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New ornithopod tracks from the Lower Cretaceous El Castellar Formation (Spain): implications for track preservation and evolution of ornithopod footprints

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ABSTRACT

Dinosaur tracks have been identified in several Upper Jurassic-Lower Cretaceous sedimentary units across the Maestrazgo Basin in eastern Iberia, which are preserved in a variety of transitional and continental paleoenvironments. Here, we described the lower Barremian San Benón tracksite with the first occurrence of clear dinosaur tracks in the El Castellar Formation within the Galve subbasin. This palustrine-lacustrine formation has yielded a rich osteological record although dinosaur tracks are notably scarce. The new footprints represent an uncommon case of dinosaur track preservation since the site has yielded several non contemporary tracks (part of different ichnoassemblages) preserved as carbonate casts at the base of a limestone bed forming a composite ichnofabric. The tracksite shows a complex history of sedimentation, track production and preservation linked to the lake level variations. The ornithopod tracks are identified to belong to the ornithopod ichnogenus *Caririchnium*, concretely to the ichnospecies *C. magnificum.* The studied tracks represent the oldest occurrence of this ichnotaxa in the Maestrazgo Basin and are coherent with other coeval (or almost coeval) occurrences in the Iberian Peninsula. The presence of *C. magnificum* in the El Castellar Formation fills a gap between the oldest (Tithonian-early Valanginian?) and younger (Barremian) occurrences of ornithopod tracks within the Maestrazgo Basin, being one of the most complete successions of ornithopod tracks in Europe. Interestingly, the underlaying formations have ichnoassemblages with *Dinehichnus*-like and *Iguanodontipus*-like tracks, whereas *Caririchnium* is mainly found in El Castellar Formation and other Barremian units. These changes in the ichnoassemblages reflect the ornithopod faunal changes shown by osteological data in the Iberian Peninsula recording a Late Jurassic-earliest Cretaceous stage dominated by basal iguanodontians followed by an Early Cretaceous stage with abundance of more derived and large-sized iguanodontians.

1. Introduction

Dinosaur footprints have been described in different coastal and continental Upper Jurassic-Lower Cretaceous sedimentary units of the Galve subbasin in the Maestrazgo Basin (Iberian Basin Rift System, NE Spain) since the early eighties (e.g. Pérez-Lorente, 2009; Alcalá et al., 2016; Aurell et al., 2016; and references therein). Among the Upper Jurassic-Lower Cretaceous units in the Galve subbasin, the lacustrine El Castellar Formation is the only one where no clear dinosaur tracksites have been described despite recent intense paleontological fieldwork carried out in this unit (e.g. Cuenca Bescós et al., 2014; Gasca et al., 2018). Many of the dinosaur tracks described in other Upper Jurassic-Lower Cretaceous units of the Galve subbasin are preserved as concave epireliefs on top bedding planes of sandstone and limestone beds, and new findings are also providing dinosaur tracks preserved as natural casts (convex hyporeliefs) (e.g. Castanera et al., 2013a; Herrero-Gascón and Pérez-Lorente, 2013; Navarrete et al., 2014). This increasing number of findings of natural casts of dinosaur footprints is a common tendency in other areas and it is probably a consequence to the fact that in earlier times these casts were either ignored or not interpreted as biological in origin (Nadon, 2001; Carvalho et al., 2021). In particular, the number of natural casts of dinosaur footprints described in Mesozoic geological units of the Iberian Peninsula (including other subbasins of the Maestrazgo Basin) has considerably increased in the last years (e.g. Avanzini et al., 2012; Cobos and Gascó, 2012; Huerta et al., 2012;; Vila et al., 2013; Piñuela, 2015; Castanera et al., 2016a, 2016b, 2020, 2021; García-Cobeña et al., 2022). Most of the aforementioned natural casts are preserved in sandstone beds, being few examples those preserved at the base of limestones (e.g. Castanera et al., 2016a; García-Cobeña et al., 2022). For instance, in the Lower Cretaceous units of La Rioja (Cameros Basin, Iberian Basin Rift System) thousands of footprints have been described, but few of them are preserved as carbonate natural casts (Pérez-Lorente, 2015). As track formation and preservation are directly linked to the paleoenvironmental settings and thus substrate properties (e.g. Laporte and Behrensmeyer, 1980; Nadon, 2001; Vila et al., 2013; Shillito and Davies, 2019), detailed studies on limestone track-bearing units are required to understand processes involved in track production and their physical preservation as track casts.

Since the first studies of dinosaur ichnology in Europe back in the 19th century (see Sarjeant et al., 1998 for an historical revision) "*Iguanodon* footprints" have been worldwide discovered, being especially abundant in Lower Cretaceous units of Europe including the Iberian Basin Rift System (see Lockley et al., 2014; Díaz-Martínez et al., 2015). Large ornithopod tracks have been identified in the Lower Cretaceous successions of the Iberian Basin Rift System since the first ichnological studies, being very common in Lower Cretaceous units of the northwestern domain (Cameros Basin: Castanera et al., 2013b; Díaz-Martínez et al., 2015; Pérez-Lorente, 2015 and references therein). This type of tracks has been also identified in several stratigraphic units since the earliest ichnological studies in the Galve subbasin (Cuenca et al., 1993; Pérez-Lorente, 2009) with the exception of the El Castellar Formation (sensu Aurell et al., 2016). Despite the scarce vertebrate ichnological record, this unit is very rich in osteological remains of several groups such as chondricthyans, osteichcthyans, mammals, testudines, lissamphibians, lacertids, crocodylomorphs, pterosaurs and dinosaurs, including iguanodontian ornithopods (e.g. Estes and Sanchiz, 1982; Ruiz-Omeñaca et al., 2004; Gasca et al., 2012; 2018; Cuenca-Bescós et al., 2014;).

The aim of this paper is the description and interpretation of a new tracksite named San Benón that show very peculiar features regarding the physical preservation of the footprints as casts at the base and lowermost part of limestone beds reflecting in detail different stages of track production. The limestone beds bearing tracks locate in the upper part of the El Castellar Formation within the Galve subbasin which is earliest Barremian in age. This is so far the only record of well recognizable dinosaur footprints from this unit in the Galve subbasin. A detailed analysis of the palustrine-lacustrine depositional facies related to the site and of the stages of track production is carried out, and the preservation potential of the footprints within the formation is evaluated. Besides, as the tracksite preserves large ornithopod footprints, the implications for the evolution of ornithopod footprints recorded within the Maestrazgo Basin are also discussed.

2. Geological setting

The San Benón tracksite is located in the upper part of the El Castellar Formation cropping out about 1 km to the southwest of the Camarillas village (Teruel province, NE Spain). This unit forms wide outcrops in the Galve subbasin, located in the western margin of the Maestrazgo Basin (Fig. 1A).

The Upper Jurassic-Lower Cretaceous successions in the Maestrazgo Basin were deposited during a major rifting stage of eastern Iberia (e.g. Salas et al., 2001; Aurell et al., 2019a), and encompass two syn-rift sequences, being the El Castellar Formation the first unit of *syn*-rift sequence 2 in the Galve subbasin (Fig. 1B; Liesa et al., 2006; Aurell et al., 2016, 2019b). The El Castellar Formation is mainly composed by limestones and marlstones that represent deposition in palustrine-shallow lacustrine environments (Meléndez et al., 2009). In the area located between Camarillas and Aguilar del Alfambra villages (Fig. 1C), the El Castellar Formation unconformably overlies the mid-Tithonian-lower Berriasian coastal-marine succession of the Aguilar del Alfambra Formation (Bádenas et al., 2018) and is conformably overlain by the continental to coastal lower Barremian Camarillas Formation (Liesa et al., 2019). The latest Hauterivian-earliest Barremian age of the El Castellar Formation in the Galve subbasin is well-constrained by the presence of a rich assemblage of charophytes. In the nearby locality of Buscajas, the lower levels of the unit have yielded a rich assemblage of *Atopochara trivolvis* var. *triquetra* (primitive form) along with few specimens of *A.t.* var. *ancora* and *A.t.* var. *micrandra* indicating a late Hauterivian-early Barremian age (e.g. Martín-Closas, 1989; Pérez-Cano et al., 2021). The upper levels of the unit including the San Benón tracksite have homogeneous populations of *Atopochara trivolvis* var. *triquetra*, indicating the onset of the lower Barremian *Atopochara trivolvis* var. *triquetra* biozone (Martín-Closas, 1989; Pérez-Cano et al., 2021).

