AN OVERVIEW OF THE LOWER CRETACEOUS DINOSAUR TRACKSITES FROM THE MIRAMBEL FORMATION IN THE IBERIAN RANGE (NE SPAIN)

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Abstract—Up to now, the ichnological vertebrate record from the Barremian Mirambel Formation (NE Spain) has remained completely unknown despite the fact that osteological findings have been reported in recent years. Here we provide an overview of 11 new dinosaur tracksites found during a fieldwork campaign in the year 2011. The majority of these tracksites (seven) preserve small- to medium-sized tridactyl tracks here assigned to indeterminate theropods. Only one footprint presents enough characters to classify it as *Megalosauripus* isp. Ornithopod tracks identified as *Caririchnium* isp. and Iguanodontipodidae indet. and sauropod tracks are recorded at two tracksites. The footprints are preserved in a variety of paleoenvironmental conditions and thus display different kinds of preservation (true tracks, shallow undertracks, natural casts and undertrack casts). The ichnological record from the Mirambel Formation seems to be theropod dominated. This is a clear discrepancy with the osteological record identified in this formation, which shows a predominance of ornithopod dinosaurs.

INTRODUCTION

The Mirambel Formation (Barremian) is one of the lithostratigraphic units included in the Wealden facies from the Lower Cretaceous of the Iberian Range. It was deposited within the Maestrazgo Basin (Fig. 1). The formation is about 150 m thick and is composed of alluvial, lacustrine and coastal plain deposits (Gasca et al., 2013, 2014). Although some of the first dinosaur remains collected in Spain were described in this formation (Lapparent et al., 1969), it is noteworthy that the number of sites remained scarce until very recently by comparison with other units belonging to the Wealden facies in the Maestrazgo Basin, such as the Blesa, the El Castellar or the Camarillas formations (Ruiz-Omeñaca et al., 2004; Canudo et al., 2010). Recent studies have notably increased the dinosaur record from the Mirambel Formation. Remains from the main groups of dinosaurs, such as theropods (Infante et al., 2005; Gasca et al., 2014), ornithopods (Lapparent et al., 1969; Viera, 1991; Gasca et al., 2009; Bauluz et al., 2014; Gasca et al., 2015a) and sauropods (Gasca and Canudo, 2015), have been described. To date, more than 20 fossil sites bearing skeletal remains have been identified (Gasca et al., 2013), as well as some dinosaur eggshell occurrences (Moreno-Azanza et al., 2015).

As in the case of the skeletal remains, dinosaur tracks have been described in other coeval (Barremian) units of the Maestrazgo Basin, such as the Camarillas Formation (Cobos and Gascó, 2012; Herrero-Gascón and Pérez-Lorente, 2013; Royo Torres et al., 2013; Navarrete et al., 2014). Recent fieldwork carried out by the Aragosaurus Research Group has led to the discovery of several dinosaur tracksites distributed throughout the formation, with tracks preserved in different sedimentological layers (Fig. 1C). The aim of this paper is to provide an overview of the dinosaur track record of the Barremian Mirambel Formation, putting special emphasis on the description of the track types, the type of preservation and the ichnotaxonomic affinities. In addition, we compare these ichnological remains with the osteological record found in the same formation in order to achieve an integrated view of the dinosaur diversity.

GEOGRAPHICAL AND GEOLOGICAL SETTING

The dinosaur tracksites are located within the municipalities of Castellote and Las Parras de Castellote in the northwestern part of Teruel Province, Spain. They are situated in two different outcrop areas: the Ladruñán anticline (Castellote) and the area of "Jaganta" (Las Parras de Castellote) (Fig. 1).

The Mirambel Formation crops out in the easternmost part of the Iberian Range, in the so-called Morella subbasin (Fig. 1B), which belongs to the Cretaceous Maestrazgo Basin (Salas et al., 2001). The unit mainly consists of alluvial and shallow lacustrine deposits with a certain marine influence (lagoon deposits) in the southern outcrops. To judge by the charophyte content, the age of the formation is early Barremian to early late Barremian (Martín-Closas, 1989).

The tracksites are located in different horizons, which cover a wide interval of the local stratigraphic series (Fig.1C). They have been named according to geographical references and are as follows: La Cadena, Voladizo del Crespol, Barrancada del Crespol and Cabezo de Ladruñán tracksites and Senda de la Pastora in the Ladruñán anticline, and the La Refoya tracksites near the village of Jaganta.

MATERIAL AND METHODS

This work studies more than 50 footprints preserved in different tracksites. The studied tracks are referred to by an acronym that is related to the name of the tracksite. These are: La Cadena (**LC**), Voladizo del Crespol (**VC**), Barrancada del Crespol (**BC**), Cabezo de Ladruñán (**CALA**), Senda de la Pastora (**SP**) and the La Refoya (**LR**) tracksites, which include Refoya 1-4, Bancales Refoya (**BR**), and Arroyo de la Refoya 0 (**AR0**).

The terminology used in this paper mainly follows the works of Thulborn (1990) and Marty (2008) for tracks preserved as concave epireliefs (mainly those of BC, CALA3.1, SP, LR, BR and AR0) and the works of Piñuela et al. (2012) and Piñuela Suárez (2015) for tracks preserved as convex hyporeliefs (mainly those of LC, VC and CALA3.2). Only the best-preserved ichnites have been described in detail. Measurements were taken for the footprint length (FL), footprint width (FW), length of the digits (LII, LIII, LIV), and the interdigital angles (II–III, III–IV). The measurements were taken in the field or with the software ImageJ from perpendicular pictures. Three blocks from the Barrancada del Crespol tracksite were mapped reticulating the tracksite in squares of 30 cm, taking perpendicular photographs of each square and then combining them using Adobe Illustrator CS2 software. The tridactyl tracks are classified as small, 10 cm < FL < 20 cm; medium, 20 cm < FL < 30 cm; or large, > 30 cm, following Marty (2008). The mesaxony index was calculated in accordance with Lockley (2009).

RESULTS: DESCRIPTION OF THE TRACKSITES

La Cadena Tracksite

This tracksite is located in the lower-mid part of the Mirambel Formation near the village of Ladruñán (Fig. 2). Several natural casts at the base of a sandstone layer have been recognized. Most of them do not show clear anatomical details, so they cannot be assigned to any concrete group. Nonetheless, some isolated natural casts with a recognizable morphology that come from the trampled layer have been found in the nearby badlands.

