

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 lithostratigraphic 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 ¹⁴C 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.

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52 The northern Iberian plateau (*meseta norte*) is the section
 53 of the central Iberian plateau that is located north of the
 54 Central system. It is characterized by a Mediterranean climate
 55 with continental climate traits. Thus, the northern plateau,
 56 even in current conditions, registers low temperatures during
 57 its long winters and an extreme range of temperatures during
 58 its short summers, which would have made it a challenging
 59 environment during the cold phases of the Pleistocene.
 60 In fact, during Marine Isotope Stage (MIS) 2 the northern
 61 plateau was sparsely populated and locally depopulated
 62 (Straus et al., 2000; Delibes and Díez, 2006), but just how is
 63 still largely unknown.

64 In the last 15 years, new human fossil remains, new sites,
 65 and new analytical approaches have resulted in a better
 66 understanding of the cultural diversity, chronology, and
 67 occupation dynamics of Neanderthals in southern Europe
 68 (see below). These new results mainly refer to coastal areas of
 69 the Iberian Peninsula, which show milder conditions than
 70 those of the Iberian interior. In the northern Iberian fringe, the
 71 important site of El Sidrón is remarkable, having yielded new
 72 and important paleobiological (including genetic) and
 73 cultural data (Lalueza-Fox et al., 2005; Rosas et al., 2006,
 74 2012). Additionally, the integrative study of the lithic
 75 remains from different Iberian Basque sites (e.g., Axlor) has
 76 resulted in a better understanding of cultural changes
 77 occurring in the northern fringe of the Iberian Peninsula
 78 (Rios-Garaizar et al., 2015a, 2015b; Rios-Garaizar, 2017).

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

90 Despite the growing evidence (e.g., Álvarez-Alonso et al.,
 91 in press; Domingo et al., in press, and references therein), the
 92 data available regarding the interior of the peninsula is still
 93 sparse. The Pinilla del Valle sites have provided human
 94 fossils and new information on the Neanderthal presence
 95 during MIS 5–4 (Baquedano et al., 2011–2012; Arsuaga
 96 et al., 2012). The cave of Gabasa has yielded a long strati-
 97 graphic sequence and several human remains (Lorenzo and
 98 Montes, 2001; Utrilla et al., 2010). In the southern Iberian
 99 plateau, Los Casares has yielded evidence of Mousterian
 100 occupations and one metacarpal bone (Basabe, 1973;
 101 Alcaraz-Castaño et al., 2015). In the northern plateau,
 102 Valdegoba has yielded several Neanderthal remains (which
 103 have also provided ancient DNA) and an abundant archaeo-
 104 paleontological assemblage (Díez et al., 1988–1989; Quam
 105 et al., 2001, Arcercedillo et al., 2011; Dalén et al., 2012).
 106 Additional Mousterian occupations have been detected
 107 around Hortigüela (Burgos): the sites of La Ermita, Millán,
 108 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 sur-
 veys 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 chrono-
 logical 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 thermo-
 luminescence dates from the *terra-rossa* forming the strati-
 graphic sequences: $27,507 \pm 2,295$ years and $29,955 \pm 2,319$
 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 archaeo-
 logical 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



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.)

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 m²) 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 m²) 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 m² and the second to ca. 6 m² (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

