

Small-mammals from the Middle Pleistocene layers of the Sima del Elefante (Sierra de Atapuerca, Burgos, northwestern Spain)

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ABSTRACT

The Sima del Elefante site, located in the Sierra de Atapuerca (Burgos, Spain), is an important Pleistocene archaeological locality that has been excavated every year since 1996. At least two main infill phases have been identified: a first (TELURU) early Pleistocene phase that has provided a rich faunal assemblage, various stone tools and the earliest human remains from western Europe; and a second phase (TEURU) attributed to the Middle Pleistocene. In this paper, for the first time we present a description of the TEURU small-mammal assemblage and its subsequent biochronological, palaeoenvironmental and palaeoclimatic implications. The small-mammal assemblage is highly diverse and comprises at least 17 species: 3 insectivores (cf. *Erinaceus* sp., *Crocidura* sp. and *Sorex* sp.); 4 chiropters (*Rhinolophus ferrumequinum*, *Rhinolophus* gr. *euryale-mehelyi*, *Myotis* gr. *myotis-oxygnathus* and *Miniopterus schreibersii*); 9 rodents (*Myodes glareolus*, *Microtus arvalis*, *Microtus agrestis*, *Iberomys brecciansis*, *Terricola* cf. *atapuerquensis*, *Arvicola* sp., *Apodemus sylvaticus*, *Eliomys quercinus* and *Allocricetus bursae*) and 1 lagomorph (*Oryctolagus* sp.). Such an association suggests a late Middle Pleistocene age (ca. 250-350 ka), a patchy landscape dominated by humid meadows and woodland areas, and mild climatic conditions. These results are compared with other proxies, such as the herpetofauna, malacofauna, large-mammals and charcoals, providing a new scenario for the climatic and environmental conditions that prevailed during the latest Middle Pleistocene in the Sierra de Atapuerca.

KEYWORDS | Small-mammals. Biochronology. Palaeoenvironment. Palaeoclimate. Middle Pleistocene. Spain.

INTRODUCTION

The palaeoanthropological sites of Atapuerca, located near the city of Burgos in northern Spain

(Fig. 1A), contain one of the most extraordinary accumulations of Pleistocene fossil humans and related stone artefacts (e.g., Arsuaga et al., 1993; Carbonell et al., 1995; Bermúdez de Castro et al,

1997). In particular, the infilled karstic cave site, the Sima del Elefante (TE) Lower Red Unit (TELRU), has yielded the oldest direct evidence of hominins in Western Europe, dating from 1.5 to 1.3 Ma (Carbonell et al., 2008). In the Gran Dolina (TD) cave, more than a hundred hominin remains have so far been recovered from the Aurora stratum within lithostratigraphic unit TD6, around 1.5 m below the Brunhes–Matuyama geomagnetic boundary (Berger et al., 2008).

In this context, the Middle Pleistocene layers of Sima del Elefante provide important data to the knowledge of the continuous fossil record of the Sierra de Atapuerca. In this paper, for the first time we describe the small-mammal assemblage from these layers, previously only included as a list in Cuenca-Bescós and García (2007) and Cuenca-Bescós et al., (2010). Hence, the aim of this paper is to propose new biostratigraphical, environmental and climatic interpretations for the latest middle Pleistocene of the Sierra de Atapuerca.

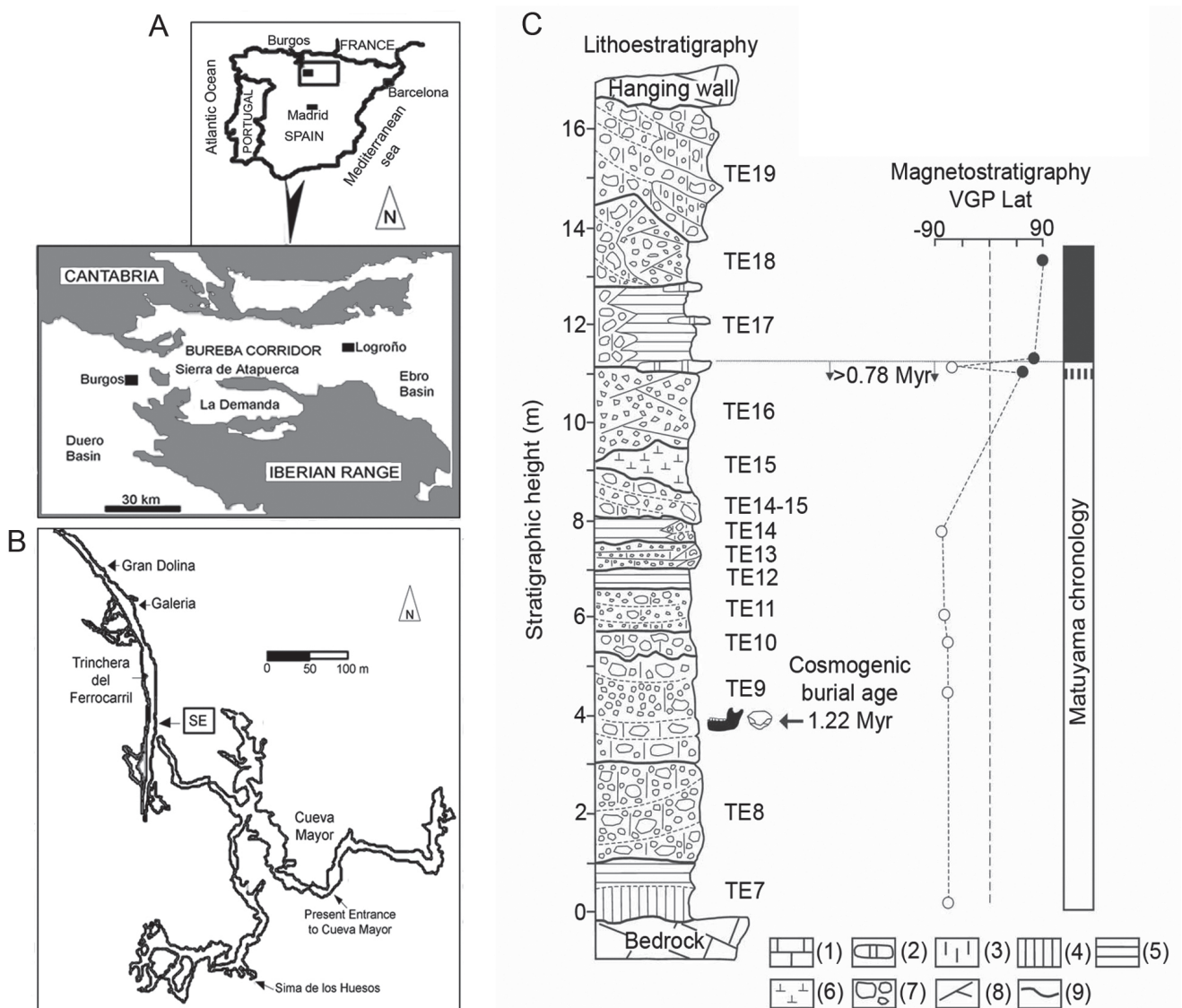


FIGURE 1 | A) Location of the Sierra de Atapuerca (Burgos, Spain). B) Location of the Trincheras del Ferrocarril (railway cutting) and Cueva Mayor karst systems of Atapuerca. SE: indicates the Sima del Elefante site (modified from Martín-Merino et al., 1981). C) Summary of the lithostratigraphy and chronology of the Sima del Elefante locality. The synthetic column on the left shows the different stratigraphic units visible at the central-north section, labelled TE. Symbols: 1) Mesozoic limestone; 2) speleothem; 3) lutite/clay; 4) bat guano; 5) clay and laminated sandy silts; 6) marls; 7) gravels and boulders; 8) cross-lamination; 9) main stratigraphic discontinuity. VGP Lat, latitude of the virtual geomagnetic pole. Cosmogenic burial ages are also shown, with the standard error given at the 68% confidence interval (modified from Carbonell et al., 2008).

