Dinosaur swim tracks from the Lower Cretaceous of La Rioja, Spain: An ichnological approach to non-common behaviours

P. Navarro-Lorbés [a, *], I. Díaz-Martínez [b, c, d, e], J.M. Valle-Melón [f], Á. Rodríguez-Miranda [f, g], J.J. Moratalla [h], M. Ferrer-Ventura [a], R. San Juan-Palacios [a], A. Torices [a, i]

[a] Department of Human Sciences, University of La Rioja, Edificio Departamental − C/ Luis de Ulloa, 2, 26004 Logroño, La Rioja, Spain
[b] Instituto de Investigación en Paleobiología y Geología (IIPG), CONICET, Av. Roca 1242, General Roca 8332, Río Negro, Argentina
[c] Universidad Nacional de Río Negro-IIPG, Av. Roca 1242, General Roca 8332, Río Negro, Argentina
[d] Geology Department, Science and Technology Faculty, University of the Basque Country UPV/EHU, Sarriena Auzoa z/g, 48940 Leioa, Basque Country, Spain
[e] Department of Earth Sciences and Condensed Matter Physics, Faculty of Sciences, University of Cantabria, Santander 39005, Cantabria, Spain
[f] Laboratory for the Geometric Documentation of Heritage (GPAC, Built Heritage Research Group), University of the Basque Country (UPV/EHU), c/ Justo Vélez de Elorriaga 1. 01006 Vitoria-Gasteiz, Spain
[g] Department of Applied Mathematics, University of the Basque Country (UPV/EHU), c/ Nieves Cano 12, 01006 Vitoria-Gasteiz, Spain
[h] Instituto Geológico y Minero de España (IGME-CSIC), Departamento de Geología y Subsuelo, Ríos Rosas, 23, 28003 Madrid, Spain
[i] Departamento de Geodinámica, Estratigrafía y Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, Calle José Antonio Novais, 12, 28040 Madrid, Spain

ARTICLE INFO

ABSTRACT

The reconstruction of behavioural patterns performed by non-avian dinosaurs is an important task of palaeontology in order to globally understand how these animals interacted with their environment. Their relation with aquatic lifestyles has always been an intriguing question that has been extensively studied during the last decades, especially focused on some specific groups. The present work describes a new tracksite with 27 swimming tracks located in a fluvial setting from the Lower Cretaceous Urbion Group of La Rioja (Spain). They are preserved as natural casts with sizes between 8.5 and 29.2 cm and a predominant orientation. The tracks have been classified into 6 different morphotypes according to their morphology, and grouped into 5 different categories depending on the different pes-substrate interactions, following the proposal of Romilio et al. (2013). Some tracks were produced while the animal was moving in partial or complete buoyancy, and displacement was conducted by water and sediment impulsion, not just a mere paddling. Other tracks could be impressed in a bottom-walked, when the trackmaker touched the digit tips on the ground vertically or sub-vertically. This new tracksite confirms the capabilities of some groups of non-avian dinosaurs to interact with shallow water environments where they could print their pedes as they moved, either in complete buoyancy or during a displacement with some vertical component in the water column. It also contributes to the better understanding of swimming track morphologies as especially dependent on pes-sediment interaction and environment more than differences in pes configuration itself, causing the high variability of swimming footprints even when they belong to the same trackway. The classification of swimming tracks and footprints into categories dependent on the pes-substrate interaction could be a good guiding principle to avoid problematics about ichnotaxonomical definition.

1. Introduction

During the Mesozoic, dinosaurs became one of the most successful vertebrates of their time, inhabiting a great variety of niches on all continents and latitudes (see Benton, 2014). Beginning as agile predators during the Triassic such as *Eoraptor* (Sereno et al., 2012), *Herrerasaurus* (Novas, 1994), or *Nyasasaurus* (Nesbitt et al., 2013), they spread all around the globe occupying almost every continental environment. Even some evolved members of non-avian dinosaurs, such as the Paraves, managed to fly (see Pei et al., 2020; Serrano and Chiappe, 2021). It is important to note

P. Navarro-Lorbés, I. Díaz-Martínez, J.M. Valle-Melón et al.

Cretaceous Research 147 (2023) 105516

that non-avian dinosaurs, as well as other well-known groups of sauropsids, are basically continental animals that, although adapted to diverse environments, are mostly obliged to terrestrial locomotion (Benton, 2004). This is confirmed by the abundant presence of sauropsid tracks and traces from the Permian-Triassic to the end of the Cretaceous (Lucas and Hunt, 2006; Klein and Lucas, 2010; Falkingham et al., 2016). Consequently, the vast majority of the record shows distinctly terrestrial locomotion consisting mainly of the presence of tracks and trackways. However, that does not always seem to have been the case. Thomson and Droser (2015) provided data from more than 100 localities with sauropsid tracks that suggested a swimming behaviour and, interestingly, it seems that this behaviour was more abundant during the Triassic (Thomson and Lovelace, 2014; Thomson and Droser, 2015), something that has also been reflected in the Iberian Peninsula record (Navarro and Moratalla, 2018).

The palaeoichnological record of dinosaurs is practically cosmopolitan and its richness has allowed paleontologists to infer very significant aspects related to their biodynamics and ethology (e.g. Whyte and Romano, 2001; Lockley et al., 2018; Navarro-Lorbés et al., 2021a), the latter understood as deducing what the trackmaker was doing and where it was, that is, in which sedimentary environment the tracks studied were produced. Regarding the latter, it should be mentioned that the formation and, above all, the preservation of dinosaur footprint sites requires special conditions. In fact, most of them have been generated in lacustrine, marshy, fluvial areas, small wetlands, etc., i.e. areas with an abundant presence of water. So, it is possible to consider that, as happens with extant terrestrial tetrapods, many non-avian dinosaurs were capable to swim to a greater or lesser extent, living even in these humid regions or certain adaptations being selected to easily cross certain flooded areas.

However, their adaptation to aquatic ecosystems has been the subject of discussion in recent years. Some discoveries have suggested that at least one clade, Spinosauridae, could have had a closer relationship with aquatic lifestyle because of their anatomical features (Charig and Milner, 1997; Ibrahim et al., 2014, 2020; Gimsa et al., 2016; Henderson, 2018; Arden et al., 2019; Gimsa and Gimsa, 2021; Beevor et al., 2021; Fabbri et al., 2022; Sereno et al., 2022; Myhrvold et al., 2022) and by isotopic reconstructions of their diet (Amiot et al., 2010; Goedert et al., 2016; Trapman, 2018; Henderson, 2018; Hassler et al., 2018; Gimsa and Gimsa, 2021). But, what happened with the rest groups of dinosaurs? could they present aquatic abilities?

Trace fossils are the result of an animal's behaviour in a given environment (e.g., Falkingham, 2014; Melchor, 2015). A true swimming behaviour could lack of an ichnological correlate if it implies an animal floating with its entire body weight supported by the water (Thomson and Lovelace, 2014) and there is no interaction with the subaqueous substrate. Nevertheless, in ichnology, the term "swim track" is used when the trackmaker contacts a subaqueous substrate when its body is at least partially buoyed by water (Lockley et al., 2010; Lee et al., 2019). Therefore, the ichnological record can contribute to answer the questions raised above. In dinosaurs, swim tracks have been described since the Early Jurassic (Milner et al., 2006) in both saurischians (e.g., Whyte and Romano, 2001; Ezquerra et al., 2007; Farlow et al., 2019) and ornithischians (e.g., Fujita et al., 2012; Romilio et al., 2013; Riguetti et al., 2021). These kinds of tracks are difficult to analyze because they are sometimes incomplete and irregular due to the exceptional nature of the interaction (Milner and Lockley, 2016). The sum of all the factors that affect aquatic locomotion − i.e. water level, water salinity, buoyancy force, irregularities in the subaqueous substrate, directional water streams, possible diving trackmaker, gravity and reaction force − makes the swim tracks a particular record that can

present consecutive footprints with different features and shapes, tracks suddenly disappearing due to the loss of contact pes-substrate, or footprints that reflect poorly the trackmaker autopod morphology (Bennett et al., 2014; Milner and Lockley, 2016). Fortunately, the dinosaur ichnological record has several examples of these kinds of tracks and it is possible to observe some interesting patterns (see Milner and Lockley, 2016; Farlow et al., 2018; and references therein).

Since the 1970s, the Cameros Basin (Late Jurassic−Early Cretaceous) has raised as an exceptional area to study dinosaur tracks and footprints (Pérez-Lorente, 2015). To date, more than 10,000 footprints and more than 170 tracksites have been identified in La Rioja (Pérez-Lorente, 2015), more than 180 tracksites in Soria province (Hernández-Medrano et al., 2005) and around 20 tracksites in the Burgos province (Torcida et al., 2001; Torcida Fernández-Baldor et al., 2012, 2021), all of them in sediments of the Cameros Basin. Among them, only two non-avian dinosaur swimming tracks had been recognized in the Enciso Group (upper Barremian-lower Aptian): Icnitas-4 (Pienkowski and Gierlinski, 1987; Casanovas et al., 1993; Pérez-Lorente, 2015) and La Virgen del Campo-4 (Ezquerra et al., 2007; Ezquerra et al., 2010; Pérez-Lorente, 2015). The scarcity of dinosaur swimming tracks is not only relevant in the Enciso Group, but in the whole Cameros Basin and in the paleoichnological record of the Iberian Peninsula. In 2020 and after days of heavy rains, a rockslide exposed a track-bearing surface (the Laguna tracksite) (Fig. 1) near the town of Laguna de Cameros, in the southern part of La Rioja province (Spain). This tracksite, found in outcrops of the Urbión Group (Valanginian-Aptian), was discovered and reported by a neighbour of that village (Navarro-Lorbés et al., 2021b). It preserved 27 natural casts with lengths between 8.5 and 29.2 cm that present natatory or pseudo-natatory features. This new finding is important not only due to the scarcity of dinosaur swimming tracks mentioned before, but because the Urbion Group presents few dinosaur tracksites (around 20) when compared with other lithological groups from the Cameros Basin like Enciso and Oncala (that combined present more than 200 tracksites) (Díaz-Martínez et al., 2015).

The aim of this work is multiple. First, to describe and analyze this new record, and compare it with other worldwide non-avian dinosaur tracks that represent swimming behaviour, leading to the analysis of how swimming tracks represent an exceptional case of ichnological record. On the other hand, tracksite location and conservation state put the tracksite at a serious risk of deterioration that rendered necessary its digital preservation, a labour that has been carried out during the last years in other tracksites of La Rioja (Spain).

2. Geographical and geological setting

The Laguna tracksite is located in the Province of La Rioja (Spain), near the village of Laguna de Cameros, situated close to the Leza river. The southeastern riverbank near Laguna de Cameros is enclosed by steep slopes almost vertical in some parts. The tracksite appears in one of those areas as a layer exposing its base.

Geologically, it is located in the Cameros basin, a high subsidence basin, produced during the second stage of the Late Jurassic−Early Cretaceous Iberian Mesozoic Rift (Mas et al., 2002).

The Cameros Basin has been traditionally divided into two main sectors: the northeastern and the southwestern sectors, which show important differences in their stratigraphy and evolution. The tracksite is located in the northeastern sector, which presents very high rates of subsidence with more than 6500 m of sediments in the depocentral areas (Martin-Chivelet et al., 2019). The age of materials in the northeastern sector ranges from Tithonian to Early Albian (Martin-Chivelet et al., 2019). The deposits of Northeastern

P. Navarro-Lorbés, I. Díaz-Martínez, J.M. Valle-Melón et al.

Cretaceous Research 147 (2023) 105516

Fig. 1. General view of the Laguna tracksite layer. Natural casts can be observed at the bottom of the layer.

sector have been traditionally divided into 5 stratigraphic groups: Tera, Oncala, Urbíón, Enciso and Oliván (Tischer, 1966) and in 8 depositional sequences (DS1−DS8) as proposed by Mas et al. (2002).

The Laguna tracksite crops out in the Urbión Group, which was deposited during the depositional sequences DS4−DS7 (Mas et al., 1993). The Urbión Group is mainly siliciclastic, with fluvial deposits composed of sandstones, siltstones and conglomerates that can evolve laterally to lacustrine carbonates, sands and marls. The age of the Urbion Group, according to depositional sequences, ranges from late Berriasian to early Aptian (Mas et al., 2011). The Laguna tracksite is located in the upper part of Urbion Group, specifically in the so called Urbion Group D (Mas et al., 1993) deposited during the DS7 (late Barremian−early Aptian) (Mas et al., 2004). These deposits are mostly siltstones with thin sandstone intercalations, interpreted as a fluvial system with alluvial plains predominance and meandering channels (Salinas and Mas, 1990). During the DS7 the materials of the Urbión Group, considered as siliciclastic fluvial deposits, are laterally equivalent to the materials of the Enciso Group, interpreted as a siliciclastic-influenced lacustrine and palustrine environment (Mas et al., 1993, 2002, 2011).

The local stratigraphy is composed of a detritic series dominated by siltstones and sandstones (Fig. 2). Lenticular layers are observed along the column, with some levels presenting lateral changes in thickness and rounded bases. This general configuration fits well with regional interpretations of the Urbión Group as a fluvial system with alluvial plains and a predominance of meandering channels (Salinas and Mas, 1990). The footprints are located in a sandy siltstone layer of 30 cm presenting a more or less tabular base

and a more sinuous top of the layer. Lateral changes in thickness are appreciated but, at least locally, the layer presents continuity. Footprints are natural casts and they seemed to have been filled in a slow process indicated by parallel laminations observed in some of the natural casts (Fig. 3B). The underlying layer (where original footprints were printed) is a 10 cm of dark grey siltstones with thin laminations (Fig. 3A). This level presents its major thickness restricted to the area beneath the natural casts, changing drastically its thickness in just a few decimetres and becoming a discontinuity between the top and bottom layers. The configuration of this layer could fit well with a briefly abandoned channel with a low energy fill.

3. Conservation of the Laguna tracksite

The Laguna tracksite is situated on the riverbank of the Leza river, the level base crops out exposing the natural casts of footprints in a steep slope, with the underlying layer lost. This fact puts the tracksite conservation in danger, exposing it to degradation if gravity causes the falling of rocks; the same process that allowed their discovery will lead to their destruction (see García-Ortiz et al., 2014). The weakening of the slope that will be caused by rock fall and fracturing of materials will eventually lead to the gravitational fall of the track layer causing its inevitable damage.

