

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

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25 **ABSTRACT**

26 The Barremian Mirambel Formation (Maestrazgo Basin, Iberian Chain, NE Spain)
27 preserves different types of dinosaur and other vertebrate fossils (skeletal, eggshell and
28 ichnological remains). A total of 31 vertebrate fossil sites and tracksites have been recognized
29 within this unit in the Ladruñán area (Teruel province). Detailed stratigraphic, sedimentological
30 and micropalaeontological analyses have also been performed in the unit. A vertical
31 sedimentary trend from alluvial-dominated facies (meandering river and related overbank areas)
32 to palustrine-lacustrine facies and back has been defined for the Mirambel Formation in this
33 area. The depositional system was located close to the coastline, as indicated by sporadic
34 marine input in the lower part of the unit.

35 Most fossil remains were recovered by surface collection as well as by the usual
36 techniques used for macrovertebrate excavations. The dinosaur record identified comprises to
37 ornithopods, theropods and sauropods. Four distinct track-bearing horizons have been
38 identified. The heterolithic nature and aggradation characteristic of the Mirambel Formation are
39 favourable factors for track formation and preservation. The dinosaur tracks consist of convex
40 hyporeliefs or concave epireliefs that record the trackmakers as they frequented lakeshores,
41 alluvial floodplains and fluvial courses. Macrovertebrate bonebeds occur in alluvial settings
42 (poorly-drained floodplains and “ponds”). Microvertebrate concentrations are located in shallow
43 lacustrine deposits. Isolated skeletal elements can be found in a great variety of deposits.
44 Attritional accumulation in a low-energy depositional context is the general pattern of origin for
45 the bone-bearing fossil sites of the Mirambel Formation. As regards the genetic framework, the
46 resulting skeletal assemblages are predominantly the result of physical factors, with
47 sedimentology as a key factor, rather than biological phenomena. Eggshell fragments are
48 frequent throughout the unit but are clearly more common in palustrine-lacustrine deposits.
49 These can be taken to be parautochthonous bioclasts from nearby areas and might be
50 indicative of the preferential affinity of the egg-layers for wetlands and lakeshores.

51 **Keywords:** bonebeds, taphonomic modes, dinosaur tracks, eggshells, palaeoenvironments,
52 Mirambel Formation.

54 **1. Introduction**

55 Dinosaur fossil sites are often analysed with the focus on the dinosaur remains
56 themselves (i.e. for systematic or palaeobiological purposes), whereas it is less common to find
57 other, holistic approaches that integrate palaeontology (systematics, taphonomy,
58 palaeoecology) and sedimentary geology to provide valuable information on palaeocommunities
59 and palaeoenvironments. Depositional environments, preservational patterns and taphonomic
60 modes are key issues on which to base the reconstruction of the original ecological scenario in
61 fossil deposits (e.g. Eberth and Currie, 2005; Csiki et al., 2010; Rogers and Brady, 2010).
62 Furthermore, the spatial and temporal resolution of the fossil assemblage, the segment of the
63 original biota represented by the fossil sample, and additional information on biological agents
64 can be established through successive levels of inference to yield a thorough palaeoecological
65 analysis of palaeontological localities (Berensmeyer and Hook, 1992). Vertebrate skeletal
66 concentrations, or “bonebeds”, provide a unique opportunity to explore an array of
67 palaeobiological and geological questions, such as the existence of genetic links between local
68 sedimentary dynamics and bonebed formation, or how vertebrate palaeoecology and behaviour
69 manifest themselves in bone-rich deposits (Rogers and Kidwell, 2007). The tetrapod track
70 record gives us invaluable information about the trackmakers (i.e. their identity, locomotion and
71 behaviour). Moreover, it contributes to the reconstruction of the palaeoenvironment and its
72 palaeoecological characteristics, and represents an extremely useful complement to the skeletal
73 record (Castanera et al., 2013; Falkingham, 2014; Melchor, 2015). Further, eggs and eggshells
74 provide limited information on the palaeobiodiversity of fossil environments, but give valuable
75 data on the palaeoecology of the egg layers and may be the source of useful information on the
76 palaeoenvironment (Erben et al., 1979; Mikhailov, 1997).

