



Bioerosion and palaeoecological association of osteophagous insects in the Maastrichtian dinosaur *Arenysaurus ardevoli*



PENÉLOPE CRUZADO-CABALLERO , JOSÉ I. CANUDO, SILVINA DE VALAIS, JAIME FRIGOLA, EDUARDO BARRIUSO AND JOSEP FORTUNY 

LETHAIA



Cruzado-Caballero, P., Canudo, J. I., De Valais, S., Frigola, J., Barriuso, E., & Fortuny, J. 2021: Bioerosion and palaeoecological association of osteophagous insects in the Maastrichtian dinosaur *Arenysaurus ardevoli*. *Lethaia*, <https://doi.org/10.1111/let.12456>.

Bioerosions produced by the osteophagous diet of animals that fed on dinosaur bones are very scarce in the European fossil record. Herein we present bioerosion on hadrosaurid remains from the Maastrichtian Tremp Formation of the Pyrenean Basin, which is only the second such case recorded from the Iberian-Occitan Plate besides a sauropod from the Jurassic-Cretaceous of Valencia. The hadrosaurid fossil record is particularly rich in the Blasi sites of the Tremp Formation located in the municipality of Arén (Huesca, Spain). In this article, bones referred to the hadrosaurid *Arenysaurus ardevoli* from the Blasi-3 site are analysed to shed light on the palaeoenvironment and on the presence of a palaeoecological interaction between the hadrosaurid carcass and osteophagous tracemakers. Bioerosions recorded on the bones comprise tunnels, roundish holes, and straight notches, similar to the traces attributed to necrophagous insects (cf. *Cuniculichnus seilacheri*). Here, we record the first instance of the activity of these animals on dinosaur bones in the Upper Cretaceous of the Ibero-Occitan Plate. The results presented lead us to infer that the *Arenysaurus* bones were possibly transported by a storm or similar event to the Blasi-3 site, where they were exposed to post-mortem biotic interactions (eaten and partially decomposed by dermestid beetles) for a prolonged time period before they were completely buried. □ *dermestid, hadrosaurid, Ibero-Occitan Plate, necrophagous, taphonomy*.

Penélope Cruzado-Caballero  [pcruzado@ull.edu.es], Área de Palaontología, Departamento de Biología Animal, Edafología y Geología, Universidad de La Laguna, San Cristóbal de La Laguna Santa Cruz de Tenerife, Spain; Penélope Cruzado-Caballero  [pcruzado@ull.edu.es], and Silvina De Valais [sdevalais@yahoo.com.ar], Instituto de Investigación en Palaobiología y Geología (IIPG) Universidad Nacional de Río Negro, Río Negro, Argentina; José I. Canudo [jicanudo@unizar.es], Grupo Aragosaurus-IUCA, Facultad de Ciencias, Universidad de Zaragoza, C/Pedro Cerbuna 12 Zaragoza 50009, Spain; Jaime Frigola [jfrigola@ub.edu], Eduardo Barriuso [barriusoeduardo@gmail.com], Departament de Dinàmica de la Terra i de l'Oceà, Facultat de Ciències de la Terra, GRC Geociències Marines Universitat de Barcelona, C/Martí i Franquès s/n Barcelona E-08028, Spain; Josep Fortuny [josep.fortuny@icp.cat], Institut Català de Palaontologia Miquel Crusafont Universitat Autònoma de Barcelona, Edifici ICTA-ICP, c/ Columnes s/n Campus de la UAB Cerdanyola del Vallès, Barcelona 08193, Spain; manuscript received on 19/04/2021; manuscript accepted on 29/10/2021.

The term bioerosion includes any form of biological penetration of hard substrates (Bromley 1992). The oldest records of continental bioerosion on bone come from the Middle-Late Triassic of China, South Africa, and Brazil (e.g. Schwanke & Kellner 1999; Xing *et al.* 2015; Paes Neto *et al.* 2016). In general, bioerosion produced by osteophagous insects are widely recorded in fossils from the Late Cretaceous but are scarce in Europe, where the only records reported are from the Hațeg Basin (e.g. de Valais *et al.* 2012; Augustin *et al.* 2019). Moreover, bioerosion produced by invertebrates is not abundant in bones of hadrosaurid dinosaurs. For instance, Rogers (1992) reported borings in two bones of the

hadrosaurid *Prosaurolophus* (a left humerus and a right pre-frontal) from the Two Medicine Formation (Campanian) in Montana (United States). Recently, Serrano-Brañas *et al.* (2018) described insect borings on hadrosaurid bones from the Cerro del Pueblo Formation (Campanian) in Coahuila (Mexico).

Hadrosaurid dinosaurs are particularly abundant—as part of a generally diverse vertebrate fauna—in the Maastrichtian of the Central Pyrenees (Iberian Peninsula) (López-Martínez *et al.* 2001; Blain *et al.* 2010; Cruzado-Caballero *et al.* 2010a, b, 2013, 2014). This area is of great interest for the study of the latest European dinosaurs, since it presents a fairly continuous sequence of continental and transitional

deposits between the Maastrichtian and the Palaeogene (Puértolas-Pascual *et al.* 2018), but no bioerosional trace fossils in bones have been reported from there. Of particular interest here is the Blasi-3 site, a vertebrate-bearing locality in the Central Pyrenees where remains of one juvenile and two adult hadrosaurid specimens have been recovered in the Tremp Formation. It is also the type locality of the hadrosaurid dinosaur *Arenysaurus* Pereda-Suberbiola *et al.* 2009b, described from numerous articulated and disarticulated remains, including cranial and postcranial elements corresponding to an adult specimen (Pereda-Suberbiola *et al.* 2009b; Cruzado-Caballero *et al.* 2013, 2015). Some post-cranial elements of this latter specimen, corresponding to the paratypes of the taxon, present trace fossils that have never been previously reported for this taxon or indeed for any terrestrial vertebrate.

In the light of the previous considerations, the main goals of this study are to describe the bioerosion preserved in some bones of the hadrosaurid *Arenysaurus*, as well as to analyse and discuss the identity and palaeobiology of the potential tracemaker. In addition to this, taphonomic and palaeoenvironmental aspects of the specimens are also discussed.

Geological setting

The vertebrate-bearing site of Blasi-3 is located 2 km to the west of the municipality of Arén (or Areny de Noguera, Huesca Province) in northeastern Spain (Fig. 1).

Blasi-3 is located stratigraphically within the Tremp Formation, being laterally equivalent to the upper Campanian-Maastrichtian of the Arén Sandstone Formation (Pereda-Suberbiola *et al.* 2009b). The Tremp Formation can be sub-divided into four informal lithological units named as follows from the base to the top: the ‘Grey Garumnian’, the ‘Lower Red Garumnian’, the Vallcebre Limestone (and lateral equivalents), and the ‘Upper Red Garumnian’ (Rosell *et al.* 2001). The ‘Grey Garumnian’ of Rosell *et al.* (2001) is equivalent to the Posa Fm, whereas the ‘Lower Red Garumnian’ is equivalent to the Conques and Talarn formations of Cuevas (1992). The ‘Grey Garumnian’ is mainly built up of greyish marls with intercalations of coal and sandstone, with abundant fossil remains of marine or brackish organisms such as benthic foraminifera, gastropods, rudists, coelenterates, chondrichthyans and osteichthyans, as well as freshwater microorganisms such as charophytes and ostracods, vascular plants and continental vertebrates such as lissamphibians, chelonians,