LC1 (Fig. 2A-C) is a pentadactyl track, and it is wider (35 cm) than long (32 cm). Digits II-IV are located in the anterior part with an anterior orientation while digits I and V are located in the posterior part,

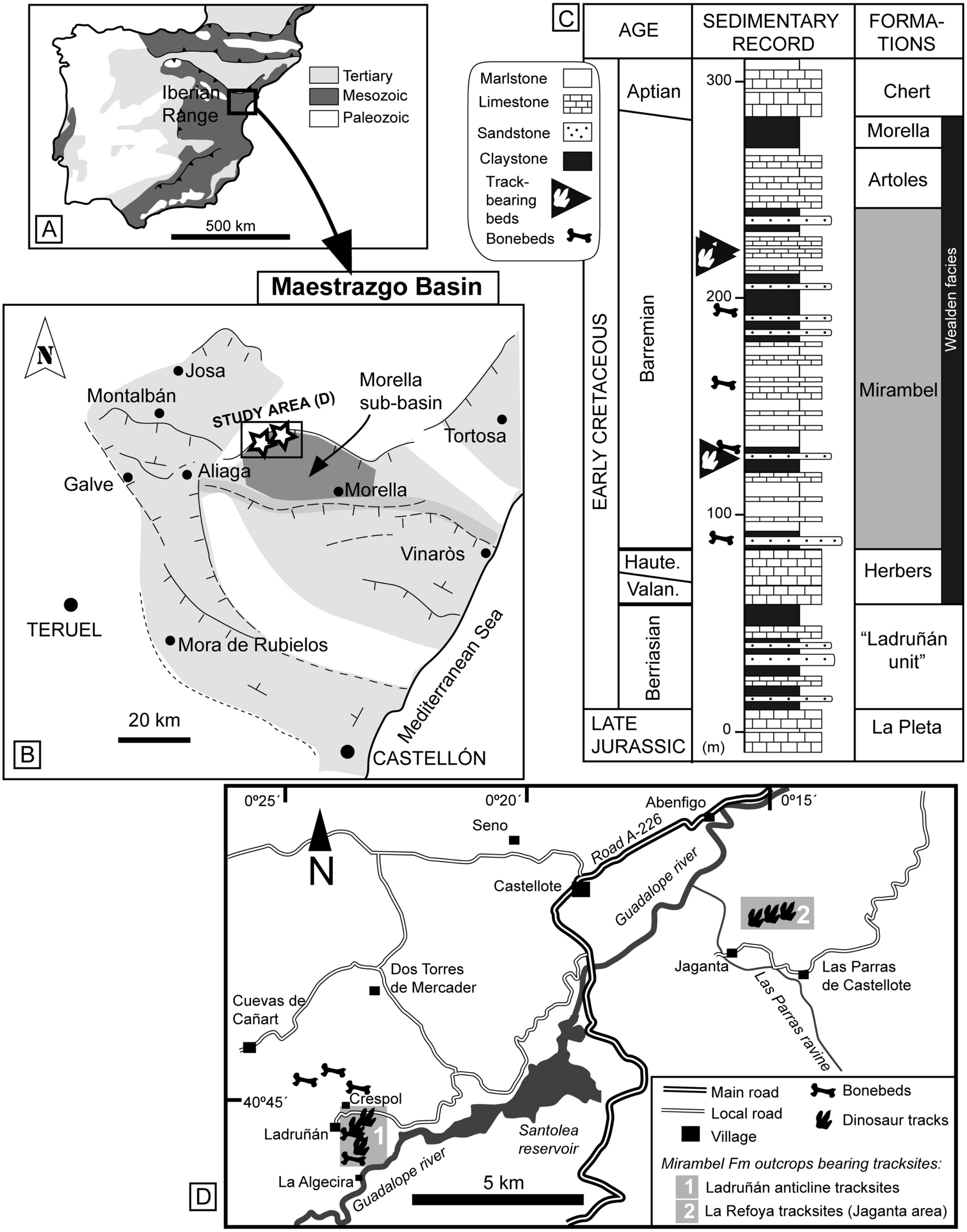

FIGURE 1. Geographical and geological location of the dinosaur tracksites from the Mirambel Formation (Teruel Province, NE Spain) (modified from Gasca et al., 2014). **A**, Iberian Peninsula. **B**, Early Cretaceous Maestrazgo Basin, with the Morella sub-basin and the study area marked. **C**, Chronostratigraphic diagram and sedimentary record of the Ladruñán area. **D**, Geographical sketch of the study area.

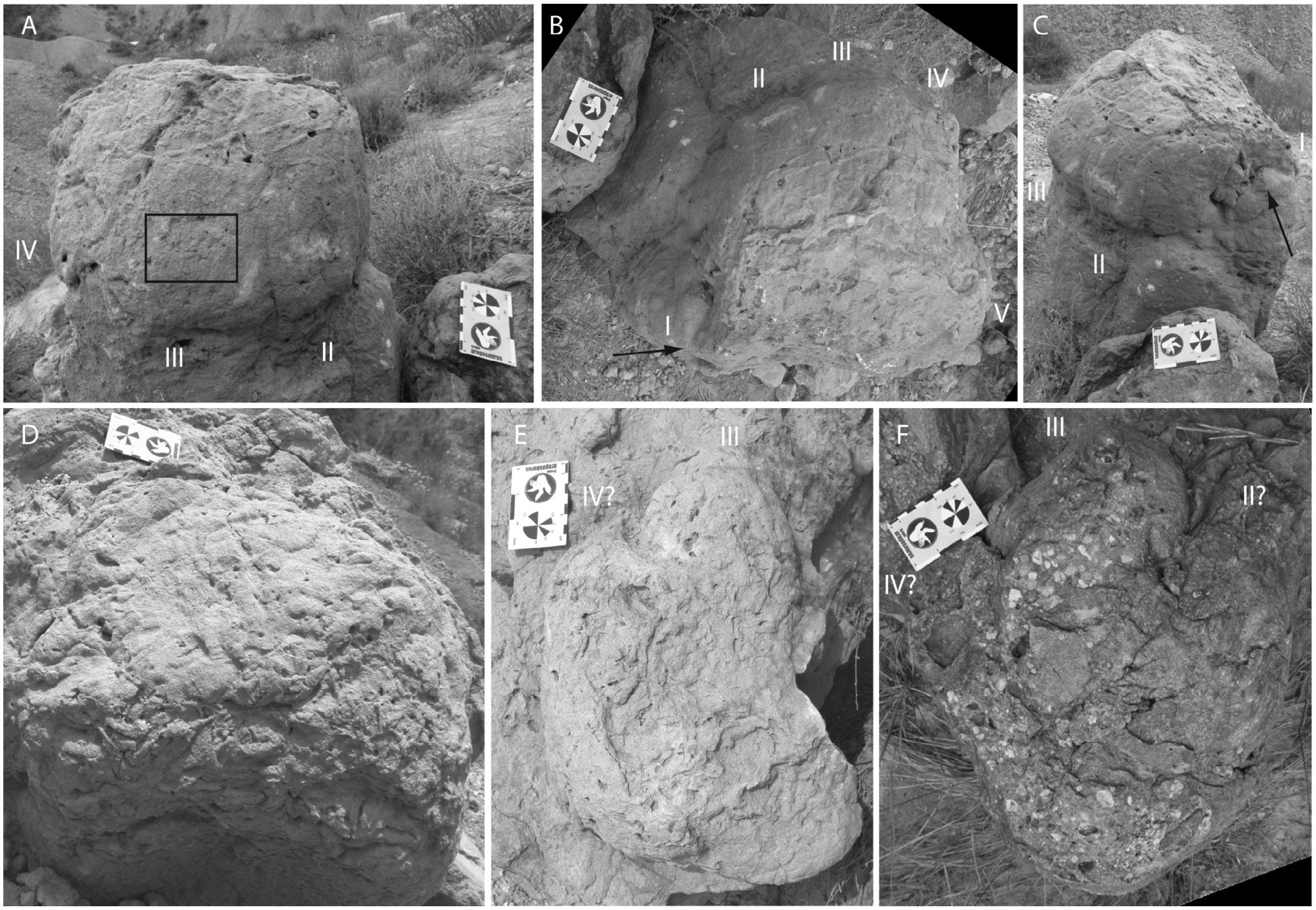

FIGURE 2. Detailed pictures of sauropod (LC1, LC2) and ornithopod (LC3, LC4) tracks from La Cadena tracksite. **A**) LC1 in anterior view. **B**) LC1 in plantar view. **C**) LC1 in lateral view. **D**) LC2 in plantar view. **E**) LC3 in plantar view. **F**) LC4 in plantar view. Scale (card) = 8 cm. ? denotes uncertainty in the interpretation of digits II and IV.

