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# Cueva de los Torrejones revisited. New insights on the paleoecology of inland Iberia during the Late Pleistocene

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## ABSTRACT

The interior of the Iberian Peninsula has orographic conditions that make this territory especially vulnerable to Quaternary climate oscillations and which actually could have made it decisive for Paleolithic human populations at critical points. For this reason, the information provided by paleontological sites is important for reconstructing climatic and environmental conditions during the Late Pleistocene and understanding how they influenced the species that inhabited them, including humans. Nevertheless, the archaeo-paleontological record is scarce in central Iberia for the Late Pleistocene. A central Iberian site that is key to addressing this issue is Cueva de los Torrejones, which was discovered and excavated during the nineties. Clues indicating the presence of Neandertal populations near the cave site were announced during prior field excavations, including Neandertal remains, Middle Paleolithic artifacts, and evidence of anthropic exploitation of faunal resources at the site. Here we report the new results from the recent excavations and research, including detailed studies on stratigraphy, micro-morphology, macro and microvertebrate paleontology, physical and molecular anthropology, taphonomy and zooarchaeology, and analysis of lithic and pottery remains. Our research has led to the detection of three Prehistoric chronologies recorded at the site. The oldest episode corresponds to between MIS 5 and MIS 4 in which the cave was used by carnivores. The second episode is represented by a faunal association dated to 30.0 ka cal BP and is indicative of cooler and more arid environmental conditions and, therefore, compatible with the worsening climate detected previously for MIS 3 in this area. The last episode corresponds to the Chalcolithic, directly dated to ~5000 cal BP in which humans used the cavity

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for funerary purposes. The DNA analysis of the human remain was assigned to mtDNA haplogroup K, which was originated in the Near East and reached western Europe through the Neolithic expansion. Human occupation during the Paleolithic has been ruled out, including Paleolithic human remains and any kind of anthropic intervention on the Hermann's tortoise and leopard as was previously proposed at the site.

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## Author statement

Nohemi Sala and Adrián Pablos designed research, analyzed the data, prepared figures, wrote the paper, and directed the excavation and research project. Antonio Rodríguez-Hidalgo, Martín Arriola-bengoa, Manuel Alcaraz-Castaño, Miriam Cubas, Cosimo Posth, Kathrin Nägele, Ana Pantoja-Perez, Mikel Arlegi, Manuel Rodríguez-Almagro, Mercedes Conde-Valverde, Gloria Cuenca-Bescos, Alfonso Arribas and Asier Gomez-Olivencia, analyzed the data, prepared figures and/or wrote the paper.

## 1. Introduction

The Iberian Peninsula is one of the key regions for the study of the European Paleolithic record due to its rich archaeological and paleontological heritage. The richness of the deposits is especially remarkable in the Cantabrian, Atlantic, and Mediterranean regions. This scenario changes towards the interior of the Iberian Peninsula, where the Paleolithic record is scarcer. In fact, the interior of the Iberian Peninsula has been considered one of the most inhospitable regions during certain critical periods of the Paleolithic due to its eco-geographical characteristics (Burke et al., 2017; Sala et al., 2020; Wolf et al., 2018). The interior part of the Iberian Peninsula can be roughly described as comprising two plateaus, divided by a mountainous system called the Sistema Central (Fig. 1A). It has been suggested that the plateau functioned as an eco-geographic barrier for human populations during the colder periods of the Pleistocene, especially during the transition from the Middle to the Upper Paleolithic (Sala et al., 2020; Wolf et al., 2018). This, together with the limited availability of caves (restricted almost exclusively to the narrow border of Cretaceous carbonate rocks bordering the Sistema Central mountains), makes central Iberia a region about which little is known and for which merely sporadic chronological and paleoecological information is available.

Between the 70s and the 90s archaeo-paleontological explorations increased in the vicinity of the Sistema Central, thus revealing some of the most significant deposits in the interior of the Iberian Peninsula, such as Cueva del Reguerillo and Pinilla del Valle in Madrid (Alfárez et al., 1982; Torres, 1996), Cueva del Búho, Pinarillo and Villacastín in Segovia (Arribas, 1994, 1995; Arribas et al., 2008; Iñigo et al., 1998), Jarama VI, Cueva de Los Casares, Peña Capón and Peña Cabra rockshelters and Cueva de los Torrejones in Guadalajara (Adán et al., 1995; Alcolea-González et al., 1997; Arribas et al., 1995; Barandiarán, 1973). Some of these deposits were recently re-excavated, and new excavation and analysis techniques have made it possible to update our current knowledge regarding paleoecological, geochronological, and archaeological aspects of Paleolithic inland Iberia (Alcaraz-Castaño 2019, 2017a, 2017b; Arsuaga et al., 2012; Sala et al., 2011, 2012). Additionally, this significant push to re-evaluate and explore this region is giving rise to the discovery of new sites, thus expanding our archaeo-paleontological records in terms of chronology and territory. Some examples are the Portalón del Tejadilla (Sala et al., 2020), Abrigo del Molino (Álvarez-Alonso et al., 2018; Kehl et al., 2018) and

Calvero de la Higuera sites (Arsuaga et al., 2011; Baquedano et al., 2014, 2016, 2018), among others.

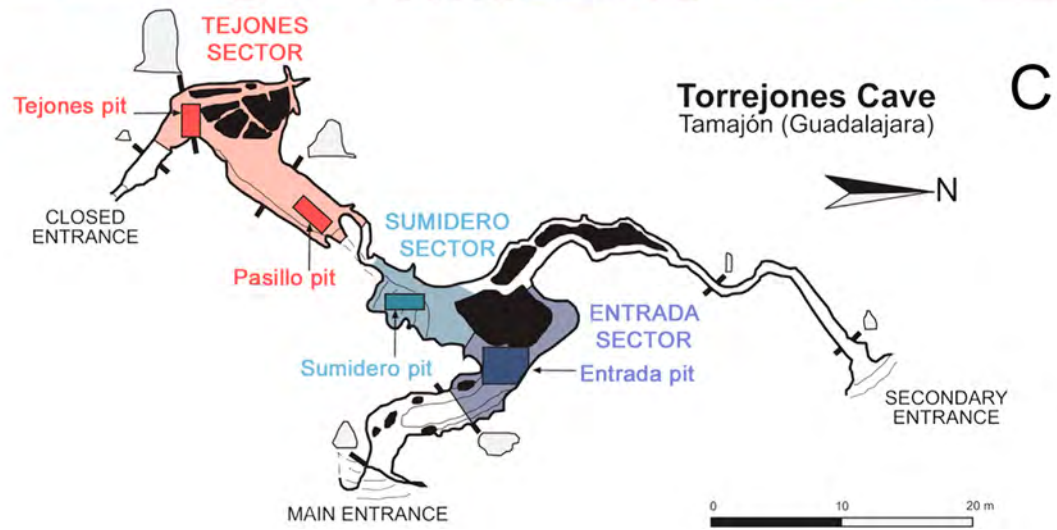
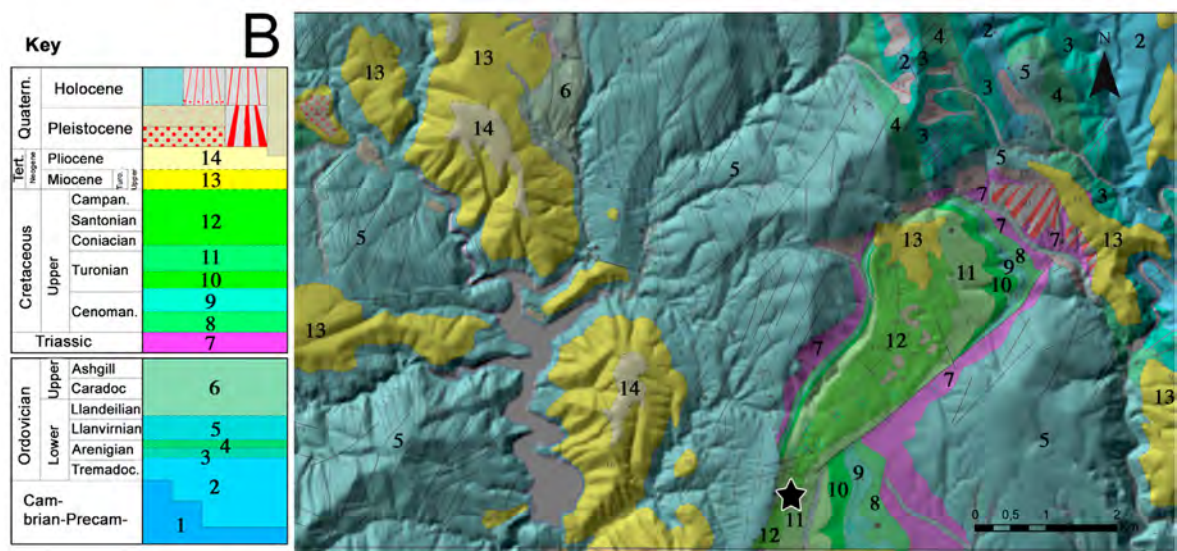
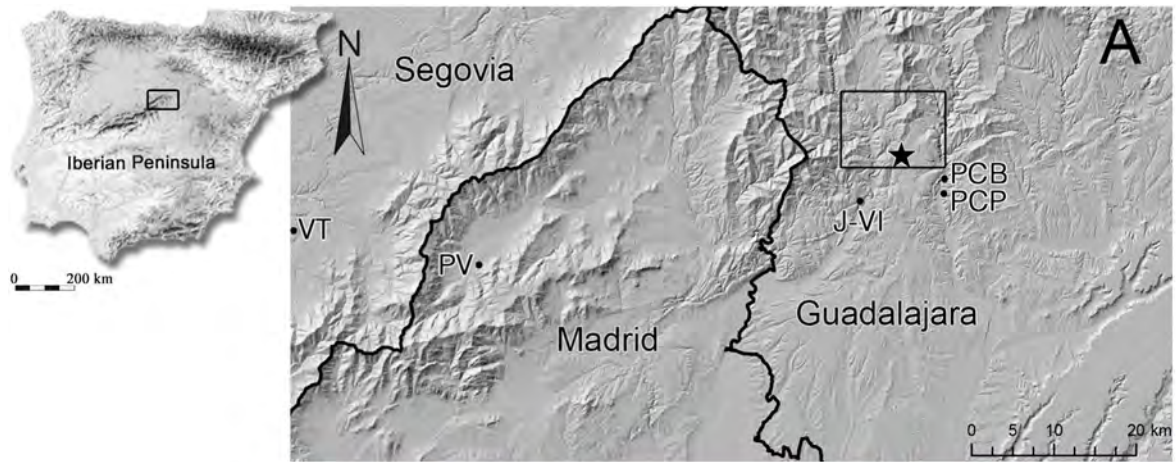
One of the key sites in this region is the Cueva de los Torrejones (hereinafter Torrejones), located in Tamajón (Guadalajara). It is situated on the southern slopes of the Ayllón Massif, in the easternmost foothills of the Sistema Central mountain range. The cave is located between the Sorbe and Jarama valleys, at 1100 m.a.s.l., just a few kilometers from other Paleolithic sites such as Jarama VI, Peña Capón, and Peña Cabra (Fig. 1B). This site is one of the most relevant archaeo-paleontological sites in this particular region because the abundant faunal association recovered could help to understand the paleoecological context during critical periods of the Late Pleistocene. Additionally, clues indicating the presence of Neandertal populations near the cave site were reported during previous field excavations, including Neandertal fossil remains, Middle Paleolithic lithic artifacts, and evidence of anthropic exploitation of faunal resources at the site (Arribas et al., 1997; Arribas, 1997; Díez Fernández-Lomana et al., 1998). Finally, remains corresponding to the Chalcolithic chronology, including human remains, pottery, and lithic artifacts, were also documented (Arribas et al., 1995, 1997).

## 2. Historical background and objectives

The first documented archaeological record in the Tamajón area was observed in 1979 by V. Cabrera and F. Bernaldo de Quirós, who conducted archaeological excavations in the Abrigo de Los Enebrales (Cabrera and Bernaldo de Quirós, 1979). In 1992 a researcher from our team (A.A.) located this rockshelter, as well as the nearby Torrejones cave (Arribas and Jordá, 1999). Torrejones is a small cave measuring about 60 m which currently has two functional entrances (Barea and Rejos, 2000). This site was excavated between 1993 and 1995 by a team led by A. Arribas, C. Díez, and J. Jordá. Despite the short duration of the excavations, a thorough study of the deposit's lithostratigraphy was carried out, numerous paleontological (including faunal and human) remains were discovered, and taphonomic analyses led to the proposal of distinct occupation models for the cave by humans and carnivores.

In this first period, different stratigraphic archaeological pits were excavated inside the cavity which were designated the Entrada, Sumidero, Pasillo, and Tejones sectors (Fig. 1C). The lithostratigraphic analyses of the different excavation zones allowed for the recognition of two main areas with differentiated sedimentary fill dynamics: i) the External Domain constituted by the Entrada sector and ii) the Internal Domain which includes the rest of the galleries (Sumidero, Pasillo and Tejones) (Arribas et al., 1997). Currently, only sediments from the Internal Domain are preserved since the entrance deposits (16 m<sup>2</sup> area) were virtually excavated in their entirety.

The External Domain (Entrada Sector) is where most of the Pleistocene fossil remains were recovered, especially in the lower units (E4 and E5), including: *Homo sapiens* ssp., *Erinaceus europaeus*, *Eliomys* sp., *Chionomys nivalis*, *Microtus arvalis-agrestis*, *Oryctolagus cuniculus* ssp., *Meles* sp., *Vulpes vulpes* ssp., *Canis lupus*



**Fig. 1.** Geographical and geological location of the Torrejones site. General geographical location and hillshade (A) of the study area with the location of other sites named in the text (VT: Valle del Tejadilla, PV: Pinilla del Valle; J-VI: Jarama VI; PCB: Peña Cabra; and, PCP: Peña Capón). B) Superposition of the Geological map (MAGNA) and digital elevation model (DEM) where the location of the Torrejones site can be observed (black star). Data from LiDAR and MAGNA (MAGNA hoja 459-Tamajón (Hernández-Huerta et al., 1994) made available by the Instituto Geográfico Nacional (IGN) and Instituto Geológico y Minero de España (IGME). C) Topographic scheme of the site map showing the different sectors. Modified from Arribas et al. (2005).

ssp., *Panthera pardus*, *Crocota spelaea*, *Ursus cf. arctos*, *Capreolus capreolus*, *Cervus elaphus*, *Bos/Bison* sp., *Sus scrofa*, *Equus ferus*, *Equus hydruntinus*, *Stephanorhinus cf. hemitoechus*, *Timon lepidus*, *Testudo cf. hermanni*, Passeriformes indet. (Arribas et al., 1997). These units (E4 and E5 units) represent a period in which the cavity acted as a hyena den site during the Late Pleistocene (Arribas et al., 1997; Díez Fernández-Lomana et al., 1998). Nevertheless, some human intervention was documented in the Entrada sector (E4 unit), illustrated by scant Middle Paleolithic lithic artifacts (Arribas et al., 1997), as well as evidences of anthropic modification (cut marks) on a leopard (*Panthera pardus*) temporal bone and a Hermann's tortoise (*Testudo hermanni*) hyoplastron (Arribas et al., 1997; Díez Fernández-Lomana et al., 1998).

The fauna recovered in the lower levels of the Internal Domain included the following species: *Homo* sp., *Erinaceus europaeus*, *Myotis* sp., Chiroptera indet., *Apodemus* sp., *Pitymys* sp., *Eliomys quercinus*, Muridae indet., *Microtus* sp., *Chionomys nivalis*, *Microtus arvalis-agrestis*, *Oryctolagus cuniculus* ssp., *Lepus* sp., *Meles meles* ssp., *Vulpes vulpes*, *Canis lupus*, *Felis silvestris*, *Crocota spelaea*, *Ursus arctos*, *Cervus elaphus*, *Capra* sp., *Sus scrofa*, *Equus* sp., *Equus hydruntinus*, *Stephanorhinus cf. hemitoechus*, Lacertidae indet., *Epidalea calamita*, Serpentes indet., Anura indet., *Testudo* sp., and Aves indet. (Arribas et al., 2005).

Both in the Internal and the External domains, the most superficial units (E1, E2 and E3 from Entrada, S1 and S2 from Sumidero, T1 and T2 from Tejones, and P1 and P2 from Pasillo) were defined as Holocene deposits (with pottery, lithic artifacts, bone remains, and badger coprolites from the last three centuries), where some Pleistocene bone remains were incorporated from the lower units (reworked fossils) (Arribas et al., 1995, 1997, 2005; Carrión et al., 2005).

Human remains were found, along with the rest of the recovered fauna, most of which came from the disturbed upper levels, and they were chronologically assigned to the Chalcolithic. Exceptionally, some human remains, including a complete radius, a fragmentary juvenile hemimandible, as well as a fourth (IV) metacarpal, found in the superficial and reworked units, were assigned to *H. sapiens cf. neanderthalensis* due to the presence of putative plesiomorphic characters (Arribas et al., 1995). Of particular interest was a hominin foot remain, a right navicular bone found in the *in situ* unit S3 in the Sumidero sector. Although this element was assigned to *Homo* sp. due to the absence of diagnostic characters, its stratigraphic designation in an *in situ* unit (associated with hyenids and ursids), suggested an older chronology of this remain compared with the rest of the human remains, assigning it to a late Middle Pleistocene, or early Late Pleistocene chronology (Arribas et al., 1995).

These results drove the current research team to resume the investigation and excavation of this site. Firstly, a detailed anthropological and morphometric study was performed on this foot remain. This study concluded that this fossil lacked the expected dimensions and morphology to be considered Neandertal or Middle Pleistocene hominin and, therefore, undoubtedly belonged to a *Homo sapiens* (Pablos et al., 2018). Due to the biostratigraphical context, a possible assignment to Upper Paleolithic *Homo sapiens* was proposed (Pablos et al., 2018). The absence of Upper Paleolithic human fossils in the interior of the Iberian Peninsula highlighted the need to re-excavate the site, especially the Sumidero Sector, with the objective of finding appropriate data allowing us to attribute this human fossil to the Paleolithic context of this region. Thus, a new excavation at the Torrejones site was initiated in 2017. In parallel, the interest sparked by this possible Upper Paleolithic hominin fossil prompted the sampling of this human remain for molecular and chronological purposes. The results of the AMS

radiocarbon direct dating on the navicular itself point to a Chalcolithic age for this human bone (Pablos et al., In press).

The current team has been working in the Tamajón karstic system since 2017, which includes Torrejones and a rockshelter called 'Abrigo de la Malia' discovered in 2017 by A.A. In this study, we focus on the new results derived from the recent excavation and research from Torrejones. The main objective of this paper is to provide new information about Torrejones, a key site in understanding the paleoecology of central Iberia during the Late Pleistocene, filling in gaps in our knowledge about how ecological conditions affected the Paleolithic human populations in this region. To that end, in this paper we present a description of the Torrejones site, including the findings recovered during the new field seasons, as well as the reanalysis of the material recovered during previous excavations, this time implementing more advanced techniques. These include: i) new data from the stratigraphy and geological sampling (mineralogy and micromorphology); ii) the description of old and new fossils, including human and faunal remains (micro and macrovertebrates); iii) taphonomic analyses of old and new remains, emphasizing the bone surface modifications and breakage patterns; iv) providing the results of the direct dating of fossil remains from different units; v) molecular analysis of human remains; and vi) the analyses of the archaeological material, including lithic and pottery remains.

### 3. Material and methods

#### 3.1. Material

For the taxonomic analysis of the faunal assemblages, the collections from the 2017–2019 excavation seasons (especially focused on the Sumidero sector) and from prior excavations have been analyzed in their entirety (total number of remains NR = 965). The materials from 2017 to 2019 comprise 217 macromammals, 210 of which correspond to the Sumidero sector. In addition, all the human remains (number of identified specimens NISP = 108) have also been analyzed. With respect to the old materials, the taxonomic study mainly focused on the Pleistocene levels of the Entrada and Sumidero sectors, of which 558 and 113 remains were analyzed, respectively. Access to the remains from the previous excavation was granted by the Museo Geominero in Madrid (Instituto Geológico y Minero de España), where the remains are stored.

Osteological collections from the Centro Nacional de Investigación sobre Evolución Humana (CENIEH, Burgos, Spain) research center were used as comparative materials. In addition, taphonomic traits were compared to actualistic data from living carnivores using the taphonomic collection from Centro Mixto UCM-ISCIII, performed by Sala and Arsuaga (2018). Lastly, the metric and morphological data of faunal remains were compared with an extensive sample, mainly from the Iberian Peninsula and other European sites (Sala et al., 2020 and references therein).

In terms of archaeological material (lithic artifacts and pottery), this study included the remains recorded during the more recent excavation seasons (2017–2019), as well as a few pieces recovered from the faunal materials from the previous excavations. In Arribas et al. (1995, 1997), 101 pieces of lithic industry and 31 pottery fragments are mentioned. Nevertheless, this material was not included in this work because its current location is unknown and, therefore, could not be analyzed. Regarding the lithic artifacts, 73 knapped products were analyzed, including from Sumidero (n = 43), Entrada (n = 12) and Pasillo (n = 18). The pottery assemblage is formed by eight fragments recorded in the upper units from the Sumidero sector (LU-S1 and LU-S2) from the

2017–2019 seasons.

### 3.2. Methodological procedure

#### 3.2.1. Stratigraphy

The lithostratigraphic units (LU) were named according to the area where they were defined (i.e., Entrada- E, Sumidero- S, Pasillo- P, Tejones- T), followed by a number in ascending order from top to bottom. Each LU was defined by sedimentary features (e.g., size, lithology, sorting, shape and roundness of clasts, matrix composition, and archaeo-paleontological remains) and grouped into different categories based on the origin of the sediment (i.e., autochthonous or allochthonous) (Bosch and White, 2007; Hughes, 2010; White, 2007). Subsequently, the different lithological units have been grouped based on allostratigraphic units (AU) since this provides an effective method for grouping sediment units that contain genetically related sedimentary deposits (Aranburu et al., 2017; Ghinassi et al., 2009; Hughes, 2010; Hunt et al., 2010; Martini, 2011; NACSN, 2005). Each AU includes different LUs grouped according to the geological processes inferred and delimited by erosive surfaces. In order to interpret and correlate the different LUs described in different sectors of the cave, we performed 11 mineralogical analyses of the bulk sediment and, another six samples were taken for the clay fraction identification, including the bedrock. These mineralogical analyses were carried out by X-ray diffraction (XRD) in the CENIEH laboratory. In addition, a thin section of the bedrock was analyzed to ascertain the composition of the insoluble fraction of the dolomite host rock. Sediment colors were determined by the Munsell® soil color charts.

Cartographical representation of digital elevation models (DEM) was obtained with the LiDAR and MAGNA data available at the Instituto Geográfico Nacional (IGN) and Instituto Geológico y Minero de España (IGME) using a geographical information system (Esri ArcGIS 10.4.1 software) (ESRI, 2011).

Nine samples (bones and teeth) were sent for AMS-ultrafiltration radiocarbon dating purposes to different labs (Oxford Radiocarbon Accelerator Unit (ORAU)-OxA in England, Beta Analytic-BETA in the United States, and Curt-Engelhorn-Zentrum Archaeometrie-MAMS in Germany), but only four of them yielded an age.

#### 3.2.2. Micromorphology

The micromorphological study was focused on the Sumidero Sector and included three unaltered sediment samples taken from: i) the contact between the LU-S2 and LU-S3A units; ii) LU-S3A, and iii) LU-S3B. The objective of the micromorphological analysis was to characterize the sedimentary features in this sector in order to address the origin of the sediments and the possible mixture of different units (Pablos et al., *In press*). A detailed explanation of the micromorphology samples obtained can be found in Supplementary Text 1.

#### 3.2.3. Paleobiological analysis

The paleobiological analysis was performed with fossil remains of micro and macro mammals. The microvertebrate assemblage from new excavations was collected by water screening the sediments excavated. In order to collect all bone and teeth fragments from the fossil assemblage, the sediment was water screened, using superimposed 1.5 mm, 1.0 mm, and 0.63 mm-mesh screens, and bagged by sector/LU, as well as manually sorted and classified. According to the information that appears in the unpublished 1995 excavation report, during the 1993–1995 excavations the micro-faunal remains were collected by dry-screening using

superimposed 5 and 2 mm sieves.

Measurements taken on macromammal bones and teeth followed the standards of von der Driesch (1976). Selected metric comparative data derive from several sources (e.g., Sala et al., 2020 and references therein). The graphs with the metric data for the different species were generated using R 3.3.1 software (R-Core-Team, 2016). The age at death of the species was estimated based on the deciduous tooth and molar wear. Furthermore, following the criteria published by Stiner (1994), three age classes were taken into consideration: juvenile, prime, and old. For postcranial elements, we differentiated adult from immature individuals based on the degree of bone fusion, such as epiphyseal fusion for limb bones.

#### 3.2.4. Anthropological analysis

The age-at-death estimation was based on the degree of dental eruption and dental attrition, as well as the degree of fusion of the principal and secondary centers of ossification in both cranial and postcranial bones (Madeline and Elster, 1995; Scheuer and Black, 2000; White and Folkens, 2005 and references therein).

In the absence of complete lower limb remains, which are the preferred element for estimating stature as they have a direct impact on it (e.g., Carretero et al., 2012; Pablos et al., 2013; Raxter et al., 2007), we used the correlation between stature and upper limb bones using the formulae by Ruff et al. (2012) in order to perform a preliminary assessment.

#### 3.2.5. Molecular analysis

The human navicular bone (T93-S3-27) was sampled for ancient DNA (aDNA) analyses in a hood at the Spanish Geological Institute (Madrid). Three aliquots of bone powder weighing 10, 20, and 38 mg were collected with a dentist drill. The entire sampling procedure was documented photographically. In the clean room facilities at the Max Planck Institute for the Science of Human History in Jena (Germany), the largest bone powder aliquot was used for DNA extraction using a protocol specifically designed to retain short DNA fragments, typical of aDNA (Dabney et al., 2013). One-fourth of the DNA extracted was converted into a double stranded UDG half library (Rohland et al., 2015) and indexed with a unique pair of barcodes (Kircher et al., 2012). The resulting DNA library was amplified to PCR plateau and shotgun sequenced for ~3 million reads on a HiSeq Illumina machine for 75 single-end cycles. The same genetic library was further amplified and used to capture the entire mitochondrial DNA (mtDNA) genome (Fu et al., 2013). The mtDNA-enriched library was then sequenced for ~1.3 million reads on a HiSeq for 75 single-end cycles.

