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Original article

Sauropod tracks of the Cameros Basin (Spain): Identification, trackway patterns and changes over the Jurassic-Cretaceous☆

Empreintes de sauropodes du bassin de Cameros (Espagne) : identification, types de traces et changement à la transition Jurassique-Crétacé

Icnitas de saurópodos de la Cuenca de Cameros (España): identificación, tipos de rastros y reemplazamiento durante el Jurásico-Cretácico

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Abstract

Sauropod tracks make up only about 2% of the Cameros Basin ichnocenosis, but they are present over the entire time span represented by the Cameros sediments. The makers of these tracks are identified in terms of their associated trackway pattern as either wide or narrow-gauge morphotypes. Narrow-gauge trackways dominate the Tithonian-Berriasian interval. Wide-gauge trackways become notably more common after the Berriasian, although narrow-gauge trackways are still present and dominate the Cameros ecosystems even during the Aptian. At this time, an interesting equilibrium between titanosauriform and non-titanosauriform sauropod trackways is evident, although the latter are somewhat more common. A review of the Iberian sauropod bone record suggests that Turiasauria + Euhelopidae, Rebbachisauridae and Titanosauriformes are the three groups mainly responsible for the Cameros Basin sauropod ichnocenosis.

Keywords: Dinosaurs; Sauropods; Lower Cretaceous; Palaeoichnology; Cameros Basin; Spain

Résumé

Les empreintes de sauropodes représentent une faible part (environ 2 %) de l'ichnocenose du Bassin de Cameros, mais on peut les trouver tout au long de la période enregistrée à Cameros. Les pistes de sauropodes du Bassin de Cameros sont principalement identifiées selon le type de traces (larges ou étroites). Les traces étroites de sauropodes sont dominantes durant l'intervalle Tithonien-Berriasien. Après le Berriasien, les pistes larges augmentent sensiblement bien que les étroites restent présentes et dominent les écosystèmes de Cameros, même pendant l'Aptien. À cette période, un équilibre intéressant est observé entre les pistes de Titanosauriformes et de non-Titanosauriformes, ce dernier groupe restant un peu plus fréquent. L'examen du registre ostéologique des sauropodes d'Espagne suggère que les Turiasauria + Euhelopidae, Rebbachisauridae et Titanosauriformes sont les trois groupes principaux impliqués dans la production de l'ichnocenose à sauropodes du Bassin de Cameros.

Mots clés : Dinosaures ; Sauropodes ; Crétacé inférieur ; Paléoichnologie ; Bassin de Cameros ; Espagne

Resumen

Las icnitas de saurópodos representan alrededor del 2% de la icnocenosis de la Cuenca de Cameros a pesar de que estén presentes durante todo el rango temporal que abarcan los sedimentos de esta región. Los autores de estas huellas se identifican en base al patrón de rastro que puede ser de tipo ancho o de tipo estrecho. Los rastros de tipo estrecho dominan el intervalo Titoniense-Berriasiense. Los rastros de tipo ancho son más comunes después del Berriasiense aunque los de tipo estrecho están aún presentes e incluso dominan los ecosistemas de Cameros durante el Aptiense.

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En este período se produce un interesante equilibrio entre rastros de saurópodos titanosauriformes y no titanosauriformes aunque estos últimos son ligeramente más abundantes. Una revisión del registro osteológico ibérico sugiere que Turiasaura + Euhelopidae, Rebbachisauridae y Titanosauriformes constituyen los tres grupos potencialmente responsables de la icnocenosis de saurópodos de la Cuenca de Cameros.

Palabras clave : Dinosaurios; Saurópodos; Cretácico Inferior; Paleoicnología; Cuenca de Cameros; España

1. Introduction

The sauropods were a group of obligate quadruped, saurischian dinosaurs that existed from the Upper Triassic to the end of the Cretaceous. They were impressive in terms of their shape and size, with some species reaching up to 35 m in length (Upchurch et al., 2004). Even the earliest sauropod specimens in the fossil record were relatively large animals, and it would seem that these dinosaurs increased their body size over time. The maximum rate of change occurred during the Upper Jurassic (especially during the Kimmeridgian) with the appearance of the clade Neosauropoda.

