

1 **Paleoecology and paleoenvironment of the Early Cretaceous theropod-dominated**
2 **ichnoassemblage of the Los Corrales del Pelejón tracksite, Teruel Province, Spain**

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4 Diego Castanera^{1*}, Marcos Aurell², José Ignacio Canudo², Gloria Cuenca-Bescós², José
5 Manuel Gasca³, Beatriz Bádenas²

6
7 *1: Fundación Conjunto Paleontológico de Teruel-Dinópolis/Museo Aragonés de*
8 *Paleontología, Avenida de Sagunto s/n, 44002 Teruel, Spain*

9
10 *2: Aragosaurus—IUCA, Facultad de Ciencias, Universidad de Zaragoza, 50009*
11 *Zaragoza, Spain.*

12
13 *3: Departamento de Geología, Universidad de Salamanca, 37008 Salamanca, Spain*

14
15 *corresponding author

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35 **Abstract**

36 The earliest Cretaceous (mid-late Berriasian) tracksite *Los Corrales del Pelejón*
37 is an important dinosaur trackway site in Teruel Province in Spain. The
38 ichnoassemblage occurs in the Galve Formation (Maestrazgo Basin) and comprises
39 around 40 tracks assigned to theropods and ornithopods. In this paper, we undertake a
40 paleoenvironmental analysis of the succession, which includes the overbank deposits of
41 a fluvial environment, and discuss the implications of these findings for trackway
42 preservation and orientation. The track-bearing unit is composed of fine- to very fine-
43 grained, thinly bedded sandstone layers with wave ripples and traces of the *Mermia*
44 ichnofacies, which were deposited as splay deposits within an ephemeral overbank
45 pond. Two different theropod ichnotaxa (*Megalosauripus* cf. *transjuranicus* and
46 Grallatoridae indet.) of three different size classes occur as small-, medium-, and large-
47 sized tracks. The ornithopod tracks are classified as cf. *Iguanodontipus* isp. Five
48 theropod trackways (*M.* cf. *transjuranicus*) show a bimodal orientation pattern with a
49 similar orientation to NW-SE wave ripple crests, suggesting that these animals were
50 walking parallel to the shoreline of the ephemeral overbank pond. Three of them walked
51 in a similar subparallel orientation, but there is no evidence suggesting gregarious
52 behavior as they have slightly different orientations and/or speed values. The *Los*
53 *Corrales del Pelejón* site is an example of environmental influence on dinosaur
54 behavior.

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68 1. Introduction

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70 Galve (Teruel Province, NE Spain) is a key locality for the analysis of Upper Jurassic-
71 Lower Cretaceous units within the Maestrazgo Basin both in terms of its stratigraphy
72 and its paleontological richness in vertebrates, including dinosaurs (e.g., Ruiz-Omeñaca
73 et al., 2004; Aurell et al., 2016). Within the paleontological record of Galve, the
74 ichnological richness stands out, with several dinosaur tracksites discovered across the
75 different Upper Jurassic-Lower Cretaceous units. The *Los Corrales del Pelejón* tracksite
76 studied in the present work was found in 1981 and represented the first dinosaur
77 tracksite discovered both in Teruel Province and the Maestrazgo Basin (Casanovas et
78 al., 1983-84; Pérez-Lorente, 2009). It also constitutes one of the first dinosaur tracksites
79 reported in Spain, just a few years after the discoveries made in the Cameros and
80 Asturian basins (Casanovas Cladellas and Santafé Llopis, 1971; García-Ramos, 1977;
81 Aguirrezabala and Viera, 1980). *Los Corrales del Pelejón* is one of the main sites in the
82 Maestrazgo UNESCO Global Geopark prepared for tourist visits (Pérez Lorente, 2009;
83 Alcalá and Cobos, 2021). In the first investigation of the site (Casanovas et al., 1983-
84 84), six dinosaur footprints attributed to medium to large theropod dinosaurs were
85 identified. Cleaning and excavation of the tracksite in 1992 allowed Cuenca-Bescós et
86 al. (1993) to provide data on 35 newly discovered tracks and seven trackways (six
87 attributed to theropods and one to an ornithopod dinosaur).

88

89 The number of dinosaur tracks recognized in the Maestrazgo Basin has notably
90 increased in recent years, with several localities with dinosaur tracksites described in
91 Upper Jurassic (Kimmeridgian-Tithonian) and Lower Cretaceous (mainly Barremian)
92 units (e.g. Pérez-Lorente, 2009; Alcalá et al., 2016; Castanera et al., 2016a, 2022; Gasca
93 et al., 2017; Campos-Soto et al., 2019; Alcalá and Cobos, 2021; García-Cobeña et al.,
94 2023). By contrast, the *Los Corrales del Pelejón* tracksite is the only dinosaur tracksite
95 from the Berriasian record discovered so far in the Maestrazgo Basin (Aurell et al.,
96 2016, 2019 and references therein). Its age is significant not only at basin scale but also
97 globally since the Berriasian-Valanginian is a rather poorly known period in terms of
98 dinosaur tracksites in Europe, in contrast with the large number of dinosaur tracks
99 described in the Kimmeridgian-Tithonian (e.g., Marty, 2008; Piñuela, 2015; Piñuela et
100 al., 2016; Razzolini et al., 2017; Rauhut et al., 2018; Castanera et al., 2018a, 2020,
101 2021; Belvedere et al., 2019) and Lower Cretaceous post-Valanginian units (e.g.,

102 Hernández-Medrano et al., 2008; Pérez-Lorente, 2015). The main areas with Berriasian-
103 Valanginian dinosaur tracks are located in the Cameros Basin (Hernández-Medrano et
104 al., 2008; Castanera et al., 2018b; Torcida Fernández-Baldor et al., 2021), the Lower
105 Saxony Basin (e.g., Hornung et al., 2012, 2016; Richter et al., 2016), and the Wealden
106 of the UK (e.g., Shillito and Davies, 2019).

107

108 Despite its scientific and heritage interest, the *Los Corrales del Pelejón* dinosaur
109 tracksite has not been described in detail, especially in terms of its ichnodiversity and
110 the paleoecological and paleoenvironmental inferences that can be drawn. In particular,
111 Cuenca-Bescós et al. (1993) identified trackways with parallelism but a variety of
112 directions and proposed (among other possibilities) a possible paleogeographic
113 influence on their orientation. The hypothesis of paleogeographic barriers controlling
114 trackway orientations has also been proposed in other cases in different areas (Lockley
115 et al., 1986; Moratalla and Hernán, 2010; Razzolini et al., 2016; Getty et al., 2017).
116 Nevertheless, when certain trackway parameters are also present (e.g., similar
117 orientations, speed, and preservation), parallelism might indicate gregarious behavior
118 (e.g., Castanera et al., 2011, 2014; García-Ortíz and Pérez-Lorente, 2014; Heredia et al.,
119 2020).

120

121 This paper aims to provide an update on *Los Corrales del Pelejón* with an emphasis on
122 integrating a detailed ichnological and sedimentological analysis of the site in order to:
123 1) analyze track preservation and ichnotaxonomy through the possible presence of one
124 or more track-bearing layers; and 2) provide a paleoenvironmental reconstruction of the
125 tracksite with a view to inferring whether the orientation of the trackways shows a
126 paleoenvironmental or paleoecological (e.g., gregarious behavior) influence. The results
127 are relevant both in adding to what is known of this significant and historic site in
128 Spain, and enlarging the poorly known Berriasian dinosaur track record in Europe.

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130 **2. Geographical and geological setting**

131

132 The *Los Corrales del Pelejón* tracksite is located near the village of Galve, a traditional
133 dinosaur village in Teruel Province (NE Spain). The tracksite is located ca. 5 km to the
134 southeast of the village, at the coordinates 40° 37' 30.49" N; 0° 50' 48.10" W.

135

136 The Upper Jurassic and Lower Cretaceous units outcropping in the Galve area belong to
137 the Galve sub-basin, located on the western margin of the Maestrazgo Basin (Fig. 1)
138 (Martín-Chivelet et al., 2019). The tracksite is located on the eastern flank of the Galve
139 syncline within the lower part of the siliciclastic Galve Fm (Aurell et al., 2016). This
140 lithostratigraphic unit has been correlated in other works (e.g., Royo-Torres et al., 2014;
141 Campos-Soto et al., 2019) to the upper part of the Villar del Arzobispo Fm defined in
142 the nearby South Iberian Basin (Mas et al., 1984). The Galve Fm forms part of the so-
143 called syn-rift sequence-1 (Fig. 1C) and is irregularly recorded (from 0 to 100 m) across
144 the eastern and western margins of the Galve sub-basin due to synsedimentary normal
145 fault activity. In the Galve syncline, the unit consists of up to 60–80 m of red mudstones
146 with intercalations of dm- to m-thick cross-bedded and tabular-burrowed sandstones
147 and locally hydromorphic soils, representing fluvial channels and overbank deposits
148 (Aurell et al., 2016, 2019).

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150 The age of the Galve Fm in the Galve syncline is constrained to the Berriasian-early
151 Valanginian by the presence of a sporomorph assemblage located in the lower part of
152 the unit at the Las Zabacheras 1 fossil site (see Fig. 1A; Santos et al., 2018). The
153 Berriasian-Barremian ostracod *Theriosynoecum fittoni* has also been found in the upper
154 part of the unit (Aurell et al., 2019). Furthermore, in the Aliaga-Molino Alto section the
155 recorded charophyte association suggests an age around the early to late Berriasian
156 transition for the onset of the sedimentation of the unit in that area. According to this
157 dataset and the sequence-stratigraphic framework (Aurell et al., 2019; Martín-Chivelet
158 et al., 2019), the *Los Corrales del Pelejón* tracksite is probably mid-late Berriasian in
159 age (Aurell et al., 2016, 2019).

160

161 **3. Materials and methods**

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163 To analyze the sedimentological context of the tracks, a detailed stratigraphic-
164 sedimentological analysis of the lower part of the Galve Fm was carried out in the
165 outcropping area of the unit around the *Los Corrales del Pelejón* tracksite (Fig. 1A).
166 This analysis encompassed: 1) a revision of the reference section of the unit established
167 previously in this area (*Pelejón* section; Aurell et al., 2016); 2) a bed-by-bed analysis of
168 a new stratigraphic section (*Los Corrales del Pelejón* section) in the specific area of the
169 *Los Corrales del Pelejón* tracksite located ca. 330 m away from the reference section;

170 and 3) a detailed, cm-thick analysis of the track-bearing beds. Paleocurrent
171 measurements and grain size analysis (12 samples of muddy and sandy lithologies)
172 using a Malvern Mastersizer 3000 laser diffractometer (see results in S3) were carried
173 out in the *Los Corrales del Pelejón* section, to complement the data obtained previously.
174 The physical tracing of key beds and orthoimages allowed the two sections to be
175 correlated.

176

177 The surface of the tracksite was photogrammetrically documented. A total of 585
178 photographs were taken with a Canon EOS 450D to cover the whole surface, and a 3D
179 model was built using the software Agisoft Photoscan Standard Edition. Several
180 orthophotos of the whole surface were taken using the software ZBrush and
181 CloudCompare, allowing a new map of the tracks and trackways of the site to be drawn.
182 This map was compared with that of Cuenca-Bescós et al. (1993). Each footprint was
183 labeled with an acronym formed by the initial letters of the tracksite (CP), followed by
184 the number of the trackway (e.g., CP1) and the number of the track (e.g., CP1.1 =
185 trackway 1, track 1). Those individual tracks not arranged in trackways were numbered
186 consecutively (e.g., CP8, CP9, etc.).

