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Pes shape variation in an ornithopod dinosaur trackway (Lower Cretaceous, NW Spain): New evidence of an antalgic gait in the fossil track record

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ABSTRACT

Trackways can provide unique insight to animals locomotion through quantitative analysis of variation in track morphology. Long trackways additionally permit the study of trackmaker foot anatomy, providing more insight on limb kinematics. In this paper we have restudied the extensive tracksite at Barranco de La Canal-1 (Lower Cretaceous, La Rioja, NW Spain) focussing on a 25-m-long dinosaur (ornithopod) trackway that was noted by an earlier study (Casanovas et al., 1995; Pérez-Lorente, 2003) to display an irregular pace pattern. This asymmetric gait has been quantified and photogrammetric models undertaken for each track, thus revealing distinct differences between the right and the left tracks, particularly in the relative position of the lateral digits II–IV with respect to the central digit III. Given that the substrate at this site is homogenous, the consistent repetition of the collected morphological data suggests that differences recorded between the right and the left tracks can be linked to the foot anatomy, but more interestingly, to an injury or pathology on left digit II. We suggest that the abnormal condition registered in digit II impression of the left pes can be linked to the statistically significant limping behaviour of the trackmaker. Furthermore, the abnormal condition registered did not affect the dinosaur's speed.

1. Introduction

The recognition of gait abnormalities in dinosaur trackways has been reported in both isolated tracks (Ishigaki, 1986, 1989; Mateus & Milàn, 2010) and trackways (Abel, 1935; Avanzini, Piñuela, & García Ramos, 2008; Dantas, Santos, Lockley, & Meyer, 1994; Lockley, Hunt, Moratalla, & Matsukawa, 1994; McCrea et al., 2014a,b; 2015). Previously published examples usually show the lack of a digit or a different value of homologous interdigital divarication angles (Avanzini et al., 2008). Palaeopathologies are more easily recognised in the osteological record (Anné et al., 2014; Rothschild & Tanke, 1992, 2005; Rega, Holmes, & Tirabasso, 2010; Tanke & Rothschild, 1997; 2002); ichnopalaeopathologies are much harder to identify because of the difficulty associated with discerning if anomalous features were due to physical abnormalities (i.e. injury, fractures, infections, deformations, swellings) were a function of unusual behaviour or merely a reflection of sediment rheology (Manning, 2004). Evidence for abnormal gaits come from trackways that display an alternating pes pace length pattern (Dantas et al., 1994; Lockley et al., 1994), although, many of these examples in literature may simply be unequal gaits of healthy animals (McCrea et al., 2015 and references therein). To date, several dinosaur trackway examples appear to correlate with a likely trackmaker limp to an actual cause, i.e., foot injury reflected in the narrow digit divarication (Abel, 1935; Avanzini et al., 2008; Ishigaki, 1986; Jenny & Jossen, 1982; Lockley et al., 1994 p. 194).

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In this study we reanalysed an ornithopod trackway (Casanovas et al., 1995; Pérez-Lorente, 2003) recently assigned to *Caririchnium lotus* (Díaz-Martínez, Pereda-Suberbiola, Pérez-Lorente, & Canudo, 2015) from the Lower Cretaceous Valdeosera-Traguajantes Unit in the Enciso Group, NW Cameros Basin, Spain. Occurring with multiple other tracks on a horizon named Barranco de La Canal (BLC) by Casanovas et al. (1995) and Pérez-Lorente (2003), this trackway (BLC1) has been previously shown to include irregular pes pace length patterns. Casanovas et al., (1995) and Pérez-Lorente (2003) noted a shortening from left to right pes pace, but did not expand with any explanation of their observation. The aim of this study is to quantify the observations made by these earlier studies and interpret the possible cause for the recorded anomaly in the alternating pace lengths in the view of potential abnormalities to trackmaker limb kinematics. Furthermore, since these tracks have only previously been documented and described as 2-D track outlines, we provide the first 3-D evaluation of the Barranco de La Canal-1 tracks, permitting a comprehensive description of track morphologies through photogrammetric models that allow us to collect more accurate morphological information and provide evidence for the possible cause of the irregular pace lengths.

2. Geological setting

The Barranco de La Canal (BLC) tracksite is situated in northern-central Spain, in the Province of La Rioja, close to the village of Munilla (Fig.1). The Cameros Basin consists of a high-subsidence basin of the Iberian Rift System displaying several tectonic phases during the Mesozoic and Cenozoic (Más et al., 2002; 2011). During the Late Jurassic and Early Cretaceous, the basin consisted of a fluvio-lacustrine system in which siliciclastic and carbonate sediments were deposited (Más et al., 2002; Doublet, 2004). The tracks are preserved on a silty sandstone slab of the Valdeosera-Traguajantes Unit, in the upper part of Enciso Group, in which sandstones, siltstones, marls and limestone are dominant (Hernández-Samaniego et al., 1990). The Enciso Group is more than 2000 m thick with its lower part mainly formed by fluvial deposits (Clemente, 2010). The middle and upper parts present a great variety of littoral and lacustrine deposits, evaporites and banks of limestones with diverse thickness, alternating with marls with desiccation cracks, fine-grained siltstones and siltstones with ripples and hummocky cross-stratification. The palaeoenvironment of the Enciso Group has been reconstructed as a siliciclastic to carbonate mixed lacustrine system with occasional marine incursions (Doublet, García, Guiraud, & Menard, 2003). Doublet (2004), based on the charophyte record (*Atopochara trivolvis* var. *triquetra*; Kneuper-Haack, 1966; Schudack, 1987, and *Clavator grovesii* var. *lusitanicus*; Grambast-Fessard, 1980; Martín-Closas, 1991), suggested that the Enciso Group is early Barremian to middle Albian in age (Fig.1).

3. Material and methods

The site has a total surface area of 250 m^2 and preserves 64 tracks divided into 7 trackways and 9 isolated tracks (Casanovas et al., 1995). The present study concentrates on trackway BLC1 (following Casanovas et al., 1995 and Pérez-Lorente, 2003 nomenclature), which is composed of 31 consecutive tracks made by what has been interpreted as a large ornithopod. The 3-D digital outcrop model (DOM) of the tracksite was first generated using a RIEGL LMS1 Z420i long range LiDAR capable of 5–10 mm resolution (Bates, Manning, Vila, & Hodgetts, 2008) and post-processed in Geomagic® software (Fig.2). The digital outcrop overview was

