

## Theropod swim traces in the Santisol tracksite (Lower Cretaceous), Cameros Basin, La Rioja, Spain

Ícnitas de natación de terópodos en el yacimiento de Santisol (Cretácico Inferior), Cuenca de Cameros, La Rioja, España

Raúl ESPERANTE  & Kevin E. NICK 

**Abstract:** Swim traces are rare in dinosaur track sites worldwide. This article reports three sets of theropod swim traces found with walking tracks in the Santisol tracksite (Cameros Basin, La Rioja, Spain). The tracksite contains over one hundred theropod and a few ornithopod walking tracks previously reported. The swim traces are well-preserved and do not show evidence of sediment collapse that characterizes the true tracks. One of the swim traces cuts through one theropod track, indicating that the walking prints formed first, followed by the rise of the water level and the formation of swim traces by swimming theropods.

**Resumen:** Las ícnitas de natación son raras en los yacimientos de ícnitas de todo el mundo. En este artículo se describen tres conjuntos de ícnitas de natación de terópodos en el yacimiento de Santisol (Cuenca de Cameros, España). El yacimiento contiene más de cien huellas de terópodos y unas pocas huellas de caminar de ornitópodos. Las ícnitas de natación están bien conservadas y no muestran el colapso sedimentario que caracteriza a las huellas. Una de las ícnitas de natación atraviesa una huella de terópodo, lo que indica que las huellas se formaron primero, seguidas por la subida del nivel del agua y la formación de las ícnitas de natación por terópodos nadadores.

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**Corresponding author:**

Raúl Esperante

[resperante@llu.edu](mailto:resperante@llu.edu)

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## INTRODUCTION

Dinosaur tracksites are abundant in the Cameros Basin (Lower Cretaceous) in the southern part of the La Rioja Autonomous Region (with more than 170 tracksites; [Pérez-Lorente, 2015](#)), in the Province of Soria (181 tracksites; [Hernández-Medrano \*et al.\*, 2005](#); [Castanera \*et al.\*, 2018](#)), and the Province of Burgos (20 tracksites; [Torcida Fernández-Baldor \*et al.\*, 2021](#)). Ornithopod, theropod and sauropod footprints have been found in Asturias ([Lires \*et al.\*, 2001](#); [Martínez \*et al.\*, 2001](#); [Piñuela \*et al.\*, 2002, 2009, 2011](#); [Rauhut \*et al.\*, 2018](#)), Teruel Province ([Germán, 2013](#); [Herrero-Gascón & Pérez-Lorente, 2013a, 2013b](#); [Royo Torres \*et al.\*, 2013](#); [Alcalá \*et al.\*, 2014](#); [Castanera \*et al.\*, 2016, 2022](#); [García-Cobeña \*et al.\*, 2023](#)), Valencia Province ([de Santisteban \*et al.\*, 2001, 2003a, 2003b, 2007, 2009](#)), Huesca Province ([Canudo \*et al.\*, 1999](#); [López-Martínez \*et al.\*, 2001](#); [Vila \*et al.\*, 2006](#)), and Jaén Province ([García-Hernández \*et al.\*, 2003](#)). The abundant scientific literature shows that in the Cameros Basin, theropod footprints predominate over sauropod and ornithopod footprints.