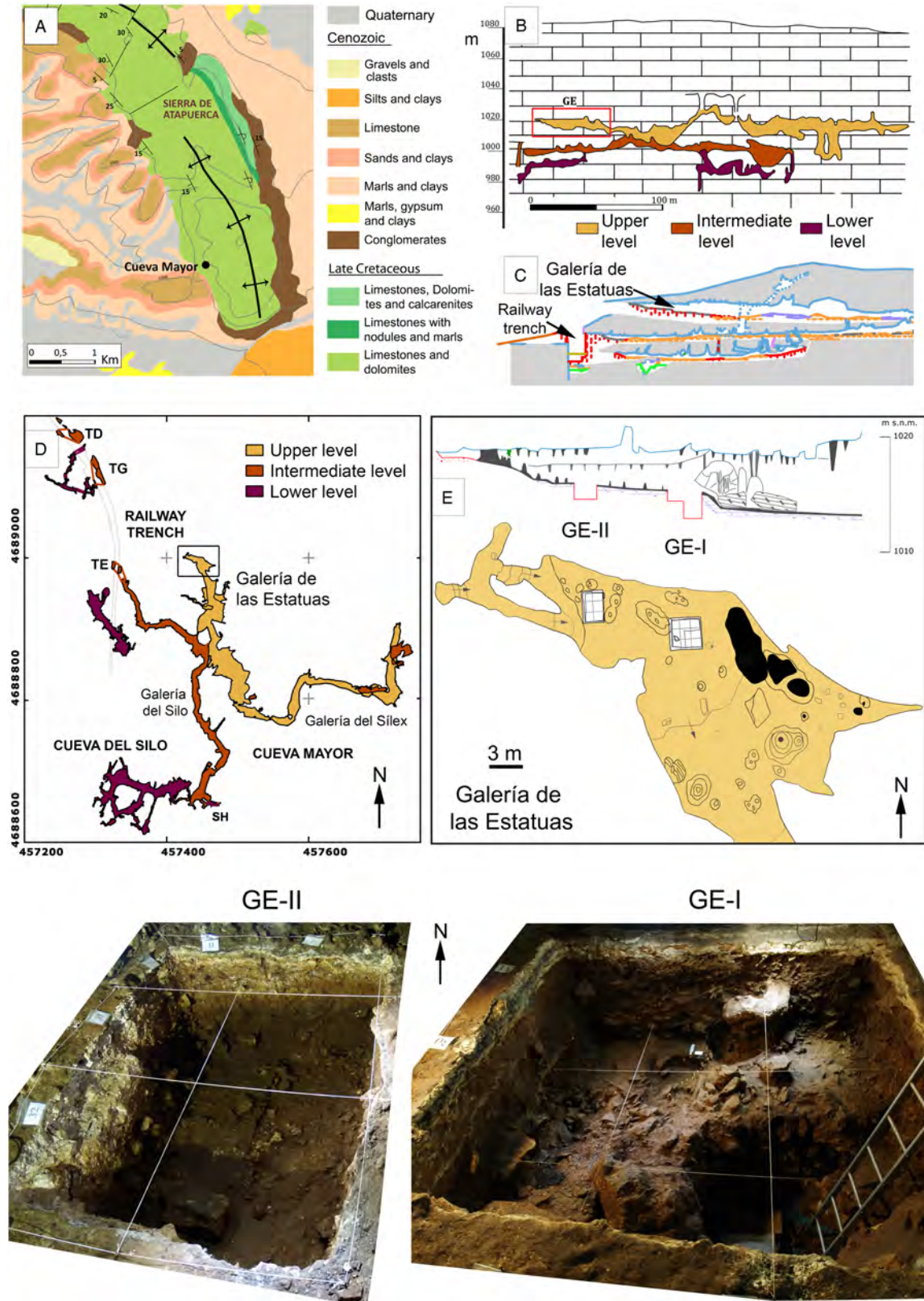


Figure 2. (color online) (A) General geological map of the Sierra de Atapuerca and the location of the Cueva Mayor cave, one of the entrances to the Cueva Mayor-Cueva del Silo cave system (modified from IGME). (B) Cross-section of Cueva Mayor-Cueva del Silo cave system on a topographical profile showing the highest point of the Sierra (modified from Ortega, 2009) and (C) a topographical profile closer to the galleries. (D) Map of the Cueva Mayor-Cueva del Silo cave system, with the location of the Galería de las Estatuas. (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. 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).

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 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 50°C, 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 (clays) 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 $\frac{1}{4}$ 1.5418 Å, $\lambda_{Cu_{K\alpha 1}}$ $\frac{1}{4}$ 1.54060 Å and $\lambda_{Cu_{K\alpha 2}}$ $\frac{1}{4}$ 1.54439 Å), a vertical goniometer (Bragg-Brentano geometry), a programmable divergence slit, an automated sample 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 (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 (M₁ or M₂, 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-ISCI (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 New *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

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322 zoom microscope and a DINO-LITE digital microscope).
 323 Photographs were taken with the digital video microscope
 324 DINO-LITE AM-TFVW-A (*DinoCapture 2.0* software).

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

336 The breakage patterns were analyzed on long bone frag-
 337 ments, following the methodology proposed by Villa and
 338 Mahieu (1991; see also Sala et al., 2015). The following
 339 parameters were taken into account: fracture outline (long-
 340 itudinal, transverse, or oblique/curved), fracture angle (right
 341 or oblique), fracture edge (smooth or jagged), shaft cir-
 342 cumference (1 = less than half of the circumference;
 343 2 = more than half of the circumference; 3 = complete cir-
 344 cumference), and shaft fragment (1 = less than one-quarter
 345 of the total diaphysis; 2 = between one-quarter and one-half
 346 of the total diaphysis; 3 = between one-half to three-quarters
 347 of the diaphysis; 4 = more than three-quarters of the dia-
 348 physis). The presence or absence of peeling was also recor-
 349 ded (White, 1992; Pickering et al., 2013).

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

358 Lithic analysis

359 The lithic assemblage was studied using the Logical
 360 Analytical System (LAS) method (Carbonell et al., 1983,
 361 1992; Rodríguez, 2004; Ollé et al., 2013). The LAS approa-
 362 ches the study of technological processes based on the stage
 363 at which the objects were produced during the reduction
 364 sequence. All the pieces, including the fragments, were
 365 analyzed, which involved the raw material, the technical
 366 attributes of every lithic category, and the integrity of the
 367 reduction sequences.

368 The Sierra de Atapuerca and its surroundings offer a wide
 369 range of raw materials, with outcrops not further than 3 km
 370 from the sites. Five primary types of rocks were archaeo-
 371 logically identified in previous work (Mallol, 1999; Navazo
 372 et al., 2008; García-Antón, 2016) and all the lithic remains
 373 correspond to six groups of lithologies. Two of them, quart-
 374 zite and metasandstone, are of metamorphic origin; two,
 375 including chert (Neogene and the Cretaceous varieties)
 376 and limestone (mainly fine mudstones), are of sedimentary

origin; and macrocrystalline quartz is of filonian or hydro-
 thermal 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 var-
 ious 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 plat-
 forms (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 morpho-
 logy), 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 allocthonous nature, based on the presence of quartz,
 phyllosilicates, and different extraclasts (sandstone, gneiss,
 and iron oxides; Aranburu et al., 2012; Fig. 3). The descrip-
 tion 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 diffractometry 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 con-
 cordance with the minimum age of the stabilization of the

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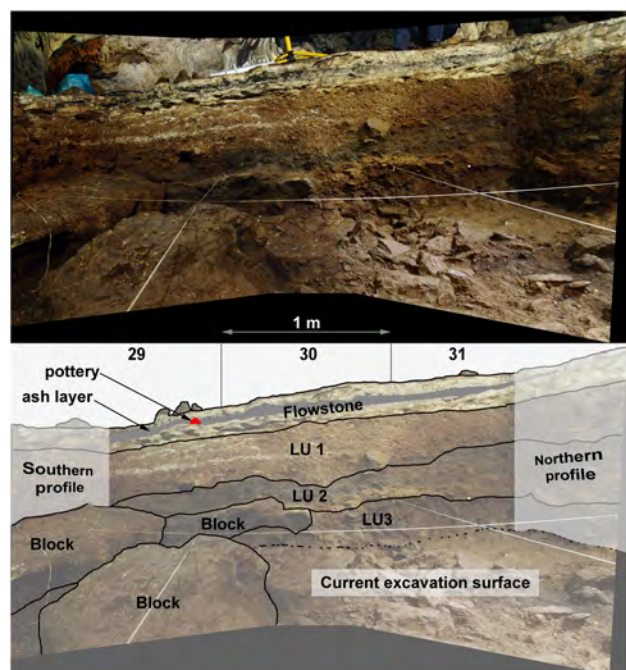


Figure 3. (color online) Western profile of GE-I at the end of the 2015 field season. LU, Lithostratigraphical unit.

water table that matches the intermediate level of the karst (Parés et al., 2016). There is a lack of available information 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 pink to pinkish silty clays with no clasts. 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 BP, 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, sharp-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 allochthonous 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 BP, 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

