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**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**

*Juan Luis Arsuaga<sup>1</sup>, Enrique Baquedano<sup>2</sup>, Alfredo Pérez-González<sup>3</sup>,  
Nohemi Sala<sup>1\*</sup>, Rolf M Quam<sup>4</sup>, Laura Rodríguez<sup>5</sup>, Rebeca García<sup>5</sup>, Nuria García<sup>1</sup>,  
Diego Álvarez<sup>6</sup>, César Laplana<sup>7</sup>, Rosa Huguet<sup>8</sup>, Paloma Sevilla<sup>9</sup>,  
Enrique Maldonado, Hugues A Blain<sup>8</sup>, M<sup>a</sup> Blanca Ruiz-Zapata<sup>10</sup>, Pilar Sala<sup>11</sup>,  
M<sup>a</sup> José Gil-García<sup>10</sup>, Paloma Uzquiano<sup>12</sup>, Ana Pantoja<sup>1</sup>, Belén Márquez<sup>7</sup>*

<sup>1</sup> Centro Mixto UCM-ISCIH de evolución y Comportamiento Humanos C/ Sinesio Delgado, 4, 28029- Madrid y Departamento de Paleontología. Facultad de Ciencias Geológicas, Universidad Complutense de Madrid. Ciudad Universitaria 28040-Madrid

<sup>2</sup> Museo Arqueológico Regional de la Comunidad de Madrid. Plaza de las Bernardas, s/n, 28801-Alcalá de Henares (Madrid)

<sup>3</sup> Centro Nacional de Investigación sobre Evolución Humana, Avenida de la Paz 28, 09004 Burgos, España y Departamento de Geodinámica, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, 28040 Madrid, España

<sup>4</sup> Department of Anthropology, Binghamton University (SUNY), Binghamton, NY 13902-6000, USA

<sup>5</sup> Laboratorio de Evolución Humana. Edificio I+D+i, Universidad de Burgos. Plaza Misael Bañuelos S/N. 09001- Burgos, Spain

<sup>6</sup> Área de Paleontología, Departamento de Geología. Universidad de Oviedo. C/ Arias de Velasco s/n, 33005 Oviedo, Spain.

<sup>7</sup> Museo Arqueológico Regional de la Comunidad de Madrid. Plaza de las Bernardas, s/n, 28801-Alcalá de Henares (Madrid), Spain.

<sup>8</sup> Institut de Paleoecologia Humana i Evolució Social Unitat associada al CSIC. Plaça Imperial Tàrraco 1, E-43005 Tarragona, Spain

<sup>9</sup> Departamento de Paleontología. Facultad de Ciencias Geológicas, Universidad Complutense de Madrid. Ciudad Universitaria 28040-Madrid, Spain.

<sup>10</sup> Departamento de Geología. Campus Universitario. Universidad de Alcalá. 28871-Alcalá de Henares- Madrid, Spain

<sup>11</sup> pilarsalabelles@yahoo.es

<sup>12</sup> U.N.E.D. Ed. Humanidades. Senda del Rey s/n 28040 Madrid, Spain

\*Corresponding author

## Abstract

The Cueva del Camino site (Pinilla del Valle, Madrid) represents the most complete MIS 5 record from the Iberian Peninsula (away from the Mediterranean margin), including a large accumulation of fossilized remains of small and large vertebrates and two human teeth. The presence of carnivores (mainly hyenas) and humans suggests that the site should be interpreted as a spotted hyena den, a human occupation, or both. During an earlier phase of excavation undertaken during the 1980s, an anthropic origin was suggested for the accumulation at the site. However, research was resumed in 2002, leading to an increase in the number of vertebrate remains recovered, as well as the recognition of new vertebrate species. These have now been incorporated into the site's list of fauna. In addition, new palaeobotanical, geochronological and stratigraphic data have been recorded and analysed, and the human teeth identified as being of Neanderthal origin. Floristic data (pollen and charcoal remains) obtained for the north sector of this site indicate an open landscape with *Pinus sylvestris-nigra* as the main arboreal taxon. The available evidence suggests this accumulation to be the result of spotted hyena activity during a warm phase of Marine Isotope Stage 5 (MIS 5) in an environment in which fallow deer was the most abundant herbivore.

**Keywords:** Late Pleistocene, MIS 5, hyena den, warm stage, Neanderthals, Central Spain

## 1. Introduction

One of the main interests in the Last Interglacial period (MIS 5) lies in the fact that it is believed to represent the last time when the earth's climate was similar to the present day. However, this period is poorly recorded in inland Iberia, and only a few scattered localities near the Mediterranean rim have been recognized in the Iberian Peninsula for MIS5. This paper presents a study of Cueva del Camino, an archaeo-palaeontological site placed in Central Iberia, which includes a very rich and diversified MIS5 fauna and flora record associated with *Homo neanderthalensis* remains.

The Late Pleistocene site of Cueva del Camino was discovered in 1979. Excavations were performed at the site from 1980 until 1989 by Alférez et al. (1982), who reported numerous remains of animals and two human molars. These animal remains have been extensively studied (Alférez and Molero, 1982; Alférez et al., 1982; Alférez et al., 1983; Alférez, 1985; Alférez et al., 1985; Alférez, 1987; Alférez and Iñigo, 1990; Toni and

Molero, 1990; Maldonado Díaz, 1991; Alférez and Roldán, 1992; Buitrago Villaplana, 1992; Alférez and Buitrago, 1994; Alférez and Chacón, 1996; Maldonado, 1996; Bochenski, 2007). The faunal association of the site led Alférez et al. (1982) to provisionally assign it to the Riss-Würm (Eemian) interglacial period or some Riss interstadial period. The two human teeth were claimed to be pre-Neanderthal (Alférez and Roldán, 1992), and the accumulation was originally interpreted as the result of human occupation (Alférez et al., 1982). Díez (1993), however, reinterpreted it as a spotted hyena den.

In 2002 a multidisciplinary research team began new excavations at the small limestone hill known as El Calvero de la Higuera. This comprises several cave deposits, those of Cueva del Camino among them. Excavations at the Cueva del Camino site were undertaken between 2002 and 2009 (one month's summertime excavation period per year) and the data gathered have led to the publishing of new articles (Laplana and Sevilla, 2006; Arsuaga et al., 2010; Huguet et al., 2010; Pérez-González et al., 2010; Arsuaga et al., 2011).

The present work describes a complete study of the Cueva del Camino site using different techniques. The fossil material studied comes from the new excavation period, but includes the human teeth recovered during the earlier excavation work. Geochronometric and biochronological data are taken into account in order to ascertain the age of the deposit. New palaeobotanical (anthracological and pollen analysis) and taxonomic (micro- and macrovertebrate) data allow the environment of the site and its surrounding area to be reconstructed. Taphonomic analyses were made to establish the origin of the accumulation. Using both classic and virtual techniques, the human teeth found at the site were compared to Neanderthals and modern humans.

## **2. Study area**

### *2.1 Geological context*

The Cueva del Camino site is part of the Calvero de la Higuera archaeological complex (Pinilla del Valle, Madrid, Spain). It is located in the upper valley of the Lozoya river in the Sierra de Guadarrama, a mountainous alignment with a NE-SW direction and general pop-up structures that form part of the Sistema Central range (Fig. 1).

The upper valley of the Lozoya River is a tectonic depression (pop-down) which runs in the same direction as the pop-up of the Sistema Central. To the north, the valley is bordered by the Montes Carpetanos (Carpetano Mountains), among which Peñalara is

the highest peak (2428 m) of the entire Sierra de Guadarrama. To the south, it borders the Cuerda Larga Mountains, of which the Cabeza de Hierro is the highest point (2380 m).

From a geological point of view, the upper valley of the Lozoya River lies within the *Esquisto-Grauváquico* Complex of the Central Iberian Zone, which is formed by deformed and metamorphosed Proterozoic to Carboniferous rocks with intrusions of different types of granitoids prior to the Permian (Vera, 2004). The main Variscan deformation occurs during the Carboniferous, although it was during the Alpine Orogeny when the pop-down of the Lozoya River formed. The oldest rock outcrops consists of orthogneisses, leucogranites, adamellites, granitoids, migmatites and to a lesser degree schists and quartzites (Arenas et al., 1991; Bellido et al., 1991). Lamprophyres, porphyries and late quartzite dykes are also present.

The Mesozoic sedimentation, of Late Cretaceous age (Bellido et al., 1991), begins with sands, clays and gravels in the so-called Utrillas facies. Over this formation, sands, lutites and carbonates can be found, as well as sandstones and dolomites, the latter with a thickness of about 35 m. Karst processes have occurred within the dolomites, forming lapies and sinkholes at the rock surface, and rock shelters within caves. The archaeological sites of Calvero de la Higuera are all associated with these types of processes.

Quaternary deposits in the Lozoya valley area are very well represented. The Calvero de la Higuera archaeological sites (1114 m) are associated with cavities that evolved on a *cuesta* from Late Cretaceous carbonate rocks, with a slight inclination towards the Lozoya River. The Lontanar and Valmaíllo streams are two affluents on the right margin of the Lozoya River that dissect the *cuesta* relief of Calvero de la Higuera, leaving the three known sites in a hanging geological position.

## 2.2 Present day vegetation

The Mediterranean landscape is divided into a series of microenvironments characterized by bioclimatic heterogeneity depending on altitude, latitude and topographic aspects (Peinado Lorca and Rivas Martínez, 1987). In the Valle de Lozoya vegetation series map (Fernández, 1988), the study area lies within the *Luzulo forsteri-Querceto pyrenaicae* series, corresponding to mesothermophilous woods comprising Pyrenean oak (*Quercus pyrenaica*), which grow on siliceous soils in mainly sub-humid, high continentality supra-Mediterranean bioclimates. This zone reaches the limit of the

Mediterranean climate, separated from typical Thermo- and Meso-Mediterranean zones where Neanderthals preferably settled (Fig. 2).

### 2.3 Site

The Cueva del Camino site is made up of four sectors (Fig. 3): the North, Central, Diaclasa Roja and South sectors (Arsuaga et al., 2010). Some 96.70% of the macrofauna remains identified (i.e., the number of identified specimens [NISP]) come from the North (Level 5) and Central sectors. The differences between the macrofauna associations of these two sectors are very small; they were therefore studied together (Arsuaga et al., 2010).

North sector: This sector is the largest in spatial terms. Seven levels (numbered 3 to 9) have been identified (Pérez-González et al., 2010; Arsuaga et al., 2011) (Fig. 3). Levels 3 and 4 are of allogenic origin and are associated with the changes to the Valmaíllo stream that occurred over time. Levels 5-9 are autochthonous in character, associated with the karst environment. Level 5, dated to  $90.961 \pm 7881$  ka by thermoluminescence (TL) in sediment samples (Pérez-González et al., 2010) (Fig. 3), contains 53.33% of the NISP of macrofauna and the greatest biodiversity. *Felis silvestris*, *Lynx* cf. *pardinus* and *Mustela putorius*, however, only appear in the upper levels (8-9), although the micromammal association of Levels 6-9 is similar to that of Level 5. Most of the microfaunal remains (>60%) come from this sector. The microvertebrate association from the North sector differs from those of the other sectors by the greater abundance of Cabrera's vole, the field mouse and the rabbit among the small mammals, and the Ladder snake and Herman's tortoise among the reptiles. The greater part of the anthracological samples studied come from this sector, mainly from Level 5.

Central sector: This has a particularly high density of macrofauna remains. The accumulation is chaotic but bears no evidence of water transport (Fig. 4). It is interpreted as a gravitational deposit. Some 38.92% of the NISP of macrofauna come from this sector. The micromammal species of this sector are the same as for the North sector, although the abundance of rabbits and field mice is lower. Fewer charcoal remains are seen than in the North sector.

Diaclasa Roja sector: This is a thin (20 cm) fossiliferous layer between the level of the stream and the bedrock (Fig. 3). This layer contains the remains of both macro- and microvertebrates (2.11% of the NISP). It lies at the same depth as the remains described for the Central sector, of which it might be a lateral continuation.

South sector: This is represented by the infilling of a fissure running along a flat surface above the Central sector (Fig. 3). Macrofaunal remains are more scarce here (1.25% of the NISP of macrofauna), and the microfauna shows some peculiar characteristics. The association is dominated by *Microtus arvalis*, alongside *Chionomys nivalis* (in small numbers). A small number of anthracological remains were also found.

### 3. Materials and Methods

#### 3.1 Palynology

Standard protocols for palynomorph extraction (Coûteaux, 1977) and the determination of the pollen concentration (Girard and Renault-Miskovsky, 1969) were followed. A Nikon Alphaphot-2 YS2 microscope (10x40 objective) has been used to examine the pollen remains. The number of grains counted always exceeded 300 per sample. Pollen taxa were quantified via pollen diagrams using TILIA® and TILIA-GRAPH® software (Grimm, 1987). Taxa were gathered and grouped according to their arboreal, shrubby or herbaceous nature. Pollen percentages for all palynomorphs are based on the sum of terrestrial pollen types. The pollen sum excludes aquatic taxa, fern and algal remains. With the aim of determining the biological diversity record, rarefaction analysis was performed (Analytic Rarefaction 1.3) (Birks and Line, 1992; Bronk Ramsey, 2000).

#### 3.2 Anthracology

Small charcoal fragments (1-2 mm) were recovered after washing and sieving the sediment, as well as by manual flotation (2007 campaign). Anthracological sampling techniques have been standardized and integrated into the methodology for excavating caves and rock shelters across Iberia (Uzquiano, 1997; Badal et al., 2003). Charcoal fragments were manually fractured to provide transversal, tangential and radial sections, and were observed by reflected light microscopy using an OLYMPUS BX60 microscope with dark/bright field objectives. Botanical determinations made use of the Atlas Keys for Fresh Wood (Greguss, 1955; Jacquot, 1955; Greguss, 1959; Jacquot et al., 1973; Schweingruber, 1978; Schweingruber, 1990) and the Charcoal Identification Guide (Vernet et al., 2001). The nomenclature employed was that of *Flora Europaea* (Tutin et al., 1964).

The North sector provided 318 charcoal fragments, of which 281 fragments came from Level 5; the Central sector yielded 62 and the South sector 47. The present study was



therefore only based on the anthracological information provided by the North sector (Level 5).

### *3.3 Microvertebrates*

After excavations were resumed in 2002, great care was taken to recover all the microvertebrate fossils given their importance as a source of biochronological data and their value as palaeoenvironmental indicators. In the excavated area of the site, 1m x 1m squares were opened and the soil was removed by natural levels. For each square and level, samples were divided vertically at intervals of 10 cm in order to detect possible variations in the small vertebrate assemblages within the levels. The sediment thus separated was freed from silt by water hosing the excavated soil in super-imposed 2 mm and 0.5 mm screens (Fig. 4). Occasionally 1 cm sieves were added to retain larger-sized sediment particles (gravel or small boulders) and thereby prevent in situ breakage of small vertebrate remains. Water sieving of all the excavated sediment was conducted during the field campaigns (Fig. 4). The resulting residues were sun-dried, packed and conveniently labelled.

Sorting of the fossils was done both during the field campaigns and later in the laboratory. For the larger-sized fraction of the residue, retained in the 2 mm sieve, the fossils were picked out directly with the naked eye, whereas the residue between 2 mm and 0.5 mm was sorted using Leica L2 binocular stereomicroscopes at 10X magnification. All the fossil bones and fragments in the samples were sorted, even when unidentifiable. Charcoal fragments, seeds and snail shells were also sorted.

The microvertebrate fossils have been studied using an Olympus SZX12 stereomicroscope provided with a drawing tube and an Olympus DP71 digital camera. For bones and teeth identification osteological keys and handbooks such as Bailon (1999), Blain (2005), Chaline (1972; 1974), Esteban and Sanchiz (1985; 1991), Holman (1998), Felten et al. (1973) and Sevilla (1988), among others, were used. The small vertebrate remains were identified with the aid of comparative material obtained from bird pellets and carnivore droppings collected in the vicinity of the site, as well as with comparative collections loaned by the Museo de Ciencias Naturales of Madrid (CSIC) and the Estación Biológica of Doñana (CSIC, Sevilla).

### *3.4 Human molar remains*



Morphological features were scored according to the criteria defined by the Arizona State University Dental Anthropology System (ASUDAS) (Turner et al., 1991) and also considered some recently-described features which reliably distinguish Neanderthals from *Homo sapiens* (Bailey, 2004; Bailey, 2006; Gómez-Robles et al., 2007). In addition to the mesiodistal (MD) and buccolingual (BL) crown dimensions, the crown and cusp base areas as well as the occlusal polygon (measured only in the M1) were measured following previously established protocols (Wood and Engleman, 1988; Bailey, 2004). The individual cusp outlines were traced in 2D digital photographs using the Photoshop<sup>TM</sup> software program following the main cusp fissures on the occlusal surface of each tooth. The measured crown area (MCA) was calculated as the sum of the individual cusp base areas. The teeth were oriented so that the cervical margin was perpendicular to the axis of the camera lens and a scale was included in each photo for calibration purposes. Location of the cusp tips in the worn M1 (for establishing the occlusal polygon) was estimated at the center of the wear facet on each cusp. Comparative analysis focused on Late Pleistocene European fossils attributed to Neanderthals and *Homo sapiens*. To determine whether these two teeth represent the same individual, their degree of attrition was compared, and a regression analysis of the MD and BL diameters was made with molars of other Neanderthal individuals with both of these teeth preserved.

Both molars were also subjected to computed-tomography (CT) scanning using a YXLON Compact (YXLON International X-Ray GmbH, Hamburg, Germany) industrial multi-slice scanner at Burgos University, Spain to study the topography of the enamel-dentine junction in the M1. Specimens were aligned along the long axis with the occlusal surface upwards and the scans were collected at the maximum resolution obtainable (pixel size = 0.027 mm) which allowed the distinction of the interface between the enamel and dentine for the entirety of the cross-sectional slice data.

### 3.5 Taphonomical analysis

This study has gathered data from the material found between 2002 and 2009. A Nikon SMZ800 (Stereoscopic zoom microscope) has been used to examine surface modification on all bone fragments (Fig. 5, 6).

Carnivore damage on the surface of bones is classified into pits, punctures, and scores. Crenulated edges, furrowing and evidences of corrosion of bone caused by stomach acid as carnivore modification (Haynes, 1980; Maguire et al., 1980; Binford, 1981; Haynes,

1983b) have also been considered. Tooth mark distribution in the bone portions is done following the methods of Selvaggio and Wilder (2001) Domínguez-Rodrigo and Piqueras (2003) and Delaney-Rivera et al (2009). Conspicuous marks were measured in length and breadth (Fig. 5). Measurements were taken with an electronic caliper. For the identification of the carnivore species that acted on the assemblage, tooth marks have been measured and then compared to data published by Domínguez Rodrigo and Piqueras (2003), Saladié et al. (2011) and Delaney-Rivera et al. (2009).

With the aim of identifying the process of breakage (green or dry bone fragmentation) all long bone fragments were analyzed following the criteria developed by Villa and Mahieu (1991), Bunn (1983), Haynes (1983a) and Lyman (1993; 1994). This method considers: the fracture location (following Lyman (1993, 1994)); the fracture outline (longitudinal, transverse and V-shaped); the angle formed by the fracture surface and the bone cortical surface (oblique, right or mixed); the characteristics of the fracture edges (jagged or smooth); shaft fragment length (1: shafts that are less than one-fourth the original length; 2: is a length comprised between one-fourth and one-half; 3: is between one-half and three-fourths; 4: is more than three-fourths, essentially a complete or almost complete shaft); and shaft circumference (1: bone circumference is less than half of the original; 2: circumference is more than half in at least a portion of the bone length and 3: complete circumference in at least a portion of the bone length).

To understand the origin of the accumulation of bone remains at the Cueva del Camino site taphonomic criteria proposed by previous authors were followed. Cruz-Urbe (1991) details some criteria for distinguishing bone assemblages accumulated by hominids from those produced by the activity of hyenas. These criteria are discussed by Pickering (2002) and Kuhn et al. (2010). The criteria used in this study are: Carnivore-ungulate ratio ( $MNI \text{ carnivores} / MNI \text{ carnivores} + MNI \text{ ungulates}$ ), bone modification and damage to bone surfaces, Bone breakage, Representation of small hard bones. Kuhn et al. (2010) suggest that of all the previously established and re-evaluated criteria, the only two that can truly differentiate between accumulations of hominids and hyenas do not form part of the criteria proposed by Cruz-Urbe or Pickering: the abundance of coprolites and/or 2) the presence of juvenile hyena remains.

## 4. Results

### 4.1 Cueva del Camino pollen data

The PVC3 pollen sequence (see SI 1.1) from the N profile represents the following levels: Fluvial (F), Level 5 (N-5), Level 6 (N-6), Level 7 (N-7) and Level 8-9 (N-8/9). 38 terrestrial taxa were identified (Fig. 7), including 11 trees, 5 shrubs and 22 herbaceous plants, as well as 6 aquatic taxa represented by monolete and trilete spores, and 3 non-pollen microfossils (NPMs). *Pinus* was the main regional element, accompanied in lesser proportions by evergreen and deciduous *Quercus* along with *Corylus* and Oleaceae. *Betula* was detected in certain samples. Riparian taxa (*Alnus*, *Salix* and *Ulmus*) were generally well represented. Ericaceae, *Juniperus*, Rosaceae and Cistaceae made up the company of shrubs, the role of which in the plant landscape was not very important. Asteraceae (Liguliflorae and tubuliflorae) were present, along with Chenopodiaceae and nitrophilous taxa such as *Plantago*, *Rumex* and *Urtica*, together being the most representative of herbaceous plants.