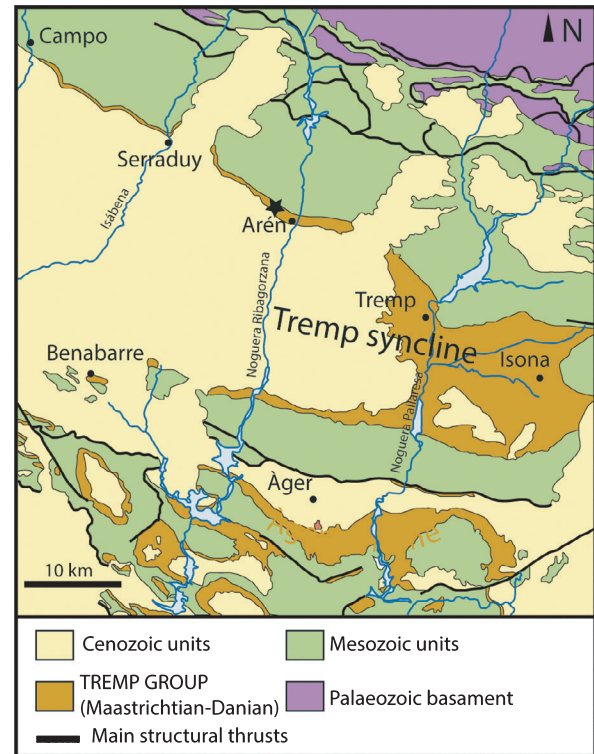


Fig. 1. Map showing the location of the Blasi-3 site (Arén, Huesca, Spain).

lizards, crocodylomorphs, and dinosaurs (López-Martínez *et al.* 2001; Pereda-Suberbiola *et al.* 2009a, b; Blain *et al.* 2010; Villalba Brea *et al.* 2012; Blanco *et al.* 2015; Company *et al.* 2015). The sediments that formed the ‘Grey Garumnian’ of the Tremp Formation (of which Blasi-3 forms part) were deposited in wide, shallow protected areas of variable salinity that are interpreted as tidal-plain, lagoonal, and estuarine environments, located laterally and proximally to the barrier-island or deltaic deposits of the Arén Formation (Puértolas-Pascual *et al.* 2018; Pérez-Pueyo *et al.* 2021).

Blasi-3 is located in a 1-m-thick, grey, massive, calcareous sandstone. The vertebrate remains of Blasi-3 were found in an area of about 70 m² (Fig. 2), most of them belonging to the partially articulated holotype of *Arenysaurus* and other disarticulated hadrosaurid ornithopods (see Pereda-Suberbiola *et al.* 2009). The sandstone of Blasi-3 is a greywacke, very different from the typical mature, calcareous sandstone of the Tremp Formation. Blasi-3 consists of a texturally immature sandstone, poorly sorted angular grains of quartz, feldspar, and small rock fragments in a compact and finegrained clay matrix. The combination in Blasi-3 of a massive deposit, with immature sandstone and the presence of a semi-articulated

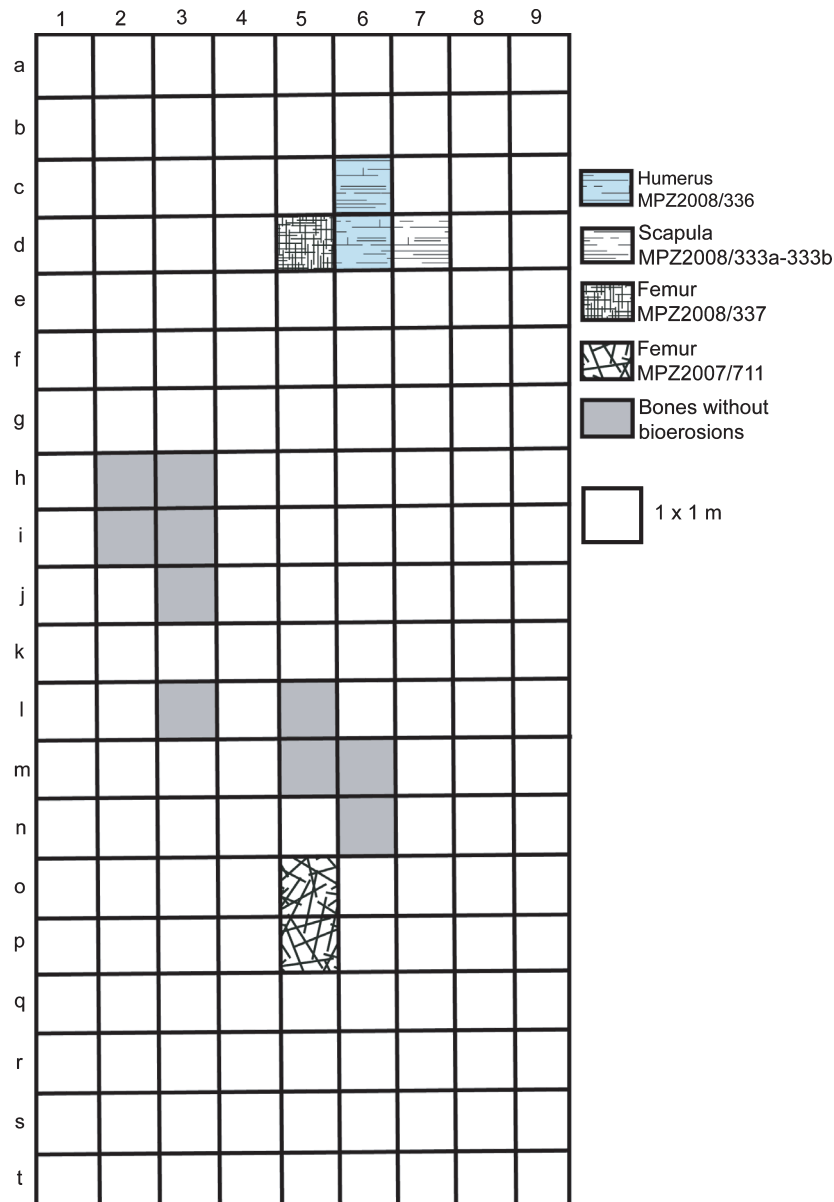


Fig. 2. Excavation grid of the Blasi-3 site.

dinosaur carcass, can be interpreted as being the result of a rapid sedimentation event, which in a coastal environment could be a storm. In Blasi-3, no typical tsunami sequences have been found (Navarrete *et al.* 2014), but the outcrop is small and the lateral relationships of Blasi-3 cannot be observed.

Blasi-3 has been included in several detailed stratigraphical, magnetostratigraphical and biostratigraphical overviews of the regional Upper Cretaceous (see Canudo *et al.* 2016, for further details). As a result, it has been ascertained that the Blasi-3 site is located in a normal-polarity chron correlated with sequence C30n, dated from 67.6 to 65.5 Ma (Canudo *et al.* 2016).

Material and methods

The trace-fossil-bearing bones are stored at the Museo de Ciencias Naturales of the Universidad de Zaragoza, under the label MPZ (Canudo 2018). The bones are paratypes of the lambeosaurine hadrosaurid *Arenysaurus* from the Blasi-3 site and include the following: in the scapula MPZ2008/333b (Fig. 3): three parallel furrows (MPZ2019/1470 to MPZ2019/1472); in the humerus MPZ2008/336 (Fig. 4): at least two furrows (MPZ2019/1473 and MPZ2019/1474) and three holes (MPZ2019/1475 to MPZ2019/1477); in the left femur MPZ2008/337 (Fig. 5): at least five

