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Palaeoenvironmental and palaeoclimatic 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 palaeoenvironmental and palaeoclimatic 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 micropalaeontological relevance for the Iberian Peninsula, especially because it contains the most ancient small vertebrate remains found in the Cantabrian Region, likely deposited during MIS 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 while 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 travelling between the Iberian Peninsula and European continent.

Keywords

Small vertebrates; Palaeoenvironment; Middle-Upper Pleistocene; Holocene; Cantabrian Range; Iberian Peninsula.

1. Introduction

During the last ten years, 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 (Aranburu et al., 2015; Castaños et al., 2014; Iriarte, 2009; Martínez-García et al., 2013). 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 travelling 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 south-western 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 (Álvarez-Alonso and Arrizabalaga, 2012; Arrizabalaga, 2006), macrofaunal investigations (Altuna, 1972; Castaños et al., 2011), descriptions of microfaunal assemblages (Chaline, 1970; Garcia-Ibaibarriaga et al., 2015a; Rofes et al., 2012), 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, since 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.

2. 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 masl 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-palaeontological infillings (Álvarez-Alonso and Arrizabalaga, 2012). In addition, there are numerous archaeo-palaeontological sites in the surrounding region, some of them with microvertebrate records (e.g. Artazu VII, Suárez-Bilbao et al., 2017; Labeko Koba, Peman, 2000; Bolinkoba, Garcia-Ibaibarriaga et al., 2015b; Askondo, 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 Jose 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 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 methodology (i.e. micromorphological analysis, palynological sampling, new dating, etc.; Arrizabalaga 2006, 2005), 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” (N-S 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 x 4).

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 paper, we 1) clarify and synthesize previously published and new chronological work at the cave, and 2) describe newly examined small vertebrate assemblages and make palaeoenvironmental inferences based on these data.

3. Material and Methods

3.1 Fieldwork and collecting techniques

The sequence from Lezetxiki II (Fig. 2B) was divided into eleven lithostratigraphic levels (Arriolabengoa et al. 2015), named using letters in alphabetical order (from A to K; Table 1). In 2011, sampling for micropalaeontological analysis was carried 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 litres of sediment), of 0.33 m^2 each, were taken through the three meters-long stratigraphic sequence in subsequent sublevels 5–10 cm thick (Fig. 2B).

The samples were processed with the water-screening method using a stack of sieves of decreasing mesh size (4 mm-0.5 mm). In subsequent years, small-mammal bony remains were analysed and quantified as part of a PhD thesis (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.

3.2 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 (1999, 1991), 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 post-cranial diagnostic element: isolated teeth for the lagomorphs; isolated teeth and mandibles for the rodents (first lower molars for the Arvicolinae); isolated teeth, mandibles and post-cranial 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 their position in the skeleton. Laterality and sex (for amphibians) were taken into account, whenever possible.

3.3 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 (Andrews et al., 1979; Fleming, 1973; Kerr and Packer, 1977), so it is possible to use diversity as a general indicator of climatic changes (Andrews and O'Brien, 2000; Blois et al., 2010; Montuire, 1995). Warmer climatic conditions are often associated with increased diversity and ecosystem complexity (Barbault, 1994; Margalef, 1974). 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 to the size of the sample, and it is more suitable when it comes to highlight minority species. The indices were calculated with the Paleontological Statistic Program (PAST; Hammer et al., 2001).

3.4 Habitat types and climate categories

Palaeoclimate and palaeoenvironmental 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 Bergeramendi (1994), International Union for Conservation of Nature (IUCN; 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, since 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 (Cuenca-Bescós et al., 2008; Iriarte-Chiapusso and Murelaga, 2012; Rofes et al., 2013; Sese, 2005).

4. Results

4.1 Chronology

Although the chronology of the cave deposits has been presented in several papers (Falguerès et al. 2006; Higham et al., 2014; Maroto et al., 2012), 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 BP (Table 2), suggesting that this level was deposited throughout the first phase of MIS 4. 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 ka and 86.8 ka, which give a mean value of 78.4 ± 8.4 ka. These results most likely represent minimum age estimates, since they are not consistent with the sedimentological 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 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).

Considering the new dating, and the data provided by the sedimentological (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, a 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 sedimentological 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 break-up of the cave environment. Therefore, we propose a 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 Palaeolithic, consistent with MIS 5d-b assignation (110-82). Althought there is a U/Th age for Level D, suggesting a deposition during the MIS 4, we consider more consistent the sedimentological assignation, which suggests the final phase of MIS 5a (ca. 82-74 Ka; Arriolabengoa et al., pers. comm.). The chronological assignation for Level C, based on archaeological material, is likely Aurignacian (MIS 3, ca. 60-30), when the cave was apparently used as a secondary settlement

(Arrizabalaga, 2003, 2001). Finally, the ceramic, faunal, and lithic fragments discovered in Levels A and B suggests 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 sedimentological and palaeontological composition of the level).

4.2 Taphonomic remarks

A preliminary study of the taphonomy of the small vertebrate assemblage from Lezetxiki II indicates that several predators likely contributed to the formation of the deposits (Andrews, 1990), while changes in preservation across the sequence indicate post-depositional 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-mammal 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 (for example, the lack of faunal remains in Level H would be related with the sedimentological composition of the level, as indicate Arriolabengoa et al., 2014).

A main characteristic of the small vertebrate assemblage is the high fragmentation of the bones. Due to 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 (4,186), followed by incisors (10.66 %, 1,091 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 around 40%. Another oddity is the conservation of ribs in Level C, fifteen 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 around 60%. Even if current natural accumulations tend to conserve 80–90%, this value indicates that these two levels suffered less postdepositional processes than the rest of the levels in this cave.

4.3 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 post-cranial bones). More than two thousands of them (2,211) have been identified at the genus and/or species level (NISP), representing a total of 432 individuals (MNI). The small vertebrates comprise 32 taxa (Fig. 6a and 6b and Table 4): one lagomorph (cf. *Oryctolagus cuniculus*), ten cricetids (*Arvicola amphibius, Arvicola sapidus, Chionomys nivalis, Clethrionomys glareolus, Pliomys lenki, Microtus oeconomus, Microtus agrestis, Microtus arvalis, Microtus (Terricola)* sp., and *Allocricetus bursae*), one murid (*Apodemus sylvaticus-flavicollis*), three glirids (*Eliomys* *quercinus, Muscardinus avellanarius*, and *Glis glis*), two sciurid (*Marmota marmota* and *Sciurus vulgaris*), one dipodid (*Sicista betulina),* one erinaceid (*Erinaceus* cf. *europaeus*), four soricids (*Sorex araneus-coronatus, Sorex minutus, Neomys* sp., and *Crocidura russula*), one talpid (*Talpa* cf. *europaea*), Chiroptera indet., two saurians (Lacertidae indet. and *Anguis fragilis*), two snakes (*Coronella girondica* and *Vipera* cf. *seoanei*), one salamandrid (*Salamandra salamandra*), one midwife toad (*Alytes obstetricans*), and one ranid (*Rana temporaria-iberica*).

