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RESEARCH ARTICLE

First pterosaur footprints from the Tera Group (Tithonian–Berriasian) Cameros Basin, Spain

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Abstract The discovery of the Larañe (La Rioja, Spain) ichnological site provides the first outcrop pterosaur footprints in the Tera Group of the Cameros Basin. The footprint have characteristics similar to some of those already known in the Oncala Group, suggesting that possibly pterosaurs, which lived in this area during the deposition of the Tithonian–Berriasian sequences, were very similar. In this case, the footprints, assigned to *Pteraichnus*-like ichnogenus, are perfectly related to with those of morphotype A of the Los Tormos site (Soria) located in sediments of the Oncala Group.

Keywords *Pteraichnus* · Cameros Basin · Tera Group · Upper Jurassic-Early Cretaceous · La Rioja · Spain

Resumen El descubrimiento del yacimiento icnológico de Larañe (La Rioja España) ha proporcionado las primeras huellas de pterosaurios en el Grupo Tera de la Cuenca de Cameros. Las huellas tienen características similares a algunas de las ya conocidas en el Grupo Oncala lo que hace pensar que posiblemente los pterosaurios que habitaron en esta zona durante el depósito de las secuencias del Titónico–Berriasiense fueron muy semejantes. En este caso las huellas asignadas al icnogénero *Pteraichnus* se relacionan perfectamente con las del morfotipo A del yacimiento de Los Tormos (Soria) perteneciente al Grupo Oncala.

Palabras clave *Pteraichnus* · Cuenca de Cameros · Grupo Tera · Jurásico Superior-Cretácico Inferior · La Rioja · España

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1 Introduction

Dinosaur tracksites are very abundant in the Cameros Basin. In fact more than 250 sites distributed among the groups of Tera, Oncala, Urbión and Enciso are known (Hernández Medrano et al. 2008; Pérez-Lorente 2015).

The pterosaur tracks are the most abundant and diversified among the non-dinosaurian reptilian footprints (Pascual Arribas and Hernández Medrano 2012) with about 50 sites and approximately 2000 footprints. These footprints are mostly located in the Oncala Group. Up to now, only one site (Los Cayos) has been reported yet from the Enciso Group (Moratalla and Hernán 2009). The broad diversity of pterosaur tracks from Cameros can be resumed as follows:

- The presence of 6 ichnospecies: *Pteraichnus palacieisaenzi* Pascual Arribas and Sanz Pérez 2000 (redescribed by Pascual-Arribas et al. 2015); *P. parvus* Fuentes Vidarte et al. 2004a; *P. manueli* Meijide Calvo 2001 (Fuentes Vidarte et al. 2004a); *P. cidacoi* Fuentes Vidarte 2001; *P. vetustior* Meijide Fuentes 2001 (Fuentes Vidarte et al. 2004a); *P. longispodus* Fuentes Vidarte et al. 2004b.
- The recognition of *Pteraichnus* cf. *stokesi* Lockley et al. 1995 (Pascual-Arribas and Hernández-Medrano 2016).

