



Ethological variations in gauge in sauropod trackways from the Berriasian of Spain

DIEGO CASTANERA, CARLOS PASCUAL, JOSÉ I. CANUDO, NIEVES HERNÁNDEZ AND JOSÉ L. BARCO

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Two sauropod trackways from the Early Cretaceous (Berriasian) of the Cameros Basin (Spain) show important variations in trackway gauge, along the same trackway. These variations seem to be associated with different behaviours; on the one hand with a significant variation in the direction of travel (turning phenomena) and on the other hand with a decrease in speed, probably associated with the properties of the substrate. These variations in sauropod trackways provide the trackway gauge debate with new data, supporting the hypothesis that the walking style and substrate properties may in some cases determine this sauropod character. The study of turning sauropod trackways improves our knowledge of sauropod locomotion. □ *Ethology, intermediate-gauge, sauropod trackways, substrate properties, wide-gauge.*

Diego Castanera [dcastanera@unizar.es] and José I. Canudo [jicanudo@unizar.es], Grupo Aragosaurus-IUCA, Paleontología, Facultad de Ciencias, Universidad de Zaragoza, C/Pedro Cerbuna 12, 50009 Zaragoza, Spain; Carlos Pascual [capascual-1@telefonica.net] C/Real, 65, 42002 Soria, Spain; Nieves Hernández [mnhernandez@terra.es] C/Jorge Vigón, 37, 26003 Logroño (La Rioja), Spain; José L. Barco [jlbarco@paleoymas.com] Paleoymás, Polígono INBISA - Empresarium - C/Retama, 17 Nave 24C, 50720 Cartuja Baja, Zaragoza, Spain; manuscript received on 11/07/2011; manuscript accepted on 20/12/2011.

Sauropod tracksites are abundant in the Upper Jurassic throughout the global record although there are only a few in the early stages of the Early Cretaceous (see Wright 2005 and references therein). Sauropod trackways have usually been differentiated into narrow-gauge and wide-gauge (Farlow 1992). Lockley *et al.* (1994a) and Meyer *et al.* (1994) also suggested the presence of an intermediate category (intermediate-gauge). The narrow-gauge trackways are considered predominant in the Jurassic (especially in the Early and Middle Jurassic) and the wide-gauge are considered more common in the Cretaceous (Lockley *et al.* 1994a,b; Wilson & Carrano 1999). In the Upper Jurassic and the Early Cretaceous there is in fact a co-occurrence of both kinds of trackways (Wright 2005; Marty 2008; Moratalla 2009). Recent works (Romano *et al.* 2007; Marty 2008; Marty *et al.* 2010) have proposed different ratios to characterize the trackway gauge, demonstrating that this division and its temporal distribution is more complex than previously suggested.

The importance of such gauge variation lies in the implications it could have in sauropod systematics. Traditionally, this subdivision provided the base for differentiating between titanosauriform and non-titanosauriform trackmakers (Farlow 1992; Lockley *et al.* 1994b; Wilson & Carrano 1999; Day *et al.* 2002; Wright 2005). Furthermore, the gauge has been used

as an important feature in sauropod ichnotaxonomy (Farlow *et al.* 1989; Lockley *et al.* 1994a; Calvo & Mazzetta 2004; González Riga & Calvo 2009; Santos *et al.* 2009). Nonetheless, Santos *et al.* (2009) suggested that some non-titanosauriform sauropods could have also produced wide-gauge trackways. Other authors have suggested that this gauge variation could also be associated with other factors such as the ontogenetic state of the trackmakers (Lockley *et al.* 2002a,b; but see Vila i Ginestí 2010), the size of the dinosaurs and the relative positions of their centres of mass (Henderson 2006), individual behaviour/substrate properties (Marty 2008), or the size and speed of the sauropod (Diedrich 2011).

A great number of sauropod tracksites of the Iberian Peninsula have been described during the Jurassic-Cretaceous interval (Tithonian-Berriasian) (see Santos 2008; Royo-Torres 2009; Moratalla 2009; Castanera & Canudo 2011; Castanera *et al.* 2011). The Huérteles Formation (Berriasian of the Cameros Basin, Spain) is known in the scientific literature for its great number of tracksites made by dinosaurs and other reptiles. From this unit, dinosaur footprints belonging to the principal clades have been described for theropods, ornithopods and sauropods (see Barco *et al.* 2005, 2006; Pascual-Arribas *et al.* 2009; Pascual-Arribas & Hernández-Medrano 2011). The number of tracksites with sauropod footprints is noteworthy

(Hernández Medrano *et al.* 2008) even though many of them do not have trackways preserved. Castanera *et al.* (2010) distinguished four different morphotypes on the basis of the trackway type, heteropody and footprint morphology, pointing out the importance of the presence of narrow and wide-gauge sauropod trackways. Two of these trackways show gauge variations along a single trackway (Meijide Fuentes *et al.* 2001; Pascual Arribas *et al.* 2008) so their classification in the above-mentioned categories is more complex. The aim of this article is to analyse these sauropod trackways, quantify their gauge variations and discuss the factors that may have produced them.

Geographical and geological setting

The tracksites are situated in the north of the province of Soria, north-central Spain (Fig. 1). Las Cuestas I tracksite is located in the village of Santa Cruz de Yanguas, and Salgar de Sillas tracksite in the village of Los Campos. Both of them belong to the region of Tierras Altas, and their UTM coordinates (ED50 datum) are: $x = 543.788$; $y = 4.656.930$ and $x = 553.517$; $y = 4.648.269$ respectively.

They are located in the eastern Cameros Basin in the northern sector of the Iberian Range. They belong to the Huérteles Formation, included in the Oncala Group, which represents an Early Cretaceous lacustrine episode (see Moratalla & Hernán 2010 and references therein). The sedimentation of the Huérteles Formation was produced in alluvial plain systems distally connected with playa-lake systems. The materials from both tracksites are of a terrigenous nature and were deposited in the proximal environments. They are interpreted as alluvial plain facies with a predominance of siltstones and sandstones (Gómez Fernández & Meléndez 1994; Moratalla & Hernán 2010).

The estimated age of the Huérteles Formation is Berriasian (Martín-Closas & Alonso Millán 1998; Salas

et al. 2001; Schudack & Schudack 2009). This dating has been proposed on the basis of the ostracod and charophyte content and by stratigraphical correlation.

Materials and methods

The sauropod trackway LCU-37-I from Las Cuestas I tracksite was described by Pascual Arribas *et al.* (2008) (Fig. 2). In this study we have used data published in the original article, and have calculated new parameters in the drawings.

The sauropod trackway SS1-R1 (nomenclature used by Moratalla 2009) at the Salgar de Sillas tracksite was described by Meijide Fuentes *et al.* (2001). In this study we remeasured the trackway parameters in the field and redrew the sketch of the trackway (Fig. 3). The sketch of the trackway produced in 2004 by the Paleoymás team in the course of the topography project for the dinosaur tracksites of the province of Tierras Altas was used. Not all the footprints at the tracksite can now be seen, so we do not have data for the first two footprints in the sketch made by Meijide Fuentes *et al.* (2001).