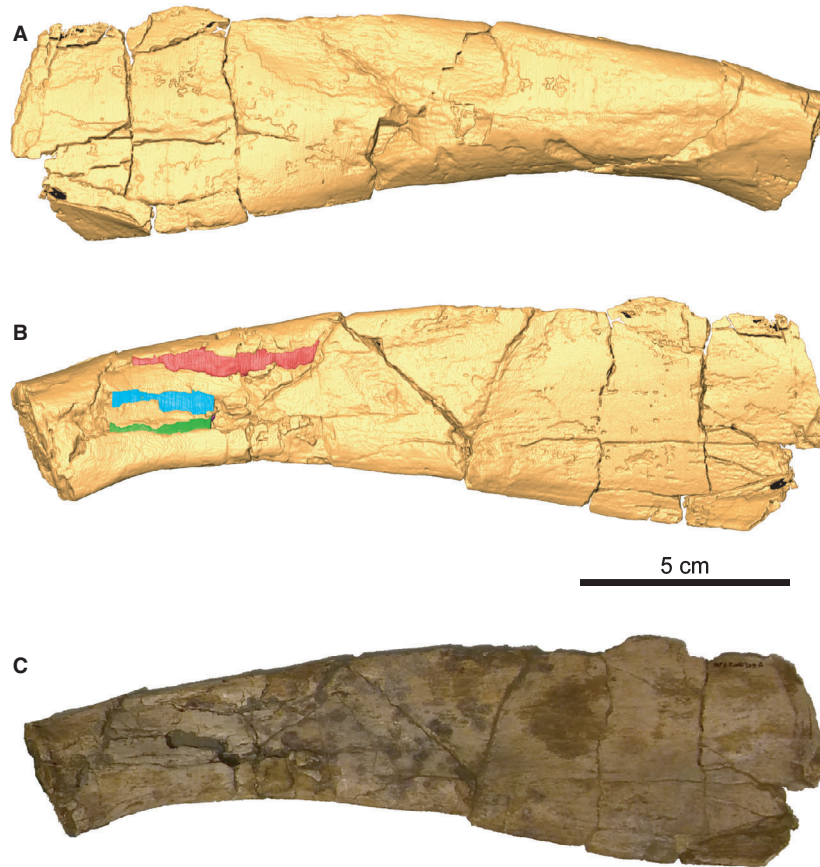


Fig. 3. 3D model of the scapula MPZ2008/333b. A, lateral view without furrows. B, C, medial views where the burrows can be seen.

furrows (MPZ2019/1478 to MPZ2019/1482), one notch (MPZ2019/1483), and many holes (MPZ2019/1484), some of them linked to furrows, and several other traces overlapping and densely preserved in the distal epiphysis (MPZ2019/1485); in the right femur MPZ2007/711 (Fig. 6): two parallel furrows (MPZ2019/1486 and MPZ2019/1487), several notches and holes, many of them overlapping and densely preserved in the distal epiphysis (see Pereda-Suberbiola et al. 2009a; Cruzado-Caballero et al. 2013, for further details of these elements).

Laboratory preparation

All the bioerosional trace fossils were originally filled with sedimentary matrix when the specimens were recovered from the field, although they were subsequently prepared in the laboratory. Currently some of the borings are partially filled with sediment or are devoid of any sediment matrix, whereas others are still completely filled. The right femur MPZ 2007/711 was cleaned using only physical methods (i.e. a pneumatic micro-hammer), whereas the right

scapula MPZ 2008/333a-333b, the right humerus MPZ2008/336 and the left femur MPZ2008/337 were cleaned using both physical and chemical methods (8% formic acid solution) to remove the surrounding rocky matrix. During bone preparation, a few bone parts were affected by the preparation process (both mechanical and chemical), and these traces are excluded from the description and discussion below. Therefore, all of the traces described below are real bioerosional trace fossils and we can exclude an artificial origin for them (i.e. that they were produced by the preparation process).

Compute tomography

A micro-focus X-ray computed tomography (micro-CT) system, the Multi-TOM Core (XRE nv, Ghent, Belgium), located in the CORELAB Laboratory (Universitat de Barcelona, Catalonia, Spain), was used. The bones were scanned at 150 kV and at a power of 58 W, using a 1.5 mm Al filter in order to reduce the beam-hardening effect (Cnudde & Boone 2013). In all cases, a complete rotation along the

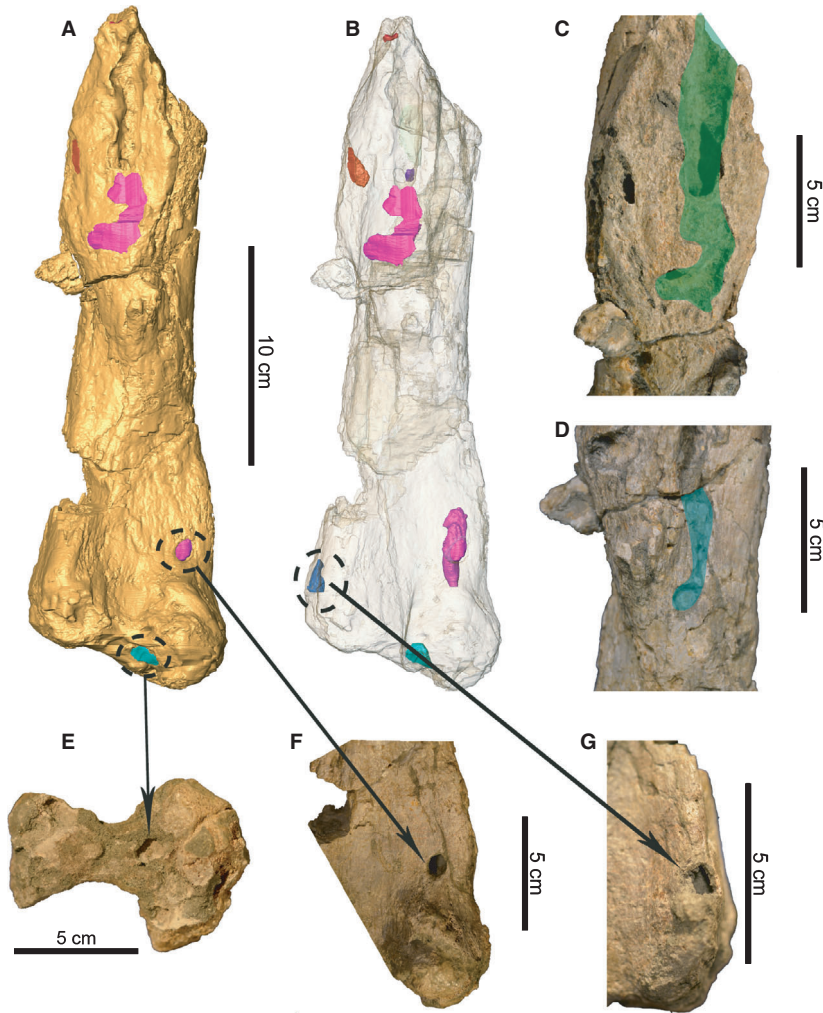


Fig. 4. 3D model of the humerus MPZ2008/336. A, anterior view. B, anterior semi-transparent view. C, furrow MPZ2019/1473. D, furrow MPZ2019/1474. E, hole MPZ2019/1475. F, hole MPZ2019/1476. G, hole MPZ2019/1477.

vertical axis for each region was performed with an exposure time of 200 ms per projection image. Source-object and source-detector distances of 228 and 499 mm, respectively, resulted in a magnification of 2.2. The acquired images were reconstructed using the ACQUILA software (www.XRE.be).

A set of 3186 projections with a voxel size of 130 μm was performed for the scapula (MPZ 2008/333a-333b), 1948 projections with a voxel size of 190 μm for the left femur (MPZ 2008/337), 3875 projections with a voxel size of 207.89 μm for the right femur (MPZ 2007/711), and 3237 projections with a voxel size of 110 μm for the humerus (MPZ 2008/336). Raw data from each scan were imported (as a stack of TIFF 8-bit files) to Avizo 7.0 to generate a 3D surface from the micro-CT images, digitally extracting the bioerosions from the bone matrix. Due to the density of the bone and internal matrix, the

CT images present several artefacts such as beam hardening, cupping artifacts and ring artifacts. As a consequence of these artifacts, automatic segmentation was difficult and not optimal, and thus semi-automatic (or manual in some regions) segmentation was required, as also reported for the study of cranial elements of the same specimen (see Cruzado-Caballero *et al.* 2015).