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

Site	LU	Sample	Sediment	Clasts	Total Mineralogy							Lithology			
					Quartz	Phyllosilicates	Calcite	Apatite	Plagioclase	K-feldspar	Dolomite	Speleothem	Other rocks	Clasts (1–2 mm)	
														Matrix	Calcite
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	1	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%		
GE-II	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	1	Pink to pinkish silty clays with roots on its top	None	15%	8%	77%	-	-	-	traces	-	-	-	
		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	1	Dark silty clay sediment	Decimetric, abundant, more sharp-edged	62%	34%	2%	-	-	-	2%	80%	2%	18%		
	2	Dark silty clay sediment	Decimetric, abundant, more sharp-edged	62%	23%	10%	1%	2%	-	2%	80%	2%	18%		

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

Site	Lithostratigraphic		Sample	Smectite	Illite	Kaolinite	Chlorite
	unit						
GE-I	1	1	-	73%	22%	5%	
		2	-	76%	19%	5%	
	2	-	-	78%	18%	4%	
		-	-	73%	22%	5%	
	3a	-	-	81%	16%	3%	
4	1	-	76%	20%	4%		
	2	-	79%	18%	3%		
GE-II	5	-	-	78%	17%	5%	
		-	-	78%	17%	5%	
	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).

Q18 514 cave floor. In Fig. 5, the percentage of presence was nor- 515
malized, according to the maximum percentage presence for 516
each of the groups.

517 The GE-I palynological sequence can be divided into three 518
pollen zones: Zone 3 is the lowermost one (LUs 5, 4 and 519
lower part of 3) and is characterized by an open environment, 520
indicative of a cool and dry climate; Zone 2 is the inter- 521
mediate (the upper part of LU3) and shows a shrub expan- 522
sion; and Zone 1 is the uppermost (i.e., the most recent, 523
comprising LU2 and the base of LU1) and shows a more 524
wooded environment (though it does not reach the threshold 525
to be considered a closed forest), which is indicative of a 526
relatively warmer and more humid climate. It is possible to 527
further divide the oldest zone (Zone 3-open environment) 528
into three phases (Fig. 5). The sequence starts with an open 529
environment with very low taxonomic diversity, which 530
indicates a very dry landscape (LU5 and base of LU4). There 531
is a slight climatic improvement throughout most of 532
LU4 with an increase in the percentage of *Pinus* pollen, 533
followed by the development of other tree species, such as 534
Betula, *Fagus*, and *Corylus*, which indicates a more mesic 535
environment. Finally, the lower half of LU3 shows a more 536
xeric climate (drier) with an expansion of Asteraceae, 537
Chenopodiaceae, *Artemisia*, and *Ephedra*. The second zone, 538
at the end of LU3, shows a transition towards the conditions 539
of Zone 1, with a warmer and wetter environment and a 540
higher taxonomic diversity demonstrated by non-arboreal 541
pollen and the expansion of shrubs. The first zone (LU2 and 542
the base of LU1) is characterized by a relatively warmer and 543
more humid climate, and the expansion of forest dominated 544
by *Pinus*; however, it becomes more taxonomically diverse. 545
The information from LU1 is sparse. While the LU1 base is 546
similar to the end of LU2, two additional samples in LU1 did 547
not contain the minimum amount of pollen required for 548
analysis (Figs. 4 and 5).

549 There is only a partial correspondence between the LUs 550
and the pollen zones. This will be the object of further study 551
in the near future. Zone 1 coincides with LU2. The upper part 552
of LU1 has not yielded a significant amount of pollen and 553
would correspond in our geological interpretation with the 554
moment when the cave starts to close. Differences in the 555
correspondence between Zones 2 and 3 and LU 3 and 4 could 556
be related to either (or both): (a) slight paleoecological 557
changes that may have not been strong enough to alter the 558
geological conditions of sedimentation; and (b) changes in 559
the occupation dynamics of the cave which could have 560
occurred, leaving an imprint on the sedimentary record 561
regardless of potential changes in the paleoenvironment of the 562
surroundings of the cave.

563 In GE-II, only a preliminary sampling was performed, 564
limited to LUs 1 and 2. The sequence starts with an open 565
environment but there is an expansion of forest, dominated 566
by *Pinus*, which parallels the record in LU2 of GE-I. In LU1, 567
the data are sparser and a deterioration of the climatic con- 568
ditions may be detected, which leads to more open environ- 569
ment conditions.

Microfaunal remains

570 Remains of several bird species and a few fish have been 571
recovered in both test pits, but are still under study. In GE-I, 572
only LUs 2 to 4 have yielded micro-vertebrate remains (see 573
Fig. 6 and Supplementary Table 1). The number of indivi- 574
duals and the taxonomic diversity is very limited in LU2, the 575
spit (artificial excavation unit) intermediate between LU2 and 576
3, and LU 4. LU3, in contrast, yielded a larger sample (both 577
in terms of MNI and diversity), which is dominated by open- 578
environment dwellers (such as *Marmota*, and voles belong- 579
ing to genera *Pliomys* and *Microtus*) and bats belonging to 580
the genus *Myotis*. The presence of forest dwellers, such as 581
Apodemus sp. and *Eliomys quercinus*, as well as the presence 582
of the porcupine, *Hystrix (Acanthion) vinogradovi*, also 583
indicates the presence of forest patches in the vicinity of the 584
cave. Humid environments are inferred near the cave, based 585
on the presence of Talpidae indet. and *Microtus oeconomus*. 586

587 In GE-II, excavation of LU2 is currently being finished, 588
and, thus, information is limited to levels 1 (1a and 1b) and 2. 589
LU1 has not yielded a large micro-mammal assemblage. 590
LU2 shows a microfaunal association dominated by open- 591
environment dwellers such as *Marmota*, and voles belonging 592
to genus *Pliomys* and *Microtus*, with the presence of forest 593
dwellers, such as *Apodemus* sp. and *Eliomys quercinus*, as 594
well as *Castor fiber*, which would be consistent with the 595
presence of water courses in the vicinity of the cave. A large 596
number of lagomorphs are also present. Both sites have also 597
yielded a small herpetological assemblage that remains to be 598
studied.