The nomenclature of the different parameters used in this article follows the works of Farlow *et al.* (1989) and Thulborn (1990). Thus, the measurements made (Tables 1 and 2) are the footprint length (FL), footprint width (FW), footprint rotation (FR), pace length (PL), pace angulation (ANG), stride length (SL), inner (internal) and external trackway width (iTW–eTW), manus–pes distance (Dm–p), and the width of the angulation pattern of pes and manus (WAP and WAM). The term m/p denotes manus and pes respectively.

The trackway ratio (Romano *et al.* 2007) and the WAP/PL ratio (Marty 2008; Marty *et al.* 2010) were calculated and analysed for the Las Cuestas I and Salgar de Sillas trackways. The pes and manus trackway ratio (PTR and MTR) were calculated as $TR = (sw/ow) \times 100$ following the procedure suggested by



Fig. 1. Geographical setting of A, Las Cuestas I tracksite (Santa Cruz de Yanguas) and B, Salgar de Sillas tracksite (Los Campos).

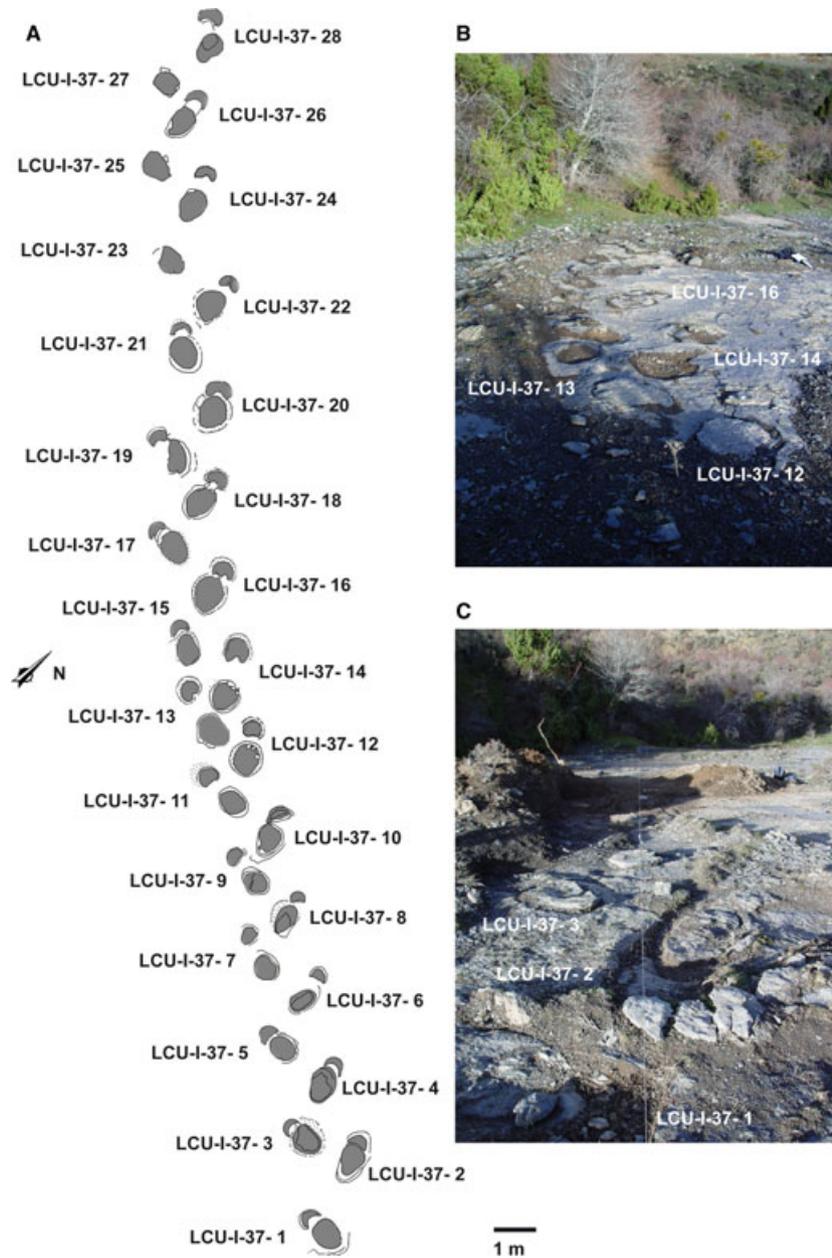


Fig. 2. Sauropod trackway LCU-I-37 from Las Cuestas I tracksite. A, sketch of the sauropod trackway LCU-I-37 (modified from Pascual Arribas *et al.* 2008). Scale: 1 m. B, picture of a part of the sauropod trackway LCU-I-37 (from LCU-I-37-12 to LCU-I-37-16). C, picture of first part of the sauropod trackway LCU-I-37 (from LCU-I-37-1 to LCU-I-37-4). Note how the gauge of the trackway varies from the first picture to the second; note also that the natural casts are inside the footprints.

Romano *et al.* (2007), where *sw* is the side width and *ow* is the overall width (in this article these parameters almost coincide with *FW* and *eTW* respectively). The *WAP/PL* ratio represents the ratio between the width of the angulation pattern (in the pes) and the pes length. Note that throughout this article we use *PL* for the pace length, and *FL* for the footprint length. Nonetheless, in the case of these ratios we have maintained the nomenclature used in the formulas from the original articles. In the case of LCU-I-37, they were calculated using the outline drawings, whereas in the

case of SS1-R1 they were calculated using the measurements taken in the field. In both cases the calculations took into consideration the interior track outline, as suggested by Marty (2008). We applied the limits for wide, intermediate and narrow-gauge trackways from the original articles. These are $\leq 35\%$, 36–49% and $\geq 50\%$ in the case of the PTR; and ≥ 1.2 , 1–1.2 and ≤ 1 for the *WAP/PL* ratio. The hip height (*h*) and the locomotion speed (*v*) were calculated using the Alexander (1976) equations ($h = 4 FL$; $v = 0.25 g \cdot 0.5 \times SL 1.67 \times h^{-1.17}$) but only with the

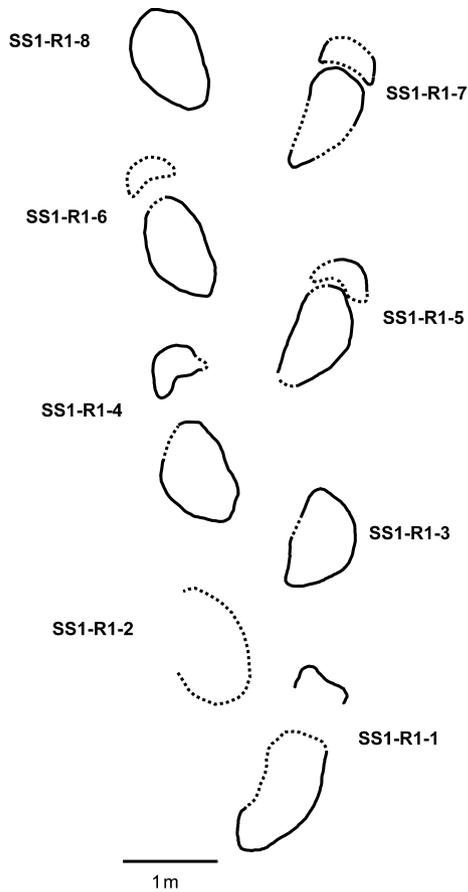


Fig. 3. Sketch of the sauropod trackway SS1-R1 from Salgar de Silas tracksite. Note that some outlines do not show the typical sauropod footprint morphology. Scale: 1 m.

purpose of showing the variation along the trackway. FL represents the footprint length, g is the constant of gravity, and SL is the stride length.