77 The Barremian Mirambel Formation is a Cretaceous sedimentary unit in the Iberian
78 Chain (NE Spain) that preserves different types of dinosaur and other vertebrate fossils
79 (skeletal, eggshell and ichnological remains). Accordingly, the palaeoenvironmental information
80 from one type can complement that from another (e.g. Mateus and Milàn, 2010). The unit crops
81 out in the Ladruñán anticline (Teruel province), providing a remarkable number of vertebrate
82 fossil localities bearing bones, ichnites and/or eggshells in a limited area. The combined

83 presence of the three types of fossil remains is uncommon (Vila et al., 2011, 2012, 2013), and
84 this case is unmatched in its temporal and regional context.

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

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

99

100 **2. Geological setting**

101 The studied outcrops of the Barremian Mirambel Formation are located around the
102 village of Ladruñán (Castellote municipality, NE Teruel province, NE Spain), in the eastern part
103 of the Iberian Chain (Fig. 1A). Palaeogeographically, this area belongs to the northwestern
104 margin of the Morella sub-basin (Fig. 1B), within the Maestrazgo Basin (Salas et al., 2001).
105 The uppermost Jurassic-Lower Cretaceous stratigraphic units in the Ladruñán area crop out in
106 a N-S-trending anticline with periclinal closure to the north (Richter and Teichmüller, 1933)
107 (Figs. 1C, D and 2). From bottom to top, they encompass the shallow marine facies of the
108 Tithonian–Berriasian La Pleta Formation, the non-marine Berriasian Ladruñán unit, the Early
109 Cretaceous (Valanginian–Barremian) Wealden facies (including the lacustrine Herbers
110 Formation, the alluvial-lacustrine Mirambel Formation, the shallow marine Artoles Formation,

111 and the transitional Morella Formation) and the Aptian Urgonian facies (i.e. Chert Formation)
112 (Martín-Closas, 1989; Salas et al., 2001).

113 The ages of the Early Cretaceous continental units were determined by the study of the
114 charophyte assemblages from the local series of Ladruñán as well as from other nearby
115 sections (Martín-Closas, 1989). In the case of the Mirambel Formation under study, the age is
116 early Barremian to early late Barremian, corresponding to the *Atopochara trivolvis triquetra*
117 biozone (Martín-Closas, 1989; Riveline et al., 1996). Further up in the series, the age of the
118 Morella Formation is late Barremian, as was recently shown by palynological studies performed
119 in other sections of the Morella sub-basin (Castellón province, Villanueva-Amadoz et al., 2015).
120 The Mirambel Formation is almost 200 m in thickness, and there is a high degree of lateral
121 bedding continuity in the outcrops of the Ladruñán anticline (see Figs. 1–2 and supplementary
122 data S1–S3). The unit is formed by an alternation of successive detrital alluvial intervals and
123 carbonate-rich palustrine-lacustrine intervals (see A to G in Fig. 1C and S1). The lowermost
124 interval A corresponds to a 15 m-thick succession of alluvial sandstones and lutites. To the
125 south (e.g., Los Menires reference section) this detrital interval intercalates with shallow
126 lacustrine grey marls and limestones, which become dominant to the east (Martín-Closas,
127 1989; Castanera et al., 2016). The basal detrital interval A is overlain by a 30-m-thick interval B
128 formed by shallow lacustrine and palustrine facies, including grey marls with reddish mottling
129 and grey burrowed and rooted limestones. The unit continues with a 15-m-thick alluvial interval
130 C, including red, yellowish and grey lutites and ochre sandstones. The next 50 m are lacustrine-
131 palustrine massive marls and limestones (interval D), which are overlain by a 20-m-thick interval
132 E of alluvial detrital facies. The unit ends with a 12-m-thick interval F formed by shallow
133 lacustrine grey massive marls and limestones and laminated limestones, and a 10-m-thick
134 interval G of detrital alluvial facies.