Measurements and nomenclature

The measurements for all the traces described in this study (length, width, and depth) were taken with a calliper, and digital measurements (from CT scan data) with the help of ImageJ 1.52v. Other measurements such as volume were obtained using Avizo 7.0 and Rhinoceros 4.0. The descriptive terminology and identification of the borings follows Roberts *et al.*

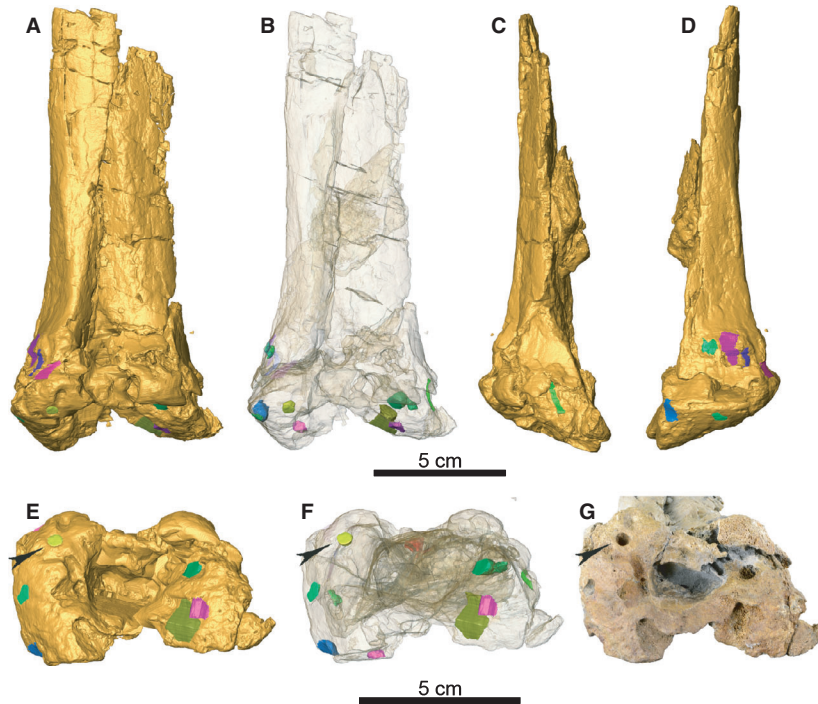


Fig. 5. 3D model of the femur MPZ2008/337. Posterior (A, B), medial (C), lateral (D) and distal (E) views. B, F, model in semi-transparent view. E–G, holes MPZ2019/1484.

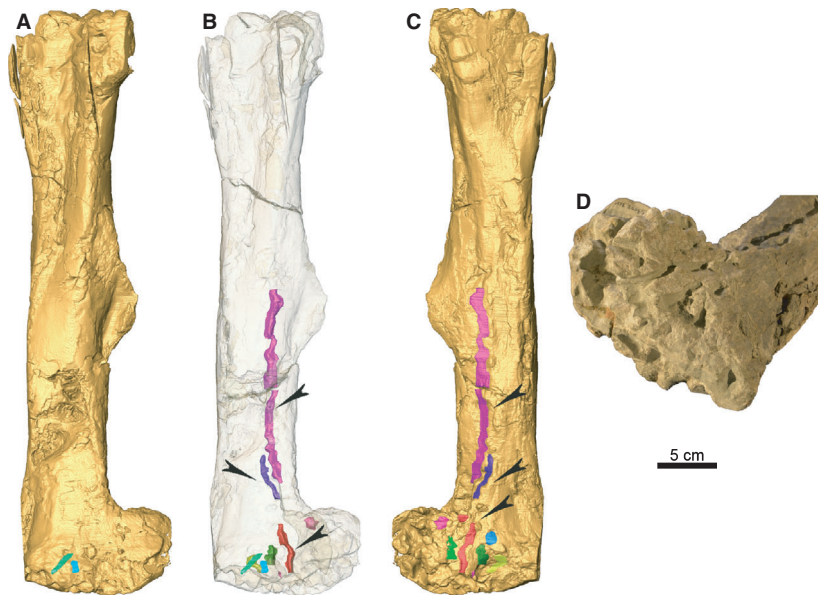


Fig. 6. 3D model of the femur MPZ2007/711. A, B, medial view. C, lateral view. D, detail of the distal condyles. B, model in semi-transparent view. B, C, furrows MPZ2019/1486 to MPZ2019/1487 marked by arrows.

(2007), Bader *et al.* (2009), Pirrone *et al.* (2014), Xing *et al.* (2015), Parkinson (2016), and Höpner & Bertling (2017). All traces were categorised, recorded, and spatially arranged on each bone, in order to record their distribution and association on the skeletal remains.

Results

Description of the trace fossils

The trace fossils described here comprise notches, holes, and furrows (*sensu* Höpner & Bertling 2017),

and may co-occur in the same bone, preserved mainly in the cortical tissue, although some of the holes also affect the spongy tissue. Both femurs are densely bioeroded, especially at the ends, whereas the humerus shows relatively fewer traces and the scapula only displays three long traces (Figs. 3–6; see Supplementary data for further details). The traces are described individually for convenience, but usually they form a continuum, so often the notches are not distinguishable from the furrows and the holes are the starting points for the furrows. Many of the trace fossils have been altered due to the preparation process (see Materials and Methods section), so it is not possible to confirm the boundaries of the walls or potential surface features, although it appears that the surface of the bioerosions is quite smooth, with no bioglyphs such as rasping or scratching microstructures on the walls.

Nevertheless, the general features of the bioerosions are still visible and distinguishable, except where they are too densely occurring and thus overlap. The furrows are unbranched structures and are almost straight, usually running parallel to the bone fibre. There are relatively few notches, all of them with irregular borders and ends, sometimes with a slight curvature and varying depth. The holes occur near the ends of the bones, normally spaced apart from each other, and are mostly rounded to irregular vertical pits, also varying in depth.

Three furrows are located in the anterior half of the scapular blade MPZ2008/333b, parallel to each other, one of them beginning with a hole (Fig. 3 B–D). They display an average depth of 2.4 mm, and a minimum and maximum depth of 0.8 mm and 5 mm, respectively. Their width varies between a minimum of 2.1 mm and a maximum of 8.5 mm, with an average of 3.6 mm, while the maximum preserved length is 142 mm.

The longer furrow in the humerus MPZ2008/336 is preserved in the distal epiphysis (MPZ2019/1473; Fig. 4C), with a length of 102.4 mm and an average width and depth of 1.14 mm and 4.4 mm, respectively. The other furrow runs parallel to the first one and begins with a hole with rounded edges (MPZ2019/1474; Fig. 4D). This furrow has a width and depth of 4.2 mm and 2.1 mm, respectively, and is at least 35.8 mm long; the hole at the beginning of the furrow is rounded but slightly irregular, and measures 9.1 mm in diameter.

There are three other holes in the humerus. One of them has irregular borders, is located on the intercondylar groove (MPZ2019/1475; Fig. 4E) and is about 10 mm in diameter and 7.4 mm in maximum depth. The second one is isolated in the diaphysis (MPZ2019/1476; Fig. 4F), with a maximum depth of

7.6 mm and a diameter of about 9 mm. The third hole of the three is almost perfectly circular, with a diameter and a depth of 9.4 mm and 10.8 mm, respectively (MPZ2019/1478; Fig. 3G).

The left femur MPZ 2008/337 has many holes and other traces densely preserved in the epiphysis (Fig. 5). One of the holes is distinctive because of its circular, rounded edge (Fig. 5E–G marked by an arrow; MPZ2019/1484), lacking any irregularity, with a diameter of 8.9 mm and a maximum depth of 6.7 mm.

The right femur MPZ 2007/711 is the most heavily bioeroded bone in the sample (Fig. 6), bearing so many trace fossils that it is difficult to distinguish them with confidence. However, some of them can be kept apart. Two furrows run parallel to each other from the distal epiphysis to the diaphysis; they extend parallel to the bone fibre and are more than 350 mm long (Fig. 6B, C; MPZ2019/1486 to MPZ2019/1487, both marked by an arrow).

To conclude, the trace fossil record in these *Arenysaurus* paratypes is characterised mainly by the presence of furrows and holes, and a few clear and well-defined notches, all of them rounded in cross-section, and more or less parallel to the surface in direction. Because these traces are mostly eroded and, in many parts, densely overlapping, it is difficult to assign them with confidence to an ichnotaxon. However, the general morphology and spatial distribution of the trace fossils allow them to be referred, tentatively, to the ichnospecies cf. *Cuniculichnus seilacheri* (see Supplementary data for more information on the ichnotaxonomy, Höpner & Bertling 2017).