Trackway descriptions

Las Cuestas I tracksite

The LCU-I-37 is composed of 28 manus-pes sets and is about 31 m long (Fig. 2; Table 1). The footprints have been preserved as true tracks (*sensu* Lockley 1991), and many of them have preserved the natural casts inside the footprint (Fig. 2). Some natural casts have been recovered (Fig. 4). The manus prints are kidney-shaped to semicircular, and some of them preserve the mark of digit I. The pes prints are subtriangular, with three claw marks decreasing in size from digit I to digit III. Moreover, the rounded marks of the digits IV and V can be discerned as well (Fig. 4).

The manus prints are farther away from the trackway midline, whereas the pes prints are closer to it, intersecting the trackway midline in some parts of the trackway.

The trackway has three different parts, differentiated by an important change in direction (Fig. 2). The first part (from LCU-I-37-1 to LCU-I-37-9) runs in a SE-NW direction and has a straight trajectory. In the middle part of the trackway (from LCU-I-37-10 to LCU-I-37-18) there is a slight change in direction (12°). Subsequently, in the last part (from LCU-I-37-19 to LCU-I-37-28) the trackway follows a sinusoidal trajectory.

In the first part of the trackway, the pes prints do not intersect the trackway midline (Fig. 2C). The values of the PTR and WAP/PL ratio (Fig. 5A, B) indicate that in this part the trackway would be intermediate-gauge, but almost wide-gauge (mean values of 35.9% PTR and 1.03 WAP/PL ratio respectively). Then, in the section where the sauropod starts to turn, the pes tracks intersect the trackway midline (Fig. 2B), and these ratios increase and decrease, respectively, so the trackway would be intermediate to narrow-gauge depending on the ratios (mean values of 44.35% PTR and 0.82 WAP/PL ratio). In the final part of the trackway, where the trajectory is sinusoidal, the values are more similar to the first part, the trackway being intermediate-gauge (mean values of 39.64% PTR and 1.02 WAP/PL ratio). At the end of the trackway, in the final two manus-pes sets, the pes prints again intersect the trackway midline in what we think could be the start of another change in direction, though this is too speculative. It is noteworthy that the variations in the manus parameters (MTR and WAM/MW) are not so great (Fig. 5A, C).

Some of the other parameters also show significant variations along the trackway. The inner trackway width, the pace length, the stride length, the speed and the footprint rotation display a marked decrease (Fig. 5D–H) just as the sauropod is about to start turning (from LCU-I-37-7 to LCU-I-37-13). The inner width (Fig. 5D) ranges from positive to negative values, the maximum being 23 cm (LCU-I-37-2p) and the minimum -12 cm (LCU-I-37-13p). The pace length (Fig. 5E) in the pes prints varies from 185 (LCU-I-37-1p) to 40 (LCU-I-37-10p) and in the manus prints from 215 (LCU-I-37-1 m) to 152 (LCU-I-37-9 m). The stride length (Fig. 5F) in the pes prints ranges from 249 (LCU-I-37-14p and LCU-I-37-20p) to 160 (LCU-I-37-12p) and in the manus prints from 269 (LCU-I-37-22 m) to 151 (LCU-I-37-13 m). The speed (Fig. 5G) varies from 3.6 to 1.9 km/h, and the footprint rotation (Fig. 5H) ranges from 50 (LCU-I-37-6p) to 15 (LCU-I-37-20p) in the pes and from 45 (LCU-I-37-6 m) to 19 (LCU-I-37-19 m) in the manus. The values just at the moment of turning are at their lowest or nearly lowest levels, and then the parameters become more similar to the first part of the trackway. Noteworthy is the variation from lower to higher values in manus pace length just at this moment of turning.

Table 1. Measurements of the sauropod trackway LCU-I-37 from Las Cuestas I tracksite (modified from Pascual Arribas *et al.* 2008).

Footprint	FL	FW	FR	PL	SL	eTW	iTW	ANG	Dp-m	v	PTR-MTR	WAP-WAM	WAP/PL
LCU-I-37-1p	72	53	35	185	238	165	x	107	14	3.6	32.12	x	x
LCU-I-37-1m	25	45	30	215	237.5	187		72			24.06	x	x
LCU-I-37-2p	72	54	27	120	203	164	23	110	15	2.7	32.93	91.5	1.27
LCU-I-37-2m	23	43	20	186	190	192		60			22.4	158	x
LCU-I-37-3p	73	53	34	145	233	156	11	116	25	3.5	33.97	85	1.16
LCU-I-37-3m	x	x	33	195	230	210		72			x	165	x
LCU-I-37-4p	73	53	35	129	230	144	4	116	0	2.2	36.81	72	0.99
LCU-I-37-4m	27	43	35	194	233	194		74			22.16	155	x
LCU-I-37-5p	72	52	32	141	216	138	9	107	14	3.1	37.68	71	0.99
LCU-I-37-5m	26	45	35	195	253	190		78			23.68	155	x
LCU-I-37-6p	71	54	50	128.5	194	149	9	100	20	2.3	36.24	79	1.11
LCU-I-37-6m	30	42	45	209	208.5	193		68			21.76	157	x
LCU-I-37-7p	70	56	22	126	216	141	14	120	44	3.1	39.72	82.5	1.18
LCU-I-37-7m	32	47	23	163	206	183		69			25.68	150	x
LCU-I-37-8p	72	50	28	125	215	128	2	130	20	2.9	39.06	64	0.89
LCU-I-37-8m	27	36	40	190	208.5	180		73			20	144	x
LCU-I-37-9p	72	52	31	113	214	147	-9	121	32	2.8	35.37	51	0.71
LCU-I-37-9m	32	47	26	152	213	175		70			26.86	135	x
LCU-I-37-10p	76	56	36	40	212.5	128	-3	121	18	2.8	43.75	57	0.75
LCU-I-37-10m	32	47	42	205	233	181		79			25.97	139	x
LCU-I-37-11p	72	54	25	113	184	127	-9	115	35	2.1	42.52	59	0.82
LCU-I-37-11m	33	47	29	156	216	181		79			25.97	136	x
LCU-I-37-12p	73	56	27	104	160	127	-5	112	30	1.9	44.09	57	0.78
LCU-I-37-12m	33	44	32	180	192	175		71			25.14	127	x
LCU-I-37-13p	72	55	24	87	202.5	122	-12	120	65	2.5	45.08	52	0.72
LCU-I-37-13m	32	47	33	154	151	181		58			25.97	135	x
LCU-I-37-14p	72	62	37	143	249	121	-9	119	60	3.6	51.24	50	0.69
LCU-I-37-14m	33	47	35	166	190	187		67			25.13	140	x
LCU-I-37-15p	73	56	20	145	247	136	6	123	15	3.4	41.18	72.5	0.99
LCU-I-37-15m	28	47	20	172	246	186		82			25.27	139	x
LCU-I-37-16p	73	58	30	136	218	130	1	115	15	3	44.62	67	0.92
LCU-I-37-16m	28	43	25	198	228.5	183		78			23.5	138	x
LCU-I-37-17p	72	53	35	124	224	133	-8	126	22	3.1	39.85	69	0.96
LCU-I-37-17m	26	50	24	189	223	200		75			25	157	x
LCU-I-37-18p	72	60	34	133	226.5	128	-3	115	23	3.2	46.88	58	0.81
LCU-I-37-18m	30	48	27	173	212	184		73.5			26.09	143	x
LCU-I-37-19p	72	x	33	136	243	138	6	110	18	3.4	x	73	1.01
LCU-I-37-19m	24	36	19	181	263	185		93			19.46	142	x
LCU-I-37-20p	72	53	15	156	249	145	12	120	2	3.6	36.55	81	1.13
LCU-I-37-20m	28	47	25	185	246	171		90			27.49	x	x
LCU-I-37-21p	73	54	34	130	221	140	5	107	15	3	38.57	70	0.96
LCU-I-37-21m	28	47	35	162	x	175		60			26.86	x	x
LCU-I-37-22p	74	x	45	148	236	154	15	112	20	3.3	x	81.5	1.1
LCU-I-37-22m	29	45	30	x	269	195		x			23.08	x	x
LCU-I-37-23p	72	53	35	137	240	151	15	113	x	3.4	35.1	79	1.1
LCU-I-37-23m	x	x	x	x	x	x		73			x	x	x
LCU-I-37-24p	73	55	35	149	209	145	10	102	32	2.8	37.93	77	1.05
LCU-I-37-24m	33	44	25	x	204	176		70			25	x	x
LCU-I-37-25p	75	53	35	121	210	149	16	127	x	2.7	35.57	83	1.11
LCU-I-37-25m	x	x	x	x	x	190		70			x	x	x
LCU-I-37-26p	75	56	25	114	188	115	-11	114	30	2.2	48.7	50	0.76
LCU-I-37-26m	32	45	40	x	178	x		70			x	x	x
LCU-I-37-27p	x	55	40	109	x	122	3	x	x	x	45.08	60	x
LCU-I-37-27m	x	x	x	x	x	x		x			x	x	x
LCU-I-37-28p	75	50	20	x	x	x	x	x	20	x	x	x	x
LCU-I-37-28m	30	45	25	x	x	x		x			x	x	x
Average pes	72.7	54.5	31.8	130.7	218.4	138.6	4.2	115.7	24.1	2.9	48.06	68.9	0.95
Average manus	29.2	43.2	29	181.9	218.5	185.8		74			25.68	140.38	x

