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Evidence of paleoecological changes and Mousterian occupations at the Galería de las Estatuas site, Sierra de Atapuerca, northern Iberian plateau, Spain

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Abstract

Here we present a new site in the Sierra de Atapuerca (Burgos, Spain): Galería de las Estatuas (GE), which provides new information about Mousterian occupations in the Iberian Plateau. The GE was an ancient entrance to the cave system, which is currently closed and sealed by a stalagmitic crust, below which a detritic sedimentary sequence of more than 2 m is found. This has been divided into five litostratigraphic units with a rich assemblage of faunal and lithic remains of clear Mousterian affinity. Radiocarbon dates provide minimum ages and suggest occupations older than 45 ^{14}C ka BP. The palynological analysis detected a landscape change to increased tree coverage, which suggests that the sequence recorded a warming episode. The macromammal assemblage is composed of both ungulates (mainly red deer and equids) and carnivores. Taphonomic analysis reveals both anthropic, and to a lesser extent, carnivore activities. The GE was occupied by Neanderthals and also sporadically by carnivores. This new site broadens the information available regarding different human occupations at the Sierra de Atapuerca, which emphasizes the importance of this site-complex for understanding human evolution in Western Europe.

Keywords: Middle Paleolithic; Neanderthal; Iberian Peninsula; Late Pleistocene

INTRODUCTION

The Iberian Peninsula is the largest of the southern European peninsulas and has played an important role as one of the multiple faunal and human refugia during the harshest glacial cycles of the Pleistocene. Despite its southern latitude, a significant proportion of this peninsula's territory exceeds 700 m above mean sea level (AMSL) and there are different mountain systems that separate/border the main fluvial basins. Together with the geology of the area, this results in a complex landscape and ecological conditions that explain its rich biodiversity with high endemism, despite being the *cul-de-sac* of the so-called European peninsula.

The northern Iberian plateau (*meseta norte*) is the section of the central Iberian plateau that is located north of the Central system (Fig. 1). It is characterized by a Mediterranean climate with continental climate traits. Thus, the northern plateau, even

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Figure 1. (color online) General location of the Sierra de Atapuerca sites (red star) in the Iberian Peninsula, and its position at the end of the Bureba corridor (small image; modified from Ortega et al., 2013). In this image we also show selected geographical elements, as well as selected Mousterian sites mentioned in the text. Foradà, Cova Foradà; Gegant, Cova del Gegant; Gibraltar, Vanguard cave and Gorham's cave; Hortigüela sites, La Mina, La Ermita, and Cueva Millán; Palomas, Sima de las Palomas site; Pinilla del Valle, Camino, Buena Pinta, Navalmaíllo, and Des-cubierta sites. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

in current conditions, registers low temperatures during its long winters and an extreme range of temperatures during its short summers, which would have made it a challenging environment during the cold phases of the Pleistocene. In fact, during Marine Isotope Stage (MIS) 2 the northern plateau was sparsely populated and locally depopulated (Straus et al., 2000; Delibes and Díez, 2006), but just how is still largely unknown.

In the last 15 years, new human fossil remains, new sites, and new analytical approaches have resulted in a better understanding of the cultural diversity, chronology, and occupation dynamics of Neanderthals in southern Europe (see below). These new results mainly refer to coastal areas of the Iberian Peninsula, which show milder conditions than those of the Iberian interior. In the northern Iberian fringe, the important site of El Sidrón is remarkable, having yielded new and important paleobiological (including genetic) and cultural data (Lalueza-Fox et al., 2005; Rosas et al., 2006, 2012). Additionally, the integrative study of the lithic remains from different Iberian Basque sites (e.g., Axlor) has resulted in a better understanding of cultural changes occurring in the northern fringe of the Iberian Peninsula (Rios-Garaizar et al., 2015a, 2015b; Rios-Garaizar, 2017).

The Iberian Levant has yielded new fossil remains from sites such as El Gegant, Cova Negra, Cova Foradà, Sima de las Palomas (Quam et al., 2001, 2015; Daura et al., 2005; Arsuaga et al., 2007; Walker et al., 2011a, 2011b; Lozano et al., 2013), and a large amount of information regarding Neanderthal occupations comes from Abric Romaní (e.g., Vallverdú et al., 2005, 2012; Burjachs et al., 2012, Rosell et al., 2012; Vaquero et al., 2015; Allué et al., 2017). The southern coast of the Iberian Peninsula is providing new data regarding landscape use, including the use of marine and avian resources (Stringer et al., 2008; Blasco et al., 2014).

Despite the growing evidence (e.g., Álvarez-Alonso et al., in press; Domingo et al., 2017, and references therein), the data available regarding the interior of the peninsula is still sparse. The Pinilla del Valle sites have provided human fossils and new information on the Neanderthal presence during MIS 5–4 (Baquedano et al., 2011–2012; Arsuaga et al., 2012). The cave of Gabasa has yielded a long stratigraphic sequence and several human remains (Lorenzo and Montes, 2001; Utrilla et al., 2010). In the southern Iberian plateau, Los Casares has yielded evidence of Mousterian occupations and one metacarpal bone (Basabe, 1973; Alcaraz-Castaño et al., 2015). In the northern plateau, Valdegoba has yielded several Neanderthal remains (which have also provided ancient DNA) and an abundant archaeo-paleontological assemblage (Díez et al., 1988–1989; Quam et al., 2001, Arceredillo et al., 2011; Dalén et al., 2012). Additional Mousterian occupations have been detected around Hortigüela (Burgos): the sites of La Ermita, Millán, and La Mina (Díez et al., 2008 and references therein). The area surrounding the Sierra de Atapuerca was also occupied by Neanderthals during MIS 4-3. The surface surveys performed at and around the Sierra de Atapuerca led to the discovery of 31 open-air sites with Middle Paleolithic lithic industries (Navazo et al., 2011; Navazo and Carbonell, 2014), which show that the Sierra de Atapuerca was inhabited by Neanderthals. Moreover, the dates of two of these sites (Hotel California and Hundidero) have yielded a chronological range from ca. 71 to 48 ka BP (Arnold et al., 2013). Furthermore, the Valle de las Orquídeas site, located at the top of the hill, was the first late Pleistocene open-air locality excavated at Sierra de Atapuerca. It yielded two thermoluminescence dates from the *terra-rossa* forming the stratigraphic sequences: 27,507 ± 2,295 years and 29,955 ± 2,319 years. The archaeological record includes 306 artifacts, which reflect a Middle Palaeolithic technical background with some Upper Palaeolithic features. No bone remains were preserved (Mosquera et al., 2007).

Despite the fact that Middle Paleolithic sites in the central Iberian plateau are known for both karstic and open-air environments, we lack information about how the abrupt climatic changes during the late Pleistocene potentially affected the ecological conditions in this large region of the Iberian Peninsula and whether or not Neanderthals changed their adaptive strategies in order to cope with these changes. Here we present the first results obtained from a new Middle Paleolithic site, Galería de las Estatuas (GE), located in the Sierra de Atapuerca, which provides a rich archaeological and paleontological (both macro and micro-vertebrate) assemblage, as well as important information on landscape changes based on pollen analysis. We provide a preliminary integrative analysis of this site, including the stratigraphy, the macro- and microfaunal analysis, and the taphonomic assessment of the macrofaunal remains, results from the palynological study of the sequence, and the study of the lithic assemblage.

SITE DESCRIPTION

The Galería de las Estatuas (GE) site within the Sierra de Atapuerca cave system

The Sierra de Atapuerca is located at the end of the Bureba corridor that connects the two most important basins (Ebro and Duero) of the Iberian Peninsula, and is also located between two mountain ranges (cordillera Cantábrica to the north, and Sierra de la Demanda to the south; Fig. 1). The Sierra de Atapuerca site complex (Burgos, northern Iberian plateau) is well known for its important middle and early Pleistocene human fossil remains, as well as its rich archaeological and paleontological assemblage that constitutes a window to more than 1 Ma of ecological and cultural changes (Arsuaga et al., 1993, 2014, 2015; Bermúdez de Castro et al., 1997; Carbonell et al., 1995, 2008; Rodríguez et al., 2011). Three additional sites (El Portalón, Galería del Sílex, and El Mirador) offer important information about the recent prehistory (Neolithic–Bronze age) in the northern Iberian plateau, and, in some cases, their sequences range from the end of the late Pleistocene to Medieval times (e.g., Carretero et al., 2008). Thus, several human species and populations have taken advantage of the Sierra de Atapuerca's strategic location during the last million years. There are some open-air sites surrounding the Sierra that have yielded Middle Paleolithic lithic remains, but no paleoecological information has been published to date. Therefore, the GE site provides new information, comprising both chronological and paleoecological aspects of the Neanderthal occupations of the Sierra de Atapuerca and the northern Iberian plateau. This information helps to fill the gap between the middle Pleistocene remains/occupations from Sima de los Huesos, Gran Dolina-TD10, upper levels of Trinchera Elefante and Trinchera Galería sites, those of the final late Pleistocene (Valle de las Orquídeas), and the Holocene sites of El Portalón, Galería del Sílex, and El Mirador.

The GE site is located in the upper level of the multilevel Torcas system, within the Cueva Mayor-Cueva del Silo complex (Fig. 1; Ortega, 2009). This upper level is a long (ca. 615 m) sub-horizontal passage, which is developed at the base level of the fluvial terrace T2 (+82/+86 m above Arlanzón River; Benito-Calvo and Pérez-González, 2015). This passage has an average size of over 10 m in width and 15 m in height, with places reaching 25 m (Ortega et al., 2013).

GE is located inside the cave and we interpret it as an ancient entrance to the cave system, which is currently closed and sealed by a stalagmitic flowstone (see below). Therefore, the site must presently be reached from one of the current entrances to the cave system, named El Portalón. The site is at ca. 1020 m AMSL and its approximate distance to the current external topography, extrapolating the orientation of the gallery, is around 18–20 m (Ortega, 2009). A first test pit (GE-I, ca. 2 m^2) was excavated in 2008 in order to assess the potential of this location as an archaeo-paleontological site. In 2009, a second test pit (GE-II, ca. 2 m^2) was opened, located west of GE-I and closer to the ancient cave entrance. In 2010, the first test pit was enlarged to ca. 9 m^2 and the second to ca. 6 m^2 (Fig. 2). Between these two pits, in the middle of the gallery, there is a large bell-shaped speleothem formation (ca. 1.5 m above the surrounding speleothem). Georadar analysis (Aranburu et al., 2012) detected that this place had different accommodation space during the deposition of the sedimentary sequence, which resulted in a kind of step from the more proximal to the cave entrance GE-II to the more distal GE-I, and which likely differentially affected the sedimentary processes in these two areas. Thus, for practical reasons, the study of the paleontological and lithic assemblages recovered from both test pits will be discussed separately. The potential correlations between the two test pits will be discussed later.

MATERIALS AND METHODS

Geological and geochemical analyses

Eight samples were taken from GE-I in order to perform the geological analysis (from clays to 3 cm clasts). Except for the first sample from lithostratigraphic (LU) unit 1 (LU1), which was taken from the excavation surface of square L30, the rest of the samples were taken from the M29-M30 northern profile, now partially destroyed due to the 2010 enlargement of the GE-I test pit. In GE-II, seven samples were analyzed: two

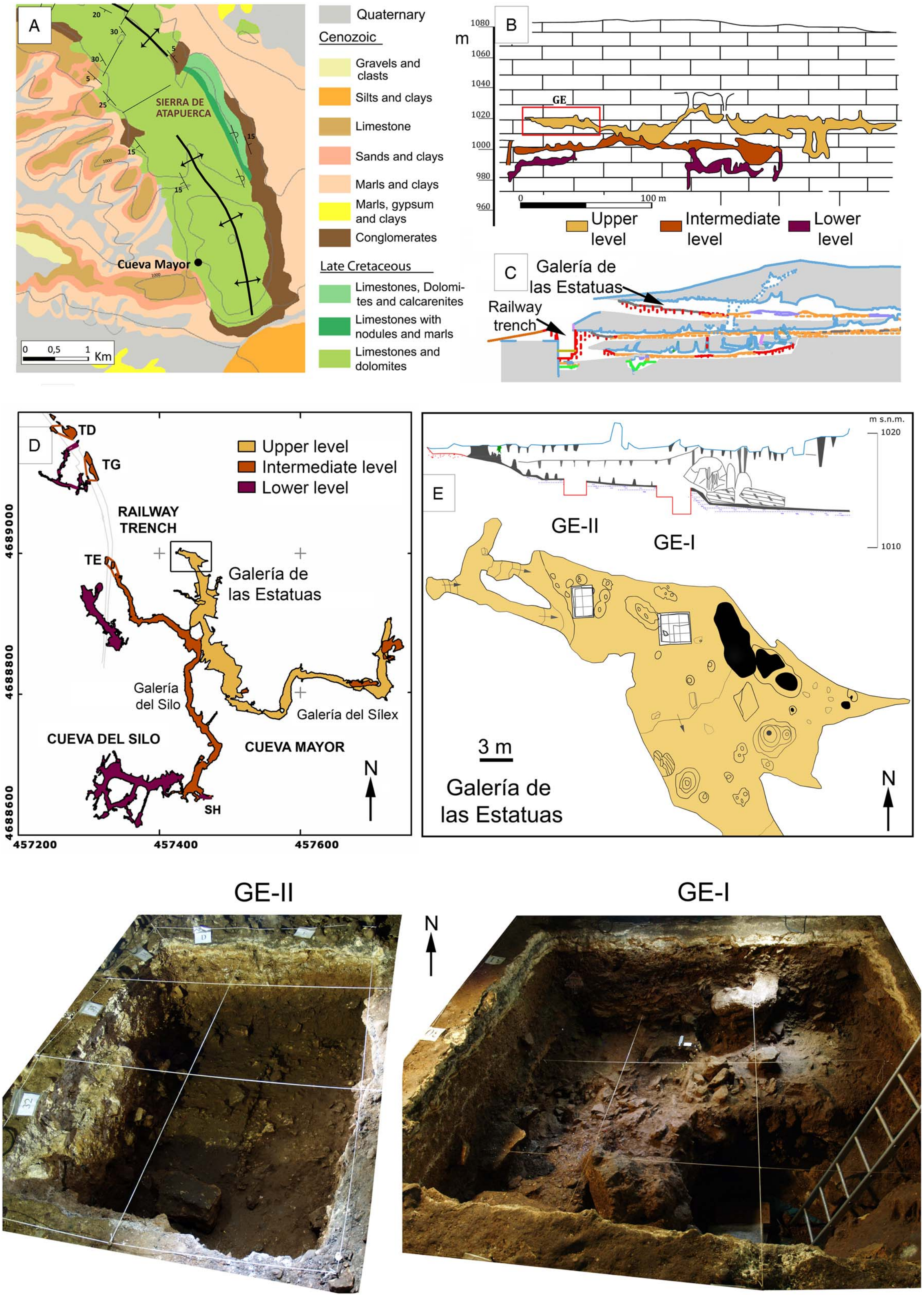

Figure 2. (color online) (A) General geological map of the Sierra de Atapuerca and the location of the Cueva Mayor cave, one of the entrances to the Cueva Mayor-Cueva del Silo cave system (modified from IGME). (B) Cross-section of Cueva Mayor-Cueva del Silo cave system on a topographical profile showing the highest point of the Sierra (modified from Ortega, 2009) and (C) a topographical profile closer to the galleries (modified from Ortega et al., 2014). (D) Map of the Cueva Mayor-Cueva del Silo cave system, with the location of the Galería de las Estatuas (modified from Ortega et al., 2013). (E) Detailed view and cross-section of the end of the Galería de las Estatuas and the position of the test pits GE-I and GE-II (based on Ortega, 2009). General view of the GE-I and GE-II test pits at the end of the 2015 field season. In the GE-I, the first test pit may be observed, before the enlargement of the excavation (the place where the stairs are located).

from LU1, which were taken from squares D34 and E33, and five more belonging to LU2, sampled from the western profile of squares D32 and D33.