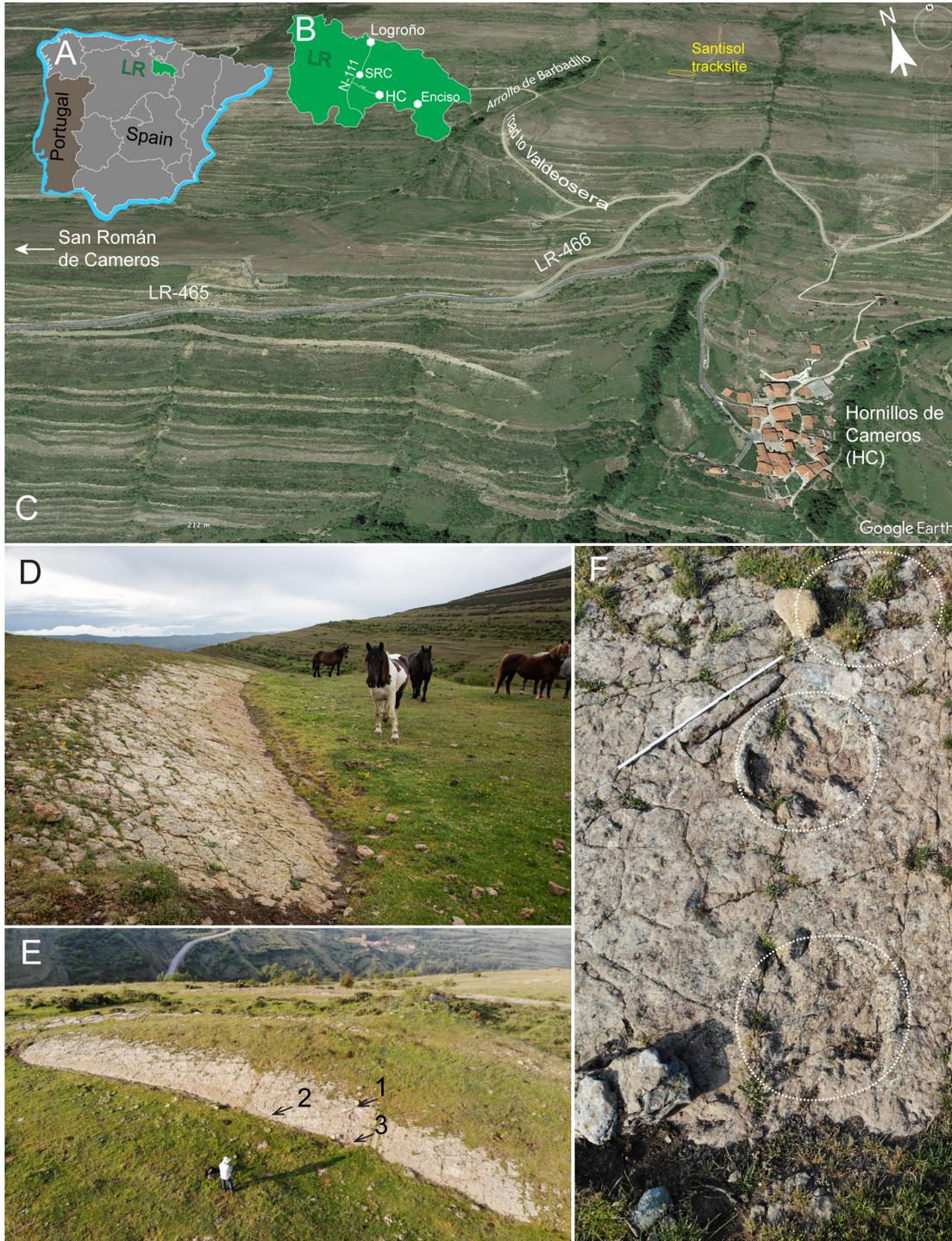
Despite the abundance of dinosaur tracksites in Spain, only three sites are known to this date with dinosaur swim traces: the Ícnitas-4 tracksite, near Enciso and between the villages of El Villar and Poyales ([Casanovas \*et al.\*, 1993](#); [Pérez-Lorente, 2015](#)); the La Virgen del Campo tracksite, in the outskirts of Enciso ([Ezquerro \*et al.\*, 2007](#); [Ezquerro, 2010](#)) and the Laguna tracksite near the town of Laguna de Cameros ([Navarro-Lorbés \*et al.\*, 2023](#)). The three tracksites with swim tracks occur within Cameros Basin in the La Rioja Region. Stratigraphically, the first two tracksites are in facies of the Enciso Group (Barremian–lower Aptian), and the third tracksite is in the Urbión Group (Valanginian–Aptian).

This article aims to present the occurrence of dinosaur swim traces in the Santisol tracksite and a detailed description of the lithology of the trackbearing layer, which has not been reported in previous studies. The author (RE) has previously published a preliminary report of the findings ([Esperante, 2022](#)).

**GEOLOGICAL SETTING**

The site is easily accessed from the road LR-465 from San Román de Cameros to Hornillos de Cameros, which continues as road LR-466 north of the latter town. An unpaved road named in online maps as Carretera de Valdeosera (road to Valdeosera) starts 325 m NE

of the junction of LR-465 and LR-466. After 600 m on this unpaved road, a trail begins uphill towards the E through a slope facing south with pastures for cattle and horses. The tracksite is situated at 30T N548153, E4673936, elevation 1170 m, facing north with a N110E strike and 18N dip at a linear distance of 700 m NNE of the town of Hornillos de Cameros (Fig. 1).



**Figure 1.** A, Map of the Iberian Peninsula with Spanish regions outlined. Source: <https://freevectormaps.com/spain/ES-EPS-01-0002?ref=atr> (Portugal added); B, La Rioja Region. HC, Hornillos de Cameros; N-111, highway; SRC, San Román de Cameros; C, satellite image of the tracksite area; D, view of the tracksite from the east; E, view of the tracksite from the NW. The location of the three sets of swim traces is indicated with the numbers in black; F, a view of swim trace 1 to the right of the 1-m scale ruler. Several theropod tracks and three ornithopod tracks are associated with this swim trace. The three ornithopod tracks are encircled in white dotted lines, forming a trackway (STS21 of Pérez-Lorente, 2003).

The Santisol tracksite occurs in the northern part of the Cameros Basin in the NW of the Iberian Cordillera, which consists of thick continental and marine siliciclastic and carbonate deposits that formed during the Upper Jurassic–Albian intraplate rifting that separated the Iberian Peninsula from the European continent (Mas *et al.*, 2002). The Cameros Basin formed in the westernmost side of the Iberian Rift System (Mas *et al.*, 1993; Salas *et al.*, 2003). According to Mas *et al.* (2002), the layers of the Cameros Basin deposited during three major sedimentary cycles: Megacycle 1 (Upper Permian–Triassic), with an upward succession of continental, shallow marine and coastal deposits, Megacycle 2 (Lower Jurassic–lower Upper Jurassic) with mudstones, wackestones, and marl deposits formed in carbonate platforms, and Megacycle 3 (upper Upper Jurassic–Lower Cretaceous) mainly alluvial and lacustrine sediments and minor marine interspersed layers that deposited in eight depositional cycles (Mas *et al.*, 1993; Arribas *et al.*, 2003; Martín-Closas & Alonso Millán, 1998). These depositional cycles, named SD1–SD8 in Mas *et al.* (2002) and Arribas *et al.* (2002), left thick alluvial clastic deposits that transition upward to lacustrine calcarenites. In general, the fossil content is scarce in the basin and of low chronostratigraphic value due to the type of facies, diagenesis and metamorphism (Mas *et al.*, 2002). According to Hernández *et al.* (1990), the Santisol tracksite is an outcrop of the Unit 21 or Hornillos de Cameros–Munilla Unit of the Enciso Group, accumulated during the depositional cycle SD7 (Upper Barremian–Lower Aptian) or SD8 (Upper Aptian–Lower Albian) in the Cameros Basin.