GEOLOGICAL SETTING

The Atapuerca sites are part of a complex karst system known as the Sierra de Atapuerca. The Sierra de Atapuerca is a Mesozoic-core hill, connected to the Iberian Range. It is located 14 km east of Burgos (Fig. 1A). It constitutes a fossil relief barely emphasized in the middle of the Neogene sediments of the Bureba Corridor which connects the Ebro and Duero Basins (Mediterranean and Atlantic realms).

The Sierra de Atapuerca has two main cave systems (Fig. 1B). From east to west these are Cueva Mayor and Trincheras del Ferrocarril. The first comprises principally the sites of Sima de los Huesos and El Portalón de Cueva Mayor. The fossils of Sima de los Huesos represent one of the most important collections of fossil human remains from the Middle Pleistocene (Arsuaga et al., 1997). The El Portalón sequence includes the end of the Late Pleistocene and much of the Holocene (López-García, 2008). The second, Trincheras del Ferrocarril, is an ancient railway cutting that exposed several fossiliferous beds as well as fossil caves, including principally the sites of Gran Dolina, Galería-Zarpazos and Sima del Elefante (Fig. 1B). The sequences of Gran Dolina and Sima del Elefante have the oldest hominin record in Europe (Carbonell et al., 1995, 2008). The Galería-Zarpazos system has provided human remains from the Middle Pleistocene that allows these levels to be correlated with those of Sima de los Huesos (Arsuaga et al., 1997).

The Sima del Elefante (also called Trincheras Elefante = TE site) is a cavity 18m deep and up to 15m wide (Rosas et al., 2001, 2004, 2006; Carbonell et al., 2008), infilled with clastic deposits. The stratigraphic section is composed of 14 lithostratigraphic levels mostly made by debris flow deposits (Fig. 1C). These lithostratigraphic units are grouped into two sedimentary phases. The first phase (also called Trincheras Elefante Lower Red Unit = TELRU) comprises levels TE7 to TE14. The second phase (Trincheras Elefante Upper Red Unit = TEURU) comprises levels TE15 to TE19 (see Rosas et al., 2006). To date, from the TEURU sequence, only levels TE18 and TE19 have furnished any vertebrate and invertebrate fossil remains. These two levels (TE18 and TE19) are separated by a stratigraphic discontinuity, although the main composition of both layers is the same: gravels and boulders with cross-lamination (Fig. 1C).

The stratigraphic section of the TE site has been sampled for dating by palaeomagnetism, U-series and cosmogenic isotopes (^{26}Al and ^{10}Be) (Rosas et al., 2004, 2006; Carbonell et al., 2008). Palaeomagnetism reveals a geomagnetic reversal, interpreted as the Matuyama-Brunhes boundary (> 0.78 Ma), in the lowermost TE7 to TE16, whereas the uppermost TE17 to TE19 display normal

polarity magnetization (Parés et al., 2006) (Fig. 1C). For the moment, despite several attempts, no radiometric dating is available for levels TE18 and TE19, since the low uranium content in the sediments precludes this dating (Rosas et al., 2004, 2006).

The large-mammal association of TE18 and TE19, including species such as *Equus caballus*, *Stephanorhinus hemithoecus*, *Cervus elaphus*, *Dama dama*, *Ursus deningeri*, *Vulpes vulpes* and *Crocota crocuta* (van der Made, 2001; Rosas et al., 2006), is typical of the last third of the Middle Pleistocene (0.35–0.15 Ma) and consistent with the advanced technical features of the lithic industry.

MATERIAL AND METHODS

The fossil remains used in this study consist of disarticulated bone fragments collected by water screening during the 2001 to 2004 excavation campaigns at the TE site. Sediments from the excavation were recovered from a surface of approximately nine square meters along the two layers in accordance with the lithostratigraphy. All the sediment (approximately 2,000kg) was water-screened using superimposed 10, 5 and 0.5mm mesh screens, and bagged by layers. In subsequent years, the fossils were processed, sorted and classified in the Department of Palaeontology of the Universidad de Zaragoza (Spain) and the Institut de Paleoecologia Humana i Evolució Social (Tarragona, Spain). Taking into account the scarcity of the microfaunal remains in the level TE18 and that the sedimentary, paleontological and archaeological composition of TE18 and TE19 seems to be similar (van der Made, 2001; Rosas et al., 2006; Carbonell et al., 2008), we have discussed the two layers as a single package (TE18–19). The small-mammal assemblage of TE18–19 is rather poor, but highly diverse, and corresponds to a total of 92 bones (a minimum number of 52 individuals), representing at least 17 taxa (Table 1; Fig. 2). The fragments were identified following the general criteria given by Reumer (1984), Rümke (1985) and Niethammer and Krapp (1990) for insectivores, Brujin and Rumke (1974), Menu (1985) and Sevilla (1988) for chiropters, van der Meulen (1973), Pasquier (1974), Damms (1981), and Cuenca-Bescós et al., (1995) for rodents, and López-Martínez (1989) and De Marfà (2009) for lagomorphs.

The specific attribution of this material rests principally on the best diagnostic elements: mandibles and isolated teeth for shrews; isolated teeth for Erinaceidae; mandibles, maxilla, isolated teeth and humerus for bats; first lower molars for Arvicolinae; and isolated teeth for *Apodemus sylvaticus*, *Eliomys quercinus*, *Allocricetus bursae* and Leporidae.

TABLE 1 | Numbers of Identified Specimens (NISP), Minimum Number of Individuals (MNI) and the percentage of Minimum Number of Individuals (%) of the small-mammal species represented in the TE18-19 layers

	TE18-19		
	NISP	MNI	%
<i>Myodes glareolus</i>	1	1	1.92
<i>Microtus agrestis</i>	4	3	5.77
<i>Microtus arvalis</i>	4	4	7.69
<i>Iberomys brecciensis</i>	21	14	26.9
<i>Terricola</i> cf. <i>atapuerquensis</i>	1	1	1.92
<i>Arvicola</i> sp.	1	1	1.92
<i>Apodemus sylvaticus</i>	17	6	11.5
<i>Eliomys quercinus</i>	1	1	1.92
<i>Allocricetus bursae</i>	1	1	1.92
<i>Oryctolagus</i> sp.	19	6	11.5
<i>Crocidura russula</i>	4	4	7.69
<i>Sorex</i> sp.	1	1	1.92
<i>Erinaceus europaeus</i>	3	2	3.85
<i>Myotis</i> gr. <i>myotis-oxygnathus</i>	9	3	5.77
<i>Rhinolophus ferrumequinum</i>	2	1	1.92
<i>R.</i> gr. <i>euryle-mehelyi</i>	1	1	1.92
<i>Miniopterus schreibersii</i>	2	2	3.85
Total	92	52	100

The taxonomic classification follows McKenna and Bell (1997) and data on the distribution and habitat of extant species are from Palombo and Gisbert (2005).

