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Paleoenvironmental and paleoclimatic interpretation of the stratigraphic sequence of Lezetxiki II Cave (Basque Country, Iberian Peninsula) inferred from small vertebrate assemblages

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Abstract

We present a paleoenvironmental and paleoclimatic reconstruction based on microfaunal assemblages preserved at Lezetxiki II Cave (Arrasate, Basque Country, Iberian Peninsula) and synthesize previously published and new chronological work from the cave to better understand the environmental history of the region. The stratigraphic sequence of this short gallery ranges from the end of the middle Pleistocene to the middle Holocene and has great micropaleontological relevance for the Iberian Peninsula, especially because it contains the most ancient small vertebrate remains found in the Cantabrian region, likely deposited during Marine Oxygen Isotope Stage 7–6. Thirty-two small vertebrate taxa, including two extinct species, were identified. Environmental reconstruction based on small vertebrates suggests an open landscape at the base of the sequence (three lower levels) that progressively changed to woodland in the upper levels. Other paleoenvironmental data suggest a similar interpretation of the environmental history of the region, and although some uncertainty in the environmental reconstruction and chronology still exists, our data provide a richly detailed record of small vertebrates from an area that likely represented an important late Quaternary migration corridor for species traveling between the Iberian Peninsula and European continent.

Keywords: Small vertebrates; Paleoenvironment; Middle-Upper Pleistocene; Holocene; Cantabrian Range; Iberian Peninsula

INTRODUCTION

During the last 10 yr, knowledge on climatic and environmental changes in terrestrial environments in the Basque area of the Iberian Peninsula has experienced a significant step forward. This has been possible on account of an increase on systematic investigations of different proxies, including vertebrate remains, palynology, sedimentology, malacology, and isotope geochemistry (Iriarte, 2009; Martínez-García et al., 2013; Castaños et al., 2014; Aranburu et al., 2015). Among terrestrial vertebrates, small vertebrates constitute an important source of information on past environments, because of their good preservation, quantity, and relatively well-understood ecology. Therefore, they are becoming increasingly used in multidisciplinary studies of the late Pleistocene and Holocene (Murelaga et al, 2008; Rofes et al., 2013; Suárez-Bilbao et al., 2017; among others). They are a particularly important source of paleoenvironmental information in places like Basque Country, likely serving as a multidirectional corridor for animal species and prehistoric populations traveling between the Iberian Peninsula and the European continent (for more information about the idea of "Basque crossroads," see Arrizabalaga, 2007).

The Lezetxiki karst complex (Arrasate, Basque Country) is situated in the southwestern tip of the province of Gipuzkoa (Iberian Peninsula), in the central sector of northern Iberia (Fig. 1). The caves within this complex contain a rich paleoenvironmental record. Previous research on the cave deposits includes synthesis studies (Arrizabalaga, 2006; Álvarez-Alonso and Arrizabalaga, 2012), macrofaunal investigations (Altuna, 1972; Castaños et al., 2011),

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descriptions of microfaunal assemblages (Chaline, 1970; Rofes et al., 2012; Garcia-Ibaibarriaga et al., 2015a), and geoarchaeology (Arriolabengoa et al., 2015).

Lezetxiki II has made a significant contribution to the paleontological and paleoenvironmental knowledge of the Pleistocene in the Iberian Peninsula, because it has yielded the first fossil record in the Cantabrian region of *Allocricetus bursae* and the southwesternmost record of *Sicista betulina* in Eurasia (Rofes et al., 2012). The site also contains the earliest Quaternary fossil remains of *Muscardinus avellanarius* in the Iberian Peninsula (Garcia-Ibaibarriaga et al., 2015a) and the first fossil remains of *Macaca sylvanus* in the Cantabrian range (Castaños et al., 2011). Therefore, additional examinations of the cave deposits are being done to better constrain the timing of faunal history and environmental conditions at this important location.

THE CAVE OF LEZETXIKI II AND STUDY OBJECTIVES

The Lezetxiki II Cave, which is formed from Cretaceous limestones, is located on a steep hillside in an area of abrupt relief (Fig. 1), at an elevation of 380 m above sea level on the eastern flank of Bostate hill. The cave is part of a larger karst complex, which includes other cavities with Quaternary sediments and archaeo-paleontological infillings (Álvarez-Alonso and Arrizabalaga, 2012). In addition, there are numerous archaeo-paleontological sites in the surrounding region, some of them with microvertebrate records (e.g., Artazu VII: Suárez-Bilbao et al., 2017; Labeko Koba: Pemán, 2000; Askondo: Garcia-Ibaibarriaga et al., 2015b; Bolinkoba: Garcia-Ibaibarriaga et al., 2015c). Even though the natural systems of Arrasate have been subjected to heavy anthropogenic pressure, *Pinus radiata* plantations still share territory with the Cantabrian Holm oak (*Quercus ilex ilex*) in the region, with beech (*Fagus sylvatica*) forests at higher altitude.

The "classic" Lezetxiki deposit was first excavated during the 1956–1968 field seasons under the direction of José Miguel de Barandiarán, revealing an extensive Late Pleistocene sequence. In addition, three human fossil remains were recovered—namely, a humerus near the entrance of Leibar Cave (level VIII; Basabe, 1966) and provisionally dated to Marine Oxygen Isotope Stage (MIS) 6 (Arrizabalaga et al., 2005) and two Neanderthal teeth from level III (Basabe, 1970). A small adjacent cavity nowadays known as Lezetxiki II, and the focus of the present work, was also explored, but its excavation was halted as it was practically sediment-filled from the accumulation of the sieved material from Lezetxiki (Arrizabalaga, 2006). In 1996, excavations were restarted on the southern side of Lezetxiki by Alvaro Arrizabalaga and María José Iriarte using updated

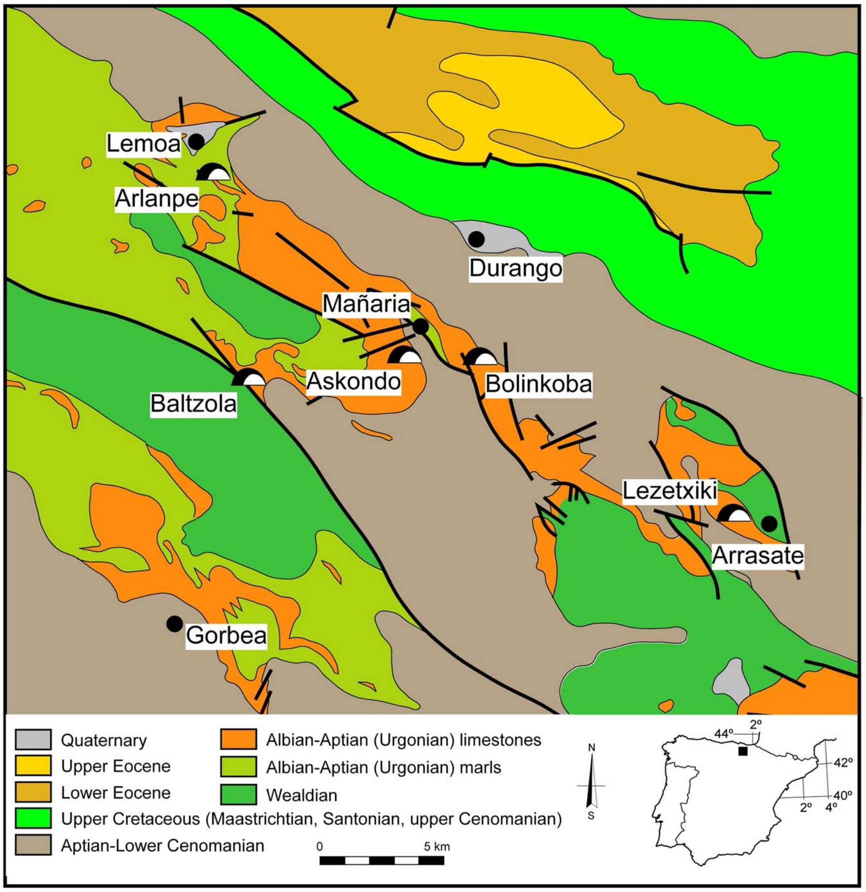

Figure 1. (color online) Geologic location of Lezetxiki Cave (Arrasate, Basque Country, Iberian Peninsula) and the location of some archaeological sites mentioned in the text. Modified from Rat (1959).

methodology (i.e., micromorphological analysis, palynological sampling, new dating, etc.; Arrizabalaga 2005, 2006), and since 1999 these efforts were extended to Lezetxiki II.

