; scale 20 cm. **J.** SHN.(JJS).ICNO.001F coloured mesh; scale 20
715 cm. **K.** SHN.(JJS).ICNO.001E coloured mesh; scale 20 cm. **L.** ML2035 coloured mesh; scale 20 cm. **M.**
716 MNHNUL.ICN1 (*Eutynichnium lusitanicum*) coloured mesh; scale 20 cm. **N.** 1AB-1-7 coloured mesh;
717 scale 20 cm.

718
719 **Figure 3.** Comparison between the mediotypes of *M. transjuranicus* and *J. curtedulensis*. **A.** False-
720 colour depth map of *M. transjuranicus* mediotype with indicated the landmarks used for track

721 registration. **B.** False-colour depth map of *J. curtedulensis* mediotype with indicated the landmarks
722 used for track registration. **C.** Registered overlap of *M. transjuranicus* (red) and *J. curtedulensis*
723 (black) mediotypes.

724

725 **Figure 4.** Depth maps and registration overlap of large theropod tracks. For comparison reasons, all
726 tracks are illustrated as right tracks. Depth gradient goes from dark blue (highest point) to white
727 (deepest point). Normals of the 3D models of tracks preserved as natural cast (positive epirelief)
728 were inverted to make the model appear in negative hyporelief. Black points indicate the landmarks
729 used for registration. *M. transjuranicus* mediotype is outlined in black. **A.** False-colour depth map of
730 the mediotype of *M. transjuranicus*. **B.** Contours of *M. transjuranicus* mediotype as created by
731 DigTrace for registration. **C.** False-colour depth map of DEIOCXXVIII/16. **D.** Registered overlap of
732 DEIOCXXVIII/16 with *M. transjuranicus* mediotype. **E.** False-colour depth map of 1AB-1-7. **F.**
733 Registered overlap of 1AB-1-7 with *M. transjuranicus* mediotype. **G.** False-colour depth map of
734 2CA1.1. **H.** Registered overlap of 2CA1.1 with *M. transjuranicus* mediotype. **I.** False-colour depth
735 map of SHN.(JJS).ICNO.001F. **J.** Registered overlap of SHN.(JJS).ICNO.001F with *M. transjuranicus*
736 mediotype. **K.** False-colour depth map of SHN.(JJS).ICNO.001E. **L.** Registered overlap of
737 SHN.(JJS).ICNO.001E with *M. transjuranicus* mediotype. **M.** False-colour depth map of ML1875. **N.**
738 Registered overlap of ML1875 with *M. transjuranicus* mediotype. **O.** False-colour depth map of
739 *Eutynichnium lusitanicum* (MNHNUL.ICN1). **P.** Registered overlap of *E. lusitanicum* (MNHNUL.ICN1)
740 with *M. transjuranicus* mediotype.

741

742 **Figure 5.** Depth maps and registration overlap of giant theropod tracks. All tracks are illustrated as
743 right tracks. Depth gradient goes from dark blue (highest point) to white (deepest point). Normals
744 of the 3D models of tracks preserved as natural cast (positive epirelief) were inverted thus to make

745 the model a negative hyporeliefs. Black points indicate the landmarks used for registration. *J.*
746 *curtedulensis* mediotype is outlined in black. **A.** False-colour depth map of the mediotype of *J.*
747 *curtedulensis*. **B.** Contours of *J. curtedulensis* mediotype as created by DigTrace for registration. **C.**
748 False-colour depth map of DEIO XLII. **D.** Registered overlap of DEIO XLII with *J. curtedulensis*
749 mediotype. **E.** False-colour depth map of 23IGR1.7. **F.** Registered overlap of 23IGR1.7 with *J.*
750 *curtedulensis* mediotype. **G.** False-colour depth map of the holotype of *Iberosauripus grandis*
751 (1CB1.4). **H.** Registered overlap of *I. grandis* (1CB1.4) with *J. curtedulensis* mediotype. **I.** False-colour
752 depth map of ML2035. **J.** Registered overlap of ML2035 with *J. curtedulensis* mediotype. **K.** False-
753 colour depth map of ML2366. **L.** Registered overlap of ML2366 with *J. curtedulensis* mediotype.