135

136 **3. Materials and methods**

137 A total of 31 vertebrate fossil sites and tracksites have been recognized within the
138 Mirambel Formation in the Ladruñán area. Their precise geographical location and stratigraphic
139 position in three reference sections (Estrecho, Cabezo Ladruñán and Los Menires) are included
140 in Fig. 2 and supplementary material S1. The complete list of sites including sedimentological

141 and palaeontological information is summarized in supplementary material S2 and S3. A
142 detailed description of the studied fossil record is provided in supplementary material S4.

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

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

161 The collection of the field data was complemented with detailed stratigraphic and
162 sedimentological analyses performed in key fossil sites, as well as the study of microfossils
163 obtained by washing and sieving sediment samples along the entire Mirambel Formation (see
164 supplementary material S3). Samples of 2kg were systematically taken from successive soft
165 horizons (lutites, marls and poorly-cemented sands), and these were processed using 2%
166 hydrogen peroxide and sieves of 2.0, 1.0 and 0.5 mm mesh. A significant amount of sediment
167 (i.e. 500 kg) was also recovered from the most remarkable microfossil bonebed (i.e. Los
168 Menires reference section, Moreno-Azanza et al., 2015). The skeletal remains and eggshell
169 fragments were sorted under a binocular microscope. To complete the micropalaeontological

170 study, other microfossils of palaeoecological or biostratigraphic significance were identified,
171 such as charophyte and ostracod remains (see supplementary information S4). Selected
172 specimens were mounted, gold-coated and viewed with a JEOL 6400 SEM at the University of
173 Zaragoza, using both secondary and backscattered electrons.

174 The ichnological terminology used in this paper mainly follows the work of Thulborn
175 (1990), Marty (2008) and Piñuela et al. (2012). Measurements were taken directly during
176 fieldwork or else by means of the digital analysis of photographs using the software ImageJ.
177 Detailed methods and measurements are described in Castanera et al. (2016).
178 Photogrammetric images were obtained using Agisoft PhotoScan™ software (version
179 0.8.5.1423). Photogrammetric models were also imported into Meshlab™ for scaling and
180 Paraview™ to generate false-colour depth maps and contour lines.

181

182 **4. Vertebrate ichnological record**

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

191 The outcrops of the Mirambel Formation are mostly exposed in cross section, which is
192 determinant in the type of track findings. Casts (convex hyporeliefs) are the most common form
193 of preservation, whereas the casual finding of tracks as concave epireliefs has been possible
194 only on stratification surfaces comprising detached rocky blocks (track level 4). Track formation
195 requires a substrate that is soft enough to be deformed by the animal but firm, cohesive and
196 dewatered enough to retain the shape of the foot until the sediment can infill the cavity (Currie
197 et al., 1991; Nadon, 2001). The heterolithic nature of the Mirambel Formation is a favourable

198 factor for track formation and preservation (Nadon, 2001). Rapid aggradation (at least in some
199 stages) must have also taken place; this is required to ensure preservation potential because
200 exposed tracks degrade rapidly after formation (Laporte and Behrensmeier, 1980; Nadon,
201 2001). A detailed description of the ichnological record was recently published by Castanera et
202 al. (2016). Further detail on the track descriptions and sedimentology of the tracksites is
203 provided in the supplementary information S4 (chapter 1.1).

204

205 **5. Skeletal record**

206 From the studied record, 22 fossil sites (sites 1-7 and 9-23 in S2) have yielded
207 vertebrate skeletal remains, contained in 12 different bone-bearing stratigraphic levels. The
208 study of the dinosaur bone record is addressed by a general description of the main bonebeds
209 and their inclusion within a classification of the taphonomic modes present in the Mirambel
210 Formation. Taphonomic modes are recurring preservational and taphonomic features and
211 geological associations among fossils from a stratigraphic interval that reflect premortem (biotic
212 and environmental) and postmortem (biostratinomic and diagenetic) influences, as well as
213 basin-scale controls on sedimentary budget and accommodation (Eberth and Currie, 2005). The
214 taphonomic modes of the Mirambel Formation are described in the supplementary information
215 S4 (chapter 1.2). The relative abundance of the differentiated types of taphonomic modes (A to
216 E) and their distribution among the main palaeoenvironments is shown in Figure 3.