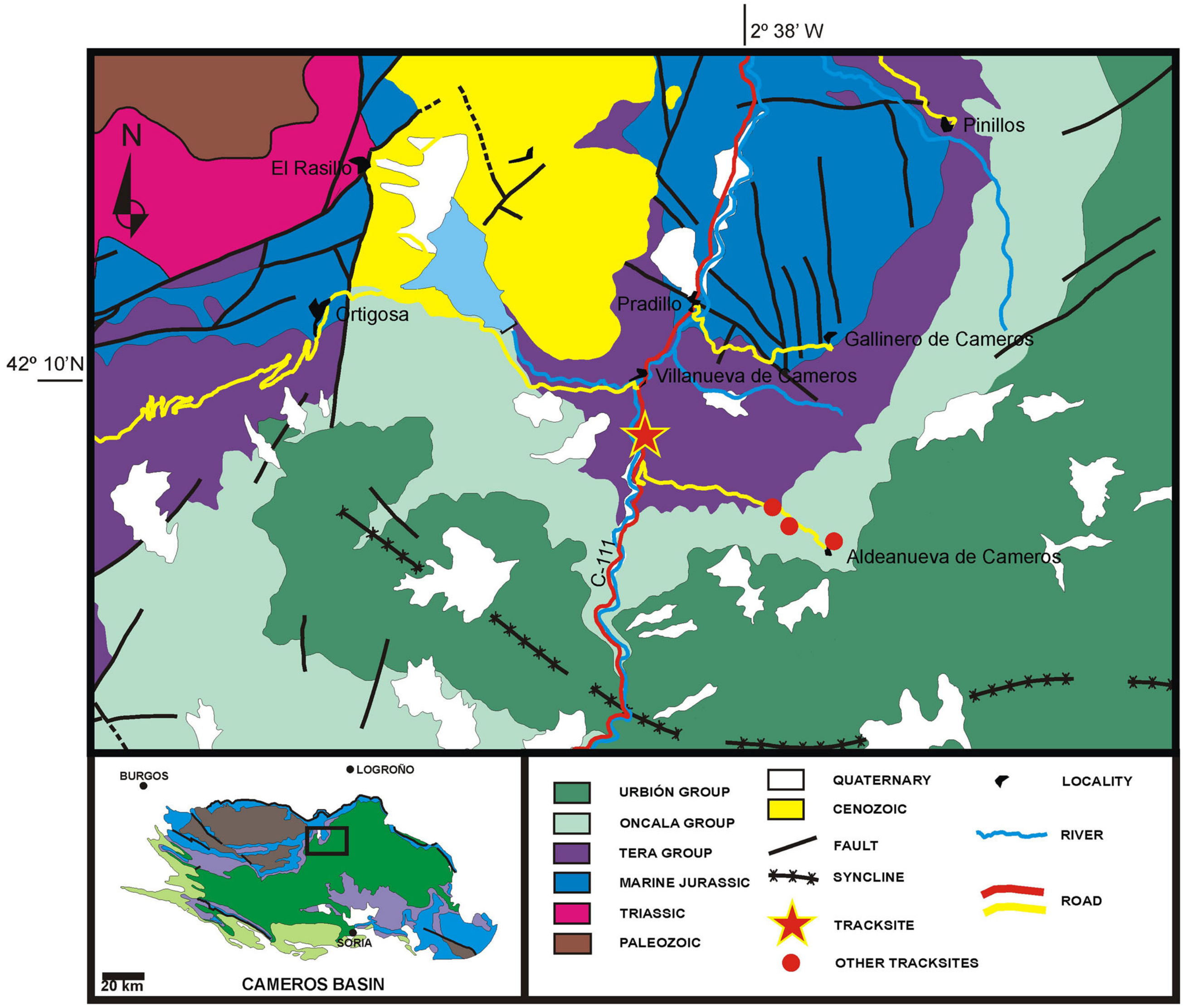

Fig. 1 Geological map displaying the location of Larañe site (Villanueva de Cameros, La Rioja, Spain). Based in Cámara and Durántez (1982)

- The presence of more morphotypes although their study is still going on (Pascual Arribas and Hernández Medrano 2012).

Larañe site in Villanueva de Cameros (La Rioja) provides the first pterosaur footprints from the Tera Group. The aim of this paper is to report the finding, to describe the tracks and to compare them with other known pterosaur ichnites, especially with other pterosaur tracks from the Cameros Basin footprints.

2 Geographical and geological situation

The Larañe site is located in the Larañe creek, about 900 m south of Villanueva de Cameros, very near of km 289.8 of the road N 111 from Soria to Logroño (UTM coordinates: x = 528,843; y = 4667,633; z = 913 m) (Fig. 1).

According to the Geological Map No. 279, of the Magna Series (Villoslada de Cameros) the new tracksite is located in the Tera Group (Tischer 1966), specifically in the Magaña Formation (Guiraud and Seguret 1985; Quijada et al. 2013) and within a sedimentary member which consists of sandstones, mudstones and some intercalated limestone levels (Cámara and Durántez 1982). The footprints (Fig. 2) are included in the top layers of a greenish-gray silty sandstone package that are part of that sedimentary area, which shows large mud cracks.

Gómez Fernández (1992) interpreted the depositional environment of the Larañe sedimentary rock as a floodplain of probably distal braided rivers.

The precise age of the sediments of the studied area is very debatable. Moreover, the ostracod *Cetacella armata* (Schudack and Schudack 2009) found at the bottom of the