Abbreviations: FL, footprint length; FW, footprint width; PL, pace length; SL, stride length; eTW-iTW, external and inner trackway width; Dm-p, manus-pes distance; WAP and WAM, width of the angulation pattern for both pes and manus, (in cm); FR, footprint rotation; ANG, pace angulation (in degrees); PTR and MTR, pes and manus trackway ratio (in %); v, locomotion speed (in km/h); m/p, manus and pes; x, no values.

The variation in other parameters such as the pace angulation (Fig. 5I) is not so significant. This ranges from 130 (LCU-I-37-8p) to 100 (LCU-I-37-6p) in the pes, and from 93 (LCU-I-37-19 m) to

58 (LCU-I-37-13 m) in the manus. The variation in the external trackway width (Fig. 5J) is significant, for it ranges from 165 (LCU-I-37-1p) to 115 (LCU-I-37-26p) in the pes, and from 210

Table 2. Measurements of the sauropod trackway SS1-R1 from Salgar de Sillas tracksite.

Footprint	FL	FW	FR	PL	SL	eTW	iTW
SS1-R1 m/p	48-50/136	55/65	x	160	260	x	x
SS1-R2 m/p	x/x	x/x	x	170	234	x	x
SS1-R3 m/p	x/110	x/66	23	160	268	210	42
SS1-R4 m/p	35-40/114	52/65	25/19	209	275	210	44
SS1-R5 m/p	28/113	61/60	24	176	241	208	51
SS1-R6 m/p	x/113	x/61	19	192	213	209	73
SS1-R7 m/p	x/112	x/55	25	168	x	x	90
SS1-R8 m/p	x/112	/66	26	x	x	x	x

Footprint	ANG	Dm-p	v	PTR/MTR	WAP	WAP/PL
SS1-R1 m/p	x	122?	x	x	x	x
SS1-R2 m/p	x	x	x	x	106	x
SS1-R3 m/p	x	x	2.556	35.8	119	1.08
SS1-R4 m/p	/87.5	124	2.58	36.9/25	125	1.09
SS1-R5 m/p	/92.5	76	2.088	33.5	131	1.16
SS1-R6 m/p	81	80?	1.69	32.7	139	1.23
SS1-R7 m/p	78	96?	x	27.5	146	1.3
SS1-R8 m/p	x	x	x	31.5	x	x

Abbreviations: FL, footprint length; FW, footprint width; PL, pace length; SL, stride length; eTW-iTW, external and inner trackway width; Dm-p, manus-pes distance; WAP, width of the angulation pattern for the pes (in cm); FR, footprint rotation; ANG, pace angulation (in degrees); PTR and MTR, pes and manus trackway ratio (in %); v, locomotion speed (in km/h); m/p, manus and pes; x, no values; ?, denotes uncertainty due to the poor preservation of the manus prints.

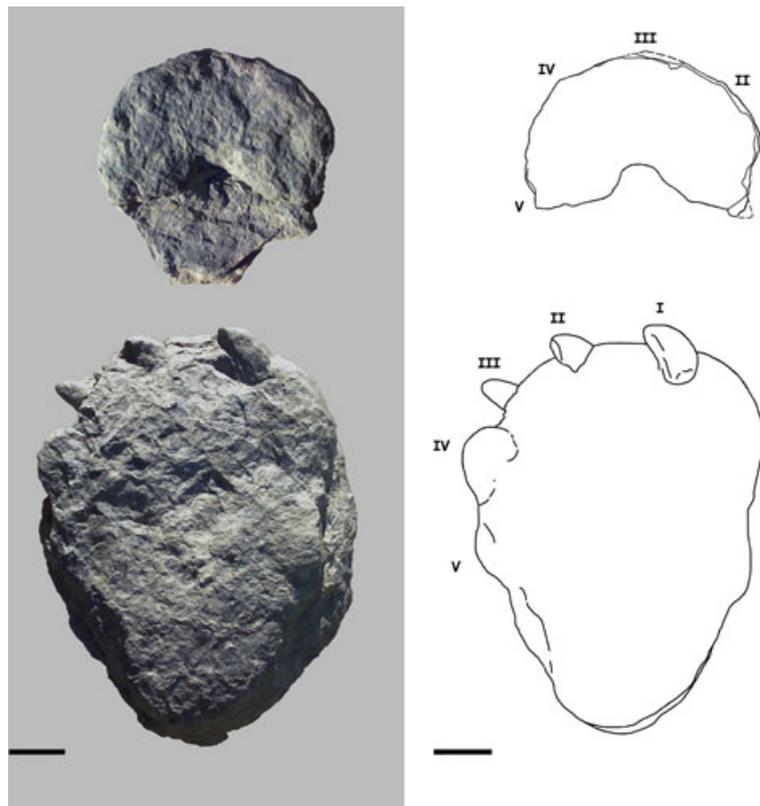


Fig. 4. Sauropod manus and pes tracks of the trackway LCU-I-37 from Las Cuestas I tracksite (after Pascual-Arribas & Hernández-Medrano 2011) A, manus cast (LCU-I-37-24 m) and pes cast (LCU-I-37-12p). B, interpretative drawings of the aforementioned manus and pes tracks. Scale: 0.1 m.

