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Late Pleistocene Environmental Reconstruction of Northeastern Iberia through the small mammal assemblages: The Case of Cudó Cave (Mont-ral, Tarragona)

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ABSTRACT

Cudó cave is a new unpublished archaeological site located in the eastern side of the Prades Mountain on the elevation of 987 m.a.s.l and belongs to the municipality of Mont-ral, Alt camp, Tarragona. The excavation since 2016 have exposing nine stratigraphic levels that provided archaeological data including faunal remains, bone and lithic artefacts, marine shell fish ornaments, pottery, as well as other glass and metal artefacts. Moreover, exceptionally rich assemblages of small mammal stand out of this site.

Dating analysis shows the range from very recent time up to ca. 31.2 ka cal BP. This work covers analysis of the small mammals from two richest levels of the site: level 107, dated to 31.2 – 24.4 ka cal BP and level 105, dated to 15.5 – 10.2 ka cal BP. This chronological frame is are interesting as it coinciding to several climatic event such as HE3, the beginning or HE2, the beginning of Last Glacial Maximum (LGM), and the warming period after the LGM. It also considering the limited terrestrial environmental data regarding this period in northeastern Iberia. For this reason, this work will provide the opportunity to increase the available knowledge about the paleoenvironment condition experienced in northeastern Iberia around the period of LGM using the small mammal assemblages.

Several methodologies covering both qualitative and quantitative approaches are used to reach this goal. These are based on the taxonomic identification and the taphonomy, complement with different paleoenvironmental methods, such as the diversity index, the chorotypes classification, the habitat weighting, the bioclimatic model, and the mutual ecogeographic range analysis. These also to recognize the main accumulation agent of the assemblages, to reconstruct the paleoenvironmental conditions in the vicinity of Cudó cave, and to get the bigger view of paleoenvironmental conditions in northeastern Iberia around LGM.

From the taxonomic analysis, up to 14 different small mammal taxa have been identified, those are *Crocidura russula*, *Sorex* gr. *araneus-coronatus*, *Rhinolophus* cf. *ferrumequinum*, *Myotis* gr. *myotis-blythii*, *Pipistrellus* cf. *pipistrellus*, *Microtus arvalis*, *Microtus agrestis*, *Microtus* gr. *arvalis*-agrestis, *Microtus* (*Terricola*) *duodecimcostatus*, *Microtus* (*Iberomys*) *cabrerae*, *Chionomys nivalis*, *Apodemus sylvaticus*, *Eliomys quercinus*, and *Sciurus vulgaris*. By the taphonomic analysis, these small mammal assemblages are mainly produced by nocturnal and diurnal raptors such as *Strix aluco, Athene noctua, Circus cyaneus, falco perregrinus,* and *Falco tinnunculus*. This number of taxa indicate a quite rich and diverse assemblages during the deposition period. The palaeoecological analysis also supports this signal with the presence of four habitat type: woodland, humid grassland, dry grassland, and rocky, even though one habitat is dominant above the others for each level. In level 107 the rocky landscape is the most represented habitat, followed by the woodland and grassland. While in level 105, the woodland landscape dominates the habitat followed by rocky and grassland. From the climatic point of view, mid-European climate is dominant in level 107, with low mean temperatures and high precipitation rates. Otherwise in level 105 it prevails a milder Mediterranean climate with higher mean temperatures and lower precipitation rates. These shows the improvement of the environmental conditions from level 107 to 105 from open and cold landscape to closer and warmer landscape.

Those results are consistent to the general trend of environmental changes in northeastern Iberia within the equivalent period. The pattern of cooling towards the beginning

of LGM and warming after the LGM are in line between Cudó cave and the other sites in this region, although the Cudó level 107 shows a colder climate. However, exceptional humidity is observed in Cudó level 107, contrast to the aridification trend. These differences could be related to the geographic peculiarities where Cudó cave situated.

Keyword: paleontology, taphonomy, paleoclimate, Heinrich Events, LGM, northeastern Iberia, Mediterranean basin

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1. INTRODUCTION AND MAIN OBJECTIVES

The end of Late Pleistocene is one critical period in human history considering the abrupt climatic fluctuations that were experienced, affecting the environment and the human subsistence. One crucial period is the Last Glacial Maximum (LGM), when the ice caps reach its maximum extend, the sea level reach its lowest point, and the sea surface temperature drops (Maier et al., 2021 and references therein). Even though numerous of studies have been done on this subject, there is still no single definitions about LGM. It could be defined based on the impact on the regional-scale ecology also depending on the proxies studied. The variation of its climatic effects also leads to the different chronology assigned to this climatic event (e.g., Mix et al., 2001; Clark et al., 2009; Lambeck et al., 2014; Hughes and Gibbard, 2015; Yokoyama et al., 2018).

Iberian Peninsula, in the southernmost part of Europe has its peculiarity regarding the effects of LGM. As the most mountainous region in Europe and strongly affected by Mediterranean Sea and Atlantic Ocean, Iberian Peninsula presents a high ecological diversity. Consequently, the global paleoclimatic information extracted from the marine and ice cores cannot always be directly used to reconstruct the terrestrial condition (e.g., Sanchez Goñi et al., 2000; Roucoux et al., 2005; Fletcher and Sánchez Goñi, 2008). Specific to the Mediterranean basin and the northeastern Iberia, the effects of global climatic fluctuation during the last glacial period were apparently milder. Several studies indicated that changes of continental environment were less contrast despite the abrupt climatic changes recorded in northern latitude. The global climatic changes are responded by the terrestrial landscape differently and locally (e.g., Carrión et al., 2003; Finlayson et al., 2008; Burjachs et al., 2012).

Despite there is no agreement for the LGM chronology, the period from ca. 26.5 to 19 ka cal BP (Clark et al., 2009) is commonly used as the timeframe of the studies in Iberian Peninsula from this context. This chronological framework is already accepted at least for the mountainous region (Cascalheira et al., 2021). In terms of human culture, the Upper Paleolithic technological groups appeared within this period in Iberian Peninsula. The main technological cultures within this period are the Gravettian, the Proto-Solutrean, the Solutrean, and the Magdalenian. According to Cascalheira et al. (2021), the development of those cultures could be linked to the eco-geographical diversity of the region with the pronounced inter-regional variability. However, the authors noted that it is still necessary to do further studies with updated methods to understand and to fill the gaps of the knowledge about the archaeological and paleoenvironmental diversity in Iberian Peninsula.

Northeastern Iberia is one of the areas with little information about archaeological and paleoenvironmental condition around or during the LGM. The only known site from this period is an open-air site of Montlleó in the southern slope of Pyrenees (Lleida), dated to 22.7 – 22.4 ka cal BP which presents Solutrean – Badegoulain lithic culture (Fullola et al., 2019) and the Banyoles Lake (Giron), covering the period for the last 30 ka cal BP. However, the local and regional environmental context of northeastern Iberia during this period is still unknown (Cascalheira et al., 2021).

The new site of Cudó cave in the Prades Mountain (*Muntanyes Prades*, Tarragona) contains archaeo-paleontological deposits contemporaneous to LGM (Vergès, 2017) which can add some information about this period. This work uses the small mammal assemblages from

the archaeo-paleontologically richest levels of the deposit, level 7 (ca. 31 – 24 ka BP) and level 105 (ca. 15 – 10 ka BP). The small mammals offer a very useful proxy to reconstruct the paleoenvironmental condition of the region and evaluated the environmental dynamics through the time. It is because the small mammal has shorter lifespan, higher reproduction rate, higher evolutionary rate, and depend on specific habitat with quick geographic dispersals (e.g., Barnosky, 1994; Van Dam et al., 2006, among others). The small mammal are very sensitive to the changes on its habitat and can be an indicator of ecological changes (e.g., Chaline et al., 1974; Andrews, 1990; Repenning, 2001 among others).

Nevertheless, the paleoenvironmental inferences from small mammal assemblage could not be straightforward. A careful consideration should be placed on the formation processes of the assemblages as it could be formed by various agents that will affects the interpretation (e.g., Andrews, 1990; Fernández-Jalvo et al., 2016 among others). Therefore, the determination of the cause of accumulation of the small mammal in Cudó cave would become the first aim in this study. This is necessary to understand the main accumulating agents of small mammal assemblages before further studies, particularly in paleoenvironmental inferences.

The second goal is to propose an environmental reconstruction based on the small mammal remains recovered from Cudó cave. Both qualitative and quantitative methodologies would be applied in this study to reach estimate the past climatic parameters and to draw the main landscape surrounding the cave. Finally, this study will get a better characterization of the paleoenvironment in northeastern Iberia and specifically in Prades Mountains during the LGM, through comparation between the obtained result to published data from the neighboring sites and other proxies within the similar chronological framework. This would also provide a better environmental understanding in the context of Magdalenian human occupation in this region.

2. STATE OF THE ART

2.2. Small mammal studies

As a part of the ecosystem, faunal communities are also affected by the changes on the landscape and environment. Changes on the climatic conditions, such as mean annual temperature and precipitation, will produce shifts on the vegetation landscape in different ecosystems. Consequently, these changes will alter the state of faunal communities by changing the composition of the taxa in a given region. Differences in species richness and diversity throughout the time also could be indicator of changes on the environment.

Although each species of fauna will respond the environmental changes differently, there are three general ways of faunal communities to encounter the changes on the environment. These are reshuffling of taxa through biogeographic range changes, including geographical movement, extinction of the taxa, and evolutionary changes within species that may or may not lead to new species (Barnosky, 1994; Lyman, 2017). It could happen to a community in a various timescale and will depends on many factors. In mammalian communities, the body size of the species could become one factors determining the timescale of the changes. As an example, the large mammal turnover could happen in a hundred-thousands of years considering its long lifespan and slow reproduction rate.

In contrast, the small mammal communities, which usually consist of mammal with less than 5kg body weight (Andrews, 1990), could be shifted just in a couple thousand years following the climatic changes as it has shorter lifespan and higher reproduction rate. Regarding to the biogeographic shifts, the changes on the large mammal communities are less obvious as its habitat covering a wide geographic area and often involved in seasonal migrations. It is not the case of most of the small mammal taxa, which are generally adapted to a particular habitat with not so wide geographic area and rarely involve in seasonal movements, with the exception on bats. These particular characters make the small mammal especially useful to evaluate the dynamics on the environment by allowing accurate climate and landscape reconstruction and also for biochronological studies (Chaline et al., 1974; Andrews, 1990; Repenning, 2001).

2.3. The origin of small mammal assemblages

In the case of faunal assemblages, paleoecological inference cannot be done directly and simply from the fossil assemblage. It is because the fossil assemblages have been subjected to a set of selective reduction before and after the deposition of the assemblage. These processes, known as taphonomic process, works on the faunal remains from its death until it recovered by the researchers. Various factors can be involved in the taphonomic process, such as the way of death, predatory selection, transportation by elements, and the condition of the burial context. Consequently, the fossil assemblages that recovered and studied would be far more less abundant than it was on the living assemblage (López, 1991). Therefore, taphonomic studies are essential to evaluate how representative is the preserved fossil assemblage in relation to the original living assemblage.

Similar processes of taphonomy also work on the small mammal assemblages. Their taphonomic history started with the selection before the deposition, which is related about how the animal died. In this regard, several cause of death can contribute to the selection from the

living assemblage, such as the death of trapped individual in the natural traps and the predation. Afterward, the death assemblages could experiencing other processes which might induce further selection such as transportation by elements (water, wind, or soil movement) or degradation by the burial context (soil acidity) (López, 1991).

Predatory selection is one of the main discussions inside the study of small mammal assemblage because this is the main cause of death and accumulation of the small mammal (Andrews, 1990). The predators forming small vertebrate assemblages mainly consist of nocturnal raptors or owls (such as *Tyto alba, Asio otus, Nyctea scaniaca, Strix aluco,* and *Bubo bubo*), diurnal raptors (such as *Circus cyaneus, Falco tinnunculus,* and *Falco peregrinus*), and small mammalian carnivores (including foxes, canids, felids, mustelids, and viverrids). These groups are often producing large accumulation of the small mammal remains as they tend to consume the prey on some preferred spots (i.e., its roosts or dens) (Andrews, 1990). Reptilian predatos including snakes, lizards, and crocodiles acan also hunt small mammals, but they are rarely considered in the small mammal studies as the reptiles did not produce accumulation of remains. Indeed, other natural elements such as water streams are also capable to produce small mammal assemblage.

Several aspects should be taken in consideration to deal with the predatory biases. The first thing is the selective predators will be preferably hunting some specific taxa while the opportunist predators hunt the species that are present within its hunting area. These two different groups of predators will make different small mammal assemblage, with over representation of some taxa in the small mammal assemblage produced by specialist predator. In contrast, the opportunistic predators will hunt wide range of prey species and will make assemblages with larger diversity. It is already known that specialist predator has wider hunting area to get the preferred preys. It will also be migrating to another area following the seasonal cycle. Otherwise, the opportunist predators will hunt on what is present in the surrounding ecosystem and will simply change the prey species following the availability on every seasons (Andrews, 1990; Fernández-Jalvo et al., 2016).

Fluctuation of prey population are also common to be happen naturally. Hence, over representation of some species over other could also be found in the opportunist predator prey assemblages. However, in the long temporal frame as in the fossil assemblages, it will not be visible. Therefore, the small mammal assemblages will be more closely representing the environment if made by opportunistic predators. However, it cannot be said that the assemblages from specialist predators are not representing the surrounding environment as it also composed by species that are present in the area, even though it from a wider area or from a specific part of the preterit ecosystem. In addition, the prey selection will also correspond to the predator's body size. It will tend to hunt smaller prey relative to its body size. Even though, exception could be found where the prey has similar or even larger body size (Andrews, 1990).

Each group of mentioned predators leave different traces on the remains of the prey considering the different eating behavior as well as the digestive system characteristics. Owls for instance, produce less fractured remains as they will swallow the whole prey without dismembering it. Its gastric acid also less corrosive so the digestion marks become less extensive or even very subtle. Otherwise, in assemblages produced by the diurnal raptors, the bone fragmentation is frequently higher as they will tear some part of the prey (frequently the head) before swallowing it (Andrews, 1990). Their gastric acid is stronger so the digestion marks will be more extensive compared to the previous group. While for the assemblages produced by mammalian predator, higher fragmentation on the prey's bones will be observed as they will

shear the prey with their teeth before swallowing it (Andrews and Evans, 1983). The mammalian carnivores also have strong gastric acid, producing extensive digestion marks (Andrews, 1990; Fernández-Jalvo et al., 2016).

Thus, identification of the predators contributing to the assemblage's formation could determine if the fossil assemblages are faithful representation of the vicinity ecosystem of the studied site or whether it is highly selected by the specialist predators. Taphonomic studies usually infers predatory origin from patterns observed on modern assemblages, mainly considering the fragmentation, the skeletal element representation, or the biochemical alteration induced by the digestion process (Andrews, 1990; Fernández-Jalvo et al., 2016). Considering modern predators ethology, the paleoenvironmental inferences can be made and possible biases can be evaluated.

2.4. Late Pleistocene environment and the LGM in the Iberian Peninsula

Extensive multi-proxy studies have been conducted to reconstruct the paleoenvironment of Iberian Peninsula during the period of Late Pleistocene to Early Holocene. As a general overview, palynological analyses from marine cores of the Iberian Peninsula margin (Sanchez Goñi et al., 2000; Sanchez Goñi and d'Errico, 2005; Fletcher and Sánchez Goñi, 2008) offer relatively continuous records of the Last Glacial Period from at least 130 ka to 10 ka BP. Vegetation composition changes are detected in several episodes, coinciding with the climatic fluctuations within this period between stadial and interstadial conditions. According to Sanchez Goñi & d'Errico (2005), at the beginning of the period, the Mediterranean forest reached maximum expansion in the Iberian Peninsula, contemporaneous to the Marine Isotope Stage 5 (MIS5). The vegetation composition changed with the increase of juniper forest and oak forest in the following period, when temperature drops were experienced. During the MIS4, the summer insolation decreased, and the polar icecaps reached greater extent. Consequently, semi desertic vegetation progressively developed in Iberia. During the 63 – 61 ka BP, it was recorded a rise in the sea surface temperatures. However, the pollen records do not show an increase in deciduous forest as the result of temperature increase.

During the late stages of Late Pleistocene, the vegetation changes increase and are commonly correlated to abrupt and short climatic events, such as Heinrich events (HE) and Dansgaard-Oescheger (DO) cycles which linked to the North Atlantic water circulation and the input of ice-rafted detritus (IRD) (e.g., Sanchez Goñi et al., 2000; Fletcher and Sánchez Goñi, 2008; Fletcher et al., 2010; Harrison and Sanchez Goñi, 2010). Palynological data of the marine core from the southwestern margin of Iberian Peninsula shows the steppe vegetation generally dominate the cold and dry periods corresponding to HEs (Sanchez Goñi et al., 2000). However, humid conditions are also observed in the beginning of HE5 (ca. 46 – 45 ka BP) and HE4 (ca. 40 – 38 ka BP), while only cold and arid condition being observed in HE3 (~31 – 29 ka) (Sanchez Goñi et al., 2000; Fletcher & Sánchez Goñi, 2008). This arid condition persists to the later period of MIS2 (ca. 29– 11 ka BP), represented by an open landscape and the presence of semi-desert vegetation such *Artemisia*, Cupressaceae, and *Helianthemum* (Fletcher and Sánchez Goñi, 2008). It is also the vegetation landscape during the LGM (26.5 – 19 ka cal BP, Clark et al., 2009), even though further expansion of semi-desertic vegetation happened during the preliminary HE2 and later on HE1 (Sanchez Goñi et al., 2000; Fletcher and Sánchez Goñi, 2008).

One interesting event during the Last Glacial Period is the LGM, when the global temperatures reached its lower point, the ice caps and mountainous glaciers reached its

maximum extent, and the average sea level on its lower point. As mentioned in the earlier chapter, this particular event is on continuous debates regarding how it affects the environment on different regions as well as the chronological position (Cascalheira et al., 2021; Maier et al., 2021 and references therein). Several authors have proposed the chronology for LGM based on multiproxy analysis referring to the maximum extent of the global ice-sheet and mountain glaciers, the main feature linked to this climatic event. Clark et al. (2009) for instance, conclude that in average the global ice sheets reached its maximum extent between 26.5 to 19 ka cal BP. The authors also noted that some locations such as mountain glaciers reached its maximum extent by ca. 30 ka BP. This change leads to several effects in global scope such as significant decrease of sea level, sea surface temperature, as well as floral and faunal changes.

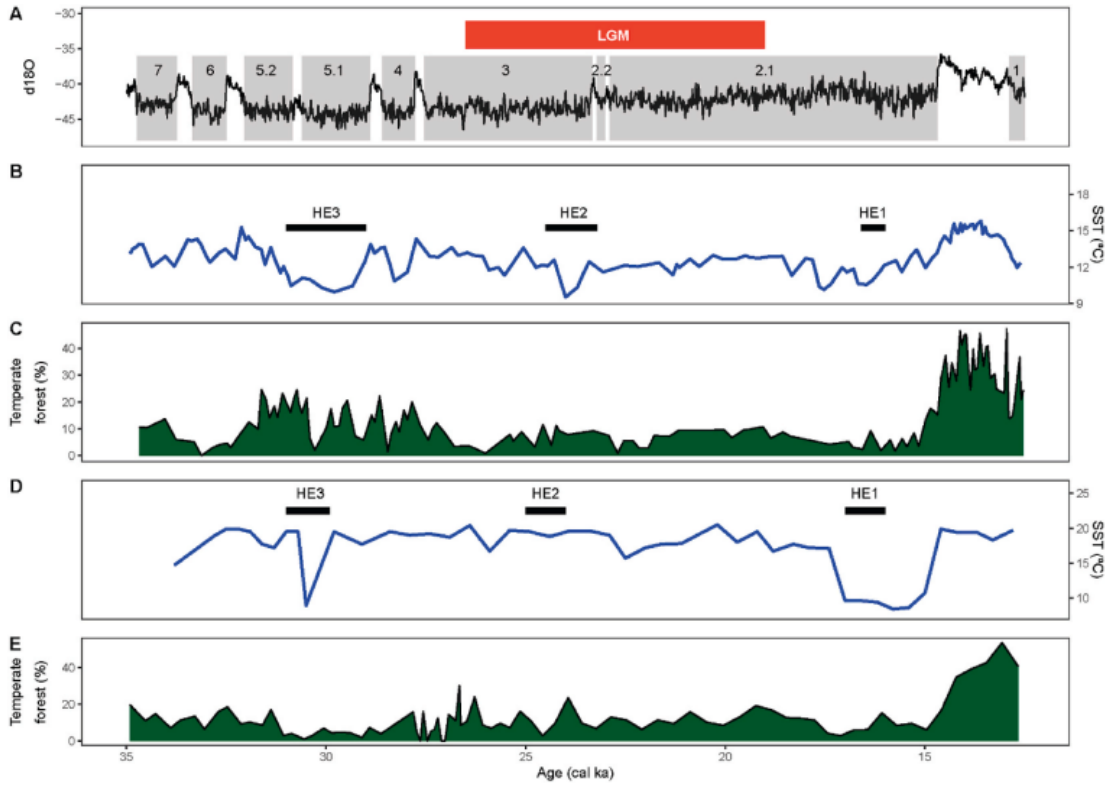

Figure 2.1. Global and regional Iberian Climatic and environmental proxies from 35 – 12.5 ka cal BP. HE, Heinrich event; SST, sea surface temperature (Cascalheira et al., 2021)

However, terrestrial data from Iberian Peninsula suggested slightly different information. In the northern region for example, the mountain glaciers reached its peak of the extension before the traditional LGM timeframe, at around 42 ka cal BP and began to melt around 38 ka cal BP (Moreno et al., 2009; Serrano et al., 2013). Unfortunately, the landscape condition during this period is still unknown (Cascalheira et al., 2021). The oldest pollen records emerged during the later period, contemporaneous to the Greenland Stadial 3 (GS-3, ca. 27.5 – 23.3 ka cal BP) (Figure 2.1). This data suggests that the landscape around Santimamiñe (Biscay) was dominated with open vegetations, in response to the cold phase, but with some degree of humidity indicated by the presence of herbaceous shrub layer. The small mammal studies also suggest the consistent information, for example with the *Sorex araneus-coronatus* remains (Rofes et al., 2014). There was an amelioration on the environment before the end of GS-3,

coinciding in chronocultural term with the final Gravettian, but then it seems to be considerably deteriorating between the end of GS-3 and before GS-2.2 (ca. 23.2 ka cal BP). The open landscape continues to predominate until the GS-2.1 (ca. 22.9 ka cal BP) (Cascalheira et al., 2021). Nevertheless, between 22 and 19 ka cal BP, the small mammal assemblages from this region display a humid climate with arboreal vegetation covers (Bañuls-Cardona et al., 2014), which means there was an amelioration of the climate from the earlier period.

In the inner Iberia, an area composed by two plateaus of Northern and Southern *Mesetas*, shows similar pattern of harsh climatic condition during the GS-2.2 and GS-2.1 (Cascalheira et al., 2021 and references therein). Moreover, in the southern Mediterranean coast, the regression of Mediterranean forest taxa was also happened around the LGM (ca. 24.5 – 15 ka cal BP), parallel to the expansion of sclerophyllous taxa and pines (Camuera et al., 2019). It is consistent to the presence of *Microtus arvalis* and *Chionomys nivalis* in the lower elevation (Cascalheira et al., 2021 and references therein) In contrast, the deep-sea cores data from Atlantic coast of western Iberia shows that the climate was not necessarily harsh during the LGM. It seems to be warmer and more humid compared to many of the stadial events at the end of MIS3 (Roucoux et al., 2005).

In the northeastern Iberia, there is not so much paleoenvironmental information that have been extracted from terrestrial proxies. Among them is the small mammal assemblage from Galls Carboners which has been correlated to the Heinrich Event 3 (HE3, ca. 31.3 – 31.1 ka cal BP). The paleoenvironmental reconstruction on this assemblage displays cool climatic condition with alternating woodland to dry meadow landscape conditions (López-García et al., 2014a). Pollen from open landscape vegetation also recorded in Banyoles Lake, northward from Galls Carboners, before 30 ka BP. It is represented by the domination of *Pinus*, *Artemisia*, and Poaceae taxa. Slight improvement appeared between 30 and 27 ka BP by the increasing mesophilous taxa such as *Quercus* and *Betula*. This amelioration is not so significant since the arboreal pollen decreasing after 27 ka BP and steppic taxa dominating the record up to ca. 14 ka BP. The environmental improvement towards current condition started around 14 ka BP with the increase of arboreal, Poaceae, and herbs pollen consistent to the decreasing steppic taxa (Pèrez-Obiol and Julià, 1994).

2.5. Human occupation around the LGM in the Iberian Peninsula

During the Late Pleistocene (MIS 3 and MIS2) two different human species were found in western Europe, Neanderthals (or *Homo neanderthalensis*) and anatomically modern humans (or *Homo sapiens*); which have been traditionally related with two different human cultural periods, the Middle Paleolithic and the Upper Paleolithic, associated respectively to each human group. Coinciding with MIS3 to MIS2 transition, and a progressive deterioration of climatic conditions, happens the extension of anatomically modern humans thorough Eurasia and they arrival to Iberia, carrying with them new technological cultures exclusively related with the Upper Paleolithic (e.g., Gravina et al., 2005; Finlayson and Carrión, 2007), which begins with Aurignacian techno-complex. Then, the expansion of global ice-sheets and mountainous glacier apparently lead to a human population shift. It could be seen by declining population in the northern Europe as the glacier built up around 30 ka BP and repopulated as the climate stabilized between 25 – 20 ka BP (e.g., Fu et al., 2016; Maier and Zimmermann, 2017). In archaeological point of view, the emergence of large number of techno-cultural units during this period could

indicate the loses of inter-group connections and the development of regionalization (Straus, 2015; 2016; Maier et al., 2021).

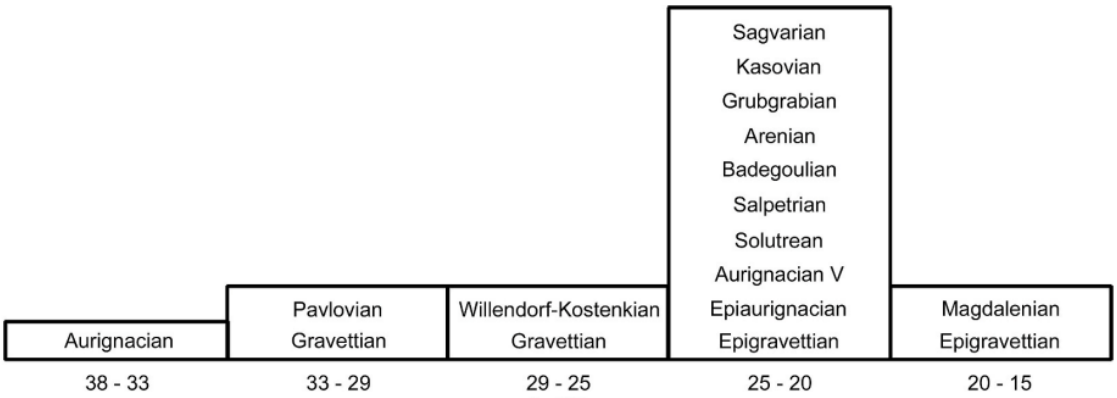

Figure 2.2. Overview of the techno-cultural units and its emergence in Europe within the period from 38 to 15 ka BP (Maier et al., 2021).