#### 4.2 Anthracological analysis

An anthracological analysis was made of the entire excavated area of this site (i.e., the North, Central and South sectors). The north sector (Level 5) provided detailed information allowing correlations with the palynological and faunal results to be established. The charcoal assemblages showed *Pinus sylvestris-nigra* to be dominant (80%), followed by *Betula* and Maloideae in very small amounts (6% and <1% respectively). Scarce meso-hygrophilous elements were also recorded (*Quercus pyrenaica* type, *Fraxinus angustifolia*, *Salix-Populus*); these must have grown in sheltered conditions bearing in mind the topographic characteristics of the area (Table 1 and Fig. 8). These results reflect a flora with montane affinities (the altitude of the site is 1114 m), with pine the most abundant taxon in the surroundings, including the calcareous slopes where the Cueva del Camino cave opens. The appearance of other taxa is related to topographic compartmentalisation of the territory where calcareous southern exposures (with pine) alternate with more humid siliceous slopes (with birch and deciduous oaks) and valleys bottom providing shelter for meso-hygrophilous elements (ash, willow /poplar).

The pollen data for the same section and level also record abundant *Pinus* located at some distance, as revealed by palynomorphological inspection. Nevertheless, the anthracological results confirm the local presence and abundance of *Pinus* on the calcareous southern slope of the El Calvero de la Higuera area.

### 4.3 Faunal Assemblage

#### 4.3.1 Microvertebrate record

Alf3rez et al. (1982) and Toni and Molero (1990) provide lists of the small vertebrates (several amphibian and reptile species, together with a wide range of micromammals) collected at the site during the 1980s, as well as a description of the rodent species found. However, no reference to any particular level is given. Among the micromammals, rodent remains stand out in terms of species richness (14 species). Four insectivore species and two lagomorphs were also recognised, as well as some unidentified species of chiroptera. On the basis of certain taxa (e.g., a small-sized porcupine, among others), the association was placed within a warm phase of either the late Riss or the Riss-W3rm interglacial period.

At least 51 species of small vertebrates are now recognised (Table 2) including 33 small mammals, 7 amphibians and 11 reptiles (Laplana and Sevilla, 2006; Arsuaga et al., 2010). The reptiles and amphibians show a relatively large increase in the number of recognised species since the earlier lists. Over 90% of the microfaunal remains analysed came from the North and Central sectors. With respect to the north sector, the great majority came from Level 5.

The rodents remain the best represented group of small mammals, with three new species added to the list: *Arvicola* cf. *terrestris*, *Chionomys nivalis* and *Microtus* cf. *vaufreyi*. Other changes with respect to earlier fauna lists include the reassignment of *M. brecciensis* to *Microtus (Iberomys) cabrerai* since the abundant material obtained in recent campaigns more closely resembles the latter species. Taxonomic revisions since the first lists are also responsible for certain changes. For example, *Pliomys coronensis* has replaced *P. lenki*, and *Clethrionomys* has been changed to *Myodes* following more recent and now generally accepted criteria (Kowalski, 2001; Wilson and Reeder, 2005). Microvertebrate remains are present in all levels and areas of the site, although richness differs from one area to another. The fluvial beds at the base contain very few microvertebrate bones (just a few, isolated remains of *Apodemus* sp. and *Microtus* sp.). Most of the microvertebrate material comes from Levels 5 to 9 in the north sector, and from the central and south sectors.

Though the majority of the microvertebrate species are represented in every sector of the site, some important exceptions exist. Thus, Male's vole (*M. aff. malei*) is only represented in the north sector, and although the Cabrera vole (*M. cabrerai*) and the hamster (*Allocricetus bursae*) are frequent in the north sector their frequencies fall in

the central sector, and reach zero in the south sector. These area-dependent differences in the rodent assemblage are probably related to slight differences in the age of the sediments, an explanation analysed in a forthcoming paper.

Remains previously identified as *M. oeconomus* and included in a faunal list built with the material from the recent excavations at Cueva del Camino (Laplana and Sevilla, 2006) have been reassigned to *M. aff. malei*. The molar morphology of these species is very similar, to the extent that some authors refer to the fossil material as *M. oeconomus-malei* (Pemán, 1985; Sesé, 2006). According to the diagnostic criteria of Nadachowski (1990; 1991), in particular the more common development of the T6 triangle and the higher values of the A/L index in *M. malei*, the first lower molars found at Cueva del Camino are closer to those of this species than to those of *M. oeconomus*. However, the “*nivalis*” morphotypes, frequent in typical *M. malei*, are absent in the samples. Thus, the material from Cueva del Camino is referred to as *M. aff. malei*. This taxon seems to have had a wider thermal tolerance range than *M. oeconomus*, given that it was a common species at the beginning of the British Late Pleistocene (Nadachowski, 1991), a period characterized by a warmer climate.

#### 4.3.2 Macrovertebrate record

The Cueva del Camino site has provided an important mammal collection including two human finds. In the present work, only the remains found during the 2002-2009 field seasons are included. Among the ungulates, six Artiodactyla species have been identified (*Dama dama*, *Cervus elaphus*, *Capreolus capreolus*, *Bos primigenius*, *Rupicapra rupicapra*, *Sus scrofa*), along with two Perissodactyla species (*Equus ferus* and *Stephanorhinus hemitoechus*). The carnivore assemblage is composed of the following species: *Canis lupus*, *Vulpes vulpes*, *Ursus arctos*, *Mustela putorius*, *Mustela nivalis*, *Crocota crocuta*, *Lynx cf. pardinus*, *Felis silvestris*, *Panthera leo*, Felidae indet. (*Panthera pardus* size). Level 5, from where this assemblage comes, have been dated by TL to  $90,961 \pm 7881$  (MIS 5) (Arsuaga et al., 2010; Pérez-González et al., 2010) (Fig. 9).

The spotted hyena is represented at Cueva del Camino by adult and immature individuals (minimum number of individuals [MNI]: juveniles = 3; MNI adults = 3), (Fig. 10). The remains of the juveniles consist of milk teeth and tooth germs, while the adult group is represented by permanent teeth showing advanced stages of wear. Compared to a modern *Crocota crocuta* specimen and some specimens of *Crocota*

*crocuta spelaea* from the Late Pleistocene, the only complete upper carnassial (P<sup>4</sup>) found at Cueva del Camino is proportionally broader compared to its length. However it does not differ significantly and no further interpretations can be made.

A few dental and postcranial remains of *U. arctos* have been recovered. The analyses of the dental material suggest a typical arctoid model, the size of which falls among the highest values for modern Iberian brown bears. The dental remains of *Canis lupus* and *Vulpes vulpes* represent one adult specimen each. The dimensions are in both cases comparable to those of modern wolves and foxes. Two adult phalanges (MNI=1) of *Panthera leo* have also been recovered. Compared to the phalanges of the large Middle Pleistocene lions arriving in Europe (García, 2003), the Cueva del Camino specimens are considerably smaller. However, they are larger than those of modern lions, in agreement with the size reduction seen from the Middle to the Late Pleistocene. A single remain (a phalange) of a medium-sized felid has been attributed to *Panthera* sp, probably a leopard. Based on size, this fossil also could be attributed to a jaguar (*P. gombaszoegensis*), although the chronological range of this species is earlier. In any event, the specimen can at least be assigned to this genus. A very small number of diagnostic remains of *Lynx pardinus*, *Felis silvestris*, *Mustela putorius* and *Mustela nivalis* show that these small felid species and mustelids were present in the Cueva del Camino area.

Fallow deer (MNI = 26) are highly predominant at the site, making up 52.5% of all ungulates. Buitrago (1992) classified these fossils as *Dama clactoniana*. However, Made (2001) assigned the remains to *Dama dama geiselana*, based on the size of the teeth. The present data support Made's assignment. *Cervus elaphus* (MNI = 7) is the second most abundant species among the ungulates, accounting for 8.2% of the total remains. Teeth and antler fragments are the most common elements. *Capreolus capreolus* is the rarest among the Cervidae (MNI = 1). *Bos primigenius* (MNI = 4) represents some 5.6 % of the ungulates. Teeth, carpal, tarsal and metapodial remains are the most abundant elements. *Rupicapra rupicapra* is represented by an isolated dental element but its presence provides interesting environmental information pointing to the presence of alpine fauna in the surroundings of the cave. *Sus scrofa* (MNI = 2) is also scanty in the assemblage with only 1.9 % of the total ungulate remains. *Equus ferus* (MNI = 4) represents 7.4% of the ungulates. Cranial and postcranial dimensions together with dental morphological traits show these remains belong to *Equus ferus*. The rhinoceros (MNI = 2) represents a small percentage (1.4%) of the ungulates.



Although the rhinoceros fossils are mostly fragmentary teeth, the morphology and dimensions are diagnostic of *Stephanorhinus hemitoechus*.

#### 4.4 Human Remains

During the 1982 field season, a right M<sup>1</sup> was recovered from square D-3. Subsequently, during the 1984 field season, a right M<sup>3</sup> was recovered from square A-3 at a depth of 124 cm below datum. Human teeth have previously been reported from Cueva del Camino (Alf3rez et al., 1982; Alf3rez and Rold3n, 1992) and have been examined in several comparative dental morphology studies (G3mez-Robles et al., 2007; Martin3n-Torres et al., 2007; Martin3n-Torres et al., 2008; Quam et al., 2009). These teeth are described below and their taxonomic affinities highlighted.

##### 4.4.1 Right M<sup>1</sup> (Figs. 11-13)

The right M<sup>1</sup> has four main cusps preserved. Slight damage to the crown surface is present along the mesial border, and wear (Grade 4; Smith, 1984) has resulted in exposure of the dentine at all four cusp tips. This wear is greater on the lingual cusps, particularly the protocone (which has essentially been worn flat) than on the buccal cusps. The mesial interproximal facet is wider (5.3 mm) and taller (2.3 mm) than is the distal (2.6 mm in height), which is limited to the upper portion of the distal enamel face, just below the level of the occlusal surface. Root formation is complete (Ac calcification stage), indicating that the tooth is fully formed. Modern human standards suggest a minimum age at death of 9.2-10.1 years (Anderson et al., 1976).

Two small areas on the distal face at the junction of the metacone and hypocone and on the hypocone might be interpreted as mild evidence of hypoplasia; here, the enamel appears thinner than on the surrounding tooth surface. There is evidence of alteration of the enamel surface on the mesial and buccal faces of the paracone as well as the distal and lingual faces of the hypocone. These alterations represent slight erosions in the form of grooves and pockmarks. The grooves, which show no predominant orientation, extend to the roots in some areas and even cross the cervicoenamel junction. This random pattern of distribution suggests they are the result of post depositional taphonomic processes.

The hypocone is well developed (ASUDAS Grade 4), but no metaconule (ASUDAS Grade 0) or Carabelli's structure (ASUDAS Grade 0) is present either on the crown surface (Fig. 11) or the enamel-dentine junction (Fig. 12). The roots are short (lingual



root length = 15.5 mm) and stout, and there is a considerable fusion of the three original roots. The mesiobuccal and distobuccal roots are fully fused, while the lingual root has a separate apex and is separated from the other roots for at least the last 6.1 mm of its length (Fig. 13). Thus, some degree of taurodontism is present.

The large MD dimension (12.0 mm) of the Cueva del Camino M<sup>1</sup> (Table 3) is just over one standard deviation above the Neanderthal mean, while the BL dimension (12.0 mm) is similar to that recorded for both Neanderthals and Upper Palaeolithic *H. sapiens* specimens. The measured crown area (MCA; 111.1 mm<sup>2</sup>) is very similar to the Neanderthal mean value.

The relative occlusal polygon area (25.3) falls within one standard deviation below the Neanderthal mean (Table 4), but is clearly outside the range of variation reported in both fossil and contemporary *H. sapiens* samples.

With respect to the relative cusp base areas, the Cueva del Camino M<sup>1</sup> also shows the reduced metacone commonly seen in Neanderthal specimens (Bailey, 2004). Finally, the angles of the occlusal polygon, centred on the main cusp tips, compare most favourably those reported for Neanderthals (Bailey, 2004) particularly in the most diagnostic of these (Angle C) centred on the metacone.

#### 4.4.2 Right M<sup>3</sup> (Figs. 14-15)

The right M<sup>3</sup> shows little tooth wear and no mesial interproximal contact facet, although the root formation is complete (Ac formation stage). This indicates the tooth had completed its formation and suggests a minimum age at death of 18.2-18.8 years by modern human standards (Anderson et al., 1976). In contrast to the M<sup>1</sup>, numerous localized hypoplastic defects can be seen on the buccal and distal faces of the enamel surface (Fig. 14). The crown outline shows two small chips on the paracone, one on the buccal side and one on the mesial side. The paracone and (extremely reduced) metacone are intact, but the crown shows some damage, with most of the protocone and the mesial portion of the hypocone missing. This fracture extends downwards to involve the cervical half of the lingual root, although the root chamber is not exposed. This fracture is argued to be premortem and to represent a localized trauma produced by a hard object travelling at high speed (Alf  rez and Rold  n, 1992).

In distal view, the root appears to show two separate buccal and lingual components, but radiographic analysis suggested the presence of only a single pulp chamber (Alf  rez and Rold  n, 1992). This has been confirmed through CT analysis, and the roots are fully

fused (Fig. 15). Thus, like the  $M^1$ , the  $M^3$  is also characterized by taurodontism. The root length is 13.6 mm in mesial view. Just below the cervico-enamel junction on the mesial face, there is a shallow groove running in the BL direction consistent with a toothpick groove.

The degree of dental wear in both molars is compatible with their belonging to the same young adult individual. The comparison of the MD and BL dimensions of  $M^1$  and  $M^3$  revealed a modest positive correlation for MD ( $r = 0.54$ ), but a stronger positive correlation ( $r = 0.74$ ) for BL. The Camino teeth fall very close to the BL Neanderthal regression line (Fig. 16), and the evidence is consistent with their belonging to the same individual.

#### *4.5 Taphonomy and the origin of accumulation*

The present work, mostly examines the material found between 2002 and 2009, from all levels and all sectors of the site. To understand the origin of the accumulation of bone remains at the Cueva del Camino site taphonomic criteria proposed by previous authors were followed. The criteria used in this study are discussed below.

*Carnivore-ungulate ratio ( $MNI\ carnivores / MNI\ carnivores + MNI\ ungulates$ ):* According to Cruz-Urbe (1991), the percentage of carnivore remains in hyena assemblages is always at least 20% of the total, whereas in archaeological assemblages carnivores always make up less than 13% of the total carnivore plus ungulate MNI (Klein and Cruz-Urbe, 1984). At the Cueva del Camino site the carnivore-ungulate ratio is 27.7%.

*Bone modification and damage to bone surfaces:* After conducting the taphonomic study on the bone collection at the deposit, marks from carnivore activity were estimated to be the most abundant alterations in all sectors and levels of the site (Fig. 17 and Table 5). Thus, 55.9% of the material analysed shows modifications allocated to carnivore activity. As can be seen in Table 5, the most characteristic marks both in the North (level 5) and Central Sectors are scores and pitting. In general, there are very few punctures and furrowing is well represented, particularly in the epiphyses of long and large-sized bones, compact bones and flat bones. Another modification typical of carnivores is the evidence of disintegration due to gastric acids. At the Cueva del Camino site, 4.91% of the total sample analysed have been found with clear evidence that they were digested. According to Cruz-Urbe (1991), damage is seen on at least 50% of bones in modern assemblages, but much less is seen in fossil assemblages.

Kuhn et al. (2010) report an average 39.2% of bones to be damaged in the ancient hyena dens they studied. Metric data on the tooth marks are summarised in Table 6.

*Bone breakage:* Of the remains analysed, 6.5% of the sample, were complete bones, with no fractures. Thus, over 93% of the bone samples had fractures. Of the fractured remains, 21.0% corresponded to unidentifiable bone splinter fragments. For bone fragments that could be identified, at least for the size of the ungulate, the fracturing characteristics were established as depicted in Table 7.

As can be seen in Table 7, the oblique orientation of the fractures is dominant in both weight sizes, where longitudinal and transversal fractures are similarly represented. With regard to the fracture angle, there is a predominance of fractures with oblique and mixed angles. The properties of the fracture edges in the majority of cases are characterised by being smooth, with a high percentage of crenulated edges in the sample. When quantifying the fracturing patterns of the long bones for diaphyseal lengths and circumferences (Table 7), the majority of the sample is represented by diaphyses with complete circumferences and incomplete diaphyseal lengths (Fig. 18). According to Cruz-Urbe (1991), hyena accumulations are characterised by many bone cylinders, while hominid collections have more broken shafts and complete epiphyses. Broken shafts alone are not diagnostic of hominid or hyena collections. Both Cruz-Urbe (1991) and Pickering (2002) indicate that hyena accumulations show an abundance of cylinder-type fragments. According to Kuhn et al. (2010), the presence of cylinders is indicative of carnivore activity, but not specifically of hyena activity.

*Representation of small hard bones:* At the Cueva del Camino site there are 139 small, high-density bones, including carpals and tarsals (excluding the astragalus and calcaneum), sesamoids and phalanges - 4.4% of the total. Cruz-Urbe (1991) indicates that elements such as sesamoids, small tarsal bones, carpal bones and phalanges are present only in small numbers in accumulations produced by hyena activity, since these animals tend to eat them. Pickering (2002) supports the idea that these bone elements usually appear, but in a digested form. Fig. 19 shows some small, hard, digested bones from the Cueva del Camino site. For Kuhn et al. (2010) these elements can be present in the range of 0-23% of the total MNI for postcranial remains at hyena dens.

The study by Kuhn et al. (2010) suggests that of all the previously established and re-evaluated criteria, the only two that can truly differentiate between accumulations of hominids and hyenas do not form part of the criteria proposed by Cruz-Urbe or Pickering: the abundance of coprolites and/or 2) the presence of juvenile hyena remains.

*Presence of hyena coprolites:* Coprolites are found both inside and outside hyena dens (Sutcliffe, 1970; Kruuk, 1972). However, at the Cueva del Camino site, only six hyena coprolites - all very fragmentary - have been recorded. They are insufficient in number to be diagnostic of a hyena den.

*Presence of juvenile hyena:* Deciduous hyena teeth are good indicators of the use of a den by cubs (Villa et al., 2010). The juvenile remains recorded consisted of milk teeth and tooth germs. An MNI of 3 has been estimated for *Crocota crocuta* among the Cueva del Camino remains.

#### 4.6 Stone tools

From 2002 to 2009, 105 lithic remains have been found at Cueva del Camino (Table 8), 52 of them belonging to Level 5. The raw materials for the lithic remains are predominantly quartz. At Camino the lithics size mean are 27 x 20 mm. Cores and retouched elements are scarce ((7.1% (N=6)), while fragments and flakes predominate the assemblage (28.6% (N=24) and 51.2% (N=43) respectively). The operative chains are fragmentary.

## 5. Discussion

### 5.1 Paleobotanical analysis

The palynological composition reflects a continental Mediterranean climate, with more temperate and humid conditions in the lower half of the sequence (Levels N-F and N-5) compared to drier, colder conditions at the top of the sequence (Levels N-6, N-8/9). A quantitative and qualitative progression can be seen between these sets of conditions in terms of the forest cover (Fig. 20), with the appearance of xerophytic over nitrophilous taxa. The presence of NPMs, i.e., *Glomus cf. fasciculatum* (type 207), *Pleospora* sp (type 3 b) and *Pseudoschizaea circula*, (Geel, 1978; López Sáez et al., 2000; Riera et al., 2006), is explained by the degradation of the landscape.

The presence of *Betula*, along with deciduous *Quercus*, *Corylus*, *Ulmus*, *Alnus* and *Salix* in the palynological spectrum, confirms the existence of refugia in more sheltered areas such as the bottom of valleys where water availability would be good. The Rosaceae recorded in the pollen diagram might correspond mainly to the Maloideae recorded in the anthracological assemblages.

The charcoal analysis suggests vegetation with a strong pioneering character, clearly reflected in the presence of *Pinus* and, to a lesser extent, *Betula*. These taxa

characteristically appear at the beginning of interstadial or interglacial climatic vegetation cycles. The date obtained for Level 5 (90 ka, TL) is contemporaneous with an interstadial event of MIS 5.

### 5.2 Biochronology of the faunal association

The faunal association of the site led Alférez et al. (1982) to provisionally assign it to the Riss-Würm (Eemian) interglacial period or some Riss interstadial period. The new faunal data have clarified the biochronological aspects as follows.

From a chronological standpoint, the rodent association of Cueva del Camino is characteristic of the first half of the Late Pleistocene in the Iberian Peninsula. Some species represented in the North and Central sectors are more common in the Middle Pleistocene, becoming progressively scarcer during the Late Pleistocene until their disappearance from the area. Such is the case of the Malaysian porcupine, which inhabited the Peninsula throughout the Middle Pleistocene and the first half of the Late Pleistocene, its most recent citations coming from the MIS 3 sites of La Mina (in Burgos; (Díez et al., 2008)) and Cueva de A Valiña (in Lugo; (Fernández Rodríguez, 2006)). Other rodents present in the Cueva del Camino assemblage are first recorded at the start of the Late Pleistocene, such as *M. cabreræ* and *A. terrestris*. The incipient differentiation observed in the enamel pattern of the molars of *A. terrestris* indicates an age within the first half of the Late Pleistocene. In the south sector, the presence of the snow vole (*Chionomys nivalis*) suggests a slightly more modern age than for the remainder of the site. The earliest record of this species in the Iberian Peninsula is from the lower levels of the Cueva de la Carihuela (Ruiz Bustos, 2000), dating from the MIS 5 or the transition to MIS4 (Fernández et al., 2007), and is more common in younger localities.