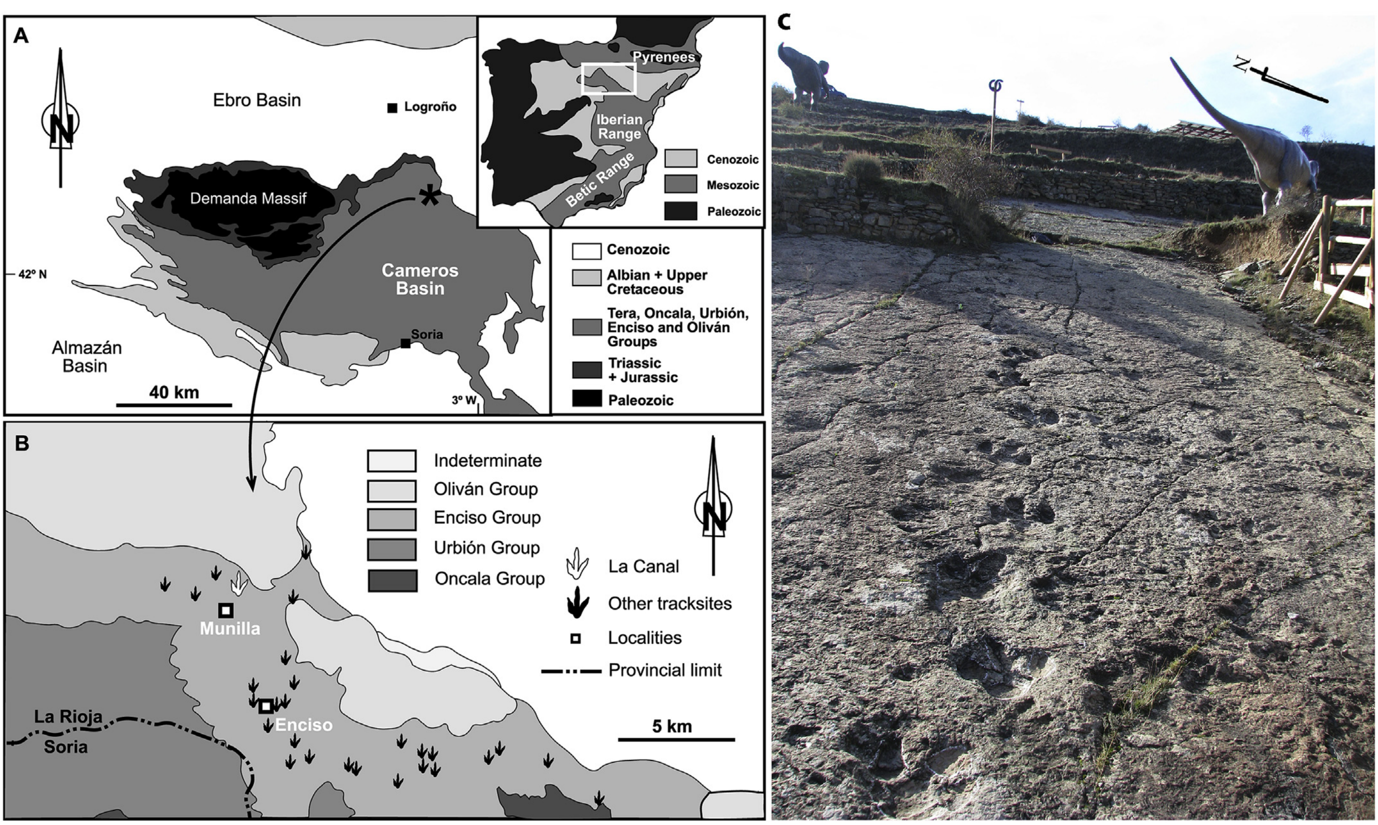


Fig. 1. A-B) Geographical and geological setting of the El Barranco de La Canal-1 tracksite from the Cameros Basin of the Munilla village, La Rioja, NW Spain. It belongs to the Enciso group. Geological map modified from Díaz-Martínez (2013). C) Field photo of the Barranco de La Canal-1 trackway with an overview of the tracksite.

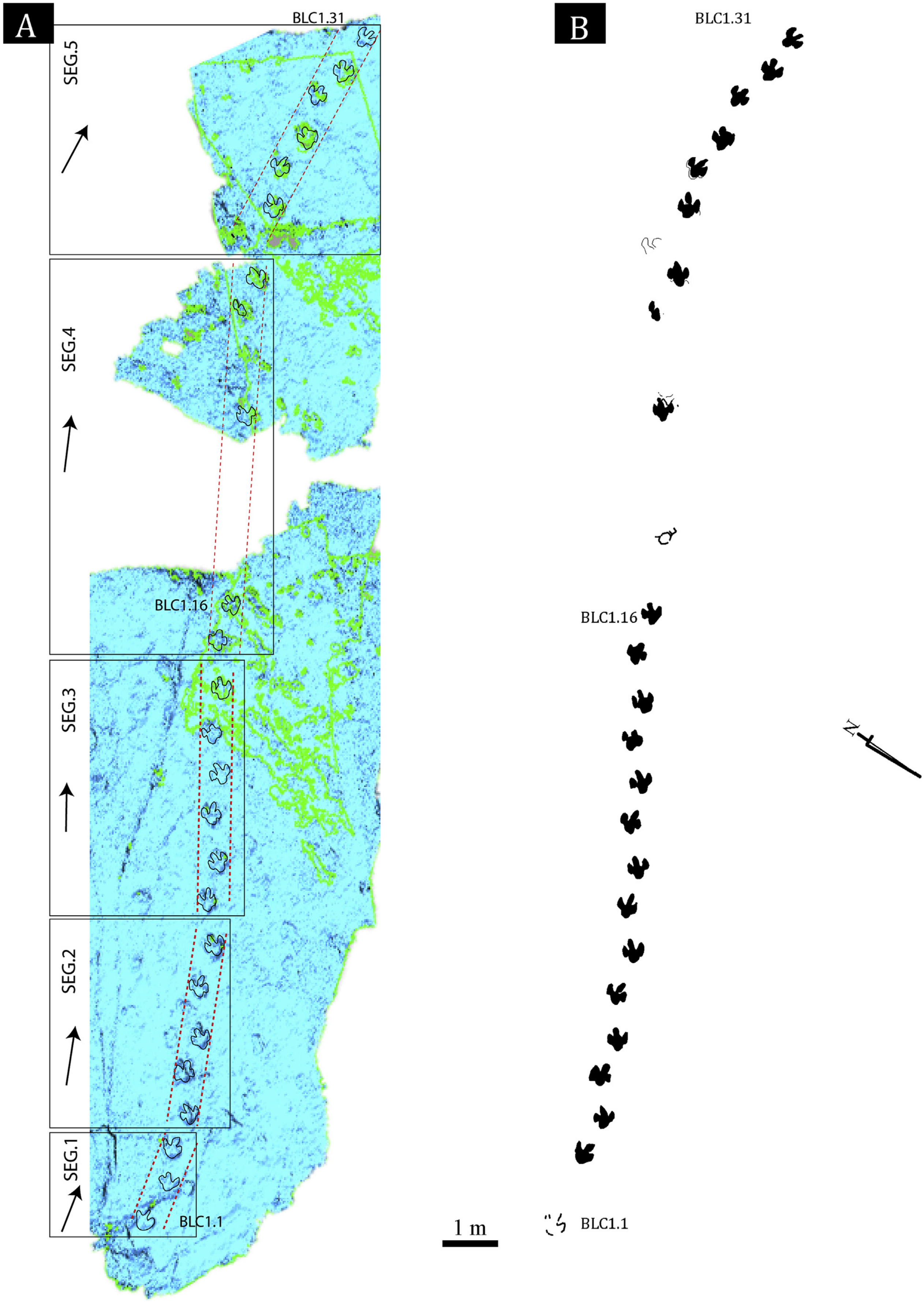


Fig. 2. A) Digital outcrop model (DOM)of the Barranco de la Canal-1 trackway (BLC1) obtained from post-processing the LiDAR scan raw data in Geomagic software. The BLC1 trackway is divided into 5 segments according to the slight change in the trackwaywidth and directional turnings. Segments are divided as follows: from 1) track BLC1.1 to track BLC1.3 and 70 cm wide; 2) track BLC1.4 to track BLC1.8 and 60 cm wide; 3) track BLC1.9 to track BLC1.14 and 60 cm wide; 4) track BLC1.15 to track BLC1.24 60 cm wide; 5) track BLC1.25 to track BLC1.31 and 95 cm wide. B) AutoCad drawing of the BLC1 trackway undertaken from the first field cartography made from a 10 × 10 m grid in the field (Pérez-Lorente, 2003). Scale bar 1 m.