Iberian Peninsula become one of the populations refugium during this period considering the milder climatic condition (Finlayson and Carrión, 2007). There are four techno-cultural complexes developed within period from ca. 26.5 to 19 ka cal BP in Iberian Peninsula, including the Gravettian, the Solutrean, the Badegoulian, and the Magdalenian (Figure 2.2). Those cultural complex appear in roughly similar temporal pattern. However, the state of the record varies in different parts of Iberia. In the northern Iberia for example, those period covers the late Gravettian, the whole Solutrean, and the early transition from Solutrean to Magdalenian, or some author defined this stage as Badegoulian culture (Cascalheira et al., 2021). Specifically, the Gravettian are recorded in this region up to the GS-3 (ca. 25 ka cal BP) followed by the beginning of the Solutrean. Roughly coinciding with the beginning of GS-2.1 (ca. 22.3 ka cal BP) the Solutrean culture was decreasing followed with the Badegoulian culture and continue thriving up to the end of LGM at around 19.5 ka cal BP (Arrizabalaga et al., 2021).

In the central Iberia, the differentiation of those four techno-cultural complex cannot be done securely since many of the data came from palimpsests (Cascalheira et al., 2021 and references therein). In the Douro basin the Gravettian layer appear until ca. 26.5 ka BP and the Proto-Solutrean appear at around 23.4 ka cal BP (Aubry et al., 2010; 2012). The Gravettian, Proto-Solutrean, middle and upper Solutrean also recorded in the Upper Jarama River valleys in the perimeter of Central System range dated to ca. 25.5 – 24 ka cal BP. Furthermore, between ca. 22.8 and 21 ka cal BP, the archaic Magdalenian culture could be recognized in the Middle Ebro basin in Zaragoza. Otherwise, in the Atlantic facade of Iberia, the records are vaguer with the lack of absolute dates. It made the transition between complexes cannot be distinguished. However, at least there are three techno-cultural complexes recorded with the chronology contemporaneous to the LGM, including the terminal Gravettian, the Proto-Solutrean, and the Solutrean (Cascalheira et al., 2021 and references therein).

The Gravettian level in southern Mediterranean Iberia in the site of Cendres (Alicante) also coincides with the early LGM (ca. 25.7 – 24.8 ka cal BP). During this period however, Lower and Middle Solutrean assemblages are also recorded in the southern part of Mediterranean Coast, in the site of La Boja, Nerja, and Ambrosio. The Gravettian technological continuity is

observed until the second half of HE2 in Cendres XV and Nerja. The Solutrean culture appeared following the diminishing Gravettian up to around the end of GS-2.2. Heat treatment of flint for producing Solutrean tools even became common between ca. 24.7 to 23.7 ka cal BP. During the later period between ca. 22.7 to 22.1 ka cal BP, the Badegoulian appeared overlapping with developed Solutrean (Aura Tortosa and Jordá Pardo, 2012). Moreover, around 19.6 – 19.2 ka cal BP the Lower Magdalenian appeared in the site of Cendres XII and La Boja OH4 (Cascalheira et al., 2021 and references therein).

There is not a lot of information from northern Mediterranean Iberia regarding techno-cultural development within this period. The only archaeological record during the LGM in this area comes from the site of Montlleó (Lleida) dated to 22.7 – 22.4 ka cal BP with some shouldered points identified as the Badegoulian culture (Fullola et al., 2019).

2.6. Late Pleistocene small vertebrate data in northeastern Iberia

Several articles have been published in regards of paleoenvironment reconstruction in the northeastern Iberian Peninsula. Those are using the terrestrial records covering botanical and paleontological data. To give a regional contextual understanding, in this section will be summarized some of the sites of late MIS3 to MIS2 with small-vertebrate studies in northeastern Iberia, to provide some clues about how small mammal communities evolved in the region in relation to climatic fluctuations (Figure. 2.3 and Table 2.1).

Figure 2.3. The sites mentioned in this chapter: 1) Cudó cave; 2) Galls Carboners; 3) Xaragalls cave; 4) Els Canyars; 5) Colomera cave; 6) Toll cave; and 7) Arbreda cave.

Sites		XA		GC	EC	TO		CO	AR				
Layers		C3	C4	107	MLU	4	3	CE-15	F	E	D	C	B
Insectivores	*Erinaceus europeus*								X	X	X	X	
	Talpa europaea		X		X					X			
	Sorex minutus			X					X	X		X	X
	Sorex gr. *araneus-coronatus*									X	X	X	X
	Crocidura cf. *russula*			X				X		X		X	
	Crocidura sp.				X								
	Neomys gr. *fodiens-anomalus*												
Bats	*Rhinolophus ferrumequinum*		X										
	Rhinolophus gr. *euryale-mehelyi*		X	X									
	Myotis gr. *myotis-blythii*			X									
	Myotis myotis											X	
	Myotis blythii							X					
	Myotis sp.			X									
	Plecotus gr. *auratus-austriacus*			X									
	Miniopterus schreibersii	X											
	Pipistrellus pipistrellus			X				X					
	Barbastrella barbastrellus							X					
	Arvicola sapidus					X			X	X	X	X	X
Rodents	*Arvicola amphibius*											X	X
	Chinomys nivalis	X	X	X		X	X	X	X	X	X	X	
	Microtus (Iberomys) brecciensis		X	X			X						
	Microtus (Iberomys) cabrerae		X		X		X		X		X		X
	Microtus (Terricola) sp.												
	Microtus (Terricola) duodecimcostatus	X	X		X	X	X	X	X	X	X	X	X
	Microtus oeconomus									X		X	X
	Microtus arvalis		X	X	X		X	X	X	X	X	X	X
	Microtus agrestis	X	X		X		X	X	X	X	X	X	X
	Microtus gr. *arvalis-agrestis*					X	X	X	X	X	X	X	X
	Microtus gregalis										X		
	Apodemus sylvaticus	X	X	X	X	X	X		X	X	X	X	X
	Eliomys quercinus	X	X	X	X		X	X	X	X	X	X	X
	Glis glis						X	X	X				
	Spermophilus cf. *citellus*											X	X

Table 2.1. Summary of small mammal species identified in the mentioned sites. XA, Xaragalls (López-García et al., 2011); GC, Galls Carboners (López-García et al., 2014a); EC, Els Canyars (López-García et al., 2013); TO, Toll cave (Fernández-García and López-García, 2013); CO, Colomera (López-García et al., 2010a); and AR, Arbreda (López-García and Cuenca-Bescós, 2010).

2.6.1. Xaragalls

Xaragalls cave is a site located around 9 km north of Cudó cave which has provided archaeological and paleoenvironmental records of the Late Pleistocene and Holocene period. It is situated in the Poblet forest within the municipality of Vimbodí-Poblet, at the UTM coordinate X 0337448 and Y 548127 on the elevation of 590 m.a.s.l. There are 8 stratigraphic layers from which radiocarbon dating analysis has been conducted to the upper part of layer C6 (>43.5 ka BP), layer C4 (45.1 – 48.2 ka BP), and layer C1 (13.7 ka BP) (Vallverdú et al., 2012).

The paleoenvironment successions during the MIS3 have been documented from the small vertebrate, large vertebrate, and archaeobotanical remains from this site. From the abundance of *Apodemus sylvaticus* species, it can be inferred that the vicinity of the site was dominated by woodland habitat throughout the period. It is partly supported by the predators contributing the small mammal assemblages in Xaragalls cave which identified from the taphonomic marks on the bones. It is known that small owl (*Athene noctua*), which prefers to live in semi open

landscape, was the accumulator of the remains. However, the changes of intensity of woodland habitat could be related to climatic events within the MIS3. In layer C8 the small mammal assemblage shows high representation of Mediterranean taxa with open-humid meadows dependent species. It indicates relatively higher MAT and lower MAP during its formation. Considering the dating result from layer C4 and C6, the assemblage from C8 could be older than 50 ka, thus it might be coinciding with the Greenland Interstadial 15 or 16 (GI-15 or GI-16, 56 – 59 ka) when the climate was warm and dry. The similar condition to what was it on the layer C8 appears on the layer C5 after it changed to be colder and wetter on layer C7 and C6. Finally, on layer C4 and C3, the MAT drops and the MAP increased, leads to the increase of mid-European taxa, represents open-humid meadows while the woodland decreased. It could be coincided with the HE5 dated around 47 ka (López-García et al., 2011; Fernández-García et al., 2019)

Furthermore, those interpretation of the paleoenvironmental condition in the vicinity of the Xaragalls cave are not only based on the small vertebrate assemblages, but also supported by the anthracological data (López-García et al., 2011) and oxygen isotopic analysis (Fernández-García et al., 2019) that shows a similar pattern. Despite of providing long paleoenvironmental record, Xaragalls cave has older chronology than the records of the Cudó cave. Nevertheless, it gives some clues on how the ecological condition and faunal communities in the northeastern Iberian Peninsula changed in accordance with the climatic dynamics.

2.6.2. Galls Carboners

The Galls Carboners is a cave that has close proximity to Cudó cave. It is located in the northeastern face of the same cliff, Motllats cliff, in the system of Prades mountain range, in the municipality of Mont-ral. The cave situated on the elevation of 965 m.a.s.l., in the Lias (Jurasic) dolomite, dolomitic breccias, sandstone, and limestone. Eight stratigraphic levels identified as level 101 to level 108 were excavated where level 105 to 108 is the archaeological levels. These levels are only separated by thin crust of limestone with similar sediment characteristics among others. In this matter, level 105 to 108 are considered as a result of a single sedimentation event. Dating analysis has been conducted to the faunal remains from level 107 which reveals an age of 26,940 ± 130 BP (31,380 – 31,170 cal BP) (López-García et al., 2014). This period contemporaneous to the Henrich Event 3 (HE3) when the climate in the Iberian Peninsula was relatively cold and dry (Sanchez Goñi et al., 2000).

There is no long paleontological record in this site to construct the sequence of paleoenvironmental evolution with a robust dating analysis. Still, from the stratigraphical information, it can be argued that the small vertebrate assemblage was deposited in a synchronous and continuous sedimentation event overlined with speleothem. There were recovered 399 remains of small vertebrates which correspond to a minimum 122 individuals, from level 105 to 108. It corresponds at least to 16 taxa of small mammal and reptile species. By the taphonomic study, the small vertebrate assemblages were accumulated by the nocturnal raptors, including *Bubo bubo* and *Strix aluco*. Some interesting findings regarding the paleoecological reconstruction are the high abundance of *Eliomys quercinus*, a generalist species but prefers woodland edge habitat. The climatic conditions during the deposition were colder than today. The cold climate conditions are supported by remains of *Microtus arvalis*, and *Rana temporaria*, which currently only distributed in the eastern Pyrenees. From the comparison of the paleontological assemblage to current small vertebrate on the region, it is argued that during the HE3 the climate of this region was colder and dryer (López-García et al., 2014).

2.6.3. Els Canyars

Els Canyars is a deposit site located in the town of Gavà in the northeastern Iberian Peninsula, at the coordinates 41°17'46" N and 1°58'47" E. It is located at the meeting point of two creeks, the Riera dels Canyars and the Riera de Can Llong. These are streams flowing from the Garraf Massif to the Mediterranean Sea. Paleontological collection consist of large mammal remains from the Upper Pleistocene were the main findings from this site. Several absolute dating analysis has been conducted by ^{14}C AMS method for level MLU (Middle Lutitic Unit), the only archaeological unit, providing an age around 34,6 ka (ca. 39,6 ka cal BP) (López-García et al., 2013), which is coinciding to the HE4 (ca. 39 – 40 ka cal BP) (Daura et al., 2013).

Small vertebrate remains have also been recovered from the deposit. In total, 362 remains which consist of 15 species of rodents, insectivores, and reptiles have been studied to obtain the information on the paleoecological condition of this area. Among the assemblage of the small mammal remains, are relevant the Mediterranean taxa, represented by *Apodemus sylvaticus, Microtus* (*Iberomys*) *cabrerae*, and *Microtus* (*Terricola*) *duodecimcostatus*. But also, the mid-European taxa, such as *Microtus arvalis*, *Microtus agrestis*, and *Talpa europaea,* are equally represented. Considering the reptiles, the presence of *Coronella* cf. *austriaca* gives an interesting information about the paleoecological condition as currently it is absent from the Catalonian coast.

The small vertebrate record of Els Canyars indicate that the landscape around the area was dominated by the Mediterranean-type woodland, but with considerable amount of open landscape (dry meadows). The humid meadows and watery landscape are also represented in the assemblage, but in small proportions. It suggests the existence of stable water body in the area that provide the favorable habitat for burrowing species found in the assemblage. Moreover, the chorotype analysis also shows that the taxa with Mediterranean requirements (chorotype 3) dominating the assemblage (50%). Apart from that, the mid-European taxa (chorotype 1 and 2) also quite well represented by 20% and 30% respectively. This cooccurrence of the temperate and cold adapted species suggest that northeastern Iberia could became a refugia for the cold adapted species during the cold periods such as HE4. In addition, from the paleoclimatic reconstruction, it is estimated that the MAT is lower than today (5.2°C) and the MAP is slightly higher than today (+99mm). It is consistent with the presence of *C. austriaca* which requires low annual temperature (<11°C) and high precipitation (>800mm) (López-García et al., 2013).

The data from Els Canyars is interesting as it gives more paleoecological information in the northeastern Iberian Peninsula during the Upper Pleistocene. In regards to the Cudó cave, it is not widely separated in distance and still in the similar climatic zone. Chronologically, the record from Els Canyars also not to old compared to the older period of Cudó (ca. 30 ky cal BP). Therefore, it is useful to get a contextual understanding on the paleoecology of the northeastern Iberian Peninsula during the Upper Pleistocene.

2.6.4. Toll cave

Toll cave is a part of the Coves del Toll karstic system located near Moià, about 50 km to the north of Barcelona, with coordinates 41°48'25" N and 2°9'2" E, on the elevation of 760 ma.a.s.l. This 2 km cave system was built up in the Neogene limestone formation through the *Torrent Mal* erosion. Archaeological intervention has been conducted in three sectors inside the

southern gallery of the Toll cave. The *Sector Entrada*, one of the excavated sectors of the Toll cave contains faunal remains with cutmarks and lithic tool. Small mammal remains were also recovered from three level of this sector, allowing to conduct biochronologcal analysis. The presence of *Microtus* (*Iberomys*) *cabrerae*, *Chionomys nivalis*, and *Glis glis* as well as the absence of *Plyomis lenki* and *Hystrix* sp. suggesting that the deposits was formed during the Late Pleistocene and not older than 35 ka. Furthermore, the presence of *C. nivalis* in level 3 and absence in level 2 indicate that the level 3 was deposited around the transition from Pleistocene to Holocene (Fernández-García and López-García, 2013). However, recently published radiocarbon dating analysis on faunal remains from level 3 and 4 shows the date around 47.1 – 45.5 ka cal BP in level 3, while level 4 dated to more than 49 ka cal BP. Still, this last result is just at the limit of radiocarbon analysis and restricting the secure inference (Ramírez-Pedraza et al., 2019).

As much as 216 remains from at least 118 individuals corresponds to 10 species of rodents have been recovered. Among the remains, the Mediterranean taxa (chorotype 3), such as *M.* (*T.*) *duodecimcostatus,* predominates the assemblages from level 3 (46.34%) and level 2 (85.92%). It is also explained the predominance of woodland habitat in the vicinity of the site. However, there are several differences between the assemblage of level 3 and level 2. The presence of mid-European species related to chorotype 1 and 2 are higher in level 3. In regards of the habitat, some species indicate the higher existence of open dry landscape. In addition, the paleoclimatic analysis shows that during the deposition of level 3, the MAT is slightly lower than it was during level 2 formation. Moreover, the MAP was higher in level 3 than it was in level 2. However, the MAT of both level still lower than today and the MAP is significantly higher than today (Fernández-García and López-García, 2013). Unfortunately, due to the limited amount of the remains, the level 4 is excluded from the paleoecological analysis.

2.6.5. Colomera

Colomera is a cave located in the western border of Catalonia, in Sierra del Montsec, in the municipality of St. Esteve de la Sarga, in coordinate of X 308339 Y 4661275 UTM. It situated in the pre-Pyrenees region, on the elevation of 670 m.a.s.l. (Oms et al., 2008). Archaeological studies have been conducted in the cave and revealed cultural records in six levels dated from 13 – 3 ka cal BP (Oms et al., 2008; Oms, et al., 2009a; b).

Colomera cave also provides small vertebrate records to add information regarding paleoecological situation in the surrounding area. In total, 809 remains from 16 taxa have been identified from the deposits (López-García et al., 2010a). These taxa were grouped into three chorotypes to observe the environmental conditions. During the older period the strict mid-European taxa (chorotype 1) and Mediterranean-tolerant mid-European taxa (chorotype 2) dominating the assemblage while the Mediterranean taxa (chorotype 3) and generalist taxa less represented. This composition gradually shifting throughout the time until the domination of Mediterranean taxa and absence of strict mid-European taxa around 3.4 ka BP (López-García et al., 2010a).

Among the assemblage, the strict mid-European taxa become the most important indicator. *Rana temporaria*, *Chionomys nivalis*, and *Microtus arvalis* are the species of this group that have been recovered from almost all along the Colomera sequences, with exception on the upper level. It suggests that these cold-adapted species are continuously thriving despite of the climatic changes on the beginning of Holocene. This is not a common case in the Iberian

Peninsula since the abrupt temperature and precipitation increase during the transition from Pleistocene to Holocene leads to the significant changes on the environment including the small vertebrate assemblages. One example of the significant environmental change is the missing or drastic drops on the strict mid-European taxa in the paleontological records (e.g. Cuenca-Bescós et al., 2009; López-García, 2008). The explanation proposed by López-García et al., (2010) is that the Pyrenees acts as a geographical barrier which control the climate changes during the Pleistocene – Holocene transition. For this reason, the transition was most likely as a gradual change for about 8000 years instead, that leads to a gradual diminishing of strict mid-European taxa before becoming totally absent around 3.4 ka BP.

2.6.6. Arbreda

Arbreda is a cave located in the northeastern part of Catalonia and it belongs to the Reclau (Serinyà) cave system in the wester margin of the Pla d'Usall and the Serinyadell river, with coordinates 24º9'38" N and 2º44'49" E. The Pla d'Usall is a part of the lacustrine basin of Banyoles-Besalú, surrounded by Eocene and Neogene reliefs and filled with Pleistocene materials. The cave itself is a rock shelter formed by travertine cascade which contains sedimentary deposit from the beginning of Late Pleistocene to the Early Holocene (López-García et al., 2014). This cave has long sequence of the paleoenvironmental records, including the small mammal deposits, spans from the Mousterian period from 40.4 to 38.5 ka BP up to the Solutrean period dated around 17.3 ka BP (López-García and Cuenca-Bescós, 2010).

The levels that are interesting for their chronological context are level E and F, which associated to the Gravettian technoculture (33.3 – 27 ka cal BP) and level B, C, and D associated to the Solutrean technoculture (23.6 – 22.4 ka cal BP) (López-García et al., 2015). Those levels are coinciding or have close proximity to the assemblages from Cudó cave by the chronology.

The recovered small mammal shows a relatively rich environment, with 21 identified taxa, including rodents and insectivores. The taphonomic traces show that several predators involved in the accumulation of the small mammal remains, which are *Strix aluco, Bubo bubo*, and particular for level E, *Falco tinnunculus* (López-García et al., 2015). In general, the small mammal assemblages from Arbreda cave are dominated by taxa with affinity to the woodland habitat (68%), such as *Myotis myotis* and *Myotis myotis-blythii*; humid open meadow habitat (21%), represented by *Myotis myotis-blythii* and *Microtus agrestis*, while the rest are rocky, open dry, and watery habitat (López-García and Cuenca-Bescós, 2010; López-García et al., 2014b; 2015). The climatic condition during the Gravettian period is related to a MAT of 6.1ºC lower than today while the MAP was 298mm higher. The MAT slightly increased during the Solutrean period (4.6ºC lower than today), but the MAP was slightly higher (309mm above the current MAP in the region). These data give more information on how the environment was on the northeastern Iberian Peninsula during the climatic event of HE3 and HE1 or Younger Dryas (YD).

3. SITE DESCRIPTION

3.1. Location and geographic condition

Cudó cave, also known as Aixàvega cave, is a natural cavity located in the municipality of Mont-ral within the Alt camp region. It is located in the Prades Mountains (*Muntanyes de Prades*), a large calcareous mountain massif which belongs to the Catalan Pre-Coastal Mountain Range (Figure 3.1). Specifically, it is situated at southern face of a cliff called the Motllats on the elevation of 987 m.a.s.l., directly facing the Aixàvega Valley where the Glorieta river flows on its base. Its coordinates are X 338355 and Y 4572037 (UTM 31/N ETRS89). In a straight line it is roughly 24 km from the coastline of Tarragona (Vergès, 2017).

The surrounding landscape shows high variability as a consequence of abrupt relief changes from high mountain ranges to low plain and by significant hydrological changes, from water springs and streams on the low land to the arid plateau (Figure 3.2). These hydrological differences lead to the widely diverse vegetation found within this area, producing a mosaic landscape. The plateau is currently covered with semi-open woodland consist of *Quercus ilex* ssp. *rotundifolia* (holm oak), *Pinus sylvestris* (Scots pine), *Juniperus communis* (common juniper), *Buxus sempervirens* (common box) as well as shrubs. The slope where Cudó cave situated is covered by a closed woodland which consists of holm oak and Scots pine on the upper parts and *Pinus halepensis* (Aleppo pine) on the lower parts. The brushwood consists mainly of boxwood, *Viburnum tinus* (laurustinus), *Rhamnus alaternus* (Mediterranean buckthorn), and *Arbutus unedo* (strawberry tree) also found within this level. The plain at the bottom of the mountains is currently used as cultivation area (López-García et al., 2014a).

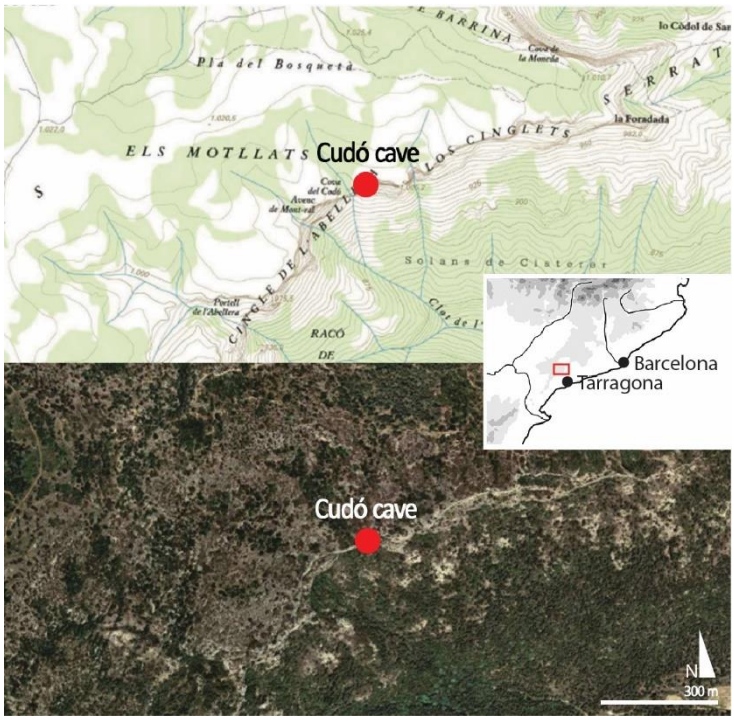

Figure 3.1. Top, topographic map in the vicinity of Cudó cave and middle, satellite image with a point shows the location of Cudó cave (Vergès, 2017).

Figure 3.2. Panoramic view facing southward from the mouth of Cudó cave. It can be recognized the vegetation gradient following the altitudinal changes.

3.2. Research history

The archaeological excavation in Cudó cave initiated in 2016 under the project of "Evolució paleoambiental i poblament prehistoric a les conques dels rius Francoli, Gaià, Siurana i rieres del Camp de Tarragona" led by Institut Catala de Paleoecologia Humana i Evolucio Social (IPHES), under the direction of Prof. Josep Maria Vergès Bosh. This project aimed to increase the paleoenvironment knowledge in this region during the Late Pleistocene, specifically on the Motllats cliff and Prades Mountains. It will also provide supplementary information on the previous paleoenvironmental studies on the Galls Carboners and Xaragalls cave situated in similar mountain system. Moreover, this project goal is to provide archaeological context to objects that nowadays found in regional museums such as *Museu municipal d'Alcover* and *Museu Salvador Vilaseca de Reus* coming from older excavation and pillaging (Vergès, 2017).

There is no archaeological intervention prior to 2016 in Cudó cave. Even though, it was assigned to the period of Late Neolithic – Ancient Iberian inside the Archaeological map of Catalonia, but there is no clear supporting evidence. The only evidence observed before the first intervention were several surface findings of bones and hand-made pottery fragments, possible to be unearthed by unauthorized excavation (Vergès, 2017).

3.3. Cave and stratigraphic description

The cave itself has been described in the *Catàleg Espeleològic de Catalunya* (1978) has the total length of the corridor of 140 m with several vertical shaft with total descend to 27m under the cave mouth (Borràs et al., 1978). The cave mouth is large enough to let the light fill the front gallery. The front gallery is straight and relatively flat with a ridge in the middle part and getting narrower towards the inside (Figure 3.3).

From the recent archaeological interventions, two different sectors have been identified, the Sector 100 and Sector 200. Sector 100 consists of two 2x1m pits located in the interior part of front gallery of the cave, on the squares 101-107 and 101-108 as well as 103-108 and 104-108 (Figure 3.4). Nine stratigraphic layers potentially from Pleistocene to Holocene

deposit have been distinguished following the geomorphological criteria, labelled from the top to the base with Level 100 to Level 108 (Figure 3.6). Those levels are described as follows.

