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Probable palaeogeographic influences of the Lower Cretaceous Iberian rifting phase in the Eastern Cameros Basin (Spain) on dinosaur trackway orientations

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ABSTRACT

The Cameros Basin sedimentary infill comprises a large, essentially continental, megasequence ranging from the Tithonian (Upper Jurassic) to the Albian (Lower Cretaceous). It occupies an area of some 5500 km^2, and is home to around 300 dinosaur tracksites. Most of these tracksites are found in either the Huérteles Formation, which is part of the Oncala Group (Berriasian), or the Enciso Group (Lower Aptian), both of which represent early Cretaceous lacustrine episodes. Dinosaur trackways ($n = 1170$) from both episodes were analysed in order to establish the preferred direction of dinosaur movement, and to determine whether these movements were influenced by the palaeogeographic and palaeoenvironmental conditions of the area.
The Huérteles Formation is interpreted as a complex record of alluvial plain systems distally connected with a playa-lake. Its dinosaur tracksites are distributed throughout its alluvial plain facies and trackways show two preferential unidirectional orientations: 1) NW, more or less parallel to the distribution of the facies belt and 2) NNE. The Enciso Group is represented by a wide and shallow lacustrine system connected with marine environments towards the SE (Iberian Basin realm) and in close proximity to marine settings to the NW (Basque–Cantabrian Basin realm), rendering the Cameros Basin as the only continental connection between the Ebro and Iberian Massifs. The fluctuating (but always shallow) water level of the system with frequent desiccations probably allowed dinosaurs to pass through the lake basin. As a consequence of these paleogeographic restrictions, the dinosaur trackways generally show a bidirectional NE–SW orientation. Despite the temporal and geographical differences between the Huérteles Formation and Enciso Group, the ichnocenoses of both are dominated by theropod dinosaur trackways (85% as a mean value). This is probably explained by these dinosaurs being more active than others, a consequence of their searching/hunting behaviour.

1. Introduction

The first Cameros Basin dinosaur tracksite was reported by Casanovas and Santafé in 1971. Since then many more such reports have been published and the literature is now rich in footprint data for this region (Moratalla and Sanz, 1997; Moratalla et al., 1997a; Pérez-Lorente, 2002, 2003 and references therein). Some 300 tracksites are now known, but every year new discoveries are made, confirming the importance of this area for the study of fossil vertebrate ichnology.

The preferred directions taken by the makers of these trackways have, however, been the focus of few studies (Martín-Escorza, 1986, 1988, 2001), and the mixing of individual footprint and trackway data from formations of different age render the results obtained difficult to interpret. The present paper tries to throw more light on this topic by examining the orientations of entire trackways associated with well-differentiated stratigraphic units.

The relationship between the preferential orientations of dinosaur trackways and palaeoenvironmental conditions has been an important area of study in dinosaur ichnology (Lockley, 1986; Lockley and Conrad, 1989; Lockley, 1991; Lockley and Hunt, 1995). The phenomenon of regionally extensive, but stratigraphically-restricted, track-bearing layers, or megatracksites (Lockley and Pittman, 1989) or "dinosaur freeways" was first noted in Jurassic and Cretaceous coastal plain deposits in the United States (Lockley and Pittman, 1989; Lockley, 1997) and Europe (Meyer, 1993). A megatracksite (*sensu* Lockley and Pittman, 1989) is a large, track-bearing layer (single surface of thin unit) covering a wide area, perhaps even hundreds to thousands of square kilometres. The Moab megatracksite in Utah (Lockley, 1991), the Glen Rose Formation in Texas (Bird, 1944; Langston, 1979; Farlow et al., 2006), the Dakota Sandstone (Gillette and Thomas, 1985; Lockley, 1985, 1987; Lockley et al., 1992; Matsukawa et al., 1999; Schumacher, 2003; Lockley et al., 2006b) and the Solothurn Limestone of Switzerland (Meyer, 1993) are outstanding examples. Lacustrine regions with track-bearing layers