The advances in the scanning and photomodelling techniques and their implementation in the case of palaeontology —and especially palaeoichnology—, provides a suitable way to preserve the information about the palaeontological heritage. Furthermore,
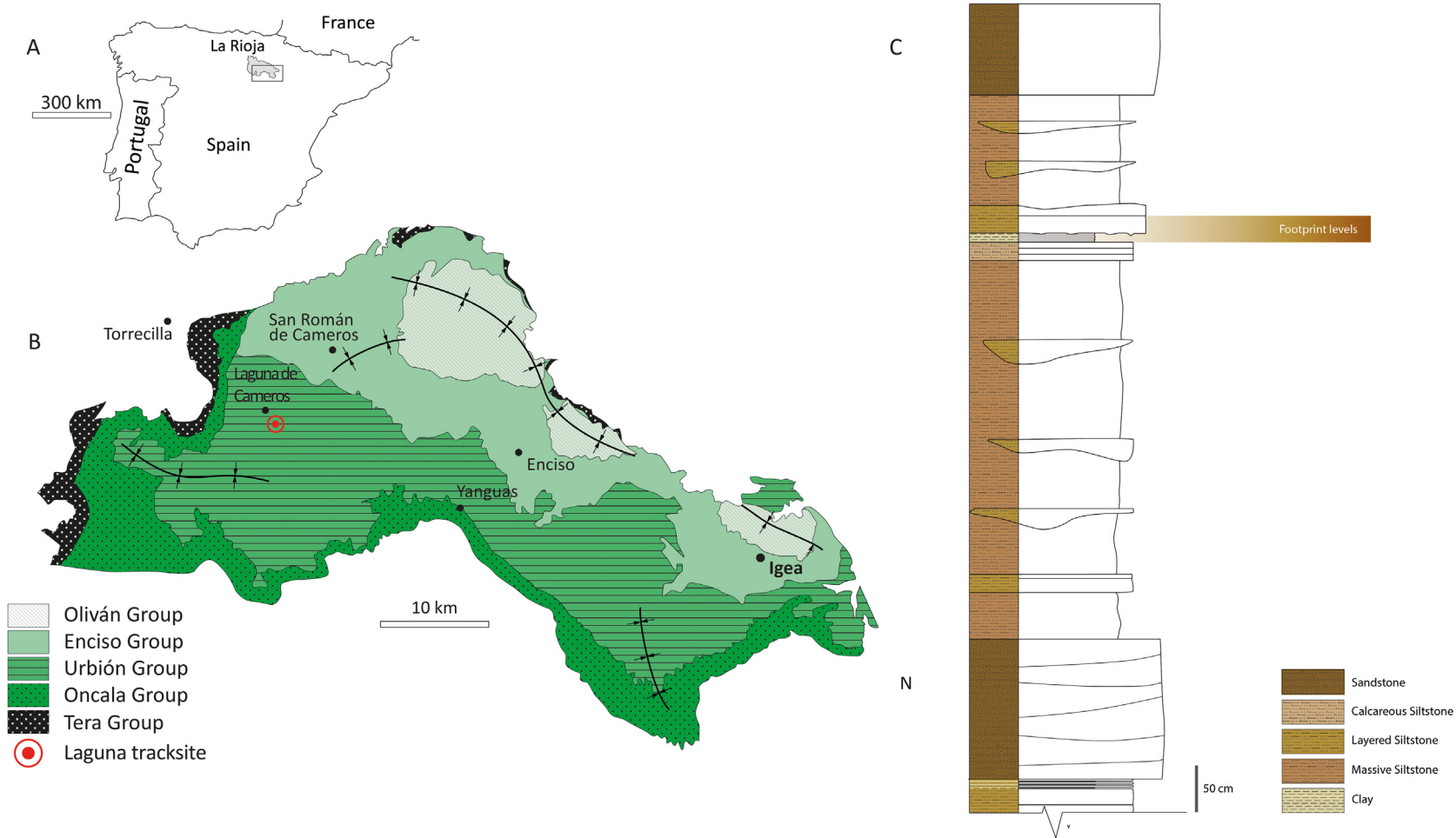
Fig. 2. Geographical and geological location of the Laguna tracksite. (A) Location of La Rioja in the Iberian Peninsula. (B) Geological map of the southern part of La Rioja, with the main stratigraphical groups of the Cameros Basin differentiated. (C) Local stratigraphic succession of the study area with the location of the natural casts layer and original tracking surface marked as "Footprint levels". Modified from Doublet et al. (2003), Suárez-González et al. (2013) and Isasmendi et al. (2020).
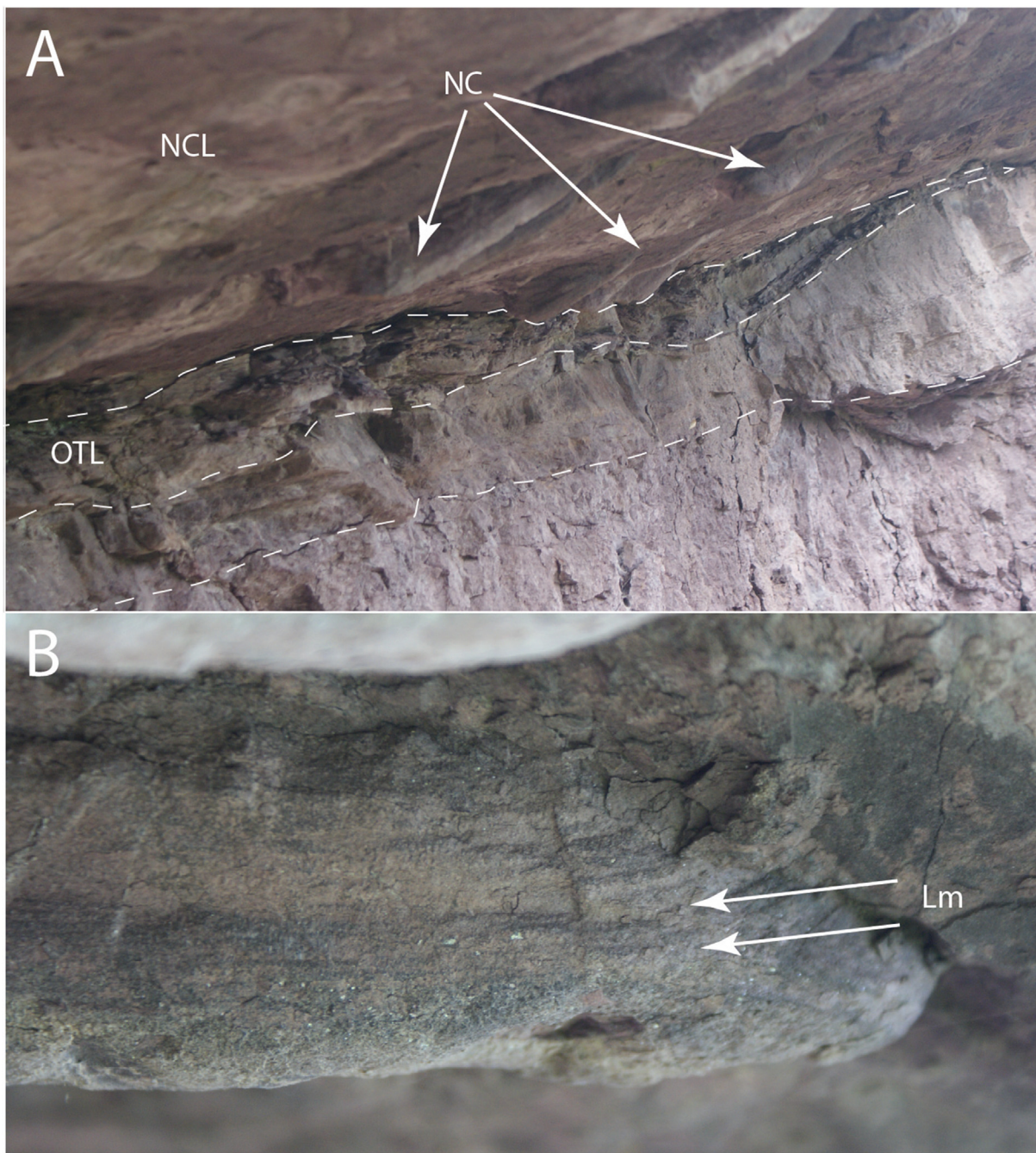
Fig. 3. Photographs of A) Detail of the natural casts layer (NCL) white arrow indicating some of the natural casts (NC) and showing the abrupt change in thickness of original tracking layer (OTL). B) Detail of Laminations (Lm) present in some of the natural casts.

the digital models not only preserve the information, but also permit to share it with museums and researchers from all over the world (Cayla et al., 2014; Díaz-Martínez et al., 2018; Herraiz et al., 2019; Torices et al., 2020). Consequently, geometrical registration and 3D modelling have become important tools in order to study tracks and footprints (Falkingham et al., 2018), expanding the classical 2D publication and registration of tracks to a three-dimensional point of view. This improvement is important due to the fact that any track or footprint presents a three-dimensional topographic surface (Falkingham et al., 2018) and many times a three-dimensional inner structure due to their complex origin as a

product of complex interaction pes-sediment (Falkingham and Gatesy, 2014).

The palaeoichnological heritage of La Rioja —due to the high amount of tracksites present in the territory and, especially, because of their situation exposed to weathering and landscape evolution— suffers from the problem of its physical conservation. This issue drove the initiative to digitally register the tracksites as they are studied and make them accessible to the public via open repositories. In this respect, the Laboratory for the Geometric Documentation of Heritage of the University of Basque Country and the Chair of Palaeontology of the University of La Rioja collaborate

P. Navarro-Lorbés, I. Díaz-Martínez, J.M. Valle-Melón et al.

Cretaceous Research 147 (2023) 105516

in the development of a catalog of tracksites of La Rioja, with the 3D models available through the repository ADDI of the University of Basque Country (https://addi.ehu.es/) and geolocated in a specific coverage provided by the Spatial Data Infrastructure (SDI) of the Government of La Rioja (https://www.iderioja.larioja.org/) (Torices et al., 2020).

4. Materials and methods

At the Laguna site, 27 swim tracks were identified. The tracks were labelled as follows: first, the tracksite identification (e.g., "L" from the Laguna tracksite); and second, separated by hyphen, the footprint (e.g., "3"). For instance, L-3 is the footprint 3 of the Laguna tracksite.

Due to the vulnerable situation of the Laguna tracksite in terms of conservation, it was necessary to generate a photogrammetric 3D model, in order to register and preserve the information of this brittle site for the current study and future uses (do take into account the difficult accessibility to the area and that it is dangerous due to rock falls).

In this case, for photogrammetric modelling the following steps were taken.

- Creating a topographic reference network all around the surrounding area to locate it in the official coordinate and reference system (UTM zone 30 in ETRS89) and scale it properly.
- Photographic record of the tracksite and its near surroundings.
- Three-dimensional modelling of the tracksite.
- Delivery of the models to the La Rioja Government database and publication in an open data repository (see the last section about "open data sources").

4.1. Establishment of topographic reference

As a previous step to the unambiguous and accurate location of the site, it is necessary to establish a network of marks with precise coordinates in the reference coordinate system. The reference network consists of two types of points.

- 3 ground permanent benchmarks are defined by means of steel nails. These points are used to reference the tracksite into the official coordinate system and remain on site in case it is necessary to return to the site in the future. The observation was performed by means of GNSS receivers (*Topcon Hiperpro*), i.e., by satellite positioning.
- 9 control points for photogrammetric reference, consisting of 3×3 cm methacrylate targets that were temporally installed over the site and its boundary. The coordinates of these points were obtained by means of measures from a total station (*Leica TCE 1205*) —set up and oriented in the official coordinate system thanks to the ground permanent benchmarks— and were removed after the photographs were taken.

All in all, the internal precision of the network defined by the control points is 3 mm, good enough for the purposes of the three dimensional modelling.

4.2. Photographic record

A Panasonic DC-GX800 camera provided with LUMIX G VARIO 12−32 mm F3.5−5.6 lens was used. The photographs were taken with extensive overlapping between the shots, which facilitates the work of the correlation algorithms run during the modelling phase.

4.3. 3D modelling

The photogrammetric model was generated using the software *Agisoft Metashape®*. The software works in successive steps: (1) relative alignment of the images and generation of a sparse point cloud of the represented area, (2) point cloud densification, (3) messing, (4) texturing and (5) georeferencing. Next, from the three-dimensional models, it is possible to derive new products such as orthographic (2D) representations; either with photographic texture or with a hypsometric scale of colours that highlights the shape of the footprints (Fig. 4A,B).

4.4. Footprint orientation

The trackmaker movement patterns were examined by plotting with PAST 4.03. In a rose diagram (following Díaz-Martínez et al., 2020), the orientations of individual tracks were plotted due to the absence of clearly preserved individual trackways (Fig. 4C). In tracks where the anterior and posterior surfaces of the track are recognized, the track direction is measured as the angle between the course of the animal's movement, using the axis of the track that is located along the digit III impression, and a local 0° (not respect the magnetic North). For convenience, track direction was oriented in a rose diagram relative to the nature of the exposure: the projection into/out of the cliff represented in the 0°−180° axis (being the 0° the out of the cliff orientation), and across the cliff represented in the 90°−270° axis.

4.5. Depth profiles

Following the methodology of Romilio et al. (2013) where the authors stablished different patterns of proximal-distal depth profiles for dinosaur swimming footprints, the depth profiles of the natural casts of the Laguna tracksite were analysed. These profiles can help to understand the peculiar shapes and morphologies of swimming tracks and footprints, probably linked to the distinctive pes motions during their generation. Once the 3D model was generated, longitudinal topography profiles of the digit impressions were performed using the slice tool in ParaView 5.10.1 (Fig. 5). In order to be more comprehensive when describing footprint generation processes, the depth profiles obtained from the natural casts were inverted (Fig. 5), simulating the depth profiles of the original footprints. The positions where the depth profiles were performed are indicated in Fig. 5.