- **Level 100:**
  Filling of circular hole with 50cm diameter and about 30cm deep, consists of ashes, charcoal, and plastic bags with various waste (battery, cans, bottles). It is probably made by hikers or speleologists who visited the cave.
- **Level 101:**
  Surface level, formed by a mixture of ashy sediment and clay, possibly from the removal of level 102 and 103. The sediment is quite loose near the wall and compact towards the middle of the cave, possibly trampled by the visitors who get into the cave. Lithic, faunal remains, pottery, and hand-glazed lathe are found in this level.
- **Level 102:**
  This is a layer formed by the remnants of a combustion episode. It composed by white – grey ash with abundant small charcoal fragments which rest on a few millimeters of carbonaceous/rubefacted sediment. This base sediment was probably formed by carbonized remains in contact with the surface where the combustion was performed. This sediment covers almost entire surface of the pit with exception on the zone affected by the hole (level 100) and the passage area where it might have been eroded. The only remains recovered is a fragment of glazed pottery.
- **Level 103:**
  This level is interpreted as a product of in situ layer removal and mixing derived from rabbit's burrows.
  Two horizontal zones could be distinguished from this level. The first zone on the sector 101-108 and the northeastern corner of 101-107, is composed by a mixture of brown silty sediment and patch of ashes of different color. The second zone, on the western side of sector 101-107 with one big stone block that fill almost all the square, no ashes are found in this sector, the filling between the blocks is loose sediment with centimeter-sized clasts. Lithic, faunal remains, as well as Roman ceramics were found in this level.
- **Level 104:**
  This consist of in-situ combustion remains, composed by white – grey ash layer and a carbonaceous/rubefacted reddish layer as it was observed in level 102. It could correspond to the same event as level 102, but the clear association could not be confirmed due to the removed areas.
- **Level 105:**
  This level formed by brown clayey sediment with abundant millimeter-sized rounded limestone nodules. The contact with level 103 is not clearly observed, so it difficult to distinguish the limit. Some filled burrows were observed, which sometimes difficult to delimit as the filling has similar characteristics to the sediment in this level. This level contains exclusively prehistoric materials such as lithic, faunal remains, and marine shell ornaments, with also abundant small mammal and bird remains.
- **Level 106:**
  This level consists of a layer of white – grey granular ash with millimeter-sized charcoal fragments found in the northeastern corner of 101-108 square. There is no reddish sediment in association to these ashes, indicating that it could have been transported from the combustion area. Only a single bovine bone fragment without thermal impact was found in this level. It is interpreted that the ashes might came from level 105.
- **Level 107:**

A reddish clayey sediment with millimeter-sized rounded calcareous nodules is the main sediment composing this level. The contact with level 105 is not clear, but the increase of clay and the decrease of calcareous nodules as well as the gradual change of color made possible to distinguish it from level 105. Lithic artefacts and marine shell ornaments were also be found as happens in level 105. Small mammal remains also abundant, although decreasing towards the base. At the base, around -10.230, several stones with 30 – 40cm long and 10 – 15cm thick could be found.

- **Level 108**
  This level contains almost pure clay without limestone nodules and apparently without microfauna or archaeological remains. The contact with level 107 is not clear, but it corresponds to the base of the stone blocks on -10.230.

The sector 200 is located in the front part of the gallery consist of one 2x1m pit, located on the squares 104-93 and 104-94 which then extended to 102-94, 103-93, and 103-94 (Figure 3.4). Only 3 levels were excavated in this sector which described as following.

- **Level 201**
  This is the surface level with grayish brown, formed by a mixture of disintegrated dung and ashes. The sediment is quite loose and generating a lot of dust during the excavation and sieving. Ashes, carbonaceous, and rubefacted layers could be identified and correspond to sub-modern combustion events. Apart from wastes, several items corresponding to modern activity were found, such as glazed pottery, lathe, and lead bullet.
- **Level 202**
  This level consists of burnt manure facies. In the top level, it formed patches, but it become continuous as it goes deeper. The thicker part of this layer is in the southern part, in contact with the stalagmite formation that form the boundary to the external part of the cave. Otherwise, it is getting thinner towards the inner part of the cave. Accumulation of small clasts are also observed in this level. The recovered remains are fragments of glazed pottery and a coin dated to 1718.
- **Level 203**
  This level composed by yellowish clayey silt with abundant clasts in various size. The clasts might be related to the formation of the stalagmite or the collapsed material of the cave ceiling. On the top of the level, small fragments of charcoal and a small flint are found, but its origin are doubtful as it could have been incorporated to the level by trampling after the formation.

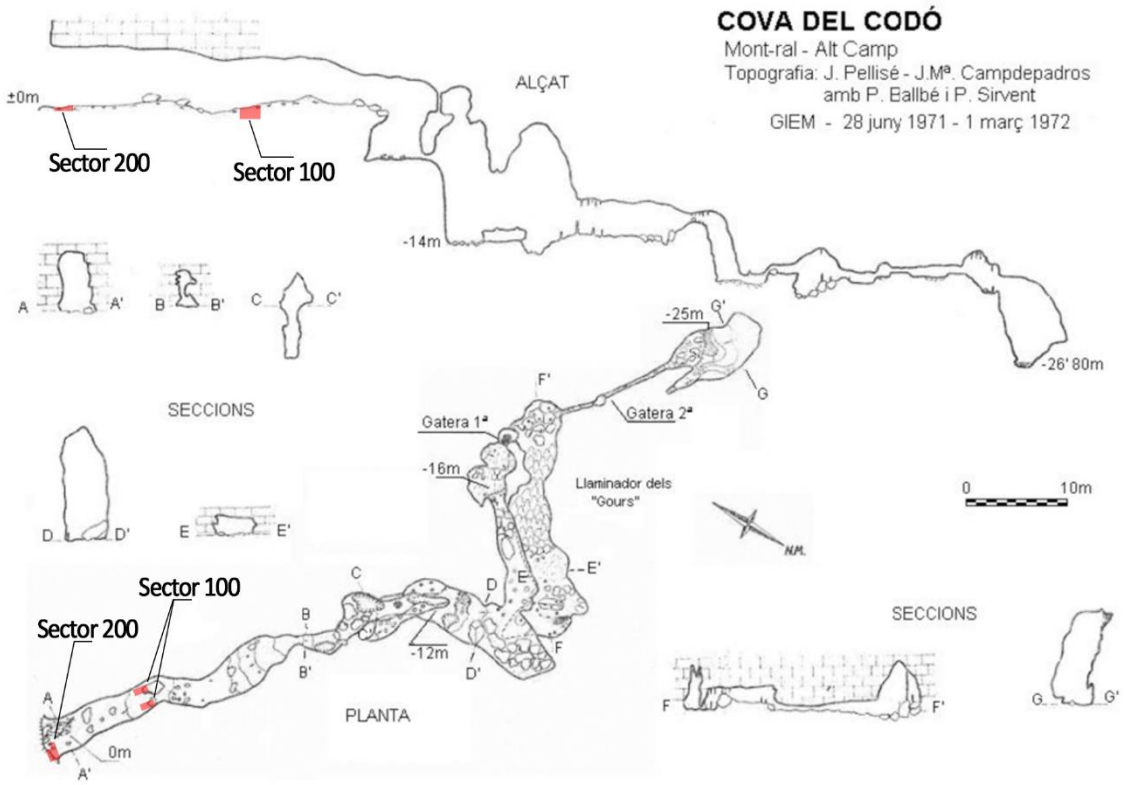

Figure 3.3. Plan, sections, and contour of Cudó cave. Red squares indicating the excavation pits in sector 100 and 200 (Vergès, 2017).

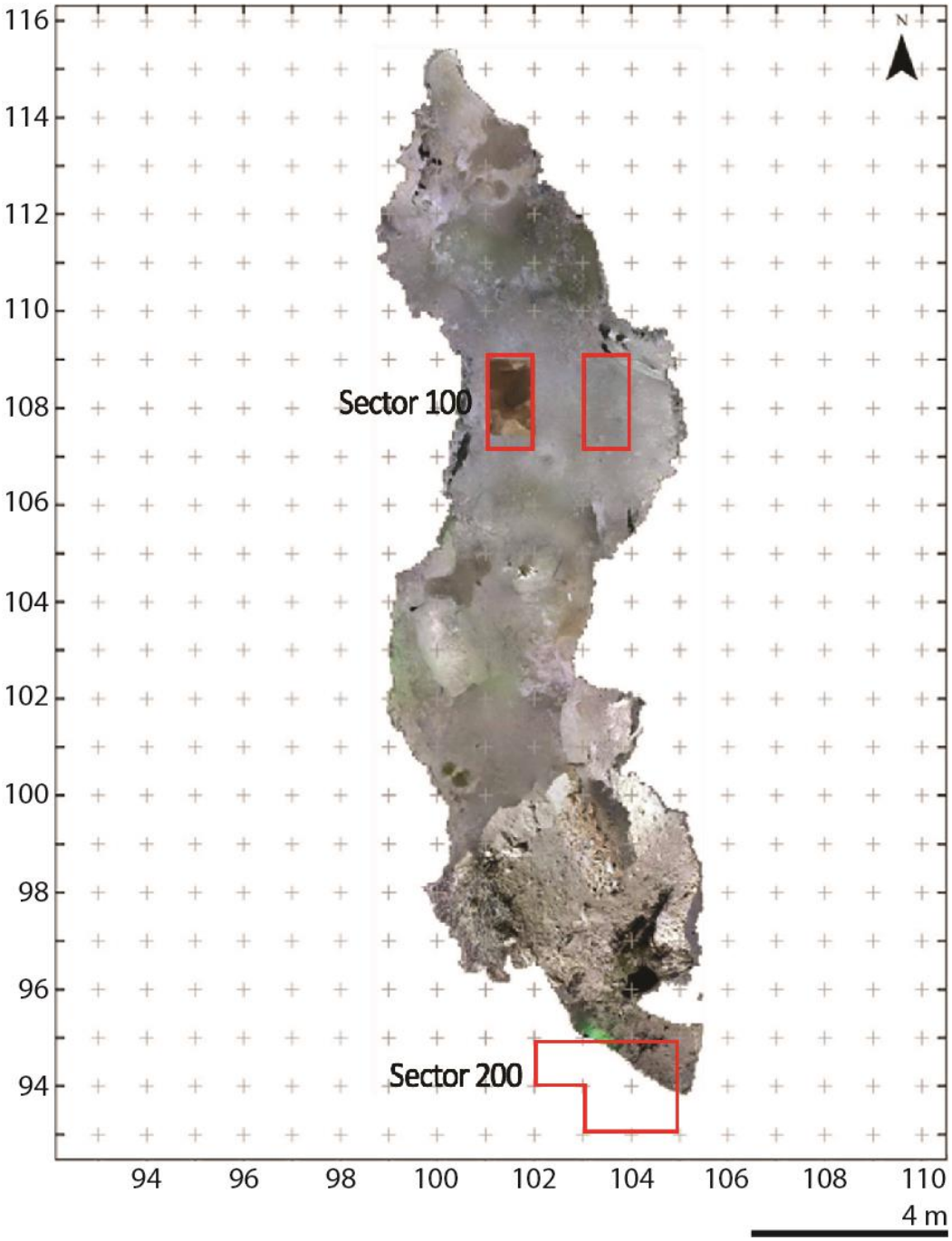

Figure 3.4. Ortography of the front gallery of Cudó cave where the excavation pits situated (red square) (modified from Vergès et al., 2017).

Figure 3.5. Left, the mouth of the Cudó cave and right, the front gallery and the excavation pits.

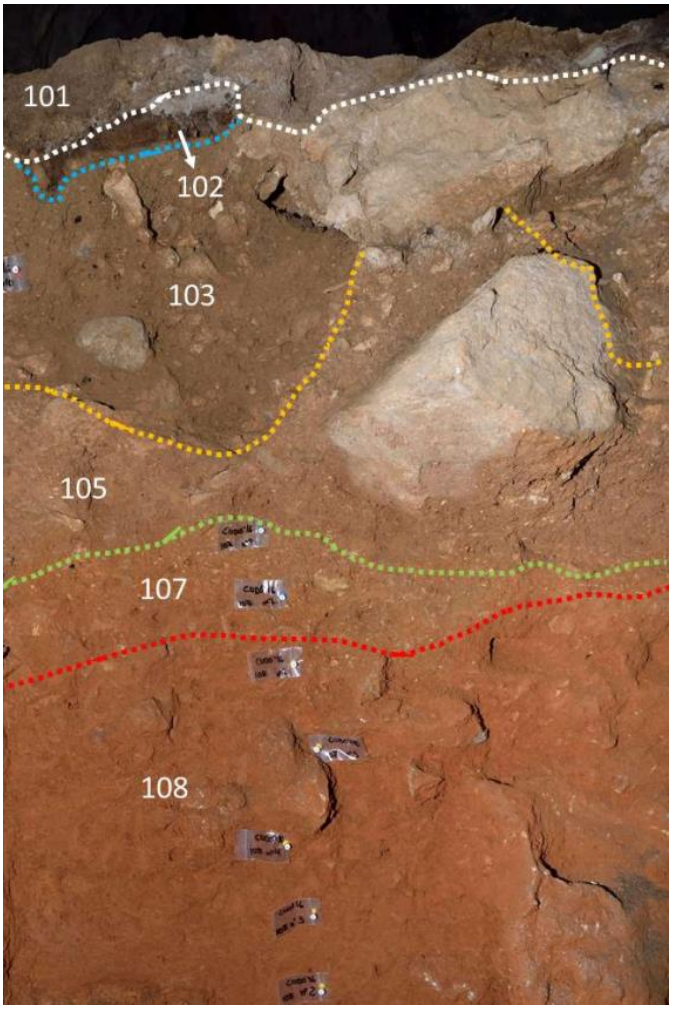

Figure 3.6. Stratigraphic levels of sector 100 Cudó cave (Vergès, 2017).

3.4. Dating analysis

Dating analysis has been done using the accelerator mass spectrometry (AMS) based on the ^{14}C isotope (Vergès, 2017; Baca et al., 2020). The results have been obtained from seven samples recovered from level 102, 105, 107, and 108 (Table 3.1). It ranges from a relatively recent period to MIS2. Among those levels, the most interesting level for its density of the remains and undisturbed stratigraphy are the level 105 dated from ca.10 – 15 ka cal. BP and level 107 dated from ca. 24 – 31 ka cal. BP.

Material	Species	Level	Laboratory ref.	Radiocarbon age (years BP)	Calibrated (years BP; 2 sigma)
Charcoal	*Buxus sempervirens*	102	Beta-455060	190 ± 30	300 – 260 220 – 140 30 post-BP
Charcoal	*Pinus t. sylvestris*	105	Beta-455058	12,900 ± 50	15,585 – 15,245
Bone	Rib indeterminate	105	Beta-455059	11,250 ± 30	13,140 – 13,070
Bone	*Pyrrhocorax pyrrhocorax*	105	Beta-489614	9,090 ± 30	10,273 – 10,199
Marine shell	*Bittium reticulatum*	107	Beta-484788	27,510 ± 120	31,245 – 30,842
Bone	Indeterminate	107	Beta-489615	20,510 ± 60	24,991 – 24,404
Bone	*Pyrrhocorax* sp.	108	Beta-489616	20,340 ± 70	24,734 – 24,157

Table 3.1. Date analysis result on the seven samples from Cudó cave (Vergès, 2017).

3.5. Archaeological remains

The archaeological remains recovered from the 2016 and 2017 campaign can be grouped into several categories based on the material and the technological aspect. Faunal remains, marine shells, lithics, bone artefacts, pottery, and metal artefacts description from the site are provided considering preliminary reports from the site (Vergès, 2017). In addition, archaeobotanical samplings have been performed in the two cave sectors for the ongoing analysis of phytoliths and pollens.

3.5.1. Faunal remains

There are 201 faunal remains that have been recovered during the last campaigns. The distribution varies among the levels, with most remains were recovered from level 103 (82 remains, 40.8%). The rest are distributed in level 105 (27.9%), level 101 (20.9%), level 107 (8.5%), and only small amounts in level 106 and 201.

From the zooarchaeological studies, 67% of the remains were able to be taxonomically identified at least to the family or genus level. Several taxa that have been identified are *Bos* sp., *Cervus elaphus*, *Capreolus capreolus*, *Sus scrofa*, Caprinae, Felidae, Leporidae, *Canis* sp., Columbae, and Corvidae. Among those taxa, the remains of Caprinae and Leporidae are the most abundant in the assemblage. Other remains that could not be taxonomically identified were assigned to the birds for its morphological characteristics (Columbae and Corvidae) and the other to small-sized group.

In the taphonomic aspect, some modifications indicating the deposition environment could be recognized from the assemblages. In this regard, the manganese oxide has been documented in the 22% of the remains, dissolution in 3%, root etching in 7%, and limestone concretion in 2.5%

of remains. Moreover, 20% of the remains, particularly on the lagomorphs, shows biostratinomic alterations that could be caused as biting, detected by depression, furrows, or tissue losses. These marks, by the morphology, location, and dimension could be caused by humans. In addition to the anthropic traces on the faunal remains, some cutmarks also have been documented on some caprids and medium-sized mammal remains (ribs, radius, and phalanx), which by the location, morphology, orientation, and the deposition indicate disarticulation, defleshing, and evisceration processes by humans. Burned bones are also presented in the assemblages with low (carbonized) or high (calcined) level of burning, but due to the high fragmentation not much taxonomical information could be obtained.

In addition, small mammal remains were recovered from sector 100. A preliminary study was conducted on the small mammal assemblages recovered from level 107 and 105. Ten species were already identified, those are *Crocidura* cf. *russula*, *Myotis* cf. *myotis*, *Pipistrellus* cf. *pipistrellus*, *Microtus arvalis*, *Microtus agrestis*, *Microtus* (*Terricola*) *duodecimcostatus*, *Microtus* (*Iberomys*) *cabrerae*, *Chionomys nivalis*, *Apodemus sylvaticus*, and *Eliomys quercinus* (Baca et al., 2020 supplementary material).

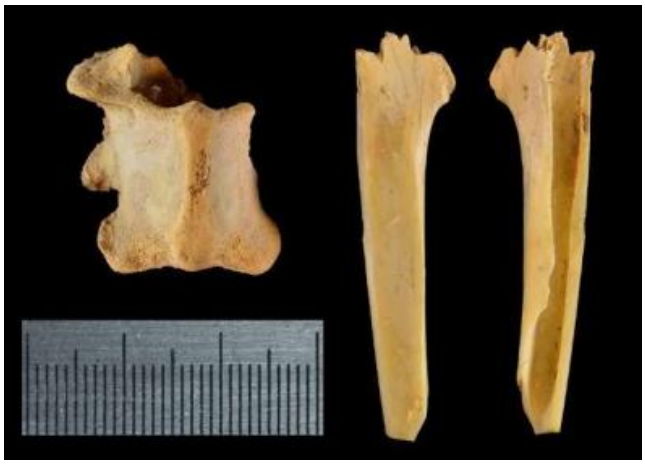

Figure 3.7. Vertebra of Leporidae (left) and femur fragment of Leporidae (right) both were recovered from level 105 (Vergès, 2017).

Figure 3.8. *Canis* sp. tooth recovered from level 105. From left, in lingual view, posterior view, labial view, and anterior view (Vergès, 2017).

3.5.2. Shells

Several marine shell remains were recovered from the washing-sieving process of the sediment and during dry sieving process in the site. They are mostly recovered from level 105 and 107 in sector 100 and could be associated to the Upper Paleolithic occupation period. Most of the recovered remains correspond to *Bittium reticulatum*. It was also recovered a fragment of *Cerastoderma* from level 105, one *Dentalium* from level 105, corresponding to the only remains that been recorded in situ with the iron oxide residues. A *Bittium reticulatum* remains recovered from level 107 was selected for the dating analysis.

3.5.3. Lithics

There are not many lithic remains that have been recovered from the campaign of 2016 and 2017. In total 77 remains were recovered, mostly from level 105 (36 pieces) and the rest are distributed on level 101, 103, 104, and 107. By raw materials, flint is the most frequent (29 pieces); while limestone, sandstone, and oncolite less abundant and cannot be surely associated to anthropic activities as can commonly be found in the cave.

On the case of flint, some technological remarks can be made from the recovered materials. In level 105, some artefacts are recognized as scrapers, splinters, blades, and points. Particular to the points, pseudo retouch possibly associated to the use wear marks can be recognized. Moreover, several positive bases also have been recovered with traces of microblade production. Considering their technological features, those items can be associated to the final Upper Paleolithic period.

More artefacts have also been recorded from level 101, 103, 104, and 107 and some of them are clearly allochthonous origin. Unfortunately, there are indications of sediment disturbance of those levels in recent period. Therefore, the provenance of the lithic items cannot be assured, except for a back-blade from level 101, which by the technological features can be attributed to the type of occupation at level 105 (Vergès, 2017).

Figure 3.9. Positive base (flakes) recovered from level 205 (Vergès, 2017).

3.5.4. Faunal artefacts

One assegai point made on cervid antler was recovered from level 103 in the square of 103-108 during the 2017 campaign. Even though the base is broken, typologically it could be categorized within the group of split-based point. As mentioned before, the level 103 is a disturbed level

with mixed chronology. However, this type of antler point could be attributed to the Upper Paleolithic period, and according to the dating analysis from level 107, it could be from 30.000 – 31.000 BP (Vergès, 2017).

3.5.5. Ceramics and metal artefacts

In total, 54 fragments of ceramics have been recovered from the 2016 and 2017 campaigns. Those were found on level 101, 102, and 103 in sector 100, also from 201 and 202 in sector 200. Among those fragments, four types of ceramics were identified, which are handmade ceramics, African sigillata, glazed ceramics, and metallic reflex ceramics. By their typology and artistic styles, those fragments could be attributed to several historical periods, from 4th to 5th century for the African sigillata to 16th to 17th century for the glazed and metallic reflex ceramics.

Some metal artefacts are also have been recovered from surface level, level 101, 103, 201, and 202, those are a brass button, an iron item, coins, and a lead bullet. Most of them are unable to be assigned to some specific period due to their poor preservation, but two bronze coins could come from the Constantine emperor, around 4th to 5th century. Two other coins also were identified from the period of Philip V, dated from 1718.

There is no ceramics or metal artefacts were found in level 104, 105, 106, 107, and 108 in sector 100.

4. MATERIALS AND METHODS

This chapter describes the recovery and analytical techniques used during the study of the small-mammal assemblages of Cudó cave. First, are described the processes performed to obtain the small mammal samples from the deposits of level 107 and 105 of Cudó cave. Second, the analytical techniques used during the taxonomic and taphonomic analysis, then exposed the palaeoecological reconstruction methods employed in this work.

4.1. Obtaining small mammal samples

The small mammal remains are recovered in a different way than the archaeological materials or the larger mammal remains. Small mammals are obtained directly from sediment samples associated to the information of their original archaeological provenance. Water-sieving of the sediments is conducted to obtain the concentrate, which comprise the mixture of coarse grain sediment, small mammal remains, and the other archaeological remains. The sieving conducted in various ways with various number of sieves depending on the characteristics of the sediment. However, in most cases, this process will use flowing water to wash the sediment on several superimposed sieve, with various mesh size from 10 to 0.5 mm (Freudenthal et al., 1976).

In the case of Cudó cave, the sediment is sandy clay that could be easily washed without leaving a lot of residues on each sieve level. Therefore, the sediment recovered from the field were directly went to the sieving processes. The sieve used for this work were with 1 mm and 0.5 mm mesh. Large stones and visible faunal or archaeological remains were hand-picked and collected during the sieving process. Then, the clean concentrate from were moved to the drying container (Figure 4.1). Finally, the extracted concentrate is air dried under the shaded area. This drying method was done to minimize alteration caused by rapid drying under direct contact to the sunlight.

After the concentrate were totally dried, the process then continued by sorting the small mammal remains from the sediment and the other archaeological remain. The sorting was conducted on all the coarse concentrate from the level 107 and 105 recovered from the 2016 – 2017 field campaign. It is considering that these two levels are the densest undisturbed levels that have been excavated from Cudó cave.

The sorting process was conducted in the Institut Català de Paleoecologia Humana i Evolució Social (IPHES) at Tarragona. The concentrate is spread thinly on the sorting tray and the remains are hand-picked using precision tweezers (Figure 4.2). The small mammal remains, and other archaeological remains such as charcoal, mollusks shells, lithic fragments, and larger bones are separated using the naked eye. Those remains are stored in separate plastic bags according to the materials with labels in each bag contains the provenance information, at least with the site name, square name, levels, and depth intervals. The taxonomically diagnostic remains such as molars, mandibles, maxillae, and humerus are collected in a separate bag for further analysis. All these remains are then deposited in the collection of IPHES.

Figure 4.1. Washing facilities for small mammal remains recovery at IPHES (left) and the drying process of the concentrate (right).

Figure 4.2. Bags of the wet-sieved sediment from the Cudó cave that need to be sorted in the laboratory (left) and the picking process at the IPHES using the sorting tray and a precision tweezer (right).

4.2. Taxonomic identification

The taxonomic identification was conducted at the IPHES by comparison to the reference collection of the Laboratory of micropaleontology (Figure 4.3 D and E) as well as to the bibliographical references and anatomical atlas. A binocular microscope (Euromax) was used with 6 – 45x magnification during the identification (Figure 4.3 C). For the photographic purpose, a Dino-Lite digital microscope with the DinoCapture 2.0 computer software were used (Figure 4.3 B). To perform observation under the binocular microscope and Dino-Lite digital microscope, the remains were mounted on acrylic base using Blue-Tack adhesive. This adhesive allows good and stable support to ease the observation and could be easily and cleanly removed. Precision tweezers were also utilized to precisely align the remains. In addition, Adobe Photoshop CC 2019 was also utilized to digitally process the photos covering brightness, contrast, color, and background adjustment. Further cleaning was also required for several remains to ease the taxonomic identification and photographing. For this purpose, ultrasonic cleaning process was used with consideration on the integrity of the remains (Figure 4.4). This process was conducted in particular to the remains with good integrity state.

The taxonomical identification was conducted using specific anatomical elements which provide valuable taxonomic information (Figure 4.3 A). It is different for each taxonomic group, such as the mandible, maxilla, and teeth for insectivores identification (Reumer, 1984; Furió, 2007); mandible, maxilla, teeth, and humerus for chiropters (Dupuis, 1986b; Sevilla, 1988; Galán,

2019); first lower molar for Arvicolinae subfamily (Nadachowski, 1982; Gosàlbez, 1987); and teeth for the Muridae, Gliridae, and Sciuridae subfamilies (Chaline, 1972; Chaline et al., 1974; Gosàlbez, 1987). The identified remains were all quantified as the number of identified specimen present (NISP). In case of maxilla and mandible, right and left part were counted as two separate remains. The NISP then grouped into the minimum number of individual (MNI), by counting the most highly represented diagnostic element for each species, considering the laterality.