The tremendous size of these animals implies an increase in limb robustness, a columnar limb posture, a shortened distal region of the limbs, etc. Such modifications are related not only to a size increase but also to the obligate quadrupedal locomotion of all known sauropod dinosaurs, including *Vulcanodon* (Cooper, 1984). Some modifications involve the manus and pes morphologies. The sauropod manus tends to be digitigrade, the metacarpals acquiring a semicircular columnar arrangement. The ungual phalanges became progressively reduced over time, and in some titanosaurs were completely lost. The metatarsals changed from a mesaxonic to an entaxonic condition since the medial digits became relatively larger. The biomechanical constraints of the sauropods therefore rendered them completely pentadactyl in both manus and pes. However, while the manus support was digitigrade, the pes support was semi-plantigrade. The position of the metacarpals during locomotion was sub-vertical, an arrangement that led to the particular form of the manus prints. In most cases, these are half-moon shaped, with the convex margin directed forward and the concave rear outline directed backward. In contrast, the pes prints are sub-elliptical in shape, broader in the anterior region, and sometimes with digital impressions showing an anterior or anterior-lateral orientation. Therefore, the shape of sauropod prints (manus and pes) depends on both autopodia morphology and support arrangement. However, the correlation between sauropod tracks and bones also involves the trackway pattern. In fact, only relatively few morphological characters (manus print morphology, number, shape and orientation of the footprint digit marks, track rotation, manus prints location with respect to pes prints, distance between manus and pes prints, etc.) are commonly used for track identification; palaeoichnologists generally consider the trackway pattern to be more important.

The Cameros Basin is an impressive sedimentary basin very rich in dinosaur and other vertebrate tracksites. It covers an area of about 8000 km^2 (Alonso et al., 1991; Mas et al., 1993) and extends over three Spanish provinces: La Rioja, Soria and Burgos (Fig. 1). The basin is a consequence of the Iberian Mesozoic rifting episode associated with Pangean drift. Although this began in the Upper Permian and involved four main events (Sánchez-Moya and Sopeña, 2004), the geological episodes that contain dinosaur tracks belong to the second phase of rifting, extending from the Oxfordian to the Albian (Alonso et al., 1995; Barrenechea et al., 1995, 2001; Salas et al., 2001; Mas et al., 2004). As a consequence of this second rifting event, the continental area now known as the Cameros Basin suffered a phase of great subsidence beginning in the Tithonian-Berriasian and with its final phase in the Aptian.

The Cameros Basin can be divided into two sub-basins – the Eastern and Western Cameros – of rather different stratigraphy (Mas et al., 1993; Martin-Closas and Alonso, 1998; Salas et al., 2001; Arribas et al., 2003). The first significant stratigraphic study of Cameros was undertaken by Tischer (1966) in the eastern sector. This author defined five geological groups: Tera, Oncala, Urbión, Enciso and Oliván. Since then, many stratigraphic studies of the Cameros Basin have been published (Alonso et al., 1995; Guimerá et al., 1995; Barrenechea et al., 2001; Salas et al., 2001; Mas et al., 2002, 2003, 2004; Arribas et al., 2003), the findings of which have modified this first proposal in many aspects. Fig. 1 has been redrawn from the stratigraphic proposals made by Mas et al. (2004); it allows the sauropod tracksites of both areas of the Cameros Basin to be described within a single stratigraphic diagram.

More than 300 dinosaur tracksites (a number that includes small and even individual track findings) have been discovered over the last 36 years of research in the Cameros region. Most of these tracksites are found in the La Rioja province. A quick look to the Cameros Basin ichnocenosis reveals it to be largely dominated by theropods (Moratalla and Sanz, 1997; Moratalla and Hernán, 2007). The most recent estimates (Moratalla and Sanz, 1997; Pérez-Lorente, 2003; Moratalla and Hernán, 2007) suggest that theropod dinosaurs were the most abundant trackmakers of the Cameros Basin (responsible for some 84%). Ornithopods were responsible for some 14% and sauropods about 2%. These data agree with the distribution of herbivorous dinosaurs expected for a Lower Cretaceous palaeocommunity. During the Upper Jurassic, the dominion of sauropods and stegosaurs was substituted by that of ornithopods (iguanodontids and hypsilophodontids) and ankylosaurs, which went on to become the dominant herbivorous dinosaurs of the Lower Cretaceous (Barrett, 2007). Consequently, according to the large number of tracksites examined, the sauropods were probably the least abundant dinosaurs of the lacustrine-dominated ecosystems that reigned throughout the Lower Cretaceous in the Cameros region. However, despite this relative scarcity, the sauropod track record of the Cameros