Most of the taxa identified at Lezetxiki II cave have extant representatives (VV.AA, 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 (VV.AA, 1989). Some other species are absent even from the Iberian Peninsula, like *M. oeconomus*, which presently has a wide range extending from north-west 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*; Meining et al., 2008), but not to *M. avellanarius*, which in Europe is only absent from Iberia, south-western France, and northern Fennoscandia and Russia (Amori et al., 2008). Finally, we have identified two extinct species at Leczetxiki 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). And 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).

4.4 Small vertebrate community changes over time

There are significant taxonomical differences in the small vertebrates between the base and the top of the Lezetxiki II cave sequence (Fig. 7a and 7b and 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 7b and 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 due to the abundance of *M. agrestis* and *S. araneus-coronatus* (Fig. 7a and 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 above. Levels J, I, H and E are the poorest subunits of the entire stratigraphic sequence (Fig. 7a and 7b) from a quantitative point of view, although it is true that only a single 5-10 cm deep sample has been taken from each of them. Level C (MIS 3) is also poor in individuals (Fig. 7a and 7b and 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 *Anguis fragilis* dominating the NISP and *Apodemus sylvaticus-flavicollis* the MNI (Fig. 7a and 7b and Table 4).

4.5 Palaeoenvironmental and palaeoclimatic evolution

The pattern of temporal changes in microfaunal assemblages from Lezetxiki was used to reconstruct environmental change using both the method of habitat weighting (Table 4 and Figure 8), and the proportion of species that predominantly occur in wooded habitats (Table 5 and Figure 9). Our data suggest a palaeoenvironment 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*), indicating that the environmental conditions could not have been extremely cold. Gradually, the climate probably warmed in Level J (Fig. 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 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 onwards, 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 was likely increased temperatures indicated by the higher diversity (H’ = 2.583), and the increase in woodlands habitat taxa (Fig. 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). Although the percentage of woodland species in Level F is somewhat lower, the highest thermophilous taxa diversity is recorded, characterized by the presence *E. quercinus, M. avellanarius, C. glareolus, P. lenki,* and *A. sylvaticus-flavicollis*. In addition, the Shannon Index shows great diversity (H’ = 2.521). Towards the end of the MIS 5 (Level E) temperatures may have slightly cooled (depending on the method 30% or 20% of woodland taxa; Fig. 8 and Fig. 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 of *A. sylvaticus-flavicollis* (50%) and *A. fragilis*. Finally, warm conditions characterize the Chalcolithic period in Lezetxiki II, with woodland dominating the landscape (Fig. 8 and Fig. 9), consistent with the climate of the present interglacial. However, these interpretations should be treated with caution due to the limited size the samples

5. Discussion

5.1 Comparison with other palaeoenvironmental 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 sedimentological data (Arriolabengoa et al. 2015) display the characteristics of fluviokarst sedimentation for Level L, indicating the concurrence of humid conditions and scarce vegetation cover. For level J, this proxy indicates the start of the warmer conditions, which is in accordance with the representation of woodlands inferred by the palynological data (Castaños et al., 2011). From Level J onwards, 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 sedimentological 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 sedimentological data is not indicated by the small vertebrate record, which suggests abundant woodlands and likely warmer conditions.”

5.2 Other palaeoenvironmental 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 palaeoenvironmental and palaeoclimatic 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 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 M6 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 microvertebates of the last-interglacial (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 small vertebrate assemblage during the MIS 3 at Lezetxiki II (Level C), is similar to the interpretations for Level 8 (ca. 29,600 cal BP) at Askondo, where transitory warming seems to correspond with the warmer tendency detected after the HE 3 event in the NGRIP-GICC05 record that culminated in the GI-4 warm event (Garcia-Ibaibarriaga et al., 2015c). One of the few sites from this period with a microfaunal study is the now disappeared neighbouring 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; Peman, 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).

6. Conclusion

The small vertebrate assemblage from Lezetxiki II cave, the oldest record of the Cantabrian Range, provides a rare opportunity to articulate the palaeonvironmental and palaeoclimatic scenario of the “Basque crossroad” during the late Middle Pleistocene and Upper 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 three 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, since 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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Table 1 Geological description of the stratigraphic levels in Lezetxiki II cave, modified from Arriolabengoa et al. (2015)

Table 2 List of numerical ages from Lezetxiki II cave (Arrasate, Basque Country, Iberian Peninsula) including cultural periods, chrono-stratigraphic units, laboratory codes, and sample details.

Table 3 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 (De) by the total dose rate.

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 chrono-stratigraphic unit.

Chal, Chalcolithic; Aurig, Aurignacian; MP, Middle Palaeolithic. Ro, Rocky; OH, Open Humid; OD, Open Dry; Wa, Water; Fo, Forest.

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

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

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 micropalaeontological samples (red boxes) and already published *Muscardinus avellanarius* (yellow star), *Sicista betulina* (red ellipse) and *Macaca sylvanus* (blue square) remains.

Figure 3 Single-grain TT-OSL 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 (Standardised 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 furthest to the right, and the least precise estimates fall furthest to the left. The grey band is centred on the weighted mean D_e value calculated using the central age model

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.

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

Figure 6a 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-4b) left molar; *Pliomys lenki* (5a-5b) 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 bar 1-14, 17-19= 1 mm; 15= 2mm; 16, 20= 0.5mm.

Figure 6b Some amphibians and reptiles from Lezetxiki II cave (Arrasate, Basque Country, Iberian Peninsula). *Salamandra salamandra* (1a) Trunk vertebrae 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.

Figure 7a 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 (MNI).

Figure 7b 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 (MNI).

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.

Figure 9 Paleoenvironmental and plaeoclimatic 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.

Table 1

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 3e4 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), while in K15 it is only circa 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 since it is interrupted by a series of large boulders

Table 2

Level	Cultural period	U ppm	U234/U238	Th230/Th232	Th230/U234	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

Table 3

Sample	Layer	Grain size (μm)	Measured water content [a]	Environmental dose rate (Gy/ka): Beta dose rate [c,d]	Gamma dose rate [c,d]	Cosmic dose rate [e]	Total dose rate [f,g]	Equivalent dose (D_e) data: 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 % 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 SAR rejection criteria of Arnold et al. (2014) and were used for D_e determination / total number of grains analysed.