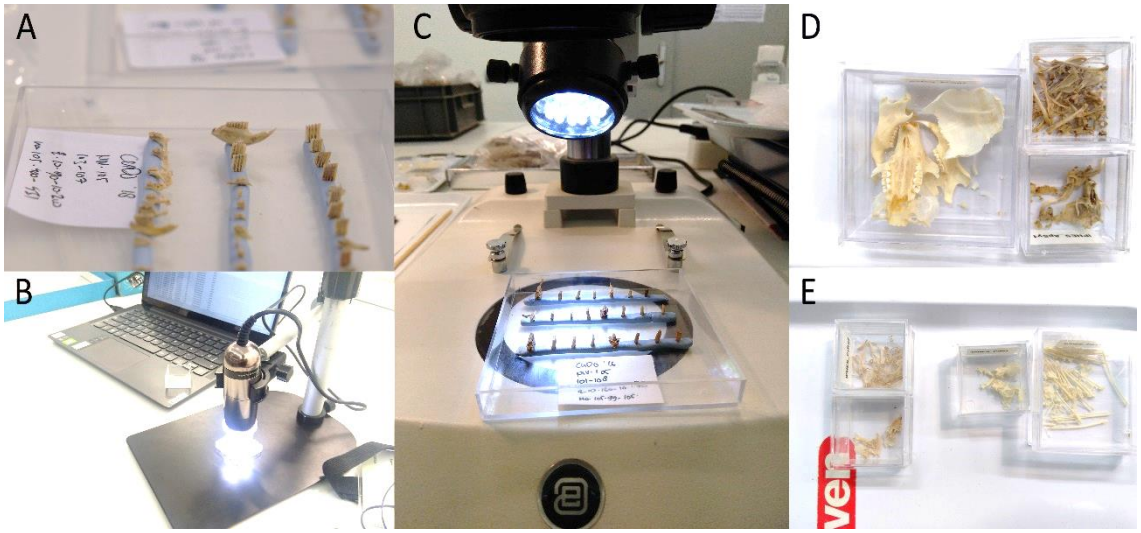

Figure 4.3. Identification processes on the remains, A) preparation of the remains for the identification, B) utilization of Dino-lite digital microscope for observation and to capture the photos, C) utilization of binocular microscope for identification, D – E) some of the small mammal reference collections of the Laboratory of Micropaleontology at IPHES.

Figure 4.4. The ultrasonic cleaner used in for cleaning several remains to ease the identification and taphonomic observation in this study.

4.3. Taphonomic analysis

Taphonomic analysis is a study on the faunal remains alteration to assess the accumulation or deposition and post-depositional processes experienced by the remains. This is based on the fact that the studied paleontological remains are the product of the processes implicated on the transition from the life assemblages, burial or fossil assemblages, up to the studied assemblages. Several agents can contribute to the assemblage formations, for instance

the predatory behavior, climatic variations, burial environments, and the research-induced alteration (López, 1991).

On the study of small mammal assemblages for paleoenvironmental reconstruction, the taphonomic processes should always be considered since the formation is highly affected by many agents. One of the most recurrent sources of the bone accumulations is the predation, with the small mammal species as the prey (Fernández-Jalvo et al., 2016). The chemical-induced alteration as the result of digestion process is the most common modification regarding the predation. Assessing the intensity of the digestion marks on the remains and its frequency could indicate the possibility of predators contributing to the formation of the assemblages (Andrews, 1990; Fernandez-Jalvo, 1992). The information about predator's species involved, its predatory behavior, and their hunting range could make the interpretation of the small mammal assemblages more accurate. The benefit of the predator identification is it can be assured that the small mammal species abundance is proportionally represented. Moreover, by knowing the hunting range of the predators, it can be inferred the scope of the reconstructed paleoenvironment. As an example, owls, diurnal raptors, and small mammalian carnivores are the main predators which produce accumulation of the small mammal remains. Among them are the opportunistic predators that hunt any species available within its range as the prey. This is the most common group and its accumulation of the small mammal remains will reflect the diversity of the surrounding ecosystem. The second group is the specialist hunter that only catch some specific species. The specialist predators will tend to migrate following the seasonal changes that lead to the decrease of its prey abundance in the initial ecosystem. The small mammal remains of this group will display unproportioned representation of certain taxa. Therefore, the environmental inferences would become less accurate. However, those groups are known to produce different traces on the prey's remains to be able to distinguished one to another (Andrews, 1990; Fernández-Jalvo et al., 2016).

The taphonomic analysis on this work follows Andrews (1990), with considering the last review by Fernández-Jalvo et el., (2016) who established four grades of the digestion marks that could be observed in the small mammal remains: light, moderate, heavy, and extreme (Table 4.1). For Cudó cave, the taphonomic analysis was only carried out on the taxonomically identified molars in order to perform a quick and preliminary approach to the origin of the accumulation. The observations on the digestion marks were conducted on the occlusal and lateral surfaces of the molars. To observe the digestion marks, binocular microscope (Euromax) is used with 6 – 45x magnification. Apart from these four grades, the teeth also been assigned to the "absent" classification for the teeth without digestion traces. Moreover, the teeth with unclear digestion mark due to the preservation state are classified as "null".

	ARVICOLINAE		MURIDAE		SORICIDAE AND CHIROPTERA
	OCCLUSAL	LATERAL	OCCLUSAL	LATERAL	
Light	Enamel gaps on salient angles, dentine emerges outlining a narrow convex shape.	Small enamel reduction (less than a third of the height of the tooth). Dentine exposed and rounded.	Rounded cusps, smoother than non-worn teeth.	Matt (loss of shiny) enamel.	No digestion can be seen, enamel is shiny, no rounding, no damage.
Moderate	Wider enamel gaps and more flattened dentine exposed on salient, dentine retracted inwards outlining a wider convex shape than in light digestion	Enamel removed along the half height of the tooth (some columns may have superficial reduction of enamel along the entire height of the column).	Pitted enamel surface, all over the tooth enamel.	Incipient enamel reduction at the crown root junction.	Matt surface enamel
Heavy	Dentine, locally removed in some salient angles outlining a concave shape on occlusal view.	Extensive removal of enamel along the entire height of the salient angles. Dentine flattened and broadly wavy.	Enamel removed from the cusps and heavily pitted. Dentine is exposed and not affected or rounded.	Enamel removed towards the height of the tooth and at the crown-root junction. Dentine/roots are not affected or rounded.	Enamel heavily pitted and partially removed, dentine exposed at the edge contact between the crown and the roots. Dentine is not affected or rounded.
Extreme	Dentine collapsed inwards, providing a concave outline in all or most salient angles.	Dentine collapsed inwards. Enamel along the sides of the original columns.	Enamel forming small islands or completely removed with or without dentine hollowed out and etched.		Enamel forming small islands or completely removed, with or without dentine hollowed out and etched.

Table 4.1. Main modifications on teeth related to digestion on the main taxonomic groups according to Fernández-Jalvo et al., (2016).

4.4. Palaeoecological analysis

Palaeoecological analysis for the landscape and climatic reconstruction performed in this work were using quantitative and qualitative methods. On the quantitative methods, relative abundance of each species was considered to get the value of a certain variables. By this means the obtained results would shows proportions or percentage of a variable over the others. The quantitative methods used in this work were Simpson's index, Chorotype analysis, and Habitat weighting method. Otherwise, on the qualitative methods were performed using the presence and absence data of identified species without considering its abundance. In this work, the qualitative analysis methods including Bioclimatic model (BM) and Mutual ecogeographic range (MER). Further explanations of each method are described as follows.

4.1.1. Simpson's index

Diversity in ecology could be split into two terms: richness, the number of taxa in a community; and evenness, a reflection of the uniformity of relative abundance of the taxa

(Olszewski, 2004). Some statistical analysis method could be used to estimate the diversity of the biological communities. Among them is the Simpson's index, which estimate the evenness of the sample by emphasizing a couple of most important species in the sample (Whittaker and Whittaker, 1972). By this means, the obtained result will show how even the composition is. The more even the lower dominance of a certain taxa, the less even means higher dominance of some taxa. The result of this index calculation lies between 0 to 1, where the value near 0 means there is domination of certain taxa and the value close to 1 means that the taxa are more equally represented. In this regard, more even or less domination could be a signal for favorable ecosystem that support complex and heterogenous community. Otherwise, the ecosystem will be less suitable to support complex community and only best-fit to some specific taxa.

The Simpson's index was used to in this work considering it was only needed to analyze the evenness from one site without comparison to the other sites. The evenness of a community can be represented by Simpson's diversity Index $1-\sum(ni/n)^2$, where the *ni* is the number of individuals of taxon *i*. This analysis was performed in the Paleontological Statistics (PAST) software (version 4.0) (Hammer et al., 2001).

4.1.2. Chorotype analysis

Chorotype is a concept of classifying species, genera, or higher taxa with overlapping geographic distribution into similar groups (Fattorini, 2015). This concept could be used to indicate several entities, such as a recurrent type of geographical distribution, assemblages of species with certain ecological requirements within geographical area, assemblages of species with common biogeographical history, group of species supposed to be phylogenetically related, and group of species with restricted biogeographical region (Vigna Taglianti et al., 1999) However, this concept is used in two different ways, which are looking for the distribution pattern globally (Vigna Taglianti et al., 1999) and in regional way depending on the studied area (Passalacqua, 2015).

This concept has been applied by Sans-Fuentes and Ventura (2000) on current insectivores and rodents species in Catalonian region. One of the main aims of the study was to climatically characterize the biotic region and the chorotypes. From the quantitative analysis that have been done, four chorotypes were identified. Those chorotypes are defined as follows.

Chorotype 1 – It is constituted by Pyrenean or Pre-Pyrenean species, which associated to mid-European environment requirement. Their environment is characterized by relatively low mean summer temperature (<20^{o}C), mean annual temperature below 10 – 12^{o}C, and the mean annual precipitation above 800 mm. The current distribution of this chorotype in northeastern Iberia is in the eastern segment of the southern Pyrenees. The species included in this chorotype are *Sorex araneus* and *Chionomys nivalis*.

Chorotype 2 – This chorotype groups species with mid-European requirements but tolerant to a certain degree of Mediterranean environment. The main factors that affect the distribution of species belongs to this chorotype is the relatively high precipitation (>600 mm). The current geographic distribution of this chorotype in northeastern Iberia overlaps with the chorotype 1 but more extended to the south and the east. Some species assigned to this chorotype are *Sorex coronatus, Microtus arvalis,* and *Microtus agrestis*.

Chorotype 3 – It is a group for species with Mediterranean environment requirement. The species within this group requires mild temperature (MAT >5^{o}C) and relatively high precipitation (MAP <1000 mm). Several species associated with this chorotype are *Crocidura russula, Microtus* (*Iberomys*) *cabrerae,* and *Microtus* (*Terricola*) *duodecimcostatus.*

Chorotype 4 – This categorizes group of Mediterranean, generalist, anthropic affected, and species with very specific habitat. Among them are *Apodemus sylvaticus, Eliomys quercinus, Sciurus vulgaris,* and the Chiroptera are some taxa assigned to this chorotype. In climatic point of view, species from this chorotype will give limited information as it could be found in a wide climatic variation. However, in term of habitat preferences, it could be useful as some species have particular habitat preferences.

In this study, these four chorotype defined for insectivores and rodents in Catalonia by Sans-Fuentes and Ventura (2000) (Table 4.2) will be used to infer the past environmental condition within the vicinity of Cudó cave. The relative abundance of species within each chorotype will be quantified to obtain the percentage of corresponding chorotype, so it would be comparable to each other.

4.1.3. Habitat weighting method

Habitat weighting is a quantitative method used for landscape reconstruction based on the habitat preferences of each taxon. As the species found in the assemblages are still living today, the habitat preferences are assumed to be similar as their living counterparts (Evans et al., 1981). The habitat weighting is based on the ordination method developed by Gauch (1989) and Rowe (1956) from the known habitat preferences of the species. It combine the presence or absence and the weighting of the preferred habitat (Gauch, 1989). One application of this method was done by Andrews (2006) on the tropical environment of Tanzania with the mammalian remains from ca. 2.6 Ma.

In this study, five habitat systems were considered by reference to the current habitats represented in the Iberian Peninsula. Those habitat systems are described below.

1. **Open dry –** meadows under seasonal change,
2. **Open humid –** evergreen meadows with dense pastures and suitable topsoil,
3. **Woodland –** mature forest, including woodland margins and forest patches with moderate ground cover,
4. **Rocky –** areas with suitable rocky or stony substratum,
5. **Water –** area along streams, lake, and ponds.

A fractioned value between 0 to 1 is assigned to each species according to its preference of the habitat, 0 means not preferred habitat, while 1 means strongly preferred habitat (Table 4.2). The atlas of modern Iberian mammals by Palomo et al. (2007) is considered for the habitat assignation of each species.

SPECIES	CHOROTYPE				HABITAT WEIGHTING			
	Ch1	Ch2	Ch3	Ch4	OD	OH	WO	R
Crocidura russula			x		0.5	0	0.5	0
Sorex gr. *araneus-coronatus*	x				0	0.5	0.5	0
Myotis gr. *myotis-blythii*				x	0		0.75	0.25
Pipistrellus cf. *pipistrellus*				x	0	0	0.5	0.5
Rhinolophus cf. *ferrumequinum*				x	0	0.5	0.5	0
Chionomys nivalis	x				0	0	0	1
Microtus (Iberomys) cabrerae			x		0	0.5	0.5	0
Microtus agrestis		x			0	0.5	0.5	0
Microtus arvalis		x			0.5	0	0.5	0
Microtus (Tericola) duodecimcostatus			x		0	0.5	0.5	0
Apodemus sylvaticus				x	0	0	1	0
Eliomys quercinus				x	0	0	0.5	0.5
Sciurus vulgaris				x	0	0	1	0

Table 4.2. Chorotype and habitat weighting valuation of each taxon recovered from the Cudó cave. Ch, chorotype; OD, open dry; OH, open humid; WO, woodland; R, rocky.

4.1.4. Bioclimatic model

Bioclimatic model analysis is a method of paleoclimatic inference proposed by Hernández Fernández (2001). It based on the relationship between the climate and the mammalian geographical distribution. This method developed using the carefully selected faunal population which represents ten climatic zone over the world (Table 4.3) (Hernández Fernández, 2001; Hernández Fernández and Peláez-Campomanes, 2003). Nevertheless, only four climatic zone will me mentioned in the next part of this work considering its presence in the assemblage from Cudó cave. These are the climatic zone IV, VI, VII, and IX.

The first step is to assign the species presented in stratigraphic level to the climatic zones. The value would be 0 if the species is does not live in the corresponding climatic zone (Table 5.4). Otherwise, if the species exists in a climatic zone, the value would be determined using the climatic restriction index (CRI) by following formula.

$$CRI_i = 1/n$$

Where *n* is the number of climate zones inhabited by the species and *i* is the climate zone which species occurs. The climate zone where the species is absent will be valued with 0 (Table 4.4) (Hernández Fernández, 2001). The CRI of each species then used for the calculation of the bioclimatic component (BC), which is the representation of each climatic typology in a specific locality. Each BC locality value is calculated with following formula:

$$BC_i = (\sum CRI_i)\ 100/S$$

Where *i* is the climate zone and *S* is the number of species found in the locality. All the BC values, represent the bioclimatic spectrum of a locality (Hernández Fernández, 2001). The next steps are to estimate the MAT, MAP, mean temperature for the coldest month (MTC), and mean temperature of the warmest month (MTW). The multiple linear regression developed

specifically for the order Rodentia corresponds to the following equations (Hernández Fernández et al., 2007).

MAT (ºC) = 26.686 + (0.024*II) – (0.029*II/III) – (0.024*III) – (0.074*IV) – (0.12*V) – (0.135*VI) – (0.217*VII) – (O-404*VIII) – (0.386*IX)

MAP (mm) = 2978.195 – (21.237*II) – (27.237*II) – (27.563*II/III) – (33.05*III) – (32.648*IV) – (6.678*V) – (5.076*VI) – (28.4*VII) – (33.109*VIII) – (25.98*IX)

MTC (ºC) = 27.538 – (0.033*II) – (0.096*II/III) – (0.080*III) – (0.175*IV) – (0.21*V) – (0.141*VI) – (0.418*VII) – (0.710*VIII) – (0.465*IX)

MTW (ºC) = 26.219 + (0.070*II) + (0.021*II/III) + (0.020*III) + (0.031*IV) – (0.032*V) – (0.113*VI) – (0.037*VII) – (0.121*VIII) – (0.287*IX)

This work only considered the order Rodentia for the application of bioclimatic model as this is the most abundant order in the assemblages compared to insectivores and chiropters, even though both groups are good for climatic inference. Furthermore, this last group is rejected for this analysis considering its seasonal migration behavior, therefore bats are mostly analyzed separately in the ecological studies(Hernández Fernández, 2001).

ZONE	CLIMATE	ZONOBIOME (MAIN VEGETATION TYPE)
I	Equatorial	Evergreen tropical rainforest
II	Tropical with summer rains	Tropical deciduous forest
II/III	Transition tropical semi-arid	Savanna
III	Subtropical arid	Subtropical desert
IV	Winter rain and summer drought	Sclerophyllous woody plants
V	Warm temperate	Temperate evergreen forest
VI	Typical temperate	Nemoral broadleaf-deciduous forest
VII	Arid temperate	Steppe to cold desert
VIII	Cold tempereate (boreal)	Boreal coniferous forest (taiga)
IX	Arctic	Tundra

Table 4.3. Climatic typology used in the Bioclimatic Model Method and its relationship with the world vegetation types (following Hernández Fernández, 2001).

SPECIES	CLIMATIC ZONE			
	IV	**VI**	**VIII**	**IX**
Microtus arvalis	0	1	0	0
Microtus agrestis	0	0.5	0.5	0
Microtus (Terricola) duodecimcostatus	0	1	0	0
Microtus (Iberomys) cabrerae	1	0	0	0
Chionomys nivalis	0.25	0.25	0.25	0.25
Apodemus sylvaticus	0.5	0.5	0	0
Eliomys quercinus	0.5	0.5	0	0
Sciurus vulgaris	0.33	0.33	0.33	0

Table 4.4. Climatic zone assignation of each species within the order of Rodentia of Cudó cave.

4.1.5. Mutual Ecogeographic Range (MER) method

Mutual Ecogeographic Range analysis is a paleoclimatic reconstruction method by determining current geographic area of co-occurrence of the species in the stratigraphic levels. This geographical area determination rely on the 10x10 km UTM grid squares where the species currently live (Blain et al., 2009; López-García et al., 2010b; Lyman, 2016). The aim of this method is to be able to infer the past climatic conditions of the stratigraphic levels by identify the climatic conditions of the co-occurrence area of the species (Fernández-García and López-García, 2013)

In this work, the current geographic distribution of the identified species in the Iberian Peninsula obtained from Palomo et al. (2007). This atlas provides species distribution area within 10x10 km UTM grid, and therefore, the climatic inferences would be under this resolution. The maps of current climatic variables, are based on climatic atlas of the Iberian Peninsula from AEMET & IMP (2011), which considered climatic information records from 1971 to 2000 (Figure 4.5 and 4.6). Moreover, for the vegetation zone, the map from Rivas Martínez et al. (1987) is used (Figure 4.7). The MAT, MTC, MTW, and MAP estimations are based on the average data obtained in intersection points of each level and then compared to the current climatic data, which obtained from the climate-data.org.

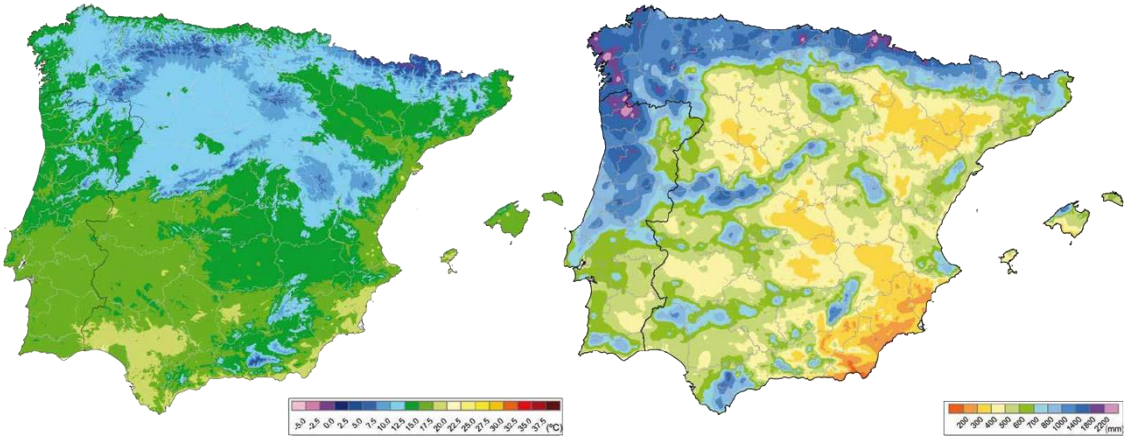

Figure 4.5. Maps of current MAP (left) and MAT (right) of the Iberian Peninsula (AEMET and IMP, 2011).

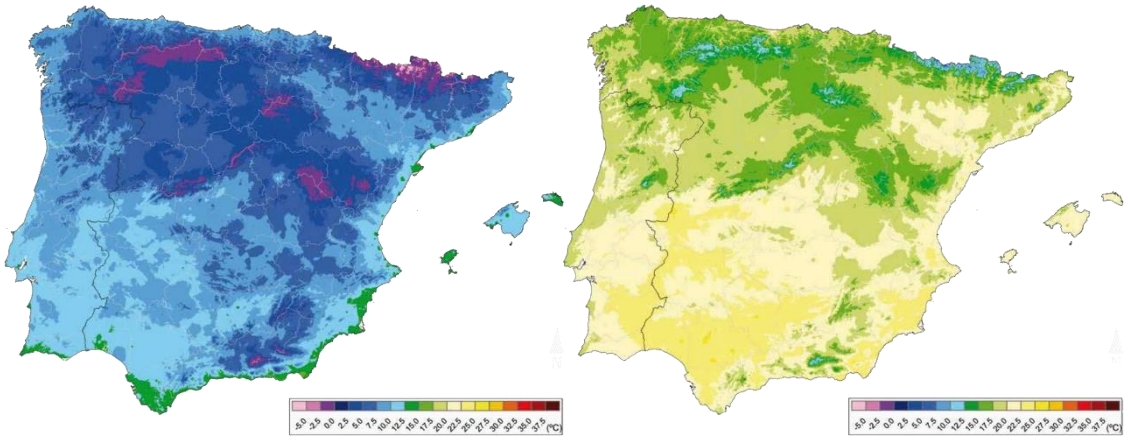

Figure 4.6. Maps of current MTC (left) and MTW (right of the Iberian Peninsula (AEMET and IMP, 2011).

Figure 4.7. Map of current vegetation zone of the Spanish Iberian Peninsula (Rivas Martínez et al., 1987)

5. TAXONOMIC IDENTIFICATION

5.1. Taxonomic and terminological remarks

In this chapter the recovered material from Cudó cave level 107 and 105 are described and discussed for the taxonomic identification. The description and taxonomical identification follows the criteria from Chaline et al. (1974), Reumer (1984), and Furió (2007) for Soricidae; Chaline (1972), De Paz & Benzal (1989), Dupuis (1986), Sevilla (1988), Menu & Popelard (1987) and Galán (2019) for Chiroptera; Nadachowski (1982) for Arvicolinae; Chaline (1972), Chaline et al. (1974), Daams (1981), and Gosàlbez (1987) for Muridae, Gliridae, and Sciuridae. Wilson & Reeder (2005) is referred for the taxonomic classification of the species.

Some terminological clarifications should be made for this work. The capital letters are used to name the upper or maxillary dentition, "I" for the upper incisors, "P" for the upper premolars, and "M" for the upper molars. The lower or mandibular dentition are written with small letter, such as "i", "p", and "m" for the lower incisors, premolars, and molars respectively. Each type of teeth is given a number following the letter, starting from the mesial side towards the distal. It corresponds to the position on the dentition rows, for example, m1 means the lower first molar, positioned in in front of or anterior to the m2. Regarding the orientation of the dental remains, the term "mesial" or "anterior" refers toward the median plane of the mandible or maxilla, while "distal" or "posterior" refers backward from the median plane or opposite to mesial. The term "labial" refers toward the outside or exterior of the mandible or maxilla while "lingual" refers toward the inside or interior of the mandible or maxilla. The term "occlusal" is used to name the mastication surface of the teeth. In case of appendicular bones, the term "proximal" refers to the parts close to the body, "distal" refers to the parts far from the body. The term "anterior" refers to the front side of the bone in the normal position respect to the body, while the "posterior" refers to the back side of the bone. The term "internal" or "medial" refers to the side close to the body, while "external" or "lateral" refers to the side far from the body.

The habitat preferential and geographic distribution of modern population of each taxa follows Palomo et al. (2007) for the Iberian Peninsula and Mitchell-Jones et al. (1999) for the Eurasian region. The habitat preferential information also acquired from several authors (Gosàlbez, 1987; Lopez-Fuster and Ventura, 1996; López-Fuster et al., 1999). Moreover, the online resources, such as IUCN Red List for Threatened Species (IUCN, 2021) and the Global Biodiversity Information Facility (GBIF, 2021) also been used for the updated geographic distribution as well as the ecological information of the species.