754

755 **Figure 6.** *M. teutonicus* comparisons with *M. transjuranicus* and *J. curtedulensis*. **A.** coloured mesh;
756 scale 20 cm. **B.** False-colour depth map of *M. teutonicus* (track B.3) **C.** Registered overlap of *M.*
757 *teutonicus* (red) with *M. transjuranicus* mediotype (black). **D.** Registered overlap of *M. teutonicus*
758 (red) with *J. curtedulensis* mediotype (black).

759

760 **Supplementary table 1.** List of specimens used for this paper, preservation, geographical, geological
761 and bibliographical information.

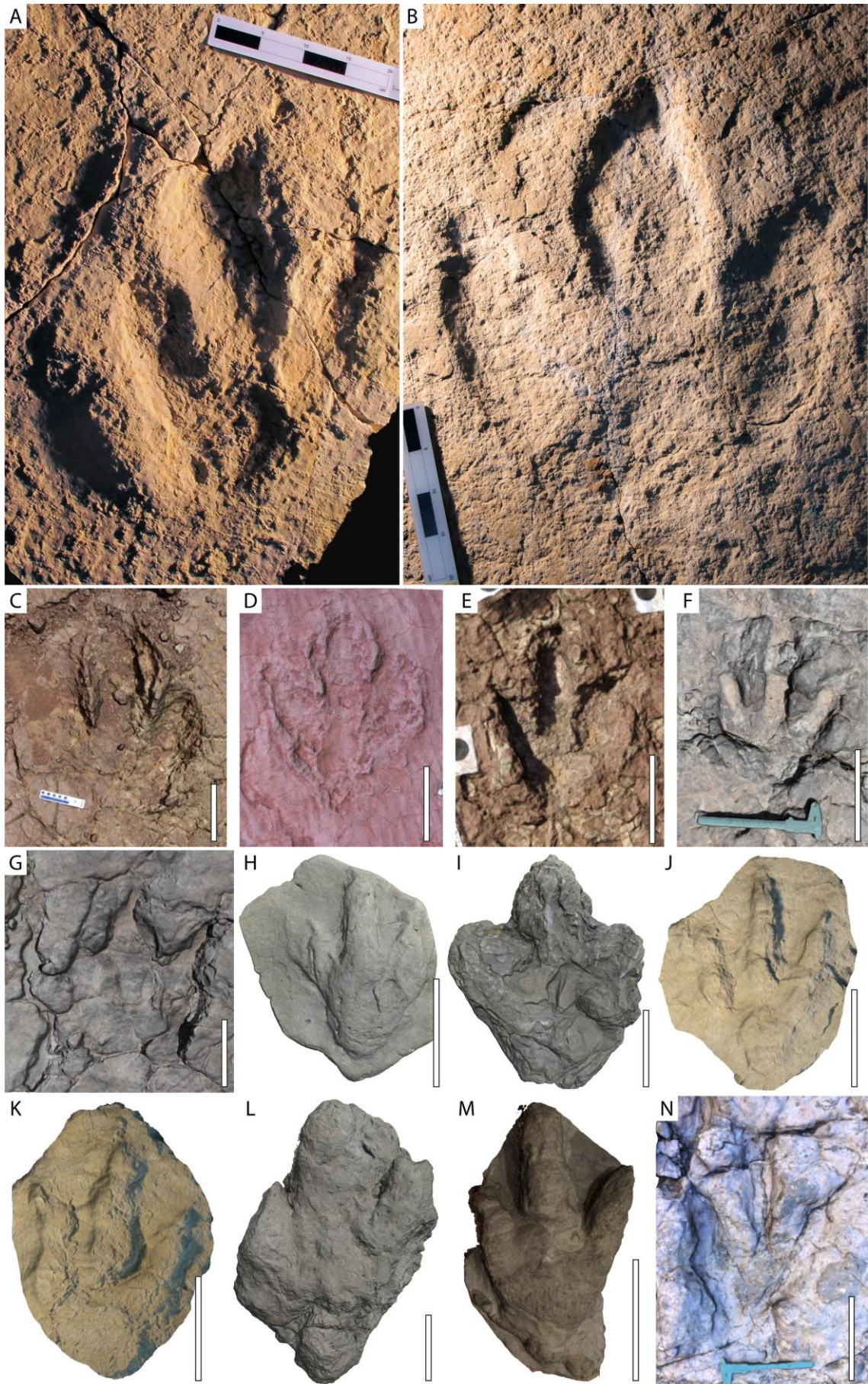
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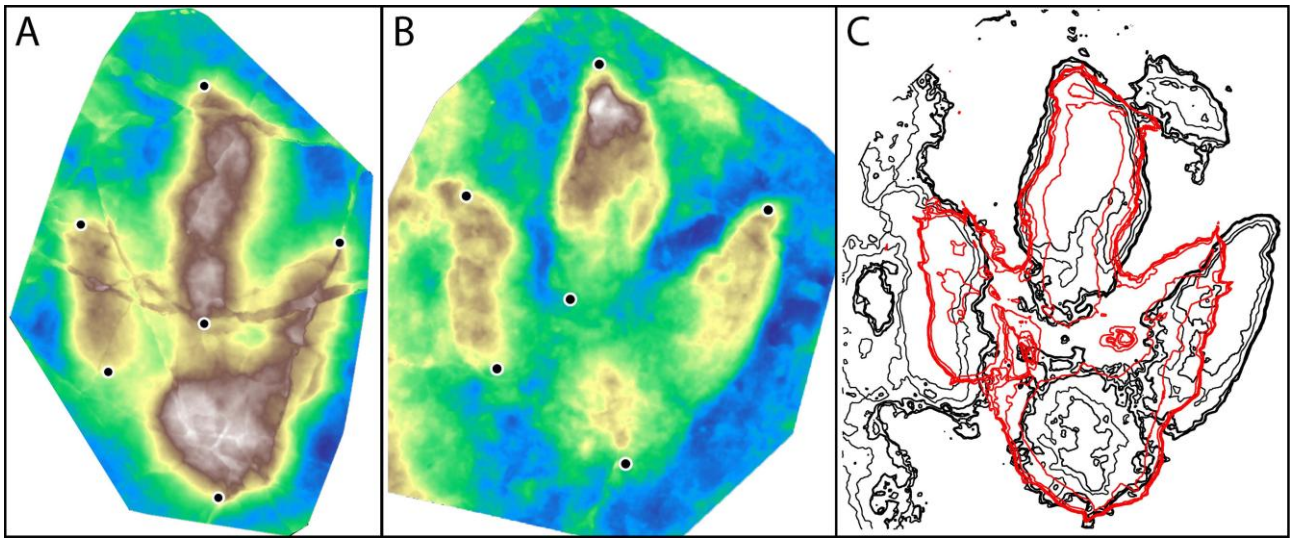
763 **Supplementary table 2.** ‘Rigid Transformation’ errors as generated by DigTrace for the comparisons
764 carried out.