The TEURU small-mammal species can be classified according to their preferences into four habitat types (in accordance with Cuenca-Bescós et al., 2005, 2009; Blain et al., 2008): open land in which dry and wet meadows can be distinguished, woodland and woodland-margin areas and surrounding water areas. These types are named as follows: *open dry*, for meadows under seasonal climate change; *open wet*, for evergreen meadows with dense pastures and suitable topsoil; *woodland*, for mature forest including woodland margins and forest patches, with moderate ground cover; and *water*, along streams, lakes and ponds.

These assemblages are a simplification because transitional habitats may exist between open wetland and water, and wet-grazing lands together with woodland habitats. Table 2 shows the habitat distribution of species represented in TEURU.

In order to reconstruct the climate at TEURU, we distributed each small-mammal taxon on the basis of its current climatic preferences. Climatic ranges were divided

into three types: Mediterranean, which includes the taxa associated with wet-winter and dry-summer climatic conditions; Euro-Siberian, which comprises the taxa associated with mild winters, cold summers and abundant

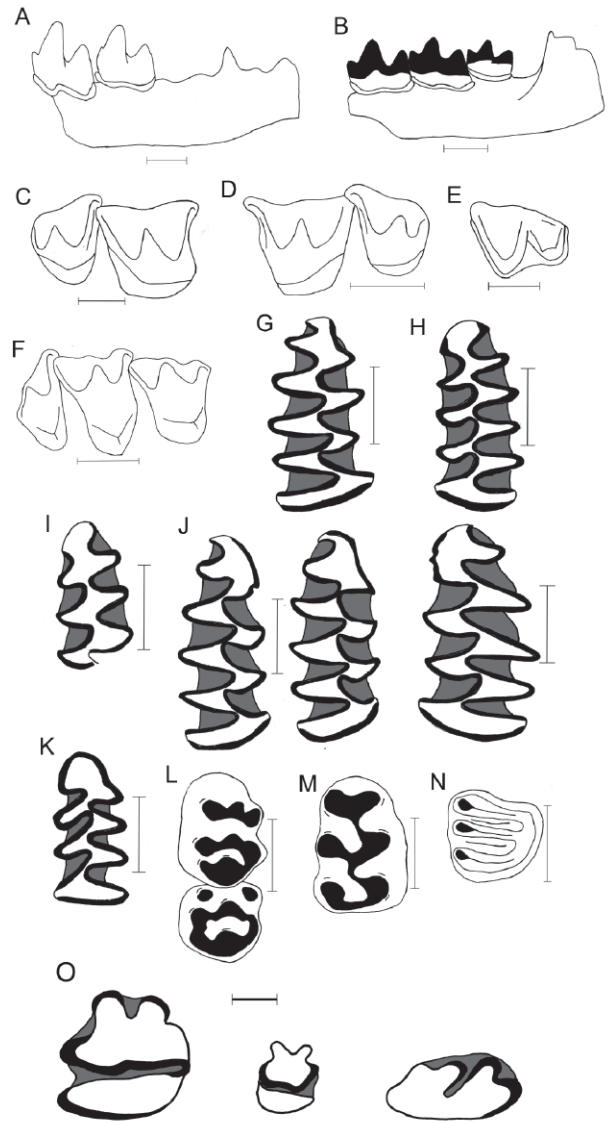


FIGURE 21 | Some small-mammal remains from the TEURU of Sima del Elefante. A) Left mandible *Crocidura* sp. (buccal view); B) Left mandible *Sorex* sp. (buccal view); C) Right upper maxilla (with M2 and M3) *Rhinolophus ferrumequinum* (occlusal view); D) Left upper maxilla (with M2 and M3) *Rhinolophus* gr. *euryle-mehelyi* (occlusal view); E) Left lower third molar (m3) *Myotis myotis-oxygnathus* (occlusal view); F) Right maxilla (with M1-M3) *Miniopterus schreibersii* (occlusal view); G) Right lower first molar (m1) *Microtus agrestis* (occlusal view); H) Left m1 *Microtus arvalis* (occlusal view); I) Left m1 *Terricola* cf. *atapuerquensis* (occlusal view); J) Two right m1 and one left m1 *Iberomys brecciensis* (occlusal view); K) Left m1 *Myodes glareolus* (occlusal view); L) Right maxilla (with M1 and M2) *Apodemus sylvaticus* (occlusal view); M) Right upper first molar (M1) *Allocricetus bursae* (occlusal view); N) Right lower second molar (m2) *Eliomys quercinus* (occlusal view); O) Left lower third premolar (p3), juvenile left p3 and right upper second premolar (P2) *Oryctolagus* sp. Scale 1 mm.

TABLE 2 | Small-mammal habitat assemblages

Small-mammal association	Habitat
<i>Microtus arvalis</i> <i>Allocricetus bursae</i> <i>Oryctolagus</i> sp. <i>Crocidura</i> sp.	Open dry meadow
<i>Microtus agrestis</i> <i>Iberomys brecciensis</i> <i>Terricola atapuerquensis</i> <i>Sorex</i> sp. cf. <i>Erinaceus</i>	Open humid meadow
<i>Myodes glareolus</i> <i>Apodemus sylvaticus</i> <i>Eliomys quercinus</i> <i>Myotis</i> gr. <i>myotis- oxygnathus</i> <i>Rhinolophus ferrumequinum</i> <i>R.</i> gr. <i>euryle-mehelyi</i> <i>Miniopterus schreibersii</i>	Woodland edge woodland
<i>Arvicola</i> sp.	Water's edge

precipitation; and ubiquitous, which includes the taxa without clear climatic preferences (Table 3).

SYSTEMATIC PALAEOLOGY

Class: Mammalia LINNAEUS, 1758

Order: Erinaceomorpha GREGORY, 1910

Family: Erinaceidae LINNAEUS, 1758

GENUS *Erinaceus* LINNAEUS, 1758

cf. *Erinaceus* sp.

Material: 1 first lower molar (m1) and 1 first upper molar (M1) from TE19; 1 m1 from TE18.

Description and discussion: The molars recovered from levels TE18-19 are characterized by their large size, displaying morphology typical of Erinaceidae. They are dilambodont, with two well-differentiated parts (trigonid and talonid). Among the material under study, the only diagnostic elements we have are a fragmented m1, of which the talonid is preserved without roots, and a juvenile m1 without roots, so we do not have enough criteria in morphological terms to be able to assign it with certainty to *Erinaceus* or *Atelerix*. However, in view of the fact that the earliest evidence in Europe to date of *Atelerix algirus* (the Algerian hedgehog) stems from the Holocene of the island of Minorca (Morales and Rofes, 2007) it is highly probable that the material from TEURU belongs to the genus *Erinaceus*.