Shotgun sequences were processed through EAGER (Peltzer et al., 2016), where DNA fragments were trimmed of the adapters, length and quality filtered, and mapped against the human reference sequence (hg19) with the following parameters (-n 0.01 -l 16,500). Furthermore, mapped reads were quality filtered (q30), duplicates were removed, and the damage pattern profile was calculated with mapDamage2.0 (Jónsson et al., 2013). Sex determination was performed by inspecting the sequence coverage on the X-chromosome compared to the coverage on the autosomes (Mittnik et al., 2016). The mtDNA-captured sequences were processed as described above but aligned to the mtDNA human reference sequence (rCRS) instead. The tool schmutzi (Renaud et al., 2015) was then used to jointly estimate mtDNA contamination levels and reconstruct complete mtDNA sequences with increasing likelihoods from q0 to q30. Finally, the online program Haplofind (Vianello et al., 2013) was implemented to assign the consensus sequences to the respective mtDNA haplogroup.

### 3.2.6. Taphonomy and zooarchaeology

All the anatomically or taxonomically identifiable remains (including the human remains), as well as those that only provide information regarding the size of the animal, were studied for taphonomic purposes. In addition, non-identifiable bone fragments larger than 2 cm were also taken into consideration. Body size was established based on the weight and age of the ungulates (Bunn, 1986). We categorized i) large sized-ungulates as adult specimens of *Bos/Bison*, equids, and rhinoceroses; ii) medium-sized ungulates as adult specimens of *Cervus*; and iii) small-sized ungulates (SSU) as adult specimens of *Capra* and *Sus scrofa*. In the taxonomically unidentifiable remains, this grouping was based on the thickness of the cortical bone. For the taphonomic analyses, all bones were studied at both macroscopic and microscopic levels by using a Motic SMZ161 Stereoscopic zoom microscope and a DINO-LITE digital microscope.

Tooth marks on bone surfaces were classified into pits, punctures, furrowing, scores, and dissolution due to gastric acids. Pits were measured (length and width) in accordance with previous studies (Sala and Arsuaga, 2018). The length and breadth of tooth marks were measured using the DINO-LITE digital microscope software tools and digital calipers. For the metric comparative analyses of tooth mark dimensions, we performed the Mann-Whitney test on all possible sample pairs to determine which differed significantly. Taphonomic studies (Andrés et al., 2012; Sala et al., 2014; Sala and Arsuaga, 2018) show that the tooth pit length on cortical surfaces is the best indicator of the size of the carnivore responsible for the tooth marks. For this reason, we focused specifically on this feature when metrically comparing the samples. The comparative samples included actualistic data with living carnivores (summarized in Sala and Arsuaga, 2018), as well as, paleontological assemblages from Central Iberia interpreted as carnivore den sites: Cueva del Camino (Arsuaga et al., 2012), Búho and Zarzamora caves (Sala et al., 2012), and Portalón del Tejadilla (Sala et al., 2020).

To evaluate the presence of cut marks, we observed the criteria established by Domínguez-Rodrigo et al. (2009). Furthermore, we used contextual criteria, such as the anatomical location of grooves, the color of grooves with respect to the color of the bone surface, the presence of chipping along the grooves, and the relationship between grooves and other taphonomic modifications. Breakage analysis, which provides valuable data regarding the timing of the fracture (fresh bone or perimortem versus dry bone or postmortem), was focused on the long bone elements. For long bone fracture patterns we followed the methodology proposed by Villa and Mahieu (1991), in terms of: fracture outline (longitudinal, transverse, or oblique/curved), fracture angle (right or oblique), fracture edge (smooth or jagged), shaft circumference (1: less than half of the circumference; 2: more than half of the circumference; 3: complete circumference), and shaft fragment (1: less than 1/4 of the total diaphysis; 2: between 1/4 and 1/2 of the total diaphysis; 3: between 1/2 and 3/4 of the diaphysis; 4: increased from 3/4 of the diaphysis).

Lastly, the study of other post-depositional alterations encompassed the presence/absence of crusting, weathering, biological (plant roots, fungi, or bacterial activities), and geological bone dissolution (e.g., cave corrosion holes due to the soil acidity); in addition, trampling marks and manganese oxide staining were documented.

### 3.2.7. Archaeological material: lithics and pottery

Lithic remains were discovered in three different sectors: Sumidero, Entrada, and Pasillo. The largest – but still relatively small – assemblage comes from the Sumidero sequence, where

pottery fragments were also recorded. Here, archaeological artifacts were gathered both by superficially cleaning the area surrounding the 1990's fieldwork and the manual excavation of an area measuring 1 × 0.80 m starting in LU-S2. Excavation methods included wet screening of sediments at 2- and 1-mm mesh sieves. The studied assemblages include part of the artifacts previously excavated by Arribas et al. (1995, 1997).

After manual cleaning, lithic artifacts were studied at the Pre-history Laboratory of the University of Alcalá under the *chaîne opératoire* or 'operational sequence' approach as described by Pelegrin et al. (1988) or Inizan et al. (1995) and discussed by others, such as Bar-Yosef and Van Peer (2009). We assigned each lithic artifact to one of the three *chaîne opératoire* stages commonly referenced in the literature. Thus, cortical flakes, preparation products, and tested cores were assigned to the initialization stage or phase I, raw blanks and core maintenance by-products to the exploitation stage or phase II, and retouched blanks and exhausted cores to the consumption and abandonment stage or phase III.

All pottery sherds were macroscopically studied whether or not they came from a representative or indeterminate morphological part of the vessel. Due to the ample fragmentation, the unit chosen for this method was the individual sherd. This was done by the naked eye, without sample preparation. The following categories were used in the systematic description of the pottery sherds: size, fabric characteristics (clay matrix and non-plastic inclusions), technological traces related to manufacturing techniques and firing temperatures, morphological characteristics, surface treatment, decorative techniques, and possible post-depositional alterations.

## 4. Geological and geochronological characterization

### 4.1. Stratigraphy and sediment characterization

The bedrock of the Torrejones cave site consists of marine limestone and dolomite deposited during the Upper Cretaceous (Coniacian-Santonian) (Fig. 1B). The bedrock is composed of a network of equigranular and anhedral dolomite crystals. Under the microscope (Supplementary Figure 1), the thin section of the bedrock shows, as an insoluble product, quartz grains scattered between the dolomite crystals, as well as clay minerals (Illite 37% and Kaolinite 63% made by oriented aggregates, XRD).

The study of the lithostratigraphic units (LU) was carried out in the different test pits in the Internal Domain of the cave: Sumidero, Pasillo, and Tejones (Fig. 1C). Fifteen lithostratigraphic units (LU) were defined, taking into consideration the remaining stratigraphic pits in the cavity (Sumidero, Tejones, and Pasillo), which were grouped into several erosive surfaces and therefore into three allostratigraphic units (AU). The Entrada sector could not be characterized stratigraphically since it was completely excavated during the 90s. Nevertheless, following the stratigraphic description available in previous publications (Arribas et al., 1995, 1997, 2005), this sector was included in the allostratigraphic scheme as an additional AU. The new sedimentological analysis expanded on previously published descriptions of the site (Arribas et al., 1995, 1997, 2005) and was mainly based on the mineralogy, texture, and grain size parameters, which allowed for the description of the units in lithostratigraphic terms in order to determine their components and to distinguish autochthonous from allochthonous sediments. The sedimentological data, taking all the sectors of the cave into account, can be found in Table 1.

### 4.2. Geochronology

The geochronological sampling was focused on the Sumidero



**Table 1**

Description of the Lithostratigraphic Units from the Internal Domain of the Torrejones cave, mineral composition (by XRD), and the archaeopalontological findings.

Sector	LU	Color	Sediment and mineral composition	Archaeo-paleontological findings
<b>Sumidero</b>	S1	Brown 7.5 YR 4/4	Variable thickness. Absence of cementation and sedimentary structures. Presence of dolostone cobbles, millimetric to centimetric well-rounded pebbles of foliated metamorphic rocks and charcoal. Matrix composition: Qtz (43%), Dol (14%), Cal (2%), Fsp (4%), Plg (4%), Hxa (6%), Phyll (27%).	Human and faunal remains. Pottery fragments and lithic industry
	S2A	Brown 7.5 YR 4/4	Thickness up to 70 cm. Cemented unit with dolostone cobbles, millimetric to centimetric well-rounded pebbles of foliated metamorphic rocks and charcoal. Matrix composition: Qtz (43%), Dol (14%), Fsp (5%), Plg (5%), Hxa (3%), Phyll (30%: Ill (43%) + Kln (49%) + Clo (4%) + IEsm (4%)).	Human and faunal remains. Pottery fragments and lithic industry
	S2B	Reddish yellow 7.5YR6/6	Thin unit at the base of S2 characterized by a lenticular morphology and clast-supported texture. Contains centimetric to decimetric dolostone cobbles and well-rounded pebbles of foliated metamorphic rocks and charcoal. Matrix composition: Qtz (33%), Dol (16%), Cal (3%), Fsp (6%), Plg (6%), Hxa (2%), Phyll (34%).	
	S3A	Reddish yellow 7.5YR7/6	60 cm maximum thickness. Chaotic matrix-supported silty deposit with millimetric and centimetric pebbles of metamorphic rocks and some scattered charcoal. Matrix composition: Qtz (33%), Dol (13%), Cal (5%), Fsp (12%), Plg (8%), Hxa (1%), Phyll (28%).	Pleistocene fauna (micro and macrovertebrates) such as bear and hyena. Human navicular bone (T93-S3.27)
	S3B	Strong brown 7.5YR5/6 (silt) Dark brown color 7.5YR3/4 (gravels)	145 cm of excavated thickness. Intercalations of fine sand/silt with internal parallel lamination in packages of 6–12 cm thickness and lenticular levels of monomictic gravels of well-sorted metamorphic rocks. The metamorphic rocks mainly consist of very rounded centimetric pebbles of greenish and grayish slate with a certain degree of imbrication. Matrix composition of the silt: Qtz (43%), Dol (8%), Cal (1%), Fsp (7%), Plg (6%), Phyll (35%: Ill (33%) + Kln (24%) + Clo (3%) + IEsm (40%)); Matrix composition of the gravels: Qtz (22%), Dol (11%), Cal (6%), Fsp (6%), Plg (5%), Phyll (50%).	
<b>Pasillo</b>	P1	Brown 7.5 YR 4/4	Superficial unit. Irregular thickness characterized by the absence of stratigraphic structures (no cemented matrix) with an intense bioturbation.	Indeterminate faunal remains
	P2A	Brown 7.5 YR 4/4	Thickness up to 45 cm with an irregular boundary with P1. Cemented unit with dolostone cobbles, millimetric to centimetric well-rounded pebbles of foliated metamorphic rocks.	Human, micro and macrovertebrate remains and coprolites.
	P2B	Brown 7.5 YR 4/4	Thickness between 90 cm and 1.5 m with irregular boundaries (dip of about 35° NE). The matrix contains planar and subangular dolomite cobbles and pebbles of well-rounded foliated metamorphic rocks. This unit is very similar to P2A, but is distinguished by its more cemented texture. Matrix composition: Qtz (36%), Dol (12%), Cal (1%), Fsp (8%), Plg (7%), Hxa (3%), Phyll (33%).	Macro and microvertebrate remains
	P3	Reddish brown 5YR4/4	50 cm minimum thickness. Fine sand/silt in packages of 10–20 cm thickness with intercalations of thin lenses gravels of metamorphic rocks (very rounded centimetric pebbles of greenish and grayish slate). Plant roots are observed in the silty horizons. Matrix composition: Qtz (40%), Cal (2%), Fsp (7%), Plg (6%), Phyll (45%: Ill (48%) + Cao (38%) + Clo (3%) + IEsm (11%)).	–
<b>Tejones</b>	T0	Dark red 10 YR 3/6	Small patches in this unit remain preserved cemented to the cave roof irregularities. Poorly sorted matrix of clay/fine silt with metamorphic pebbles. Matrix composition: Qtz (27%), Dol (5%), Cal (29%), Fsp (2%), Plg (2%), Phyll (35%: Ill (40%) + Cao (53%) + Clo (3%) + IEsm (4%)).	–
	T1	Brown 7.5 YR 4/4	Superficial unit. Irregular thickness characterized by the absence of stratigraphic structures (no cemented matrix) with an intense bioturbation.	Human and faunal remains
	T2	Yellowish red 5 YR 4/6	10 cm thickness. Clayish/silty matrix with internal parallel lamination with some metamorphic rock pebbles.	Human and faunal remains
	T3A	Dark reddish Brown 5 YR 3/3	20 cm maximum thickness. Fine sand/silt matrix with metamorphic pebbles and red clay chips.	Faunal remains
	T3B	Dark reddish Brown 5 YR 3/3	30 cm max thickness. Unit very similar to T3A (same matrix) but characterized by its more cemented texture, the presence of planar and subangular dolomite cobbles, as well as galleries produced by current bioturbation.	
T4	Red 2.5 YR 4/6	70 cm thickness. Fine sand/silt red matrix with abundant red clay chips, dolomite cobbles, metamorphic rock pebbles, and disseminated charcoal. Abundant plant roots at its base. This unit's base has contact with a dolomite rock (floor bedrock?).	–	

Qtz: Quartz; Cal: Calcite; Fsp: Feldspar; Plg: Plagioclase; Hxa: Hidroxiapatite; Phyll: Phyllosilicates; Clo: Clorite; IEsm: Smectite; Ill: Illite; Kln: Kaolinite. The color codes used correspond to those of the Munsell color system for wet sediment.

and Entrada sectors, covering relevant LUs (LU-S1, LU-S2 and LU-S3 from Sumidero and LU-E4/LU-E5 from Entrada), in order to characterize the chronology of the sequence (Pablos et al., *In press*). Two dates on human remains provided a range of around 5300–4500 cal years BP, confirming the Chalcolithic attribution for the uppermost levels (LU-S1 and LU-S2). These dates are compatible with the lithic industry, the micromammal association, and the presence of pottery in these lithostratigraphic units. Radiocarbon

dating placed an equid lower molar from level LU-S3 (Beta-481,425) at 30,750–29,950 cal years BP. However, the human navicular recovered in the same LU (from exactly the same bag with the same field information as the horse molar) provided a Chalcolithic age (MAMS-34581). Five additional remains from Entrada and Tejones sectors were unable to be dated due to inappropriate C:N ratio, % C and % N and the  $\delta^{13}\text{C}$  parameters for dating. Detailed results of the AMS radiocarbon dating can be found in

## Supplementary Table 1.

### 4.3. Micromorphology

In this study we have focused on the micromorphological analysis of the Sumidero. The micromorphological examination of the thin sections from units LU-S2/LU-S3 reveals variations in the texture, fabric, and organization of the main constituents. The basic components are consistent throughout most of the sequence, though their organization and proportion change locally within the deposits. The micromorphological examination results are presented in stratigraphic order from the bottom to the top of the sequence (Supplementary Text 1), resumed in Table 2 and detailed in Fig. 2 and Supplementary Figures 2 to 4.

## 5. Paleontological analysis

### 5.1. Microvertebrates

The microvertebrate taxonomic association encompasses 23 taxa. Nevertheless, the high fragmentation of the remains implies that many of them have only been identified at the genus level (Table 3). The microvertebrate analysis in the Entrada sector was carried out based on some materials recovered in the nineties, published in Arribas et al. (1997). In the upper units (LU-E1/2), *Microtus arvalis*, *Terricola* sp. and *Eliomys quercinus* are present, species that are replaced by *Chionomys nivalis* in the lower levels (LU-E4/5).

The materials excavated during recent excavations were taken into consideration when analyzing the microvertebrates from the Sumidero sector, and the taxonomic list published by Arribas et al. (1997) was also taken into account (Table 3). The small vertebrate fauna is dominated by lagomorphs (*Oryctolagus* and *Lepus*), rodents, and insectivores. There are also some chiropterans, though they constitute a minority group in the association. With respect to rodents, the most abundant in LU-S2 and LU-S3 are: *Microtus arvalis*, *Eliomys quercinus*; *Apodemus* sp., *Terricola* sp., and *Chionomys nivalis*. Noteworthy is that, *Iberomys cabrerae* and *Sciurus vulgaris* only appear in LU-S2. Regarding insectivores, *Erinaceus* has been identified in both LU-S2 and LU-S3. Moles of the *Talpa* genus have only been recognized in LU-S2. Finally, the presence of the alpine marmot, *Marmota marmota*, has been documented in LU-S1, LU-S3, and LU-S3B.

### 5.2. Macrovertebrates

Taxonomic analysis has led to the identification of 19 macrovertebrate species. The taxonomic assemblages from the different lithostratigraphic units were analyzed separately (Table 4).

#### 5.2.1. Internal Domain

The Holocene units, LU-S1 and LU-S2 from Sumidero, and T1 and T2 from the Tejones sectors are very similar with respect to their faunal content, as they are all dominated by small carnivores, mainly badgers (*Meles meles*) and foxes (*Vulpes vulpes*) (Table 4). The badger is the most abundant species in units LU-S1 and LU-S2, represented by elements of the whole skeleton. Additionally, coprolites of this species have also been identified, especially in LU-S1, which attest to these mustelids' repeated occupation of the cavity, most of them sub-recent, from the last 300 years (Carrión et al., 2005). In LU-S1, small felids have also been identified, including a hemimandible, a canine, and a phalanx. It has not been possible to discern whether they are from a wild (*Felis silvestris*) or domestic cat (*Felis catus*). Additionally, two proximal phalanges and

two lower canines show felid morphological characters (longitudinal grooves in the enamel), but a larger size than that expected for cats (Supplementary Table 2) and, therefore, are classified as *Lynx*. According to Rodríguez-Varela et al. (2016), there is no current evidence that the Eurasian lynx (*Lynx lynx*) reached latitudes south of the Cantabrian Mountain Range. On the contrary, only *L. pardinus* (Rodríguez et al., 2011) is represented in the southernmost latitudes of the Iberian Peninsula; therefore, the species found in Torrejones is most likely *Lynx* cf. *pardinus*. Finally, hyena fossils were recovered from these upper units (LU-S1, LU-S2 and LU-T1), strictly Pleistocene species and, therefore, reworked from underlying units.

Both ovicaprines and horses are the most abundant species of ungulate found in the upper units of the Internal sector, followed by large bovids and suids. Given the Holocene chronology of these units, it is very likely that a large percentage of these bone remains correspond to domestic species. Wild species have also been documented: a few roe deer (*Capreolus capreolus*) remains in LU-S1 and LU-T2, as well as two red deer (*Cervus elaphus*) remains in LU-T1 and LU-T2. Additionally, two tortoise plates have been recovered from LU-S2, probably corresponding to *Testudo hermanni* reworked from the underlying units due to the abundance of this species in the lower units and their similar taphonomic features.

A total of 98 macrovertebrate remains have been recovered from the lower unit of the Sumidero sector (LU-S3), which differs from the overlying units. In relation to carnivores, we observe a considerable decrease in the representation of badgers which, although still present, are no longer a dominant species. Instead, six hyena remains have been recovered, mainly dental fragments displaying the typical morphology and size of genus *Crocota*, compatible with a single young adult individual (Fig. 3). Metrically, the *Crocota* upper carnassial P<sup>4</sup> (T93-S3-57), which preserves a mesio-distal fragment of the labial side with paracone and metacone, falls within the range of variation for the Late Pleistocene *C. spelaea* from the Iberian Peninsula and is slightly larger than extant African spotted hyenas (*C. crocuta*) from Masai Mara (Supplementary Table 3).

LU-S3 has also yielded a second lower right molar corresponding to a young bear individual who did not yet complete the development of the root apex (Fig. 3). In occlusal view, this tooth shows a complex cusp pattern, especially in the metaconid and entoconid. The dimensions of this molar falls within the range, though below the mean for *U. spelaeus* and outside the range for a large *U. arctos* sample (Fig. 4 and Supplementary Table 4). However, due to the absence of additional diagnostic fossil remains, we cautiously assign this molar to *Ursus* sp.







Finally, there is a complete canine whose dimensions are compatible with *Canis lupus* among the carnivores from LU-S3; however, in the absence of more diagnostic elements, this identification remains uncertain (Fig. 3).

Horse is the dominant species of ungulate in the LU-S3 assemblage, and the 17 dental elements correspond to a minimum of two individuals (an adult and an immature). Despite not being complete, the dental piece dimensions are compatible with the expected values for *Equus ferus*. One of these teeth (T93-S3-24) was sampled for radiocarbon dating, yielding a chronology within the Pleistocene (Supplementary Table 1).

Cervid remains have been identified, including permanent and deciduous dentition, representing a minimum of two individuals. Although the size of the remains suggests that they belong to a red deer, a comparative metric study was not performed due to the lack of complete pieces.

Lastly, an artiodactyl intermediate phalanx (T93-S3-39) recovered from LU-S3 displays dimensions that fall more comfortably within the range of variation for the Pleistocene

**Table 2**  
Synthetic micromorphological description and interpretation.

Thin section	LU	Description	Interpretation
	LU-S2	Matrix-supported, massive microstructure and poor sorting. Skeleton grains (40%): dark slate lithoclasts (40%), rip-up clasts (25%), dolostone lithoclasts (15%), bones (10%), coprolites and organic aggregates (10%). Groundmass (60%): yellowish-brown sandy (70 quartz, 30% dolomite) silt.	Most components are autochthonous (resedimented from other stratigraphic levels). Relatively low transport. Deposited by hyperconcentrated runoff events. Low diagenesis of some phosphatisation.
	LU-S2/S3A	Highly irregular and clear contact.	Erosive hiatus.
	LU-S3A	Clast-supported, massive microstructure and not fair sorting. Skeleton grains (65%): dark slate lithoclasts (35%), rip-up clasts (25%), dolostone lithoclasts (20%), bones (10%), coprolites and organic aggregates (8%), well-preserved charcoal (2%). Groundmass (35%): dark-brown sandy (70% quartz, 25% dolomite, 5% opaque) silt.	Most components are autochthonous (resedimented from other stratigraphic levels or upper soils). Low transport. Deposited by hyperconcentrated runoff events. Low diagenesis with some phosphatisation.
	LU-S3A	2 (sub) microfacies: 1) matrix-supported; 2) clast-supported. Massive microstructure with an incipient lamination, and not fair sorting. Skeleton grains: black slate lithoclasts (45%), rip-up clasts (25%), dolostone lithoclasts (15%), bones (8%), coprolites and organic aggregates (5%), charcoal (2%). Groundmass: dark-brown on clast-supported microfacies, while brown on matrix-supported microfacies. Sandy silt compound (70% quartz, 25% dolomite, 5% opaque).	
	LU-S3B	3 (sub) microfacies: 1) sandy matrix-supported; 2) silty clay matrix-supported; 3) clast-supported. Horizontally laminated microstructure and good sorting. Skeleton grains: dark slate lithoclasts (70%), rip-up clasts (20%), dolostone lithoclasts (8%), bones (2%). Groundmass: yellow-pale brown, alternation of fine sand lamina (80% quartz, 20% dolomite), and silty clay lamina.	Most components are allochthonous (coming from others rock formations located in the area). Relatively long transport. Fluvio-karstic processes. Absent of diagenesis.
			

See Fig. 2 and Supplementary text and Supplementary Figures 2 to 4 for detailed description and the images of thin sections.

*Rupicapra pyrenaica* than in the case of *Capra pyrenaica* (Supplementary Table 5). Due to the scarcity of the material recovered for this species and because the metric comparison is not definitive, we believe this bone belongs to *cf. Rupicapra pyrenaica*.

### 5.2.2. External Domain

The Entrance sector was virtually completely excavated during the 90s and, therefore, the results described here correspond to the re-study of the paleontological assemblage from previous excavations. The Entrada sector shows a similar pattern of faunal associations between the upper and lower levels which parallels what is observed in the Internal Domain (Table 4). Units LU-E1, LU-E2, and LU-E3 are characterized by the abundance of extant species. The carnivore assemblage is dominated by badgers and foxes with some hyena tooth fragments that were reworked from the underlying units. The ungulate association from the upper levels consists basically of potentially domestic species (ovicaprine, pigs, and

perhaps horses) with some remains of wild species such as red deer (Table 4).

This panorama changes drastically in the lower units (LU-E4/E5), where domestic species are replaced by extinct species in Europe during the Pleistocene (Table 4). The best-represented carnivore species with respect to NISP is a medium-sized felid identified as a leopard by Arribas (1997). Nearly half a hundred remains corresponding to the same individual were analyzed (Supplementary Figure 5). The leopard dentition from Torrejones is small as it is within the lower limit or just outside the range of variation for a relatively large Pleistocene sample from the Iberian Peninsula (Fig. 4 and Supplementary Tables 6 and 7) but closer to the large Italian sample from Equi (Ghezzi and Rook, 2015). It is, however, larger than the Middle Pleistocene (MIS 14) L'Arage individual, at least in terms of the lower teeth (Testu et al., 2011). When compared to a large extant leopard sample, the Torrejones specimen is close to its mean. The Iberian fossil record is very limited in regard to the postcranium, and thus the Torrejones

individual helps to enhance our understanding of the range of variation of this species (Supplementary Table 8). Thus, the new metric data are consistent with the previous taxonomic classification. It is worth mentioning that some elements of this individual's remains were found in anatomical connection at the site (Supplementary Figure 6) (Arribas, 1997).