Macrofaunal remains

599 In terms of NISP, the macrofaunal assemblage is dominated by 600
ungulate remains, though the presence of carnivores is

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	$^{13}\text{C}/^{12}\text{C}$ 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	42720–out of range (>48000)	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	43043–out of range (>48000)	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	43106–out of range (>48000)	45,106–out of range (>49,500)	This study
Hotel California	2	E-022	Bone	OxA-24564	-18.85	AMS-Ultrafiltration	> 46,300		48,200 ± 3300	This study
		HC10-1				SG-OSL			Arnold et al., 2013	
	V (top)									
Valdegoba Prado Vargas	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	Human bone	OxA-21970		AMS-ultrafiltration	48400 ± 3300		71,000 ± 5600	Arnold et al., 2013
La Ermita Cueva Millán	5a		Tooth (horse)			Aminoacid racemization			46,400	Dalén et al., 2012
		1a	Charcoal	OxA-4603		Conventional C14	31100 ± 550	32,135–34,240	34,135–36,240	Diez et al., 2008
	1b	Charcoal	GrN-11021		Conventional C14	37600 ± 700	38,923–41,082	40,923–43,082	40,923–43,082	Moure Romanillo et al., 1997
La Mina			Charcoal	GrN-1161		Conventional C14	37450 ± 650	38,869–40,892	40,869–42,892	Moure Romanillo et al., 1997
			Tooth (rhinoceros)	LEB-6012		Aminoacid racemization			52,500	Diez et al., 2008

Calibration was performed with OxCal 4.2 (Bronk Ramsey, 2013), using the IntCal13 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.

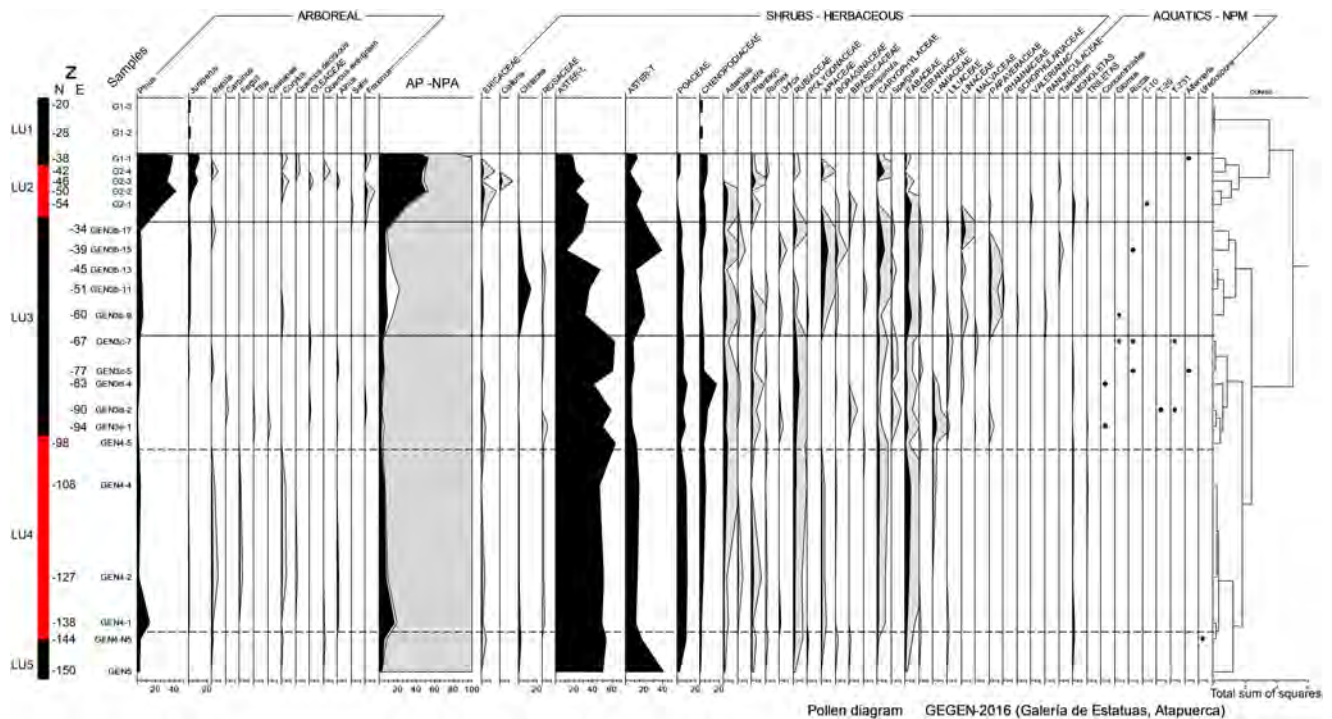


Figure 4. (color online) The horizontal lines subdivide the sequence into the main zones and subzones (see Fig. 5). From LU5 to the middle of LU3 the palynological record is characteristic of open environments. The upper part of LU3 shows a development of shrubs, while LU2 shows an increase in arboreal 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.

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

617 *Equus hydruntinus* mtDNA

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

624 Taphonomic analysis

625 The taphonomic traits of the GE-I and GE-II pits differ
 626 depending on the LU analyzed. In general terms, anthropo-
 627 genic modifications (cut marks and anthropogenic breakage)
 628 are more abundant than carnivore activity in all LUs
 629 (Table 6). Due to the scarcity of remains recovered from LUs
 630 1 and 5 of GE-I, the study will focus on LUs 2, 3, and 4 of this
 631 pit, and on LUs 1 and 2 of GE-II.

632 Sixty-eight bone remains from GE-I LU2 were analyzed.
 633 Anthropogenic activity (i.e., cut marks, anthropogenic
 634 breakage, and burned bones) is present in 35.3% of the ana-
 635 lyzed sample (Supplementary Table 3). The types of cut
 636 marks (Supplementary Table 4) show that defleshing, peri-
 637 osteum removal, and marrow access took place mainly on
 638 ribs and long bone fragments. The analysis of breakage pat-
 639 terns (Supplementary Table 5) shows that fresh-bone frac-
 640 tures are dominant for all taxa. The presence of percussion
 641 marks and peeling suggests anthropogenic breakage as the
 642 origin for these fresh-bone fractures. Three bone fragments
 643 display evidence of combustion, though at a low degree
 644 (stages 1 and 2 of Stiner, 1995). In addition to the anthro-
 645 pogenic traces, one fossil remain (a long bone fragment of an
 646 indeterminate species) displays scores and tooth pits (Fig. 9)
 and two additional bones have features compatible with