The ungulates of Cueva del Camino provide a clear example of an interglacial faunal complex. Similar mammal associations are documented at a number of Eemian *s.l.* sites, such as Barrington and Trafalgar Square (Great Britain) (Stuart, 1982), Taubach and Burgtonna I (Germany) (Kolfshoten, 2000; Kahlke, 2002). The term Eemian is here used in a broad sense, referring to the warm (interglacial) period preceding the cold episodes of the Late Pleistocene. The Cueva del Camino site is of special interest in the Iberian Peninsula given the high proportion of *Dama dama* remains and because it is one of the earliest known Iberian assemblages of this species.

In the Iberian Peninsula, spotted hyenas first occur in late Early Pleistocene sites (García and Arsuaga, 1999). The most recent occurrence of *Crocota crocuta* is at Cueva de las Ventanas (Granada), a tardiglacial site about 12.500 cal radiocarbon BP (Carrión et al., 2001). Brown bears (*Ursus arctos*) first occur in Europe during the late Middle Pleistocene at a moment when *U. spelaeus* fully occupied the continent. The latest clear occurrence of *Panthera pardus* in the Iberian Peninsula was between 30 and 22 ka at Cueva Morín (Cantabria; Level 5b: Gravettian-Aurignacian; (Altuna, 1971)) and Amalda VI (Basque Country; Gravettian Level; (Altuna, 1984)).

The carnivore assemblage of Cueva del Camino provide little detail in terms of age range, but points to an interval from the late Middle Pleistocene to around 30-22 ka: thus it is consistent with the radiometric age obtained by TL ( $90.961 \pm 7881$  years), corresponding to isotopic stage 5c which was a generally temperate time.

### 5.3 Environmental reconstruction from faunal remains

The faunal analysis developed by Alférez's team confirms a paleoenvironment characterized by open forest and warm climate. The new data supports this hypothesis. Regarding the microvertebrate assemblage, the most outstanding feature of the Cueva del Camino is its high species richness. Several factors may be responsible for this, not least the steep valley in which the locality lies. The altitude differs by about 1000 m from the base of the valley to the summits of the surrounding mountains, favouring the development of a variety of biotopes, each with its distinctive species. Another factor favouring a high diversity of small vertebrates might be the nearby Pico de Peñalara (2428 m), which lies at the head of the valley. This mountain determines that the area enjoys more rainfall and more humid conditions than the surrounding regions. A positive correlation has been described between rainfall and mammalian species richness (Moreno-Rueda and Pizarro, 2009). For these same reasons, the Sierra de Guadarrama, and particularly the high part of the Lozoya Valley, is even now one of the areas of Central Spain with the highest vertebrate species richness (Tellería, 1999).

From a paleoenvironmental point of view, several microvertebrates identified in the fossil assemblage at Cueva del Camino can be considered typically thermophilous, e.g., the Cabrera vole or the Malaysian porcupine. Herman's tortoise and the Montpellier snake can be similarly viewed. These taxa, together with the absence of cold climate-adapted species are indicative of warm environmental conditions during the formation of the North and Central sectors of the site. The scarcity or absence of these



thermophilous taxa, together with the presence of the snow vole and the abundance of the field vole in the South sector, suggest colder conditions for this part of the site.

Interestingly, typically forest-dwelling rodents such as the squirrel or the bank vole (*Myodes* cf. *glareolus*) were also found in the North and Central sectors, although only in proportions of around 0.1%. These animals are very rare in other micromammal associations of the Iberian Pleistocene. The abundance of field mouse remains (>40% of all rodent remains) is also indicative of forest masses, which must have alternated with more open areas occupied by different types of vole. In the South sector, the absence of forest species, the lesser abundance of the fieldmouse (10%), and the dominance of rodent associations by the common vole (*M. arvalis*) indicate a more open landscape than within the other sectors.

Analysis of the macrofauna allows the reconstruction of the Lozoya Valley's early Late Pleistocene palaeoecology. The ungulate association at Cueva del Camino shows an environmental complex composed of different ecosystems. During the Late Middle and Late Pleistocene interglacial periods, *Bos primigenius* inhabited the forests, although these must have had open patches. A forest environment is also supported by the presence of *Dama dama*, *S. scrofa* and *C. capreolus*. Open areas (grasslands) were inhabited by *E. ferus* and *S. hemitoechus*. A third ecological component related to the altitude of the site is suggested by the presence of *R. rupicapra*, a species characteristic of rocky, high mountain areas. The absence of *U. spelaeus* at Cueva del Camino an abundant species in the nearby site of Reguerillo (Torres, 1974), might be explained by the different preferences of these taxa. Cave bear remains are rarely recovered in sites other than deep caves (as in the case of Reguerillo), while brown bear remains are often found in open air, cave entrance or rock shelter sites. Mild climatic conditions might also explain the predominance of brown bears at Cueva del Camino.

The carnivore species recovered from Cueva del Camino have a wide climatic tolerance range, allowing them to be found associated with both warm and cold faunas. No typically cold taxa such as *Alopex lagopus* or *Gulo gulo* have been recovered. The absence of such species cannot provide much of a clue with respect to the climate, but it is in line with the suggested mild period reflected by Cueva del Camino – a time when browsing ungulates were common on open land, when brown bears would have inhabited the forests, and when lions would have patrolled the steppeland. Lions and hyenas today occupy open areas such as savannas, but during the Pleistocene these species might have occupied a wider range of habitats. Pole cats, wolves and foxes can



also inhabit different habitats but are more commonly found in woodlands, i.e., in environments similar to that in the area of Cueva del Camino. Thus a varied, temperate ecosystem can be interpreted, where there were forested areas but also more open spaces attractive to lions and hyenas.

#### 5.4 Human Remains

The degree of hypocone development in the M<sup>1</sup> is similar to that commonly found among Neanderthals, which generally show large hypocones. However, a metaconule and some development of a Carabelli structure are seen in about 64% and 68% of Neanderthal specimens respectively (Bailey, 2006). The frequencies of these traits are somewhat lower (53% and 40% respectively) in Upper Palaeolithic modern humans, but their absence in the Cueva del Camino M<sup>1</sup> is not diagnostic with respect to taxonomic affinity. While not as pronounced as in some Neanderthal specimens, the external crown outline of this tooth shows what can be characterized as a bulging hypocone, which seems to conform to the derived shape identified in specimens attributed to the Neanderthal evolutionary lineage (Gómez-Robles et al., 2007). The presence of a taurodont pulp chamber is a variable feature found at low frequency (<5%) in living humans (Hillson, 1996) but at high frequency in Neanderthals (Kallay, 1963). This chamber has also been documented in *Homo erectus* teeth from Zhoukoudian (Weidenreich, 1937).

In its overall crown dimension, the Cueva del Camino M<sup>1</sup> compares most favorably with European Neanderthal specimens. The relative sizes of the occlusal polygon and cusp base areas also provide clear indications of the taxonomic affinities. Low values for the relative occlusal polygon area, as in the Camino M<sup>1</sup>, indicate relatively internally placed cusp tips, a feature argued to represent a derived Neanderthal condition (Smith, 1989; Bailey, 2004). Although the reduction of the metacone is known to occur in earlier *Homo* species (Quam et al., 2009), it reaches its maximum expression in specimens attributed to the Neanderthal evolutionary lineage (Bailey, 2004). The very small metacone in the Cueva del Camino M<sup>1</sup> indicates Neandertal taxonomic affinities. The M<sup>3</sup> is the most variable of the upper molars, and the crown and root morphology are largely undiagnostic as to taxonomic affinities. Nevertheless, this tooth is not inconsistent with a Neandertal classification.

#### 5.5 Taphonomy and signs of human presence at Cueva del Camino

The first interpretations of the site indicated that this cave was probably occupied by humans (Alf3rez et al., 1982). Subsequently, D3ez (1993) reinterpreted the origin of the accumulation as a spotted hyena den. The present work tends to corroborate the interpretation of the latter author. The presence of human teeth at the site obliges the possibility that some human activity took place either within the cave or at its mouth. Unfortunately clues on what that activity was have likely been lost through erosion or the building of the road that passes by the site. These teeth may, however, have been transported to the site by hyenas or other carnivores, which are thought to be the main (perhaps only) agents responsible for the accumulation of the large mammal remains.

The proportion of possible cut marks is just 0.4%, and only on the acetabulum of a single innominate that belongs to a specimen of *Cervus elaphus* are cut marks clear. Thus, there is little reason to think that humans commonly processed the bodies of animals at the site. The raw materials for the lithic remains (predominantly quartz) are the same as those documented at the other archaeological sites in the surrounding area (Navalma3llo Shelter, Descubi3rta and Buena Pinta caves). However, in contrast to those other archaeological sites, the frequency of lithics compared to faunal remains is minor (it represents 2.8 % of the record).

Because of the infrequency of lithics at Camino, the possibility that their presence at the site was due to taphonomic processes and not of anthropogenic origin must be tested. Different criteria were used for assessment (Villa and Soressi, 2000), including the lithic record composition as well as special features of the faunal record such as the scarcity of cut marks and the lack of evidence for anthropogenic fracturing of bones.

The proximity of Descubi3rta cave, an earlier locality, with a very rich lithic sample, provides an abundance of stone tools at the surface of the hill, just above Cueva del Camino. It is possible that this material could have entered through different fractures in the rock walls of the cave. Support for this hypothesis is provided by comparing the size of the lithic artifacts found at Cueva del Camino with those of Descubi3rta cave. At Camino the lithics are typically smaller (mean 27 x 20 mm) while being larger at Descubi3rta (mean 58 x 44 mm). In this case, this small size would mean selective transport by natural processes. Additionally, cores and retouched elements are scarce, while fragments and flakes predominate in the assemblage. The operative chains are fragmentary, which support this hypothesis.

No burned bones were discovered during the 2002-2009 campaigns; such findings would have been clear evidence of controlled fire being used. The isolated pieces of charcoal recovered might indicate that fires were made close by. Indeed, these charcoal pieces do not seem to have been the product of natural fires for the following reasons: i) the stratigraphy does not include any layer of ash that might represent a bushfire. Further, carbon microparticles on the pollen slides are very scarce and discontinuous; ii) the carbonised remains only correspond to wood; no carbonised fruits, seeds, leaves or bark have been found; iii) many species with different ecological (e.g., sunny or shady) and soil (silicic and calcic) requirements are represented by these charcoal pieces. This might indicate that the original wood was brought from different places.

It is therefore possible that the small charcoal remains found at the site were transported there by geological means from nearby human dwelling areas, probably higher up the slope. None of the evidence above goes against interpreting the Cueva del Camino as a den used by carnivores, particularly hyenas. Furthermore the data suggest the Neanderthals of the area only rarely, if ever, used the cave.

Human remains or traces of human presence have also been recorded in other carnivore dens, such as: Wezmeh cave (Iran) (Trinkaus et al., 2008; Mashkour et al., 2009), Geula cave (Israel) (Monchot, 2005), Les Auzières 2 and Bois Roche (France) (Marchal et al., 2009; Villa et al., 2010) or Zourah cave (Morocco) (Monchot and Aouraghe, 2009).

Fracturing pattern results show that there is a predominance of fractures with bevelled and mixed angles with respect to the fracture angle. The properties of the fracture edges in the majority of cases are characterised by being smooth, with a high percentage of crenulated edges in the sample. These data suggest that the majority of the sample was fractured during a biostratigraphic stage and that carnivores played a role in the fracturing processes. There is abundant evidence of carnivorous activity in the fossiliferous association at this site. However, it is not easy either to assign a taxon responsible for modifying and accruing these bones. Tooth mark metric data from this site have been compared with those published earlier. Fig. 21 shows an important overlapping of the tooth mark values in relation with published data. The high frequency of gnaw marks and digested bones, the carnivore/ungulate ratio, the abundance of juvenile hyena and the patterns of bone breakage suggest that the Cueva del Camino was a hyena den (*Crocuta crocuta*).

## 6. Conclusions

Iberian Peninsula is rich in Neanderthal occupations dated to Middle-Upper Paleolithic through the entire Mediterranean coast margin, ranging from the French border to the Straits of Gibraltar (Arsuaga et al., 1989; Arsuaga et al., 2005; Daura et al., 2005; Finlayson et al., 2006; Walker et al., 2011). However the Cueva de Camino fossil assemblage, located in a mountain habitat (in the limit of Mediterranean conditions), is of special interest because it constitutes the most complete and ancient inland Iberian record, where the Neanderthals lived.

In general, the pollen composition of the site corresponds to the installation of a continental Mediterranean climate, with more temperate and more humid conditions represented in the lower half of the sequence (Levels N-F and N-5), and drier, colder conditions represented towards the top (Levels N-6, N-8/9). This change was accompanied by a progressive loss (both qualitative and quantitative) of forest cover, the appearance of xerophytic taxa, and the gradual loss of nitrophilous plants.

The results of charcoal analysis suggest a strong pioneering character for the site's vegetation, dominated by *Pinus* and to a lesser extent *Betula*. These taxa are characteristic of the beginning of interstadial and interglacial vegetation cycles. Certainly, the date obtained for Level 5 (90 ka TL) is contemporaneous with one of the interstadial events of MIS 5. This stadial-interstadial cyclicality might have been responsible for this pioneering character of the vegetation.

Several of the microvertebrates identified in the fossil assemblage at Cueva del Camino are typically thermophilous species. From a chronological point of view, the rodent assemblage is characteristic of the first half of the Late Pleistocene in the Iberian Peninsula.

The ungulates of Cueva del Camino provide a clear example of an interglacial faunal complex. The site is of special interest in the Iberian Peninsula given the high proportion of *Dama dama* remains, and because it is one of the earliest known Iberian assemblages for this species. The carnivore species recovered from the site showed a wide climatic tolerance range, and have been reported associated with both warm and cold faunas. Thus, a varied, temperate ecosystem can be interpreted, with forested areas but also more open spaces attractive to lions and hyenas.

The M<sup>1</sup> specimen from Cueva del Camino shows a number of derived features seen at high frequencies in Neanderthals, including the shape of the crown outline, the crown and cusp dimensions, the relative size and internal placement of the individual cusps and the taurodont pulp chamber. While the external morphology of M<sup>3</sup> is largely

undiagnostic, it is not inconsistent with a Neanderthal classification, and both teeth likely belonged to the same individual. These results are broadly similar with previous suggestions (Alfárez and Roldán, 1992) of Neanderthal affinities for the specimens. However, the present study provides a more detailed analysis based on recent findings, places the human teeth within a clear Upper Pleistocene context and provides comparative data for further studies of Neanderthal dental morphology and evolution. The high frequency of gnaw marks and digested bones, the carnivore/ungulate ratio, and the patterns of bone breakage suggest that the Cueva del Camino megafaunal assemblage was accumulated by carnivores. The abundance of juvenile hyena suggests that the site was a hyena den (*Crocuta crocuta*) during the Late Pleistocene.

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#### *References*

- Alfárez, F., 1985. Dos molares humanos procedentes del yacimiento del Pleistoceno Medio de Pinilla del Valle (Madrid). In, Resúmenes IV Congreso Español de Antropología Biológica. Trabajos de Antropología, pp. 303.
- Alfárez, F., 1987. Paleoambiente y rasgos culturales de los homínidos del Pleistoceno Medio de Pinilla del Valle (Madrid). In, Abstracts of XII Internacional Congreso of INQUA, pp. 119.

Alfárez, F., Molero, G., 1982. Descubrimiento de un fósil humano (Riss-Würm) en Pinilla del Valle (Madrid). In, Résumés des Communications du I Congrès International de Paléontologie Humane. Section IV: *Homo sapiens neandertalensis*/Neandertaliens et Neandertaloides.

Alfárez, F., Iñigo, C., 1990. Los restos de *Dicerorhinus hemitoechus* (*Perissodactyla*; *Mammalia*) del Pleistoceno medio de Pinilla del Valle (Madrid). *Acta Salmanticensia* 68, 25-45.

Alfárez, F., Roldán, B., 1992. Un molar humano Anteneandertal con patología traumática procedente del yacimiento cuaternario de Pinilla del Valle (Madrid). *Munibe* 8, 183-188.

Alfárez, F., Buitrago, A.M., 1994. Los restos de *Sus scrofa* (*Artiodactyla*, *Mammalia*) del Pleistoceno Medio de Pinilla del Valle (Madrid). In, Comunicaciones de las X Jornadas de Paleontología, pp. 12-13.

Alfárez, F., Chacón, B., 1996. New data on the Middle Pleistocene bear from the Pinilla del Valle, Madrid. In, 44th Symposium of Vertebrate Palaeontology and Comparative Anatomy (SVPCA).

Alfárez, F., Molero, G., Maldonado, E., 1985. Estudio preliminar del úrsido del yacimiento del cuaternario medio de Pinilla del Valle (Madrid). *Coloquios de Paleontología* 40, 59-67.

Alfárez, F., Molero, G., Maldonado, E., Bustos, V., Brea, P., Buitrago, A.M., 1982. Descubrimiento del primer yacimiento cuaternario (Riss-Würm) de vertebrados con restos humanos en la provincia de Madrid (Pinilla del Valle). *Coloquios de Paleontología* 37, 15-32.

Alfárez, F., Molero, G., Maldonado, E., Brea, P., Bustos, V., Buitrago, A.M., Toni, I., 1983. Paleontología del Cuaternario. Yacimiento cuaternario de Pinilla del Valle. . In: D. y. T. Comunidad de Madrid. Consejería de Cultura (Ed.) Madrid en sus orígenes. pp. 1-11.

Altuna, J., 1971. Los mamíferos del yacimiento prehistórico de Morín (Santander)Cueva Morín. Excavaciones 1966-1968, Publicaciones del patronato de las cuevas prehistóricas de la provincia de Santander, Santander. pp. 368-401.

Altuna, J., 1984. Cueva de Amalda (Cestona, Guipúzcoa)VI campaña de excavaciones. Arkeoikuska: Investigación arqueológica pp. 32-35.

Anderson, D., Thompson, G., Popovich, F., 1976. Age of attainment of mineralization stages of the permanent dentition. *Journal of Forensic Science* 21, 191-200.

Arenas, R., Fuster, J.M., Martínez-Salnova, d.O., A., Villaseca, C., 1991. Mapa Geológico de España 1:15.000, Segovia (843). IGME, Madrid.

Arsuaga, J.L., Baquedano, E., Pérez-González, A., 2011. Neanderthal and carnivore occupations in Pinilla del Valle sites (Community of Madrid, Spain). In: L. Oosterbeek, C. Fidalgo (Eds.), *Proceedings of the XV World Congress of the International Union for Prehistoric and Protohistoric Sciences*, BAR International Series. Archaeopress, Oxford. pp. 111-119.

Arsuaga, J.L., Gracia, A., Martínez, I., Bermúdez de Castro, J.M., Rosas, A., Villaverde, V., Fumanal, M.P., 1989. The human remains from Cova Negra (Valencia, Spain) and their place in European Pleistocene human evolution. *Journal of Human Evolution* 18, 55-92.

Arsuaga, J.L., Quam, R., Villaverde, V., Martínez, I., Lorenzo, C., Carretero, J.M., Gracia, A., 2005. New Neandertal remains from the site of Cova Negra (Spain). *American Journal of Physical Anthropology* S40, 66-67.

Arsuaga, J.L., Baquedano, E., Pérez-González, A., Sala, M.T.N., García, N., Álvarez-Lao, D., Laplana, C., Huguet, R., Sevilla, P., Blain, H.-A., Quam, R., Ruiz-Zapata, M.B., Sala, P., García, M.J.G., Uzquiano, P., Pantoja, A., 2010. El yacimiento arqueopaleontológico del Pleistoceno Superior de la Cueva del Camino en el Calvero de la Higuera (Pinilla del Valle, Madrid). *Zona arqueológica* 13 (1ª Reunión de científicos



sobre cubiles de hiena (y otros grandes carnívoros) en los yacimientos arqueológicos de la Península Ibérica), 422-442.

Badal, E., Carrión, Y., Rivera, D., Uzquiano, P., 2003. La Arqueobotánica en cuevas y abrigos: objetivos y métodos de muestreo. In: R. Buxó, R. Piqué (Eds.), La recogida de muestras en arqueobotánica: objetivos y propuestas metodológicas. La gestión de los recursos vegetales y la transformación del paleopaisaje en el Mediterráneo Occidental. Encuentro del Grupo de Trabajo de Arqueobotánica de la Península Ibérica (G.T.A.P.I.), Museu d'Arqueologia de Catalunya, Barcelona/Bellaterra.

Bailey, S., 2004. A morphometric analysis of maxillary molar crowns of Middle-Late Pleistocene hominins. *Journal of Human Evolution* 47, 183-198.

Bailey, S., 2006. Beyond shovel-shaped incisors: Neandertal dental morphology in a comparative context. *Periodicum Biologorum* 108 (3), 253-267.

Bailey, S., Glantz, M., Weaver, T., Viola, B., 2008. The affinity of the dental remains from Obi-Rakhmat Grotto, Uzbekistan. *Journal of Human Evolution* 55, 238-248.

Bailon, S., 1999. Différenciation ostéologique des Anoures (Amphibia, Anura) de France. In: J. Desse, N. Desse-Berset (Eds.), Fiches d'ostéologie animale pour l'archéologie, Centre de Recherches Archéologiques-CNRS, Valbonne. pp. 38.

Basabe, J.M., 1973. Dientes humanos del Musteriense de Axlor (Dima, Vizcaya). *Trabajos de Antropología* 4, 287-202.

Bellido, F., Escuder, J., Klein, E., del Olmo, A., 1991. Mapa Geológico de España 1:50.000, Buitrago de Lozoya (484). IGME, Madrid.

Bermúdez de Castro, J.M., 1993. The Atapuerca dental remains. New evidence (1987-1991 excavations) and interpretations. *Journal of Human Evolution* 24, 339-371.

Bilsborough, A., Thompson, J.L., 2005. The dentition of Le Moustier 1. The Neanderthal adolescent Le Moustier 1: New aspects, new results, Staatliche Museen Zu Berlin-Preussischer Kulturbesitz, Berlin. pp. 157-186.