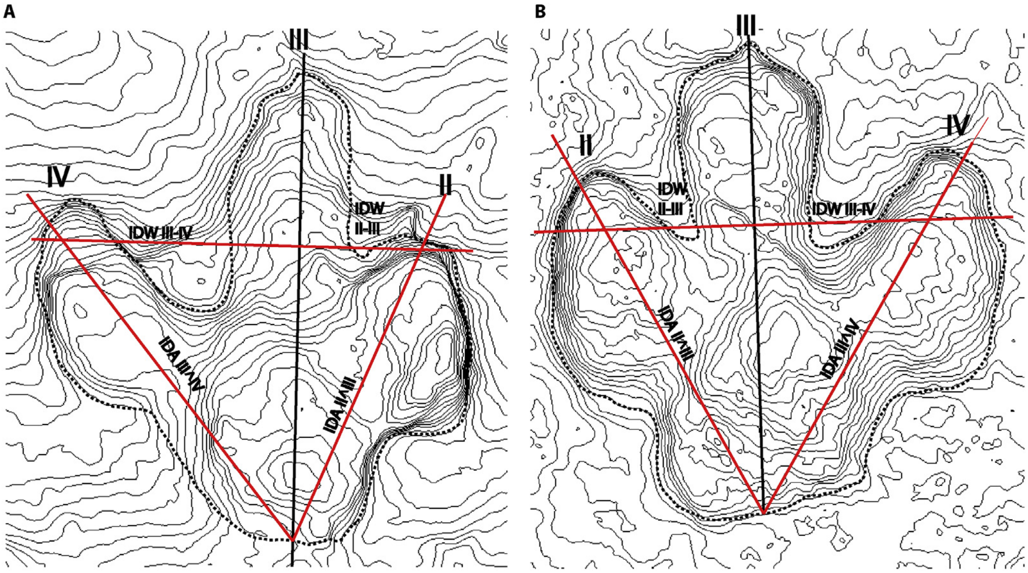


Fig. 3. Materials and methods explanation on:A)left track BLC1.9; B) right track BLC1.30. Isolines (contour lines) of height (Z coordinate) obtained from Paraview software every centimetre. To draw the track profile, one isoline was treated as an independent track contour line to use in the interdigital angle (IDA) and interdigital width (IDW) measurements (red lines). The IDW measurement (horizontal red line) was calculated by tracing the perpendicular segment (red line) to the track middle line (black line) and by accommodating it on the first isoline outside the hypexes. II, III, IV number of digit impressions; IDA II^III, III^IV: interdigital angle between II^III and III^IV; IDW II-III, III-IV, interdigital width between II-III, III-IV. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Measurements undertaken on right tracks from the BLC1 trackway of the Barranco de La Canal-1 tracksite. Abbreviations are as follows: TL: track length, TW: track width, PL: pace length, SL: stride length, IDA II^III: interdigital angle between digits II and III, IDA III^IV: interdigital angle between digits III and IV, DH: depth of the metarsodigital pad impression, DII: depth of digit II, DIII: depth of digit III, DIV: depth of digit IV, IDW II-III: index of the interdigital width between digits II and Table 1 III, IDW III-IV: index of the interdigital width between digits III and IV. Interdigital angles in degree and all other measurements are in centimetres.

Right	TL	TW	PL	SL	IDA II^III	IDA III^IV	D H	D II	D III	D IV	IDW II-III	IDW III-IV
BLC1.2	46.1	45.7	86.7		0	35	4.4	3.3	3.2	4.9	3.2	12.0
BLC1.4	30.3	29.3	90.0	178.7	35	36	4.3	3.0	3.5	2.2	3.3	2.2
BLC1.6	45.3	38.3	107.7	175.1	0	32	4.5	3.8	4.1	3.1	2.9	7.7
BLC1.8	43.5	40.3	102.1	198.5	0	28	6.1	4.2	5.0	5.6	3.3	7.4
BLC1.10	33.3	39.7	102.5	183.5	0	30	3.0	2.3	2.7	3.1	4.3	4.8
BLC1.12	39.9	40.6	96.7	185.9	0	31	2.2	2.4	1.5	2.2	2.5	7.2
BLC1.14	45.0	40.8	102.6	174.8	0	28	3.1	2.9	2.6	2.1	2.7	2.5
BLC1.16	38.4	39.7	76.5	192.1	0	34	4.2	3.0	3.3	1.5	5.1	2.5
BLC1.22	40.2	41.3	96.7	186.0	30	35	4.0	3.1	3.3	2.8	2.5	2.7
BLC1.24	47.2	39.3	104.0	173.4	0	30	2.9	2.6	3.4	4.3	2.9	7.7
BLC1.26	50.6	43.8	107.7	165.8	0	30	2.7	1.6	1.6	1.7	3.8	3.4
BLC1.28	39.8	38.3	105.6	187.5	0	38	3.6	2.8	3.2	2.8	2.1	2.8
BLC1.30	43.3	42.4	99.6	188.0	0	37	3.8	3.4	2.5	2.7	3.3	4.1
AVERAGE	**41.8**	**40.0**	**98.3**	**184.7**	**5**	**32**	**3.7**	**3.0**	**3.1**	**3.0**	**3.2**	**5.1**

Table 2
Measurements undertaken on left tracks from the BLC1 trackway of the Barranco de La Canal tracksite. Abbreviations are as follows: TL: track length, TW: track width, PL: pace length, SL: stride length, II^III: interdigital angle between digits II and III, III^IV: interdigital angle between digits III and IV, DH: depth of the metarsodigital pad impression, DII: depth of digit II, DIII: depth of digit III, DIV: depth of digit IV, IDW II-III: index of the interdigital width between digits II and III, IDW III-IV: index of the interdigital width between digits III and IV. Interdigital angles in degree and all other measurements are in centimetres.

Left	TL	TW	PL	SL	IDA II^III	IDA III^IV	D H	D II	D III	D IV	IDW II-III	IDW III-IV
BLC1.3	41.1	38.2	92.1	171.4	19?	28	5.5	4.1	4.0	6.1	2.5	7.4
BLC1.5	46.3	35.9	92.1	193.6	24?	32	7.0	2.4	3.2	6.1	3.0	11.3
BLC1.7	47.6	40.9	97.3	192.8	17?	32	2.9	3.1	2.5	3.2	1.9	6.1
BLC1.9	46.2	35.9	89.7	185.7	13?	31	4.8	7.0	3.3	3.4	2.1	6.6
BLC1.11	43.1	35.4	91.2	180.4	16?	30	4.5	4.7	3.2	3.6	1.8	7.9
BLC1.13	41.5	36.2	83.6	183.3	18?	31	4.2	3.8	2.9	4.3	2.0	4.5
BLC1.15	40.8	39.7	93.7	192.0	16?	32	4.3	5.7	3.6	5.0	1.9	4.7
BLC1.21	36.9	40.1	84.9	185.0	14?	35	4.0	3.2	2.4	2.9	1.6	8.0
BLC1.23	41.1	37.4	91.1	177.9	18?	32	5.2	4.2	3.6	3.9	1.5	6.7
BLC1.25	x	x	x	181.4	x	x	x	x	x	x	x	x
BLC1.27	41.2	39.0	89.7	184.5	19?	32	2.7	2.0	2.2	2.5	1.6	5.7
BLC1.29	39.3	37.2	92.8	188.3	19?	42	3.0	3.5	0.5	1.9	1.4	6.4
BLC1.31	30.3	41.2	x	191.8	19?	34	2.3	2.6	1.8	2.0	0.9	4.6
AVERAGE	**41.3**	**38.1**	**90.7**	**185.0**	**18?**	**32**	**4.2**	**3.9**	**2.8**	**3.7**	**1.8**	**7.4**