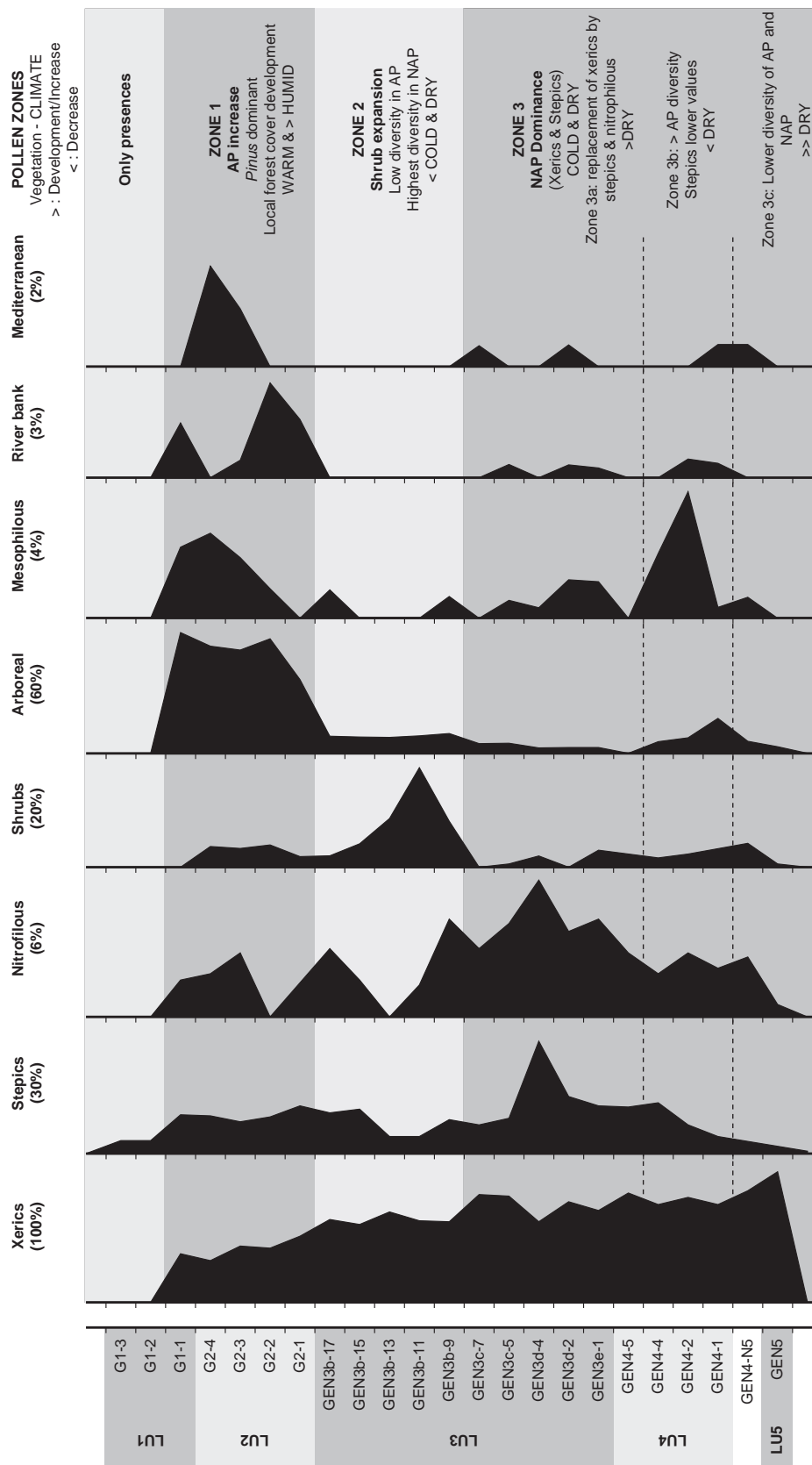


Figure 5. Interpretative diagram of the palynological sequence of GE-I. Note that the samples have been represented one after the other regardless of the depth. Note that the zones based on the palynological content are different from the stratigraphy. GEN4-N5 was taken in the limit between LU 4 and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

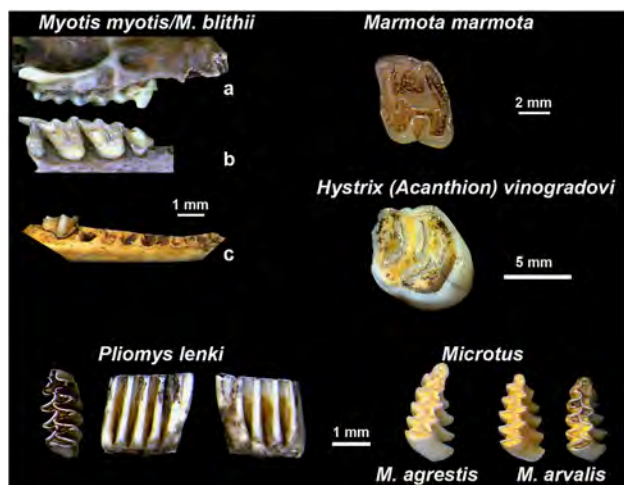


Figure 6. (color online) Selected micro-mammal remains from Galería de las Estatuas. *Myotis myotis/M. blithii*: a right maxilla in (A) lateral and (B) occlusal views. (C) A right mandible with lower M3. *Marmota marmota* from GE-II-level 2: left lower M2. *Hystrix (Acanthion) vinogradovi* from GE-I-level 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.