The sedimentary succession of the tracksite consists mainly of alternating marls and detritic deposits. The tracked lithology is a very fine-grained, submature sandstone with laminae of sandy mudstone in a bed 10–20 cm thick. Petrographic examination showed three lithologies with sharp to gradational contacts (Fig. 2A). Some early deformation of bedding planes and later brittle fractures are present. Two lithologies are very fine-grained sandstones, and the third is laminated mudstone. All the lithologies are rich in muscovite and biotite micas.

Sandstone 1 is a compacted, micaceous arkose (Fig. 2B). Detrital components are quartz, altered K-feldspars, plagioclase, muscovite, and biotite. Detrital grains, averaging about 90 µm, are moderate to poorly sorted, subangular, with mostly long but some sutured grain contacts. The K-feldspars are partially altered and show some dissolution, and most biotite grains are weathered. A small amount of clay is present between grains, and pyrite framboids have replaced some unknown detrital grains. Porosity of 1–2% is visible, and original intergranular spaces appear to have been eliminated mainly by early compaction. This lithology has gradational contacts over short distances into Sandstone 2 and is in sharp or gradational contact with mudstones. The micas are not oriented in parallel, suggesting deformation, which supports the same

conclusion inferred by deformation of mudstone laminae.

Sandstone 2 is a porous micaceous arkose (Fig. 2C). Detrital components are quartz, altered K-feldspar, plagioclase, muscovite, and biotite, as in Sandstone 1. The grains average about 100 µm with some muscovite grains up to 400 µm long, are moderately well sorted, subangular, and are dominated by point to long grain contacts. The K-feldspars are partially dissolved and altered, and biotite is weathered. A small amount of clay is present in the intergranular areas, and pyrite framboids have replaced some unknown detrital grains. Porosity is mostly intergranular and estimated at 12%. It is most likely secondary since this sandstone type is not compacted like Sandstone 1, which it is intimately associated with, implying the removal of cement. Sandstone 2 has gradational contacts over a short distance into Sandstone 1.

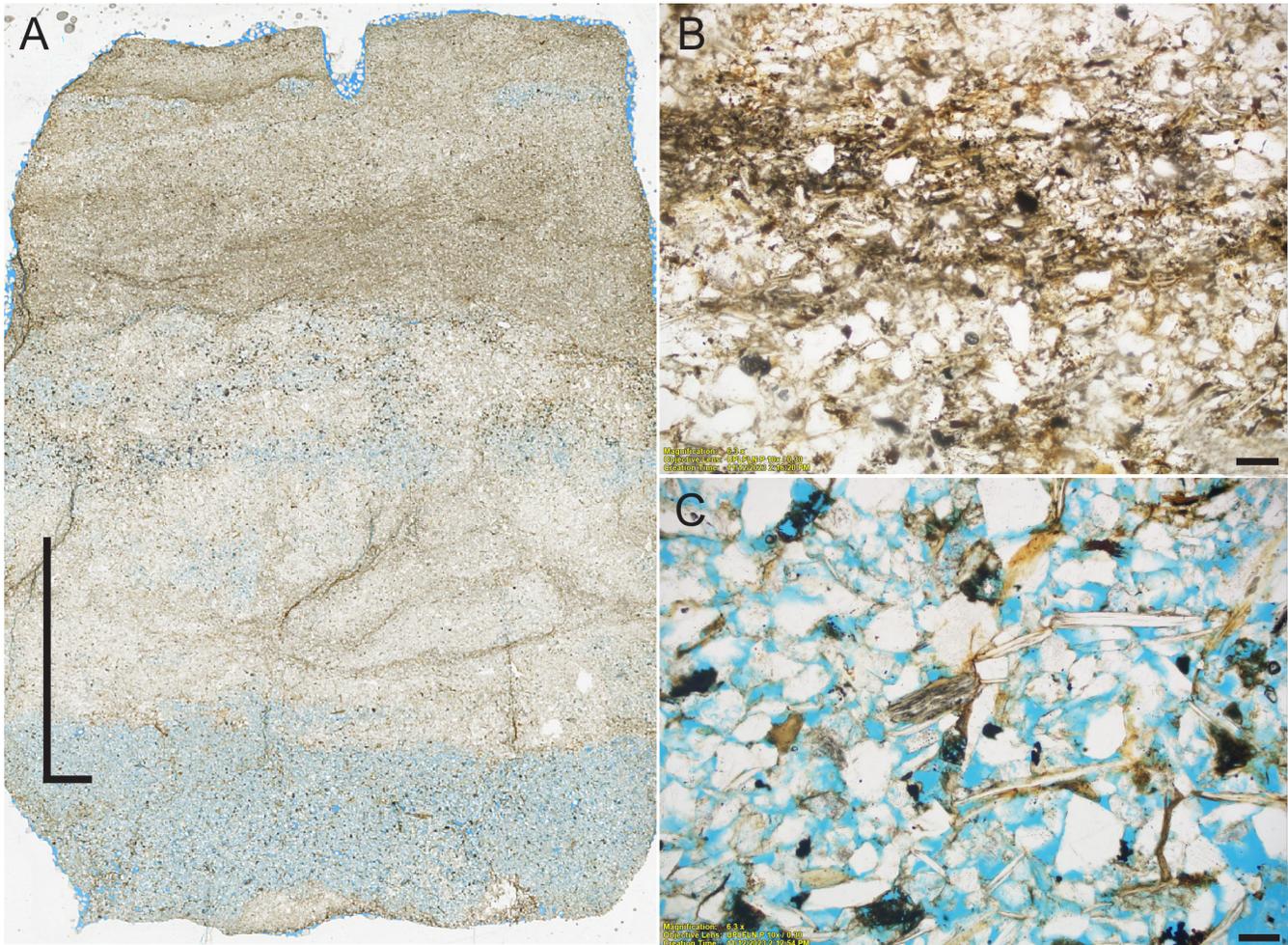
Mudstone occurs as laminae within the sandstones. Mudstones are dominated by very fine-grained and moderately oriented biotite grains with lesser clay, quartz, and feldspar silt. The laminae contain abundant, partially oxidized pyrite framboids scattered through the lamina rather than concentrated in grain shapes like the sandstones. The laminae are not visibly porous. Some mudstone laminae have sharp contacts with Sandstone 2 or 1, and others are gradational. One mudstone lamina shows grading in the abundance of silt clastic grains. Tracing the continuity of the mudstone laminae indicates that the rock sample was deformed before lithification.