oriented posterolaterally and posteromedially, respectively. The FL/FW ratio is about 0.9. This natural cast bears some striations and some polygonal traces in digit III; these are interpreted as skin impressions. LC2 (Fig. 2D) is a large natural cast, kidney-shaped to semicircular in shape. It is clearly wider than long. No clear digit traces can be discerned. LC3 (Fig. 2E) seems to be a tridactyl natural cast, although digit II? is broken. It is longer (40 cm) than wide (32 cm). LC4 (Fig. 2F) is a tridactyl natural cast, longer (42 cm) than wide (35). In LC3 and LC4, the digit impressions are thick and rounded at the distal ends, and the digit III impression is slightly longer than the lateral ones. In addition, the heel impression is broad and rounded, and there is no evidence of claw marks or phalangeal pads.

Voladizo del Crespol Tracksite

At least 10 footprints preserved as casts at the base of a limestone bed from the upper part of the Mirambel Formation have been identified in this tracksite near the village of Crespol (Fig. 3). According to their size and preservation, two different kinds of track can be discerned. The small-sized (about 10-cm-long) tracks are tetradactyl (Fig. 3A-C), have slender digits with acuminate ends, and possible claw mark impressions. They also show hallux and metatarsal impressions. There is no evidence of phalangeal pads, but this might be due to preservation processes (see discussion). Some of them belong to the same trackway and continue inside the outcrop.

The deformation seen in the tracks has prevented us from measuring any of the morphometric parameters. The medium-to-large-sized tracks are tridactyl (Fig. 3D-F) and are also preserved as casts. In specimen VC1 the length and the width are similar (29 cm). Digit III is longer, and digits II and IV are subequal in length. The three digits are slender and have sharp distal ends. The divarication angle is high, at 84º. By contrast, track VC2 is slightly longer (29 cm) than wide (25 cm), and the divarication angle is lower than that of specimen VC1 (68º). The digits are also slender with sharp distal ends, digit III being the longest and digits II and IV being subequal in length. It is noteworthy that despite being larger in size, these tracks have not deformed the substrate, as the smaller ones have.

Barrancada del Crespol Tracksite

This tracksite consists of nine rocky blocks that have fallen from the same calcareous bed stratigraphically close to the Voladizo del Crespol level (slightly lower than it) and are now located on the slope of the hill (Figs. 4-5). About 25 dinosaur footprints preserved as concave epireliefs have been identified. Blocks 1 and 2 have three and two poorly preserved footprints, respectively, two of which (~45 cm in length) are the largest found on the blocks (large-sized tridactyl tracks). Blocks 3 to 5 contain most of the tracks. The cartography of the blocks (Fig. 4) shows the presence of at least four/five medium-to-large-sized tridactyl footprints (two complete and two/three partially preserved) as well as other undetermined traces in block 3 (Fig. 4A); three partially complete footprints that seem medium-to-large-sized and other undetermined traces in block 4 (Fig. 4B); and two almost complete (one medium-sized and the other large-sized) footprints and other undetermined traces in block 5 (Figs. 4C, 5A). All of them are tridactyl footprints, and their preservation is variable. Some footprints are shallow, with their outline contour poorly defined, whereas others show mud collapse and deformation structures. Block 6 is small and has preserved two partially complete footprints and one complete tridactyl footprint characterized by slender digits and high divarication angles between digits II-IV with mud collapse inside digit III (Fig. 5B), suggesting significant extramorphological features (see discussion). Block 7 preserves an isolated tridactyl track with slender digits and a possible hallux impression (Fig. 5C). Block 8 is a highly dinoturbated area where at least seven tridactyl tracks have been identified. Finally, block 9 contains a partially preserved tridactyl footprint.

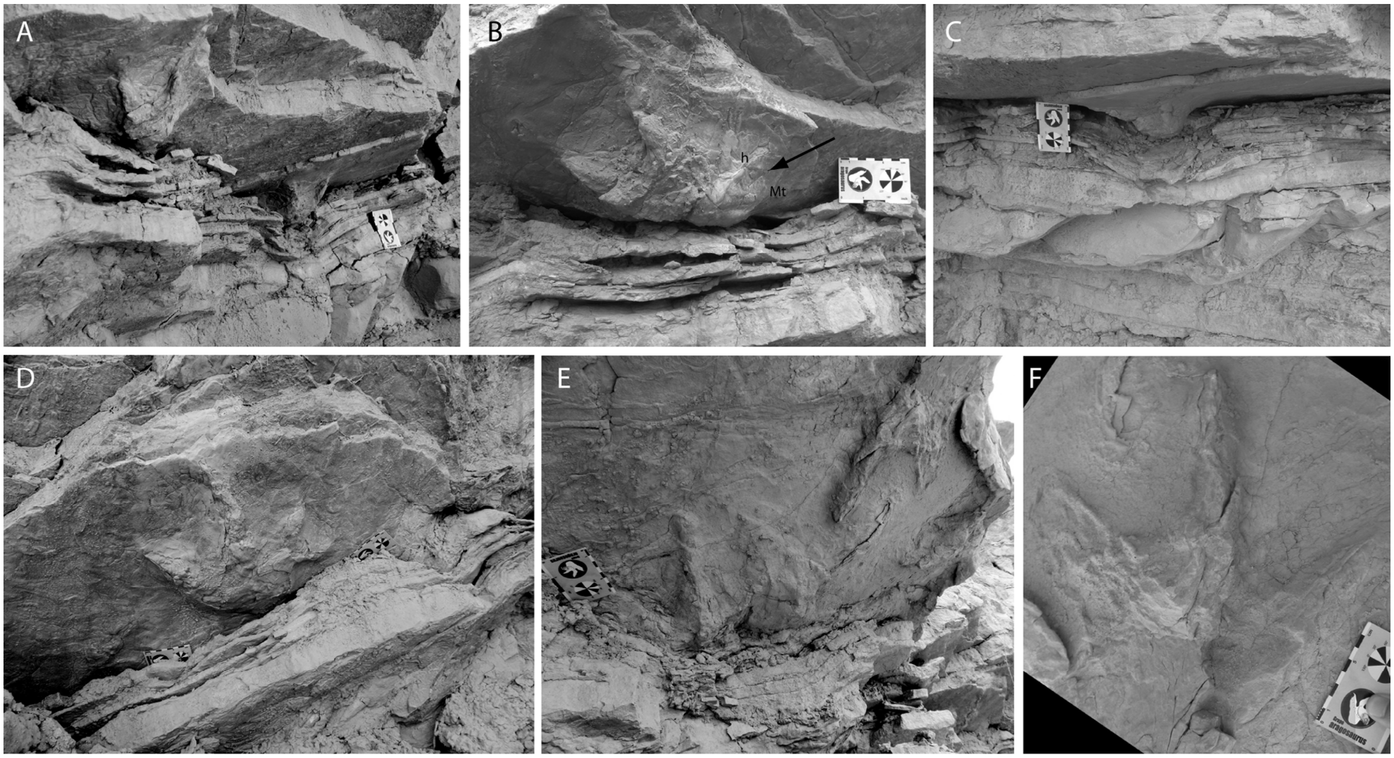

FIGURE 3. Theropod tracks from Voladizo del Cantalar tracksite. **A**) VC4 and VC5 in anterior view. **B**) VC6 in lateral view. **C**) VC5 in lateral view. **D**) VC1 in plantar view. **E**) VC2 and VC3 in plantar view. **F**) VC2 in plantar view. Scale (card) = 8 cm.