5. Footprint description

The footprints of the Laguna tracksite are preserved as convex hyporeliefs in a decametric sandy-clay layer. Originally, the track-maker modified a 10 cm marly-siltstone level which is the tracking-surface (*sensu* Fornós et al., 2002). Moreover, some natural casts have preserved longitudinal scale scratch marks or drag marks. Scale scratch marks (sensu Milner et al., 2006) are millimetric parallel striations that are usually found in true tracks (or natural casts) and indicate the direction of both digits and pes motion. This is due to the impression of both pes morphology and motion, when the digits, scales and other irregularities of the skin can leave longitudinal striations of different sizes. These features, added to the homogeneous lithology of the casts and the presence of parallel infill laminations (Fig. 3B) allow to interpret the studied materials as natural casts (infillings of true tracks). In total, 27 footprints have been recognized (Fig. 4A-C). Although some of them have similar morphology (see next section), there are no identified clear trackways. The dimensions of the Laguna tracksite (Fig. 4) are not
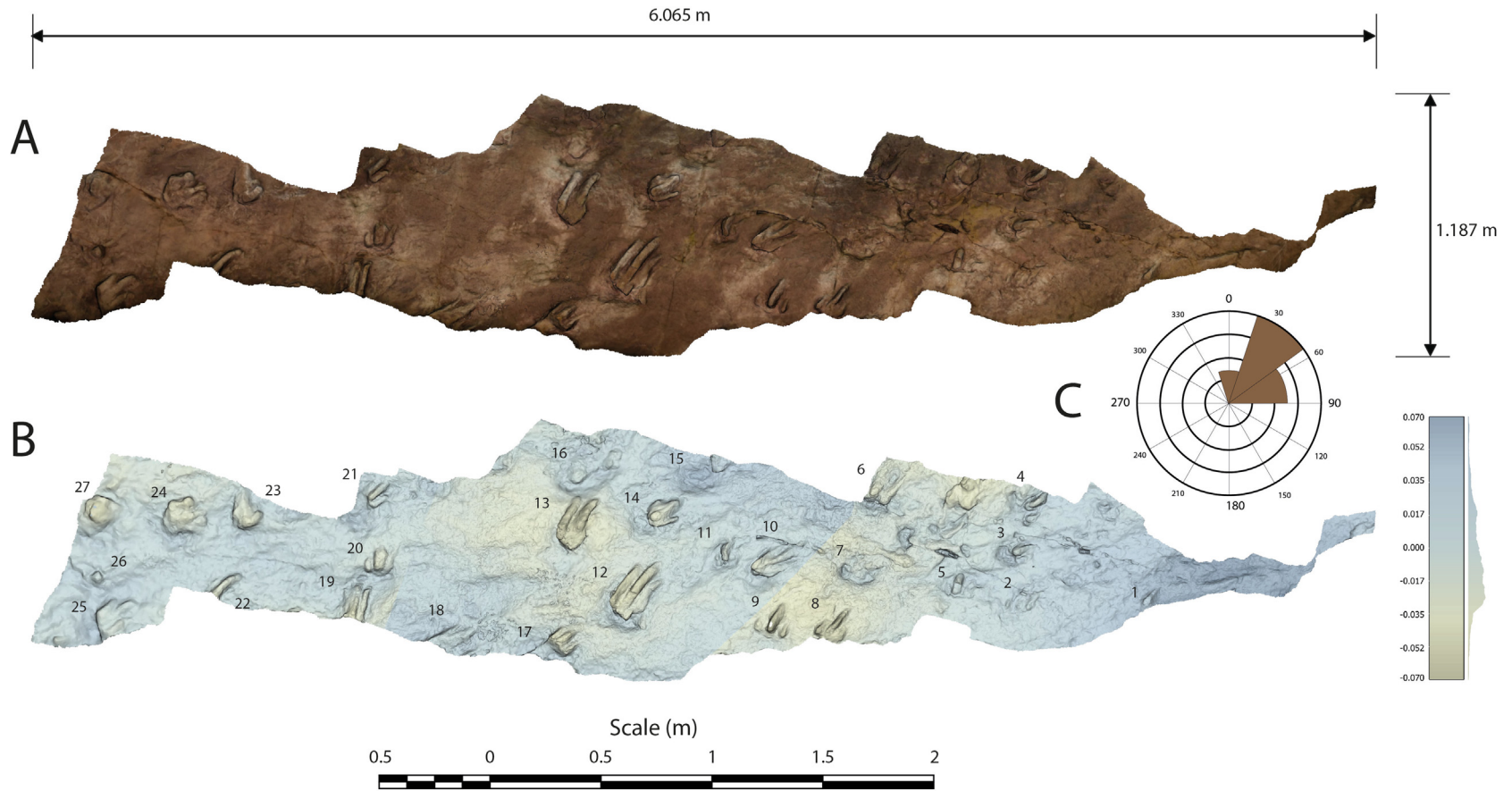
Fig. 4. Detail of the Laguna tracksite. A) Orthographic projection and normal. B) Hypsometric projection and normal. C) Graphical representation of footprint orientation in a rose diagram.
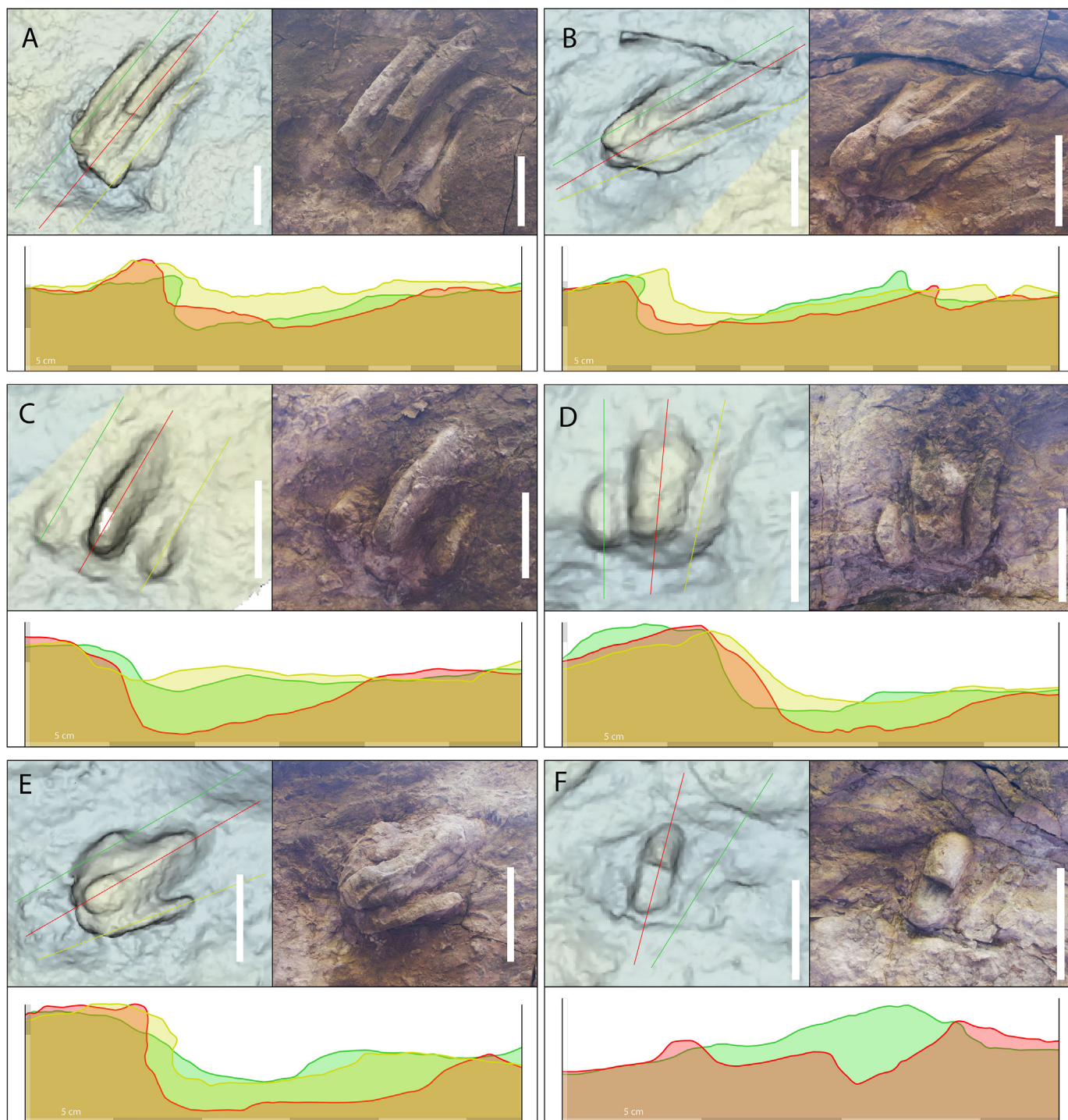
P. Navarro-Lorbés, I. Díaz-Martínez, J.M. Valle-Melón et al.

Cretaceous Research 147 (2023) 105516

Fig. 5. Different images of the best representatives of each Morphotype described in the tracksite: A) Morphotype 1 (L-12). B) Morphotype 2 (L-10). C) Morphotype 3 (L-9). D) Morphotype 4 (L-20). E) Morphotype 5 (L-14). F) Morphotype 6 L-5). Each morphotype is represented with 3 different images: Top left: Captures of different footprints taken from the hypsometric projection and normal model. Scale bar: 10 cm. Top right: Photographies of the footprints taken in the tracksite. Scale bar: 10 cm. Bottom: Proximal-distal depth profiles of each digit impressions. The depth profile is represented inverted, in order to reflect real footprint profile. The position of each depth profile is represented by lines in top left images.

excessively large but it presents a relatively high footprint density (5.91 footprints per square meter). Taking into account the rose diagram information (Fig. 4C), the tracks present a predominant direction of 30° (local angular value).

5.1. Footprint morphology

According to the general morphology, footprints have been divided into 6 morphotypes.

- Morphotype 1 (L-12, L-13, L-17, L-18, L-19, L-25) (Fig. 5A): The tracks are 25−30 cm long and around 15 cm wide. They present parallel impressions of two or three digits, scale scratch lines (sensu Milner et al., 2006), evidence of claw impressions in the distal parts and depressions in the proximal part of the footprint, which would represent sediment accumulation in the true tracks. The best preserved of them are L-13 and L-12, which are located in the middle part of the tracksite. Their depth profile has a steeped proximal part with a flat base in the first third of the footprint and a slope to the distal end, being deeper in the proximal area.

- Morphotype 2 (L-10, L-6) (Fig. 5B): The footprint of this morphotype shows a traditional theropod footprint configuration. It is mesaxonic and has three digit impressions converging in a "heel". Moreover, it has elongated digit impressions (specially digit III) and evidence of sediment accumulation in the proximal part behind the "heel". Its depth profile is similar to Morphotype 1, being steeped in its proximal part, presenting a slope to the distal part and with the proximal area deeper (Fig. 5B, Table 1).

- Morphotype 3 (L-2, L-3, L-4, L-8, L-9, L-11) (Fig. 5C): Footprints with an elongated distal impression of digit III (or claw impression) and short digit II and IV impressions, sometimes showing just an oval or subcircular shape. Their depth profile presents a long slope from the distal part to almost the proximal end, reaching its deeper part in this area, and then a steeped proximal edge. The sediment accumulation behind the "heel" is also present but not as evident as in Morphotypes 1 and 2 (Fig. 5C, Table 1).

- Morphotype 4 (L-20, L-21) (Fig. 5D): Footprints with similar lengths and widths, even in some cases being wider than long. They present impressions of the three digits, with digit III longer than the other two, but all of them show especially wide shapes. These digit impressions show rounded shapes distally, with slight mesaxony. The proximal end of the footprint is abrupt, with the three digit impressions ending in the same line and sediment accumulation backward in the best-preserved footprint (L-20). Their depth profile is similar to Morphotype 3 with a slope from the proximal part and proximal steeped end (Fig. 5D, Table 1).

- Morphotype 5 (L-14, L-24) (Fig. 5E): Into this morphotype are classified those footprints that show a more or less defined tridactyl footprint contour, but present grooves (ridges in the natural casts) deeper than the rest of the pes impression. They present abrupt proximal and distal ends, being the proximal ones the deepest. Their base is almost flat with a slight slope that reaches their deeper part in the proximal part of digit III impression.

- Morphotype 6 (L-1, L-5, L-22) (Fig. 5F): Impressions of isolated digits (probably digit III) that sometimes present shallower impressions of digits II and IV.

- Undefined (L-23, L-26, L-27): They are classified as footprints due to their presence as elevations in the slab, but they are poorly preserved. Moreover, the slab presents some subcircular irregularities that could be caused by sediment mobilization due to water flow as the pes paddle near the sediment but not touching it (L-16, L-15, L-7).

6. Discussion

6.1. Different Lower Cretaceous swimming traces from the Cameros Basin

Swim tracks present great morphologic variations due to the processes implied in their production (Whyte and Romano, 2001; Romilio et al., 2013; Milner and Lockley, 2016). Because of this is difficult to assess a specific producer as it occurs in many tracks produced during terrestrial locomotion. The morphology of swim tracks reflects complex dynamic processes that mask the main

Table 1
Measurements taken in the Laguna trracksite. max L: Footprint maximum length. max W: Footprint maximum width. O: Orientation. II L: Digit II impression length. IIIL: Digit III impression length. IV L: Digit IV impression length. II W: Digit II impression width. III W: Digit III impression width. IV W: Digit IV impression width. III proxD: Digit III impression proximal depth. III distD: Digit III impression distal depth. min II−III: Minimum distance between digit II and III impressions. max II−III: Maximum distance between digit II and III impressions. min III−IV: Minimum distance between digit III and IV impressions. max III−IV: Maximum distance between digit III and IV impressions. Distances measured in cm.

	max L	max W	O	II L	III L	IV L	II W	III W	IV W	III proxD	III distD	min II−III	max II−III	min III−IV	max III−IV
L-1	8.5		41		8.5			3.6		1.53	0.11				
L-2	15.1	11.2	28	11.7	15.1	4.2	2.6		2	2.96	0.65				
L-3	12.2	4	73		12.2			4		2.96	0.65				
L-4	11.9	14.1?	62	7.2	11.9	2.5?	3.1	4.1	2.5	3.09	1.45	2	2.9	2.3?	2.3?
L-5	10.6	3.7	18		10.6			3.7		2.26	0.65				
L-6	23.4?	12.4	22	17	23.4?		4.7	4.6?		2.26	1.35	1.2	3.4?		
L-7			63												
L-8	17.6	12.3	37	7.1	17.6	7.8	3	3.1	2.9	2.2	1.17	0	1.9	0	1.8
L-9	13.9	14.6	30	6.9	13.9	6.3	2.5	4.8	3.3	2.51	1.07	2.9	2.9	3.2	3.2
L-10	27.1	10	62	??	??	??	??	??	??	2.36	0.44	??	??	??	??
L-11	8.8	9.2	−5	5.2	8.9	3.0?	2.5	3.8	2	1.19	0.68	1.1	1.1	1.2	1.2
L-12	29.2	16.2	37	22.5	29.2	23.6	3.9	4.1	4.5*	4.28	1.64	0	1.8	0	1.5
L-13	25.8	14.1	31	20.6	25.8		4.5	5.76		4.03	1.16	0	1.5		
L-14	16.5	11.9	60							5.01	2.86				
L-15															
L-16															
L-17			54							3.52	2.98				
L-18															
L-19			4							4.99	2.76				
L-20	13.9	18.2	8	6.73	12	13.9	2.9	6.1	3.6	2.01	1.25	1.2	1.2	0.5	0.5
L-21	14	9.9	52	9.1	12	7.1	2.5	3.3	3.2	3.32	1.74	0.5	0.5	0	1.2
L-22			46							2.65	2.03				
L-23															
L-24			71							5.12	4.58				
L-25			62							1.62	2.06				
L-26			26												
L-27															

P. Navarro-Lorbés, I. Díaz-Martínez, J.M. Valle-Melón et al.

Cretaceous Research 147 (2023) 105516

features of the animal feet. Just some features can be recognized (digit thickness, foot width or claw and scale impressions) and sometimes, even these features are difficult to measure and recognize if the sediment conditions are not suitable for their impression or there is an important lateral component in the movement.

The paleoichnological record of the Cameros Basin (La Rioja, Soria and Burgos provinces) makes this area one of the better places in the world to study non-avian dinosaur tracks and footprints. More than 250 tracksites (see Hernández-Medrano et al., 2005; Torcida Fernández-Baldor et al., 2012; Pérez-Lorente, 2015) located to date, only two of them show evidences of swimming non-avian dinosaurs (both in the Enciso Group). The Laguna tracksite would be the third record for the Cameros Basin, and the first one at the Urbión Group.

The scarcity of tracksites with swimming evidence even in such an ichnological rich area shows the exceptional nature of this kind of footprints. The first interpretation of swimming behaviour in the Enciso Group was made in the track EVP12, located in the Icnitas-4 tracksite (La Rioja) of the complex Villar-Poyales (Pienkowski and Gierlinski, 1987; Casanovas et al., 1993; Pérez-Lorente, 2015). It is composed by five footprints (EVP12.1-EVP12.5) that show a curious shape evolution along the track: the first footprint (EVP12.1) presents a common morphology made by terrestrial locomotion, with the pes morphology reflected in the impression showing three digits of regular proportions convergent in the proximal area. The second one (EVP12.2) has elongated digits, interpreted as the product of the foot slipping in the mud (Pérez-Lorente, 2015). The third footprint (EVP12.3) shows three elongated roughly parallel toe impressions not convergent in the proximal area. These parallel impressions are a common feature in swimming tracks, being one of the definitory features in the ichnogenus *Characichnos* (Whyte and Romano, 2001). The last two footprints (EVP12.4 and EVP12.5) have tip toe and claw impressions with a characteristic mud elevation in the back, probably due to the traction generated during the interaction pes-substrate, again a common feature in some non-avian dinosaur swimming tracks. The trackway shows an evolution of the conditions from the first footprint presenting the highest sole pressure in the sediment (Pérez-Lorente, 2015) and progressively less pressure between pes and sediment due to buoyancy force, with the second and third footprints showing sliding toe and claw impressions and the last two presenting just drag marks of claws and sediment accumulation backwards. Several studies have interpreted this tracksite as evidence of a dinosaur transitioning from walking to swimming in a submerged slope (Pienkowski and Gierlinski, 1987; Casanovas et al., 1993; Pérez-Lorente, 2015).