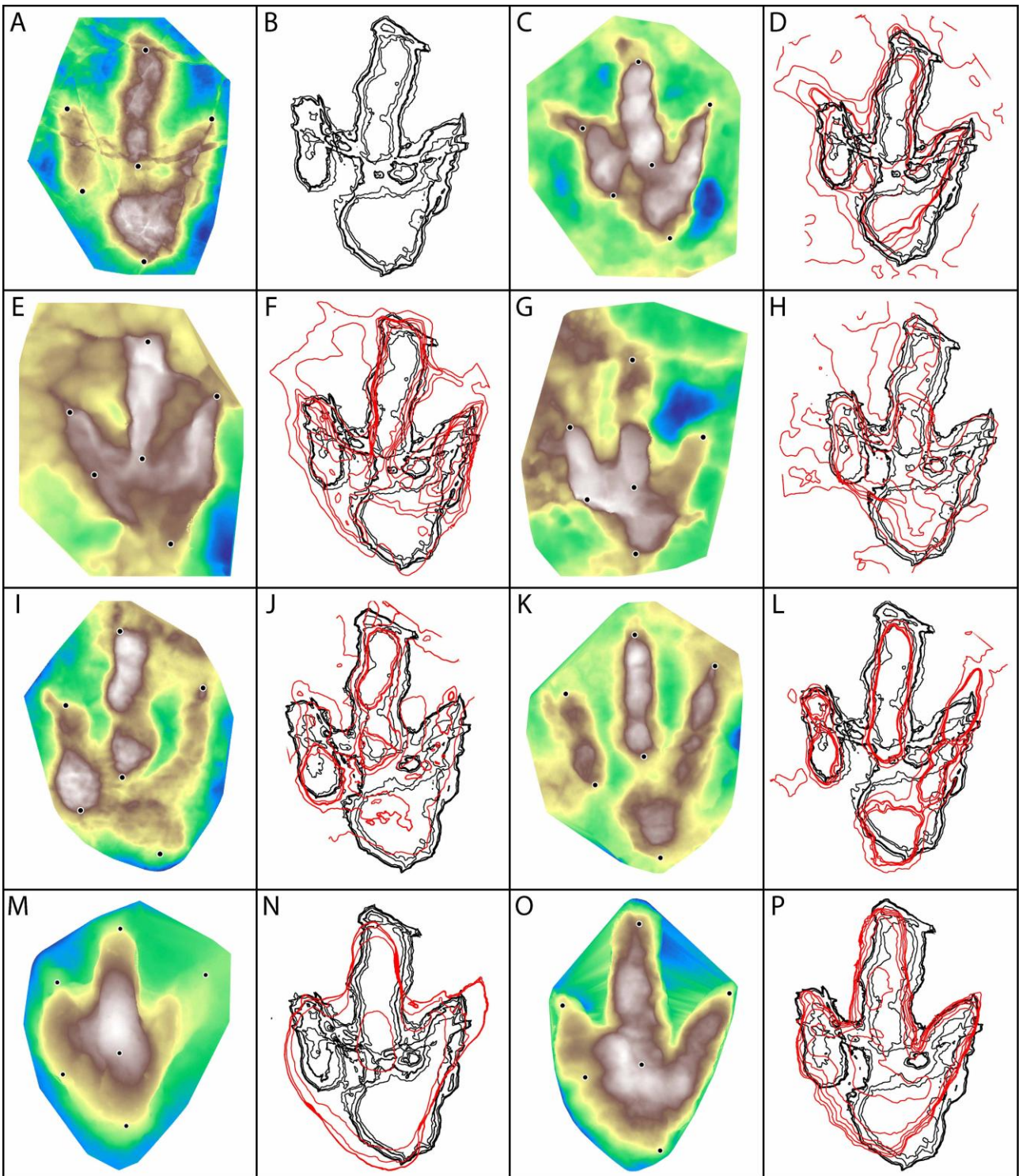
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