Binford, L.R., 1981. Bones: ancient men and modern myths. Academic Press, London, 320p.

Birks, H.J.B., Line, J.M., 1992. The use of rarefaction analysis for estimating palynological richness from Quaternary pollen-analytical data. *The Holocene* 2 (1), 1-10.

Blain, H.-A., 2005. Contribution de la paleoherpétofaune (Amphibia and Squamata) à la connaissance de l'évolution du climat et du paysage du Pliocène supérieur au Pléistocène moyen d'Espagne.

Bochenski, Z., 2007. The Middle Pleistocene avifauna from Pinilla del Valle (Spain). *Geobios* 40, 31-37.

Bronk Ramsey, C., 2000. OxCal Version 3.5  
<http://www.uga.edu/strata/software/Software.html> ANALYTIC RAREFACTION 1.3  
<http://www.rlaha.ox.ac.uk/orau/index.htm>.

Buitrago Villaplana, A.M., 1992. Estudio de los Artiodáctilos del yacimiento del Pleistoceno medio de Pinilla del Valle (Madrid). Ph.D.

Bunn, H.T., 1983. Comparative analysis of modern bone assemblages from a San hunter-gatherer camp in the Kalahari desert, Botswana and from spotted hyena den near Nairobi, Kenya. In: J. Clutton-Brock, C. Grigson (Eds.), *Animals and archaeology: Hunters and their prey*, 1, BAR International Series, Oxford. pp. 143-148.

Carrión, J.S., Riquelme, J.A., Navarro, C., Munuera, M., 2001. Pollen in hyaena coprolites reflects late glacial landscape in southern Spain. *Palaeogeography, Palaeoclimatology, Palaeoecology* 176 (1-4), 193-205.

Chaline, J., 1972. Les rongeurs du Pléistocène Moyen et Supérieur de France. Cahiers de Paléontologie. Éditions du Centre national de la recherche scientifique Paris 410p.

Chaline, J., 1974. Les Proies des Rapaces. Doin Editeurs, Paris, 141p.

Coûteaux, M., 1977. À propos de l'interprétation des analyses polliniques de sédiments minéraux, principalement archéologiques. In: H. Laville, J. Renault-Miskovsky (Eds.), Approche écologique de l'homme fossile. Supplément du Bulletin de l'Association française pour l'Etude du Quaternaire, 47 pp. 259-276.

Cruz-Uribe, K., 1991. Distinguishing Hyena from Hominid Bone Accumulations. *Journal of Field Archaeology* 18 (4), 467-486.

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.

Delaney-Rivera, C., Plummer, T.W., Hodgson, J.A., Forrest, F., Hertel, F., Oliver, J.S., 2009. Pits and Pitfalls: Taxonomic Variability and Patterning in Tooth Mark Dimensions. *Journal of Archaeological Science* 36 (11), 2597-2608.

Díez, J.C., 1993. Estudio tafonómico de los macrovertebrados de yacimientos del Pleistoceno medio. *Complutum* 4, 21-40.

Díez, J.C., Alonso, R., Bengoechea, A., Colina, A., Pardo, J.F.J., 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 Cuaternario y Geomorfología 22 (3-4), 135-157.

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.

Esteban, M., Sanchiz, B., 1985. Herpetofauna de Erralla. *Munibe (Antropología y Arqueología)* 37, 81-86.

Esteban, M., Sanchiz, B., 1991. Sobre la presencia de *Rana iberica* en el Pleistoceno burgales. *Revista Española de Herpetología* 5, 93-99.

Felten, H., Helfricht, A., Storch, G., 1973. Die Bestimmung der europäischen Fledermäuse nach der distalen Epiphyse des Humerus. *Senckenbergiana biologica* 54 (4/6), 291-297.

Fernández, F., 1988. Estudio florístico y fitosociológico del Valle del Paular (Madrid).

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

Fernández, S., Fuentes, N., Carrión, J.S., González-Sampériz, P., Montoya, E., Fil, G., Vega-Toscano, G., Riquelme, J.A., 2007. The Holocene and Upper Pleistocene pollen sequence of Carihuela Cave, southern Spain. *Geobios* 40, 75-90.

Finlayson, C., Giles-Pacheco, F., Rodríguez-Vidal, J., Fa, D.A., Gutierrez-López, J.M., Santiago-Pérez, A., Finlayson, G., Allue, E., Baena-Preysler, J., Cáceres, I., Carrión, J., Jalvo, Y.F., Gleed-Owen, C.P., Espejo, F.J.J., López, P., Sáez, J.A.L., Cantal, J.A.R., Marco, A.S., Guzman, F.G., Brown, K., Fuentes, N., Valarino, C.A., Villalpando, A., Stringer, C.B., Ruiz, F.M., Sakamoto, T., 2006. Late survival of Neanderthals at the southernmost extreme of Europe. *Nature* 443, 850-853.

Freyer, D., 1977. Metric dental change in the European Upper Paleolithic and Mesolithic. *American Journal of Physical Anthropology* 46, 109-120.

García, N., 2003. Osos y otros carnívoros de la sierra de Atapuerca. Fundación Oso de Asturias, Asturias.

García, N., Arsuaga, J.L., 1999. Carnivores from the Early Pleistocene hominid-bearing Trinchera Dolina 6 (Sierra de Atapuerca, Spain). *Journal of Human Evolution* 37 (3-4), 415-430.

Geel, B.v., 1978. A palaeoecological study of Holocene peat bog sections in Germany and The Netherlands. *Review of Palaeobotany and Palynology* 25, 1-120.

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

Gómez-Robles, A., Martínón-Torres, M., Bermúdez de Castro, J.M., Margvelashvili, A., Bastir, M., Arsuaga, J.L., Pérez-Pérez, A., Estebaranz, F., Martínez, L.M., 2007. A geometric morphometric analysis of hominin upper first molar shape. *Journal of Human Evolution* 53, 272-285.

Greguss, P., 1955. Identification of living Gymnospermes on the basis of xylotomy. *Akademikai Kiado, Budapest*, 263p.

Greguss, P., 1959. *Holzanatomie der Europäischen Laubhölzer und Sträucher*. *Akademikai Kiado, Budapest*

Grimm, E.C., 1987. CONISS: a FORTRAN 77 program for stratigraphically constrained cluster analysis by the method of incremental sum of squares. *Computers Geosciences* 13 (1), 13-35.

Haynes, G., 1980. Evidence of carnivore gnawing on Pleistocene and Recent mammalian bones. *Paleobiology* 6 (3), 341-351.

Haynes, G., 1983a. Frequencies of spiral and green-bone fractures on ungulate limb bones in modern surface assemblages. *American Antiquity* 48 (1), 102-114.

Haynes, G., 1983b. A guide for differentiating mammalian carnivore taxa responsible for gnaw damage to herbivore limb bones. *Paleobiology* 9 (2), 164-172.

Hillson, S., 1996. *Dental Anthropology*. Cambridge University Press, Cambridge.

Holman, J.A., 1998. *Pleistocene amphibians and reptiles in Britain and Europe*. Oxford University Press, New York and Oxford, 254p.

Huguet, R., Arsuaga, J.L., Pérez-González, A., Arriaza, M.C., Sala-Burgos, M.T.N., Laplana, C., Sevilla, P., García, N., Álvarez-Lao, D., Blain, H.-A., Baquedano, E., 2010. Homínidos y hienas en el Calvero de la Higuera (Pinilla del Valle, Madrid) durante el Pleistoceno Superior. Resultados preliminares. *Zona Arqueológica* 13 (1<sup>a</sup> Reunión de científicos sobre cubiles de hiena (y otros grandes carnívoros) en los yacimientos arqueológicos de la Península Ibérica), 444-458.

Jacquot, C., 1955. *Atlas d'Anatomie des Bois de Conifères*. Texte et Planches. Centre Technique du Bois, CNRS, Paris.

Jacquot, C., Trenard, Y., Dirol, D., 1973. *Atlas d'anatomie des bois des Angiospermes (essences feuillues)*. Centre Technique du Bois, CNRS, Paris.

Kahlke, R.D., 2002. The Quaternary large mammal faunas of Thuringia (Central Germany). In: R. A. Meyrick, D. C. Schreve (Eds.), *The Quaternary of Central Germany (Thuringia and surroundings)*, Field Guide, Quaternary Research Association, London. pp. 59-78.

Kallay, J., 1963. A radiographic study of the Neanderthal teeth from Krapina, Croatia. In: D. Brothwell (Ed.) *Dental Anthropology*, Pergamon Press, Oxford. pp. 75-86.

Klein, R.G., Cruz-Urbe, K., 1984. *The Analysis of Animal Bones from Archaeological Sites*. The University of Chicago Press, Chicago, London, 266p.

Kolfschoten, T.v., 2000. The Eemian fauna of central Europe. *Geologie en Mijnbouw / Netherlands. Journal of Geosciences* 79 (2/3), 269-281.

Kowalski, K., 2001. Pleistocene rodents of Europe. *Folia Cuaternaria* 72, 1-389.

Kruuk, H., 1972. The spotted hyena: a study of predation and social behavior. The University Chicago Press.

Kuhn, B.F., Berger, L.R., Skinner, J.D., 2010. Examining Criteria for Identifying and Differentiating Fossil Faunal Assemblages Accumulated by Hyenas and Hominins using Extant Hyenid Accumulations. *International Journal of Osteoarchaeology* 20 (1), 15-35.

Laplana, C., Sevilla, P., 2006. Nuevos datos sobre los micromamíferos (Roedores, Insectívoros y Quirópteros) del yacimiento Camino (Pleistoceno Superior, Pinilla del Valle, Madrid). In: E. E. Fernández-Martínez (Ed.), XXII Jornadas de Paleontología, pp. 135-137.

López Sáez, J.A., van Geel, B., Martín Sánchez, M., 2000. Aplicación de los microfósiles no polínicos en Palinología Arqueológica. In: V. Oliveira Jorge (Ed.) *Actas 3º Congresso de Arqueologia Peninsular. Contributos das Ciências e das Tecnologias para a Arqueologia da Península Ibérica*, IX, Adecap, Porto. pp. 11-20.

Lumley, M.A., 1973. *Anteneandertaliens et Neandertaliens du Basin Méditerranéen Occidental Européen*. Laboratoire de paléontologie humaine et de préhistoire. Université de Provence, Marseille.

Lyman, R.L., 1993. Density-Mediated Attrition of Bone Assemblages: New Insights. In: J. Hudson (Ed.) *From Bones to Behavior: Ethnoarchaeological and Experimental Contributions to the Interpretation of Faunal Remains* Southern Illinois University press, Illinois. pp. 324-341.



Lyman, R.L., 1994. *Vertebrate Taphonomy*. Cambridge University Press, Cambridge, 524p.

Made, J.V.d., 2001. Les Ongulés d'Atapuerca. Stratigraphie et biogéographie. *L'Anthropologie* 105 (1), 95-113.

Maguire, J.M., Pemberton, D., Collett, M.H., 1980. The Makapansgat limeworks grey breccia: Hominids, hyaenas, hystrioids or hillwash? *Palaeontologia Africana* 23, 75-98.

Maldonado Díaz, E., 1991. El yacimiento cuaternario de Pinilla del Valle (Madrid). *Cuadernos de INICE* 38, 9-22.

Maldonado, E., 1996. Revisión de los équidos del Pleistoceno Medio y Superior de España. Tesis doctoral

Manzi, G., Santandrea, E., Passarello, P., 1997. Dental size and shape in the Roman Imperial Age: two examples from the area of Rome. *American Journal of Physical Anthropology* 102, 469-479.

Marchal, F., Monchot, H., Coussot, C., Desclaux, E., Deschamp, P., Thiébaud, C., Bahain, J.-J., Falguères, C., Dolo, J.-M., 2009. Neandertals paleoenvironment in Western Provence: The contribution of Les Auzières 2 (Méthamis, Vaucluse, France). *Comptes Rendus Palevol* 8, 493-502.

Martinón-Torres, M., Bermúdez de Castro, J.M., Gómez-Robles, A., Margvelashvili, A., Prado, L., Lordkipanidze, D., Vekua, A., 2008. Dental remains from Dmanisi (Republic of Georgia): Morphological analysis and comparative study. *Journal of Human Evolution* 55 (2), 249-273.

Martinón-Torres, M., Bermúdez de Castro, J.M., Gómez-Robles, A., Arsuaga, J.L., Carbonell, E., Lordkipanidze, D., Manzi, G., Margvelashvili, A., 2007. Dental evidence on the hominin dispersals during the Pleistocene. *Proceedings of the National Academy of Sciences* 104 (33), 13279-13282.

Mashkour, M., Monchot, H., Trinkaus, E., Reyss, J.L., Biglari, F., Bailon, S., Heydari, S., Abdi, K., 2009. Carnivores and their Prey in the Wezmeh Cave (Kermanshah, Iran): A Late Pleistocene Refuge in the Zagros. *International Journal of Osteoarchaeology* 19 (6), 678-694.

Monchot, H., 2005. Un assemblage original au Paléolithique moyen : le repaire à hyènes, porcs-épics et hominidés de la grotte Geula (Mont Carmel, Israël). *Paléorient* 31 (2), 27-42.

Monchot, H., Aouraghe, H., 2009. Deciphering the taphonomic history of an Upper Paleolithic faunal assemblage from Zouhrah Cave/El Harhoura 1, Morocco. *Quaternaire* 20 (2), 239-253.

Moreno-Rueda, G., Pizarro, M., 2009. Relative influence of habitat heterogeneity, climate, human disturbance, and spatial structure on vertebrate species richness in Spain. *Ecological Research* 24, 335-344.

Nadachowski, A., 1990. Comments of variation, evolution and phylogeny of *Chionomys* (Arvicolidae) International Symposium. Evolution, phylogeny and biostratigraphy of arvicolids (Rodentia, Mammalia), Rohanov. pp. 353-368.

Nadachowski, A., 1991. Systematics, geographic variation, and evolution of snow voles (*Chionomys*) based on dental characters. *Acta Theriologica* 36 (1-2), 1-45.

Olejniczak, A.J., Smith, T.M., Feeney, R.N.M., Macchiarelli, R., Mazurier, A., Bondioli, L., Rosas, A., Fortea, J., de la Rasilla, M., Garcia-Tabernero, A., Radovic, J., Skinner, M.M., Toussaint, M., Hublin, J.-J., 2008. Dental tissue proportions and enamel thickness in Neandertal and modern human molars. *Journal of Human Evolution* 55 (1), 12-23.

Peinado Lorca, M., Rivas Martínez, S., 1987. La vegetación de España. Colección Aula Abierta, Universidad de Alcalá de Henares, Alcalá de Henares.

Pemán, E., 1985. Aspectos climáticos y ecológicos de los micromamíferos del yacimiento de Erralla. *Munibe* 37, 49-57.

Pérez-González, A., Karampaglidis, T., Arsuaga, J.L., Baquedano, E., Báñez, S., Gómez, J.J., Panera, J., Márquez, B., Laplana, C., Mosquera, M., Huguet, R., Sala, P., Arriaza, M.C., Benito, A., Aracil, E., Maldonado, E., 2010. Aproximación geomorfológica a los yacimientos del Pleistoceno Superior del Calvero de la Higuera en el Valle Alto del Lozoya (Sistema Central Español, Madrid). *Zona arqueológica* 13, 404-419.

Pickering, T.R., 2002. Reconsideration of criteria for differentiating faunal assemblages accumulated by hyenas and hominids. *International Journal of Osteoarchaeology* 12 (2), 127-141.

Quam, R., Bailey, S., Wood, B., 2009. Evolution of M<sup>1</sup> crown size and cusp proportions in the genus *Homo*. *Journal of Anatomy* 214 (5), 655-670.

Riera, S., López Sáez, J.A., Julià, R., 2006. Lake responses to historical land use changes in northern Spain: the contribution of non-pollen palynomorphs in a multiproxy study. *Review of Palaeobotany and Palynology* 141, 127-137.

Rivas Martínez, S., 1987. Memoria del mapa de series de vegetación de España. Ministerio de Agricultura, Pesca y Alimentación, Madrid.

Ruiz Bustos, A., 2000. Estudio paleoecológico de los sedimentos con presencia del hombre de Neandertal en la Cueva de la Carihuela (Piñar, Granada). Instituto Andaluz de Ciencias de la Tierra, Consejo Superior Investigaciones Científicas, Granada, 91p.

Saladié, P., Huguet, R., Díez, C., Rodríguez-Hidalgo, A., Carbonell, E., 2011. Taphonomic modifications produced by modern brown bears (*Ursus arctos*). *International Journal of Osteoarchaeology*, doi: 10.1002/oa.1237.

Schweingruber, F.H., 1978. Mikroskopische holzanatomie microscopic wood anatomy. Eidgenössische Anstalt für das forstliche Versuchswesen, Birmensdorf, Switzerland.

Schweingruber, F.H., 1990. Anatomie europäischer Hölzer - Anatomy of European woods. Eidgenössische Forschungsanstalt für Wald Schnee und Landschaft, Birmensdorf Bern, Stuttgart, Haupt.

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

Sesé, C., 2006. Micromamíferos (Rodentia, Insectivora, Lagomorpha y Chiroptera) de la Peña de Estebanvela (Segovia). In: C. Cacho Quesada, L. Ripoll, S., F. J. Muñoz Ibáñez (Eds.), *La Peña de Estebanvela (Estebanvela-Ayllón, Segovia). Grupos Magdalenienses en el Sur del Duero*, 17, *Arqueología en Castilla y León*. pp. 145-166.

Sevilla, P., 1988. Estudio paleontológico de los Quirópteros del Cuaternario español. *Paleontologia i evolució* 22, 113-233.

Smith, B., 1984. Patterns of molar wear in hunter-gatherers and agriculturalists. *American Journal of Physical Anthropology* 63, 39-56.

Smith, P., 1989. Dental evidence for phylogenetic relationships of Middle Paleolithic hominids. In: M. Otte (Ed.) *L'Homme de Néandertal, Vol 7 L'Extinction*, Université de Liege, Liege. pp. 111-120.

Smith, T.M., Olejniczak, A.J., Reid, D.J., Ferrell, R.J., Hublin, J.J., 2006. Modern human molar enamel thickness and enamel-dentine junction shape. *Archives of Oral Biology* 51, 974-995.

Stuart, A.J., 1982. *Pleistocene vertebrates in the British Isles*. Longman, London.

Sutcliffe, A.S., 1970. Spotted hyaena: Crusher, gnawer, digester and collector of bones. *Nature* 227, 1110-1113.

- Tellería, J.L., 1999. La diversidad de vertebrados del Valle de El Páular (Madrid). In: J. A. Vielva-Juez (Ed.) Primeros Encuentros Científicos del Parque Natural de Peñalara y del Valle de El Páular, Consejería de Medio Ambiente, Comunidad de Madrid, Madrid. pp. 155-162.
- Toni, I., Molero, G., 1990. Los roedores (*Rodentia*, *Mammalia*) del yacimiento cuaternario de Pinilla del Valle (Madrid). *Acta Salmantica* 68, 359-373.
- Torres, T., 1974. El oso de las cavernas de la cueva del Reguerillo, Torrelaguna (Madrid) III Congreso Nacional de Espeleología, Madrid. pp.
- Trinkaus, E., 1983. The Shanidar Neandertals. Academic Press, New York, 1-502p.
- Trinkaus, E., Biglari, F., Mashkour, M., Monchot, H., Reyss, J.-L., Rougier, H., Heydari, S., Abdi, K., 2008. Late Pleistocene Human Remains From Wezmeh Cave, Western Iran. *American Journal of physical anthropology* 135, 371-378.
- Turner, C., Nichol, C., Scott, G., 1991. Scoring procedures for key morphological traits of the permanent dentition: the Arizona State University Dental Anthropology System. In: M. Kelley, C. Larsen (Eds.), *Advances in Dental Anthropology*, Wiley-Liss, New York. pp. 13-31.
- Tutin, T.G., Heywood, V.H., Burgues, N.A., Valentine, D.H., Walters, S.M., Webb, D.A., 1964. *Flora europaea*. Cambridge University press.
- Uzquiano, P., 1997. Antracología y métodos: implicaciones en la Economía prehistórica, Etnoarqueología y Paleoecología. *Trabajos de Prehistoria* 54 (1), 145-154.
- Vera, J.A., 2004. Geología de España, pp. 884. SGE-IGME, Madrid.
- Vernet, J.L., Ogereau, P., Figueras, I., Machado, C., Uzquiano, P., 2001. Guide d'identification des charbons de bois préhistoriques et récents. Sud-Ouest de l'Europe: France, Péninsule Ibérique, Îles Canaries. CNRS, Paris, 395p.

Villa, P., Mahieu, E., 1991. Breakage patterns of human long bones. *Journal of Human Evolution* 21 (1), 27-48.

Villa, P., Soressi, M., 2000. Stone tools in carnivore sites: the case of Bois Roche<sup>1</sup>. *Journal of Anthropological Research* 56, 187-215.

Villa, P., Sánchez Goñi, M.F., Bescós, G.C., Grün, R., Ajas, A., García Pimienta, J.C., Lees, W., 2010. The archaeology and paleoenvironment of an Upper Pleistocene hyena den: An integrated approach. *Journal of Archaeological Science* 37 (5), 919-935.

Walker, M.J., Ortega, J., López, M.V., Parmová, K., Trinkaus, E., 2011. Neandertal postcranial remains from the Sima de las Palomas del Cabezo Gordo, Murcia, southeastern Spain. *American Journal of physical anthropology* 144 (4), 505-515.

Weidenreich, F., 1937. The Dentition of *Sinanthropus pekinensis*. *Paleontologica Sinica*. New Series D. Geological Survey of China, Beijing.