A few ovoid or truncated spots of Sandstone 1 in contact with Sandstone 2 or the mudstone may be small burrows preserved by early cementation. Their width is 1 to 3 mm.

## MATERIALS AND METHODS

The exposed tracksite is 30 m long and 1.5–4 m wide (Fig. 1). The dinosaur tracks are heavily covered with lichens and show evidence of weathering and cracking. The degree of preservation ranges from poorly preserved to well preserved. The site has been exposed to recent erosion, and the rock surface has been subjected to weathering and breakage. Some of the tracks show evidence of smoothing by running water, and plant roots are opening cracks in the layer. The fieldwork was done in May 2021, June 2022 and September 2023. Because a detailed description of the tracks has already been carried out by Pérez-Lorente (2003), the current study focused on the swim traces. We used a ruler to measure the traces' dimensions, including length, width, and depth.

We calculated the width of the traces from the estimated highest point of the expulsion rim on each side of the trace. Field photos were taken with a Canon 6D using a 28–105 mm lens. Geographic orientation was taken using an iPhone 13. Drone photos were taken using a DJI Mavic Air. Photogrammetric 3D models were



**Figure 2.** Thin section petrography. **A**, Scan of the thin section showing disrupted clay-rich laminae and contacts between the three lithologies. Some disruptive textures are small burrows. Pores are filled with blue-dyed epoxy and notch marks the top; **B**, sandstone 1 and mudstone with small, dark biotite mostly replaced by pyrite. Note the close packing of grains. This photo is from the upper quarter of 2A; **C**, sandstone 2 contrasts with sandstone 1 with open grain packing, suggesting the removal of an early cement. Dark areas contain pyrite framboids. This photo is from the lower quarter of A; the vertical and horizontal scale bars in A are 10 mm and 2 mm, respectively scale bar in C and D is 100 mm.

made using MetaShape (v. 1.7.5 and v. 2.0.1). The 3D models were then imported into Meshlab (v. 2022.02) for rotation to the XY plane. Scale bars were added, and false-color depth maps created using ParaView (v. 5.10.0). Thin section scan was from an Epson Perfection V600 Photo scanner at 4800 dpi resolution. Photomicrographs were taken with Olympus BX53 microscope and DP74 camera.