Each 100 to 150 g sample was weighed in dry conditions to determine the total weight before undergoing laboratory procedures. The samples were sieved into different fractions, to separate clay, sand and gravel using 1, 2 and 4 mm mesh sizes. This sieving was carried out in wet conditions, to decant the clay. The resulting samples were dried in an oven around 50ºC, while periodically controlling the evaporation to avoid firing the clay fraction. Once dry, the samples were weighed again to determine the proportion of each fraction based on the total initial weight. Fractions of more than 4mm (coarse gravels), between 2 and 4 mm (fine gravel), and between 1 and 2 mm were studied visually when possible and under a binocular loupe. An approximate count was performed to determine the percentage of the different lithologies present in each sample, identifying authigenic materials from those outside of the cavity. Those grains of rock or mineral that were too small to be identified in hand specimens were prepared in a solution of epoxy resin (Norsodyne® O AL 13155 with a PMEK catalyst) to make thin sections and study them under optical microscopy.

The <1mm fraction sediment was divided to perform X-ray diffraction. The analysis of the total rock composition and clay mineralogy was conducted in the SgiKer laboratories of the Universidad del País Vasco/Euskal Herriko Unibertsitatea. Diffractograms were measured using a diffractometer PANalytical Xpert PRO equipped with a copper tube ($\lambda Cu_{K\alpha}$ mean ¼ 1.5418 Å, $\lambda Cu_{K\alpha 1}$ ¼ 1.54060 Å and $\lambda Cu_{K\alpha 2}$ ¼ 1.54439 Å), a vertical goniometer (Bragg-Brentano geometry), a programmable divergence slit, an automated simple changer, a secondary graphite monochromator and a PixCel detector.

Palynomorph extraction

The standard protocol for palynomorph extraction (Coûteaux, 1977) and pollen concentration (Girard and Renault-Miskovsky, 1969) was followed. The number of grains counted always exceeded 300. Pollen taxa were quantified using pollen diagrams with the computer package TILIA and TILIA-GRAPH (v.2; Grimm, 1987, 1992). Taxa were grouped as arboreal, shrubby, and herbaceous. Frequencies were computed from supreme base, excluding the pollen and spores from the aquatic vegetation. These percentages were calculated as the total sum of the palynomorph content in every sample.

Macrofaunal analysis

The taxonomical assessment was performed using osteological collections, as well as both standard atlases and specialized literature (Pales and Garcia, 1981a, 1981b; García, 2003; Sala et al., 2010). All the bone fragments were identified and quantified following the Number of Identified Specimens (NISP), Minimum Number of Elements (MNE), and Minimum Number of Individuals (MNI), according to skeletal element and portion (Lyman, 1994 and references therein). All the taxonomically identifiable remains and the fossil remains that provided a size of the animal were studied. Body size was established based on body mass and age-at-death of the animals (Bunn, 1986). In this study we divided taxa into three size classes: small, medium, and large. Small carnivores (i.e., *Vulpes vulpes*, *Meles meles*) are considered small-sized taxa; b) *Cervus elaphus* are considered medium-sized taxa; and c) large-sized ungulates (i.e., adult *Bos/Bison*, *Equus* sp.) are considered large-sized taxa.

Genetic analysis of equid remains

In order to identify the presence of *Equus hydruntinus* using a molecular approach, genetic analysis was performed on a lower right molar (M_1 or M_2, sample GE-189) recovered from GE-I, and based on external morphology, tentatively associated with *Equus hydruntinus*. The GE-189 DNA extraction was performed in the ancient DNA laboratory at Centro Mixto UCM-ISCIII (Madrid, Spain) using silica spin columns (Lira et al., 2010). Primers 15.425F–15.625R from Vilà et al. (2001) were incorporated into the mtDNA hypervariable region I (HVR-I) amplification step (nucleotide positions according to the newly proposed *Equus caballus* Reference Sequence, JN398377 from Achilli et al., 2012). Polymerase chain reaction setup was performed as in Lira et al. (2010). These primers amplify a fragment with a 28 base pair deletion between np. 15.533–15.560, only detected in *Equus kiang*, *Equus hemionus*, and *Equus hydruntinus* (Orlando et al., 2006).

Microfaunal analysis

All the sediment recovered from the site was wet-sieved using 0.5-mm screens. The mammals were classified in accordance with works by Chaline (1972), van der Meulen (1973), and Cuenca-Bescós (1999, 2009).

Taphonomic analysis

The taphonomic analysis was restricted to the macro-mammal assemblage. We studied all the taxonomically identifiable bone remains, as well as those that provide information about the size of the animal. In addition, non-identifiable bone fragments larger than 2 cm were also considered for the taphonomic analysis. The dental remains were studied but excluded from the taphonomic quantification. A total of 601 bone remains were studied, from all LUs from both GE-I (Number of remains, NR = 500) and GE-II (NR = 101).

The taphonomic study included: anthropogenic traces, fracture patterns, carnivore modification, and post-depositional alterations. All bones were macroscopically and microscopically examined (using a Nikon SMZ800 stereoscopic zoom microscope and a DINO-LITE digital microscope). Photographs were taken with the digital video microscope DINO-LITE AM-TFVW-A (*DinoCapture* 2.0 software).

Stone-tool modifications were classified as: cut marks (including incisions or slicing cut marks, scrape marks, and chop marks) and percussion marks (percussion pits, conchoidal scars and flakes, and adhered flakes; Shipman and Rose, 1983; Blumenschine and Selvaggio, 1988; Capaldo and Blumenschine, 1994; Blumenschine et al., 1996; Saladié et al., 2012; Rodríguez-Hidalgo et al., 2015). The location of cut marks was recorded since they may be used as criteria for distinguishing different butchery activities (Binford, 1981; White, 1992; Saladié et al., 2012). For the study of burned bones we followed the stages defined by Stiner et al. (1995).

The breakage patterns were analyzed on long bone fragments, following the methodology proposed by Villa and Mahieu (1991; see also Sala et al., 2015). The following parameters were taken into account: 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 one-quarter of the total diaphysis; 2 = between one-quarter and one-half of the total diaphysis; 3 = between one-half to three-quarters of the diaphysis; 4 = more than three-quarters of the diaphysis). The presence or absence of peeling was also recorded (White, 1992; Pickering et al., 2013).

Tooth marks on bone surfaces were classified as pits, punctures, furrowing, scores, and dissolution due to gastric acids. Punctures, scores, and pits were measured (length and width) in accordance with previous studies (Selvaggio and Wilder, 2001; Domínguez-Rodrigo and Piqueras, 2003; Sala et al., 2014; Sala and Arsuaga, in press). The length and breadth of tooth marks were measured using DINO-LITE digital microscope software tools.

Lithic analysis

The lithic assemblage was studied using the Logical Analytical System (LAS) method (Carbonell et al., 1983, 1992; Rodríguez, 2004; Ollé et al., 2013). The LAS approaches the study of technological processes based on the stage at which the objects were produced during the reduction sequence. All the pieces, including the fragments, were analyzed, which involved the raw material, the technical attributes of every lithic category, and the integrity of the reduction sequences.

The Sierra de Atapuerca and its surroundings offer a wide range of raw materials, with outcrops not further than 3 km from the sites. Five primary types of rocks were archaeologically identified in previous work (Mallol, 1999; Navazo et al., 2008; García-Antón, 2016) and all the lithic remains correspond to six groups of lithologies. Two of them, quartzite and metasandstone, are of metamorphic origin; two, including chert (Neogene and the Cretaceous varieties) and limestone (mainly fine mudstones), are of sedimentary origin; and macrocrystaline quartz is of filonian or hydrothermal origin.

Five lithic categories were taken into consideration: (1) hammerstones and percussive material (mainly pebbles and fractured pebbles, which we also refer to as "natural bases"); (2) cores; (3) flakes (whole flakes, broken flakes, and flake fragments); (4) flake tools or retouched flakes; and (5) knapping fragments. According to the LAS, there are two types of knapping sequences: exploitation sequences and configuration sequences (Rodríguez, 2004). The objective of the exploitation sequences (also called production sequences) is to obtain flakes. These processes for producing flakes consist of reducing the cores, which may be done using various knapping methods. Knapping methods were identified only when the technical features of the objects were clear. Knapping methods are defined by means of faciality (number of flaked faces), direction of extractions (unidirectional, bidirectional, centripetal), and arrangement of striking platforms (Rodríguez, 2004; Ollé et al., 2013). Archaeologically, they have been identified both on cores and to a lesser extent in products, which are much more difficult to assign.

The aim of the configuration processes is to retouch flakes or pebbles in order to obtain cutting edges with a certain morphology and angle. The result of these configuration processes can be pebble tools or flake tools (retouched flakes). Configuration processes were studied in accordance with LAS analytical procedures (Rodríguez, 2004), which focus on faciality, retouch attributes (portion of the perimeter modified, angle, extent, direction, delineation, and morphology), as well as on typological aspects (Laplace, 1972).

RESULTS

Geological and geochemical results

In both GE-I and GE-II, a detrital sequence is sealed with a stalagmitic flowstone of varying thickness, depending on its location. The stalagmitic crust thickens from GE-I towards the ancient cave entrance (GE-II). The detrital phase is of a clearly allochtonous nature, based on the presence of quartz, phyllosilicates, and different extraclasts (sandstone, gneiss, and iron oxides; Aranburu et al., 2012; Fig. 3). The description of the sediment, clasts, and lithology from the detrital sequences for both GE-I and GE-II is presented in Table 1. The analysis of clay minerals from the detrital sequences for both GE-I and GE-II using X-ray diphractometry is given in Table 2.

In GE-I, the excavations extend to a depth of ca. 2 m. From top to bottom, the geological sequence at the excavation zone starts with a stalagmitic flowstone, which is of varying thickness depending on its location, and which seals the site. This detrital sequence overlies an ancient flowstone that also occupies the east wall of the cave (Aranburu et al., 2012). The chronology of this flowstone appears to correspond to the Matuyama chron, but falls before 1.22 Ma, which is in concordance with the minimum age of the stabilization of the water table that matches the intermediate level of the karst (Parés et al., 2016). There is a lack of available information

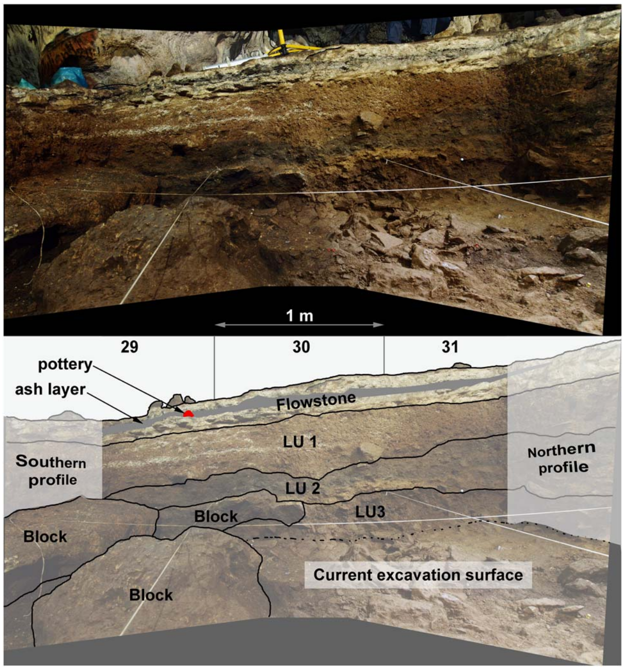

Figure 3. (color online) Western profile of GE-I at the end of the 2015 field season. LU, Lithostratigraphical unit.

regarding what happened between the deposition of the Matuyama age flowstone and the start of the GE-I detrital sequence. This detrital sequence has been divided into five LUs: LU5 is the oldest and LU1 is the most recent (Tables 1 and 2). LU5 is composed of pinkish degraded speleothem. LU4 is composed of dark clays with decimetric, planar, isolated, and very heterometric clasts. LU3 is composed of orangish silty clays, which are browner towards the base; it is matrix-supported and clasts are oblong at the base and more rounded at the top. LU2 is composed of black clays with silty orange sublevels and has abundant clasts, the size of which decreases towards the top of the level. LU1 is composed of orange clays with millimetric subhorizontal clast fragments. The detrital sequence is sealed by a speleothem, formed during the late Pleistocene (more than 14 ka, according to Martínez-Pillado et al., 2014) and evolves to dripping speleothem forms developed during the Holocene. Some ash-rich layers and charcoal fragments have been found within these stalagmites, corresponding to Neolithic and Bronze age human activity (Martínez-Pillado et al., 2014). A fine sediment layer, which contains some pottery fragments and is embedded inside the base of the stalagmites in certain areas of the site, is also attributed to these same periods.

In GE-II, the excavation has reached a depth of 1.5 m and there are differences in the composition from that of GE-I (Table 2), which could be due to the location of this sector (closer to the cave entrance, which is also evident from the abundance of plant roots in this sector of the cave), and/or to potential chronological differences between these two sectors. Future correlation analyses will provide more information about this particular aspect. The detrital sequence of GE-II has been divided into two LUs, the uppermost of which is further subdivided into two sublevels (see Tables 1 and 2). LU2, which is the lowermost level from GE-II, is composed of dark silty clay with decimetric, abundant, sharped-edged clasts. LU1b from GE-II is composed of orange clays with decimetric isolated clasts, while LU1a from GE-II is composed of light sands with subhorizontal, whitish, altered clasts.