217

218 **6. Eggshell record**

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

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

232

233 **7. Discussion**

234 *7.1. Evolution of the depositional system and palaeoenvironments*

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

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

245 The diversity of preservational patterns in the fossiliferous sites is related with the
246 variety of palaeoenvironments found in the Mirambel Formation (Fig. 3B). Within shallow
247 lacustrine environments there are microfossil bonebeds (taphonomic mode E) as well as
248 isolated bones (taphonomic mode D). Within alluvial settings, taphonomic mode C (i.e. isolated
249 elements) is present in coarse-grained deposits, whereas undifferentiated bonebeds
250 (taphonomic mode B) and isolated bones (taphonomic mode D) are present in the floodplains.
251 In poorly-drained floodplain/palustrine areas, macrofossil bonebeds (taphonomic mode A) are

252 also present. A general reconstruction of the sedimentary system with the distribution of the
253 bone accumulations is shown in Fig. 5.

254 *7.2. Track production*

255 *7.2.1. Tracks in alluvial, near-channel and channel settings*

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

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

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

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

291 *7.2.2. Tracks in marginal lacustrine settings*

292 Like track level 4, other cases with both kinds of ichnite preservation (i.e. convex
293 hyporeliefs and concave epireliefs) in the same tracksite have already been described (e.g. Fig.
294 3B in Xing et al., 2012). Similar preservational conditions occurred in some sequences of
295 shallow lacustrine deposits bearing dinosaur tracks as well (e.g. Villanueva de Huerva
296 Formation, Gasca et al., 2012). Such tracks are preserved in the only interval of laminated
297 palustrine-lacustrine sediments (interval F) of the Mirambel Formation; they are preserved as
298 convex hyporeliefs in the Voladizo del Crespel and Cabezo Ladruñán 3 outcrops, as well as
299 concave epireliefs in Senda de la Pastora, Barrancada del Crespel and again in Cabezo
300 Ladruñán 3. The different preservational style would be conditioned by the position of thin marly
301 beds within sequences as well as differential erosion in the outcrop cross-sections.

302 In contrast to the laminated limestones, vertebrate tracks are rare in the massive
303 limestones and rooted palustrine limestones (see intervals B and D in S1), with only one
304 isolated cast identified in the massive limestones "Near LAD8-10". This indicates that the effects
305 of persisting palustrine conditions are less favourable for track preservation and/or track
306 production. Accordingly, the ubiquitous root traces in the marl-limestone sequences indicate the
307 recurrent presence of vegetal cover that would have hampered the transit of dinosaurs. In
308 addition, the high level of root penetration (see S4: Fig. 7F) and the intense pedogenic features

309 are evidence of long periods of subaerial exposure (Platt and Wright, 1992). These palustrine
310 facies, which are the most common in the Ladruñán area, are more similar to those of the El
311 Castellar Formation (Meléndez et al., 2009), where unequivocal dinosaur tracks are absent
312 (*contra* Meléndez et al., 2009).

313 7.3. *Origins of the bonebeds*

314 Understanding the diverse mechanisms of vertebrate hardpart concentration is vital for
315 accurate palaeoecological and palaeoenvironmental reconstructions (Rogers and Kidwell,
316 2007). Local geological data indicate that the genesis of the bone-bearing sites studied here
317 was in a low-energy context. As in the case of the Mirambel Formation (see S4), dinosaur fossil
318 sites are frequently described in deposits corresponding to lentic systems (e.g. Buscalioni et al.,
319 2008; Canudo et al., 2010; Rogers and Brady, 2010). There is no evidence of catastrophic
320 events or of biogenic concentrations but rather the evidence suggests attritional accumulations.
321 The genetic framework for the vertebrate skeletal sites would have been physical
322 concentrations, with sedimentology as a key factor. Overprinting and dispersion would have
323 been post-concentration effects (Rogers and Kidwell, 2007) that might be relevant in the origin
324 of some taphonomic modes. Overprinting might be revealed in the Camino de la Algecira
325 macrofossil bonebed (taphonomic mode A), when the colonization of dinosaur bones by marine
326 invertebrates took place. Dispersion, reworking and/or destruction could be invoked in the
327 poorly-preserved and scattered bioclasts of taphonomic modes C (isolated elements in sandy
328 beds) and D (isolated bones).

