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Integrated overview of the vertebrate fossil record of the Ladruñán anticline (Spain): Evidence of a Barremian alluvial-lacustrine system in NE Iberia frequented by dinosaurs

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ABSTRACT

The Barremian Mirambel Formation (Maestrazgo Basin, Iberian Chain, NE Spain) preserves different types of dinosaur and other vertebrate fossils (skeletal, eggshell and ichnological remains). A total of 31 vertebrate fossil sites and tracksites have been recognized within this unit in the Ladruñán area (Teruel province). Detailed stratigraphic, sedimentological and micropalaeontological analyses have also been performed in the unit. A vertical sedimentary trend from alluvial-dominated facies (meandering river and related overbank areas) to palustrine-lacustrine facies and back has been defined for the Mirambel Formation in this area. The depositional system was located close to the coastline, as indicated by sporadic marine input in the lower part of the unit. Most fossil remains were recovered by surface collection as well as by the usual techniques used for macrovertebrate excavations. The dinosaur record identified comprises ornithopods, theropods and sauropods. Four distinct track-bearing horizons have been identified. The heterolithic nature and aggradation characteristic of the Mirambel Formation are favourable factors for track formation and preservation. The dinosaur tracks consist of convex hyporeliefs or concave epireliefs that record the trackmakers as they frequented lakeshores, alluvial floodplains and fluvial courses. Macrovertebrate bonebeds occur in alluvial settings (poorly-drained floodplains and "ponds"). Microvertebrate concentrations are located in shallow lacustrine deposits. Isolated skeletal elements can be found in a great variety of deposits. Attritional accumulation in a low-energy depositional context is the general pattern of origin for the bone-bearing fossil sites of the Mirambel Formation. As regards the genetic framework, the resulting skeletal assemblages are predominantly the result of physical factors, with sedimentology as a key factor, rather than biological phenomena. Eggshell fragments are frequent throughout the unit but are clearly more common in palustrine-lacustrine deposits. These can be taken to be parautochthonous bioclasts from nearby areas and might be indicative of the preferential affinity of the egg-layers for wetlands and lakeshores.

1. Introduction

Dinosaur fossil sites are often analysed with the focus on the dinosaur remains themselves (i.e. for systematic or palaeobiological purposes), whereas it is less common to find other, holistic approaches that integrate palaeontology (systematics, taphonomy, palaeoecology) and sedimentary geology to provide valuable information on palaeocommunities and palaeoenvironments. Depositional environments, preservational patterns and taphonomic modes are key issues on which to base the reconstruction of the original ecological scenario in fossil deposits (e.g. Eberth and Currie, 2005; Csiki et al., 2010; Rogers and Brady, 2010). Furthermore, the spatial and temporal resolution of the fossil assemblage, the segment of the original biota represented by the fossil sample, and additional information on biological agents can be established through successive levels of inference to yield a thorough

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palaeoecological analysis of palaeontological localities (Berensmeyer and Hook, 1992). Vertebrate skeletal concentrations, or "bonebeds", provide a unique opportunity to explore an array of palaeobiological and geological questions, such as the existence of genetic links between local sedimentary dynamics and bonebed formation, or how vertebrate palaeoecology and behaviour manifest themselves in bone-rich deposits (Rogers and Kidwell, 2007). The tetrapod track record gives us invaluable information about the trackmakers (i.e. their identity, locomotion and behaviour). Moreover, it contributes to the reconstruction of the palaeoenvironment and its palaeoecological characteristics, and represents an extremely useful complement to the skeletal record (Castanera et al., 2013; Falkingham, 2014; Melchor, 2015). Further, eggs and eggshells provide limited information on the palaeobiodiversity of fossil environments, but give valuable data on the palaeoecology of the egg layers and may be the source of useful information on the palaeoenvironment (Erben et al., 1979; Mikhailov, 1997).

The Barremian Mirambel Formation is a Cretaceous sedimentary unit in the Iberian Chain (NE Spain) that preserves different types of dinosaur and other vertebrate fossils (skeletal, eggshell and ichnological remains). Accordingly, the palaeoenvironmental information from one type can complement that from another (e.g. Mateus and Milàn, 2010). The unit crops out in the Ladruñán anticline (Teruel province), providing a remarkable number of vertebrate fossil localities bearing bones, ichnites and/or eggshells in a limited area. The combined presence of the three types of fossil remains is uncommon (Vila et al., 2011, 2012, 2013), and this case is unmatched in its temporal and regional context.

The first dinosaur remains from the Mirambel Formation were discovered in the second half of the 20th century (Lapparent et al., 1969). Recent studies have notably increased what is known of the dinosaur record from the unit, reporting fossil remains from theropods (Infante et al., 2004; Gasca et al., 2014), ornithopods (Viera, 1991; Gasca et al., 2009; Bauluz et al., 2014; Gasca et al., 2015) and sauropods (Gasca and Canudo, 2015). Up to now, roughly 20 fossil sites bearing skeletal remains have been cited, as well as an occurrence of dinosaur eggshell (Moreno-Azanza et al., 2015) and 11 dinosaur tracksites (Castanera et al., 2016).

In this paper we present an integrated overview of the various dinosaur fossil sites in the Ladruñán anticline, specifying their stratigraphic setting, palaeoenvironments and taphonomic features. Additional information is also provided from local sedimentological observations and from other fossils (micropalaeontological analysis). Furthermore, the relationships between the types of vertebrate fossil sites and palaeoenvironments, their origins and preservational histories are considered. Finally, issues relating to the evolution of the depositional system as well as some palaeoecological inferences are discussed.

2. Geological setting

The studied outcrops of the Barremian Mirambel Formation are located around the village of Ladruñán (Castellote municipality, NE Teruel province, NE Spain), in the eastern part of the Iberian Chain (Fig. 1A). Palaeogeographically, this area belongs to the northwestern margin of the Morella sub-basin (Fig. 1B), within the Maestrazgo Basin (Salas et al., 2001).

The uppermost Jurassic-Lower Cretaceous stratigraphic units in the Ladruñán area crop out in a N-S-trending anticline with periclinal closure to the north (Richter and Teichmüller, 1933) (Figs. 1C, D and 2). From bottom to top, they encompass the shallow marine facies of the Tithonian–Berriasian La Pleta Formation, the non-marine Berriasian Ladruñán unit, the Early Cretaceous (Valanginian–Barremian) Wealden facies (including the lacustrine Herbers Formation, the alluvial-lacustrine Mirambel Formation, the shallow marine Artoles Formation, and the transitional Morella Formation) and the Aptian Urgonian facies (i.e. Chert Formation) (Martín-Closas, 1989; Salas et al., 2001).