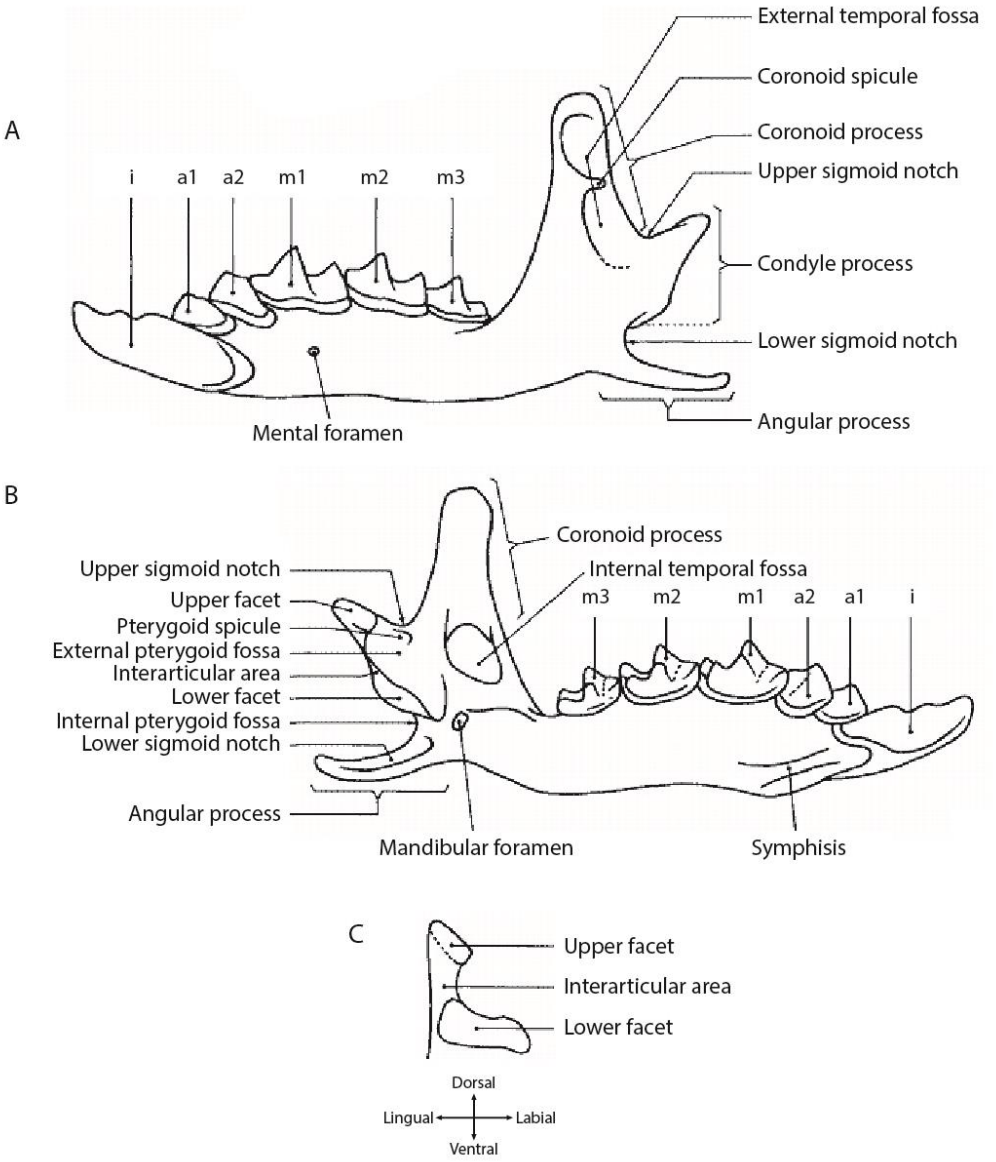

Figure 5.1 – Soricidae nomenclature of the mandible: A) from labial view, B) from lingual view, C) the articular facet of the condylar process from posterior view (modifed from Reumer, 1984).

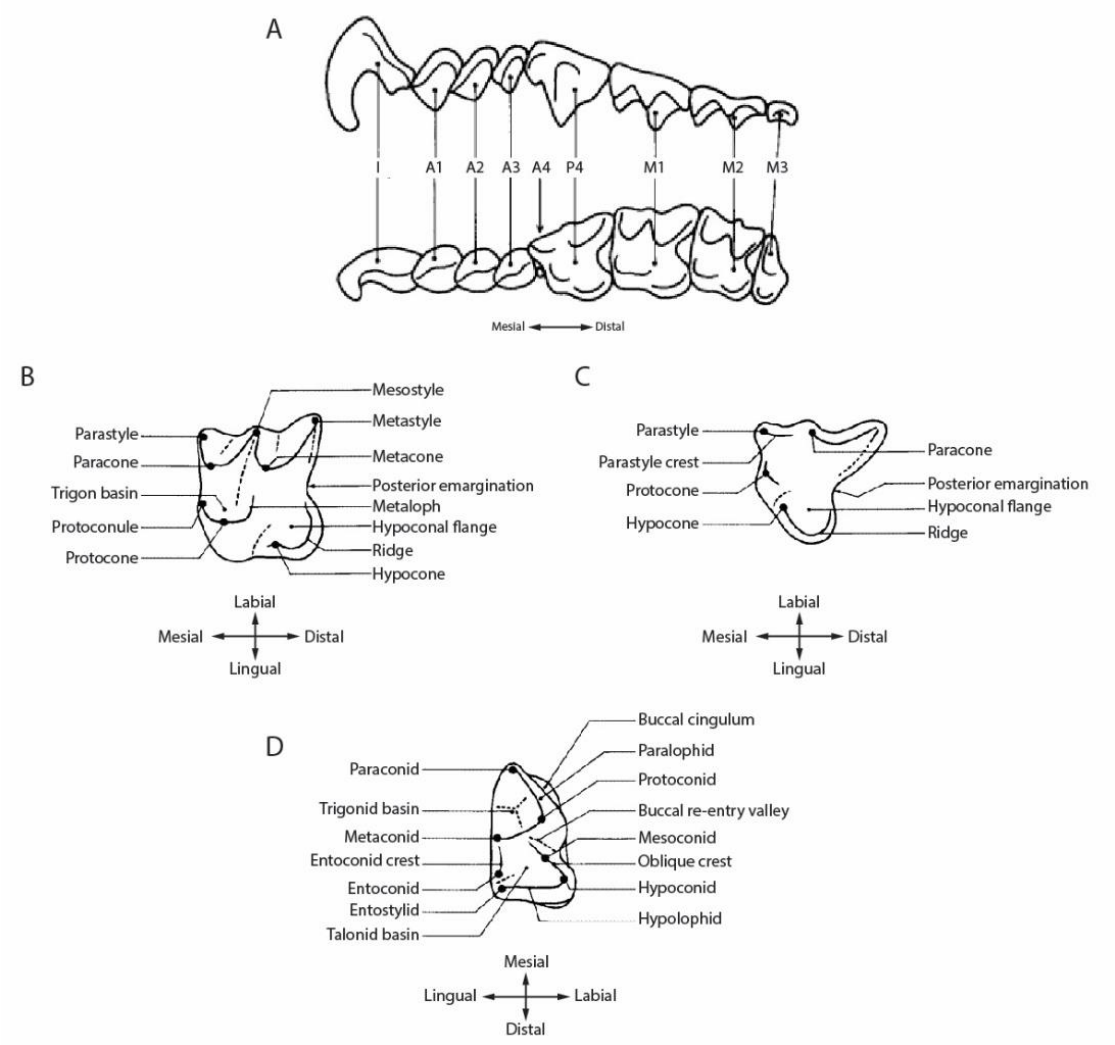

Figure 5.2. – The teeth nomenclature from the occlusal view of the family Soricidae, A) upper dentition in labial view (top) and occlusal view (bottom), B) for M1 and M2, C) for P4, D) for m1 – m3 (modified from Reumer, 1984).

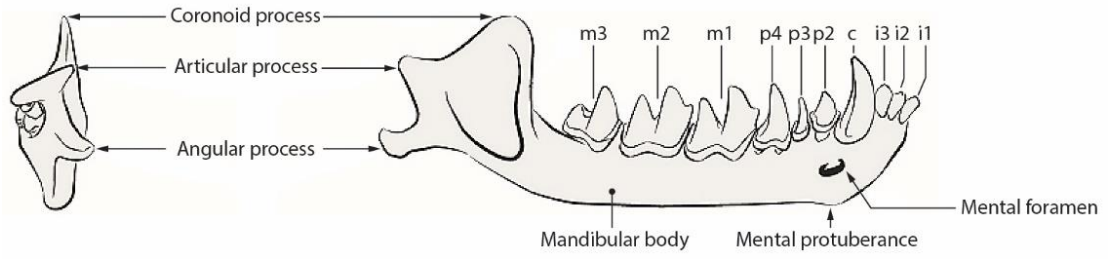

Figure 5.3 – Chiroptera mandible nomenclature: in posterior view (left) and labial view (right) (modified from Galán, 2019)

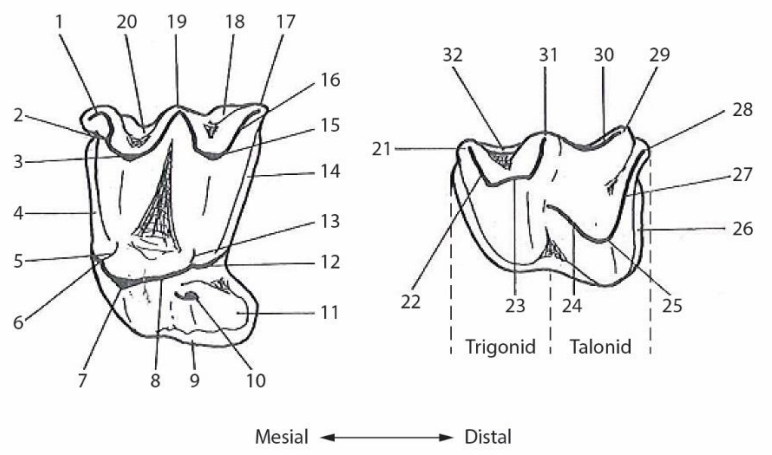

Figure 5.4 – The nomenclature of the order Chiroptera: upper molars (left) and lower molar (right). 1) parastyle; 2) praparacrista; 3) paracone; 4) anterior cingulum; 5) paralophe; 6) paraconule; 7) protocone; 8) postprotocrista; 9) labial cingulum; 10) hipocone; 11) talon; 12) metaconule; 13) metalophe; 14) distal cingulum; 15) metacone; 16) postmetacrista; 17) metastyle; 18) labial cingulum of metaflex; 19) mesostyle; 20) labial cingulum of paraflex; 21) paraconid; 22) paralophid; 23) protoconid; 24) oblique crest; 25) hypoconid; 26) distal cingulum; 27) postcrestid; 28) hypoconulid; 29) entoconid; 30) entocrestid; 31) metaconid; 32) lingual cingulum of trigonid (modfied from Sevilla, 1988).

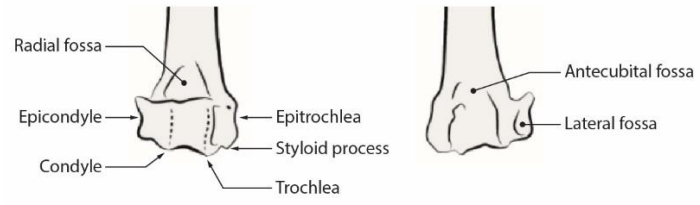

Figure 5.5 – Chiroptera nomenclature: distal part of right humerus in external view (left) and internal view (right) (modified from Galán, 2019).

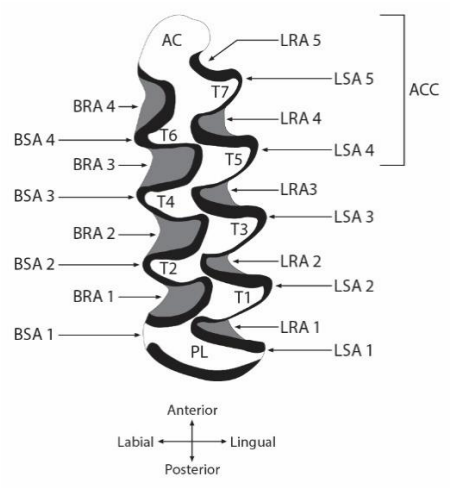

Figure 5.6 – Arvicolinae nomenclature: left first lower molar of (m1) of *Microtus arvalis* from level 105 Cudó cave. AC, anterior cap; T, triangle; LRA, lingual reentrant angle; LSA, lingual salient angle; BRA, buccal reentrant angle; BSA, buccal salient angle; PL, posterior lobe; ACC, anteroconid complex. Grey represents cementum and black represent enamel.

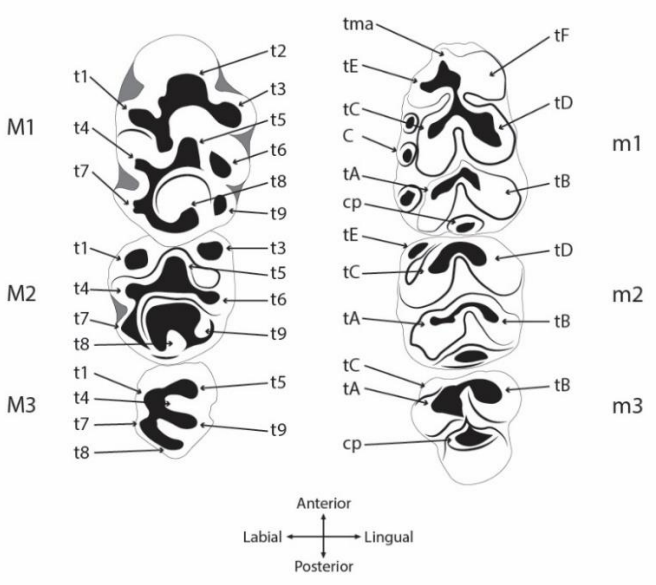

Figure 5.7 – Murinae nomenclature: upper (left) and lower (right) molars of *Apodemus sylvaticus* from level 105 of Cudó cave. t, tubercles; t5, protocone; t6, paracone; t8, hypocone; t9, metacone; c, labial accessory cusps; cp, posterior accessory cusps; tma, medium anterior tubercle; tF, principal antero-lingual tubercle; tE, principal antero-labial tubercle; tD, metaconid; tC, protoconid; tB, entoconid, tA, hypoconid.

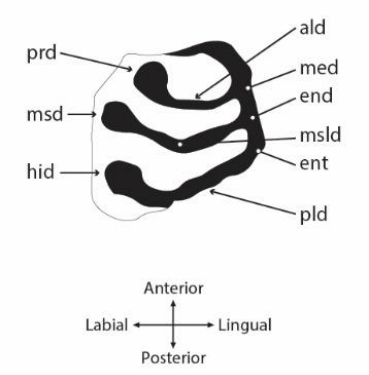

Figure 5.8 – Glirinae nomenclature: first right lower molar of *Eliomys quercinus* from level 5 Cudó cave. ald, anterolophid; prd, protoconid; med, metaconid; end, endolophid; msd, mesoconid; msld, mesolophid; ent, entoconid; hid, hypoconid; pld, posterolophid.

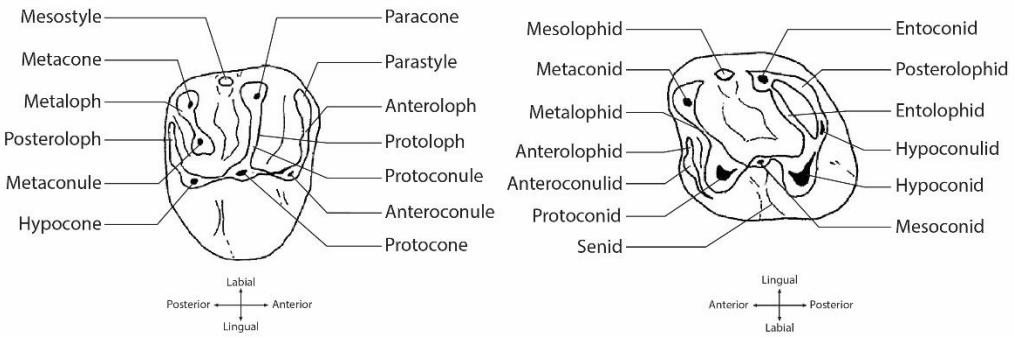

Figure 5.9 – Sciuridae nomenclature: first upper molar (left) and first lower molar (right) (modified from Cuenca-Bescós, 1988).

5.2. Identified species

Class MAMMALIA Linnaeus, 1758
Order EULIPOTYPHLA Waddell, 1999
Family SORICIDAE Fischer, 1814
Subfamily CROCIDURINAE Milne-Edwards, 1872
Genus ***Crocidura*** Wagler, 1832
Crocidura russula Hermann, 1780

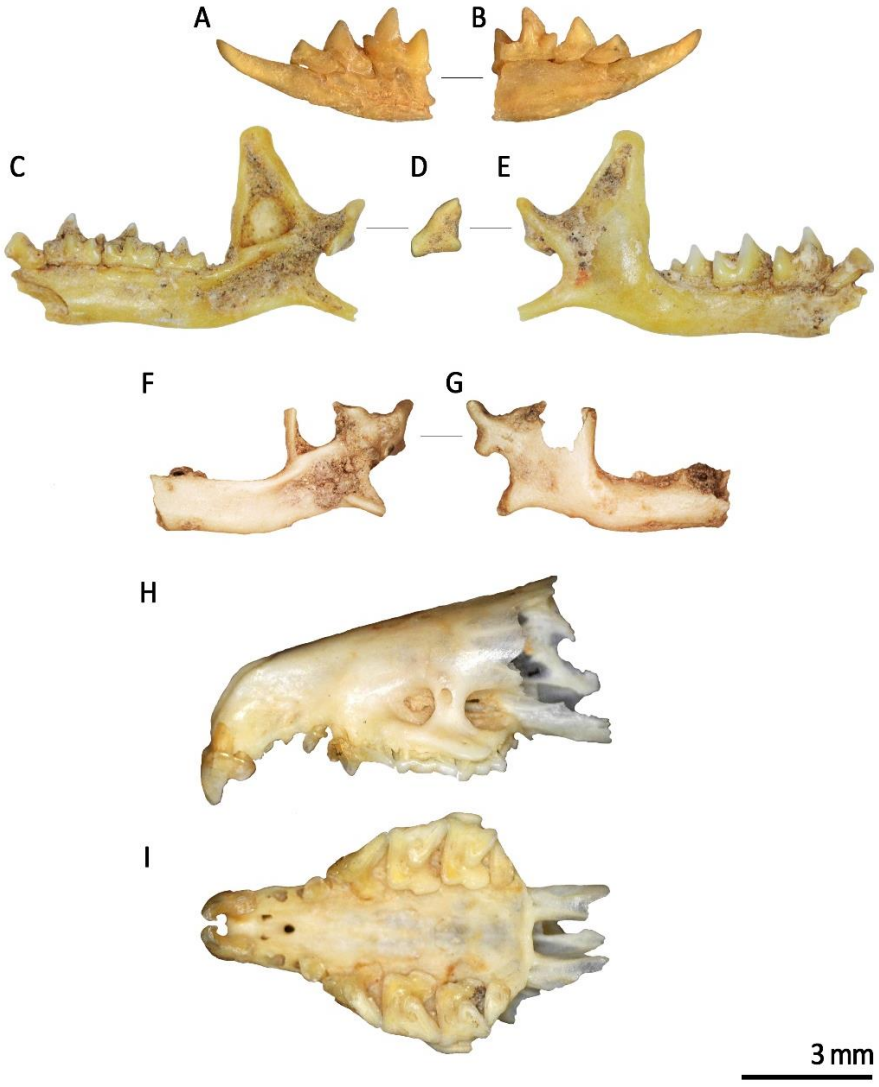

Figure 5.10 – *Crocidura russula* remains: A) left mandible from level 105 with i – m1 in labial view and B) in lingual view; C) right mandible from level 105 with a4 – m3 in lingual view, D) the articular facet in posterior view, and E) in labial view; F) right mandible without teeth from level 105 in lingual view; G) the same mandible in labial view; H) cranium from level 105 in lateral view; and I) in occlusal view. Scale in 3mm.

Material – Level 107: 18 mandibles (eight without teeth; one with a4 – m2; two with a4 – m3; one with i – m3; one with m1; four with m1 – m3; one with m2) and one maxilla (with M1 and M3). **Level 105**: 21 mandibles (three with a4 – m3; one with i; two with i – m1; one with i – m3; one with i – a4 and m3; four with m1 – m3; one with m1 – m2; one with m1, m3; one with m2;

three with m2 – m3; one with m3; and three without teeth), 15 maxillae (one with P4; two with P4 – M1; three with P4 – M2; one with I1; two with I1 – P4; one complete maxilla with a pair I1 – M3; two with I1 – M2; one with M1 – M3; one with P4 – M3), and one isolated a4.

Description – The mandibular ramus is robust curved upward on the dorsal margin and slightly curved on the ventral margin. The coronoid process is high and upright with large, well-defined or robust margin, and triangular-shaped internal temporal fossa on its lingual side. On the posterior view, the articular facet of condylar process appears a single articular facet with no clear separation between upper and lower facet. The remains in this group have dental formula of 1-4-3/1-2-3 with non-pigmented teeth and in lateral view, the protoconid of lower molars appear remarkably high compared to the paraconid and hypoconid. The lower incisor has straight upper edge from the alveolus to the anterior end and curving upwards. There are two premolars on the mandible which called antemolar. The a4 has tetrahedron shape without additional cuspids. The talonid of m3 are reduced and makes small crest or cuspid on the posterior. Cingulum are present on the mandibular teeth and can be observed on the labial and lingual side with fine irregular thickness. On the maxilla, there are 4 premolars, with P1 – P3 called antemolar from its unicuspid incisiform. The first antemolar is larger than the second and third. The P4 and the molars have labio-lingually developed talonid. It has non-clearly separated protocone and hypocone in occlusal view. As on the m3, the size of maxillary M3 is significantly reduced on the dorsal margin to the paracone. On the upper dentition, the cingulum only appears on the incisor and antemolars.

The single large incisor in each dental rows brings it to the family of Soricidae and particularly the non-pigmented teeth, tetrahedron-shaped a4, and single articular facet resemble to the genus *Crocidura*, inside the subfamily of Crocidurinae (Chaline et al., 1974; Furió, 2007). However, there are currently two extant species of the genus *Crocidura* in the Iberian Peninsula since the Late Pleistocene, which are *Crocidura suaveolens* and *Crocidura russula* (Furió, 2007). Apart from the size difference, these two species could be distinguished from its dental characteristics. *C. russula* has undulating labial cingulum on the lower m2 while it is straight on the *C. suaveolens* (Poitevin, 1984). Furthermore, according to Rey & Landín (1973), the upper P4 also shows diagnostic features, where the protocone and hyocone are not clearly separated in *C. russula* while it clearly separated in *C. suaveolens*. Moreover, the coronoid process of *C. russula* is robust and forming a right angle towards the mandibular ramus while the *C. suaveolens* has more gracile posteriorly leaned coronoid process. The internal temporal fossa of *C. russula* also appears to be more robust with well-defined edges while it more gracile in the *C. suaveolens*. Following those characteristics of two extant species, the remains from Cudó cave apparently closer to the *C. russula*. Therefore, it could confidently be assigned to the species of *Crocidura russula.*

Habitat and geographical distribution – Greater white-toothed shrew or *Crocidura russula* is a species which prefers more open landscape with good vegetation covers on the ground level such as grassland, shrubland, and forest edges. It can be found within elevation up to 2,000 meters above the sea level (m.a.s.l.), but frequently below the 1,200 m.a.s.l. It also been reported to live around artificial environment such as garden, urban, and agriculture. It is a Mediterranean species, but widely dispersed throughout Europe from the Iberian Peninsula to the southern Germany and United Kingdom islands, also in north Africa as well as in the Canary

Islands. In the Iberian Peninsula, the distribution covers the coastal area, both Mediterranean and Atlantic coasts, as well as the mountainous landscape in central Iberia (Palomo et al., 2007).

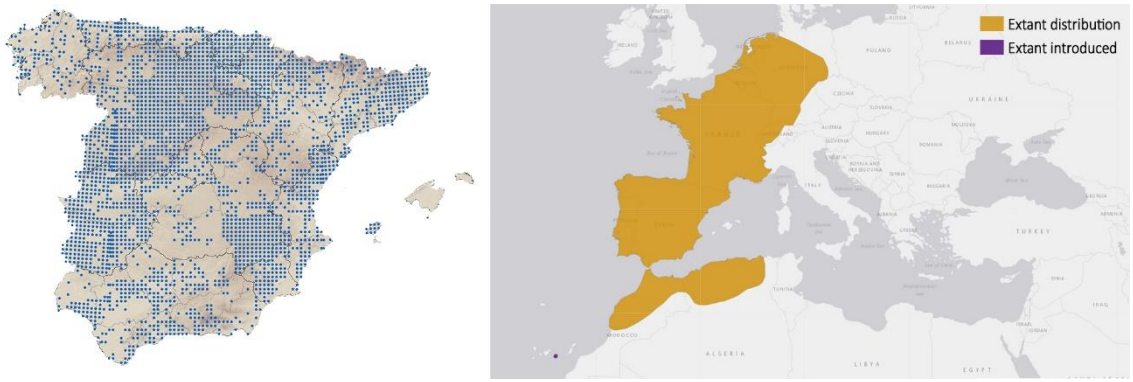

Figure 5.11 – Current distribution maps of *Crocidura russula* in the Iberian Peninsula (left) (Palomo et al., 2007) and Eurasia (right) (IUCN, 2021).

Subfamily SORICINAE Fischer, 1814
Genus ***Sorex*** Linnaeus 1758
Sorex* gr. *araneus-coronatus Linnaeus, 1758 – Millet, 1828

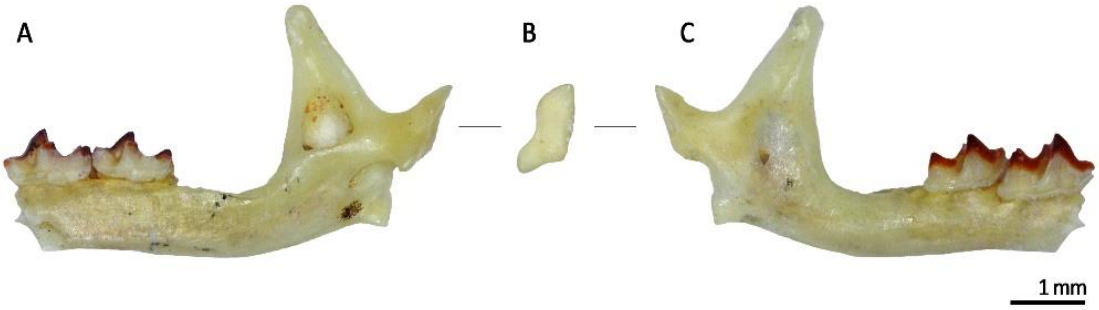

Figure 5.12 – *Sorex* gr. *araneus-coronatus* A) right mandible from level 107 with m2 – m3 in lingual view, B) the articular facet of the condylar process in posterior view, and C) in labial view. Scale in 1mm.

Material – Level 107: one mandible with m1 and m2.

Description – One mandible with m1 and m2 from level 107 appears to have red pigmentation on its teeth. Fine undulated cingulum with regular thickness present in the labial side of the m1 and straighter on the m2. The mandibular ramus is more gracile with slight curvature on the ventral and dorsal margin of its horizontal ramus. The coronoid process is high, forming a right angle towards the horizontal mandibular ramus, with slight inclination towards the anterior part. The internal temporal fossa has triangular shape with straight clear inferior margin and vague line on the superior line. On the posterior view of condyle process, the upper and lower facets are clearly separated by an interarticular area.