Palaeoenvironment

The vertebrate-bearing site of Blasi-3 is located in a 1-m-thick, channelized, massive calcareous sandstone with abundant *Ophiomorpha* specimens. The sandstone containing bones has a complex depositional history influenced by a variety of factors. The site has yielded hadrosaurid bones that, as mentioned above, are present partially in anatomical connection (*Arenysaurus*) and partially disarticulated (indeterminate hadrosaurids), covering an area of about 70 m² (Fig. 2). Moreover, isolated fossils, such as turtle plates and crocodyliform bones, have also been recovered (Fig. 7; López-Martínez *et al.* 2001; Murelaga & Canudo 2005).

The presence of bothremydid and solemydid turtles and crocodyliform remains suggests an aquatic palaeoenvironment. On the other hand, *Ophiomorpha* burrows are interpreted as being the products of crustaceans that lived near the coast (Boggs 1995).

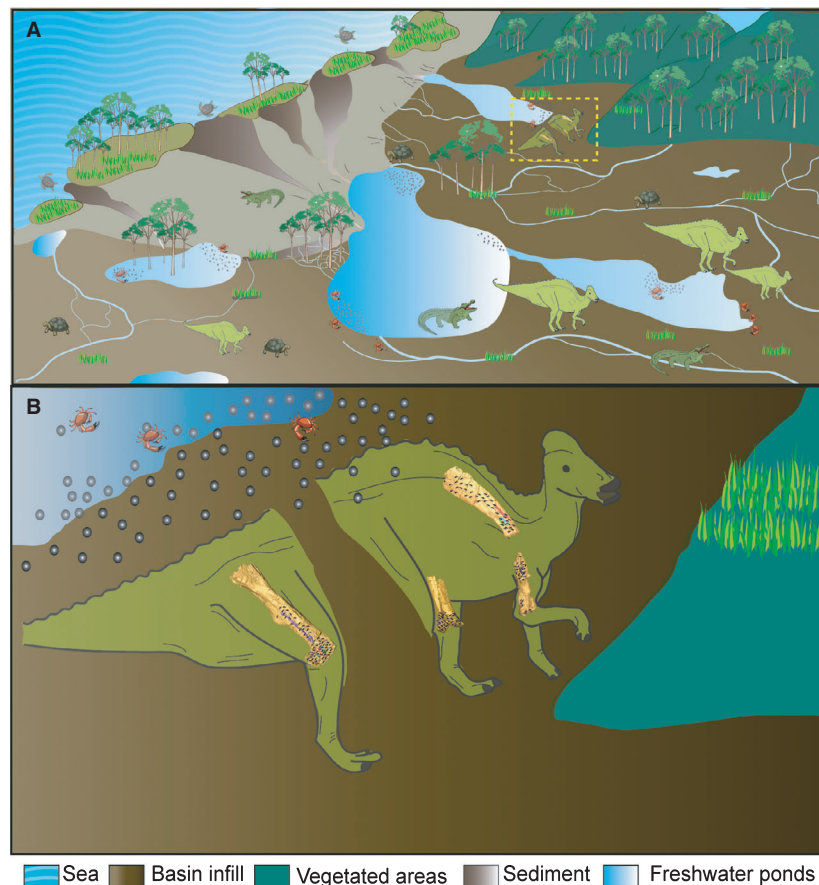


Fig. 7. Palaeoecological reconstruction of the Blasi-3 site. A, at the headwaters of the delta-front, lagoonal and coastal deposits, in the 'Grey Garumnian' unit within the Trepmp Group. B, detail of the probable necrophagous colonisation of the *Arenysaurus* carcass.

Furthermore, the absence of bivalves suggests that water was not permanently present at the site. The occurrence of dry periods during the sedimentation of the Blasi-3 site is now also confirmed by the presence of bioerosion (Fig. 7).

Weathering stages

Hadrosaurid remains are concentrated in three main areas. The outcrop where the remains were recovered is sloping (at around 55°). The first area corresponds to the top of the slope (Fig. 2 grids 5D; 6C-D; 7), whereas the second area represents the central part of the site (Fig. 2 grids 2H-I; 3H-J, L) and the third area corresponds to the middle western section (Fig. 2 grids 3L; 5L-M, O-P; 6M-N). Of the specimens showing bioerosion, the scapula (MPZ 2008/333a-333b), the right humerus (MPZ 2008/336) and the left femur (MPZ 2008/337) were recovered from the first area. The second area was where the anterior section of the holotype *Arenysaurus* tail with its vertebrae in anatomical connection was recovered,

together with post-cranial remains of a juvenile individual (two sacral vertebrae MPZ 2005/300a-300b, a right ilium MPZ 2005/90 and a right pubis MPZ 2005/301; Cruzado-Caballero *et al.* 2005) and post-cranial remains of a small adult individual (a partial sacrum MPZ 2005/318 and a right pubis MPZ 2005/302; Cruzado-Caballero 2012), indicating the rapid burial of the bones in this area. In the third area, several cranial and post-cranial remains of *Arenysaurus* were recovered, all of them disarticulated. For this study, of particular interest among the remains recovered from this area of the site is the right femur (MPZ 2007/711).

The right femur (MPZ 2007/711) is the most bioeroded bone, with almost its entire surface bearing traces, whereas the left femur (MPZ 2008/337) is partially preserved and only shows traces in the condyles. In the case of the right humerus (MPZ 2008/336), the traces are distributed over part of the diaphysis and the condyles. Finally, the scapula has only one surface that is bioturbated. These spatial distributions and the fact that the bones do not show signs

of abrasion due to transport and only show flaking and cracking in restricted parts of the bones suggest that the bones were only partially exposed while the bioerosion took place, and that they hardly moved once they were deposited in the Blasi-3 site.

The external surfaces of the bones recovered in area 1 present weathering stages that are intermediate between the final stages of 'Stage 1' and early stages of 'Stage 2' weathering, as defined by Behrensmeyer (1978). The humerus MPZ 2008/336 presents a cracked and flaked surface along its length, which, according to Behrensmeyer (1978), suggests 'Stage 2'. The femur MPZ 2008/337 also presents a cracked and flaked surface, but less developed, which may indicate 'Stage 1' or early 'Stage 2' weathering. Regarding the scapula MPZ 2008/333a-333b, this bone element is less damaged but nevertheless has equally cracked and flaked surfaces. The damage is concentrated around the scapular neck, whereas the scapular lamina does not present any signs of weathering. This could mean that the scapula was partially buried while its weathering took place. In accordance with Behrensmeyer (1978), the features seen in the femur and the scapula thus indicate 'Stage 1' or early 'Stage 2' weathering.

The external surface of the femur MPZ 2007/711 recovered in the third area presents cracked and flaked surfaces in the middle and the distalmost parts of the bone, whereas the proximal parts have an undamaged surface. This suggests that the femur may have been partially buried, too, during sub-aerial weathering. These features of surface damage indicate 'Stage 1' or early 'Stage 2' weathering.

Discussion

Identity of the potential producer of the trace fossils at Blasi-3

There is an extensive record of trace-fossil-bearing bones preserved either in terrestrial and freshwater or in marine environments (e.g. Hasiotis 2004; Rouse *et al.* 2004; Britt *et al.* 2008; Höpner & Bertling 2017). Regarding trace-fossil-bearing bones preserved in marine environments as shown by Antonelli *et al.* 2019, with remains deposited in a possible tidal-plain, lagoonal or estuarine, with variable salinity, clearly contrasts with the presence of cracking and desquamation on the surface of the bioeroded bones of *Arenysaurus*. Even more, the absence of bivalve remains and the presence of burrows of *Ophiomorpha* indicates that the remains of *Arenysaurus* should not have been submerged under the water, but rather in an area near

the coast with parts of the bones exposed to dry periods while bioerosion occurred.