The ages of the Early Cretaceous continental units were determined by the study of the charophyte assemblages from the local series of Ladruñán as well as from other nearby sections (Martín-Closas, 1989). In the case of the Mirambel Formation under study, the age is early Barremian to early late Barremian, corresponding to the *Atopochara trivolvis triquetra* biozone (Martín-Closas, 1989; Riveline et al., 1996). Further up in the series, the age of the Morella Formation is late Barremian, as was recently shown by palynological studies performed in other sections of the Morella sub-basin (Castellón province, Villanueva-Amadoz et al., 2015).

The Mirambel Formation is almost 200 m in thickness, and there is a high degree of lateral bedding continuity in the outcrops of the Ladruñán anticline (see Figs. 1–2 and Supplementary data S1–S3). The unit is formed by an alternation of successive detrital alluvial intervals and carbonate-rich palustrine-lacustrine intervals (see A to G in Fig. 1C and S1). The lowermost interval A corresponds to a 15-m-thick succession of alluvial sandstones and lutites. To the south (e.g., Los Menires reference section) this detrital interval intercalates with shallow lacustrine grey marls and limestones, which become dominant to the east (Martín-Closas, 1989; Castanera et al., 2016). The basal detrital interval A is overlain by a 30-m-thick interval B formed by shallow lacustrine and palustrine facies, including grey marls with reddish mottling and grey burrowed and rooted limestones. The unit continues with a 15-m-thick alluvial interval C, including red, yellowish and grey lutites and ochre sandstones. The next 50 m are lacustrine-palustrine massive marls and limestones (interval D), which are overlain by a 20-m-thick interval E of alluvial detrital facies. The unit ends with a 12-m-thick interval F formed by shallow lacustrine grey massive marls and limestones and laminated limestones, and a 10-m-thick interval G of detrital alluvial facies.

3. Materials and methods

A total of 31 vertebrate fossil sites and tracksites are recognized within the Mirambel Formation in the Ladruñán area. Their precise geographical location and stratigraphic position in three reference sections (Estrecho, Cabezo Ladruñán and Los Menires) are included in Fig. 2 and Supplementary material S1. The complete list of sites including sedimentological and palaeontological information is summarized in Supplementary material S2 and S3. A detailed description of the studied fossil record is provided in Supplementary material S4.

The fossil material recovered for this work is now housed entirely in the Natural History Museum of the University of Zaragoza (MPZ, Museo de Ciencias Naturales de la Universidad de Zaragoza). Previously studied specimens from some fossil sites in the Ladruñán area (Gasca et al., 2014; Gasca and Canudo, 2015) are housed in museums in Teruel province: the Museo Aragonés de Paleontología (fossils from the sites of Barrancada del Convento and Ladruñán 6 and 8) and the Museo de Mas de las Matas (one sauropod bone from Ladruñán 0 site).

Most palaeontological and geological data were collected during fieldwork campaigns between 2008 and 2011. Most vertebrate remains were recovered by means of surface collecting during palaeontological prospections. Furthermore, special efforts were focused on the macrofossil bonebed Camino de la Algecira (CALG). The fossil remains were extracted from the site by the usual techniques for macrovertebrate excavations (Eberth et al., 2007b). First, an excavator fitted with a tilting bucket removed the overburden. The extraction of elements was carried out with the aid of tools such as hammers, chisels or gravers, after consolidating all fossil remains with acrylic adhesives (Paraloid B-72, a copolymer of methyl acrylate and ethyl methacrylate, and cellulose nitrate adhesive), as well as plaster jackets in the case of larger elements. Typical fieldwork data (e.g., coordinates, orientation, preservational features) were collected for the characterization of the bonebed (Eberth et al., 2007a).

The collection of the field data was complemented with detailed stratigraphic and sedimentological analyses performed in key fossil sites, as well as the study of microfossils obtained by washing and sieving sediment samples along the entire Mirambel Formation (see