187

188 For each track, the morphological preservation (MP) was evaluated according to the
189 scale of Marchetti et al. (2019), and the descriptions were based on those specimens
190 with the highest MP values (avoiding extramorphological features in the descriptions).
191 The open nomenclature follows the recommendations of Bengston (1998). Each track
192 was analyzed individually by measuring footprint length (FL), footprint width (FW), the
193 length and width of digits II (LII, WII), III (LIII, WIII), and IV (LIV, WIV), the “heel”
194 (metatarsophalangeal) area (HA), and the divarication angles (II[^]III, III[^]IV) following
195 previously used procedures (e.g., Castanera et al., 2020, 2021). The FL/FW ratio,
196 LIII/FL, and the mesaxony (AT) were calculated accordingly. LIII/FL was calculated
197 following Lockley et al. (2021) and Xing et al. (2021a). AT was calculated as the ratio
198 between the anterior triangle length (ATl) and the anterior triangle width (ATw),
199 following Lockley (2009). Different size classes were distinguished following Marty
200 (2008) on the basis of the pes footprint length (FL) as: (1) minute = FL < 10 cm; (2)
201 small = 10 cm < FL < 20 cm; (3) medium = 20 cm < FL < 30 cm; and (4) large = 30 cm
202 < FL < 50 cm. Trackway data were characterized by measuring pace length (PL), stride
203 length (SL), pace angulation (PA), trackway width (TW), and width of angulation

204 pattern (WAP) measured from the midpoint of the footprint. Locomotion speed was
205 estimated to compare the relative values among the trackways. The hip height (h) and
206 the locomotion speed (v) were estimated using Alexander's (1976) formulas: hip height
207 (h) = 4FL; speed (v) = $0.25 g^{0.5} * SL^{1.67} * h^{-1.17}$, where g = 9.8 and is the acceleration due
208 to gravity, and SL = stride length. We also calculated the speed according to the formula
209 $v = 0.226 g^{0.5} * SL^{1.67} * h^{-1.17}$, as proposed by Ruiz and Torices (2013) and Navarro-
210 Lorbés, (2021). The values of SL and h used in the formulas were mean values for each
211 trackway. The measurements were taken with the software ImageJ from false-color
212 depth maps in the case of the individual tracks, and in situ in the tracksite for the
213 trackway data. The false-color depth maps were obtained from the 3D models generated
214 from pictures taken of individual tracks with a SONY ILCE-5000, using Agisoft
215 Photoscan Standard Edition. The scaled meshes were exported as OBJ files and then
216 processed in CloudCompare (v.2.7.0) to obtain the false-color depth maps using the
217 color schemes provided by Belvedere (2020). It should be emphasized that there are two
218 different photogrammetries, one for the orthomosaic and a detailed one to characterize
219 each individual footprint. The photogrammetric meshes of individual tracks used in this
220 study are available for download in the supplementary information ([link to be included](#)),
221 following the recommendation of Falkingham et al. (2018). The orientation of the
222 trackways was plotted in a rose diagram using the software GeoRose
223 (<http://www.yongtechnology.com/download/georose>).

224

225 **4. Results**

226

227 *4.1. Facies analysis*

228

229 In the study area, the Galve Fm is ~65 m thick, although its thickness varies laterally
230 due to synsedimentary normal fault activity (Aurell et al., 2016). The stratigraphic
231 successions of the lower part of the unit in the *Pelejón* and *Los Corrales del Pelejón*
232 sections are shown in Figure 2A. Physical tracing and orthoimages allowed the lateral
233 continuity of some sandstone packages to be deciphered (G1 to G7 in Fig. 2A) and a
234 normal fault controlling variations in thickness to be identified, from ca. 30 m in
235 *Pelejón* to ca. 18.5 m in *Corrales del Pelejón*. Packages G1 to G3 are only present in
236 the thicker *Pelejón* section, whereas packages G4 to G7 are laterally continuous,
237 although with lateral facies variations. The *Los Corrales del Pelejón* tracksite is located

238 in package G6 in the *Los Corrales del Pelejón* section (Fig. 2A). The differentiated
239 facies (Fig. 2A) are in accordance with those previously identified and interpreted as
240 fluvial channels and overbank deposits by Aurell et al. (2016), but they are here
241 described and interpreted in more detail (see Supplementary data S1 to S3 for detailed
242 descriptions and interpretations) to provide a new paleoenvironmental scheme of the
243 unit for the studied area (Fig. 2B).

244

245 The unit is dominated by red to ocherish mudstones accumulated in a sparsely vegetated
246 floodplain, with local ponds (gray mudstones). The intercalated cross-bedded
247 sandstones and laminated and/or bioturbated sandstones that are laterally related (e.g.,
248 G5 and G6 in Fig. 2A, see Supplementary material S1 and S2) correspond to fluvial
249 channels and splay deposits, respectively. Paleocurrents indicate that the fluvial
250 channels were very variable in orientation, but mainly ran southward (parallel to the
251 orientation of the Galve sub-basin). The paleocurrents of the splay deposits are NE-
252 directed (Fig. 2). The *Los Corrales del Pelejón* tracksite is judged to correspond to
253 laminated and/or bioturbated splay deposits accumulated in an ephemeral pond, as 1)
254 they are laterally equivalent to channel deposits in package G6, 2) they are overlying
255 gray mudstones (pond deposits), and 3) they present wave ripples (Figs. 2A, B). In
256 particular, four cm-thick, fine to very fine sandstone layers can be distinguished in the
257 surface of the tracksite (layers 1 to 4 in Fig. 3A), including parallel-laminated layers 1
258 and 4 and rippled layers 2 and 3. Two main sectors (A and B) can be differentiated in
259 the tracksite (see Figures 3 and 4). In sector B, it is mainly layer 1 that crops out due to
260 current erosion of the overlying layers. In sector A, the four layers can be distinguished,
261 except in some areas where ripples disappear laterally (Fig. 3A, D). These ripples are
262 asymmetric and symmetric wave ripples (with bifurcation, zig-zag, and hourglass crest
263 morphology; e.g., Perron et al., 2018) and are present in the very fine sandstone layers 2
264 and 3 (Fig. 3), thus reflecting subaqueous deposition and a NW-SE paleowind direction
265 (Fig. 2). Several invertebrate traces can be identified in the different layers of the
266 tracksite. Simple horizontal (e.g., *Helminthopsis*, *Gordia*) and vertical burrows are
267 present in layer 1. The rippled layer 3 is characterized by arthropod trackways (e.g.,
268 *Diplopodichnus*), simple horizontal burrows and trails (e.g., *Helminthopsis*,
269 *Helminthoidichnites*), and simple vertical burrows. The topmost very fine sandstone
270 layer 4 (presumably the dinosaur tracking surface) has parallel lamination and an
271 exclusive presence of grazing trails (indeterminate and simple horizontal trails of

272 *Helminthopsis*). Floodplain red mudstones cover the track-bearing beds (Fig. 3A). This
273 invertebrate ichnoassemblage, with its rather low ichnodiversity, represents an example
274 of the *Mermia* ichnofacies, characterized by a predominance of horizontal grazing traces
275 produced in low-energy environments such as floodplain ponds and under subaqueous
276 conditions (Buatois and Mangano, 2011; Melchor et al., 2012). Bioturbation traces are
277 recorded close to some tracks, but there is no clear evidence to decipher their cross-
278 cutting relationships, especially in layer 4, so it is difficult to infer whether the dinosaur
279 tracks and the invertebrate traces were coeval or not.

280

281

282 4.2. Track preservation

283

284 Around 40 dinosaur tracks are identified in the *Los Corrales del Pelejón* tracksite,
285 including five clear theropod trackways (CP1, CP2, CP3, CP5 and CP6) (Fig. 4). As
286 well as this, three pairs of two tracks might be part of two different trackways (CP4 and
287 CP7). In addition, some isolated tridactyl tracks (CP8-C11) and four large, rounded
288 depressions (CP12-CP15) of indeterminate origin (possibly undertracks) are identified.
289 Most of these tracks were previously reported by Cuenca-Bescós et al. (1993), except
290 for the first tracks in trackways CP1-CP3 and track CP6.5, which were unearthed in
291 cleaning operations and excavations carried out in subsequent years. Tracks CP10 and
292 CP11 can only be identified under certain light conditions. All the tracks are preserved
293 as concave epireliefs. Trackways CP1 and CP2, and track CP11, are located in Sector A
294 of the tracksite (left side of the map in Fig. 4), and the tracks are mainly preserved on
295 top of layers 4 and 3 (e.g., CP2, Fig. 3B). In the upper area of sector A, where rippled
296 layers 2 and 3 change laterally to the topmost part of layer 1 (Fig. 3), the tracks are
297 preserved on top of this layer (e.g., CP1.1, Fig. 3B). By contrast, in sector B (right side
298 of the map in Fig. 4), trackways CP3 to CP7 and isolated tracks CP8 to CP10 are
299 preserved on top of layer 1 (Fig. 3), and the overlying layers are absent. The observed
300 track preservation thus indicates that all the dinosaurs possibly impressed their
301 footprints on layer 4 (this layer would be the original tracking surface), so trackways
302 CP1 and CP2 are preserved as true tracks, and those preserved in the underlying layers
303 (e.g., trackways CP3 to CP7 and isolated tracks CP8 to CP10) are shallow undertracks.
304 This interpretation is also in accordance with the MP values, which are higher in
305 trackways CP1 and CP2 (see Table 1, Fig. 4C, Fig. 5).

306

307 4.2 Dinosaur morphotypes

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309 4.1.1 Theropod tracks

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311 Based on footprint size and morphology, two different theropod morphotypes of three
312 different size classes can be distinguished (Table 1): one small-sized (CP4, FL = 15.5
313 cm, Fig. 5K), one medium-sized (CP1, CP5, CP9, CP10; FL = 26-28 cm, Fig. 5A-B, G-
314 H, J), and one large-sized (CP3 and CP6, FL = 35, 39 cm, Fig. 5C-F, I). The tracks are
315 tridactyl and notably gracile, showing differences between the different size classes,
316 especially in the FL/FW ratio and mesaxony. Generally, the smaller specimens have
317 higher values for FL/FW and mesaxony (CP4.1-CP4.2 = 1.53-1.63/0.66-0.74) than the
318 medium (CP1.1-CP1.4 = 1.48-1.64/0.56-0.6; CP5.1 = 1.54/0.6) and larger specimens
319 (CP2.4-CP2.5 = 1.44-1.43/0.48-0.55; CP3.3 = 1.61/0.57; CP6.2 = 1.57/0.55). The tracks
320 with higher morphological preservation values are characterized by a large, rounded,
321 metatarsophalangeal pad impression, as shown in individuals of both the medium and
322 large-sized classes (e.g., CP1.1, CP1.3, CP2.4, CP3.3, CP5.1, CP6.2). The digits are
323 slender in all the trackways, except in CP6, where they are somewhat robust (Fig. 5I).
324 Digit III is clearly the longest, digit IV being generally slightly longer than digit II. The
325 digit divarication is low in the three different size classes (generally lower than 50°, see
326 Table 1). The distal ends of the digits are acuminate, showing clear claw impressions in
327 the best-preserved tracks (e.g., CP1.4, Fig. 5B).

328

329 4.1.2 Ornithopod tracks

330

331 CP7 is the only trackway possibly attributable to ornithopods. It is composed of two
332 pairs of two footprints, which might represent part of the same trackway showing a
333 slight change in direction. CP7.4 has the highest morphological quality. It is a large-
334 sized tridactyl track (FL = 35.5 cm), slightly longer than wide (FL/FW ratio = 1.09),
335 with medium mesaxony (AT = 0.44). The footprints are symmetrical, with a rounded to
336 quadrangular metatarsophalangeal pad impression. The digits are robust (9 cm in
337 width), digit III being slightly longer than digits II and IV, which are subequal in length.
338 The hypices are symmetrical, and the digits possibly show one phalangeal pad per digit.

339 The distal end of the digits is rounded, without evidence of clear claw marks (indicative
340 of blunt claws). The interdigital angle is medium (63°), and III^{IV} slightly higher than
341 II^{III}.

342

343 *4. 3 Orientation and locomotion speed values of the dinosaur trackways*

344

345 The dinosaur trackways of the *Los Corrales del Pelejón* tracksite are not very long, with
346 no more than seven footprints. They have different orientations (see Fig. 4, Table S1),
347 showing a generally multidirectional pattern. Of the theropod trackways, CP1, CP2 and
348 CP3 are heading to the SW, the former two being parallel and CP3 subparallel with a
349 higher SW orientation. The three trackways have speed values close to 2 m/s (see Table
350 S1), CP2 and CP3 having rather similar speed values. CP1 is the fastest trackway (2.15-
351 2.37 m/s). CP6 is parallel to CP3 but is heading in the opposite direction (NE), with a
352 slightly lower speed value (1.59-1.76 vs 1.98-2.19 m/s respectively). CP5 has a NE
353 orientation, with the lowest speed value (1.5-1.66 m/s). CP4 is heading SE. By contrast,
354 the ornithopod tracks in CP7 are heading NW, with a change in the direction of travel to
355 the W from the first pair to the second pair. No speed values are calculated in the latter
356 since there are not three consecutive tracks preserved.