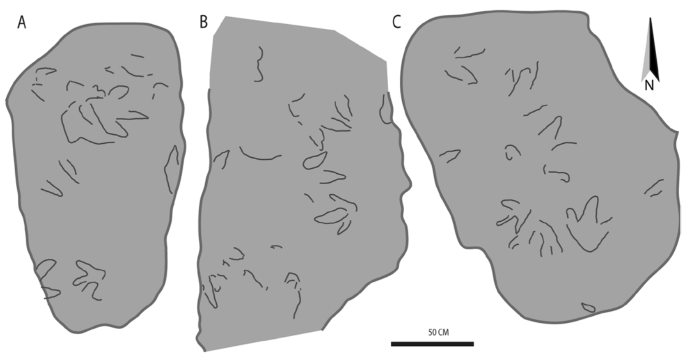

FIGURE 4. Sketch map of blocks 3-5 from Barrancada del Crespol tracksite.

Cabezo de Ladruñán Tracksites

These tracksites consist of three small outcrops with a few footprints, located on the slope of the mountain opposite the village of Ladruñán (Fig. 6). Cabezo de Ladruñán 2 (CALA2) represents the lowest tracksite in the stratigraphic series of Cabezo de Ladruñan, and a large natural cast has been identified. It is preserved at the base of a sandstone layer. No digit traces can be discerned, so it is difficult to assign it to a concrete group (Fig. 6A).

Cabezo de Ladruñán 3 (CALA3) represents an upper level, lateral to the limestone interval comprising the above-mentioned Voladizo and Barrancada tracksites. CALA3.1 comprises three blocks where three tridactyl tracks (one in each block) preserved as concave epireliefs can be discerned. The blocks are from a laminated limestone layer. In block 1, CALA3.1a (Fig. 6C) is longer (27 cm) than wide (19 cm). Digit III is clearly the longest, and digits II and IV are subequal in length. All of them are quite slender and acuminated (V-shaped) at their distal ends. The divarication angle is low (50º). Some constriction denoting the digital pads can be discerned. The mesaxony is medium, with a mesaxony index of about 0.45. In block 2, CALA3.1b (Fig. 6D) is a

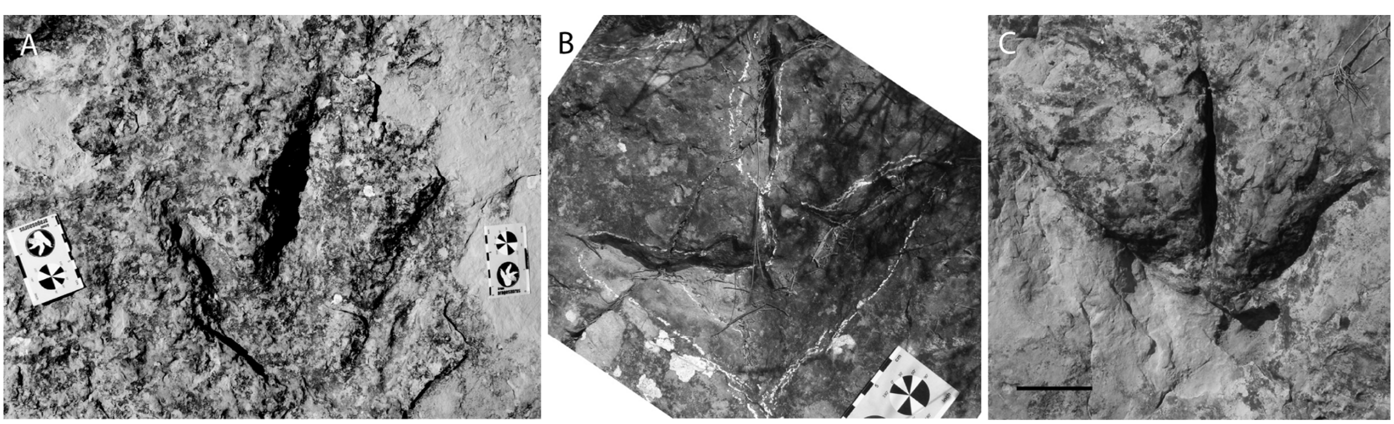

FIGURE 5. Detailed pictures of the footprints from Barrancada del Crespol tracksite. **A**) BC5.1. **B**) BC6.1. **C**) BC7.1. Scale bar = 5 cm. Scale card = 8 cm. Note the mud collapse within the digits in BC6.1. and BC7.1.