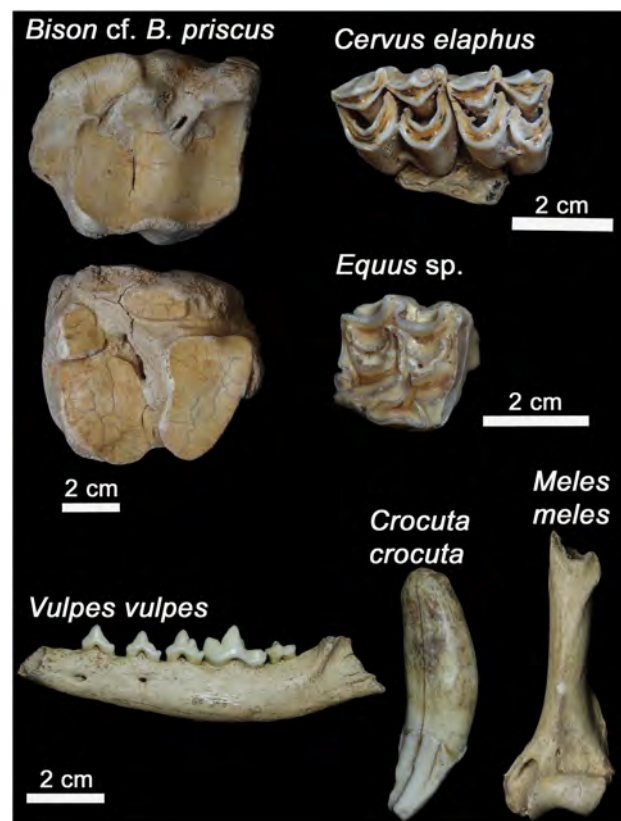


Figure 7. (color online) Selected macrofaunal remains from Galería de las Estatuas, including both ungulates and carnivores. Scaphocuboid of *Bison cf. B. priscus* (GE-1174; LU3 of GE-I) in proximal and distal views. Occlusal view of a *Cervus elaphus* right maxilla preserving the M¹–M² (GE-106; LU2 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 P₂–M₂ (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

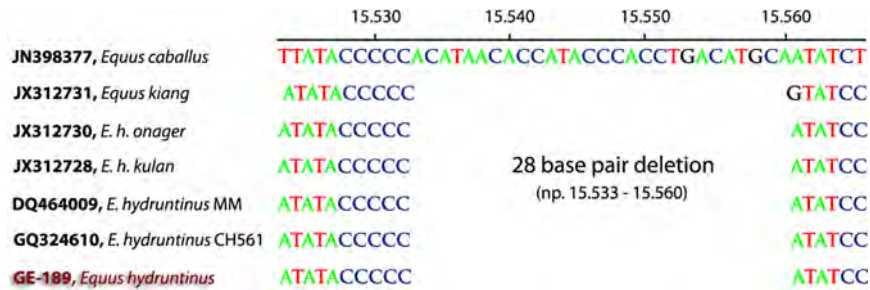


Figure 8. (color online) Informative 28-base pair deletion found in mtDNA HVR-I *Equus hydruntinus*/*Equus hemionus*/*Equus kiang* lineage, which is also present in a lower right molar (M₁ or M₂, GE-189) from GE-I. JN398377 is the *Equus caballus* reference sequence (Achilli et al., 2012). Complete mitochondrial 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.

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

699 In general terms, chert is the most common (83.8%) raw
700 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.

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, however, 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. The majority of the plat-
forms are plain or unifaceted (46.1%), but it is noteworthy
that 20.2% of the striking platforms are dihedral and 29.2%
multifaceted. 85.4% of the dorsal surfaces of flakes are non-
cortical, 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 ham-
merstones (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 assem-
blage. 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

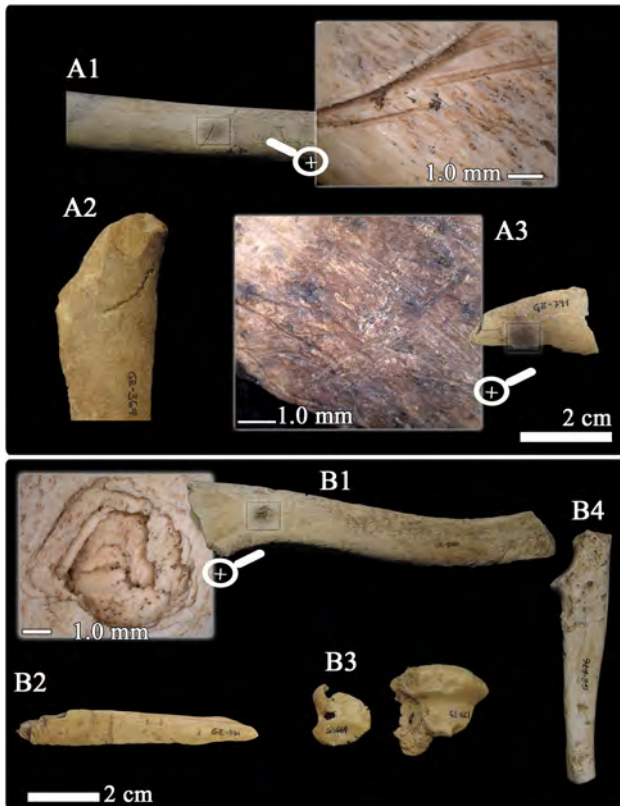


Figure 9. (color online) Selected (A) anthropogenic and (B) carnivore modifications on the Galería de las Estatuas fossil remains. (A1) General and detailed images of cut marks on the rib GE-545 from LU4 of GE-I. (A2) Percussion pits on a long bone fragment (GE-369) from LU4 of GE-I. (A3) Burned and 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.