357

358 In summary, although the rose diagram shows a generally multidirectional pattern of
359 trackway directions (Fig. 4), it indicates a rather bimodal (NE-SW) pattern in the
360 medium to large theropod trackways (CP1-CP3, CP5-CP6). It is interesting to observe
361 that the theropod trackways are very narrow, with high pace angulations (greater than
362 165°, see Table S1). Also noteworthy is the difference in speed values among trackways
363 produced by similar-sized theropods: for example, CP1 moved considerably faster
364 (longer PL and SL and higher PA) than CP5; CP2 and CP3 moved at rather similar
365 speeds and slightly faster than CP6. Despite these differences in speed values and the
366 fact that according to their footprint length they can be included in the range of the
367 “good runner” dinosaurs (see Navarro-Lorbés et al., 2021), all the theropod trackways
368 show a rather low absolute value. Thus, they were moving with a walking gait with a
369 low speed, as also evidenced by the low values (1.42-1.97) of their relative stride length
370 (values lower than 2, Thulborn, 1990).

371

372 **5. Discussion**

373

374 5.1 Ichnotaxonomic affinities and candidate trackmakers

375

376 Some tracks from *Los Corrales del Pelejón* (CP3 and CP6, and possibly CP1.4) were
377 previously compared by Casanovas et al. (1983-84) to various ichnotaxa such as
378 *Eubrontes giganteus* Hitchcock, 1845 (Fig. 6A), *Eutynichnium lusitanicum* Nopcsa,
379 1923 (Fig. 6B), *Megalosauropus broomensis* Colbert and Merrilees, 1967 (Fig. 6C), and
380 *Bueckeburgichnus maximus* Kuhn, 1958 (Fig. 6D). The authors noted the similarities,
381 especially with respect to *Eubrontes*, but emphasized that this ichnotaxon is mainly
382 found in the Upper Triassic and Lower Jurassic and so did not classify the tracks. Pérez-
383 Lorente (2009) suggested that track CP1.4 could be classified as *Eubrontes*. Generally,
384 *Eubrontes* tracks are indeed typical of the Late Triassic-Early Jurassic (Olsen et al.,
385 1998; Lucas et al., 2006), but they have also been described in the Cretaceous of Asia
386 (e.g., Xing et al., 2016, 2021). Although some of the tracks in CP3 and CP6 might
387 resemble *Eubrontes*-like tracks (see fig. 6 in Xing et al., 2021), the heel pad impression
388 of Cretaceous *Eubrontes* (e.g., *E. nobitai*, Fig. 6E) is bilobed with a third phalangeal
389 pad in digit II close to the heel pad impression. In the studied theropod tracks (CP1-
390 CP6) this pad is not present, and the heel pad impression is rounded and centered in
391 relation to the track axis. Moreover, CP1.4 is more gracile than many of the tracks
392 classified as *Eubrontes*.

393

394 The other three ichnotaxa mentioned by Casanovas et al. (1983-84) are now either
395 considered *nomem dubium* or related to *Megalosauripus* Lockley, Meyer, & Santos,
396 1996 (Lockley et al., 1996, 2000; Belvedere et al., 2019). Certainly, both the medium
397 and large-sized theropod tracks from *Los Corrales del Pelejón* show similarities with
398 the tracks assigned to *Megalosauripus* (Fig. 6F-6G), which is typical of Middle
399 Jurassic-Lower Cretaceous successions, including several sites in the Iberian Peninsula
400 and the Maestrazgo Basin (Lockley et al., 1996, 2000; Fanti et al., 2013; Razzolini et
401 al., 2016, 2017; Belvedere et al., 2019; Castanera et al., 2021). *Megalosauripus* tracks
402 are characterized as being large and gracile in contrast to coeval robust and giant tracks
403 such as *Jurabrontes curtedulensis* Marty, Belvedere, Razzolini, Lockley, Paratte, Cattin,
404 Meyer, 2018 (Fig. 6H) or *Iberosauripus grandis* Cobos, Lockley, Gascó, Royo-Torres,
405 Alcalá, 2014 (Fig. 6I), the latter of which is also identified in Tithonian-Berriasian units
406 of the Iberian Range (Cobos et al., 2014; Castanera et al., 2015; Marty et al., 2018;

407 Belvedere et al., 2019). Two ichnospecies of *Megalosauripus* are currently considered
408 valid (Razzolini et al., 2017; Belvedere et al., 2019; Meyer et al., 2021): *M.*
409 *uzbekistanicus* Lockley, Meyer, & Santos, 1996 (Fig. 6F) and *M. transjuranicus*
410 Razzolini, Belvedere, Marty, Paratte, Lovis, Cattin, & Meyer, 2017 (Fig. 6G). The *Los*
411 *Corrales del Pelejón* tracks show greater similarities with *M. transjuranicus*, especially
412 in their gracility and the rounded heel mark morphology. A diagnostic feature of *M.*
413 *uzbekistanicus* is its elongated heel impression (Lockley et al., 2000), whereas in *M.*
414 *transjuranicus* the heel impression is circular and rounded, and generally has twice the
415 width of the rest of the dIV impression. In the tracks from *Los Corrales del Pelejón*
416 with high MP values that do have a characteristic circular and rounded heel pad
417 impression (e.g., CP1.1; CP1.4, Fig. 5), this is not as wide as in *M. transjuranicus* (the
418 width is around 1.5 times the width of dIV). It should be noted that these tracks are
419 slightly smaller than *M. transjuranicus*. This would be a difference with respect to both
420 ichnospecies of *Megalosauripus* since generally *Megalosauripus* tracks are larger than
421 35-40 cm (Fanti et al., 2013; Razzolini et al., 2017).

422

423 Distinguishing between *Eubrontes* and *Megalosauripus* can be difficult when the tracks
424 do not have high MP values. Recently, Lockley et al. (2021) suggested that the two
425 ichnotaxa might differ in the length of digit III with respect to the length of the
426 footprint, *Eubrontes* having a longer digit. Xing et al. (2021a) provide copious data on
427 this parameter in different *Eubrontes*-like tracks, showing a variation from 0.57 to 0.71.
428 The authors propose this ratio to quantify digitigrady and indicate that it is also
429 quantitatively related to the presence or absence of a digit II metatarsal phalangeal pad.
430 In the case of *Los Corrales del Pelejón* (see Table 1, S4), the values of this ratio vary
431 from 0.67 (CP3.6) to 0.81 (CP2.6). In the best-preserved tracks, the ratios are between
432 0.70 (CP3.3) and 0.75 (CP5.3). As already mentioned, the tracks do not show any sign
433 of the impression of the digit II metatarsal phalangeal pad, so attribution to a *Eubrontes*-
434 related ichnotaxon is not justified. This is also reinforced by the length/width ratio and
435 the mesaxony, *Eubrontes*-like tracks having generally lower values in both parameters
436 (see S4).

437

438 A large, rounded heel pad impression is also a diagnostic feature of *Asianopodus*.
439 *Asianopodus pulvinicalx* Matsukawa, Shibata, Kukihara, Koarai, & Lockley 2005, the
440 type ichnospecies, was described from the Valanginian-Barremian of Japan (Fig. 6J).

441 This ichnotaxon is diagnosed by a “small to medium sized tridactyl, mesaxonic and
442 subsymmetrical track with distinct bulbous heel impression. Track is longer than wide.
443 The digital divarication angles are rather narrow” (Matsukawa et al., 2005).
444 Subsequently, Li et al. (2011) described a second ichnospecies, *A. robustus* Li 2011
445 (Fig. 6K), from the Lower Cretaceous of Inner Mongolia. The main differences of this
446 ichnospecies are its size and a separated heel pad impression. A third ichnospecies, *A.*
447 *niui* Li, Jiang, & Wang, 2020 (Fig. 6L), was defined by Li et al. (2020) but subsequently
448 designated a *nomen dubium* (Xing et al., 2021b, 2021c). Xing et al. (2021c) described
449 another ichnospecies, *A. wangi* Xing, Lockley, Mao, Klein, Gu, Bai, Qiu, Liu, Romilio,
450 Scott Parsons IV & Wan 2021, from the Berriasian of China (Fig. 6K), characterized by
451 higher mesaxony and a longer digit III than the other ichnospecies. *Asianopodus*-like
452 tracks have also been described in the Lower Cretaceous of Mongolia and China (Xing
453 et al., 2014) and Argentina (Heredia et al., 2020). The overall dimensions (FL/FW ratio
454 and mesaxony) of the *Asianopodus* ichnospecies are slightly different (see S4) from
455 those of the *Los Corrales del Pelejón* tracks (1.43-1.6 and 0.43-0.67, in the best-
456 preserved tracks, see Table 1) and vary between the ichnospecies (1.44/0.45 in *A.*
457 *pulvinicalx*; 1.23/0.40 in *A. robustus*; 1.7/0.64 in *A. wangi*). In the *Los Corrales del*
458 *Pelejón* tracks, these values vary between those of *A. pulvinicalx* (e.g., CP2) and *A.*
459 *wangi* (e.g., CP1.4) (see Table 1, Table S1). Razzolini et al. (2017) noted that *M.*
460 *transjuranicus* and *Asianopodus* have some features in common regarding the
461 metatarsophalangeal pad area and argued that in the latter this is located in a more
462 central position and separated from the digit impressions (a feature not seen in *A.*
463 *wangi*), the track being more symmetrical. Xing et al. (2021c) also noted the similarities
464 between the two ichnotaxa, emphasizing that the main differences are in the heel pad,
465 which is located “rather laterally to the digit III axis” in *Megalosauripus* and “in
466 continuation with digit III” in *Asianopodus*. The previous considerations suggest that
467 the medium to large *Los Corrales del Pelejón* tracks are more similar to *M.*
468 *transjuranicus* and *Asianopodus wangi* than to any other ichnotaxa, although they do
469 not strictly have all the diagnostic features of either of them. It is interesting to note that
470 the best-preserved footprints from *Los Corrales del Pelejón* only show slight variations
471 in the parameters despite the differences in the MP values associated with the track-
472 bearing layers where they are preserved (tracks and shallow undertracks, with just a cm
473 of difference between the layers in which they are preserved) (see the previous section
474 and Fig. 3). Nonetheless, they show considerable variations in MP even within the same

475 trackway, and only CP1.4 has an MP value higher than 2. In the light of these data, the
476 tracks are tentatively classified as *M. cf. transjuranicus*. This attribution is also
477 consistent with the length/width ratio and mesaxony as compared with the main
478 theropod ichnotaxa in a bivariate plot (see Supplementary data S4), although the values
479 from both *M. transjuranicus* and *Asianopodus* overlap partially. This discussion opens a
480 new window onto the question of how properly to distinguish between *M.*
481 *transjuranicus* (an ichnotaxon typical of the Kimmeridgian-Berriasian interval of
482 Europe) and *Asianopodus* (an ichnotaxon typical of the Lower Cretaceous of Asia).

483

484 As regards the small-sized theropod (CP4) morphotype, just a few small-sized theropod
485 ichnotaxa have been described in the Kimmeridgian-Berriasian interval of Europe. The
486 main ichnotaxa identified in the Kimmeridgian-Tithonian include *Grallator*,
487 *Carmelopodus*, *Wildeichnus*, cf. *Jialingpus*, and *Therangospodus*-like tracks (see
488 Castanera et al., 2016b, 2018a and references therein). In Berriasian areas, by contrast,
489 identified small-sized tridactyl theropod ichnotaxa are almost absent (e.g. Hernández-
490 Medrano et al., 2008; Hornung et al., 2012), with the exception of *Kalohipus*
491 *bretunensis* Fuentes Vidarte and Meijide Calvo 1998 (Fig. 6R). This latter ichnotaxon
492 and the small-sized theropod (CP4) morphotype resemble tracks included in
493 Grallatoridae (Lull, 1904; see Melchor et al., 2019). According to the latter authors,
494 these footprints are characterized by moderate to marked elongation ($FL/FW > 1.50$)
495 and mesaxony. The morphological quality of CP4 is rather low, but the tracks meet
496 these parameters. Grallatorid tracks are common in the Kimmeridgian-Berriasian
497 successions of the Iberian Peninsula (Castanera et al., 2015, 2016b, 2021), including the
498 aforementioned *Kalohipus bretunensis* (Fig. 6R) and *Grallator* isp. (Fig. 6S). The main
499 differences between them lie in mesaxony and the FL/FW ratio. The values of CP4 are
500 more similar to those of *Kalohipus*, but taking into account the low MP values of the
501 CP4 tracks they are classified as Grallatoridae indet.