EVP12 was the first tracksite of the Cameros Basin attributable to non-avian dinosaurs swimming behaviour, but years later another example of non-avian dinosaur swimming trackway was published in this exceptional area. The track (4LVC17) is located in La Virgen del Campo-4 tracksite (La Rioja) and is one of the best examples of non-avian dinosaur swimming tracks worldwide. The footprints show a theropod swimming into a leftward water current (Ezquerra et al., 2007; Ezquerra et al., 2010; Pérez-Lorente, 2015; Milner and Lockley, 2016). This trackway presents a set of S-shaped scratch marks; showing claw impressions of two or three fingers (Ezquerra et al., 2007) (Fig. 6). This track is distinctive due to the orientation of the left and right sets of footprints. The left ones are parallel to the trackway axis, while the right ones have an approximate orientation of an inward rotated angle of 40° to the trackway axis. The peculiar distribution of right and left footprints is added to information extracted from ripple crests direction, being calculated a slow water current from the leftside at ~30° of trackway axis (Ezquerra et al., 2007). Combined information led the

authors to the conclusion that the animal was swimming into a leftward water current with the body orientated approximately at 20° to the left of the trackway axis (Ezquerra et al., 2007). Otherwise, a rotation of right pes at 40° of the sagittal plane of the animal would have been anatomically difficult to justify (Ezquerra et al., 2007). The footprints present features similar to those of *Characichnos*, with parallel toe and claw impressions not convergent, and sediment accumulation around the scratch marks. The footprints are very similar in their characteristics along the track, showing a similar water level along the tracking surface, differentiating this track from the one of Icnitas-4, where the animal entered into a submerged slope, progressively loosing contact with the sediment while it began to swim.

The Laguna tracksite adds one more example of dinosaur swimming tracks to the paleoichnological record of the Cameros Basin. The variety of morphologies present in the three tracksites (Icnitas-4, La Virgen del Campo-4 and Laguna) allow to observe the heterogeneity of this kind of tracks, probably caused by the different factors and physical complexities involved in the generation of swimming tracks: water level, buoyancy force, irregularities in the subaqueous substrate, directional water streams, displacements of the centre of buoyancy, gravity and reaction force.

6.2. Track formation dynamics

The morphotypes described in the Footprint description section have been classified into five categories according to the trackmaker posture, grade of interaction pes-sediment and track depth profile following the proposal of Romilio et al. (2013), but with some modifications. The idea of this section is to link the Laguna morphotypes (footprints with morphological common features) and other morphologies present in the Cameros Basin swimming tracks with their biodynamic origin, in order to explain the different morphologies present in footprints with a similar biodynamical generation (swimming). The categories proposed by Romilio et al. (2013) have been applied in this classification, but including a new category and adding a variant to Category 2 based in the track morphologies seen in the Laguna tracksite.

- Category 1: Into this group are included footprints known typically as "scratch marks", where the biomechanical interaction between pes and sediment is minimal or almost minimal. This minimal interaction is related to the low influence that it has in the displacement of the animal, being the displacement highly performed by paddling or classical swimming. Into this group would be classified the majority of 4LVC17 track footprints, such as 4LVC17-7 (Fig. 6A), which present morphologies typical of the ichnogenus *Characichnos* as being two to three parallel straight or sinusoidal marks with a light sediment elevation in their contours but without posterior relevant sediment elevation. Romilio et al. (2013) already related 4LVC17 to this Category 1 for those footprints of the track that show longitudinal scratches with a more or less symmetrical depth profile, with slopes in the proximal and distal parts. The posterior elevation showed by some swimming footprints (like some examples of the Laguna tracksite as Morphotype 1 and 4LVC17-4, Fig. 6B) reveals a more functional interaction between pes and sediment, having a higher influence in the animal displacement. This "backward" sediment elevation would discard a footprint from Category 1 in this paper proposal.
- Category 2: There are no evidences of footprints within this category in the Laguna tracksite nor in other deposits of the Cameros Basin, being described by Romilio et al. (2013) as "three circle-shaped impressions in dorsal view, with steep distal and proximal margins in the track depth profile width." These tracks

P. Navarro-Lorbés, I. Díaz-Martínez, J.M. Valle-Melón et al.

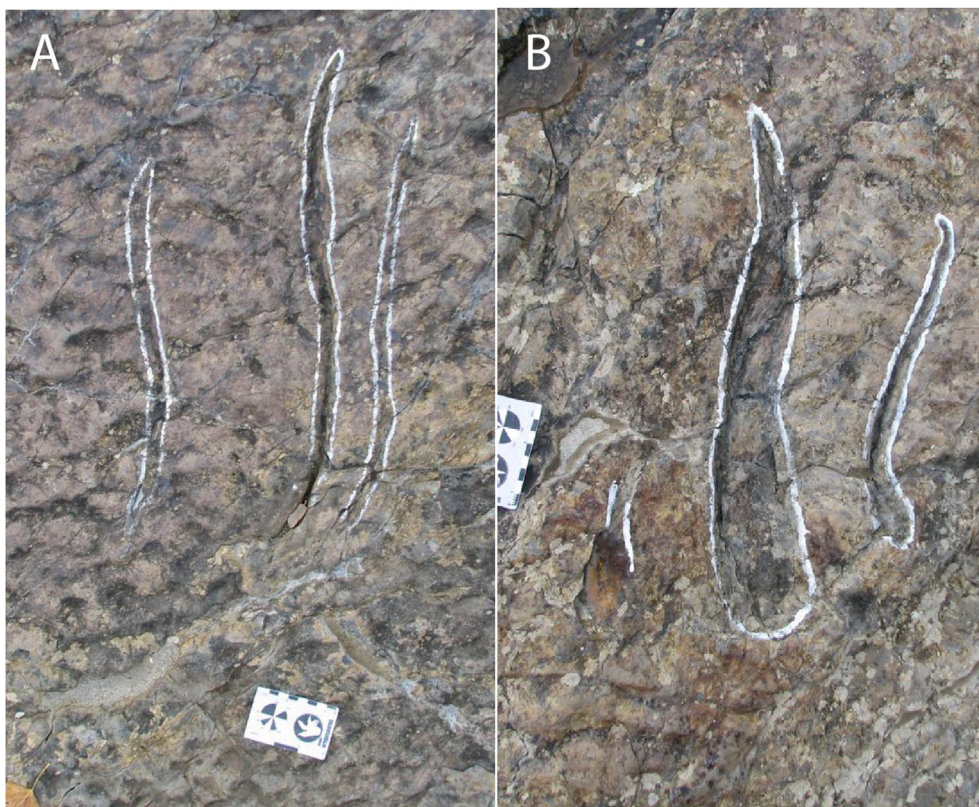*Cretaceous Research 147 (2023) 105516*

Fig. 6. Photographs of 4LVC17 swimming footprints: A) 4LVC17-7 footprint. B) 4LVC17-4 footprint.

were made by a buoyant trackmaker which pes entered and exited the sediment in an almost unguligrade position, with vertical movement and very little longitudinal component. As noted by Romilio et al. (2013), some footprints within this category can show proximal or distal drag marks made by the digits and/or unguals.

- Category 3 (Morphotypes 1 (Fig. 5A) and 2 (Fig. 5B) of the Laguna tracksite and 4LVC17-4 (Fig. 6B)) (Fig. 7B):Usually present elongated digital impressions, some of them with rounded elevations in the proximal part of the track. Their depth profile shows a steeped proximal part and a slope to the distal part or a similar depth profile but with a more or less horizontal base located in the proximal area. The trackmaker placed the pes more vertically at the proximal part during the touchdown phase, probably due to the sediment resistance progressively raised by sediment compaction during pes movement (Romilio et al., 2013) and partial leg extension or due to the presence of a slight slope that made the pes-substrate interaction shallower in the distal part and deeper in the proximal one. This category implies a deep interaction of pes-substrate scratching the substrate with the digits. The Morphotype 1 of the Laguna tracksite presents two to three elongated digit impressions, mesaxonic in the distal part and truncated in the proximal one. The sediment elevation (depression in the natural casts) is present immediately behind the footprint (Fig. 5A) with steeped proximal region and a slope in the distal part. Morphotype 2 (Fig. 5B) footprints present elongated digit impressions and sediment accumulation in the proximal part, the generation of footprints into this morphotype would have implied more contact of the pes with the substrate, impressing the "heel".
- Category 4 (Morphotypes 3 (Fig. 5C), 4 (Fig. 5D) and 6 (Fig. 5F) of the Laguna tracksite) Fig. 7A: The tracks are generally composed

of one to three subcircular to elliptical impressions in apical view. The digit III impression is the most developed and the deeper one (highest in the natural cast), with the track depth profile showing steeped proximal and distal margins. These tracks have been formed when the autopod entered in contact with the substrate (touch-down phase *sensu* Thulborn and Wade, 1989) in a subunguligrade position and craniocaudally movement. After that, the pes exited (weight-bearing and kick-off phases *sensu* Thulborn and Wade, 1989) the sediment in an almost vertical position with little longitudinal component. The range of movement described by the pes during footprint generation determines the elongation of digit impressions, from shapes just oval or subcircular to more elliptical ones. However, there are differences into this category that can lead to the definition of two subcategories: while in the Laguna Morphotype 3 the trackmaker lightly scratched the substrate with the distal part of the digits in the kick-off phase when propelling forward in a more digitigrade position (new Category 4A, Fig. 5C, Fig. 7A), in Morphotypes 4 and 6 the trackmaker made a more vertical pressure with a more unguligrade contact during the weight-bearing phase that could allow short and wide digital impressions (new Category 4B, Figs. 5D, 5F).
- Category 5 (Morphotype 5 (Fig. 5E)) (Fig. 7C): The footprints indicate a different position of the pes during the touch-down phase and kick-off phase, with a more plantar-digitigrade impression in the moment of contact (leaving the tridactyl pes contour impression) and a more unguligrade position of the pes when it left the substrate, leaving the impression of the exiting point of digit III in a proximal position. The exiting point is also the deepest part of the footprint, with lateral digits deepening in the substrate, leaving drag marks from the initial position to the final. This category is different from those proposed by Romilio
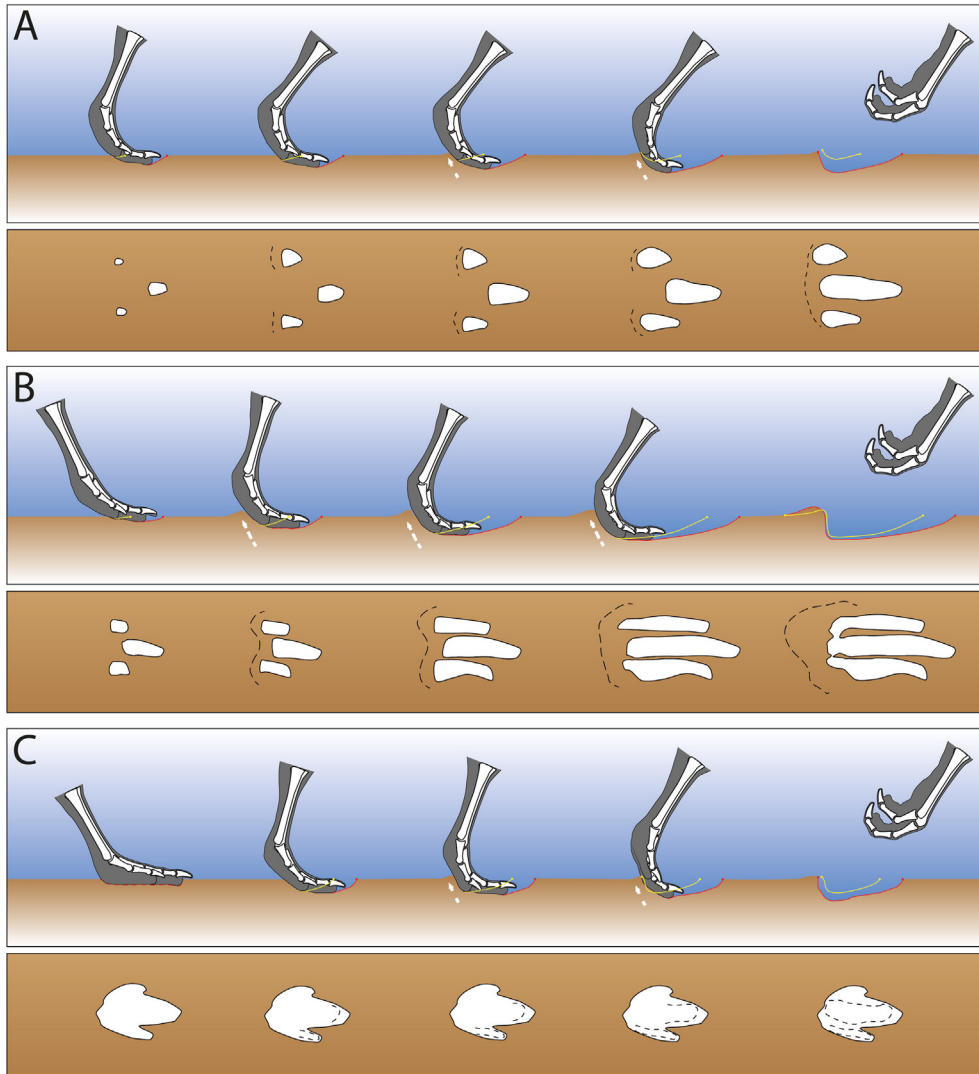
P. Navarro-Lorbés, I. Díaz-Martínez, J.M. Valle-Melón et al.

Cretaceous Research 147 (2023) 105516

Fig. 7. Hypotheses for the different footprint group formation, with successive steps of foot movement and the generation of the depth profiles and footprint shape in apical view. A: Category 3 formation hypothesis. B: Category 4A formation hypothesis. C: Category 5 formation hypothesis.
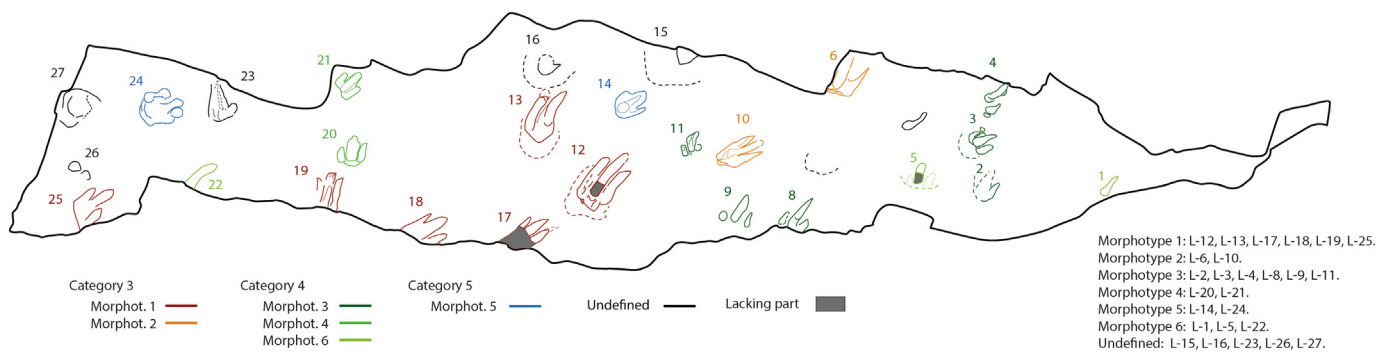

Morphotype 1: L-12, L-13, L-17, L-18, L-19, L-25.
Morphotype 2: L-6, L-10.
Morphotype 3: L-2, L-3, L-4, L-8, L-9, L-11.
Morphotype 4: L-20, L-21.
Morphotype 5: L-14, L-24.
Morphotype 6: L-1, L-5, L-22.
Undefined: L-15, L-16, L-23, L-26, L-27.