3. Materials and methods

Dinosaur tracks of the San Benón tracksite are included in different limestone blocks that were removed from the original beds during the construction of the road A-228 and accumulated along its roadside (Fig. 1). More than 10 large blocks preserving tracks (or partial tracks) have been identified. Latitude-longitude coordinates of the area are 40º 36' 20" and 0º 46' 19". The majority of them mainly preserve indeterminate isolated digit impressions but four of them (named SB1 to SB4) also preserve ornithopod footprints. Among them, block SB3 stands out by their large and well-preserved ornithopod footprints and is described here in detail. Block SB3 has been relocated and is currently on display in Camarillas village. All the tracks are preserved as casts (convex hyporeliefs). We have distinguished between natural casts that represent the infill of the true track (Lockley, 1991) and undertrack casts that represent the deformed underlying layers seen from below in the base of the bed (Milàn and Bromley, 2006; Piñuela, 2015; Marty et al., 2016).

A detailed stratigraphic-sedimentological log has been carried out in the El Castellar Formation, in a continuous outcrop located c. 500 m south of the location area of the limestone blocks (Figs. 1C and 2A). The log summarizes both field observations of lithology, texture, components, bedding and sedimentary structures, and the petrographic description of limestone samples in thin sections and microfossil content in marlstone samples. This analysis allowed to precise the stratigraphic location of the limestones bearing the tracks, to identify the substrate (facies and related paleoenvironment) on which they were produced and to interpret the stages of track formation and preservation in relation with evolution of sedimentation.

The morphological preservation (MP) has been evaluated in the ornithopod tracks according to the scale of Marchetti et al. (2019). Each track has been analyzed individually by measuring footprint length (FL), footprint width (FW), the length and width of digits II (LII, WII), III (LIII, WIII), and IV (LIV, WIV), the "heel" (metatarsophalangeal) area (HA), and the divarication angles (II^III, III^IV) following previous procedures for the analysis of ornithopod tracks (e.g. Castanera et al., 2013b, 2020). The FL/FW ratio and the mesaxony (AT: anterior triangle length (ATl)/width (ATw) ratio), following Lockley (2009) were calculated accordingly. The measurements were taken with the software ImageJ from the false-colour depth maps exported from the 3D-photogrammetric models. These were generated from pictures taken with a Panasonic DMZ-FZ7, using the software Agisoft Metashape Standard Edition. The meshes were exported as OBJ files and then scaled and processed in CloudCompare (v.2.6.2) in order to obtain false-colour depth maps. All photogrammetric meshes used in this study are available for download in the supplementary information, following the recommendations of Falkingham et al. (2018).

4. Sedimentological context of San Benón tracksite

The studied facies succession of the El Castellar Formation (Fig. 2) roughly fit with the low-energy lake margin facies association described within the unit at regional scale. This facies association is characterized by stacked successions of marls to marlstones to limestones with subaerial features on top (root traces, brecciation and nodulization; Meléndez et al., 2009). The sedimentological analysis performed in the present work indicates that there is a vertical facies stacking from marlstones to mud-supported and grain-supported limestones (Fig. 2C), although some subaerial exposure features cited by Meléndez et al. (2009) (e.g. brecciation and nodulization) are absent and root traces are possibly overprinted by other types of bioturbation.

Grey to brown marlstones with plant remains, and characean and ostracod mudstones/wackestones (with bivalves, gastropods, osteichtyan, chondrichtyans and plant remains) were accumulated in low-energy shallow lacustrine areas with different detrital input. These two facies were eventually subaerially exposed in palustrine conditions as indicates the local presence of root traces (Fig. 2C; e.g. Alonso-Zarza, 2003). These two facies can pass vertically to characean and ostracod wackestones/packstones with frequent accumulations of disarticulated bivalves and gastropods, and sharp and locally irregular erosive bases. Undulate (wavy) lamination, and root traces/burrows filled with muddier sediment are frequent (Fig. 2A, B). These features indicate deposition in shallow lacustrine areas with alternating low-energy and high-energy conditions eventually exposed in palustrine conditions (Fig. 2C). The packstone/grainstone facies (either dominated by characean algae or by ostracods) overlying the characean and ostracod mudstones/wackestones facies (Fig. 2C) represents the highest-energy lacustrine facies of the succession, as indicated by the grain-supported texture and the presence of irregular erosive bases and undulate lamination. Possible hydrodynamic sorting gave rise to domination either of characean debris or disarticulated ostracod valves. Very locally, there are also mudstones with fenestral porosity and mudcracks formed in palustrine conditions.

The observed facies and facies stacking reflect deposition in a palustrine-shallow lacustrine area of very low-angle depositional topography as suggested by Meléndez et al. (2009). This lacustrine area had to have some connection with marginal marine environments located to the east (Aurell et al., 2019b), as indicates the occasional presence of ostreid remains in the uppermost part of the unit (Fig. 2C). Falls and rises in lake level originated sharp changes in the environmental conditions. In particular, eventual lowering in lake water level involved the subaerial exposure of shallow lacustrine sediments, both low-energy muddy sediments (grey to brown marlstones, characean and ostracods mudstones/wackestones) and relative high-energy grainy sediments (characean packstones/grainstones and ostracod packstones/grainstones).

The texture and sedimentary structures recognized in the blocks bearing the tracks, and in particular in block SB3, indicate they come from two possible limestone packages located at the upper part of the limestone-dominated middle succession of the unit (see packages 1 and 2 in Fig. 2). These two packages are not outcropping in the area were the blocks are located because they were removed during the construction of the road. Nonetheless, the packages do not show significant sedimentological differences, as both are characean and ostracod wackestones/packstones with bivalve and gastropod accumulations, root traces and burrowing. In addition, both packages overly grey to brown marlstone beds, although package 1 also overlies a thin discontinuous mudstone/wackestone bed (Fig. 2A). This thin bed has not been clearly identified in SB3 block (and some of the other blocks), but its absence/presence is not a good criterion to precise the original location of blocks (either from package 1 or 2), as this marlstone bed can be absent due to lateral facies variations or to erosion during removing of blocks.

5. Description of the dinosaur tracks

Block SB3 has a surface area of around 4 m^2 and has the largest concentration of tracks showing a rather moderate to high dinoturbation index (Fig. 3). Two ornithopod tracks (SB3.1 and SB3.2) can be clearly identified. In addition, two isolated digit impressions (SB3.3, SB3.4), a possible tridactyl track (SB3.5) and several isolated smaller digit impressions (SB3.6) are also present.

SB3.1 and SB3.2 are large sized ornithopod tracks (FL = 53-54 cm, Table 1) showing medium to high MP value (2.5 and 1.5 respectively). SB3.1 has the highest MP value, and although it has half of digit II broken, it can be considered an elite track. Both footprints are tridactyl, mesaxonic with robust digits. DIII is the longest, DIV and DII are slightly shorter and subequal in length. They are almost as wide as long (length/width ratio close to 1) with a low mesaxony (AT close to 0.3). The tracks show one pad impression per digit and one large heel pad, thus showing a clear quadripartite morphology. Digital pads are clearly longer than wide. The heel pad has a subtriangular morphology. It is wide (wider than the proximal part of the digit III impression) and has a subrounded to subrectangular posterior margin. The tracks show well-developed notches in the proximal part both medially and laterally, being one of those (possibly DII?) slightly more marked. The tracks are very symmetrical with similar interdigital divarication angles II^III and III^IV and low total divarication angle (II^IV lower than 60º). SB3.1 and SB3.2 have some differences since SB3.2 show evidence of blunt claw impressions, the mesaxony is slightly higher, the digital pads are considerably shorter and the heel pad is slightly wider.