(LCU-I-37-3 m) to 171 (LCU-I-37-20 m) in the manus. Nonetheless, in the turning area this variation is not as marked as the variation in the other parameters.

Salgar de Sillas tracksite

The SS1-R1 is composed of eight manus-pes sets and is about 8 m long, but the manus prints have not been

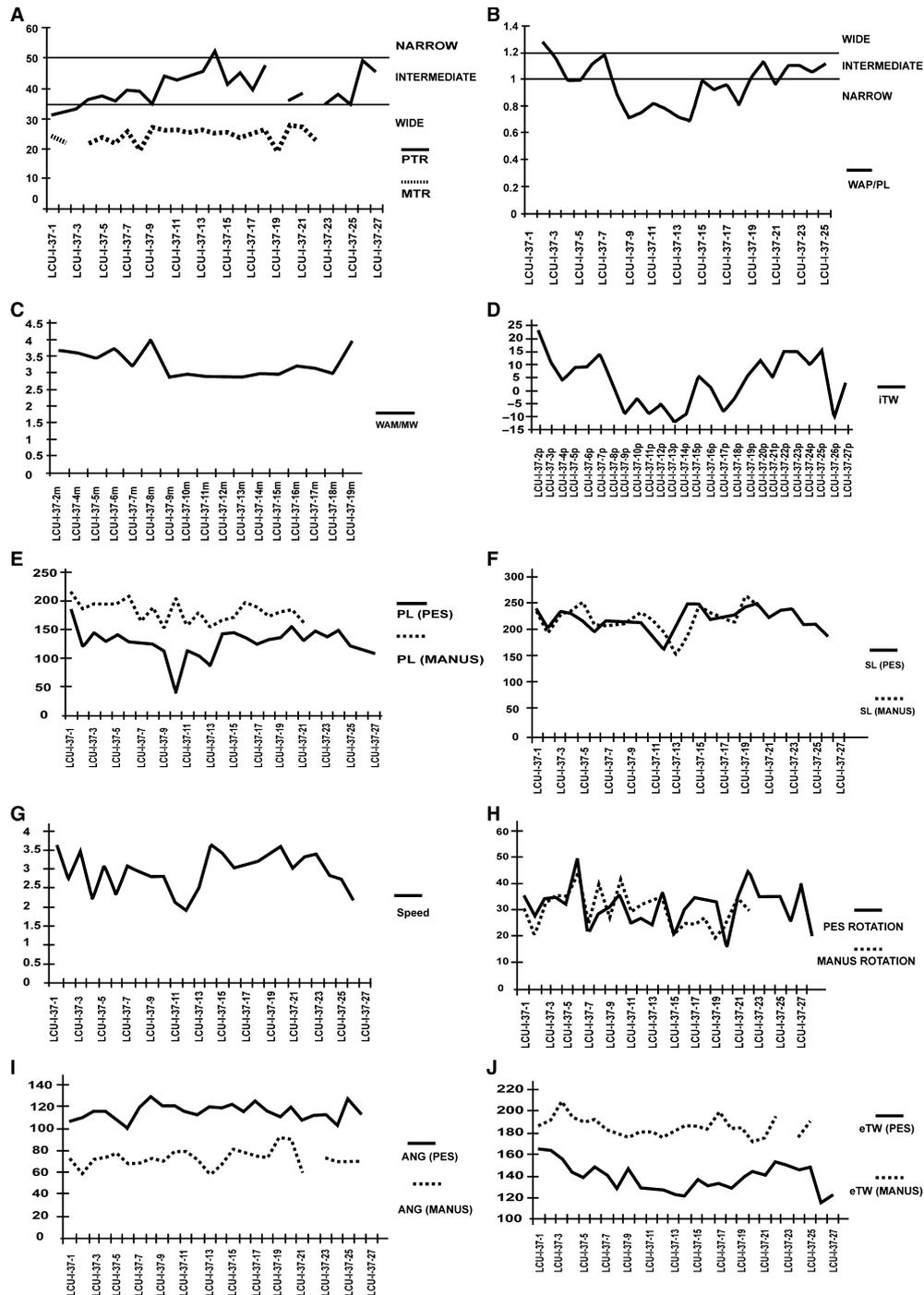


Fig. 5. Plots showing the variations in the different parameters of LCU-I-37 along the whole trackway. A, PTR and MTR ($TR = (sw/ow) \times 100$, *sensu Romano et al. 2007* where *sw* is side width and *ow* the overall width). B, WAP/PL ratio (*sensu Marty 2008*), where WAP is the width of the angulation pattern in the pes and PL the footprint (pes) length. C, WAM/MW ratio (*sensu Marty 2008*), where WAM is the width of the angulation pattern in the manus and MW is the manus width. D, inner trackway width. E, pace length. F, stride length. G, speed. H, footprint rotation. I, pace angulation. J, external trackway width.

preserved in the first part of the trackway (Fig. 3). The mode of preservation of the footprints is a little confusing due to deformation of the different layers produced by the dinosaur as it passed. The tracksite is particularly spectacular because the tracks form raised

pedestals. There is some doubt about which layer the footprints were produced in. It is difficult to know whether the top layer of the pedestals is the tracking surface or whether this is above the top layer and the tracks may thus represent undertracks (Fig. 6).

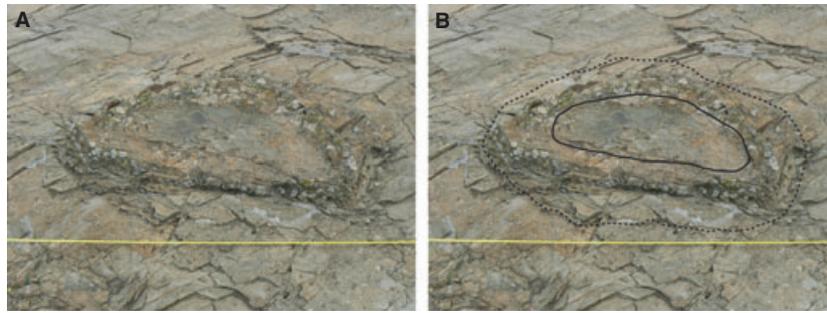


Fig. 6. Right pes track (SS1-R1-3p) of the sauropod trackway SS1-R1 from Salgar de Sillas tracksite. A, pes track SS1-R1-3p. B, pes track SS1-R1-3p, stating the preservation of the undertrack layers (inside the broken line) and the top layer (continuous line) that could represent the tracking surface. Scale (ruler) = 1.6 m.