## CRITERIA FOR SWIM TRACES

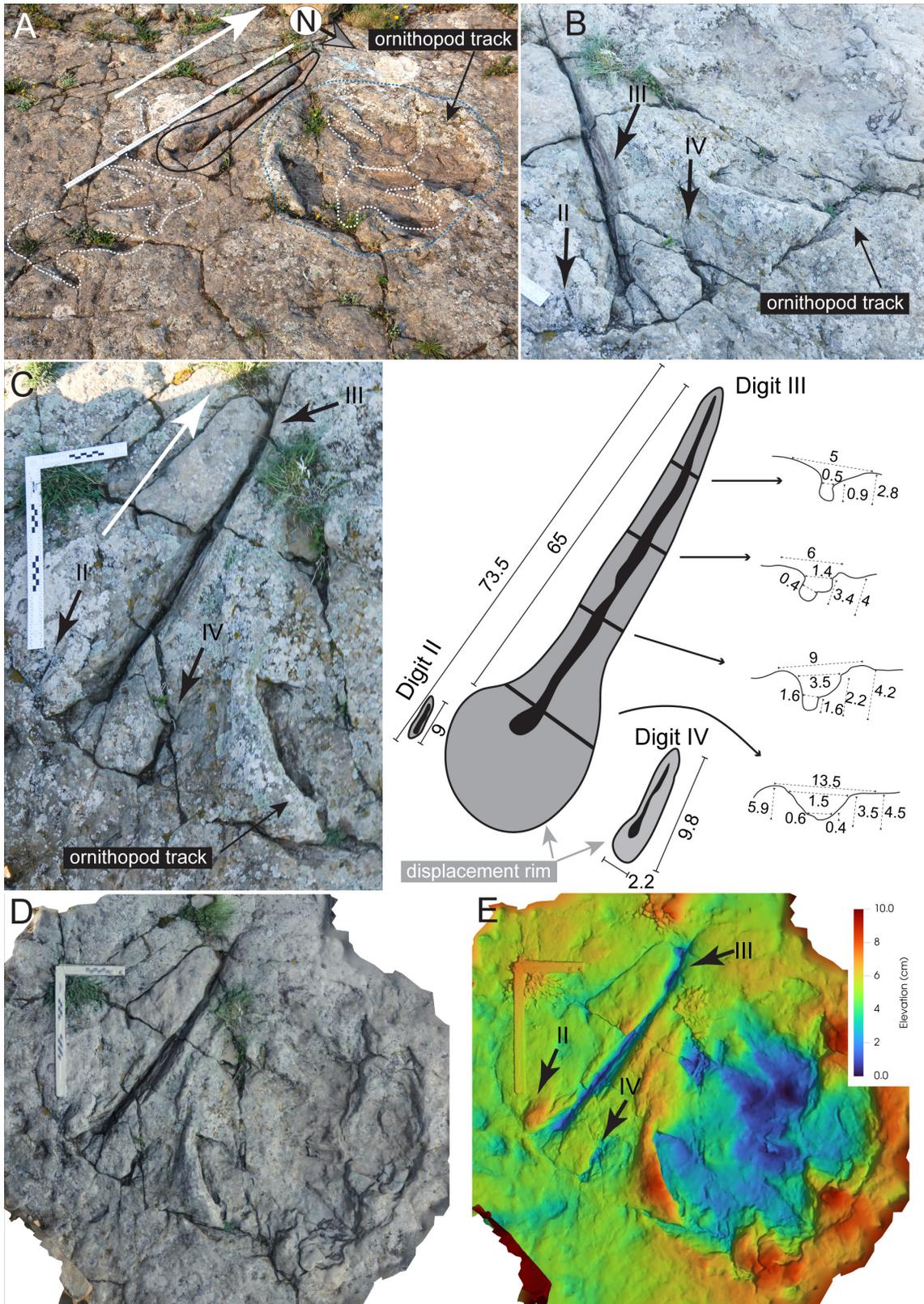
The swim traces in the Santisol tracksite occur alongside regular dinosaur tracks and consist of scratches preserved as concave epireliefs corresponding with the tridactyl autopodium. The narrow and small size of the Santisol tracksite prevents checking if the swim traces occur in successions of alternate right-left prints and, therefore, from checking the regular spacing of scratches. Yet, the morphology of the scratches is like the prints identified as swim traces in other tracksites.

## DESCRIPTION OF THE SWIM TRACES

Three sets of swim traces are reported here. They are isolated and do not form part of the same trackway (Fig. 1E). They are relatively well preserved, without collapse structures that characterize many of the theropod tracks on the surface (see below).

### Swim trace 1

This swim trace consists of three subtraces. The longest corresponds to digit III and is a slightly curved, 65 cm-long groove with a prominent displacement rim in the posterior end (Fig. 3). The rim of displacement is 0.6–2 cm higher than both sides of the central segment of the trace. The oval-shaped posterior end shows a prominent, partially eroded, curved displacement rim that partially cuts across a theropod track. Two smaller subtraces correspond to digits II and IV. They are smaller and narrower than the longer subtrace (dimensions in Fig. 3C). The disproportional length of the trace of digit III compared to those of digits II and



**Figure 3.** Swim trace 1. The white arrows indicate the direction of movement of the swimming theropod. **A**, Swim trace 1 (within the black line) and associated theropod tracks (white dotted lines). The blue dotted line outlines the exterior edge of the rim left by the large ornithopod track, which has two theropod tracks preserved within (more conspicuous in the depth color photogrammetry model in **E**). The scale ruler is 1 m long; **B**, another view of swim trace 1 with the adjacent ornithopod track; **C**, plain view of swim trace 1 with a partial view of the ornithopod track to the right. The four black lines across the trace indicate the places where the dimensions were measured, indicated in the cross-section outlines to the right. Dimensions of the cross-section in cm. The longer side of the scale ruler is 30 cm; **D**, 3D model of the set of swim traces and associated ornithopod and theropod tracks; **E**, depth color photogrammetry model showing the large and small swim traces and the associated ornithopod and theropod tracks. The black arrows and Roman numbers indicate the digits.

IV is observed in other tracksites, and documented by [Esperante \*et al.\* \(2023\)](#) in the El Molino Formation in Bolivia. In theropod dinosaurs, the digit III is oriented anteriorly compared to digits II and IV and can be longer than the latter. In a swimming behavior, digit III would scratch the substrate first and longer than digits II and IV, thus leaving longer traces. The trace of digit IV is longer than that of the digit II, a feature also present in multiple swim ichnites in the el Molino Formation in Bolivia (our own observations). Based on the curvature of the long groove, the traces were made by the right foot of the swimming theropod.