SB3.3 is a digit impression that belongs to a partial track cut by the block surface. It shows a sharp claw mark. SB3.4 is also a digit impression that might be part of the tridactyl track SB5, being the central digit (digit III) of the track. SB3.6 refers to indeterminate scratch-like impressions. They are elongated, straight with a rather acuminated end, and shallow impressions randomly distributed in the bedding plane of the block (dot lines in Fig.3C).

6. Stages of sedimentation and track production

The facies sequence involving the tracks of block SB3 of the San Benón tracksite encompasses a grey marlstone bed and the overlaying limestone package of shallow-lacustrine characean and ostracod wackestone-packstone facies (see *a* and *b* in Fig. 4, respectively). Detailed analysis of tracks of the lowermost cm-thick sediment layers of the limestone (Fig. 4A) allows establishing a complex history of stages of sedimentation and track formation and preservation, linked to raises and falls in water level (Fig. 4B), involving at least three episodes of track production in different tracking surfaces. As is detailed below, the presence of different tracking surfaces (instead of a unique tracking surface with variable water content) is justified by: 1) the presence of two initial sediment layers (*b-1*/*b-2*) at the bottom of the block that are not preserved across the whole surface, but just inside of some footprints. These two layers seem not to be distorted by the footprint but accommodated, the base of the footprint being flat; 2) the presence, overlying the *b*1-*b*2 footprint infill, of younger sediment layers (*b-2*/*b-4* and *b-n*) that indeed are disturbed by other tracks.

The first episode of track generation corresponds to the tracks located on the left side of the block in Figs. 3 and 4A (track SB3.1 and possibly SB3.4 plus SB3.5). After deposition of low-energy lacustrine marly layer *a* (stage 1 in Fig. 4B), the marly substratum became firm most probably because of subaerial exposure due to lowering of water level (see stage 2); soon thereafter, track SB3.1 was produced on this surface (see stage 3) where the lack of collapse associated to this track also suggests that the marlstone substrate was firm (e.g. Jennings et al., 2006) (see stage 3). The nature of the substratum would explain the high MP quality of SB3.1. Thus, these tracks were formed in the marly layer *a* and subsequently filled by the first cm-thick bioclastic layers of wackestone-packstone facies (in particular grain-supported layer *b-1* and the lower part of mud-supported layer *b-2*). This filling is deduced by the absence of these layers in other areas of the block, the parallelism between the base of the limestone bed and the *b-1/b-2* boundary and the fact that these layers are mainly preserved inside the SB3.1 track and are not affected by the trampling itself but filling the track (Fig. 4). Thus, these tracks would be preserved as a natural cast of the true track. Absence of detailed claw impressions or scale impressions in SB3.1 might be explained by the nature of grainy layer *b-1*, in particular by the poor size classification of its skeletal grains (with both sub-mm to mm-size ostracods and characean algae, and mm to cm-sized gastropods and bivalves; e.g. Fig. 2B), which would avoid the preservation of those features. Other substrate properties relevant to the absence of features might be a coarse grain size of the grainy layer or a high water content of the marls which would be relatively wet but not saturated enough to collapse (e.g. Falk et al., 2017).

After the generation of the tracks in stage 3, water level rose allowing the deposition of shallow-lacustrine grainy and muddy layers *b-1* to *b-4* (characean and ostracod wackestone-packstone facies) that sealed the tracks of first episode of trampling (stage 4). The second episode of track generation would correspond to a trampling episode where scratch-like indeterminate impressions (e.g. SB3.6, dot lines in Fig. 3C) have been identified. This episode affects part of layer *b-2* and overlaying layers *b-3* and *b-4* (Fig. 4A). The disturbance indicates these tracks were produced at least after deposition of layers *b-1/b-4* when they were still soft and probably in subaqueous conditions (stage

5 in Fig. 4B). Therefore, the actual mode of preservation of the tracks of episode 2 is difficult to interpret since the footprint morphology is not clear. Thus, the scratch-like impressions could be either interpreted as undertrack casts of swimming traces (Milner and Lockley, 2016) or as penetrative tracks (Gatesy and Falkingham 2020).

Finally, after generation of the impressions in stage 5, there was a stage of sedimentation (stage 6 in Fig. 4B) of at least layer *b-n*, but probably of more layers, followed by an episode of generation of tracks SB3.2 and SB3.3 (stage 7), making layer *b-n* penetrating downwards to layer b4. These tracks are very shallow (considerably shallower than SB3.1) and preserve the whole track morphology but with less sharp footprint contours and morphological features and thus lower MP value than track SB3.1 of the first episode (stage 3). Thus since they show some morphological features such as claw impressions, they might be preserved as shallow undertrack casts (Milàn and Bromley, 2006; Piñuela 2015). However, there are not clear criteria to interpret if tracks of stage 7 were generated in a subaqueous or a subaerial sediment surface (Fig. 4B). The precise production of the tracks of stages 5 and 7 is difficult to evaluate since it is not possible to know where the tracking surfaces are located.

7. Discussion

7. 1. Unusual dinosaur track preservation in the El Castellar Formation

The footprints of San Benón were preserved as casts at the lowermost part of the same limestone bed. The detailed sedimentological analysis tells us a complex and singular history of different stages of footprint formation and preservation. The bed shows a moderate dinoturbation index (Lockley, 1991), but the tracks were not coeval so they are part of different ichnoassemblages forming a composite ichnofabric (Ekdale et al., 2012) of tracks. The detailed analysis of track formation in relation with sedimentation layers reflects the importance of analyzing the location of the tracking surface to understand track preservation (e.g. Marty et al., 2016). In San Benón, the tracks were produce at different times and have different modes of preservation depending on the moment of trampling (Fig. 4), mainly: 1) natural cast of the true tracks (stage 3) that walked on a firm marly layer; 2) undertrack casts or penetrative tracks (i.e. scratch marks and indeterminate tracks) of stage 5 that step and disturbed soft shallow-lacustrine bioclastic layers in subaqueous conditions; and 3) shallow undertrack casts (stage 7) that walked on shallow-lacustrine bioclastic layers deforming the underlaying firm layer with no clear evidences of subaqueous or subaerial conditions at the moment of track generation. Therefore, a variation in substrate conditions from firm to soft (and firm again) during track production (episodes 1, 2, 3 in stages 3, 5 and 7, respectively), possibly linked with water content (from moist to wet to indeterminate, respectively), can satisfactorily explain both the different types of preservation observed in the tracksite and the differences of the MP values and morphological features (e.g.: claw impressions) of the large ornithopod tracks recorded in stages 3 and 7.

The San Benón tracksite preserves the first clear dinosaur tracks identified within the El Castellar Formation in the Galve subbasin and shows a good example about how the environmental conditions for track production and preservation were both optimal (e.g. Falk et al., 2017). For instance, in stage 3 a short period of subaerial exposure that prevented destruction after track formation either by physical or biological agents (e.g. wave action, plant colonization, bioturbation/burrowing or mudcrack generation), but also a rapid rise in lake level that drove to the deposition of the shallow lacustrine cm-think grainy and muddy layers *b1–b4* sealing the tracks. Rapid aggradation (deposition) has been highlighted to be an important factor for track preservation (e.g. Laporte and Behresmeyer, 1980; Nadon, 2001; Gasca et al., 2017). In particular, the probably short-lasting alternating high- and low-energy sedimentation conditions of the cm-thick grainy and muddy layers of bed *b* favoured track preservation of track of stage 3, with energy not high enough to erode the track. Besides, the sediment was not subsequently so heavily trampled (stages 5 and 7) to destroy the previously produced tracks either in stage 3 or 5.

As exposed in the introduction section, the presence of dinosaur tracks in the San Benón tracksite not only represents an uncommon type of preservation, but also an uncommon example of preservation of casts in carbonate/calcareous sediments in the Iberian Peninsula. In this regard, Pérez-Lorente, (2015) noted that most of the casts found in La Rioja are preserved in sandstones and that “natural casts in limestone have only been found after reservoir explosions and during road-widening work after breaking through thick calcareous sedimentary formations or units”. This is precisely the case of the San Benón tracksite where the construction of the road has allowed the motion of the blocks.