502

503 The tracks of the ornithopod trackway (CP7) have a very low MP value except for
504 CP7.4. This track has many of the diagnostic features of the ichnofamily
505 Iguanodontipodidae (sensu Díaz-Martínez et al., 2015), such as one pad impression in
506 each digit and the heel, the pads being longer than wide, and also well-developed
507 notches in the proximal part of digit II and digit IV. On the other hand, the track is
508 slightly longer than wide (not as wide as or wider than long). The track also has

509 diagnostic features of the ichnogenus *Iguanodontipus*, such as a small, rounded, and
510 centered heel impression that is narrow. Although the preservation of the heel mark is
511 rather poor, it is possibly similar in width to the proximal part of digit III. Castanera et
512 al. (2022) suggested that this track “can be considered as *Iguanodontipus*-like”.
513 *Iguanodontipus*-like tracks (Fig. 6T-6V) have been described in a variety of European
514 Berriasian localities, including England (Sarjeant et al., 1998 and references therein),
515 Germany (Dietrich, 1927; Hornung et al., 2012, 2016), and Spain (Castanera et al.,
516 2013). Díaz-Martínez et al. (2015) compiled information on this ichnotaxon and
517 concluded that *Iguanodontipus burreyi* Sarjeant, Delair, & Lockley 1998 (Fig. 6T-V) is
518 the only valid ichnospecies within *Iguanodontipus*. Subsequently, Piñuela et al. (2016)
519 described new tracks (Fig. 6W) from the Upper Jurassic of Asturias (Spain) and
520 questioned the validity of *Iguanodontipus* due to the poor preservation of the holotype,
521 even suggesting that the trackmaker might not be an ornithopod. New tracks assigned to
522 Iguanodontipodidae have also been described in the Upper Jurassic of Portugal (Fig.
523 6X, Castanera et al., 2020). Given the current state of knowledge, therefore, a review of
524 the type and the referred material of *Iguanodontipus burreyi* is needed in order properly
525 to classify the CP7 tracks, and to understand 1) whether *Iguanodontipus* is a
526 monospecific ichnogenus, and 2) whether the stratigraphic range of *I. burreyi* would be
527 restricted to the Berriasian of Europe. In the light of this discussion and the fact that
528 track CP7.4 shows slight differences with respect to the diagnostic features of the
529 emended diagnosis proposed by Díaz-Martínez et al. (2015), we classify the CP7 tracks
530 as cf. *Iguanodontipus* isp. Even though the tracks from *Los Corrales del Pelejón* could
531 not be assigned with confidence to a specific ichnospecies/ichnogenus and most of them
532 are classified in open nomenclature, the ichnoassemblage is of particular interest since it
533 provides new data that shed light on whether or not there might be an ichnofaunal
534 change across the Tithonian-Berriasian boundary. In the current state of knowledge,
535 *Asianopodus* and *Iguanodontipus* are restricted to the Lower Cretaceous of Asia and
536 Europe respectively, so further work is needed to ascertain whether these ichnotaxa are
537 already present in the Late Jurassic (Kimmeridgian/Tithonian) or whether there might
538 be a change in both theropod (*Megalosauripus transjuranicus*/*Asianopodus*) and
539 ornithopod tracks (unnamed Iguanodontipodidae/*Iguanodontipus*) through the
540 Jurassic/Cretaceous (Tithonian-Berriasian) transition.
541 The identity of the trackmakers of the trackways is especially difficult to ascertain due
542 to the poor osteological record of theropods and ornithopods in the Tithonian-

543 Valanginian interval in the Maestrazgo and South Iberian basins. The sauropod
544 *Aragosaurus ischiaticus* Sanz, Buscalioni, Casanovas, & Santafé, 1987 is the only
545 dinosaur formally named in the Berriasian of the Maestrazgo Basin (Sanz et al., 1987;
546 Canudo et al., 2012; Royo-Torres et al., 2014). Other dinosaur remains have been
547 assigned to dromaeosaurs and stegosaurs (Ruiz-Omeñaca et al., 2004; Pereda
548 Suberbiola et al., 2005). Theropod remains assigned to large tetanurans (possible
549 megalosaurids), middle-sized allosaurids, and small dromaeosaurs have been described
550 on the basis of their teeth in slightly older (Tithonian) deposits in both basins (Canudo,
551 2006; Gascó et al., 2012; Cobos et al., 2014). Berriasian ornithopod remains are absent
552 in the area although Kimmeridgian-Tithonian remains have been recovered in the South
553 Iberian Basin (Sánchez Fenollosa et al., 2022, 2023 and references therein).

554

555 The Berriasian/Valanginian theropod record in Europe is also quite sparse. Remains of
556 the dromaeosaur *Nuthetes destructor* have been described in the Berriasian of the UK
557 (Milner, 2002) and France (Pouech et al., 2014). Turmine-Juhel et al. (2019) reported
558 teeth of theropod dinosaurs assigned to *Baryonyx* and to an allosauroid from the
559 Valanginian Wadhurst Clay Formation. The largest European sample of theropod
560 remains comes from the Berriasian of France, concretely from Angeac-Charente. Four
561 different non-avian theropod taxa have been described based on teeth and postcranial
562 material: cf. *Nuthetes* sp., Tyrannosauroida indet., Megalosauridae? indet., and
563 Ornithomimosauria indet. (Allain et al., 2022). Traditionally, Late Jurassic
564 *Megalosauripus transjuranicus*-like tracks have been associated with allosauroids or
565 ceratosaurs as their most plausible trackmakers (Razzolini et al., 2017; Rauhut et al.,
566 2018; Castanera et al., 2021). With the data currently available, it is not possible to
567 associate the *Los Corrales del Pelejón* tracks with any of the abovementioned groups,
568 since none of the criteria proposed by Carrano and Wilson (2001) for correlations
569 between tracks and trackmakers (synapomorphy-based, phenetic or coincidence
570 correlations) can be confidently applied to the studied tracks.

571

572 As regards the candidate trackmaker for the ornithopod trackway CP7, Angeac-
573 Charente is also the site with the highest diversity of ornithopod remains from the
574 Berriasian of Europe. Remains from three different ornithopod taxa have been described
575 in this site: teeth belonging to the heterodontosaurid *Echinodon* sp. and
576 Hypsilophodontidae indet. and teeth and postcranial material assigned to

577 ankylopollexians (Allain et al., 2022). The former two taxa are too small to have
578 produced the CP7 tracks, whereas the ankylopollexians would fit better. However, the
579 footprint length (FL > 35 cm) is slightly higher than the estimates calculated for the Late
580 Jurassic taxa *Camptosaurus dispar* (FL = 26 cm; Gierlinski et al., 2009) and
581 *Oblitosaurus bunnueli* (FL = 29-31 cm; Sánchez Fenollosa et al., 2023). *Iguanodontipus*
582 tracks have usually been associated with Ankylopollexia or basal Styracosterna (Díaz-
583 Martínez et al., 2015), so the presence of ankylopollexians in the slightly older deposits
584 of the nearby South Iberian Basin (Sánchez Fenollosa et al., 2022, 2023) and in the
585 Berriasian of Europe (Agneac; Allain et al., 2022) suggests by the coincidence
586 correlation (Carrano and Wilson, 2001) that an ankylopollexian is the most plausible
587 trackmaker for the CP7 tracks.

588

589 *5.2 Paleoenvironmental and paleoecological influence on the dinosaur trackway* 590 *orientations*

591

592 As previously mentioned, (see section 4.1), all the dinosaurs have been interpreted as
593 impressing their footprints on layer 4 (the interpreted tracking surface), suggesting that
594 all the trackways were coeval. This interpretation is significant for understanding
595 whether the trackway orientation might show any paleoenvironmental or
596 paleoecological influence. Parallelism in dinosaur trackways has usually been used to
597 infer gregarious behavior (e.g.: Ostrom, 1972; Castanera et al., 2011, 2014; García-Ortíz
598 and Pérez-Lorente, 2014). In addition, some reports (Moratalla and Hernán, 2010;
599 Razzolini et al., 2016; Getty et al., 2017) have also shown the importance of
600 paleogeographical barriers such as ancient shorelines (either coastal or lacustrine) for
601 the orientation of the trackways. The latter authors have shown the importance of not
602 assuming either gregariousness or a paleogeographic barrier solely from the parallelism
603 of the trackways. The dinosaur trackway orientations among the medium and large-
604 sized theropod trackmakers of the *Los Corrales del Pelejón* tracksite show both a clear
605 bimodal pattern (NE-SW) and a multidirectional but perpendicular pattern (NW-SE),
606 where the ornithopod trackway CP7 and the small-sized theropod trackway CP4 are
607 included (Fig. 4). The orientation of the individual tracks (CP8, CP10 and CP11) also
608 shows rather similar directions (see Fig. 4B). Generally, a bimodal orientation pattern is
609 associated with paleogeographic constraints/natural barriers such as shorelines, river-
610 banks or even basin configuration (Lockley et al., 1986; Thulborn, 1990; Lockley,

611 1991; Moratalla and Hernán, 2010; Razzolini et al., 2016), especially when the
612 trackways have similar directions but opposite orientations, as in the case of trackways
613 CP1-CP2 (and tracks CP8 and CP11) vs CP5 (and track CP10) and CP3 vs CP6.
614 Cuenca-Bescós et al. (1993) highlighted that the latter two trackways were subparallel
615 but were moving in opposite directions, so a geographic barrier would be a possible
616 explanation for their orientation. Ostrom (1972) even suggested “that the presence of
617 parallel trackways in opposite directions is a starting point for suspecting the existence
618 of some kind of physical barrier that affected the passage of individuals.” The tracks
619 formed on layer 4 can be compared with the orientation of the ripple crests of layers 2
620 and 3, as the entire track-bearing package of layers 1 to 4 formed in an ephemeral pond
621 (see section 4.1). In particular, the orientation of trackways CP1, CP2, C5, (and roughly
622 CP3 and CP6 and the individual tracks CP8, CP10 and CP11) is similar to that of the
623 crest of the ripple marks (NE-SW) in layers 2 and 3 (Figs. 2B, 3B). Given that the wave
624 ripples probably formed parallel to the shoreline of the ephemeral pond, the medium
625 and large theropods may have walked across the site parallel to this shoreline whereas
626 the ornithopod and the small theropod walked perpendicular to it. Despite the shortness
627 of the trackways, the six theropod trackways show a directional pattern (linear
628 trackways), as a consequence of the dinosaurs crossing the site with no evidence of
629 milling behavior (Cohen et al., 1993). Taking into account these data and the fact that
630 the trackways differ in their speed values (see Table S1), it is thus plausible that the
631 orientations of the trackways do show a paleoenvironmental influence. As regards any
632 possible paleoecological influence, it should be highlighted that CP1 and CP2 show a
633 parallel configuration and a close inter-trackway space (just a meter); CP2 and CP3 are
634 subparallel and show a rather similar speed value (see Table S1). However, the slight
635 differences in speed values, preservation, size and the inferred paleoenvironmental
636 influence preclude the suggestion that these theropods were walking together, so there is
637 no clear evidence of an ethological/paleoecological influence.

638

639 **6. Conclusions**

640

641 This analysis of the *Los Corrales del Pelejón* dinosaur tracksite in Galve has provided
642 significant new data on the preservation and ichnotaxonomy of the tracks and the
643 paleoenvironmental influence on the orientation of the dinosaur trackways. The
644 tracksite is located in a sandstone package composed of four cm-thick sandstone layers,

645 with wave ripples and simple grazing trails and burrows of the *Mermia* ichnofacies,
646 representing splay deposits accumulated in an ephemeral pond. All the dinosaurs
647 impressed their footprints in the uppermost layer, but the trackways are preserved in
648 different layers, either as true tracks (layer 4) or shallow undertracks (layers 1-3).
649 Despite the differences in morphological preservation, the tracks do not show great
650 variation in their morphometric data, probably due to the reduced thickness of the
651 layers. The tracks are assigned to *M. cf. transjuranicus* and Grallatoridae indet.
652 (produced by indeterminate theropods) and cf. *Iguanodontipus* isp. (possibly produced
653 by an ankylopollexian ornithopod). Analysis of the trackway orientations and
654 paleocurrents indicates that the dinosaurs crossed the site individually and at slightly
655 different speeds. Concretely, the medium to large theropods (CP1-CP3, CP5-CP6) were
656 possibly walking parallel to the shoreline of the ephemeral pond, whereas the small
657 theropod (CP4) and the ornithopod (CP7) were walking perpendicular to it. This
658 paleogeographic constraint was thus a considerable influence on the dinosaur trackway
659 orientations.