Wilson, D.E., Reeder, D.M., 2005. *Mammal species of the World. A Taxonomic and Geographic Reference*. The Johns Hopkins University Press.

Wood, B., Engleman, C., 1988. Analysis of the dental morphology of Plio-Pleistocene hominids V. Maxillary postcanine tooth morphology. *Journal of Anatomy* 161, 1-35.

## Figures

**Fig. 1:** Location of the Sierra de Guadarrama. Detail of the Lozoya Valley, home to the Cueva del Camino site.

**Fig. 2:** Climatic zone distribution and main Neanderthal sites of the Iberian Peninsula. Modified from Rivas Martínez (1987).

**Fig. 3:** a) Site map showing the four sectors defined for the excavated areas; b) stratigraphic section (I-I') and c) TL dates for the main levels. Modified from Pérez-González et al. (2010).

**Fig. 4:** View of three activities involved in obtaining small vertebrates during the excavation. In the foreground, sorting fossils, in the background sieve washing of sediment. Farther back the residue of the different samples left to dry can be seen.

**Fig. 5:** Examples of SEM images of tooth marks (a: scores; b: punctures and c-d: pits) showing the measurements considered in this study.

**Fig. 6:** Detail of the large accumulation of long bones (at least 3 equid metapods are represented) characteristic of the Central sector of the site. Photograph taken during the 2009 campaign. Scale in centimetres.

**Fig. 7:** Pollen histogram.

**Fig. 8:** Anthracological histogram showing the main woody species identified in the North sector (Level 5)

**Fig. 9:** MNI of ungulates (left) and carnivores (right) of the site

**Fig. 10:** Cranial remains and dentition of *Crocota crocuta* juveniles. **A)** Fragment of a right maxilla with dP<sup>3</sup> and dP<sup>2</sup> (05/34/C/05/C4/146); **B)** Right hemimandible with dP<sub>4</sub>, dP<sub>3</sub> and dC<sub>0</sub> (04/20/C/Z8/5/91); **C)** left dP<sup>3</sup> (03/35/C/X7/05/41); **D)** left dP<sup>3</sup> (03/35/C/B5/05/205); **E)** left dP<sup>3</sup> (03/35/C/A5/06/1); **F)** right dP<sup>3</sup> (03/35/C/B5/05/103) **G)** left dP<sub>4</sub> (03/35/B5/05/227); **H)** right dP<sub>3</sub> (03/35/C/B5/05/236); **I)** right dP<sub>3</sub> (germ) (03/35/C/X7/05/15). Scale = 2 cm.

**Fig. 11:** The Cueva del Camino M<sup>1</sup> in mesial (A), distal (B), occlusal (C), buccal (D) and lingual (E) view. Scale = 1 cm.

**Fig. 12:** Virtual reconstruction of the Cueva del Camino M<sup>1</sup> showing the topography of the enamel dentine junction. Note the absence of both a metaconule and any trace of a Carabelli's structure.



**Fig. 13:** Virtual reconstruction of M<sup>1</sup> showing the enamel (white), dentine (green) and pulp chamber (red).

**Fig. 14:** The Cueva del Camino M<sup>3</sup> in mesial (A), distal (B), occlusal (C), buccal (D) and lingual (E) view. Scale = 1 cm

**Fig. 15:** Virtual reconstruction of M<sup>3</sup> showing the enamel (white), dentine (green) and pulp chamber (red).

**Fig. 16:** Relationship between the BL diameters of Neanderthal M<sup>1</sup> and M<sup>3</sup> teeth. Regression line:  $y = 6.935 + 0.437(x)$ .  $r = 0.7449$ ;  $p < 0.001$ ;  $r^2 = 0.5549$ . Neanderthal sample: Axlor (Basabe, 1973); La Quina 5 (JMBC pers. Com.); Le Moustier (Bilsborough and Thompson (2005); Saccopastore 2 (Lumley, 1973); Shanidar (Trinkaus, 1983); Spy (Lumley, 1973); Tabun (Lumley, 1973).

**Fig. 17:** Carnivore-made marks on some bone remains from the site. a) Left mandible of *Dama dama* (04/20/C/Y8/5/122) showing crenulated edges. b) Right calcaneum of *Dama dama* (06/37/C/05/B3/12): note the pitting and scoring. c) *Equus ferus* innominate fragment (05/34/C/05/C4/49) showing pitting and scoring. d) *Equus caballus* femur (04/20/C/Z8/5/24) with a “cylinder shape” and crenulated edges. e) Medial phalange of *Cervus elaphus* (03/35/CA4/05/29) showing a puncture. f) Left antler of *Dama dama* (05/34/C/05/B4/101) with gnaw marks. g) Right metatarsal of red deer (03/35/C/C4/05/101). h) Left innominate of *Equus ferus* (06/37/C/05/C4/74). Scale = 1 cm.

**Fig. 18:** Three-dimensional bar diagrams showing relative frequencies of shaft fragment by shaft circumference in big sized (superior image) and medium sized ungulates (inferior image). *Shaft length* categories are: 1:  $< 1/4$  of the original length; 2:  $1/4$  to  $1/2$ ; 3:  $1/2$  to  $3/4$  and 4:  $> 3/4$  or complete. *Shaft circumference* categories are: 1: bone circumference is less than half of the original; 2: circumference is more than half, and 3: complete circumference in at least a portion of the bone length.

**Fig. 19:** Small hard bones digested. Scale = 1 cm.

**Fig. 20:** Change in main plant taxa groups.

**Fig. 21:** Mean  $\pm$  1 Standard Deviation of carnivore tooth pit sizes according to bone type and length/breadth recovered from Cueva del Camino site. A: Length in dense cortical; B: breadth in dense cortical. Legend data from: \*Domínguez-Rodrigo and Piqueras, 2003; ^Delaney-Rivera *et al.*, 2009; ´Saladié *et al.*, 2011

## Tables

**Table 1:** Summary of the anthracological information obtained from the site's stratigraphic record (Norte sector).

**Table 2:** Microvertebrates identified at the site. The data listed by Alférez *et al.* (1982) and Toni and Molero (1990) refer to excavations conducted in the 1980s. The right-hand column shows the species identified in the recent excavations (2002-2005 campaigns).

**Table 3:** Dimensions of the two human teeth recovered at the site compared with the teeth of Upper Pleistocene and recent humans.

**Table 4:** M<sup>1</sup> occlusal polygon, cusp base areas and cusp angles in the recovered teeth and those of contemporary humans.

**Table 5:** Tooth mark frequencies of in the Cueva del Camino assemblage according to the distribution in the bone portions, geological unit and ungulate size. PE: Proximal Epiphysis; DE: Distal Epiphysis; DPH: Diaphysis.

**Table 6:** Statistical values of pits, punctures and scores analyzed in the sample of the Cueva del Camino assemblage. The data displayed in the table show length and width in dense cortical (n: number of cases; Max: maximum value; Min: minimum value; C.I.: Confidence Interval for mean and St. Desv.: Standard Deviation).

**Table 7:** Fracture properties in Cueva del Camino assemblage. \*Long bones only.

**Table 8:** Number of lithic artefacts from the different sectors and levels of the site.

Figure 1

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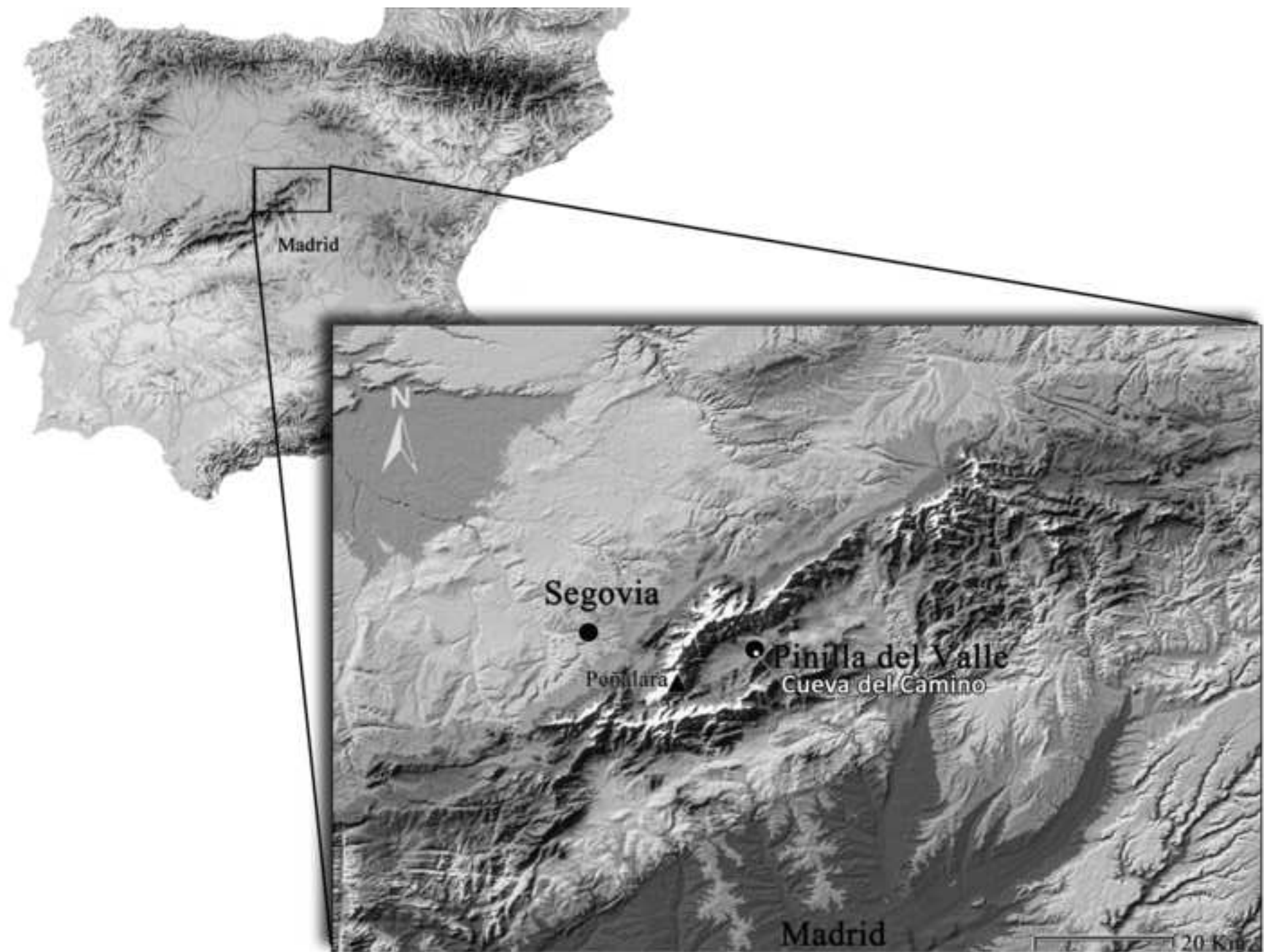


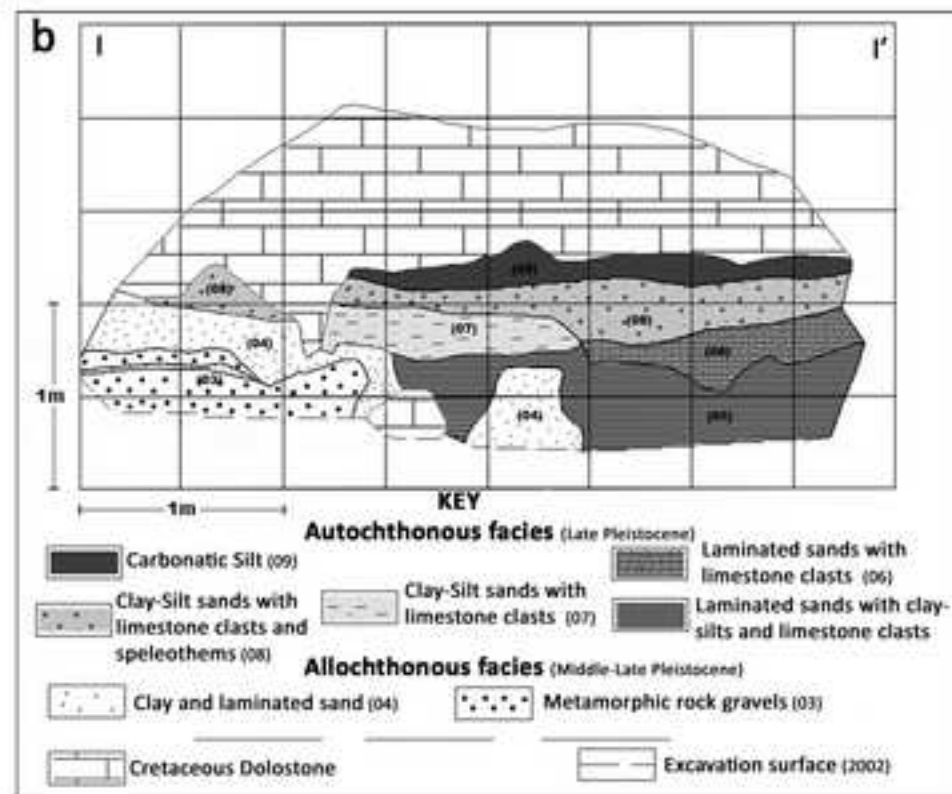
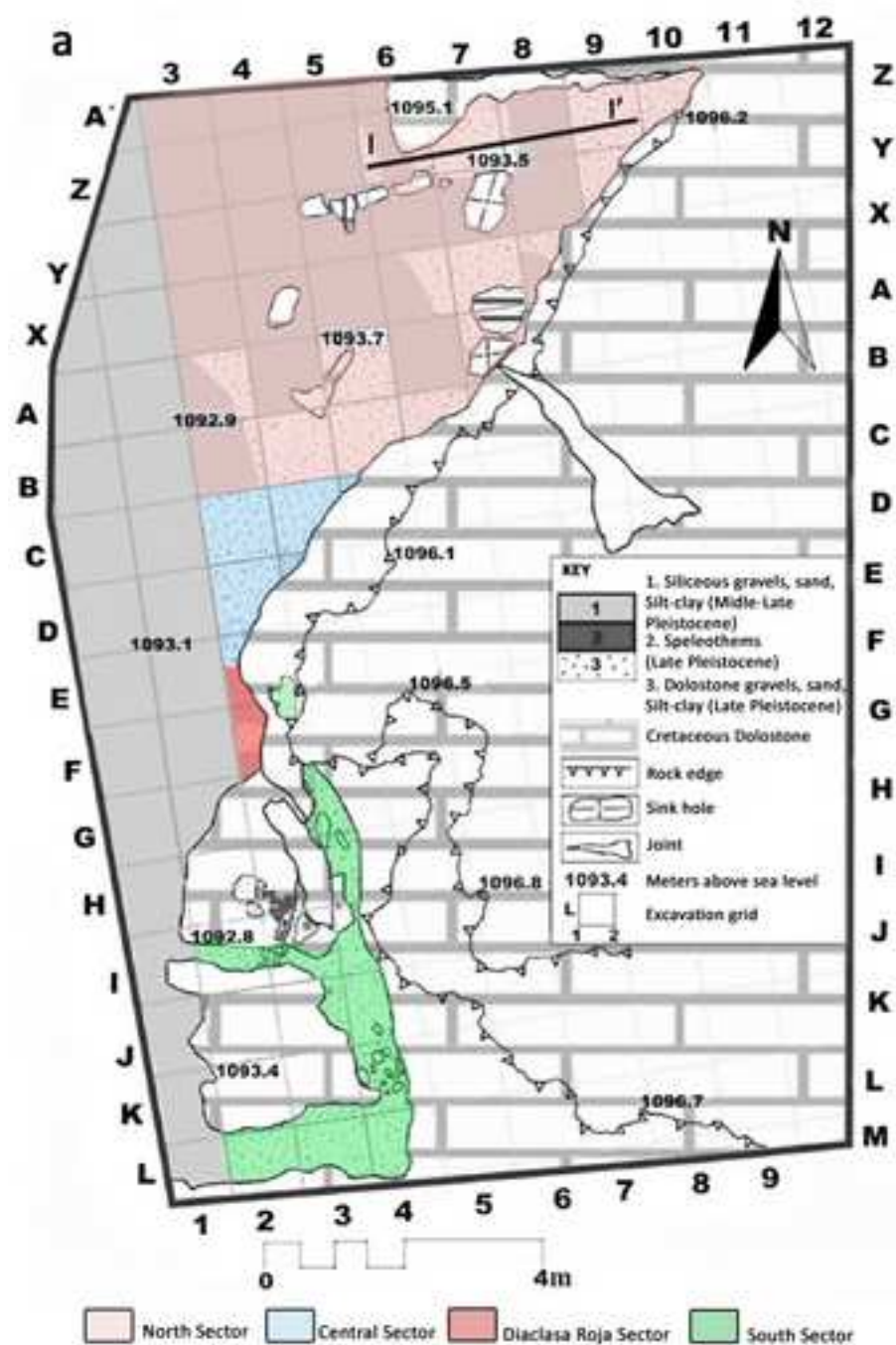


Figure 2



Figure 3

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Sample	Level	Material	Date (Kyr)
Mad-3287	3 (fluvial)	Quartz grain	140.4 ± 11.3
Mad-3738	5 (Square A6)	Sediment	90.9 ± 7.8
Mad-3743	8 (Square Y8)	Sediment	91.6 ± 8.1
Mad-3749	South sector (Square J3)	Sediment	74.5 ± 6.3





Fig 5

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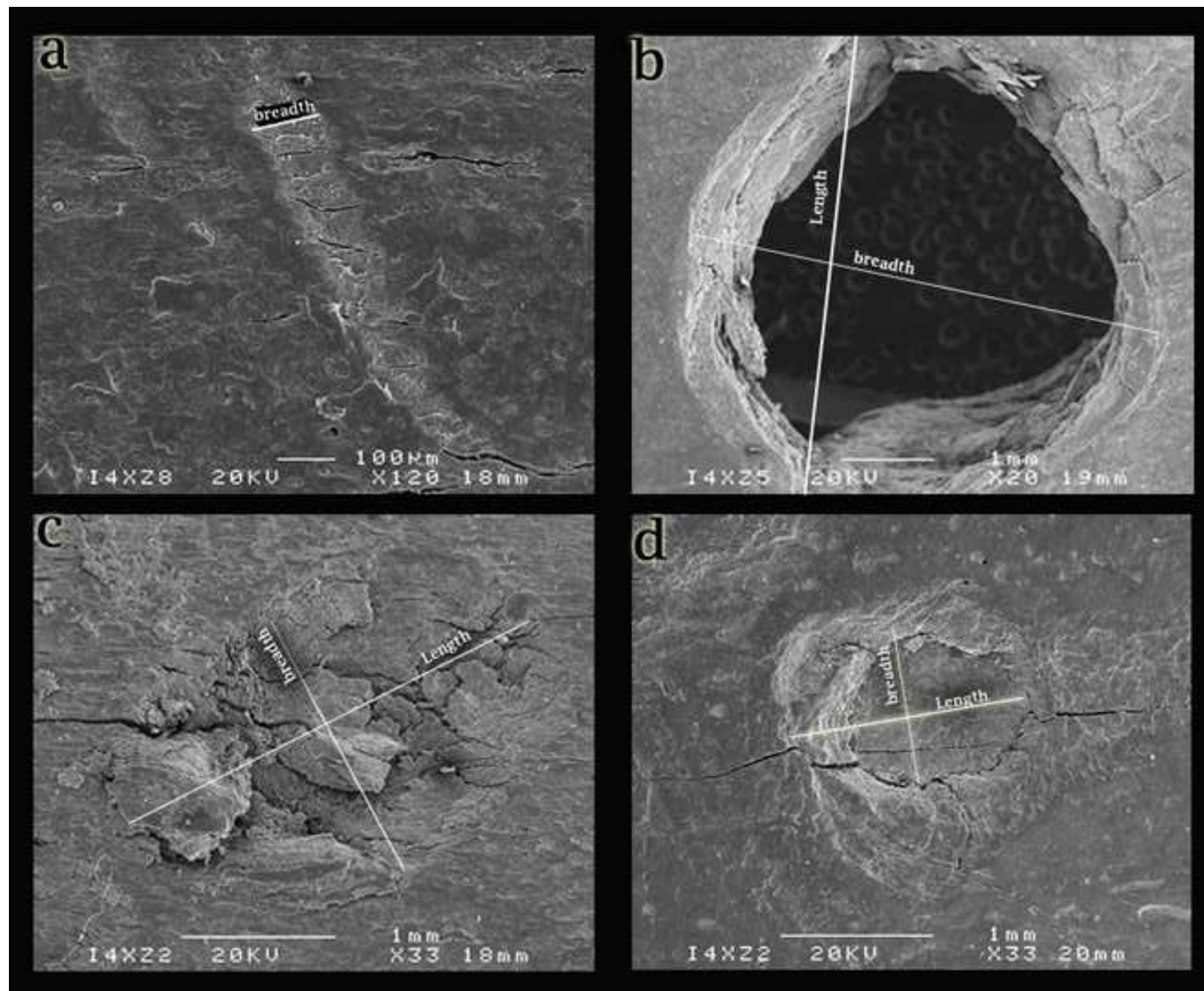