After the leopard, the best-represented carnivore is the hyena. Two individuals were identified as hyenas, corresponding to a juvenile individual represented by a right hemimandible fragment with definitive P<sub>3</sub> and P<sub>4</sub> (T95-CE-L4-4-1) and another younger individual represented by a right hemimandible fragment with the unerupted M<sub>1</sub> germ (T95-CE-L5-4-26). The metric comparisons of the dental pieces with fossil specimens from the Iberian Pleistocene fossil record and the fossils from Torrejones are entirely compatible with *C. spelaea* (Supplementary Table 3). No postcranial remains have been identified as hyenas in the fossil association. In addition to the crania-dental remains, 12 fragments of fossilized feces have been identified as hyena coprolites (Fig. 3). This assignment is made based on criteria previously described by various authors (Arribas, 1994; Carrión et al., 2001, 2007; Kruuk, 1972; Larkin et al., 2000; Sala et al., 2012) such as: i) their spherical morphology; ii) their size (between 3 and 6 cm) is consistent with the measurements taken at different European Pleistocene sites; iii) the presence of partially digested bone fragments; and iv) their porous and powdery texture with the presence of numerous vesicles in their interior. Other carnivore species have been documented from isolated elements such as some fox and wolf remains.

Horse is the dominant species of ungulate in the assemblage, representing 52% of the ungulate NISP, followed by cervids (33%), large bovids (8.5%), rhinoceroses (3.7%) and, finally, wild boars (2.4%) (Table 4).

Teeth are the most abundant remains among the horses, though limb bones, including humerus, radius, metapodials and phalanxes, are present as well. Both adult and immature individuals have been recognized, including several immature long bones and a phalanx that surely correspond to the same individual, given its similar state of development (Fig. 5). Generally, *E. ferus* and *E. hydruntinus* are differentiated by a combination of metric (i.e., *E. hydruntinus* is smaller than *E. ferus*) and anatomical criteria. However, this differentiation is still complicated and controversial due to the great morphometric variability for different species of Pleistocene horses (Eisenmann and Mashkour, 1999; Maldonado, 1996). In this research we consider only adult individuals, and we took metric criteria into consideration at first and then we studied the anatomical features of the smaller pieces that potentially belonged to *E. hydruntinus*. In the interest of acting conservatively, we classified the fossil remains to a species level (*E. ferus* or *E. hydruntinus*) only in those cases where both criteria (metrics and morphology) concurred. *Equus ferus* is the dominant species in the assemblage, although some elements are evaluated as possible candidates for *E. hydruntinus* due to their smaller dimensions: a lower molariform (T95-CE-M3-4.10), an upper molar (M<sup>1-2</sup>) (T95-CE-M3-4.11) (Fig. 5), a proximal phalanx (T93-E4-46) (Fig. 5), and a proximal fragment of a third metatarsal (T-93-E45). The lower molar T95-CE-M3-4.10 dimensions are in the overlapping zone between *E. ferus* and *E. hydruntinus* (Supplementary Table 9). Its morphology indicates some features that are typical of caballine equids such as: a U-shaped entoflexid, short-length ectoflexids, or a well-developed plicostilid fold. For this reason, we consider this remain an *E. ferus*. The postcranial remains, including the proximal phalanx T93-E4-46 and the metatarsal T-93-E4/5, do not present sufficient definitive metric criteria to be able to classify them reliably (Supplementary Table 10) and, due to the absence of morphological criteria, they are identified as *Equus* sp.

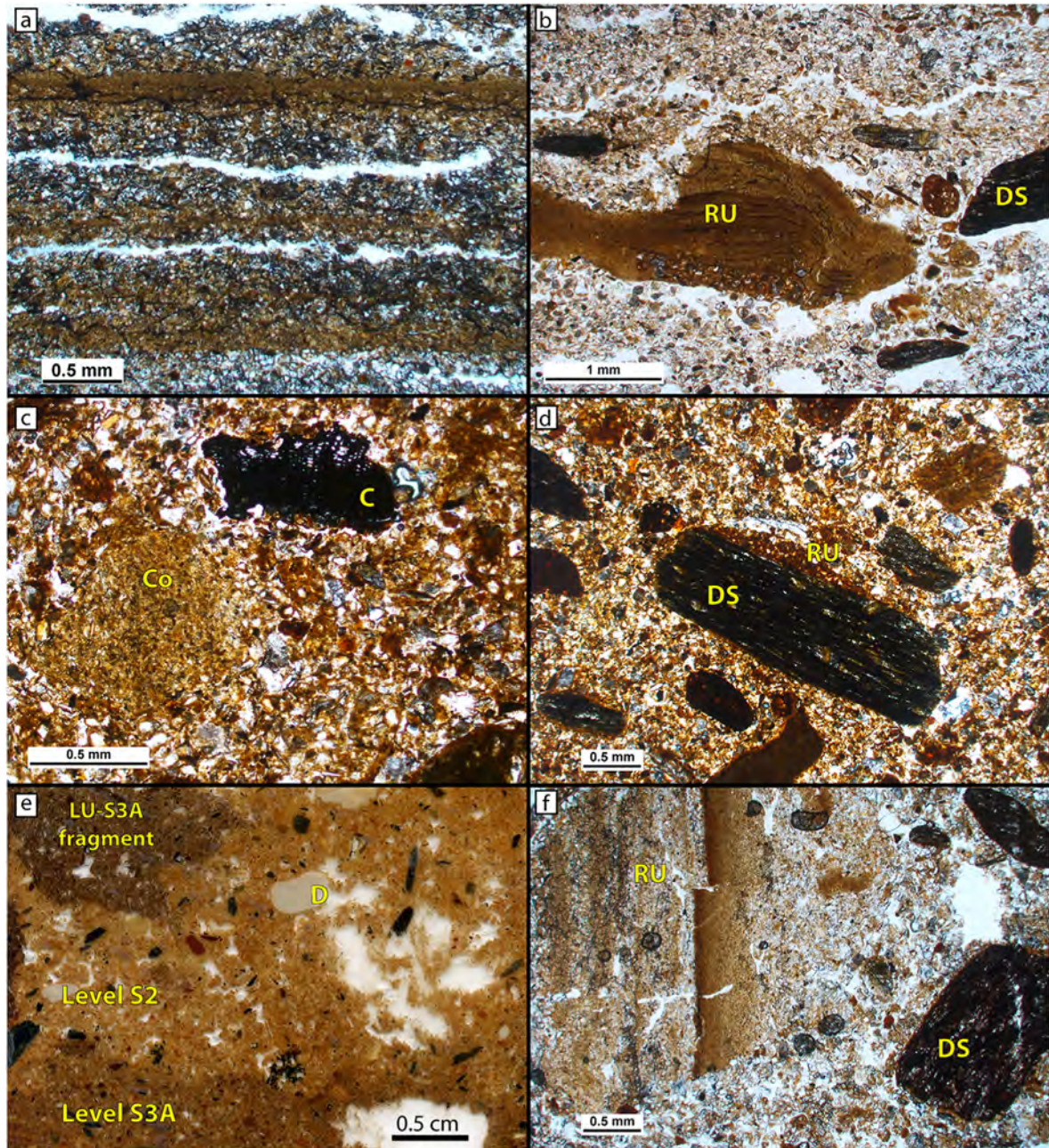
Although the dimensions of the upper molar (M<sup>1-2</sup>) T95-CE-M3-4-11 fall within the overlapping zone between the two equid species (Supplementary Table 10), it contains distinctive features for the stenoian lineage, which are compatible with *Equus hydruntinus*, such as: short protocone with a mesial portion that is shorter than the distal portion, subtriangular shape of the protocone instead of bilobulated, weak longitudinal groove in the protocone, and rudimentary pli caballin. For these reasons we consider this upper molar to be the single specimen out of the entire faunal assemblage that could be identified as *E. hydruntinus*.

Among the Perissodactyls, three fossil remains were identified as belonging to rhinoceros. Two of them preserved anatomical features that are taxonomically useful for determining species (either *Coelodonta antiquitatis* or *Stephanorhinus hemitoechus*) with a great degree of confidence (Fig. 5). The upper third molar (T95-CE-M3-4-1) corresponds to an adult individual (wear stage 5/6 following the patterns proposed by Álvarez-Laó (2007)), displays a triangular shape, absence of middle fossa, and a curved ectometalophe instead of differentiated ectoloph and metaloph typical of the woolly rhino (Fig. 5). These anatomical criteria, in addition to the metric comparison with other Pleistocene samples (Fig. 4 and Supplementary Table 11), place this specimen within the expected range for *Stephanorhinus hemitoechus*. On the other hand, an innominate bone recovered in the LU-4b (T95-CE-L5-4b-1) displays metric and anatomical features compatible with *Stephanorhinus hemitoechus*. The acetabulum dimensions fall within the expected values for the steppe rhinoceros, which are smaller than *C. antiquitatis* (Supplementary Table 11). Furthermore, the acetabular notch is slightly wider, and the acetabular fossa is not evident, in contrast to the marked and deeper acetabular notch present in woolly rhinoceroses (Pandolfi and Tagliacozzo, 2015; Rodríguez-Almagro et al., 2020). The third one, a fragment of a radius T95-CE-L2-3-1, is considered a taxonomically indeterminate rhinoceros (Rhinocerotidae indet.) as its fragmentary condition does not allow for morphological or metrical comparative studies.

After equids, cervids are the most represented family in the ungulate assemblage (Table 4). The small-sized cervids correspond to the expected metrical values for *Capreolus capreolus* (Supplementary Table 12) and represent a minimum of three individuals: two adults, represented by two right lower third molars, and a juvenile individual with deciduous dentition (Fig. 5). Additionally, 15 elements have been identified of a larger-sized cervid, including dental, antler, and postcranial remains, which corresponds to a minimum of two individuals (Fig. 5), one of which is an antler remain (T95-CE-L5-4-7) and is of large dimensions. A metric and morphological study, following Lister (1996), conducted on this cervid's diagnostic elements shows that these fall within the range of variation of red deer (*Cervus elaphus*) and outside that of the fallow deer (*Dama dama*) (Supplementary Table 12).

Large bovids comprise 8.5% of the NISP corresponding to ungulates. The anatomical differences between bovines are limited, and most of the elements preserved in the assemblage do not provide enough reliable diagnostic features to distinguish between *Bos* and *Bison*. There is an exception, the metatarsal III-IV (T95-CE-L4-4b-26), which allows for taxonomic identification. Firstly, the relationship between the antero-posterior and medio-lateral dimensions of the proximal epiphysis falls within the Pleistocene *Bison priscus* range of variation (Fig. 4; Supplementary Table 13). Morphologically, the proximal articular facets for the 2nd/3rd tarsal and cubonavicular are clearly confluent (Fig. 5), suggesting a *Bison*-like morphology following Gee (1993). Thus, for the bovines we assign one remain to *Bison* cf. *priscus* (T95-CE-L4-4b-26), but the rest of the large bovid remains are *Bos/Bison*.

Lastly, in regard to the artiodactyls, wild boar remains comprise



**Fig. 2.** Microphotographs of the Sumidero sedimentary sequence. a) LU-S3B, rhythmic alternation of silty clay and silty sand layers; b) LU-S3B, rip-up clasts and dark slate lithoclast oriented lamina within a silty sand matrix; c) LU-S3A, remains of a coprolite and charcoal fragment; d) LU-S3A, slate fragment with a rip-up clast attached to the upper part; e) Irregular and clear boundary between LU-S3A and LU-S2 and a reworked fragment from LU-S3A within LU-S2; f) LU-S2, rip-up clast preserving the same microfacies as LU-S3B. RU: rip-up clast; DS: dark slate; C: charcoal; Co: coprolite; D: dolostone.

2.4% of the ungulate assemblage (Table 4), and include two dental remains, an incisor, and a molar fragment, which could correspond to a single individual. Unfortunately, the sample is too small to allow for comparative metric studies.

A total of 17.4% of the faunal assemblage is represented by tortoises: mainly isolated plastron and carapace plates, though a fairly complete carapace was found (T95-CE-M2-5-1: Fig. 7). The relatively thick bone plates and marked growth suture lines on the plates lead us to suggest classifying them as *Testudo hermanni*, following the criteria proposed Cheylan (1981) and Bailon (2001). This is compatible with the initial taxonomic proposal by Arribas et al. (1997) and Arribas (1997). Additionally, pursuant to the

fossil record review of the genus *Testudo* in the Iberian Peninsula by Morales-Pérez and Sanchis-Serra (2009), *T. hermanni* was the only species of the genus *Testudo* present in the Iberian Peninsula during the Pleistocene and for most of the Holocene.

### 5.3. Human remains

#### 5.3.1. Anthropological analysis

Torrejones has yielded 108 human remains representing all anatomical regions of the skeleton (Table 5). All these remains have been assigned to *Homo sapiens* (Supplementary Text 2). Radiocarbon dating of three remains has yielded a Chalcolithic age

**Table 3**  
Microvertebrate species identified in the Entrada and Sumidero sectors from Cueva de los Torrejones.

Order	Species	Entrada			Sumidero				
		LU-E1	LU-E2	LU-E4/5	LU-S1	LU-S2	LU-S3	LU-S3A	LU-S3B
<b>Rodentia</b>	Rodentia indet.					X	X		X
	<i>Microtus</i> sp.					X	*		
	<i>Microtus arvalis</i>	X				X	X	X	
	<i>Microtus agrestis</i>					X	X		
	<i>Microtus arvalis-agrestis</i>			*			*		
	<i>Chionomys nivalis</i>			*		X	X*		
	<i>Arvicola scherman</i>					X			
	<i>Terricola</i> sp.	X				X			
	<i>Terricola lusitanicus</i>					X			
	<i>Terricola pyrenaicus</i>					X			
	<i>Terricola duodecimcostatus</i>					X			
	<i>Iberomys cabreræ</i>					X			
	<i>Eliomys quercinus</i>	X				X		X*	X
	<i>Eliomys</i> sp.			*					
	<i>Pitymys</i> sp.							*	
	<i>Apodemus</i> sp.						X	X*	X
	<i>Apodemus sylvaticus</i>						X	X	
	<i>Sciurus vulgaris</i>						X		
	<i>Marmota marmota</i>				X			X	X
	<b>Eulipotyphla</b>	Eulipotyphla indet.						X	
<i>Talpa</i> sp.			X			X			
<i>Crocidura</i> sp.						X			
<i>Erinaceus</i> sp.			X			X	X		X
<b>Lagomorpha</b>	<i>Erinaceus europæus</i>			*			X*		
	Lagomorpha indet.		X		X	X	X	X	X
	<i>Oryctolagus cuniculus</i> ssp.			*			*		
<b>Chiroptera</b>	<i>Lepus</i> sp.						*		
	Chiroptera indet.					X	X*		X
	<i>Myotis</i> sp.						*		
<b>Aves</b>	<i>Myotis myotis</i>						X		
	Aves indet.		X		X	X	X*		X
<b>Anura</b>	Passeriformes indet.			*					
	Anura indet.					X	X*		
	<i>Epidalea calamita</i>						*		
<b>Squamata</b>	<i>Pelobates</i> sp.					X	X	X	
	Lacertidae indet.				X	X	X*	X	
	<i>Timon lepidus</i>			*					
	Serpentes					X	X*	X	

x: species identified during the analysis of new and old material. \*species identified by [Arribas et al. \(1997\)](#).

([Supplementary Table 1](#)). From a stratigraphic and spatial point of view, most of the remains come from the most superficial units throughout the cave. Several refitting bones have allowed us to connect three of the excavation sectors (Entrada, Pasillo, and Sumidero), which have yielded 96.3% of the human assemblage.

This assemblage represents a minimum of five individuals ([Fig. 7](#)): two immature, one adolescent, and two adults ([Table 5](#)). The youngest (<6 years) is represented by the left hemi-arc of a thoracic vertebrae (MUPA-TMJ-293) and a rib (MUPA-TMJ-277). An individual around 8–9 years of age is represented by a left mandibular fragment (Torrejones-2), preserving the dm<sub>2</sub> with visible wear on the buccal cusps, and a M<sub>1</sub> with no evidence of wear, as well as the Torrejones 3 temporal bone ([Fig. 7](#)). An adolescent is represented by a right maxilla (Torrejones-5) preserving the erupted M<sup>1</sup> and a M<sup>2</sup> that is not completely erupted but already in occlusion, the temporal bone T95-S2-1 with no sign of closure of the occipitomastoidal synchondrosis, and an isolated lower premolar (MUPA-TMJ-289). Two adult individuals are represented by both dentition with a large degree of attrition and the presence of other adult postcranial remains (Torrejones 1, 4, T95-S2-1, and MUPA-TMJ-258, among others).

The stature of the individuals represented by the complete long bones of adult individuals was estimated ([Supplementary Table 14](#)). The three different formulae used in the complete 'Torrejones-4' right humerus yielded a result ranging from 165.1 to 166.6 cm. A complete right radius (Torrejones-1) yielded a stature estimation of

around 160 cm. The other complete right radius (MUPA-TMJ-258) yielded a stature estimation ranging between 152.7 and 154.2 cm. In summary, if we assume the presence of only two adults, the tallest would be around 166 cm, and the shortest would be ca. 153 cm, which could correspond to two individuals of different sexes and would be consistent with the stature found in other Chalcolithic populations, such as Abautz ([Utrilla et al., 2013](#)).

It has also been possible to estimate the sex of other elements corresponding to adult individuals. First, the width and mastoid projection values of the late adolescent (or young adult) temporal bone T95-S2-1 ([Fig. 7](#)) which is closer to male values than those of females from a modern human sample of known sex ([Supplementary Table 15](#)). The navicular bone (T93-S3-27) also corresponds to an adult male individual, taking into consideration its developmental stage ([Pablos et al., 2018](#)) and the molecular analysis provided in this study.

The Torrejones assemblage also shows some paleopathological lesions. An I<sub>1</sub> (MUPA-TMJ-272) shows evidence of caries in its neck. Several of the teeth show tartar. A thoracic vertebra (refitted from four different fragments; MUPA-TMJ-5, 8, 10 and 11) shows an abnormal porosity on the left costal facet, as well as ossification of the yellow ligament. T93-S2-62 corresponds to the ankylosis of two lumbar vertebrae, with the presence of osteophytes, Schmorl nodes, and ossification of the anterior ligament ([Fig. 7](#)). The head of the complete right humerus (Torrejones-4) shows a slight osteophytic rim. Finally, the distal fibular fragment MUPA-TMJ-288

**Table 4**  
Quantification of the macrovertebrate assemblage from the Cueva de los Torrejones site.

Order	Species	Internal Domain						External Domain				Total
		Sumidero			Tejones			Entrada				
		S1	S2	S3	T1	T2	T3	E1	E2	E3	E4-5	
<b>Primates</b>	<i>Homo sapiens</i>	39 (-)	17 (-)	2 (-)	1 (-)	1 (-)	0 (-)	35 (-)	2 (-)	0 (-)	3 (-)	<b>100</b>
<b>Carnivora</b>	<i>Crocuta spelaea</i>	1 (1)	1 (1)	6 (1)	1 (1)	0 (0)	0 (0)	1 (1)	4 (1)	0 (0)	11 (2)	<b>25</b>
	<i>Panthera pardus</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	46 (1)	<b>46</b>
	<i>Lynx cf. pardinus</i>	3 (1)	0 (0)	0 (0)	0 (0)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	<b>4</b>
	<i>Felis sp.</i>	4 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	<b>4</b>
	<i>Ursus sp.</i>	0 (0)	0 (0)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)	<b>2</b>
	<i>Canis lupus</i>	0 (0)	0 (0)	0 (0)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)	<b>2</b>
	<i>Canis sp.</i>	2 (1)	0 (0)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	<b>3</b>
	<i>Vulpes vulpes</i>	5 (1)	5 (2)	6 (2)	3 (1)	2 (1)	0 (0)	2 (1)	0 (0)	1 (1)	4 (1)	<b>28</b>
	<i>Meles meles</i>	24 (3)	34 (3)	5 (2)	5 (2)	10 (2)	1 (-)	10 (2)	1 (1)	1 (1)	0 (0)	<b>91</b>
	Carnivora indet.	13 (-)	2 (-)	2 (-)	3 (-)	5 (-)	0 (0)	9 (-)	3 (-)	1 (-)	6 (-)	<b>44</b>
	Coprolites	5 (-)	1 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	1 (-)	1 (-)	12 (-)	<b>20</b>
<b>Artiodactyla</b>	<i>Cervus elaphus</i>	0 (0)	0 (0)	7 (2)	1 (1)	1 (1)	0 (0)	0 (0)	1 (1)	3 (1)	15 (2)	<b>28</b>
	<i>Capreolus capreolus</i>	3 (1)	0 (0)	0 (0)	0 (0)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	12 (3)	<b>16</b>
	<i>Bos/Bison</i>	2 (-)	1 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	0 (-)	6 (-)	<b>9</b>
	<i>Bison cf. priscus</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)	<b>1</b>
	<i>Ovis/Capra</i>	8 (2)	2 (1)	0 (0)	5 (1)	3 (2)	0 (0)	31 (6)	0 (0)	0 (0)	0 (0)	<b>18</b>
	<i>cf. Rupicapra pyrenaica</i>	0 (0)	0 (0)	1 (1)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	<b>1</b>
	<i>Sus scrofa</i>	3 (1)	3 (2)	1 (1)	0 (0)	1 (1)	0 (0)	8 (2)	0 (0)	0 (0)	2 (1)	<b>18</b>
<b>Perissodactyla</b>	<i>Equus ferus/caballus</i>	1 (1)	0 (0)	17 (2)	0 (0)	0 (0)	0 (0)	6 (1)	6 (2)	0 (0)	15 (3)	<b>45</b>
	<i>Equus sp.</i>	5 (-)	9 (-)	0 (-)	0 (-)	2 (-)	0 (-)	0 (-)	0 (-)	0 (-)	28 (-)	<b>44</b>
	<i>Equus hydruntinus</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)	<b>1</b>
	<i>Stephanorhinus hemitoechus</i>	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	2 (1)	<b>2</b>
	Rhinocerotidae indet.	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (-)	0 (-)	<b>1</b>
<b>Testudines</b>	<i>Testudo hermanni</i>	0 (0)	2 (1)	1 (0)	0 (0)	0 (0)	0 (0)	0 (0)	1 (1)	1 (1)	40 (1)	<b>45</b>
<b>Indet.</b>	Ungulate indet.	4 (-)	22 (-)	9 (-)	1 (-)	2 (-)	0 (0)	23 (-)	13 (-)	4 (-)	67 (-)	<b>145</b>
	Indeterminate	46 (-)	18 (-)	43 (-)	2 (-)	7 (-)	2 (-)	27 (-)	28 (-)	13 (-)	107 (-)	<b>293</b>
<b>Total</b>		<b>168</b>	<b>117</b>	<b>102</b>	<b>23</b>	<b>36</b>	<b>3</b>	<b>121</b>	<b>60</b>	<b>26</b>	<b>380</b>	<b>1036</b>

Number of identified specimens (NISP). In brackets: minimum number of individuals (MNI) of the identified species.

shows periostitis on the internal surface of the bone and abnormal bone growth on the anterior part of the metaphysis.

### 5.3.2. Paleogenetic analysis

The human navicular bone from Torrejones (T93-S3-27) was sampled for ancient DNA analyses and radiocarbon dating. DNA was extracted from a 38 mg aliquot of bone powder, converted into double stranded libraries, and shotgun sequenced. Sequences were aligned to the human reference genome resulting in 1.25% of human DNA with an average fragment length of 61.5 bp and a deamination level of 6.4% at the 5' terminal position. The latter two values confirmed the presence of ancient DNA preserved in the Torrejones genetic library. We thus estimated the genetic sex of the individual as male, as indicated by an Rx value of  $0.49 \pm 0.01$ , which corresponds to a XY karyotype. Moreover, we captured the complete mitochondrial DNA (mtDNA) followed by sequencing. Sequences were then aligned against the mtDNA reference sequence which in turn resulted in 1.9% of mapped fragments with 49.4-fold mtDNA average coverage. The complete mtDNA sequence of the individual was reconstructed and mtDNA contamination was estimated to be low ( $4 \pm 1\%$ ). Finally, the generated mtDNA sequence was assigned to mtDNA haplogroup K1a2b. Haplogroup K is thought to have originated in the Near East and reached Europe through the Neolithic expansion (Brandt et al., 2013). The specific haplogroup found in the Torrejones navicular was already reported for other Chalcolithic individuals from Spain (Olalde et al., 2019; Valdiosera et al., 2018). Therefore, the obtained mtDNA haplogroups are consistent with the radiocarbon dating of the specimens to ~5000 cal BP.