Red pigmentation on the teeth and the separated lower articular facet are the unique feature leads to the assignation on the genus *Sorex*. However, there are three medium-sized species

among this genus currently living in Iberian Peninsula that also present during the Pleistocene, which are *S. araneus*, *S. coronatus*, and *S. granarius* (Furió, 2007). The last species however, currently has a geographic distribution restricted to the western Iberian Peninsula and the Central System (Lopez-Fuster and Ventura, 1996; López-Fuster et al., 1999; Palomo et al., 2007). The differentiation between the remaining species of *S. araneus* and *S. coronatus* is usually inferred from the coronoid process inclination towards the horizontal mandible ramus. The forward-inclined coronoid process is more often found in *S. araneus* then in *S. coronatus* (Gosàlbez, 1987). Nevertheless, it is difficult to distinguish these two species with only one mandible. Therefore, this remain from Cudó cave is identified as *Sorex* gr. *araneus-coronatus*.

Habitat and geographical distribution – *Sorex araneus* or the common shrew is a species that prefers cool, damp, and shady boreal and subalpine forest with deciduous and coniferous mixing. In the Iberian Peninsula, it found between 600 and 2,000 m.a.s.l. with quite high precipitation, above 800 mm. *S. araneus* are a common species in central Europe, from the United Kingdom islands in the west to Siberia in the east. It also found in Scandinavia through the eastern Pyrenees in the south. This last region is the only region where *S. araneus* population can be found today in the Iberian Peninsula. The preferred habitat and the geographic distribution of *S. araneus* is partly overlapped with the geographic distribution and preferred habitat of *S. coronatus*. Basically, *S. coronatus* is Atlantic forest dependent species with humid environment and good vegetation cover of deciduous and conifer mixture. But it also found in northern part of Iberian System. It can be found from the sea level until the elevation of 2.200 m.a.s.l. The modern population of *S. coronatus* or millet's shrew is found in southwestern Europe from the northern Iberian Peninsula to the Elba River in Germany as well as some island of United Kingdom. In Iberian Peninsula, it found in the Atlantic coast from the eastern part of Galicia to the northern Catalunya. Indeed, currently both species could be found in a same area in northeastern Iberian Peninsula, such as in the Catalan Pyrenees.

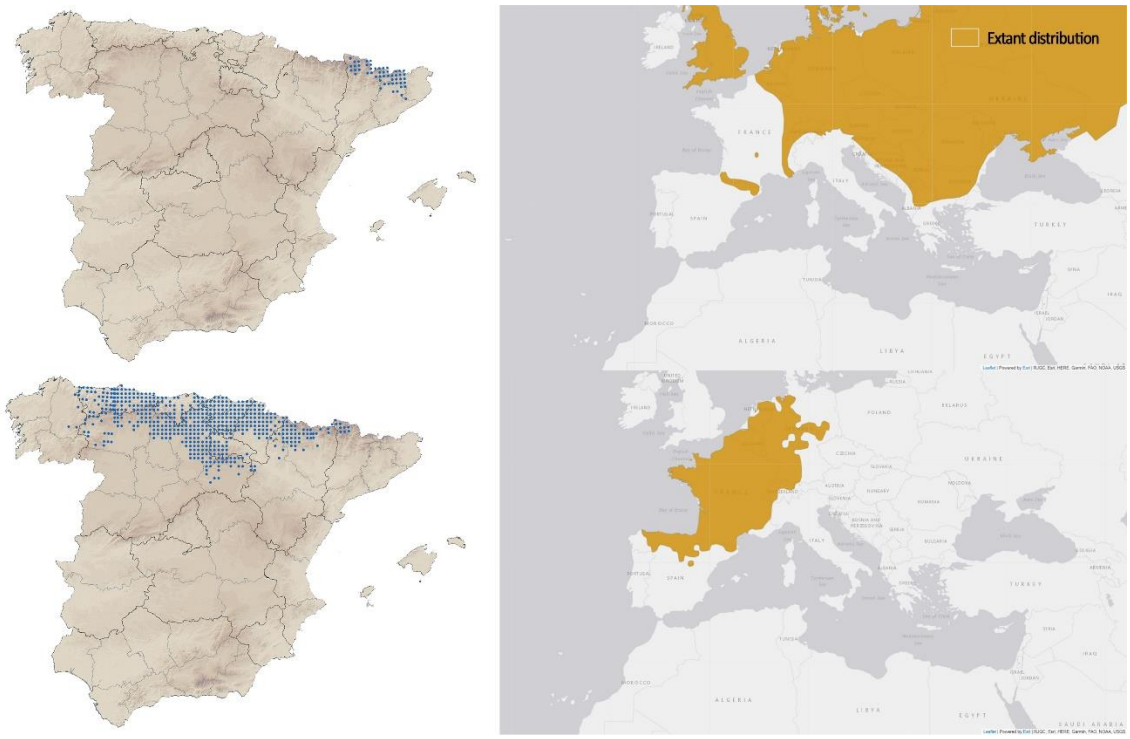

Figure 5.13 – Current distribution maps of *Sorex araneus* (top) and *Sorex coronatus* (bottom) in Iberian Peninsula (left) (Palomo etal 2007) and Eurasia (right) (IUCN, 2021).

Order CHIROPTERA Blumenbach, 1779

Chiroptera indet.

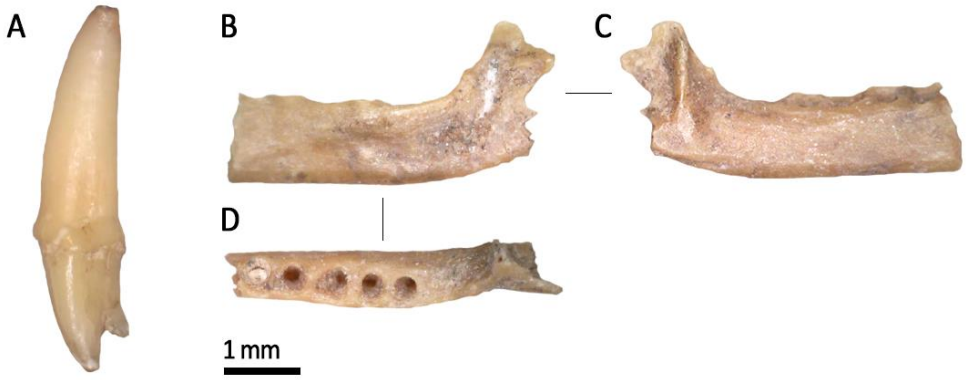

Figure 5.14 – Indeterminate remains of the order Chiroptera: A) isolated upper left incisor and B – D) left mandible without teeth in lingual, labial, and occlusal view respectively. Those remains are from level 105. Scale in 1mm.

Material – Level 105: one mandible without teeth and one isolated upper incisor.

Description – In this denomination, the remains providing general morphology corresponds to the order Chiroptera such as gracile mandible and bicuspided incisor. However, the lack of other diagnostic parts makes the specific identification to the genus or species level is difficult.

Family RHINOLOPHIDAE Gray, 1825
Genus ***Rhinolophus*** Lacépède, 1799
Rhinolophus* cf. *ferrumequinum Schreber, 1774

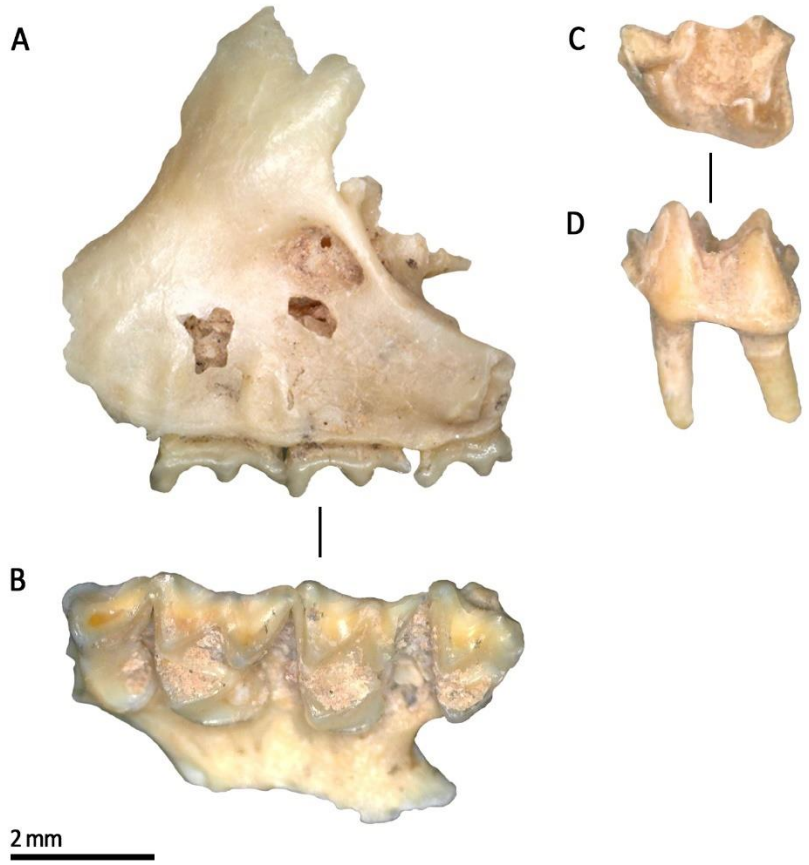

Figure 5.15 – *Rhinolophus* cf. *ferrumequinum* remains A) left maxilla with P4 – M3 in lateral view; B) the same left maxilla with P4 – M3 in occlusal view, C) isolated left m1 in occlusal view and D) the same isolated m1 in labial view. All the remains are from level 105. Scale in 2mm.

Material – Level 105: one maxilla (with P4 – M3) and one isolated m1.

Description –The remains under this group have remarkably large dimension compared to the other remains of Chiroptera within the Cudó cave assemblage. The upper P4 contour close to rectangular shape, with well-developed talon, with a single cuspid that slightly angled mesio-labially. The M1 have subrectangular contour, with wide well-developed talon, and without hypocone. The parastyle is well-developed and right-angled towards the paracrista, the metastyle is straight, and the protocone is displaced towards the anterior margin. There is cingulum on the base of protocone and on the talon, continuous to the distal cingulum. The M2 have rectangular contour, with less developed talon than the M1. The parastyle is well-developed but the metastyle is absent. The protocone is displaced towards the anterior margin. The M3 is slightly reduced on the post-paracrista and still preserving metacrista and metacone. The lower m1 has nyctalodont morphology, which the hypoconulid become a single part with postcrestid and slightly displaced lingually, so it does not align with the hypoconulid. The trigonid morphology is open, the protoconid and metaconid are close in distance, the paralophid has

remarked notch, and the entocrista is curved. The hypoconulid is located more to the labial than the entoconid, and the labial cuspids are not aligned. From the lateral view, it can be observed the fine and regular cingulum.

Several characteristics allows the remains to be assigned to the genus *Rhinolophus*, the large-size chiropters, such as the generally large size, less reduced M3, and nyctalodont-type lower m1 with fine and regular cingulum (Sevilla, 1988; Galán, 2019). There are three extant species of this genus that appears since the Pleistocene, which are *R. ferrumequinum*, *R. mehelyi*, and *R. euryale*. Those species have quite high similarity on the dental morphology but with distinct dimension (Sevilla, 1988). The characteristics of the remains from Cudó cave described above, such as the developed talon and absence of hypocone on the upper molars as well as the nyctalodont lower molars with fine and regular cingulum, resembles to the *R. ferrumequinum* (Sevilla, 1988). However, since there is only a small amount of remains, it is hard to eliminate the equivocality. Therefore, these remains are identified as the *Rhinolophus* cf. *ferrumequinum*.

Habitat and geographical distribution – *Rhinolophus ferrumequinum* or the greater horseshoe bat is a nocturnal insectivore with a 200 – 3,000 m hunting range from its roost and have migrating behaviour up to 180 km. The preferred habitat is forest or woodland with some open landscape with temperate or Mediterranean climate. Its roosting spot is the caves or other subterranean cavity and forms colonies up to 900 individuals. It could be found from the sea-level up to the elevation of 1,600 m.a.s.l., even though it commonly found under 800 m (Palomo et al., 2007). The greater horseshoe bat is a common species in the southern palearctic. In Europe, the northern limit of its distribution is the southern United Kingdom, and the eastern limit is Greece. Particularly in the Iberian Peninsula, it is widely dispersed in almost the entire region, with exception of Aragon, Galicia, and Castillas region.

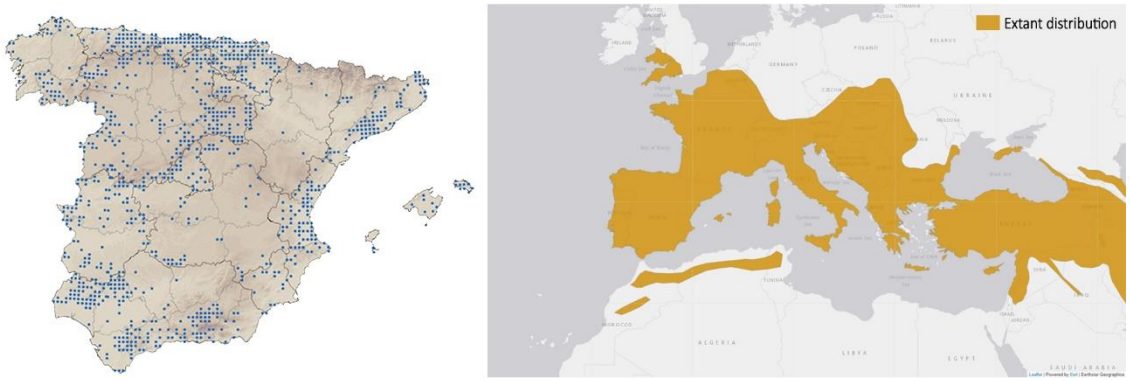

Figure 5.16 – Current distribution map of *Rhinolophus ferrumequinum* in the Iberian Peninsula (left) (Palomo et al., 2007) and Eurasia (right) (IUCN, 2021).

Suborder MICROCHIROPTERA Dobson, 1875
Family VESPERTILIONIDAE Gray, 1821
Subfamily VEPERTILIONINAE Gray, 1821
cf. Myotis (Kaup, 1829)

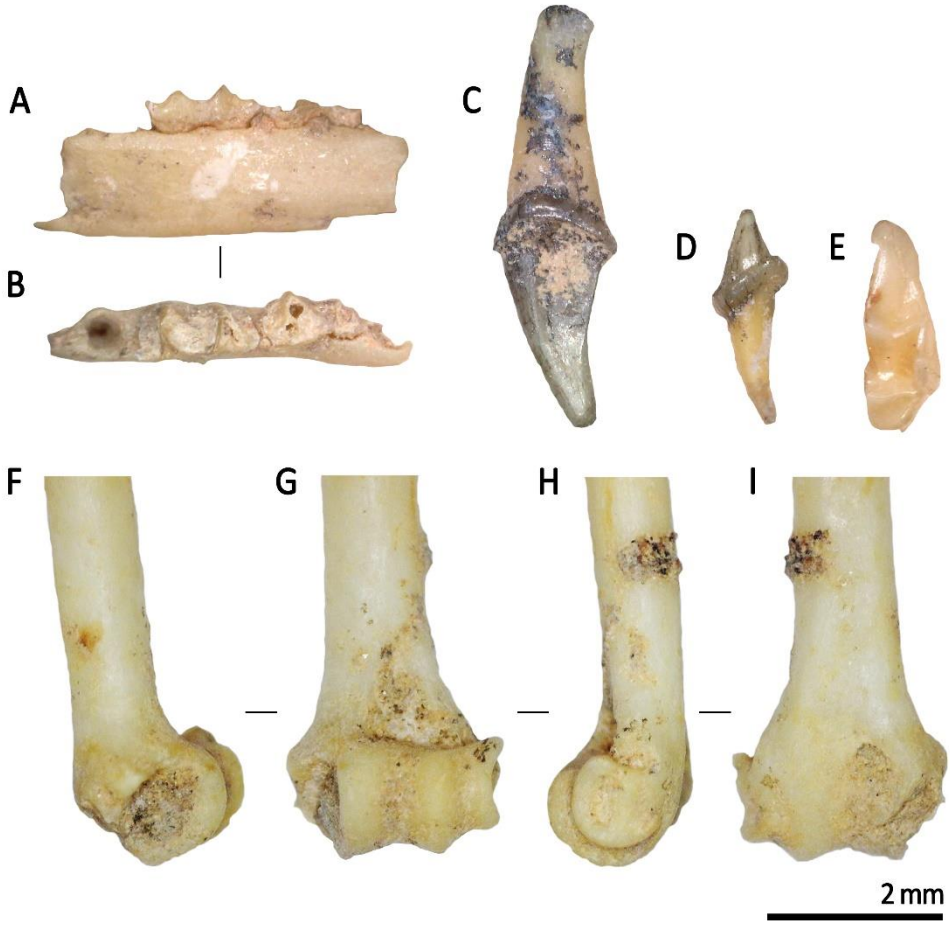

Figure 5.17 – Remains attributed to cf. *Myotis* A) left mandible with m2 – m3 in lateral view; B) the same mandible in occlusal view; C) isolated left upper canine in lingual view; D) isolated left p2; E) isolated left M3; and E – H) distal epiphysis of left humerus, in anterior, external, posterior, and internal view, respectively. All remains recovered from level 105. Scale in 2mm.

Material – Level 105: one mandible (with m2 – m3), one p2, one C, one M3, and one humerus.

Description – The remains generally have a small size. The superior canine has oval contour and the root and corona forming a curve. There is clear ridge separating the labial and lingual faces on the distal part, while none in the mesial part, therefore appears three faces. The cingulum is thick and irregular. The second premolar also has oval contour with single cuspid that displaced towards the lingual. The cingulum is continuous and slightly thickening mediomesial and mediodistally with the maximum width on the most labial and lingual margin. The M3 is very reduced on the posterior part, has triangular contour, and the parastyle is well developed. On the mandibular m2 and m3 shows myotodont pattern, which the hypoconulid is separated from the postcrestid and entoconid, and it aligned labially in respect to entoconid. However, it is difficult to observe the detailed features due to the poor preservation. The styloid process, one

of the diagnostic features on the humerus distal epiphysis, is not developed in this remain. On the external view, the trochlea and condyle have narrow width, more equal height, and shallow notch in between. The epitrochlear appears to have concave-convex morphology with blunt-point edge. On the internal side, the antecubital fossa is very subtle.

Among two family of chiropters in Europe, according to its small size, the remains from the Cudó cave are likely belong to the small-sized chiropters of Vespertilionidae (Sevilla, 1988). The general morphology of the dental remains and the humerus described above apparently resemble to the genus *Myotis* (Sevilla, 1988). Still, the isolated remains and poor preservation did not allow further identification to the specific level. Therefore, these five specimens are assigned to cf. *Myotis.*

Genus ***Myotis*** Kaup, 1829
Myotis* gr. *myotis-blythii Borkhausen, 1797 – Tomes, 1857

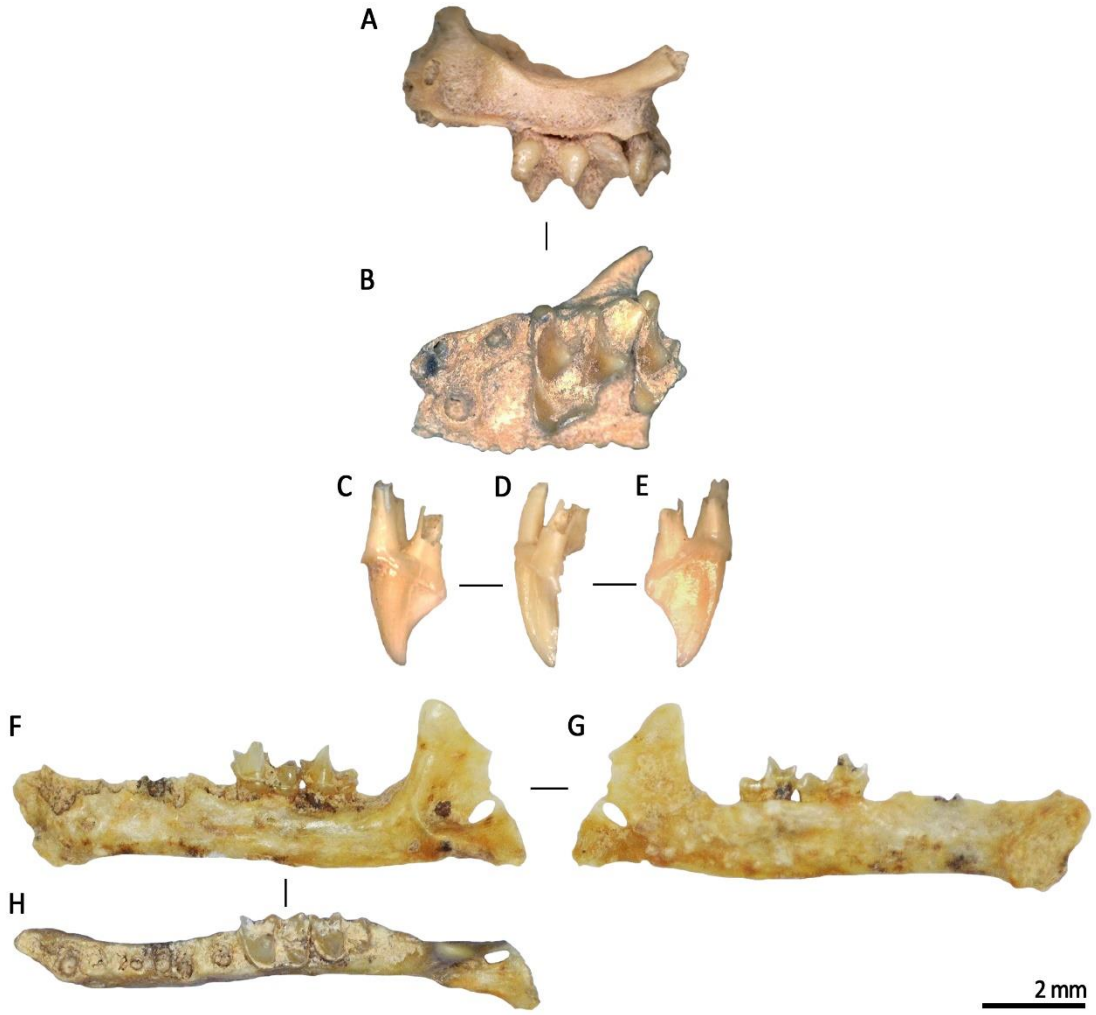

Figure 5.18 – Remains of *Myotis* gr. *myotis-blythii* A) left maxilla with M2 – M3 in lateral view; B) the same maxilla from occlusal view; C – E) isolated left P4; F) left mandible with m2 – m3 in labial view; G) the same mandible in occlusal view; and C) in lingual view. All remains are from level 105. Scale in 2mm.

Material – Level 107: one mandible with m2. **Level 105**: 5 mandibles (three with m2 – m3; one with p4 – m1; one with p4 – m2), three maxillae (one with M2 – M3; one with P4 – M2; one with P4 – M3), two m1, one m2, one m3, one p4, and one P4.

Description – The upper premolar has three roots with triangular contour and convex labial face on the mesial side also concave on the distal side. The mesiolingual face is straighter and the distolingual face is slightly concave. It has a single cuspid located in the mesiolabial corner. The cingulum is present in all side except on the distolabial corner. The upper second molar has subrectangular contour, without talon and hypocone, developed parastyle with slightly curved morphology. The metacone is higher than the paracone, the metalophe and paralophe are absent, and the metaconule is present. The third upper molar has triangular contour with highly reduced posterior part. The parastyle is well developed with slight curved morphology. The post paracresta is highly reduced with the absence of metastyle. The metacone also reduced and lower than the paracone. On the mandible, the preserved alveoli show the dental formula of 3-1-3-3. From the occlusal view, the m2 and m3 appear to have myotodont morphology with separated hypoconulid from postcrestid and entoconid. The cingulum is irregular in thickness, from medium to thick. The trigonids are closed, the entocrista is convex, the paralophid is angled, and the hypoconid of the m3 is reduced and displaced towards labial.

Those characteristics resemble to the small-sized chiropters of Vespertilinoidae. The lower dental formula and the myotodont type lower molars could specify the remains from the Cudó cave to the genus *Myotis* and *Plecotus* (Dupuis, 1986a). However, from the regular medium to thick cingulum of the lower molars, the subrectangular contour of the upper molars and premolar, and the labially displaced postprotocresta of the upper molars, the remains can be classified to the genus *Myotis* (Sevilla, 1988). Nevertheless, there are two species correspond to these characteristics, the *Myotis myotis* and *Myotis blythii* and it is difficult to morphologically distinguish the *M. myotis* and *M. blythii*. A slight difference could be acknowledged by the measurement on the bone or dental remains (Galán, 2019), but with a small amount of remains, it cannot be done. Therefore, these remains are assigned to the group of *Myotis* gr. *myotis-blythii.*

Habitat and geographical distribution – *Myotis myotis* or greater mouse-eared bat prefers to dwells on caves, rock shelters, other subterranean cavities, even the artificial cavities such as attics and basement. Forest and shrubland vegetation are its preferred habitat in correspondence with its insectivore diets. It is commonly found in the se-level area up to 1,500 m.a.s.l., even though has been reported to be found in the elevation of 2,060 m.a.s.l. It can be found in the southern palearctic region, roughly southward from Netherland, German – Poland coast, and Crimea, from the Azores Islands, mainland of Europe, to the West Asia. In the Iberian Peninsula, it is frequently found in the Mediterranean coast and in the Central System. The distribution is highly dependent to the roosting and hunting range availability. Therefore, in some region such as Sierra de Morena and other Andalusian region with arid environment, *M. myotis* are nearly absent.

The geographic distribution however, overlapping to the geographic distribution of *M. blythii* or the lesser mouse-eared bat. Indeed, morphologically these two species are similar. Nevertheless, *M. blythii* is more likely to live in the grassland or steppe, with some specific case

such as in Swiss, it commonly found near the woodland. It could be found under the 1,380 m.a.s.l. elevation in most of the Iberian Peninsula and until 2,100 m.a.s.l. in the Sierra Nevada.