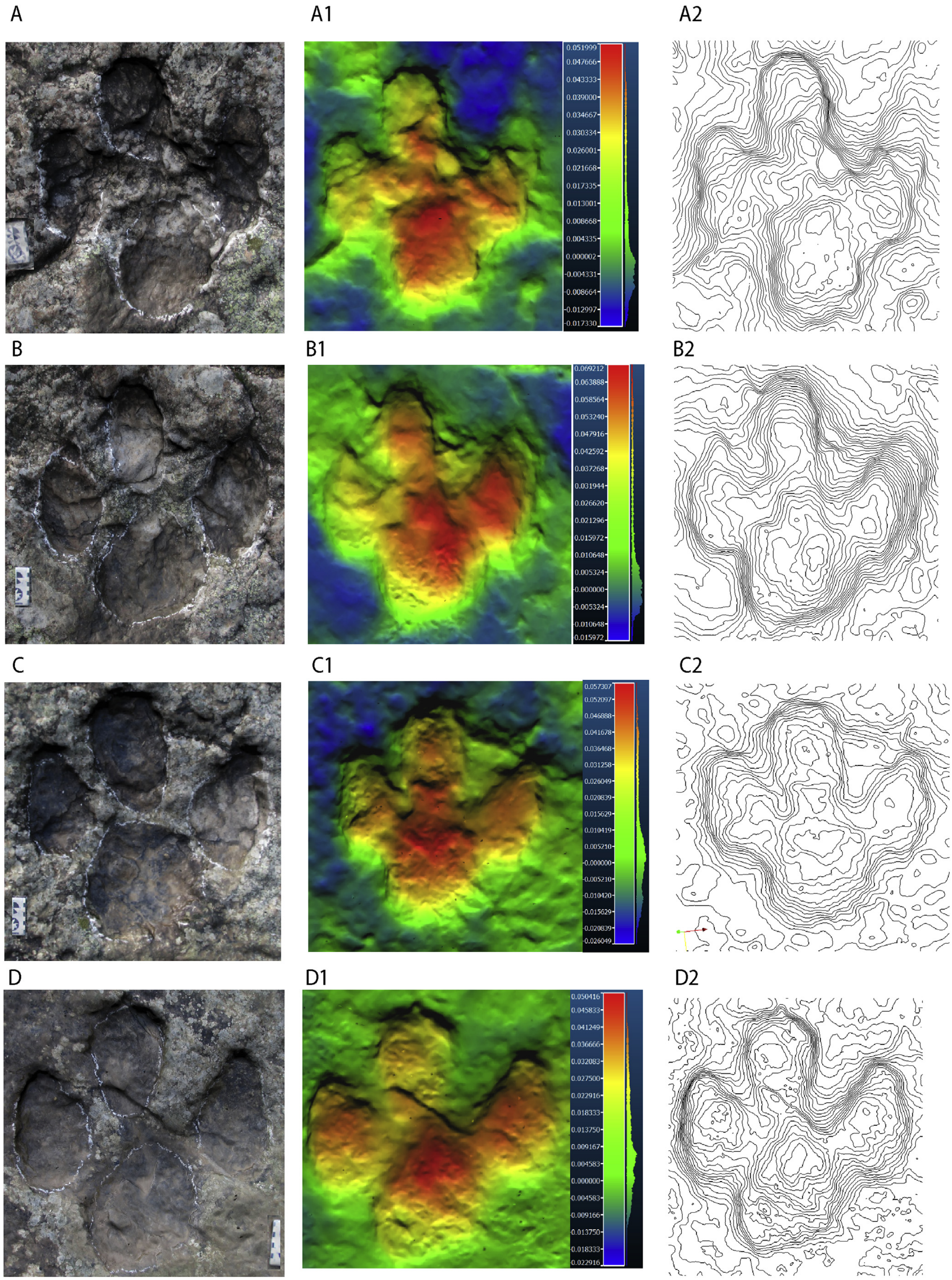
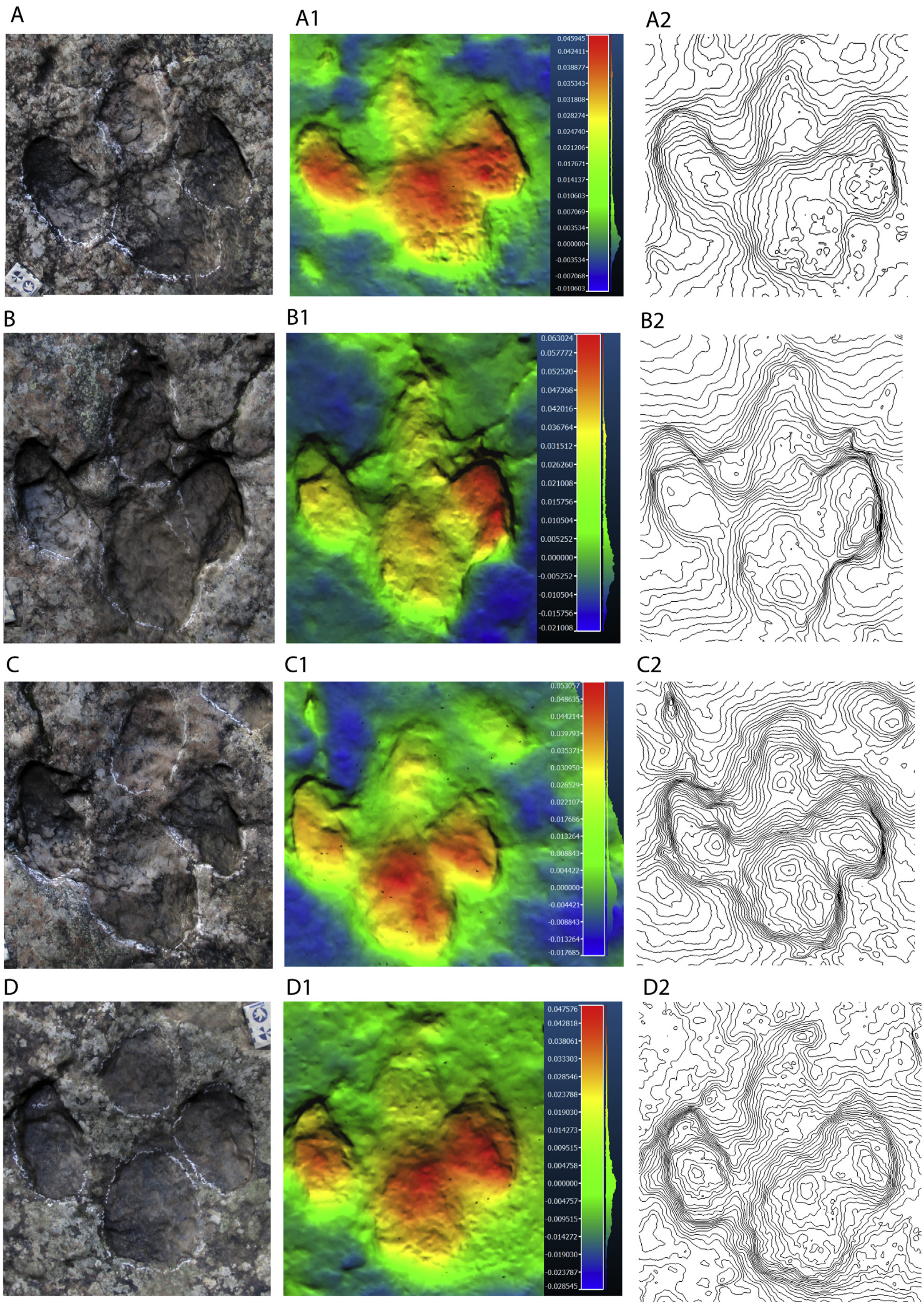


Fig. 4. Right tracks in A-D) Field photos of BLC1.6, BLC1.8, BLC1.28 and BLC1.30 respectively, scale bar 8 cm; A1-D1)height map of right tracks BLC1.6, BLC1.8, BLC1.28 and BLC1.30 respectively calculated in CloudCompare, colour scale bar in metres; A2-D2) Isolines of height (Z coordinate) of right tracks BLC1.6, BLC1.8, BLC1.28 and BLC1.30 respectively, generated using the free software Paraview. Each track displays a contour line every centimetre in order to provide a dense and objective outline of the right track morphologies. Tracks recall the *Caririchnium lotus* quadripartite and well discernible shape, with subparallel disposition and equal lengths of digits II and IV impressions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)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0.030950
0.026529
0.022107
0.017686
0.013264
0.008843
0.004422
0.000000
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-0.008843
-0.013264
-0.017685
D
D1
D2
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0.042818
0.038061
0.033303
0.028546
0.023788
0.019030
0.014273
0.009515
0.004758
0.000000
-0.004757
-0.009515
-0.014272
-0.019030
-0.023787
-0.028545

complemented with close-range photogrammetric models obtained from the best-preserved tracks (right: BLC1.6, BLC1.8, BLC1.28, BLC1.30; left: BLC1.7, BLC1.9, BLC1.11, BLC1.29).