329 The source of the different bone concentrations in the Mirambel Formation mainly fits
330 with a passive attritional model. The concentrations are derived from a set of processes in
331 which autochthonous to parautochthonous, articulated, disassociated and/or fragmentary
332 remains are accumulated (Behrensmeyer, 2007). Sometimes sediment accumulation is slow
333 relative to bone input (as in the case of Los Menires bonebed), whereas most of the time
334 moderate sedimentation rates prevent significant bone concentrations. Taphonomic modes A, B
335 and E have features in common with other bonebeds described in distal environments (low
336 energy, slow sedimentation) of continental settings, with the vertebrate remains being randomly
337 scattered, incomplete and scarcely or not at all articulated (e.g. bonebeds G2 and R2 in

338 Cambra-Moo et al., 2012). In the case of the Pepe site (taphonomic mode A) and some
339 bonebeds characterized by taphonomic mode B, their origins would have been on the
340 floodplain, where physicochemically resistant vertebrate hardparts accumulated to produce a
341 relatively concentrated level of micro- and macroremains by attritional processes.

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

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

357 Aquatic ecosystems typically support diverse communities of vertebrate animals,
358 including abundant fish, crocodylians and amphibians. They also tend to attract terrestrial
359 animals to their shores and shallows for feeding, drinking and wallowing purposes. Over time,
360 many generations of aquatic, semiaquatic, and terrestrial animals may perish in and around
361 ponds and lakes for a plethora of reasons (senescence, disease, predation), and their skeletal
362 hardparts may in turn contribute to cumulative death assemblages. Whether skeletal elements
363 accrue to concentrated levels would depend on numerous factors, including the density and
364 fecundity of vertebrate populations, and the intensity of biological recycling (Rogers and Kidwell,
365 2007). Attritional accumulations of vertebrate skeletal hardparts, regardless of their sedimentary
366 context, should be time-averaged to a greater or lesser degree (Rogers and Kidwell, 2007;

367 Rogers and Brady, 2010). According to previous proposals (Martin, 1999), the time-averaging
368 represented by the vertebrate skeletal concentrations of the Mirambel Formation would range
369 from less than decades in bonebeds from floodplain environments (taphonomic mode A) to
370 centuries and millennia in microfossil bonebeds from shallow lacustrine environments
371 (taphonomic mode E).

372 Other proposals for the classification of taphonomic modes and taphonomic history
373 have been put forward for Mesozoic vertebrate fossil assemblages in continental settings (e.g.
374 Eberth and Currie, 2005; Csiki et al., 2010). Taphonomic mode A (macrofossil bonebeds),
375 which is the most important type in terms of the completeness and quality of dinosaur bones in
376 the Mirambel Formation record, is consonant with taphonomic mode C13 (macrofossil
377 bonebeds: lenticular bonebeds preserved in poorly-drained floodplain deposits) of the
378 Maastrichtian Hateg Basin (Csiki et al., 2010). In order of importance, the relevant taphonomic
379 processes would here be scavenging and disarticulation of the carcasses followed by
380 weathering and –to a far lesser extent– transport, as schematized in Fig. 10 by Csiki et al.
381 (2010), whose account is congruent with the observations made at the fossil sites of the
382 Mirambel Formation. Apart from this, further correlations between the taphonomic modes of the
383 Mirambel Formation and the fluvial-dominated Hateg Basin cannot be successfully established.
384 Apart from ecological and methodological factors, the differences in depositional context with
385 respect to the fluvial-dominated upland Hateg Basin appear to be decisive for the presence of
386 distinct kinds of vertebrate fossil sites.