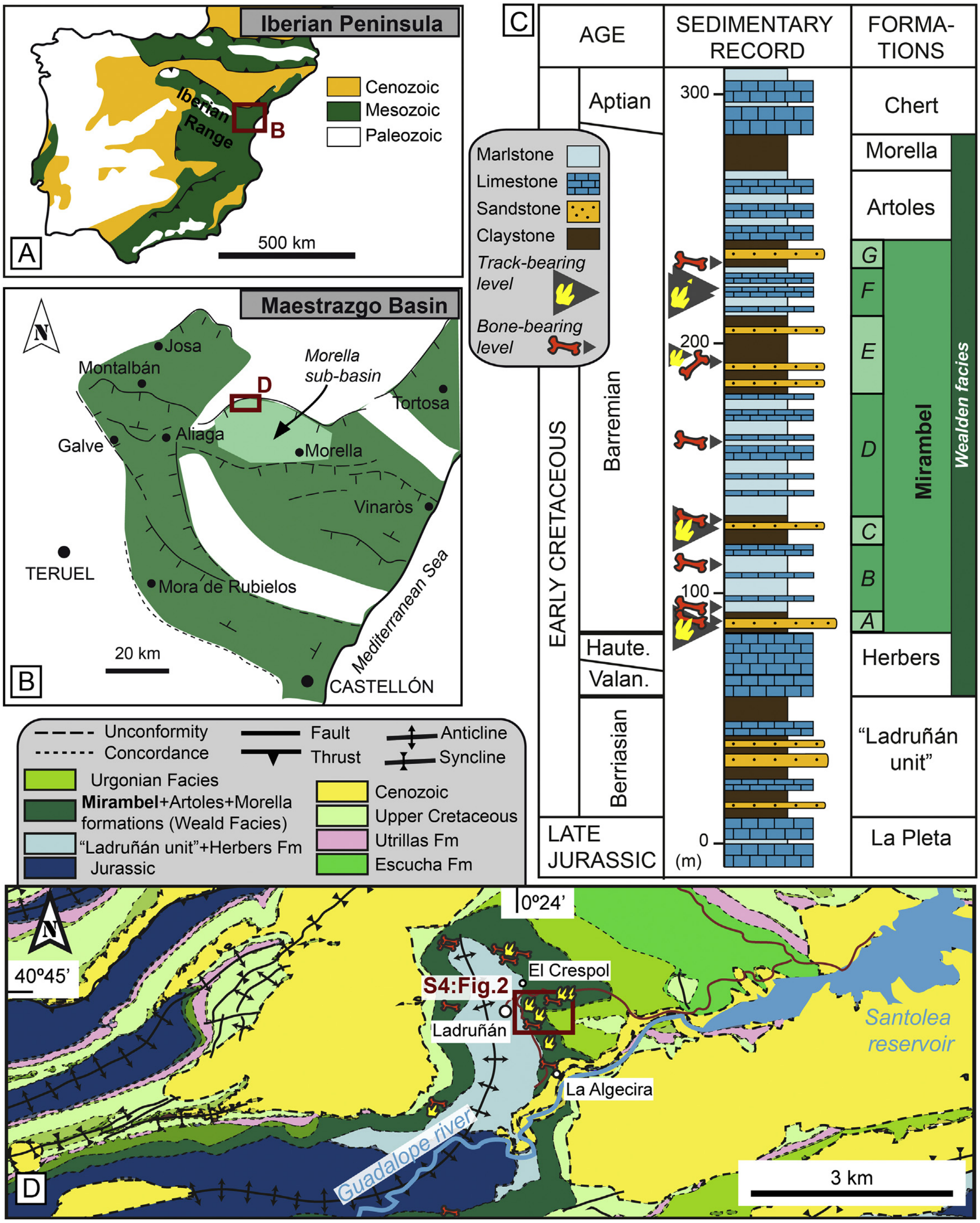

Fig. 1. A and B, geographical and geological location of the dinosaur tracksites from the Early Cretaceous Mirambel Formation (Teruel Province, NE Spain) within the Morella sub-basin of the Maestrazgo Basin (modified from Gasca et al., 2014). C, synthetic log of the uppermost Jurassic-Early Cretaceous sedimentary units in the Ladruñán area, including the distribution of the main dinosaur tracksites and fossil sites described in the Mirambel Formation in previous works. Within the Mirambel Formation, A to F indicate successive detrital and carbonate-rich intervals (see also S1). D, geological mapping of the studied area, indicating the area included in Fig. 2 of the Supplementary material S4.

Supplementary material S3). Samples of 2 kg were systematically taken from successive soft horizons (lutites, marls and poorly-cemented sands), and these were processed using 2% hydrogen peroxide and sieves of 2.0, 1.0 and 0.5 mm mesh. A significant amount of sediment (i.e. 500 kg) was also recovered from the most remarkable microfossil bonebed (i.e. Los Menires reference section, Moreno-Azanza et al., 2015). The skeletal remains and eggshell fragments were sorted under a binocular microscope. To complete the micropalaeontological study, other microfossils of palaeoecological or biostratigraphic significance were identified, such as charophyte and ostracod remains (see Supplementary information S4). Selected specimens were mounted, gold-coated and viewed with a JEOL 6400 SEM at the University of Zaragoza, using both secondary and backscattered electrons.

The ichnological terminology used in this paper mainly follows the work of Thulborn (1990), Marty (2008) and Piñuela et al. (2012). Measurements were taken directly during fieldwork or else by means of the digital analysis of photographs using the software ImageJ. Detailed methods and measurements are described in Castanera et al. (2016).

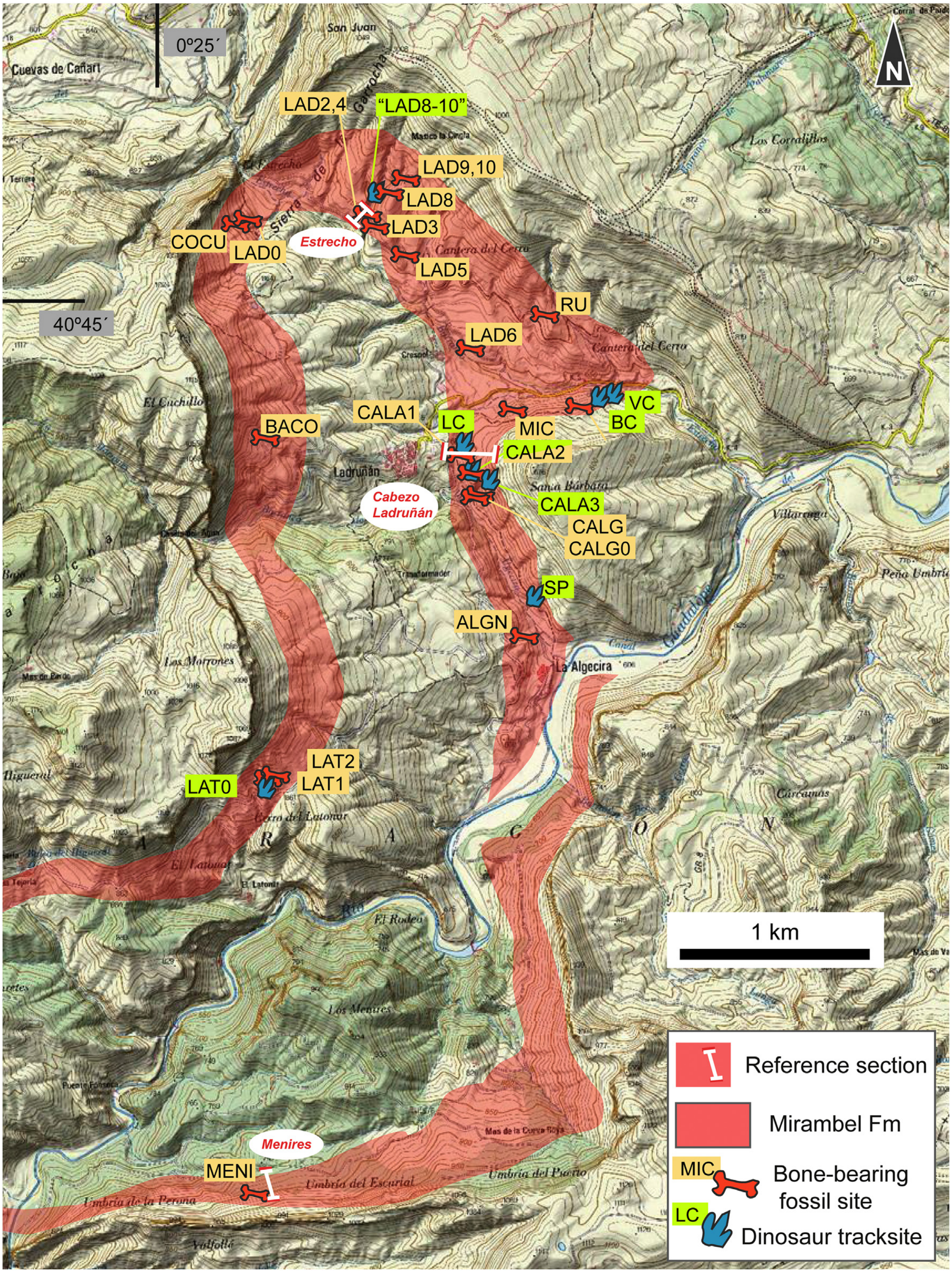

Fig. 2. Detailed geographic location of the 31 fossil sites and tracksites within the Mirambel Formation in the Ladruñán area. Topographic map (1:25,000) obtained from SIGPAC, Government of Spain (available at http://sigpac.mapa.es/fega/visor/). Abbreviations: LAT1 – Cerro Latonar 1, BACO – Barrancada del Convento, LAD0 – Ladruñán 0, LAD3 – Ladruñán 3, LAD6 – Ladruñán 6, LAD2 – Ladruñán 2, LAD4 – Ladruñán 4, LAT2 – Cerro Latonar 2, LAD5 – Ladruñán 5, COCU – Collado del Cuchillo, MENI – Los Menires, LAD1 – Ladruñán 1, CALG0 – Camino de la Algecira 0, CALA1 – Cabezo Ladruñán 1, CALG – Camino de la Algecira, LAD8 – Ladruñán 8, LAD9 – Ladruñán 9, LAD10 – Ladruñán 10, CALA2 – Cabezo Ladruñán 2, ALGN – La Algecira Norte, MIC – Mirador del Crespol, RU – Masico El Rullo, PEPE – Pepe, LAT0 – Cerro Latonar 0, LC – La Cadena, LAD8-10 – "Near LAD8-10", CALA2 – Cabezo Ladruñán 2, CALA3 – Cabezo Ladruñán 3, SP – Senda de la Pastora, BC – Barrancada del Crespol, VC – Voladizo del Crespol.