660

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677

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1009 **Figure captions**

1010 **Figure 1:** Geographical and geological setting of the *Los Corrales del Pelejón* tracksite.

1011 A) Orthophoto showing the distribution of the lithostratigraphic units outcropping in the
1012 Galve syncline. B) Geological setting of the Maestrazgo Basin in northeast Spain
1013 showing the distribution of the sub-basins (modified from Martín-Chivelet et al., 2019).
1014 C) Synthetic log showing the stratigraphy (based on Aurell et al., 2016, 2019) of the
1015 Galve sub-basin.

1016

1017 **Figure 2:** Stratigraphic and sedimentological analysis of the lower part of the Galve Fm

1018 in the studied area. A) Facies distribution and correlation between the *Pelejón* and *Los*
1019 *Corrales del Pelejón* sections, indicating the sandstone packages G1 to G7 used as
1020 reference levels for lateral correlation. Note the normal fault controlling sedimentation
1021 in the lowermost part (see packages G1 to G3) and the location of the *Los Corrales del*
1022 *Pelejón* tracksite in sandstone package G6. B) Paleoenvironmental interpretation of the
1023 studied successions and the broader-scale sedimentary context in the Galve sub-basin.
1024 The location of the *Los Corrales del Pelejón* tracksite and paleocurrent data from
1025 different facies are indicated in the paleoenvironmental scheme (see also Supplementary
1026 data S1 and S2).

1027

1028 **Figure 3:** Sedimentological context of the *Los Corrales del Pelejón* tracksite beds. A)

1029 Detailed log of the tracksite beds, indicating the four sedimentary layers where the
1030 dinosaur tracks are preserved. B-C) Outcropping layers in the tracksite in the different
1031 sectors. Note that mainly layer 1 is outcropping in Sector B due to current erosion (see
1032 also log in A), whereas layers 1 to 4 crop out in Sector A. Nevertheless, in the upper
1033 area of Sector A, the ripples in layers 2 and 3 disappear laterally, so that these layers are
1034 laterally equivalent to the uppermost layer 1 in this sector (see Fig. 3A). Notice peaked-
1035 and rounded-crest wave ripples in layers 2 and 3, respectively, and the tracks of
1036 trackways CP1 and CP2 on layers 4 and 1, parallel to the ripple crests. D) Detailed

1037 picture of C. Note the invertebrate traces on layers 3 and 4 and the lateral disappearance
1038 of rippled layer 3 (see also log in A). E) Detailed picture of the upper area of Sector A.

1039

1040 **Figure 4:** Tracks and trackways of the *Los Corrales del Pelejón* tracksite. A) Solid
1041 three-dimensional model (obtained with ParaView) of the surface of the tracksite. B)
1042 Sketch map of the tracksite. Note that the tracks have been numbered consecutively,
1043 including missing tracks. Note also that the sketch map in B has not been directly drawn
1044 from A. C) Historic picture taken in 1992 of track CP1.4. D) Rose diagram showing the
1045 orientation of the midline of the trackways CP1-CP7. Note that the orientations of the
1046 trackways represented in the diagram have been measured from the map.

1047

1048 **Figure 5:** Dinosaur tracks of high morphological quality from the *Los Corrales del*
1049 *Pelejón* tracksite. *Megalosauripus* cf. *transjuranicus* (A-J), Grallatoridae indet. (K), cf.
1050 *Iguanodontipus* isp. (L). A) CP1.1. B) CP1.4. C) CP2.2. D) CP2.4. E) CP3.3. F) CP3.7.
1051 G) CP5.1. H) CP5.3. I) CP6.4. J) CP9. K) CP4.2. L) CP7.4. Scale bars = 15 cm (K), 25
1052 cm (A, B, F, J), 30 cm (E, G, H, L), 35 cm (C, D, I).

1053

1054 **Figure 6:** A) *Eubrontes giganteus* Hitchcock, 1845 (redrawn from Olsen et al., 1998);
1055 B) *Eutynichnium lusitanicum* Nopcsa, 1923 (redrawn from Lockley et al., 2000); C)
1056 *Megalosauropus broomensis* (Colbert and Merrilees, 1967); D) *Bueckeburgichnus*
1057 *maximus* (redrawn from Lockley, 2000); E) *Eubrontes nobitai* (redrawn from Xing et
1058 al., 2021a); F) *Megalosauripus uzbekistanicus* (redrawn from Lockley et al., 1996); G)
1059 *Megalosauripus transjuranicus* (redrawn from Razzolini et al., 2017); H) *Jurabrontes*
1060 *curtedulensis* (redrawn from Marty et al., 2018); I) *Iberosauripus grandis* (redrawn
1061 from Cobos et al., 2014); J) *Asianopodus pulvinicalx* (redrawn from Matsukawa et al.,
1062 2005); K) *Asianopodus robustus* (redrawn from Xing et al., 2021b); L) *Asianopodus*
1063 *niui* (redrawn from Xing et al., 2021b); M) *Asianopodus wangi* (redrawn from Xing et
1064 al., 2021c); N) CP1.1; O) CP1.4; P) CP2.4; Q) CP3.7; R) *Grallator* isp. from the Late
1065 Jurassic of Asturias (redrawn from Castanera et al., 2016b); S) *Kalohipus bretunensis*
1066 from the Berriasian of Spain (redrawn from Castanera et al., 2015, after Fuentes Vidarte
1067 and Meijide Calvo, 1998); T) *Iguanodontipus burreyi* (holotype, redrawn from Sarjeant
1068 et al., 1998); U) *Iguanodontipus burreyi* (previously *Wealdenichnites iguanodontoides*)
1069 (redrawn from Díaz-Martínez et al., 2015, after Dietrich, 1927); V) *Iguanodontipus*
1070 *burreyi* (previously *Iguanodontipus? oncalensis*) (redrawn from Castanera et al., 2013);

1071 W) unnamed ornithopod track from the Late Jurassic of Asturias (redrawn from Piñuela
1072 et al., 2016); X) Iguanodontipodidae from the Late Jurassic of Portugal (redrawn from
1073 Castanera et al., 2020); Y) CP7.4. Scale bars = 10 cm (A-Q), 5 cm (R-S).

1074

1075 **Table 1:** Measurements of the dinosaur tracks of the *Los Corrales del Pelejón* tracksite.
1076 MP, Morphological preservation value (following Marchetti et al., 2019); FL, footprint
1077 length; FW, footprint width; FL/FW, footprint length/footprint width ratio; LII, LIII,
1078 LIV, digit total length (from the tip to the heel pad impression); DIII, digit III length
1079 excluding the heel pad; WII, WIII, WIV, digit width; HPL, heel pad length; HPW, heel
1080 pad width. II[^]III, III[^]IV, II[^]IV, interdigital divarication angles; ATI, anterior triangle
1081 length; ATw, anterior triangle width; AT ratio (ATI/ATw (mesaxony). FL, FW, LII,
1082 LIII, LIV, DIII, WII, WIII, WIV, HPL, HPW, ATI, ATw, in cm. II[^]III, III[^]IV, II[^]IV in
1083 degrees (°). NP, not preserved. NM, not measured due to poor preservation. ? denotes
1084 uncertainty in the measurement.

1085

1086 **Supplementary data**

1087

1088 **S1:** Facies description and interpretation of red to ocherish mudstones, gray mudstones,
1089 and laminated and/or bioturbated sandstones. The stratigraphic location of sandstone
1090 packages (e.g., G4, G5, etc.), paleocurrent data, and the paleoenvironmental scheme are
1091 shown in Fig. 2 of the main text. Grain size results are in Supplementary data S3.

1092

1093 **S2:** Facies description and interpretation of cross-bedded sandstones and poorly bedded
1094 conglomerates. The stratigraphic location of sandstone packages (G5, G7 in A),
1095 paleocurrent data, and the paleoenvironmental scheme are shown in Fig. 2 of the main
1096 text. Grain size results are in Supplementary data S3.

1097

1098 **S3:** Grain size analysis of muddy and sandy facies of the lower part of the Galve Fm in
1099 the *Corrales del Pelejón* section, including the data from beds 1, 3 and 4 of the *Los*
1100 *Corrales del Pelejón* tracksite. For the location of samples and beds see Figs. 2A and 3
1101 of the main text.

1102

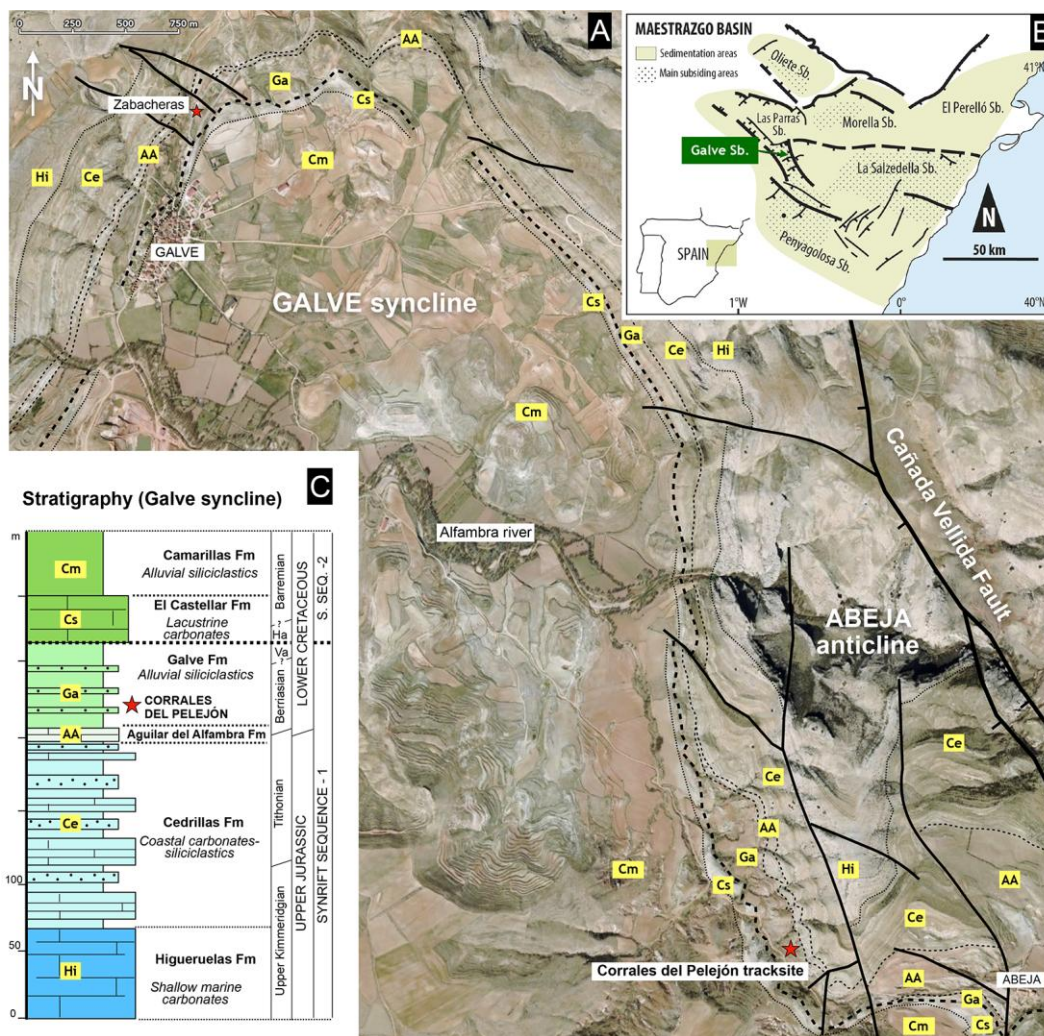
1103 **S4:** Bivariate graph plotting the footprint length/footprint width ratio against the
1104 mesaxony of the studied tracks with some of the main tridactyl theropod ichnotaxa

1105 mentioned in the text. Data taken from Lockley et al. (2021), Xing et al. (2021a),
 1106 Castanera et al. (2021) and references therein.

1107

1108 **Table S1:** Measurements of the dinosaur trackways. Orientation of the trackway. PLh,
 1109 pace length measured from the heel pad impression; PLt, pace length measured from the
 1110 tip of DIII; SLh, stride length measured from the heel pad impression; SLt, stride length
 1111 measured from the tip of DIII; FL, footprint length; h, height to the acetabulum; speed
 1112 following the Alexander (1976) and Ruiz and Torices (2013) formulas. All
 1113 measurements in meters.