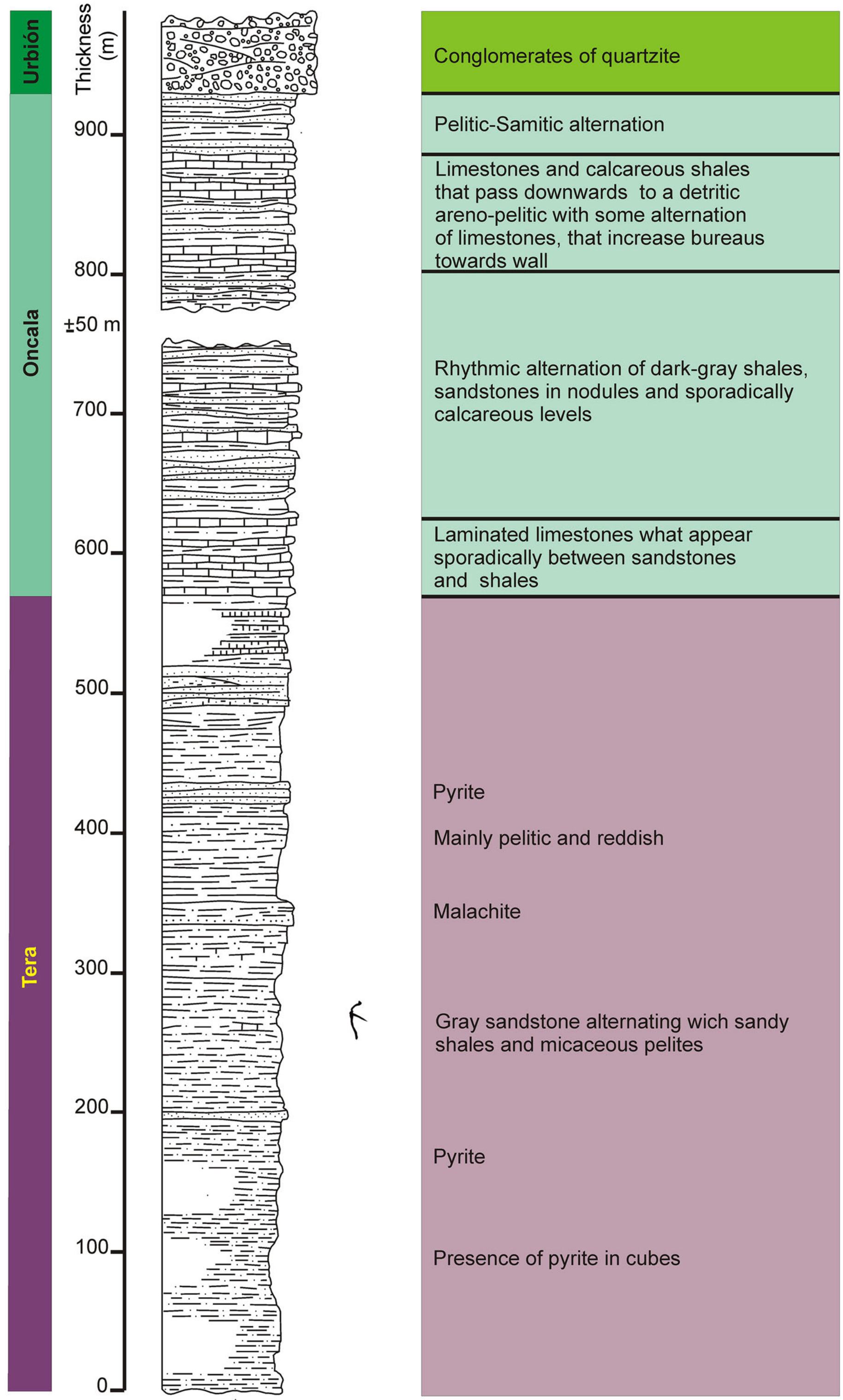

Fig. 2 Stratigraphic column near the Larañe site. Modified from Cámara and Durántez (1982). The pterosaur footprint indicates the level at which the Larañe site is located

Tera Group in the vicinity of Villoslada (near Villanueva de Cameros) indicates Tithonian, and the overlying layers of the Huérteles Formation (Oncala Group), are considered Berriasian (Schudack and Schudack 2009). In consequence, as the Larañe tracksite is located at the top of the Tera Group, we suggest that its age would be close to the Tithonian–Berriasian boundary.

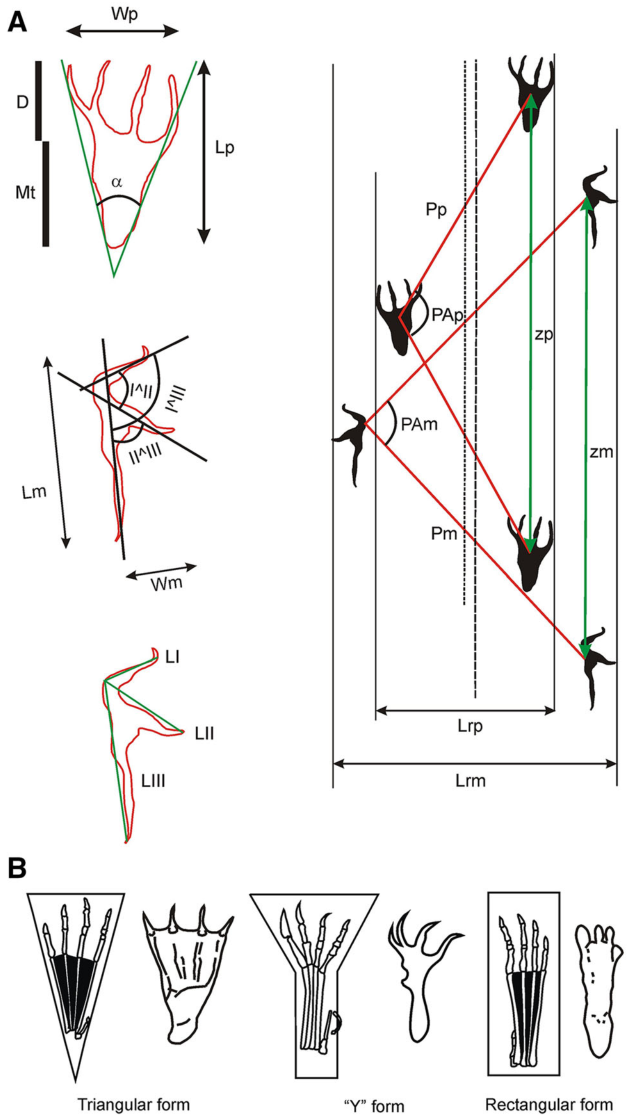

Fig. 3 **a** Key for the abbreviations of the description of tracks and trackways measurements. L–W, length–width of the footprint; I, II, III, IV represent the manus or pes digits; I^II^III interdigital angles; α angle between the toes I^IV; P, pace; z, stride; PA, pace angle; m, manus; p, pes; Lr, external width of the trackway; LI, LII, LIII, length of the toe print; Mt, length of metatarsal part; D-, length of digits part. Modified from de Pascual Arribas and Hernández Medrano 2012. **b** Form of pes. Modified from Pascual-Arribas and Hernández-Medrano (2016)