Lezetxiki II has a tunnel-type morphology, with an octagonal orientation to the "classic site" (north–south orientation) and is a minimum of 4 m in length (Fig. 2A). The entrance of the cave, located at the eastern end, is 1 m wide and 0.4 m high. The cavity was probably principally used as a hibernation and breeding den of *Ursus spelaeus* (Villaluenga, 2013), although the presence of other carnivores and ungulates may be related with sporadic occupation of the cave by carnivores and humans (anthropogenic activity is evidenced by scarce lithic tools). The origin and formation of endokarst fill in Lezetxiki II Cave was the product of multiple episodes of deposition and erosion (Arriolabengoa et al., 2015), so the stratigraphic sequence is not homogeneous in the excavated area (a test trench of 1 × 4).

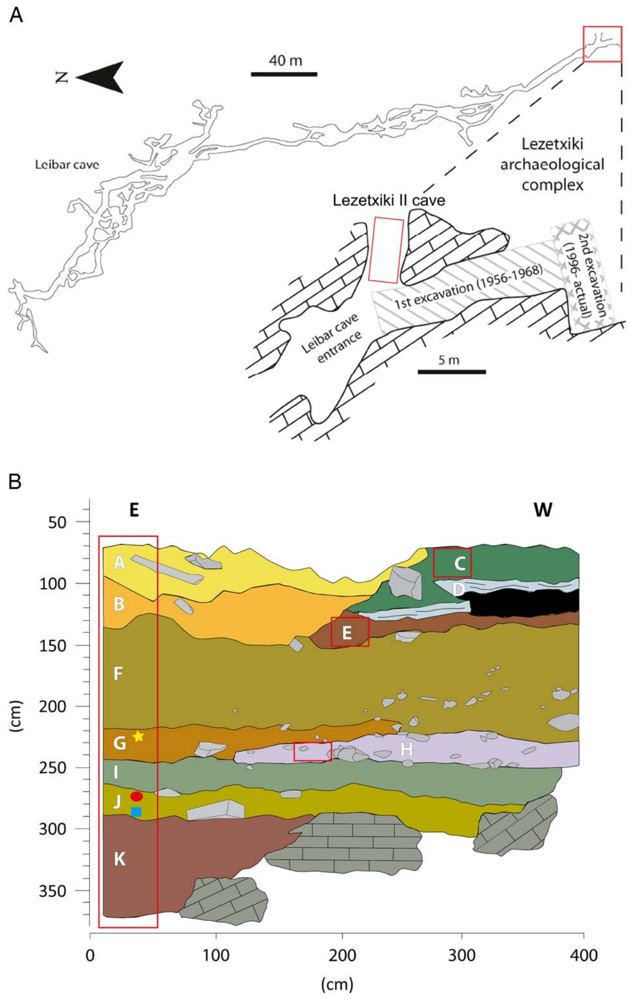

Figure 2. (A) Topography of Leibar Cave with the exact location of Lezetxiki II Cave (Arrasate, Basque Country, Iberian Peninsula) in red. (B) Stratigraphy of Lezetxiki II, indicating the location of micropaleontological samples (red boxes) and already published *Muscardinus avellanarius* (yellow star), *Sicista betulina* (red ellipse), and *Macaca sylvanus* (blue square) remains. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

The absence of a systematic geochronology framework remains one of the most difficult methodological problems for interpreting the infilling history al Lezetxiki II. In this article, we (1) clarify and synthesize previously published and new chronological work at the cave and (2) describe newly examined small vertebrate assemblages and make paleoenvironmental inferences based on these data.

MATERIAL AND METHODS

Fieldwork and collecting techniques

The sequence from Lezetxiki II (Fig. 2B) was divided into 11 lithostratigraphic levels (Arriolabengoa et al., 2015), named using letters in alphabetical order (from A to K; Table 1). In 2011, sampling for micropaleontological analysis was carried

Table 1. Geologic description of the stratigraphic levels in Lezetxiki II Cave, modified from Arriolabengoa et al. (2015).

Level	Description
A	Silty matrix with gastropods and some decimetric limestone fragments (deepest point −76 cm). Deposited only in the first half of the gallery (L15 and M15), filling the gap left by the dismantling of the Pleistocene levels.
B	Clay and silty matrix level, deposited only in L15 and M15. Depth of about 22 cm at the eastern end and 40 cm depth in inner areas. The ceramic, faunal, and lithic fragments discovered suggest a Chalcolithic occupation.
C	Silty clay matrix with gastropods and fragments of flint and iron oxides. Uppermost level in squares J15 and K15 (deepest point −76 cm). The base is abruptly displaced in square J15 (20 cm in the vertical and 20 cm to the east).
D	Speleothem, flowstone of 15 cm thick, identified only in the second half of the gallery. Fractured with a latero-vertical displacement of 20 cm, forming a small hole in the basement of this level. No microfaunal sampling.
E	Concretionary silty clay matrix, sterile in micropaleontological remains. It appears only in the inner part of the cave with 10 cm in the west side (J15) and 30 cm in band K15.
F	Clayey silt matrix with 3-4 millimetric rounded gravels of quartzite and iron oxides. It extends along the whole profile with about 1 m thick.
G	Clayey silt matrix with some limestone fragments, occurring between squares K15 and M15. It is thicker at its east end (30 cm), whereas in K15 it is only about 10 cm.
H	Clay matrix with millimetric clasts of calcite concretion, between 20 and 30 cm thick. It lies beneath level F (J15) or level G (K15).
I	Silty sand matrix with fragments of iron oxides nodules, 10 cm thick. It is below level G on the east side and below level H on the west side.
J	Silty matrix sediment with centimetric rounded pebbles of sandstone and some iron oxide nodules. Between 5 and 30 cm thick.
K	Decreasing grain-size sequence with centimetric rounded pebbles of sandstone and some iron oxide nodules. It mainly occupies square M15 and part of L15 because it is interrupted by a series of large boulders.

out at the entrance of the cave, where most of the stratigraphic units were present. In addition, samples were taken from levels identified in deeper parts of the gallery (levels C, E, and H; Fig. 2B), with the exception of level D (stalagmite flow). A total of 52 samples (279 L of sediment), of 0.33 m^2 each, were taken through the 3-m-long stratigraphic sequence in subsequent sublevels 5 to 10 cm thick (Fig. 2B).

The samples were processed with the water-screening method using a stack of sieves of decreasing mesh size (4 mm to 0.5 mm). In subsequent years, small-vertebrate bony remains were analyzed and quantified as part of a Ph.D. dissertation (Garcia-Ibaibarriaga, 2015). With the aid of a stereomicroscope, the disarticulated bone fragments and isolated teeth were separated from the concentrates, classified, quantified, and photographed at the University of the Basque Country UPV/EHU.

Systematic attribution and quantification

For the identification of bones, we followed the general criteria given by López-Martínez (1989) for lagomorphs; Cuenca-Bescós (1988), Daams (1981), Heinrich (1982), Pasquier (1974), Pucek (1982), and Van der Meulen (1973) for rodents; and Furió (2007), Niethammer and Krapp (1982), and Reumer (1984) for eulipotyphlans. The specific attribution of squamate and amphibians followed the criteria established previously by Bailon (1991, 1999), Blain (2009), and Szyndlar (1984). The taxonomic classification for small mammals was in accordance with Tesakov et al. (2010), Waddell et al. (1999), and Wilson and Reeder (2005). Additionally, the systematical nomenclature used for amphibians and reptiles was based on Speybroeck et al. (2010). Specific taxonomic attributions rest mainly on the best cranial and/or postcranial diagnostic element: isolated teeth for the lagomorphs; isolated teeth and mandibles for the rodents (first lower molars for the Arvicolinae); isolated teeth, mandibles, and postcranial skeleton for the insectivores; the vertebrae for newts, lacertids, and snakes; vertebrae, dental material, and osteoderms for *Anguis fragilis*; and the humerus, the ilium, and the scapula for the anurans.