Fig. 8. Location of each morphotype in the tracksite surface.

et al. (2013), so it is considered here as a new category. Nevertheless, the Category 3b of Romilio et al. (2013) shows some common features, such as the trydactil-like contour, the distal position of the digits in the touch-down phase, and the more proximal position during the kick-off phase. The main difference is that Category 3b of Romilio et al. (2013) is produced with an

unguligrade entrance of the pes in the sediment and the distal lengthening of the footprint when the digits exited (something similar to the case described by Gatesy et al., 1999), and in the new Category 5 the exiting point is located in the proximal area of the footprint, something possible if buoyancy is present, allowing the existence of a vertical component in the animal movement.

Indeed, the classification of swim tracks into categories dependent on the pes-substrate interaction is a good guiding principle to avoid problematics with ichnotaxonomical definitions. During more than a decade, the only monospecific ichnogenus related to non-avian dinosaur swimming tracks was *Characichnos trydactilus* (Whyte and Romano, 2001). The original ichnogenus definition and subsequent works have noted that this ichnotaxon can be related not only to theropods but to various groups of vertebrates swimming ((Milner and Lockley, 2016) and references therein), produced by any trackmaker that used three digits to impress parallel ridges or traces (Lockley and Foster, 2006). In this case, the Categories 3 and 4 share almost all the features proposed in the *Characichnos* diagnosis, so, those tracks could be classified as *C. trydactilus*. On the other hand, the tracks of the Category 1 present some of the features characteristic of the ichnogenus *Characichnos*, but for example the trackway 4LVC17 presents two rows of tracks, but not parallel to each other as proposes the diagnosis of the ichnogenus. The features of these tracks, which are well preserved, could be used either to amend the diagnosis of *Characichnos*, or to propose a new ichnospecies within this ichnogenus. Finally, the Categories 2 and 5 are outside of the diagnosis of *Characichnos*, therefore it could be considered if it is also a variability and the diagnosis would have to be amended, or if it is truly a new ichnogenus. Considering that an ichnotaxonomic revision of swimming tracks is necessary, together with the difficulty of cases where tracks belonging to the same pathway can be labelled as different ichnotaxa (Lockley and Foster, 2006), we have considered classifying traces from the Laguna tracksite as *Characichnos*-like pending further findings and works.

The length of the tracks is very variable (from 8.5 to 29.2 cm) and mainly depends on the trackmaker posture and the movement that it made when touching the substrate. The tracks of Category 3 are longer than those belonging to Category 4 and 5. In the former, the trackmaker touched the substrate subvertically and scratched it with the digits horizontally during pes movement. Nevertheless, the trackmakers of Category 2 and 4 touched the substrate in a subunguligrade posture producing high vertical pressure and little horizontal movement, and in Category 5 the pes has a more plantar-digitigrade impression when touching the substrate and a vertical component when lifting it. In this case, the width of the tracks is a more conservative measure. All the width data taken from footprints with 3 digit impressions are between 9.2 and 18.2. The highest width values range from 14.1 to 18.2 cm, while the rest are in the range of 9.2 to 12.3 cm. If the assumption of the posture and movement of the pes affects in less proportion the wideness of the track, and the width of the track would be correlated with the width of the pes, it is possible to deduce that the footprints at this tracksite were left by trackmakers of similar pes configuration, but with two different sizes. It is difficult to confirm if this differences in size are related to different taxa or ontogenetical-sexual differences of the same taxon.

The morphology and formation dynamics of the studied tracks are particular and different from those expected by an animal walking in a subaerial substrate. In general, they have clear digit impressions (whit different configurations) and lack "heel" impressions. These features have been related in the literature to tracks made in aquatic environments (e.g., Whyte and Romano, 2001; Romilio et al., 2013; Thomson and Droser, 2015; Milner and Lockley, 2016), so we propose that the Laguna tracks were made underwater by swimming animals.

6.3. Trackmakers and behaviour inferred from the studied tracks

Swim tracks have been related to several groups of Mesozoic vertebrates. Pseudosuchians leave tracks similar to those studied here, but normally they are tetradactyls–pentadactyls and present a quadrupedal gait arrangement (e.g., Vila et al., 2015; Navarro and Moratalla, 2018; Castanera et al., 2022). Swimming tracks of turtles have short and parallel claw impressions, and are smaller and also tetradactyl–pentadactyl (e.g., Avanzini et al., 2005; Kim and Lockley, 2016). Pterosaurs only impressed the pes tracks when swimming and they are tetradactyls (Lockley and Wright, 2003; Lockley and Schumacher, 2014). Nevertheless, some ichnogenera related to swimming Crocodylomorpha can show morphologies similar to those generated by non-avian dinosaurs, in part because of the extramorphological dependence of this kind of tracks. Ichnogenera like *Hatcherichnus* (Foster and Lockley, 1997) related to swimming or bottom-walking crocodylomorphs, can show tridactyl pes impressions in some individual tracks, when just three digits are clearly marked. But the digit impressions tend to be short in length due to the presence of an interdigital web connecting digits II–IV (Lockley et al., 1992; Avanzini et al., 2010), a feature that is not present in the natural casts of the Laguna tracksite. The manus impressions of *Hatcherichnus* are trydactil, with impression of digits I–III, being digit I and II impressions nearly parallel and slightly separated from digit III, being the latter the longest one (Foster and Lockley, 1997; Avanzini et al., 2010). There are no examples in Laguna tracksite of non-mesaxonical trydactil footprints that could correspond to *Hatcherichnus* manus impressions, and there are no evidences of tetradactyl pes impressions. Other swimming crocodylomorph ichnogenera like *Indosuchipes* (Rajkumar et al., 2015), *Antisuchipes* (Mustoe, 2019) or *Kangyuampus* Lockley et al., 2010 and *Laiyangpus* (Lockley et al., 2010) show tetradactyl pes impressions with no mesaxony and use to be associated with manus impressions. Among crocodylomorph swimming tracks, the most similar morphologies to some of the Laguna tracks can be found in the ichnogenus *Albertasuchipes* (McCrea et al., 2004), with trydactil pes impressions that are very similar to Morphotype 1-Category 3 Laguna tracks. This similarity can be caused by the nature of footprint generation: both made by an animal partially buoyed up in aquatic conditions (McCrea et al., 2004). However, *Albertasuchipes* pes footprints are associated with manus impressions, usually located immediately anterior to pes (McCrea et al., 2004). . The size and configuration of the Laguna tracks with tridactyl, mesaxonic pes impressions and the absence of manus and tetradactyl pes footprints makes non-avian tridactyl dinosaurs the most plausible trackmakers for the Laguna tracksite. While large ornithopod swimming tracks have three separated, broad and rounded distal digit impressions, and lack plantar impressions (Fujita et al., 2012; Moklestad et al., 2018), small ornithopod ones are similar to those made by theropods: one to three elongate, parallel sets of distal phalangeal digit or/and claw impressions which may be straight, gently curved or slightly sinuous (*sensu* Whyte and Romano, 2001; Milner and Lockley, 2016). Sharp claw impressions have been generally related to theropod swimming tracks (Milner et al., 2006; Ezquerra et al., 2007; Xing et al., 2013) and were classified within the ichnogenera *Characichnos* and *Paravipus* (Whyte and Romano, 2001; Mudroch et al., 2011). But indeed, sharp claw traces were also found in some small ornithopod swimming trackways, such as in *Wintonopus* (*sensu* Romilio et al., 2013; but see also Thulborn, 2013 for other interpretations) and tracks similar to *Dinehichnus* (Lockley and Foster, 2006). In this sense, it is not possible to assign the Laguna tracks to a particular group of dinosaurs, so we relate them to undetermined bipedal dinosaurs.

Swim tracks are produced when the animal is partially or completely submerged in water with the body buoying and the pes (and sometimes other parts of the body) entered in contact with the subaqueous substrate (Milner and Lockley, 2016; Farlow et al., 2018; Lee et al., 2019). McAllister (1989) and McAllister and Kirby

(1998) proposed a series of criteria for the identification of footprints that had potentially been produced in an underwater environment: 1) reflecture of digits; 2) Z traces; 3) kick-off scours; 4) impressions of only digital tips; 5) absence of a regular locomotion pattern, etc. (see Navarro and Moratalla, 2018 for further reading). In a broad sense, swim tracks can be divided into two groups respecting the position of the trackmaker in the water sheet: buoyancy tracks and punting tracks. Buoyancy tracks are produced by animals floating on the water surface that touch the subaqueous substrate with their autopod tips (e.g., Romilio et al., 2013; Milner and Lockley, 2016). Although they are also identified in sauropods and ankylosaurus (e.g., Farlow et al., 2018; Riguetti et al., 2021), they are the typical swim tracks related to bipedal dinosaurs characterized by subparallel long slender grooves and were usually classified as *Caracichnos* (Whyte and Romano, 2001; Milner et al., 2006; Ezquerra et al., 2007). Moreover, these tracks are useful to know the bathymetry of that area because the acetabular height of the trackmaker would be approximately the thickness of the water (Melchor, 2015). On the other hand, punting tracks are those impressed in subaquatic locomotion (bottom walking) in which the animal pushes off the bed of a water body with its limbs to maintain forward motion (Martinez et al., 1998; Bennett et al., 2014). Punting has been applied across several extinct and extant tetrapods as crocodilians (Farlow et al., 2018; Lee et al., 2019; Mustoe, 2019), turtles (Gaillard et al., 2003; Avanzini et al., 2005), undetermined Permian vertebrates (Brand and Tang, 1991), placodonts (Xing et al., 2020) and hippopotami (Bennett et al., 2014), but not yet in non-avian dinosaurs.

In tracksites with swimming tracks of different sizes and preservation (e.g., Whyte and Romano, 2001; Romilio et al., 2013; Xing et al., 2013; Farlow et al., 2018) changes in the water level have been proposed to explain the presence of these diverse tracks at the same tracking surface. As commented above, considering the wide of the tracks of the Laguna, their trackmakers present, at least, two different sizes. This could be explained in two different ways: 1) The footprints were made in two different moments, with variation of the water level. 2) The trackmakers were able to move vertically in the water column. L-14, which is quite a complete pes track, allows calculating the acetabular height with footprint length (16.5 cm). Applying Alexander (1976) approach (acetabular height = 4*Footprint length) the trackmaker, and hence the water level, was at least 66 cm.

The tracks of Category 3 (morphotypes 1 and 2) are located in the central area of the tracksite (Fig. 8) and due to their morphology and formation dynamics can be related to buoyancy tracks, but the reduced extension of the tracksite does not make it possible to ensure if it is a consequence of different water depth areas or a coincidental conservation-behaviour bias. They are classified as Category 3 of Romilio et al. (2013) in which the scratches of the digits in the substrate were formed while the animal body moved partially or completely buoying with a mixed sediment and water impulsion and not just a mere paddling. Within the Laguna tracksite, tracks of Category 4 (morphotypes 3, 4 and 6) are on the sides of Category 3. The morphology of these tracks is very different from the typical swim tracks. They are similar to those studied by Romilio et al. (2013) (categories 2 and 4) interpreted as small ornithopods buoying. Here, we propose two different hypotheses for the formation of these tracks: 1) variations in the water column or changes in the position of the animal from a more buoyant position or submerged one could provoke the impression of just the claws or the tips of the digits; and 2) the trackmaker, which would be bottom-walked, touched the digit tips on the ground vertically or sub-vertically to balance an unstable pattern of gait or to maintain the forward momentum of the glide alternating phases of thrust and glide through the water. If we consider no differences in the water level and the size of the trackmakers, hypothesis 1 would be the most correct option and Category 3 and 4 tracks are the consequence of variation in the buoyancy swimming. However, considering that the general shape and formation dynamics of Category 4 tracks are similar to the called prod-marks shown by Bennett et al. (2014) for punting swimming hippos and very different from those of *Caricichnos*-like tracks, we propose that the trackmakers have a different swimming behaviour. In addition to prod-marks, Bennett et al. (2014) observed other tracks which had the impression of the plantar-digital surface more developed in bottom-walk hippopotami. The tracks of Category 5 (morphotype 5), which are located on the tracksite close to Category 3 ones, present the same features cited by Bennett et al. (2014). Therefore, in our opinion, it is necessary to explore through new ichnological and other palaeontological evidence the possibility that at least some dinosaurs could move underwater and not just float as previously thought.

6.4. Possible dinosaur trackmakers and swimming strategies

Almost since the beginning of palaeontology, dinosaurs were related to aquatic ecosystems (Owen, 1841). Even many years later, this possibility continued to be considered. For instance, sauropods had been restricted to inhabit the water (aquatic or semiaquatic) due to their immense size and their particular anatomical features (see Romer, 1966; Coombs, 1975). Some hadrosaurs were considered amphibious due to their anatomy and feeding in swampy pools or at their margins (see Osborn, 1912; Romer, 1966; Morris, 1981). Most of these hypotheses have been ruled out over the years (see Alexander, 1985; Henderson, 2004) but other new proposals have been pointed out. Interestingly, Tereschenko (2008) summarized some anatomical features that would prove the adaptation of some neoceratopsian to aquatic life (see also Ford and Martin, 2010). The possible relationships with the aquatic environments of theropods (members of dromaeosaurids, ornithomimosaurs and spinosaurids) are an interesting subject of discussion (Lee et al., 2014; Ibrahim et al., 2014, 2020; Cau et al., 2017; Fabbri et al., 2022). Particularly, the habitat of spinosaurids is paying a lot of scientific attention in the last few years. Anatomical (Ibrahim et al., 2014, 2020; Vullo et al., 2016; Arden et al., 2019), osteological (Aureliano et al., 2018; (Fabbri et al., 2022)) and isotopic (Amiot et al., 2010; Goedert et al., 2016; Trapman, 2018; Henderson, 2018; Hassler et al., 2018; Gimsa and Gimsa, 2021) data seem to show that at least part of the spinosaurids (i.e. *Spinosaurus* and *Baryonyx*) have had adaptations to aquatic life (but see also Henderson, 2018; Hone and Holtz, 2021; Sereno et al., 2022 for other interpretations).