Field photos were taken with Canon Power Shot S5IS camera (focal length 35 mm, resolution 3264 × 2448). Photogrammetry was undertaken following the general methodology explained in Mallison and Wings (2014) and terminology was used following Lockley, McCrea, and Buckley (2015). Point clouds were processed in Agisoft Photoscan standard version 1.1.4. build 2021software (http://www.agisoft.ru/) from a minimum of 10 to a maximum of 30 photos per track. Three-dimensional models were converted to colour maps in the open source CloudCompare software (v.2.6.1, http://www.danielgm.net/cc/). Contour lines (isolines profile) were obtained in free software Paraview 4.4.0 version (http://www.paraview.org/), importing scaled and oriented models with respect to the Z axis from CloudCompare (v.2.6.1) and they were set at a 0.25 cm distance according to maximum and minimum heights of the plane where tracks are. Pace length (PL), stride length (SL) and trackmaker velocity (Alexander, 1976) were estimated from the trackway DOM. The ratio of short/long pes pace length (*sensu* Lockley et al., 1994) was used as a numerical aid to compare the degree of gait irregularity. Track length (TL), track width (TW), interdigital angle (IDA) and a new parameter, interdigital width (IDW) were measured from 3-D models in Paraview 4.4.0. We developed the limping hypothesis on the basis of observation and quantification of an irregular gait in the BLC1 trackway. To test this hypothesis, we carefully examined each track in search of morphological clues. The left tracks were consistently deemed qualitatively different in the disposition of digit II with respect to that of right tracks. In this specific case of the BLC1 trackway, measurement of the interdigital angle between digits II-III impressions in left tracks was problematic due to the unclear orientation of digit II. Therefore, we developed a new parameter (IDW) exclusively for this case of the BLC1 trackway in order to quantify the qualitatively evident morphological difference in left tracks digit II impressions with respect to the contralateral counterpart. Although we acknowledge the confusion that may be generated by adding new parameters in the already established ichnological methodology (i.e., interdigital angles have been used as a diagnostic parameter with a large consensus), this parameter is simple to reproduce and is statistically significant in this restricted example. Unlike the interdigital angle parameter (IDA), the interdigital width (IDW) does not require knowledge of the orientation of the digits because it measures the separation between the medial/lateral edges of digit III and medial/lateral edges of digits II/IV. The IDW between digits II-III and III-IV impressions is determined by the perpendicular segment to the track middle line, found on the first contour line outside one of the hypexes (Fig.3). The higher the value of the IDW parameter, the bigger the interdigital distance. We restrict the use of the IDW parameter to this specific case of the BLC1 trackway to quantify the morphological differences that we observed qualitatively. To more broadly apply this parameter, future studies should further test the repeatability and reliability of this parameter in a more explicit methodological study, which is beyond the scope of the present work.

Relative depths of the metatarsodigital pad impression (DH) and digits II (DII), III (DIII), IV (DIV) digits impressions were calculated using Cloudcompare (v.2.6.1http://www.danielgm.net/cc/) in order to generalize the qualitative distribution within the track. Pace, stride lengths, track lengths, track widths, interdigital angles and interdigital widths were measured through ImageJ software (http://imagej.nih.gov/ij/). Statistical differences in the pace lengths and in the averages of the interdigital width parameter between right and left tracks were compared through the two-paired sample statistic analysis, suited to testing the hypothesis that the left pace length was consistently smaller than the right paired pace length and whether this difference might be linked to a cause. The test is used to compare two population means, where there are two samples in which observations in one sample (left pes morphologies) can be paired with observations in the other sample (right pes morphologies). Tracks BLC1.2, BLC1.26 and BLC1.31 were excluded because the corresponding paired tracks BLC1.1, BLC1.25 and BLC1.32 are either absent or preserved as partial prints in the tracksite. The statistical tests also took into account the 11 pairs of tracks (11 for the left and 11 for the right pedes impressions).

4. Results

The Barranco de La Canal-1 trackway (BLC1) measures 25 m in length and it is the longest trackway at the site. The trackway consists of 31 pes tracks, 25 of which are well preserved and could be measured (Tables 1 and 2). Manus tracks are observed in front of three of the pes tracks (BLC1.7, BLC1.11, BLC1.12).

Photogrammetric models undertaken on 25 out of 31 pes tracks of the BLC1 show a general well discernible morphology that fits the typical ornithopod track morphotype, which is mesaxonic, tridactyl with three stout and broad spreading toes ending in blunt hoof-mark toes and generally symmetric (*sensu* Pérez-Lorente, 2001; Thulborn, 1990). The tracks also display a quadripartite division corresponding to the pes anatomy (single pad print per digit and a subtriangular to rounded metatarsodigital pad impression). The common track shape is hexagonal because of the notches developing from the proximal parts of digits II and IV. The tracks are interpreted as true tracks because of the presence of clear blunt hoof marks in some of the tracks (e.g. track BLC1.16) and of the distinct outline of the entire track. The average track length (TL) and width (TW) range from 41.3 to 41.7 cm and from 38.1 to 40.0 cm respectively, resulting in a TL/TW index of ~1. The BLC1 tracks do not present evidence of sediment deformation such as displacement rims or mud collapse within the digits, although there is a low degree of homogenous erosion (probably current). The average pes stride length (SL) is 185 cm (for both sides of the trackway) and the average pes pace length (PL) is 94.5 cm ($n = 25$). However, the pace is uneven, 98.3 cm for the right-left pes pace length (range of 76.5–107.7 cm) and 90.7 cm for the left-right pes pace length (range 83.6–97.3 cm) (Tables 1 and 2). The “two-sample paired test” statistical analysis undertaken resulted in $t = 2516$; $p = 0{,}030596$ with 95% confidence level, therefore the left pace length was consistently smaller than the right paired pace length, showing a 81.8% of pace-shortening occurrence along the trackway (9 out of 11 paired paces) and displaying a 92% of gait irregularity (pace length ratio *sensu* Lockley et al., 1994). The BLC1 trackway can be divided into five segments that coincide with major orientation changes and variations in the external trackway widths (Fig. 2). Velocity estimations were calculated for each of these segments (Fig. 2) and resulted in: 1) 1.106 m/s; 2) 1.214 m/s; 3) 1.171 m/s; 4) 1.209 m/s; 5) 0.998 m/s following the Alexander's (1976) formula

Fig. 5. Left tracks in A-D) Field photos of left tracks BLC1.7, BLC1.9, BLC1.11 and BLC1.29 respectively, scale bar 8 cm; A1-D1)height map of left tracks BLC1.7, BLC1.9, BLC1.11 and BLC1.29 respectively calculated in CloudCompare, colour scale bar in metres; A2-D2) Isolines of height (Z coordinate) of right tracks BLC1.7, BLC1.9, BLC1.11 and BLC1.29 respectively, generated using the free software Paraview. Each track displays a contour line every centimetre in order to provide a dense and objective outline of the left track morphologies. Left tracks recall the *Caririchnium magnificum* or *C.* isp morphology, in which the metatarsodigital pad impression in laterally compressed and bigger in size. Digits II and IV impressions are divergently positioned and unequal in size and digit III is usually faintly impressed. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(standard deviation ± 0.09).

Besides the statistically significant of pace length irregularity, morphological differences between right and left pes tracks were clearly observed in the BLC1 trackway. These include: 1) the shape of the metatarsodigital pad impression; 2) the degree of symmetry between impressions of digits II and IV (notch development); 3) the interdigital width (IDW) and interdigital angles (IDA), where measurable, between II-III and III-IV and 4) the depth distribution and values for metatarsodigital pad (DH) and impressions of digits II, III and IV (DII, DIII, DIV, see Tables 1 and 2 for measurements).

The shape of metatarsodigital pad impression in the right pes tracks ($n = 13$, Fig. 4, Table 1) is rounded to subtriangular, easily discernible in all tracks. It divides the track space into two even areas in which the antero-posterior length of the metatarsodigital pad impression equals that of impression of digit III. The notches that develop from the proximal parts of both impressions of digit II and IV toward the metatarsodigital pad impression region are very symmetric and consistent in all the right tracks, giving the impressions of digits II and IV an overall comparable geometry and morphology, being all three digit impressions straight-pointing (Fig. 4 A2-D2). Noteworthy features of right tracks are the subparallel orientation of digits II and III impressions (IDA range 0°–35°; IDW range 2.06–5.06 cm, Table 1) and the slight angulation and higher distance range between digits III and IV impressions (IDA range 28°–38°; IDW range 2.24–7.69, Table 1). Depth distribution appears qualitatively homogenous within the track. Maximum depths values are recorded in the metatarsodigital pad impression (range 2.2–6.1 cm), while digits II, III and IV impressions displayed the same average and range of depths (range 1.5–5.6 cm) (Fig. 4 A1-D1, Table 1).