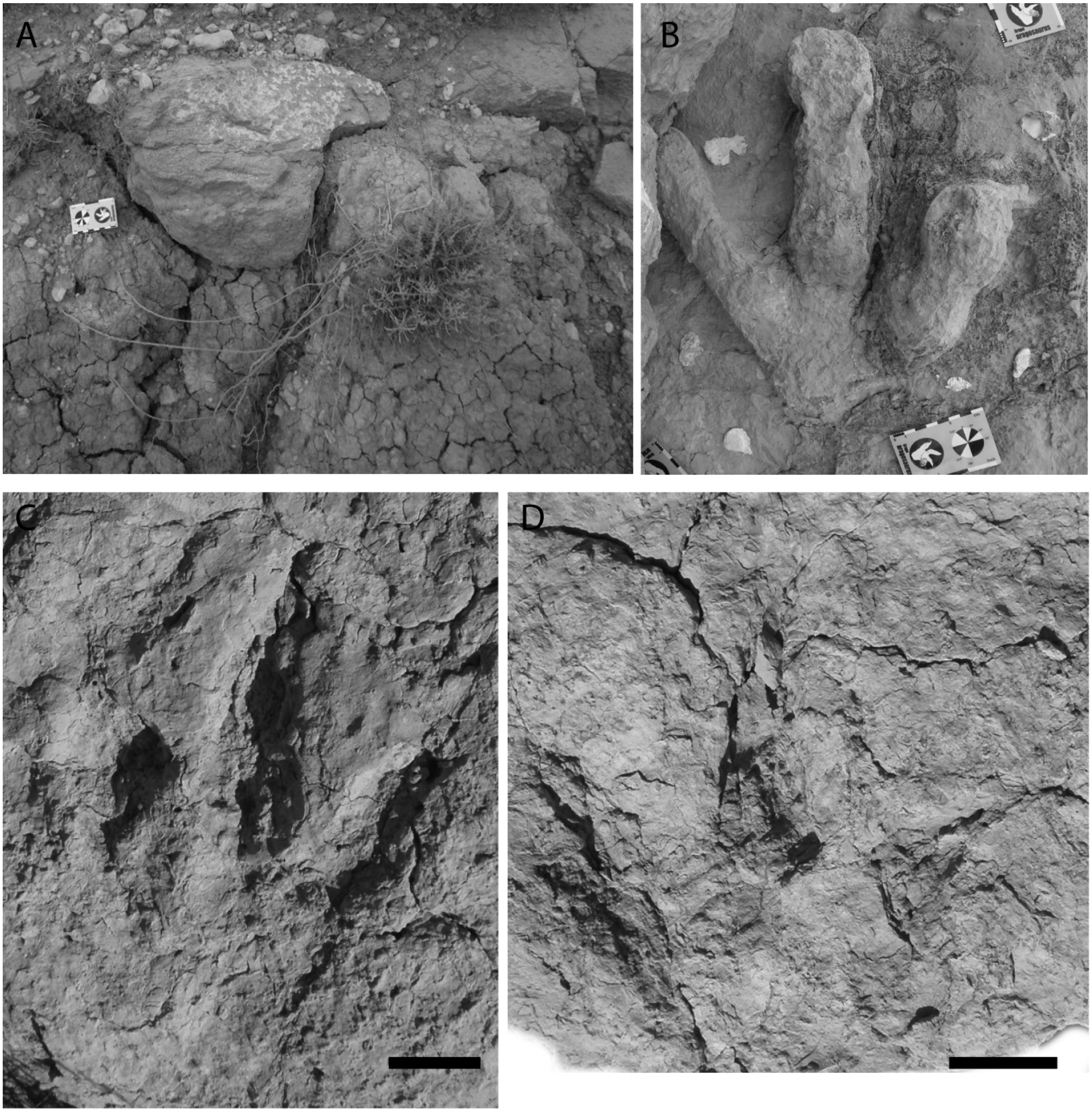

FIGURE 6. Detailed pictures of the footprints from Cabezo de Ladruñán. **A**) CALA2. **B**) CALA 3.2. **C**) CALA3.1a. **D**) CALA3.1b. Scale (card) = 8 cm. Scale bar = 5 cm.

little bit longer (22? cm) than wide (21 cm), although the "heel" mark is poorly preserved, and the total track length might be more. Digit III is the longest, and digits II and IV are almost subequal in length. All three digits are quite slender and acuminate (V-shaped) at their distal ends. The divarication angle (76º) is higher than in CALA3.1a. CALA3.1c is a poorly preserved tridactyl footprint located in block 3.

CALA3.2 (Fig. 6B) is an impressive tridactyl cast preserved at the base of a laminated limestone layer. It is longer (34 cm) than wide (30? cm). Digit III is the longest (22 cm), digits II (17 cm) and IV (19 cm) being smaller and of different sizes. Digits II and III are quite robust/thick and digit IV is slender. The depth of the digits also varies; digits III 5 cm) and II (4.5 cm) are deeper than digit IV (2 cm). The distal ends of the digits are rounded, with evidence of sharp claw traces preserved in digit II, but not well preserved in III or IV. Discrete phalangeal pads can be recognized in digits II (2) and III (3). Digit II shows a slight indentation on the posterior margin. The heel is subtriangular and is shallower (2 cm) than the rest of the footprint. The mesaxony is low (with a mesaxony index of 0.38). The divarication angle II-IV is moderate (67º).

Farther south, another tracksite (Senda de la Pastora) has been found at the same level that bears the CALA3.1 tracks. An isolated tridactyl track can be discerned in a fallen block. It is medium-sized and characterized by slender digits with acuminate endings.

La Refoya Tracksites

These tracksites, located near the village of Jaganta, also consist of small outcrops where some isolated tracks have been identified. All of the tracks are preserved in limestone layers (Fig. 7).

In Refoya 1-2, different casts have been identified at the base of a limestone layer, while an isolated tridactyl track has been identified at the top of the layer. LR1-2.1 is probably preserved as a true track (Fig. 7A). It is mesaxonic, wider (52 cm) than long (45 cm), and presents one pad impression in each digit and one in the heel. The heel impression is rounded and broad. The digit impressions are broad and have blunt claw mark impressions.

In Refoya 3, a trackway with small tridactyl footprints has been identified. The trackway is composed of three footprints characterized by their small size and by clear extramorphological features such as a mud collapse in the hypex and a high interdigital angle. In track 1, there is also a small metatarsal mark.

In Refoya 4, two isolated and poorly preserved tridactyl tracks have been identified.

In Arroyo de la Refoya 0, an isolated track has also been identified (Fig. 7C). AR0.1 is a shallow tridactyl track that is preserved as a true track or shallow undertrack. Digit III is the longest, and digits II and IV are subequal in length.

In Bancales de la Refoya (Fig. 7B), an isolated manus-pes set can be discerned (BR1). It belongs to a quadrupedal animal. The manus print is kidney-shaped to semicircular, while the pes print is quite rounded. These tracks are probably undertracks.

DISCUSSION

Track Preservation

The dinosaur tracks found in the Mirambel Formation show a high variety of modes of preservation related to the environment where they were produced. There are some examples where the tracks are preserved as convex hyporeliefs that represent casts (La Cadena, Voladizo del Crespol, CALA 2, CALA3.2, Figs. 2, 3, 6A-6B), while there are others (Barrancada del Crespol, CALA3.1, Senda de la Pastora and the Refoya tracksites, Figs. 4, 5, 6C-6D, 7) where they are preserved as concave epireliefs, which represent true tracks and probably undertracks. Several studies have pointed out the importance of the type of preservation for the shape of the tracks and its significance for correctly identifying the trackmaker (e.g. Milàn and Bromley, 2006, 2008; Marty et al., 2009; Avanzini et al., 2012; Piñuela et al., 2012; Piñuela Suárez, 2015) and in ichnotaxonomic studies (e. g. Bertling et al., 2006; Díaz-Martínez et al., 2009, 2015; Castanera et al., 2012, 2013a; Vila et al., 2013; Piñuela Suárez, 2015).

Certain points should be clarified regarding both the convex hyporeliefs and the concave epireliefs, especially for inferring the identity of the trackmakers. In the case of the casts from the La Cadena (Fig. 2A-2C) and CALA2 (Fig. 6A) tracksites, the tracks are preserved in sandstone layers as "casts of true tracks or shallow undertracks" (*sensu* Piñuela et al., 2012; Piñuela Suárez, 2015). One of the ideal conditions for preserving anatomical details (digit and claw impressions, phalangeal pads, skin impressions) is when the footprint is produced in a muddy and firm substrate and then covered by sand (Piñuela et al., 2012; Piñuela Suárez, 2015). This would be the case for some of the footprints preserved in La Cadena such as LC1 (Fig. 2A-C), where digital and skin impressions can be discerned. The skin traces seem to have a hexagonal pattern. Skin traces preserved in sauropod tracks have been described in different localities in Spain (Navarrete et al., 2014; Lires et al., 2001; Piñuela Suárez, 2015) and in other localities around the world (see Kim et al., 2010).