Pérez-Lorente, (2015) also noted the importance of the lithology for the preservation of the footprints as casts, suggesting that "it is probably easier for casts to become separated from sandstone than from limestone". This is also the case of San Benón, where the change in facies from marlstone to limestone and their contact (*a-b* in Fig. 4) have also undoubtedly played a role for track preservation. Interestingly, Nadon (2001) indicated that generally the casts (in sandstones) are infilled in a single event, but in the case of SB3.1 it was infilled by two high- (*b-1* layer) and low-energy (*b-2* layer) deposition events.

Regarding the low number of dinosaur tracks in the El Castellar Formation, previous reports of tracks in this unit in the Galve subasin were mainly based in observations of "deformations" on tops of limestone beds (i.e. on top of shallowing-upward sequences of lake margin facies) rather than well-defined dinosaur footprints (Meléndez et al., 2009). This mode of preservation is completely different to that of San Benón tracksite or to the recently described tracks from Cabra de Mora also preserved as casts in limestone (Level 1)/sandy limestone (Level 2) beds (García-Cobeña et al., 2022). Outcrop conditions in the area of San Benón tracksite allow the exposition of large areas of top bedding planes of several limestone strata, but no clear dinosaur footprints could be identified. The low number of reports of clear dinosaur tracks up to now within the formation might be a consequence of several factors, mainly linked to the paleonvironmental conditions. Nadon (2001) proposed that intertidal regions and anastomosed fluvial systems are the best paleoenvironments for track preservation. Nonetheless, several dinosaur tracksites have been also described in lacustrine to palustrine units of the Iberian Range showing also the high preservation potential for dinosaur tracks on top of bedding planes of these facies successions in the Iberian Basin Rift System (e.g. Moratalla and Hernán, 2010; Gasca et al., 2017; Moratalla et al., 2017; Torcida et al., 2021). Thus, this low number of reports of dinosaur tracks described up to now in the El Castellar Formation would be an anomaly since a high preservation potential of footprints would be expected in such palustrine-shallow lacustrine paleonvironments. Gasca et al. (2017) noted that in the Mirambel Formation the tracks are considerably scarce in massive limestones and rooted palustrine limestones (in contrast to laminated limestones) and proposed that "the effects of persisting palustrine conditions are less favourable for track preservation and/or track production". This fits with our observations in San Benón, where short periods of subaerial exposition in palustrine conditions favoured track preservation of tracks in stage 3. Laporte and Behresmeyer (1980) noted the biases in vertebrate track preservation along the Lake Turkana as a consequence of waves, longshore currents and winds but also noted the importance of the intense vertebrate trampling in the obliteration of primary sedimentary structures (thus including previous footprints). This latter factor combined with intense bioturbation on top of some limestone beds, and the fact that many top bedding surfaces correspond to relatively deeper facies within the lake system might be the factors to explain the footprint preservation bias seen in the tops of many strata within El Castellar Formation. This new results would be applicable to other similar palustrine-lacustrine carbonate successions and can be used for further searching of dinosaur tracks.

7. 2 Ichnotaxonomy

In the last years there has been a considerable advance for the “stabilization” of a robust ichnotaxonomy in large ornithopod footprints and several reviews of the main ichnotaxa have been carried out (e.g. Lucas et al., 2011; Lockley et al., 2014; Díaz-Martínez et al., 2015). Díaz-Martinez et al. (2015) analyzed 34 ichnogenera and 44 ichnospecies, many of them considered invalid because of the poor morphological quality preservation or inadequate diagnosis. These authors only considered as valid eight ichnospecies belonging to the ichnogenera *Iguanodontipus* (Berriasian-Valanginian, Fig. 5C), *Caririchnium* (Berriasian-Albian, Fig. 5D) and *Hadrosauropodus* (Aptian-Maastrichtian, Fig. 5E). It should be noted that some Lower Cretaceous ichnogenera considered as *nomen dubium* by Díaz-Martinez et al. (2015), such as *Amblydactylus* (Fig. 5F) or *Ornithopodichnus* (Fig. 5G), are considered valid for other authors (Lockley et al., 2014; Kim et al., 2016; Xing et al., 2016). Main differences seen among the aforementioned ichnogenus rely on the pes tracks with variations in length/width ratios, mesaxony, digit termination (e.g. pointed toes, ungual traces), features of the digital pads (quadripartite or nonquadripartite configuration) or the heel shape (rounded, oval, triangular, bilobed). Other differences are the absence/presence of manus tracks and their shape, as well as the possible skin traces, rotation of manus and pes and trackway width and pace angulation (Lockley et al., 2014; Díaz-Martínez et al., 2015).

The features of the studied tracks in SB3 block (in particular, SB3.1 and SB3.2) show considerable differences with the aforementioned ichnotaxa in many of the mentioned features (see Fig. 5) with the exception of *Caririchnium*. The SB3 ornithopod tracks fit all the features of the emended diagnosis of the ichnogenus provided by Díaz-Martínez et al. (2015). According to the authors, four ichnospecies can be considered valid: *C. magnificum* (Fig. 5D), *C. kortmeyeri* (Fig. 5H, previously referred to *Amblydactylus*), *C. billsarjeanti* (Fig. 5I, previously referred to *Iguanodontipus*) and *C. lotus* (Fig. 5J). Since the revision of Díaz-Martínez et al. (2015) new data regarding *Caririchnium* tracks have been published. Xing et al. (2015) emended the diagnosis of *C. lotus* emphasizing the quadripartite morphology and the pronounced ridges that separate the heel pad impression. Besides, two new ichnospecies *C. yeongdongensis* (Fig. 5K, Kim et al., 2016) and *C. liucixini* (Fig. 5L, Xing et al., 2016) have been defined. Main differences among the ichnospecies are in the heel pad dimensions and morphology, the shape of the claw impressions and the mesaxony in the pes prints (Díaz-Martínez et al., 2015; Xing et al., 2016) and also in the manus morphology (Kim et al., 2016).

Both SB3.1 and SB3.2 differ from many of the ichnospecies in the shape of the heel pad impression (Fig. 5). The outline of the heel pad impression is subtriangular in the San Benón tracks, whereas is rounded/subeliptical in many ichnospecies (e.g. *C. billsarjeanti*, *C. yeongdongensis*, *C. lotus*, *C. liucixini*). The track morphotype of San Benón clearly differs from *C. kortmeyeri* because it shows pointed claw impressions. The greatest similarities are with *C. magnificum* and *C. lotus*. Both ichnospecies have differences in the dimensions of the heel pad impression since it “is as wide as or wider than long” in the former and longer than wide in the latter. Regarding this parameter, the San Benón tracks show dimensions that would be proportionally more similar to *C. lotus* although morphologically it is closer to *C. magnificum.* Xing et al. (2016) carried out a bivariate analysis, analyzing differences in length/width ratio and mesaxony. Interestingly, San Benón tracks would fall close to the range of both ichnospecies. The main morphology of the tracks is more reminiscent to *C. magnificum* since the track and the digits are more robust and the heel pad impression is subtriangular. Besides, tracks of *C. lotus* are generally more gracile and produced by smaller individuals (FL < 40 cm) and the heel pad morphology is more rounded. Thus, we tentatively classified the San Benón tracks as *C. magnificum*. This ichnospecies was defined from the Antenor Navarro Formation (Berriasian-Hauterivian) in Brazil by Leonardi (1984) and has been posteriorly identified in several sites from the Enciso Group in Spain (late Hauterivian-Barremian; Díaz-Martínez et al., 2015) and recently in the Berriasian-Valanginian of England (Shillito and Davies, 2019). The new material from San Benón provides a new evidence of this ichnotaxon in Europe and for the first time outside of the Cameros Basin in the Iberian Peninsula. This confirms the presence of the ichnotaxon in the lower Barremian of the Iberian Peninsula representing most probably a coeval occurrence to those recorded in the Enciso Group (e.g. Muñoz et al., 2020).