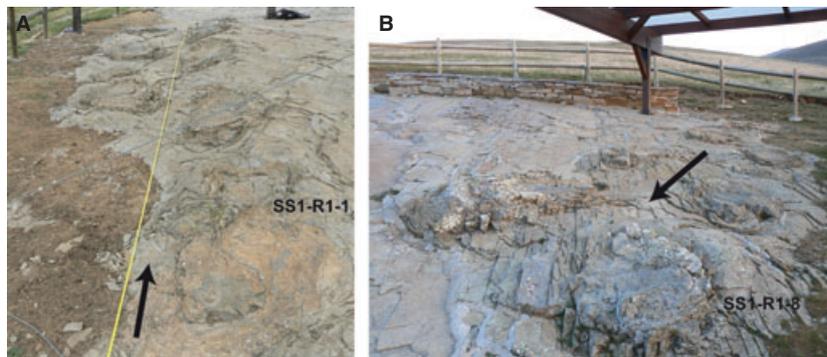


Fig. 7. Sauropod trackway SS1-R1 from Salgar de Sillas tracksite. Note how the trackway gauge increases in the direction of travel. The arrows show the direction of travel.

Different layers below the top surface can be seen which represent undertracks or transmitted prints (*sensu* Thulborn 1990; Lockley 1991). We cannot rule out the possibility that the top layer was the true tracking surface. Whatever the case, the morphology of the manus prints is semicircular, and the pes prints are oval in shape. However, this morphology is completely conditioned by the preservation of the prints and does not represent anatomical features.

The trackway starts with the pes prints relatively close to the trackway midline, and the inner width (Figs 3, 7) and WAP (and the WAP/PL ratio) increase in the direction of travel (northwards), while the PTR decreases (Fig. 8A, B). The preserved manus prints are always far from the trackway midline, and except in the case of SS1-R1-4 m (Fig. 9A) they are overprinted by the pes prints (Fig. 9B).

The variation in parameters such as the inner trackway width (Fig. 8C), the pace length (Fig. 8D), the stride length (Fig. 8E), the speed (Fig. 8F) or the manus-pes distance (Table 2) is considerable, and these parameters are influenced by the mode of preservation. The inner width increases in the direction of travel (Fig. 8C) while the speed decreases (Fig. 8F). The pace length (Fig. 8D), and the stride length (Fig. 8E) are irregular and decrease a little. Other

parameters do not show a major variation (footprint rotation (Fig. 8G), pace angulation (Fig. 8H) and external trackway width (Fig. 8I)). The pace angulation is relatively low, no more than 92° , and the rotation is about $20\text{--}25^\circ$.

Discussion

Gauge variation in LCU-I-37 and SS1-R1

Farlow (1992) suggested that the differences between narrow and wide-gauge sauropod trackways ‘conceivably reflect differences in the skeletal structure of the trackmakers’. Farlow (1992) and Wilson & Carrano (1999) also suggested that the speed and the substrate consistency likewise exert an important influence on the inner width of the trackways. Moreover, the gauge can change along the length of a single trackway (Romano *et al.* 2007). These authors thus argue that to assign a single trackway to a particular trackway type may be an oversimplification.

In the case of LCU-I-37 and SS1-R1 there is considerable variation in the gauge along the trackways themselves, which can thus be classified as narrow/intermediate (LCU-I-37) and intermediate/wide

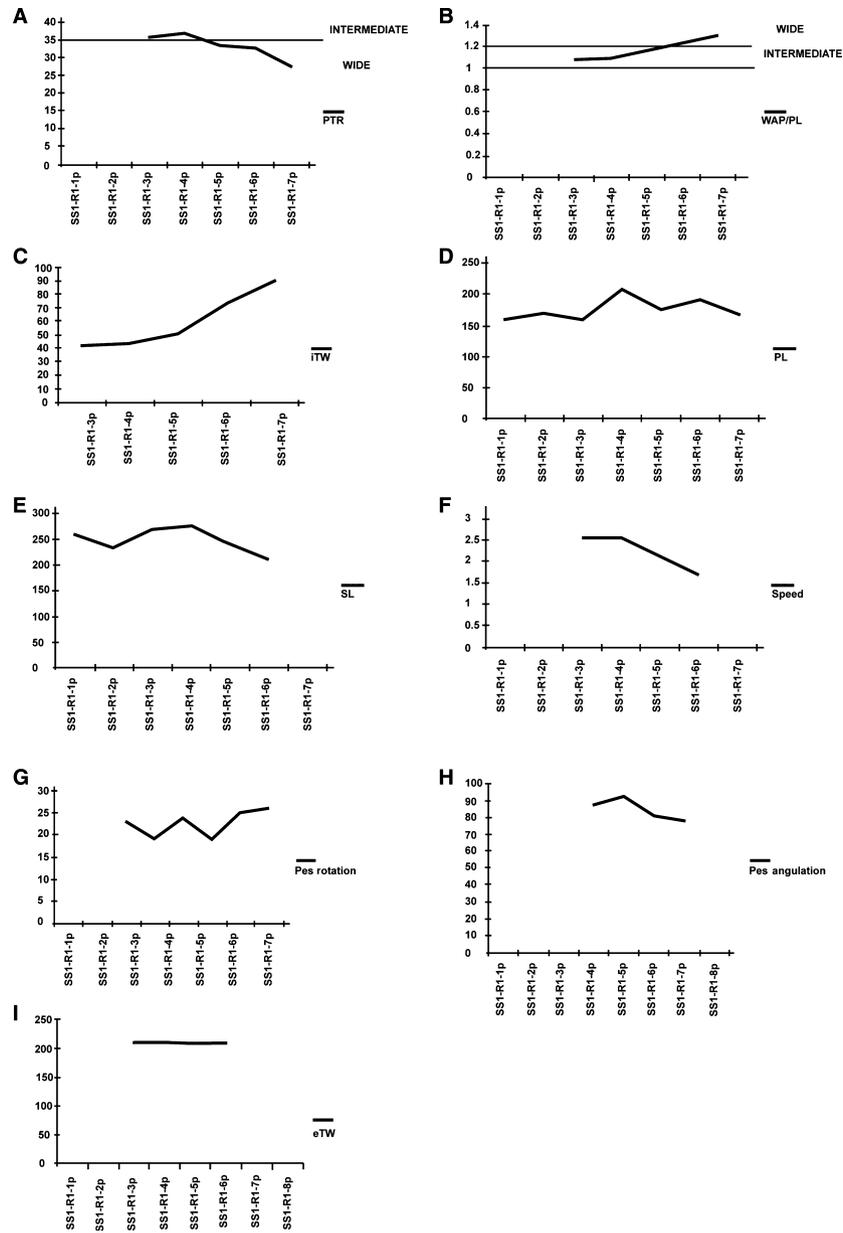


Fig. 8. Plots showing the variations in the different parameters of SS1-R1 along the whole trackway. A, PTR ($TR = (sw/ow) \cdot 100$, *sensu* Romano *et al.* 2007 where *sw* is side width and *ow* the overall width). B, WAP/PL ratio (*sensu* Marty 2008), where WAP is the width of the angulation pattern in the pes and PL the footprint (pes) length. C, inner trackway width. D, pace length. E, stride length. F, speed. G, footprint (pes) rotation. H, ANG, pace (pes) angulation. I, external trackway width.