387 *7.4. Origin of the eggshell assemblages*

388 Previous experimental taphonomical studies of eggshell transport and sedimentation
389 have been carried out with significantly bigger eggshell fragments (around 1 cm²: (Tokaryk and
390 Storer, 1991; Oser and Jackson, 2014; Imai et al., 2015). The eggshells recovered here by
391 sieving sediments are between two and three orders of magnitude smaller, so any extrapolation
392 of the conclusions from the previous analysis should be undertaken with caution. Nevertheless,
393 all the previous data agree in indicating that eggshell breakage during transport is minimal (
394 Tokaryk and Storer, 1991; Oser and Jackson, 2014), and that large eggshell fragments are not
395 easily transported by hydraulic currents (Imai et al., 2015). On the other hand, small eggshell

396 fragments do not present a marked concavity, thus minimising the differences in critical bed
397 shear stress between concave-down and concave-up eggshells. We here hypothesize that sub-
398 centimetre eggshell fragments behave like planar particles, and may easily be transported by
399 low-energy currents. Nevertheless, this hypothesis needs to be tested by means of
400 appropriately designed experiments.

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

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

419 In the Mirambel Formation, eggshell assemblages are restricted to lacustrine and
420 palustrine palaeoenvironments. Although highly fragmented and modified, the eggshell remains
421 are here considered parautochthonous, as the sedimentology of the eggshell-bearing beds
422 does not substantiate the occurrence of long-distance transport. The absence of eggshell
423 fragments in channel deposits and floodplains suggests that dinosaurs, turtles and crocodiles
424 preferred more humid environments to lay their eggs. Clutches and nests, probably laid in small

425 emergent areas within the lacustrine and palustrine systems, were dismantled by biological
426 processes (hatching, trampling and predation) but mainly by physical processes, and were then
427 incorporated into the lake sediments. Eggshell remains accrued together with skeletal remains,
428 providing a time-averaged record of the nesting taxa in the area surrounding the system.

429 7.5. Consistency between the types of vertebrate fossil evidence

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

448 Eggshell record apart, another relevant issue to be resolved is whether or not the
449 ichnological record is consistent with the skeletal record (Lockley, 1991). Some examples have
450 come to light elsewhere where the skeletal and the ichnological record represent a similar
451 faunal assemblage (Lockley et al., 1986), while in other cases there are considerable
452 differences between the two records (e.g. Belvedere et al., 2013). The ichnological record of the
453 Mirambel Formation is theropod-dominated. This scenario has been reported in other

454 ichnoassemblages, where possible preservational biases have been invoked to account for this
455 kind of census (Thulborn, 1990). In the skeletal record of the Ladruñán sites, theropods are
456 represented by 11 occurrences, but often they are only tooth remains. Ornithopods are also
457 common, being present in 9 sites and furthermore providing more complete bone evidence.
458 Sauropods are less frequent (3 sites). Note that the data size is too modest to justify robust
459 palaeoecological inferences. In any event, preservational biases in the vertebrate record of the
460 Mirambel Formation are evidenced by the fact that other archosaurs such as crocodylomorphs
461 are well represented by skeletal fossils but are absent in the track assemblage.

462 *7.6. Vertebrate biota of the Mirambel Formation*

463 The dinosaurs from the Barremian of the Ladruñán area were sauropods
464 (Titanosauriformes: Gasca and Canudo, 2015), theropods (spinosaurids, carcharodontosaurids
465 and coelurosaurs: Infante et al., 2004; Gasca et al., 2014;) and ornithopods (Gasca et al.,
466 2009, 2015). As well as the skeletal evidence, this scenario is reinforced by the ichnological and
467 oological records.

468 In addition to dinosaurs, shallow-water environments, wetlands and/or the nearby areas
469 were populated by vertebrates such as osteichthyans, chondrichthyans, lissamphibians, turtles,
470 crocodylomorphs and mammals. For these taxa there is skeletal evidence. Recognition of much
471 of the vertebrate diversity can be achieved especially by means of information provided by the
472 vertebrate microfossil sites (e.g. Sweetman, 2015). A list of the vertebrate taxa recorded from
473 the Mirambel Formation is provided in Table 1. The taxonomic diversity identified in the
474 Mirambel Formation (17 vertebrate taxa) is still low in comparison with other Barremian units
475 from the Iberian Range (e.g. Canudo et al., 2010). However, this count is provisional because
476 the majority of vertebrate fossil groups in the Ladruñán anticline have not been studied in depth.
477 For now the taxa of the Mirambel Formation are common to those registered in other fossil
478 associations belonging to the Wealden facies of the Maestrazgo Basin (Canudo et al., 2010;
479 Cuenca-Bescós et al., 2014).