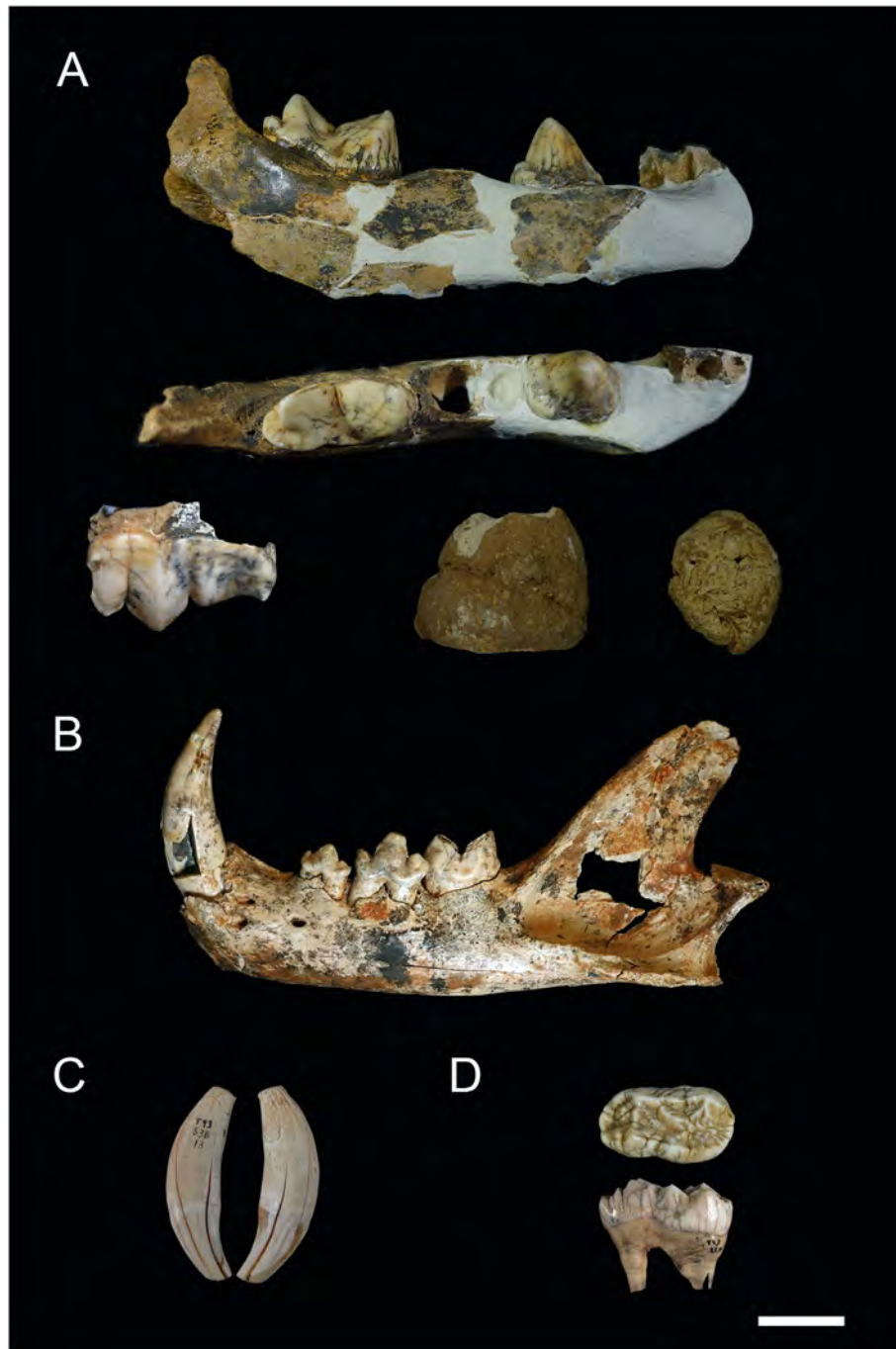
## 6. Taphonomic and zooarchaeological analyses

### 6.1. Human remains

Most of the human remains were recovered from the upper units (Table 4), scattered along the surface of the cave with no spatial association between them. Some refitted bones from different units and sectors were documented, corresponding to LU-S1 + LU-S2, LU-S1 + LU-E1 and LU-E1 + LU-P2. Their discovery distributed throughout the different sectors of the cave can be explained by intense bioturbation by small mammals (badgers, foxes and lagomorphs), thus scattering the remains. For this reason, the sample of human remains was considered a single set, regardless of the area (sector and LU) where they were recovered. Nevertheless, special attention was paid to those remains from the lower units (LU-S3 and LU-E4) for the purpose of determining whether their taphonomic alterations are indicative of different deposition contexts.

The human remains are generally well preserved, evidenced by the fact that 28% are complete and have no alterations on the bone surfaces. No cut marks, percussion marks, nor any other traces of butchering have been documented among the anthropological remains. Three burned bones have been identified (Table 6). Despite the low percentage of burned bones (3.1%), high stages of combustion (stages 1, 3 and 4) were observed, according to Stiner et al. (1995) (Supplementary Figure 7). Calcinations only occur in bones when they have been directly exposed to fire (Stiner et al., 1995). While the first two cases could have been carbonized postmortem, in the case of the humerus, the data indicate that this remain was directly exposed to fire.

Regarding biological alterations, tooth marks have been documented for three remains, including tooth pits, punctures, and/or scores. Therefore, we cannot rule out sporadic scavenging by small



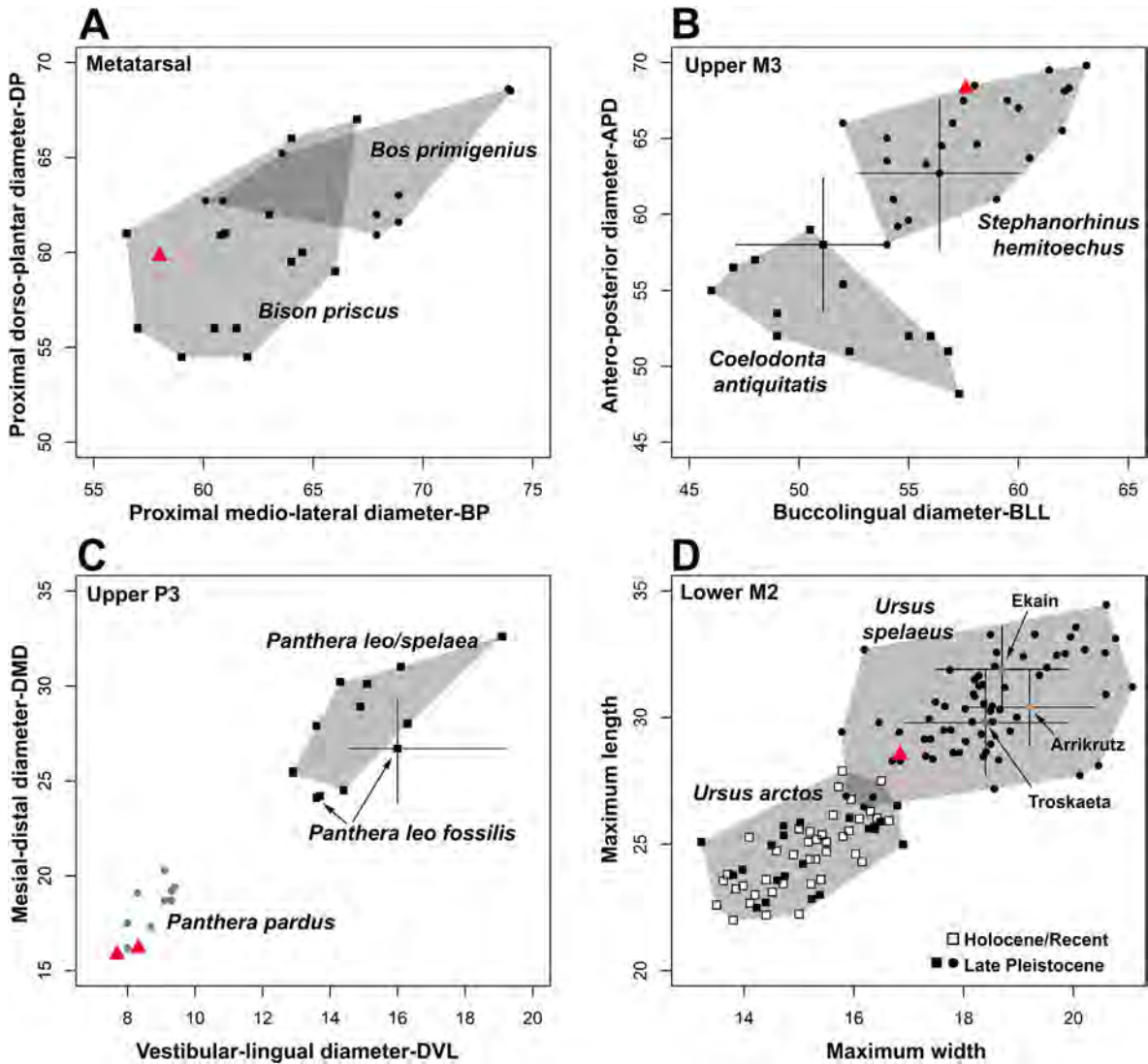
**Fig. 3.** Carnivore remains from the Torrejones site. A) Hyena (*C. spelaea*) including: a left hemimandible fragment with P<sub>3</sub> and M<sub>1</sub> from the Entrada LU-E2 (T93-E2-32) in lingual and occlusal views, fragment of an upper carnassial P<sub>4</sub> (T93-S3-57) from Sumidero (LU-S3) in labial view, and coprolites from LU-E4/5. B) Left hemimandible of a leopard (*P. pardus*) which preserves canine, P<sub>3</sub> to M<sub>1</sub> (T95-CE-L3-4-1) from Entrada LU-E4 in labial view. C) Left upper canine of *C. lupus* from Sumidero LU-S3 (T93-S3B-13) in medial and distal views. D) Right second lower molar of *Ursus cf. spelaeus* (T93-S3-19) from Sumidero LU-S3 in occlusal and lingual views. Scale bar 2 cm.

carnivores. Although rodent activity has not been documented in the human remains sample, the presence of vermiculations produced by plant roots on a hand phalanx has been recognized.

In terms of non-biological alterations, the absence of signs of weathering on the bone remains (stage 0 according to Behrensmeier, 1978) would indicate that they have not been exposed to atmospheric agents. Almost 42% of the human remains show abundant striations on the bone surfaces. Their microscopic study reveals the following features: broad groove shape, sinuous trajectories, the presence of numerous superimposed striae on the

main grooves, scarce micro-striation which, when it does appear, is discontinuously at the base of the main groove (Supplementary Figure 8). These features are to be expected for trampling marks (scratches caused by sediment abrasion on bone surfaces) (Domínguez-Rodrigo et al., 2009). This indicates that the bones were subject to moderate transport along the surface of the cave probably caused by intense surface bioturbation. It should be noted here that most of the human bone collection was recovered directly on the surface or from superficial units. This bioturbation was probably caused by humans and small mammals, such as badgers,





**Fig. 4.** Bivariate comparison (in mm) for different taxa from Torrejones (red triangle): A) Proximal dorso-plantar diameter (DP) and proximal medio-lateral diameter (BP) of the metatarsal T95-CE-L4-4b-26 from Torrejones compared *B. priscus* and *B. primigenius* samples (see [Supplementary Table 13](#) and [Appendix 2](#) for sample composition); B) Antero-posterior diameter (APD) and buccolingual diameter (BLL) of the rhinoceros M<sup>3</sup> (T95-CE-M3-4-1) from Torrejones compared to *S. hemitoechus* and *C. antiquitatis* samples ([Supplementary Table 11](#) and [Appendix 4](#)); C) Upper P<sup>3</sup> meso-distal diameter (DMD) and vestibular-lingual diameter (DVL) of the leopard from Torrejones (T95-CE-L3-4b-1 and T95-CE-L3-4b-2) compared to other Iberian *P. pardus* ([Supplementary Table 7](#) and [Appendix 1](#)), *P. leo spelaeus* and *P. leo fossilis* ([Gómez-Olivencia et al., 2015](#)) and references therein. D) Length (L) and width (W) of a Torrejones bear M<sub>2</sub> (T93-S3-19) compared to Iberian specimens of *U. spelaeus* and *U. arctos* ([Supplementary Table 4](#) and [Appendix 1](#)). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

which wandered around the cavity during the Holocene ([Carrión et al., 2005](#)). In addition, and as previously mentioned, refitted human bones from separated sectors confirm that the bones were subjected to certain transport within the cavity and, therefore, their abrasion against the sedimentary particles is the most likely cause. Lastly, scattered circular-shaped stains of manganese oxide dendrites have been documented on most of the human bones, with a presence on more than 83% of the collection ([Table 6](#)).

In relation to fracturing, the human remains from the assemblage mostly display transversal outlines, jagged surfaces with right angles of fracture planes, and complete circumferences of the long bone diaphysis. All these features are to be expected for dry bone (postmortem) fractures ([Sala et al., 2015](#); [Villa and Mahieu, 1991](#)).

Finally, the taphonomy is remarkably consistent between the Chalcolithic human remains recovered from the upper units (LU-S1 and LU-S2 in Sumidero and LU-E1 and LU-E2 in the Entrada sector) and those recovered from the lower units (LU-S3 and LU-E4), which

are ascribed to the Pleistocene units, including the navicular bone from LU-S3. The results of this comparative study conclude that, according to criteria such as mineralization, bone surface modifications, manganese oxide staining, and fracturing patterns, the bones recovered from the lower units are taphonomically indistinguishable from the bones recovered from the Chalcolithic units.

## 6.2. Faunal remains

The taphonomic analysis of the faunal assemblage focused on the Sumidero and Entrada sectors since they contained the majority of the material recovered. Regarding Sumidero, we considered all of the materials from the lithostratigraphic sequence, including both the new and previous excavations. The Chalcolithic units (LU-S1 and LU-S2) were analyzed separately from the lower unit (LU-S3). Regarding Entrada, we considered only the materials from the unaltered units excavated during the previous field seasons,



**Fig. 5.** Selected ungulate remains from Torrejones mentioned in the text: A) Proximal fragment of a metatarsal (T95-CE-L4-4b-26) of *Bison* cf. *pricus* from LU-E4. B) Right innominate (T95-CE-L5-4b-1) and upper third molar (T95-CE-M3-4-1) of *S. hemitoechus* from LU-E4. D) Upper molars (left to right:  $M^{1/2}$  T95-CE-L5-4-3 and  $M^3$  T95-CE-L5-4-25) and antler fragment (T95-CE-L4-4b-15 + 16) of *C. elaphus* from LU-E4. C) Lower dentition of *C. capreolus* from LU-E4: lower third molars on the right side (left to right: T95-CE-N2-4-1 and T95-CE-L34-4-13) and right hemimandible with  $D_2$  (T95CE-M3-4-22). E) Equid remains from LU-E4 including an upper molar  $M^{1-2}$  (T95-CE-M3-4-11) of *E. hydruntinus* and a proximal phalanx of *Equus* sp. (T93-E4-46). Scale bars 2 cm.

corresponding to the lower units (LU-E4/5). The results of the taphonomic analysis are detailed in [Table 6](#).

The taphonomic analysis of Sumidero reveals two different sets corresponding to the upper units (LU-S1 and LU-S2) and the lower unit (LU-S3). In the upper units, badger and fox remains are generally well preserved without fractures or bone surface modification, thus indicating that they were not introduced into the cavity by any external agent (carnivores, humans, or geological

agents) but rather correspond to dead animals inside the cave since the Chalcolithic. Besides carnivores, ungulate taxa were analyzed in Sumidero LU-S1 and LU-S2, mostly corresponding to undetermined or potentially domestic species. In these taxa we observe that both the carnivore induced modifications and the anthropogenic alterations are very scarce. There is just one case in which conspicuous tooth marks were identified (in the equid metapodial fragment MUPA-TMJ-51), though three remains show evidence of dissolution

**Table 5**

Anatomical representation of the human fossil remains, including the number of identified specimens (NISP), minimum number of elements (MNE), and minimum number of individuals (MNI), and the criterium used for the latter.

	NR-NISP	MNE	MNI	MNI-Criterium	Immature (<6)	Immature (8-9)	Adolescent (~16)	Adult
Cranial bones	12	7	4	2 right maxillae and age-at-death incompatibilities (juvenile parietal and temporal bones)		1	1	2
Mandibles	2	1	1	Age-at-death incompatibilities		1		
Isolated dentition	10	10	3	2 adult lower i1s (with wear) and a lower P <sub>3</sub> with no wear			1?	2
Cervical vertebrae	4	4	2	Vertebral body			1	1
Thoracic vertebrae	12	5	3	Neural arc; age-at-death incompatibilities	1			2
Lumbar vertebrae	3	2	2	Age-at-death incompatibilities			1	1
Ribs	26	12	3	Age-at-death incompatibilities	1		1	1
Clavicles	1	1	1				1	
Scapulae	4	2	1	Acromion				1
Humeri	4	4	3	Age-at-death incompatibilities and repetition of the shaft from the right side	1?			2
Radii	4	3	2	Two complete right radius				2
Hand bones	13	13	2	Second right metacarpal				2
Pelvic bones	2	2	1					1?
Fibulae	3	2	1					1
Foot bones	8	8	3	Age-at-death incompatibilities; 2 right navicular bones			1	2
<b>Total</b>	<b>108</b>				<b>1</b>	<b>1</b>	<b>1</b>	<b>2</b>

**Table 6**

Taphonomic trait frequencies for the main assemblages from Cueva de los Torrejones.

	Human remains <sup>a</sup>	Sumidero		Entrada	
		LU-S1/S2	LU-S3	LU-E3/4	
Tooth marks	Pits	1 (1%)	0	2 (0.7%)	7 (2.5%)
	Punctures	2 (2.1%)	0	0	3 (1.1%)
	Scores	1 (1%)	0	3 (1.0%)	8 (2.9%)
	Furrowing	0	1 (0.9%)	2 (0.7%)	10 (3.6%)
Anthropic modifications	Digested bones	0	3 (2.6%)	26 (8.5%)	24 (8.6%)
	Cut marks	0	3 (2.6%)	1 (0.3%)	0
	Burned bones	3 (3.1%)	3 (2.6%)	3 (1.0%)	0
Others	Trampling	40 (41.2%)	35 (29.9%)	28 (9.2%)	20 (7.1%)
	Weathering	0	0	0	0
	Manganese oxides staining	80 (82.5%)	113 (96.6%)	304 (99.3%)	252 (90.0%)
	Plant roots	1 (1%)	0	0	0
Fractures	Rodent gnawing	0	4 (3.4%)	2 (0.7%)	3 (1.1%)
	Transversal outline	19 (19.6%)	22 (18.8%)	18 (5.9%)	30 (10.7%)
	Oblique outline	14 (14.4%)	30 (25.6%)	61 (19.9%)	57 (20.4%)
	Right angles	17 (17.5%)	48 (41%)	61 (19.9%)	79 (28.2%)
	Oblique angles	6 (6.2%)	24 (20.5%)	56 (18.3%)	59 (21.1%)
	Smooth surface	2 (2.1%)	21 (17.9%)	54 (17.6%)	50 (17.9%)
	Jagged surface	45 (46.4%)	52 (44.4%)	59 (19.3%)	76 (27.1%)
	Complete circumference <sup>b</sup>	21 (21.6%)	7 (6.0%)	64 (20.9%)	14 (5.0%)
	1/2 circumference <sup>b</sup>	3 (3.1%)	1 (0.9%)	1 (0.3%)	3 (1.1%)
	<1/2 circumference <sup>b</sup>	0	24 (20.5%)	64 (20.9%)	45 (16.1%)

<sup>a</sup> Human remains are considered as a single set regardless of the Sector/unit (see text).

<sup>b</sup> Long bones only.

by gastric acids. Regarding anthropic modifications, two bone remains display cut marks (one chop mark and one slicing mark). The rest of the bones with evidence of anthropic manipulation correspond to alteration by fire (NR = 3). The fracturing of the bones in these superficial units is characterized by right-angle edges and jagged surfaces and, therefore, are interpreted as dry bone (post-mortem) fractures (Villa and Mahieu, 1991) in most of the documented cases.

The bone surface modification pattern changes in Sumidero's lower units (LU-S3) with respect to the Holocene units. The anthropogenic activity is also scarce, but we observe an increase in the frequency of modifications produced by carnivores, especially with regard to modification by gastric acids. Although tooth marks

have only been documented for six bone elements (1.9% of the LU-S3 sample), 26 bones show evidence of modification by gastric acids (8.5%). Trampling marks are relatively abundant (9.7% of the sample). Only one remain displays clear cut marks (0.3%) and three remains show evidence of burning. This leads us to conclude that, taphonomically, a mixture of bone assemblages in this unit cannot be ruled out.

Regarding the lower units from the Entrada sector (LU-E4/5), 17.1% of the bone assemblage analyzed displays some kind of carnivore modification. Evidence of dissolution by gastric acids is the most documented alteration (8.6%), followed by furrowing, scores, pits, and punctures. Tooth-pit dimensions on cortical bone (Supplementary Table 16) are compatible with hyena activity when

compared with central Iberian Pleistocene hyena den assemblages, such as Portalón del Tejadilla ( $p = 0.67$ ), Zaramora and Búho caves ( $p = 0.93$ ), or the Cueva del Camino site ( $p = 0.97$ ), and compared with the living hyenas documented in experimental taphonomic analyses ( $p = 0.07$ ). On the other hand, differences in tooth-mark dimensions are statistically different ( $p < 0.05$ ) when compared to larger carnivores such as bears or lions.

On the other hand, the fracture patterns display a high percentage of oblique fractures together with smooth surfaces and oblique fracture angles (Table 6). These attributes are to be expected for biostratigraphic (perimortem) breakage. Nevertheless, the presence of right angles, jagged surfaces, and the mixture of these attributes also indicates certain postmortem (dry-bone) fracturing of the sample. Moreover, other post-depositional modifications are present, including trampling marks (7.1%) and rodent gnawing (1.1%).

Taphonomically, and contrary to what was observed in the Sumidero sector, we can affirm that the lower units of the Entrance constitute practically unaltered deposits given the following criteria: i) homogeneity in the observed taphonomic characteristics (mineralization, bone surface modifications, manganese oxide staining, and fracturing patterns) in most of the recovered macrofaunal remains; ii) the preservation of a leopard in anatomical connection (Supplementary Figure 6) suggests that there has been no major postdepositional alterations; iii) The few signs of burrows (small inclusions of LU-E2 in LU-E3 that could reach the top of LU-E4) were perfectly localized and visible as shown in the Supplementary Figure 6. In consequence, although the burrowing animals could have slightly modified the upper part of LU-E4, incorporating some isolated remains from more recent units, there is no sign of a generalized bioturbation of the LU-E4 and LU-E5 original deposits. Therefore, we have no evidence to rule out that the faunal evidence correspond to the same chronological period.

The new analysis of the taphonomic traits of the Torrejones assemblage includes the detailed evaluation of the cut marks on the leopard and the tortoise described by Arribas et al. (1997) and Díez Fernández-Lomana et al. (1998).

### 6.2.1. Tortoise

In the case of the tortoise, we observed three clusters of grooves on its surface: two groups on the ventral side of the plastron and one on the dorsal side of the carapace. The first group is located on the left hypoplastron and epiplastron on its ventral view (Fig. 6). This group includes the concentration of the largest number of linear marks (at least 28), which are distributed into three subgroups that can be sequenced in time by overlapping: one subgroup of nine oblique and parallel marks, a second subgroup of 12 longitudinal and parallel marks, and a final subgroup of two transversal marks that are parallel to each other (Fig. 6). The second group presents five sub-parallel linear marks on the humeral-axillary incision on the ventral surface (Fig. 6). The third group shows six marks in two subgroups (two and four parallel marks) on the dorsal view of a sixth right peripheral plaque (Fig. 6).

The linear marks generally exhibit a straight but somewhat sinuous trajectory (Fig. 6.3). In section they are deep and present V-sections, with the occasional presence of internal micro-striations and abundant flaking on the shoulders. There are no micro-striations on the surface between the grooves, nor polished surfaces. The marks show a different color as opposed to the natural patina of the bone, always lighter though more visible in the areas where varnish was not applied for curation purposes (Fig. 6.1). Several grooves show cortical lifts in the form of large flakes in different parts along the marks (Fig. 6.1). In several cases, the marks overlap manganese dendrites and dissolution domes, thus erasing

these modifications. No signs of burning or percussion marks were observed (Fig. 6). The only grooves observed on the interior surface of the shell were of anatomical origin.

### 6.2.2. Leopard

Observation of the leopard remains has allowed us to locate three groups of marks on the neurocranium (Fig. 8). No other element shows linear marks. The first group is on the right temporal and parietal. This group shows at least 29 marks clustered in the area of the temporal fossa, generally oblique and longitudinal in orientation, with different marks overlapping in the group, which are somewhat chaotic. The second "group" is located on the left tympanic bulla. It is an isolated groove with a sinuous trajectory. The last group is on the occipital, on the right occipital condyle where two parallel sinuous marks are located. All the grooves observed on the leopard remains are similar in trajectory (sinuous), morphology (slightly U-shaped), and depth (shallow). Grooves cross and remove post-depositional taphonomic modifications. The most striking is the removal of a fine concretion of carbonated clay on the bone surface exposing a lighter color (Figs. 8.1–2). They also overlap manganese dendrites and small fissures (Fig. 8.3), providing evidence that all these grooves are subsequent to post-depositional modifications. In addition, the marks are shallow and display a rounded bottom (Fig. 8.3), they do not have any conspicuous internal or external micro-striations but they are abundant at higher magnifications.

## 7. Material culture

### 7.1. Lithics

The lithic assemblage from LU-S1 is composed of 39 items, 34 of which have been classified as knapping products. The remaining five are fragmented cobbles, perhaps brought into the cave by humans, but bearing no hint of anthropogenic modifications. 23 products (67.6%) are complete, while 11 (32.4%) present fractures. Surface alterations are scarce: no rounding, dehydration, or patinas have been recorded. Pseudo-retouches are only marginally found on some quartz pieces, and thermal alterations (color change and internal cracking interpreted as the result of accidental fire exposure) are found on two flint artifacts. Quartz and flint are the most common rocks, followed by quartzite and rock crystal. Raw blanks are the most represented technological category, followed by core maintenance by-products (mainly *débordant* or lateral core edge flakes), retouched tools, chunks and, lastly, cortical and preparation products (Table 7). No cores or natural blocks have been recorded. Among the retouched artifacts, two were produced on laminar blanks, two on elongated flakes, and one on a flake fragment.

According to these data, the exploitation stage (phase II) is the most represented (70.6%), followed by the consumption and abandonment stage (phase III) (14.7%), and the initialization stage (phase I) (5.9%). Retouched artifacts include a denticulated backed blade (Fig. 9.2), a bec/denticulate on a blade fragment (Fig. 9.4), an atypical endscraper produced on the platform of a laminar flake (Fig. 9.3), a denticulate on a laminar flake, and a flake with inverse retouch.