The relative abundance of fossil species in Lezetxiki II was established using the minimal number of individuals (MNI), determined considering the best diagnostic element and its position in the skeleton. Laterality and sex (for amphibians) were taken into account, whenever possible.

Diversity

Diversity refers to the number of taxa present in a community or region and their relative evenness in proportions. It is likely related to environmental conditions and climate, as well as other variables (Fleming, 1973; Kerr and Packer, 1997; Andrews et al., 1979), so it is possible to use diversity as a general indicator of climatic changes (Montuire, 1995; Andrews and O'Brien, 2000; Blois et al., 2010). Warmer climatic conditions are often associated with increased diversity and ecosystem complexity (Margalef, 1974; Barbault, 1994). In this study, we used the Shannon index (sometimes referred to as Shannon-Weaver or Shannon-Wiener index) to quantify diversity, as the final result is independent of the size of the sample, and it is more suitable when it comes to highlight minority species. The indices were calculated with the Paleontological Statistics program (PAST; Hammer et al., 2001).

Habitat types and climate categories

Paleoclimate and paleoenvironmental inferences from microvertebrate fossils were made based on knowledge of modern ecological preferences using two methods. Details of ecological preferences of the different small vertebrate species from Lezetxiki II Cave are extensively documented in Garcia-Ibaibarriaga (2015). We used the taxonomic habitat index, a method developed by Nesbit Evans et al. (1981) and Andrews (1990, 2006), based on habitat weighting. According to this method, we organized the taxa identified at Lezetxiki II Cave by their ecological preferences in biotopes following Álvarez et al. (1985), Cuenca-Bescós et al. (2008), Gosá and Bergerandi (1994), International Union for Conservation of Nature (2014), Palomo and Gisbert (2005), Pleguezuelos et al. (2002), Pokines (1998), Salvador (1998), and Sesé (2016). In the case of fossil taxa, values were applied depending on the ecological affinities of related modern species, as established by Bartolomei et al. (1975) and Sesé (2005). However, we acknowledge that this approach induces considerable uncertainty, because it is not possible to establish the actual proportion represented by each species in different habitats. Consequently, we also examined the proportion of species that predominantly occur in wooded habitats (*Eliomys quercinus*, *Muscardinus avellanarius*, *Glis glis*, *Sicista betulina*, *Clethrionomys glareolus*, *Apodemus sylvaticus-flavicollis*, *Sciurus vulgaris*, *Sorex araneus-coronatus*, *Sorex minutus*, *Anguis fragilis*, and *Salamandra salamandra*). Numerous previous studies have shown that deciduous forests expanded in the Cantabrian region in response to warmer climates (Sese, 2005; Cuenca-Bescós et al., 2008; Iriarte-Chiapusso and Murelaga, 2012; Rofes et al., 2013).

RESULTS

Chronology

Although the chronology of the cave deposits has been presented in several studies (Falguerès et al. 2006; Maroto et al., 2012; Higham et al., 2014), uncertainty still remains about the infilling history of Lezetxiki II Cave. In 2003, a U/Th age was obtained from a speleothem located at level D by CNRS specialists C. Falguères, H. Valladas, and N. Mercier (Arrizabalaga, 2004). This sample had been contaminated by thorium from the detrital part of the speleothem (intercalated clays), so it had to be corrected (Falguerès et al., 2006). The sample provided an age of 74 ka (Table 2), suggesting that this level was deposited throughout the first phase of MIS 4.

Table 2. List of numeric ages from Lezetxiki II Cave (Arrasate, Basque Country, Iberian Peninsula) including cultural periods, chronostratigraphic units, laboratory codes, and sample details.

Level	Cultural period	U ppm	$^{234}U/^{238}U$	$^{230}Th/^{232}Th$	$^{230}Th/^{234}U$	Date (ka)	Corrected date	Lab code	Sample
D	Middle Paleolithic	0.1	1.198 ± 0.071	2	0.674 ± 0.042	117 +15/–13	74 ka	IPH-Lz16	Stalagmite flowstone

Additionally, in 2010, two *Ursus* teeth found in the level J were dated by amino acid racemization at the Polytechnic University of Madrid using aspartic acid D/L ratios (Castaños et al., 2011). The individual results are 70 and 86.8 ka, which give a mean value of 78.4 ± 8.4 ka. These results most likely represent minimum age estimates, because they are not consistent with the sedimentologic and archaeological analyses.

Recently, level K has been dated by single-grain thermally transferred optically stimulated luminescence (TT-OSL), which we are presenting for the first time in this work. It provides an estimate of when quartz grains were last exposed to light prior to deposition and burial at the site, using a methodology presented in Arnold and Demuro (2015), Arnold et al. (2015), and Demuro et al. (2014, 2015). A single sample (LZ12-6) was collected from level K using a PVC tube, and dated using the TT-OSL methodological procedures and quality assurance criteria outlined in Arnold et al. (2014). Suitability of the single-grain equivalent dose (D_e) estimation procedures was confirmed with a dose-recovery test, and the natural D_e distribution (n = 84 grains) displayed a low overdispersion value of 25 ± 5%, which is indicative of sufficient optical resetting prior to burial (Fig. 3). The single-grain TT-OSL age for sample LZ12-6 (obtained using the central age model) is 215.7 ± 15.1 ka, with a 1-sigma error (Table 3).

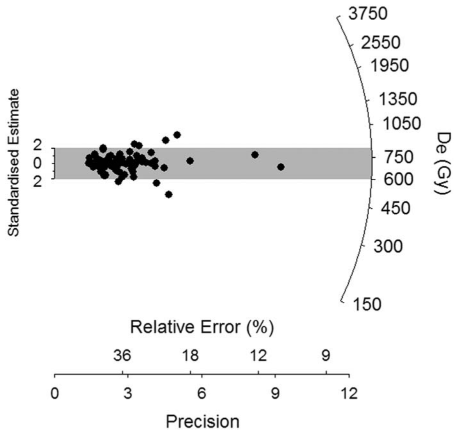

Figure 3. Single-grain thermally transferred optically stimulated luminescence equivalent dose (D_e) distribution for sample LZ12-6, shown as a radial plot. The D_e value for each grain is read by drawing a line from the origin of the y-axis ("Standardized Estimate"), through the data point of interest, to the radial axis (plotted on a log scale) on the right-hand side; the point of intersection is the D_e (in Gy). The measurement error on this D_e is obtained by extending a line vertically to the x-axis, where the point of intersection is the relative standard error (shown as a percentage of the D_e value) and its reciprocal (precision). In radial plots, the most precise estimates fall farthest to the right, and the least precise estimates fall farthest to the left. The gray band is centered on the weighted mean D_e value calculated using the central age model.

Considering the new dating, and the data provided by the sedimentologic (Arriolabengoa et al., 2015) and microfaunal analysis, we propose the following chronological description. Level K contains the MIS 7–MIS 6 transition, TT-OSL dated to 215.7 ± 15.1 ka. Therefore, we propose for levels J and I, an MIS 6 age (190–130 ka) based on stratigraphic relations with surrounding levels. Subsequent in the stratigraphic sequence are levels H–G, which do not have any direct age control. Both the sedimentologic evidence (i.e., the predominance of autochthonous material and speleothem formation) and the microfaunal analyses (the increase and diversity in woodland species) suggest that levels G–H represent a notorious breakup of the cave environment. Therefore, we propose an MIS 5e (ca. 128–110 ka) assignation for these levels. Consequently, the probable assignation for levels F–E, based on different lithic remains and their typological criteria, could be Middle Paleolithic, consistent with MIS 5d–b assignation (110–82 ka). Although there is a U/Th age for level D, suggesting a deposition during the MIS 4, we consider more consistent the sedimentologic assignation, which suggests the final phase of MIS 5a (ca. 82–74 ka; M.A., E.I., A.A., I.Y., A.A, personal communication). The chronological assignation for level C, based on archaeological material, is likely Aurignacian (MIS 3, ca. 60–30 ka), when the cave was apparently used as a secondary settlement (Arrizabalaga, 2001, 2003). Finally, the ceramic, faunal, and lithic fragments discovered in levels A and B suggest a Chalcolithic occupation (MIS 1: 14 ka–present; Arrizabalaga, 2000).