Our current working hypothesis is that allochtonous sediment started entering the cave once GE opened to the exterior. The detrital LUs display a high content of limestone clasts that likely come from the cave entrance and were probably formed due to cryoclastic activity. Afterwards, these were transported into the cave via gravitational mass transport of variable density, embedded into the water-saturated clays. Neanderthal and (to a lesser extent) carnivore activities explain the archaeo-paleontological record recovered from this site (see below). Despite the similarity in the geochemistry, the differences in color between LU3 and LU4 are likely due to a higher content of organic matter in LU4, which is also slightly siltier and has a lower limestone content than LU3. LU2 presents the highest amount of organic matter, including charcoal fragments (visible during the geochemical preparation), and a high percentage of extraclasts, which were detected during a visual assessment of the clasts during the water-sieving of the sediment from this unit, likely the result of anthropogenic activities. At some point, the cave entrance closed and the flowstone started to form, which eventually became a dripping speleothem.

Chronological framework

The base of the dripping speleothem is dated to more than 14 ka, according to Martínez-Pillado et al. (2014), which should be viewed as a very conservative minimum age for the detrital sequence as there is still a laminar part of the speleothem that has not yet been dated. A series of radiocarbon dates performed on bone from both GE-I and GE-II are presented in Table 3 and compared to other sites from the province of Burgos. In GE-I, only the uppermost three levels have been dated so far (and those bones from level 1 likely belong to the interface between level 1 and 2). In GE-II, levels 1b and 2 were dated. In all cases, the results are close to the limit of resolution of the ^{14}C techniques and five out of the eight dates are infinite. Thus, we prefer to cautiously interpret these results and we believe that the archaeologically and paleontologically rich levels from Galería de las Estatuas have a minimum age of ~45 ka.

The palynological record

In GE-I, we were able to obtain a composite sequence of ca. 2 m depth from the five detrital LUs that are found between the two stalagmitic flowstones. In Fig. 4, we show the raw data for the palynological analysis in depths relative to the cave floor. In Fig. 5, the percentage of presence was normalized, according to the maximum percentage presence for each of the groups.

Table 1. Description of the sediment, clasts, and lithology of the GE-I and GE-II detritic sequences. LU, lithostratigraphic unit.

					Total Mineralogy						Lithology		
					Matrix						Clasts (1–2 mm)		
Site	LUl	Sample	Sediment	Clasts	Quartz	Phyllosilicates	Calcite	Apatite	Plagioclase	K-feldspar	Calcite/ Dolomite	Speleothem	Other rocks
GE-I	1	1	Orange clays	Millimetric subhorizontal fragments	40%	19%	41%	-	-	-	95%	4%	1%
		2	Orange clays	Millimetric subhorizontal fragments	44%	22%	34%	-	-	-	95%	4%	1%
	2		Black clays with silty orange sublevels	Abundant. Their size increases towards the bottom of the level	57%	34%	9%	-	-	traces	98%	2%	-
	3a		Orangish silty clays, browner towards the base	Rounded, matrix-supported	29%	19%	47%	5%	-	-	97%	2%	1%
	3b		Orangish silty clays, browner towards the base	Oblong, matrix-supported	28%	21%	45%	6%	-	-	97%	2%	1%
	4	1	Dark clays	Decimetric, planar, isolated, and very heterometric	29%	32%	39%	-	-	-	90%	2%	8%
		2	Dark clays	Decimetric, planar, isolated, and very heterometric	30%	29%	41%	-	-	-	90%	2%	8%
	5		Pinkish degraded speleothem	Centimetric, planar (fragments of speleothem)	15%	8%	77%	-	-	traces	-	-	-
GE-II	1a		Light sands with abundant roots	Subhorizontal, whitish, altered	43%	25%	29%	-	-	3%	92%	5%	3%
	1b		Orange clays	Decimetric, isolated	58%	25%	17%	-			90%	3%	7%
	2	1	Dark silty clay sediment	Decimetric, abundant, more sharp-edged	49%	27%	9%	13%	2%	-	80%	2%	18%
		2	Dark silty clay sediment	Decimetric, abundant, more sharp-edged	53%	42%	3%	-	-	2%	80%	2%	18%
		3	Dark silty clay sediment	Decimetric, abundant, more sharp-edged	44%	38%	12%	5%	-	1%	80%	2%	18%
		4	Dark silty clay sediment	Decimetric, abundant, more sharp-edged	62%	34%	2%	-	-	2%	80%	2%	18%
		5	Dark silty clay sediment	Decimetric, abundant, more sharp-edged	62%	23%	10%	1%	2%	2%	80%	2%	18%

Table 2. Analysis of clay minerals by X-ray diphractometry of the GE-I and GE-II detritic sequences.

Site	Lithostratigraphic unit	Sample	Smectite	Illite	Kaolinite	Chlorite
GE-I	1	1	-	73%	22%	5%
		2	-	76%	19%	5%
	2		-	78%	18%	4%
	3a		-	73%	22%	5%
	3b		-	81%	16%	3%
	4	1	-	76%	20%	4%
		2	-	79%	18%	3%
	5		-	78%	17%	5%
GE-II	1a		21%	56%	16%	7%
	1b		15%	64%	16%	5%
	2	1	-	82%	14%	4%
		2	-	76%	18%	6%
		3	traces	76%	20%	4%
		4	traces	79%	15%	6%
		5	-	75%	18%	7%

The smectite contents from level 1 of GE-II (especially LU1a) could be related to a recent intrusion of clays due to bioturbation (see text).

The GE-I palynological sequence can be divided into three pollen zones: Zone 3 is the lowermost one (LUs 5, 4 and lower part of 3) and is characterized by an open environment, indicative of a cool and dry climate; Zone 2 is the intermediate (the upper part of LU3) and shows a shrub expansion; and Zone 1 is the uppermost (i.e., the most recent, comprising LU2 and the base of LU1) and shows a more wooded environment (though it does not reach the threshold to be considered a closed forest), which is indicative of a relatively warmer and more humid climate. It is possible to further divide the oldest zone (Zone 3-open environment) into three phases (Fig. 5). The sequence starts with an open environment with very low taxonomic diversity, which likely indicates a very dry landscape (LU5 and base of LU4). There is a slight climatic improvement throughout most of LU4 with an increase in the percentage of *Pinus* pollen, followed by the development of other tree species, such as *Betula, Fagus*, and *Corylus*, which indicates a more mesic environment. Finally, the lower half of LU3 shows a more xeric climate (drier) with an expansion of Asteraceae, Chenopodiaceae, *Artemisia*, and *Ephedra*. The second zone, at the end of LU3, shows a transition towards the conditions of Zone 1, with a warmer and wetter environment and a higher taxonomic diversity demonstrated by non-arboreus pollen and the expansion of shrubs. The first zone (LU2 and the base of LU1) is characterized by a relatively warmer and more humid climate, and the expansion of forest dominated by *Pinus*; however, it becomes more taxonomically diverse. The information from LU1 is sparse. While the LU1 base is similar to the end of LU2, two additional samples in LU1 did not contain the minimum amount of pollen required for analysis (Figs. 4 and 5).

There is only a partial correspondence between the LUs and the pollen zones. This will be the object of further study in the near future. Zone 1 coincides with LU2. The upper part of LU1 has not yielded a significant amount of pollen and would correspond in our geological interpretation with the moment when the cave starts to close. Differences in the correspondence between Zones 2 and 3 and LU 3 and 4 could be related to either (or both): (a) slight paleoecological changes that may have not been strong enough to alter the geological conditions of sedimentation; and (b) changes in the occupation dynamics of the cave which could have occurred, leaving an imprint on the sedimentary record regardless of potential changes in the paleonvironment of the surroundings of the cave.

In GE-II, only a preliminary sampling was performed, limited to LUs 1 and 2. The sequence starts with an open environment but there is an expansion of forest, dominated by *Pinus*, which parallels the record in LU2 of GE-I. In LU1, the data are sparser and a deterioration of the climatic conditions may be detected, which leads to more open environment conditions.

Microfaunal remains

Remains of several bird species and a few fish have been recovered in both test pits, but are still under study. In GE-I, only LUs 2 to 4 have yielded micro-vertebrate remains (see Fig. 6 and Supplementary Table 1). The number of individuals and the taxonomic diversity is very limited in LU2, the spit (artificial excavation unit) intermediate between LU2 and 3, and LU 4. LU3, in contrast, yielded a larger sample (both in terms of MNI and diversity), which is dominated by open-environment dwellers (such as *Marmota,* and voles belonging to genera *Pliomys* and *Microtus*) and bats belonging to the genus *Myotis.* The presence of forest dwellers, such as *Apodemus* sp. and *Eliomys quercinus*, as well as the presence of the porcupine, *Hystrix (Acanthion) vinogradovi*, also indicates the presence of forest patches in the vicinity of the cave. Humid environments are inferred near the cave, based on the presence of Talpidae indet. and *Microtus oeconomus*.

In GE-II, excavation of LU2 is currently being finished, and, thus, information is limited to levels 1 (1a and 1b) and 2. LU1 has not yielded a large micro-mammal assemblage. LU2 shows a microfaunal association dominated by open-environment dwellers such as *Marmota,* and voles belonging to genus *Pliomys* and *Microtus*, with the presence of forest dwellers, such as *Apodemus* sp. and *Eliomys quercinus*, as well as *Castor fiber*, which would be consistent with the presence of water courses in the vicinity of the cave. A large number of lagomorphs are also present. Both sites have also yielded a small herpetological assemblage that remains to be studied.

Macrofaunal remains

In terms of NISP, the macrofaunal assemblage is dominated by ungulate remains, though the presence of carnivores is significant in terms of taxonomic diversity (Fig. 7 and

Table 3. Direct ^{14}C dates (uncal BP) performed on bone remains in GE-I and GE-II compared to other dates of other sites from the northern plateau mentioned in the text. LU,Lithostratigraphic unit.

Site/Pit	LU	Field label	Sample	Lab label	$^{13}C/^{12}C$ ratio	Method	Age uncal BP	Calibrated age (calBCE)[a] 95.4% probability range	Calibrated age (calBP)[a] 95% probability range	Reference
GE-I	1	A-168	Bone	Beta - 247626	−20.3	AMS-Standard	> 45,000			This study
		GE-191	Bone	OxA-21523	−20.15	AMS-Ultrafiltration	43,500 ± 1800	42,720–out of range (>48,000)	44,670–out of range (>49,500)	This study
	2	A-101	Bone	Beta - 247627	−19.1	AMS-Standard	> 45,000			This study
		GE-175	Bone	OxA-21524	−21.09	AMS-Ultrafiltration	> 45,600			This study
	3	A-129	Bone	Beta - 247628	−19.9	AMS-Standard	> 45,000			This study
		GE-189	Bone	OxA-21525	−20.55	AMS-Ultrafiltration	44,000 ± 1900	43,043–out of range (>48,000)	45,043–out of range (>49,500)	This study
GE-II	1b	GE-773 (E-011)	Bone	OxA-24563	−20.21	AMS-Ultrafiltration	44,200 ± 2000	43,106–out of range (>48,000)	45,106–out of range (>49,500)	This study
	2	E-022	Bone	OxA-24564	−18.85	AMS-Ultrafiltration	> 46,300			This study
Hotel California	V (top)	HC10-1				SG-OSL			48,200 ± 3300	Arnold et al., 2013
	V (top)	HC10-4				SG-OSL			48,200 ± 3900	Arnold et al., 2013
	II (top)	HC10-2				SG-OSL			57,600 ± 5700	Arnold et al., 2013
	I (top)	HC10-3				SG-OSL			71,000 ± 5600	Arnold et al., 2013
Valdegoba			Human bone	OxA-21970		AMS-ultrafiltration	48,400 ± 3300			Dalén et al., 2012
Prado Vargas			Tooth (horse)			Aminoacid racemization			46,400	Navazo et al., 2005
La Ermita	5a		Charcoal	OxA-4603		Conventional C14	31,100 ± 550	32,135–34,240	34,135–36,240	Díez et al., 2008
Cueva Millán	1a		Charcoal	GrN-11021		Conventional C14	37,600 ± 700	38,923–41,082	40,923–43,082	Moure Romanillo et al., 1997
	1b		Charcoal	GrN-1161		Conventional C14	37,450 ± 650	38,869–40,892	40,869– 42,892	Moure Romanillo et al., 1997
La Mina			Tooth (rhinoceros)	LEB-6012		Aminoacid racemization			52,500	Díez et al., 2008

Calibration was performed with OxCal 4.2 (Bronk Ramsey, 2013), using the Intal13 atmospheric curve by Reimer et al., 2013. Before Common Era (BCE) calibrated results were obtained by subtracting 2000 years from the calBP (Before Present) dates.