Necrophagous insects are present in terrestrial environments, where they colonise exposed carcasses (see references in Csiki 2006; Xing *et al.* 2015; Pirrone & Buatois 2016; Serrano-Brañas *et al.* 2018; Augustin *et al.* 2019). These insects belong to six orders: (1) Isoptera, termites of the families Termitidae, Rhinotermitidae and Mastotermitidae; (2) Coleoptera, beetles of the families Silphidae, Dermestidae, Cleridae and Tenebrionidae; (3) Diptera, blow flies (Calliphoridae); (4) Ephemeroptera, mayflies; (5) Hymenoptera, sweat bees (Halictidae), sphecoid wasps (Sphecidae), and some species of ants (Formicidae); and (6) Lepidoptera, tineid moths. The first possible tracemakers to be ruled out are ants and termites due to their social character, since the tracks left by these organisms have variable star-shaped features (Backwell *et al.* 2012; Xing *et al.* 2015). Other producers that can be excluded are the tineid moths, which are specialists in the consumption of keratinised structures such as horns and hooves (Behrensmeyer 1978; Hill *et al.* 1987; Serrano-Brañas *et al.* 2018). Moreover, some mayflies (polymitarcids) produce U-shaped burrows that are separated by a thin wall; they do not bore furrows or pupation chambers (Serrano-Brañas *et al.* 2018).

Beetles, and more specifically the dermestids, are the most common tracemakers that produce pupation chambers (see references in Xing *et al.* 2015; Serrano-Brañas *et al.* 2018; Augustin *et al.* 2019). The first fossil record of dermestid beetles comes from the Late Cretaceous (Parkinson 2013). According to actualistic experiments performed by Zanetti *et al.* (2019), the dermestid beetles could produce pupation chambers on bones. Besides, it is known that dermestid larvae feed on carrion and perforate various durable substrates (wood and stone) during pupation (Hefti *et al.* 1980; Kirkland & Bader 2010; Holden *et al.* 2013; Zanetti *et al.* 2014, 2019). To infest a corpse, these insects need a carcass of a dead animal with dry skin and dried soft tissues (muscles, tendons, and cartilage), in other words to be in a dry stage of decomposition. At this stage, the carcass is above water and dry, and the bones are not buried quickly (Bornemissza 1957; Reed 1958; Coe 1978; Timm 1982; Hasiotis 2004; Serrano-Brañas *et al.* 2018; Augustin *et al.* 2019). Moreover, these insects are able to bore into cortical and spongy bone, producing pupation chambers, tunnels and furrows (Timm 1982; Jodry & Stanford 1992; Schroeder *et al.* 2002; Roberts *et al.* 2007; Britt *et al.* 2008; Huchet *et al.* 2013; Höpner & Bertling 2017). Our results suggest that most of the traces found in *Arenysaurus* were possibly produced by dermestid beetles.

However, experimental and/or additional observational data will be necessary to confirm it with confidence.

Taphonomic stage

Bioerosions give us information about the behaviour and biotic interactions of the organism that produced them and the palaeoenvironment in which it lived (Saneyoshi *et al.* 2011; Xing *et al.* 2013; Serrano-Brañas *et al.* 2018), as well as about the taphonomic history of vertebrate remains (e.g. Rogers 1992; Bader *et al.* 2009; Saneyoshi *et al.* 2011; Serrano-Brañas *et al.* 2018; Augustin *et al.* 2019, 2021).

In the Blasi-3 site, the sedimentological data show the presence of a massive deposit of immature sandstone, together with the spatial arrangement of the specimens and the different degrees of articulation and weathering stages of these remains (Fig. 1-6; see Weathering Stages section). These data suggest that the carcass of *Arenysaurus*, partially decomposed, was possibly transported by a storm or similar event (Fig. 7; Navarrete *et al.* 2014). During transport the carcass was fragmented, leaving an articulated part in the middle eastern and western section of the site (Fig. 2 grids 2 H-I; 3H-J, L; 5L, M; 6M-N); this was quickly buried and was not subject to attack from osteophagous insects. Meanwhile, the bones located in the top and middle parts of the sloping western section of the site were not buried or only partially so, as indicated by the distribution of the traces (i.e. the scapula MPZ 2008/333a-333b, the distal portion of the diaphysis of the femora MPZ 2008/337 and MPZ 2007/711, and the humerus MPZ 2008/336; Fig. 2 grids 5D, O, P; 6C-D; 7D; Fig. 7).

On the other hand, the presence of bioerosions produced by insect activity only in some bones suggests that these were sub-aerially exposed above the water level for a certain period of time, allowing them to dry out (Behrensmeyer 1978). This is indicated by the presence of bioerosions produced by necrophagous insects such as the dermestid beetle, which colonises carcasses only if they are sub-aerially exposed and at the dry stage of decomposition, which occurs several days or weeks after death (Fig. 7; Bornemissza 1957; Reed 1958; Martin & West 1995; Mariani *et al.* 2014; Augustin *et al.* 2021).

Conclusions

The bones of the hadrosaurid dinosaur *Arenysaurus* are the first that record the activity of necrophagous insects (cf. *C. seilacheri*) in the Maastrichtian of the

Ibero-Occitan Plate. The fossil fauna recorded in the Blasi-3 site indicates that the *Arenysaurus* carcass was deposited in wide, shallow protected areas of variable salinity that are interpreted as a coastal environment. Our taphonomic reconstruction suggests that the *Arenysaurus* bones along with other indeterminate hadrosaurids were possibly transported by a storm or similar event, being partially fragmented and disarticulated during transport. The dinosaur remains were not buried or only partially so, with the sub-aerial exposure of the carcass lasting for at least several days or weeks resulting in the dry stage of decay that allowed the osteophagous insects to infest it. Dermestid beetles are proposed as the most probable tracemakers.

Acknowledgements. – We acknowledge two anonymous reviewers for their valuable comments and suggestions that have greatly improved the manuscript. Financial support has been provided by the Spanish Ministerio de Ciencia e Innovación and the European Regional Development Fund (AEI/FEDER EU) (CGL2017-85038-P; to P.C.-C. and J.I.C. and J.I.C. and CGL2017-82654-P and PID2020-117118GB-I00 by MCIN/AEI/10.13039/501100011033 to J.F.), partially by the Agencia Nacional de Promoción Científica y Tecnológica (PICT 2016-0419; PICT 2016-0481; to P.C.-C.), partially by the Universidad Nacional de Río Negro (PI 40-A-737; PI 40-A-660; to P.C.-C.) and the Catalan Government Grups de Recerca Consolidats grant to GRC Geociències Marines (ref. 2017 SGR 315 to J. Frigola). J. Fortuny was supported by the CERCA Programme (Generalitat de Catalunya) and J. Frigola is supported by the Generalitat de Catalunya through a Serra Hünter Tenure-eligible Lecturer contract. We thank sincerely Rupert Glasgow, who revised the translation of the text into English.

References

- Antonelli, F., Ricci, S., Petriaggi, B.D. & Ortuño, M.B. 2019: Study of the bioerosion of Phoenician elephant tusks from the shipwreck of Bajo de la Campana: lots of hypotheses, few certainties. *Facies* 6, 10.
- Augustin, F.J., Matzke, A.T., Csiki-Sava, Z. & Pfretzschner, H.U. 2019: Bioerosion on vertebrate remains from the Upper Cretaceous of the Hațeg Basin, Romania and its taphonomic implications. *Palaeogeography, Palaeoclimatology, Palaeoecology* 534, 109318.
- Augustin, F.J., Matzke, A.T., Maisch, M.W. & Pfretzschner, H.U. 2021: Dinosaur taphonomy of the Jurassic Shishugou Formation (Northern Junggar Basin, NW China) – insights from bioerosional trace fossils on bone. *Ichnos* 28, 87–96. <https://doi.org/10.1080/10420940.2021.1890590>.
- Backwell, L.R., Parkinson, A.H., Roberts, E.M., d'Errico, F. & Huchet, J.B. 2012: Criteria for identifying bone modification by termites in the fossil record. *Palaeogeography, Palaeoclimatology, Palaeoecology* 337, 72–87.
- Bader, K.S., Hasiotis, S.T. & Martin, L.D. 2009: Application of forensic science techniques to trace fossils on Dinosaur bones from a quarry in the upper Jurassic Morrison formation, northeastern Wyoming. *Palaio* 24, 140–158.
- Behrensmeyer, A.K. 1978: Taphonomic and ecologic information from bone weathering. *Paleobiology* 4, 150–162.
- Blain, H.A., Canudo, J.L., Cuenca-Bescós, G. & López-Martínez, N. 2010: Amphibians and squamates from the latest Maastrichtian (Upper Cretaceous) of Blasi 2 (Huesca, Spain). *Cretaceous Research* 31, 433–446.
- Blanco, A., Fortuny, J., Vicente, A., Luján, À.H., García-Marçà, J.A. & Sellés, A.G. 2015: A new species of *Allodaposuchus*