The left pes tracks ($n = 12$, Fig. 5, Table 2) shape of metatarsodigital pad impression is laterally compressed and large, suboval in shape. Visually, it occupies more than half of the track area and it is antero-posteriorly longer thatdigit III impression. The notches developing from the proximal parts of both digits II and IV impressions toward the metatarsodigital pad impression region are not symmetrically organized. The notch that forms from digit II to the metatarsodigital pad impressions is steeper than the one that forms from digit IV impression and it is usually closer to the distal end of the metatarsodigital pad impression. Further important features of left tracks are the asymmetric arrangement and dissimilarity in shape and lengths of digits II and IV impressions, also evidenced by the divergence in the interdigital widths measurement. The interdigital angle between digits II and III impressions is not confidently measured since the arrangement and orientation of digit II impression is not clear also because of a more pronounced inward rotation of digit III impression (IDA range 13°–24°; IDW rage from 1.35 to 3.04). Interdigital angle range between digits III and IV impressions is similar to the right tracks one (IDA range 28°–42°), while IDW range is 4.53–11.31 cm (Fig. 5 A3-D3). Depth distribution and ranges within the left track are quite similar (DH range 2.3–7.0 cm, DII range 2.0–7.0 cm; DIII range 0.5–4.0 cm; DIV range 1.9–6.1 cm), (Fig. 5 A2-D2, Table 2).

In summary, the BLC1 trackmaker shows a 92% ratio of gait irregularity (*sensu* Lockley et al., 1994), corresponding to an 8% difference between the left-right (short) and right-left (long) consecutive steps in 81.8% of the footfalls, resulted in a statistical significance. Left tracks IDA II-III range (13°–24°) fall into the right tracks range (0°–35°), although this measurement is doubtful due to the unclear orientation of left digit II impression. Left and right tracks IDA III-IV range is very similar (20°–42°). More importantly, IDW for II-III and III-IV distances in left and right tracks were tested in the two-paired sample analysis and both resulted statistically significant in 95% of confidence level (two-paired sample test for IDW II-III: $t = 4.43$; $p = 0.0012$ and for IDW III-IV: $t = 3.36$; $p = 0.007$).

5. Discussion

The Barranco de La Canal-1 tracks are located in a decametric, fine-grained non-cohesive sandstone that lacks clear sedimentary structures (e.g., ripples, mud cracks, dunes). The tracks break the sandy layer and do not display sedimentary deformation structures, such as displacement rims, mud collapse, interdigital mud rims, which are often substrate-controlled features (Falkingham & Gatesy, 2014; Kuban, 1989; Razzolini et al., 2014; Scrivner & Bottjer, 1986). If erosion of the sediment is considered, it is simulated that tracks emplaced in a sufficiently deep sediment of homogenous composition and subjected to conditions of light and uniform erosion usually retain their basic dimensions and shapes (Henderson, 2006). Although it is true that a wide number of external factors that influence track morphology and the trackway quality can be either contemporaneous or post-depositional in origin (Schulp, 2002), a selective weathering on digit II impression of left tracks is unlikely in such a narrow trackway. The possibility that the BLC1 trackmaker was crossing different substrate consistencies throughout the tracksite, causing morphological changes according to the soil response (Dai et al., 2015; Manning, 2004; Milan & Bromley, 2006; Padian & Olsen, 1984) has also to be taken into consideration. Nevertheless, considering the sinuosity of the trackway, if the sediment was characterized by different consistencies, the track morphologies would uniformly or gradually display the bias caused by the trackmaker's trampling on the substrate (*sensu* Razzolini et al., 2014).

The Barranco de La Canal-1 trackway geometry shows that the right-left pace length is8% longer than the left-right pace length. This observation is usually quantified by the ratio of the average between short and long steps: the farther from the 1/1 ratio (equidimensional consecutive steps), the higher the degree of asymmetric movement. The alternating pes pace length noted and mentioned in Casanovas et al. (1995) and Perez-Lorente et al. (2003) is here quantified in a ratio of short/long pace length of 92%, such variation can be explained by an abnormal gait, such as a limping (Dantas et al., 1994; Ishigaki & Lockley, 2010; Lockley et al., 1994; Reineck & Flemming, 1997). However, left and right pes stride lengths in the BLC1 trackway show identical values for both sides (185 cm), despite the differences in the length of consecutive step (Tables 1 and 2). This stride length regularity is linked to a bipedal and narrow gait, since it is not usually visible in quadrupedal trackways (Lockley et al., 1994). Velocity variations calculated here for every turning segment in the trackway indicates that the animal was not significantly accelerating/decelerating along the trackway and that its locomotion was steady. Although we agree that trackmaker's behaviour can bias the trackway geometry, as shown by the recorded irregularities on pace lengths producing “anomalies” in the tracks that are not necessarily linked to a foot injury (McCrea et al., 2015), the noticeable difference on the placement of left digit II impressions with respect to the contralateral counterpart (Figs. 3–5) cannot be fully discarded as the causation of the irregular gait. The fact that limb dynamics (*sensu* Falkingham, 2014) is not playing a significant role in causing morphological differences recorded in right and left tracks is also shown through depth analyses, which resulted in similar values for both right and left tracks. Therefore, from our results, we believe that recorded significantly different morphologies on right and left tracks (left digit II impression placement with respect to the right digit II impression) depend on the foot anatomy of the trackmaker rather than being a consequence of the turnings and slight accelerations-decelerations recorded in the dynamic estimations.

The Barranco de La Canal-1 tracks have been identified as *Caririchnium lotus* (Díaz-Martínez et al., 2015), although, it is worth mentioning that Díaz-Martínez (2013) suggested that if the

Barranco de La Canal-1 right and left tracks were analysed separately, they could be easily assigned to different *Caririchnium* ichnospecies (*Caririchnium magnificum*, *C. lotus* and *C.* isp). Right pes tracks closely resemble those of *Caririchnium lotus* described by Xing, Wang, Pan, and Chen (2007; 2012).

Parameters such as the quadripartite subdivision of the track geometry, the subequal lengths and very similar morphologies of digit II and IV impressions and the subtriangular metatatarsodigital pad impression characterizing right tracks and more specifically, the shapes observed in tracks BLC1.6, BLC1.8, BLC1.28, BLC1.30 (Fig. 4), all agree with *C. lotus* assignation (Díaz-Martínez, 2013; Díaz-Martínez et al., 2015). The similar values of the interdigital widths and the homogenous depth distribution within the tracks point out the quadripartite and symmetrical large-ornithopod foot arrangement in the substrate (Lockley et al., 1994; Moratalla, Sanz, Melero, & Jiménez, 1989; Pérez-Lorente, 2003; Xing et al., 2007). On the contrary, left tracks do not display similarity between digit II and IV impressions as the statistically significant smaller values for the interdigital width parameter (digits II-III) pointed out, implying that digit II impression is closer to or overlapping that of digit III, displaying a different arrangement of digit II pad with respect the homologous on the right tracks. This dissimilarity in the distance between digit II-III impressions of the right and left pes tracks, confirmed by the statistical significance, suggests asymmetry in the pedal anatomy in the left pes. A similar scenario to the one we are proposing for the BLC1 tracks is found in the graphic scale of exostosis cases presented in Fig. 23 of McCrea et al. (2015), in which features characterizing the placement of the affected lateral digit involve interdigital width (short), interdigital angle (low) and digit length (small) parameters. Additional data such as the 92% degree of limping in the trackway (with the short step on the left side of the midline) also support an abnormal condition in the left digit II pad impression. This altered rhythm according to which the pes are placed along the trackway reveals a gait alteration, as it is shown by the 8% difference between right and left pes pace lengths.