TABLE 3 | Small-mammal climatic preferences

Small-mammal association	Climatic Preferences
<i>Iberomys brecciensis</i> <i>Terricola atapuerquensis</i> <i>Allocricetus bursae</i> <i>Crocidura</i> sp. <i>R.</i> gr. <i>euryle-mehelyi</i> <i>Miniopterus schreibersii</i>	Mediterranean
<i>Microtus agrestis</i> <i>Sorex</i> sp.	Euro-Siberian
<i>Microtus arvalis</i> <i>Myodes glareolus</i> <i>Apodemus sylvaticus</i> <i>Arvicola</i> <i>Eliomys quercinus</i> cf. <i>Erinaceus</i> sp. <i>Myotis</i> gr. <i>myotis- oxygnathus</i> <i>Rhinolophus ferrumequinum</i>	Ubiquist

Distribution and habitat: *Erinaceus europaeus* is the only current representative of the genus *Erinaceus* on the Iberian Peninsula. This is an autochthonous species that is distributed over almost all the Peninsula, except for the Balearic Islands and the Canaries. This species shows a very varied range of habitats, both open and wooded, in preferentially humid areas, normally beneath 1000m in altitude.

Order: Soricomorpha GREGORY, 1910

Family: Soricidae FISCHER VON WALDHEIM, 1817

Subfamily: Crocidurinae WAGLER, 1832

GENUS *Crocidura* WAGLER, 1832

Crocidura sp.

Fig. 2 (A)

Material: 2 left mandibles (1 with m3, 1 with m1-m3) from TE19; 2 right mandibles (1 with m3, 1 with m1-m3) from TE18.

Description and discussion: The material at our disposal from levels TE18-19 is characterized by dentition typical of the crocidurines, with white teeth. Without pigmentation and medium-sized, the teeth are typical of the genus *Crocidura*. The lack of complete mandibles in the specimens analysed makes it impossible to assign them to a concrete species, since the diagnostic characters established by Poitevin (1984) for the lower dentition of *Crocidura* need to be accompanied by other criteria such as the morphology of the ascending mandibular ramus and the fourth upper premolar, which are absent in our fossils. For

this reason we have decided to designate our specimens to *Crocidura* sp.

Distribution and habitat: In the Iberian Peninsula the genus *Crocidura* is currently represented by two autochthonous species (*C. russula* and *C. suaveolens*), which extend over almost the whole region. Both species are generalists and display basically Mediterranean requirements, preferring open spaces. In general they live in areas with annual precipitation of less than 1000mm and with average temperatures greater than 5°C, reaching altitudes of up to 1200-1600metres.

Subfamily: Soricinae FISCHER VON WALDHEIM, 1817
 GENUS *Sorex* LINNAEUS, 1758
Sorex sp.
 Fig. 2 (B)

Material: 1 left mandible (with m1-m3) from TE19.

Description and discussion: The material is characterized by being medium-sized and by the pigmentation of the molars, typical of the genus *Sorex*. Given the scantiness of the remains (a single mandible fragment), we have assigned this specimen to *Sorex* sp.

Distribution and habitat: There are three present-day representatives of the genus *Sorex* in the Iberian Peninsula: *S. araneus*, *S. coronatus* and *S. granarius*. These three species are currently distributed across the northern half of the Peninsula and are characteristic of humid environments with good herbaceous or shrub vegetation cover (Pemán, 1990a; Pokines, 1998; Zubeldia Garmendia, 2006; Cuenca-Bescós et al., 2008).

Order: Chiroptera BLUMENBACH, 1779
Suborder: Microchiroptera DOBSON, 1875
Family: Rhinolophidae GRAY, 1866
 GENUS *Rhinolophus* LACÉPÈDE, 1779
Rhinolophus ferrumequinum (SHREBER, 1774) /
Rhinolophus gr. *eryale-mehelyi*
 Fig. 2 (C and D)

Material: 1 right maxilla (with M1–M3), 1 left lower second molar (m2) from TE19 of *Rhinolophus ferrumequinum*. 1 left maxilla (with M2 and M3) from TE19 of *Rhinolophus* gr. *eryale-mehelyi*.

Description and discussion: The two first upper molars in our specimens are characterized by the presence of a talon without a hypocone; the third upper molar has a scarcely reduced post-paracristid; and the m2 has a delicate cingulum and shows a nyctalodont pattern (the hypoconulid connected with the entoconid), typical of the genus

Rhinolophus. These morphological characters coincide with the size of the material under study, as reflected in the measurements (in mm) taken for our specimens: M1: L=2.20, W=2.05; M2: L=2.14, W=2.22; M3: L=1.62, W=1.85; m2: L=2.03, W1=1.27, W2=1.08; M2: L=1.63, W=1.71; M3: L=1.37, W=1.55.

Comparison of our material with the measurements for *R. ferrumequinum* and *Rhinolophus* gr. *eryale-mehelyi* according to Sevilla (1988) allows us to ascribe part of the material under study to the greater horseshoe bat (*R. ferrumequinum*) and the other part to the group of medium-sized rhinolophids (*R. gr. eryale-mehelyi*).

Distribution and habitat: Both *R. ferrumequinum* and *R. gr. eryale-mehelyi* are species with a broad geographical distribution over the Peninsula. They are found in a wide range of environments, with a preference for wooded areas with open spaces. Moreover, *R. gr. eryale-mehelyi* are thermophilous species that prefer to inhabit valley bottoms, being found at altitudes ranging from sea-level to 1600 metres.

Family: Vespertilionidae GRAY, 1821
Subfamily: Vespertilioninae GRAY, 1821
 GENUS *Myotis* KAUP, 1829
Myotis gr. *myotis-oxygnathus*
 Fig. 2 (E)

Material: 1 left mandible (with p4-m3), 1 left third lower molar (m3), 1 right third m3, 2 left first upper molars, 1 right upper canine from TE19; 1 left mandible (with p4-m3), 1 right first lower molar (m1), 1 lower canine, 1 right upper first molar (M1) from TE18.

Description and discussion: In morphological terms, the material available is characterized by the absence of talon and hypocone in the upper molars, the third upper molar (M3) with an intense distal reduction, and lower molars that are myotodont (the hypoconulid completely separate from the entoconid) with a reasonably thick cingulum, typical of the genus *Myotis*. The large size of the molars under study leads us to ascribe our material to the group of large-sized mouse-eared bats (*Myotis* gr. *myotis-oxygnathus*), since *M. myotis* and *M. oxygnathus* are the two biggest species of the genus in Europe. These two species are difficult to differentiate from one another on the basis of their dentition alone on account of their great morphological and morphometric similarity (overlapping of size ranges) (Sevilla, 1988). Given that the shortage of diagnostic material makes it impossible to separate the two species, the fossils from TEURU have been assigned to *M. gr. myotis-oxygnathus*.

Distribution and habitat: Both species are frequent in the Mediterranean region of the Iberian Peninsula, but whereas

the preferred habitat of *M. myotis* (the greater mouse-eared bat) is mature woodland and humid wooded pastures, *M. oxygnathus* (the lesser mouse-eared bat) prefers more open areas, though equally humid. The two species are even known to form mixed colonies in a single location. Both species are distributed over altitudes ranging from sea-level to 1400metres.