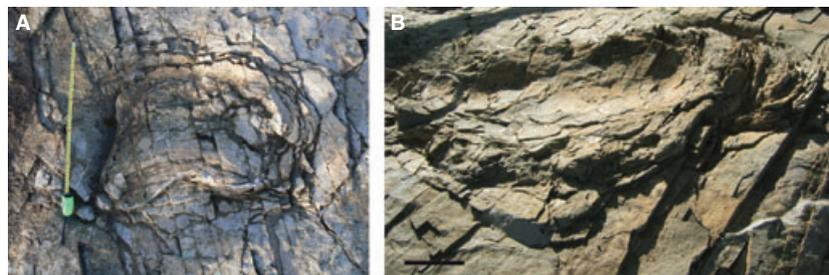


Fig. 9. Tracks of the sauropod trackway SS1-R1 from Salgar de Sillas tracksite. A, manus print SS1-R1-4 m, scale (ruler) = 0.5 m. B, manus-pes set SS1-R1-5p and SS1-R1-5 m, scale = 0.3 m. Note the overprinting phenomenon.

(SS1-R1). In both cases there is a relationship between the speed and the gauge, as suggested by Diedrich (2011) in reference to other sauropod trackways from Germany. The author based this relationship on the fact that the ‘faster the animal runs, the narrower the track gauge’ is. Nonetheless, in LCU-I-37 and SS1-R1 there are contrary situations. In LCU-I-37 the calculated decrease in speed corresponds to a narrower section of the trackway, whereas in SS1-R1 the opposite is the case. The decrease in speed in SS1-R1 is associated with the wider part of the trackway, whereas the first part, where the speed is greater, is narrower. As trackway SS1-R1 is so short, however, it cannot be known for certain whether this variation in speed is directly related to the inner width of the trackway or is just an artefact.

These differences can perhaps be explained by different behaviours in the two trackways. In LCU-I-37 it seems to be clear that the narrower pattern is determined by the change in the direction of travel associated with a decrease in speed. In SS1-R1 the marked variation in some parameters suggests an abnormal gait that could be a consequence of the substrate consistency, though other factors cannot be ruled out either. This is also reflected in the considerable deformation (Figs 6, 7, 9B) below the footprints (transmitted prints) and in the overprinting phenomenon (Fig. 9B). The features of the majority of the tracks clearly do not show the autopod morphology of the sauropods, and no anatomical features can be seen. The deformation of the layers below the top surface (as mentioned above, there is some doubt as to whether this corresponds to the tracking surface) is so substantial that the variation in the gauge could be very different depending on what the internal edge is considered to be.

There are specific problems that could arise in measuring the inner width of the trackways (Lockley *et al.* 2002; Marty 2008). Some of these problems are related with the variation of these parameters with depth and the preservation of the footprints below the walking surface (Romano *et al.* 2007; Jackson *et al.* 2009). In the case of Salgar de Sillas, Meijide Fuentes *et al.* (2001) considered the trackway to be narrow-gauge. Comparing the data of their measurements with ours, it can be seen that for example in the footprint length their values are about 20% greater than ours. Their measurements are more similar to the data that we obtained measuring in the lowest layer of the undertracks (Table 3; Fig. 6). As a result, measurements in the transmitted print layers imply that the sauropod trackway might be narrow whereas in fact it is not. Moratalla (2009) classified this trackway as narrow-gauge, but also added that ‘nothing else is clear’.

In the case of Las Cuestas I tracksite, in the lower layer where LCU-I-37 is preserved, other sauropod

Table 3. Measurements of the footprint length (FL) and footprint width (FW) of the sauropod trackway SS1-R1 from Salgar de Sillas tracksite, taken in the lowest undertrack layer.

Footprint	FL	FW
SS1-R1-1p	152	106
SS1-R1-2p	x	x
SS1-R1-3p	172	11
SS1-R1-4 m/p	50/156	109
SS1-R1-5 m/p	41/153	70/104
SS1-R1-6p	177	107
SS1-R1-7 m/p	38/145	60/103
SS1-R1-8p	153	101

Abbreviation: x, no values.

trackways have been described (Pascual-Arribas & Hernández-Medrano 2011). All of them are smaller in size than LCU-I-37 and seem to be narrower-gauge. Pascual Arribas *et al.* (2008) proposed that these differences could be ontogenetic in origin (cf. Lockley *et al.* 2002a,b), but another explanation may also be possible. Some footprints do not show any anatomical details so they are probably undertracks. The gauge variation could also be a consequence of depth, in that the trackways appear to be narrower (cf. Moratalla *et al.* 1994). Jackson *et al.* (2009) have shown experimentally that transmitted tracks may widen (increase in size) with depth, thus producing potentially narrower-gauge trackways. Some articles have pointed out the important variations in some parameters with respect to the track preservation quality and depth (Manning 2004; Milàn & Bromley 2006; Romano *et al.* 2007; Falkingham *et al.* 2010). These authors note the importance of the tracking surface, the surface where the measurements are taken, the substrate type, the moisture content and the force applied. All this should be taken into account before classifying a trackway type. Despite having classified SS1-R1 as intermediate/wide-gauge, we are conscious that this is just an approximation because we remain uncertain whether the top layer is the tracking surface. This means that the ‘real gauge’ of the trackway could in fact be greater. Some parameters in SS1-R1 have been estimated only to bring to light the degree of variation.

Romano *et al.* (2007) also noticed the correlation between the pace angulation and the PTR in trackways from Paluxy River (USA) and Galinha (Portugal). The higher the pace angulation, the higher the PTR; in other words, the narrower is the trackway. The authors also suggested that the PTR could be related with the speed and stride length. In the case of LCU-I-37 and SS1-R1 there is not such a great variation in pace angulation (Figs 5I, 8H). The former trackway varies from 100 (LCU-I-37-6p) to 130 (LCU-I-37-8p), which corresponds to the part where the sauropod is going to start the turning, and in this part the

trackway is still intermediate (PTR = 36 and 39 respectively). In the case of SS1-R1 the pace angulation does not vary so much, but this correlation could be possible. Marty (2008) also noted the importance of footprint rotation in the gauge variation. In the case of LCU-I-37 it is noteworthy that just at the point where it becomes narrower, the footprint rotation is lower, contrary to what we might have expected (Figs 5B, H).

Another parameter that is worthy of comment is the external width (Tables 1 and 2). In LCU-I-37 this varies from 115 (LCU-I-37-26p) to 165 (LCU-I-37-1p) cm in the pes and from 171 (LCU-I-37-20m) to 210 (LCU-I-37-3m) cm in the manus. It is noteworthy that just in the part of the trackway where the sauropod is turning, the pes values are very variable whereas the manus values are not (Figs 2, 5J). This could be a consequence of the major role of the hindlimbs in sauropod progression (Christiansen 1997). This could also be reflected in the largely constant values for the MTR and WAM/MW ratios (Fig. 5A, C).

Comparison of LCU-I-37 with other turning trackways

The variation in some parameters due to changes in direction or sinuous trajectories of travel has also been described in other sauropod trackways (Casanovas *et al.* 1997; Calvo & Mazzetta 2004; González Riga & Calvo 2009; Ishigaki & Matsumoto 2009). Other turning sauropod trackways have been reported, but in these cases the variations in parameters were not described in detail (Meyer 1993; Meyer *et al.* 1994; Mezga & Bajraktarevic 1999).