Photogrammetric images were obtained using Agisoft PhotoScanTM software (version 0.8.5.1423). Photogrammetric models were also imported into MeshlabTM for scaling and ParaviewTM to generate false-colour depth maps and contour lines.

4. Vertebrate ichnological record

Seven dinosaur tracksites have been identified within the Mirambel Formation in the Ladruñán anticline (sites 24–25 and 27–31 in S2). The tracks are located in four stratigraphic horizons (track levels tr1–tr4 in S1) and are preserved in a variety of facies that have allowed different types of preservation: true tracks, shallow undertracks, natural casts and undertrack casts. Moreover, an isolated ornithopod cast preserved in grey limestones was found ex-situ and is referred to as "Near LAD8-10" (site 26 in S2). This probably came from a layer within the middle part of the Mirambel Formation between tr2 and tr3 (see palustrine-shallow lacustrine interval D in S1).

The outcrops of the Mirambel Formation are mostly exposed in cross section, which is determinant in the type of track findings. Casts (convex hyporeliefs) are the most common form of preservation, whereas the casual finding of tracks as concave epireliefs has been possible only on stratification surfaces comprising detached rocky blocks (track level 4). Track formation requires a substrate that is soft enough to be deformed by the animal but firm, cohesive and dewatered enough to retain the shape of the foot until the sediment can infill the cavity (Currie et al., 1991; Nadon, 2001). The heterolithic nature of the Mirambel Formation is a favourable factor for track formation and preservation (Nadon, 2001). Rapid aggradation (at least in some stages) must have also taken place; this is required to ensure preservation potential because exposed tracks degrade rapidly after formation (Laporte and Behrensmeyer, 1980; Nadon, 2001). A detailed description of the ichnological record was recently published by Castanera et al. (2016). Further detail on the track descriptions and the sedimentology of the tracksites is provided in the Supplementary information S4 (Chapter 1.1).

5. Skeletal record

Of the studied record, 22 fossil sites (sites 1–7 and 9–23 in S2) have yielded vertebrate skeletal remains, contained in 12 different bone-bearing stratigraphic levels. The study of the dinosaur bone record takes the form of a general description of the main bonebeds and their inclusion within a classification of the taphonomic modes present in the Mirambel Formation. Taphonomic modes are recurring preservational and taphonomic features and geological associations among fossils from a stratigraphic interval that reflect premortem (biotic and environmental) and postmortem (biostratinomic and diagenetic) influences, as well as basin-scale controls on sedimentary budget and accommodation (Eberth and Currie, 2005). The taphonomic modes of the Mirambel Formation are described in the Supplementary information S4 (Chapter 1.2). The relative abundance of the differentiated types of taphonomic modes (A to E) and their distribution among the main palaeoenvironments are shown in Fig. 3.

6. Eggshell record

A total of 18 distinct horizons host eggshell fossils (see Supplementary information S1). The richest levels, with up to 50 eggshell fragments per 2 kg of sediment, correspond to lacustrine or palustrine deposits, whereas fragments are scarce or absent in alluvial deposits. There is no evidence of autochthonous eggs or eggshell concentrations (i.e., nests or clutches). Details on the parataxonomy and taphonomy of the eggshells are provided in Supplementary information S4.

Eggshell fragments are the most abundant vertebrate fossil remains in most of the samples, and are present in beds both where bone concentrations occur (e.g., Los Menires) and where they do not (e.g. samples CL2, SM8). Eggshell accumulations are more common in palustrine and lacustrine levels, as in other non-marine Barremian units from nearby sub-basins (Canudo et al., 2010; Moreno-Azanza et al., 2014a, 2015). This contrasts with the global record, where eggshell fragments and eggs are often recovered in fluvial and alluvial deposits (Imai et al., 2015 and references within).

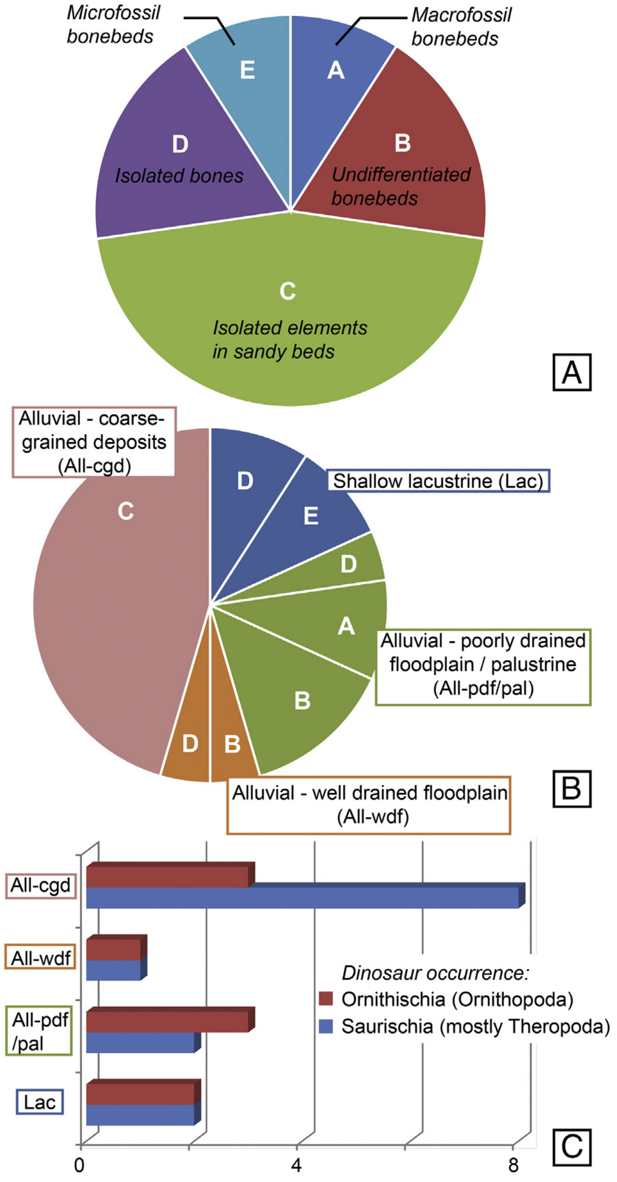

Fig. 3. Taphonomic modes and palaeoenvironments of the Mirambel Formation. A, pie chart showing relative abundances of the taphonomic modes. B, pie chart showing the distribution of the fossil localities and their taphonomic modes within palaeoenvironments. C, bar graph showing the number of dinosaur occurrences within each palaeoenvironment.