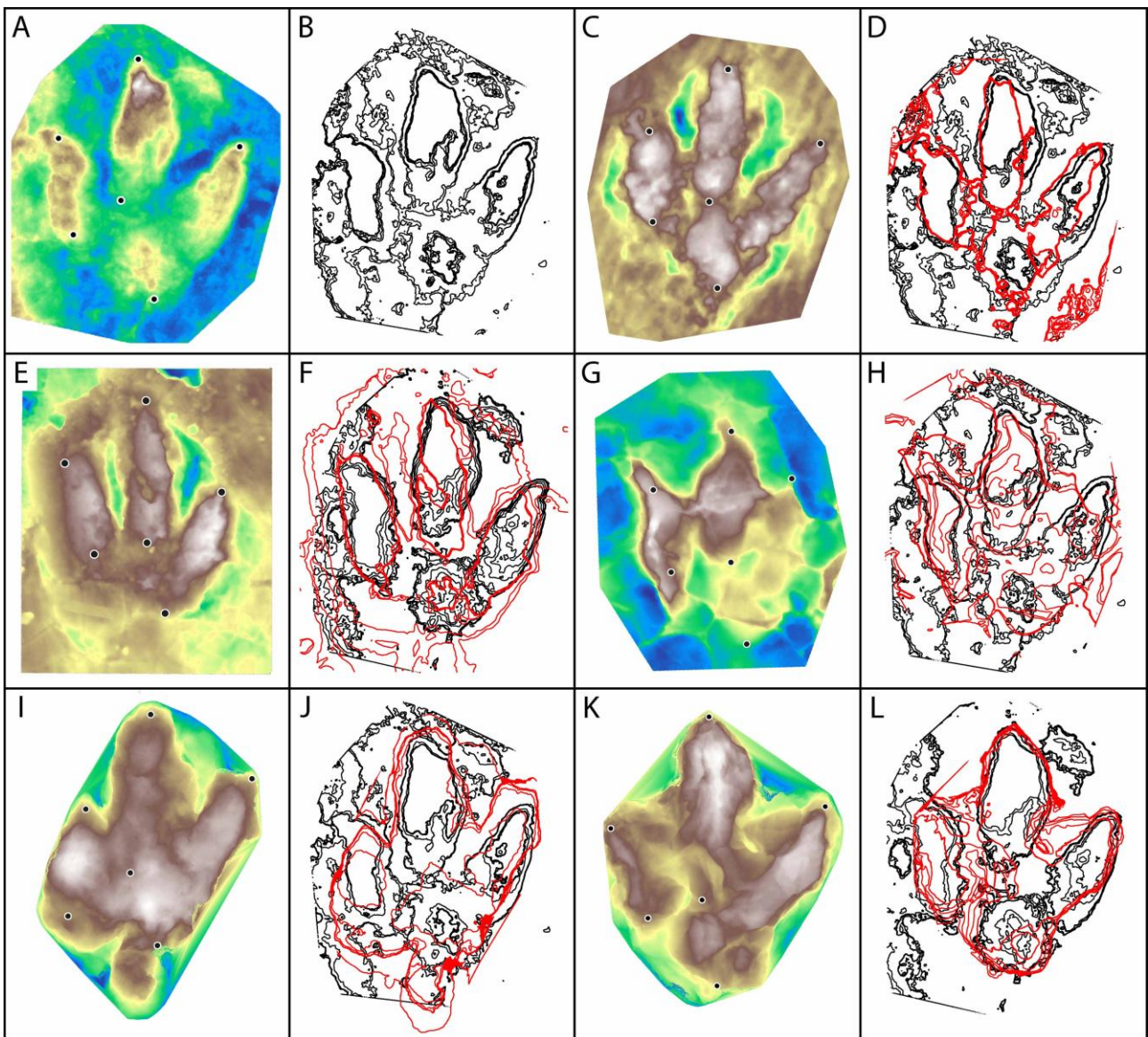
766 **Figure 1**