### Swim trace 2

This swim track consists of two subtraces of different dimensions (Fig. 4A–4D). Based on the curvature of the minor groove, the traces were made by the right foot of the swimming theropod. The longest subtrace corresponds to digit III and is sinuous (elongate S-shaped) with a prominent (although partially eroded) displacement rim in the posterior end. The shortest subtrace trace is slightly curved, corresponds to the scratch made by digit II, and is shallower and narrower than the other subtrace, with a smaller displacement rim in the posterior end. Both subtraces have an overall V-section.

### Swim trace 3

This swim trace consists of a single wide and slightly curved groove made by the digit III (Fig. 4E–4D). It has an asymmetric V-shape in cross-section with an overall comma-shape that widens toward the posterior end. Based on the curvature of the groove, the trace was made by the left foot of the swimming theropod.

## DISCUSSION

The Santisol tracksite north of the town of Hornillos de Cameros (La Rioja) (Fig. 1) was studied by Félix Pérez-Lorente, who published a description of the trackways ([Pérez-Lorente, 2003](#)) and a revision later with a summary and discussion of relevant taphonomic features ([Pérez-Lorente, 2015](#)). In his description of the tracksite, he states that 104 tracks are preserved, most of them of large theropods and some of small theropods. The abundance of tracks in the narrow and small outcrop makes distinguishing trackways difficult. In the first description, Pérez-Lorente states that “the most abundant sequences of tracks show 2 tracks (12 pairs) or three (10 sequences)” (“*las secuencias de pisadas más abundantes son de dos huellas (12 pares) o tres (10 secuencias)*”) ([Pérez-Lorente, 2003](#)). It is uncertain what he means by “12 pairs”. In Table 1 of the same publication, he indicates the occurrence of twenty-five theropod trackways and one ornithopod trackway. In the text, he describes the characteristics of twelve theropod trackways and one ornithopod trackway. Of the twelve theropod trackways, eight

consist of three tracks, three of five tracks, and one of four tracks. The ornithopod trackway (STS21) consists of three tracks. In none of the two publications that deal with the tracksite does Pérez-Lorente mention the existence of theropod swim traces.

[Milner \*et al.\* \(2006\)](#) and [Lockley \*et al.\* \(2014\)](#) in their studies of “scrape marks” in the Lower Jurassic of Utah and the Cretaceous of Colorado observed several characteristics that suggest that those structures are swim tracks. Building on those observations and based on their own studies of scrape marks in the El Molino Formation in Bolivia, [Esperante \*et al.\* \(2023\)](#) proposed eight features for the classification of these scratches as theropod swim traces as opposed to walking tracks or tail traces: 1) the successive linear occurrence of scratches with similar morphology (interpreted here as scratches of digit III); 2) the disposition of three or more scratches in a pattern of alternative right and left sides of a medial line; 3) the occurrence of three or more scratches with a shape curved to the right alternating with a shape curved to the left; 4) the presence of smaller, scratches (interpreted here as scratches of digits II and IV) on both sides of a medial scratch (interpreted as the claw mark of digit III), in alternating sets of traces, these smaller lateral traces are not present in between the sets; 5) the regular spacing of the sets of scratches; 6) the same geographic orientation of all the scratches within any given succession; and 7) the absence of metatarsophalangeal impressions. This criteria also distinguishes the swim traces produced by theropod dinosaurs from those made by crocodiles, which often show four scratches instead of three in each set.