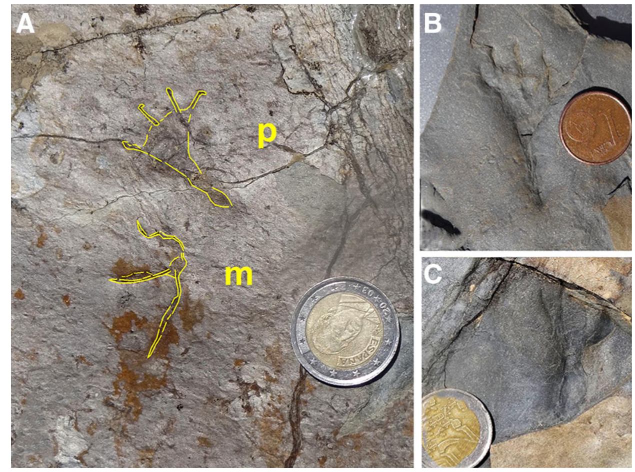

Fig. 4 Pes and manus prints from Larañe site. **a** Pes print (p) and manus print (m) from the trackway LAR-R1 (Coin diameter = 25.75 mm); **b** Isolated pes prints with collapse (Coin diameter = 16.25 mm); **c** Y-shaped pes footprint (Coin diameter = 25.75 mm)

3 Material and methodology

The studied material consists of a pterosaur trackway (10 manus and 4 pes) and 10 isolated pterosaur tracks described herein as "in situ", i.e. in the same Larañe site (LAR), and three isolated slabs (2 manus and 1 pes) that have been deposited in the Museum of Enciso (LAR-1m, LAR-2p, LAR-3m).

The footprints were first drawn on a plastic sheet and then drawn in a vectorial format. The variables (Fig. 3a) of the trackway have been measured on the trackway, using a measuring tape whereas the footprints were measured used digital caliper. The criteria, measurements and descriptions of Lockley et al. (1995); Billon-Bruyat and Mazin (2003), and Pascual-Arribas and Hernández-Medrano (2016) are followed in this paper.

The classification of Larañe's ichnites has been based on their biomorphic characteristics and metric values, specially the shape of the pes morphology (Fig. 3b) and the relative size of pes and manus. The same criteria were used to compare them with other defined ichnotaxa.

4 Description

The footprints (14 completed and 13 partially preserved) are locate on several levels, but most of them (19) occur in one, called the main level. There are 8 isolated footprints on levels below the main level. All tracks are similar in size and shape.

At least 14 tracks of the main level form a trackway, which consists of 10 manus prints (6 complete) and 4 pes prints. It is possible that two footprints considered as isolated, would be part of the trackway (LAR-R1-0p, LAR-R1-0m). If so, its position is irregular.

The pes footprints (Fig. 4a-p) are "Y" shaped (Pascual-Arribas and Hernández-Medrano 2016); small (3.29 × 2.13 cm; Table 1); longer than wide (Lp/Wp = 1.55). They show four digits, the central two being slightly longer than the others. The claw marks are the deepest part of the digit prints. These marks are rounded probably due to fact that they contacted the sediment almost perpendicular. The metatarsal area is narrow,

Table 1 Measurements of pterosaur tracks from Larañe (La Rioja, España)

Track	L (mm)	W (mm)	L/W	I^II^III(°) α(°)	P (mm)	z (mm)	PA (°)
LAR-R1-0m	>	–	–	–	120	(145)	–
LAR-R1-0p	(35.93)	21.48	(1.67)	–	85	–	95
LAR-R1-1m	32.48	16.27	2.00	110–70–180	131	190	–
LAR-R1-1p	32.96	22.96	1.44	20	115	205	(138)
LAR-R1-2m	34.75	17.30	2.00	107–73–180	102	205	–
LAR-R1-2p	33.20	22.66	1.47	20–25	–	–	(147)
LAR-R1-3m	35.47	17.20	2.06	–	160	220	–
LAR-R1-3p?	(31.3)	20.78	(1.51)	–	130	–	
LAR-R1-4m	(39.26)	(16.74)	(2.01)	–	–	195	–
LAR-R1-4p	32.61	18.66	1.74	–	–	–	–
LAR-R1-5m	>12	–	–	–	110	–	–
LAR-R1-6m	39.07	19.08	2.04	60–40–100	118	205	–
LAR-R1-7m	>27	(16.9)	–	–	110	–	130
LAR-R1-8m	34.69	17.35	2.00	107–73–180	135	215	103
LAR-R1-9m	35.48	17.86	1.99	81–60–141	140	–	104
LAR-R1-10m	40.33	19.85	2.03	93–77–170	–	–	–
Mean pes	32.92	21.31	1.55	20–25	11.0	–	(142.5)
Mean manus	36.18	17.84	2.03	93–65.5–158.5	13.4	20.8	105
LAR-Ap	>42	22	–	25	–	–	–
LAR-Bp	29	20	1.45	25	9.24	–	–
LAR-Cm	36.97	15.74	2.35	93–87–180	–	–	–
LAR-Dp	34.5	18.9	1.83	(23)	–	–	–
LAR-Ep	26.5	18.2	1.46	(33)	–	–	–
LAR-Fm	>35		–	–	–	–	–
LAR-Gm	>18	17.98	–	–	–	–	–
LAR-Hm	>12	–	–	–	–	–	–
LAR-1m	28.5	12.7	2.24	115–50–165	–	–	–
LAR-2p	37.1	16.1	2.30	(15)	–	–	–
LAR-3m	24.3	9.0	2.7	110–40–150	–	–	–

Lp/Lm = 0.91; Lrm = 13.1 cm = 6.15; pes orientation = +17° −15°

L–W length width of the footprint, *I^II^III* interdigital angles, α angle between the toes I^IV, *P* pace, *z* stride, *PA* pace angle, *m* manus, *p* pes, *Lr* external width of the trackway

somewhat longer than the digital area (LMT/Ld = 1.17). The heel, very poorly marked, is rounded. The interdigital angle between digits I and IV is about 20°–25°. The pes prints of the lower layers of the site are better preserved. The track LAR 2p shows both very narrow digit and metatarsal marks (Fig. 4b). This track, with very thin claw marks, is located on a slab that was detached from the sedimentary levels. Claws cross through the rock fragment (about 5 mm) so they show up well at the bottom of the fragment. Both the digits and the metatarsus traverse the upper surface but not the bottom one. The digits do not penetrate the track-bearing surface, probably because they are joined by a web or tissue that prevents penetration in the sediment. The metatarsus produces a relatively long and wide depression with a rounded heel, similar to the other isolated track (Fig. 4c), also located below the main level (about 1 cm). The LAR-2p footprint shows a clear "Y" shape morphology.