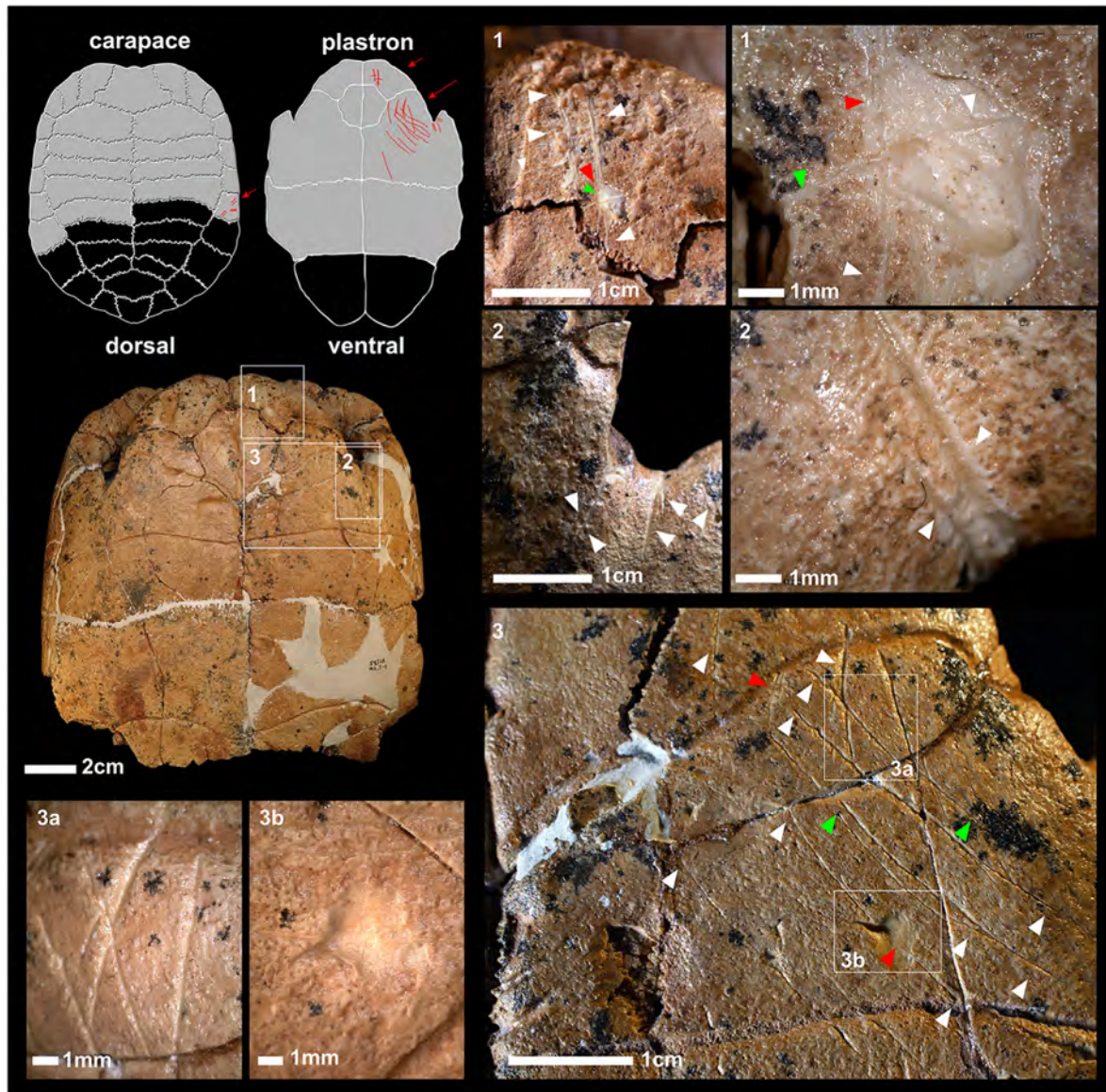
Although the studied assemblage is very scarce, the obtained results strongly point to a largely fragmented operational sequence, showing that lithic products were brought into the cave after the initial preparation and first knapping of cores were performed elsewhere. It is noteworthy that all the retouched artifacts were produced on flint, thus showing a clear preference for this rock when producing curated tools. Quartz and quartzite blanks could have been used as unretouched tools.



**Fig. 6.** Selected human remains from Torrejones mentioned in the text: A) Elements of an immature individual around 8–9 years of age represented by: a left temporal bone (Torrejones 3) and a left mandibular fragment with  $dm_2$  and  $M_1$  (Torrejones-2). B) Elements of an adolescent individual represented by: Right maxilla with  $M^1$  and  $M^2$  (Torrejones-5) and a right temporal bone T95-S2-1 of a male individual. All the postcranial elements represented in the figure are compatible with adult individuals: C) Torrejones-4 right humerus belonging to an adult (likely male) individual. D) Right radius (Torrejones-1) of an adult individual. E) Right radius (MUPA-TMJ-258) of an adult (likely female). F) Distal part of a right fourth metacarpal of an adult individual (T94-CT-S1). G) Ankylosis of two lumbar vertebrae T93-S2-62 in ventral and dorsal views. Scale bars 2 cm.

Exacerbating the already scarce assemblage, typological data do not enable us to reach a conclusion regarding a chrono-cultural assignment for the lithics of LU-S1. Nonetheless, technical attributes recorded for the piece shown in Fig. 9.2, including its strongly parallel ridges and overall thinness, show that this blade was produced using the pressure technique, thus indicating a Holocene age, as this technique has not been documented in the European Paleolithic record (Desrosiers, 2012). Keeping in mind both the

presence of pottery in this level and the radiocarbon dates that were obtained for the upper sequence of Sumidero, these traits suggest a Chalcolithic attribution for the LU-S1 lithic assemblage, thus confirming a previous interpretation by Arribas et al. (1995, 1997). This is also reinforced by the absence of any technological or typological feature typical of the Middle or Upper Paleolithic technological strategies. Excavation of LU-S2 has revealed only four knapping products, to which we have added five more pieces from



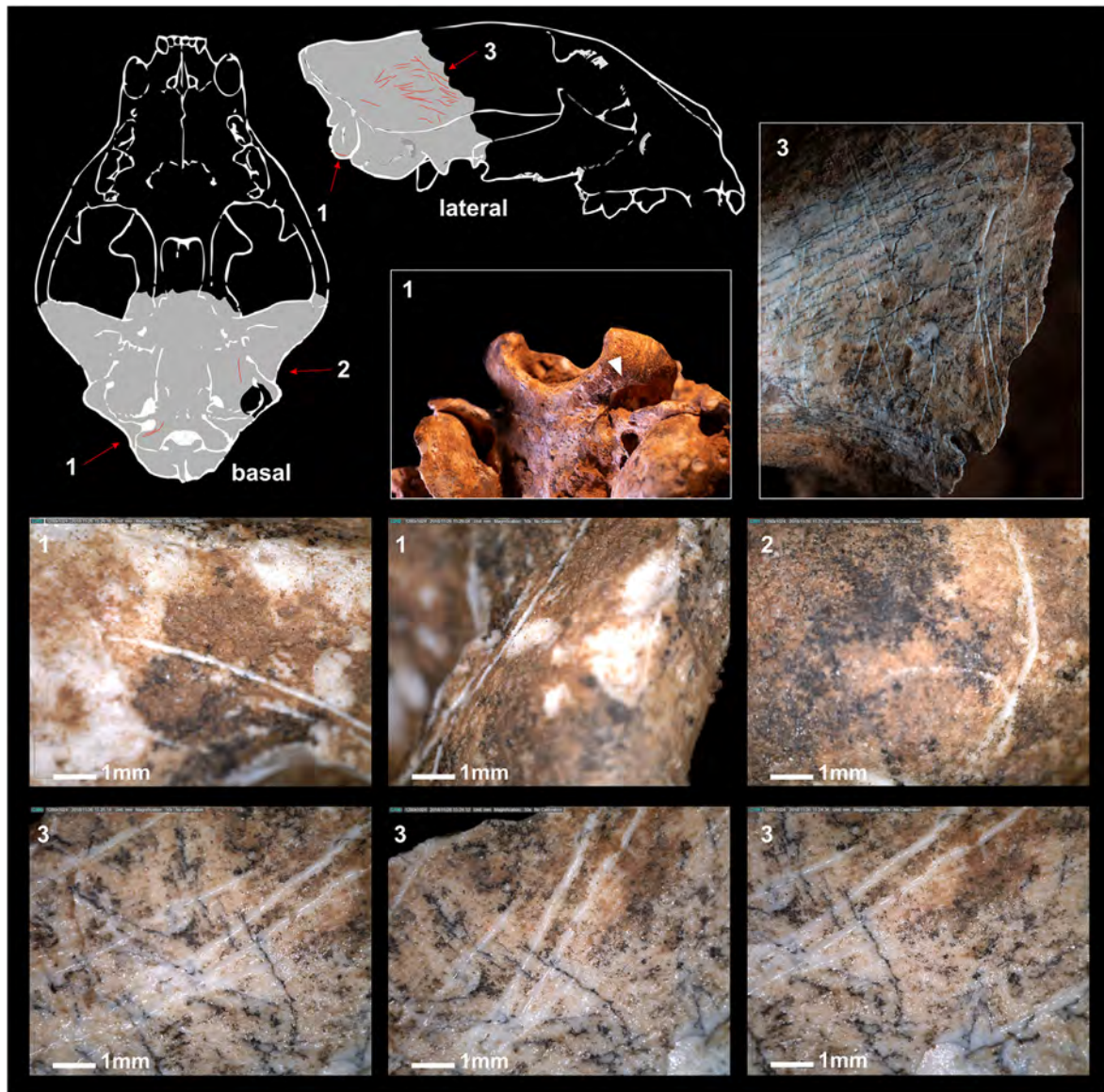
**Fig. 7.** *Testudo hermanni* carapace (T95-CE-M2-5-1) showing the preserved area (grey), the location (red lines), and detailed images of the linear marks (white arrows) from the plastron described in the text. Red arrows point to the cortical flakes associated with the groove trajectories. Green arrows point to the overlapping of grooves with manganese dendrites. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

the previous excavation. Although there are no clear technological traits allowing for a chrono-cultural assignment of this assemblage, the presence of three pottery sherds and the direct dating of the hominin remains suggest a Late Prehistory chronology for the entire assemblage.

All lithic products from the Entrada and Pasillo sectors came from the excavations conducted by Arribas and colleagues. Seven lithic artifacts from Entrada LU-E4 were studied, among which they defined two flakes obtained 'from centripetal cores', a 'point with partial retouch on elongated flint Levallois flake' and "a quartzite point with abrupt retouch" (Diez Fernández-Lomana et al., 1998: 67; see also Arribas et al., 1997: 60). Supported by the faunal assemblages from LU-E4 and LU-E5, which they assigned to the Late Pleistocene, they proposed, as a working hypothesis, that lithics from LU-E4 belonged to the end of the Middle Paleolithic (Diez Fernández-Lomana et al., 1998: 67; Arribas et al., 1997: 60). Unfortunately, none of these artifacts were available to us, given that their location is currently unknown. Since no drawings or photos of

these pieces were published, we cannot support or refute this hypothesis. Furthermore, the lithic artifacts from this LU that we were able to directly analyze were scarce and do not allow for proper chrono-cultural assignments. Among them, a pointed laminar flake on flint (Fig. 9.5) and a quartzite flake obtained by centripetal core reduction (Fig. 9.6) could point to Middle Paleolithic technological strategies but also to other chrono-cultural contexts. All things considered, our view is that a Middle Paleolithic assignment for LU-E4 is indeed possible, but no final conclusions should be drawn in this regard. In fact, the possibility that lithics found at this LU belong to the same Neolithic/Chalcolithic context as proposed for most of the archaeological assemblages recorded in the cave cannot be ruled out.

In LU-E3 we recorded a small, thin blade with a straight central ridge (Fig. 9.7). Although this artifact's platform is broken, and thus percussion technique is difficult to assess, it is likely that this blade matches the chrono-cultural context for Sumidero LU-S1 and LU-S2, as is also suggested by the presence of domestic faunal



**Fig. 8.** *Panthera pardus* neurocranium fragment (T95-CE-L3-4b-3) showing the preserved area (grey), the location (red lines), and detailed images of the linear marks (white arrows) described in the text. 1) Grooves on the right occipital condyle. 2) Grooves on the left tympanic bulla. 3) Grooves on the right temporal. Note the lighter color of the grooves in comparison with the bone surface and how the grooves cross post-depositional modifications such as: concretion patches, manganese dendrites, and small fissures of the bone. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

remains in this unit.

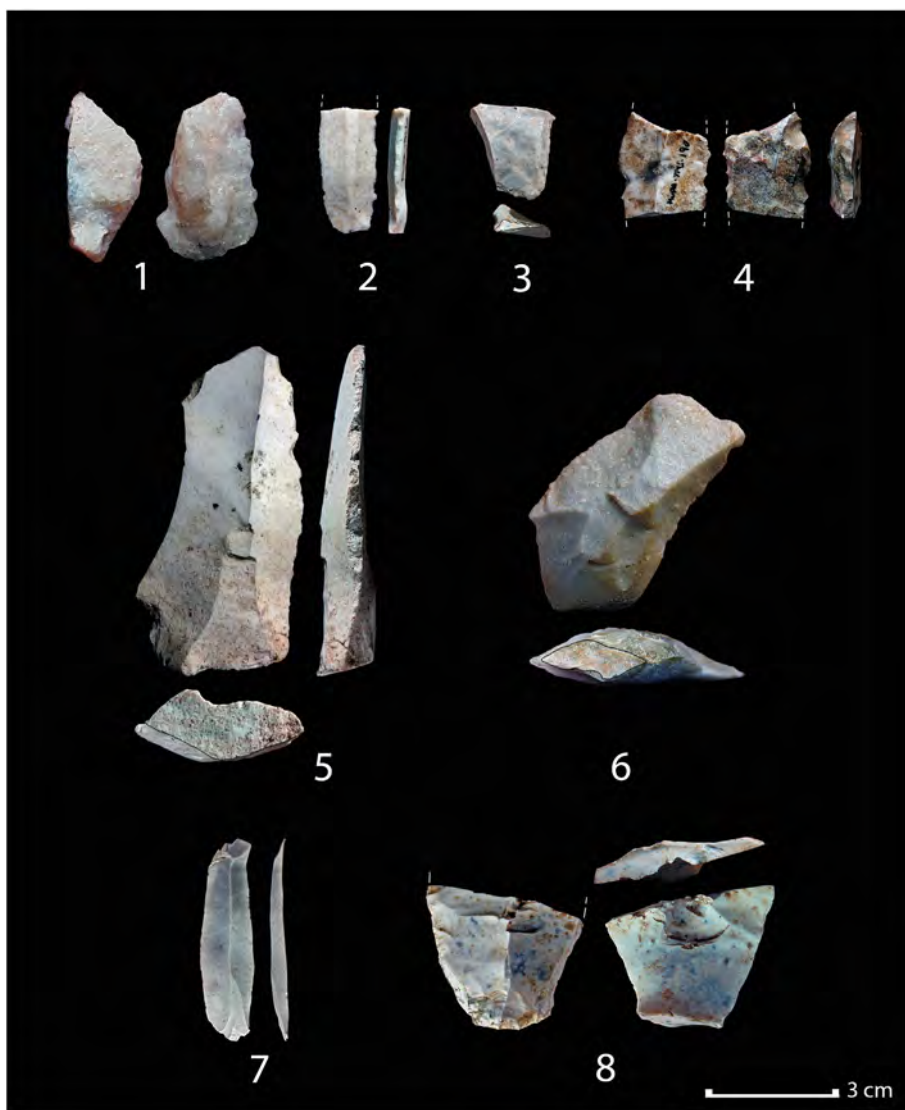
Lastly, in the Pasillo sector we studied nine lithic products from LU-P2, and nine more assigned to LU-P3. All of them are uninformative in terms of chronology or technological methods, and only one artifact from level LU-P3 shows relevant techno-typological traits. This is a laminar flake fragment in flint, with continuous retouch on one edge, bearing at least two small removals using the fracture as a platform (Fig. 9.8). These core-on-tool pieces are known to have been in existence from the Middle Paleolithic onwards, so its presence is irrelevant in chronological terms.

## 7.2. Pottery

The median size of the eight pottery fragments is  $41.7 \pm 5.7$  mm in length. Macroscopic observations reveal a very high density of voids and non-plastic inclusions, mainly mineral, in the clay matrix.

The non-plastic inclusions reach a size of 3 mm. In general, all these sherds have smooth internal and external surfaces. In some cases, technological traces linked to other surface treatments (burnishing and scraping) can be observed. The color of the sherds denotes mixing ( $n = 7$ ) and reduced ( $n = 1$ ) atmosphere conditions during the firing process. These alterations are clearly representative of a low controlled firing process in open hearths.

Pottery sherds are classified according to their morphological features: body ( $n = 6$ ), non-determined ( $n = 1$ ), and rim ( $n = 1$ ). Body sherds are convex, allowing for the proposal of a globular or hemispherical vessel morphology. The only rim sherd recorded shows a straight and rounded lip morphology (Supplementary Figure 9). Decoration is difficult to address. The external surface of the lip shows some impressions that might be interpreted as decoration. However, the erosion of the rim cannot substantiate this with certainty.



**Fig. 9.** Lithic artifacts from Torrejones. 1) *Débordant* flake (quartz) (LU-S1). 2) Denticulated backed blade (flint) (LU-S1). 3) Atypical endscraper on a laminar flake (flint) (LU-S1). 4) Bec/denticulate on a blade fragment (flint) (LU-S1). 5) Retouched pointed flake (flint) (LU-E4). 6) Centripetal flake (quartzite) (LU-E4). 7) Blade (flint) (LU-E3). 8) Retouched laminar flake recycled into a core (flint) (LU-P3).

**Table 7**  
Quantitative distribution of lithic technological categories and raw materials recorded in the LU-S1 from Torrejones.

Technological categories/Raw materials	Flint	Quartz	Rock cristal	Quartzite	TOTAL	%
Cores	0	0	0	0	0	0
Cortical flakes and preparation products	1	1	0	0	2	5.9
Core maintenance by-products	0	5	0	2	7	20.6
Knapping waste (chunks and <i>débris</i> )	0	2	3	0	5	14.7
Raw blanks	6	7	0	2	15	44.1
Retouched blanks	5	0	0	0	5	14.7
<b>TOTAL</b>	<b>12</b>	<b>15</b>	<b>3</b>	<b>4</b>	<b>34</b>	<b>100.0</b>
<b>%</b>	<b>35.3</b>	<b>44.1</b>	<b>8.8</b>	<b>11.8</b>	<b>100.0</b>	



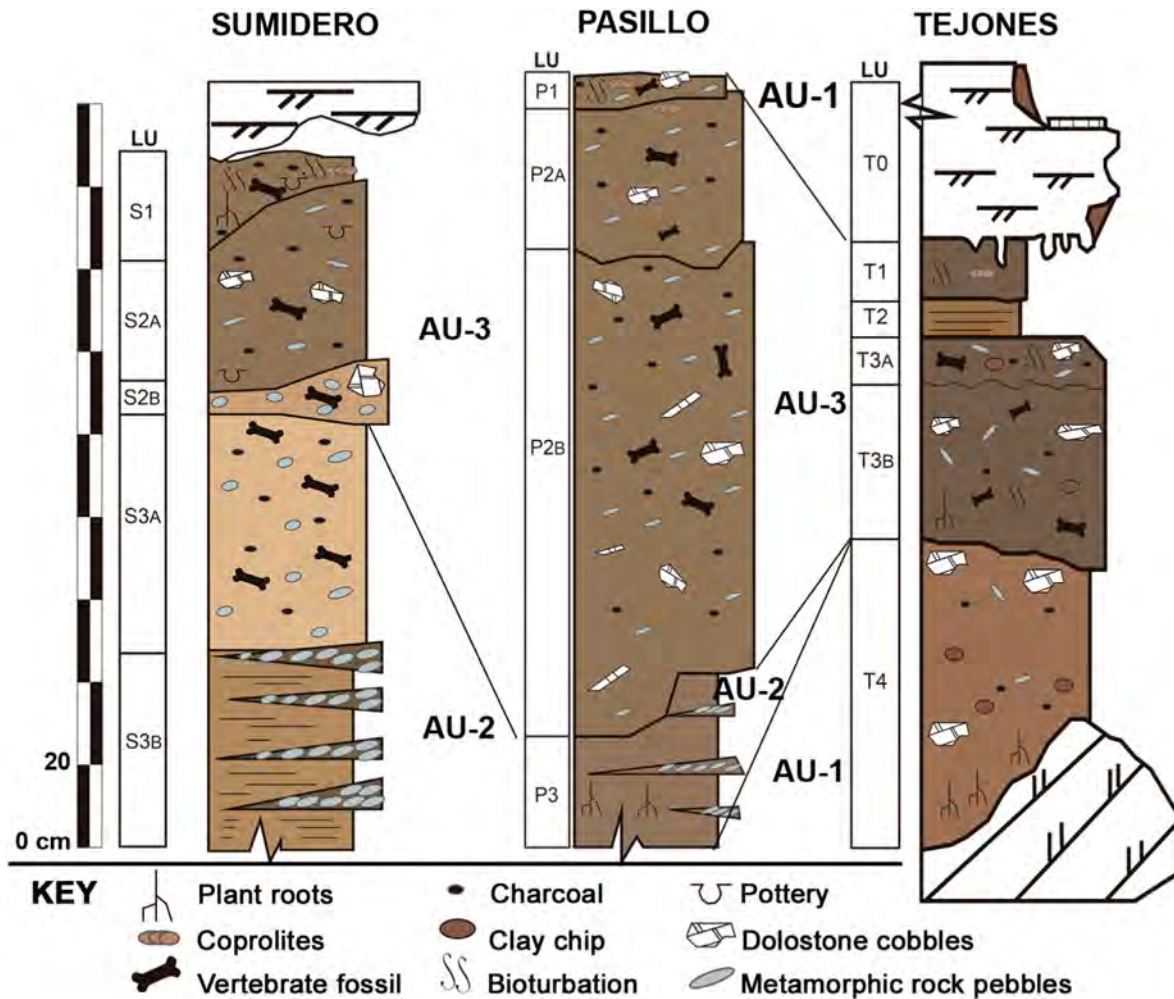


Fig. 10. Stratigraphic columns throughout the site: Sumidero, Pasillo and Tejonés sectors. The colors used correspond to those of the Munsell color system for wet sediment. LU: Lithostratigraphic Unit. AU: Allostratigraphic Unit. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

## 8. Discussion

### 8.1. Depositional sequence and interpretation of geological processes

The analysis and correlation of the identified lithostratigraphic units described in Table 1 have allowed us to redefine the depositional sequence for the cave's Internal Domain based on three allostratigraphic units described as follows (Fig. 10).

#### 8.1.1. Allostratigraphic unit AU-1

This allostratigraphic unit includes units LU-T0 and LU-T4, which are restricted to the Tejonés pit. This constitutes a deposit of reddish clay with cobbles of allochthonous composition (metamorphic rocks) deposited in this sector. At present, the only *in situ* remnant of the original unit remains attached to the cave wall reaching a height of 4.40 m. The unsorted and unbedded sediment consists of a chaotic mixture of particle sizes. Consequently, an erosive process (probably a karstic reactivation) partially washed these units leaving small *in situ* patches cemented at the irregularities in the cavity roof. The presence of abundant reddish clay chips in LU-T4 leads us to interpret this unit as the reworked deposit resulting from this erosional event. Its chronology remains unknown due to the lack of archaeo-paleontological materials.

#### 8.1.2. Allostratigraphic unit AU-2

The second allostratigraphic unit is composed of detrital sediment (LU-S3 in Sumidero and LU-P3 in the Pasillo sector). Although we do not know the nature of the lower contacts for these units (unexcavated), the boundaries are irregular and erosional (see Fig. 10). These facies are characterized by the intercalations of fine sand/silt with internal parallel lamination with lenticular levels of monomictic gravels of well-sorted metamorphic rocks. These metamorphic rocks are considered undoubtedly allochthonous to the cave system and the source area could correspond to the Roda Formation II (Hernández-Huerta et al., 1994), which outcrops at the top of El Lomo hill.

This type of cave deposit would correspond to the channel facies according to the classification of endokarstic sediments proposed by Bosch and White (2007) and defined as "sediments, transported mainly as bedload, that have been sorted or partially sorted by transport along the conduit." These facies are usually associated with fluviokarstic episodes transporting and depositing different particle sizes (from clay to gravel) depending on the flow regimes or hydraulic energy.

The new stratigraphic analysis of the Sumidero Sector has led to distinguishing two subunits in the unit originally named LU-S3: LU-S3A and LU-S3B. The lower unit (LU-S3B) is composed of well-preserved intercalations of fine sand/silt and gravels and shows no signs of mixing of geological materials. The micromorphological

analysis corroborates the fluviokarstic origin of this deposit due to the well sorting of the sediment and the imbrication of the lithoclasts. Under the microscope it is possible to observe, in addition to the allochthonous elements (metamorphic lithoclasts and quartz), some autochthonous elements, such as dolomite pebbles and rip-up fragments, which could correspond to the same unit or another underlying eroded and resedimented unit. The micromorphological analysis does not reveal signs of diagenetic alteration processes for LU-S3B after the original deposition by fluviokarstic processes.

On the contrary, the upper unit (LU-S3A) has no recognizable fluviokarstic sedimentary structures, nor does it have pebble imbrications nor good sediment sorting. However, both the fine and coarse fractions have the same composition with respect to LU-S3B. It is likely that the deposit in LU-S3A was formed during isolated surface runoff events saturated in sediment, which may occur during flooding periods (Bertran and Texier, 1999). The presence of bones that do not have signs of rounding and charcoal with a well-preserved internal structure could indicate inclusions from the upper unit. These observations suggest that LU-S3A could represent a sublevel with a mixture of Holocene (LU-S2) and Pleistocene (LU-S3B) units. Fine inclusions of LU-S2 in LU-S3 were described during previous excavations (Arribas et al., 1995, 2005). Macrovertebrate fossils were recovered in unit LU-S3 during the excavations conducted in the 1990s. Different taxa have been described, including equids, bear, and hyena. Direct dating of an equid lower molar recovered from LU-S3 during the 1993 field season reveals an age of 30,750–29,950 cal years BP (Supplementary Table 1), confirming the Late Pleistocene chronology proposed by Arribas et al. (1995, 2005). However, the human navicular also recovered from LU-S3 (from the same bag as the directly dated equid lower molar) provided a Holocene age of 5036–4855 cal years BP (Supplementary Table 1). Therefore, radiocarbon dating on the fauna and human remains indicates a doubtless mixture of chronologies. In the new stratigraphic scheme, two subunits have been described for LU-S3 (LU-S3A and LU-S3B), a distinction that gives rise to two possible scenarios for contextualizing this deposit's chronology, including the mixture of chronologies detected. The first scenario contemplates the possibility that the navicular remain could correspond to LU-S3A (a subunit with a mixture of LU-S2 and LU-S3B) and the equid molar could correspond to LU-S3B, a fluviokarstic unit deposited in the Late Pleistocene. The second possibility could be that both the navicular bone and the Pleistocene equid tooth originated in LU-S3B. In this case, the only explanation is that LU-S3B was deposited during the Holocene, incorporating Pleistocene fossils from previous units that are not preserved in their original position with Holocene remains. If this second scenario is confirmed, it would mean that the Internal Domain (dark zone of the cave) does not preserve unaltered Pleistocene units. Given that the fossiliferous units of the External Sector (twilight zone of the cave) were excavated in the 1990s, this would imply that there are no Pleistocene units currently preserved *in situ* at the Torrejones site.