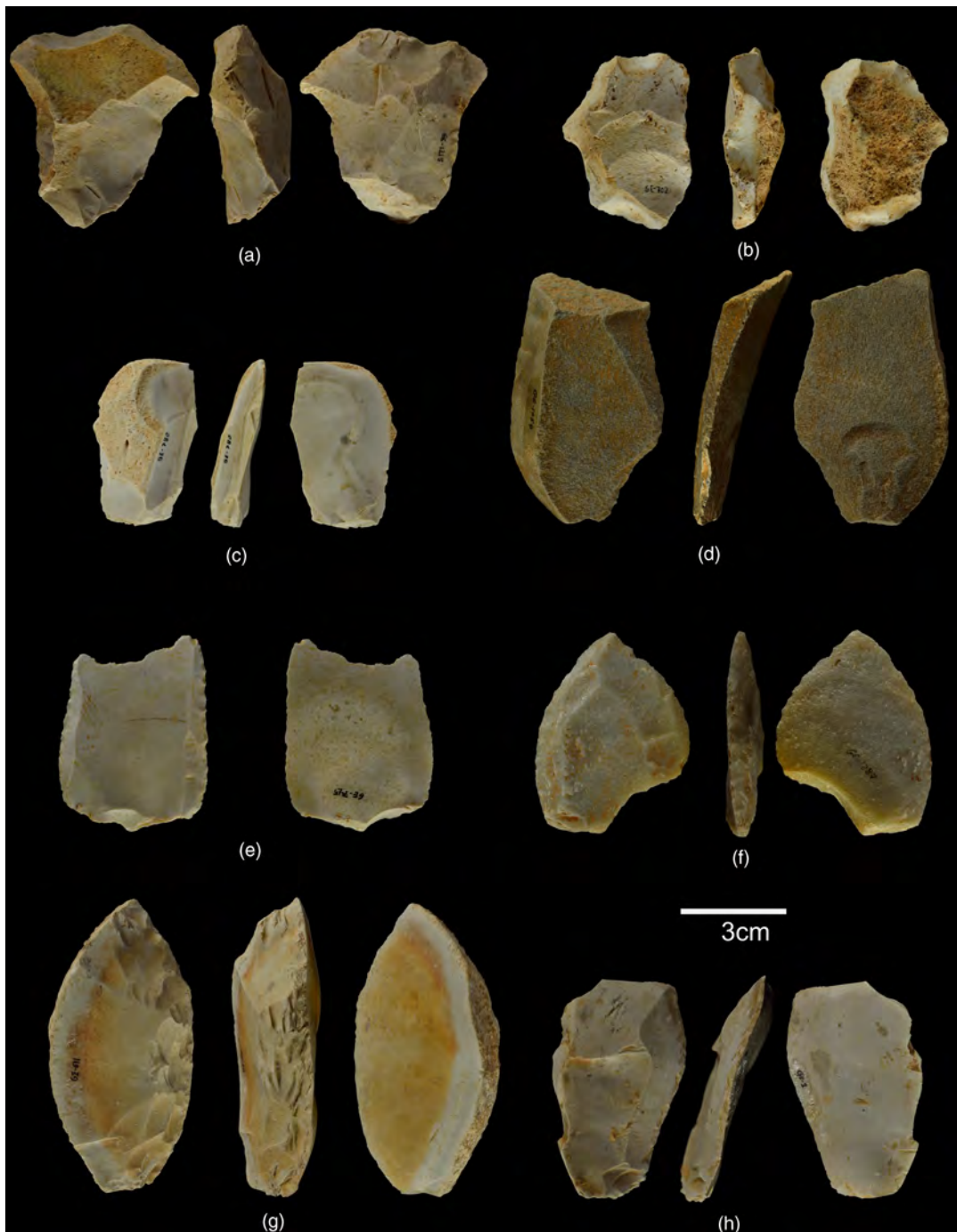


Figure 10. (color online) Selection of stone tools from the Galería de las Estatuas. (A) Centripetal flake core on chert (GE-II, LU2). (B) Chert core with a clearly hierarchised exploitation surface (GE-II, LU2). (C) Chert flake (GE-II, LU2). (D) Quartzite flake (GE-I, LU3). (E) Chert double marginal 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).

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743 than débitage, which is scarce, particularly with regard to the
 744 initial stages of the cores exploitation, as we mention previously.
 745 For example, LU2 of GE-I (including the contact between LUs
 746 1-2) shows a large amount (76.5%) of small sized-flakes that are
 747 smaller than 20 mm, which suggests that some retouching
 748 activities took place there. However, the percentage of retouch-
 749 ed tools in this LU is very small (1.7%). Therefore, retouched
 750 tools were used (and abandoned) elsewhere.

DISCUSSION

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Interpretation of the site

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753 The GE corresponds to a site located at an ancient entrance of
 754 the Cueva Mayor-Cueva del Silo karst system. Both GE-I and
 755 GE-II pits have yielded new information regarding the
 756 Neanderthal occupations of the site that include lithic remains

757 and bone remains with anthropogenic marks. Additionally,
758 the palynological sequence indicates that there was a climatic
759 improvement from LU3 to LU2, as the latter was warmer and
760 more humid.

761 The bone remains from GE display several features that
762 indicate human manipulation in all the LUs (Fig. 9). Cut marks,
763 including slicing marks, scrape marks, and chop marks, are
Q24 764 present on different preserved anatomical parts. Most of the cut
765 marks – mainly slicing and scraping marks – are present in long
766 bone shaft fragments and ribs, which indicate that defleshing,
767 evisceration, and periosteum removal took place. Most of the
768 cut marks are present on unidentifiable bone fragments, how-
769 ever, making it difficult to interpret the butchering processes. In
770 addition to the lithic tool traces, intentional breakage was also
771 recorded in all LUs. None of the carnivore fossil remains from
772 GE-I display cut marks, but tooth marks are present in LUs 3
773 and 4. Cut marks are more common in large-sized ungulates
774 (equids and bovids) than in any other taxa in all LUs from GE-I.
775 Although no hearths were documented in the cave site, some
776 bone fragments show evidence of fire activity in the LU2 from
777 GE-I and LU1 from GE-II (Fig. 9). The scarcity of tooth marks
778 on the GE sample makes it difficult to statistically compare their
779 dimensions with experimental and archaeological samples, in
780 order to assess the carnivore taxa that produced them.

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

791 **Galería de las Estatuas and the Mousterian in the** 792 **northern plateau**

793 The best sites for contextualizing the Middle Paleolithic
794 occupations in the GE within the northern plateau are the
795 open-air contexts found at and around the Sierra de
796 Atapuerca, the Valdegoba and Prado Vargas sites, and three
797 additional sites in the Arlanza River valley (Hortigüela): the
798 La Ermita and La Mina cave sites and the Millán rock-shelter.
799 Direct dating completed on these sites indicate that
800 Neanderthals occupied the Sierra de Atapuerca and the
801 northern plateau, at least from the end of MIS 4 and
802 throughout MIS 3 (Table 3). The comparison of the lithic
803 remains and the main prey species found at these sites reveals
804 some similarities and some slight discrepancies (Table 4).
805 Equids, red deer, wild goat, and chamois are the most abun-
806 dant prey species in the northern plateau. The presence/
807 absence of caprids (wild goat and chamois) at different sites
808 could be the effect of ecological differences among them.
809 Additionally, some differences in technology could be the
810 result of differences in the raw materials available and,

therefore, differences in the management of these raw mate- 811
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Navazo et al. (2011) believe that the tendency towards 822
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835 **Galería de las Estatuas: completing the sierra de** 836 **Atapuerca record**