7. Discussion

7.1. Evolution of the depositional system and palaeoenvironments

Taking into account all the palaeoenvironmental data provided by the vertebrate associations, the additional data from ostracod and carophyte associations (see S4), as well as the sedimentological data, one can identify a vertical sedimentary trend from alluvial-dominated facies (meandering river and related overbank areas) to palustrine-lacustrine facies and back for the Mirambel Formation (Fig. 4).

The depositional system was located close to the coastline, as indicated by sporadic marine input in the lower part of the unit. The marine influence is suggested by levels bearing ostreids (Fig. 4), as occurs in the Cerro Latonar outcrop (see S4: Fig. 1A) and the Camino de la Algecira bonebed (see S4: Fig. 6), as well as by the presence of allochthonous benthic foraminifera in the fossil assemblage of Los Menires microfossil bonebed.

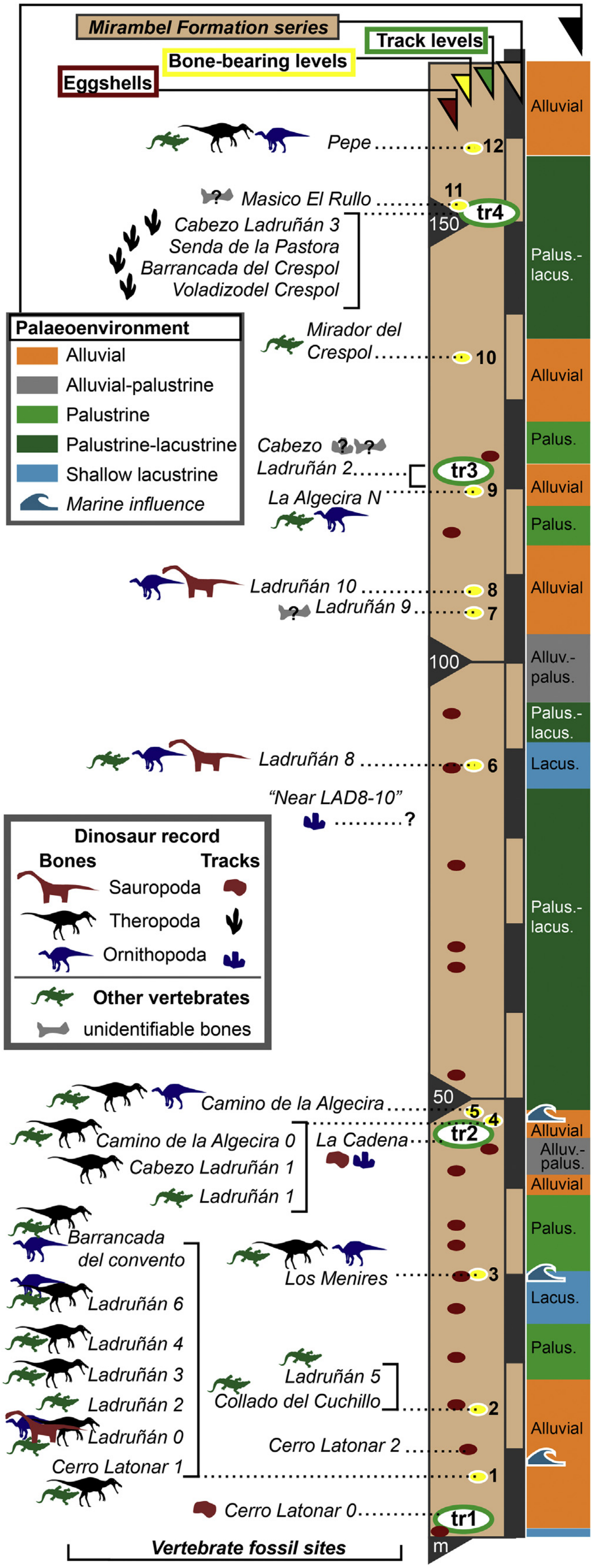

Fig. 4. Synthesis of the vertebrate fossil record of the Mirambel Formation in the Ladruñán anticline, showing the vertical distribution of tracksites, bone-bearing sites, eggshell occurrences and palaeoenvironments.

The diversity of preservational patterns in the fossiliferous sites is related with the variety of palaeoenvironments found in the Mirambel Formation (Fig. 3B). Within shallow lacustrine environments there are microfossil bonebeds (taphonomic mode E) as well as isolated bones (taphonomic mode D). Within alluvial settings, taphonomic mode C (i.e., isolated elements) is present in coarse-grained deposits, whereas undifferentiated bonebeds (taphonomic mode B) and isolated bones (taphonomic mode D) are present in the floodplains. In poorly-drained floodplain/palustrine areas, macrofossil bonebeds (taphonomic mode A) are also present. A general reconstruction of the sedimentary system with the distribution of the bone accumulations is shown in Fig. 5.

7.2. Track production

7.2.1. Tracks in alluvial, near-channel and channel settings

The floodplains of some river systems allow for the optimum formation and preservation of tracks due to the combination of vegetation and water that attract animals, and the seasonal inundation (Nadon, 2001). Such scenarios would give rise to the clastic deposits of the Mirambel Formation that bear dinosaur tracks, in particular track levels 2 and 3, which formed in floodplain fines and were sealed by crevasse-splay deposits. In addition, the formation and preservation of dinosaur tracks on point-bar deposits are also recognized (track level 1). The same kind of track preservation has previously been described in settings that are similar in lithology and depositional environment, such as the natural cast tracks of the Lanzhou-Minhe Basin (Xing et al., 2015), which are found at the base of sandstone beds, within sandstone beds (i.e., on accretion surfaces), or as sandy casts within mudstone levels. The infilling by fine-grained sandy material of a moderately deep track made in a soft substrate forming a track cast is a mode of preservation that is common in alluvial/fluvial settings (Lockley, 1991). The late Maastrichtian tracksites of the Pyrenees (Spain) have similar preservational and sedimentary features (Vila et al., 2013).

Most of the tracks are poorly preserved and appear as rounded, amorphous bulges, but some tracks exhibit morphological features of the autopod such as skin impressions (Fig. 2in Castanera et al., 2016). The best cases of preservation showing skin impressions (track level 2: La Cadena tracksite) indicate that the trampled muddy sediment was cohesive enough to resist erosion during the subsequent overbank flood (e.g. Vila et al., 2013). However, it should also be noted that the vertical stacking of crevasse splay deposits recorded in La Cadena tracksite reflects aggradation, which can increase the potential for track preservation. On the other hand, the poorly-preserved and deformed casts recorded in point-bar IHS deposits (track level 1: Cerro Latonar tracksite) indicate a low proportion of cohesive substrate, which prevented the proper preservation of the autopod shape (e.g. Vila et al., 2013).