Factors that can cause pathologies affecting morphology and locomotion have been recently dived into five categories (McCrea et al., 2015). We suggest that the abnormality in the left digit II pad belongs to the second category defined as a "biomechanical injury: defects due to physical damage to the body, possibly affecting the movement of the limp and its elements" (McCrea et al., 2015). The BLC1 trackmaker's injury was localized on its left digit II pad causing on the overall trackway geometry just a slight gait asymmetry (antalgic gait), small velocity changes and few differences in depth distributions within the tracks. A compensatory type of gait occurs where movement of the centre of gravity is such that there is an accommodation in the gait pattern to minimize muscle effort by the affected leg (Harrington, 2005).

Lockley et al. (1994) noted a trackway in which the shorter step was recorded on the opposite side to the supposed injured hind limb. On the contrary, in the Barranco de la Canal-1 trackway we suggest an antalgic gait for the individual, attempting to take less weight on the affected limb, shortening the duration of the support phase on the injured side (Harrington, 2005) and extending the pace length of the normal side. It would be mechanically coherent and convenient to have the shorter step (left-right) on the same side of the pedal injury (left digit II), since the right hind limb could still use all of its muscular strength to take the longer step (right-left).

6. Conclusions

A long trackway of *Caririchnium lotus* from the Barranco de la Canal-1 site (NW Cameros Basin, La Rioja, Spain) is here restudied using LiDAR and a photogrammetric-based approach. Previous work on the tracksite observed an asymmetric gait pattern in this 25-m-long trackway (Casanovas et al., 1995; Pérez-Lorente, 2003), which has been subject to in depth analysis for the first time and quantified in a 92% ratio of gait irregularity, corresponding to an 8% difference between the left-right (short) and right-left (long) consecutive steps in the 81.8% of the footfalls. Furthermore, 3-D photogrammetric models together with quantitative analyses undertaken on all the digital outcrop model point to a difference in the morphology of right and left tracks. These statistically significant differences refer to a distinct shape and placement of digit II impression with respect to digit III impression. The significant morphological and quantitative differences recorded between the right and left pes tracks suggest that an injury on the left digit II pad resulted in a pathology causing an antalgic limping behaviour. Moreover, it is also suggested that due to the low percentage in the discrepancy between consecutive steps, the pathological or abnormal condition inferred for digit II pad of the left track did not significantly affect the locomotion of the trackmaker. This ornithopod trackway provides new insight to antalgic gaits and offers a more quantitative approach to the analysis of dinosaur track and trackway abnormal conditions. The BLC 1 trackway adds new data on the occurrences of ichnopathologies in ornithopod dinosaurs, scarcely documented with respect to those relative to theropod dinosaurs.

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References

Abel, O. (1935). *Vorzeitliche Lebenspuren* (pp. 1–644). Jena: Gustav Fischer.
Alexander, R. M. N. (1976). Estimates of speeds of dinosaurs. *Nature, 261*, 129–130.
Anné, J., Wogelius, R. A., Edwards, N. P., Tumarkin-Deratzian, A. R., Sellers, W. I., Bergmann, U.… Manning, P. L. (2014). Synchrotron imaging reveals bone healing and remodelling strategies in extinct and extant vertebrates. *Journal of the Royal Society of Interface, 11*, 20140277 http://dx.doi.org/10.1098/rsif.2014.0277.
Avanzini, M., Piñuela, L., & García Ramos, J. C. (2008). Theropod palaeopathology inferred from a Late Jurassic trackway, Asturias (N. Spain). *Oryctos, 8*, 71–75.
Bates, K. T., Manning, P. L., Vila, B., & Hodgetts, D. (2008). Three-dimensional modelling and analysis of dinosaur trackways. *Palaeontology, 51*, 999–1010.
Casanovas, M. L., Ezquerra, R., Fernández, A., Montero, D., Pérez-Lorente, F., Santafé, J. V.… Viera, L. V. (1995). El yacimiento de La Canal (Munilla, La Rioja, España). La variación de velocidad en función del tamaño del pie de los