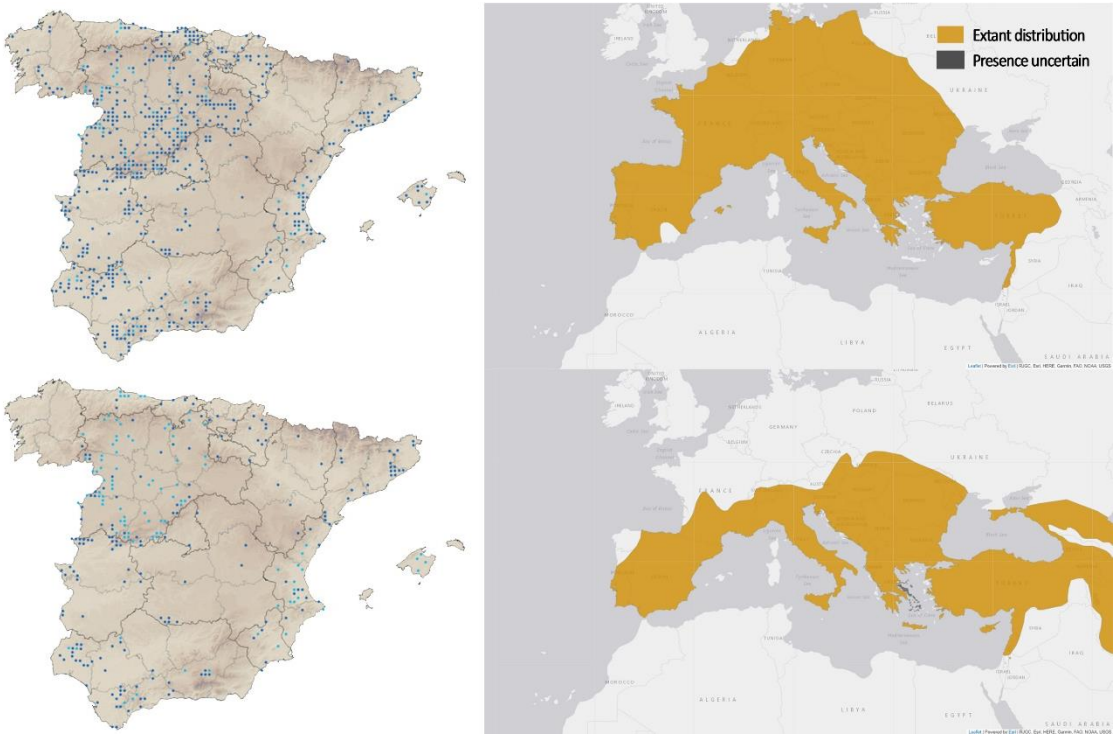

Figure 5.19 - Recent distribution map of *Myotis blythii* (top) and *Myotis myotis* (bottom) in the Iberian Peninsula (left) (Palomo et al., 2007) and Eurasia (right) (IUCN, 2021).

cf. Pipistrellus Kaup, 1829

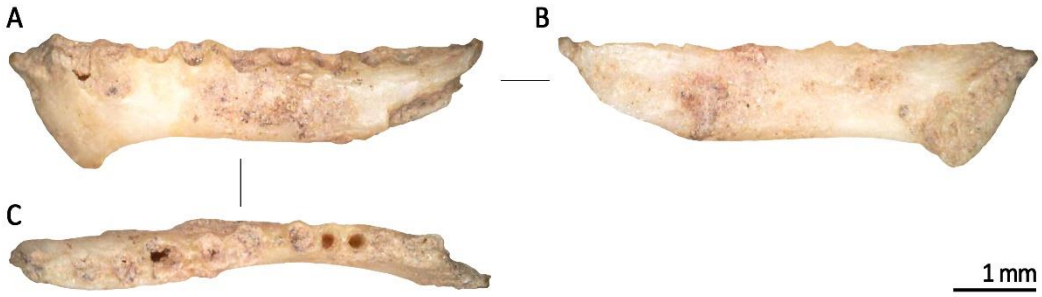

Figure 5.20 – Left mandible without teeth of cf. *Pipistrellus* from level 105 A) in labial view, B) in lingual view, and C) in occlusal view. Scale in 1mm.

Material – Level 105: one mandible without teeth.

Description – From the alveolus, it can be inferred that the specimen has at least one canine, two premolars, and three molars. So, it could be distinguished from the group of chiropters with three premolars, such as the genus *Myotis* and *Miniopterus* (Dupuis, 1986a). The well-developed chin and a small general size allow us to ascribe this mandible to genus *Pipistrellus*. However, it

is the only specimen and the teeth, coronoid process, condylar process, and angular process are not preserved. Thus, it does not have enough diagnostic features to ensure the genus or to be identified specifically to the species level.

Genus ***Pipistrellus*** Kaup, 1829
Pipistrellus* cf. *pipistrellus Schreber, 1774

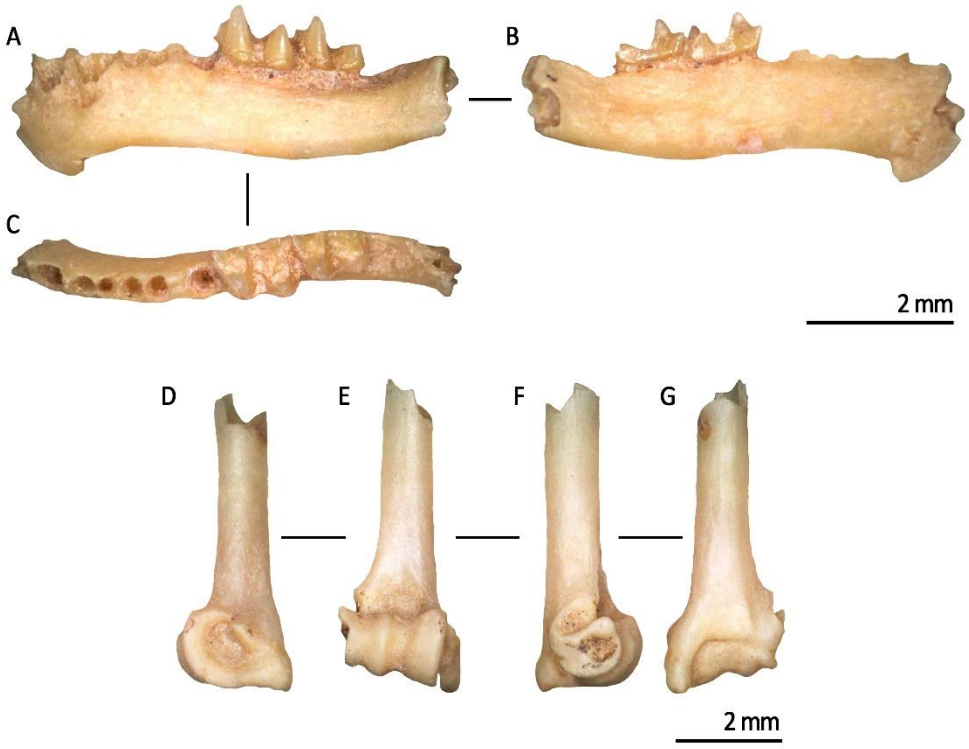

Figure 5.21 – Remains of *Pipistrellus* cf. *pipistrellus* A-C) left mandible with m2-m3 in labial view, lingual vies, and occlusal view respectively; D-G) epiphysis distal of right humerus in anterior, external, posterior, and interior view respectively. These two remains are from level 105. Scale in 2mm.

Material – Level 107: one mandible (with m1 – m3). **Level 105**: 5 mandibles (one with c, m1, m2; one with m2 – m3; one with p4 – m3; one with p4, m2, and m3; one without teeth) and four humeri.

Description – In general, the mandibles have small size with slender mandibular ramus and well-defined mental protuberance. From the alveoli, it can be observed the lower dentition with at least one canine, two premolars, and three molars (3-1-2-3). The alveoli present less diastema, particularly between the i3 and the canine. From the occlusal view, the lower molars show nyctalodont in shape with joined hypoconulid to postcrestid but separated and unaligned to entoconid. On the labial view, the cingulum appears irregular medium thickness. The trigonids are more closed, the distance of protoconid and metaconid are similar to the distance between metaconid and paraconid. The paralophid is concave without notch, and the entoconid is the highest labial cuspids. The entocrista is curved; paraconid, metaconid, and entoconid are aligned. The hypoconulid is more displaced towards lingual than the entoconid. The m3, the

entoconid is more displaced towards labial, the hypoconulid displaced toward lingual, and the hypoconid is displace toward lingual.

On the humerus the styloid process is present with short length, only slightly longer than the trochlea. The trochlea and condyle have medium width with shallow notch in between, and the trochlea higher than the condyle. The antecubital fossa is deep, and the epicondyle visible from external view. There are several species sharing similar characteristic of the skeletal remains in the period of the upper Pleistocene in Iberian Peninsula, those are *P. kuhlii, P. nathusii,* and *Hypsugo savii* (Galán, 2019). Nevertheless, several features such as the diastema between each incisivus and between incisivus and canine, as well as the morphology of the humerus distal epiphysis could distinguish the species. The assemblage from Cudó cave show absence of diastema between i3 and canine on the mandible as well as the high epicondyle on the humerus distal epiphysis. Those features resemble to the *P. pipistrellus* (Dupuis, 1986a; Sevilla, 1988). However, the quantity of the remains still too small to confidently identify as *P. pipistrellus*. Therefore, it is identified as the *P.* cf. *pipistrellus.*

Habitat and geographical distribution – *Pipistrellus pipistrellus* or common pipistrelle are a generalist insectivore that can be found in wide range of habitat, including urban area. It dwells on the cervices, trees, and anthropic structures with only occasionally in the caves. It can be found from the sea-level elevation up to 2,000 m.a.s.l. It widely distributed in Europe, North Africa, Arabian Peninsula, and Indian Subcontinent. In Europe, it can be found in almost all region, from Spain in the south to Denmark in the north. In the Iberian Peninsula, it mostly found in the northern part, while in the Mediterranean coast only sparsely can be found.

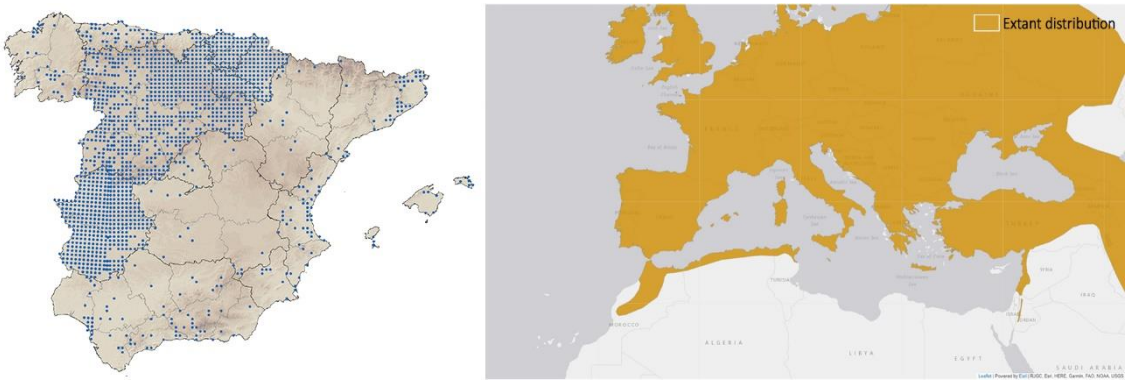

Figure 5.22 – Recent distribution map of *Pipistrellus pipistrellus* in the Iberian Peninsula (left) (Palomo et al., 2007) and Eurasia (right) (IUCN, 2021).

Order RODENTIA Gregory, 1910
Family CRICETIDAE Fischer, 1817
Subfamily ARVICOLINAE Gray, 1821
Genus ***Microtus*** Schrank, 1798
Microtus arvalis Pallas, 1778 / ***Microtus agrestis*** Linnaeus, 1761

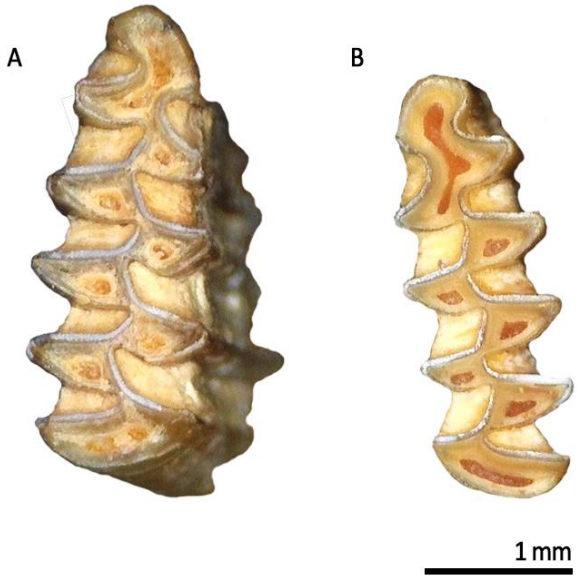

Figure 5.23 – A) Right m1 of *Microtus agrestis* and B) Left m1 of *Microtus arvalis*. Both are from level 105. Scale in 1mm.

Material – *Microtus arvalis* – Level 107: 21 isolated m1, 9 mandibles (two with m1; six with m1 – m2; one with m1 and m3). **Level 105**: 14 isolated m1, 5 mandibles (two with m1; three with m1 – m2). **– *Microtus agrestis* – Level 107**: 21 isolated m1, 9 mandibles (three with m1; 4 with m1 – m2; two with m1 and m3). **Level 105**: 12 isolated m1, 4 mandibles with m1 – m2. **– *Microtus* gr. *arvalis-agrestis* – Level 107**: one isolated m1.

Description – The first lower molar from genus *Microtus* is characterized by seven triangles with closed T4 – T5 and marked BRA 4 and LRA 5. The enamel is thicker on the anterior side of the triangles. The anterior cap is rounded while the salient angle of the triangles is sharp. Several features appear distinctively between *Microtus arvalis* and *Microtus agrestis*. *M. arvalis* molars are generally smaller and more delicate than those of *M. agrestis*. The T6-T7 are more open and confluent in the *M. arvalis* while it more closed in the *M. agrestis.* Moreover, the triangles also appear to be more symmetrical in *M. arvalis*. These characteristics are consistent with the description of *M. arvalis* and *M. agrestis* by several authors (e.g. Chaline et al., 1974; Gosàlbez, 1987; Nadachowski, 1982). However, it could be difficult to distinguish *M. arvalis* and *M. agrestis* from the skeletal remains due to high similarities in morphology. Nevertheless, only one specimen recovered from the level identified as *M.* gr. *arvalis-agrestis* because of this difficulty.

Habitat and geographical distribution – The common vole or *Microtus arvalis* is an European species with habitat preferences on moist forest, meadows, steppe, grassland, or shrubland as

the habitat. It normally can be found on elevation between 500 and 1,500 m.a.s.l., but the population of *M. arvalis* in the Pyrenees, it reaches elevation between 900 and 2,200 m.a.s.l. Geographically, it can be found almost all-over European continent, from the Atlantic coast of the Iberian Peninsula to central Russia. It absents in the most part of the United Kingdom, the Mediterranean basin, Fennoscandia, and north Russia. Particular to the Iberian Peninsula, it can be found in the northern half of the area, including the Cantabrian mountain range, Central System, Iberian System, and also the Pyrenees. Otherwise, *M. agrestis*, prefers meadows, grassland, woodland, and wetland. It generally needs more humid environment compared to *M. arvalis*. *M. agrestis* commonly found within elevation range of 1 – 1,600 m.a.s.l. It is also widely distributed in Eurasia, even though slightly different in the Iberian Peninsula compared to *M. arvalis*. In the Iberian Peninsula, *M. agrestis* is commonly found in the Atlantic coast of Spain, Portugal, also in the north of Catalonia, from the Mediterranean coast to the Pyrenees.

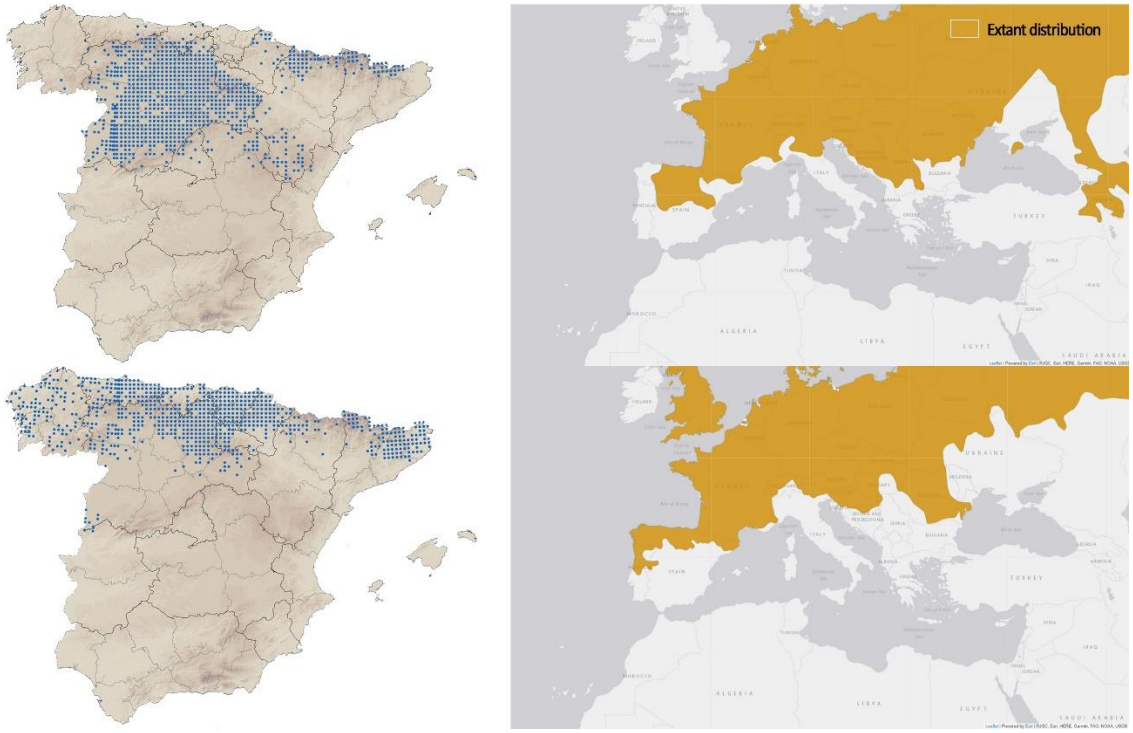

Figure 5.24 – Distribution map of *Microtus arvalis* (top) and *Microtus agrestis* (bottom) in the recent Iberian Peninsula (left) (Palomo et al., 2007) and Eurasia (right) (IUCN, 2021).

Subgenus ***Terricola*** Fatio, 1867

Microtus (Terricola) duodecimcostatus Sélys-Longchamps, 1839

Figure 5.25 – Left m1 *Microtus (Terricola) duodecimcostatus* from level 105 in occlusal view. Scale in 1mm.

Material – Level 107: 11 isolated m1, 2 mandibles (one with m1, one with m1 – m2). **Level 105**: 30 isolated m1, 5 mandibles (two with m1, three with m1 – m2).

Description – The m1 in this group has seven triangles with closed T1 – T3 and open, confluent T4 – T5 forming a pytimian rhombe. The T6 – T7 are also open and symmetrically confluent forming the second pytimian rhombe. The anterior cap is rounded but less developed, widely confluent with T6 and T7 with less marked BRA 4 and LRA 5. The triangles are symmetrical between the lingual and labial side and the enamel is uniformly distributed, with exception on the anterior cap and the lateral side of posterior lobe.

The pytimian rhombe formed by T4 – T5 and T6 – T7 is the particular characteristic of the subgenus *Terricola*, under the genus *Microtus*. There are two extant species living in the northeastern Iberian Peninsula, *M.* (*T*). *duodecimcostatus* and *M.* (*T*). *gerbei*. It is not easy to distinguish these two species with the high similarities and the high interindividual variability. Still, the characteristic of the anterior cap and the second pytimian rhombe could be distinctive. On *M.* (*T*). *gerbei,* the anterior cap is well developed with marked BRA 4 and LRA 5, and also the second pytimian rhombe is more isolated and more asymmetric. Otherwise, on the *M.* (*T*). *duodecimcostatus* the anterior cap is less developed or reduced and the second pytimian rhombe is not isolated (Chaline et al., 1974; Gosàlbez, 1987; Brunet-Lecomte, 1990; Cuenca-Bescós et al., 2008). The remains from Cudó cave show characteristics resemble to the species of *Microtus (Terricola) duodecimcostatus,* and (Chaline et al., 1974; Gosàlbez, 1987; Cuenca-Bescós et al., 2008)herefore, it could be identified as this species.

Habitat and geographical distribution – *Microtus (Terricola) duodecimcostatus* or the Mediterranean pine vole prefers open landscape with herbaceous covers and stable humid-loose soil as the habitat. It can be found on the sea-level elevation and up to 3,000 m.a.s.l. It is a Mediterranean species that can be found in most of the Iberian Peninsula with exception on the northwest Iberian Peninsula. It also can be found in the southern France.

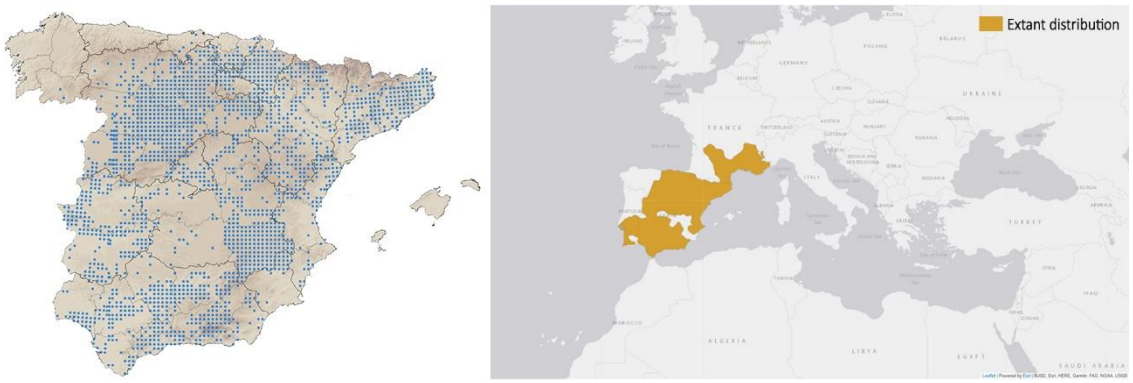

Figure 5.26 – Current distribution map of *Microtus (Terricola) duodecimcostatus* in the Iberian Peninsula (left) (Palomo et al., 2007) and Eurasia (right) (IUCN, 2021).

Subgenus ***Iberomys*** Chaline, 1972
Microtus (Iberomys) cabrerae Thomas, 1906

Figure 5.27 – Left m1 of *Iberomys cabrerae* from level 105 in occlusal view. Scale in 1mm.

Material – Level 107: one isolated m1. **Level 105**: 26 isolated m1, 6 mandibles (one with m1, five with m1 – m2).

Description – The lower first molars inside this classification are large and wide. It has seven triangles, with closed T4-T5 and open T6-T7. The BRA 4 is less developed while the LRA 5 is

deeper. The ACC has triangular form with the anterior cap is pointing to the lingual side. The triangles are very asymmetric, with significantly larger triangles on the lingual side. Those features generally forming the labio-lingual asymmetry of the molar. The salient and reentrant angles are acutely marked and sharp pointed. Those characteristics are consistent with the description of *Iberomys cabrerae* by Chaline (1972), Gosàlbez (1987) and Cuenca-Bescós et al. (2014). Thus, the remains from Cudó cave could be inferred as *Iberomys cabrerae*.

Habitat and geographical distribution – *Iberomys cabrerae*, also known as Cabrera vole is a species strictly dependent on the Mediterranean climate and prefers open landscapes with herbaceous covers such as perennial grass. It is distributed in the meso and supra-Mediterranean bioclimatic floors with elevation range of 250 – 1,500 m.a.s.l., although more frequent within 500 – 1,200 masl. It is an endemic species of the Iberian Peninsula, with current distribution on some areas of Spain and Portugal, such as the southern Iberian System, Central System, and the south part of Portugal. This distribution is highly fragmented due to the anthropic factors. The fossil or sub-fossil record shows it was presented in the southern France and the Sierra Nevada.

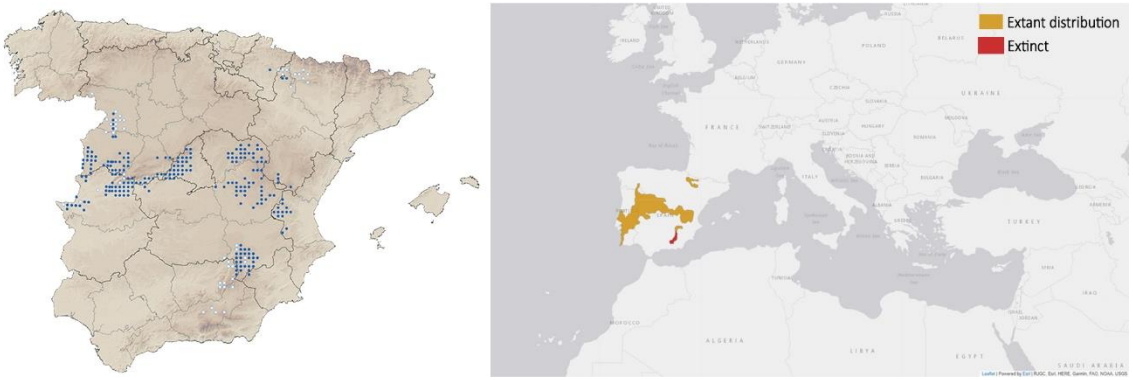

Figure 5.28 – Current distribution map of *Iberomys cabrerae* in the Iberian Peninsula (left) (Palomo et al., 2007) and Eurasia (right) (IUCN, 2021).

Genus ***Chionomys*** Miller, 1908
Chionomys nivalis Martins, 1842

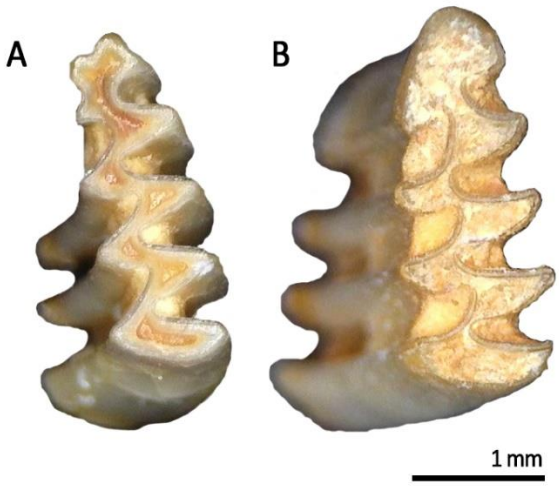

Figure 5.29 – A) Left m1 of juvenile *Chionomys nivalis* and B) Left m1 of adult individual. Both recovered from Cudó cave level 105. Scale in 1mm.

Material – Level 107: 229 isolated m1, 92 mandibles (25 with m1; 58 with m1 – m2; 2 with m1 – m3; 7 with m1 and m3). **Level 105**: 96 isolated m1, 28 mandibles (7 with m1; 20 with m1 – m2; one with m1 – m3).