We take this opportunity to clarify some already published chronological assignations. In light of the new TT-OSL dating result, we propose that both *Macaca sylvanus* and *Sicista betulina* remains (Castaños et al., 2011 and Rofes et al., 2012, respectively) have been found in levels that could be attributed to MIS 6. We support the previous assignation of the hazel dormouse (*Muscardinus avellanarius*) remains with an interstadial period of MIS 5 (Garcia-Ibaibarriaga et al., 2015a), probably with MIS 5e (taking into account the sedimentologic and paleontological composition of the level).

Taphonomic remarks

A preliminary study of the taphonomy of the small vertebrate assemblage from Lezetxiki II indicates that several

Table 3. Thermally transferred optically stimulated luminescence (TT-OSL) dose rate data, single-grain equivalent dose, and final age for sample LZ12-6. The final TT-OSL age has been derived by dividing the weighted mean equivalent dose (D_e) by the total dose rate.

				Environmental dose rate (Gy/ka)				Equivalent dose (D_e) data				
Sample	Layer	Grain size (μm)	Measured water content[a]	Beta dose rate[b,c]	Gamma dose rate[c,d]	Cosmic dose rate[e]	Total dose rate[f,g]	No. of grains[h]	Overdispersion (%)[i]	Age model[j]	D_e (Gy)[f]	TT-OSL age (ka)[f,k]
LZ12-6	K	90–125	17 ± 2	1.94 ± 0.1	1.27 ± 0.05	0.06 ± 0.01	3.29 ± 0.15	84/2300	25 ± 6	CAM	71.0 ± 34.8	215.7 ± 15.1

[a] Field water content, expressed as percent of dry mass of mineral fraction, with an assigned relative uncertainty of ±10%.

[b] Calculated on dried and powdered sediment samples using a Risø GM-25-5 low-level beta counter.

[c] Specific activities and radionuclide concentrations have been converted to dose rates using the conversion factors given in Guérin et al. (2011), making allowance for beta-dose attenuation (Mejdahl, 1979; Brennan, 2003).

[d] Calculated from in situ measurements made at each sample position with a NaI:Tl detector, using the "energy windows" approach (e.g., Arnold et al., 2012).

[e] Cosmic-ray dose rates were calculated using the approach of Prescott and Hutton (1994), and assigned a relative uncertainty of ±10%.

[f] Mean ± total uncertainty (68% confidence interval), calculated as the quadratic sum of the random and systematic uncertainties.

[g] Includes an internal dose rate of 0.03 Gy/ka with an assigned relative uncertainty of ±30%.

[h] Number of D_e measurements that passed the single-aliquot regenerative-dose (SAR) rejection criteria of Arnold et al. (2014) and were used for D_e determination/total number of grains analyzed.

[i] The relative spread in the D_e data set beyond that associated with the measurement uncertainties for individual D_e values, calculated using the central age model (CAM) of Galbraith et al. (1999).

[j] The CAM was used to calculate the final D_e as this sample had a low overdispersion value, consistent with that observed in "ideal" well-bleached and unmixed sample from similar settings (Arnold and Roberts, 2009; Arnold et al., 2014, 2015; Demuro et al., 2014).

[k] Total uncertainty includes a systematic component of ±2% associated with laboratory beta-source calibration.

predators likely contributed to the formation of the deposits (Andrews, 1990), and changes in preservation across the sequence indicate postdepositional processes varied through time. The mainly extensive alterations caused by digestion found in some remains, especially those of Gliridae and Murinae (Fig. 4A), suggest that the agent responsible for these small-vertebrate accumulations was likely to be a predator with great to extreme modification capacity. In contrast, other small mammal taxa digestion traces were practically absent or moderate. Among the herpetofauna, frog remains have evident signs of digestion, probably by a small carnivore (Fig. 4B). Regarding the causative agents that have altered the faunal composition, some of the remains could have surface modifications that may be related with weathering (Fig. 4C), whereas others show clear traces of chemical abrasion (Fig. 4D). An in-depth study is necessary to address these alterations in more detail, e.g., the lack of faunal remains in level H would be related with the sedimentologic composition of the level, as indicated by Arriolabengoa et al. (2015).

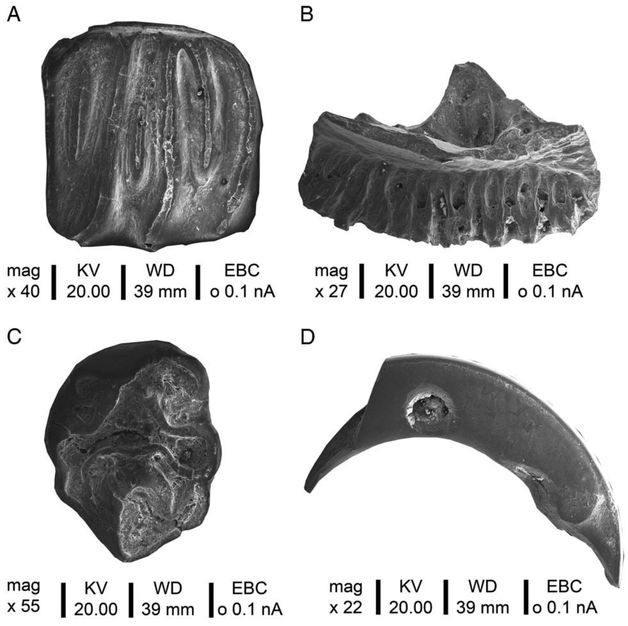

Figure 4. Alteration traces identified in some small vertebrates remains from Lezetxiki II Cave (Arrasate, Basque Country, Iberian Peninsula). (A) *Glis glis* left m2 with extreme digestion. (B) *Rana temporaria-iberica* premaxilla with evident signs of digestion. (C) *Apodemus sylvaticus-flavicollis* right M1 weathered. (D) Small mammal incisor abrased.

A main characteristic of the small vertebrate assemblage is the high fragmentation of the bones. Because of the high breakage, the number of identified skeletal elements is quite low, with 10,309 specimens out of more than 66,000 recovered remains. Among all identified fossils, 40% are metapodials and phalanges (4186), followed by incisors (10.66%, 1091 remains). Taking into account the raw frequency in which elements occur in a complete skeleton, the most represented elements are incisors (24.5%), followed by molars (17.5%).

The fragmentation and skeletal element representation changed over time (Fig. 5). The similar preservation stage of proximal limb bones compared with the conservation of femora and tibia-fibulae suggests that generally the predator consumed the whole carcasses in the cave. The identification of incisors in levels I, B, and A is quite low. Level K has noteworthy numbers of both radii and humeri, whereas in level F the identification of calcanei and astragali is about 40%. Another oddity is the conservation of ribs in level C, 15 times more than in the rest of the levels. Finally, the excellent preservation of the mandibles in levels K and J should be noted, with conservation of about 60%. Even if current natural accumulations tend to conserve 80–90%, this value indicates that these two levels suffered fewer postdepositional processes than the rest of the levels in this cave.