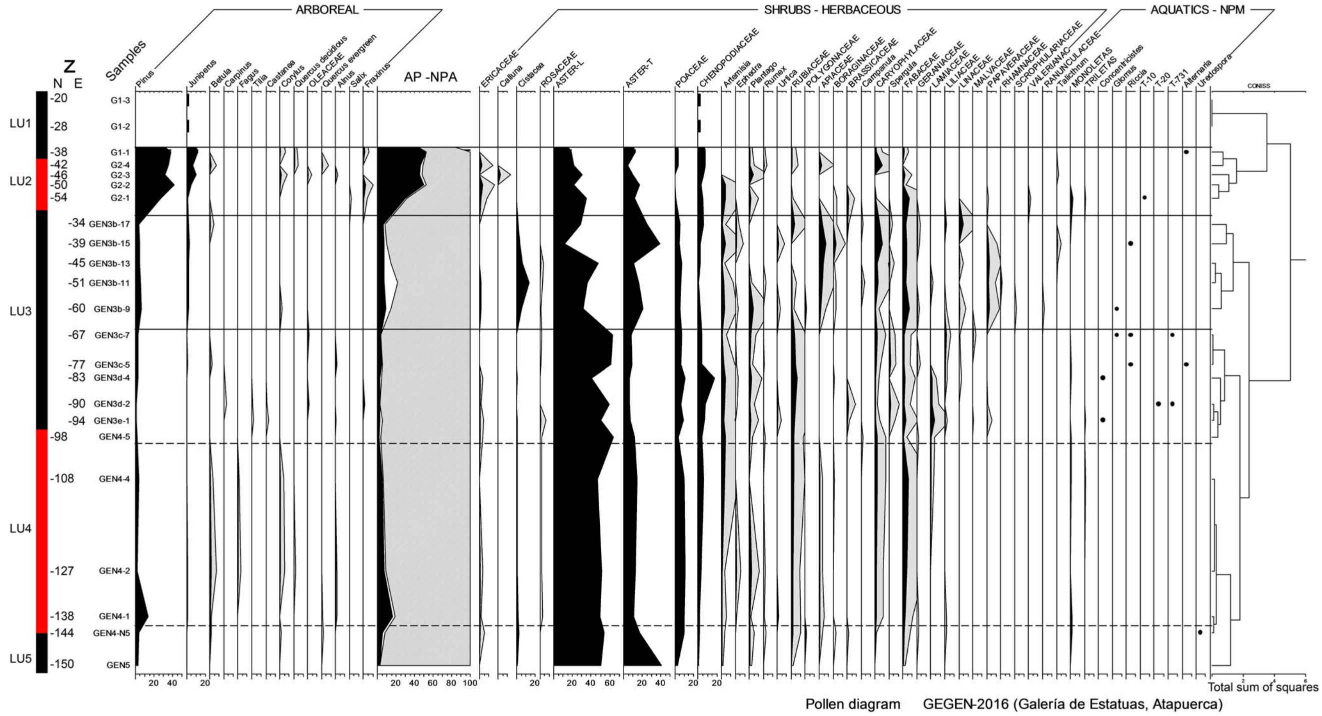

Figure 4. (color online) The horizontal lines subdivide the sequence into the main zones and subzones (see Fig. 5). From LU5 to the middle of LU3 the palynological record is characteristic of open environments. The upper part of LU3 shows a development of shrubs, while LU2 shows an increase in arboreal pollen. The samples from LU1 did not reach the minimum necessary in order to be able to perform the necessary statistical analysis and, thus, only their presence is reported here. The depth (Z) is relative to the cave floor. The samples from LU1, LU2, LU4 and L5 were taken at the northern profile (N) of square M30. The samples from LU3 were taken in the eastern profile (E) of N30 which shows a thinner flowstone, thinner LU1 and LU2, and whose cave floor is lower topographically compared to the northern profile of M30.

Supplementary Table 2). Ungulates are dominated by equids (*Equus* sp.) and red deer (*Cervus elaphus*). In the case of equids, the presence of *Equus hydruntinus* was suspected based on a morphological basis and confirmed based on genetic evidence (see below), while some postcranial remains have dimensions that are compatible with large size *Equus ferus*. Additional analysis will provide a more exact determination in the near future. In GE-I LU3, we have identified a scaphocuboid bone belonging to genus *Bison* (*Bison* cf. *B. priscus* based on the chronology of the deposit; Fig. 7). It should be noted that, despite its limited excavation surface, LU4 has yielded evidence for a minimum of four ungulates and four carnivores. Red foxes (*Vulpes vulpes*) and spotted hyenas (*Crocuta crocuta*) are the best-represented carnivores, though other species are represented, albeit more sparsely.

Equus hydruntinus mtDNA

We found the 28 base pair deletion in the mtDNA HVR-I nucleotide positions 15.533–15.560 in the fossil GE-189 from GE-I. Figure 8 shows the deletion previously detected in other *Equus hydruntinus* specimens and characteristic of the *Equus hydruntinus*/*Equus hemionus*/*Equus kiang* lineage (Orlando et al., 2006, 2009).

Taphonomic analysis

The taphonomic traits of the GE-I and GE-II pits differ depending on the LU analyzed. In general terms, anthropogenic modifications (cut marks and anthropogenic breakage) are more abundant than carnivore activity in all LUs (Supplementary Table 3). Due to the scarcity of remains recovered from LUs 1 and 5 of GE-I, the study will focus on LUs 2, 3, and 4 of this pit, and on LUs 1 and 2 of GE-II.

Sixty-eight bone remains from GE-I LU2 were analyzed. Anthropogenic activity (i.e., cut marks, anthropogenic breakage, and burned bones) is present in 35.3% of the analyzed sample (Supplementary Table 3). The types of cut marks (Supplementary Table 4) show that defleshing, periosteum removal, and marrow access took place mainly on ribs and long bone fragments. The analysis of breakage patterns (Supplementary Table 5) shows that fresh-bone fractures are dominant for all taxa. The presence of percussion marks and peeling suggests anthropogenic breakage as the origin for these fresh-bone fractures. Three bone fragments display evidence of combustion, though at a low degree (stages 1 and 2 of Stiner, 1995). In addition to the anthropogenic traces, one fossil remain (a long bone fragment of an indeterminate species) displays scores and tooth pits (Fig. 9) and two additional bones have features compatible with

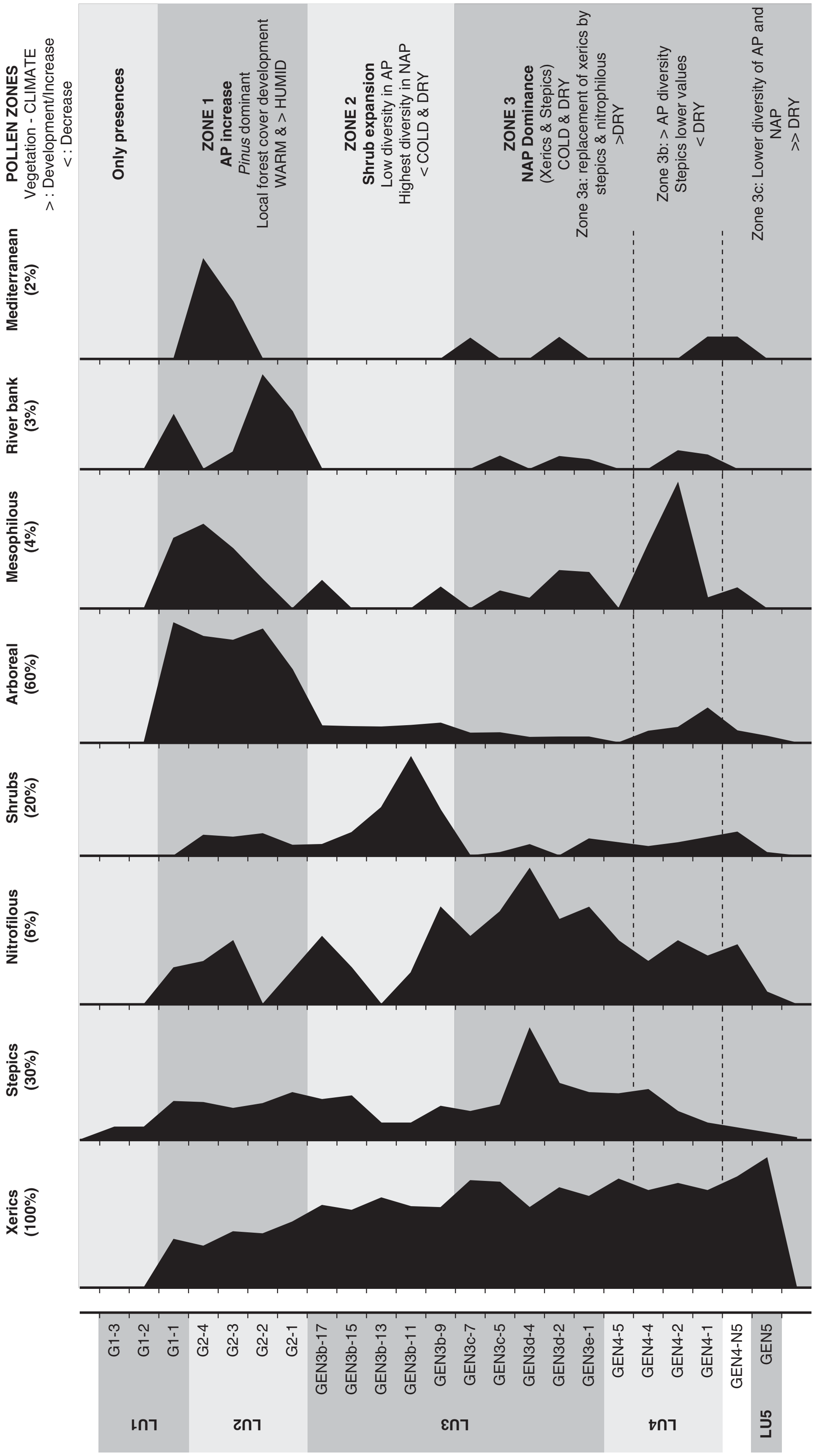

Figure 5. Interpretative diagram of the palynological sequence of GE-I. Note that the samples have been represented one after the other regardless of the depth. Note that the zones based on the palynological content are different from the stratigraphy. GEN4-N5 was taken in the limit between LU 4 and LU5. AP, Arboreal pollen; NAP, Non-arboreal pollen; LU, Lithostratigraphical unit.

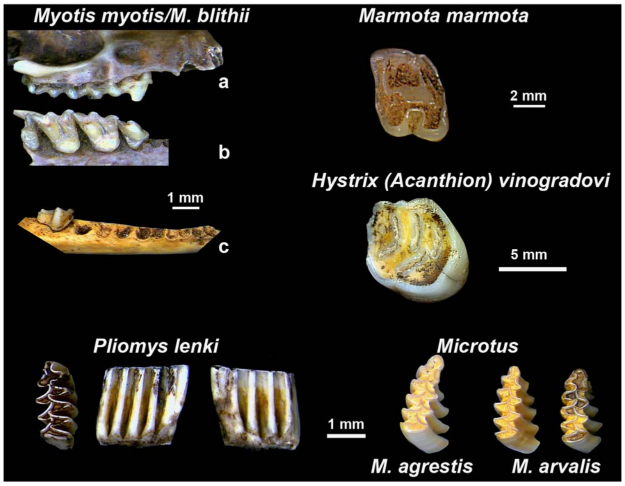

Figure 6. (color online) Selected micro-mammal remains from Galería de las Estatuas. *Myotis myotis/M. blithii*: a right maxilla in (A) lateral and (B) occlusal views. (C) A right mandible with lower M3. *Marmota marmota* from GE-II-level 2: left lower M2. *Hystrix (Acanthion) vinogradovi* from GE-I-level 3: right upper M1. *Pliomys lenki*: lower left M1; *Microtus*: lower right M1 of one specimen of *M. agrestis* and two specimens of *M. arvalis*.

dissolution by gastric acids. None of these three remains display anthropogenic cut marks.

Two hundred and twenty-nine bone remains from GE-I LU3 were analyzed. Around 19% of the sample shows anthropogenic activity in terms of stone tool marks and anthropogenic breakage. No burned bones were identified in this LU. Cut marks, skinning, defleshing, and periosteum removal is evident on cranial remains, ribs, and long bones (Supplementary Table 4). Longitudinal and curved outlines, oblique angles, smooth surfaces, and incomplete diaphysis circumferences in long bones dominate, which indicates that long bones in all taxa represented in this LU were broken when they were fresh (Supplementary Table 5). Fourteen remains display conspicuous tooth marks (pits, scores, and punctures) and 12 remains show evidence of dissolution by gastric acids. Tooth marks affect both carnivores and large size ungulates (Fig. 9) and are also present in other, taxonomically indeterminate small fragments. Tooth marks appear together with anthropogenic cut marks in only three cases, including a leporid tibia. We cannot rule out the possibility that these tooth marks were made by humans.

Eighty faunal remains from GE-I LU4 were analyzed. Based on the type and location of cut marks on long and flat bones, nearly half of this sample (43.7%) shows anthropogenic modification, including defleshing, periosteum removal, and disarticulation (Supplementary Table 4). No burned bones were identified in this unit. In all the long bones, the type of breakage is consistent with fresh-bone breakage (Supplementary Table 5). Tooth marks are present on five specimens belonging to both carnivores and medium sized ungulates, as well as on indeterminate bone fragments (Fig. 9). Only in a taxonomically indeterminate tibia fragment, tooth marks are associated with slicing marks. The tooth marks could correspond to human tooth marks.

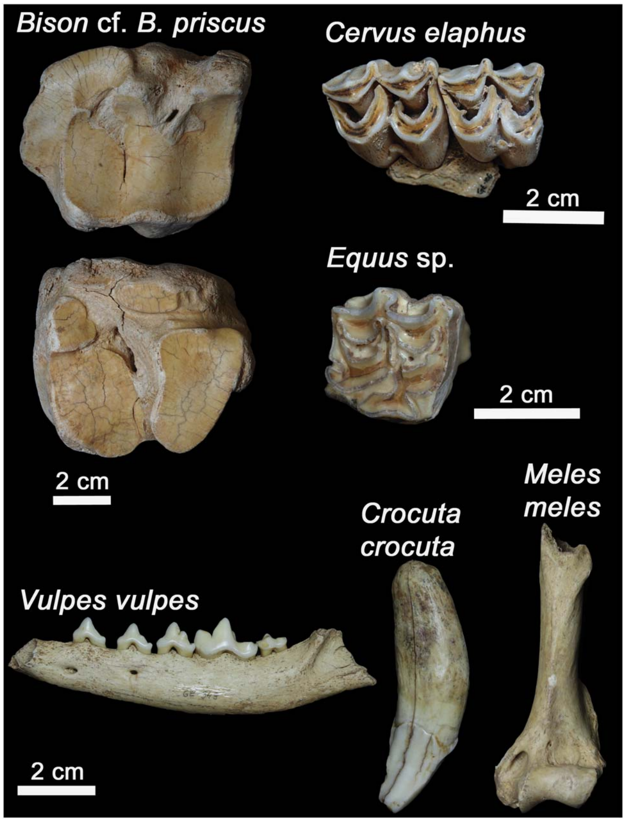

Figure 7. (color online) Selected macrofaunal remains from Galería de las Estatuas, including both ungulates and carnivores. Scaphocuboid of *Bison* cf. *B. priscus* (GE-1174; LU3 of GE-I) in proximal and distal views. Occlusal view of a *Cervus elaphus* right maxilla preserving the M^1–M^2 (GE-106; LU2 of GE-I). Occlusal view of a *Equus* sp. upper right molariform (GE-1051; LU2 of GE-I). Lateral view of a red fox (*Vulpes vulpes*) left hemimandible preserving P$_2$–M$_2$ (GE-348; LU3 of GE-I). Mesial view of a hyena (*Crocuta crocuta*) upper right canine (GE-407; LU3 of GE-I). Anterior view of a badger (*Meles meles*) left humerus (GE-420; LU4 of GE-I).