Some of the other casts (LC2-LC4, Fig. 2) preserved in the La Cadena or Voladizo del Crespol (Fig. 3) tracksites and the CALA3.2 (Fig. 6B) tracksite do not preserve details such as clear phalangeal pads or skin impressions, despite the fact that some of them do preserve anatomical details such as claw mark impressions or metatarsal traces. The CALA3.2 and Voladizo del Crespol tracksites are preserved in laminated limestone, so one might infer that such features are not preserved as well in calcareous substrates. Another possible explanation is that these footprints in fact represent the cast of the shallow undertracks (*sensu* Piñuela et al., 2012; Piñuela Suárez, 2015). Recent research has shown the significance of the deformation produced in subjacent horizons by the pressure of dinosaur feet (Gatesy, 2003; Milàn and Bromley, 2006, 2008; Jackson et al., 2009; Falkingham et al., 2011; Avanzini et al., 2012; Falkingham and Gatesy, 2014; Piñuela Suárez, 2015). The tracks from Voladizo del Crespol are exceptional examples of preservation (Fig. 3). Some footprints manifest the whole range of types of preservation within the same specimen. It is difficult to determine where the tracking surface is located, but they preserve all the deformed layers above (overtracks) and beneath (undertracks) the footprint. Depending on where the tracking surface is considered to be, the dinosaur would thus have deformed 6 or 7 layers beneath, which is especially significant given that the dinosaur was relatively small (footprint length no more than 10 cm).

In the case of the studied concave epireliefs, it is difficult to determine whether the tracks are preserved as true tracks or shallow undertracks. Some of the studied tracks (Fig. 5) have certain of the features characteristic of true tracks described by Leonardi (1997), such as mud collapse. These features are indicative of deep tracks and do not reflect clear anatomical details, although they may give information about foot motion and substrate consistency (Gatesy, 2003; Avanzini et al., 2012; Piñuela Suárez, 2015). In other cases (Figs. 4, 6C-6D, 7), the absence of details might be taken to indicate an undertrack mode of preservation or to be a consequence of variations in substrate consistency that result in the preservation of fewer details in these calcareous layers (Piñuela Suárez, 2015).

Ichnotaxonomy

According to our description, there are at least two types of tridactyl footprints in the Mirambel Formation. The first presents short, wide digit impressions, and rounded, symmetrical heel impressions (LC3, LC4 and LR1-2.1). These features have been related in the literature with so-called "large ornithopod tracks" (see Díaz-Martínez et al., 2015). Recently, the ichnotaxonomical validity of this group of tracks has been discussed; the use of the ichnofamily Iguanodontipodidae Vialov, 1988, has been accepted, although it remains a matter of debate which ichnogenera belong to this ichnofamily (Lockley et al., 2014; Díaz-Martínez et al., 2015). Footprints LC3 and LC4 are not well enough preserved (LC3 is incomplete) to ascribe them to a concrete ichnogenus within Iguanodontipodidae, but they present features characteristic of this ichnofamily (mesaxonic, tridactyl, subsymmetrical pes tracks, wide or wider than long). Therefore, we classify them as Iguanodontipodidae indet. On the other hand, LR1-2.1 is better-preserved than the latter and presents one pad impression in each digit and one in the heel, and blunt claw marks. These features are typical of the ichnogenus *Caririchnium* Leonardi, 1984 (*sensu* Díaz-Martínez et al., 2015). Nevertheless, the left area of this track is somewhat deformed, and an ichnospecific classification is risky. Thus, we classify LR1-2.1, as *Caririchnium* isp.

The other tridactyl footprints from the Mirambel Formation have

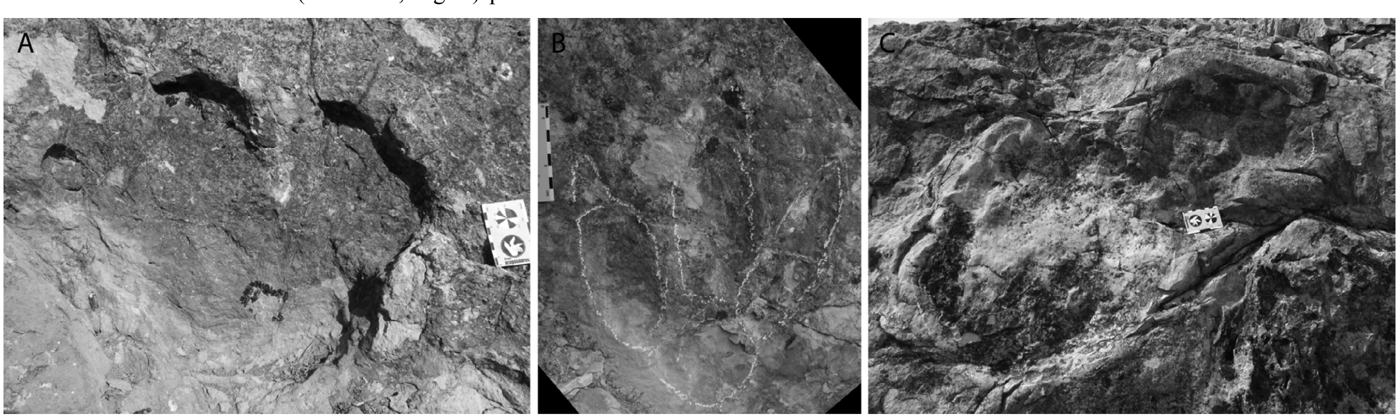

FIGURE 7. Detailed pictures of the footprints from the La Refoya tracksites. **A**) LR1-2.1. **B**) AR0.1. **C**) BR1. Scale (card) = 8 cm.

long, slender digit impressions with an acuminate end and asymmetrical heel impressions. These features are commonly associated with theropod footprints (Thulborn, 1990; Romero-Molina et al., 2003). Almost all the footprints lack anatomical details such as pad impressions and claw marks, and present extramorphological features (mud collapse) that obscure the shape of the trackmaker autopod. When the footprints preserve hallux and metatarsal impressions, the rest of the footprint is deformed (collapsed), suggesting that the mud was very soft. Trying to classify these footprints, in which extramorphological features prevail over morphological ones, within an ichnogenus or ichnospecies is therefore artificial and unwise. Ichnotaxonomically, we consider them to be indeterminate theropod footprints.

However, there is one theropod footprint, CALA3.2 (Fig. 6A), which is very well preserved and shows pad impressions and claw marks. The outline of this footprint is very similar to the sketches of the ichnogenus *Megalosauripus* Lessertisseur, 1955, shown in Lockley et al. (2000, fig. 8). CALA3.2 presents a shape similar to the footprints classified as *Megalosauripus uzbekistanicus* (Gabuniya and Kurbatov, 1982) and *Megalosauripus* isp. by Lockley et al. (2000), found in the Upper Jurassic of the USA, Portugal and Uzbekistan-Turkmenistan. Accordingly, we consider that the Mirambel Formation footprint belongs to the ichnogenus *Megalosauripus*, but that its ichnospecific affinity is not clear. Taking into account that there is only one footprint for comparison, we classify CALA3.1 as *Megalosauripus* isp.