#### 8.1.3. Allostratigraphic unit AU-3

An irregular boundary marks the base of the third allostratigraphic unit, which is particularly pronounced in the Pasillo sector (dip of 35°). This AU is composed of detrital sediments from the Sumidero LU-S2 (LU-S2A and LU-S2B), Pasillo LU-P2 (P2A and P2B), and Tejones LU-T3 (LU-T3A and LU-T3B) sectors. These units have been correlated based on their similar color, texture, and mineralogical composition, as well as their archaeological content. This unit corresponds to the Chalcolithic occupation of the site, given the characteristics of the pottery and lithic assemblages, as well as the radiocarbon dating of the human bones (Supplementary

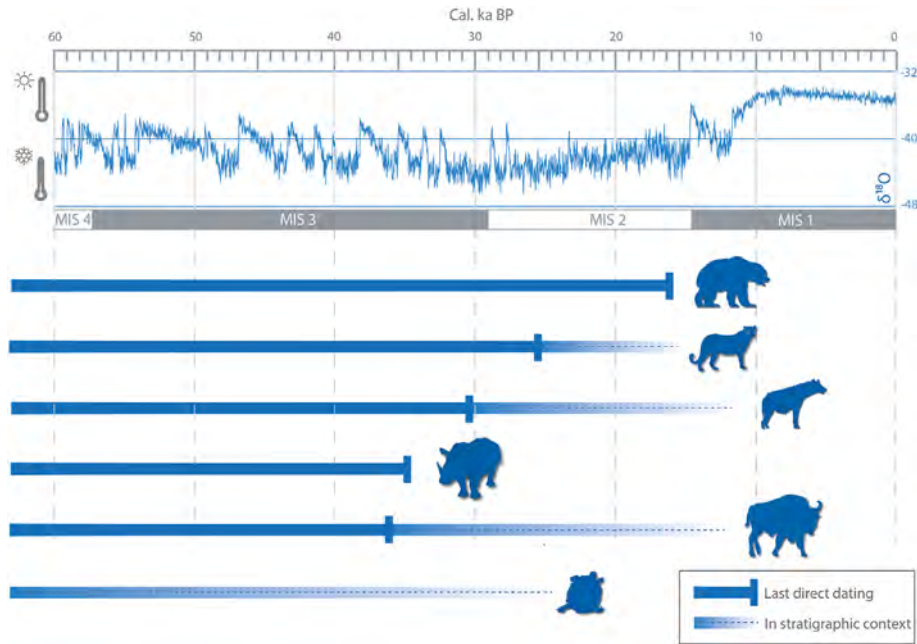
Table 1). In addition, the use of the cave by small carnivores, such as mustelids (badgers) and canids (foxes), is evident since numerous skeletal remains and coprolites of these species have been recovered (Arribas et al., 1997; Carrión et al., 2005). Although the sediment is highly compacted or cemented today, no internal sedimentary structure can be observed for these homogeneous deposits. At the microscopic level, LU-S2 facies are very similar to LU-S3A but have a higher fine fraction percentage, thus the energy of these surface runoffs should be lower. In addition, there is evidence of eroded sediments from previous units. There is a superficial deposit on top of these units, which is observed throughout the entire cavity (LU-S1, LU-P1 and LU-T1) and which differs from the underlying units due to the absence of compaction or cementation and because of its intense bioturbation (historical and current). This detritic deposit is characterized by having virtually the same mineral composition, color, and archaeological findings as the AU-3 units. Additionally, some human remains have been refitted corresponding to LU-S1 + LU-S2, LU-S1 + LU-E1 and LU-E1 + LU-P2 as a testament to the fact that they were originally the same units but were later remobilized and bioturbated. The material from the Sumidero sector could partially have been remobilized due to different causes, either biological or geological. No evidence of the presence of burrows has been detected in the stratigraphic sections or in the micromorphological samples in the LU-S3A/LU-S3B. Nevertheless, we cannot conclusively discard burrowing animals as agents for the bioturbation due to the lack of information from the excavation volume. Due to the abundance of badgers and foxes and the evidences of their activity (e.g. scats and bone remains) in the upper units (LU-S1 and LU-S2), these species could have been the responsible for the bioturbation and possible mixing of materials with the lower unit LU-S3. On the other hand, we do not discard geological agents such as runoff processes or small lateral mass movements could have remobilized older materials and sediments (Fig. 2e, f) to LU-S1 and LU-S2 levels.

#### 8.1.4. Allostratigraphic unit AU-0

Finally, although this was not mentioned in the sedimentological description (since there are currently no preserved LUs in the site), it is worth noting that we have the analysis of the fossil remains, as well as the documentation published by the former team from the Entrada sector (twilight zone of the cave). According to the documentation at hand, an additional allostratigraphic unit should be added to the depositional sequence (AU-0), composed of detritic sediments (LU-E4 and LU-E5) and formed mainly by autochthonous materials (dolostone fragments and detritic sediment originated by the weathering of the dolomite bedrock) with allochthonous material contributions (quartz and slate pebbles) (Supplementary Figure 6). The composition of the sedimentary matrix was interpreted as weathering or arenization of the cave rock dolostone with allochthonous contributions incorporated by low energy processes (diffused stream) (Arribas et al., 1997). In these units carnivores (mainly hyenas) deposited bone remains of different species and coprolites during the Late Pleistocene (Arribas, 1995, 1997; Arribas et al., 1997; Carrión et al., 2007).

## 8.2. Chronological inferences

From a chronological point of view, at least four sets have been differentiated. Firstly, the upper units from all the sectors (AU-3) have a Holocene chronology (Chalcolithic and historical record) as evidenced by both direct dating and the techno-typological deriving from the archaeological artifacts, which is compatible with the faunal association, despite having reworked fossils from the lower units. Regarding the lower units, two different locations



**Fig. 11.** Schematic chronological disappearance of some species documented in Torrejones in reference to the Marine Isotopic Stages (MIS). From top to bottom: *U. spelaeus*, *P. pardus*, *C. spelaea*, *S. hemitoechus*, *B. priscus*, and *T. hermanni*. The chronological distribution until the most recent direct dating chronology of the species is represented by dark blue continuous line and their distribution, taking into consideration stratigraphic or archaeological contexts only, is in light blue pointed line. The NGRIP  $\delta^{18}\text{O}$  curve from the Greenland ice core record is shown as a representation of temperature oscillations during this period (data from NGRIP Dating Group, 2008). Detailed citations of the chronological aspects are described in the text. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article).

contain faunal assemblages: the External Domain located in the Entrada Sector's lower units (AU-0; LU-E4/5) and LU-S3 in the Sumidero Sector in the Internal Domain (AU-2). The faunal association from these two locations includes species that were extinct during the Late Pleistocene (Fig. 11).

### 8.2.1. AU-0: External Domain (LU-E4/5)

From a biochronological perspective, the rodent association from the lower units in the Entrada sector is representative of the Late Pleistocene in the Iberian Peninsula. Particularly, the snow vole (*Chionomys nivalis*) appears in Iberia at the base of the Late Pleistocene; moreover, the earliest record of this species was in the MIS 5 units from the Cueva de la Carihuela (Fernández et al., 2007; Ruiz Bustos, 2000). This species continues occupying the Iberian Peninsula, though its distribution is currently restricted to high mountain regions (1000–4700 m.a.s.l.). After a strong expansion during the Pleistocene, the populations were reduced to small nuclei in specific biotopes of the mountainous regions (Luque-Larena and Gosálbez, 2007).

The LU-E4/5 faunal association includes macromammal species with biostratigraphic significance: hyena, leopard, steppe rhino, bison, and Hermann's tortoise. The oldest hyena of the genus *Crocuta* on record in Iberia is the Early Pleistocene remains from unit TD4-5 in Gran Dolina in Atapuerca (García and Arsuaga, 1999). Although *C. spelaea* has been found in archaeological contexts at the end of the Late Pleistocene (e.g., 15.0–11.8 ka cal BP in Santa Catalina level III (Castaños, 2014)), direct dating of hyena remains suggests an earlier disappearance (Fig. 11), around 32.0–30.0 ka cal BP in the Las Ventanas (Cortés-Sánchez et al., 2018) and La Garma sites (Cueto et al., 2020), which is in accordance with other direct dates at a European level (Stuart and Lister, 2014).

*P. pardus* was present in the Iberian landscapes since the Middle Pleistocene (e.g., Level VI of the Lezetxiki site (Altuna, 1972; Falgouères et al., 2005)), and inhabited Iberian ecosystems during a

large part of the Late Pleistocene (Sanchis et al., 2015b; Sauqué et al., 2013). The last appearance of Iberian leopards differs chronologically if we take into account the archaeological context or direct dating (Fig. 11). Although they are cited in the Gravettian and Magdalenian contexts of some sites in the north of the Iberian Peninsula, such as Astigarraga (Castaños, 2010), El Juyo (González Echegaray and Freeman, 1992/1993, (González Echegaray, 2015), or Bolinkoba (Castaños, 1983), the most recent direct dating of a leopard in Iberia provides an age of 26.8–25.3 ka cal BP (Aintzulo; Altuna and Mariezkurrena (2013); Mariezkurrena (2011)).

The steppe rhino was a relatively abundant species in Iberian ecosystems starting in the Middle Pleistocene (Cerdeño, 1990), including in the central region of the Iberian Peninsula, as documented by its presence in the MIS 5 units from Cueva del Camino (Arsuaga et al., 2012), and in the MIS 3 units from Valle del Tejadilla sites (Sala et al., 2020). The latest occurrences of *Stephanorhinus hemitoechus* took place around 34 ka cal BP, both in stratigraphic context in Portalón del Tejadilla (Sala et al., 2020) and Arbreda (Estévez, 1987; Maroto et al., 2012) and in direct dating at El Castillo (37.8–34.4 ka cal BP following Castaños, 2018) (Fig. 11).

Early representations of the *Bison priscus* lineage appear in the Middle Pleistocene units from Galería and Gran Dolina TD10/2 (Made, 2013) and are present in stratigraphic contexts up until unit D from Kiputz IX dated to 18.9–13.4 ka cal BP (Castaños et al., 2012). Nevertheless, the last direct dated steppe bison in Iberia (without ultrafiltration pretreatment protocol) date to 43.1–36.3 ka cal BP at the site of Padul (Álvarez-Laó et al., 2009) (Fig. 11).

Lastly, Hermann's tortoise remains were recovered from the lower units in the Entrada sector of Torrejones. *Testudo hermanni* had inhabited Mediterranean Iberian ecosystems since the Lower Pleistocene (Morales-Pérez and Sanchis-Serra, 2009). Despite the absence of direct dating (as far as we know), the disappearance of *T. hermanni* from the Iberian Peninsula roughly coincides with the end of the Middle Paleolithic (Morales-Pérez and Sanchis-Serra,

2009). Nevertheless, *T. hermanni* has recently been described in Aurignacian contexts from Cova Foradada as well, with a chronology of 34.6–33.9 ka cal BP (Morales et al., 2019) and in the pre-Gravettian unit from Nerja (Aura-Tortosa et al., 2002; Morales-Pérez and Sanchis-Serra, 2009) (Fig. 11). Due to its ecological preferences, this species is abundant on the Mediterranean and Atlantic coasts of the Iberian Peninsula but is rarely found in inland Iberia, especially in the vicinity of the Sistema Central. In addition to its discovery at Torrejones, *T. hermanni* remains have been reported at two additional central Iberian sites: in the MIS 5 site Cueva del Camino (90.9 ± 7.9 ky BP by TL) (Arsuaga et al., 2010, 2011, 2012) and the MIS 4/5 units of Abrigo de Navalmaíllo (77.2 ± 6.0 and 71.7 ± 5.1 ka BP by TL) (Arsuaga et al., 2011; Huguet et al., 2010). Both sites belong to the Pinilla del Valle archaeopaleontological complex (Madrid) located in the Sierra de Guadarrama mountains (1114 m.a.s.l.). This species is not featured in the faunal lists from Units 2 to 5 of the Cueva de la Buena Pinta (Huguet et al., 2010), also in Pinilla del Valle, which is considered chronologically younger (MIS 4) than the two aforementioned sites (63.4 ± 5.5 to 60.5 ± 5.0 ka BP by TL) (Arsuaga et al., 2011; Laplana et al., 2016). Rodent and lagomorph species (*Ochotona cf. pusilla*, *Microtus oeconomus*, *Microtus gregalis* and *Chionomys nivalis*), indicators of cold climates, were recorded at these units in the Cueva de la Buena Pinta hyena den site, suggesting a climatic cooling in this area (Laplana et al., 2015, 2016). This climatic deterioration is most evident in Portalón de Tejadilla (Segovia), also located in the vicinity of the Sistema Central, at an altitude similar to Pinilla del Valle. In this hyena den site, extreme cold and arid conditions have been inferred for a chronological range of between 40.4 and 34.2 cal kyr BP, including the Heinrich 4 event (Sala et al., 2020). These climate conditions, and especially the gradual increase in aridity, could be responsible for the disappearance of Hermann's tortoises from this high-altitude region. It is possible, therefore, that this central Iberian region witnessed a premature disappearance of Hermann's tortoises, (ca. 70 ka BP), which survived to more recent chronologies in the refuges of the Mediterranean and Atlantic coastal regions.

In sum, the vertebrate association from the lower units of the Entrada Sector at the Torrejones site suggests a Late Pleistocene chronology in a temporal range between MIS 5 to MIS 4 (~90.0–70.0 ka cal BP). However, given the exiguous record of *T. hermanni* in central Iberia, alternatively, we do not rule out slightly younger dates for this assemblage, which could imply new paleobiogeographical information for this testudine.

### 8.2.2. AU-2: Internal Domain (LU-S3)

As in the case of the Entrada Sector, the rodent association from the lower units of Sumidero, which also includes *C. nivalis*, is representative of the Late Pleistocene to the Holocene. The macromammal association from LU-S3 comprises hyena and bear (*Ursus* sp.). The cave bear (*Ursus spelaeus*) appears in the Iberian Peninsula at the end of MIS 6 (García, 2003; Torres, 1984) and becomes more abundant between MIS 5 and MIS 3 (Quam et al., 2001; Torres, 1984). Numerous radiocarbon dating results signal the prevalence of this species in chronologies of around 28.0–26.0 ka cal BP (Grandal-d'Anglade et al., 2006, 2019). Nevertheless, this species is cited in stratigraphic contexts up until more recent chronologies, including a singular direct dating of 17.1–16.3 ka cal BP for the O Rebolal site (Grandal-d'Anglade et al., 2006), which could be considered the youngest direct dating in all of Europe (Fig. 11).

The presence of snow vole and hyena here seems congruent with the direct dating of an equid lower molar to 30.7–29.9 ka cal BP. The presence of cave bear, if confirmed, would also be consistent

with the equid dating. We could therefore infer that LU-S3 represents a younger association (final MIS 3) with respect to the lower units of the Entrada sector. Nevertheless, given the ample evidence of the possible mixing of units in LU-S3, we cannot guarantee the congruence of this association here, which prevents us from attempting precise biochronological interpretations.

### 8.2.3. AU-3: superficial units

The lithic artifact analysis shows that archaeological assemblages recorded mainly in the upper units from the Sumidero sequence strongly point to an exclusively Late Prehistory human occupation of this area of the cave. The classification and systematic description of the pottery assemblage has made it possible to evaluate its integrity in order to assess whether it is technologically, morphologically, and decoratively coherent. This initial assessment is required for estimating the scope of the results and conclusions that can be obtained from the ceramic study. The pottery assemblage presents an undoubtedly technological coherence, and no fragment made by the throwing-wheel technique has been recovered, so there is no observed presence of materials from the modern or contemporary period. The pottery assemblage's technological characteristics denote a hand-made manufacturing process and firing conditions typical of an undetermined period attributed to Late Prehistory. Although it is impossible to specify this occupation's chronology given the scarcity of items and the absence of diagnostic decorative motifs, the pottery recovered from the site's upper units is compatible with the Chalcolithic chronology obtained by radiocarbon dating.

Lastly, the faunal association dominated by species that still survive today (small carnivores, domestic species, and humans) is compatible with the Chalcolithic chronology obtained by direct dating (Supplementary Table 1). Additionally, we have evidence of recent repeated occupation of the cavity by mustelids based on the presence of badger coprolites directly dated from the last three centuries (Carrión et al., 2005).

## 8.3. Paleoenvironmental and paleoclimatic implications

Since the chronological implications point to at least three prehistoric periods documented in Torrejones, we will make distinct paleoecological inferences in temporal order: first for the MIS4/5 (AU-0), next for the final MIS3 (AU-2), and lastly for the Chalcolithic (AU-3).

### 8.3.1. MIS-4/5 (AU-0: LU-E4/5)

In general terms, the macromammal association from this unit is characterized by the presence of eurythermal species with a wide climatic tolerance range, such as leopard, hyena, red deer, horse, or steppe rhinoceros. Regarding reptiles, the abundance of Hermann's tortoise, together with the absence of cold-climate adapted species, could be indicative of tempered environmental conditions during the formation of LU-E4/5. On the other hand, grazing species adapted to open environments, such as horses, rhinoceroses, and bison, are equally represented as species like red deer, roe deer, or wild boar. Likewise, the microvertebrate association (Table 3) suggests that a variety of environments were present in the vicinity of the cave since forest species like *Eliomys* sp. have been recovered, in addition to species that inhabit mountain environments (*C. nivalis*). This is compatible with the analysis of pollen recovered from hyena coprolites from LU-E4 by Carrión et al. (2007), which documented different vegetation types in several coprolites sampled including: steppe-grasslands, open pine forests, and parkland/savannah vegetation of pine stands. Among the arboreal pollen, temperate trees were documented (*Taxus*, *Quercus* and

*Betula*). The predominantly herbaceous vegetation was interpreted by Carrión et al. (2007) as potentially conditioned by the montane conditions surrounding the site.

In sum, taking into consideration macro and microvertebrate associations, together with the collective pollen analysis, we can suggest that there was a mosaic environment in the cave's surroundings during a temperate period for the LU-E4/5 assemblage.

#### 8.3.2. MIS-3 (AU-2: LU-S3)

LU-S3 comprises a small mammal association consisting of open-environment dwellers such as *Marmota marmota*, voles belonging to the genera *Microtus* (*M. agrestis* and *M. arvalis*), and bats belonging to the genus *Myotis* (Table 3). The presence of forest dwellers, such as *Eliomys quercinus* and *Apodemus sylvaticus*, suggest the presence of forest patches in the vicinity of the cave. Additionally, *C. nivalis* illustrates the proximity of summits to the cave (e.g., Ocejón peak 2049 m.a.s.l). The association of *C. nivalis* with *M. marmota* could suggest cold and open landscapes, indicating a possible deterioration of climatic conditions as compared to LU-E4/5. However, it is advisable to be cautious in this interpretation since, in view of the available data of material mixing in LU-S3, the congruence in this association cannot be guaranteed.

Regarding the macrovertebrate association from the Pleistocene unit in the Entrada sector, there is a drastic reduction or even disappearance of roe deer, rhinoceros, leopard, and Hermann's tortoises. This reduction in macrovertebrate species, together with the increase in open-environment species, would suggest an environmental deterioration.

#### 8.3.3. Chalcolithic (AU-3: LU-S1, LU-S2, LU-E1, LU-E2, LU-T1, LU-T2)

The majority of the AU-3 (mainly recovered from LU-S2) microvertebrate species are indicators of woods and/or forest edges, such as *A. sylvaticus*, *E. quercinus*, and *S. vulgaris*. Furthermore, there are meadow species represented, such as *Iberomys*, *Arvicola*, *Terricola*, and *Microtus*. The large number of small lizards, together with the abundance of *T. duodecimcostatus*, indicates an open landscape, with some sporadic forests. Most of the taxa from the small mammal association indicate a humid Mediterranean climate for the Holocene units from the Torrejones site.

### 8.4. Site formation processes and origin of the skeletal accumulation

The taphonomic data suggest different accumulation processes for the skeletal assemblages, depending on the assemblage and chronology.

#### 8.4.1. MIS-4/5 (AU-0: LU-E4/5)

Evidence of carnivore activity marks have been documented in the lower units of Entrada. The tooth marks, together with the presence of large carnivores in LU-E4/5 (mainly hyena and leopard), as well as the abundance of hyena coprolites, suggest occupation by carnivores that used the Entrance sector as a den during the Late Pleistocene. Pleistocene hyenas (unlike other large carnivores such as bears or lions) have a great knack for accumulating their prey in their lairs (Sala and Arsuaga, 2018 and references therein). This behavior generates large bone accumulations in caves occupied by hyenas, which is documented in numerous Iberian Pleistocene sites, including some recorded in the vicinity of the Central System (Arribas, 1995; Arribas et al., 2008; Arsuaga et al., 2012; Sala et al., 2012, 2020). Thus, in this sense, the data obtained in the present study are compatible with previous interpretations (Arribas et al., 1995, 1997; Arribas, 1997; Díez Fernández-Lomana et al., 1998).

Some lithic products from the Entrada sector could suggest a

human presence in the vicinity of the cave during the Middle Paleolithic, though it has not been possible to verify this with any degree of accuracy, since they correspond typologically to the Middle Paleolithic or a later chronology. In any case, it is not uncommon to find some lithics in Pleistocene hyena dens (Villa and Soressi, 2000), as has been observed in sites that are geographically close by and that have been interpreted as hyena lairs (Arsuaga et al., 2012; Sala et al., 2012, 2020). Nevertheless, in the Late Pleistocene units from Entrada sector of Torrejones, signs of interaction or competition between hominin and carnivores has not been observed. Given the exiguous signs of anthropic activity in the fossil assemblage, it is possible that humans used the cave sporadically as a refuge in the periods of non-occupation by carnivores, taking into account that carnivores usually have a seasonal cave occupation pattern (Villa and Soressi, 2000; Rosell et al., 2010). The presence of humans in the area during the Middle Paleolithic is demonstrated by the existence of at least two archaeological sites bearing Mousterian sequences within a radius of less than 10 km: Jarama VI (Kehl et al., 2013; Navazo Ruiz et al., 2020) and Peña Cabra (Alcaraz-Castaño et al., 2016, 2017b).

The marks observed on the tortoise depict characteristics that are compatible with those inflicted by a dihedral or at least by a pointed object. Their depth, section, orientation, and relationship between marks render them incompatible with trampling. The superposition of the groups of marks observed on the hypoplastron and epiplastron indicates that this is probably a response to a repetitive and sequential action, which is unlikely to occur in this sequence due to natural (geological) causes. However, their sinuous trajectory, the presence of abundant flaking in the shoulders, the color changes, the manganese dendrite erasure, and the recurrent flaking along the groove's trajectories, demonstrate that the marks were performed on dry bone, long after burial. In addition, the marks are located on the outside of the shell, where the epidermal scutes should have been, which could greatly hinder the possibility of producing permanent marks. Finally, the anatomical location of the marks cannot be related to any butchering activity since there are no profitable resources located in this position. Upon review of the literature about anthropogenic processing of turtles, common taphonomic characteristics can be summarized by; i) large breakage, including percussion marks on the shells and peeling on long bones, ii) abundant cremations, especially on the dorsal view of the carapaces, and iii) cut marks on the ventral surface of the plastron and carapaces. In the literature we only found one cut mark on the exterior surface of the shell, in a dorsal view of a plate (Sanchis et al., 2015a: 112). None of these taphonomic features can be observed at Torrejones, thus indicating that the marks are probably not related to prehistoric butchering activity.

In the case of the grooves on the leopard's neural skull, the overlap of the grooves with other post-depositional modifications and the fact that they erase some of them as manganese or concretions clearly indicate that the scratches occurred long after burial. Furthermore, its U-shape is not compatible with cut marks. Its position and location are not compatible with skinning either, since marks during fur processing are inflicted on many areas of the skull and jaw rather than the masseter fossa, where they are not typically observed (e.g., Luff and Moreno García, 1995; Val and Maille, 2011). The total lack of anthropic modifications on the rest of this leopard's skeleton, found in less than 2 m<sup>2</sup> in anatomical position, reinforces a post-depositional origin for the modifications. The absence of certain skeletal elements of this individual could be due to numerous postdepositional processes, such as carnivore removal, non-preservation of the most fragile elements, or bioturbation, but not necessarily due to anthropogenic activity.

Both in the case of the tortoise and in the case of the leopard, the

marks described were previously interpreted as cut marks (Arribas, 1997; Díez Fernández-Lomana et al., 1998). The results of our re-evaluation show that the marks were made after burial. The similarity of some of them to cut marks is evident. However, many non-anthropogenic agents and processes may cause some properties of the linear marks to be similar (Domínguez-Rodrigo et al., 2009). In Torrejones, these marks are compatible with accidents during the excavation-restoration process (Krasinski, 2018; Marin-Monfort et al., 2018) or with the claws of digging animals (Pokines and Symes, 2013). From the date of its publication, the marks on the tortoise and the leopard from Torrejones have been used as archaeological parallels in investigations into Neandertal diet and behavior (Blasco, 2008; Blasco et al., 2010, 2011; Gabucio et al., 2014; Rosell and Blasco, 2009; Sanchis et al., 2015a, 2017) among others. Considering our reassessment of the marks, this parallel should cease to be made.

#### 8.4.2. MIS-3 (AU-2: LU-S3)

No evidence of human occupation of the cave has been detected in LU-S3, as there are no Paleolithic human remains, nor Paleolithic lithic industry, nor traces of human butchery on the bones. Instead, modification produced by carnivores, especially digested bones, has been documented. Sedimentological, micromorphological, geochronological, and taphonomic analyses allowed us to detect mixing of Pleistocene and Holocene materials, especially in the upper part of LU-S3 (specifically LU-S3A).