[i] The relative spread in the D_e dataset 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 of 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.

Table 4

Cultural period	**Chal.**		**Chal.**		**Aurig.**		**MP**		**MP**		**MP**		**MP**		**MP**		**MP**				**Habitat**				
Level	**A**		**B**		**C**		**E**		**F**		**G**		**H**		**I**		**J**		**K**						
	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		
Apodemussylvaticus-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 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						

Table 5

Level	A	B	C	E	F	G	H	I	J	K
Apodemussylvaticus-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

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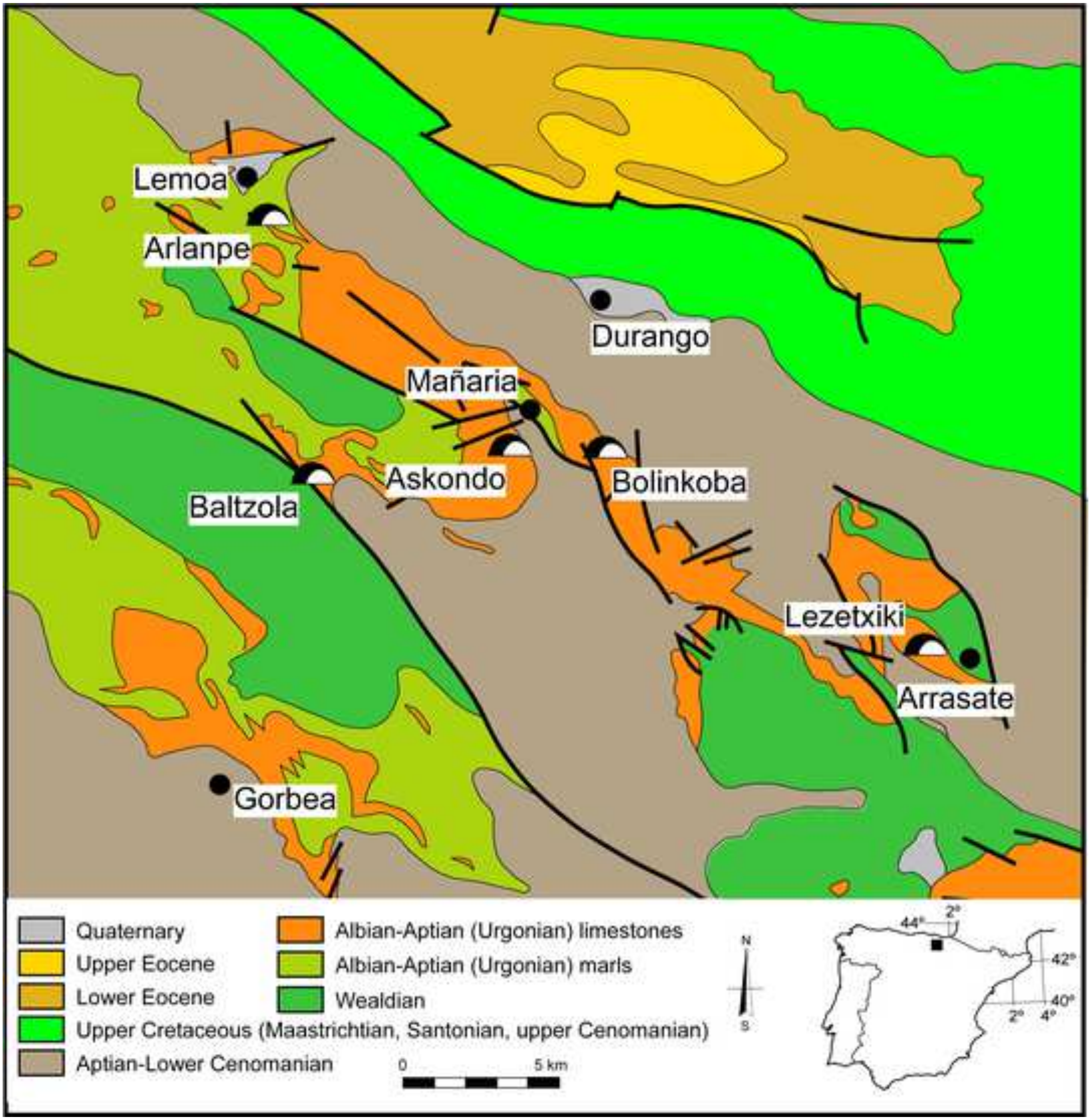

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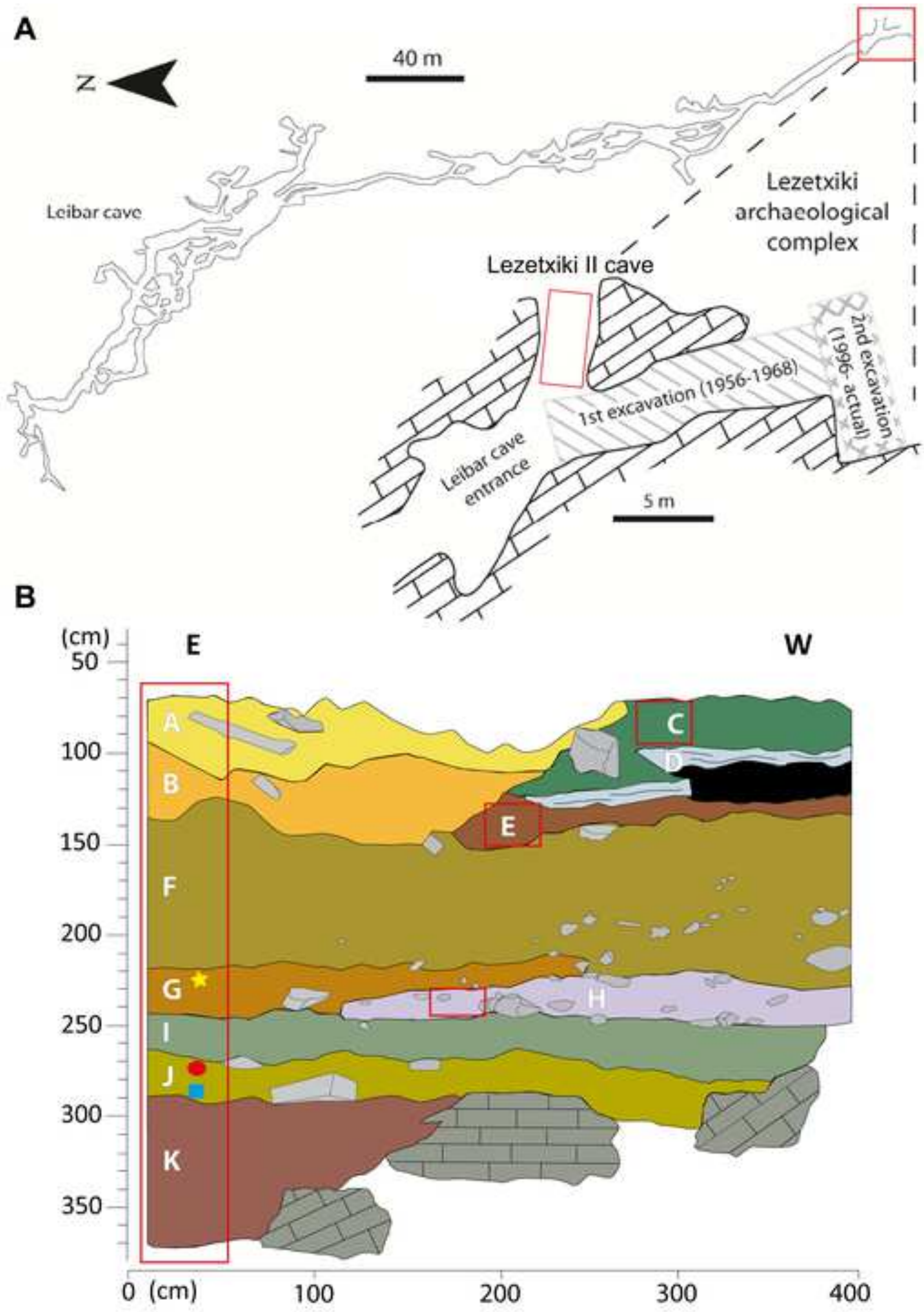