As in the case of GE-I, in GE-II the anthropogenic traces on the bones are more abundant than those produced by carnivore activity. In the LU1 of GE-II, 36.4% of the remains show cut marks and/or evidence of intentional breakage and three remains show signs of combustion. No conspicuous tooth marks were recorded in this upper unit, though evidence of corrosion from gastric acids was identified in two remains (indeterminate bone and antler fragments). In LU2 from GE-II, 52.8% of the remains display anthropogenic modifications, either cut marks or signs of intentional breakage. In addition, five indeterminate bone fragments show tooth marks; however, due to the small sample size it was not possible to statistically compare the dimensions of the tooth marks with experimental and archaeological samples.

Lithic tool analysis

To date, excavations at GE have yielded a total of 499 lithic objects in both test pits. The study of the GE's lithic

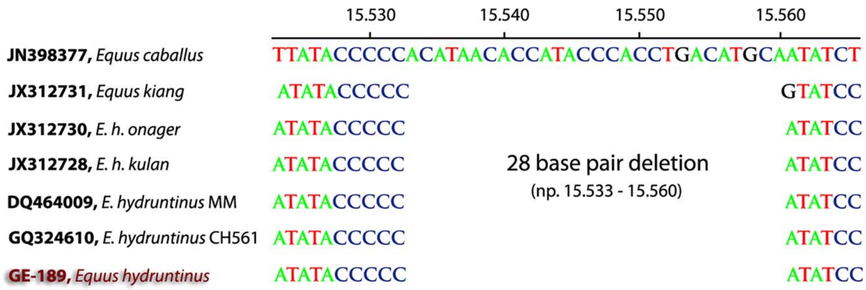

Figure 8. (color online) Informative 28-base pair deletion found in mtDNA HVR-I *Equus hydruntinus*/*Equus hemionus*/*Equus kiang* lineage, which is also present in a lower right molar (M_1 or M_2, GE-189) from GE-I. JN398377 is the *Equus caballus* reference sequence (Achilli et al., 2012). Complete mitochondrial genomes from *Equus hemionus kulan* (JX312728), *Equus hemionus onager* (JX312730), and *Equus kiang* (JX312731) from Vilstrup et al., 2013. Partial *Equus hydruntinus* mtDNA sequences DQ464009 and GQ324610 from Orlando et al., 2006, 2009.

industry shows a clear Mousterian affinity for the entire assemblage (Fig. 10).

In general terms, chert is the most common (83.8%) raw material in both pits, and additional raw materials include quartzite, sandstone, quartz, and limestone, among others (Supplementary Table 6). It should be noted that all of these raw materials are present in the Sierra de Atapuerca and surroundings (Ollé et al., 2013 and references therein). Therefore, the raw material procurement was local. The size of the lithic remains varies depending on the raw material. For example, in LU3 from GE-I the mean size of the flakes made of chert are smaller (from the 12 complete flakes, 5 are <5 mm) than those made of quartzite (all of them >36 mm). This could be indicative of differential management of the raw material.

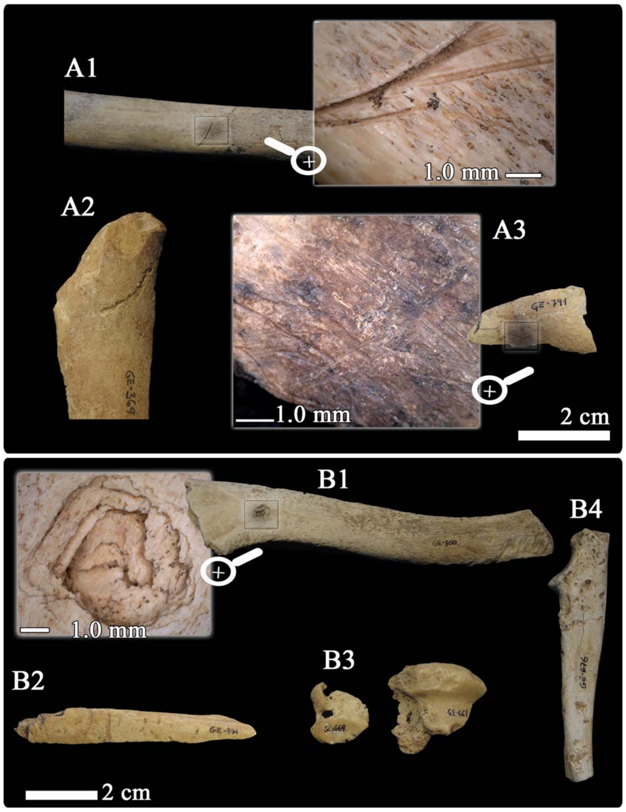

Figure 9. (color online) Selected (A) anthropogenic and (B) carnivore modifications on the Galería de las Estatuas fossil remains. (A1) General and detailed images of cut marks on the rib GE-545 from LU4 of GE-I. (A2) percussion pits on a long bone fragment (GE-369) from LU4 of GE-I. (A3) Burned and cut-marked long bone fragment (GE-791) from LU2 of GE-I. Note the slicing and scraping marks in the detailed view. (B1) Carnivore puncture on the vertebra GE-300 from GE-I LU3; B2) long bone fragment (GE-871 from LU2 of GE-I) with scores and tooth pits. (B3) Bone fragments (GE-669 and GE-661 from LU1 of GE-II unit 1) with evidence of corrosion by stomach acids. (B4) Carnivore ulna fragment (GE-576 from LU4 of GE-I) with tooth pits and punctures.

Most of the artifacts recovered are knapping products (simple flakes, broken flakes, and flake fragments; n = 402, 80.56%) (Supplementary Table 7). The low number of cores (n = 8, 1.6%) and their high degree of exploitation make it difficult to identify the strategies employed for the production of the flakes. Analysis conducted on the cores and on some of the flakes reveals centripetal knapping, huowever, some of which depict the characteristic features of Levallois débitage. Additionally, one small quartzite core shows evidence of bipolar-on-anvil technique. There is also one Kombewa chert flake on in LU2 of GE-I. Most (88.8%) of the flakes lack cortex in their striking platforms. Only 4.5% of the flake platforms are completely cortical. Platforms are mainly plain or unifaceted (46.1%), but it is noteworthy that 20.2% of the striking platforms are dihedral and 29.2% multifaceted. Dorsal surfaces of flakes are non-cortical (85.4%), and there is only one flake (0.5%) with a completely cortical dorsal surface. These data likely indicate that the earlier stages of flake production are not represented in this lithic assemblage. Pebbles and broken pebbles were recovered at both test pits, of which three were classified as hammerstones (two of quartzite and one of limestone), with an average size of 58.7 × 52.3 × 43.3 mm.

Retouched flakes represent 8% (n = 40) of the assemblage. From a typological point of view, the most common elements are side-scrapers (n = 18; some of which have "Quina"-type retouching), and denticulates (n = 12). There are also points (n = 3), endscrapers (n = 2), and one piece with abrupt retouching (Supplementary Table 8).

The fact that 64.3% of the lithic objects have a maximum length of <20 mm suggests that retouching was more common

Figure 10. (color online) Selection of stone tools from the Galería de las Estatuas. (a) Centripetal flake core on chert (GE-II, LU2). (b) Chert core with a clearly hierarchised exploitation surface (GE-II, LU2). (c) Chert flake (GE-II, LU2). (d) Quartzite flake (GE-I, LU3). (e) Chert double marginal sidescraper (GE-I, LU1). (f) Quartzite convergent scraper (GE-II, LU2). (g) Chert sidescraper with Quina retouch (GE-II, LU1A). (h) Chert sidescraper with marginal retouch (GE-I, LU1-2).

than débitage, which is scarce, particularly with regard to the initial stages of the cores exploitation, as we mention previously. For example, LU2 of GE-I (including the contact between LUs 1-2) shows a large amount (76.5%) of small sized-flakes that are smaller than 20 mm, which suggests that some retouching activities took place there. However, the percentage of retouched tools in this LU is very small (1.7%). Therefore, retouched tools were used (and abandoned) elsewhere.

DISCUSSION

Interpretation of the site

The GE corresponds to a site located at an ancient entrance of the Cueva Mayor-Cueva del Silo karst system. Both GE-I and GE-II pits have yielded new information regarding the Neanderthal occupations of the site that include lithic remains and bone remains with anthropogenic marks. Additionally, the palynological sequence indicates that there was a climatic improvement from LU3 to LU2, as the latter was warmer and more humid.

The bone remains from GE display several features that indicate human manipulation in all the LUs (Fig. 9). Cut marks, including slicing marks, scrape marks, and chop marks, are present on different preserved anatomical parts. Most of the cut marks – mainly slicing and scraping marks – are present in long bone shaft fragments and ribs, which indicate that defleshing, evisceration, and periosteum removal took place. Most of the cut marks are present on unidentifiable bone fragments, however, making it difficult to interpret the butchering processes. In addition to the lithic tool traces, intentional breakage was also recorded in all LUs. None of the carnivore fossil remains from GE-I display cut marks, but tooth marks are present in LUs 3 and 4. Cut marks are more common in large-sized ungulates (equids and bovids) than in any other taxa in all LUs from GE-I. Although no hearths were documented in the cave site, some bone fragments show evidence of fire activity in the LU2 from GE-I and LU1 from GE-II (Fig. 9). The scarcity of tooth marks on the GE sample makes it difficult to statistically compare their dimensions with experimental and archaeological samples, in order to assess the carnivore taxa that produced them.

The results from the taphonomic analysis indicate that, although carnivores occupied the cave sporadically, this site was mainly used by hominins during the late Pleistocene. This is consistent with the presence of lithic artifacts in all LUs. Carnivore modification on bones could be interpreted as a result of occasional scavenging activities. Future analyses, once larger samples are available, will test whether or not there are significant differences in the taphonomic traits and in the lithic sample, which could indicate changing subsistence strategies along the stratigraphic sequence.

Galería de las Estatuas and the Mousterian in the northern plateau

The best sites for contextualizing the Middle Paleolithic occupations in the GE within the northern plateau are the open-air contexts found at and around the Sierra de Atapuerca, the Valdegoba and Prado Vargas sites, and three additional sites in the Arlanza River valley (Hortigüela): the La Ermita and La Mina cave sites and the Millán rock-shelter. Direct dating completed on these sites indicate that Neanderthals occupied the Sierra de Atapuerca and the northern plateau, at least from the end of MIS 4 and throughout MIS 3 (Table 3). The comparison of the lithic remains and the main prey species found at these sites reveals some similarities and some slight discrepancies (Table 4). Equids, red deer, wild goat, and chamois are the most abundant prey species in the northern plateau. The presence/absence of caprids (wild goat and chamois) at different sites could be the effect of ecological differences among them. Additionally, some differences in technology could be the result of differences in the raw materials available and, therefore, differences in the management of these raw materials and/or the nature of the occupation at the site. A common feature of the lithic industry of these sites is the predominance of small-sized (<40 mm) flakes. Moreover, the Mousterian sites found on the northern plateau extend for more than 20 ka, as is the case for the Mousterian occupations of the Sierra de Atapuerca (including both cave and open-air sites). Therefore, differences in lithic technology are to be expected: for a similar time frame, differences have been detected in the Mousterian sites on the northern Iberian Peninsula (Rios-Garaizar, 2017).

Navazo et al. (2011) believe that the tendency towards microlithism observed in some of the open-air sites of Atapuerca (e.g., Hundidero), which can also be found in GE, is due to cultural tradition. This microlithism cannot be explained by the need to exploit the raw materials to the maximum due to their scarcity, because of the presence of abundant raw materials (especially Neogene flint) found close to these sites (Navazo et al., 2011). The re-use/recycling of stone tools detected in Hundidero indicates repeated visits, though short in duration (Navazo et al., 2011; Navazo and Carbonell, 2014). In the Arlanza valley, La Ermita seems to reflect specialized short visits, while Millán were longer and/or more diversified occupations (Díez et al., 2008).

Galería de las Estatuas: completing the Sierra de Atapuerca record

The Sierra de Atapuerca site complex has yielded not only important archaeo-paleontological assemblages from the lower and middle Pleistocene (Arsuaga et al., 1993, 1999, 2014, 2015; Carbonell et al., 1995, 2008; Bermúdez de Castro et al., 1997), but also important stratigraphic sequences that are providing a plethora of data on the macro- and microfaunal assemblages, as well as on the lithic technology, among others. While the Holocene is well-represented by several sites in the Sierra de Atapuerca as well, the late Pleistocene was only scarcely represented (Mosquera et al., 2007) up until now. Thus, the GE sequence provides important technological, paleoecological and taphonomic information about the derthal populations that inhabited the Sierra de Atapuerca.

There are clear differences between the lithic tools found in the GE and the technological complexes found in the middle Pleistocene levels of Gran Dolina or Trinchera Galería (Ollé et al., 2013 and references therein). For example, while Neanderthals used local raw materials in a fashion similar to the previous human populations that inhabited the Sierra de Atapuerca, there is a clear trend towards the use of better quality materials. Additional differences refer to the absence of large-sized tools in GE, the type of débitage, and the consolidation of hierarchized exploitation strategies like the Levallois débitage. Indeed, many of the technical features from GE are shared with the Valle de las Orquídeas assemblage, particularly regarding the knapping methods (Mosquera et al., 2007).

The GE site provides new information regarding the Sierra de Atapuerca Neanderthal occupations, which adds to the

Table 4. Comparison of the main prey species and lithic raw materials and technological aspects between Galería de las Estatuas and other northern Iberian Plateau sites.