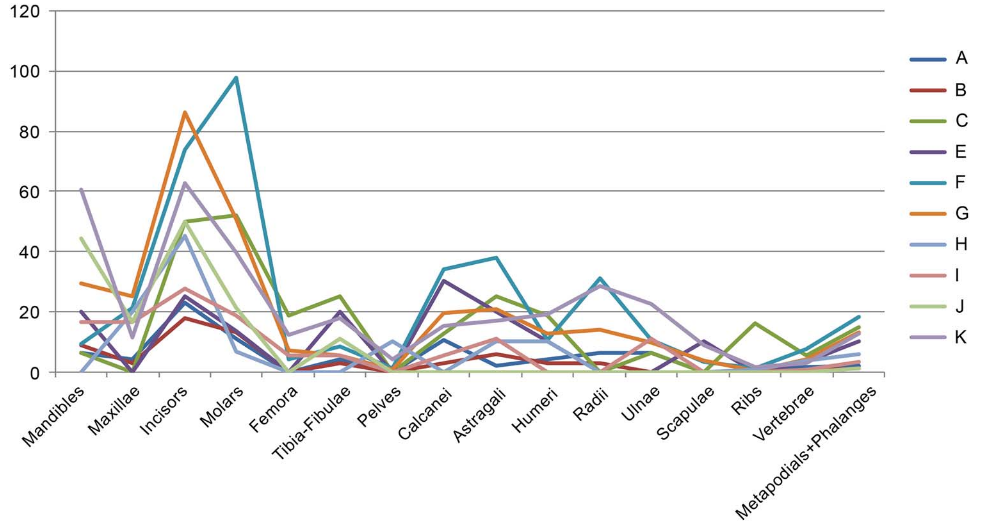

Figure 5. (color online) Relative abundance of small mammal skeletal elements from Lezetxiki II Cave (Arrasate, Basque Country, Iberian Peninsula).

Small vertebrate assemblage from Lezetxiki II

The small vertebrate assemblage comprises 66,300 identified and unidentified disarticulated bone fragments (teeth, isolated mandibles, skull fragments, and postcranial bones). More than 2000 of them (2,211) have been identified at the genus and/or species level (number of identified specimens [NISP]), representing a total of 432 individuals (MNI). The small vertebrates comprise 32 taxa (Fig. 6A and B; Table 4): 1 lagomorph (cf. *Oryctolagus cuniculus*), 10 cricetids (*Arvicola amphibius*, *Arvicola sapidus*, *Chionomys nivalis*, *Clethrionomys glareolus*, *Pliomys lenki*, *Microtus oeconomus*, *Microtus agrestis*, *Microtus arvalis*, *Microtus* [*Terricola*] sp., and *Allocricetus bursae*), 1 murid (*Apodemus sylvaticus-flavicollis*), 3 glirids (*Eliomys quercinus*, *Muscardinus avellanarius*, and *Glis glis*), 2 sciurid (*Marmota marmota* and *Sciurus vulgaris*), 1 dipodid (*Sicista betulina*), 1 erinaceid (*Erinaceus* cf. *europaeus*), 4 soricids (*Sorex araneus-coronatus*, *Sorex minutus*, *Neomys* sp., and *Crocidura russula*), 1 talpid (*Talpa* cf. *europaea*), Chiroptera indet., 2 saurians (Lacertidae indet. and *Anguis fragilis*), 2 snakes (*Coronella girondica* and *Vipera* cf. *seoanei*), 1 salamandrid (*Salamandra salamandra*), 1 midwife toad (*Alytes obstetricans*), and 1 ranid (*Rana temporaria-iberica*).

Most of the taxa identified at Lezetxiki II Cave have extant representatives (País Vasco, Viceconsejería de Medio Ambiente, 1989), albeit some of them only inhabit other parts of the Iberian Peninsula. This is the case of the common shrew (*S. araneus*), as well as of *A. amphibius*, *E. quercinus*, and *O. cuniculus*, among others (Aranzadi, 1989). Some other species are absent even from the Iberian Peninsula, like *M. oeconomus*, which presently has a wide range extending from northwest Europe in the west to Alaska in the east (Linzey et al., 2008). The western limit (Denmark, Norway, and Austria) is similar to the birch mouse (*Sicista betulina*; Meinig et al., 2008), but not to *M. avellanarius*, which in Europe is only absent from Iberia, southwestern France, and northern Fennoscandia and Russia (Amori et al., 2008). Finally, we have identified two extinct species at Lezetxiki II. One is *P. lenki*, whose last occurrence is recorded in the Upper Magdalenian levels from El Mirón Cave, in Cantabria (Cuenca-Bescós et al., 2010). The other is *A. bursae*, identified for the last time in the Iberian Peninsula in Ambrosio Cave (17,000 yr BP; Sesé and Soto, 1998).

Small vertebrate community changes over time

There are significant taxonomic differences in the small vertebrates between the base and the top of the Lezetxiki II Cave sequence (Fig. 7A and B, Table 4). The small-mammal distribution from the lower layers (levels K–E) is characterized by the predominance of *M. agrestis* with 88 MNI (Fig. 7A and B, Table 4), followed by *A. sylvaticus-flavicollis* (26 individuals). Few insectivorous and herpetofaunal remains occurred within these lower levels. Observing the internal variations among them, levels K, G, and F are the most numerous in both NISP and MNI, which turn out to comprise, in terms of overall coverage, the largest stratigraphic sequences. Level K (end of MIS 7) is the subunit with the most identified specimens (389) and determined individuals (205), mostly because of the abundance of *M. agrestis* and *S. araneus-coronatus* (Fig. 7A, Table 4). On the other hand, the small vertebrate distribution from levels G (MIS 5e?) and F (MIS 5d–b?) are characterized by the prevalence of *A. sylvaticus-flavicollis*, followed by the two species mentioned previously. Levels J, I, H, and E are the poorest subunits of the entire stratigraphic sequence (Fig. 7A and B) from a quantitative point of view, although it is true that only a single 5- to 10-cm-deep sample has been taken from each of them. Level C (MIS 3) is also poor in individuals (Fig. 7A and B, Table 4), although it has the highest NISP, related to the presence of numerous postcranial slowworm remains (notwithstanding that they correspond to a single individual). Finally, the last two levels (B and A) are similar to level C, with *A. fragilis* dominating the NISP and *A. sylvaticus-flavicollis* the MNI (Fig. 7A and B, Table 4).