7.3 The ornithopod ichnological and osteological record in the Maestrazgo Basin: implications for ornithopod evolution

As mentioned in the introduction section, the Iberian Basin Rift System is one of the key areas for the study of large ornithopod footprints, especially the Cameros Basin (Díaz-Martínez et al., 2015). In the southeastern domain, in the Maestrazgo Basin, aside from the first identifications of ornithopod footprints (Cuenca et al., 1993; Pérez-Lorente, 2009 and references therein) recent findings come from the Barremian units, including the El Castellar Formation (in the neighbouring Peñagolosa subbbasin: García-Cobeña et al., 2022), Camarillas Formation (Cobos and Gascó, 2012; Herrero-Gascón and Pérez-Lorente, 2013; Navarrete et al., 2014), the Mirambel Formation (Castanera et al., 2016; Gasca et al., 2017) and the Artoles Formation (Cobos et al., 2016). This footprint record, despite the low number of reports in each unit, is one of the most complete stratigraphic records of ornithopod tracks in Europe since it ranges from the Tithonian to the Barremian, with ornithopod tracks discovered up to now in almost each of the stages (Fig. 6). However it should be noted that the sedimentary record is not continuous, because there is a widespread sedimentary gap of variable amplitude around the Valanginian-Hauterivian interval in the Maestrazgo Basin (e.g. Aurell et al., 2019b). In this regard, the San Benón tracksite and the recently described tracks from Cabra de Mora (García Cobeña et al., 2022) fill a gap on the Barremian ornithopod track record known so far, and they are now reported in all the transitional-continental stratigraphic units exposed in the western Maestrazgo Basin, from the Cedrillas to the Artoles formations (see Figs 1 and 6).

The overall ornithopod ichnological and osteological record of the Maestrazgo Basin allows to understand how the faunas evolved in a concrete area through a period of time of more than 25 My. Despite the new reports, the ichnotaxonomic affinities of the ornithopod tracks are not well understood since in many cases the tracks have just been considered as "ornithopod tracks". The oldest reports (Fig. 6) from Las Cerradicas tracksite (upper Cedrillas Formation, early Tithonian, Aurell et al., 2019b) have been related with *Dinehichnus*-like tracks (Lockley et al., 2009; Castanera et al., 2013a). *Dinehichnus* is an ornithopod ichnotaxon typical from the Late Jurassic, also identified in other areas including the Iberian Peninsula, and traditionally attributed to dryosaurid trackmakers (Lockley et al., 1998; Castanera et al., 2020). Cobos et al. (2015) related ornithopod footprints from the Aguilar del Alfambra Formation (mid-Tithonian-earliest Berriasian; Aurell et al., 2019b) with the ichnogenus *Iguanodontipus*, typical from the Berriasian of Europe and traditionally attributed to basal members of Ankylopollexia or Styracosterna (Castanera et al., 2013b; Díaz-Martínez et al., 2015). The ornithopod tracks from Los Corrales del Pelejón in the Galve Formation (late Berriasian-early Valanginian; Aurell et al., 2016) have not been classified (Cuenca et al., 1993), although their features are more related with *Iguanodontipus* than to any other ornithopod ichnotaxa (Figs. 5 and 6), and can be considered as *Iguanodontipus*-like. Although further work is needed in order to understand the clear ichnotaxonomic affinities of the tracks from the Tithonian-Valanginian? sites in the Maestrazgo Basin, it is interesting to note that the morphology and size of these tracks are clearly different from that of the post-Valanginian (mainly Barremian) tracksites. These are dominated by larger ornithopod tracks in several cases related to *Caririchnium*-like morphologies such as the case of San Benón or other tracksites from the El Castellar, Camarillas and Mirambel formations (Díaz-Martínez et al., 2015; Castanera et al., 2016a; García Cobeña et al., 2022).

It is interesting to note that in the Upper Jurassic-Lower Cretaceous units in the Maestrazgo Basin, there is not always a good correlation in the quality of the ichnological and the osteological ornithopod record with considerable preservation bias against certain groups and types of fossils through the stages. Despite the above-mentioned occurrences of ornithopod tracks in the older units (e.g. Cedrillas, Aguilar del Alfambra and Galve formations), the osteological evidence from the Tithonian-Berriasian units in eastern Spain is considerably scarce and the record very fragmentary, being the material related to dryosaurids and ankylopollexians (see Sánchez-Fenellosa et al., 2022 and references therein). The only ornithopod record described so far within these units in the Maestrazgo Basin is a fragmentary tooth from the Galve outcrops (i.e., Las Cerradicas) (Sánchez Hernández et al., 2007; Galton, 2009). In contrast, the Barremian deposits of the Maestrazgo Basin are much richer in bone remains, being medium to large-sized ornithopods the most frequent macrofossils, with at least three different forms belonging to non-hadrosaurid styracosternans (e.g. Gasca et al., 2014, 2015). Several taxa have been erected such as "*Delapparentia turolensis*" and *Iguanodon galvensis* from the lower Barremian of the Galve subbasin (Ruiz-Omeñaca, 2011; Verdú et al., 2015; 2021) or *Portellsaurus sosbaynati* from the lower Barremian Mirambel Formation (Santos-Cubedo et al., 2021) and *Morelladon beltrani* in the upper Barremian Morella Formation from the Morella subbasin (e.g. Gasulla et al., 2015). Besides, the presence of other classic European ornithopods such as *Iguanodon bernissartensis* and *Mantellisaurus atherfieldensis* has also been reported (Gasulla et al., 2014; 2022). Some of these taxa are the best candidates to be the trackmakers of the San Benón tracksite. Regarding the ornithopod record of the El Castellar Formation in the Galve subbasin, teeth and disarticulated bones are the main fossils discovered (e.g. Gasca et al., 2009; Gasca, 2011), whereas complete specimens assignable to a concrete species are unknown. Bone remains of a robust styracosternan have been described such as a fragmentary tibia recovered from the Masía de los Cerezos fossil site, in Allepuz (Gasca, 2011), 10 km to the south of San Benón tracksite. In the Peñagolosa subbasin, Verdú et al. (2019) identified two different ornithopod taxa on the basis of the morphometric and systematic study of several vertebrae. The authors identified two large indeterminate styracosternans, one that would be more related to a robust morphotype that would fit with taxa such as *Magnamanus* (described in the Cameros Basin, Fuentes Vidarte et al., 2016) or *Iguanodon*; and the second that would be related to a smaller trackmaker such as *Morelladon*. Recently, García-Cobeña et al. (2022) have provided new data on this coexistence of two different styracosternans in the El Castellar Formation and have identified *Iguanodon galvensis* in the unit. The presence of different styracosternan species during the Hauterivian-Barremian interval in the Maestrazgo Basin makes difficult to assign a concrete styracosternan trackmaker to the San Benón tracks and this high diversity might be responsible of the differences seen among the Barremian tracks within the basin and even within the San Benón tracks (Fig. 6).

8. Conclusions

The San Benón tracksite represents the first occurrence of indubitable ornithopod footprints within the palustrine-lacustrine El Castellar Formation (Fig.7) in the Galve subbasin. The tracksite is uncommon, as it contains a composite ichnofabric of non coeval dinosaur tracks. Successive stages of sedimentation and at least three episodes of track production have allowed the preservation of the footprints as natural and undertrack casts. These stages were linked to changes in the environmental conditions driven by falls and rises in lake level in this kind of palustrine-lacustrine environment of very low-angle depositional topography. The changes in sedimentary conditions explain the variety of tracks and modes of track preservation.

The paleoenvironmental conditions deduced bring some light on the preservational bias of the ichnological record in palustrine-lacustrine units. The preservation and the finding of the dinosaur tracks of San Benón tracksite required a conjunction of sedimentological (e.g. short periods of subaerial conditions, variations in lake level, heterolithic horizons with different marl-limestone facies), biological (not very intense bioturbation and vertebrate trampling), geological (outcrop conditions and availability) and even human (construction of the road) factors. Nonetheless, the successive episodes of dinosaur trampling show that the area was persistently frequented by dinosaurs, especially large-sized ornithopods.

The ornithopod tracks can be assigned to *Caririchnium magnificum*. This identification is the oldest occurrence of *Caririchnium* and represents the first occurrence of large ornithopod tracks within the Galve subbasin of the Maestrazgo Basin. Thus, this new ichnological record reports an ornithopod faunal change from Tithonian-Valangian units (with *Dinehichnus*-like and *Iguanodontipus*-like tracks and a poor osteological record) to the Barremian (with *Caririchnium* tracks and the presence of abundant large-sized styracosternan iguanodontians).