	Estatuas	Hundidero (Levels 1, 2, and 3)	Valdegoba	Prado Vargas	Sites of the Arlanza river	
					La Ermita (levels 5a and 5b) (Arlanza river)	Millán (Surface level) (Arlanza river)
Main prey species (MNI)	GE-I: Equids (8), red deer (8)	No faunal remains	Chamois (114), red deer (40), Equids (33)	Equids (2), red deer (2), chamois (2), wild goat (2)		Equids (8), red deer (7), chamois (7), wild goat (7)
Raw materials	Chert (83.8%); Quartzite (12.8%)	Chert (92.1%); Quartzite (6.7%)	Quartzite (45.4%); Flint (42%)	Chert (97%); Quartzite (2%)	Chert (61.3%); Quartzite (35.4%)	Chert (90%); Quartzite (10%)
Cores	1.6%	5.1%	1.7%	9.5%	3.8%	4%
Knapping methods	Centripetal; Levallois; bipolar on anvil	Discoidal; Centripetal; Scarce Levallois	Centripetal; Scarce presence of Levallois	Discoidal; Quina; Levallois	Discoidal; Quina; Levallois	Discoidal; Quina; Levallois;
Flake percentage	80.6%	76.7%	68.3%	74.25%	61.1%	70%
Retouched flakes	8%	16.2%	17.2%	12%	20.1%	20%
Typology of the most abundant retouched flakes	Side scrapers (45%); denticulates (30%); points (7.5%); end scrapers (5%)	Denticulates; notches; side scrapers; end scrapers	Side scrapers (37.6%); denticulates (33.4%); points (7.1%)	Side scrapers (50%); denticulates; points; end scrapers	Side scrapers; denticulates; notches	Side scrapers; denticulates

Information from Galería de las Estatuas from this work.

already known Middle Paleolithic open-air sites (Navazo et al., 2011; Navazo and Carbonell, 2014; see above). From a paleontological point of view, some of the faunal species represented were already present in older levels at different sites within the Sierra de Atapuerca karst complex. In other cases, GE provides the first evidence of certain taxa present at the Sierra de Atapuerca sites. Starting with carnivores, the hyena *Crocuta crocuta* and lynxes (*Lynx* sp.) have inhabited the Sierra de Atapuerca since the end of the early Pleistocene, while the fox *Vulpes vulpes* and the badger *Meles meles* appeared at the middle Pleistocene site of Sima de los Huesos (Rodríguez et al., 2011). In GE, the only remain attributed to genus *Panthera* corresponds to a phalanx of an immature individual, which, based on the chronology of this site, likely belonged to either a lion (*P. leo/spelaea*) or a leopard (*P. pardus*). If these remains belonged to the latter species, it would be the first appearance of this taxon in the Sierra de Atapuerca.

In the case of the ungulates, *Sus scrofa* and *Cervus elaphus*, they are known in the Sierra de Atapuerca starting at the end of the early Pleistocene. *Equus hydruntinus* and *E. ferus* make their first appearance in the middle middle Pleistocene. In GE, it has been possible to identify *Bison* cf. *B. priscus* among the scarce large bovid remains. This is the first evidence of this taxon in the Sierra de Atapuerca and the second for the northern plateau after that of the Cueva del Búho-Zarzamora cave complex (Sala et al., 2010), though the latter would be younger chronologically.

In the case of the microfaunal assemblage from the GE, bats from genera *Myotis* and *Miniopterus* were known to be present in the Sierra de Atapuerca since the end of the Early Pleistocene, as well as shrews from the genus *Sorex* and talpids (Rodríguez et al., 2011). *Hystrix (Acanthion) vinogradovi, Microtus arvalis*, *Microtus agrestis*, *Pliomys lenki*, and *Arvicola sapidus* were present in the Sierra de Atapuerca since the middle Pleistocene (Cuenca-Bescós, 1999) while marmots (genus *Marmota*), field mice belonging to genus *Apodemus*, and the dormouse *Eliomys quercinus* were present since the end of the early Pleistocene. Beavers are a scarce taxon in Atapuerca, limited to the lower Pleistocene levels from Gran Dolina and Sima del Elefante (ca. 0.9 Ma in TD6 and ca. 1.2 Ma in TE9) and to the Holocene remains from El Portalón (Cuenca-Bescós et al., 2017), and, therefore, their presence in the GE expands their chronological range in the Sierra de Atapuerca record. Finally, the GE provides the first reference for several species: *Terricola lusitanica/duodecimcostatus, Terricola gerbei/pyrenaicus, Microtus oeconomus*, and there is potentially an *Iberomys cabrerae* remain.

Paleoenvironmental and paleoecological changes during the late Pleistocene in the Iberian Peninsula: new insights from the Galería de las Estatuas

During the late Pleistocene, there were not only dramatic climatic changes that occurred. There were also ecological changes, including extinctions of certain species at a local/

global level. A better understanding of these dynamics can offer insights into the extinction of Neanderthals. Here, we discuss the palynological record compared to the chronological data provided by the radiocarbon direct dating, as well as aspects of the macro-mammal record.

The GE has yielded several *Hystrix vinogradovi* remains in LUs 3 and 4 of GE-I. The presence of porcupine in the Late Pleistocene of the Iberian Peninsula is restricted to 9–10 sites, most of which are associated or contemporaneous with Neanderthal occupations. The first porcupine remain was identified in Devil's Tower (Gibraltar) by Bate (1928; see her figure 25), where Mousterian tools and the remains of a Neanderthal child were found (Buxton, 1928; Garrod, 1928). The Cueva del Camino site provides the earliest (MIS 5) evidence of *Hystrix* in the Iberian Peninsula (Arsuaga et al., 2012; Laplana et al., 2013). Additional sites that have yielded Neanderthal remains/occupations with the presence of this species include: two caves in the province of Burgos, Valdegoba (Díez et al., 1988–1989) and La Mina (Díez et al., 2008); level I of Cova del Gegant (Daura et al., 2005, 2010; López-García et al., 2008); the nearby Cova del Muscle (López-García et al., 2007); and Sima de las Palomas (Rhodes et al., 2013). Finally, the youngest (in chronological terms) *Hystrix* on record was found in level IV at A Valiña (Fernández Rodríguez, 2006), dated to 31,730 + 2880/-2110 ^{14}C yr BP GrN-20833 (Ramil Rego and Fernández, 1995 in Fernández Rodríguez, 2006). There are other sites with the presence of *Hystrix*, such as Cova d'Olopte (Cova B; López-García et al., 2007), the age of which is not certain (Villalta, 1972).

The Sierra de Atapuerca site complex has yielded evidence of the presence of different *Bison* species throughout the lower and middle Pleistocene (Rodríguez et al., 2011 and references therein). However, the presence of the steppe bison *Bison priscus* in the Iberian Peninsula south of the Cantabrian mountain range during the late Pleistocene is almost unheard of. Its presence has been identified at only two sites, both of which are located on the northern plateau: the GE and the slightly younger Búho-Zarzamora site complex (Sala et al., 2010). It should be noted that the paleoecological conditions of the latter site are those of an herbaceous-dominated open environment, based on both palynological and microfaunal studies. The dominance of equids, steppe rhinoceros (*Stephanorhinus hemitoechus*), and the presence of *Bison priscus* is consistent with the other paleoecological proxies (Sala et al., 2011, 2012). In the case of GE, the presence of *Bison* cf. *B. priscus* in LU3 is consistent with the open environments, as is also suggested by the palynological and microfaunal analyses. Nevertheless, the absence of this taxon in the record could be partially for biogeographical reasons, and the Cantabrian mountain range could have acted as a barrier, allowing only some animals to sporadically cross it, similar to that which occurred with other species (e.g., reindeer; Álvarez-Lao and García, 2011; Gómez-Olivencia et al., 2014). However, since there are difficulties entailed in distinguishing between *Bos* and *Bison* remains, certain diagnostic elements are required in order to successfully do so (e.g., Altuna, 1972; Sala et al., 2010).

The absence of other ungulates is also noticeable, such as the fallow deer (*Dama dama*), which is not present in any of the late Pleistocene sites from the northern plateau (Arceredillo, 2016). In fact, all these sites are from the second half of the late Pleistocene (ca. <70 ka). In older chronologies, such as the MIS 5 central Iberian site of Camino (Arsuaga et al., 2012; Álvarez-Lao et al., 2013), *Dama dama* is the most abundant species of the fossil assemblage. However, the presence of fallow deer in the Buena Pinta cave, which has yielded chronologies around 60–70 ka (Laplana et al., 2015 and references therein), would suggest a more prolonged survival in this part of the Iberian Peninsula. Thus, the absence of *Dama dama* in GE could be related to the fact that the taxon had a more restricted biogeographical range that did not include the Sierra de Atapuerca. Therefore, additional chronological data from different sites are still necessary in order to assess the extinction of this taxon in Iberia during the late Pleistocene. In this case, it is easier to distinguish between genus *Cervus* and *Dama* than between *Bos/Bison* due to their differences in general size.

Finally, another important aspect that must be taken into account is the high micro-mammal biodiversity, likely linked to the strategic geographical location of the Sierra de Atapuerca within the northern plateau and the landscape variation within 5 km from the Sierra itself. The Sierra de Atapuerca is located in the Duero basin, at the entrance of the Bureba corridor that connects the Ebro and the Duero basins. This corridor is limited by the Cantabrian mountain range to the north and the Central system to the south. The Sierra de Atapuerca has several natural springs, and, together with the limestone nature of this hill, and the fact that it is surrounded by the terraces of the nearby Arlanzón River, it provides a variety of landscapes, which is reflected in high levels of biodiversity preserved in the different Atapuerca sites throughout the Pleistocene (Rodríguez et al., 2011). The GE is no exception and the palynological and micropaleontological studies presented here show that, despite the general rigorous climatic conditions, a varied plant and micro-mammal community inhabited the surroundings of the Sierra de Atapuerca.

SUMMARY AND CONCLUSIONS

The GE site, in which two test pits have been excavated, is located at an ancient entrance of the Cueva Mayor-Cueva del Silo karst system. Here a detrital sequence has yielded both stone artifacts of clear Mousterian affinity, as well as paleontological remains. In general terms, chert is the most common raw material and most of the artifacts are knapping products. Among the retouched flakes, side scrapers are the most common elements, and some of them have "Quina"-type retouching. The macrofaunal spectrum is dominated by ungulates, mainly equids and red deer, with the presence of large bovids (including *Bison*) and several carnivores (mainly red fox and spotted hyena). The taphonomic analysis reveals traces of both anthropogenic and, to a lesser extent, carnivore activity. Thus, although carnivores occupied the cave sporadically, this site was mainly used by hominins during the late Pleistocene. The current chronological framework is based on a series of ^{14}C dates that indicate a minimum age of 45 ^{14}C ka BP for the human occupations of this site. The palynological analysis indicates a warming episode in a more open environment compared to that of the present day. This is consistent with the very diverse and rich micro-mammal assemblage, dominated by open-habitat taxa. GE provides insights into the Neanderthal occupations of the more inland Iberian Peninsula, which contrasts with the climatically milder, more coastal sites. Moreover, it also shows the diversity of strategies in which Neandertal engaged to survive in the different ecosystems/ecotones on the northern Iberian Plateau in which different species of prey existed (caprids in more mountainous areas; cervids and equids in more open environments). It indicates the resilience of these hunter-gatherer groups that inhabited the Sierra de Atapuerca despite ecological changes that occurred during the late Pleistocene. Finally, GE provides new evidence of the Neanderthal occupation at the Sierra de Atapuerca, which helps to complete the more than one million-year-old sequence of human occupations at this site complex.

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SUPPLEMENTARY MATERIAL

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REFERENCES

Achilli, A., Olivieri, A., Soares, P., Lancioni, H., Kashani, B.H., Perego, U.A., Nergadze, S.G., *et al.*, 2012. Mitochondrial genomes from modern horses reveal the major haplogroups that underwent domestication. *Proceedings of the National Academy of Sciences* 109, 2449–2454.

Alcaraz-Castaño, M., Weniger, G.-C., Alcolea, J., de Andrés-Herrero, M., Baena, J., de Balbín, R., Bolin, V., *et al.*, 2015. Regreso a la cueva de los Casares (Guadalajara). Un nuevo proyecto de investigación para el yacimiento del seno A. ARPI. *Arqueología y Prehistoria del Interior Peninsular* 2, 68–89.

Allué, E., Solé, A., Burguet-Coca, A., 2017. Fuel exploitation among Neanderthals based on the anthracological record from Abric Romaní (Capellades, NE Spain). *Quaternary International* 431A, 6–15.

Álvarez-Lao, D.J., Arsuaga, J.L., Baquedano, E., Pérez-González, A., 2013. Last Interglacial (MIS 5) ungulate assemblage from the Central Iberian Peninsula: the Camino Cave (Pinilla del Valle, Madrid, Spain). *Palaeogeography, Palaeoclimatology, Palaeoecology* 374, 327–337.

Álvarez-Alonso, D., de Andrés-Herrero, M., Díez-Herrero, A., Medialdea, A., Rojo-Hernández, J., (in press). Neanderthal settlement in central Iberia: geo-archaeological research in the Abrigo del Molino site, MIS 3 (Segovia, Iberian Peninsula). *Quaternary International*. https://doi.org/10.1016/j.quaint.2016.05.027.

Álvarez-Laó, D.J., García, N., 2011. Geographical distribution of Pleistocene cold-adapted large mammal faunas in the Iberian Peninsula. *Quaternary International* 233, 159–170.

Altuna, J., 1972. Fauna de mamíferos de los yacimientos prehistóricos de Guipúzcoa. *Munibe Antropologia-Arkeologia* 24, 1–492.

Aranburu, A., Martínez-Pillado, V., García, F., Arsuaga, J.L., Alcázar de Velasco, A., Bonmatí, A., García, N., *et al.* 2012. La variabilidad de los rellenos endokársticos de la Galería de Estatuas (Atapuerca, Burgos) y su caracterización paleoambiental. In: González-Díez, A., Fernández-Maroto, G., Doughty, M.W., Remondo, J., Bruschi, V. M., Bonachea, J., Díaz de Terán, J.R. *et al.*, (Eds.), *Avances de la Geomorfología en España 2010–2012. Actas de la XII Reunión Nacional de Geomorfología* (Santander, 17–20 septiembre de 2012. PUbliCan Ediciones. Universidad de Cantabria, Santander, pp. 397–400.

Arceredillo, D., 2016. Análisis paleobiológico de los ungulados del Pleistoceno Superior de Castilla y León (España). BAR publishing, Oxford.

Arceredillo, D., Gómez-Olivencia, A., García-Pérez, A., 2011. Three statistical methods for sex determination in extant and fossil caprines: assessment of the *Rupicapra* long bones. *Journal of Archaeological Science* 38, 2450–2460.

Arnold, L.J., Demuro, M., Navazo, M., Benito-Calvo, A., Pérez-González, A., 2013. OSL dating of the Middle Palaeolithic Hotel California site, Sierra de Atapuerca, north-central Spain. *Boreas* 42, 285–305.

Arsuaga, J.L., Baquedano, E., Pérez-González, A., Sala, N., Quam, R.M., Rodríguez, L., García, R., *et al.*, 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. *Quaternary International* 275, 55–75.

Arsuaga, J.L., Carretero, J.-M., Lorenzo, C., Gómez-Olivencia, A., Pablos, A., Rodríguez, L., García-González, R., *et al.*, 2015. Postcranial morphology of the middle Pleistocene humans from Sima de los Huesos, Spain. *Proceedings of the National Academy of Sciences* 112, 11524–11529.

Arsuaga, J.L., Lorenzo, C., Carretero, J.M., Gracia, A., Martínez, I., García, N., Bermúdez de Castro, J.M., Carbonell, E., 1999. A complete human pelvis from the Middle Pleistocene of Spain. *Nature* 399, 255–258.