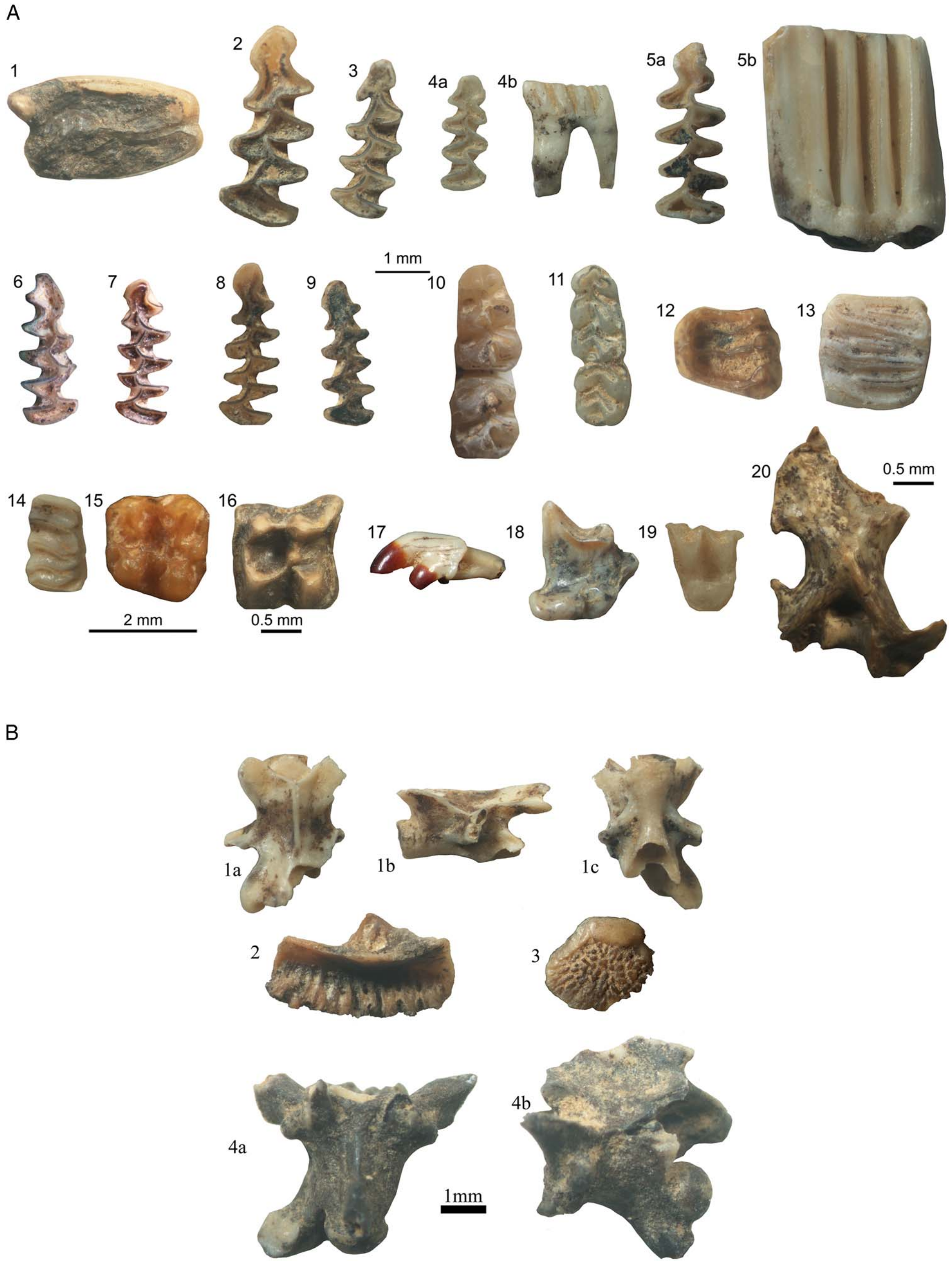

Figure 6. (color online) (A) Some small mammals from Lezetxiki II Cave (Arrasate, Basque Country, Iberian Peninsula). cf. *Oryctolagus cuniculus* (1) right m2; *Arvicola amphibius* (2) left m1; C*hionomys nivalis* (3) left m1; *Clethrionomys glareolus* (4a–b) right molar; *Pliomys lenki* (5a–b) left m1; *Microtus oeconomus* (6) right m1; *Microtus agrestis* (7) left m1; *Microtus arvalis* (8) left m1; *Microtus (Terricola)* sp. (9) left m1; *Allocricetus bursae* (10) left m1-m2; *Apodemus sylvaticus-flavicollis* (11) right m1-m2; *Eliomys quercinus* (12) right m1; *Glis glis* (13) left m2; *Muscardinus avellanarius* (14) right M1; *Sicista betulina* (15) right P4; *Erinaceus* cf. *europaeus* (16) left m1; *Sorex araneus-coronatus* (17) left I; *Neomys* sp. (18) right P4; *Crocidura russula* (19) right M1/2; *Talpa* cf. *europaea* (20) left humerus. Scale bars: 1–14, 17–19 = 1 mm; 15 = 2 mm; 16, 20 = 0.5 mm. (B) Some amphibians and reptiles from Lezetxiki II Cave (Arrasate, Basque Country, Iberian Peninsula). *Salamandra salamandra* (1a) trunk vertebra dorsal view, (1b) idem lateral view, (1c) idem ventral view; *Rana temporaria-iberica* (2) left premaxilla; *Anguis fragilis* (3) osteoderm; *Vipera* cf. *seoanei* (4a) trunk vertebra ventral view, (4b) idem lateral view. Scale bar = 1 mm.

Paleoenvironmental and paleoclimatic evolution

The pattern of temporal changes in microfaunal assemblages from Lezetxiki II was used to reconstruct environmental change using both the method of habitat weighting (Table 4, Fig. 8) and the proportion of species that predominantly occur in wooded habitats (Table 5, Fig. 9). Our data suggest a paleoenvironment composed mainly of open humid habitats (53 vs. 77%), for the beginning of the sequence (level K), associated with species such as *Microtus agrestis* and *Microtus* (*Terricola*) sp. There are also thermophilous affinity species (like *Eliomys quercinus* or *Sciurus vulgaris*),

Table 4. Number of identified specimens (NISP) and minimum number of individuals (MNI) of small vertebrate species from Lezetxiki II (Arrasate, Basque Country, Iberian Peninsula), organized by cultural period and chronostratigraphic unit. Chal., Chalcolithic; Aurig., Aurignacian; MP, Middle Paleolithic; Ro, rocky; OH, open humid; OD, Open dry; Wa, water; Fo, forest.

	Chal.		Chal.		Aurig.		MP		MP		MP		MP		MP		MP								
Cultural period	A		B		C		E		F		G		H		I		J		K		Habitat				
Level	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	Ro	OH	OD	Wa	Fo
cf. *Oryctolagus cuniculus*											1	1							1	1			1		
Arvicola amphibius									2	2	2	1					3	2	30	22		0.5		0.5	
Arvicola sapidus									1	1									3	2				1	
Chionomys nivalis							1	1	1	1											1				
Clethrionomys glareolus									7	3	9	4													1
Pliomys lenki									15	3	16	5	2	1	1	1			28	12					1
Microtus oeconomus																			9	6		0.5			0.5
Microtus agrestis	2	2	2	2	1	1	1	1	15	11	16	12	1	1	4	3			99	61		0.8			0.2
Microtus arvalis									18	10	3	2					5	4	8	7			0.5		0.5
Microtus (Terricola) sp.	1	1	1	1					6	4	7	5			1	1			35	25		0.5			0.5
Allocricetus bursae									3	2									4	4	0.2		0.8		
Apodemus sylvaticus-flavicollis	19	9	15	6	31	4			95	19	71	16			6	4	2	1	11	6					1
Eliomys quercinus											3	2							10	8			0.2		0.8
Muscardinus avellanarius											3	2													1
Glis glis	1	1							2	2															1
Sicista betulina																	1	1	1	1		0.2			0.8
Marmota marmota																			1	1	1				
Sciurus vulgaris																			1	1					1
Erinaceus cf. *europaeus*											1	1										0.5			0.5
Sorex araneus-coronatus	4	3	3	2	1	1	2	1	54	12	37	6					1	1	96	22					1
Sorex minutus									1	1	1	1	1	1					2	1		0.5			0.5
Neomys sp.									1	1												0.5			0.5
Crocidura russula			1	1	8	1			1	1	8	4							7	3				1	
Talpa europaea							1	1	7	2	10	2											0.5		0.5
Chiroptera indet.	1	1	1	1					4	1	30	2			1	1	10	3	20	2					
Lacertidae indet.									2	2									2	2					
Anguis fragilis	488	8	128	5	615	1			10	3	24	4	3	1					6	4		0.3			0.7
Coronella girondica									1	1											0.2		0.6		0.2
Vipera cf. *seoanei*									1	1									2	2	0.3	0.2			0.5
Alytes obstetricans							1	1														0.3		0.2	0.5
Salamandra salamandra											4	2							1	1	0.1	0.2			0.7
Rana temporaria-iberica											7	2	4	1					33	14					
Totals	516	25	151	18	656	8	6	5	247	83	253	74	11	5	13	10	22	12	410	208					
No. of species	6		6		5		5		20		18		5		4		5		22						