The dinosaur ichnological record hoards evidence of swimming from at least the Lower Jurassic (Milner et al., 2006). Manus-only and manus-dominated trackways had been originally associated with sauropods swimming with the forelimb touching the bottom and the hindlimb floating (Bird, 1944; Ishigaki, 1989; Farlow et al., 2019; Demathieu et al., 2022). Nevertheless, some of these trackways have been questioned and explained by the under-tracking hypothesis (e.g., Vila et al., 2005; Ishigaki and Matsumoto, 2009; Falkingham et al., 2011, 2012). Other manus-only trackways have been also proposed for swimming ankylosaurids (Riguetti et al., 2021). Swim trackways have been also cited for both large (Fujita et al., 2012; Moklestad et al., 2018) and small ornithopods (Lockley and Foster, 2006; Romilio et al., 2013). Regarding theropods, there are many examples, summarized in Milner and Lockley (2016), which show *Caracichnos*-like swimming tracks. This record is abundant since the Lower−Middle Jurassic (e.g., Whyte and Romano, 2001; Milner et al., 2006), long before the appearance of the mentioned above theropod clades with aquatic adaptations. Nevertheless, all these examples of swimming tracks are typical

P. Navarro-Lorbés, I. Díaz-Martínez, J.M. Valle-Melón et al.

Cretaceous Research 147 (2023) 105516

ones left by animals through buoying on a water surface and do not mean that they have adaptations to aquatic life, but rather that they have the ability to move at least circumstantially through the water. On the other hand, bottom-walking is known for extant aquatic and semi-aquatic animals (Lee et al., 2019) such as crabs (Martinez et al., 1998), chondrichthyans (Koester and Spirito, 2003; Maia et al., 2012), turtles (Zug, 1971; Avanzini et al., 2005), crocodiles (Farlow et al., 2018), hippopotami (Bennett et al., 2014). If Category 4 and 5 tracks were made by a trackmaker punting, it would imply the capability of some non-avian dinosaurs to perform a bottom-walk behaviour, a behaviour already known to be performed by other groups.

The diversity of medium-sized bipedal dinosaurs in the Iberian Peninsula during the Early Cretaceous is mainly composed of three theropod groups, and two groups of small ornithopods: 1) Spinosaurids have raised during the last decades as a very successful group in Europe and especially in the remains found all along the Iberian Peninsula. Their skeletal remains had led to the identification of *Baryonyx* (Fuentes-Vidarte et al., 2001; Mateus et al., 2011) as well as the description of two new spinosaurid species: *Vallibonavenatrix cani* (Malafaia et al., 2020) and *Iberospinus natarioi* (Mateus and Estraviz-López, 2022). The maxilla fragment previously assigned as belonging to *Baryonyx walkeri* by Viera and Torres, 1995, is now classified as Baryonychinae indet. (Isasmendi et al., 2022) and could indicate the presence of a new baryonychine taxon in the Early Cretaceous of Iberia. In addition, *Camarillasaurus* was classified as a basal ceratosaur (Sánchez-Hernández and Benton, 2014) but in the last years, new studies have classified these remains as belonging to a spinosaurid and no longer a ceratosaur (Rauhut et al., 2019; Barker et al., 2021; Samathi et al., 2021). Besides the mentioned skeletal remains, isolated spinosaurid teeth and bones are very common fossil remains in the Lower Cretaceous of the Iberian Peninsula (e.g., Pereda-Suberbiola et al., 2012; Alonso and Canudo, 2016; Gasca et al., 2018; Mateus and Estraviz-López, 2022; Isasmendi et al., 2022). 2) Carcharodontosaurids are also present in the Lower Cretaceous of the Iberian Peninsula with the definition of *Concavenator corcovatus* (Ortega et al., 2010; Cuesta et al., 2018a,b, 2019) and the recovery of isolated teeth (Alonso et al., 2018) and skeletal remains (Gasca et al., 2014). 3) Ceratosaurs have been reported from the Late Jurassic of Portugal by findings of their isolated teeth as well as dental remains assigned to *cf. Abelisauridae* in the Cenomanian of Algora. 4) Small to medium sized ornithopods from the Iberian Peninsula are referred to basal Euornithopods (previously classified into the paraphyletical family "Hypsilophodontidae") and Dryosaurids (Pereda-Suberbiola et al., 2012 and references therein).

If part of the tracks studied herein were made by an aquatic or semiaquatic animal, and taking into account the above-mentioned state of knowledge about dinosaur adaptations of aquatic life, maybe spinosaurids could be a good candidate as trackmaker of the Laguna footprints.

7. Conclusions

The discovery of the new the Laguna tracksite in the Urbión Group (Lower Cretaceous) is very significant given the scarcity of non-avian dinosaur swimming tracks in the fossil record. The 27 studied footprints were classified into 6 morphotypes due to their morphology. Moreover, these morphotypes were categorized into 5 categories based on the interaction pes-sediment and track depth profile: Category 1, footprints with two to three elongated and subparallel scratch marks, where the biomechanical interaction between pes and sediment is minimal or almost minimal, with no evidence of traction in the proximal part in form of elevated sediment and depth profiles with distal and proximal slopes, the

deepest part located between them; Category 2, penetrative digit impressions with subcircular contour in apical view, presenting a steeped proximal and distal depth profile and in some cases showing proximal and/or distal drag marks; Category 3, elongated subparallel fingerprints, some of them with rounded elevations in the proximal part of the footprint, with a depth profile that shows generally a steep proximal part and a slope towards the distal part; Category 4, one to three subcircular to slight elongate impressions in apical view, with the digit III impression the most developed and the deeper one (highest in natural casts), with the track depth profile showing steeped proximal and distal margins; and the new Category 5, more or less defined tridactyl footprint contour, but present grooves, deeper than in a common tridactyl footprint. While Category 3 tracks were formed while the animal body moved partially or completely buoying with a mixed sediment and water impulsion and not just a mere paddling, Categories 2, 4 and 5 could be impressed during a bottom-walk behaviour, when the trackmaker touched the digit tips on the ground vertically or subvertically to balance an unstable pattern of gait or to maintain the forward momentum.

The studied tracksite of Laguna, produced by an undetermined bipedal non-avian dinosaur, provides new information about the swimming capabilities of this group of vertebrates, and how the high variability of this kind of footprints is more related to motion and behaviour rather to different anatomical features present in the trackmaker. This fact also emphasizes the problem of how to classify this kind of tracks, being an interesting option for the characterization of tracks and footprints into categories depending on the pes-substrate interaction in order to avoid ichnotaxonomical problems in multishaped swimming track assemblies where more than one ichnogenera could be recognized.

Open data sources

The 3D model of the exposed stratum —and an additional cast located in a fallen rock— containing the tracks are available, together with the descriptive report of the photogrammetric documentation (in Spanish) at the open repository of the University of the Basque Country (ADDI) https://addi.ehu.es/handle/10810/53971 (Rodríguez-Miranda and Valle-Melón, 2021).

Data availability

Data will be made available on request.

References

Alexander, R.M., 1976. Estimates of speeds of dinosaurs. Nature 261 (5556), 129−130.

Alexander, R.M., 1985. The ideal and the feasible: physical constraints on evolution. Biological Journal of the Linnean Society 26 (4), 345−358.

Alonso, A., Canudo, J.I., 2016. On the spinosaurid theropod teeth from the Early Barremian (Early Cretaceous) Blesa Formation (Spain). Historical Biology 28, 823−834.

Alonso, A., Gasca, J.M., Navarro-Lorbés, P., Rubio, C., Canudo, J.I., 2018. A new contribution to our knowledge of the large-bodied theropods from the Barremian of the Iberian Peninsula: the "Barranco del Hocino" site (Spain). Journal of Iberian Geology 44, 7−23.

Amiot, R., Buffetaut, E., Lécuyer, C., Wang, X., Boudad, L., Ding, Z., Fourel, F., Hutt, S., Martineau, F., Medeiros, M.A., Mo, J., Simon, L., Suteethorn, V., Sweetman, S., Tong, H., Zhang, F., Zhou, Z., 2010. Oxygen isotope evidence for semi-aquatic habits among spinosaurid theropods. Geology 38, 139−142.

Arden, T.M., Klein, C.G., Zouhri, S., Longrich, N.R., 2019. Aquatic adaptation in the skull of carnivorous dinosaurs (Theropoda: Spinosauridae) and the evolution of aquatic habits in spinosaurids. Cretaceous Research 93, 275−284.

Aureliano, T., Ghilardi, A.M., Buck, P.V., Fabbri, M., Samathi, A., Delcourt, R., Fernandes, M.A., Sander, M., 2018. Semi-aquatic adaptations in a spinosaur from the Lower Cretaceous of Brazil. Cretaceous Research 90, 283−295.

Avanzini, M., García-Ramos, J.C., Lires, J., Menegon, M., Pinuela, L., Fernández, L.A., 2005. Turtle tracks from the late Jurassic of Asturias, Spain. Acta Palaeontologica Polonica 50 (4), 743−755.

Avanzini, M., García-Ramos, J.C., Lires, J., Piñuela, L., Lockley, M.G., 2010. Preservational morphotypes of *Crocodylopodus* from the Late Jurassic of Asturias (Spain). New Mexico Museum of Natural History and Science Bulletin 51, 239−244.

Barker, C.T., Hone, D.W.E., Naish, D., Cau, A., Lockwood, J.A.F., Foster, B., Clarkin, C.E., Schneider, P., Gostling, N.J., 2021. New spinosaurids from the Wessex Formation (Early Cretaceous, UK) and the European origins of Spinosauridae. Scientific Reports 11 (1), 19340.

Beevor, T., Quigley, A., Smith, R.E., Smyth, R.S., Ibrahim, N., Zouhri, S., Martill, D.M., 2021. Taphonomic evidence supports an aquatic lifestyle for Spinosaurus. Cretaceous Research 117, 104627.

Bennett, M.R., Morse, S.A., Falkingham, P.L., 2014. Tracks made by swimming hippopotami: an example from Koobi Fora (Turkana Basin, Kenya). Palaeogeography, Palaeoclimatology, Palaeoecology 409, 9−23.

Benton, M.J., 2004. Origin and relationships of Dinosauria. In: Weishampel, D.B., Dodson, P., Osmólska, H. (Eds.), The Dinosauria, 2nd edition. University of California Press, Berkeley, CA, pp. 7−24.

Benton, M.J., 2014. Vertebrate Palaeontology. John Wiley and Sons.

Bird, R.T., 1944. Did *Brontosaurus* ever walked on land? Natural History 53, 60−69.

Brand, L.R., Tang, T., 1991. Fossil vertebrate footprints in the Coconino Sandstone (Permian) of northern Arizona: evidence for underwater origin. Geology 19 (12), 1201−1204.

Casanovas, M.L., Ezquerra, R., Fernández, A., Pérez-Lorente, F., Santafé, J.V., Torcida, F., 1993. Icnitas digitígradas y plantígradas de dinosaurios en el afloramiento de El Villar-Poyales (La Rioja-España). Zubia - Monografico 5, 135−163.

Castanera, D., Pascual-Arribas, C., Canudo, J.I., Puértolas-Pascual, E., 2022. A new look at *Crocodylopodus meijidei*: implications for crocodylomorph locomotion. Journal of Vertebrate Paleontology 41 (5), e2020803. https://doi.org/10.1080/02724634.2021.2020803.

Cau, A., Beyrand, V., Voeten, D.F., Fernandez, V., Tafforeau, P., Stein, K., Barsbold, R., Tsogtbaatar, K., Currie, P.J., Godefroit, P., 2017. Synchrotron scanning reveals amphibious ecomorphology in a new clade of bird-like dinosaurs. Nature 552 (7685), 395−399.

Cayla, N., Hobléa, F., Reynard, E., 2014. New digital technologies applied to the management of geoheritage. Geoheritage 6 (2), 89−90.

Charig, A.J., Milner, A.C., 1997. *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. Bulletin of Natural History Museum. Geology Series 53 (1), 11−70.

Coombs Jr., W.P., 1975. Sauropod habits and habitats. Palaeogrography, Palaeoclimatology, Palaeoecology 17, 1−33.

Cuesta, E., Ortega, F., Sanz, J.L., 2018a. Appendicular osteology of *Concavenator corcovatus* (Theropoda: Carcharodontosauridae) from the Lower Cretaceous of Spain. Journal of Vertebrate Paleontology 38 (4), 1−24.

Cuesta, E., Ortega, F., Sanz, J.L., 2019. Axial osteology of Concavenator corcovatus (Theropoda; Carcharodontosauria) from the Lower Cretaceous of Spain. Cretaceous Research 95, 106−120.

Cuesta, E., Vidal, D., Ortega, F., Sanz, J.L., 2018b. The cranial osteology of *Concavenator corcovatus* (Theropoda; Carcharodontosauria) from the Lower Cretaceous of Spain. Cretaceous Research 91, 176−194.

Demathieu, P., Izart, A., Charrière, A., Vianey-Liaud, M., 2022. Small sauropod tracks in the Hettangian of Southern France—a case of ichnite fossilization in an intertidal zone. Paleovertebrata 45 (2), 1−14.

Díaz-Martínez, I., García-Ortiz, E., Pérez-Lorente, F., 2015. A new dinosaur tracksite with small footprints in the Urbión Group (Cameros Basin, Lower Cretaceous, La Rioja, Spain). Journal of Iberian Geology 41 (1), 167−175.

Díaz-Martínez, I., Citton, P., de Valais, S., García-Ortiz, E., 2018. La fotogrametría se convierte en una poderosa herramienta para la conservación y difusión del patrimonio paleontológico. revista PH, Instituto Andaluz del Patrimonio Histórico 94, 20−22.

Díaz-Martínez, I., Suarez-Hernando, O., Larrasoaña, J.C., Martínez-García, B.M., Beceta, J.I., Murelaga, X., 2020. Multi-aged social behaviour based on artiodactyl tracks in an early Miocene palustrine wetland (Ebro Basin, Spain). Scientific Reports 10, 1099. https://doi.org/10.1038/s41598-020-57438-4.

Doublet, S., García, J.P., Guiraud, M., Ménard, A., 2003. Wave-dominated siliciclastic and carbonate sedimentation in a Lower Cretaceous lake (Cameros basin, northern Spain). Journal of Iberian Geology 29, 11−28.

Ezquerra, R., Doublet, S., Costeur, L., Galton, P.M., Pérez-Lorente, F., 2007. Were non-avian theropod dinosaurs able to swim? Supportive evidence from an Early Cretaceous trackway, Cameros Basin (La Rioja, Spain). Geology 35 (6), 507−510.

Ezquerra, R., Costeur, L., Pérez-Lorente, F., 2010. Los dinosaurios también nadaban. Investigación y ciencia diciembre 2−8.

Fabbri, M., Navalón, G., Benson, R.B.J., Pol, D., O'Connor, J., Bhullar, B.A.S., Erickson, G.M., Norell, M.A., Orkney, A., Lamanna, M.C., Zouhri, S., Becker, J., Emke, A., Dal Sasso, C., Bindellini, G., Maganuco, S., Auditore, M., Ibrahim, N., 2022. Subaqueous foraging among carnivorous dinosaurs. Nature 603, 852−857.

Falkingham, P.L., 2014. Interpreting ecology and behaviour from the vertebrate fossil track record. Journal of Zoology 292 (4), 222−228.

Falkingham, P.L., Gatesy, S.M., 2014. The birth of a dinosaur footprint: subsurface 3D motion reconstruction and discrete element simulation reveal track ontogeny. Proceedings of the National Academy of Sciences 111, 18279−18284.

Falkingham, P.L., Bates, K.T., Margetts, L., Manning, P.L., 2011. The 'Goldilocks' effect: preservation bias in vertebrate track assemblages. Journal of the Royal Society Interface 8 (61), 1142−1154. https://doi.org/10.1098/rsif.2010.0634.

Falkingham, P.L., Bates, K.T., Mannion, P.D., 2012. Temporal and palaeoenvironmental distribution of manus-and pes-dominated sauropod trackways. Journal of the Geological Society 169 (4), 365−370.