1114



1115

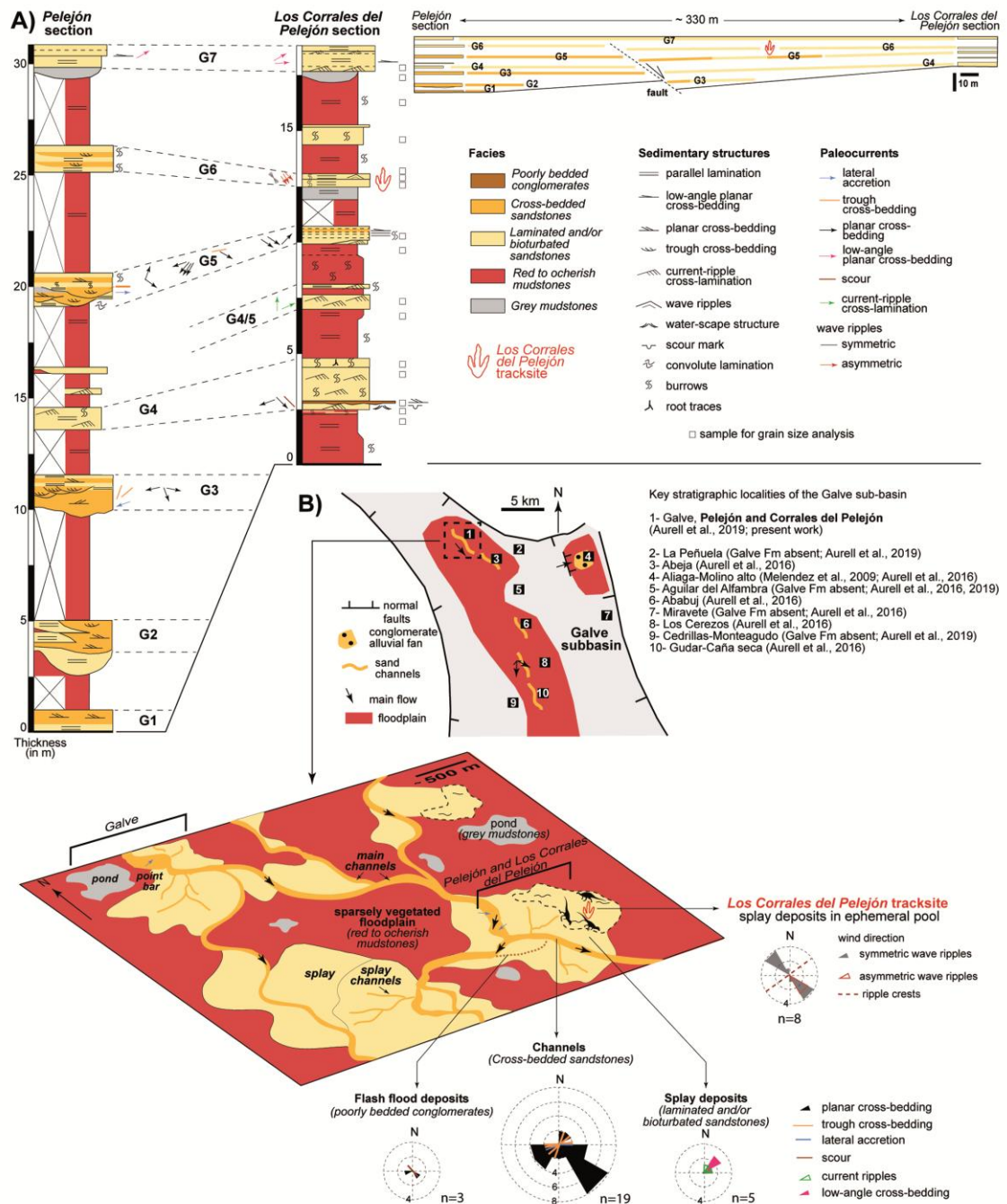
1116 Figure 1

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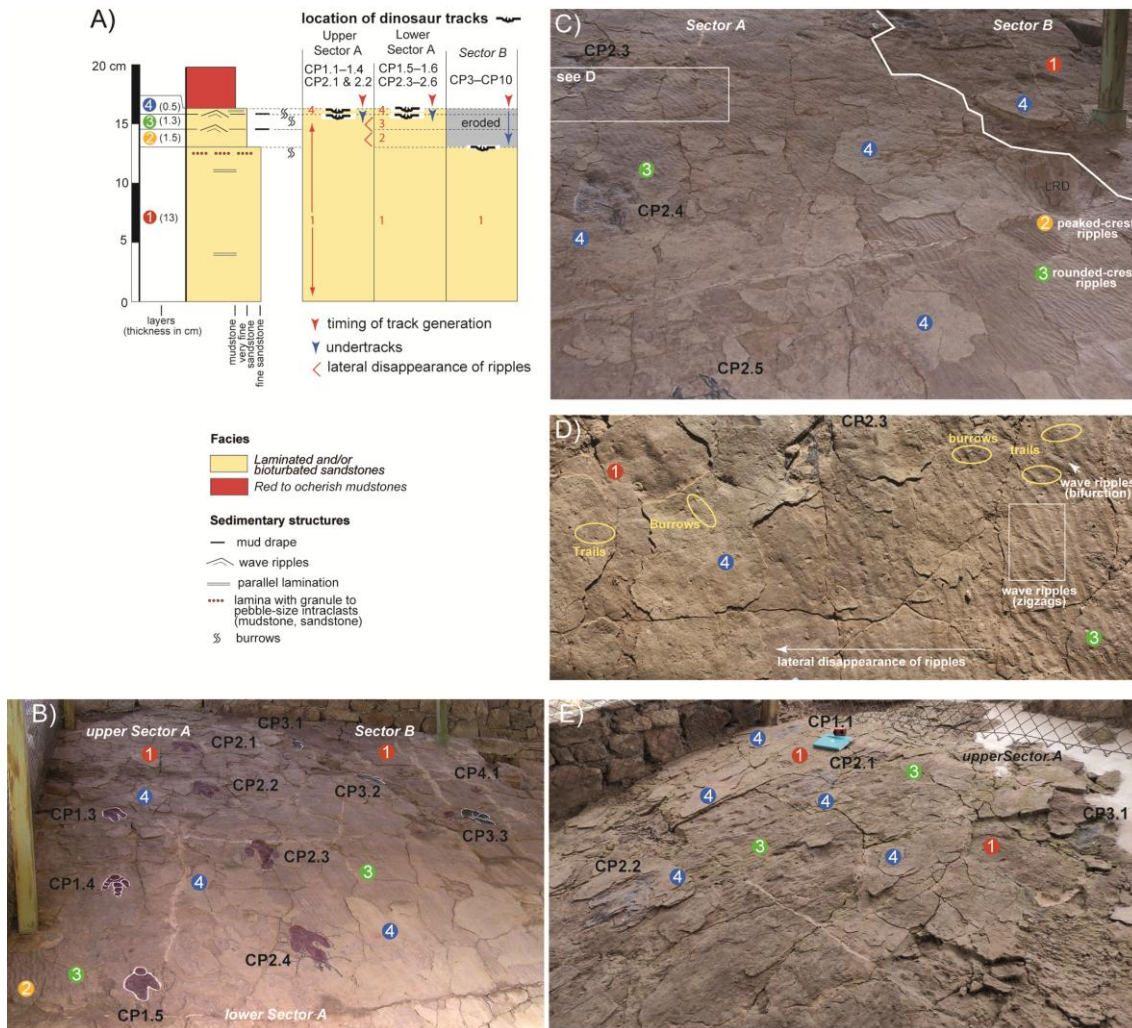
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1122 Figure 2

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1125 Figure 3

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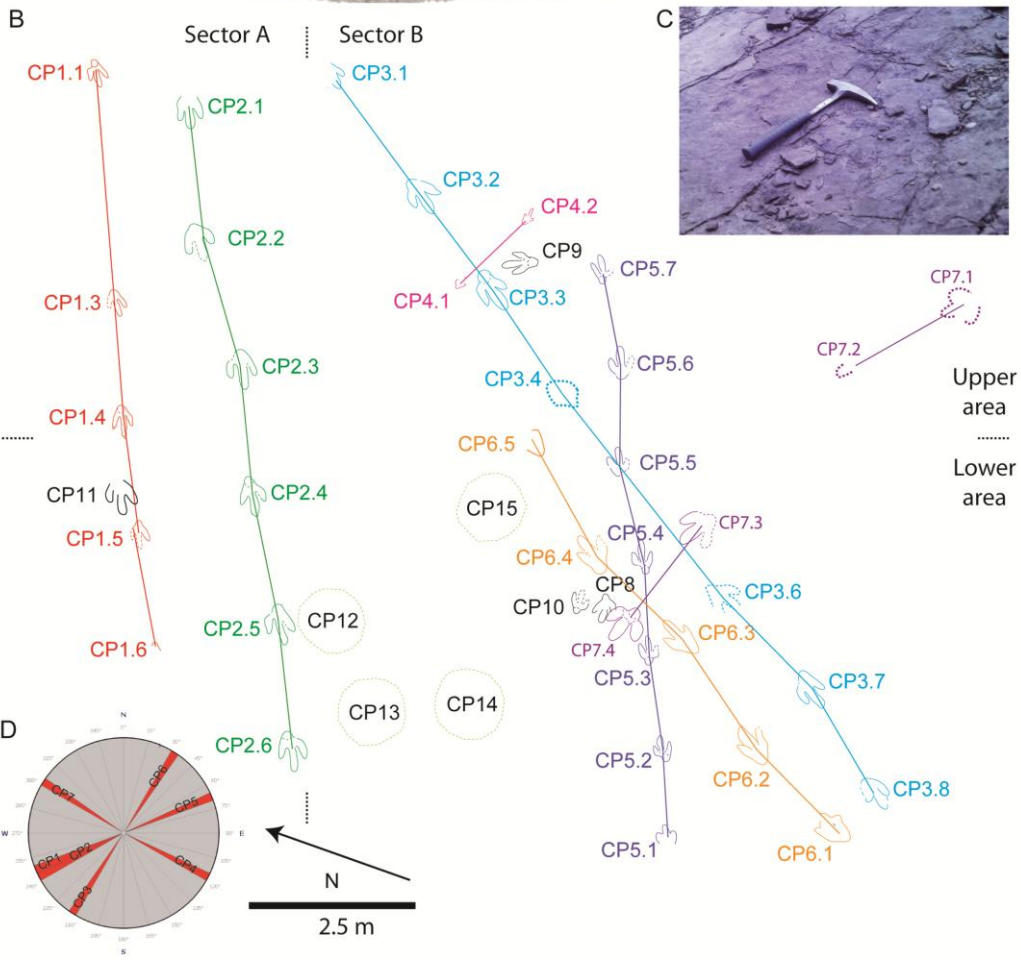
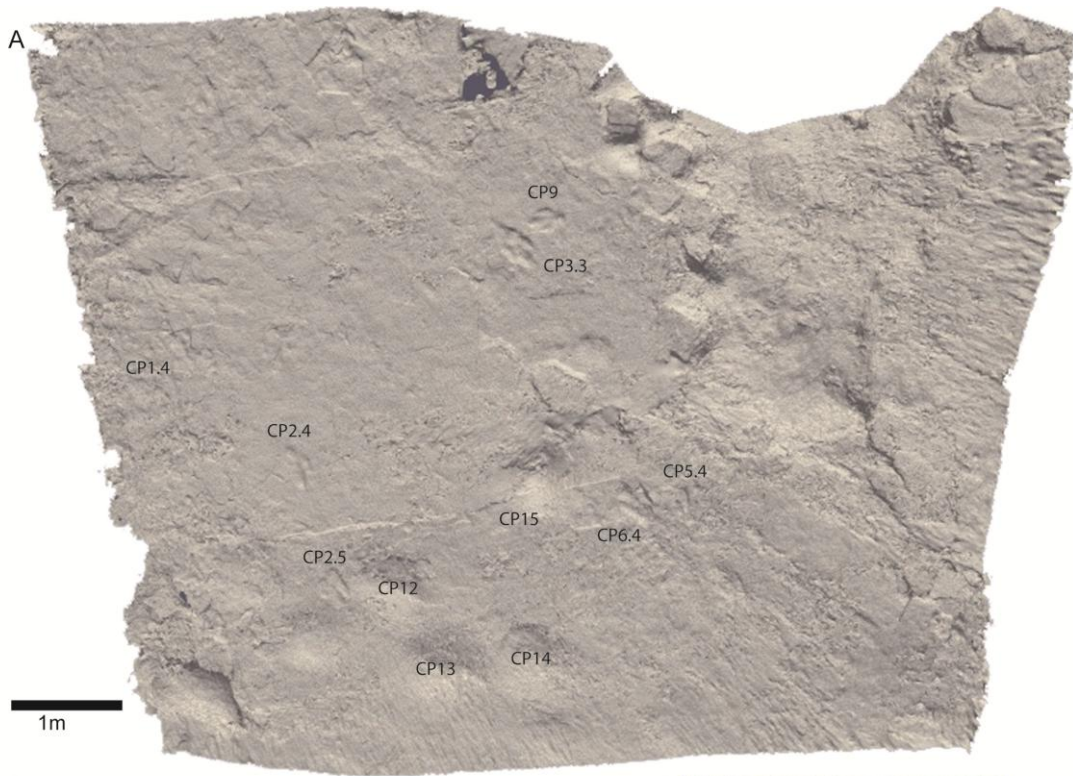
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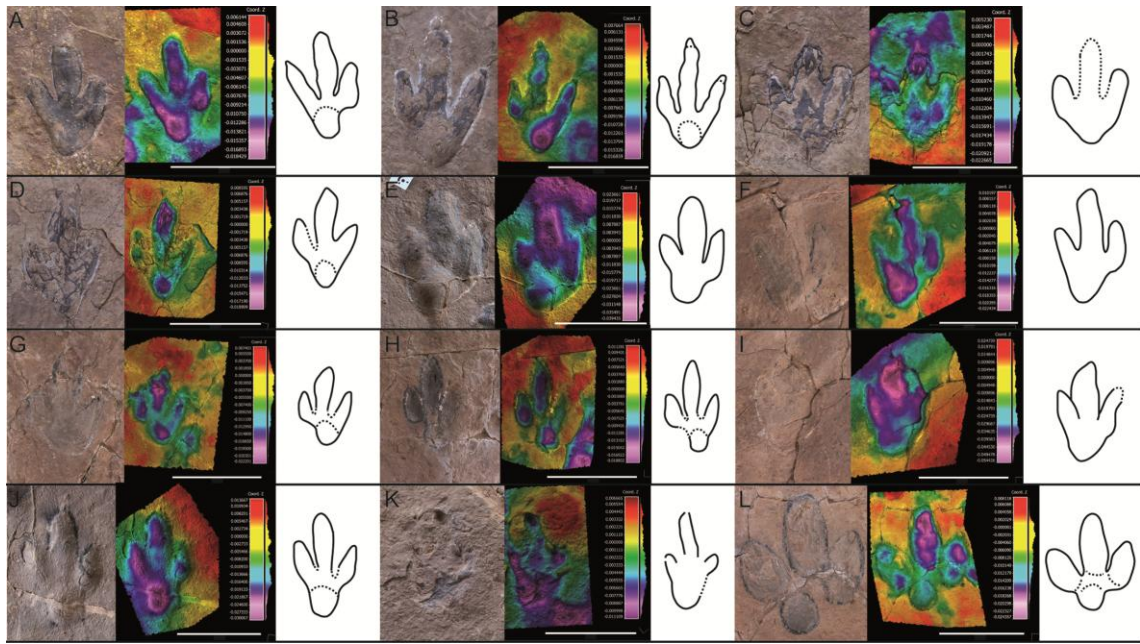
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1140 Figure 4