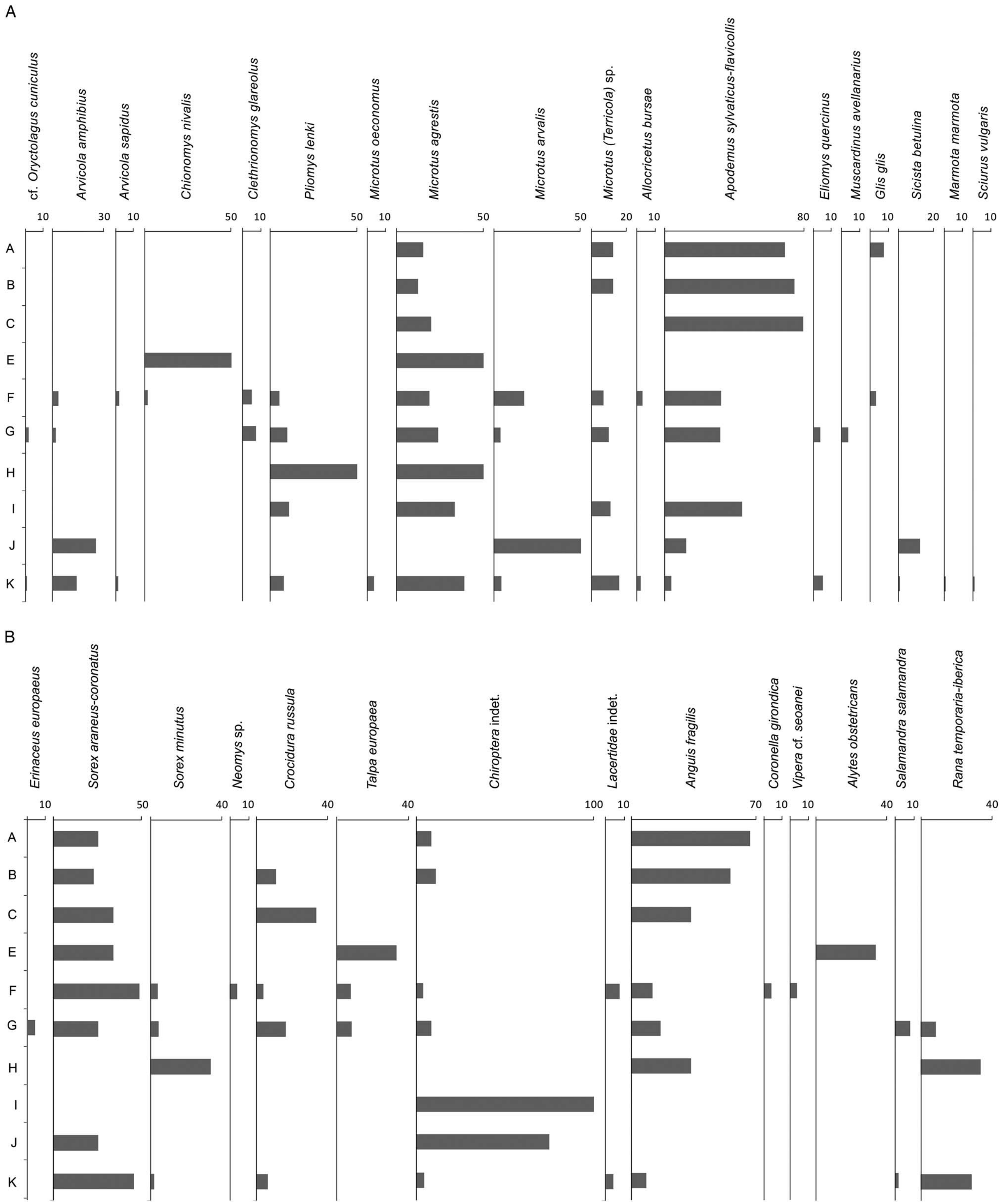

Figure 7. (A) Relative variations of abundance in a part of small mammals from Lezetxiki II Cave (Arrasate, Basque Country, Iberian Peninsula), expressed as the percentage of the minimum number of individuals. (B) Relative variations of abundance in a part of small mammals and herpetofauna from Lezetxiki II Cave (Arrasate, Basque Country, Iberian Peninsula), expressed as the percentage of the minimum number of individuals.

indicating that the environmental conditions could not have been extremely cold. Gradually, the climate probably warmed in level J (Figs. 8 and 9), with an increase of temperature and the decrease of humidity, bringing an increase in forest-dwelling taxa (48% vs. 33%). Therefore, this level may be linked to warm and humid conditions

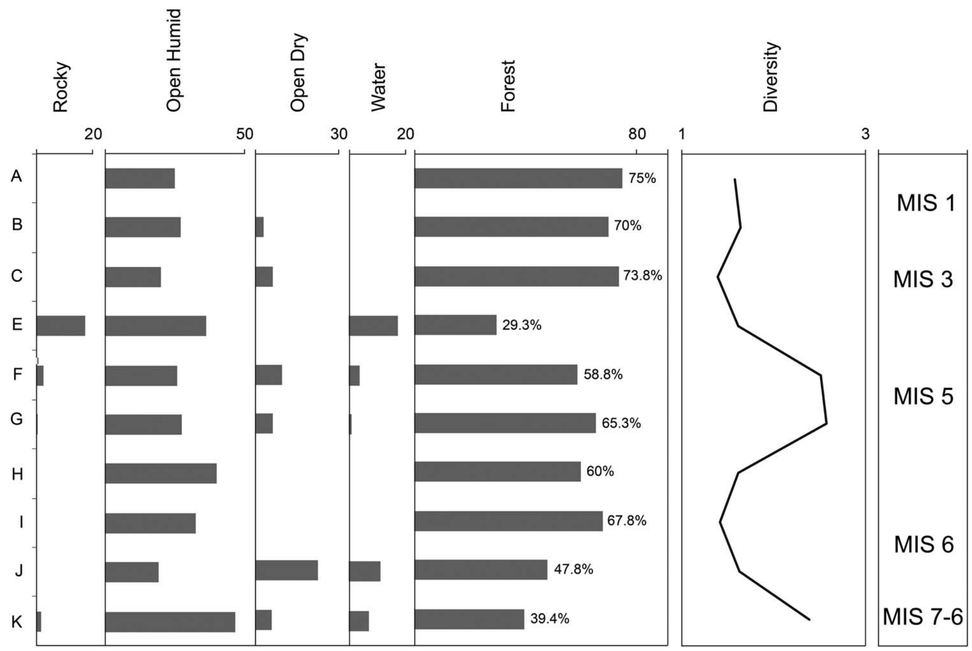

Figure 8. Habitat reconstruction of Lezetxiki II Cave (Arrasate, Basque Country, Iberian Peninsula) using the taxonomic habitat index method, and the diversity index, based on the small vertebrate assemblage. MIS, Marine Oxygen Isotope Stage.

associated with an interstadial period of MIS 6. The survival of taxa currently associated with continental steppes, such as *Sicista betulina*, reflect that the conditions were still quite different than today. This development of the forest is more noticeable from level I onward, although the two methodologies applied in this study differ in their inferred rates of change. Habitat-weighting indicates that the advance of forests slowed down at level H (Fig. 8); the methodology established based on the proportion of forest species suggests that the forest continued to increase during the deposition of level H (Fig. 9).

Throughout level G there were likely increased temperatures indicated by the higher diversity ($H' = 2.583$) and the increase in woodlands habitat taxa (Figs. 8 and 9). These changes may have been brought on by warm and humid conditions associated with an interstadial period of MIS 5, most likely MIS 5e (Eemian interglacial period). Although the percentage of woodland species in level F is somewhat lower, the highest thermophilous taxa diversity is recorded, characterized by the presence of *E. quercinus*, *M. avellanarius*, *C. glareolus*, *P. lenki*, and *A. sylvaticus-flavicollis*. In addition, the Shannon index shows great diversity ($H' = 2.521$). Toward the end of the MIS 5 (level E), temperatures may have slightly cooled (the presence of woodland taxa is 30% or 20% for each methods; Figs. 8 and 9). The progressive climatic warming continued during MIS 3 (level C, Aurignacian period), with a patchy landscape surrounding the cave dominated by forests. This is determined by the great representation of *A. sylvaticus-flavicollis* (50%) and *A. fragilis*. Finally, warm conditions characterize the Chalcolithic period in Lezetxiki II, with woodland dominating the landscape (Figs. 8 and 9), consistent with the climate of the present interglacial period. However, these interpretations should be treated with caution because of the limited size of the samples.