Figure 6

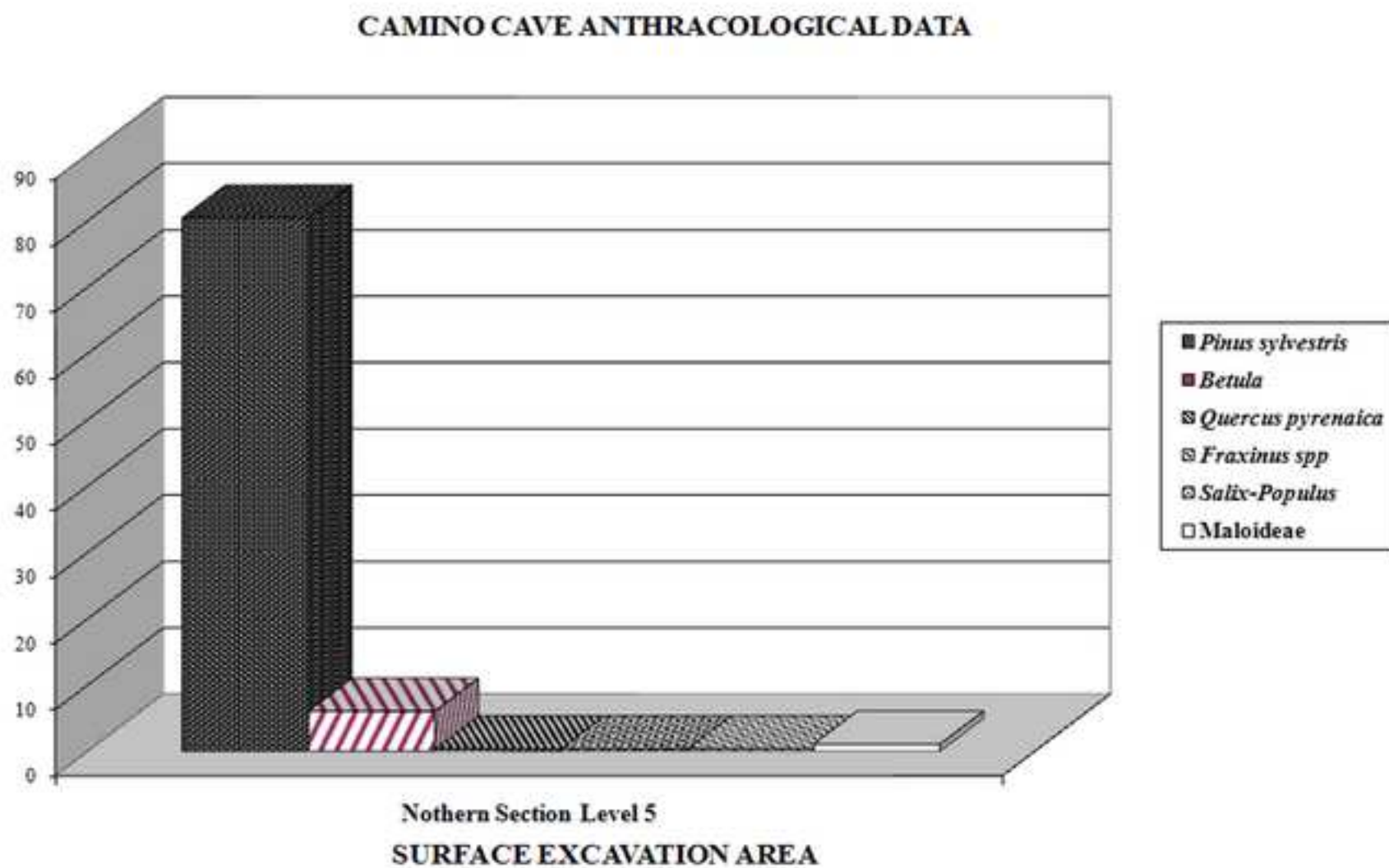
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Figure 8

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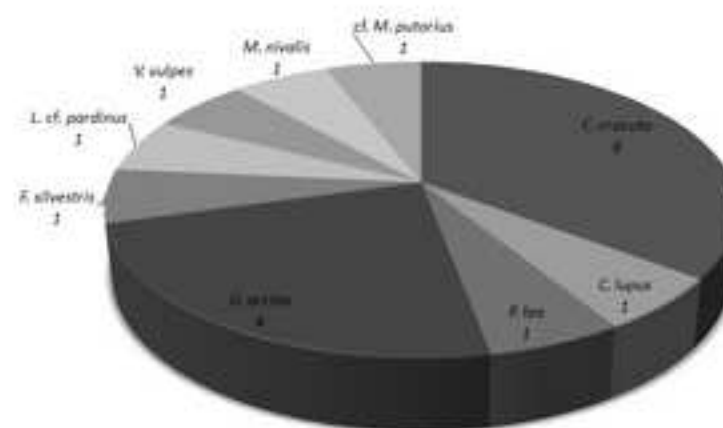
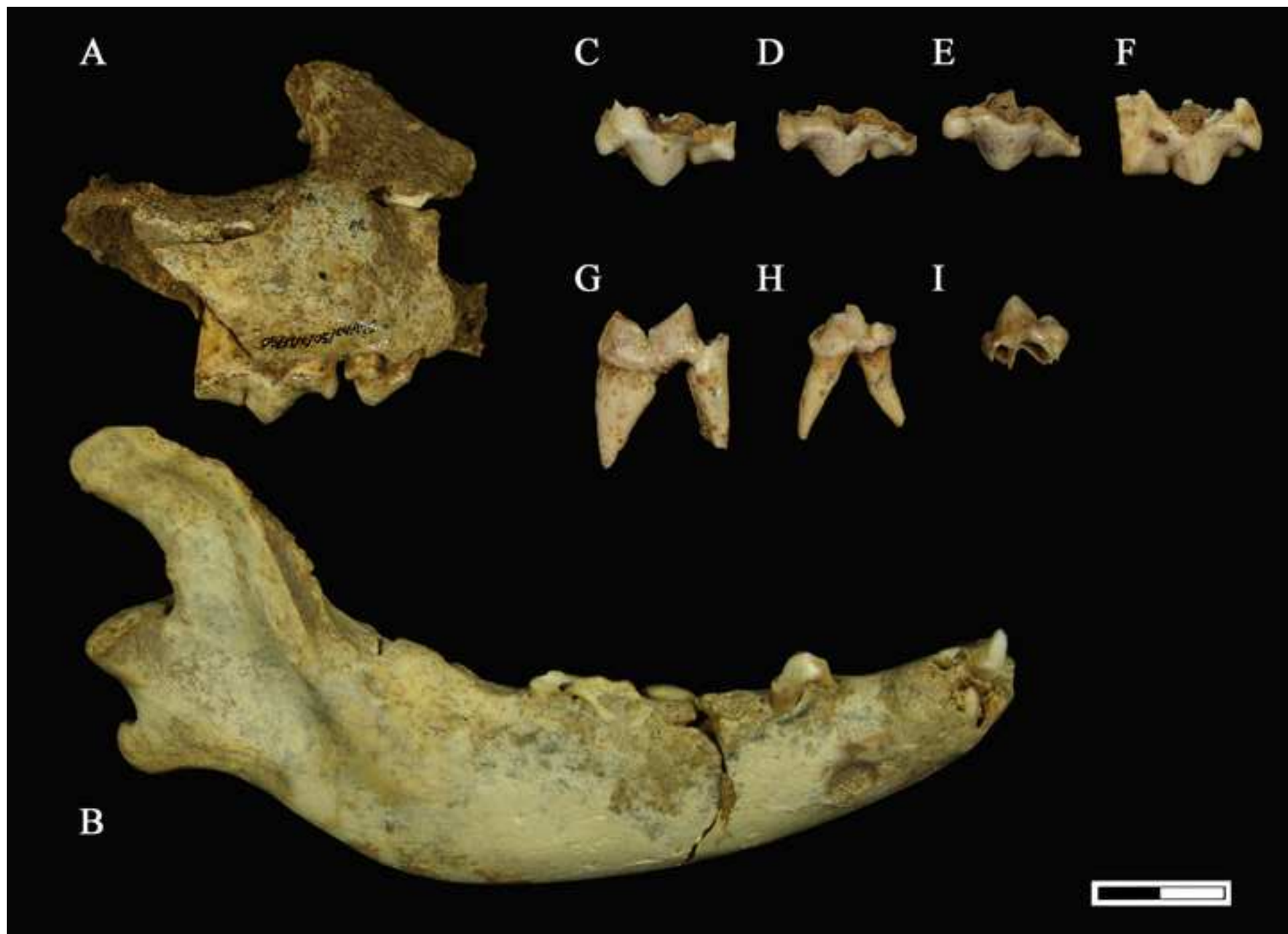


Figure 10

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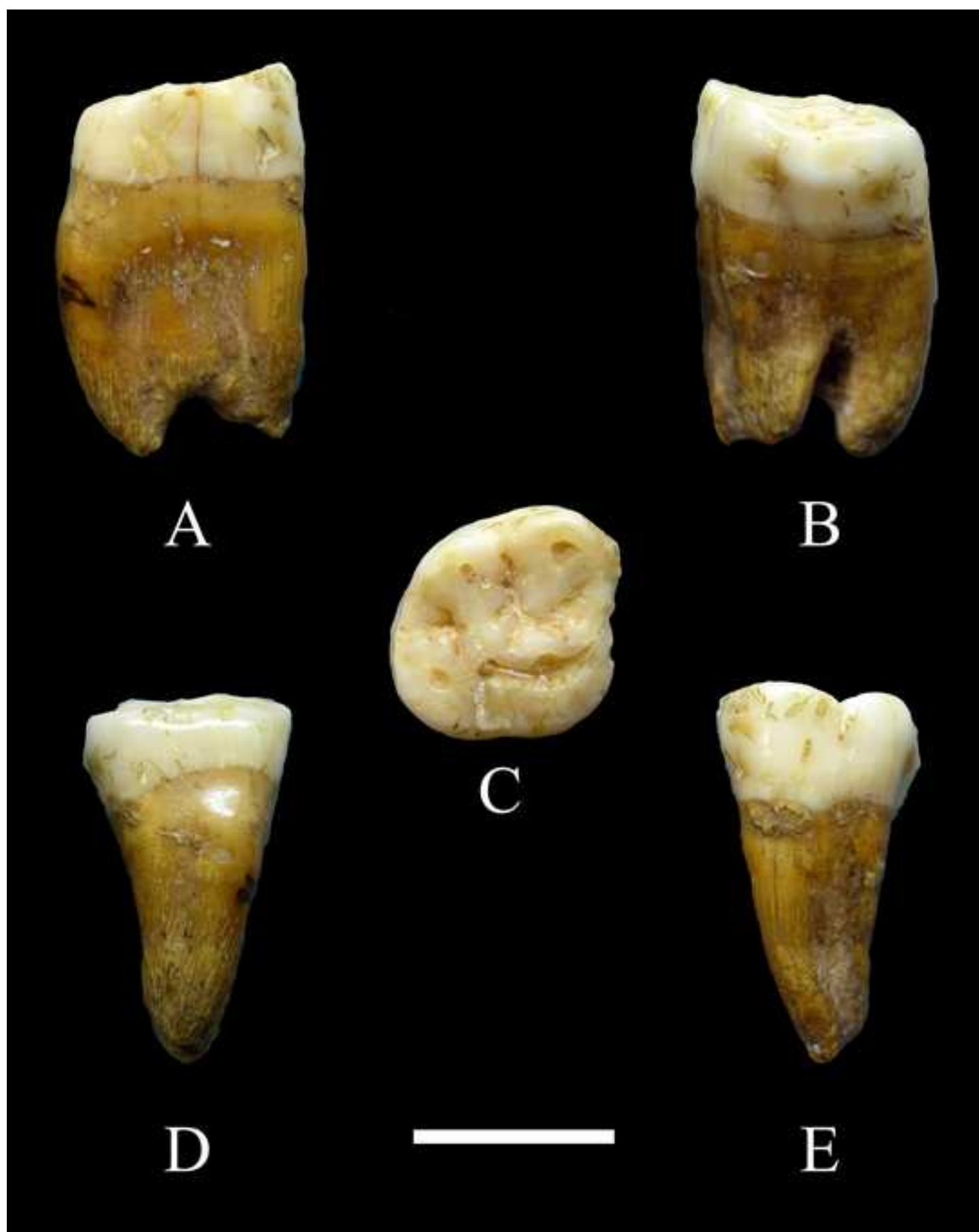


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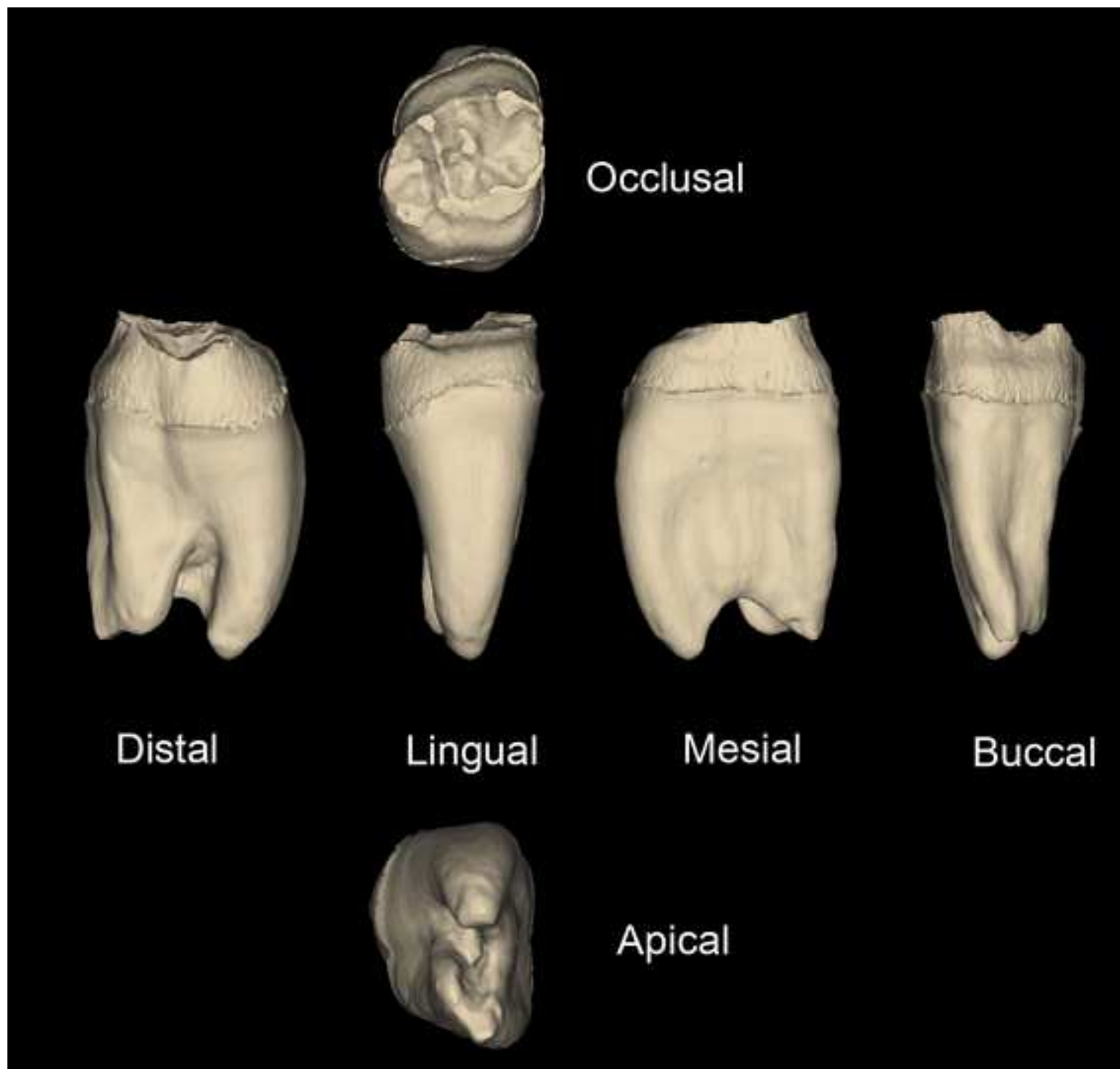
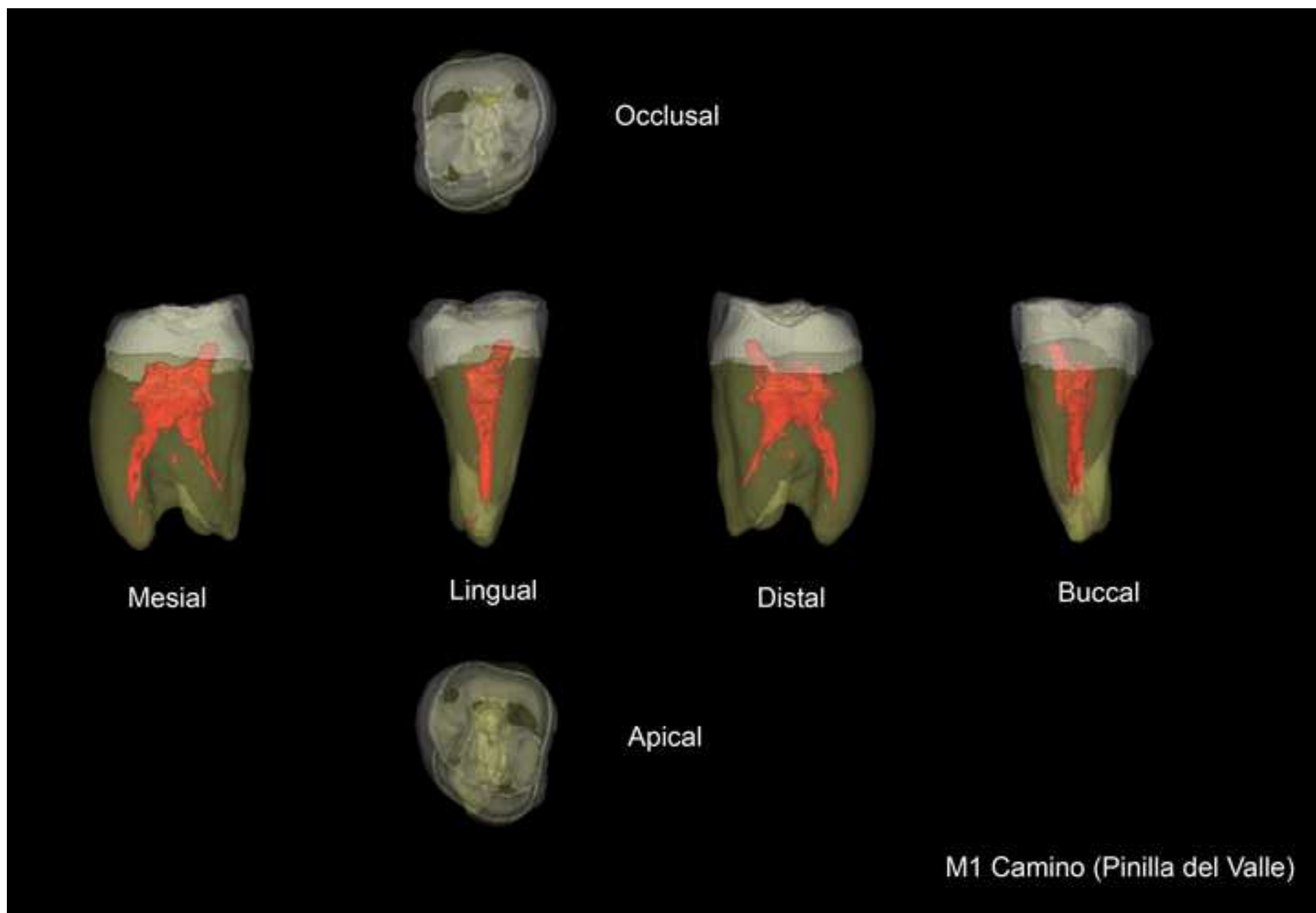




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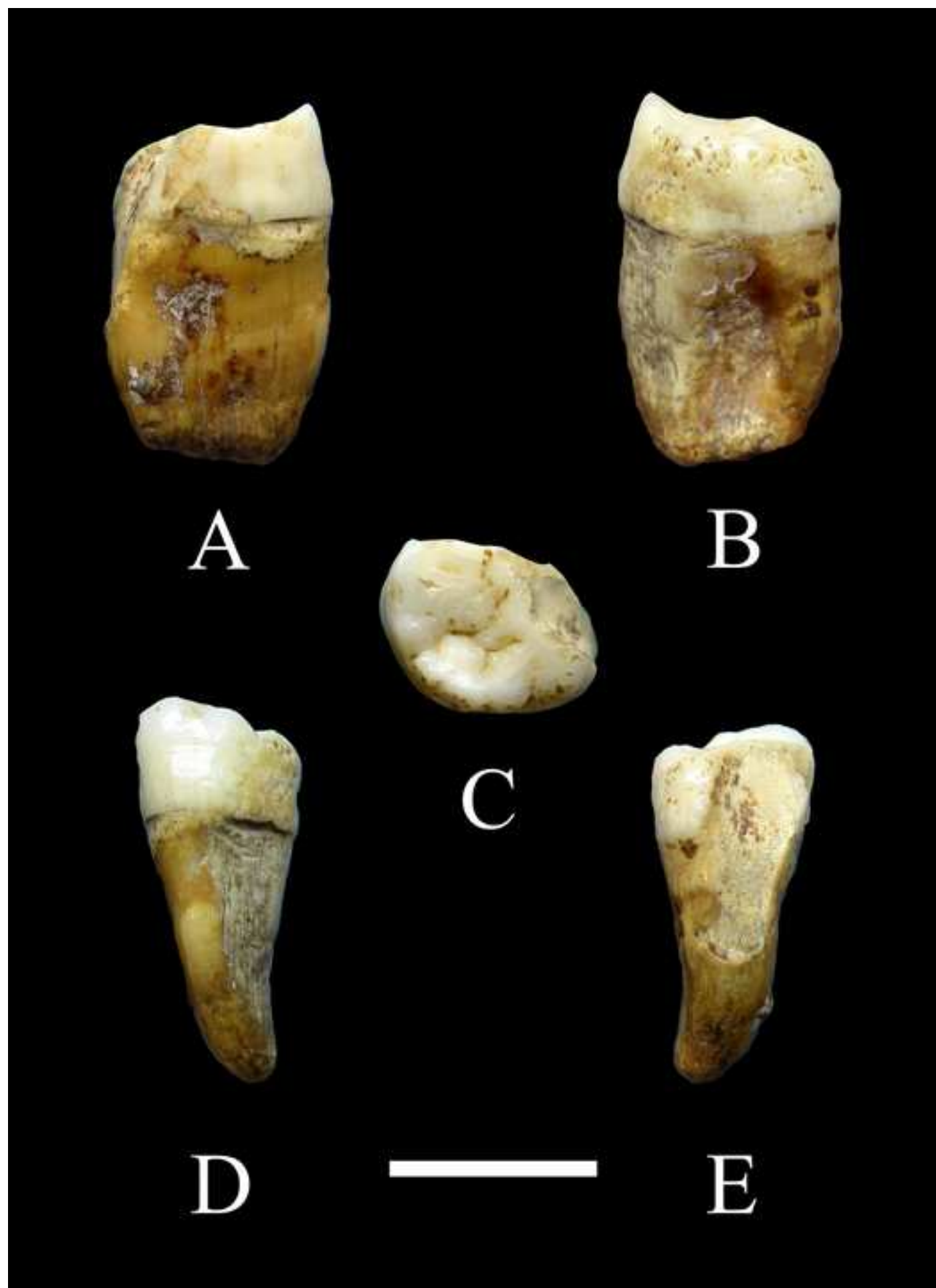