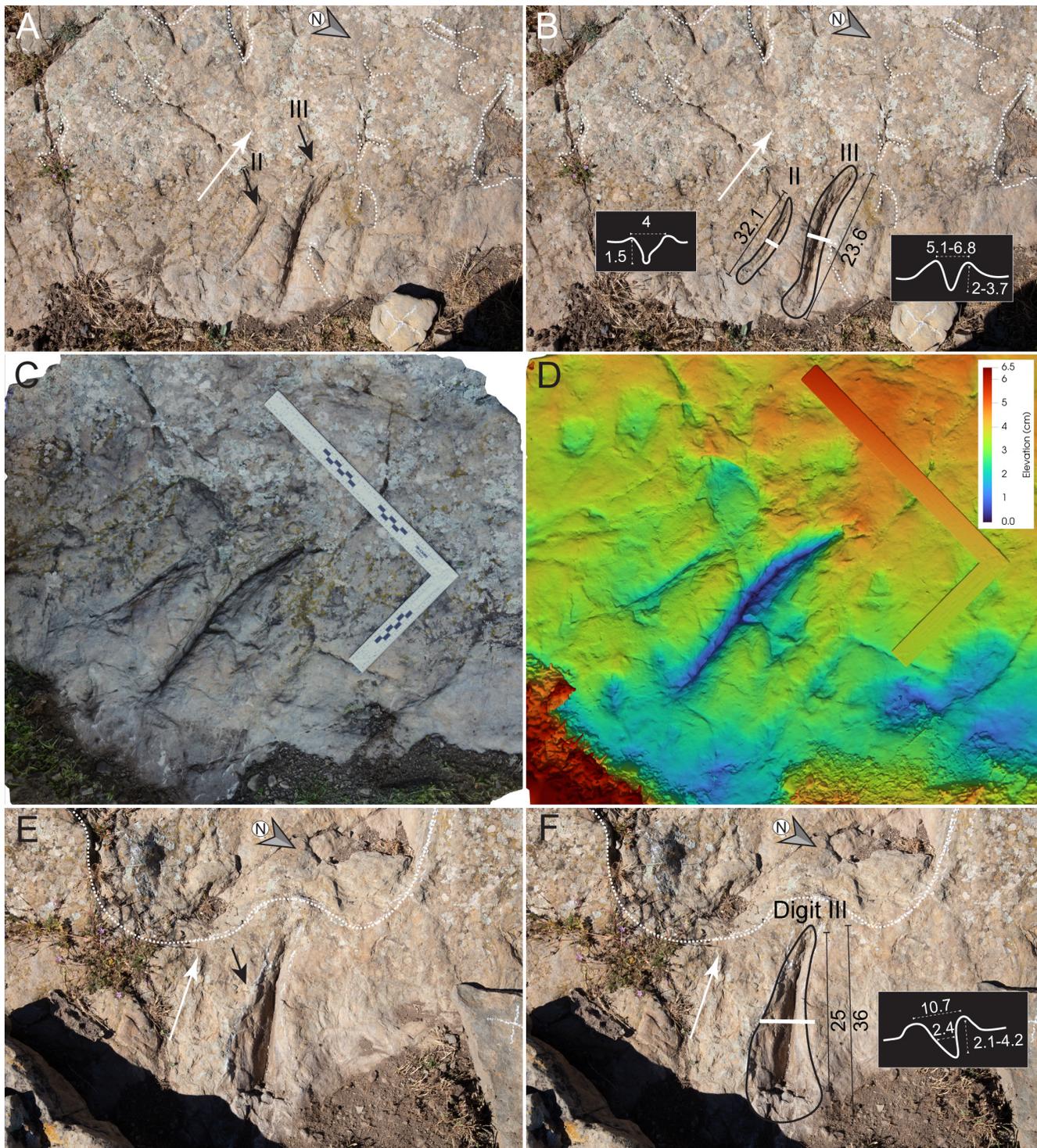
The Santisol swim traces are like those reported by [Esperante \*et al.\* \(2023\)](#) from the Upper Cretaceous (Maastrichtian) from El Molino Formation in the Torotoro National Park (TTNP), Bolivia. At the TTNP–Km99 tracksite, [Esperante \*et al.\* \(2023\)](#) describe three swim morphotypes: morphotype 1, consisting of long, deep grooves (10–35 cm), rectilinear, slightly curved or comma-shaped; morphotype 2, composed of deep short grooves (2–5 cm) and tear-drop-shaped; and morphotype 3, consisting of very long (30–120 cm) shallow, slim scratches. The Santisol swim trace 1 is of morphotype 1, and the swim traces 2 and 3 are of morphotype 2.

The Santisol swim traces are very similar to those found at the Virgen del Campo tracksite, Enciso, La Rioja, Spain, reported by [Ezquerro \*et al.\* \(2007; fig. 2\)](#). At this tracksite, a 15 m-long trackway is preserved with theropod swim traces, consisting of a succession of 12 traces (6 asymmetric pairs) of 2 or 3 curved scratch marks. Each trace consists of two or three slender grooves corresponding to digits II, III and IV of the theropod hindfeet. These swim traces correspond to morphotypes 1 and 3 or TTNP–Km99 of [Esperante \*et al.\* \(2023\)](#).

The Santisol swim traces resemble several tracks found in the Icnitas-4 tracksite along the road LR-286 between El Villar and Poyales, near Enciso (La Rioja,

Spain), which are also of the morphotype 1 described here. This tracksite was first described by Casanovas *et al.* (1993) and further discussed by Pérez-Lorente (2015), who labeled the tracksite as EVP. The latter author describes trackway EVP12 as beginning with a

footprint of “normal shape,” followed by a track that has “inordinately long toe marks,” continuing with a track that consists of “three long, roughly parallel toe marks that do not meet at the proximal end of the footprint” and the last two tracks of the trackway are “simply drag



**Figure 4.** Swim traces 2 (A–D) and 3 (E–F). The white arrow indicates the direction of movement of the trace maker (swim direction). **A**, Swim track 2 consisting of a set of two subtraces. The longest corresponds to digit III, whereas the shortest corresponds to digit II. Note the multiple theropod true tracks associated; **B**, swim track 2 marked in black lines, with indicated lengths (in cm). The cross-section’s dimensions (in cm) are indicated in white on the side of each trace; **C**, 3D model of swim track 2. The longer side of the ruler is 30 cm; **D**, depth color photogrammetry model of swim track 2; **E**, swim trace 3 with the posterior side of the associated ornithopod track in the dotted white line. The white arrow indicates the direction of movement of the swimming theropod; **F**, interior and exterior dimensions and cross-section dimensions of swim trace 3.

marks of claws and the tips of toes". Pérez-Lorente interprets such a trackway as a theropod transitioning from walking to swimming. The three swim traces in the Santisol tracksite are of morphotype 1 in the TTNP-Km99 tracksite of [Esperante et al. \(2023\)](#), and they are not interpreted as transitioning from walking to swimming.

The Icnitas-4 (EVP) tracksite has other swim traces in figures 3 and 9 of [Casanovas et al. \(1993\)](#) but not labeled or described. The author (RE) has visited the tracksite and compared the morphology of these traces with those of TTNP-Km99 and Santisol tracksites, concluding that they are also of swim morphotypes 1 and 2.