The general model for track formation and preservation in alluvial/fluvial settings highlights the fact that fluctuations related with the hydraulic dynamics are essential for facilitating a suitable substrate (Lockley and Conrad, 1991; Vila et al., 2013).

The occurrence of tracks preserved as convex hyporeliefs is favoured by the alternating high- and low-water stages of fluvial deposits. In meandering fluvial systems the successive high-water stages provide suitable conditions for infilling the tracks produced in the floodplain or in the accretion surfaces within the channel. Braided systems are generally less stable than meandering ones, so they have a lower preservation potential for vertebrate tracks. The dinosaurs produced these tracks on mudstones or sandstones (Fig. 5) in low-water stage conditions, and during the high-water stage (stream reactivation) the track holes were infilled by sands (Vila et al., 2013).

7.2.2. Tracks in marginal lacustrine settings

Like track level 4, other cases with both kinds of ichnite preservation (i.e. convex hyporeliefs and concave epireliefs) in the same tracksite have already been described (e.g. Fig. 3B in Xing et al., 2012). Similar

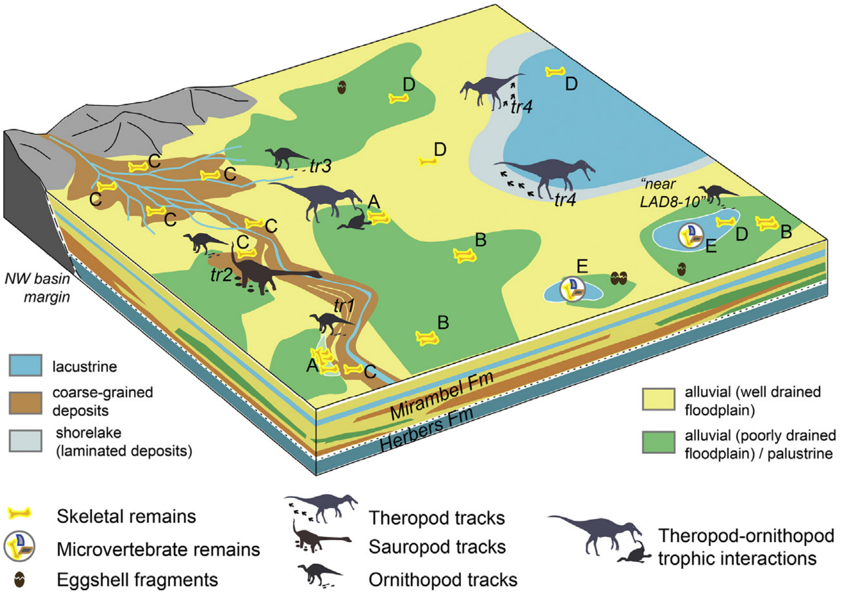

Fig. 5. Reconstruction of the alluvial-lacustrine system of the Mirambel Formation in the Ladruñán area, dinosaur track production, and location of the skeletal accumulations indicating their taphonomic modes.

preservational conditions occur in some sequences of shallow lacustrine deposits bearing dinosaur tracks as well (e.g. Villanueva de Huerva Formation, Gasca et al., 2012). Such tracks are preserved in the only interval of laminated palustrine-lacustrine sediments (interval F) of the Mirambel Formation; they are preserved as convex hyporeliefs in the Voladizo del Crespol and Cabezo Ladruñán 3 outcrops, as well as concave epireliefs in Senda de la Pastora, Barrancada del Crespol and again in Cabezo Ladruñán 3. The different preservational style is conditioned by the position of thin marly beds within sequences as well as differential erosion in the outcrop cross-sections.

In contrast to the laminated limestones, vertebrate tracks are rare in the massive limestones and rooted palustrine limestones (see intervals B and D in S1), with only one isolated cast identified in the massive limestones "Near LAD8-10". This indicates that the effects of persisting palustrine conditions are less favourable for track preservation and/or track production. Accordingly, the ubiquitous root traces in the marl-limestone sequences indicate the recurrent presence of vegetal cover that would hamper the transit of dinosaurs. In addition, the high level of root penetration (see S4: Fig. 7F) and the intense pedogenic features are evidence of long periods of subaerial exposure (Platt and Wright, 1992). These palustrine facies, which are the most common in the Ladruñán area, are more similar to those of the El Castellar Formation (Meléndez et al., 2009), where unequivocal dinosaur tracks are absent (*contra* Meléndez et al., 2009).

7.3. Origins of the bonebeds

Understanding the diverse mechanisms of vertebrate hardpart concentration is vital for accurate palaeoecological and palaeoenvironmental reconstructions (Rogers and Kidwell, 2007). Local geological data indicate that the genesis of the bone-bearing sites studied here was in a low-energy context. As in the case of the Mirambel Formation (see S4), dinosaur fossil sites are frequently described in deposits corresponding to lentic systems (e.g. Buscalioni et al., 2008; Canudo et al., 2010; Rogers and Brady, 2010). There is no evidence of catastrophic events or of biogenic concentrations in the Mirambel Formation, but rather the evidence suggests attritional accumulations. The genetic framework for the vertebrate skeletal sites was physical concentrations, with sedimentology as a key factor. Overprinting and dispersion were post-concentration effects (Rogers and Kidwell, 2007) that might be relevant in the origin of some taphonomic modes. Overprinting is possibly revealed in the Camino de la Algecira macrofossil bonebed (taphonomic mode A), where the colonization of dinosaur bones by marine invertebrates took place. Dispersion, reworking and/or destruction can be invoked in the poorly-preserved and scattered bioclasts of taphonomic modes C (isolated elements in sandy beds) and D (isolated bones).

The source of the different bone concentrations in the Mirambel Formation mainly fits with a passive attritional model. The concentrations are derived from a set of processes in which autochthonous to parautochthonous, articulated, disassociated and/or fragmentary remains are accumulated (Behrensmeyer, 2007). Sometimes sediment accumulation is slow relative to bone input (as in the case of Los Menires bonebed), whereas most of the time moderate sedimentation rates prevent significant bone concentrations. Taphonomic modes A, B and E have features in common with other bonebeds described in distal environments (low energy, slow sedimentation) of continental settings, with the vertebrate remains being randomly scattered, incomplete and scarcely or not at all articulated (e.g. bonebeds G2 and R2 in Cambra-Moo et al., 2012). In the case of the Pepe site (taphonomic mode A) and some bonebeds characterized by taphonomic mode B, their origins were on the floodplain, where physicochemically resistant vertebrate hardparts accumulated to produce a relatively concentrated level of micro- and macroremains by attritional processes.

