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

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ABSTRACT

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

1. Introduction

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

In this study we reanalysed an ornithopod trackway (Casanovas

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

2. Geological setting

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

3. Material and methods

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

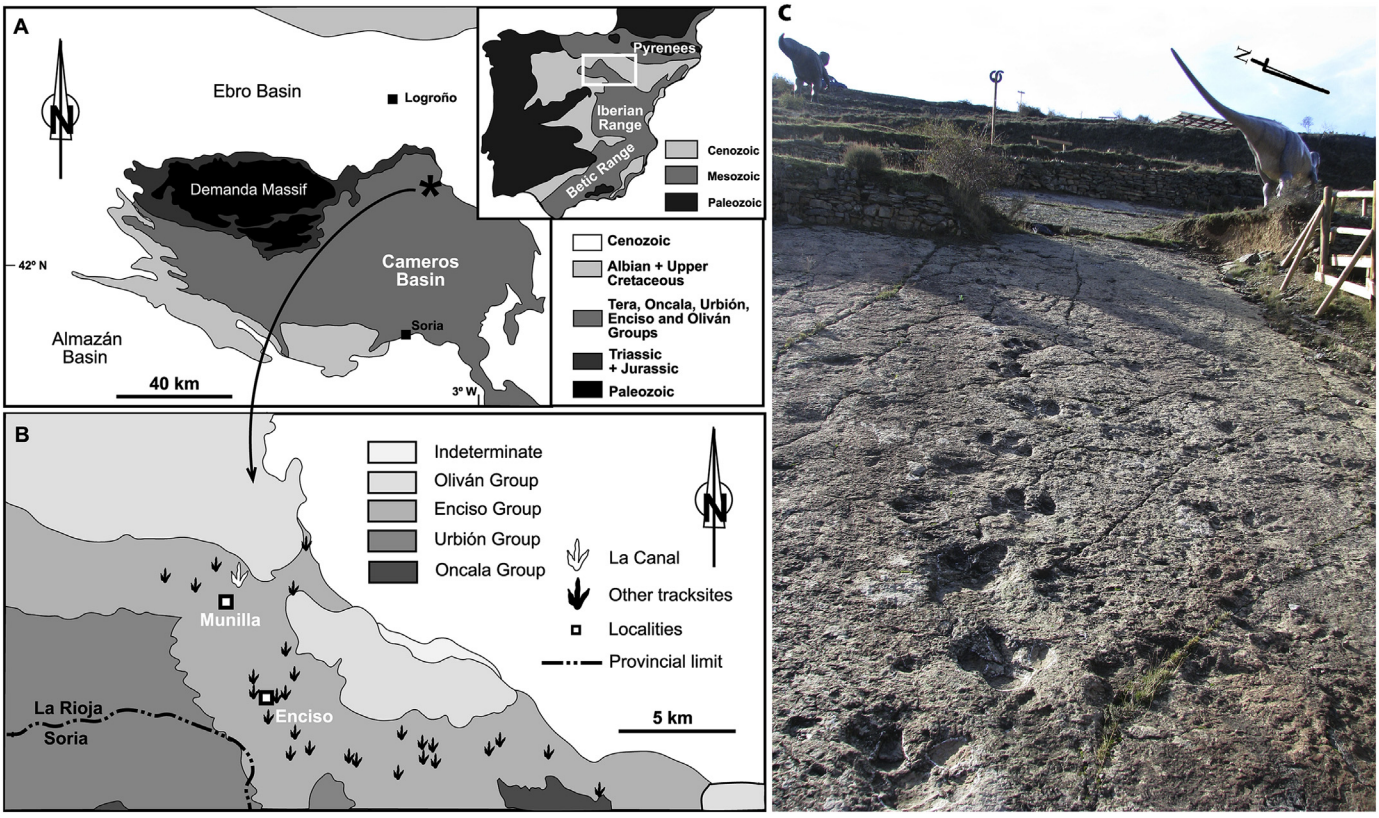

Fig. 1. A-B) Geographical and geological setting of the El Barranco de La Canal-1 tracksite from the Cameros Basin of the Munilla village, La Rioja, NW Spain. It belongs to the Enciso group. Geological map modified from Díaz-Martínez (2013). C) Field photo of the Barranco de La Canal-1 trackway with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