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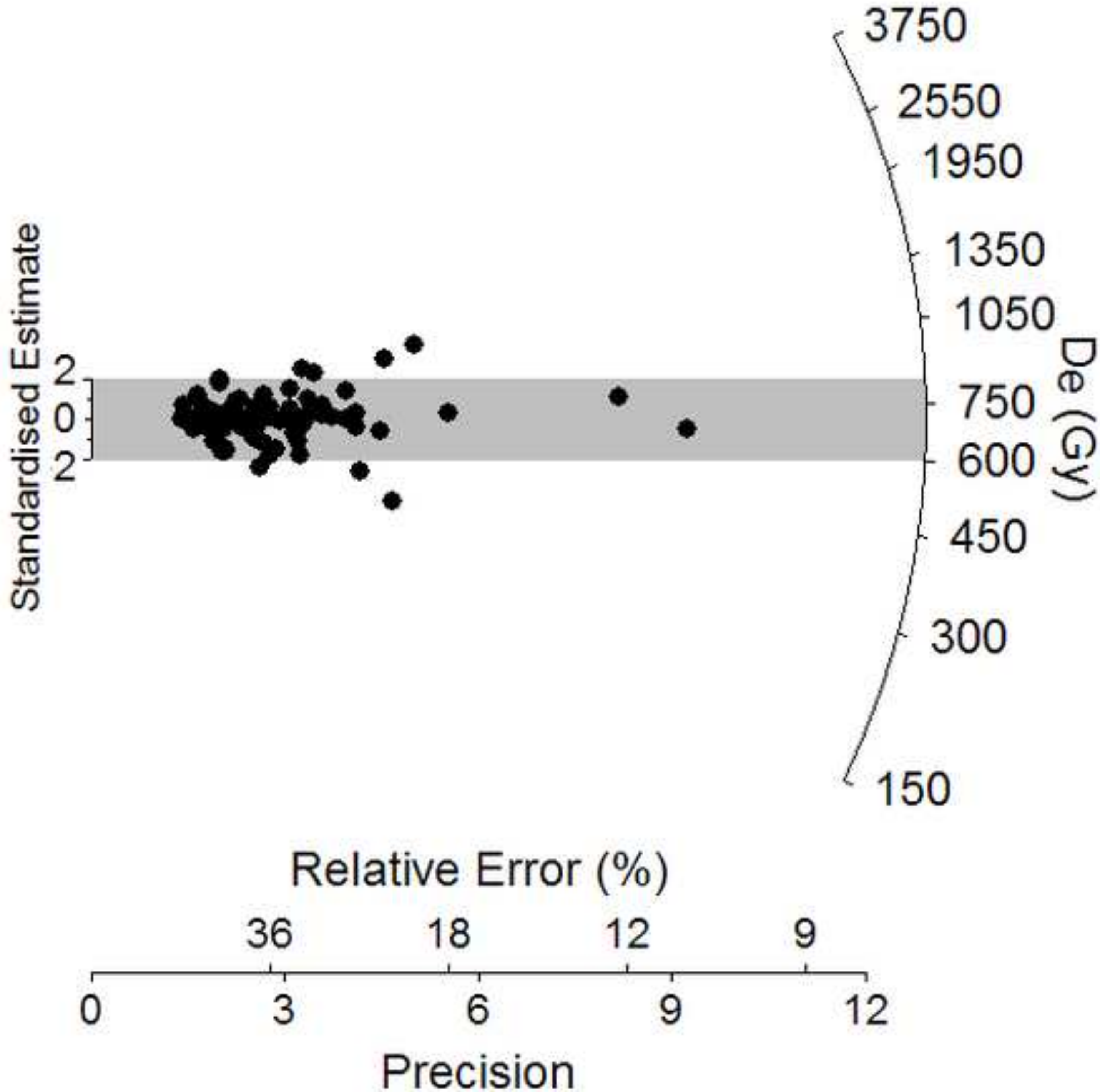