Taphonomic mode C, i.e. isolated elements in sandy beds, can be assumed to be abiotic in origin in the sense that these concentrations of disarticulated bones or bone fragments provide evidence that transport processes or variations in sediment supply were primarily responsible for forming the bonebed (Behrensmeyer, 2007). This is coherent with the fluvial channel deposits in which the remains are preserved. There is no evidence to suggest biotic causes in the Mirambel Formation skeletal record given the absence of carcasses or skeletal parts that indicate mass or clustered death events. The key feature of the genetic framework of the recorded fossil sites is that the final concentration of vertebrate skeletal components is predominantly the result of physical factors, whether hydraulic processes or sedimentary budgets, rather than biological phenomena.

Floodplain ponds and lakes (taphonomic modes B and E) are typical settings for the attritional accumulation of vertebrate bioclasts (e.g. Rogers and Kidwell, 2007). Palustrine-lacustrine bonebeds are excellent targets for palaeoecological studies that seek to reconstruct overall community membership and structure, as they are preserved in situ at the scale of the local palaeoenvironment (Rogers and Brady, 2010).

Aquatic ecosystems typically support diverse communities of vertebrate animals, including abundant fish, crocodilians and amphibians. They also tend to attract terrestrial animals to their shores and shallows for feeding, drinking and wallowing purposes. Over time, many generations of aquatic, semiaquatic and terrestrial animals may perish in and around ponds and lakes for a plethora of reasons (senescence, disease, predation), and their skeletal hardparts may in turn contribute to cumulative death assemblages. Whether skeletal elements accrue to concentrated levels depends on numerous factors, including the density and fecundity of vertebrate populations, and the intensity of biological recycling (Rogers and Kidwell, 2007). Attritional accumulations of vertebrate skeletal hardparts, regardless of their sedimentary context, may be time-averaged to a greater or lesser degree (Rogers and Kidwell, 2007; Rogers and Brady, 2010). According to previous proposals (Martin, 1999), the time-averaging represented by the vertebrate skeletal concentrations of the Mirambel Formation ranges from less than a decade in bonebeds from floodplain environments (taphonomic mode A) to centuries and millennia in microfossil bonebeds from shallow lacustrine environments (taphonomic mode E).

Other proposals for the classification of taphonomic modes and taphonomic history have been put forward for Mesozoic vertebrate fossil assemblages in continental settings (e.g. Eberth and Currie, 2005; Csiki et al., 2010). Taphonomic mode A (macrofossil bonebeds), which is the most important type in terms of the completeness and quality of dinosaur bones in the Mirambel Formation record, is consistent with taphonomic mode C13 (macrofossil bonebeds: lenticular bonebeds preserved in poorly-drained floodplain deposits) of the Maastrichtian Hateg Basin (Csiki et al., 2010). In order of importance, the relevant taphonomic processes here were scavenging and disarticulation of the carcasses followed by weathering and – to a far lesser extent – transport, as schematized in Fig. 10 by Csiki et al. (2010), whose account is congruent with the observations made at the fossil sites of the Mirambel Formation. Apart from this, further correlations between the taphonomic modes of the Mirambel Formation and the fluvial-dominated Hateg Basin cannot be successfully established. In addition to ecological and methodological factors, the differences in depositional context with respect to the fluvial-dominated upland Hateg Basin appear to be decisive for the presence of distinct kinds of vertebrate fossil sites.

7.4. Origin of the eggshell assemblages

Previous experimental taphonomical studies of eggshell transport and sedimentation have been carried out with significantly bigger eggshell fragments (around 1 cm^2: (Tokaryk and Storer, 1991; Oser and Jackson, 2014; Imai et al., 2015). The eggshells recovered here by sieving sediments are between two and three orders of magnitude smaller, so any extrapolation of the conclusions from the previous analyses should be undertaken with caution. Nevertheless, all the previous data agree in indicating that eggshell breakage during transport is minimal (Tokaryk and Storer, 1991; Oser and Jackson, 2014), and that large eggshell fragments are not easily transported by hydraulic currents (Imai et al., 2015). On the other hand, small eggshell fragments do not present a marked concavity, thus minimising the differences in critical bed shear stress between concave-down and concave-up eggshells. We here hypothesize that sub-centimetre eggshell fragments behave like planar particles, and may easily be transported by low-energy currents. Nevertheless, this hypothesis needs to be tested by means of appropriately designed experiments.

In addition to this, prolonged transport of eggshell fragments between nesting sites and accumulation areas may also be indicated by the degradation of the eggshell fragments. Most of the eggshells are slightly rounded, and present a medium (see S4: Fig. 8A) to high degree of modification of the eggshell surfaces, making some fragments unidentifiable (see S4: Fig. 8E, F). Oser and Jackson (2014) postulate that the degree of abrasion and rounding of eggshell fragments is a good proxy for assessing whether or not eggshell fragments have been transported. According to their results, the eggshell assemblages of the Mirambel Formation are to be regarded as allochthonous.

Problems arise when the evidence for long-distance transport is tested against the sedimentological and taphonomical model for the formation of the microfossil bonebeds (see Section 7.3). Most of the eggshell-bearing beds were deposited in lacustrine-palustrine, low-energy, low-sedimentation-rate conditions. In such contexts, the dismantling of the clutches, fragmentation of the eggs and degradation of the eggshell fragments is the equivalent of the disarticulation, breakage and weathering of skeletal remains. The remobilization and possible reworking of the eggshells over extended time periods explains the great modification undergone by the specimens. In this context, the weathering and breakage of the specimens can best be explained by a protracted period of transport, not necessarily implying a long distance between the production and accumulation areas.

In the Mirambel Formation, eggshell assemblages are restricted to lacustrine and palustrine palaeoenvironments. Although highly fragmented and modified, the eggshell remains are here considered parautochthonous, as the sedimentology of the eggshell-bearing beds does not substantiate the occurrence of long-distance transport. The absence of eggshell fragments in channel deposits and floodplains suggests that dinosaurs, turtles and crocodiles preferred more humid environments to lay their eggs. Clutches and nests, probably laid in small emergent areas within the lacustrine and palustrine systems, were dismantled by biological processes (hatching, trampling and predation) but mainly by physical processes, and were then incorporated into the lake sediments. Eggshell remains accrued together with skeletal remains, providing a time-averaged record of the nesting taxa in the area surrounding the system.