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covering a relatively small area but spanning a relatively long period of time represent another palaeoenvironment providing large accumulations of dinosaur tracksites. Abundant examples of lacustrine systems with rich dinosaur ichnofaunas have been identified for the Mesozoic ranging from the: (1) Triassic, e.g., the Fleming Fjord Formation (Jenkins et al., 1994; Milàn et al., 2004) and Chinle Group (Gaston et al., 2003), through the (2) Jurassic, e.g., the Whitmore Point Member of the Moenave Formation (Milner et al., 2006), the Morrison Formation (Lockley et al., 1998), and the East Berlin Formation (Getty, 2005), to the (3) Cretaceous, e.g., the Sousa Formation (Leonardi, 1994; Leonardi and Dos Santos, 2004), the Jindong Formation (Lockley and Matsukawa, 1998; Paik et al., 2001; Lockley et al., 2006a), the Uhangi Formation (Huh et al., 2003), the Haman Formation (Huh et al., 2003), and the El Molino Formation (Meyer et al., 2001).

Despite their structural differences, both megatracksites and the latter, vertically extensive, "basinal" track-bearing systems have yielded important clues regarding dinosaur fauna composition, behaviour and movement patterns. The features of ichnocenoses reflect the composition of palaeocommunities and provide testimony to the abundance of dinosaurs over relatively large areas. Dinosaur abundance can be estimated from the number of trackways and the number of tracksites (Lockley, 1997). It should be remembered, however, that ichnocenoses can show bias with respect to animal size, activity rates and preservation potential.

The study of dinosaur trackway orientation patterns has two main aims: 1) to provide information on the relationships between different trackways within the same tracksite, thus yielding information about the behaviour of different individuals, and 2) to determine the general orientation pattern of dinosaur trackways on a regional scale (which implies the analysis of several tracksites) (Moratalla et al., 1997b). The presence of parallel dinosaur trackways can be indicative of gregarious behaviour or the passage of individuals along a physically constrained pathway (Ostrom 1972; Lockley, 1986, 1991). The presence of parallel, bidirectional trackways has long been associated with physical restriction to movement, e.g., walking along the shores of a lake (checked against ripple-mark directions or other indications of shoreline orientation) (Lockley et al., 1986; Lockley, 1987, 1991, 1997). Sometimes, movements appear to be unidirectional, even with regular spacing between the trackways (intertrackway spacing, *sensu* Lockley, 1989). Such a pattern is usually interpreted as the consequence of gregarious behaviour (Bird, 1944; Ostrom, 1972; Currie and Sarjeant, 1979; Lockley, 1989; Lucas, 1998). These general preferential movements may, however, also have been influenced by palaeogeographic conditions structures at a more regional scale.

The Cameros Basin is in fact a mixture of the two types of extensive track-bearing deposits mentioned above, and has thick sediments (total combined stratigraphic thickness up to 10000 m) covering a wide area (about 5500 km^2) (Moratalla, 2008). However, the frequent lateral change shown by its facies does not allow for track-bearing layers to persist over long distances; the conditions of the megatracksite concept of Lockley and Pittman (1989) are therefore not met. The basin lies in the most northwestern part of the Iberian Range, outcropping into the Spanish provinces of Burgos, Soria and La Rioja (Fig. 1). It can be divided into two sub-basins — the Eastern and Western Cameros — of rather different stratigraphic framework (see General geological setting for further details). The preservation conditions responsible for maintaining the fossil record were different in the two sub-basins. Indeed, the Western Cameros sub-basin is characterized by the predominance of osteological remains (Torcida, 2006), while the Eastern Cameros is characterized by ichnological sites (Moratalla et al., 1997a; Sanz et al., 1997; Pérez-Lorente, 2003; Hernández-Medrano et al., 2005–2006).