Table 5. Minimum number of individuals (MNI) of small vertebrate species from Lezetxiki II (Arrasate, Basque Country, Iberian Peninsula) used to establish the paleoclimatic and paleoenvironmental evolution.

Level	A	B	C	E	F	G	H	I	J	K
Apodemus sylvaticus-flavicollis	9	6	4		19	16		4	1	6
Eliomys quercinus						2				8
Muscardinus avellanarius						2				
Glis glis	1				2					
Sicista betulina									1	1
Clethrionomys glareolus					3	4				
Sciurus vulgaris										1
Sorex araneus-coronatus	3	2	1	1	12	6			1	22
Sorex minutus					1	1	1			1
Anguis fragilis	8	5	1		3	4	1			4
Salamandra salamandra						2				1

DISCUSSION

Comparison with other paleoenvironmental proxies

In addition to small vertebrates, certain other paleoenvironmental proxies have provided useful information to compare with our data. These include sediment and pollen data, which combined with our results, provide a more general picture of the climatic and environmental changes that occurred in the region. The mineralogical and sedimentologic data (Arriolabengoa et al., 2015) display the characteristics of fluviokarst sedimentation for level K, indicating the concurrence of humid conditions and scarce vegetation cover.

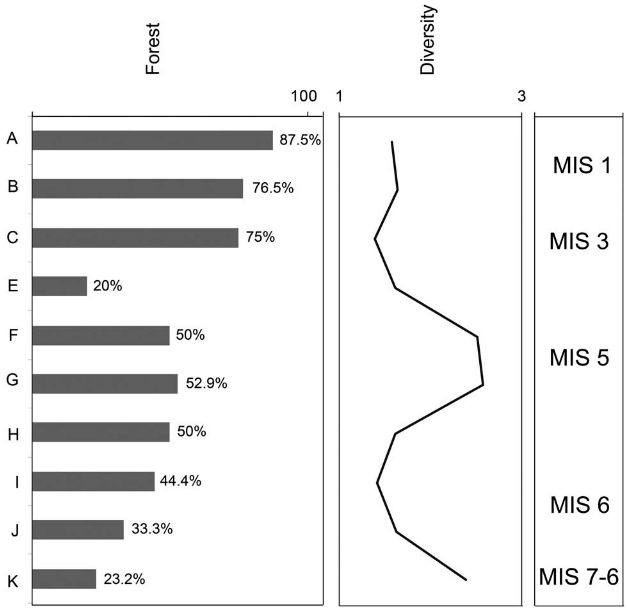

Figure 9. Paleoenvironmental and paleoclimatic reconstruction of Lezetxiki II Cave (Arrasate, Gipuzkoa) using the relative proportion of species predominantly of wooded habitats, and the diversity index, based on the small vertebrate assemblage. MIS, Marine Oxygen Isotope Stage.

For level J, this proxy indicates the start of warmer conditions, which is in accordance with the representation of woodlands inferred by the palynological data (Castaños et al., 2011). From level J onward, the endokarst sediment reflects the infiltration of autochthonous soils, denoting lesser fluviokarst activity and an increase in water infiltration, as well as the precipitation of speleothems in levels H and D. The presence of finer allochthonous sediments in level C suggests greater fluviokarst activity and erosion as a consequence of cooler conditions. Finally, the autochthonous sediments and slight calcite precipitation of levels B and A are related with warmer and wetter conditions.

Comparing our results with those obtained from the mineralogical and sedimentologic study (and the single pollen reference) of Lezetxiki II, we generally find more agreement among the various environmental proxies; however, some differences occur. For example, the small vertebrates suggest that any warming within level J was likely not long-lasting, as meadow-inhabiting taxa still dominate this interval. Additionally, the cooler conditions suggested by mineralogical and sedimentologic data are not indicated by the small vertebrate record, which suggests abundant woodlands and likely warmer conditions.

Other paleoenvironmental reconstructions with small vertebrates from northern Iberia

In the Iberian Peninsula, there are several sites where Middle–Late Pleistocene and Holocene sequences with small vertebrates have been studied from a paleoenvironmental and paleoclimatic point of view, comparable with our data. In this sense, the first site is Arlanpe Cave, a small cave situated in the Arratia Valley (Lemoa, Bizkaia), where a speleothem has been dated at 184,271 +34,258/−26,576 yr BP (Rios-Garaizar et al., 2013). Comparing the paleoenvironmental reconstruction of level K from Lezetxiki II with the corresponding time span at Arlanpe, we find a very similar pattern of habitat, with woodland landscape albeit with considerable meadows, especially ones with wet soil (Garcia-Ibaibarriaga et al., 2013).

For the MIS 6, we focus again on Arlanpe, where both level VI of the entrance and level 4 of the central sector correspond to this period. As in Lezetxiki II, the microvertebrate species associated with open habitats are in the majority, ranging from 53% (level 4) to 47% (level IV). Additionally, the herpetofaunal assemblage from the archaeological site Estanque de Tormentas de Butarque H-02 (Manzanares Valley, central Iberian Peninsula) pointed out that during MIS 6, the climate was colder (−3.0°C) and slightly wetter (+122.8 mm) than at present, with a large representation of dry environments (Blain et al., 2017).

The microfauna of MIS 5 has been studied mainly on the coast of Catalonia sites, for example in Teixoneres (López-García et al., 2012a) and Cova Gegant (López-García et al., 2012b). Any perspective that these Mediterranean sites might supply therefore likely diverges significantly from the Cantabrian sites. Nevertheless, the microvertebrates of the last interglacial period (late MIS 5) identified at the archaeological site of Cueva del Camino (Pinilla del Valle, Madrid) are typically thermophilous species (Arsuaga et al., 2012), similarly to the level F of Lezetxiki II.

The woodland domains inferred by the small vertebrate assemblage during the MIS 3 at Lezetxiki II (level C), is similar to the interpretations for level 8 (ca. 29,600 cal yr BP) at Askondo, where transitory warming seems to correspond with the warmer tendency detected after the Heinrich Event 3 in the NGRIP-GICC05 (North Greenland Ice Core Project-Greenland Ice Core Chronology 2005) record that culminated in the warm Greenland Interstadial 4 (Garcia-Ibaibarriaga et al., 2015b). One of the few sites from this period with a microfaunal study is the now disappeared neighboring site of Labeko Koba (Arrasate, Basque Country), which records a complete lack of cold-related taxa and a relatively high abundance of *Glis glis* for the Aurignacian period (levels VII to IV; Pemán, 2000). It is important to highlight that in both cases, the microfaunal data are in contradiction with the data obtained from other environmental proxies.

Finally, microvertebrate fossil remains from the uppermost levels (B and A) of Lezetxiki II Cave have been assigned to the Chalcolithic period. The results coincide with a Holocene climate, with a warm, wet climate similar to the current one. Woodlands were the dominant landscape as in many archaeological sites of similar chronology (El Mirón: Cuenca-Bescós et al., 2009; Santimamiñe: Rofes et al., 2014; El Mirador: Bañuls-Cardona et al., 2013).

CONCLUSION

The small vertebrate assemblage from Lezetxiki II Cave, the oldest record of the Cantabrian Range, provides a rare opportunity to articulate the paleonvironmental and paleoclimatic scenario of the "Basque crossroad" during the late middle Pleistocene and late Pleistocene, improving additionally our knowledge of the northern third of the Peninsula. In addition, the significance of the basal levels from Lezetxiki II should be noted as they represent the possible context of the human humerus found in 1964 in Leibar Cave (Arrizabalaga et al., 2005), which represents the oldest human fossil of the Basque Country.

The 3-m-deep deposit began with a cold period, at the end of MIS 7 or beginning of MIS 6 (level K), while levels J–I could correspond to MIS 6. The small vertebrate assemblage from Lezetxiki II Cave could provide useful information about the internal variations of MIS 5, because the changes observed in levels H–E could correspond to these fluctuations. Likewise, during MIS 3 (level C) warming is suggested by the small vertebrate remains. Finally, the woodland reconstruction of the uppermost two levels (B and A) is consistent with their middle Holocene age.

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