Tracks interpreted as swim traces have been reported from the La Laguna tracksite in La Rioja, Spain, preserved as longitudinal scale scratch marks or drag marks ([Navarro-Lorbés et al., 2023](#)). They are morphologically different from those identified in the Santisol tracksite, the other tracksites in La Rioja with swim traces, and those identified in the TTNP in Bolivia. The La Laguna swim traces are preserved as convex epireliefs in six different morphotypes. Some of the tracks show the cast of the posterior part of the autopodium, where the impressions of the three digits converge in a "heel". In the Santisol traces, the groove interpreted as the scratch of the claw of digit III does not coalesce with any other parallel scratch or structure. The impressions of the digits in the La Laguna tracks are uniform in width and thickness from the anterior to the posterior end. In contrast, the traces in the Santisol tracksite have an acuminate tip in the anterior end and a wider, round drop-like shape in the posterior end.

Morphologically, the Santisol swim traces differ from the long (dm-scale) very thin, curved or sinuous semi-parallel scratches found in several localities in the world, including the Blätterton Member/Hornburg Formation of the Konberg Quarry in Germany ([Buchwitz et al., 2020](#)); the Praia da Amoreira tracksite of the Porto Novo Formation in Portugal, classified as *Characichnos* isp. ([Castanera et al., 2021](#)); the Irati Formation of the Paraná Basin in NE Brazil, interpreted as mesosaurid swim traces by [da Silva and Sedor \(2017\)](#); the St. George dinosaur Discovery Site of the Lower Jurassic Kayenta Formation in SE Utah ([Milner et al., 2016](#), fig. 10.3, 10.4; [Milner et al., 2006](#)).

The Santisol swim traces differ from those preserved as sets of four cm-scale, curved parallel scratches in the Blätterton Member/Hornburg Formation of Konberg Quarry in Germany ([Buchwitz et al., 2020](#)).

Morphologically, the Santisol swim traces resemble the impression of the central digit in the *Paravipus didactyloides* tracks reported in the Irhazer tracksite of the ?Middle Jurassic Irhazer Group on the plains of Agadez, Niger ([Mudroch et al., 2011](#)), therein interpreted as tracks made by didactyl theropods. Like the Santisol traces, the *Paravipus didactyloides* tracks lack the metatarsophalangeal joints and digital nodes.

The Santisol swim traces resemble the "category 1 swim trace" of *Wintonopus latonorum* figured by [Romilio et al. \(2013\)](#), figs. 6, 7 and 12) from the Lark Quarry Tracksite in Western Australia. The authors state that "The elongated, didactyl or tridactyl, longitudinal scratches that characterize category 1 strongly resemble previously recognized dinosaur swim traces", citing several references. They indicate that such traces are considered as swim traces of theropod dinosaurs (*Charaichnos*). However, the resemblance with the Santisol swim traces is difficult to assess because they provided only one photograph of the swim traces on the site.

The occurrence of swim traces in the Santisol tracksite has significant palaeoenvironmental implications. The theropod and ornithopod tracks indicate that those animals walked on the surface when the substrate was wet and deformable. [Pérez-Lorente \(2003\)](#) describes tracks with evidence of the collapse of sediment into the prints, particularly into the traces of the digits, closing or almost closing the depression made during the impact of the autopodium onto the sediment. This indicates that the substrate must have been soft and not very firm.

Swim trace 1 clearly cuts through a theropod track, which indicates that the water level rose after several dinosaurs walked on the surface of the track-bearing layer, leaving prints on the substrate. The absence of collapse structures in any of the swim traces suggests that the substrate had achieved a higher degree of firmness than when the dinosaurs walked on the surface. Remarkably, the sediment reaches that degree of plasticity again without the previous ichnites being excessively affected or directly disappearing.

## CONCLUSION

Three sets of theropod swim traces were found in the previously studied Santisol tracksite in La Rioja, Spain. These traces occur alongside more than one hundred theropod true tracks and several ornithopod tracks, all preserved as concave epirelief. The swim traces consist of curved or sinuous scratches with a rim of displaced sediment in the posterior end. Their morphology is very different from true dinosaur tracks, and they are like swim traces identified in two nearby tracksites in La Rioja and in several tracksites in the Torotoro National Park, Bolivia. One of the swim traces in the Santisol tracksite cuts through a true theropod track, indicating that the true tracks formed first, and the water level rose before the tracks cemented. Theropod dinosaurs swam in the area during the high water level stage, leaving scratches on the substrate, which later indurated and preserved the tracks and traces.

**Supplementary information.** The article has no additional data

**Author's Contributions.** RE, field work, wrote the manuscript, prepared Figures 1, 3, 4. KEN, thin sections, wrote the lithological description, manuscript review, prepared Figure 2.

**Competing interests.** The authors declare that they do not have any competing interests

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**Author details.** Raúl Esperante<sup>1</sup> & Kevin E. Nick<sup>2</sup>.

<sup>1</sup>Geoscience Research Institute, 11060 Campus Street, Loma Linda, California, 92350, USA; [resperante@llu.edu](mailto:resperante@llu.edu);

<sup>2</sup>Department of Earth and Biological Sciences, School of Medicine, Loma Linda University, Loma Linda, California 92350, USA; [knick@llu.edu](mailto:knick@llu.edu).

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