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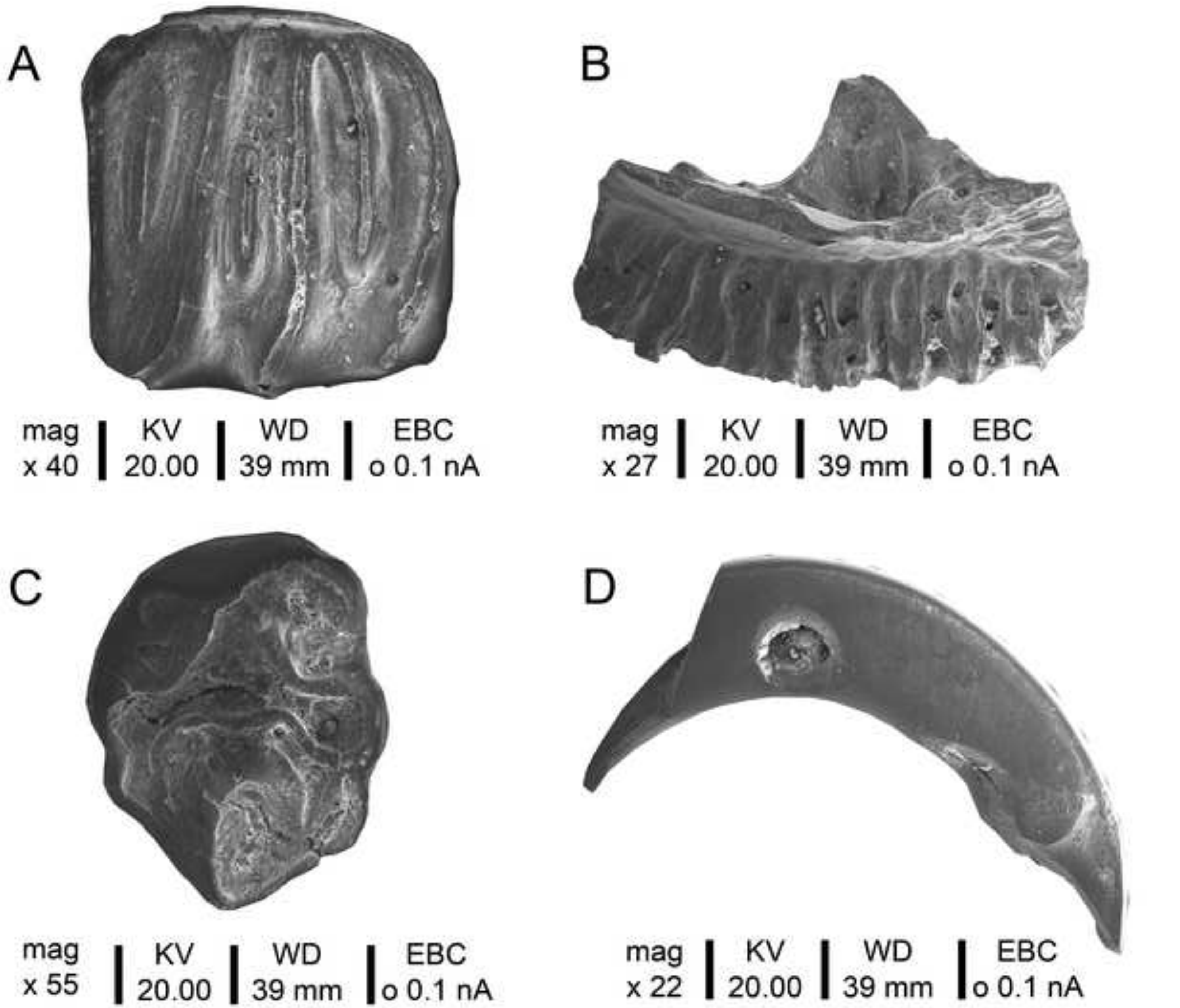

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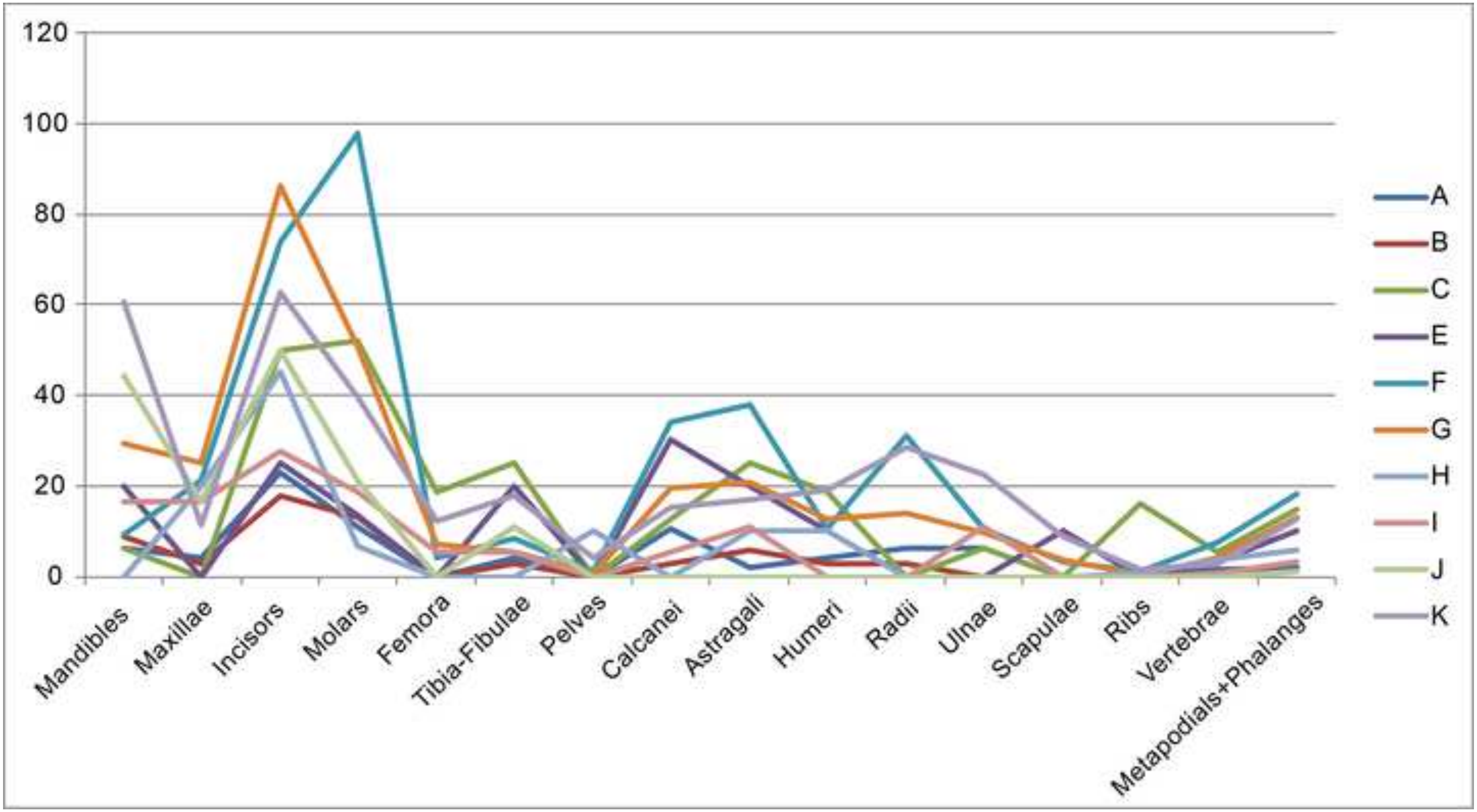