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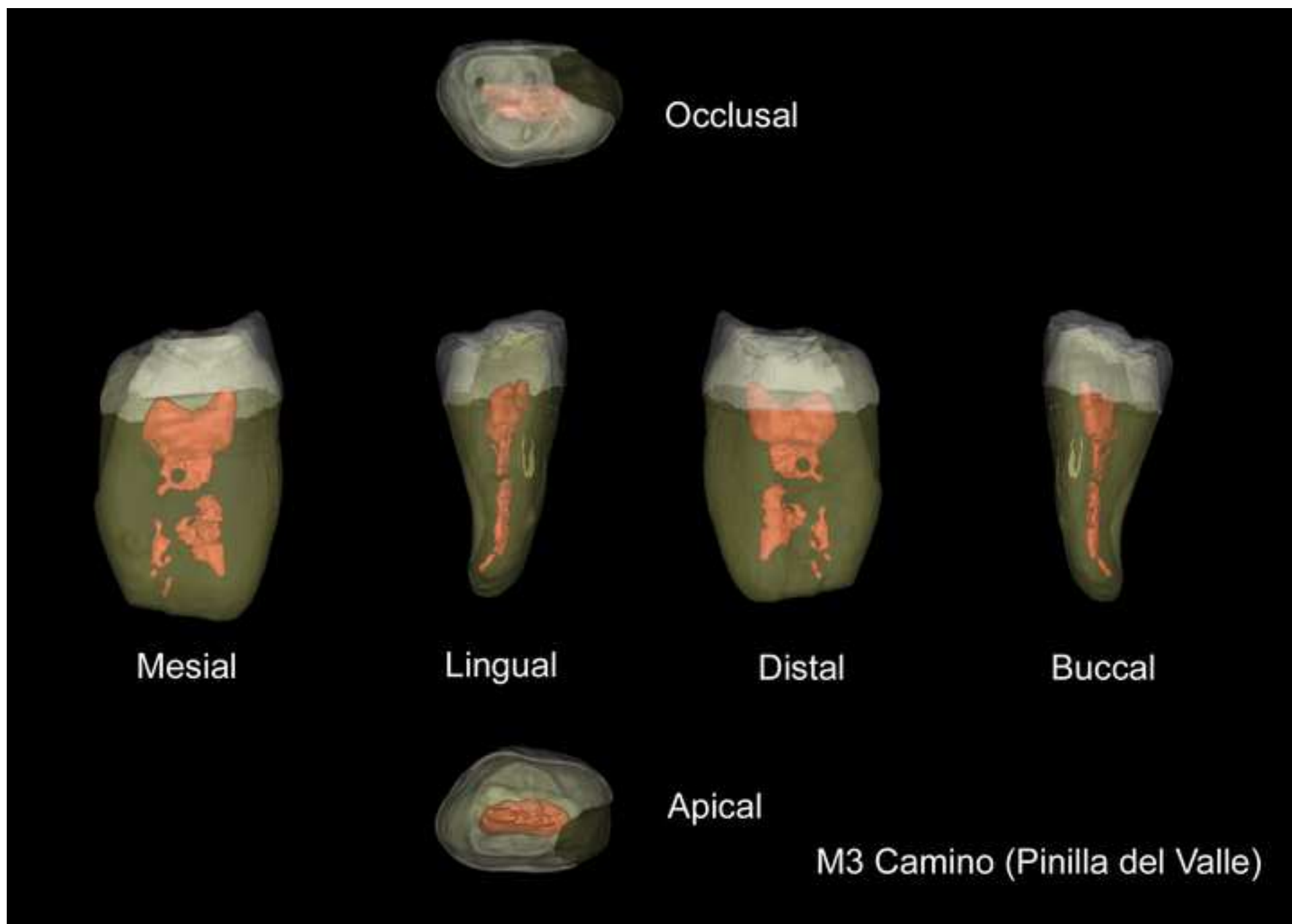


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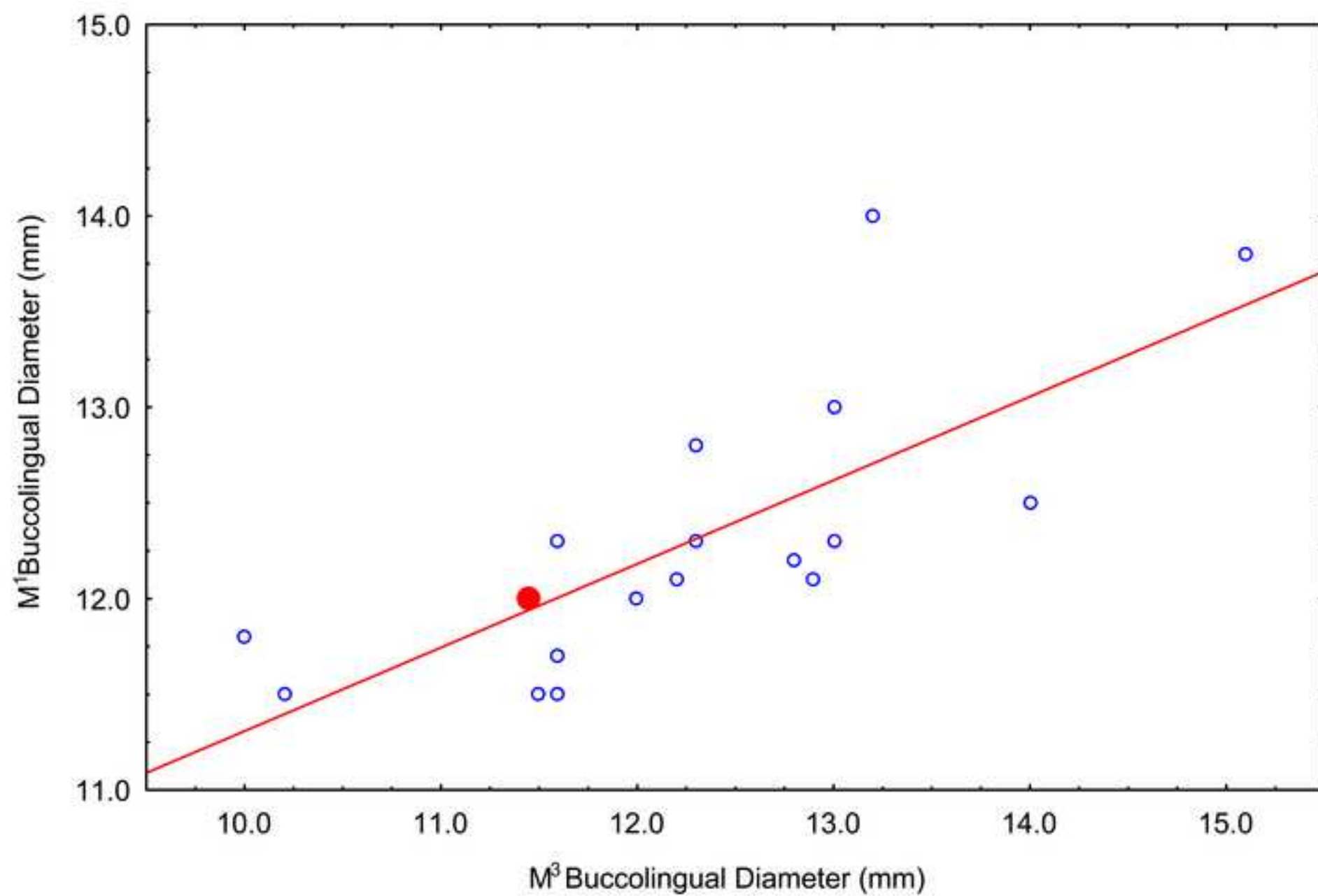


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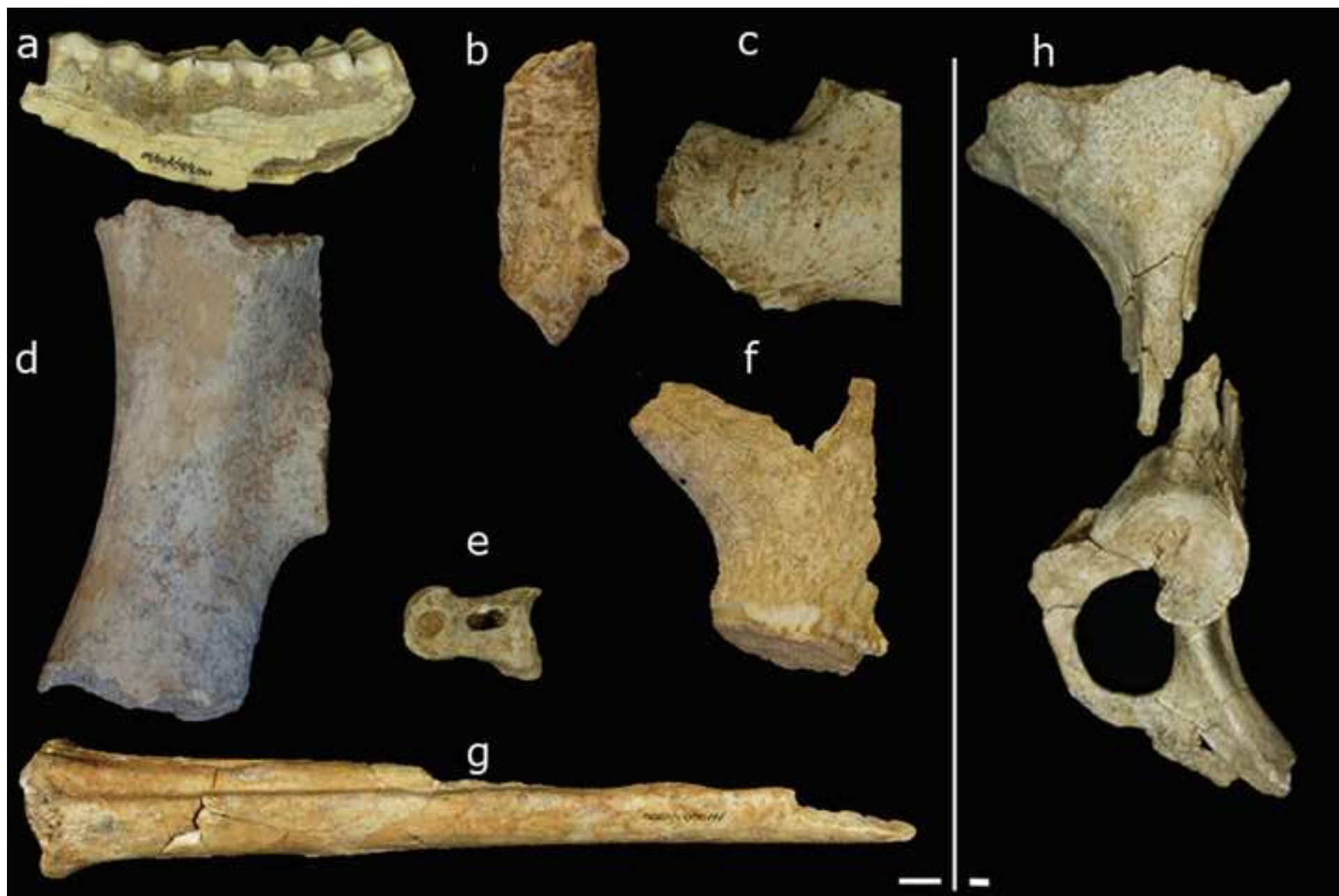




Figure 18

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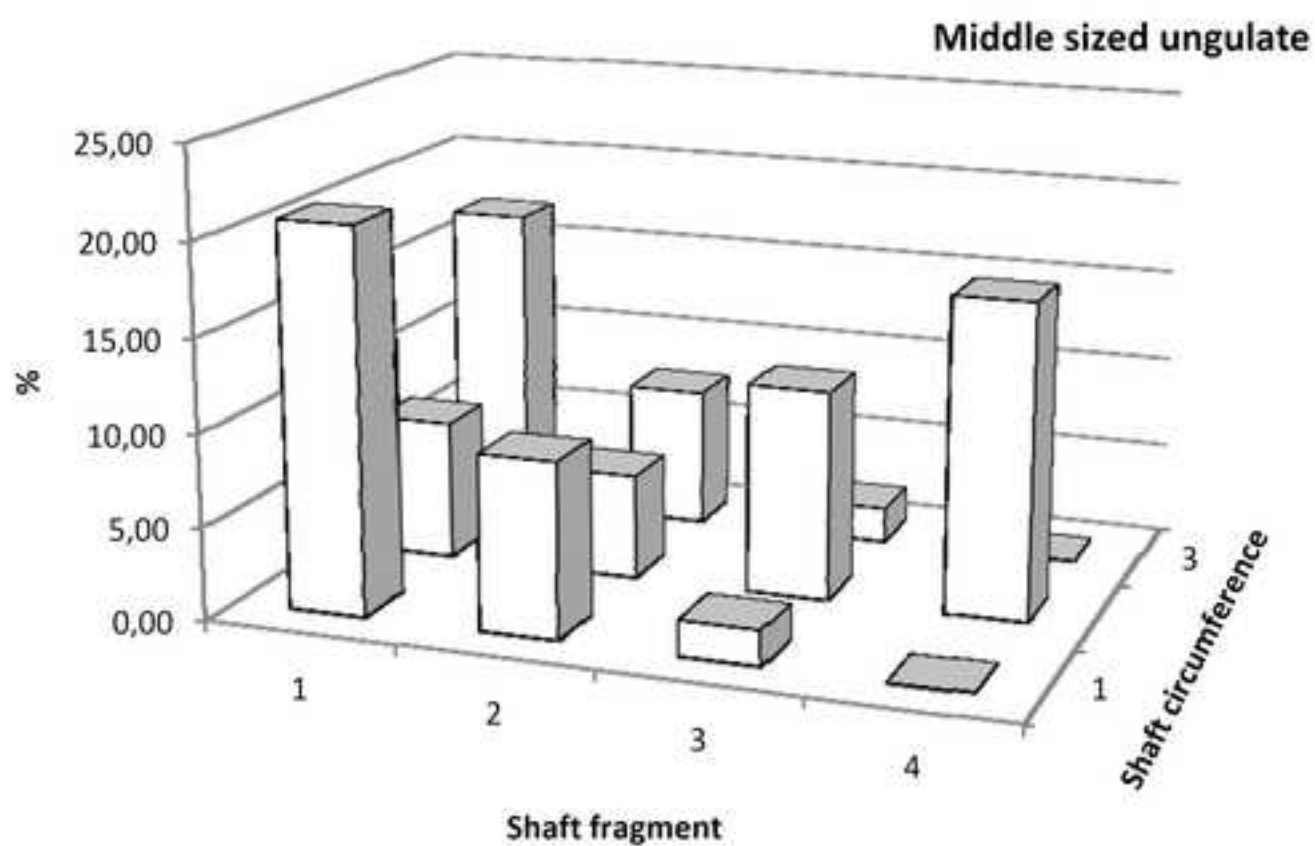
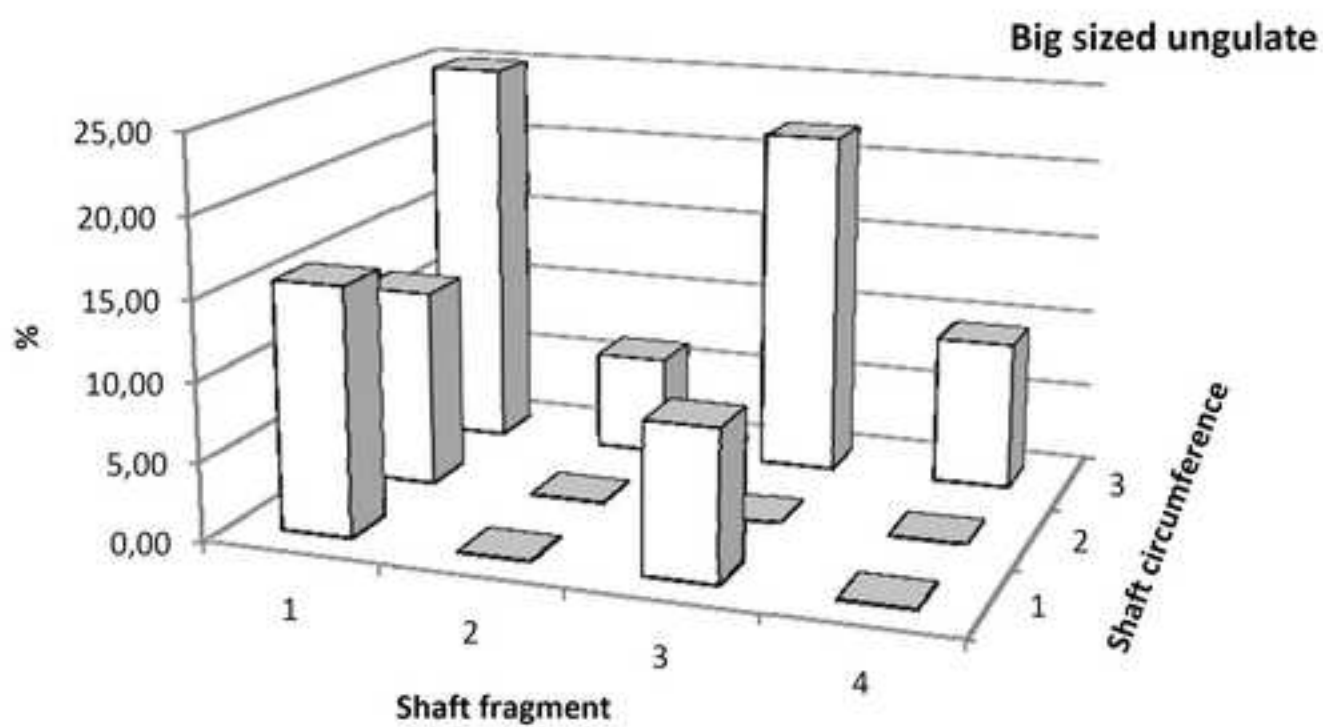


Figure 19

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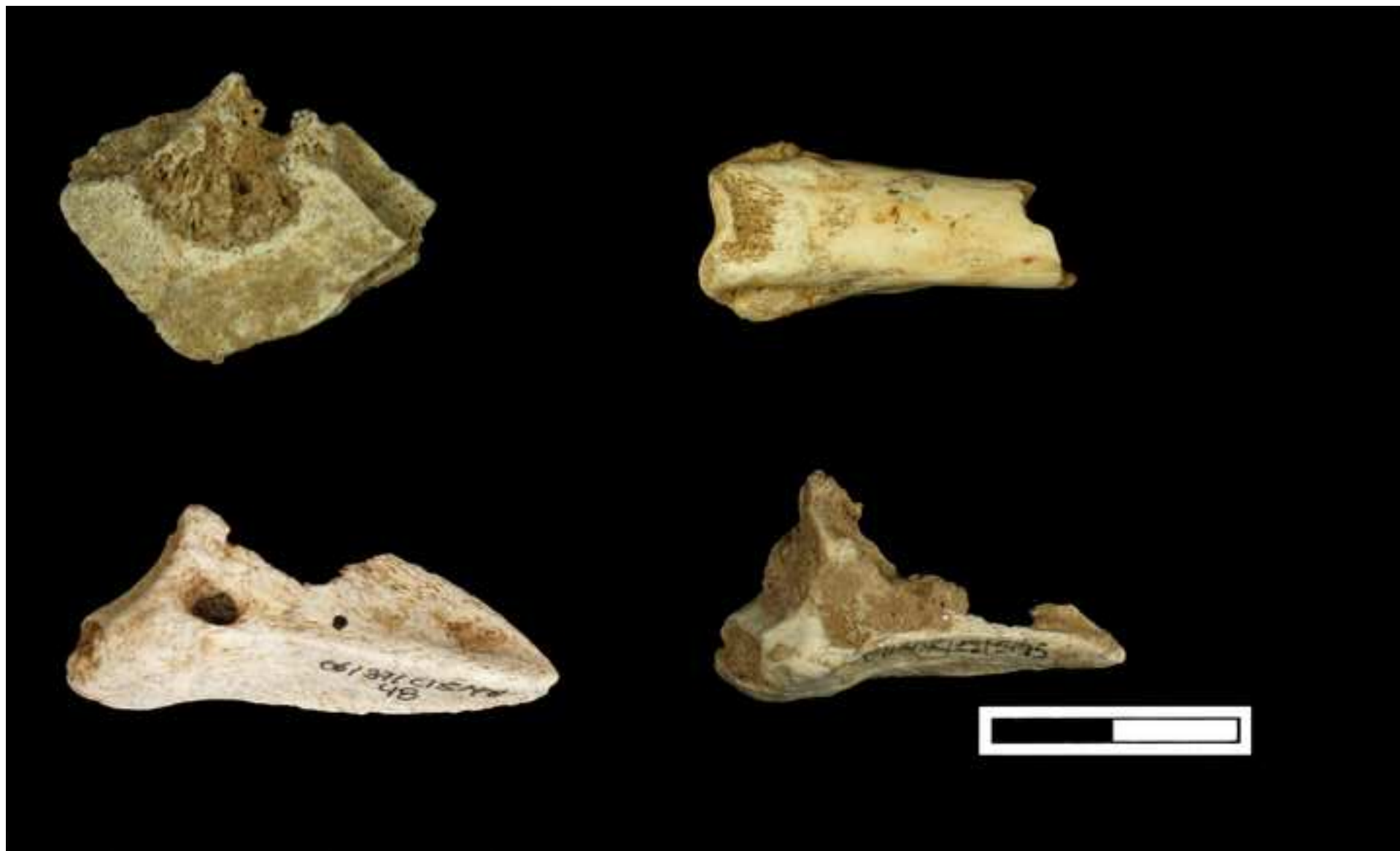