Ishigaki & Matsumoto (2009) reported one turning trackway from the Upper Jurassic of Morocco and described the phenomenon of 'off-tracking' in this and other sauropod turning trackways from the literature (Lockley 1991; Meyer 1993). This consists in the existence of a maximum gap between the trackway midlines of manus and pes prints at the moment of turning. In the case of LCU-I-37 (Fig. 10) the trackway midlines for both manus and pes coincide in

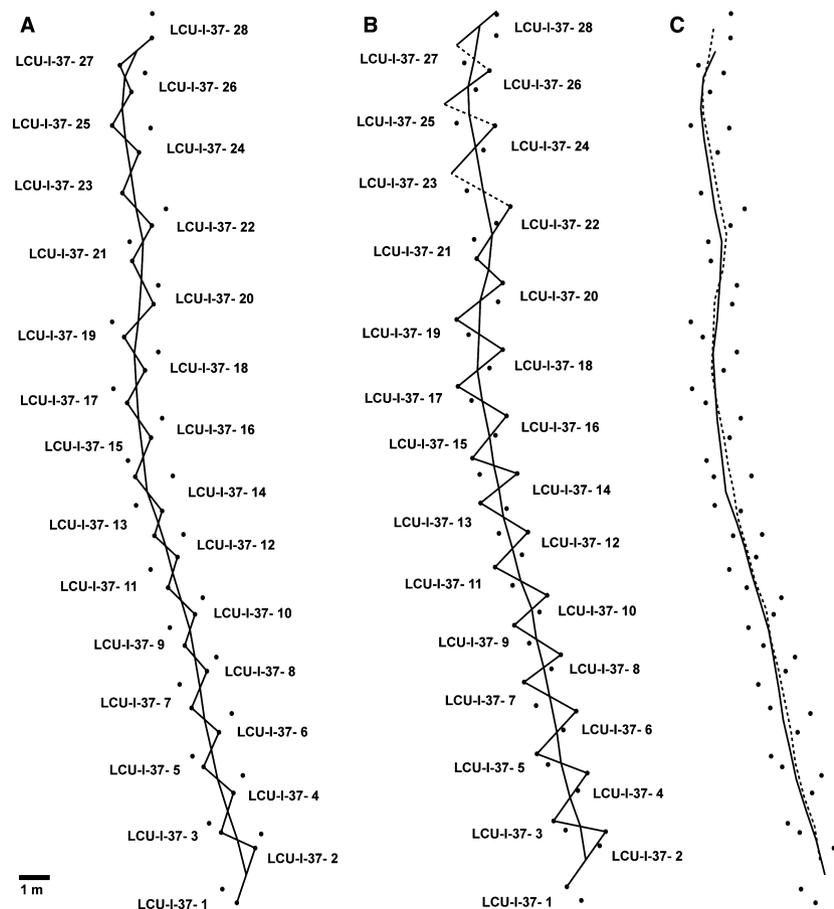


Fig. 10. Trackway midlines (manus and pes) of the sauropod trackway LCU-I-37 from Las Cuestas I tracksite. A, LCU-I-37 pes pace lengths and trackway midline for the pes. B, LCU-I-37 manus pace lengths and trackway midline for the manus. C, comparison of the two trackway midlines, pes (continuous line) and manus (broken line). Note the gaps between the two midlines. The dots indicate the middle point of the footprints.

great parts of the trackway although at times there is a gap that varies in extent. At the turning point a maximum is reached between LCU-I-37-14 and LCU-I-37-15, although this is no more than 20–25 cm. This gap is not as significant as in the cases mentioned above, and the off-tracking, if it exists, is minimal. One possible explanation for this is that the turning is not as pronounced as in the other cases, where the turning angles are greater than 50°. Other possible explanations could be that in LCU-I-37 the hindlimbs seem to control the turning (see section Gauge variation in LCU-I-37 and SS1-R1) or that the sauropod is smaller in size and in its glenoacetabular distance. Ishigaki & Matsumoto (2009) suggested that in the Moroccan trackway the turning may be controlled by the forelimbs. They also stated that in smaller sauropods (Mezga & Bajraktarevic 1999) there is no evidence of the off-tracking phenomenon and a consequence could be that the ‘hindlimbs worked to steer the body together with the forelimbs’. These differences in size between the two trackways (FL = 115 and 72 cm) could explain why the off-tracking phenomenon is not so clearly in evidence in LCU-I-37. Other topics that call for consideration are the possible taxonomical differences between the track-makers of the trackways and the differences in the relative positions of their centres of mass (Henderson 2006).

Ishigaki & Matsumoto (2009) calculated a PTR value of 50% in the Moroccan trackway, which indicates that it belongs to the narrow-gauge category. In their drawings the trackway does not seem to show a significant gauge variation and remains narrow-gauge throughout. Some of the trackways studied by these authors from the literature have been classified as, or seem to be, wide-gauge (Lockley 1991; Meyer 1993; Mezga & Bajraktarevic 1999). The turning sauropod from Cabo Espichel belongs to the intermediate-gauge category (Meyer *et al.* 1994). Another turning sauropod trackway reported by Casanovas *et al.* (1997) and two sauropod trackways from Argentina with sinuous trajectories (Calvo & Mazzetta 2004; González Riga & Calvo 2009) have also been classified as wide-gauge. The absence of accurate data for the new parameters (PTR or WAP/PL) in all of these trackways makes it impossible to establish whether they are intermediate or wide (except in the case of the latter Argentinean trackway, which is truly wide, González Riga & Calvo 2009). Whatever the case, the drawings in the original articles show no strong evidence of a narrower part at the turning points or in the sinuous parts. Thus, LCU-I-37 shows the importance of quantifying the gauge in turning trackways, as whether it is classified as narrow or intermediate may depend on the segment of the trackway.

Even though we initially believed that any sauropod taxon in a ‘normal gait situation’ could only produce one particular trackway type (narrow, intermediate or wide), LCU-I-37 and SS1-R1 show that in certain situations the gauge can change along the same trackway for ethological or preservational reasons. This means that the individual walking style (e.g. the turning phenomenon), individual behaviour associated (or not) with the substrate properties (abnormal gaits), and the preservation (undertracks) exert an important influence on the trackway gauge-type. Consequently, care must be taken before applying a trackway type category, especially in the case of those trackways that seem to be intermediate, because a slight variation in the factors that control the gauge can here represent a different trackway type.

Conclusions

The inner width of sauropod trackways (the trackway gauge-type) plays an important role in sauropod classification and ichnotaxonomy. Nonetheless, this parameter can change along the same trackway. The gauge variations in the sauropod trackways LCU-I-37 and SS1-R1 from the Berriasian of the Cameros Basin (Iberian Range) seem to be associated with an individual behaviour represented by a change in the direction of travel (LCU-I-37) and with an abnormal gait that could be associated with the substrate consistency (SS1-R1) or other ethological/preservational factors. The variations in this character along the same trackway and due to variations in the state of track preservation alert us to the problems that sauropod classification could face. The near-absence of the off-tracking phenomenon in LCU-I-37 opens a new window onto the study of turning trackways and sauropod locomotion.

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