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FIGURES:

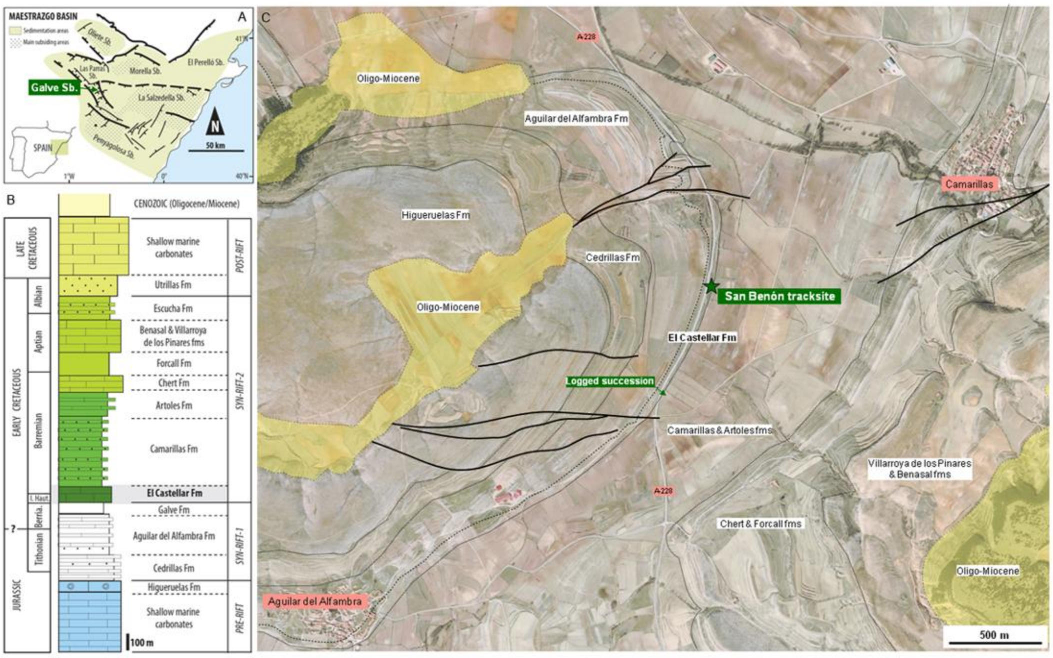

Figure 1: Geographical and geological setting of the San Benón tracksite. A) Geological setting of the Maestrazgo Basin in northeast Spain showing the distribution of subbasins (modified from Liesa et al., 2019). B) Synthethic log showing the stratigraphy of the Galve subbasin. The San Benón tracksite is located in the El Castellar Formation, in the lowermost part of the *syn*-rift sequence 2. C) Ortophoto showing the distribution of the lithostratigraphic units outcropping in the area located between Alguilar del Alfambra and Camarillas villages.

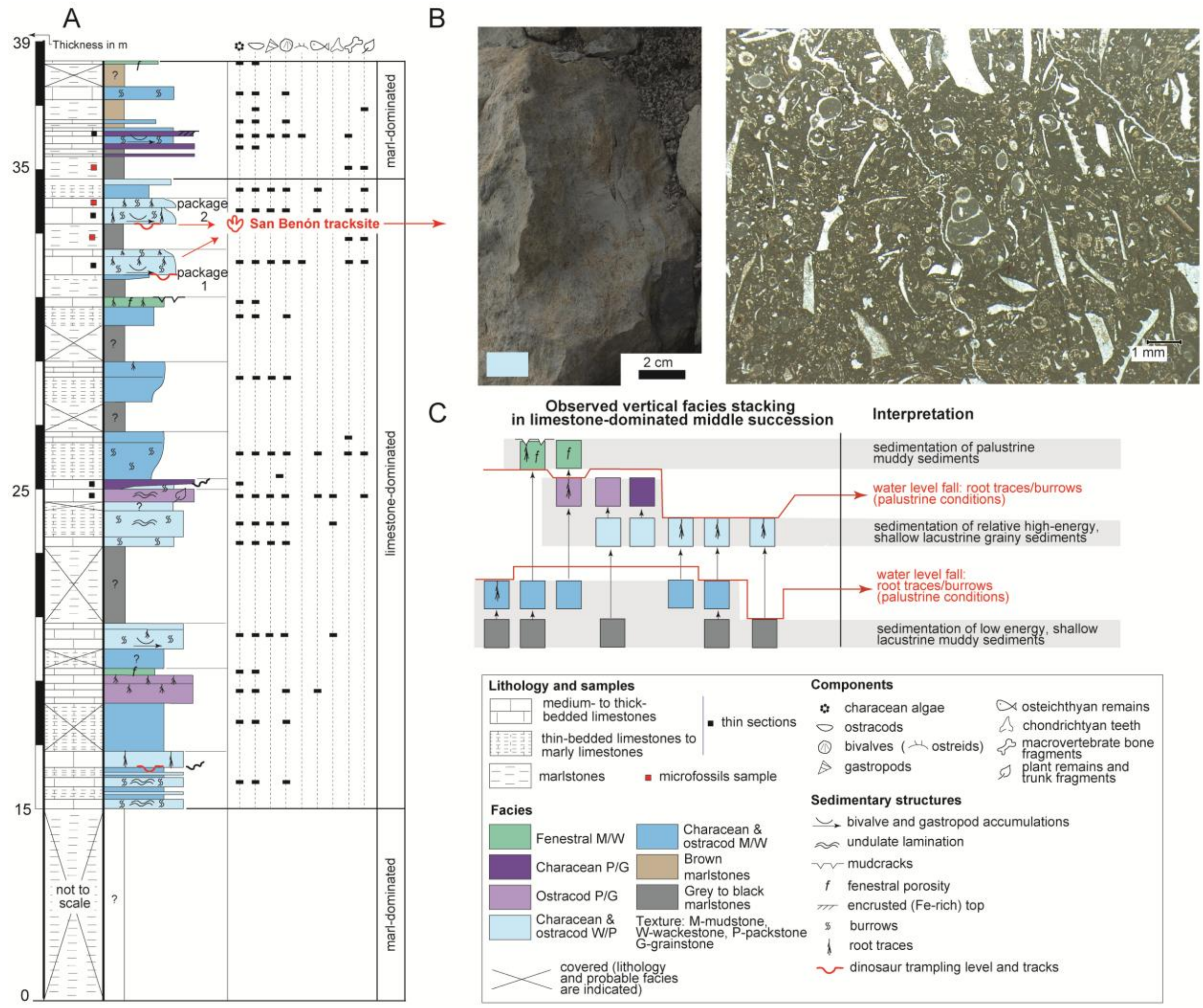

Figure 2: Stratigraphic-sedimentological context of the San Benón tracksite. A) Stratigraphic log of the El Castellar Formation, indicating the vertical distribution of different shallow palustrine-lacustrine facies and the location of the limestone packages (see packages 1 and 2) at the uppermost part of the middle limestone-dominated succession from which the San Benón tracksite limestone blocks come from. B) Field image and thin section image (in plane-polarized light) of the limestone package 2, belonging to characean and ostracod wackestone-packstone facies. Notice in the field image the presence of cm-thick grainy (skeletal) and muddy layers within the bed. C) Summary of vertical facies stacking within the middle limestone-dominated succession and sedimentological interpretation (see explanation in text).