The manus prints (Fig. 4a-m) are also small (3.62 × 1.78 cm; Table 1), tridactyl, longer than wide (Lm/Wm = 2.03), asymmetrical and have unequal digits (LI < LII < LIII). Usually, the divarication angle between I and II is about 110° or less, but between I and III ranges between 100° and 180° (average 158.5°). The claw marks of the first digit are clearly marked, while those of II and III are not always distinct.

The manus and pes prints are arranged on a trackway which direction is curved to the right (Fig. 5). The trackway shows a wide gauge pattern, sensu Farlow (1992). The width varies along the trackway (less in the first tracks and greater in the end, being minimal in the sector of major curvature). As a result, PAm is wider (115°) at the

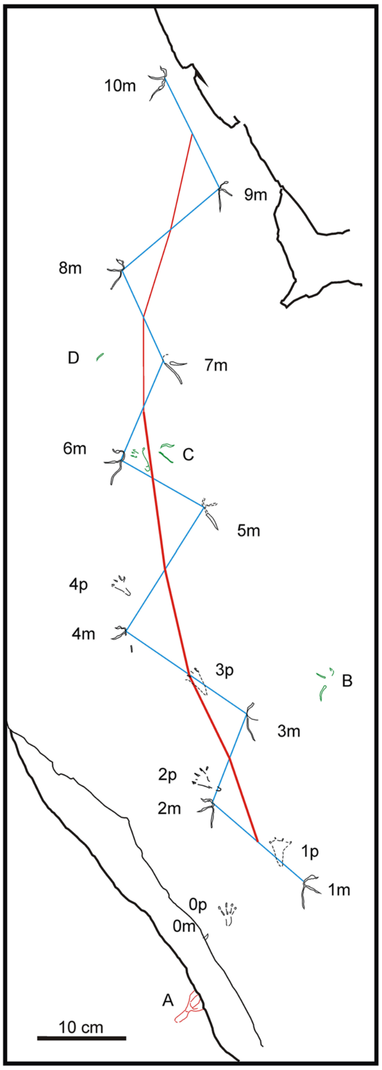

Fig. 5 Pterosaur trackway LAR-R1 of Larañe site (La Rioja, Spain)

beginning and narrower at the end (100°). PAm is reduced to 90° at the segment of greater curvature. PAp is wider (about 145°) but only measurable at the beginning of the trackway.

The pes prints are directed outwards (+17). The manus prints are more separated than the pes prints. This results in a greater pace length between the manus (13.1 cm) than the pes (11 cm), but not in the stride length because in both manus and pes, it is about 20 cm. Stride length sharply decreases in the portion of greater curvature of the trackway. If the footprint "0p" would belong to the trackway, its orientation and so small pace length would not be normal. Only a bigger change in the direction of movement by the trackmaker would justify the inclusion of this track in the studied trackway. Its curvature causes that the manus and pes midlines not to match due to the effect of "off tracking" stated in sauropod tracks by Ishigaki and Matsumoto (2009). The three manus-pes pairs indicate that although the size of the feet and hands is approximately equal, the hands are always a little longer (Lp/Lm = 0.91).

5 Discussion

The size and shape of the Larañe tracks suggest that they are different from the ichnogenera *Haenamichnus* Hwang et al. 2002, *Purbeckopus* Delair 1963, or *Agadirichnus* Ambroggi and Lapparent 1954 (Fig. 6, Table 2).

On the contrary, the morphometric characteristics of the Larañe footprints are similar to those of the ichnogenus *Pteraichnus* 1957 Stokes (emend Lockley et al.1995; emend Billon-Bruyat and Mazin 2003): the triangular shape of the pes (in this case, the form is "Y"); the similar length of the digits (the two central digits slightly longer than the lateral two), the difference in the manus digit length (LI < LII < LIII), the backward or slightly lateral position of the manus, relative to the pes position, and the good impression of claw I, being worse the II and lastly the claw III barely marked or unmarked. The Lp/Wp ratio is similar to other small *Pteraichnus* ichnospecies. However, because the pes morphology is like a "Y" (Pascual-Arribas and Hernández-Medrano 2016), they could belong to a new ichnogenus (Fig. 6).

Among the *Pteraichnus* published ichnospecies, the Larañe footprints resemble the footprints of A morphotype from the Los Tormos site (Pascual Arribas and Hernández Medrano 2012) and the unpublished tracks of the La Laguna site (Fig. 7). In fact, the best preserved pes print shape (LAR-2p; Fig. 7b) and the A morphotype (Fig. 7a) are virtually identical. The pes and manus prints of Larañe, Los Tormos and La Laguna are similar in length (the smallest being those of La Laguna; Fig. 7c). The manus prints are always slightly longer than the pes prints (Lp/Lm = 0.95–0.90). The same occurs in *P. saltwashensis*, but in this ichnospecies, the difference between the manus and pes prints is greater (Lp/Lm ≈ 0.8).