Falkingham, P.L., Bates, K.T., Avanzini, M., Bennett, M., Bordy, E.M., Breithaupt, B.H., Castanera, D., Citton, P., Díaz-Martínez, I., Farlow, J.O., Fiorillo, A.R., Gatesy, S.M., Getty, P., Hatala, K.G., Hornung, J.J., Hyatt, J.A., Klein, H., Lallensack, J.N., Martin, A.J., Marty, D., Matthews, N.A., Meyer, C.A., Milàn, J., Minter, N.J., Razzolini, N.L., Romilio, A., Salisbury, S.W., Sciscio, L., Tanaka, I., Wiseman, A.L.A., Xing, L.D., Belvedere, M., 2018. A standard protocol for documenting modern and fossil ichnological data. Palaeontology 61, 469−480. https://doi.org/10.1111/pala.12373.

Farlow, J.O., Robinson, N.J., Turner, M.L., Black, J., Gatesy, S.M., 2018. Footfall pattern of a bottom-walking crocodile (Crocodylus acutus). PALAIOS 33 (9), 406−413.

Falkingham, P.L., Marty, D., Richter, A., 2016. Dinosaur tracks: the next steps. Indiana University Press, Bloomington & Indianapolis.

Farlow, J.O., Galton, P.M., Hyatt, J.A., 2019. Dinosaur footprints from Dinosaur State Park (East Berlin Formation, Lower Jurassic, Rocky Hill, Connecticut, USA). Hallesches Jahrbuch für Geowissenschaften/Beiheft 46, 27−29.

Ford, T.L., Martin, L.D., 2010. A semi-aquatic life habit for *Psittacosaurus*. In: New Perspectives on Horned Dinosaurs: The Royal Tyrrell Museum Ceratopsian Symposium. Indiana University Press, pp. 328−339.

Fornós, J.J., Bromley, R.G., Clemmensen, L.B., Rodriguez-Perea, A., 2002. Tracks and trackways of *Myotragus balearicus* Bate (Artiodactyla, Caprinae) in Pleistocene aeolianites from Mallorca (Balearic Islands, Western Mediterranean). Palaeogeography, Palaeoclimatology, Palaeoecology 180 (4), 277−313.

Foster, J.R., Lockley, M.G., 1997. Probable crocodilian tracks and traces from the Morrison Formation (Upper Jurassic) of eastern Utah. Ichnos 5, 121−129.

Fuentes-Vidarte, C., Meijide-Calvo, M., Izquierdo, L.A., Montero, D., Pérex, G., Torcida, F., Urién, V., Meijide-Fuentes, F., Meijide-Fuentes, M., 2001. Restos fósiles de *Baryonyx* (Dinosauria, Theropoda) en el Cretácico inferior de Salas de los Infantes (Burgos, España). In: Actas de las I Jornadas internacionales sobre Paleontología de Dinosaurios y su entorno (CAS ed.) Salas de los Infantes, pp. 349−359.

Fujita, M., Lee, Y.N., Azuma, Y., Li, D., 2012. Unusual tridactyl trackways with tail traces from the Lower Cretaceous Hekou Group, Gansu Province, China. PALAIOS 27 (8), 560−570.

Gaillard, C., Bernier, P., Barale, G., Bourseau, J.P., Buffetaut, E., Ezquerra, R., Gall, J.-C., De Lapparent De Broin, F., Renous, S., Wenz, S., 2003. A giant Upper Jurassic turtle revealed by its trackways. Lethaia 36 (4), 315−322.

García-Ortiz, E., Fuertes-Gutiérrez, I., Fernández-Martínez, E., 2014. Concepts and terminology for the risk of degradation of geological heritage sites: fragility and natural vulnerability, a case study. Proceedings of the Geologists' Association 125 (4), 463−479.

Gasca, J.M., Canudo, J.I., Moreno-Azanza, M., 2014. A large-bodied theropod (Tetanurae: Carcharodontosauria) from the Mirambel Formation (Barremian) of Spain. Neues Jahrbuch für Geologie und Paläontologie 273, 13−23.

Gasca, J.M., Díaz-Martínez, I., Moreno-Azanza, M., Canudo, J.I., Alonso, A., 2018. A hypertrophied ungual phalanx from the lower Barremian of Spain:

P. Navarro-Lorbés, I. Díaz-Martínez, J.M. Valle-Melón et al.

Cretaceous Research 147 (2023) 105516

implications for the diversity and palaeoecology of Spinosauridae (Theropoda) in Iberia. Cretaceous Research 84, 141–152.

Gatesy, S.M., Middleton, K.M., Jenkins Jr., F.A., Shubin, N.H., 1999. Three-dimensional preservation of foot movements in Triassic theropod dinosaurs. Nature 399, 141–144.

Gimsa, J., Gimsa, U., 2021. Contributions to a discussion of Spinosaurus aegyptiacus as a capable swimmer and deep-water predator. Life 11 (9), 889.

Gimsa, J., Sleigh, R., Gimsa, U., 2016. The riddle of Spinosaurus aegyptiacus dorsal sail. Geological Magazine 153 (3), 544–547.

Goedert, J., Amiot, R., Boudad, L., Buffetaut, E., Fourel, F., Godefroit, P., Kusuhashi, N., Suteethorn, V., Tong, H., Watabe, M., Lécuyer, C., 2016. Preliminary investigation of seasonal patterns recorded in the oxygen isotope compositions of theropod dinosaur tooth enamel oxygen isotope seasonality in theropod teeth. PALAIOS 31 (1), 10–19.

Hassler, A., Martin, J.E., Amiot, R., Tacail, T., Arnaud Godet, F., Allain, R., Balter, V., 2018. Calcium isotopes offer clues on resource partitioning among Cretaceous predatory dinosaurs. Proceedings of the Royal Society B: Biological Sciences 285 (1876), 20180197.

Herraiz, J.L., Villena, J.A., Vilaplana-Climent, A., Conejero, N., Cocera, H., Botella, H., García-Forner, A., Martínez-Pérez, C., 2019. The palaeontological virtual collection of the University of Valencia's Natural History Museum: a new tool for palaeontological heritage outreach (La colección virtual de paleontología del Museo de Historia Natural de la Universitat de València: una nueva herramienta para la difusión del patrimonio paleontológico). Spanish Journal of Palaeontology 34 (1), 139–144.

Hone, D.W., Holtz Jr., T.R., 2021. Evaluating the ecology of Spinosaurus: shoreline generalist or aquatic pursuit specialist? Palaeontologia Electronica 24 (1), a03. https://doi.org/10.26879/1110.

Henderson, D.M., 2004. Tipsy punters: sauropod dinosaur pneumaticity, buoyancy and aquatic habits. Proceedings of the Royal Society of London. Series B: Biological Sciences 271 (Suppl_4), S180–S183.

Henderson, D.M., 2018. A buoyancy, balance and stability challenge to the hypothesis of a semi-aquatic Spinosaurus Stromer, 1915 (Dinosauria: Theropoda). PeerJ 6, e5409.

Hernández-Medrano, N., Pascual-Arribas, C., Latorre-Macarrón, P., Sanz-Pérez, E., 2005. Contribución de los yacimientos de icnitas sorianos al registro general de Cameros. Zubía 23–24, 79–120.

Ibrahim, N., Sereno, P.C., Dal Sasso, C., Maganuco, S., Fabbri, M., Martill, D.M., Zouhri, S., Myhrvold, N., Iurino, D.A., 2014. Semiaquatic adaptations in a giant predatory dinosaur. Science 345 (6204), 1613–1616.

Ibrahim, N., Maganuco, S., Dal Sasso, C., Fabbri, M., Auditore, M., Bindellini, G., Martill, D.M., Zouhri, S., Mattarelli, D.A., Unwin, D.M., Wiemann, J., Bonadonna, D., Amane, A., Jakubczak, J., Joger, U., Lauder, G.V., Pierce, S.E., 2020. Tail-propelled aquatic locomotion in a theropod dinosaur. Nature 581 (7806), 67–70.

Isasmendi, E., Saez-Benito, P., Torices, A., Navarro-Lorbés, P., Pereda Suberbiola, X., 2020. New insights about theropod palaeobiodiversity in the Iberian Peninsula and Europe: Spinosaurid teeth (Theropoda, Megalosauroidea) from the Early Cretaceous of La Rioja (Spain). Cretaceous Research 116, 104600. https://doi.org/10.1016/j.cretres.2020.104600.

Isasmendi, E., Navarro-Lorbés, P., Sáez-Benito, P., Viera, L.I., Torices, A., Pereda-Suberbiola, X., 2022. New contributions to the skull anatomy of spinosaurid theropods: Baryonychinae maxilla from the Early Cretaceous of Igea (La Rioja, Spain). Historical Biology. https://doi.org/10.1080/08912963.2022.2069019.

Ishigaki, S., 1989. Footprints of swimming sauropods from Morocco. In: International Symposium on Dinosaur Tracks and Traces, 1, pp. 83–86.

Ishigaki, S., Matsumoto, Y., 2009. Re-examination of manus-only and manus-dominated sauropod trackways from Morocco. Geological Quarterly 53, 441–448.

Kim, J.Y., Lockley, M., 2016. First report of turtle tracks from the Lower Cretaceous of Korea. Cretaceous Research 64, 1–6.

Klein, H., Lucas, S.G., 2010. Tetrapod footprints – their use in biostratigraphy and biochronology of the Triassic. In: Lucas, S.G. (Ed.), The Triassic Timescale, Geological Society, London, Special Publications, vol. 334, pp. 419–446.

Koester, D.M., Spirito, C.P., 2003. Punting: an unusual mode of locomotion in the little skate, Leucoraja erinacea (Chondrichthyes: Rajidae). Copeia 2003 (3), 553–561.

Lee, Y.-N., Barsbold, R., Currie, P.J., Kobayashi, Y., Lee, H.-J., Godefroit, P., Escuillié, F., Chinzorig, T., 2014. Resolving the long-standing enigmas of a giant ornithomimosaur Deinocheirus mirificus. Nature 515 (7526), 257–260.

Lee, Y.N., Lee, H.J., Kobayashi, Y., Paulina-Carabajal, A., Barsbold, R., Fiorillo, A.R., Tsogtbaatar, K., 2019. Unusual locomotion behaviour preserved within a crocodyliform trackway from the Upper Cretaceous Bayanshiree Formation of Mongolia and its palaeobiological implications. Palaeogeography, Palaeoclimatology, Palaeoecology 533, 109239.

Lockley, M.G., Foster, J., 2006. Dinosaur and turtle tracks from the Morrison Formation (Upper Jurassic) of Colorado National Monument, with observations on the taxonomy of vertebrate swim tracks. In: Foster, J.R., Lucas, S.G. (Eds.), Geology and Paleontology of the Morrison Formation. New Mexico Museum of Nature and Science, Bulletin 36, pp. 193–198.

Lockley, M.G., Schumacher, B., 2014. A new pterosaur swim tracks locality from the Cretaceous Dakota Group of eastern Colorado: implications for pterosaur swim track behavior. Fossil Footprints of Western North America. Bulletin of the New Mexico Museum of Natural History and Science 365–371.

Lockley, M.G., Wright, J.L., 2003. Pterosaur swim tracks and other ichnological evidence of behaviour and ecology. Geological Society, London, Special Publications 217 (1), 297–313.

Lockley, M.G., Holbrook, J., Hunt, A.P., Matsukawa, M., Meyer, C., 1992. The dinosaur freeway: a preliminary report on the Cretaceous megatracksite, Dakota Group, Rocky Mountain Front Range and Highplains; Colorado, Oklahoma and New Mexico. In: Flores, R. (Ed.), Mesozoic of the Western Interior, SEPM Midyear Meeting Fieldtrip Guidebook, pp. 39–54.

Lockley, M.G., Lucas, S.G., Milan, J., Harris, J.D., Avanzini, M., Foster, J.R., Spielmann, J.A., 2010. The fossil record of crocodilian tracks and traces: an overview. In: Milan, J., Lucas, S.G., Lockley, M.G. (Eds.), Crocodyle Tracks and Traces, New Mexico Museum of Natural History and Science Bulletin, pp. 1–13.

Lockley, M., Houck, K., Matthews, N., McCrea, R., Xing, L., Tsukui, L., Ramezani, J., Breithaupt, B., Cart, K., Martin, J., Buckley, L., Hadden, G., 2018. New theropod display arena sites in the Cretaceous of North America: clues to distributions in space and time. Cretaceous Research 81, 9–25.

Lucas, S.G., Hunt, A.P., 2006. Permian tetrapod footprints: biostratigraphy and biochronology. Geological Society, London, Special Publications 265 (1), 179–200.

Maia, A.M., Wilga, C.A., Lauder, G.V., 2012. Biomechanics of Locomotion in Sharks, Rays, and Chimaeras. In: Biology of Sharks and their Relatives, vol. 1, pp. 125–151.

Malafaia, E., Gasulla, J.M., Escaso, F., Narváez, I., Sanz, J.L., Ortega, F., 2020. A new spinosaurid theropod (Dinosauria: Megalosauroidea) from the upper Barremian of Vallibona, Spain: implications for spinosaurid diversity in the Early Cretaceous of the Iberian Peninsula. Cretaceous Research 106, 104221.

Martinez, M.M., Full, M.R.J., Koehl, M.A.R., 1998. Underwater punting by an intertidal crab: a novel gait revealed by kinematics of pedestrian locomotion in air versus water. Journal of Experimental Biology 201, 2609–2623.

Mas, J.R., Alonso, A., Guimera, J., 1993. Evolución tectonosedimentaria de una cuenca extensional intraplaca: La cuenca finijurásica-eocretácica de Los Cameros (La Rioja-Soria). Revista de la Sociedad Geológica de España 6 (3–4), 129–144. ISSN 2255-1379.

Mas, R., Benito, M.I., Serrano, A., Guimerà, J., Millán, A., Azcárate, J., 2002. La Cuenca de Cameros: desde la extensión finijurásica-eocretácica a la inversión terciaria-implicaciones en la exploración de hidrocarburos. Zubía (), 9–64.

Mas, R., García, A., Mas, R., García, A., Salas, R., Meléndez, A., Alonso, A., Aurel, M., Bádenas, B., Benito, M.I., Carenas, B., García-Hidalgo, J.F., Gil, J., Segura, M., 2004. Segunda Fase de rifting: Jurásico Superior-Cretácico Inferior. In: Vera, J.A. (Ed.), Geología de España. Sociedad Geológica de España, Instituto Geológico y Minero, Madrid, pp. 503–510.

Mas, J.R., Benito, M.I., Arribas, J., Millán, A., Arribas, E., Lohmann, K., González-Acebrón, L., Hernán, J., Quijada, I., Suárez-Gonzalez, P., Omodeo-Salé, S., 2011. Evolution of an intra-plate rift basin: the Latest Jurassic-Early Cretaceous Cameros Basin (Northwest Iberian Ranges, North Spain). Geo-Guías 8, 117–154.

Martin-Chivelet, J., López-Gómez, J., Aguado, R., Arias, C., Arribas, J., Arribas, E., Aurell, M., Bádenas, B., Benito, M.I., Bover-Arnal, T., Casas-Sainz, A., Castro, J., Coruña, F., Guillén, G.A., Fornós, J., Fregenal-Martínez, M., García-Senz, J., Garófano, D., Gelabert, B., Vilas, L., 2019. The Late Jurassic-Early Cretaceous Rifting. In: Quesada, C., Oliveira, J.T. (Eds.), The Geology of Iberia: A Geodynamic Approach, The Alpine Cycle. Regional Geology Reviews, Vol. 3. Springer, pp. 169–249.