ornitópodos. *Zubía, 13*, 55–81.
Clemente, P. (2010). Review of the Upper Jurassic-Lower Cretaceous stratigraphy in western Cameros Basin,Northern Spain. *Revista de la Sociedad Geológica de España, 23*, 101–143.
Dai, H., Xing, L., Marty, D., Zhang, J., Persons, W. S., Hu, H. … Wang, F. (2015). Microbially-induced sedimentary wrinkle structures and possible impact of microbial mats for the enhanced preservation of dinosaur tracks from the Lower Cretaceous Jiaguan Formation near Qijiang (Chongqing, China). *Cretaceous Research, 53*, 98–109.
Dantas, P., Santos, V. F., Lockley, M. G., & Meyer, C. (1994). Footprint evidence for limping dinosaurs from the upper Jurassic of Portugal. *Gaia, 10*, 43–48.
Díaz-Martínez, I. (2013) (PhD thesis). *Icnitas de dinosaurios bípedos de La Rioja (Cuenca de Cameros, Cretácico Inferior): icnotaxonomía y aplicación paleobiológica* (Vol. 1, pp. 1–253). Universidad de La Rioja. xii + 632 pp, Vol. 2 (anexos).
Díaz-Martínez, I., Pereda-Suberbiola, X., Pérez-Lorente, F., & Canudo, J. I. (2015). Ichnotaxonomic review of large ornithopod dinosaur tracks: temporal and geographic implications. *PLoS One*. http://dx.doi.org/10.1371/journal.pone.0115477.
Doublet, S. (2004). *Contrôles tectonique et climatique de l'enregistrement stratigraphique dans un bassin continental de rift: le bassin de Cameros*. Tésis doctoral. Inédito (pp. 1–512). Université de Bourgogne.
Doublet, S., García, J. P., Guiraud, M., & Menard, A. (2003). Wave dominated siliciclastic and carbonate sedimentation in a Lower Cretaceous lake (Cameros basin, northern Spain). *Journal of Iberian Geology, 29*, 11–30.
Falkingham, P. L. (2014). Interpreting ecology and behaviour from the vertebrate fossil track record. *Journal of Zoology, 292*, 222–228.
Falkingham, P. L., & Gatesy, S. M. (2014). The birth of a dinosaur footprint: Subsurface 3D motion reconstruction and discrete element simulation reveal track ontogeny. *Proceedings of the National Academy of Sciences, 111*, 18279–18284.
Grambast-Fessard, N. (1980). Les charophytes du Montien de Mons (Belgique). *Review of Palaeobotany and Palynology, 30*, 67–88.
Harrington, I. J. (2005). Symptoms in the opposite or uninjured leg. In *Discussion paper prepared for the Workplace Safety and Insurance Appeals Tribunal, province of Ontario* (pp. 1–21).
Henderson, D. M. (2006). Simulated weathering of dinosaur tracks and the implications for their characterization. *Canadian Journal of Earth Sciences, 43*, 691–704.
Hernández-Samaniego, A., Ramírez Merino, J. I., Olivé Davó, A., Álvaro López, M., Ramírez del Pozo, J., Aguilar, M. J. … Meléndez Hevia, A. (1990). *Mapa Geológico de España a escala 1:50.000, Hoja 242, Munilla, Segunda Serie-Primera edición* (pp. 1–55). Hoja y Memoria: Instituto Tecnológico y GeoMinero de España.
Ishigaki, S. (1986). Dinosaur footprints of the Atlas mountains. *Nature Study, 32*, 6–9 (In Japanese).
Ishigaki, S. (1989). Footprints of swimming sauropods from Morocco. In G. G. Gillette, & M. G. Lockley (Eds.), *Dinosaur tracks and traces*. D.D. Gillette and M.G.Lockley (Eds.) Cambridge UniversityPress, 83–86.
Ishigaki, S., & Lockley, M. G. (2010). Didactyl, tridactyl and tetradactyl theropod trackways from the Lower Jurassic of Morocco: evidence of limping, labouring and other irregular gaits. *Historical Biology, 22*, 100–108.
Jenny, J., & Jossen, J. A. (1982). Découverte d'empreintes de pas de Dinosauriens dans le Jurassique inférieur (Pleinsbachian) du Haut Atlas central (Maroc). *Compte Rendu de l'Académie de Sciences, 294*, 223–226.
Kneuper-Haack, F. (1966). Ostracoden aus dem Wealden der Sierra de los Cameros (Nordwestliche Iberische Ketten). In *Beih. Geol. Jb* (Vol. 44, pp. 165–209).
Kuban, G. J. (1989). Elongate dinosaur tracks. In D. D. Gillette, & Y. M. G. Lockley (Eds.), *Dinosaur tracks and traces* (pp. 57–72). Cambridge University Press.
Lockley, M. G., Hunt, A. P., Moratalla, J., & Matsukawa, M. (1994). Limping Dinosaurs? Trackway evidence for abnormal gaits. *Ichnos, 3*, 193–202.
Lockley, M. G., McCrea, R. T., & Buckley, L. G. (2015). A review of dinosaur track occurrences from the Morrison Formation in the type area around Dinosaur Ridge. *Palaeogeography, Palaeoclimatology, Palaeoecology, 433*, 10–19.
Mallison, H., & Wings, O. (2014). Photogrammetry in paleontology – a practical guide. *Journal of Paleontological Techniques, 12*, 1–31.
Manning, P. L. (2004). A new approach to the analysis and interpretation of tracks: examples from the Dinosauria. In D. McIlroy (Ed.), *Geological Society,London, Special Publications: Vol. 228. The application of ichnology to palaeoenvironmental and stratigraphic analysis* (pp. 93–123).
Martín-Closas, C. (1991). *Els caròfits del Cretaci inferior de les conques periferiques del Bloc de l'Ebre*. Col·lecció de Tesis doctorals Microfitxades, numero 904 (pp. 1–581). Publicacions de la Universitat de Barcelona.
Mas, J. R., Benito, M. I., Arribas, J., Alonso, A., Arribas, M. E., Lohmann, K. C. … Omodeo, S. (2011). Evolution of an intra-plate rift basin: the Latest Jurassic-Early Cretaceous Cameros Basin (Northwest Iberian ranges, North Spain). In *Post-Meeting Field trips28th IAS Meeting, Zaragoza. Geo-Guías 8. Sociedad Geológica de España, Zaragoza* (pp. 119–154).
Más, R., Benito, I., Arribas, J., Serrano, A., Guimerá, J., Alonso, A. … Alonso-Azcarate, J. (2002). La Cuenca de Cameros: Desde la extensión Finijurásica –Eocretácica a la inversión terciaria-Implicaciones en la exploración de hidrocarburos. *Zubía, 14*, 9–64.
Mateus, O., & Milàn, J. (2010). A diverse Upper Jurassic dinosaur ichnofauna from central-west Portugal. *Lethaia, 43*, 245–257.
McCrea, R. T., Buckley, L. G., Farlow, J. O., Lockley, M. G., Currie, P. J., Matthews, N. A. … Pemberton, S. G. (2014a). A 'terror of tyrannosaurs': the first trackways of tyrannosaurids and evidence of gregariousness and pathology in Tyrannosauridae. *PLoS One, 9*, e103613. http://dx.doi.org/10.1371/journal.pone.0103613.
McCrea, R. T., Buckley, L. G., Plint, A. G., Currie, P. J., Haggart, J. W., Helm, C. W. … Pemberton, S. G. (2014b). A review of vertebrate track-bearing formations from the Mesozoic and earliest Cenozoic of western Canada with a description of a new theropod ichnospecies and reassignment of an avian ichnogenus. *New Mexico Museum of Natural History and Sciences Bulletin, 52*, 5–93.
McCrea, R. T., Darren, H., Tanke, D. H., Lisa, G., Buckley, L. G., Martin, G. … Breithaupt, B. H. (2015). Vertebrate Ichnopathology: pathologies inferredfrom dinosaur tracks and trackways from the Mesozoic. *Ichnos, 22*, 235–260. http://dx.doi.org/10.1080/10420940.2015.1064408.
Milan, J., & Bromley, R. G. (2006). True tracks, undertracks and eroded tracks, experimental work with tetrapod tracks in laboratory and field. *Palaeogeography, Palaeoclimatology, Palaeoecology, 231*, 253–264.
Moratalla, J. J., Sanz, J. L., Melero, I., & Jiménez, S. (1989). Yacimientos paleoicnologicos de la Rioja: Huellas de dinosaurios. *Gobierno de la Rioja y Iberduero*, 1–95.
Padian, K., & Olsen, P. E. (1984). The fossil trackway *Pteraichnus*: not pterosaurian, but crocodilian. *Journal of Paleontology, 58*, 178–184.
Pérez-Lorente, F. (2001). *Paleoicnología: los dinosaurios y sus Huellas en la Rioja; apuntes para los cursos y campos de trabaja de verano. Cultural Joven Gobierno de la Rioja y fundación caja Rioja* (pp. 1–227). Fundación Patrimonio Paleontológico de La Rioja.
Pérez-Lorente, F. (2003). Aportaciones de los yacimientos de La Barguilla, Santisol y Santa Juliana (Hornillos de Cameros, La Rioja. España). In *Dinosaurios y otros reptiles mesozoicos en España, Pérez-Lorente, F. coord* (pp. 161–194).
Razzolini, N. L., Vila, B., Castanera, D., Falkingham, P. L., Barco, J. L., Canudo, J. I. … Galobart, À. (2014). Intra-trackway morphological variations due to substrate consistency: the El Frontal Dinosaur tracksite (Lower Cretaceous, Spain). *PLoS One, 9*, e93708. http://dx.doi.org/10.1371/journal.pone.0093708.
Rega, E., Holmes, R. B., & Tirabasso, A. (2010). Habitual locomotor behavior inferred from manual pathology in two Late Cretaceous chasmosaurine ceratopsid dinosaurs, Chasmosaurus irvinensis (CMN 41357) and Chasmosaurus belli (ROM 843). In *New perspectives on horned dinosaurs: The Ceratopsian Symposium at the Royal Tyrrell Museum* (pp. 340–354).
Reineck, H. E., & Flemming, W. B. (1997). Unusual tracks, traces, and other oddities. In *CaUL Farsch.-Inst. Senckenberg* (Vol. 20, pp. 349–360).
Rothschild, B. M., & Tanke, D. H. (1992). Paleopathology: Insights to lifestyle and health in the geological record. *Geoscience Canada, 19*, 73–82.
Rothschild, B. M., & Tanke, D. H. (2005). Theropod paleopathology: state-of-the-art review. In *The carnivorous dinosaurs* (pp. 351–365).
Schudack, M. E. (1987). Charophytenflora und fazielle Entwicklung der Grenzschichtenmariner Jura/Wealden in den Nordwestlichen Iberischen Ketten (mit Vergleichenzu Asturien und Kantabrien). *Palaeontographica Abteilung B, 204*, 1–108.
Schulp, A. S. (2002). The effects of tectonic deformation on dinosaur trackway-morphology. Sargetia. *Acta Musei Devensis, Series Scientia Naturae, Deva, 19*, 27–32.
Scrivner, P. J., & Bottjer, D. J. (1986). Neogene avian and mammal tracks from Death Valley National Monument, California: their context, conservation and preservation. *Paleogeography, Paleoclimatology, Paleoecology, 57*, 285–331.
Tanke, D. H., & Rothschild, B. M. (1997). *Paleopathology. encyclopedia of dinosaurs* (pp. 525–530). San Diego: Academic Press.
Tanke, D. H., & Rothschild, B. M. (2002). Dinosores: an annotated bibliography of dinosaur paleopathology and related topics, 1838–2001. *New Mexico Museum of Natural History and Science*, 1–96. Bullettin 20.
Thulborn, T. (1990). *Dinosaur tracks* (pp. 1–410). London: Chapman and Hall.
Xing, L. D., Bell, P. R., Harris, J. D., & Currie, P. J. (2012). An unusual, three dimensionally preserved, large Hadrosauriform pes track from "Mid" Cretaceous Jiaguan Formation of Chongqing, China. *Acta Geologica Sinica, 86*, 304–312. English Edition.
Xing, L. D., Wang, F., Pan, S., & Chen, W. (2007). The discovery of dinosaur footprints from the middle Cretaceous Jiaguan formation of Qijiang county, Chonqing city. *Acta Geologica Sinica, 81*, 1591–1602 [in Chinese].