Regarding the sauropod footprints, the kidney-shaped to semicircular tracks LC1 and LC2 have been associated with sauropod manus prints. It should be noted that stegosaur tracks such as those belonging to the ichnogenus *Deltapodus* are also kidney-shaped, and it is difficult to distinguish between the two groups unless the pes prints are preserved (Piñuela Suarez, 2015 and references therein). Nonetheless, stegosaur prints seem to be much wider than long, which is not the case at least in specimen LC1. In addition, BR1 has been identified as a sauropod manus-pes set. Although there are no impressions of the digits in this case, the length/width ratio would not fit with the described stegosaur footprints, where the length/width ratio is substantially higher than in sauropod footprints, and the anterior part of the footprint is wider than the posterior (Piñuela Suarez, 2015). The general morphology of the tracks does not fit with other thyreophoran ichnotaxa described in Cretaceous deposits either (see Pascual et al., 2012; Xing et al., 2013). It is difficult to classify these tracks within any sauropod ichnogenus. Generally, the pes print shape as well as the type of trackway (narrow or wide gauge) have played a major role in sauropod ichnotaxonomy (Lockley et al., 1994; Wright, 2005; Marty et al., 2010), although the manus print shape may also be different enough to distinguish between different ichnotaxa (Castanera et al., 2016). LC1 and LC2 are isolated manus prints, so it is not possible to relate them with any ichnotaxa just on the basis of the manus morphology. In the case of BR1 the manus-pes set is also poorly preserved (no digit traces can be discerned). Thus, we classify them as indeterminate sauropod footprints.

Tracks and Trackmakers of the Mirambel Formation

The final morphology of the footprints is a consequence of a variety of factors (Díaz-Martínez et al., 2009; Falkingham, 2014; Razzolini et al., 2014). Assigning a footprint to a concrete taxonomic category may seem an easy task, but this is not so when a combination of the aforementioned factors apply, especially when comparing dinosaur groups with similar foot arrangements (e.g., tridactyl dinosaurs such as theropods and ornithopods). Most of the tracks preserved in the tracksites from the Mirambel Formation are tridactyl (or tetradactyl in the case of some deep tracks that preserve a hallux impression). Taking into account the general features of the tracks and the skeletal record, theropods and ornithopods are the best candidates for producing this kind of track (Thulborn, 1990; Lockley, 1991). It is noteworthy that of the whole sample, only in two tracksites (see Table 1) have we identified ornithopod tracks. The tridactyl tracks from the other tracksites have the features (high length/width ratio, acuminated digits, presence of claw marks) that have traditionally been used to describe theropod tracks (Thulborn, 1990; Lockley, 1991).

Recent research (Castanera et al., 2013a,b) has shown the difficulties of distinguishing between theropod and ornithopod tracks in older deposits (Jurassic-Cretaceous transition), because some of the general features previously used to differentiate them (e.g. length/width ratio, acuminated digits) may not differ greatly in certain groups of ornithopods (e.g., dryosaurids or basal ankylopollexians). In the Barremian of Teruel two broad groups of ornithopods have been described: medium to large styracosternans (Ruiz-Omeñaca, 2011; Gasca et al., 2015a, 2015b; Verdú et al., 2015) and small-bodied basal forms (Ruiz-Omeñaca et al., 2012). In the former case, the general morphology of the tracks generally assigned to these large-bodied ornithopods (Díaz-Martínez et al., 2015) is quite different from that of theropods. In fact, the ornithopod tracks of the Mirambel Formation resemble those of the typical ornithopod *Caririchnium*. This ichnogenus has usually been associated with basal styracosternans and “iguanodonts” (see Lockley et al., 2014; Díaz-Martínez et al., 2015). In the case of the small ornithopod footprints, some papers have pointed out that some small tridactyl tracks from the Lower Cretaceous of the Valdebrajes tracksite in La Rioja might have been produced by small ornithopods rather than theropods (see Díaz-Martínez, 2011; Pérez-Lorente, 2015). This raises the question of whether some of the small-sized tridactyl tracks described here might have been produced by small ornithopods, bearing in mind the extramorphological features of the tracks. Despite this uncertainty, given the absence of criteria for distinguishing between theropods and basal forms of ornithopods, we have considered that the tridactyl tracks with “theropod” features (Thulborn, 1990; Lockley, 1991) are indeed theropods.

Regarding the sauropod record, LC2 and BR1 are not well enough preserved to allow an interpretation of the trackmakers. Nonetheless, LC1 preserves some features that are worthy of mention. It shows

TABLE 1. Tracksites reported from the Mirambel Formation.

Tracksite	Number of footprints	Mode of preservation	Identification
La Cadena	4	natural casts	Sauropod (LC1; LC2); Ornithopod (LC3, LC4, Iguanodontipodidae indet)
Voladizo del Crespol	10	natural casts + undertrack casts?	Theropods
Barrancada del Crespol	25	undertracks?	Theropods
Cabezo de Ladruñan 2 (CALA2)	1	natural cast + undertrack cast?	undetermined
Cabezo de Ladruñan 3 (CALA3)	4	true tracks (CALA3.1) Cast (CALA 3.2)	Theropods *Megalosauripus* isp.
Senda de la Pastora	1	true tracks	Theropod
Refoya 1-2	1	true tracks	Ornithopod (*Caririchnium*)
Refoya 3	3 (1 trackway)	true tracks	Theropod
Refoya 4	2	shallow undertrack	Theropod
Bancales de la Refoya	1	undertrack	Sauropod
Arroyo de la Refoya 0	1	shallow undertrack	Theropod

digital impressions of five digits, digits II-IV located in an anterior position and digits I and V in a posterior position. This disposition of the digits suggests a horseshoe-type shape. This morphology and the fact that the impression of digit I seems to be small (reduction of the pollex mark) are features typical of titanosauriform sauropods (Wright, 2005; Castanera et al., 2016). Titanosauriform sauropods have also been identified on the basis of osteological remains in the Mirambel Formation (Gasca and Canudo, 2015). Horseshoe-shaped tracks have been identified in the coeval Camarillas Formation in the Maestrazgo Basin; these include specimens MPZ-2013/67 and Mi-3.1m (fig. 6c and 6d in Navarrete et al., 2014). Another significant feature of specimen LC1 is the presence of the digital marks as discrete digit traces. Milàn et al. (2005) reported a sauropod manus cast that lacks any sign of individual digits (except for digit I). This is also seen in the case of MPZ-2013/67 and Mi-3.1m. Taking into account the sauropod footprint record of the Iberian Peninsula (Castanera et al., 2016), LC1 is the second occurrence of a sauropod manus print with individual digits, as these features have only been described in the Galinha tracksite, although the trackmakers of these footprints would be a different group of sauropods, dating from the Middle Jurassic (Santos et al., 2009; Castanera et al., 2016). Recently, Kim and Lockley (2012) have reported sauropod manus prints from the Lower Cretaceous of Korea with discrete digit traces, with digits II-IV also located in an anterior position. LC1 also shows another remarkable feature: namely that it is not preserved as a clear tubular structure (as is the case with the manus print reported by Milán et al. (2005) and specimens MPZ-2013/67 and Mi-3.1m). The main differences lie in the posterior digits (I and V), which did not achieve the same depth during the step cycle (Fig. 2A-C). Thus, digits II-IV sank deeper into the mud than digits I and V. This might be a consequence of the sauropod putting more weight on the anterior part of the manus during the touch-down and weight-bearing phases (Thulborn, 1990); the movement of the manus would thus not be completely vertical (as in the aforementioned specimens). This also suggests that the actual dimensions of the track might be greater than the original dimensions. It is noteworthy that it is precisely in this anterior part where the skin traces (Fig. 2A) have been preserved. Although all the features point to sauropods as the trackmakers of LC1 and possibly of LC2 and BR1, other possible quadrupedal trackmakers such as thyreophorans cannot be ruled out entirely, especially given that stegosaur remains have been described in the Hauterivian-Barremian of the Iberian Range (Pereda Suberbiola et al., 2005) and both stegosaurs and ankylosaurs have sauropod-like metacarpal configurations (Senter, 2010, 2011).