Arsuaga, J.L., Martínez, I., Arnold, L.J., Aranburu, A., Gracia-Téllez, A., Sharp, W.D., Quam, R.M., *et al*., 2014. Neandertal roots: Cranial and chronological evidence from Sima de los Huesos. *Science* 344, 1358–1363.

Arsuaga, J.L., Martínez, I., Gracia, A., Carretero, J.M., Carbonell, E., 1993. Three new human skulls from the Sima de los Huesos Middle Pleistocene site in Sierra de Atapuerca, Spain. *Nature* 362, 534–537.

Arsuaga, J.L., Villaverde, V., Quam, R., Martínez, I., Carretero, J.M., Lorenzo, C., Gracia, A., 2007. New Neandertal remains from Cova Negra (Valencia, Spain). *Journal of Human Evolution* 52, 31–58.

Baquedano, E., Márquez, B., Pérez-González, A., Mosquera, M., Huguet, R., Espinosa, J.A., Sánchez-Romero, L., Panera, J., Arsuaga, J.L., 2011–2012. Neanderthales en el valle del Lozoya: los yacimientos paleolíticos del calvero de la Higuera (Pinilla del Valle, Madrid). *Mainake* XXXIII, 83–100.

Basabe, J.M., 1973. Metacarpiano humano de la cueva de Los Casares (Guadalajara). La Cueva de los Casares (en Riba de Saelices, Guadalajara). *Excavaciones Arqueológicas en España* 76, 117–122.

Bate, D.M., 1928. The animal remains. In: Garrod, D.A.E., Buxton, L.H.D., Smith, G.E., Bate, D.M.A. (Eds.), *Excavation of a Mousterian rock-shelter at devil's tower, Gibraltar*. Royal Anthropological Institute of Great Britain and Ireland, London, pp. 92–110.

Benito-Calvo, A., Pérez-González, A., 2015. Geomorphology of the Sierra de Atapuerca and the Middle Arlanzón Valley (Burgos, Spain). *Journal of Maps* 11, 535–544.

Bermúdez de Castro, J.M., Arsuaga, J.L., Carbonell, E., Rosas, A., Martínez, I., Mosquera, M., 1997. A hominid from the Lower Pleistocene of Atapuerca, Spain: possible ancestor to Neandertals and modern humans. *Science* 276, 1392–1395.

Binford, L.R., 1981. *Bones: Ancient Men and Modern Myths*. Academic Press, London.

Blasco, R., Finlayson, C., Rosell, J., Marco, A.S., Finlayson, S., Finlayson, G., Negro, J.J., Pacheco, F.G., Vidal, J.R., 2014. The earliest pigeon fanciers. Nature Scientific Reports, A5971. http:/hx.doi.org/ 10.1038/srep05971.

Blumenschine, R.J., Marean, C.W., Capaldo, S.D., 1996. Blind tests of inter-analyst correspondence and accuracy in the identification of cut marks, percussion marks, and carnivore tooth marks on bone surfaces. *Journal of Archaeological Science* 23, 493–507.

Blumenschine, R.J., Selvaggio, M.M., 1988. Percussion marks on bone surfaces as a new diagnostic of hominid behaviour. *Nature* 333, 763–765.

Bunn, H.T., 1986. Patterns of skeletal representation and hominid subsistence activities at Olduvai Gorge, Tanzania, and Koobi Fora, Kenya. *Journal of Human Evolution* 15, 673–690.

Burjachs, F., López-García, J.M., Allué, E., Blain, H.-A., Rivals, F., Bennàsar, M., Expósito, I., 2012. Palaeoecology of Neanderthals during Dansgaard–Oeschger cycles in northeastern Iberia (Abric Romaní): From regional to global scale. *Quaternary International* 247, 26–37.

Buxton, L.H.D., 1928. Human remains. In: Garrod, D.A.E., Buxton, L.H.D., Smith, G.E., Bate, D.M.A. (Eds.), *Excavation of a Mousterian Rock-Shelter At Devil's Tower, Gibraltar*. Royal Anthropological Institute of Great Britain and Ireland, London, pp. 57–85.

Capaldo, S.D., Blumenschine, R.J., 1994. A quantitative diagnosis of notches made by hammerstone percussion and carnivore gnawing on bovid long bones. *American Antiquity* 59, 724–748.

Carbonell, E., Bermúdez de Castro, J.M., Arsuaga, J.L., Díez, J.C., Rosas, A., Cuenca-Bescós, G., Sala, R., Mosquera, M., Rodríguez, X.P., 1995. Lower pleistocene hominids and artefacts from Atapuerca-TD6 (Spain). *Science* 269, 826–830.

Carbonell, E., Bermúdez de Castro, J.M., Parés, J.M., Pérez-González, A., Cuenca-Bescós, G., Ollé, A., Mosquera, M., *et al*., 2008. The first hominin of Europe. *Nature* 452, 465–469.

Carbonell, E., Guilbaud, M., Mora, R., 1983. Utilización de la lógica analítica para el estudio de Tecno-complejos a cantos tallados. *Cahier noir*, 1, 3–64.

Carbonell, E., Mosquera, M., Ollé, A., Rodríguez, X.P., Sala, R., Vaquero, M., Vergès, J.M., 1992. New elements of the logical analytic system. First International Meeting on Technical Systems to Configure Lithic Objects of scarce elaboration (Montblanc, 1992). Laboratori d'Arqueologia de la Universitat Rovira i Virgili/ Reial Societat Arqueològica Tarraconense, Tarragona.

Carretero, J.M., Ortega, A.I., Juez, L., Pérez-González, A., Arsuaga, J.L., Pérez-Martínez, R., Ortega, M.C., 2008. A late Pleistocene-early Holocene archaeological sequence of Portalón de Cueva Mayor (Sierra de Atapuerca, Burgos, Spain). *Munibe Antropologia-Arkeologia* 59, 67–80.

Chaline, J., 1972. *Les rongeurs du Pleistocène moyen et supèrieur de France*. Centre National de la Recherche Scientifique, Paris.

Coûteax, M., 1977. A propos de l'interpretation des analyses polliniques de sediments minéraux, principalement archéologiques. In: Le Milieu Végétal, les faunas et l'Homme. *Supplément au Bulletin de l'AFEQ* 47, 259–276.

Cuenca-Bescós, G., Canudo, J.I., Laplana, C., 1999. Análisis bioestratigráfico de los roedores del Pleistoceno medio del yacimiento de Galería (Sierra de Atapuerca, Burgos). In: Carbonell, E., Rosas, A., Díez, J.C. (Eds.), *Atapuerca: Ocupaciones Humanas y Paleoecología del Yacimiento de Galería*. Junta de Castilla y León, Valladolid, pp. 189–210.

Cuenca-Bescós, G., Rosell, J., Morcillo-Amo, A., Galindo-Pellicena, M.A., Santos, E., Moya Costa, R., (2017). Beavers (Castoridae, Rodentia, Mammalia) from the Quaternary sites of the Sierra de Atapuerca, in Burgos, Spain. *Quaternary International* 433, 263–277.

Cuenca-Bescós, G., Straus, L.G., González Morales, M.R., García Pimienta, J.C., 2009. The reconstruction of past environments through small mammals: from the Mousterian to the Bronze Age in El Mirón Cave (Cantabria, Spain). *Journal of Archaeological Science* 36, 947–955.

Dalén, L., Orlando, L., Shapiro, B., Durling, M.B., Quam, R., Gilbert, M.T.P., Díez Fernández-Lomana, J.C., Willerslev, E., Arsuaga, J.L., Götherström, A., 2012. Partial genetic turnover in neandertals: continuity in the east and population replacement in the west. *Molecular Biology and Evolution* 29, 1893–1897.

Daura, J., Sanz, M., Pike, A.W.G., Subirà, M.E., Fornós, J.J., Fullola, J.M., Julià, R., Zilhão, J., 2010. Stratigraphic context and direct dating of the Neandertal mandible from Cova del Gegant (Sitges, Barcelona). *Journal of Human Evolution* 59, 109–122.

Daura, J., Sanz, M., Subirá, M.E., Quam, R., Fullola, J.M., Arsuaga, J.L., 2005. A Neandertal mandible from the Cova del Gegant (Sitges, Barcelona, Spain). *Journal of Human Evolution* 49, 56–70.

Delibes, G., Díez, F., 2006. ¿Una Meseta desolada? Estado actual de la investigación sobre el Paleolítico Superior en las regiones interiores de la Península Ibérica. In: Delibes de Castro, G., Díez Martin, F. (Eds.), *El Paleolítico Superior en la Meseta Norte Española*. Universidad de Valladolid, Secretariado de Publicaciones, Valladolid, Spain, pp. 11–40.

Díez, C., Alonso, R., Bengoechea, A., Colina, A., Jordá, J.F., Navazo, M., Ortiz, J.E., Pérez, S., Torres, T., 2008. El Paleolítico Medio en el valle del Arlanza (Burgos). Los sitios de la Ermita, Millán y la Mina. *Revista C* & G 22, 135–157.

Díez, C., García, M.A., Gil, E., Jordá, J.F., Ortega, A.I., Sánchez, A., Sánchez, B., 1988–1989. La cueva de Valdegoba (Burgos). Primera campaña de excavaciones. *Zephyrus* 41–42, 55–74.

Domingo, R., Peña-Monné, J.L., de Torres, T., Ortiz, J.E., Utrilla, P., (2017). Neanderthal highlanders: Las Callejuelas (Monteagudo del Castillo, Teruel, Spain), a high-altitude site occupied during MIS 5. *Quaternary International* 435, 129–143.

Domínguez-Rodrigo, M., Piqueras, A., 2003. The use of tooth pits to identify carnivore taxa in tooth-marked archaeofaunas and their relevance to reconstruct hominid carcass processing behaviours. *Journal of Archaeological Science* 30, 1385–1391.

Fernández Rodríguez, C., 2006. De humanos y carnívoros: la fauna de macromamíferos de la cueva de A Valiña (Castroverde, Lugo). In: Maillo, J.M., Baquedano, E. (Eds.), *Miscelánea en homenaje a Victoria Cabrera* Zona Arqueológica 7. Vol I. Museo Arqueológico Regional, Alcalá de Henares, pp. 290–303.

García, N., 2003. *Osos y otros carnívoros de la Sierra de Atapuerca*. Fundación Oso de Asturias, Oviedo.

García-Antón, M.D., 2016. *La captación, selección y gestión de recursos líticos en la Prehistoria: una visión diacrónica del uso del territorio y sus recursos en el entorno de la Sierra de Atapuerca (Burgos) durante el Pleistoceno inferior y medio*. Ph.D. Dissertation. Universitat Rovira i Virgili, Tarragona, Spain.

Garrod, D.A.E., 1928. Archaeology and geology. In: Garrod, D.A.E., Buxton, L.H.D., Smith, G.E., Bate, D.M.A. (Eds.), *Excavation of a Mousterian rock-shelter at devil's tower, Gibraltar*. Royal Anthropological Institute of Great Britain and Ireland, London, pp. 34–56.

Girard, M., Renault-Miskovsky, J., 1969. Nouvelles techniques de préparation palynologie appliques à trois sédiments du Quaternaire final de l'Abri Cornille (Istres, Bouches-du Rhone). *Bulletin de l'Association Française pour l´Etude du Quaternaire* 4, 275–284.

Gómez-Olivencia, A., Arceredillo, D., Álvarez-Lao, D.J., Garate, D., San Pedro, Z., Castaños, P., Rios-Garaizar, J., 2014. New evidence for the presence of reindeer (*Rangifer tarandus*) on the Iberian Peninsula in the Pleistocene: an archaeopalaeontological and chronological reassessment. *Boreas* 43, 286–308.

Grimm, E.C., 1987. CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers and Geosciences* 13, 13–35.

Grimm, E.C., 1992. TILIA v. 2. Illinois State Museum, Research and Collection Center, Springfield.

Lalueza-Fox, C., Sampietro, M.L., Caramelli, D., Puder, Y., Lari, M., Calafell, F., Martínez-Maza, C., Bastir, M., Fortea, J., de la Rasilla, M., Bertranpetit, J., Rosas, A., 2005. Neandertal Evolutionary Genetics: mitochondrial DNA data from Iberian Peninsula. *Molecular Biology and Evolution* 22, 1077–1081.

Laplace, G., 1972. La typologie analytique et structurale: Base rationnelle d'étude des industries lithiques et osseuses, Banques des données archéologiques. *Colloques nationaux du CNRS* 932, 91–143.

Laplana, C., Blain, H.A., Sevilla, P., Arsuaga, J.L., Baquedano, E., Pérez-González, A., 2013. Un assemblage de petits vertébrés hautement diversifié de la fin du MIS 5 dans un environnement montagnard au centre de l'Espagne (Cueva del Camino, Pinilla del Valle, Communauté autonome de Madrid). *Quaternaire* 24, 207–216.

Lira, J., Linderholm, A., Olaria, C., Brandström Durling, M., Gilbert, M.T.P., Ellegren, H., Willerslev, E., Lidén, K., Arsuaga, J.L., Götherström, A., 2010. Ancient DNA reveals traces of Iberian Neolithic and Bronze Age lineages in modern Iberian horses. *Molecular Ecology* 19, 64–78.

López-García, J.M., Agustí, J., Cuenca-Bescós, G., 2007. Catalogue of the late Quaternary Iberian micro-mammals (Rodentia, Eulipotyphla, Chiroptera) from the Museu de Geologia de Barcelona, Spain. *Treballs del Museu de Geologia de Barcelona* 15, 5–23.

López-García, J.M., Blain, H.-A., Cuenca-Bescós, G., Arsuaga, J.L., 2008. Chronological, environmental, and climatic precisions on the Neanderthal site of the Cova del Gegant (Sitges, Barcelona, Spain). *Journal of Human Evolution* 55, 1151–1155.

Lorenzo, J.I., Montes, L., 2001. Restes néandertaliens de la Grotte de "Los Moros de Gabasa" (Huesca, Espagne). In: Zilhão, J., Aubry, T.H., Carvalho, A.F. (Eds.), *Les premiers hommes modernes de la Péninsule Ibérique*. Trabalhos de Arqueologia vol. 17. Instituto Português de Arqueologia, Lisboa, pp. 77–86.

Lozano, M., Subirà, M.E., Aparicio, J., Lorenzo, C., Gómez-Merino, G., 2013. Toothpicking and Periodontal Disease in a Neanderthal Specimen from Cova Foradà Site (Valencia, Spain). *PLoS ONE* 8, e76852. http://dx.doi.org/10.1371/journal.pone.0076852.