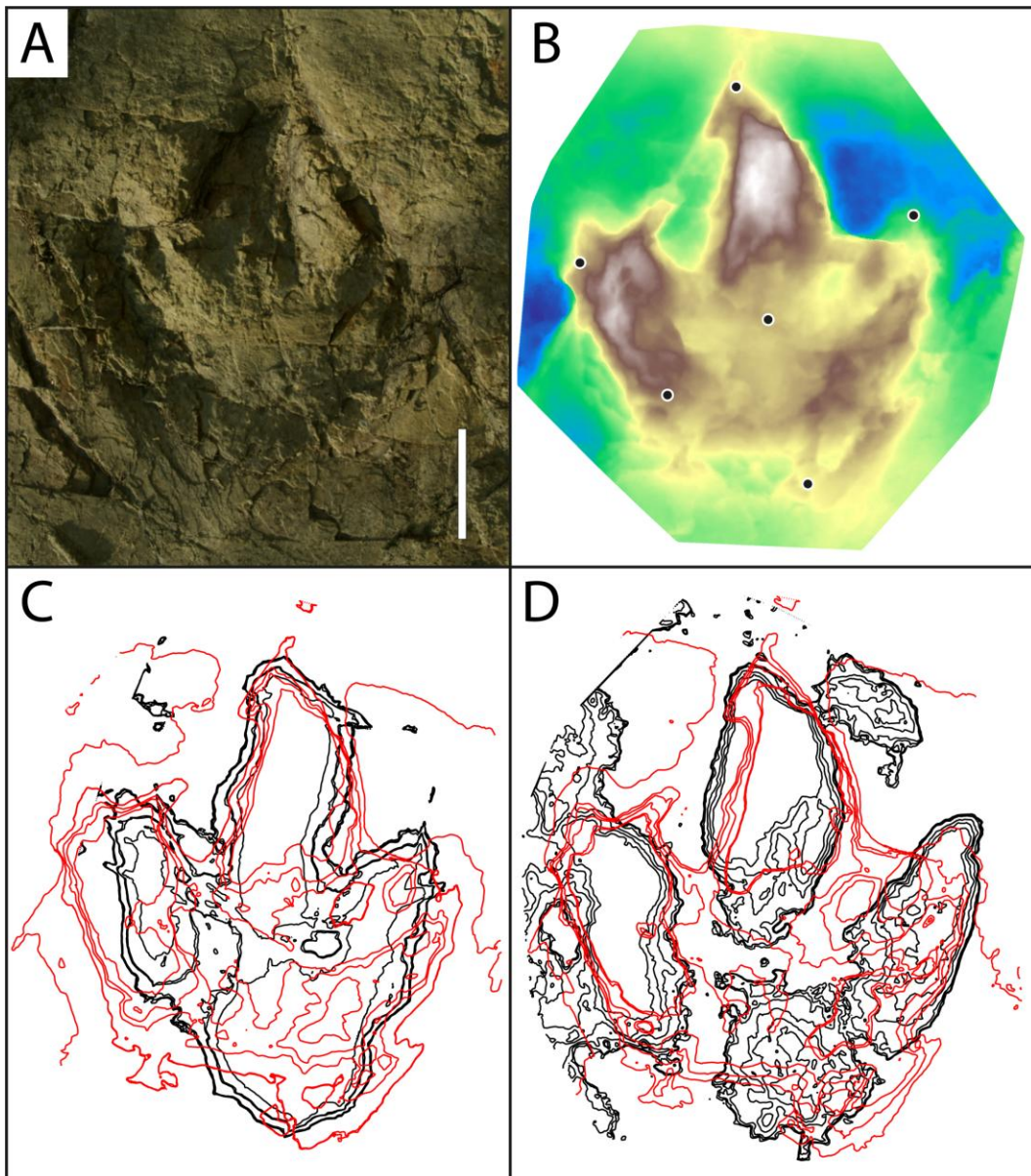












Acronym	Left/right + Conservation	Tracksite	Country	Formation	Age	Lithology	Reference
MNHN-MG-P261	Left Hyporelief	Cabo Mondego	Portugal	Cabaco	Oxfordian	Sandstone	Gomes, 1916 ; Lapparent and Zbyszewsky, 1957
B. 3	Right Epirelief	Barkhausen	Germany	Sand-Tonkomplex Member	middle Upper Kimmeridgian acanthicum/ mutabilis ammonoid biozone	Mud-cracked biolaminated siltstones/sandstones	Diedrich, 2011
TCH1030-T6-L1	Left Epirelief	Courtédoux—Tchâfoué	Switzerland	Reuchenette	late Early to early Late Kimmeridgian, Cymodoce to Mutabilis (Boreal), and Divisum to Acanthicum (Tethyan) biozones	Calcareous tidal laminites	Razzolini et al., 2017
SCR1500-T1-L8	Left Epirelief	Courtédoux—Sur Combe Ronde	Switzerland	Reuchenette	late Early to early Late Kimmeridgian, Cymodoce to Mutabilis (Boreal), and Divisum to Acanthicum (Tethyan) biozones	Calcareous tidal laminites	Marty et al., 2018
ML2366	Right Hyporelief	Porto Dinheiro	Portugal	Lourinhã	Kimmeridgian-Tithonian	Bivalve-rich carbonate bed	Mateus and Milan, 2010
ML2035	Left Hyporelief	Porto Dinheiro	Portugal	Lourinhã	Kimmeridgian-Tithonian	Bivalve-rich carbonate bed	Mateus and Milan, 2010
DEIO CXXVIII/16	Left Epirelief	Taghbalout	Morocco	louaridène	?Oxfordian-Kimmeridgian-Tithonian	Alternated pelites and consolidated silt/sandstones (trampled)	Charriere et al., 2005 ; Belvedere 2008 ; Belvedere et al., 2010
DEIO XLII	Left Epirelief	Taghbalout	Morocco	louaridène	?Oxfordian-Kimmeridgian-Tithonian	Alternated pelites and consolidated silt/sandstones (trampled)	Charriere et al., 2005 ; Belvedere 2008 ; Belvedere et al., 2010