Other characters shared by the Larañe and Los Tormos footprints are:

- The interdigital angle I^III from the manus is large (in some cases it is almost 180°).
- The interdigital angle I^IV in the pes print is only 20°–25° (lower than other ichnoespecies (Fig. 8, Table 2) such as *P. saltwashensis* or *P. palacieisaenzi*, between 30°–40°).
- The exterior width of the trackway (Lr) is about 3–4 times the width of the pes print.
- The pace angle of the pes (between 100° and 115°).
- The outward orientation of the pes (about 20° or more, but in no case reaching, the 40° of *P. stokesi*).

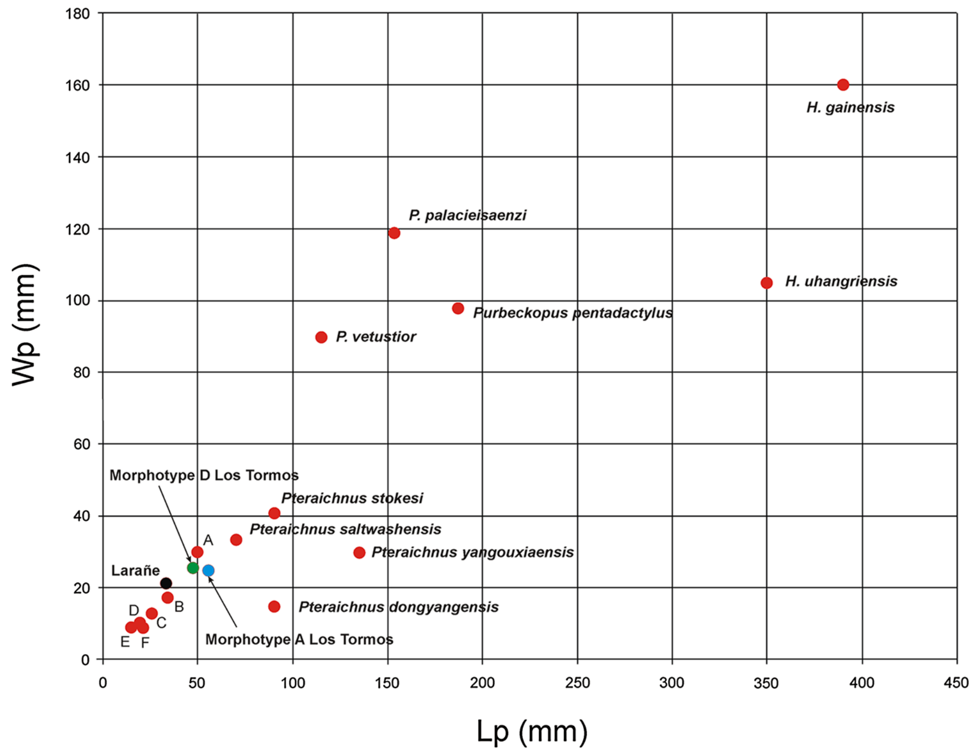

Fig. 6 Comparison between Lp/Wp ratios of various pterosaur footprints icnogenus and Larañe site footprints. *a Pteraichnus cidacoi*; *b P. longispodus*; *c P. koreanensis*; *d P. nipponensis*; *e P. parvus; f P. manueli*. The data comes from the original publication in which the ichnospecies were defined (see text)

Although we do not know with certainty the pes pace angle (PAp) of the Larañe footprints, the value obtained—taking into account the situation of the first two and the fourth pes (the third LAR-R1-3p is doubtful)—it is similar to two PAp of the A morphotype trackway from Los Tormos site (mean 147.5°).

The shape and size of the Larañe footprints are relatively similar to those of the D morphotype from Los Tormos. However, they differ because the pes digits of the first ones arise from the same point from which they fan out, while the digits of D morphotype are curved and their start is staggered, which implies that the length of the each digit is different (Fig. 8).

The Larañe ichnites primarily differ in their shape from *P. cidacoi, P. manueli* and *P. parvus* (also from the Cameros Basin—Fig. 8). In these last cases, the footprints are more rectangular than triangular in shape and the ratio Lp/Wp is small (short metatarsus). The pes of *P. longispodus* is "Y" shaped, and it is similar to the Larañe tracks only when they show signs of obliteration (LAR-2p) or are well marked (LAR-Ap).

The characteristics of the Larañe tracks that differ from those of *P. palacieisaenzi* seem to be more apparent than in the previous cases (Fig. 8, Table 2). This last ichnospecies is large (pes length 15.3 × 11.9 cm); low Lp/Wp ratio (1.29); I^IV interdigital angle of about 35°–40°; pes print always longer than manus print (Fig. 8) and by the curvature of the heel outside the trackway.

The F morphotype footprints from Los Tormos differs from the Larañe footprints, not only in being slightly larger, but also in the arrangement of the toes, and the extension of the metatarsal area. The same difference, regarding the Los Tormos F morphotype, can be observed in the ichnospecies *P. cf. stokesi* of La Muela site (Pascual-Arribas and Hernández-Medrano 2016), which are similar in size.

Outside the Cameros Basin, small footprints of Jurassic pterosaurs in Asturias (Piñuela et al. 2002; García-Ramos et al. 2006), are similar in size but their shape is different. The pes prints of Asturias are triangular and do not show a narrow process between the digital to the metatarsal zone. The value of the Lp/Lm ratio is not known, as there are no manus-pes pairs, but statistically the pes are of similar size or slightly larger than the manus, contrary to what observed in Larañe footprints.