#### 8.4.3. Holocene (AU-3: LU-S1, LU-S2, LU-E1, LU-E2, LU-T1, LU-T2)

The upper units of the different sectors of the cavity contain differentiated assemblages: skeletal remains of small carnivores (mainly badgers and foxes), humans, and domestic species (horses, ovine/caprines, and suids) that present different mineralization and patina patterns compared to the Pleistocene species (less mineralization, absence of tooth marks and similar pattern of patinas of manganese oxides). The presence of these skeletal remains in terms of the use of the cavity can be explained by small carnivores who contributed their own skeletal remains to the deposit (Rodríguez-Hidalgo et al., 2020). Chalcolithic communities used the cave for funerary purposes, as is directly supported by radiocarbon dating. In addition to this activity, older elements have been recognized in the upper levels (Pleistocene species) that must have been incorporated into the Holocene deposit by biological (bioturbation) and/or geological processes (fluvio-karstic reactivation).

Radiocarbon dating indicates diachronic use of the cave for funerary purposes during the Chalcolithic. In other words, Torrejones does not represent a single funerary event, but rather the corpses were accumulated over the course of a long period of time (Supplementary Table 1). The presence of the remains of several individuals, which are scattered and commingled in the superficial units of the cave, are compatible with the non-simultaneous collective burials inside other caves that have been reported for the funerary activities of Early Chalcolithic populations in Central Iberia such as El Rebollosillo or Cueva de Juan Barbero in Madrid (Aliaga Almela, 2008), Jarama II in Guadalajara (Jordá-Pardo and Mestres Torres, 1999), or Mirador in Burgos (Vergès et al., 2016). In some of the aforementioned sites, burned bones were recovered and interpreted as using fire as a way of purifying and cleaning burial sites in karstic contexts (Aliaga Almela, 2008; Fabián García, 1995; Martínez Navarrete, 1984).

## 9. Conclusions

Paleoecological conditions in central Iberia are crucial to understanding the role of climatic oscillations in order to address

Paleolithic population dynamics in this particular area. However, archaeo-paleontological evidence is scarce in this region. One of the key sites from central Iberia for broaching this matter was discovered and excavated during the nineties and is called the Cueva de los Torrejones. This site is one of the most relevant archaeo-paleontological sites in the region because of its rich and diverse faunal association, which could help to bring to light the full paleoecological panorama during critical periods of the Late Pleistocene.

The site's most recent excavation, as well as restudying the previously recovered materials with the implementation of new techniques, has allowed us to expand upon our knowledge of the site. The new stratigraphic and micromorphological analysis of the deposits led us to define four allostratigraphic units (AU) and to propose geological factors for the site formation processes. Analyzing the distinct faunal assemblages from the different sectors and units in the cavity allowed us to propose three main occupation episodes for the cave. The oldest episode (AU-0) is represented by a faunal assemblage indicative of a rich ecosystem formed by a mosaic of environments during a temperate climate period in a temporal range between MIS 5 to MIS 4. During this period the cave was occupied mainly by carnivores (hyenas and leopards) who used the cavity as a den. Although few lithics recovered in this unit could point to Middle Paleolithic technologies as suggested in previous studies, no direct evidence of human presence in the cave has been documented; i.e., there were no Paleolithic human remains nor butchery activities on faunal remains. The new taphonomic analysis rules out any kind of anthropic intervention on the Hermann's tortoise and leopard in the Torrejones cave during the Middle Paleolithic. The second episode (AU-2) is represented by a faunal association dated to 30.0 ka cal BP, indicative of cooler and more arid environmental conditions and, therefore, consistent with the worsening climate detected during MIS 3 in other central Iberian sites. Human occupation of the cavity has not been detected in these units (neither Paleolithic human remains nor evidence of butchering of faunal assemblages). The last episode (AU-3) is represented by the upper units from all sectors of the cavity and corresponds to the Holocene including Chalcolithic (III millennia cal BC), directly dated to ~5000 cal BP and sporadic occupations of small carnivores until historical times. Lithic and pottery elements have been recovered which are compatible with this chronology and associated with human remains. These communities used the cavity for funerary purposes during late prehistory as non-simultaneous collective burials. A minimum of five individuals has been estimated for the human remains recovered, including immature individuals and adults for which both male and female individuals have been distinguished. The generated mtDNA sequence of one of the human remains was assigned to mtDNA haplogroup K, which is thought to have originated in the Near East and reached western Europe through the Neolithic expansion, and has been well documented during the Chalcolithic in Spain.

The Torrejones cave has therefore made it possible to understand the paleoenvironment during different periods of the Late Pleistocene and Holocene. Finally, as a result of the Torrejones cave excavations, other nearby deposits have been discovered, which hopefully will aid in enhancing our understanding of the Late Pleistocene archaeological and paleoecological record for central Iberia.

## Declaration of competing interest

The authors have no competing interests to declare.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.quascirev.2020.106765>.

## References

- Adán, G., Arribas, A., Barbadillo, J., Cervera, J., Estrada García, R., García-Valero, M.Á., Jordá Pardo, J.F., Pastor Muñoz, J., Sánchez Chillón, B., Sánchez-Marco, A., Sanchiz, B., Sesé, C., 1995. Prospecciones y excavaciones arqueológicas en el Valle del Jarama. In: Balbín, R.d., Valiente, J., Mussot, M.T. (Eds.), *Patrimonio Histórico-Arqueológico de Castilla la Mancha*. Arqueología en Guadalajara, Guadalajara, pp. 112–124.
- Alcaraz-Castaño, M., Alcolea-González, J., Weniger, G.-C., Baena-Preysler, J., De Balbín-Behrmann, R., Cuartero, F., Kehl, M., López-Sáez, J.A., Piqué, R., Yravedra, J., 2016. Neandertal adaptations in central Iberia: a multi-proxy investigation of the Middle Paleolithic site of Peña Cabra, Guadalajara, Spain. Guadalajara, Spain, 6th annual meeting of the European Society for the Study of Human Evolution (ESHE). European Society for the Study of Human Evolution (ESHE) 31.
- Alcaraz-Castaño, M., Alcolea-González, J., Kehl, M., Albert, R.-M., Baena-Preysler, J., de Balbín-Behrmann, R., Cuartero, F., Cuenca-Bescós, G., Jiménez-Barredo, F., López-Sáez, J.-A., Piqué, R., Rodríguez-Antón, D., Yravedra, J., Weniger, G.-C., 2017a. A context for the last Neandertals of interior Iberia: los Casares cave revisited. *PLoS ONE* 12 e0180823.
- Alcaraz-Castaño, M., Alcolea González, J., Weniger, G.C., Álvarez-Figueras, I., Arteaga, A., Baena-Preysler, J., de Balbín-Behrmann, R., Bustos-Pérez, G., Cabaleiro, A., Cuartero, F., Cuenca-Bescós, G., Dávila, A., Herrero, D., Kehl, M., Lamas, V., López-López, A., López-Sáez, J.A., Marinas-Díez, E., Ortiz, I., Picazo, Z., Piqué, R., Polo, E., Sáez-Martínez, M., Salinero-Sánchez, I., Sánchez, J., Vaca, A., Vizcaino-Trueba, J., Yravedra, J., 2017b. Neandertales y humanos modernos en Guadalajara. *Boletín de la Asociación de Amigos del Museo de Guadalajara* 8, 13–44.
- Alcaraz-Castaño, M., Alcolea-González, J., Balbín-Behrmann, R., de Kehl, M., Weniger, G.C., 2019. Recurrent human occupations in central Iberia around the Last Glacial Maximum. The Solutrean sequence of Peña Capón updated. In: Schmidt, I., Cascalheira, J., Bicho, N., Weniger, G.-C. (Eds.), *Human Adaptations to the Last Glacial Maximum: the Solutrean and its Neighbors*. 3rd International Conference on the Solutrean. Cambridge Scholars Publishing, Faro (Portugal), pp. 148–170.
- Alcolea-González, J.J., Balbín, R.d., García Valero, M.Á., Jiménez Sanz, P.J., Aldecoa Quintana, A., Casado Mateos, A.B., Andrés Lorient, B.d., Ruiz Pedraza, S., Sainz-Rubio, P., Suárez-Rueda, N., 1997. Avance al estudio del poblamiento paleolítico del Alto Valle del Sorbe (Muriel, Guadalajara). In: Balbín, R.d., Bueno, P. (Eds.), *II Congreso de Arqueología Peninsular*, Zamora (Spain), pp. 201–218.
- Alfárez, F., Molero, G., Maldonado, E., Bustos, V., Brea, P., Buitrago, A.M., 1982. Descubrimiento del primer yacimiento cuaternario (Riss-Würm) de vertebrados con restos humanos en la provincia de Madrid (Pinilla del Valle). *Coloq. Paleontol.* 37, 15–32.
- Aliaga Almela, R., 2008. El mundo funerario calcolítico de la región de Madrid. *Cuadernos de Prehistoria y Arqueología* 34, 23–39.
- Altuna, J., 1972. Fauna de mamíferos de los yacimientos prehistóricos de Guipúzcoa. *Munibe* 24, 1–464.
- Altuna, J., Mariezkurrena, K., 2013. Cráneos de pantera en Allekoaitze (Ataun) y Aintzulo (Errezil) (Gipuzkoa). *Kobie* 32, 29–38.
- Álvarez-Alonso, D., de Andrés-Herrero, M., Díez-Herrero, A., Medialdea, A., Rojo-Hernández, J., 2018. Neandertal settlement in central Iberia: geoarchaeological research in the Abrigo del Molino site, MIS 3 (Segovia, Iberian Peninsula). *Quat. Int.* 474, 85–97.
- Álvarez-Laó, D.J., 2007. Revisión paleontológica de los macromamíferos indicadores de clima frío en el Pleistoceno de la Península Ibérica, Departamento de Geología. Universidad de Oviedo.
- Álvarez-Laó, D.J., Kahlke, R.-D., García, N., Mol, D., 2009. The Padul mammoth finds – on the southernmost record of *Mammuthus primigenius* in Europe and its southern spread during the Late Pleistocene. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 278, 57–70.
- Andrés, M., Gidna, A.O., Yravedra, J., Domínguez-Rodrigo, M., 2012. A study of dimensional differences of tooth marks (pits and scores) on bones modified by small and large carnivores. *Archaeol. Anthropol. Sci.* 4, 209–219.
- Aranburu, A., Arsuaga, J.L., Sala, N., 2017. The stratigraphy of the Sima de los Huesos (Atapuerca, Spain) and implications for the origin of the fossil hominin accumulation. *Quat. Int.* 433, 5–21.
- Arribas, A., 1994. Paleontología de macromamíferos del yacimiento mesopleistoceno de Villacastín (Segovia, España). *Bol. Geol. Min.* 105, 22–39.
- Arribas, A., 1995. Consideraciones cronológicas, tafonómicas y paleoecológicas del yacimiento Cuaternario de Villacastín (Segovia, España). *Bol. Geol. Min.* 106, 3–22.
- Arribas, A., 1997. Un leopardo, *Panthera pardus* (Linnaeus, 1758), en el Pleistoceno de la Cueva de los Torrejones (Tamajón, Guadalajara, España). *Geogaceta* 22, 19–22.
- Arribas, A., Jordá, J.F., 1999. Los mamíferos del Cuaternario kárstico de Guadalajara (Castilla-La Mancha, España). In: Aguirre, E., Rábano, I. (Eds.), *La Huella del Pasado. Fósiles de Castilla-La Mancha*. Patrimonio Histórico. Arqueología Castilla-La Mancha, pp. 327–353.
- Arribas, A., Díez, J.C., Jordá, F.J., 1995. El yacimiento cuaternario de la Cueva de los Torrejones (Tamajón, Guadalajara, Castilla-La Mancha): resultados preliminares. In: Balbín, R., Valiente, J., Musat, M.T. (Eds.), *Arqueología en Guadalajara*. Patrimonio Histórico-Arqueología Castilla-La Mancha, Guadalajara (Spain), pp. 97–110.
- Arribas, A., Díez Fernández-Lomana, C., Jordá Pardo, J.F., 1997. Primeras ocupaciones en los depósitos Pleistocenos de la Cueva de los Torrejones (Sistema Central español, Guadalajara): litografía y actividad biológica. *Cuaternario Geomorfol.* 11, 55–66.
- Arribas, A., Garrido, G., García Solano, J.A., 2005. Depósitos retrabajados y fósiles Pleistocenos reelaborados en un karst de la provincia de Guadalajara (Cueva de los Torrejones). Evidencias de ocupaciones biológicas Pleistocenas y Holocenas, de reactivación kárstica postcalcolítica y de una ocupación biológica histórica. In: Martinell, J., Doménech, R., Gibert, J.M. (Eds.), *2nd International Meeting Taphos*. Universitat de Barcelona, Barcelona (Spain).
- Arribas, A., Solano, J.G., Garrido, G., Carroza, J., 2008. El registro diferencial de carnívoros y homínidos en los karst del Pleistoceno del Sistema Central español: condicionantes geológicos y espaciales. In: Díez Fernández-Lomana, C. (Ed.), *Zoarquología hoy*. Encuentros Hispano Argentinos. Universidad de Burgos, pp. 39–52.
- Arsuaga, J.L., Baquedano, E., Pérez-González, A., Sala, N., García, N., Álvarez-Laó, D., Laplana, C., Huguet, R., Sevilla, P., Blain, H.-A., Quam, R., Ruiz Zapata, M.B., Sala, P., Gil García, M.J., Uzquiano, P., Pantoja, A., 2010. El yacimiento arqueopaleontológico del Pleistoceno superior de la Cueva del Camino en el Calvero de la Higuera (Pinilla del Valle, Madrid). *Zona Arqueológica* 13, 349–368.
- Arsuaga, J.L., Baquedano, E., Pérez-González, A., 2011. Neandertal and carnivore occupations in Pinilla del Valle sites (Community of Madrid, Spain). In: Oosterbeek, L., Fidalgo, C. (Eds.), *Union Internationale des Sciences Préhistoriques et Protohistoriques*. BAR International Series, Lisbon (Portugal), pp. 111–119.
- Arsuaga, J.L., Baquedano, E., Pérez-González, A., Sala, N., Quam, R.M., Rodríguez, L., García, R., García, N., Álvarez-Laó, D., Laplana, C., Huguet, R., Sevilla, P., Maldonado, E., Blain, H.A., Ruiz-Zapata, M.B., Sala, P., Gil-García, M.J., Uzquiano, P., Pantoja, A., Márquez, B., 2012. Understanding the ancient habitats of the last-interglacial (late MIS 5) Neanderthals of central Iberia: paleoenvironmental and taphonomic evidence from the cueva del Camino (Spain) site.

- Quat. Int. 275, 55–75.
- Aura-Tortosa, J.E., Jordá Pardo, J.F., Pérez Ripoll, M., Rodrigo García, M.J., Badal García, E., Guillem Calatayud, P., 2002. The far south: the Pleistocene–Holocene transition in Nerja cave (Andalucía, Spain). *Quat. Int.* 93–94, 19–30.
- Bailon, S., 2001. Revisión de la asignación a *Testudo cf. graeca* del yacimiento del Pleistoceno superior de Cueva Horá (Darro, España). *Rev. Española Herpetol.* 15, 61–65.
- Baquedano, E., Márquez, B., Laplana, C., Arsuaga, J.L., Pérez-González, A., 2014. The archaeological sites at Pinilla del Valle (Madrid, Spain). In: Sala Ramos, R., Carbonell, E., Bermúdez de Castro, J.M., Arsuaga, J.L. (Eds.), *Pleistocene and Holocene hunter-gatherers in Iberia and the Gibraltar strait: The current archaeological record*. Universidad de Burgos. Fundación Atapuerca, Burgos, pp. 577–584.
- Baquedano, E., Arsuaga, J.L., Pérez-González, A., Márquez, B., Laplana, C., Ortega, M.C., Huguet, R., Poza-Rey, E.M., Rodríguez, L., Alonso, J.I., Ortega, A.I., Galindo-Pellicena, M.A., García, N., Álvarez-Lao, D., 2016. The Des-Cubierto Cave (Pinilla del Valle, Comunidad de Madrid, Spain): a Neanderthal site with a likely funerary/ritualistic connection, 6th annual meeting of the European Society for the Study of Human Evolution (ESHE). *European Society for the Study of Human Evolution (ESHE)*, Alcalá de Henares (Spain) 41.
- Baquedano, E., Márquez, B., Laplana, C., Pérez-González, A., Arsuaga, J.L., 2018. Human occupations at Navalmaíllo Rock Shelter (Pinilla del Valle, Madrid, Spain). In: XVIII world UISPP Congress, Paris (France).
- Bar-Yosef, O., Van Peer, P., 2009. The chaîne opératoire approach in Middle Paleolithic archaeology. *Curr. Anthropol.* 50, 103–131.
- Barandiarán, I., 1973. La Cueva de los Casares (en Riba de Saelves, Guadalajara). In: Ministerio de Educación y Ciencia. Dirección General de Bellas Artes. Comisaría General de Excavaciones Arqueológicas.
- Barea, J., Rejos, J., 2000. Últimas exploraciones en el karst de Tamajón (Guadalajara). *Boletín del Grupo de Espeleología SECJA de Alcobendas* 2, 47–53.
- Behrensmeier, A.K., 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology* 4, 150–162.
- Bertran, P., Texier, J.-P., 1999. Facies and microfacies of slope deposits. *Catena* 35, 99–121.
- Blasco, R., 2008. Human consumption of tortoises at level IV of Bolomor cave (Valencia, Spain). *J. Archaeol. Sci.* 35, 2839–2848.
- Blasco, R., Rosell, J., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2010. The hunted hunter: the capture of a lion (*Panthera leo fossilis*) at the Gran Dolina site, Sierra de Atapuerca, Spain. *J. Archaeol. Sci.* 37, 2051–2060.
- Blasco, R., Blain, H.-A., Rosell, J., Carlos Díez, J., Huguet, R., Rodríguez, J., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2011. Earliest evidence for human consumption of tortoises in the European Early Pleistocene from Sima del Elefante, Sierra de Atapuerca. *Spain. J. Hum. Evol.* 61, 503–509.
- Bosch, R.F., White, W.B., 2007. Lithofacies and transport of clastic sediments in karstic aquifers. In: Sasowsky, I.D., Mylroie, J. (Eds.), *Studies of Cave Sediments: Physical and Chemical Records of Paleoclimate*. Springer, Dordrecht, pp. 1–22.
- Brandt, G., Haak, W., Adler, C.J., Roth, C., Szécsényi-Nagy, A., Karimnia, S., Möller-Rieker, S., Meller, H., Ganslmeier, R., Friederich, S., Dresely, V., Nicklisch, N., Pickrell, J.K., Sirocko, F., Reich, D., Cooper, A., Alt, K.W., 2013. Ancient DNA reveals key stages in the formation of Central European mitochondrial genetic diversity. *Science* 342, 257–261.
- Bunn, H.T., 1986. Patterns of skeletal representation and hominid subsistence activities at Olduvai Gorge, Tanzania, and Koobi Fora, Kenya. *J. Hum. Evol.* 15, 673–690.
- Burke, A., Kageyama, M., Latombe, G., Fasel, M., Vrac, M., Ramstein, G., James, P.M.A., 2017. Risky business: the impact of climate and climate variability on human population dynamics in Western Europe during the Last Glacial Maximum. *Quat. Sci. Rev.* 164, 217–229.
- Cabrera, V., Bernaldo de Quirós, F., 1979. Abrigo de Tamajón. Ministerio de Cultura. Carretero, J.M., Rodríguez, L., García-González, R., Arsuaga, J.L., Gómez-Olivencia, A., Lorenzo, C., Bonmatí, A., Gracia, A., Martínez, I., Quam, R., 2012. Stature estimation from complete long bones in the Middle Pleistocene humans from the Sima de los Huesos, Sierra de Atapuerca (Spain). *J. Hum. Evol.* 62, 242–255.
- Carrión, J.S., Riquelme, J.A., Navarro, C., Munuera, M., 2001. Pollen in hyaena coprolites reflects late glacial landscape in Southern Spain. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 176, 193–205.
- Carrión, J.S., Gil, G., Rodríguez, E., Fuentes, N., García-Antón, M., Arribas, A., 2005. Palynology of badger coprolites from central Spain. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 226, 259–271.
- Carrión, J.S., Scott, L., Arribas, A., Fuentes, N., Gil-Romera, G., Montoya, E., 2007. Pleistocene landscapes in central Iberia inferred from pollen analysis of hyena coprolites. *J. Quat. Sci.* 22, 191–202.
- Castaños, P., 1983. Estudio de los macromamíferos del yacimiento prehistórico de Bolinkoba (Abadiano-Vizcaya). *Kobie. Serie Paleantropología* 13, 261–298.
- Castaños, P., 2010. Nuevas cavidades con carnívoros y humanos en el Cantábrico oriental. *Zona Arqueológica* 13, 263–268.
- Castaños, P., 2014. Estudio de los macromamíferos del yacimiento de Santa Catalina. *Kobie. Serie Paleantropología* 4, 331–360.
- Castaños, P., 2018. Revisión sistemática de la fauna a lo largo de los distintos niveles y horizontes culturales, in: Castaños, P.M. (Ed.), *El Castillo: Historia de una fauna olvidada. La fauna de las excavaciones históricas (1910-1914) de la cueva de El Castillo (Puente Viesgo, Cantabria)*. Monografías del Museo de Prehistoria y Arqueología de Cantabria, Cantabria (Spain), pp. 88–135.
- Castañón, J., Castañón, P., Murelaga, X., Alonso-Olazabal, A., 2012. Kiputz IX: un conjunto singular de bisonte estepario (*Bison priscus* Bojanus, 1827) del Pleistoceno superior de la Península Ibérica. *Ameghiniana* 49, 247–261.
- Cerdeño, E., 1990. *Stephanorhinus hemitoechus* (falc.) (Rhinocerotidae, Mammalia) del Pleistoceno Medio y Superior de España. *Estud. Geol.* 46, 465–479.
- Cheyland, M., 1981. Biologie et écologie de la tortue d'Hermann *Testudo hermanni* Gmelin, 1789. In: *Contribution de l'espèce à la connaissance des climats quaternaires de la France*. EPHE, Montpellier (France).
- Cortés-Sánchez, M., Riquelme-Cantal, J.A., Simón-Vallejo, M.D., Parrilla Giráldez, R., Odriozola, C.P., Calle Román, L., Carrión, J.S., Monge Gómez, G., Rodríguez Vidal, J., Moyano Campos, J.J., Rico Delgado, F., Nieto Julián, J.E., Antón García, D., Martínez-Aguirre, M.A., Jiménez Barredo, F., Cantero-Chinchilla, F.N., 2018. Pre-Solutrean rock art in southernmost Europe: evidence from Las Ventanas Cave (Andalusia, Spain). *PLOS ONE* 13, e0204651.
- Cueto, M., Camarós, E., Castaños, P.M., Ontañón, R., Arias, P., 2020. Highlighting the role of carnivores as a multifunctional resource among the middle Magdalenian: the case of the lower gallery of La Garma (Cantabria, Spain). *J. Archaeol. Sci. Report* 30, 102221.
- Dabney, J., Knapp, M., Glocke, I., Gansauge, M.-T., Weihmann, A., Nickel, B., Valdiosera, C., García, N., Pääbo, S., Arsuaga, J.L., Meyer, M., 2013. Complete mitochondrial genome sequence of a Middle Pleistocene cave bear reconstructed from ultrashort DNA fragments. *Proc. Natl. Acad. Sci. Unit. States Am.* 110, 15758–15763.
- Desrosiers, P.M., 2012. *The Emergence of Pressure Blade Making: from Origin to Modern Experimentation*. Springer-Verlag, New York (USA).
- Díez Fernández-Lomana, C., Jordá Pardo, J.F., Arribas Herrera, A., 1998. Torrejones (Tamajón, Guadalajara, Spain). A hyaena den on human occupation. *Economie préhistorique: les comportements de subsistance au Paléolithique*. Editions APDCA. Sophia Antipolis 63–72.
- Dominguez-Rodrigo, M., de Juana, S., Galán, A.B., Rodríguez, M., 2009. A new protocol to differentiate trampling marks from butchery cut marks. *J. Archaeol. Sci.* 36, 2643–2654.
- Driesch, A.V.d., 1976. *A Guide to Measurement for Animals Bones from Archaeological Sites*. Harvard University Peabody Museum of Archaeology and Ethnology.
- Eisenmann, V., Mashkour, M., 1999. The small equids of Binagady (Azerbaijan) and Qazvin (Iran): *E. hemionus* Binagadensis nov. subsp. and *E. hydruntinus*. *Geobios* 32, 105–122.
- ESRI, 2011. Release 10. Environmental Systems Research Institute. ArcGIS Desktop.
- Estévez, J., 1987. La fauna de L'Arbreda (sector Alfa) en el conjunt de faunes del Pleistocè superior. *Cypsel* 6, 73–87.
- Fabián García, J.F., 1995. El aspecto funerario durante el Calcolítico y los inicios de la Edad de Bronce en la Meseta Norte. In: *El enterramiento colectivo en fosa de «El Tomillar» (Bercial de Zapardiel, Ávila)*. Ediciones Universidad de Salamanca, Salamanca (Spain).
- Falguères, C., Yokoyama, Y., Arrizabalaga, A., 2005. La Geocronología del yacimiento pleistocénico de Lezetxiki (Arrasate, País Vasco). *Crítica de las dataciones existentes y algunas nuevas aportaciones*. *Munibe* 57, 93–106.
- Fernández, S., Fuentes, N., Carrión, J.S., González-Sampériz, P., Montoya, E., Gil, G., Vega-Toscano, G., Riquelme, J.A., 2007. The Holocene and Upper Pleistocene pollen sequence of Carihuela cave, southern Spain. *Geobios* 40, 75–90.
- Fu, Q., Meyer, M., Gao, X., Stenzel, U., Burbano, H.A., Kelso, J., Pääbo, S., 2013. DNA analysis of an early modern human from Tianyuan Cave, China. *Proc. Natl. Acad. Sci. Unit. States Am.* 110, 2223–2227.
- Gabucio, M.J., Cáceres, I., Rodríguez-Hidalgo, A., Rosell, J., Saladié, P., 2014. A wildcat (*Felis silvestris*) butchered by neanderthals in level O of the Abric Romaní site (Capellades, Barcelona, Spain). *Quat. Int.* 326–327, 307–318.
- García, N., 2003. Osos y otros carnívoros de la Sierra de Atapuerca. Fundación Oso, Asturias, Oviedo.
- García, N., Arsuaga, J.L., 1999. Carnívoros from the Early Pleistocene hominid-bearing trinchera Dolina 6 (Sierra de Atapuerca, Spain). *J. Hum. Evol.* 37, 415–430.
- Gee, H., 1993. The distinction between postcranial bones of *Bos primigenius* Bojanus, 1827 and *Bison priscus* Bojanus, 1827 from the British Pleistocene and the taxonomic status of *Bos* and *Bison*. *J. Quat. Sci.* 8, 79–92.
- Ghezzo, E., Rook, L., 2015. The remarkable *Panthera pardus* (Felidae, Mammalia) record from Equi (Massa, Italy): taphonomy, morphology, and paleoecology. *Quat. Sci. Rev.* 110, 131–151.
- Ghinassi, M., Colonese, A.C., Giuseppe, Z.D., Govoni, L., Vetro, D.L., Malavasi, G., Martini, F., Ricciardi, S., Sala, B., 2009. The Late Pleistocene clastic deposits in the Romito Cave, southern Italy: a proxy record of environmental changes and human presence. *J. Quat. Sci.* 24, 383–398.
- Gómez-Olivencia, A., Sala, N., Arceredillo, D., García, N., Martínez-Pillado, V., Rios-Garaizar, J., Libano, I., 2015. The Punta Lucero Quarry site (Zierbena, Bizkaia): a window into the Middle Pleistocene in the Northern Iberian Peninsula. *Quat. Sci. Rev.* 121, 52–74.
- González Echegaray, J., Freeman, L.G., 2015. Excavando la cueva de El Juyo. Un santuario de hace 14000 años. Museo Nacional y Centro de Investigación de Altamira.
- González Echegaray, J., Freeman, L.G., 1992/1993. Las excavaciones de la cueva del Juyo (Cantabria). *Kobie* 20, 29–42.
- Grandal-d'Anglade, A., Vidal-Romaní, J.R., Vaquero-González, M., Méndez, E., 2006. A new cave in Galicia (NW Spain) with recent cave bear remains: preliminary report. In: *Scientific Annals. School of Geology Aristotle University of Thessaloniki (AUTH)* 98, pp. 173–177.
- Grandal-d'Anglade, A., Pérez-Rama, M., García-Vázquez, A., González-Fortes, G.M., 2019. The cave bear's hibernation: reconstructing the physiology and behaviour of an extinct animal. *Hist. Biol.* 31, 429–441.