Subfamily: Miniopterinae, DOBSON, 1875

GENUS *Miniopterus* BONAPARTE, 1837

Miniopterus schreibersii (KUHL, 1817)

Fig. 2 (F)

Material: 1 right upper maxilla (with M1-M3) from TE19; 1 humerus from TE18.

Description and discussion: The upper molars are subrectangular (M1 and M2) or triangular (M3) in outline; there is a well-developed parastyle on all the molars and a metastyle that is developed (M1 and M2) or reduced (M3). On its distal epiphysis, the humerus is characterized by a long styloid process in the shape of a hook; the epitrochlea is not very wide, and the condyle and epicondyle are separated by a marked constriction. These morphological characteristics make it possible to ascribe the specimens under study to the species *Miniopterus schreibersii*.

Distribution and habitat: *M. schreibersii* (the common bent-wing bat) is a species that inhabits the whole of the Iberian Peninsula and much of the Balearic Islands, although it is more abundant on the Mediterranean fringe and in the southern half of the Peninsula. It is typically a cave-dwelling species, which normally locates its refuges in Mediterranean areas with or without vegetation cover, where it may form colonies together with *Myotis myotis*. It is found at altitudes ranging from sea-level to 1400metres.

Order: Rodentia BOWDICH, 1821

Family: Arvicolidae GRAY, 1821

GENUS *Arvicola* LACÉPÈDE, 1779

Arvicola sp.

Material: 1 first upper molar from TE19.

Description and discussion: This is a first upper molar (M1) that is large in size, with a rounded morphology in the salient angles of the triangles, and thick enamel and cement in the re-entrant angles, typical of the genus *Arvicola*. The enamel, which is thicker in the posterior than the anterior parts of the triangles, leads us to believe that the *Arvicola* sp. from TE19 lies within the line of the modern-day *Arvicola sapidus*.

Distribution and habitat: The genus *Arvicola* is currently represented by two species in the Iberian Peninsula:

A. sapidus (southern water vole) and *A. terrestris* (European water vole). The two species have a different distribution over the Peninsula. Whereas *A. sapidus* is represented throughout the Iberian Peninsula, *A. terrestris* is distributed only along the northern fringe. *A. sapidus* is a semi-aquatic rodent associated with the presence of flowing or stationary bodies of water, while in the Iberian Peninsula *A. terrestris* is a hypogean species that prefers to inhabit natural meadows.

GENUS *Microtus* SCHRANK, 1798

Microtus agrestis (LINNAEUS, 1761) / *Microtus arvalis* (PALLAS, 1779)

Fig. 2 (G and H)

Material: *Microtus agrestis*: 1 right lower first molar (m1), 2 left lower first molars from TE19 and 1 right lower first molar from TE18; *Microtus arvalis*: 4 left lower first molars from TE19.

Description and discussion: The (m1) assigned to *M. agrestis* are characterized by their reduced size and by the presence of three closed triangles in the posterior complex (TTC) and four triangles that are closed or minimally confluent in the anterior complex (ACC). Marked asymmetry and alternation in the T4/T5 and T6/T7 triangles is also in evidence, as well as marked alternation in the re-entrant angles; the salient angles are pointed in shape and curved towards the anterior part of the tooth, and the T9 triangle is strongly developed. These features distinguish it from the specimens belonging to the species *M. jansoni* of Galería (Cuenca-Bescós et al., 1999) and from the m1 recovered from TE19 of *M. arvalis*, which are characterized by the almost symmetrical and parallel arrangement of T4/T5 and especially of T6/T7, as well as the corresponding re-entrant angles, giving a rounded shape to the ACC by contrast with the angular form in *M. agrestis*.

Distribution and habitat: *M. agrestis* (the field vole) is a species concentrated in the northern third of the Iberian Peninsula, in a fringe ranging from the Pyrenees to Galicia and including all the Sierra de la Demanda and the north of Portugal, but absent in the Mediterranean area. It inhabits open spaces close to deciduous woodland, in humid areas with abundant grass, such as ponds and riverbanks up to altitudes of 1900metres.

M. arvalis (the common vole) displays a similar geographical distribution to the field vole, although it is a more generalist species and more widely distributed. In the Iberian Peninsula it is more extensively spread over the southern region and may be found in many environments, from pasture to deciduous and coniferous woodland. It is also distributed over the whole of the region of Castilla

y León. Its most frequent habitat is subalpine and alpine meadows; it is a species that prefers open, not very humid spaces without high vegetation, that does not penetrate closed woodland and that avoids swamped areas. It is found at altitudes greater than 900metres and up to 2000metres, with an annual rainfall greater than 800mm.

GENUS *Terricola* FATIO, 1867
Terricola cf. *T. atapuerquensis* GIL, 1996
 Fig. 2 (I)

Material: 1 left lower first molar (m1) from TE19.

Description and discussion: The confluence of T4-T5 in our specimen leads us to assign it to the genus *Terricola*. Moreover, the T4-T5 and T6-T7 triangles are slightly alternating; the labial apex is slightly developed and is inclined towards the posterior part of the tooth; the neck formed by T6-T7 with the anterior lobe (AC) is wide; the fourth lingual re-entrant (LRA4) is semicircular in shape; and the labial triangles (T2 and T4) are curved towards the anterior part of the tooth. These morphological characteristics are typical of the species *Terricola atapuerquensis* (Gil, 1996; Cuenca-Bescós et al., 1999) and differ from other extant Iberian *Terricola* (Brunet-Lecomte, 1988; Brunet-Lecomte et al., 1987; Brunet-Lecomte and Chaline, 1990, 1993). Nevertheless, given the scantiness of the remains available to us we have decided to assign our specimen cautiously to *T. cf. T. atapuerquensis*.

Distribution and habitat: To date, the palaeogeographical distribution of the fossil species *T. atapuerquensis* has been restricted to the Sierra de Atapuerca, where it is abundantly present in the Middle Pleistocene sites of Gran Dolina and Galería-Zarpazos (Cuenca-Bescós et al., 1999), and one record, still to be confirmed owing to the scarceness of the material, in the northeast of the Peninsula in the Middle Pleistocene site of Cueva de Mollet (Maroto et al., in press).

In ecological terms, its preferred biotope can be inferred on the basis of the present-day representatives of the genus *Terricola* in the Iberian Peninsula: *T. duodecimcostatus* (the Mediterranean pine vole), *T. lusitanicus* (the Lusitanian pine vole) and *T. pyrenaicus-gerbei* (the Pyrenean pine vole). These three species have diverging geographical distributions in the Iberian Peninsula, but all of them are associated with open spaces and the presence of stable, moist soils that are easy to dig and have abundant herbaceous cover.

GENUS *Iberomys* CHALINE, 1972
Iberomys brecciensis (GIEBEL, 1847)
 Fig. 2 (J)

Material: 5 right lower first molars (m1), 11 left lower first molars from TE19; 2 right lower first molars, 3 left lower first molars from TE18.