Some footprints of Crayssac (specifically the B ichnospecies), in France (Mazin et al. 1997, 2003), are triangular in shape, like the footprints of the Larañe site (Fig. 8, Table 2). Nevertheless, in this case, the footprints have a more triangular shape, the difference between the digits length of the pes is lower and these are disposed in a fan shape less opened. On the other hand, in the trackways, the manus prints of Crayssac are separated the same distance from the trackway midline than the pes, meanwhile the ones in Larañe are more separated than the pes ones. (Lrm > Lrp).

Table 2 Some morphometric data of pterosaur ichnospecies in the world

Ichnospecies	Formation Edad	$L_p \times W_p$ (mm)	$L_m \times W_m$ (mm)	L_p/W_p	Lp/Lm	PAp (°)
Haenamichnus uhangriensis	Uhangri Fm. Santonian–Campanian	350 × 105	330 × 110	2.4	1.06	–
Haenamichnus gainensis	Haman Fm. Lower Cretaceous	390 × 160	–	2.4	–	136–154
Purbeckopus pentadactylus	Purbeck Limestone Fm. Berriasian	187 × 98 225 × 123	140 × (85)	1.9	(1.34)	–
Pteraichnus saltwashensis	Morrison Fm. Upper Jurassic	70 × (33–34)	90 × (36)	2–2.1	0.78	105–115
Pteraichnus stokesi	Sundance Fm Middle-Upper Jurassic	90 × (41)	70 × (34)	2.2	1.39	90
Pteraichnus palacieisaenzi	Huérteles Fm. Berriasian	153.4 × 119	130.2 × 48.5	1.29	1.18	82–137
Pteraichnus parvus	Huérteles Fm. Berriasian	15 × 9	23 × 9	1.6	0.65	–
Pteraichnus longipodus	Huérteles Fm. Berriasian	36.6× 34 × 17.4	30 × 15.7 24.5 × 17	1.95	(1.2) 1.39	–
Pteraichnus vetustior	Huérteles Fm. Berriasian	115 × 90	70 × 32	1.3	1.64	–
Pteraichnus manueli	Huérteles Fm. Berriasian	21 × 9	25.3 × 8.3	2.3	0.91	–
Pteraichnus cidacoi	Huérteles Fm. Berriasian	50 × 30	46 × 23	1.6	1.09	–
Pteraichnus nipponensis	Kitadani Fm. Barremian	19.4 × 10.5	20.1 × 8.8	1.87	0.96	98–111
Pteraichnus koreanensis	Hasandong Fm. Hauterivian-Albian	25.7 × 12.8	25.6 × 12.3	2.0	1.00	126
Pteraichnus yanguoxiaensis	Hekou Fm. Lower Cretaceous	130–140 × 30	(120 × 48)	4.3–4.7	(1.19)	122–145
Pteraichnus dongyangensis	Jinhua Fm. Upper Cretaceous	90 × 15	65 × 40	6.0	1.38	–
Morfotipo A de Los Tormos	Huérteles Fm. Berriasian	55.5 × 25.0	59.5 × 25.0	2.22	0.93	147.5
Morfotipo D de Los Tormos	Huérteles Fm. Berriasian	47.4 × 25.7	58.1 × 21.0	1.84	0.82	–
Pteraichnus isp. Larañe	Magaña Fm. Tithonian-Berriasian	32.9 × 21.3	26.2 × 17.8	1.55	0.91	145

L–W length width of the footprint, *PA* pace angle, *m* manus, *p* pes

Pterosaur footprints from Wierzbica in Poland (Pieńkowski and Niedźwiedzki 2005) are very poorly preserved. Although there are no trackways to confirm it, the pes prints are somewhat larger than the manus prints.

The ichnospecies from North America (*P. saltwashensis* Stokes 1957, and *P. stokesi* Lockley et al. 1995) are larger (Fig. 8, Table 2). The pes prints are triangular, but the metatarsal area does not narrow as those of Larañe and also the Lp/Wp ratio is different. Footprints of South America considerably different from those of North America not only in age, but also in very elongated feet, and very high Lp/Wp ratio (e.g., Lake Ezequiel Ramos Mexia site, Argentina).

Diverse pterosaur tracks from China [*Pteraichnus isp,* of several Chinese sites: for example Lotus Fortress, Dongyang, Zhaojue, (Xing et al. 2012, 2013, 2015; Lü et al. 2010)] differ from the Larañe prints in the shape of the pes and the Lp/Wp ratio, which is higher and rectangular in shape. On the contrary, Korean and Japanese prints (*P.*

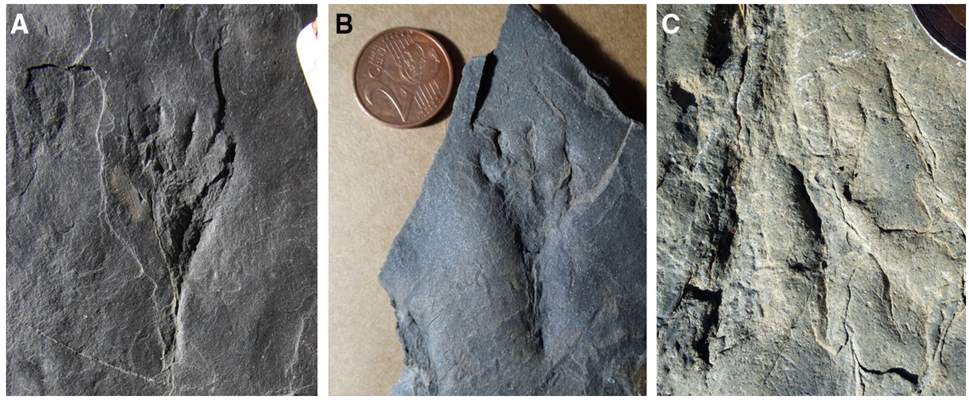

Fig. 7 Pterosaur footprints of the Los Tormos (**a**), Larañe (**b**), and La Laguna (**c**) sites. *Scale bar* 20 mm