- Hernández-Huerta, P.P., López Olmedo, F., Cabra Gil, P., Rodríguez Fernández, L.R., 1994. Tamajón, mapa Geológico de España escala 1: 50.000. Instituto Geológico y Minero de España. Hoja 459, 20.
- Hughes, P.D., 2010. Geomorphology and Quaternary stratigraphy: the roles of morpho-, litho-, and allostratigraphy. *Geomorphology* 123, 189–199.
- Huguet, R., Arsuaga, J.L., Pérez-González, A., Arriaza, M.C., Sala, N., Laplana, C., Sevilla, P., García, N., Álvarez-Laó, D., Blain, H.-A., Baquedano, E., 2010. Homínidos y hienas en el Calvero de la Higuera (Pinilla del Valle, Madrid) durante el Pleistoceno Superior. Resultados preliminares. *Zona Arqueológica* 13, 444–458.
- Hunt, C., Davison, J., Inglis, R., Farr, L., Reynolds, T., Simpson, D., el-Rishi, H., Barker, G., 2010. Site formation processes in caves: the Holocene sediments of the Haua Fteah, Cyrenaica, Libya. *J. Archaeol. Sci.* 37, 1600–1611.
- Iñigo, C., Molero, G., Maldonado, E., 1998. Los carnívoros del yacimiento Pleistoceno de Cueva del Búho (Segovia, España) y sus huellas de actividad. *Estud. Geol.* 54, 65–73.
- Inizan, M.L., Reduron, M., Roche, H., Tixier, J., 1995. Technologie de la pierre taillée. "Préhistoire de la Pierre Taillée". CREP, Meudon.
- Jónsson, H., Ginolhac, A., Schubert, M., Johnson, P.L.F., Orlando, L., 2013. mapDamage2.0: fast approximate Bayesian estimates of ancient DNA damage parameters. *Bioinformatics* 29, 1682–1684.
- Jordá-Pardo, J.F., Mestres Torres, J.S., 1999. El enterramiento Calcólico pre-campaniforme de Jarama II: una nueva fecha radiocarbónica para la Prehistoria Reciente de Guadalajara y su integración en la cronología de la región. *Zephyrus* 52, 175–190.
- Kehl, M., Burrow, C., Hilgers, A., Navazo, M., Pastoors, A., Weniger, G.-C., Wood, R., Jordá Pardo, J.F., 2013. Late Neanderthals at Jarama VI (central Iberia)? *Quat. Res.* 80, 218–234.
- Kehl, M., Álvarez-Alonso, D., de Andrés-Herrero, M., Díez-Herrero, A., Klasen, N., Rethemeyer, J., Weniger, G.-C., 2018. The rock shelter Abrigo del Molino (Segovia, Spain) and the timing of the late Middle Paleolithic in Central Iberia. *Quat. Res.* 90, 180–200.
- Kircher, M., Sawyer, S., Meyer, M., 2012. Double indexing overcomes inaccuracies in multiplex sequencing on the Illumina platform. *Nucleic Acids Res.* 40 e3–e3.
- Krasinski, K.E., 2018. Multivariate evaluation of criteria for differentiating cut marks created from steel and lithic implements. *Quat. Int.* 466, 145–156.
- Kruuk, H., 1972. *The Spotted Hyena: a Study of Predation and Social Behavior*. The University Chicago Press, Chicago.
- Laplana, C., Sevilla, P., Arsuaga, J.L., Arriaza, M.C., Baquedano, E., Pérez-González, A., López-Martínez, N., 2015. How far into Europe did pikas (Lagomorpha: Ochotonidae) go during the Pleistocene? New evidence from central Iberia. *PLoS ONE* 10, e0140513.
- Laplana, C., Sevilla, P., Blain, H.-A., Arriaza, M.C., Arsuaga, J.L., Pérez-González, A., Baquedano, E., 2016. Cold-climate rodent indicators for the Late Pleistocene of Central Iberia: new data from the Buena Pinta Cave (Pinilla del Valle, Madrid Region, Spain). *C.R. Palevol* 15, 696–706.
- Larkin, N.R., Alexander, J., Lewis, M.D., 2000. Using experimental studies of recent faecal material to examine hyaena coprolites from the West Runton Freshwater bed, Norfolk, U.K. *J. Arch. Sci.* 27, 19–31.
- Lister, A.M., 1996. The morphological distinction between bones and teeth of fallow deer (*Dama dama*) and red deer (*Cervus elaphus*). *Int. J. Osteoarchaeol.* 6, 119–143.
- Luff, R.M., Moreno García, M., 1995. Killing cats in the medieval period. An unusual episode in the history of Cambridge. *Archaeofauna* 4, 93–114.
- Luque-Larena, J.J., Gosálbez, J., 2007. Topillo nival (*Chionomys nivalis* martini, 1842). In: Palomo, L.J., Gisbert, J., Blanco, J.C. (Eds.), *Atlas y libro rojo de los mamíferos terrestres de España*. Dirección General para la Biodiversidad-SECEM-SECEMU, Madrid, pp. 410–412.
- Made, J.V.d., 2013. First description of the large mammals from the locality of Penal, and updated faunal lists for the Atapuerca ungulates *Equus altidens*, *Bison*; and human dispersal into Western Europe. *Quat. Int.* 295, 36–47.
- Madelaine, L.A., Elster, A.D., 1995. Suture closure in the human chondrocranium: CT assessment. *Radiology* 196, 747–756.
- Maldonado, E., 1996. Revisión de los équidos del Pleistoceno Medio y Superior de España. Universidad Complutense de Madrid. Madrid (Spain).
- Mariezcurrera, K., 2011. Hallazgos de macromamíferos poco frecuentes en yacimientos arqueológicos y paleontológicos del Pleistoceno de la región cántabra. *Kobie. Serie Paleantropología* 30, 83–110.
- Marin-Monfort, M.D., Suñer, M., Fernández-Jalvo, Y., 2018. Characterization of recent marks produced on fossil bone surface during sullegic and trephic processes and their influence on taphonomic studies. *Quat. Int.* 481, 3–13.
- Maroto, J., Vaquero, M., Arrizabalaga, A., Baena, J., Baquedano, E., Jordá, J., Juliá, R., Montes, R., Van Der Plicht, J., Rasines, P., Wood, R., 2012. Current issues in late Middle Palaeolithic chronology: new assessments from northern Iberia. *Quat. Int.* 247, 15–25.
- Martínez Navarrete, M.I., 1984. El comienzo de la metalurgia en la provincia de Madrid: la cueva y el cerro de Juan Barbero (Tielmes). *Trab. Prehist.* 41, 17–128.
- Martini, I., 2011. Cave clastic sediments and implications for speleogenesis: new insights from the Mugnano cave (Montagnola Senese, northern Apennines, Italy). *Geomorphology* 134, 452–460.
- Mittnik, A., Wang, C.-C., Svoboda, J., Krause, J., 2016. A molecular approach to the sexing of the triple burial at the Upper Paleolithic site of Dolní Věstonice. *PLOS ONE* 11, e0163019.
- Morales, J.L., Cebrià, A., Burguet-Coca, A., Fernández-Marchena, J.L., García-Argudo, G., Rodríguez-Hidalgo, A., Soto, M., Talamo, S., Tejero, J.-M., Vallverdú, J., Fullola, J.M., 2019. The Middle-to-Upper Paleolithic transition occupations from Cova Foradada (Calafell, NE Iberia). *PLOS ONE* 14.
- Morales-Pérez, J.V., Sanchis-Serra, A., 2009. The Quaternary fossil record of the genus *Testudo* in the Iberian Peninsula. Archaeological implications and diachronic distribution in the western Mediterranean. *J. Archaeol. Sci.* 36, 1152–1162.
- NACSN, 2005. North American stratigraphic code. AAPG (Am. Assoc. Pet. Geol.) Bull. 89, 1547–1591.
- Navazo Ruiz, M., Jordá Pardo, J.F., Burrow, C., Kehl, M., Pastoors, A., Weniger, G.C., Wood, R., 2020. Last neanderthal occupations at central Iberia: the lithic industry of Jarama VI rock shelter (Valdesotos, Guadalajara, Spain). *Archaeol. Anthropol. Sci.* 12, 45.
- NGRIP Dating Group, 2008. Greenland ice core chronology 2005 (GICC05) 60,000 Year, 20 year resolution. <ftp://ftp.ncdc.noaa.gov/pub/data/paleo/icecore/greenland/summit/ngrip/gicc05-60ka-20yr.txt>.
- Olalde, I., Mallick, S., Patterson, N., Rohland, N., Villalba-Mouco, V., Silva, M., Dulias, K., Edwards, C.J., Gandini, F., Pala, M., Soares, P., Ferrando-Bernal, M., Adamski, N., Broomandkshobacht, N., Cheronet, O., Culleton, B.J., Fernandes, D., Lawson, A.M., Mah, M., Oppenheimer, J., Stewardson, K., Zhang, Z., Jiménez Arenas, J.M., Toro Moyano, I.J., Salazar-García, D.C., Castanyer, P., Santos, M., Tremolela, J., Lozano, M., García Borja, P., Fernández-Eraso, J., Mujika-Alustiza, J.A., Barroso, C., Bermúdez, F.J., Viguera Mínguez, E., Burch, J., Coromina, N., Vivó, D., Cebrià, A., Fullola, J.M., García-Puchol, O., Morales, J.L., Oms, F.X., Majó, T., Vergès, J.M., Díaz-Carvajal, A., Ollich-Castanyer, I., López-Cachero, F.J., Silva, A.M., Alonso-Fernández, C., Delibes de Castro, G., Jiménez Echevarría, J., Moreno-Márquez, A., Pascual Berlanga, G., Ramos-García, P., Ramos-Muñoz, J., Vijande Vila, E., Aguilera Arzo, G., Esparza Arroyo, A., Lillios, K.T., Mack, J., Velasco-Vázquez, J., Waterman, A., Benítez de Lugo Enrich, L., Benito Sánchez, M., Agustí, B., Codina, F., de Prado, G., Estalrich, A., Fernández Flores, Á., Finlayson, C., Finlayson, G., Finlayson, S., Giles-Guzmán, F., Rosas, A., Barciela González, V., García Atiénzar, G., Hernández Pérez, M.S., Llanos, A., Carrión Marco, Y., Collado Beneyto, I., López-Serrano, D., Sanz Tormo, M., Valera, A.C., Blasco, C., Liesau, C., Ríos, P., Daura, J., de Pedro Michó, M.J., Díez-Castillo, A.A., Flores Fernández, R., Francés Farré, J., Garrido-Pena, R., Gonçalves, V.S., Guerra-Doce, E., Herrero-Corral, A.M., Juan-Cabanilles, J., López-Reyes, D., McClure, S.B., Merino Pérez, M., Oliver Foix, A., Sanz Borrás, M., Sousa, A.C., Vidal Encinas, J.M., Kennett, D.J., Richards, M.B., Werner Alt, K., Haak, W., Pinhasi, R., Lalueza-Fox, C., Reich, D., 2019. The genomic history of the Iberian Peninsula over the past 8000 years. *Science* 363, 1230–1234.
- Pablos, A., Gómez-Olivencia, A., García-Pérez, A., Martínez, I., Lorenzo, C., Arsuaga, J.L., 2013. From toe to head: use of robust regression methods in stature estimation based on foot remains. *Forensic Sci. Int.* 226, 299.e1–299.e7.
- Pablos, A., Sala, N., Arribas, A., 2018. Taxonomic reassignment of the Paleolithic human navicular from Cueva de los Torrejones (Guadalajara, Spain). *Archaeol. Anthropol. Sci.* 10, 1867–1880.
- Pablos, A., Sala, N., Arribas, A., In press. Direct dating of the human navicular from the Cueva de los Torrejones (Guadalajara, Spain). *Radiocarbon* <https://doi.org/10.1017/RDC.2020.92>.
- Pandolfi, L., Tagliacozzo, A., 2015. *Stephanorhinus hemitoechus* (Mammalia, Rhinocerotidae) from the late Pleistocene of Valle Radice (Sora, central Italy) and re-evaluation of the morphometric variability of the species in Europe. *Geobios* 48, 169–191.
- Pelegrin, J., Karlin, C., Bodu, P., 1988. Chaînes opératoires: un outil pour le préhistorien, Technologie préhistorique. "Notes et Monographies techniques" CNRS. Paris (France).
- Peltzer, A., Jäger, G., Herbig, A., Seitz, A., Kniep, C., Krause, J., Nieselt, K., 2016. EAGER: efficient ancient genome reconstruction. *Genome Biol.* 17, 60.
- Pokines, J., Symes, S.A., 2013. *Manual of Forensic Taphonomy*. CRC Press.
- Quam, R.M., Arsuaga, J.L., Bermúdez de Castro, J.M., Díez, J.C., Lorenzo, C., Carretero, J.M., García, N., Ortega, A.I., 2001. Human remains from Valdegoba cave (Huérmedes, Burgos, Spain). *J. Hum. Evol.* 41, 385–435.
- R-Core-Team, 2016. A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna (Austria).
- Raxter, M.H., Ruff, C.B., Auerbach, B.M., 2007. Technical note: revised fully stature estimation technique. *Am. J. Phys. Anthropol.* 133, 817–818.
- Renaud, G., Slon, V., Duggan, A.T., Kelso, J., 2015. Schmutzi: estimation of contamination and endogenous mitochondrial consensus calling for ancient DNA. *Genome Biol.* 16, 224.
- Rodríguez, R., Ramírez, O., Valdósera, C.E., García, N., Alda, F., Madurell-Malapeira, J., Marmi, J., Doadrio, I., Willerslev, E., Götherström, A., Arsuaga, J.L., Thomas, M.G., Lalueza-Fox, C., Dalén, L., 2011. 50,000 years of genetic uniformity in the critically endangered Iberian lynx. *Mol. Ecol.* 20, 3785–3795.
- Rodríguez-Almagro, M., Sala, N., Wißing, C., Arriolabengoa, M., Etxeberria, F., Rios-Garaizar, J., Gómez-Olivencia, A., 2020. Ecological conditions during the Middle to Upper Paleolithic transition (MIS 3) in Iberia: the cold-adapted faunal remains from Mainea, northern Iberian Peninsula. *Boreas*. <https://doi.org/10.1111/bor.12501>.
- Rodríguez-Hidalgo, A., Sanz, M., Daura, J., Sánchez-Marco, A., 2020. Taphonomic criteria for identifying Iberian lynx dens in quaternary deposits. *Sci. Rep.* 10, 7225.
- Rodríguez-Varela, R., García, N., Nores, C., Álvarez-Laó, D., Barnett, R., Arsuaga, J.L., Valdósera, C., 2016. Ancient DNA reveals past existence of Eurasian lynx in Spain. *J. Zool.* 298, 94–102.
- Rohland, N., Harney, E., Mallick, S., Nordenfett, S., Reich, D., 2015. Partial uracil-DNA-glycosylase treatment for screening of ancient DNA. *Phil. Trans. R. Soc.* 370,

- 20130624.
- Rosell, J., Blasco, R., 2009. Home sharing: carnivores in anthropogenic assemblages of the Middle Pleistocene. *J. Taphonomy* 7, 305–324.
- Rosell, J., Blasco, R., Rivals, F., Chacón, M.G., Menéndez, L., Morales, J.L., Rodríguez-Hidalgo, A., Cebriá, A., Carbonell, E., Serrat, D., 2010. A stop along the way: the role of Neanderthal groups at level III of Teixoneres cave (Moià, Barcelona, Spain). *Quaternaire* 21, 139–154.
- Ruff, C.B., Holt, B.M., Niskanen, M., Sladák, V., Berner, M., Garofalo, E., Garvin, H.M., Hora, M., Maijanen, H., Niinimäki, S., Salo, K., Schuplerová, E., Tompkins, D., 2012. Stature and body mass estimation from skeletal remains in the European Holocene. *Am. J. Phys. Anthropol.* 158, 601–617.
- Ruiz Bustos, A., 2000. Estudio paleoecológico de los sedimentos con presencia del hombre de Neandertal en la Cueva de la Carihuela (Piñar, Granada). Ayuntamiento de Piñar.
- Sala, N., Arsuaga, J.L., 2018. Regarding beasts and humans: a review of taphonomic works with living carnivores. *Quat. Int.* 466, 131–140.
- Sala, N., Arsuaga, J.L., Laplana, C., Zapata, B.R., Gil García, M.J., García, N., Aranburu, A., Algaba, M., 2011. Un paisaje de la meseta durante el Pleistoceno Superior. Aspectos paleontológicos de la Cueva de la Zarzamora (Segovia, España). *Bol. R. Soc. Esp. Hist. Nat.* 105, 67–85.
- Sala, N., Algaba, M., Arsuaga, J.L., Aranburu, A., Pantoja, A., 2012. A Taphonomic study of the Búho and Zarzamora caves. Hyenas and humans in the Iberian Plateau (Segovia, Spain) during the Late Pleistocene. *J. Taphonomy* 10, 477–498.
- Sala, N., Arsuaga, J.L., Haynes, G., 2014. Taphonomic comparison of bone modifications caused by wild and captive wolves (*Canis lupus*). *Quat. Int.* 330, 126–135.
- Sala, N., Arsuaga, J.L., Martínez, I., Gracia-Téllez, A., 2015. Breakage patterns in Sima de los Huesos (Atapuerca, Spain) hominin sample. *J. Archaeol. Sci.* 55, 113–121.
- Sala, N., Pablos, A., Gómez-Olivencia, A., Sanz, A., Villalba, M., Pantoja-Pérez, A., Laplana, C., Arsuaga, J.L., Algaba, M., 2020. Central Iberia in the Middle MIS 3. Paleocological inferences during the period 34–40 cal kyr BP. *Quat. Sci. Rev.* 228, 106027.
- Sanchis, A., Morales, J.V., Pérez, L.J., Hernández, C.M., Galván, B., 2015a. La tortuga mediterránea en yacimientos valencianos del Paleolítico Medio: distribución, origen de las acumulaciones y nuevos datos procedentes del Abric del Pastor (Alcoi, Alacant). In: Sanchis Serra, A., Pascual Benito, J.L. (Eds.), *Preses petites i grups humans en el passat. II Jornades d'arqueozoologia*. Museu de Prehistòria de València, Valencia (Spain), pp. 97–120.
- Sanchis, A., Tormo, C., Sauqué, V., Sanchis, V., Díaz, R., Ribera, A., Villaverde, V., 2015b. Pleistocene leopards in the Iberian Peninsula: new evidence from palaeontological and archaeological contexts in the Mediterranean region. *Quat. Sci. Rev.* 124, 175–208.
- Sanchis, A., Tormo, C., Sauqué, V., 2017. Leopards del Pleistoceno en el territorio valenciano. In: Sanchis, A., Pascual Benito, J.L. (Eds.), *Interaccions entre felins i humans. III Jornades d'arqueozoologia*. Museu de Prehistòria de València, Valencia (Spain), pp. 81–92.
- Sauqué, V., Cuenca-Bescós, G., 2013. The Iberian Peninsula, the last European refugium of *Panthera pardus* Linnaeus 1758 during the Upper Pleistocene. *Quaternaire* 24, 35–48.
- Scheuer, L., Black, S., 2000. *Developmental Juvenile Osteology*. Academic Press, London.
- Stiner, M.C., 1994. *Honor Among Thieves. A Zooarchaeological Study of Neandertal Ecology*. Princeton University Press, New Jersey.
- Stiner, M.C., Kuhn, S.L., Weiner, S., Bar-Yosef, O., 1995. Differential burning, recrystallization, and fragmentation of archaeological bone. *J. Archaeol. Sci.* 22, 223–237.
- Stuart, A.J., Lister, A.M., 2014. New radiocarbon evidence on the extirpation of the spotted hyaena (*Crocuta crocuta* (Erxl.)) in northern Eurasia. *Quat. Sci. Rev.* 96, 108–116.
- Testu, A., Moigne, A.M., De Lumley, H., 2011. La panthère *Panthera pardus* des niveaux inférieurs de la Caune de L'Arago à Tautavel (Pyrénées-Orientales, France) dans le contexte des Felidae (Felinae, Pantherinae) de taille moyenne du Pléistocène européen. *Quaternaire. Hors-série* 4, 271–281.
- Torres, T.J.d., 1984. Úrsidos del Pleistoceno-Holoceno de la Península Ibérica, Ingeniería Geológica. E.T.S.I. Minas (UPM).
- Torres, T.d., 1996. El yacimiento paleontológico de la Cueva del Reguerillo. In: Espeleología, F.M.d. (Ed.), *La Cueva del Reguerillo y su entorno: un estudio multidisciplinar*, pp. 7–18.
- Utrilla, P., Mazo, C., Lorenzo, J.J., 2013–2014. Rituales funerarios en el Calcolítico de Abauntz. Un ejemplo de lesión con supervivencia. *Saldvie* 13–14, 297–314.
- Val, A., Maille, J.-B., 2011. Small carnivore skinning by professionals: skeletal modifications and implications for the European Upper Palaeolithic. *J. Taphonomy* 9, 221–243.
- Valdiosera, C., Günther, T., Vera-Rodríguez, J.C., Ureña, I., Iriarte, E., Rodríguez-Varela, R., Simões, L.G., Martínez-Sánchez, R.M., Svensson, E.M., Malmström, H., Rodríguez, L., Bermúdez de Castro, J.M., Carbonell, E., Alday, A., Hernández Vera, J.A., Götherström, A., Carretero, J.M., Arsuaga, J.L., Smith, C.I., Jakobsson, M., 2018. Four millennia of Iberian biomolecular prehistory illustrate the impact of prehistoric migrations at the far end of Eurasia. *Proc. Natl. Acad. Sci. Unit. States Am.* 115, 3428–3433.
- Vergès, J.M., Allué, E., Fontanals, M., Morales, J.L., Martín, P., Carrancho, Á., Expósito, I., Guardiola, M., Lozano, M., Marsal, R., Oms, X., Euba, I., Rodríguez, A., 2016. El Mirador cave (Sierra de Atapuerca, Burgos, Spain): a whole perspective. *Quat. Int.* 414, 236–243.
- Vianello, D., Sevinci, F., Castellani, G., Lomartire, L., Capri, M., Franceschi, C., 2013. HAPLOFIND: a new method for high-throughput mtDNA haplogroup Assignment. *Hum. Mutat.* 34, 1189–1194.
- Villa, P., Mahieu, E., 1991. Breakage patterns of human long bones. *J. Hum. Evol.* 21, 27–48.
- Villa, P., Soressi, M., 2000. Stone tools in carnivore sites: the case of Bois Roche. *J. Anthropol. Res.* 56, 187–215.
- White, W.B., 2007. Cave sediments and paleoclimate. *J. Cave Karst Stud.* 69, 76–93.
- White, T.D., Folkens, P.A., 2005. *The Human Bone Manual*. Elsevier Academic Press, New York.
- Wolf, D., Kolb, T., Alcaraz-Castaño, M., Heinrich, S., Baumgart, P., Calvo, R., Sánchez, J., Ryborz, K., Schäfer, I., Bliedtner, M., Zech, R., Zöller, L., Faust, D., 2018. Climate deteriorations and Neanderthal demise in interior Iberia. *Sci. Rep.* 8, 7048.