Description and discussion: The genus *Iberomys* is characterized by clear labio-lingual asymmetry (Ayarzagüena and López Martínez, 1976), providing it with greater width in comparison to other microtines; on the labial side of m1 there are only three re-entrants filled with cement; in some specimens there is a fourth, greatly reduced re-entrant (BRA4), allowing these specimens to be distinguished from the genus *Microtus* and *Terricola*. Furthermore, the triangular-subtriangular morphology formed by the T6-T7 triangles in conjunction with the anterior lobe (AC), the clear alternation of the T4-T5 triangles in our specimens, the complete development of the AC, as well as the presence of enamel-free areas and the reduced width of the teeth, lead us to attribute our material to the species *I. brecciensis*, thus distinguishing it, moreover, from the present-day species *I. cabreræ* and from the fossil species from the lower Pleistocene *I. huescarensis*.

Distribution and habitat: The palaeogeographical distribution of the fossil species *I. brecciensis* is typically Mediterranean. Only a few Pleistocene localities are known in areas of Atlantic influence: L'Abri Vaufrey in France (Marquet, 1993), Spessa II in Italy (Sala and Masini, 2007) and the sites of Gran Dolina and Galería-Zarpazos in the Sierra de Atapuerca (Cuenca-Bescós et al., 1999).

In ecological terms, its preferred biotope can be inferred on the basis of its current representative *I. cabreræ* (Cabrera's vole), a species endemic to the Iberian Peninsula. *I. cabreræ* occupies various main centres in the foothills of the Pyrenees, the southern Iberian System, the Baetic Sierras and the Central System, as well as in the southern half of Portugal. It inhabits exclusively Mediterranean areas, with herbaceous cover all year round and a high water table, from 250 to 1500metres in altitude.

GENUS *Myodes* PALLAS, 1811
Myodes glareolus (SCHREBER, 1780)
 Fig. 2 (K)

Material: 1 left lower first molar (m1) from TE19.

Description and discussion: The presence of roots, the cement on the labial and lingual re-entrants of the triangles, the enamel that is unbroken and the same thickness on all the occlusal perimeter, except for a small enamel-free area on the labial part of the posterior lobe (PL) and the confluence of the triangles, are the morphological characteristics that make it possible to distinguish our specimen from the extinct genus *Pliomys* and assign our m1 to the present-day species *Myodes glareolus*.

Distribution and habitat: *M. glareolus* (the bank vole) is one of the few extant arvicolines that live in deciduous woodland that is more or less open or in areas where the vegetation consists of shrubs or high grasses. It is a good indicator of the presence of vegetation cover in a temperate climate with a humid atmosphere (Permán, 1985, 1990a, b; Cuenca-Bescós et al., 2008). Within the Iberian Peninsula its current distribution is northern (Ventura et al., 1993; Pokines, 1998), although it may be found in mountainous massifs in the eastern part of the Peninsula where the climate is Euro-Siberian, such as Montseny in Catalonia (Arrizabalaga et al., 1986).

Family: Muridae ILLIGER, 1811

GENUS *Apodemus* KAUP, 1829

Apodemus sylvaticus (LINNAEUS, 1758)

Fig. 2 (L)

Material: 1 right mandible (with m1-m2), 2 left mandibles (without teeth), 3 right lower first molars (m1), 3 left lower first molars, 1 right lower second molar (m2), 1 left lower third molar (m3), 1 right maxilla (with M1-M2), 1 right upper first molar (M1), 1 left upper first molar, 2 right upper second molars (M2) from TE19.

Description and discussion: The presence in the fossil lower molars (m1) of a low occlusal surface with six main cusps, the anterolingual and anterolabial cusps confluent in an X-shape and separated by a deep, narrow groove, in conjunction with a posterior cusp (cp) that is low, rounded and well developed and the presence of secondary cusps (c) on the labial face of the m1 and of a mesial tubercle (tma) allow us to assign our specimens to the genus *Apodemus*. Further, the confluence of the tubercles t4 and t7 in the upper first molar (M1) of our material, together with the development of the tubercle t9 in the upper second molar (M2), lead us to ascribe our specimens to the species *A. sylvaticus*.

Distribution and habitat: *A. sylvaticus* (the wood mouse) is one of the most abundant micromammals in the Iberian Peninsula, present throughout the whole territory. Although it may be found in almost all types of habitats, it prefers to inhabit areas with good shrub or tree cover. In regions of homogeneous woodland, however, it prefers the marginal areas.

Family: Cricetidae ROCHEBRUNE, 1883

GENUS *Allocricetus* SCHAUB, 1930

Allocricetus bursae SCHAUB, 1930

Fig. 2 (M)

Material: 1 right upper molar (M1) from TE19.

Description and discussion: The fossil M1 is characterized by its small size and the presence of an

anterostyle, a double anterolophule, the lingual longer than the labial, and a relatively high proportion of the protolophule and metalophule that is double. These characters allow it to be assigned to the fossil species *Allocricetus bursae*, while distinguishing it from the extant species *Cricetulus migratorius*.

Distribution and habitat: The palaeogeographical distribution of this fossil species in the middle Pleistocene of the Iberian Peninsula is typically Mediterranean. Only three Pleistocene localities are known in areas of Atlantic influence: Gran Dolina, Galería-Zarpazos and Sima de los Huesos, all of them in the Sierra de Atapuerca (Cuenca-Bescós, 2003; Cuenca-Bescós et al., 1997, 1999).

In ecological terms, its preferred biotope can be inferred on the basis of the present-day species that is closest to it phylogenetically, though unrepresented in the Iberian Peninsula, *Cricetulus migratorius* (the grey hamster). The present range of the grey hamster extends from eastern Europe through Russia and central Asia to Mongolia and western China. It originally occurred in dry grasslands, steppes and semi-deserts. Now, it also inhabits agricultural land and gardens, sometimes even living in houses. Arid areas with relatively sparse vegetation are preferred, and forests and damp habitats are avoided (Mitchell-Jones et al., 1999).

Family: Gliridae THOMAS, 1897

Subfamily: Leithinae LYDEKKER, 1896

GENUS *Eliomys* WAGNER, 1840

Eliomys quercinus (LINNAEUS, 1766)

Fig. 2 (N)

Material: 1 right lower second molar (m2) from TE19.

Description and discussion: The fossil m2 is characterized by its possession of a concave occlusal surface, with simple main crests that cross the tooth labio-lingually, and main cusps projecting due to their great development at the lingual and labial ends. Together with the absence of supplementary extra-ridge typically of *E. intermedius* species, make them possible to assign our specimen to the species *Eliomys quercinus*.

Distribution and habitat: *E. quercinus* (the garden dormouse) is an ubiquitous species generally found in low-density deciduous woodland and in shrubland throughout the Peninsula, associated with rocky clearings at forest edges, and which can also be an occasional commensal. Areas with abundant herbaceous vegetation seem to be a limiting factor on its presence. It is found at altitudes of up to 2000metres.

Order: Lagomorpha BRANDT, 1855

Family: Leporidae GRAY, 1821

GENUS *Oryctolagus* LILLJEBORG, 1874

Oryctolagus sp.

Fig. 2 (O)

Material: 2 left juvenile mandible fragments, 1 right juvenile fragment, 1 upper molar, 1 upper juvenile molar, 1 right juvenile maxilla fragment, 1 right lower third premolar (p3), 2 right upper second premolars (P2), 1 calcaneum, 1 proximal ulna fragment, 1 proximal tibia fragment from TE19. 1 lower molar, 2 upper molars, 3 juvenile upper molars, 1 right juvenile P2 from TE18.