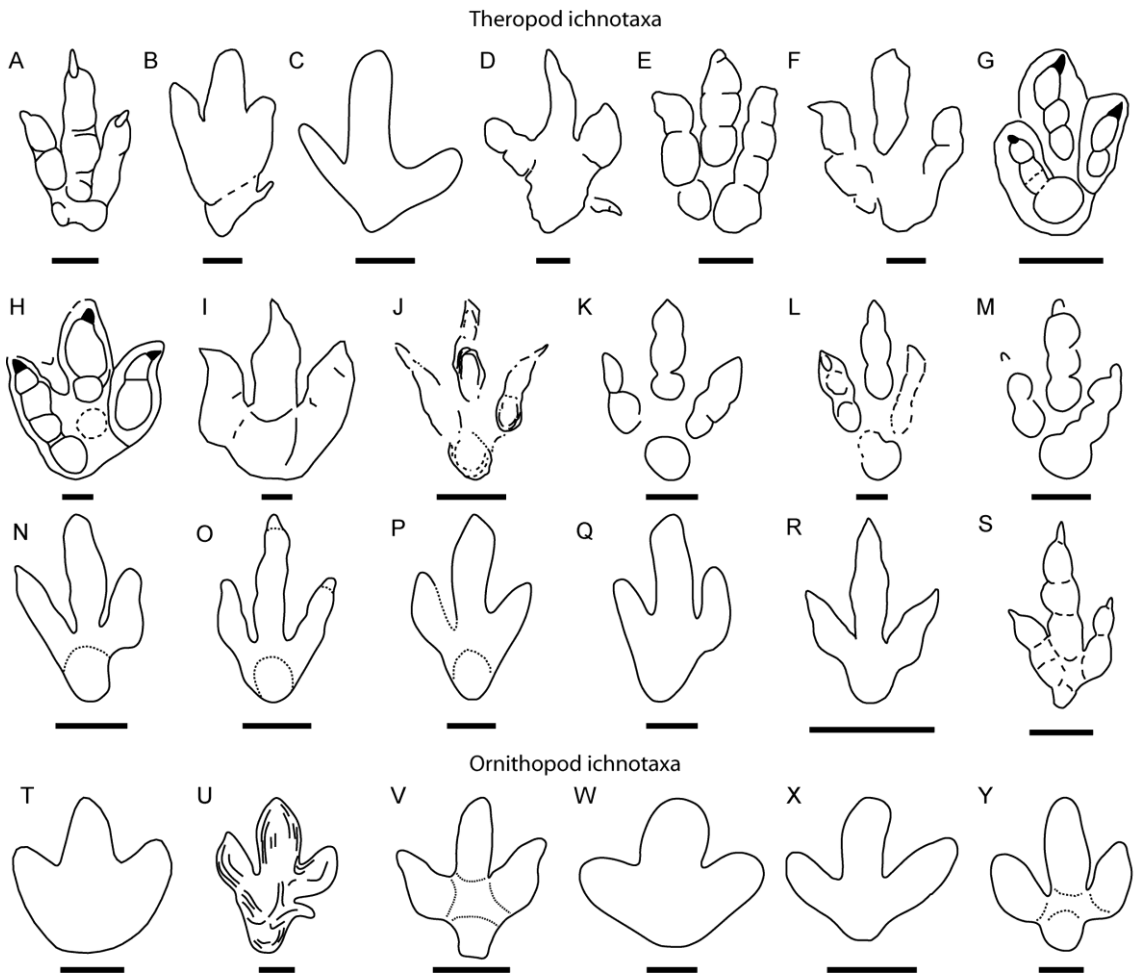
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1143 Figure 5


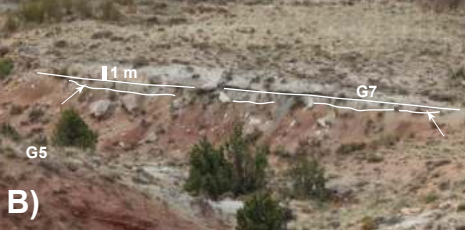
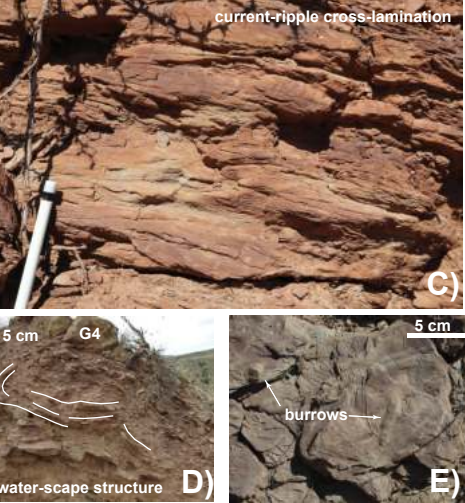
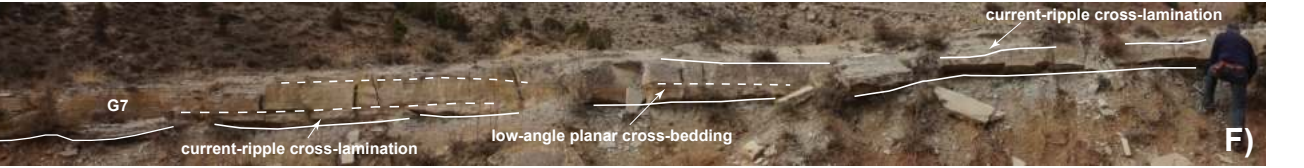

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1146

1147 Figure 6

Description	Interpretation	
<p>Red to ocherish mudstones</p> 	<p>Red to ocherish, locally white, mudstones (see red circles in A) with median grain size of medium silt (see S3), and local intercalated fine sandstones</p> <ul style="list-style-type: none"> - mudstones are stratified in laterally extensive tabular beds, a few dm- to 5 m-thick. They are massive or parallel laminated and have local burrows, root traces and mud cracks - fine sandstones are arranged in parallel or wavy cm-thick laminae <p>Occurrence: dominant facies</p>	<p>Floodplain fines: unchanneled flows when discharge exceeded the bank-full capacity of the channel network (e.g., Bridge, 2003; Cain and Mountney, 2009):</p> <ul style="list-style-type: none"> - mudstones: settling of suspended sediments during waning flows - fine sandstones: bedload transport under lower-flow regime conditions <p>Local root traces and mud cracks indicate very local vegetated areas and probably rapid sedimentation preventing soil development and desiccation</p>
<p>Gray mudstones</p> 	<p>Massive or parallel laminated gray mudstones (see white arrows in B) with median grain size of very fine silt (see S3), arranged in tabular or concave-plane beds, 0.5 m-thick and a few decimeters in lateral extension. Presence of crocodylomorph teeth</p> <p>Occurrence: very local; underlying laminated and/or bioturbated sandstones</p>	<p>Small ponds in the floodplain with stagnant waters; less likely mud-filled small channels (e.g., Makaske, 2001)</p>
<p>Laminated and/or bioturbated sandstones</p> 	<p>Fine sandstones (median grain size: very fine sand; see S3) stratified in dm-thick beds to 2.5 m-thick bed packages, including:</p> <ul style="list-style-type: none"> - Current-ripple cross-laminated sandstones with mud drapes (see C), burrows (see E), and local root traces, and upward-oriented water-scape structures and convolute beds - parallel-laminated sandstones, occasionally with low-angle planar cross-bedding, associated with the current-ripple cross-laminated beds (see F) - Massive sandstones, usually burrowed <p>Occurrence:</p> <ul style="list-style-type: none"> - Intercalated and pinching out to red to ocherish mudstones - Beds with parallel lamination locally observed laterally (attached) to cross-bedded sandstones 	<p>Unconfined sheet-like splay deposits emanating from the main fluvial channels (e.g., Burns et al., 2019) or from points where fluvial channels terminated on the alluvial plain (e.g., Tooth, 2000; Cain and Mountney, 2009). Beds laterally (attached) to cross-bedded sandstones would represent levee deposits:</p> <ul style="list-style-type: none"> - dominant bedload transport, under upper flow regime (parallel lamination) and low-flow regime (current-ripple cross lamination), and suspended load component (i.e. mud-drapes) (e.g. Hampton and Horton, 2007) - massive sandstones may represent rapid deposition (e.g., Cain and Mountney, 2009)
	<p> Los Corrales del Pelejón tracksite: see specific description and interpretation in main text</p>	

S1. Facies description and interpretation of red to ocherish mudstones, gray mudstones and laminated and/or bioturbated sandstones. Stratigraphic location of sandstone packages (e.g. G4, G5, etc), paleocurrent data and paleoenvironmental scheme are shown in Fig. 2 of main text. Grain size results are in Supplementary data S3.

References:

Bridge, J.S., 2003. Rivers and Floodplains: Forms, Processes, and Sedimentary Record. Wiley-Blackwell, Oxford, UK., 512 p.

Burns, C.E., Mountney, N.P., Hodgson, D.M., Colombera, L., 2019. Stratigraphic architecture and hierarchy of fluvial overbank splay deposits. Journal of the Geological Society 176, 629–649.

Cain, S.A., Mountney, N.P., 2009. Spatial and temporal evolution of a terminal fluvial fan system: the Permian Organ Rock Formation, South-east Utah, USA. Sedimentology 56, 1774–1800.