Figure 6a

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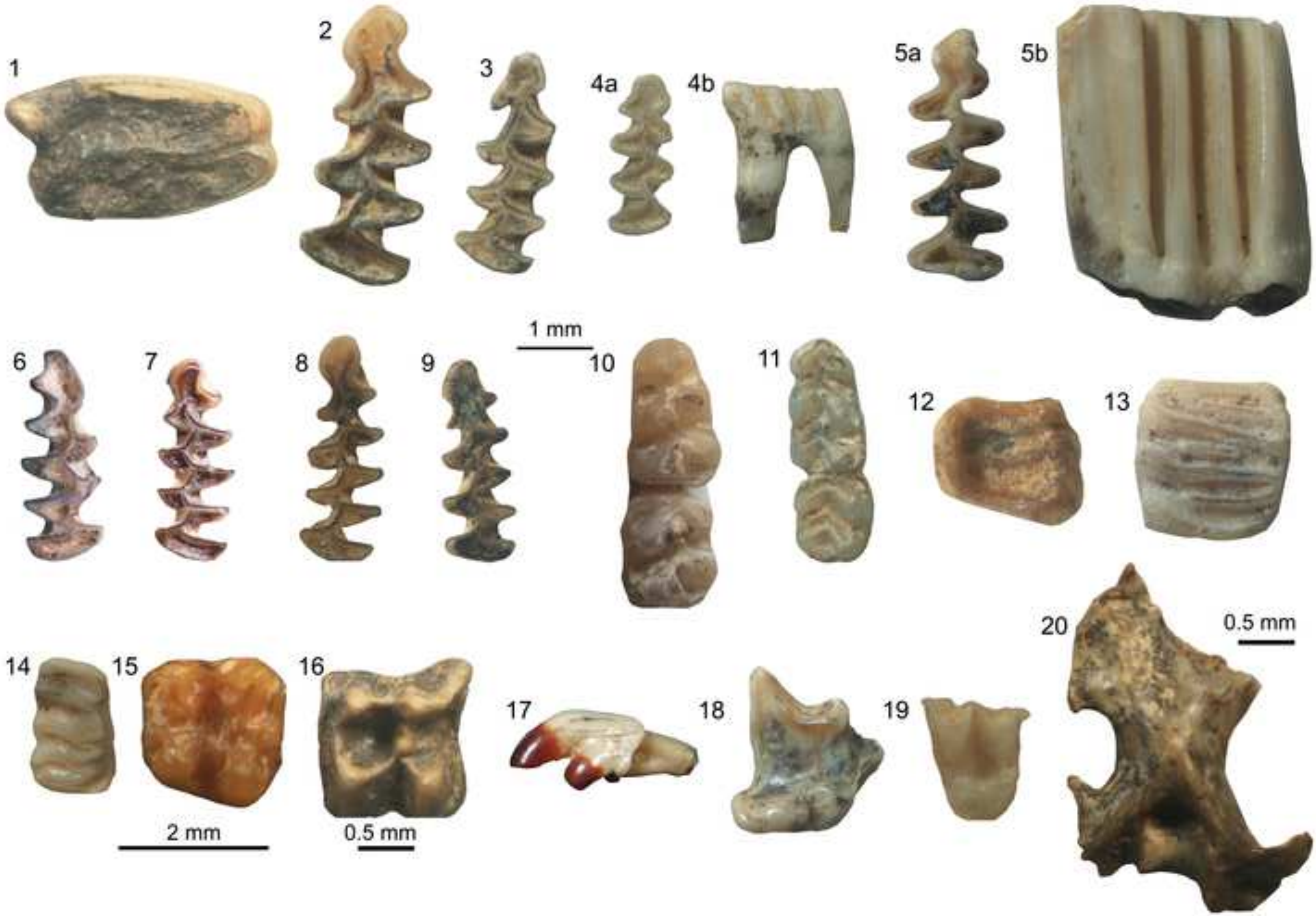

Figure 6b

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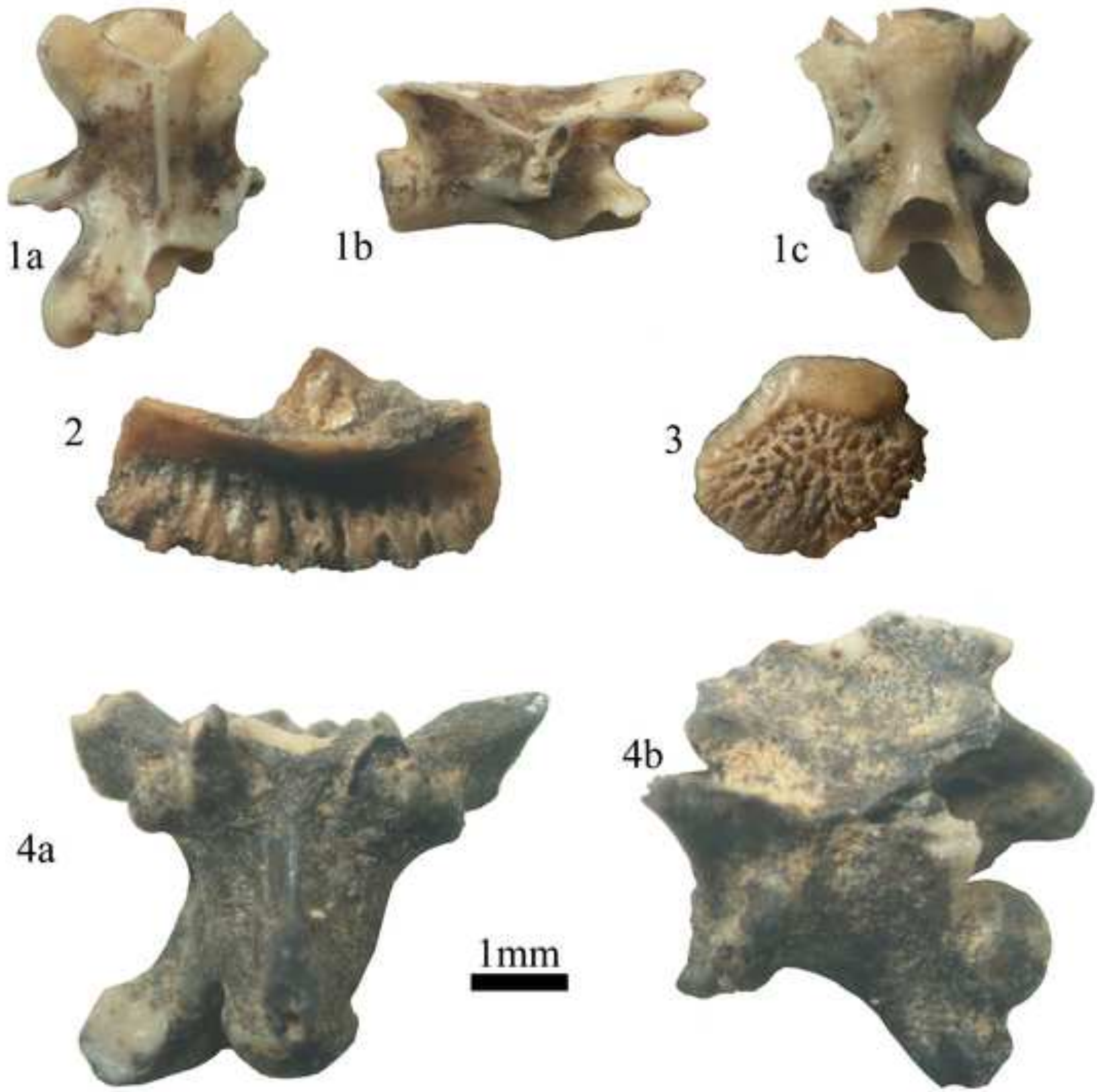