Description and discussion: The P2s have a lagicone similar in size to the mesial hypercone; the paraflexus penetrates obliquely halfway across the tooth, and the mesoflexus is well-marked but shorter in relation to the hypoflexus. The rest of the upper dentition is characterized by the presence of a convoluted hypoflexus that penetrates a little more than half the width of the tooth. As regards the p3, the anteroconids are similar in size. The labial anteroconid is more elongated and more compressed in the juvenile individuals, whereas in the adults it displays an ellipsoidal or rectangular morphology. The anteroflexid is straight and relatively deep, with convergent margins towards the interior of the tooth. The protoflexid is wide and smooth and forms an angle of 90° or more between the anteroconid and the protoconid. The hypoflexid crosses almost the whole width of the tooth, and its anterior margin does not present many undulations. All these morphological characteristics allow our fossil material to be assigned to the genus *Oryctolagus*. Within the genus *Oryctolagus*, the dental remains from TE18-19 differ from *O. lacosti*, a species from the upper Pliocene – Lower Pleistocene of France and Italy, displaying a morphology that is identical to *O. cuniculus* (Middle Pleistocene to present) and *O. giberti* (Lower-Middle Pleistocene of Spain). Given the impossibility of distinguishing between *O. cuniculus* and *O. giberti* on the basis of the dentary remains (De Marfà, 2008), we have attributed our fossil material to the genus level.

Distribution and habitat: Present-day representatives of the genus *Oryctolagus* are very sedentary and may inhabit diverse biotopes, although they require sandy soils to be able to dig their warrens. They are very abundant in Mediterranean climates and in general prefer relatively open terrain, although they may also inhabit woodland clearings. They do not usually go beyond altitudes of 1500 metres, preferring warm climates. As regards rainfall, the European rabbit (*O. cuniculus*) prefers arid climates, although on a small scale it tends to be very abundant in riverbank areas.

TAPHONOMICAL REMARKS

The taphonomic analysis of levels TE18-19 incorporates 85 bony cranial and post-cranial micromammal remains. Alterations caused by digestion (rounded fractures in bones and enamel progressive reduction in teeth) are to be seen in slight measure in 14.5% of the small-mammal teeth and large bones remains. This suggests that the accumulation of micromammals in the upper levels of Sima del Elefante is due to the action of a category 1 predator (*sensu* Andrews, 1990), such as a nocturnal bird of prey. The characteristics of the remains under study do not permit us to specify the predator responsible for the accumulation, yet there is no indication or alteration suggesting that the TEURU assembly is not representative of the ecosystem in the immediate vicinity of the cave at the time when the remains were deposited.

BIOCHRONOLOGICAL DATA

The small-mammal assemblage of the TE uppermost layers (TEURU) is similar to the other late Middle Pleistocene sites of the Sierra de Atapuerca, such as TD10 (Cuenca-Bescós et al., 2010), Sima de los Huesos (Cuenca-Bescós et al., 1997) and Galería (Cuenca-Bescós et al., 1999).

Among the small-mammal association of TEURU one rodent species, *Iberomys brecciensis*, is particularly useful for biochronological purposes (Ayarzagüena and López Martínez, 1976; López-García et al., 2008; López-García, 2008; Maroto et al., in press). *I. brecciensis* is a pseudo-extinct vole, which disappears in the Middle-Upper Pleistocene transition. This vole is the ancestor of the extant *I. cabrerae*. *I. brecciensis* is characterized by several features that are also present in the TEURU specimens: a relatively long and wide lower molar (m1), the reduction of the triangles of the anteroconid complex (ACC), a noticeable labio-lingual asymmetry, a fourth buccal salient angle (BSA4) with a triangular form, and enamel not covering completely the labial wall of the ACC (Fig 2J).

As pointed out by various authors such as Chaline (1972), Ayarzagüena and López-Martínez (1976), Cuenca-Bescós et al., (1995), and Laplana and Cuenca-Bescós (1998), the main morphological character in the evolution of the first lower molars of the representatives of the genus *Iberomys* is the tendency to antero-posterior flattening, which results in a widening of the molars. An analysis of the variability in size (width) of the TE18-19 specimens in relation to those from the Middle Pleistocene of Gran Dolina (TD10), Galería (Cuenca-Bescós et al., 1999) and Mollet cave (Maroto et al., in press) and the Upper

Pleistocene sites of the Cova del Gegant (López-García et al., 2008) and Abric Romaní (López-García, 2008) would place our specimens between the age of TD10 (ca. 245–430 ka) and Galeria (ca. 250–500 ka) (Berger et al., 2008) (Fig. 3), thus situating TE18–19 between ca. 250–350ka, i.e. slightly younger than TD10 and quite similar to Galería.

Such data are in accordance with previous studies (van der Made, 2001; Rosas et al., 2006), which attributed to TEURU an age of late Middle Pleistocene (i.e. between 150–350 ka; Marine Isotopic Stages [MIS] 7–9).

PALAEOENVIRONMENTAL AND PALAEOCLIMATIC DATA

Previous studies of the TEURU environments (Rosas et al., 2006) have mainly been based on charcoal and large-mammal proxies. In particular, the presence in TEURU of charcoal pieces of *Pinus silvestris/nigra* together with the preponderance of horses has been interpreted as an indicator of cold, dry climatic conditions, with the development of open landscapes. Nevertheless, the presence of horses together with other herbivores, such as *Stephanorhinus hemitohecus*, *Cervus elaphus*, *Dama dama* and *Bos* sp., is indicative of open forest meadows, and the occurrence of taxa representative of temperate Europe, such as *C. elaphus* and *D. dama*, could be associated with milder climatic conditions.

As far as small-mammals are concerned, in the assemblage from layers TE18–19 *Iberomys brecciensis*, *Apodemus sylvaticus* and *Oryctolagus* sp. are the most abundant species, accounting for 50 % of the total sample. Among the fossil material analysed here, *I. brecciensis* corresponds to 21 remains and 14 individuals, *A. sylvaticus* corresponds to 17 remains and 6 individuals and *Oryctolagus* sp. corresponds to 19 remains and 6 individuals (Table 1). These species are related with humid forest and open areas with probably drier conditions. The other half of the small-mammal sample from TE18–19 follows the same ecological pattern of the most abundant species. It consists of taxa linked to humid grasslands and woodland edges, such as *Terricola atapuerquensis*, *Sorex* sp., *Arvicola* sp., *Microtus agrestis*, cf. *Erinaceus* sp., *Myodes glareolus*, *Eliomys quercinus* and bats in general (Fig. 4), and taxa related with dry grassland environments, such as *Microtus arvalis*, *Allocrietus bursae*, and *Crocidura* sp. (Fig. 4). From a climatic point of view, the assemblage is dominated by temperate-Mediterranean taxa, such as *I. brecciensis*, *T. atapuerquensis*, *Oryctolagus* sp., *Crocidura* sp., *Miniopterus schreibersii* or *Rhinolophus euryale-mehelyi* (Fig. 4).