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

926 The GE has yielded several *Hystrix vinogradovi* remains in
 927 LUs 3 and 4 of GE-I. The presence of porcupine in the Late
 928 Pleistocene of the Iberian Peninsula is restricted to 9–10 sites,
 929 most of which are associated or contemporaneous with
 930 Neanderthal occupations. The first porcupine remain was
 931 identified in Devil's Tower (Gibraltar) by Bate (1928; see her
 932 figure 25), where Mousterian tools and the remains of a
 933 Neanderthal child were found (Buxton, 1928; Garrod, 1928).
 934 The Cueva del Camino site provides the earliest (MIS 5)
 935 evidence of *Hystrix* in the Iberian Peninsula (Arsuaga et al.,
 936 2012; Laplana et al., 2013). Additional sites that have yielded
 937 Neanderthal remains/occupations with the presence of this
 938 species include: two caves in the province of Burgos,
 939 Valdegoba (Díez et al., 1988–1989) and La Mina (Díez et al.,
 940 2008); level I of Cova del Gegant (Daura et al., 2005, 2010;
 941 López-García et al., 2008); the nearby Cova del Muscle
 942 (López-García et al., 2007); and Sima de las Palomas (Rhodes
 943 et al., 2013). Finally, the youngest (in chronological terms)
 944 *Hystrix* on record was found in level IV at A Valiña (Fernández
 945 Rodríguez, 2006), dated to 31,730 + 2880/-2110 ¹⁴C yr BP
 Q26 946 GrN-20833 (Ramil Rego and Fernández, 1995 in Fernández
 947 Rodríguez, 2006). There are other sites with the presence of
 948 *Hystrix*, such as Cova d'Olopte (Cova B; López-García et al.,
 949 2007), the age of which is not certain (Villalta, 1972).

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

The absence of other ungulates is also noticeable, such
 978 as the fallow deer (*Dama dama*), which is not present in any
 979 of the late Pleistocene sites from the northern plateau
 980 (Arceredillo, 2015). In fact, all these sites are from the second
 981 half of the late Pleistocene (ca. <70 ka). In older chron-
 982 ologies, such as the MIS 5 central Iberian site of Camino
 983 (Arsuaga et al., 2012; Álvarez-Lao et al., 2013), *Dama dama*
 984 is the most abundant species of the fossil assemblage.
 985 However, the presence of fallow deer in the Buena Pinta
 986 cave, which has yielded chronologies around 60–70 ka
 987 (Laplana et al., 2015 and references therein), would suggest
 988 a more prolonged survival in this part of the Iberian
 989 Peninsula. Thus, the absence of *Dama dama* in GE could be
 990 related to the fact that the taxon had a more restricted
 991 biogeographical range that did not include the Sierra de
 992 Atapuerca. Therefore, additional chronological data from
 993 different sites are still necessary in order to assess the
 994 extinction of this taxon in Iberia during the late Pleistocene.
 995 In this case, it is easier to distinguish between genus *Cervus*
 996 and *Dama* than between *Bos/Bison* due to their differences in
 997 general size.
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999 Finally, another important aspect that must be taken into
 1000 account is the high micro-mammal biodiversity, likely linked
 1001 to the strategic geographical location of the Sierra de
 1002 Atapuerca within the northern plateau and the landscape
 1003 variation within 5 km from the sierra itself. The Sierra de
 1004 Atapuerca is located in the Duero basin, at the entrance of the
 1005 Bureba corridor that connects the Ebro and the Duero basins.
 1006 This corridor is limited by the Cantabrian mountain range to
 1007 the north and the Central system to the south. The Sierra de
 1008 Atapuerca has several natural springs, and, together with the
 1009 limestone nature of this hill, and the fact that it is surrounded
 1010 by the terraces of the nearby Arlanzón River, it provides
 1011 a variety of landscapes, which is reflected in high levels
 1012 of biodiversity preserved in the different Atapuerca sites
 1013 throughout the Pleistocene (Rodríguez et al., 2011). The
 1014 GE is no exception and the palynological and micro-
 1015 paleontological studies presented here show that, despite
 1016 the general rigorous climatic conditions, a varied plant and
 1017 micro-mammal community inhabited the surroundings of the
 1018 sierra de Atapuerca.

1019 SUMMARY AND CONCLUSIONS

1020 The GE site, in which two test pits have been excavated, is
 1021 located at an ancient entrance of the Cueva Mayor-Cueva del
 1022 Silo karst system. Here a detrital sequence has yielded both
 1023 stone artifacts of clear Mousterian affinity, as well as paleonto-
 1024 logical remains. In general terms, chert is the most common
 1025 raw material and most of the artifacts are knapping products.
 1026 Among the retouched flakes, side scrapers are the most
 1027 common elements, and some of them have “Quina”-type
 1028 retouching. The macrofaunal spectrum is dominated by
 1029 ungulates, mainly equids and red deer, with the presence of
 1030 large bovids (including *Bison*) and several carnivores (mainly
 1031 red fox and spotted hyena). The taphonomic analysis reveals
 1032 traces of both anthropogenic and, to a lesser extent, carnivore

1033 activity. Thus, although carnivores occupied the cave spor- 1087
 1034 adically, this site was mainly used by hominins during the 1088
 1035 late Pleistocene. The current chronological framework is 1089
 1036 based on a series of ^{14}C dates that indicate a minimum age of 1090
 1037 45 ^{14}C ka BP for the human occupations of this site. The 1091
 1038 palynological analysis indicates a warming episode in a more 1092
 1039 open environment compared to that of the present day. This is 1093
 1040 consistent with the very diverse and rich micro-mammal 1094
 1041 assemblage, dominated by open-habitat taxa. GE provides 1095
 1042 insights into the Neanderthal occupations of the more inland 1096
 1043 Iberian Peninsula, which contrasts with the climatically 1097
 1044 milder, more coastal sites. Moreover, it also shows the 1098
 1045 diversity of strategies in which Neanderthal engaged to sur- 1099
 1046 vive in the different ecosystems/ecotones on the Northern 1100
 1047 Iberian Plateau in which different species of prey existed 1101
 1048 (caprids in more mountainous areas; cervids and equids in 1102
 1049 more open environments). It indicates the resilience of these 1103
 1050 hunter-gatherer groups that inhabited the Sierra de Atapuerca 1104
 1051 despite ecological changes that occurred during the late 1105
 1052 Pleistocene. Finally, GE provides new evidence of the 1106
 1053 Neanderthal occupation at the Sierra de Atapuerca, which 1107
 1054 helps to complete the more than one million-year-old 1108
 1055 sequence of human occupations at this site complex. 1109

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Supplementary material

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