Figure 20

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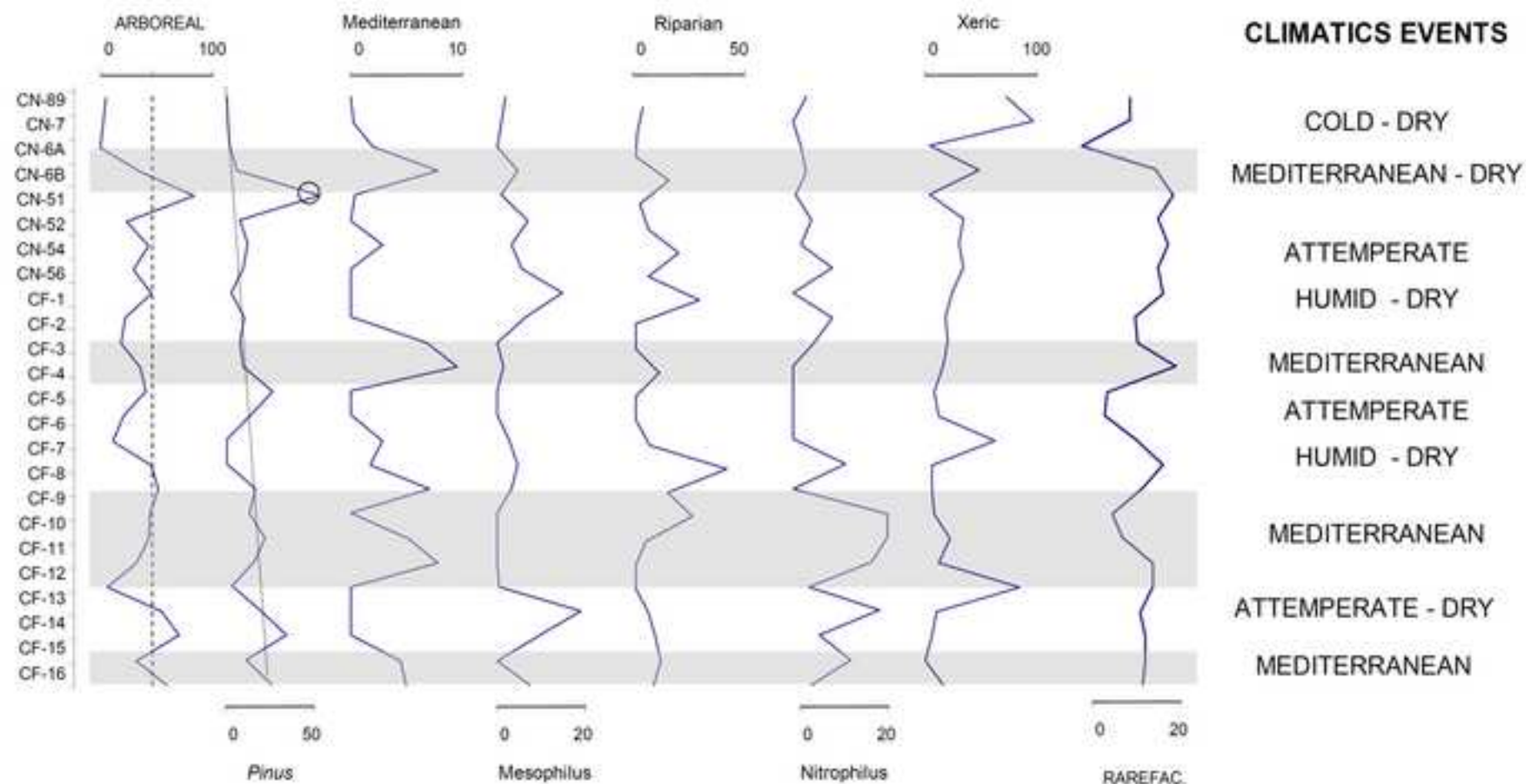


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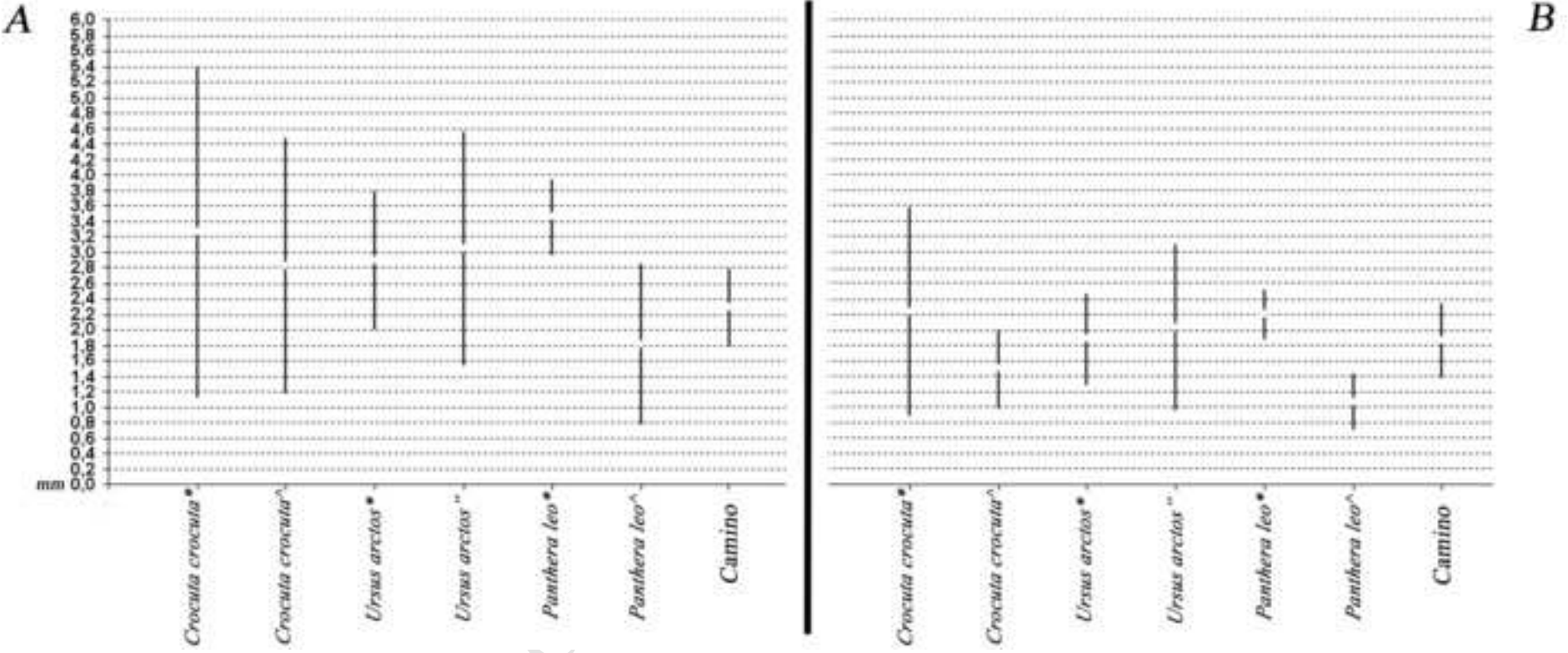


Table 1

SECTOR	North sector					Central & Diacasa Roja sector		South sector
LEVEL	4	5	6	7	8/9			
	N	N	%	N	N	N	%	N
<i>Pinus sylvestris</i>	5	226	80,42	8	2	12	35	56,45
<i>Betula</i> sp.	2	17	6,04			5	3	4,83
<i>Quercus pyrenaica</i>		1	0,35				11	17,74
<i>Fraxinus angustifolia</i>		1	0,35					26
<i>Salix-Populus</i>		1	0,35					
<i>Quercus ilex</i>								5
<i>Quercus</i> sp.								2
Maloideae		3	1,06				4	6,45
Indeterminables		32	11,38	1	2	2	9	14,51
<b>TOTAL</b>	7	281		9	2	19	62	47

Table 2

Alfárez <i>et al.</i> (1982)	Toni & Molero (1990)	This paper	
<u>Order Rodentia</u>			
<i>?Allocricetus bursae</i>	<i>Allocricetus bursae</i>	<i>Allocricetus bursae</i>	Extinct hamster
<i>Apodemus sylvaticus</i>	<i>Apodemus sylvaticus</i>	<i>Apodemus sylvaticus</i>	Wood mouse
<i>Arvicola</i> aff. <i>sapidus</i>	<i>Arvicola sapidus</i>	<i>Arvicola sapidus</i>	Southern water vole
		<i>Arvicola</i> cf. <i>terrestris</i>	Water vole
<i>Castor fiber</i>	<i>Castor fiber</i>	<i>Castor fiber</i>	European beaver
		<i>Chionomys nivalis</i>	Snow vole
<i>Eliomys quercinus</i>	<i>Eliomys quercinus</i>	<i>Eliomys quercinus</i>	Garden dormouse
	<i>Hystrix</i> sp.	<i>Hystrix</i> cf. <i>brachyura</i>	Malayan porcupine
<i>Microtus arvalis-agrestis</i>	<i>Microtus agrestis</i>	<i>Microtus agrestis</i>	Field vole
<i>Microtus arvalis-agrestis</i>	<i>Microtus arvalis</i>	<i>Microtus arvalis</i>	Common vole
<i>Microtus brecciensis</i>	<i>Microtus brecciensis</i>	<i>Microtus cabreræ</i>	Cabrera's vole
<i>Pitimys</i> cf. <i>savii</i> group	<i>Pitimys</i> cf. <i>duodecimcost.</i>	<i>Microtus</i> gr. <i>duodecimcost.</i>	Mediterranean pine vole
	<i>Microtus</i> cf. <i>malei</i>	<i>Microtus</i> aff. <i>malei</i>	Male's vole
		<i>Microtus</i> cf. <i>vaufreyi</i>	Vaufrey's vole
<i>Clethrionom. cf. glareolus</i>	<i>Clethrionomys glareolus</i>	<i>Myodes</i> cf. <i>glareolus</i>	Bank vole
	<i>Pliomys lenki</i>	<i>Pliomys coronensis</i>	Brasov's vole
	<i>Sciurus vulgaris</i>	<i>Sciurus vulgaris</i>	Red squirrel
<u>Order Lagomorpha</u>			
<i>Lepus</i> sp.		<i>Lepus</i> sp.	Hare
<i>Oryctolagus</i> sp.		<i>Oryctolagus cuniculus</i>	Rabbit
<u>Order Erinaceomorpha</u>			

<i>Erinaceus</i> sp.	<i>Erinaceus europaeus</i>	Western hedgehog
	<i>Erinaceus</i> sp.	Hedgehog
<hr/>		
Order Soricomorpha		
<i>Crocidura</i> cf. <i>russula</i>	<i>Crocidura russula</i>	Greater white-toothed shrew
<i>Sorex araneus</i>	<i>Sorex</i> gr. <i>araneus</i>	Common shrew
	<i>Sorex minutus</i>	Pygmy shrew
	<i>Galemys pyrenaicus</i>	Pyrenean desman
	<i>Neomys fodiens/anomalus</i>	Water shrew
<i>Talpa</i> cf. <i>caeca</i>	<i>Talpa europaea</i>	Common mole
	<i>Talpa occidentalis</i>	Iberian mole
<hr/>		
Order Chiroptera		
Chiroptera indet.	<i>Rhinol. ferrumequinum</i>	Greater horseshoe bat
	<i>Rhinolophus hipposideros</i>	Lesser horseshoe bat
	<i>Myotis myotis/oxygnathus</i>	Mouse-eared bat
	<i>Myotis nattereri</i>	Natterer's bat
	<i>Plecotus auritus/austriacus</i>	Long-eared bat
<hr/>		
Order Anura		
Discoglossidae indet.	<i>Alytes</i> cf. <i>obstetricans</i>	Common midwife toad
	<i>Pelobates cultripes</i>	Western spadefoot
<i>Bufo bufo</i>	<i>Bufo bufo</i>	Common European toad
<i>Bufo calamita</i>	<i>Bufo calamita</i>	Natterjack toad
	<i>Hyla meridionalis</i>	Stripeless treefrog
	<i>Rana</i> cf. <i>iberica</i>	Iberian frog
	<i>Pelophylax perezi</i>	Southern marsh frog

## Order Chelonia

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*Testudo* sp.

Emydidae indet.

*Testudo hermanni*

Hermann's tortoise

## Order Squamata

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*Lacerta* sp.*Timon lepidus*

Ocellated lizard

Lacertidae indet.

"Small-sized lizards"

*Anguis fragilis*

Slow worm

## Order Serpentes

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Colubridae indet.*Natrix maura*

Viperine snake

*Natrix natrix*

Grass snake

*Coronella* cf. *austriaca*

Smooth snake

*Coronella* cf. *girondica*

Southern smooth snake

*Malpolon monspessulanus*

Montpellier snake

*Rhinechis scalaris*

Ladder snake

*Vipera latasti*Lataste's viper

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Specimen/Sample	Tooth	MD (mm)	BL (mm)	Measured Crown	Source
		Mean $\pm$ s.d. (n) (range)	Mean $\pm$ s.d. (n) (range)	Area (mm <sup>2</sup> ) Mean $\pm$ s.d. (n)	
Pinilla del Valle	M <sup>1</sup>	12,0	12,0	111,1	Present study
Neandertals		11.1 $\pm$ 0.8 (22)	11.9 $\pm$ 0.4 (22)	112.3 $\pm$ 16.6 (21)	Bermudez de Castro (1993); Quam et al. (2009)
UP <i>H. sapiens</i>		10.7 $\pm$ 0.8 (24)	12.3 $\pm$ 0.7 (24)	99.6 $\pm$ 10.2 (15)	Fruyer (1977); Quam et al. (2009)
Contemporary <i>H. sapiens</i>		9.7 $\pm$ 0.9 (57)	10.8 $\pm$ 1.1 (64)	96.6 $\pm$ 14.0 (59)	Manzi et al. (1997); Quam et al. (2009)
Pinilla del Valle	M <sup>3</sup>	8,4	11,5		Present study
Neandertals		9.6 $\pm$ 0.7 (16)	12.0 $\pm$ 1.0 (16)		Bermudez de Castro (1993)
UP <i>H. sapiens</i>		9.5 $\pm$ 1.0 (12)	11.1 $\pm$ 1.2 (14)		Fruyer (1977)
Contemporary <i>H. sapiens</i>		8.2 $\pm$ 0.9 (49)	10.3 $\pm$ 1.4 (49)		Manzi et al. (1997)

Table 4

Specimen/Sample <sup>1</sup>	Relative Occlusal Polygon Mean ± s.d.(n) (range)	Relative Protocone Area Mean ± s.d.(n) (range)	Relative Paracone Area Mean ± s.d.(n) (range)	Relative Metacone Area Mean ± s.d.(n) (range)	Relative Hypocone Area Mean ± s.d.(n) (range)	Angle A (deg.) Mean ± s.d.(n) (range)	Angle B (deg.) Mean ± s.d.(n) (range)	Angle C (deg.) Mean ± s.d.(n) (range)	Angle D (deg.) Mean ± s.d.(n) (range)
Pinilla del Valle	25,3 26.7 ± 1.8 (17)	34,6 29.7 ± 2.4 (18)	27,1 25.4 ± 2.1 (18)	17,1 21.0 ± 1.5 (18)	21,2 23.8 ± 2.2 (18)	102,8 106.1 ± 5.2 (17) (98.5-115.7)	68,1 66.7 ± 6.7 (17)	118,7 118.0 ± 10.0 (17)	71,1 69.0 ± 6.1 (17)
Neandertals	(23.2-30.5)	31.8 ± 1.7 (12)	25.8 ± 2.7 (12)	23.0 ± 1.6 (18)	19.5 ± 3.1 (12)		(53.9-76.8)	(98.0-137.5)	(53.3-80.8)
Upper Paleolithic <i>H. sapiens</i>	32.7 ± 1.9 (5) (28.6-33.5)					106.3 ± 4.4 (5) (100.8-110.6)	71.1 ± 2.7 (5) (67.6-73.3)	110.3 ± 4.9 (5) (100.3-112.9)	73.3 ± 4.8 (5) (68.8-80.8)
Contemporary <i>H. sapiens</i>	37.5 ± 5.4 (24) (27.0-50.4)	30.1 ± 2.0 (59)	25.8 ± 2.1 (59)	22.9 ± 1.8 (59)	20.5 ± 2.5 (59)	101.4 ± 10.1 (24) (80.3-128.3)	74.3 ± 4.0 (24) (62.9-79.0)	106.2 ± 5.5 (24) (95.5-115.7)	78.6 ± 7.7 (24) (59.0-90.2)

<sup>1</sup>Comparative data from Bailey et al. (2008)

Relative occlusal polygon area = Absolute occlusal polygon area/MCA

Relative cusp areas = Absolute cusp areas/MCA

Table 5

ACCEPTED MANUSCRIPT

Central Sector			Big-sized Ungulate			
	Long bones			Flat bones		Articular bones
	PE	DPH	DE	Cortical	Cancellous	Dense cortical
Pits	5,13	53,85	2,56	40,00	20,00	45,45
Scores	10,26	48,72	10,26	40,00	20,00	27,27
Punctures	0,00	2,56	0,00	0,00	0,00	9,09
Furrowing	5,13	5,13	2,56	0,00	50,00	36,36
Middle-sized Ungulate						
	Long bones			Flat bones		Articular bones
	PE	DPH	DE	Cortical	Cancellous	Dense cortical
Pits	0,00	52,00	2,00	0,00	0,00	27,27
Scores	2,00	36,00	2,00	33,33	0,00	36,36
Punctures	0,00	0,00	0,00	11,11	0,00	0,00
Furrowing	0,00	4,00	2,00	0,00	0,00	27,27
North Sector (Level 5)			Big-sized Ungulate			
	Long bones			Flat bones		Articular bones
	PE	DPH	DE	Cortical	Cancellous	Dense cortical
Pits	3,03	24,24	3,03	54,55	18,18	19,05
Scores	9,09	39,39	3,03	36,36	18,18	9,52
Punctures	3,03	6,06	0,00	9,09	0,00	0,00
Furrowing	9,09	15,15	3,03	9,09	9,09	4,76
Middle-sized Ungulate						
	Long bones			Flat bones		Articular bones
	PE	DPH	DE	Cortical	Cancellous	Dense cortical
Pits	1,20	37,95	4,82	28,85	3,85	4,88
Scores	0,60	32,53	3,01	26,92	1,92	19,51
Punctures	1,20	3,01	1,20	9,62	1,92	9,76
Furrowing	0,00	4,82	0,60	7,69	1,92	2,44

Table 6

## ACCEPTED MANUSCRIPT

		<i>n</i>	<i>Mean</i>	<i>Min</i>	<i>Max</i>	<i>St. Dev.</i>	<i>IC -95%</i>	<i>IC + 95%</i>	<i>CV</i>
PITS	Length	14	2,29	1,61	3,21	0,49	2,01	2,58	21,55
	Width	14	1,86	1,13	2,85	0,47	1,60	2,13	24,95
PUNCTURES	Length	11	3,36	2,00	4,50	0,94	2,73	3,99	27,94
	Width	7	2,77	1,72	4,32	0,96	1,88	3,66	34,72
SCORES	Width	12	1,75	0,93	3,35	0,78	1,25	2,24	44,39

		Big-sized Ungulates	Middle-sized Ungulates
<b>Fracture outline</b>	Longitudinal	7,14	6,00
	Transversal	9,52	6,67
	Curved	83,33	87,33
<b>Fracture angle</b>	Oblique	64,71	78,57
	Right	11,76	16,07
	Mixed	23,53	5,36
<b>Edges</b>	Smooth	46,15	60,94
	Jagged	35,90	15,63
	Crenulated	17,95	23,44
<b>Shaft circumference*</b>	< 1/2	22,58	32,69
	> 1/2	12,90	25,00
	Complete	64,52	42,31
<b>Shaft fragment*</b>	<1/4	54,84	46,15
	1/4-1/2	6,45	30,77
	1/2-3/4	29,03	21,15
	>3/4	9,68	1,92

\* Long bones only

Table 8

ACCEPTED MANUSCRIPT

SECTOR		North Sector							Central
LEVEL	3	3 - 4	4	5	7	8	8-9		5
NR	11	32	6	52	1	1	1		1