480 Furthermore, the evidence recorded in macrovertebrate bonebeds (i.e. tooth traces on
481 ornithopod bones in Pepe or shed spinosaurid teeth in Camino de la Algecira, S4: Fig. 7D and

482 6C) is indicative of trophic interactions between theropods and ornithopods, whether in the form
483 of predation or scavenging (Farlow and Holtz, 2002).

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

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

497

498 **8. Conclusions**

499 The dinosaur record of the Mirambel Formation in the Ladruñán anticline comprises
500 ornithopods, theropods and sauropods and consists of track-, bone- and eggshell-bearing fossil
501 sites (see further data in supplementary information). Four distinct track-bearing horizons have
502 been identified in the Ladruñán area. The dinosaur tracks consist of convex hyporeliefs or
503 concave epireliefs that record the trackmakers as they frequented lakeshores, alluvial
504 floodplains and fluvial courses. Macrovertebrate bonebeds with significant accumulations of
505 dinosaur skeletal remains, and even with associated specimens, occur in alluvial settings
506 (poorly-drained floodplains and "ponds"). Microvertebrate concentrations are located in shallow
507 lacustrine deposits. Isolated skeletal elements can be found in a great variety of deposits.
508 Attritional accumulation in a low-energy depositional context would be the general pattern of
509 origin for the bone-bearing fossil sites of the Mirambel Formation. Eggshell fragments are

510 frequent throughout the unit but are clearly more common in palustrine-lacustrine deposits.
511 These can be taken to be parautochthonous bioclasts from nearby areas and might be
512 indicative of the preferential affinity of the egg-layers for wetlands and lakeshores.

513

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525

526 **Appendix A. Supplementary data**

527 Supplementary data associated with this article provide detailed information on the
528 stratigraphic location (S1) and the main features of the vertebrate fossil sites (S2) and sampled
529 beds (S3) from the Mirambel Formation in the Ladruñán anticline. Furthermore, detailed
530 observations and descriptions of the fossil record are disclosed in S4 (1: vertebrate record; 2:
531 micropalaeontological analysis).

532

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733 FIGURE CAPTIONS

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

742 **Fig. 2.** Detailed geographic location of the 31 fossil sites and tracksites within the Mirambel
743 Formation in the Ladruñán area. Topographic map (1:25000) obtained from SIGPAC,
744 Government of Spain (available at <http://sigpac.mapa.es/fega/visor/>). Abbreviations: LAT1 –
745 Cerro Latonar 1, BACO – Barrancada del Convento, LAD0 – Ladruñán 0, LAD3 – Ladruñán 3,
746 LAD6 – Ladruñán 6, LAD2 – Ladruñán 2, LAD4 – Ladruñán 4, LAT2 – Cerro Latonar 2, LAD5 –
747 Ladruñán 5, COCU – Collado del Cuchillo, MENI – Los Menires, LAD1 – Ladruñán 1, CALG0 –
748 Camino de la Algecira 0, CALA1 – Cabezo Ladruñán 1, CALG – Camino de la Algecira, LAD8
749 – Ladruñán 8, LAD9 – Ladruñán 9, LAD10 – Ladruñán 10, CALA2 – Cabezo Ladruñán 2, ALGN
750 – La Algecira Norte, MIC – Mirador del Crespól, RU – Masico El Rullo, PEPE – Pepe, LAT0 –
751 Cerro Latonar 0, LC – La Cadena, LAD8-10 – “Near LAD8-10”, CALA2 – Cabezo Ladruñán 2,
752 CALA3 – Cabezo Ladruñán 3, SP – Senda de la Pastora, BC – Barrancada del Crespól, VC –
753 Voladizo del Crespól. **Fig. 3.** Taphonomic modes and palaeoenvironments of the Mirambel
754 Formation. A, pie chart showing relative abundances of the taphonomic modes. B, pie chart
755 showing the distribution of the fossil localities and their taphonomic modes within
756 palaeoenvironments. C, bar graph showing the number of dinosaur occurrences within each
757 palaeoenvironment.

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

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

764 **Table 1.** Vertebrates recorded in the Mirambel Formation.