Figure 7a

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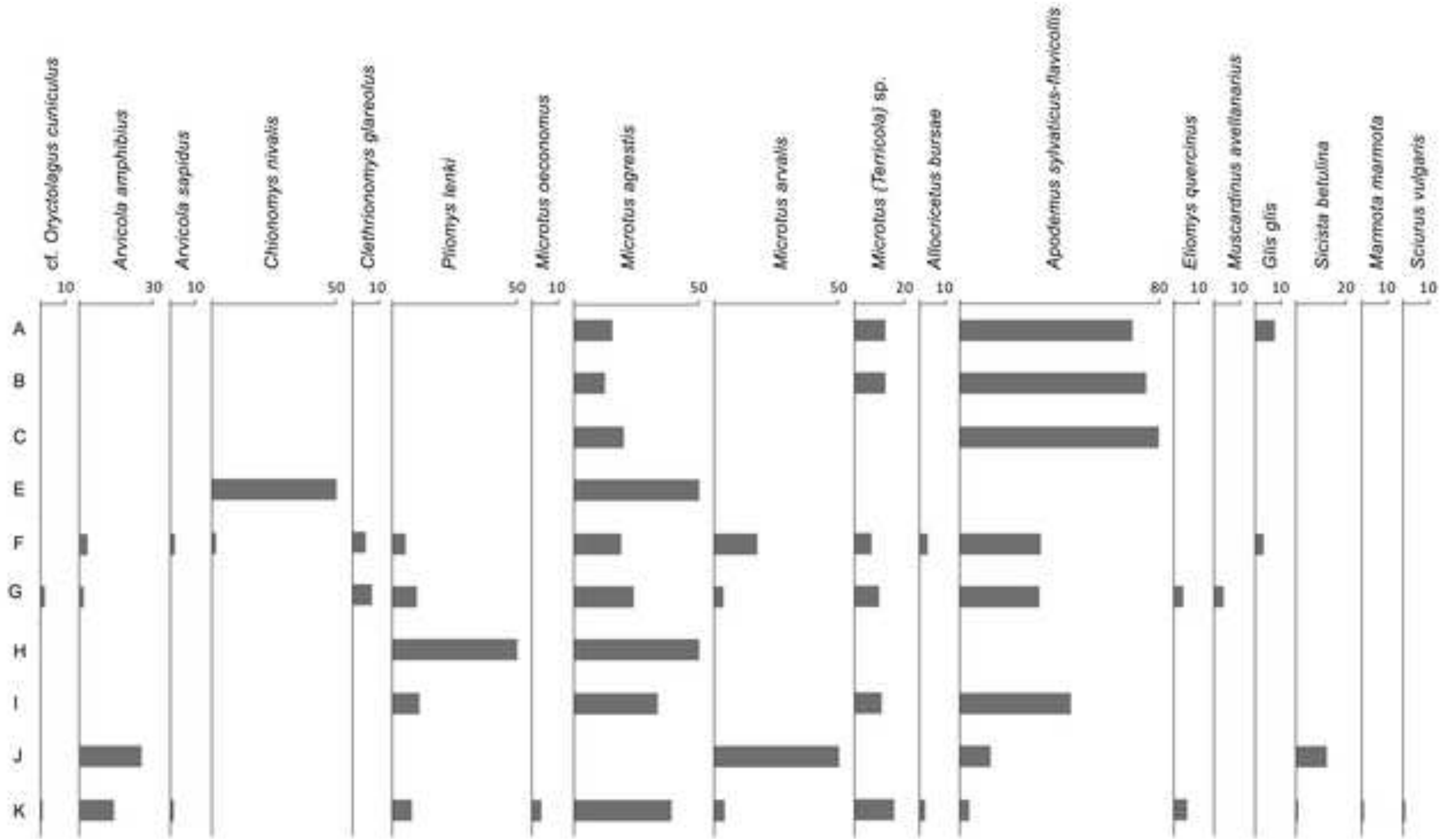