Traditionally, it has been suggested that geological units that preserve a large number of skeletal remains usually have a poor ichnological record and vice-versa (Lockley, 1991). In the Iberian Range, there are some Cretaceous examples, such as the Huérteles Formation and the Enciso Group, where a large number of tracksites have been described while the skeletal record is poor (Hernández Medrano et al., 2008; Moratalla and Hernàn, 2010; Pérez-Lorente, 2015). By contrast, the Mirambel Formation is one of those that preserves both kind of fossils (skeletal and ichnological remains), and thus the information taken from one can complement the other (e.g., Mateus and Milàn, 2010). In this regard, a combination of both sources of data can represent the census for a paleoecological reconstruction of the unit, thus indicating whether the ichnological record is consistent or not with the skeletal record (Lockley, 1991). Some examples have come to light where the skeletal and the ichnological record represent a similar faunal assemblage (e.g., Lockley et al., 1986) while in other cases there are considerable differences between the two records (e.g., Belvedere et al., 2013). Thulborn (1990) warns of possible preservational biases produced in this kind of census (e.g. "favouring bigger and heavier trackmakers") and reports a census of different ichnoassemblages from different geological units around the world, noting that some examples are theropod-dominated. The author states that this finding "is decidedly puzzling because one would expect the predatory dinosaurs to have been outnumbered by plant-eaters" and suggests a number of hypothetical reasons for it, such as behavioural or environmental factors or possible misinterpretations to the detriment of ornithopod tracks.

This is precisely the case with the Mirambel Formation, where most of the footprints recorded in the surveys seem to be theropod tracks (Fig. 8; Table 1). Assuming that all the footprints were indeed made by theropods, it is remarkable that the skeletal record suggests a predominance of ornithopods (Fig. 8; Table 2). These discrepancies between the ichnological and the skeletal record might be due to an

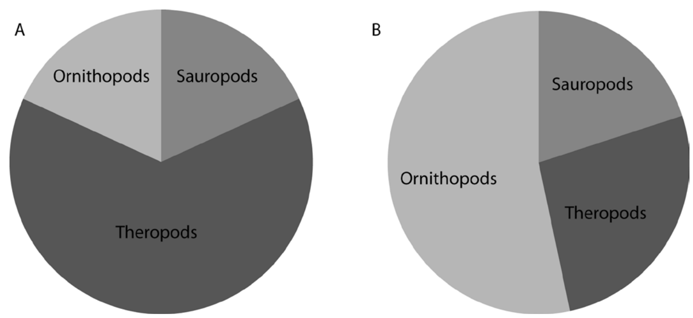

FIGURE 8. Circular diagrams representing the occurrence of the main taxa (Theropoda, Ornithopoda and Sauropoda) in the tracksites (**A**) and skeletal sites (**B**). The number of tracksites recorded for each group is 2-Sauropoda, 7-Theropoda and 2-Ornithopoda, whereas the number of sites is 3-Sauropoda, 4-Theropoda and 8-Ornithopoda for the skeletal record.

TABLE 2. Sites with osteological remains reported from the Mirambel Formation.

Fossil bone site	TAXA	Reference
Ladruñán 0 (Castellote)	Titanosauriformes (Sauropoda)	Gasca and Canudo 2015
Ladruñán 8 (Castellote)	Titanosauriformes (Sauropoda)	Gasca and Canudo 2015
Cerro Marín (Mirambel)	Titanosauriformes (Sauropoda)	Gasca and Canudo 2015
Ladruñán 0 (Castellote)	Spinosauridae (Theropoda)	Infante et al., 2005
Ladruñán 4 (Castellote)	Allosauroidea (Theropoda)	Infante et al 2005
Ladruñán 3 (Castellote)	Carcharodontosauridae (Theropoda)	Gasca et al., 2014
Camino de la Algecira (Castellote)	Theropoda	Bauluz et al., 2014
Camino de la Algecira (Castellote)	Styracosterna (Ornithopoda)	Bauluz et al., 2014
La Tolellera (Tronchón)	Styracosterna (Ornithopoda)	Gasca et al., 2015a
Ladruñán 6 (Castellote)	Styracosterna (Ornithopoda)	Gasca et al., 2015a
Ladruñán 8 (Castellote)	Styracosterna (Ornithopoda)	Gasca et al., 2015a
Ladruñán 10 (Castellote)	Styracosterna (Ornithopoda)	Gasca et al., 2015a
Barrancada del Convento (Castellote)	Styracosterna (Ornithopoda)	Gasca et al., 2015a
Barranco del Abad (Mirambel)	Styracosterna (Ornithopoda)	Viera 1991
"Ejulve" (Ejulve)	Styracosterna (Ornithopoda)	Lapparent et al., 1969

ecological signal or a preservational bias (Belvedere et al., 2013). However, it should be borne in mind that the small amount of data might not be representative enough to register a real ecological signal. A preservational bias against ornithopod and sauropod tracks might be a possible explanation, since theropod tracks also dominate in other ichnoassemblages that have been described. For instance, Moratalla and Hernàn (2010) suggest that theropods are the dominant dinosaurs in the Huérteles Formation and the Enciso Group (Lower Cretaceous of the Iberian Range), probably due to the higher activity entailed by their searching/hunting behaviour. Finally, possible misidentifications of certain tridactyl tracks that might have been produced by small ornithopods, resulting from the lack of criteria for distinguishing them, should also be kept in mind.

CONCLUSIONS

Fieldwork carried out during the year 2011 has allowed the discovery of 11 new dinosaur tracksites in the Mirambel Formation. These new tracksites considerably increase the dinosaur fossil record of the formation, which was overlooked until recent years. The footprints are preserved in a variety of environments that have allowed different types of preservation: true tracks, shallow undertracks, natural casts and undertrack casts. Ichnotaxonomic analysis has allowed identification of the theropod ichnotaxon *Megalosauripus* isp. and the ornithopod ichnotaxa *Caririchnium* isp. and Iguanodontipodidae indet. The other tracks have been classified as indeterminate theropod and sauropod tracks. The ichnological record is dominated by theropods, with about 80% of the tracks. These data are not concordant with the osteological record, according to which ornithopod dinosaurs seem to be dominant in the Mirambel Formation. Further work is needed in order to understand whether this discrepancy represents a real ecological signal or results from possible biases associated with the paleoenvironmental conditions where the tracksites and osteological sites were preserved, or whether it is just a bias produced by the small sample of sites.

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