23IGR1.7	Right Epirelief	Tirika	Morocco	louaridène	?Oxfordian-Kimmeridgian-Tithonian	Alternated pelites and consolidated silt/sandstones (trampled)	Ishigaki 1985 ; Charriere et al., 2005 ; Boutakiout et al., 2009
SHN.(JUS).ICNO.001F	Right Hyporelief	Praia de Porto Barril	Portugal	Freixial	Tithonian	Limestones	Castanera et al., 2017
SHN.(JUS).ICNO.001E	Right Hyporelief	Praia de Porto Barril	Portugal	Freixial	Tithonian	Limestones	Castanera et al., 2017
1CB1.4	Left Epirelief	El Castellar (CT-1), level A	Spain	Villar del Arzobispo	Tithonian	Peloidal limestone	Cobos et al., 2014 ; Campos-Soto et al., 2017
2CA1.1	Right Epirelief	El Castellar (CT-1), level B	Spain	Villar del Arzobispo	Tithonian	Peloidal limestone	Cobos et al., 2014 ; Campos-Soto et al., 2017
1AB-1-7	Right Epirelief	Ababuj	Spain	Villar del Arzobispo	Tithonian-Berriasian	Limestones	Alcalá et al., 2012 ; Badenas et al., 2018

773 **Supplementary table 2**

Track	'Rigid Transformation' error	Figure
<i>M. transjuranicus</i> vs. <i>J. curtedulensis</i>	70.0018	3
<i>M. transjuranicus</i> mediotype vs.		4A, B
DeioCXXVIII/16	23.9238	4C, D
1AB-1-7	44.0285	4E, F
2CA1.1	44.5901	4G, H
SHN.(JJS).ICNO.001F	44.7367	4I, J
SHN.(JJS).ICNO.001E	50.7065	4K, L
ML1875	55.6470	4M, N
<i>E. lusitanicum</i> (MNHNUL.ICN1)	36.3121	4O, P
<i>J. curtedulensis</i> mediotype vs.		5A, B
Deio XLII	36.1539	5C, D
23IGR1.7	61.1915	5E, F
<i>I. grandis</i> (1CB1.4)	68.5210	5G, H
ML2035	93.8900	5I, J
ML2366	51.5200	5K, L
<i>M. transjuranicus</i> vs. <i>M. teutonicus</i> (B.3)	55.1519	6B
<i>J. curtedulensis</i> vs. <i>M. teutonicus</i> (B.3)	45.7026	6C