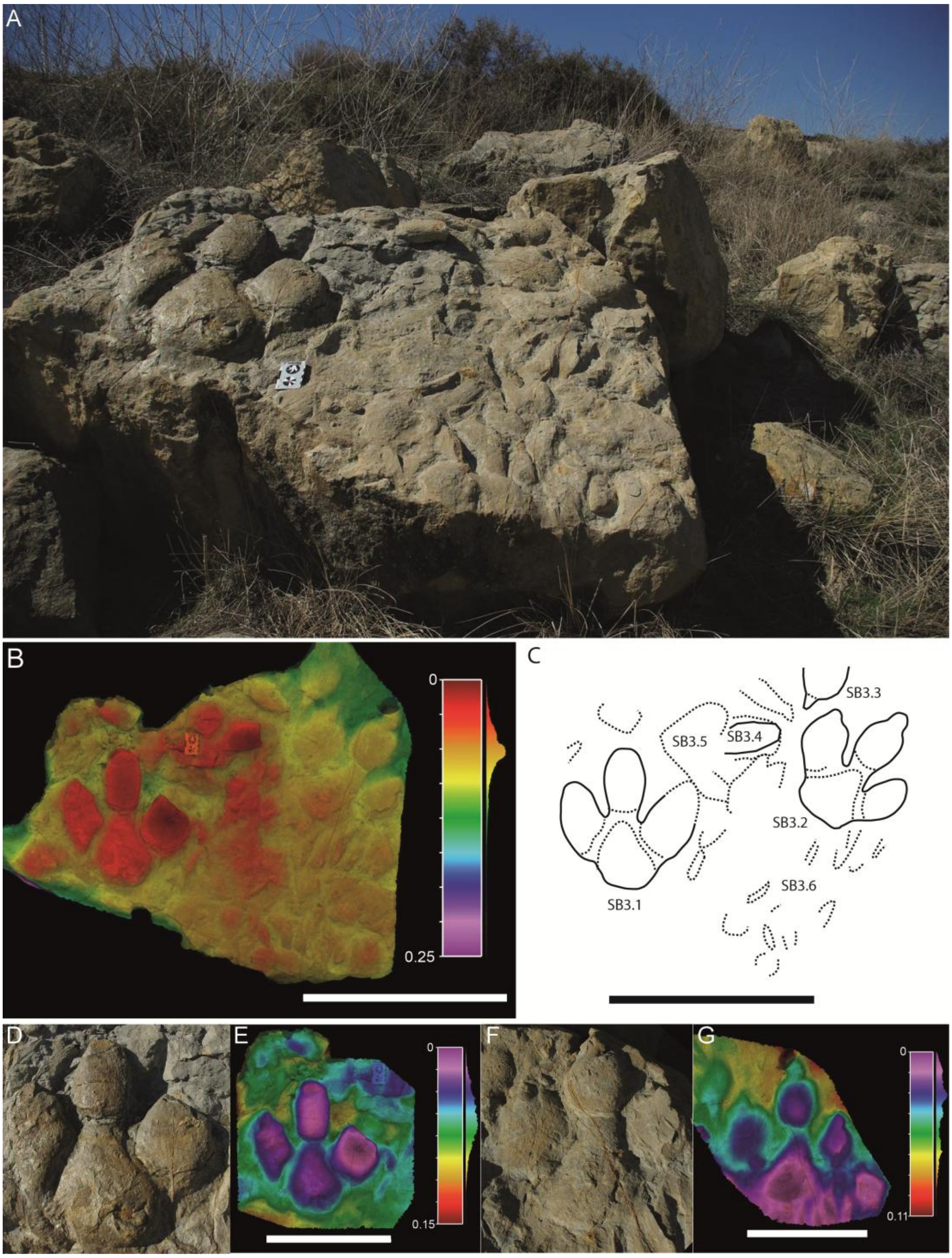

Figure 3: Block SB3 from San Benón tracksite. A) Field picture of the block. B) False colour depth map of the block. C) Outline drawing of the tracks identified in the block. D) Detailed picture of track SB3.1. E) False colour depth map of track SB3.1. F) Detailed picture of track SB3.2. G) False colour depth map of tracks SB3.2 and SB3.3. Scale bars 0.8 m (B), 0.5 m (E), 0.45 m (G).

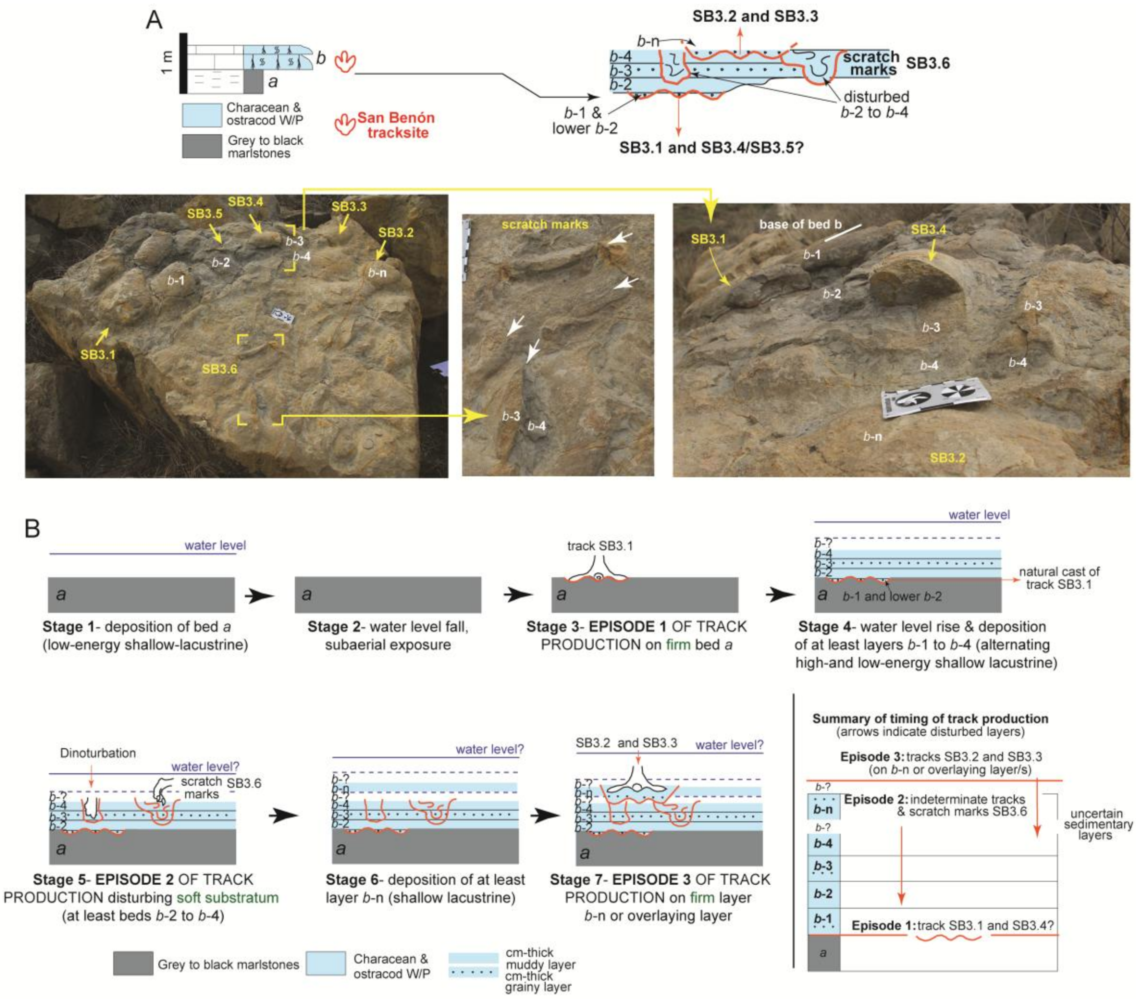

Figure 4: Track generation and preservation in the San Benón tracksite. A) Reconstructed stratigraphic position of the block SB3 in a section showing the trampling sequence within the layers. Field pictures of limestone block SB3 (bed *b* of the sedimentological profile), illustrating the relationship between tracks and lowermost sediment layers of bed *b* (see explanation in text). Note the flat base of track SB3.1 (layer *b-1*) in the left part of the block and the disturbed layers (*b-2*/*b-4* and *b-n*). B) Stages of sedimentation and episodes of track production and trampling deduced. Scale (card) = 8 cm.