Lyman, R.L., 1994. *Vertebrate Taphonomy*. Cambridge University Press, Cambridge.

Mallol, C., 1999. The selection of lithic raw materials in the Lower and Middle Pleistocene levels TD6 and TD10A of Gran Dolina (Sierra de Atapuerca, Burgos, Spain). *Journal of Anthropological Research* 55, 385–407.

Mosquera, M., Ollé, A., Pérez-González, A., Rodríguez, X.P., Vaquero, M., Vergès, J.M., Carbonell, E., 2007. Valle de las Orquídeas: un yacimiento al aire libre del Pleistoceno superior en la Sierra de Atapuerca (Burgos). *Trabajos de Prehistoria* 64, 143–155.

Moure Romanillo, A., Delibes de Castro, G., Castanedo Tapia, I., Hoyos Gómez, M., Cañaveras, J.C., Iriarte Chiapusso, M.J., 1997. Revisión y nuevos datos sobre el Musteriense de la cueva de La Ermita (Hortigüela, Burgos). In: Balbín Behrmann, R., Bueno Ramírez, P. (Eds.), *II Congreso de Arqueología Peninsular, Tomo I-Paleolítico y Epipaleolítico*. Fundación Rei Alfonso Henriques, Zamora, pp. 67–83.

Navazo, M., Alonso-Alcalde, R., Benito-Calvo, A., Díez, J.C., Pérez-González, A., Carbonell, E., 2011. Hundidero: MIS 4 open air Neanderthal occupations in Sierra de Atapuerca. *Archaeology, Ethnology and Anthropology of Eurasia* 39, 29–41.

Navazo, M., Carbonell, E., 2014. Neanderthal settlement patterns during MIS 4–3 in Sierra de Atapuerca (Burgos, Spain). *Quaternary International* 331, 267–277.

Navazo, M., Colina, A., Dominguez-Bella, S., Benito-Calvo, A., 2008. Raw stone material supply for Upper Pleistocene settlements in Sierra de Atapuerca (Burgos, Spain): flint characterization using petrographic and geochemical techniques. *Journal of Archaeological Science* 35, 1961–1973.

Navazo, M., Díez, J.C., Torres, T., Colina, A., Ortiz, J.E., 2005. La cueva de Prado Vargas. Un yacimiento del Paleolítico Medio en el sur de la Cordillera Cantábrica. In: Lasheras, J.A., Montes, R. (Eds.), *Neandertales cantábricos, estado de la cuestión*. Museo de Altamira, Santander, pp. 151–166.

Ollé, A., Mosquera, M., Rodríguez, X.P., de Lombera-Hermida, A., García-Antón, M.D., García-Medrano, P., Peña, L., *et al*., 2013. The

Early and Middle Pleistocene technological record from Sierra de Atapuerca (Burgos, Spain). *Quaternary International* 295, 138–167.

Orlando, L., Mashkour, M., Burke, A., Douady, C.J., Eisenmann, V., Hänni, C., 2006. Geographic distribution of an extinct equid (*Equus hydruntinus*: Mammalia, Equidae) revealed by morphological and genetical analyses of fossils. *Molecular Ecology* 15, 2083–2093.

Orlando, L., Metcalf, J.L., Alberdi, M.T., Telles-Antunes, M., Bonjean, D., Otte, M., Martin, F., *et al*., 2009. Revising the recent evolutionary history of equids using ancient DNA. *Proceedings of the National Academy of Sciences* 106, 21754–21759.

Ortega, A.I., 2009. Evolución geomorfológica del Karst de la Sierra de Atapuerca (Burgos) y su relación con los yacimientos pleistocenos que contiene. Ph.D. Dissertation. Universidad de Burgos.

Ortega, A.I., Benito-Calvo, A., Pérez-González, A., Carbonell, E., Bermúdez de Castronez, J.M., Arsuaga, J.L., 2014. Atapuerca Karst and its Palaeoanthropological Sites. In F. Gutiérrez and M. Gutiérrez (eds.), *Landscapes and Landforms of Spain*, World Geomorphological Landscapes. Springer Science, Dordrecht, pp. 101–111.

Ortega, A.I., Benito-Calvo, A., Pérez-González, A., Martín-Merino, M.A., Pérez-Martínez, R., Parés, J.M., Aramburu, A., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2013. Evolution of multilevel caves in the Sierra de Atapuerca (Burgos, Spain) and its relation to human occupation. *Geomorphology* 196, 122–137.

Pales, L., Garcia, M.A., 1981a. *Atlas ostéologique pour servir à l'identification des mammifères du Quaternaire: Herbivores*. Centre National de la Recherche Scientifique, Paris.

Pales, L., Garcia, M.A., 1981b. *Atlas ostéologique pour servir à l'identification des mammifères du Quaternaire: Carnivores, Homme*. Centre National de la Recherche Scientifique, Paris.

Parés, J.M., Ortega, A.I., Benito-Calvo, A., Aranburu, A., 2016. Paleomagnetic constraints of the Atapuerca karst development (N Spain). *Geological Society of America Special Papers* 516, SPE16–SPE22.

Pickering, T.R., Domínguez-Rodrigo, M., Heaton, J.L., Yravedra, J., Barba, R., Bunn, H.T., Musiba, C., *et al*., 2013. Taphonomy of ungulate ribs and the consumption of meat and bone by 1.2-million-year-old hominins at Olduvai Gorge, Tanzania. *Journal of Archaeological Science* 40, 1295–1309.

Quam, R., Sanz, M., Daura, J., Robson Brown, K., García-González, R., Rodríguez, L., Dawson, H., *et al*., 2015. The Neandertals of northeastern Iberia: New remains from the Cova del Gegant (Sitges, Barcelona). *Journal of Human Evolution* 81, 13–28.

Quam, R.M., Arsuaga, J.L., Bermúdez de Castro, J.M., Díez, C.J., Lorenzo, C., Carretero, J.M., García, N., Ortega, A.I., 2001. Human remains from Valdegoba Cave (Huermeces, Burgos, Spain). *Journal of Human Evolution* 41, 385–435.

Rhodes, S., Walker, M.J., López-Martínez, M., Haber-Uriarte, M., López-Jiménez, A., Buitrago-López, A.T., Dewar, G., 2013. Analysis of *Hystrix* specimens recovered from Sima de las Palomas, Murcia, Spain: identification and paleoenvironmental revision (abstract). In: Silcox, M.T., Schillaci, M.A., Sumra, M.K. (Eds.), *41st Annual Meeting Canadian Association for Physical Anthropology. Program with abstracts*. University of Toronto, Scarborough, pp. 47–48.

Rios-Garaizar, J., 2017. A new chronological and technological synthesis for late Middle Paleolithic of the Eastern Cantabrian Region. *Quaternary International* 433B, 50–63.

Rios-Garaizar, J., Eixea, A., Villaverde, V., 2015a. Ramification of lithic production and the search of small tools in Iberian Peninsula Middle Paleolithic. *Quaternary International* 361, 188–199.

Rios-Garaizar, J., Garate Maidagan, D., Gómez-Olivencia, A., Iriarte, E., Arceredillo-Alonso, D., Iriarte-Chiapusso, M.J., Garcia-Ibaibarriaga, N., *et al*., 2015b. Short-term Neandertal occupations in the late Middle Pleistocene of Arlanpe (Lemoa, northern Iberian Peninsula). *Comptes Rendus Palevol* 14, 233–244.

Rodríguez, J., Burjachs, F., Cuenca-Bescós, G., García, N., Van der Made, J., Pérez González, A., Blain, H.A., *et al*., 2011. One million years of cultural evolution in a stable environment at Atapuerca (Burgos, Spain). *Quaternary Science Reviews* 30, 1396–1412.

Rodríguez, X.P., 2004. Technical Systems of Lithic Production in the Lower and Middle Pleistocene of the Iberian Peninsula: technological variability between north-eastern sites and Sierra de Atapuerca sites. *British Archaeological Reports, International Series S1323*. John and Erica Hedges Ltd., Oxford.

Rodríguez-Hidalgo, A., Saladié, P., Ollé, A., Carbonell, E., 2015. Hominin subsistence and site function of TD10.1 bone bed level at Gran Dolina site (Atapuerca) during the late Acheulean. *Journal of Quaternary Science* 30, 679–701.

Rosas, A., Estalrrich, A., García-Tabernero, A., Bastir, M., García-Vargas, S., Sánchez-Meseguer, A., Huguet, R., *et al*., 2012. Les Néandertaliens d'El Sidrón (Asturies, Espagne): actualisation d'un nouvel échantillon. *L'Anthropologie* 116, 57–76.

Rosas, A., Martinez-Maza, C., Bastir, M., Garcia-Tabernero, A., Lalueza-Fox, C., Huguet, R., Ortiz, J.E., *et al*., 2006. Paleobiology and comparative morphology of a late Neandertal sample from El Sidrón, Asturias, Spain. *Proceedings of the National Academy of Sciences* 103, 19266–19271.

Rosell, J., Cáceres, I., Blasco, R., Bennàsar, M., Bravo, P., Campeny, G., Esteban-Nadal, M., *et al*., 2012. A zooarchaeological contribution to establish occupational patterns at Level J of Abric Romaní (Barcelona, Spain). *Quaternary International* 247, 69–84.

Sala, M.T.N., Arsuaga, J.L., Laplana, C., Ruiz Zapata, B., 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). *Boletín de la Real Sociedad Española de Historia Natural Sección Geología* 105, 67–85.

Sala, M.T.N., Pantoja, A., Arsuaga, J.L., Algaba, M., 2010. Presencia de bisonte (*Bison priscus* Bojanus, 1827) y uro (*Bos primigenius* Bojanus, 1827) en las cuevas del Búho y de la Zarzamora (Segovia, España). *Munibe Antropologia-Arkeologia* 61, 43–55.

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. *Journal of Taphonomy* 10, 477–497.

Sala, N., Arsuaga, J.L., (in press). Regarding beasts and humans: A review of taphonomic works with living carnivores. *Quaternary International*. https://doi.org/10.1016/j.quaint.2016.03.011.

Sala, N., Arsuaga, J.L., Haynes, G., 2014. Taphonomic comparison of bone modifications caused by wild and captive wolves (*Canis lupus*). *Quaternary International* 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. *Journal of Archaeological Science* 55, 113–121.

Saladié, P., Huguet, R., Rodríguez-Hidalgo, A., Cáceres, I., Esteban-Nadal, M., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2012. Intergroup cannibalism in the European Early Pleistocene: the range expansion and imbalance of power hypotheses. *Journal of Human Evolution* 63, 682–695.

Selvaggio, M.M., Wilder, J., 2001. Identifying the Involvement of Multiple Carnivore Taxa with Archaeological Bone Assemblages. *Journal of Archaeological Science* 28, 465–470.

Shipman, P., Rose, J., 1983. Early hominid hunting, butchering, and carcass-processing behaviors: Approaches to the fossil record. *Journal of Anthropological Archaeology* 2, 57–98.

Stiner, M.C., Weiner, S., Bar-Yosef, O., Kuhn, S.L., 1995. Differential burning, recrystallization, and fragmentation of archaeological bone. *Journal of Archaeological Science* 22, 223–237.

Straus, L., Bicho, N., Winegardner, A., 2000. The Upper Palaeolithic settlement of Iberia: first-generation maps. *Antiquity*, 553–566.

Stringer, C.B., Finlayson, J.C., Barton, R.N.E., Fernández-Jalvo, Y., Cáceres, I., Sabin, R.C., Rhodes, E.J., *et al*., 2008. Neanderthal exploitation of marine mammals in Gibraltar. *Proceedings of the National Academy of Sciences* 105, 14319–14324.

Utrilla, P., Montes, L., Blasco, F., Torres, T., Ortiz, J.E., 2010. La cueva de Gabasa revisada 15 años después: un cubil para las hienas y un cazadero para los Neandertales. *Zona Arqueológica* 13, 376–390.

Vallverdú, J., Allué, E., Bischoff, J.L., Cáceres, I., Carbonell, E., Cebrià, A., García-Antón, D., *et al*., 2005. Short human occupations in the Middle Palaeolithic level i of the Abric Romaní rock-shelter (Capellades, Barcelona, Spain). *Journal of Human Evolution* 48, 157–174.

Vallverdú, J., Alonso, S., Bargalló, A., Bartrolí, R., Campeny, G., Carrancho, Á., Expósito, I., *et al*., 2012. Combustion structures of archaeological level O and mousterian activity areas with use of fire at the Abric Romaní rockshelter (NE Iberian Peninsula). *Quaternary International* 247, 313–324.

van der Meulen, A.J., 1973. Middle Pleistocene smaller mammals from the Monte Peglia (Orvieto, Italy) with special reference to the phylogeny of *Microtus* (Arvicolidae, Rodentia). *Quaternaria* 17, 1–144.

Vaquero, M., Bargalló, A., Chacón, M.G., Romagnoli, F., Sañudo, P., 2015. Lithic recycling in a Middle Paleolithic expedient context: Evidence from the Abric Romaní (Capellades, Spain). *Quaternary International* 361, 212–228.

Vilà, C., Leonard, J.A., Götherström, A., Marklund, S., Sandberg, K., Lidén, K., Wayne, R.K., Ellegren, H., 2001. Widespread origins of domestic horse lineages. *Science* 291, 474–477.

Villa, P., Mahieu, E., 1991. Breakage patterns of human long bones. *Journal of Human Evolution* 21, 27–48.

Villalta, J.F., 1972. Presencia de la Marmota y otros elementos de la fauna esteparia en el Pleistoceno catalán. *Acta Geológica Hispánica* VII, 170–173.

Vilstrup, J.T., Seguin-Orlando, A., Stiller, M., Ginolhac, A., Raghavan, M., Nielsen, S.C.A., Weinstock, J., *et al*., 2013. Mitochondrial phylogenomics of modern and ancient equids. *PLoS ONE* 8, e55950. http://dx.doi.org/10.137.journal.pone.0055950.

Walker, M.J., Ortega, J., López, M.V., Parmová, K., Trinkaus, E., 2011a. Neandertal postcranial remains from the Sima de las Palomas del Cabezo Gordo, Murcia, southeastern Spain. *American Journal of Physical Anthropology* 144, 505–515.

Walker, M.J., Ortega, J., Parmová, K., López, M.V., Trinkaus, E., 2011b. Morphology, body proportions, and postcranial hypertrophy of a female Neandertal from the Sima de las Palomas, southeastern Spain. *Proceedings of the National Academy of Sciences* 108, 10087–10091.

White, T.D., 1992. *Prehistoric cannibalism at Mancos 5Mtumr-2346*. Princeton University Press, Princeton.