The first large stratigraphic study of the region was undertaken in the eastern sector by Tischer (1966), who defined five geological groups: Tera, Oncala, Urbión, Enciso and Oliván, ranging from the Tithonian to the Albian. The Tera, Urbión and Oliván Groups are characterized by fluvio-lacustrine sediments, while both the Oncala and Enciso Groups are dominated by limestones of clearly lacustrine origin. The Tithonian to Albian synrift infill of the Eastern Cameros sub-basin has yielded a significant but irregular record of dinosaur ichnofaunas covering a period of some 42 million years, providing important ichnological evidence of dinosaur activity for most of the early Cretaceous. This record is particularly associated with lacustrine environments such as those of the Huérteles Formation and Enciso Group.

Given the long period of time between the Berriasian (Huérteles Formation) and the Aptian (Enciso Group), it might be expected that many differences should be found between their ichnological records, which would be influenced by their respective palaeogeographic and palaeoenvironmental conditions, sedimentation rates, fauna and flora etc. Dinosaur track morphotypes might, therefore, also differ, as might the general tracksite features. The differences in the palaeogeographic conditions between the Berriasian interval and the Lower Aptian lacustrine episodes were probably great enough that they might easily have had a significant influence on preferential dinosaur movements throughout the entire Cameros area.

The aim of the present paper is to examine the preferential orientations of the dinosaur trackways made during the Berriasian and Aptian, and to attempt to correlate them with the palaeoenvironmental and paleogeographic reconstructions of the basin for these periods. In the study area, two distinct temporal lacustrine episodes and a large number of dinosaur trackways (1170) were analysed. Two original palaeogeographic maps (based on the information available in the literature) corresponding to the age of the units discussed in this paper are presented; they illustrate the close relationship between the palaeogeography and sedimentary environments of these times and the main patterns of dinosaur movement.

2. General geological setting

The Cameros Basin is placed in the Cameros structural unit which consists of an intracratonic fold-and-thrust belt with a dominant NW–SE orientation, a result of the Palaeogene–Lower Miocene compressional phase (Guimerà et al., 1995). The northern border is a 100 km-long striking thrust veering from E–W to NW–SE (traditionally known as the Cameros or North Cameros thrust) over the Tertiary Ebro Basin. The southern margin is characterized by NE–SW to NW–SE-oriented folds and thrusts over the Tertiary Duero and Almazán Basins (Fig. 1A). Thus, the Cameros unit has an overall asymmetric pop-up structure and represents the result of the Tertiary inversion of the uppermost Jurassic–early Cretaceous extensional Cameros Basin (Guimerà et al., 1995).

During Mesozoic times the Iberian plate underwent an extensional regime leading to the widespread development of pericratonic rift systems, including the South-Iberian Continental Margin (Vera, 2001), the North Iberian Margin (García-Mondéjar et al., 1996; Vergés and García-Senz, 2001), and the Western Iberian Margin (Pinheiro et al., 1996), as well as intracratonic rifting named the Mesozoic Iberian Rift System (MIRS) or Iberian Basin (Salas et al., 2001). The MIRS comprises four evolutionary stages of the Mesozoic: (a) the Late Permian–Hettangian rift cycle 1, (b) the Sinemurian–Oxfordian postrift stage 1, (c) the latest Oxfordian–middle Albian rift cycle 2, and (d) the Late Albian–Maastrichtian postrift stage 2. During the onset of the second rifting cycle, which showed a NNE–SSW regional extension related to the opening of the Bay of Biscay and the North Atlantic, four strongly subsiding and well-differentiated sedimentary domains were generated: (1) the Cameros Basin (both Eastern and Western sub-basins), (2) the Maestrazgo Basin, (3) the offshore Columbretes Basin and, (4) the South-Iberian Basin (Salas and Casas, 1993; Salas et al., 2001). Thus, the Cameros Basin is the most interior and northwesterly sedimentary basin of the MIRS. As a result, it differs from the other MIRS basins in that it shows continental infilling with only slight