- (Eusuchia, Crocodylia) from the Maastrichtian (Late Cretaceous) of Spain: phylogenetic and paleobiological implications. *PeerJ* 3, e1171.
- Boggs, S.J. 1995: *Principles of Sedimentology and Stratigraphy*. 2nd edn, 774 pp. University of Oregon, Prentice Hall.
- Bornemissza, G.F. 1957: An analysis of arthropod succession in carrion and the effect of its decomposition on the soil fauna. *Australian Journal of Zoology* 5, 1–12.
- Britt, B.B., Scheetz, R.D. & Dangerfield, A. 2008: A suite of dermestid beetle traces on dinosaur bone from the Upper Jurassic Morrison Formation, Wyoming, USA. *Ichnos* 15, 59–71.
- Bromley, R.G. 1992: Bioerosion: eating rocks for fun and profit. In Maples, C.G. & West, R.R. (eds): *Trace Fossils, Paleontological Society Short Course Notes, volume 5*, Cambridge: Cambridge University Press, 121–129.
- Canudo, J.I. 2018: The collection of type fossils of the Natural Science Museum of the University of Zaragoza (Spain). *Geohistory* 10, 385–392.
- Canudo, J.I., Oms, O., Vila, B., Galobart, A., Fondevilla, V., Puértolas-Pascual, E., Sellés, A.G., Cruzado-Caballero, P., Dinarés-Turell, J., Vicens, E., Castanera, D., Company, J., Burrell, L., Estrada, R., Marmi, J. & Blanco, A. 2016: The upper Maastrichtian dinosaur fossil record from the southern Pyrenees and its contribution to the topic of the Cretaceous-Palaeogene mass extinction event. *Cretaceous Research* 57, 540–551.
- Cnudde, V. & Boone, M.N. 2013: High-resolution X-ray computed tomography in geosciences: a review of the current technology and applications. *Earth-Science Reviews* 123, 1–17.
- Coe, M. 1978: The decomposition of elephant carcasses in the Tsavo (East) National Park, Kenya. *Journal of Arid Environments* 1, 71–86.
- Company, J., Cruzado Caballero, P. & Canudo, J.I. 2015: Presence of diminutive hadrosaurids (Dinosauria: Ornithomimidae) in the Maastrichtian of the south-central Pyrenees (Spain). *Journal of Iberian Geology* 41, 71–81.
- Cruzado-Caballero, P. 2012: *Restos directos de dinosaurios hadrosáuridos (Ornithomimidae, Hadrosauridae) del Maastrichtense superior (Cretácico Superior) de Arén (Huesca)*. Unpublished PhD Thesis. Universidad de Zaragoza, 403 pp.
- Cruzado-Caballero, P., Canudo, J.I. & Ruiz-Omeñaca, J.I. 2005: New evidence of lambeosaurine hadrosaurs (Dinosauria) in the Upper Maastrichtian of the Iberian Peninsula (Arén, Huesca Province, NE Spain). *Geogaceta* 38, 47–50.
- Cruzado-Caballero, P., Canudo, J.I., Moreno-Azanza, M. & Ruiz-Omeñaca, J.I. 2013: New material and phylogenetical position of *Arenysaurus ardevoli*, a lambeosaurine dinosaur from the Late Maastrichtian of Arén (Northern Spain). *Journal of Vertebrate Paleontology* 33, 1376–1384.
- Cruzado-Caballero, P., Fortuny, J., Llacer, S. & Canudo, J.I. 2015: Paleoneuroanatomy of the European lambeosaurine dinosaur *Arenysaurus ardevoli*. *PeerJ* 3, e802.
- Cruzado-Caballero, P., Pereda-Suberbiola, X. & Ruiz-Omeñaca, J.I. 2010a: *Blasisaurus canudo* gen. et sp. nov., a new lambeosaurine dinosaur (Hadrosauridae) from the latest Cretaceous of Arén (Huesca, Spain). *Canadian Journal of Earth Sciences* 47, 1507–1517.
- Cruzado-Caballero, P., Ruiz-Omeñaca, J.I. & Canudo, J.I. 2010b: Evidencias de la coexistencia de dinosaurios hadrosaurinos y lambeosaurinos en el Maastrichtiano superior de la Península Ibérica (Arén, Huesca, España). *Ameghiniana* 47, 153–164.
- Cruzado-Caballero, P., Ruiz-Omeñaca, J.I., Gaete, R., Riera, V., Oms, O. & Canudo, J.I. 2014: A new hadrosaurid dentary from the latest Maastrichtian of the Pyrenees (north Spain) and the high diversity of the duck-billed dinosaurs of the Ibero-Armorican Realm at the very end of the Cretaceous. *Historical Biology* 26, 619–630.
- Csiki, Z. 2006: Insect borings in dinosaur bones from the Maastrichtian of the Hațeg Basin, Romania—paleoecological and paleoclimatic implications. In Csiki, Z. (ed.): *Mesozoic and Cenozoic Vertebrates and Paleoenvironments. Tributes to the Career of Dan Grigorescu*, Cambridge: Cambridge University Press, 95–104. *Ars Docendi*, 213.
- Cuevas, J.L. 1992: Estratigrafía del «Garumniense» de la Conca de Tremp. *Prepirineo De Lérida. Acta Geológica Hispánica* 27, 95–108.
- De Valais, S., Apesteeguía, S. & Garrido, A. 2012: Cretaceous small scavengers: feeding traces in tetrapod bones from Patagonia, Argentina. *PLoS One* 7, e29841.
- Hasiotis, S.T. 2004: Reconnaissance of Upper Jurassic Morrison Formation ichnofossils, Rocky Mountain Region, USA: paleoenvironmental, stratigraphic, and paleoclimatic significance of terrestrial and freshwater ichnocoenoses. *Sedimentary Geology* 167, 177–268.
- Hefti, E., Trechsel, U., Rufenacht, H. & Fleisch, H. 1980: Use of dermestid beetles for cleaning bones. *Calcified Tissue International* 31, 45–47.
- Hill, A., Leakey, M.D. & Harris, J.M. 1987: Damage to some fossil bones from Laetoli. In Leakey, M.D. & Harris, J.M. (eds): *Laetoli: a Pliocene site in Northern Tanzania*, 543–545. Clarendon Press, Oxford.
- Holden, A.R., Harris, J.M. & Timm, R.M. 2013: Paleocological and taphonomic implications of insect-damaged Pleistocene vertebrate remains from Rancho La Brea, southern California. *PLoS One* 8, e67119.
- Höpner, S. & Bertling, M. 2017: Holes in bones: ichnotaxonomy of bone borings. *Ichnos* 24, 259–282.
- Huchet, J.-B., Le Mort, F., Rabinovich, R., Blau, S., Coqueugniot, H. & Arensburg, B. 2013: Identification of dermestid pupal chambers on Southern Levant human bones: inference for reconstruction of Middle Bronze Age mortuary practices. *Journal of Archaeological Science* 40, 3793–3803.
- Jodry, M.A. & Stanford, D.J. 1992: Stewart's Cattle Guard site: an analysis of bison remains in a Folsom kill-butchery campsite. *Ice Age Hunters of the Rockies* 101–168.
- Kirkland, J. & Bader, K. 2010: Insect trace fossils associated with *Protoceratops* carcasses in the Djadokhta Formation (Upper Cretaceous). In Ryan, M.J., Chinnery-Allgeier, B.J., Eberth, D., Currie, P. & Ralrick, P.E. (eds): *New perspectives on Horned Dinosaurs: The Royal Tyrrell Museum Ceratopsian Symposium*, 509–519. Indiana University Press, Bloomington.
- López-Martínez, N., Canudo, J.I., Ardèvol, L., Suberbiola, X.P., Orue-Etxebarria, X., Cuenca-Bescós, G., Ruiz-Omeñaca, J.I., Murelaga, X. & Feist, M. 2001: New dinosaur sites correlated with Upper Maastrichtian pelagic deposits in the Spanish Pyrenees: implications for the dinosaur extinction pattern in Europe. *Cretaceous Research* 22, 41–61.
- Mariani, R., García-Mancuso, R., Varela, G. L. & Inda, A. M. (2014) Entomofauna of a buried body: Study of the exhumation of a human cadaver in Buenos Aires, Argentina. *Forensic Science International*, 237, 19–26.
- Martin, L. D. & West, D. L. (1995) The recognition and use of dermestid (Insecta, Coleoptera) pupation chambers in paleoecology (*Palaeogeography, Palaeoclimatology, Palaeoecology*, 113, (2–4), 303–310.
- Murelaga, X. & Canudo, J.I. 2005: Descripción de restos de quelonios del Maastrichtense superior de Arén y Serraduy (Huesca). *Geogaceta* 38, 51–54.
- Navarrete, R., Liesa, C.L., Castanera, D., Soria, A.R., Rodríguez-López, J.P. & Canudo, J.I. 2014: A thick Tethyan multi-bed tsunami deposit preserving a dinosaur megatracksite within a coastal lagoon (Barremian, eastern Spain). *Sedimentary Geology* 313, 105–127.
- Paes Neto, V.D., Parkinson, A.H., Pretto, F.A., Soares, M.B., Schwanke, C., Schultz, C. & Kellner, A.W. 2016: Oldest evidence of osteophagous behavior by insects from the Triassic of Brazil. *Palaeogeography, Palaeoclimatology, Palaeoecology* 453, 30–41.
- Parkinson, A.H. 2013: *Dermestes maculatus* and *Periplaneta americana*: Bone Modification Criteria and Establishing their Potential as Climatic Indicators. Unpublished PhD Thesis, 204 pp. University of the Witwatersrand
- Parkinson, A.H. 2016: Traces of insect activity at Cooper's D fossil site (Cradle of Humankind, South Africa). *Ichnos* 23, 322–339.
- Pereda-Suberbiola, X., Canudo, J.I., Company, J., Cruzado-Caballero, P. & Ruiz-Omeñaca, J.I. 2009a: Hadrosaurid