Such a reconstruction is very much at odds with the previous data of Rosas et al., (2006), yet it is supported by

new data available from the malacofauna and herpetofauna. However according to the herpetofauna data (H.-A. Blain, unpublished data) we can observe that the TEURU may correspond to a dry and cold period in comparison with the other Pleistocene sites of the Sierra de Atapuerca, but that the climate is rather similar to the present climatic data from the region of Burgos.

The malacofauna of TEURU (A. García, unpublished data) is rather poor, but comprises several taxa linked with humid grassland environments, such as *Oxychilus cellarius*, *Oxychilus* sp. and *Punctum pygmeum*. On the other hand, the presence of *Chendrus niso*, *Xerocrassa* sp., *Xeroplexa gigaxii*, *Granopupa* sp., *Truncatellina cylindrica* and *Pomatias* sp. is associated with dry loose soils and rocky biotopes, and the presence of the Mediterranean taxa *Granopupa* sp. and *Pomatias* sp indicates temperate climatic conditions.

A preliminary study of the amphibians and squamate reptiles (H.-A. Blain, unpublished data) suggests that the TEURU assemblage is one of the most diverse from the Pleistocene of the Sierra de Atapuerca, with at least 18 taxa, including salamandrids, anurans, lacertid and anguid lizards, and several snakes. From an environmental point of view, this assemblage suggests a patchy landscape with a predominance of humid meadows and open woodland areas (*Salamandra salamandra*, *Alytes* sp., *Pelodytes punctatus*, *Bufo bufo*, *Hyla arborea*, cf. *Rana* sp., *Anguis fragilis*, *Natrix natrix*, *Coronella girondica*). However, the presence of *Pelobates cultripes*, *Bufo calamita*, *Lacerta* s.l., *Podarcis* sp. and *Vipera latasti* points to dry loose soils and rocky biotopes. Sunny aquatic environments in proximity to the cave are well attested by the

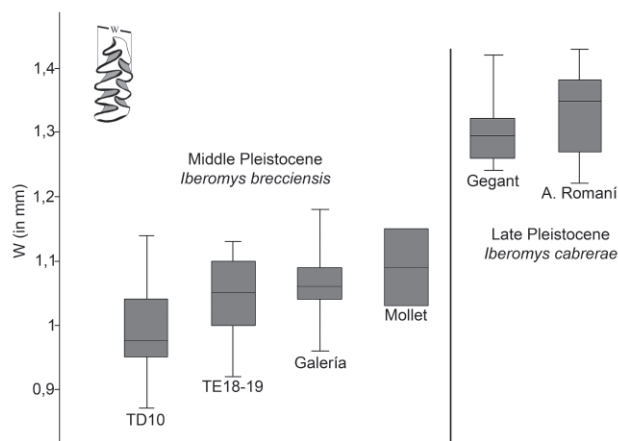


FIGURE 3 | Comparison of the width of the first lower molars (m1) of the TE18–19 Sima del Elefante specimens (n=15), with *Iberomys brecciensis* from Atapuerca-TD10 (n=34), Atapuerca-Galería (n=6; Cuenca-Bescós et al., 1999), Mollet (n=4; Maroto et al., in press) and *Iberomys cabrerae* from Gegant (n=7; López-García et al., 2008), Abric Romaní (n=26; López-García, 2008). Measures are taken in mm.

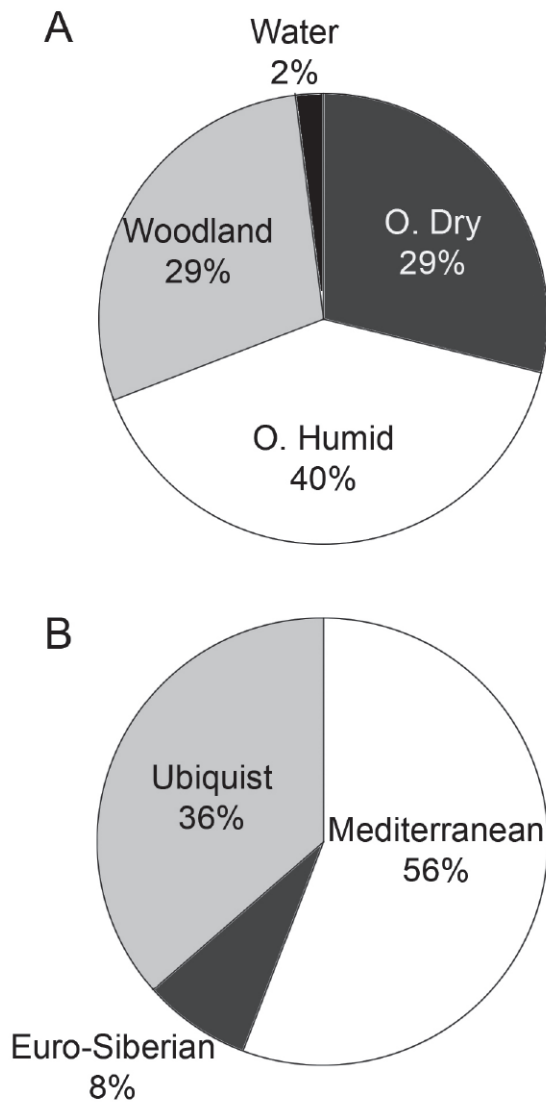


FIGURE 4 | **A)** Small-mammal association by habitat. **B)** Small-mammal association by climatic preferences. Data have been taken from the percentage of the Minimum Number of Individuals.

presence of *Lissotriton helveticus*, *Discoglossus* sp., *Natrix natrix* and *Natrix maura*. From a climatic point of view, we might note the predominance of Mediterranean taxa and the poor representation of Euro-Siberian taxa (*Salamandra salamandra*, cf. *Rana* sp. and *Anguis fragilis*) that are reasonably abundant in other localities of the Sierra de Atapuerca such as TELRU, Gran Dolina and Portalón cave (Blain et al., 2008, 2009; López-García et al., 2009). As a whole, such an assemblage is characteristic of the moistest environments of the Mediterranean area.

In conclusion, such environmental and climatic data suggest that TEURU may correspond to a mild, temperate period and that, taking into account the biochronological data, it can probably be correlated with MIS8/MIS9.

CONCLUSIONS

Our studies of the small-mammals from the uppermost layers of Sima del Elefante (TEURU) add new data to what is known about the late middle Pleistocene of the Sierra de Atapuerca. The small-mammal bone remains from TEURU have been analysed and quantified. There are a total of 92 fragments, which correspond to a minimum of 52 small-mammal specimens, representing at least 17 taxa, including insectivores, bats, rodents and rabbits. The small-mammal fossil remains were grouped by the minimum-number-of-individuals (MNI) method, bearing in mind that taphonomic factors might have influenced the record of the assemblages and abundances of the species. In the late Middle Pleistocene layers of Sima del Elefante, the animal responsible for the assemblage was probably a nocturnal bird of prey.

On the basis of the small-mammal assemblage, the age of the TEURU is estimated at MIS9 or MIS8 (i.e. ca. 250-350 ka) at the end of the Middle Pleistocene, corroborating the previously acquired large-mammal biostratigraphic data.

The landscape surrounding the cave was composed of a humid forest, with open areas with probably drier conditions. The climate had a clear Mediterranean pattern, somewhat similar to the climatic conditions that we can observe today in the Burgos area.

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