Mateus, O., Estraviz-López, D., 2022. A new theropod dinosaur from the early cretaceous (Barremian) of Cabo Espichel, Portugal: Implications for spinosaurid evolution. PLoS One 17 (2), e0262614.

Mateus, O., Araujo, R., Natario, C., Castanhinha, R., 2011. A new specimen of the theropod dinosaur Baryonyx from the Early Cretaceous of Portugal and taxonomic validity of Suchosaurus. Zootaxa 2827, 54–68.

McAllister, J.A., 1989. Dakota Formation tracks from Kansas: implications for the recognition of tetrapod subaqueous traces. In: Gillette, D.D., Lockley, M.G. (Eds.), Dinosaur Tracks and Traces. Cambridge University Press, Cambridge, U.K, pp. 343–348.

McAllister, J.A., Kirby, J., 1998. An occurrence of reptile subaqueous traces in the Moenkopi Formation (Triassic) of Capito Reef National Park, south central Utah, USA. Journal of Pennsylvania Academy of Science 71 (Suppl. and Index), 174–181.

McCrea, R.T., Pemberton, S.G., Currie, P.J., 2004. New ichnotaxa of mammal and reptile tracks from the Upper Paleocene of Alberta. Ichnos 11 (3–4), 323–339.

Melchor, R.N., 2015. Application of vertebrate trace fossils to palaeoenvironmental analysis. Palaeogeography, Palaeoclimatology, Palaeoecology 439, 79–96.

Milner, A.R.C., Lockley, M.G., 2016. Dinosaur swim track assemblages: characteristics, contexts, and ichnofacies implications. In: Falkingham, P.L., Marty, D., Richter, A. (Eds.), Dinosaur Tracks: The Next Steps. Indiana University Press, Bloomington and Indianapolis, IA, pp. 152–178.

Milner, A.R., Lockley, M.G., Kirkland, J.I., Harris, J.D., 2006. A large collection of well-preserved theropod dinosaur swim tracks from the Lower Jurassic Moenave Formation, St. George, Utah. New Mexico Museum of Natural History and Science Bulletin 37, 315–328.

Moklestad, T., Caneer, T., Lucas, S.G., 2018. The "Lost Tracks" at Dinosaur Ridge, Colorado, from the base of the Cretaceous (Late Albian-Early Cenomanian) Mowry Shale Member of the Benton Formation, show a swimming (?) ornithopod affected by a current. Bulletin 79, 503–511.

P. Navarro-Lorbés, I. Díaz-Martínez, J.M. Valle-Melón et al.

Cretaceous Research 147 (2023) 105516

Morris, W.J., 1981. A new species of hadrosaurian dinosaur from the Upper Cretaceous of Baja California:? *Lambeosaurus laticaudus*. Journal of Paleontology 453−462.

Mudroch, A., Richter, U., Joger, U., Kosma, R., Idé, O., Maga, A., 2011. Didactyl tracks of paravian theropods (Maniraptora) from the ?Middle Jurassic of Africa. PLoS One 6 (2), e14642. https://doi.org/10.1371/journal.pone.0014642.

Mustoe, G.E., 2019. Lower Eocene footprints from Northwest Washington, USA. Part 1: Reptile tracks. Geosciences 9 (7), 321.

Myhrvold, N.P., Sereno, P.C., Baumgart, S.L., Formoso, K.K., Vidal, D., Fish, F.E., Henderson, D.M., 2022. Spinosaurids as 'subaqueous foragers' undermined by selective sampling and problematic statistical inference.. bioRxiv.

Navarro, O., Moratalla, J.J., 2018. Swimming reptile prints from the Keuper facies (Carnian, Upper Triassic) of Los Gallegos new tracksite (Iberian Range, Valencia province, Spain). Journal of Iberian Geology. https://doi.org/10.1007/s41513-018-0060-0.

Navarro-Lorbés, P., Ruiz, J., Díaz-Martínez, I., Isasmendi, E., Sáez-Benito, P., Viera, L., Pereda-Suberbiola, X., Torices, A., 2021a. Fast-running theropods tracks from the Early Cretaceous of La Rioja, Spain. Scientific Reports 11 (1), 23095. https://doi.org/10.1038/s41598-021-02557-9.

Navarro-Lorbés, P., Valle-Melón, J.M., Rodríguez, A., Moratalla, J.J., Ferrer-Ventura, M., San Juan-Palacios, R., Torices, A., 2021b. Digital preservation of a new endangered swimming dinosaur tracksite from the Lower Cretaceous of La Rioja (Spain). In: Abstract book of the XVIII Conference of the European Association of Vertebrate Palaeontologists, p. 125.

Nesbitt, S.J., Barrett, P.M., Werning, S., Sidor, C.A., Charig, A.J., 2013. The oldest dinosaur? A Middle Triassic dinosauriform from Tanzania. Biology Letters 9 (1), 20120949.

Novas, F.E., 1994. New information on the systematics and postcranial skeleton of *Herrerasaurus ischigualastensis* (Theropoda: Herrerasauridae) from the Ischigualasto Formation (Upper Triassic) of Argentina. Journal of Vertebrate Paleontology 13 (4), 400−423.

Ortega, F., Escaso, F., Sanz, J.L., 2010. A bizarre, humped Carcharodontosauria (Theropoda) from the Lower Cretaceous of Spain. Nature 467, 203−206. https://doi.org/10.1038/nature09181.

Osborn, J.F., 1912. Integumento of the iguanodont dinosaur *Trachodon*. American Museum of Natural History Memoir, New Series 1 (3), 33−54.

Owen, R., 1841. Report on British Fossil Reptiles, Part II. Reports of the British Association for the Advancement of Science, London, pp. 60−65.

Pei, R., Pittman, M., Goloboff, P.A., Dececchi, T.A., Habib, M.B., Kaye, T.G., Larsson, H.C.E., Norell, M.A., Brusatte, S.L., Xu, X., 2020. Potential for powered flight neared by most close avialan relatives, but few crossed its thresholds. Current Biology 30 (20), 4033−4046.e8. https://doi.org/10.1016/j.cub.2020.06.105.

Pereda-Suberbiola, X., Ruiz-Omeñaca, J.I., Canudo, J.I., Torcida, F., Sanz, J.L., 2012. Dinosaur faunas from the Early Cretaceous (Valanginian-Albian) of Spain. In: Godefroit, P. (Ed.), Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems. Indiana University Press, Bloomington (In), pp. 379−407.

Pérez-Lorente, F., 2015. Dinosaur Footprints and Trackways of La Rioja. In: Series: Life of the Past. Indiana University Press.

Pienkowski, G., Gierlinski, G., 1987. New finds of dinosaur footprints in Liassic of the Holy Cross mountains and its paleoenvironmental background. Prezegl'd Geologiczny 4, 199−205.

Rajkumar, H.S., Mustoe, G.E., Khaidem, K.S., Soibam, I., 2015. Crocodylian Tracks from Lower Oligocene Flysch deposits of the Barail Group, Manipur, India. Ichnos 22, 122−131.

Rauhut, O.W.M., Canudo, J.I., Castanera, D., 2019. A reappraisal of the Early Cretaceous theropod dinosaur *Camarillasaurus* from Spain. In: Abstract Book of the 17th Annual Meeting of the European Association of Vertebrate Palaeontologists (EAVP) 96, Brussels.

Riguetti, F., Citton, P., Apesteguía, S., Zacarías, G.G., Pereda-Suberbiola, X., 2021. New ankylosaurian trackways (cf. *Tetrapodosaurus*) from an uppermost Cretaceous level of the El Molino Formation of Bolivia. Cretaceous Research 124, 104810.

Rodríguez-Miranda, Á., Valle-Melón, J.M., 2021. Documentación geométrica de las huellas de dinosaurio nadador en Laguna de Cameros (La Rioja). http://hdl.handle.net/10810/53971.

Romer, A.S., 1966. Vertebrate Paleontology. University of Chicago Press, Chicago, p. 468.

Romilio, A., Tucker, R.T., Salisbury, S.W., 2013. Reevaluation of the Lark Quarry dinosaur tracksite (late Albian-Cenomanian Winton Formation, central-western Queensland, Australia): no longer a stampede? Journal of Vertebrate Paleontology 33, 102−120.

Salinas, F.J., Mas, J.R., 1990. Estudio sedimentológico y tectosedimentario de la cubeta de Cervera del Río Alhama (La Rioja) durante la sedimentación del Grupo Urbión (Cretácico inferior). Estudios Geológicos 46, 245−255.

Samathi, A., Sander, P.M., Chanthasit, P., 2021. A spinosaurid from Thailand (Sao Khua Formation, Early Cretaceous) and a reassessment of *Camarillasaurus cirugedae* from the Early Cretaceous of Spain. Historical Biology. https://doi.org/10.1080/08912963.2021.18743.72.

Sánchez-Hernández, B., Benton, M.J., 2014. Filling the ceratosaur gap: A new ceratosaurian theropod from the Early Cretaceous of Spain. Acta Palaeontologica Polonica 59 (3), 581−600.

Sereno, P.C., Martínez, R.N., Alcober, O.A., 2012. Osteology of *Eoraptor lunensis* (Dinosauria, Sauropodomorpha). Journal of Vertebrate Paleontology 32 (Suppl. 1), 83−179.

Sereno, P.C., Myhrvold, N., Henderson, D.M., Fish, F.E., Vidal, D., Baumgart, S.L., Keillor, T.M., Formoso, K.K., Conroy, L.L., 2022. *Spinosaurus* is not an aquatic dinosaur. Elife 11, e80092. https://doi.org/10.7554/eLife.80092.

Serrano, F.J., Chiappe, L.M., 2021. Independent origins of powered flight in paravian dinosaurs? Current Biology 31 (8), R370−R372. https://doi.org/10.1016/j.cub.2021.03.058.

Suárez-González, P., Quijada, I.E., Benito, M.I., Mas, R., 2013. Eustatic versus tectonic control in an intraplate rift basin (Leza Fm., Cameros Basin). Chronostratigraphic and paleogeographic implications for the Aptian of Iberia. Journal of Iberian Geology 39, 285−312.

Tereschenko, V.S., 2008. Adaptive features of protoceratopoids (Ornithischia: Neoceratopsia). Paleontological Journal 42 (3), 273−286.

Thomson, T.J., Droser, M.L., 2015. Swimming reptiles make their mark in the Early Triassic: delayed ecologic recovery increased the preservation potential of vertebrate swim tracks. Geology 43 (3), 215−218.

Thomson, T.J., Lovelace, D.M., 2014. Swim track morphotypes and new track localities from the Moenkopi and Red Peak formations (lower-middle Triassic) with preliminary interpretations of aquatic behaviors. In: Lockley, M.G., Lucas, S.G. (Eds.), Fossil Footprints of Western North America: New Mexico Museum of Natural History and Science Bulletin, 62, pp. 103−128.

Thulborn, R.A., 2013. Lark Quarry revisited: a critique of methods used to identify a large dinosaurian track-maker in the Winton Formation (Albian-Cenomanian), western Queensland, Australia. Alcheringa 37, 312−330.

Thulborn, R.A., Wade, M., 1989. A footprint as a history of movement. In: Gillette, D.D., Lockley, M.G. (Eds.), Dinosaur Tracks and Traces. Cambridge University Press, Cambridge, U.K, pp. 51−56.

Tischer, G., 1966. Uber die Wealden-Ablagerung und die tektonik der ostlichen Sierra de los Cameros in den nordwestlichen Iberischen Ketten (Spanien). In: Beuther, A., Dahm, H., Kneuper-Haak, F., Mensink, H., Tischer, G., Brinkmann, R., De Lôme, D., Lötgers, H. (Eds.), Der Jura und Wealden in Nordost-Spanien, Beihefte zum Geologischen Jahrbuch, 44, pp. 123−164.

Torcida, F., Izquierdo, L.A., Montero, D., Pérez, G., Urién, V., 2001. Primera cita de huellas de saurópodos en Burgos (España). In: Colectivo Arqueológico-Paleontológico Salense (Ed.), Actas I Jornadas internacionales sobre Paleontología de Dinosaurios y su entorno, Salas de los Infantes, Burgos, pp. 427−434.

Torcida Fernández-Baldor, F., Díaz-Martínez, I., Huerta, P., Contreras-Izquierdo, R., Izquierdo Montero, L.A., Montero Huerta, D., Urién-Montero, V., 2012. Estudio previo del yacimiento de icnitas de dinosaurios de Las Sereas (Cuenca de Cameros, Jurásico Superior-Cretácico Inferior). In: Huerta Hurtado, P., Torcida Fernández-Baldor, F., Canudo Sanagustín, J.I. (Eds.), Actas V Jornadas internacionales sobre Paleontología de Dinosaurios y su entorno, pp. 197−204.

Torcida Fernández-Baldor, F., Díaz-Martínez, I., Huerta, P., Montero Huerta, D., Castanera, D., 2021. Enigmatic tracks of solitary sauropods roaming an extensive lacustrine megatracksite in Iberia. Scientific Reports 11 (1), 16939.

Torices, A., Valle Melón, J.M., Elorriaga Aguirre, G., Navarro-Lorbés, P., Rodríguez-Miranda, A., 2020. Multiscale geometric 3D recording of palaeontological heritage in La Rioja (Spain): regional context, sites, tracks and individual fossils. Journal of Iberian Geology 46, 465−474. https://doi.org/10.1007/s41513-020-00132-1.

Trapman, T.H., 2018. Stable Isotope Analysis of Theropod Teeth from the Kem Kem Beds, North Africa-Niche Differentiation Among Large Predatory Dinosaurs (Master's thesis).

Viera, L.I., Torres, J.A., 1995. Presencia de *Baryonyx walkeri* (Saurischia, Theropoda) en el Weald de La Rioja (Espana), Nota previa. Munibe 47, 57−61.

Vila, B., Oms, O., Galobart, A., 2005. Manus-only titanosaurid trackway from Fumanya (Maastrichtian, Pyrenees): further evidence for an underprint origin. Lethaia 38 (3), 211−218.

Vila, B., Castanera, D., Marmi, J., Canudo, J.I., Galobart, À., 2015. Crocodile swim tracks from the latest Cretaceous of Europe. Lethaia 48 (2), 256−266.

Vullo, R., Allain, R., Cavin, L., 2016. Convergent evolution of jaws between spinosaurid dinosaurs and pike conger eels. Acta Palaeontologica Polonica 61 (4), 825−828.

Whyte, M.A., Romano, M., 2001. A dinosaur ichnocenosis from the Middle Jurassic of Yorkshire, UK. Ichnos 8, 223−234.

Xing, L.D., Lockley, M.G., Zhang, J.P., Milner, A.R.C., Klein, H., Li, D.Q., Persons IV, W.S., Ebi, J.F., 2013. A new Early Cretaceous dinosaur track assemblage and the first definite non-avian theropod swim trackway from China. Chinese Science Bulletin 58, 2370−2378. https://doi.org/10.1007/s11434-013-5802-6.

Xing, L., Klein, H., Lockley, M.G., Wu, X.C., Benton, M.J., Zeng, R., Romilio, A., 2020. Footprints of marine reptiles from the Middle Triassic (Anisian-Ladinian) Guanling Formation of Guizhou Province, southwestern China: the earliest evidence of synchronous style of swimming. Palaeogeography, Palaeoclimatology, Palaeoecology 558, 109943.

Zug, G.R., 1971. Buoyancy, Locomotion, Morphology of the Pelvic Girdle and Hindlimb, and Systematics of Cryptodiran Turtles. In: Miscellaneous Publications Museum of Zoology, University of Michigan, 142, pp. 1−98.