- dinosaurs from the Latest Cretaceous of the Iberian Peninsula. *Journal of Vertebrate Paleontology* 29, 946–951.
- Pereda-Suberbiola, X., Canudo, J.I., Cruzado-Caballero, P., Barco, J.L., López-Martínez, N., Oms, O. & Ruiz-Omeñaca, J.I. 2009b: The last hadrosaurid dinosaurs of Europe: a new lambeosaurine from the uppermost Cretaceous of Arén (Huesca, Spain). *Comptes Rendus Palevol* 8, 559–572.
- Pérez-Pueyo, M., Cruzado-Caballero, P., Moreno-Azanza, M., Vila, B., Castanera, D., Gasca, J.M., Puértolas-Pascual, E., Bádenas, B. & Canudo, J.I. 2021: The Tetrapod Fossil Record from the Uppermost Maastrichtian of the Ibero-Armorican Island: An Integrative Review Based on the Outcrops of the Western Tremp Syncline (Aragón, Huesca Province, NE Spain). *Geosciences* 11, 162.
- Pirrone, C.A., Buatois, L.A. & González Riga, B. 2014: A new ichnospecies of *Cubiculum* from Upper Cretaceous dinosaur bones in Western Argentina. *Ichnos* 21, 251–260.
- Pirrone, C.A. & Buatois, L.A. 2016: Bioeroded dinosaur bones: novel signatures of necrophagous activity in a Cretaceous continental environment. *Ichnos* 23, 340–348.
- Puértolas-Pascual, E., Arenillas, I., Arz, J.A., Calvin, P., Ezquerro, L., García Vicente, C., Sánchez Moreno, E.M., Villalain, J. & Canudo, J.I. 2018: Chronostratigraphy and new vertebrate sites from the upper Maastrichtian of Huesca (Spain), and their relation with the K/Pg boundary. *Cretaceous Research* 89, 36–59.
- Reed, H.B. 1958: A study of dog carcass communities in Tennessee, with special reference to the insects. *American Midland Naturalist* 59, 213–245.
- Roberts, E.M., Rogers, R.R. & Foreman, B.Z. 2007: Continental insect borings in dinosaur bone: examples from the Late Cretaceous of Madagascar and Utah. *Journal of Paleontology* 81, 201–208.
- Rogers, R.R. 1992: Non-marine borings in dinosaur bones from the Upper Cretaceous Two Medicine Formation, northwestern Montana. *Journal of Vertebrate Paleontology* 12, 528–531.
- Rosell, J., Linares, R. & Llompart, C. 2001: El 'Garumniense' prepirenaico. *Revista De La Sociedad Geológica De España* 14, 47e56.
- Rouse, G.W., Goffredi, S.K. & Vrijenhoek, R.C. 2004: Osedax: bone-eating marine worms with dwarf males. *Science* 305, 668–671.
- Saneyoshi, M., Watabe, M., Suzuki, S. & Tsogtbaatar, K. 2011: Trace fossils on dinosaur bones from Upper Cretaceous eolian deposits in Mongolia: Taphonomic interpretation of paleoecosystems in ancient desert environments. *Palaeogeography, Palaeoclimatology, Palaeoecology* 311, 38–47.
- Schroeder, H., Klotzbach, H., Oesterhelweg, L. & Puschel, K. 2002: Larder beetles (Coleoptera, Dermestidae) as an accelerating factor for decomposition of a human corpse. *Forensic Science International* 127, 231–236.
- Schwanke, C. & Kellner, A. 1999: Presence of insect? Borings in synapsid bones from the terrestrial Triassic Santa Maria Formation, southern Brazil. *Journal of Vertebrate Paleontology* 19 (Suppl. 3), 74A.
- Serrano-Brañas, C.I., Espinosa-Chávez, B. & Maccracken, S.A. 2018: Insect damage in dinosaur bones from the Cerro del Pueblo Formation (Late Cretaceous, Campanian) Coahuila, Mexico. *Journal of South American Earth Sciences* 86, 353–365.
- Timm, R.M. 1982: Dermestids. *Field Museum of Natural History Bulletin* 53, 14–18.
- Villalba Brea, S., Martín Closas, C., Marmi, J., Gómez, B. & Fernández Marrón, M.T. 2012: Peat-forming plants in the Maastrichtian coals of the Eastern Pyrenees. *Geologica Acta* 10, 189–207.
- Xing, L., Parkinson, A.H., Ran, H., Pirrone, C.A., Roberts, E.M., Zhang, J., Burns, M.E., Wang, T. & Chioniere, J. 2015: The earliest fossil evidence of bone boring by terrestrial invertebrates, examples from China and South Africa. *Historical Biology* 28, 1108–1117.
- Xing, L., Roberts, E.M., Harris, J.D., Gingras, M.K., Ran, H., Zhang, J., Xu, X., Burns, M.E. & Dong, Z. 2013: Novel insect traces on a dinosaur skeleton from the Lower Jurassic Lufeng Formation of China. *Palaeogeography, Palaeoclimatology, Palaeoecology* 388, 58–68.
- Zanetti, N.I., Ferrero, A.A. & Centeno, N.D. 2019: Depressions of *Dermestes maculatus* (Coleoptera: Dermestidae) on bones could be pupation chambers. *The American Journal of Forensic Medicine and Pathology* 40, 122–124.
- Zanetti, N.I., Visciarelli, E.C. & Centeno, N.D. 2014: Taphonomic marks on pig tissue due to cadaveric coleoptera activity under controlled conditions. *Journal of Forensic Science* 59, 997–1001.

Supporting Information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Supplementary Material