7.5. Consistency between the types of vertebrate fossil evidence

Even though the eggshell record of the Mirambel Formation has yet to be studied in depth, some preliminary relationships between taxa and parataxa can be established. Ornithopod dinosaurs most probably produced cf. *Guegoolithus* eggshells, matching their ubiquitous presence in the skeletal record. One of the several small theropod dinosaur morphotypes present in the area may have produced the indeterminate three-layered eggshells. More interesting is the absence of sauropod eggshells in any of the assemblages, even though sauropods are present in both the ichnological and skeletal records. To date, sauropod eggshells have only been recognized in the Iberian Chain in a single locality, Pochancalo 1 (Villanueva de Huerva Formation), which happens to be alluvial (avulsion deposits: Gasca et al., 2012). In view of the above considerations, it is possible that sauropods actively avoided lacustrine or palustrine sediments to lay their eggs. Well-documented corroboration of this scenario is provided by the Maastrichtian outcrops of the southern Pyrenees, where sauropod eggs are very abundant in fluvial environments (e.g. Vila et al., 2010). By contrast, palustrine and lacustrine Maastrichtian environments are dominated by ornithopod and crocodylomorph eggshells, whereas sauropods are absent (Moreno-Azanza et al., 2014b; Sellés et al., 2014). As regards non-dinosaurian taxa from the Mirambel Formation, two of the several crocodyloid taxa present in the skeletal record can tentatively be attributed to *Mycomorphoolithus* and *Krokolithes*. Finally, both turtle eggshells and bones have been identified.

Eggshell record apart, another relevant issue to be resolved is whether or not the ichnological record is consistent with the skeletal record (Lockley, 1991). Some examples have come to light elsewhere where the skeletal and the ichnological record represent a similar faunal assemblage (Lockley et al., 1986), while in other cases there are considerable differences between the two records (e.g. Belvedere et al., 2013). The ichnological record of the Mirambel Formation is theropod-dominated. This scenario has been reported in other ichnoassemblages, where possible preservational biases have been invoked to account for this kind of census (Thulborn, 1990). In the skeletal record of the Ladruñán sites, theropods are represented by 11 occurrences, but often they are only tooth remains. Ornithopods are also common, being present in 9 sites and furthermore providing more complete bone evidence. Sauropods are less frequent (3 sites). Note that the data size is too modest to justify robust palaeoecological inferences. In any event, preservational biases in the vertebrate record of the Mirambel Formation are evidenced by the fact that other archosaurs such as crocodylomorphs are well represented by skeletal fossils but are absent in the track assemblage.

7.6. Vertebrate biota of the Mirambel Formation

The dinosaurs from the Barremian of the Ladruñán area were sauropods (Titanosauriformes: Gasca and Canudo, 2015), theropods (spinosaurids, carcharodontosaurids and coelurosaurs: Infante et al., 2004; Gasca et al., 2014) and ornithopods (Gasca et al., 2009, 2015). As well as the skeletal evidence, this scenario is reinforced by the ichnological and oological records.

In addition to dinosaurs, shallow-water environments, wetlands and/or the nearby areas were populated by vertebrates such as osteichthyans, chondrichthyans, lissamphibians, turtles, crocodylomorphs and mammals. There is skeletal evidence of these taxa in the Mirambel Formation. Much of the vertebrate diversity can be recognized especially by means of information provided by the vertebrate microfossil sites (e.g. Sweetman, 2015). A list of the vertebrate taxa recorded from the Mirambel Formation is provided in Table 1. The taxonomic diversity identified in the Mirambel Formation (17 vertebrate taxa) is still low in comparison with other Barremian units from the Iberian Range (e.g. Canudo et al., 2010). However, this count is provisional because most of the vertebrate fossil groups in the Ladruñán anticline have not been studied in depth. At present, what is known is that the taxa of the Mirambel Formation are common to other fossil associations belonging to the Wealden facies of the Maestrazgo Basin (Canudo et al., 2010; Cuenca-Bescós et al., 2014).

Furthermore, the evidence recorded in macrovertebrate bonebeds (i.e., tooth traces on ornithopod bones in Pepe or shed spinosaurid teeth in Camino de la Algecira, S4: Fig. 7D and 6C) is indicative of trophic interactions between theropods and ornithopods, whether in the form of predation or scavenging (Farlow and Holtz, 2002).

Dinosaur tracks also provide direct evidence of the presence of their trackmakers on lakeshores and in areas near watercourses. The disparate eggshell record testifies to the preferential affinity of tetrapods for performing certain vital activities (nesting?) in environments near shallow waters (palustrine-lacustrine).

Table 1
Vertebrates recorded in the Mirambel Formation.

Higher taxa	Taxa
Chondrichthyes	Hybodontidae indet.
Osteichthyes	Pycnodontiformes indet.
	Semionotiformes indet.
	Amiiformes indet.
Lissamphibia	Lissamphibia indet.
Squamata	Squamata indet.
Chelonia	Solemydidae indet.
	Pleurosternidae indet.
Crocodylomorpha	Goniopholididae indet.
	Atoposauridae indet.
	Bernissartiidae indet.
Ornithopoda	Styracosterna indet.
Sauropoda	Titanosauriformes indet.
Theropoda	Spinosauridae indet.
	Carcharodontosauridae indet.
	Maniraptoriformes indet.
Mammalia	Spalacotheriidae indet.

As regards their ecological categorization, the bonebeds of the Mirambel Formation preserve aquatic (Osteichthyes, Chondrichthyes), semiaquatic (Chelonia, Crocodyliformes) and terrestrial animals (Dinosauria, Mammalia). In relation to the depositional environments, dinosaur occurrences are widely distributed within the alluvial-lacustrine system, but a comparison of the main groups (Fig. 3C) reveals that ornithopods are underrepresented in coarse-grained deposits. This could be indicative of the ornithopod preference for lower and near-water areas and for avoiding uplifted and exposed areas. In contrast, the conspicuous occurrence of theropods may be indicative of the wide spatial range they adopted for their vital activity.

8. Conclusions

The dinosaur record of the Mirambel Formation in the Ladruñán anticline comprises ornithopods, theropods and sauropods and consists of track-, bone- and eggshell-bearing fossil sites (see further data in supplementary information). Four distinct track-bearing horizons are identified in the Ladruñán area. The dinosaur tracks consist of convex hyporeliefs or concave epireliefs that record the trackmakers as they frequented lakeshores, alluvial floodplains and fluvial courses. Macrovertebrate bonebeds with significant accumulations of dinosaur skeletal remains, and even with associated specimens, occur in alluvial settings (poorly-drained floodplains and “ponds”). Microvertebrate concentrations are located in shallow lacustrine deposits. Isolated skeletal elements can be found in a great variety of deposits. Attritional accumulation in a low-energy depositional context is the general pattern of origin for the bone-bearing fossil sites of the Mirambel Formation. Eggshell fragments are frequent throughout the unit but are clearly more common in palustrine-lacustrine deposits. These can be taken to be parautochthonous bioclasts from nearby areas and might be indicative of the preferential affinity of the egg-layers for wetlands and lakeshores.

Supplementary data associated with this article provide detailed information on the stratigraphic location (S1) and the main features of the vertebrate fossil sites (S2) and sampled beds (S3) from the Mirambel Formation in the Ladruñán anticline. Furthermore, detailed observations and descriptions of the fossil record are disclosed in S4 (1: vertebrate record; 2: micropalaeontological analysis). Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.palaeo.2017.01.050.

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