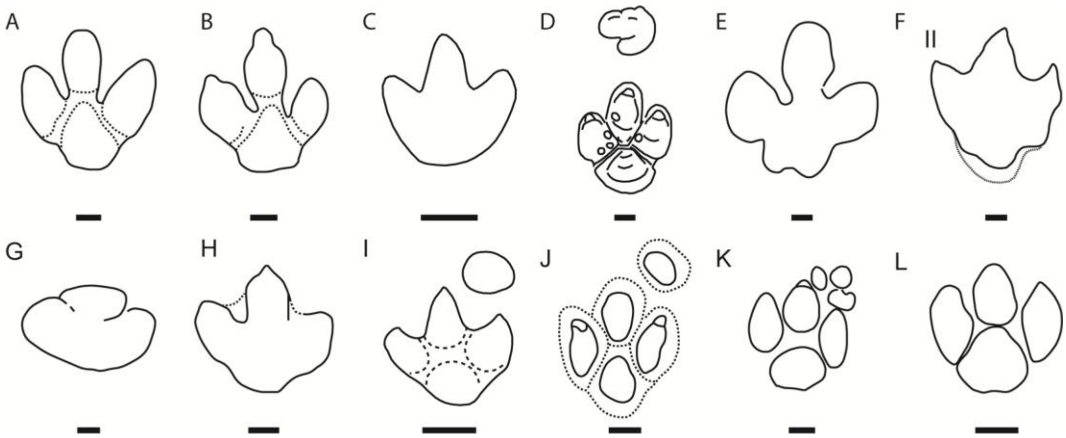

Figure 5: Comparison of San Benón tracks with the holotypes of the main large ornithopod ichnotaxa. A) SB3.1. B) SB3.2. C) *Iguanodontipus burreyi* (redrawn from Sarjeant et al., 1998). D) *Caririchnium magnificum* (redrawn from Leonardi, 1984). E) *Hadrosauropodus langstoni* (redrawn from Lockley et al., 2003). F) *Amblydactylus gethingi* (redrawn from Sternberg, 1932). G) *Ornithopodichnus masanensis* (redrawn from Kim et al., 2009). H) *Caririchnium kortmeyeri* (redrawn from Currie and Sarjeant, 1979). I) *Caririchnium billsarjeanti* (redrawn from Meyer and Thuring, 2003). J) *Caririchnium lotus* (redrawn from Xing et al., 2015). K) *Caririchnium yeongdongensis* (redrawn from Kim et al., 2016). L) *Caririchnium liucixini* (redrawn from Xing et al., 2016). Scale bar: 10 cm.

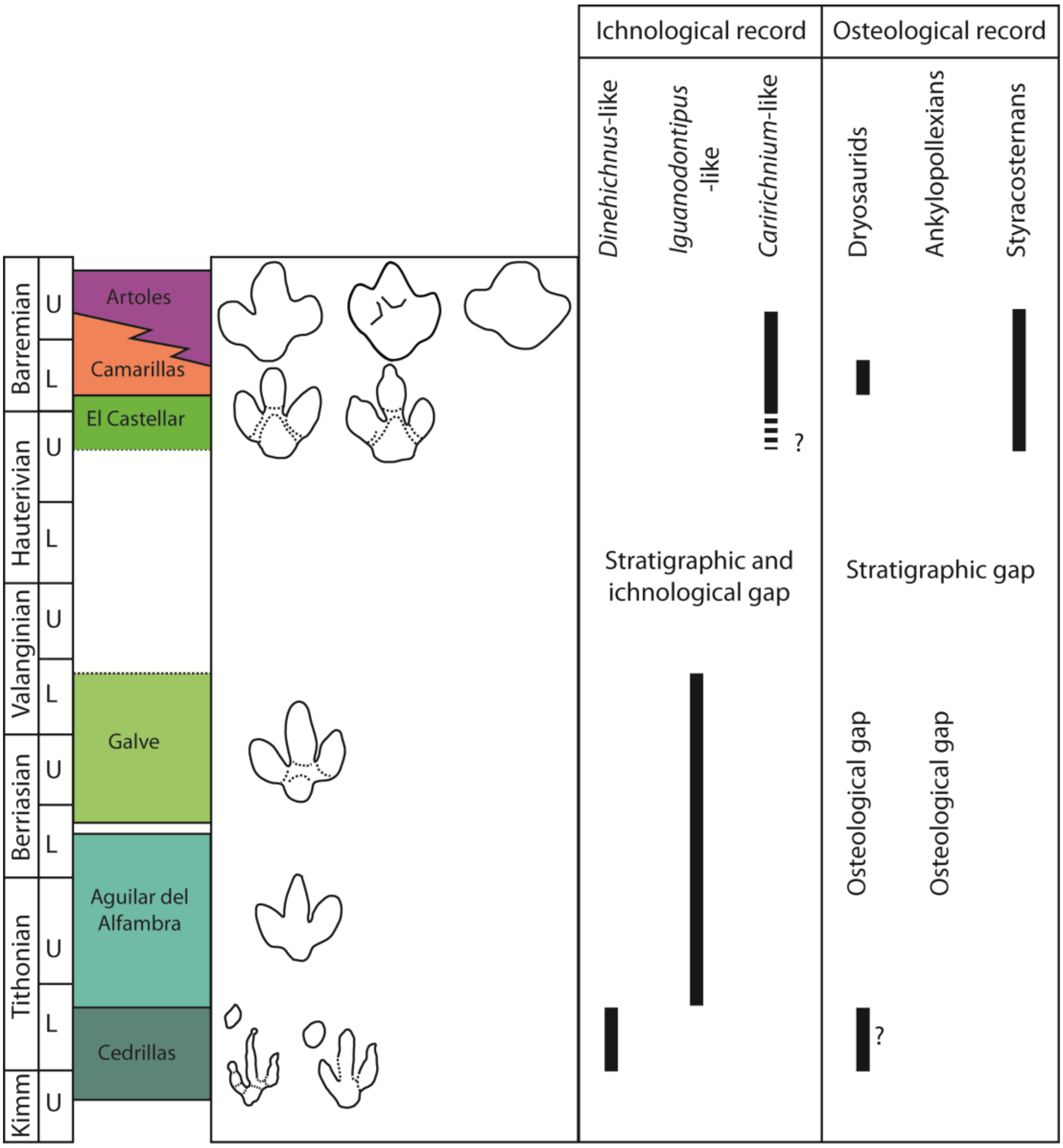

Figure 6: Comparison of the iguanodontian ornithopod ichnological and osteological record in the western Maestrazgo Basin showing the faunal faunal changes in ornithopod faunas (references of the data in the text). Drawings not to scale. Geological units from the Galve subbasin (based on Aurell et al., 2016; 2019b).

Figure 7: Paleoenvironmental reconstruction of the Camarillas area during the early Barremian showing the ornithopod that produced the San Benón tracks (drawing by Paleoymás S.L.).

TRACK	Left/ right	MP	FL	FW	FL/FW	LII	DPLII	LIII	DPLIII
SB3.1	right	2.5	53.5	52	1.02	46.5?	28.5	53.5	24.5
SB3.2	left	1.5	54*	47	1.14	42	21	54*	19
			LIV	DPLIV	WII	WIII	WIV	HPL	HPW
SB3.1	right	2.5	46	23	18.5	14	15.5	26	22
SB3.2	left	1.5	40	18	18	14.5	12.5	24	23
			II^III	III^IV	II^IV	ATL	ATW	AT	
SB3.1	right	2.5	33	26	59	13	44	0.29	
SB3.2	left	1.5	29	28	57	13	36.5	0.35	

Table 1: Measurements of the ornithopod tracks SB3.1 and SB3.2 from San Benón tracksite. MP, Morphological preservation value (Marchetti et al., 2019); FL, footprint length; FW, footprint width; FL/FW, footprint length/footprint width ratio; LII, LIII, LIV, digit length; DPLII, DPLIII, DPLIV, digital pad length; WII, WIII, WIV, digit width; HPL, heel pad length; HPW, heel pad width. II^III, III^IV, II^IV, interdigital divarication angles. ATL, anterior triangle length; ATW, anterior triangle width; AT, ratio ATL/ATW (mesaxony). FL, FW, LII, LIII, LIV, DPLII, DPLIII, DPLIV, WII, WIII, WIV, HPL, HPW, ATL, ATW, in cm. II^III, III^IV, II^IV in degrees (º). ? digit broken. * presence of claw impressions.