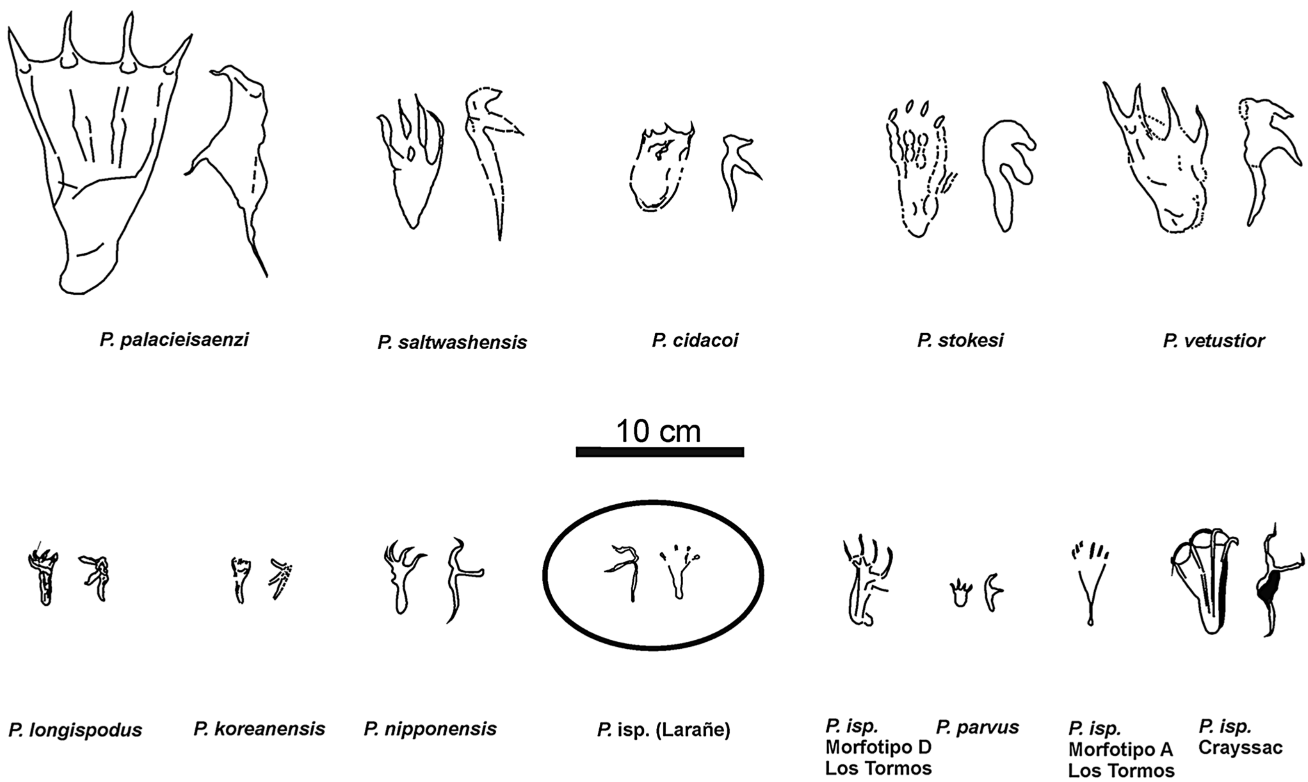

Fig. 8 Representation of the Larañe pterosaur footprints and *Pteraichnus* ichnoespecies. The figures have been modified from the original publications in which they were drawn (see text). (Pascual-Arribas et al. 2015; Stokes 1957; Lockley et al. 1995; Fuentes Vidarte et al. 2004a, b; Lee et al. 2008, 2010; Mazin et al. 2003)

koreanensis Lee et al. 2008 and *P. nipponensis* Lee et al. 2010) are "Y"-shaped or almost rectangular (Fig. 8, Table 2). Ichnites of *P. nipponensis*, as with *P. longispodus* (Early Cretaceous), are similar to the best-preserved Larañe samples.

6 Conclusions

The Larañe site (La Rioja) has yielded the first pterosaur footprints from the Jurassic (Tera Group) of the Cameros Basin (NW of the Iberian Range).

The morphometric characters of the Larañe tracks, similar to the A morphotype of the Los Tormos site and to the unpublished site of La Laguna (Soria, Spain), they are classified as *Pteraichnus*-like ichnogenus. However, the lack of well-preserved footprints, does not allow to assign them to a known ichnospecies of *Pteraichnus*, or to a new one ("Y" form of pes).

The most similar pterosaur tracks outside of the Iberian Peninsula come from the Crayssac locality (France) (ichnospecies B), of similar age (Tithonian).

The similarity between the Larañe pterosaur tracks and those from the Oncala Group suggests that the pterosaur fauna could be relatively similar through both periods (Tithonian–Berriasian).

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