Hampton, B.A., Norton, B.K., 2007. Sheetflow fluvial processes in a rapidly subsiding basin, Altiplano plateau, Bolivia. Sedimentology 54, 1121–1147.

Makaske, B., 2001. Anastomosing rivers: a review of their classification, origin and sedimentary products. Earth-Science Reviews 53, 149–196.

Tooth, S., 2000. Downstream changes in dryland river channels: the Northern Plains of arid central Australia. Geomorphology 34, 33–54.

Description

Interpretation

Cross-bedded sandstones

Fine and medium sandstones in m-thick packages, including ribbons ($W:T < 15$) both isolated and offset stacked and narrow sheets ($15 > W:T < 100$); ($W:T$, width-thickness ratio, following Gibling, 2006):

- complex internal vertical stacking of planar and trough cross-bedding
- lateral accretion surfaces in the *Pelejón* section (Aurell et al., 2016)
- local conglomerates at the base

Occurrence:

- Intercalated in red to ocherish mudstones and changing laterally to laminated and/or bioturbated sandstones (see Fig. 2A in the main text)
- locally eroding laminated and/or bioturbated sandstones



Fluvial channels: SE-directed main fluvial channels (running roughly parallel to the orientation of the Galve sub-basin) and SW and NE-directed splay channels (see Fig. 2 in the main text)

Poorly bedded conglomerates



Matrix-supported conglomerates, with coarse sandstone matrix and unsorted subangular to subrounded, granule to pebble-size clasts of limestones (Aguilar del Alfambra Fm), sandstones and red mudstones. Local fish teeth and macrovertebrate bone fragments

Occurrence: very local; three individual lens-shaped beds (0.1- to 0.4 m-thick) overlying current-ripple cross-laminated sandstones and intercalated with massive and trough cross-bedded fine and medium sandstones, defining fining-upward and coarsening upward units

Slightly channeled erosional bases with scour marks and burrows on top

Flashflood deposits transporting extraclasts (Aguilar Fm limestones), intraclasts (mudstone rip-up clasts and sandstone clasts) and skeletal remains (Aurell et al., 2016):

- fining-upward and coarsening upward units indicate they likely were deposited by several flood events

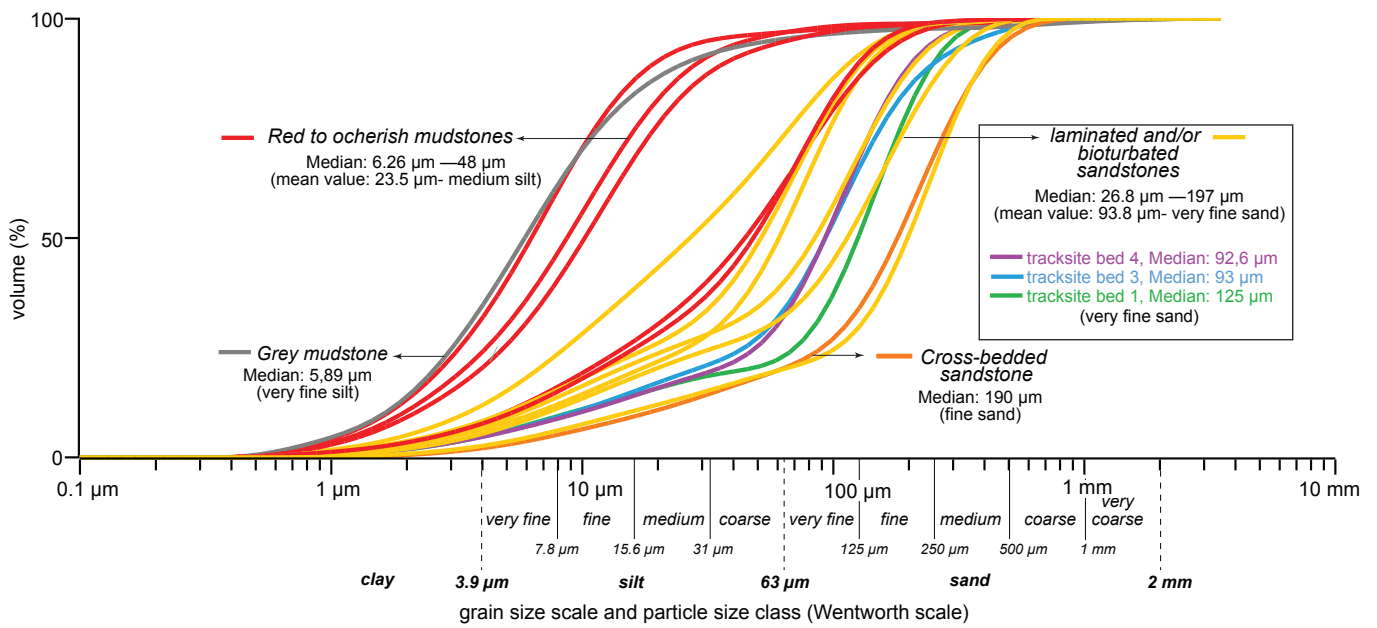
- scour marks and intercalated trough cross-bedded sandstones (i.e. migration of 2-D dunes at lower flow velocities) indicate a SE paleocurrent

S2. Facies description and interpretation of cross-bedded sandstones and poorly bedded conglomerates. Stratigraphic location of sandstone packages (G5, G7 in A), paleocurrent data and paleoenvironmental scheme are shown in Fig. 2 of main text. Grain size results are in Supplementary data S3.

References:

Aurell, M., Bádenas, B., Gasca, J. M., Canudo, J. I., Liesa, C. L., Soria, A. R., ... & Najes, L. (2016). Stratigraphy and evolution of the Galve sub-basin (Spain) in the middle Tithonian–early Barremian: implications for the setting and age of some dinosaur fossil sites. *Cretaceous Research*, 65, 138-162.

Gibling, R. (2006). Width and Thickness of Fluvial Channel Bodies and Valley Fills in the Geological Record: A Literature Compilation and Classification. *Journal of Sedimentary Research* 76 (5), 731–770.



S3. Grain size analysis of muddy and sandy facies of the lower part of the Galve Fm at the *Corrales del Pelejón* section, including the data from beds 1, 3, 4 of the *Los Corrales del Pelejón* tracksite. For location of samples see Figs. 2A and 3 of the main text.

TRACK	Left/ right	MP	FL	FW	FL/ FW	LII	LIII	DIII	LIV	WII	WIII	WIV	HPL	HPW	II^III	III^IV	II^IV	AT1	ATw	AT	DIII/FL
CP1.1	left	2	26	17.5	1.48	19	26	19	20	4	5	4	7	6.5	23	23	46	8.5	15	0.56	0.73
CP1.2	right	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP
CP1.3	left	1	25	16.5	1.51	17.5	25	18.5	20	4.5	5	5	6.5	6	23	21	44	7.5	13.5	0.55	0.74
CP1.4	right	2.5	28	17	1.64	19	28	20.5	20.5	4	5	4	7.5	6	22	25	47	9	15	0.6	0.73
CP1.5	left	1	26?	16.5	1.57	17.5	26?	20.5	20.5	4.5	5	5	5.5?	5?	22	24	46	9?	14	0.64	0.78
CP1.6	right	0.5	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP
CP2.1	left	1	31	25	1.24	23.5	30	NM	26.5	6	7.5	7	NP	NP	25	27	52	10	20.5	0.48	NM
CP2.2	right	1.5	35?	25.5	1.37	26	35?	NM	27	5.5	6	5.5	NP	NP	26	24	50	10.5?	21.5	0.48?	NM
CP2.3	left	1	36	24.5	1.46	26.5	36	NM	27	5.5	5.5	5	NP	NP	24	23	47	11.5	20	0.57	NM
CP2.4	right	2	37.5	26	1.44	28	37.5	28	29	6.5	7.5	6	9.5	7.5	23	24	47	11	22.5	0.48	0.74
CP2.5	left	2	34.5	24	1.43	25.5	34.5	NM	27	6	6.5	6.5	?	8	26	21	47	11	20	0.55	NM
CP2.6	right	1.5	35.5			26.5?	35.5	29	26.5	6?	6	6	6.5	7.5	23	27	50	10.5	21	0.5	0.81
CP3.1	right	1	27	19	1.42	22	27	NP	23	5	6.5	?	NP	NP	26	18?	44?	6.7	16.5	0.4?	NM
CP3.2	left	1.5	34	22	1.54	22?	34	NM	26.5	5.5	6.5	5.5	NP	NP	23	26	49	12	19	0.63	NM
CP3.3	right	2	35.5	22	1.61	25.5	35.5	25	28	6.5	8.5	6.5	10.5	9.5	23	23	46	11.5	20	0.57	0.70
CP3.4	left	0	32.5	22.5	1.44	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP
CP3.5	right	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP
CP3.6	left	1	34?	23	1.47	23	34?	23	26	5.5	6.5	5.5	11	8.5	24	24	48	12?	20	0.6	0.67
CP3.7	right	2	35	22.5	1.55	27	35	NP	26	5.5	6	5.5	?	?	21	23	44	11	18.5	0.59	NM
CP3.8	left	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM
CP4.1	right	1	13.5?	8.8	1.53	9.5?	13.5?	NP	10	?	?	2	3	3	23	28	51	7.5?	5?	0.66?	NM
CP4.2	left	2?	15.5	9.5	1.63	10.5	15.5	NP	10.5	1.5	2	1.5	?	?	20	25	45	6.3	8.5	0.74	NM

TRACK	Left/ right	MP	FL	FW	FL/ FW	LII	LIII	DIII	LIV	WII	WIII	WIV	HPL	HPW	II^III	III^IV	II^IV	ATl	ATw	AT	DIII/FL	
CP5.1	right	2	25.5	16.5	1.54	19.5	25.5	19	19.5	4	4	3.5	6.5	7	24	22	46	8.5	14	0.6	0.74	
CP5.2	left	1.5	26	18	1.44	17	26	19.5	19	4.5	5	4.5	6.5	6	27	22	49	10	15	0.66	0.75	
CP5.3	right	2	29	17	1.7	20.5	29	22	19	5	5	4	7	5.5	23	22	45	10.5	15.5	0.67	0.75	
CP5.4	left	1	24	18	1.3	17	24	NP	19.2	4.5	5	5	NP	NP	25	24	49	8	15	0.53	NM	
CP5.5	right	1.5	29	22	1.3	21	29	21	22	5	6	5	8	7	25	27	52	10	18	0.55	0.72	
CP5.6	left	1.5	24.5	20	1.2	19?	24.5	NP	20.5	4?	4.5	4	6	6	30	23	53	7.5	17.5	0.42	NM	
CP6.1	right	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM
CP6.2	left	2	38.5	24.5	1.57	29.5	38.5	NP	29	5.5	8.5	6.5	?	?	27	19	46	12	21.5	0.55	NP	
CP6.3	right	1	39	24.5	1.59	34	39	NP	29	9	9	6	NP	NP	22	20	42	13	21	0.59	NP	
CP6.4	left	1	35.5	24.5	1.44	29?	35.5	NP	28.5?	7.5	8	7.5	ND	ND	24	21	45	20.5	13	0.63	NP	
CP6.5	right	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM
CP7.1	right	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP
CP7.2	left	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP	NP
CP7.3	right	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM	NM
CP7.4	left	2	35.5	32.5	1.09	28	35.5		27.5	9	9.5	9.5	?	?	28	35	63	12.5	28	0.44	NM	
CP8	right	2	28.5	22.5	1.26	22?	28.5	24	22	5	5	4	4.5	5	34	28	62	8.5	19.5	0.43	0.84	
CP9	left	2	29.5	18	1.63	20	29.5	21	22	5	5.5	5	8.5	7	23	18	41	9.5	15	0.63	0.71	
CP10	left	2	26	18	1.44	19.5?	26	20	20.5	4.5	5	4.5	6	6.5	30	21	51	8	15.5	0.51	0.76	
CP11	left	1.5	32	26	1.23	25	32	NP	26	6	5	6	NP	NP	27	25	52	21	9.5	0.45	NP	

Speed ** (Km/h)	Relative stride length SL/FL	
		* Alexander 1976 Formula (estimated with SLt)
		** Ruiz and Torices, 2013 Formula (estimated with SLt)
		PLh and SLh = measured from the heel
		PLt and SLt =measured from the tip
7.74	1.97	
6.63	1.57	
7.14	1.57	
5.4	1.5	
5.7	1.42	
		This trackway has a slight change in direction, and the trackway midline has been estimated