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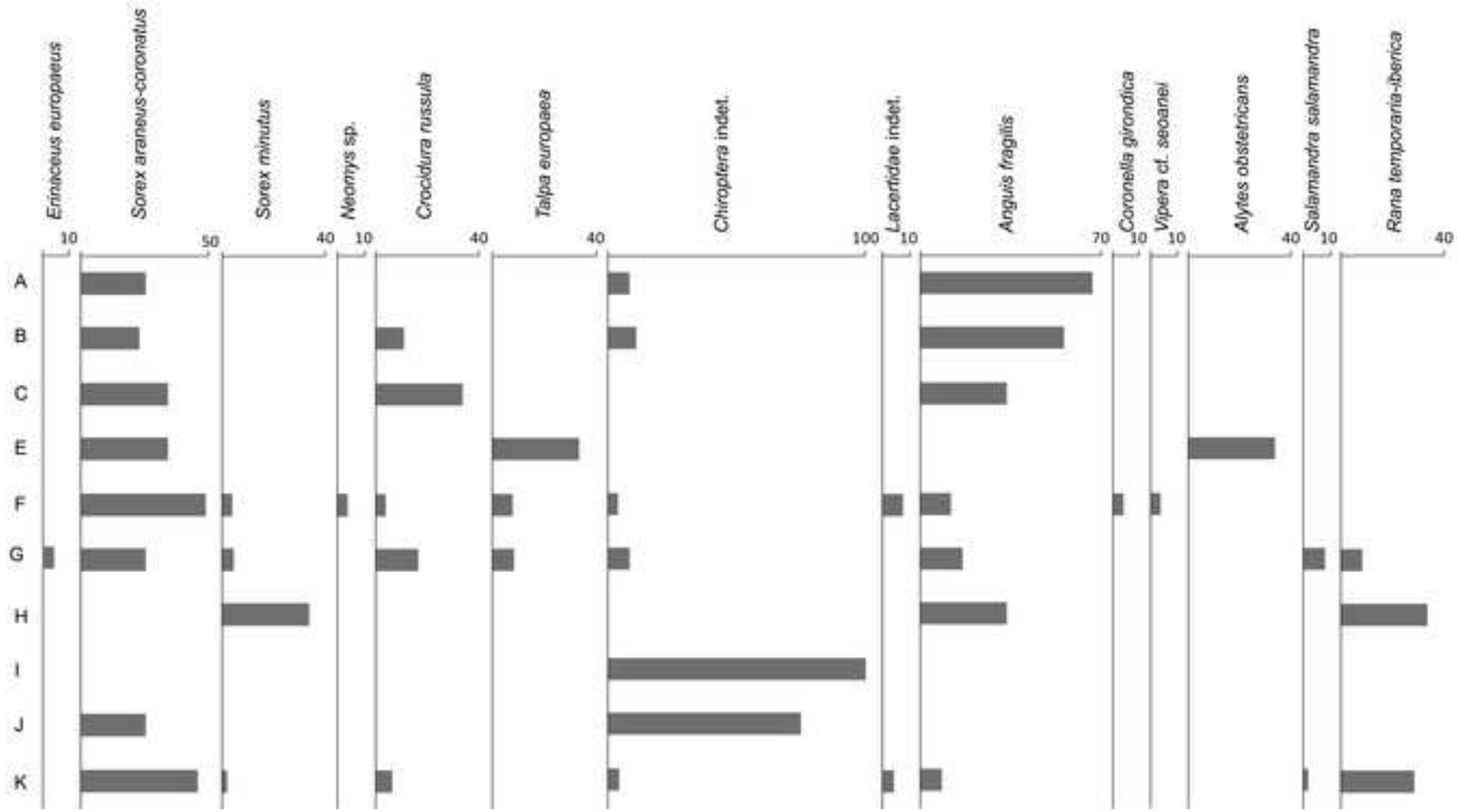

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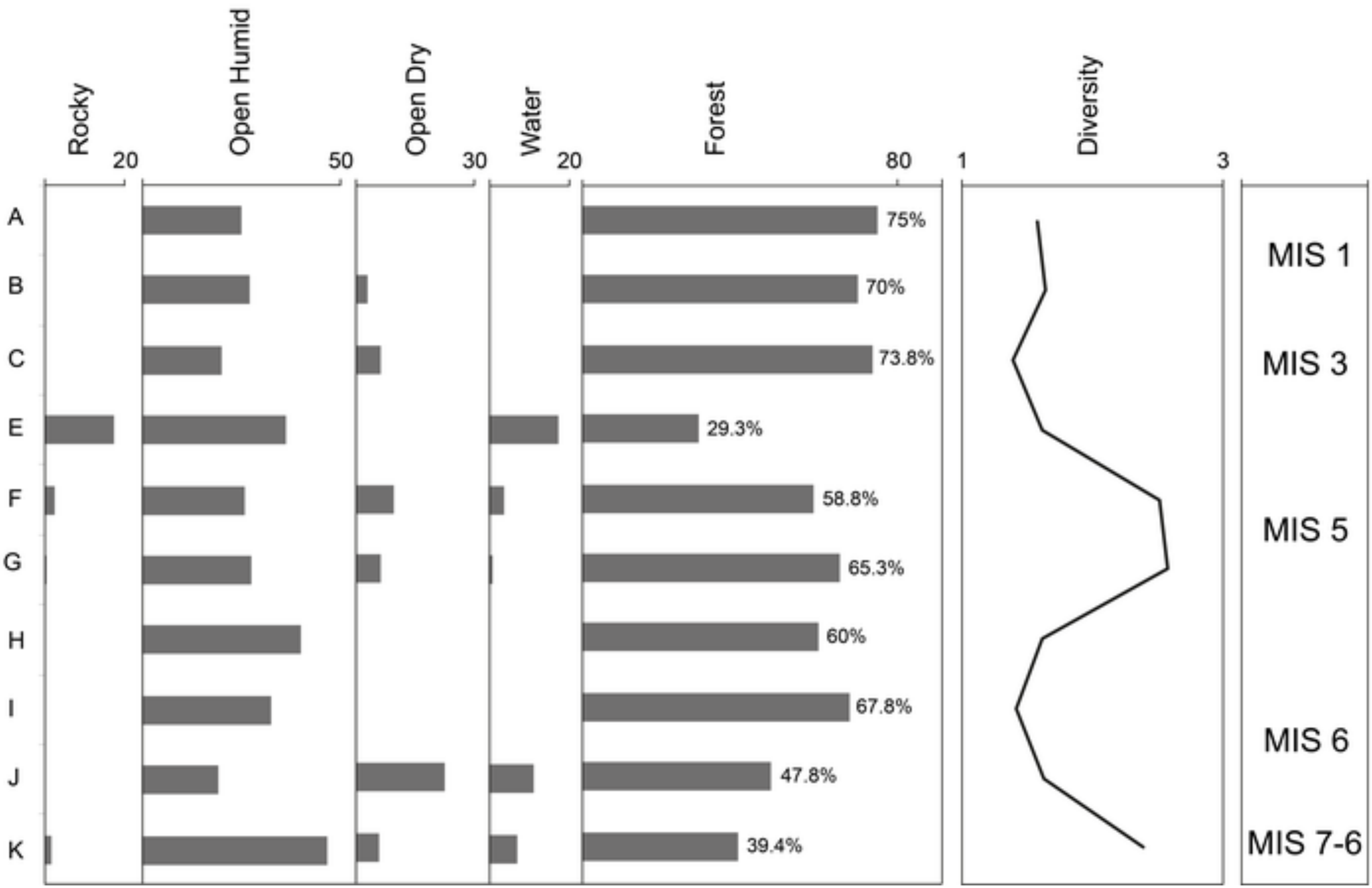

Figure 9

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