Description – The first lower molar inside the genus *Chionomys* has five triangles. From the occlusal view, it shows posterior lobe, the T1 – T4 are closed and in general case, one triangle in communication with the posterior lobe (T5). The triangles are more symmetrical, even though it more developed on the lingual side. The anterior cap has mushroom-like shape with rounded anterior part and marked BRA 3 and LRA 4, as marked as the other BRAs and LRAs. It has no LRA 5 or sometimes represented by a subtle notch, while the BRA 4 is more variable from the complete absent, shallow wave, to considerably deep notch, even though still smaller than the other BRAs. When it present, the T6 is small and pointed, while T7 is more open and rounded. Juvenile teeth often appeared in the assemblage with non-fully developed triangles. It makes the identification more difficult, but still possible to observe the diagnostic features. Those characteristics are consistent to what described by Chaline (1972), Gosàlbez (1987), and Nadachowski (1982). Therefore, the remains from Cudó cave could be confidently classified as *Chionomys nivalis*.

Habitat and geographical distribution – *Chionomys nivalis* or commonly known as the snow vole is a species specially adapted to the rocky terrain with medium to large boulder and either stable or loose rocks. It commonly found in the elevation between 1,000 to 2,600 m.a.s.l. Altough, some particular cases it found in the elevation of 250 masl and up to 4,000 m.a.s.l. After the maximum glacial expansion during the Late Pleistocene, *Chionomys nivalis* population reduced to some specific mountainous biotopes. It occupying the mountain range from the southwest Europe to the southeast Asia, such as in the Alpines, Balkan, and Caucasus. In the Iberian

Peninsula it is isolated on some areas such as Pyrenees, Cantabrian Mountain range, some part of Iberian System, Sierra de Guadarama, and Sierra de Nevada.

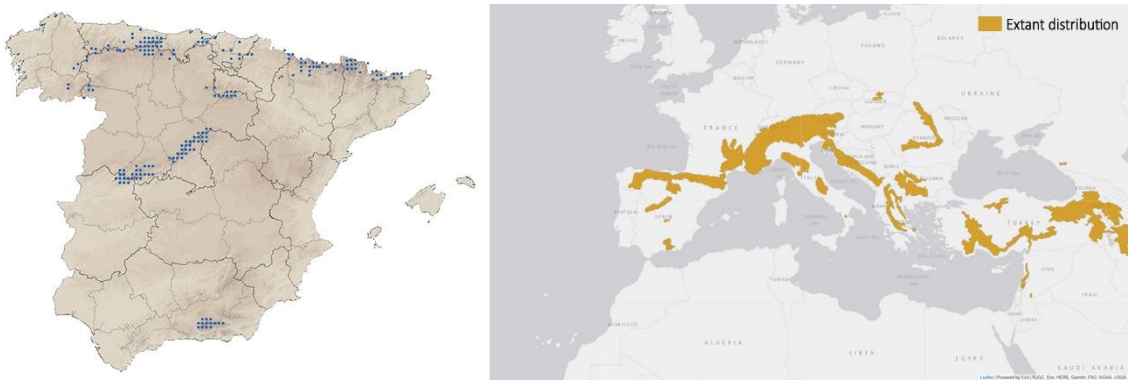

Figure 5.30 – Current distribution map of *C. nivalis* in the Iberian Peninsula (left) (Palomo et al., 2007) and Eurasia (right) (IUCN, 2021).

Family MURIDAE Illiger, 1811
Subfamily MURINAE Illiger, 1811
Genus ***Apodemus*** Kaup, 1829
Apodemus sylvaticus Linnaeus, 1758

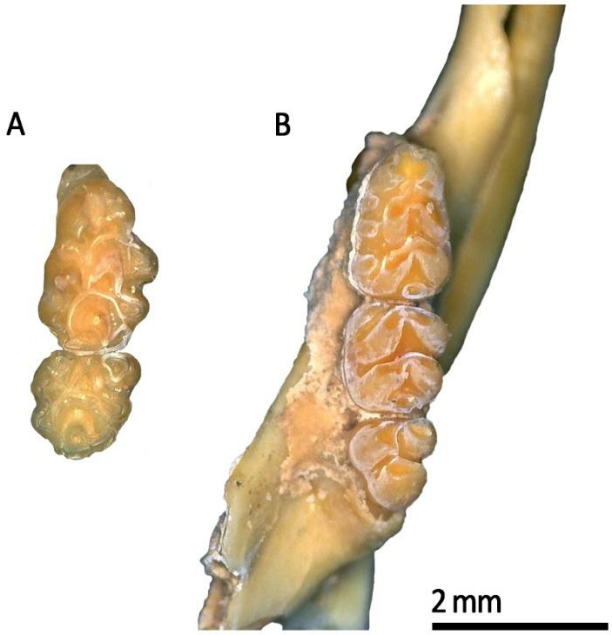

Figure 5.31 – Remains of *Apodemus sylvaticus* from Cudó cave level 105: A) right M1 and M2 in occlusal view, B) left mandible with m1 – m3 in occlusal view. Scale in 2mm.

Material – Level 107: 26 isolated m1, 3 isolated m2, 1 isolated m3, 2 isolated M2, 40 mandibles (6 with m1; 9 with m1 – m2; 8 with m1 – m3; 7 with m1 and m3; 5 with m2; 4 with m2 – m3; 1 with m3), 28 maxillae (4 with M1; 9 with M1 – M2; 9 with M1 and M3; 1 with M2; 3 with M2 – M3; 1 with M3; 1 without teeth). **Level 105**: 54 isolated m1, 9 isolated m2, 4 isolated m3, 37

isolated M1, 5 isolated M2, 116 mandibles (28 with m1; 39 with m1 – m2; 26 with m1 – m3; 1 with m1 and m3; 14 with m2; 5 with m2 – m3; 2 with m3; 1 without teeth), 82 maxillae (26 with M1; 24 with M1 – M2; 19 with M1 – M3; 2 with M1 and M3; 2 with M2; 7 with M2 – M3; 2 with M3).

Description –The dental remains within this group has low corona and bunodont occlusal pattern. There are six main cuspids on the first molar and four main cuspids on the second and third molars. Those patterns appear in both upper and lower molars. The upper first and second molars have three longitudinal rows, with the middle row is much bigger than the two lateral rows. The M1 has nine tubercles, with T7 connected to the T4, the external tubercle is simple, and the anterior tubercle is not laterally compressed. The three anterior tubercles (T1 – T3) separated from the six other tubercles and forms an oblique transversal line, leaning labially. The M2 has 8 tubercles with similar morphology to the M1, with absence of T2 while the T1 and T3 are isolated. The M3 is reduced, with only six tubercles (absence of T2, T3, and T6). On the lower dentition, the m1 has six principal tubercles, one medium anterior tubercle, and four accessory tubercles. The two pairs of principal tubercles on the anterior part and the medium anterior tubercle are connected to a star-like shape. A pair of posterior principal tubercle is also connected. The accessory tubercles, which three on the labial side and one on posterior, are isolated. The m2 has five principal tubercles, with isolated principal antero-labial tubercle, and one accessory tubercle on the posterior part. The m3 is pretty much reduced with only three principal tubercles, in many cases only two that well developed. Moreover, the posterior accessory tubercle of m3 is developed to the size and morphology of principal tubercle.

Several characteristics such as low crown molars and bunodont occlusal pattern with 4 – 6 principal tubercles leads the identification to the genus *Apodemus* (Cuenca-Bescós et al., 2008). There are two extant species in the Iberian Peninsula, the *Apodemus sylvaticus* and *Apodemus flavicollis*. Although those species share high morphological similarities on the teeth, some features are unique to each species. On the *A. sylvaticus,* the T4 – T7 of M1 are connected, the T9 of M2 is expanded but relatively small, and the lateral accessory tubercles of m1 are isolated (Cuenca-Bescós et al., 1997). Those distinctive characteristics however, consistent to the assemblage from Cudó cave. Therefore, the remains from Cudó cave level 107 and 105 could be classified as *Apodemus sylvaticus*.

Habitat and geographical distribution – *Apodemus sylvaticus*, or the wood mouse is a generalist species. It prefers the forest ecosystem, although could also be found in the margin of homogenous forest, shrubland, and grassland. It can live on the wide climatic range, from the semi desertic to the subalpine, from the sea level up to 1,850 masl. Currently, it widely dispersed across Europe, west Asia, and the north Africa, including the Mediterranean islands. It also widely distributed in Spain and considered as one of the most abundant species of micromammals.

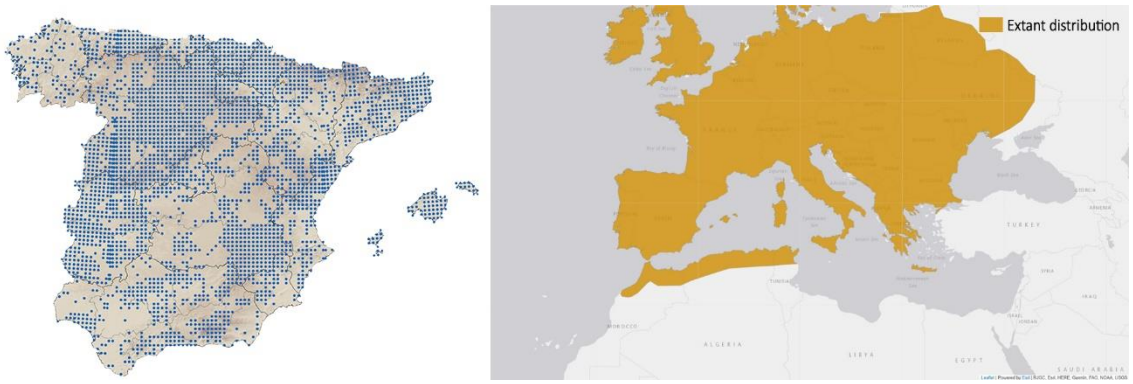

Figure 5.32 – Current distribution map of *Apodemus sylvaticus* on the Iberian Peninsula (left) (Palomo et al., 2007) and Eurasia (right) (IUCN, 2021).

Family GLIRIDAE Muirhead, 1819
Subfamily LEITHINAE Lydekker, 1895
Genus ***Eliomys*** Wagner, 1840
Eliomys quercinus Linnaeus, 1766

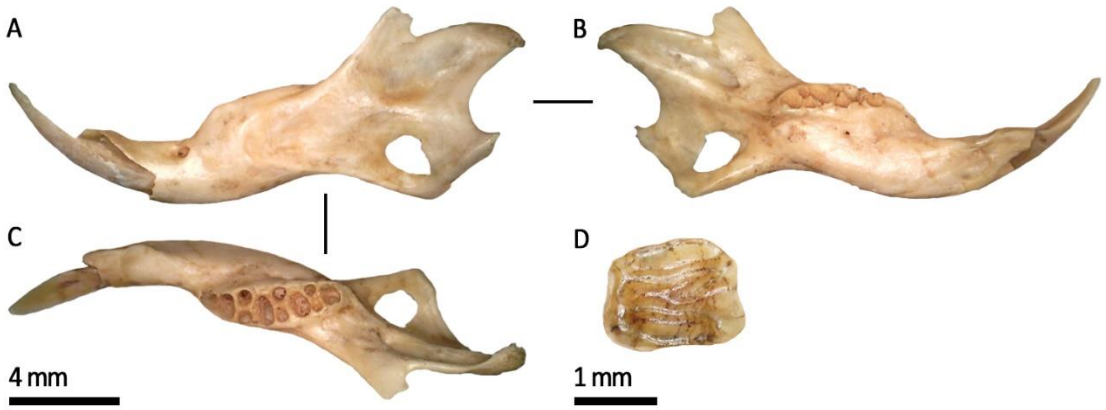

Figure 5.33 – The remains of *Eliomys quercinus* from the Cudó cave level 105: A – C) left mandible without teeth in labial, lingual, and occlusal view, respectively; and D) left M1 in occlusal view. Scale in 4mm for the mandibles and 1mm for the isolated molars.

Material – Level 107: 3 isolated m1, 4 mandibles without teeth. **Level 105**: 6 isolated m1, 9 isolated m2, 3 isolated p4, 11 isolated M1, 6 isolated M2, 6 isolated M3, 3 isolated P4, 7 mandibles without teeth, 4 maxillae (2 with P4; 1 with P4 – M1; 1 with P4 – M3).

Description – The mandible is quite large, with a hole on the angular apophysis. It has four molariform teeth both on the mandible and maxilla, which are one premolar and three molars. The lower molars have three roots, with two small roots on the anterior and one big root on the posterior side. The occlusal surface of the molars is concave, with the high lateral cupids. On the lower dentition, the premolar has triangular contour with only one lateral crest on the posterior. The molars have trapezoid contour with three marked transversal crests connecting the large labial cuspids (protoconid, mesoconid, and hypoconid) to the lingual cuspids). The m1 is wider

and more trapezoid compared to the m2, while the m3 is more rhomboidal and is the smallest compared to the other molars. On the upper dentition, the premolar is trapezoid, with two cuspids on the labial side. The molars are more quadrangular on its contour with two large labial cuspids (paracone and metacone). Four transversal crests, finer than the transversal crest of inferior molars, are connecting the labial and lingual cuspids. A transversal crest from paracone to the middle point of the M1 and M2. These features resemble to the description of *Eliomys quercinus* by Chaline et al. (1974) and Gosàlbez (1987). Moreover, it differs from the *Glis glis*, another species of the family Gliridae, where the *Glis glis* has more number of lateral crests and more complex in its pattern (Chaline et al., 1974; Daams, 1981; Gosàlbez, 1987). Therefore, the remains recovered from Cudó cave level 107 and 105 could be confidently classified as *Eliomys quercinus*.

Habitat and geographical distribution – The garden dormouse or *Eliomys quercinus* is a generalist species that inhabits woodland, rocky, and artificial landscape. It can live from the sea level elevation to altitude of 1,500 m.a.s.l. Currently, it is widely distributed over Europe from the Baltic and Finland to the southern Europe and from Ural to the Atlantic coast. In Spain, it also can be found roughly in all region.

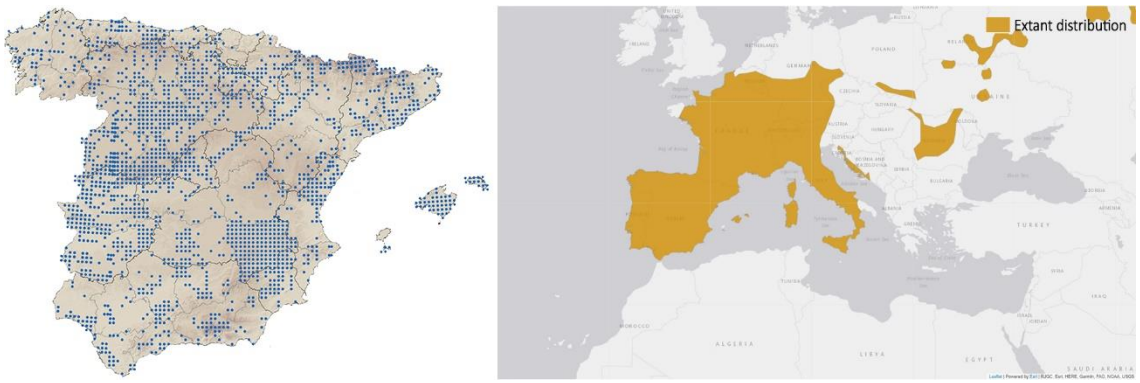

Figure 5.34 – Current distribution maps of *Eliomys quercinus* on the Iberian Peninsula (left) (Palomo et al., 2007) and Eurasia (right) (IUCN, 2021).

Family SCIURIDAE Fischer & Waldheim, 1817
Subfamily SCIURINAE Braid, 1857
Genus ***Sciurus*** Linnaeus, 1758
Sciurus vulgaris Linnaeus, 1758

Figure 5.35 – Left m1 of *Sciurus vulgaris* recovered from Cudó cave level 105. Scale in 1mm.

Material – Level 105: one isolated m1.

Description – The molar has trapezoiidal contour on the occlusal view with remarkably longer posterior side compared to the anterior. The occlusal surface is concave surrounded by ridges with two large tubercles (protoconid and hypoconid) and one small isolated tubercle (mesoconid) in between on the labial side. On the lingual side, the metaconid and entoconid are developed and connected to the labial cuspids by anterolophid and posterolophid, while the mesolophid is developed isolated from the other cuspids. Those features are resemble to the description of *Sciurus vulgaris* by Cuenca-Bescós (1988) and Gosàlbez (1987). Therefore, the left m1 from the Cudó cave level 105 could be classified as *Sciurus vulgaris*.

Habitat and geographical distribution – *Sciurus vulgaris* or the red squirrel is a common species in the palearctic forest. It inhabits all type of forest, from conifers, hardwood, homogenous, to the artificial forest. It is common in the elevation range from the littoral to 1,900 m.a.s.l. In Europe, it is currently widely distributed while in the Iberian Peninsula it is present in the Eurosiberian region from Galician to Catalonian region. It can also be found in several parts of the Central System and in the Mediterranean Coast.

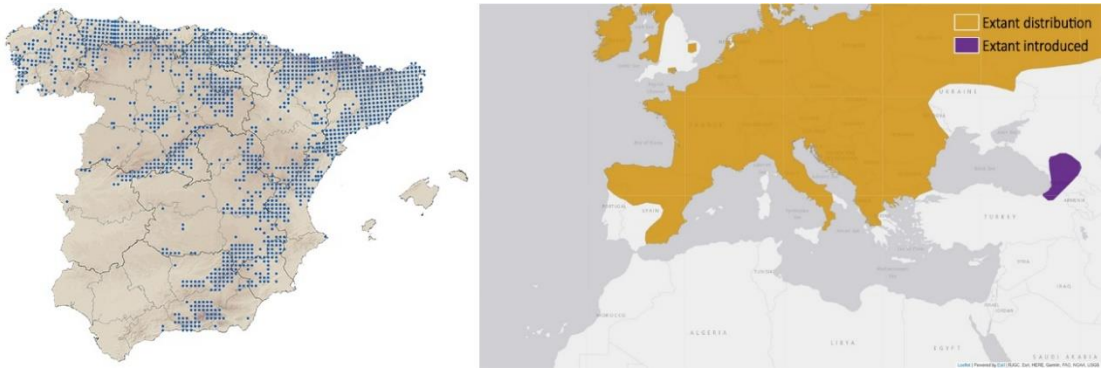

Figure 5.36 – Current distribution maps of *Sciurus vulgaris* on the Iberian Peninsula (left) (Palomo et al., 2007) and Eurasia (right) (IUCN, 2021).

6 RESULTS

6.1 Quantification of remains

This study has identified a total of 1185 remains, which correspond to a minimum of 502 individuals (Table 6.1). Those numbers are distributed into 528 taxonomically identified specimens in level 107, which corresponds to minimum of 264 individuals, and 658 in level 105, which corresponds to minimum of 238 individuals.

From the taxonomical analysis, 14 different taxa have been identified: *Crocidura russula*, *Sorex* gr. *araneus-coronatus*, *Rhinolophus* cf. *ferrumequinum*, *Myotis* gr. *myotis-blythii*, *Pipistrellus* cf. *pipistrellus*, *Microtus arvalis*, *Microtus agrestis*, *Microtus* gr. *arvalis*-agrestis, Microtus (*Terricola*) *duodecimcostatus*, *Microtus* (*Iberomys*) *cabrerae*, *Chionomys nivalis*, *Apodemus sylvaticus*, *Eliomys quercinus*, *Sciurus vulgaris*. However, several specimens were unable to be identified into species level, therefore they were grouped at the genus level (cf. *Myotis*, cf. *Pipistrellus*) and order level (Chiroptera indet). These groups, with addition of *Microtus* gr. *arvalis-agrestis* are not considered for the environmental reconstruction since they provide little ecological information.

Considering relative abundance of the taxa, in level 107, *C. nivalis* appears dominating the assemblage with a relative abundance of 66.3%, calculated considering the minimum number of individual (MNI). It is significantly higher than the other taxa. *A. sylvaticus*, which is the second most abundant taxon, only reach 10.6%. Other taxa with relevant abundance in level 107 are *M. arvalis*, *M. agrestis*, and *M. (T) duodecimcostatus*, with 8.7%, 6.4%, and 3%. The remaining taxa are scarce within the assemblage, representing less than 2% such as *Crocidura russula* (1.9%), *Eiomys quercinus* (1.1%), *M. (I) cabrerae* (0.4%), *Myotis* gr. *myotis-blythii* (0.4%), *Pipistrellus* cf. *pipistrellus* (0.4%), and *Sorex* gr. *araneus-coronatus* (0.4%).

The taxonomic relative abundance in level 105 appears slightly different from the level 107. The species *C. nivalis* is still highly represented with an MNI of 64 (26.9%), but it is not dominating the assemblage due to a significant increase of the abundance of *A. sylvaticus* (37%). Other taxa are well represented in level 105, such as *M. (T) duodecimcostatus* (7.6%), *M. (I) cabrerae* (7.1%), *M. agrestis* (5.5%), *M. arvalis* (4.6%), *C. russula* (4.2%), *E. quercinus* (3.4%), *M.* gr. *myotis-blythii* (1.7%), and *P.* cf. *pipistrellus* (1.3%).

Apart from the evidence change on the relative abundance decrease of *C. nivalis* and the increase of *A. sylvaticus*, the changes are also noticed in other species representation (Figure 6.1). The abundance of *M. agrestis* and *M. arvalis* decreased from 6.4% to 5.5% for *M. agrestis* and from 8.7% to 4.6% for *M. arvalis*. The species of *Sorex* gr. *araneus-coronatus* however, is totally absent in the level 105. Otherwise, some significant increases are represented in the other taxa, such as *M. (T) duodecimcostatus* from 3.0% to 7.6%, *M. (I) cabrerae* from 0.4% to 7.1%, *C. russula* from 1.9% to 4.2%, *E. quercinus* from 1.1% to 3.4%, *M.* gr. *myotis-blythii* and *P.* cf. *pipistrellus* from 0.4% to 1.4% and 1.3%, respectively. Moreover, in level 105 appears two taxa that absent in level 107, which are *S. vulgaris* and *R.* cf. *ferrumequinum*.

	107			105		
	NISP	MNI	%	NISP	MNI	%
Crocidura russula	19	5	1.9	38	10	4.2
Sorex gr. *araneus-coronatus*	1	1	0.4	0	0	0
Chiroptera indet	0			2		
Rhinolophus cf. *ferrumequinum*	0	0	0	2	1	0.4
cf. *Myotis*	0			4		
Myotis gr. *myotis-blythii*	1	1	0.4	14	4	1.7
cf. *Pipistrellus*	0			1		
Pipistrellus cf. *pipistrellus*	1	1	0.4	9	3	1.3
Microtus arvalis	30	23	8.7	19	11	4.6
Microtus agrestis	30	17	6.4	16	13	5.5
Microtus gr. *arvalis-agrestis*	1	1	0.4	0	0	0
Microtus (Tericola) duodecimcostatus	15	8	3	35	18	7.6
Microtus (Iberomys) cabrerae	1	1	0.4	32	17	7.1
Chionomys nivalis	321	175	66.3	124	64	26.9
Apodemus sylvaticus	100	28	10.6	306	88	37
Eliomys quercinus	7	3	1.1	55	8	3.4
Sciurus vulgaris	0	0	0	1	1	0.4
TOTAL	**527**	**264**	**100**	**658**	**238**	**100**

Table 6.1. Quantification table of the small mammal remains recovered from level 107 and 105 Cudó cave. NISP, number of identified specimen present; MNI, minimum number of individuals.

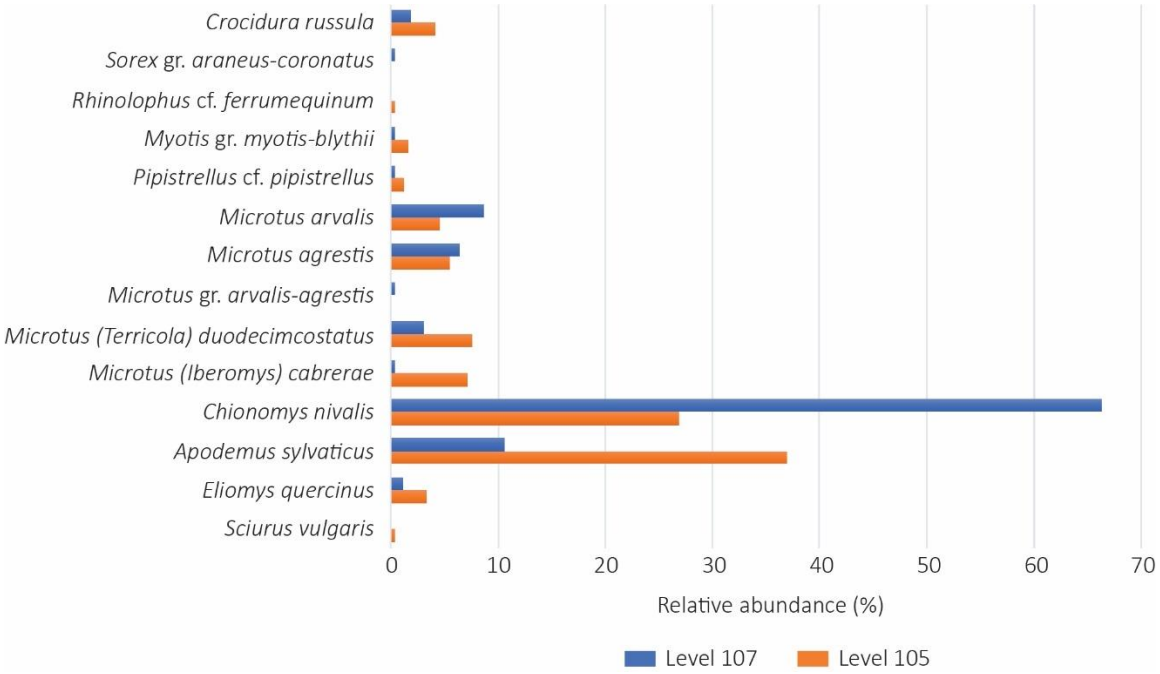

Figure 6.1. Comparison of relative abundance of taxa from level 107 and 105, considering the minimum number of individuals.

6.2 Taphonomy

Up to 1131 small mammal teeth from both levels have been included in this analysis, with 495 remains from level 107 and 636 remains from level 105. Wide range of digestion marks are detected on the remains from both levels, including the digestion degree from light to heavy (table 6.2).

In level 107, 209 remains (42.2%) are digested. Considering the digestion categories, 43 remains (8.7%) are observed with light digestion, 76 remains (15.4%) with moderate digestion, while 90 remains (18.2) with heavy digestion mark. In level 105, 43 remains (6.8%) show light digestion mark, 96 remains (15.1%) with moderate digestion, and 68 remains (10.7%) with heavy digestion. Thus, the quantification result is just slightly different in level 105 and in both levels moderate and heavy digested remains are significantly higher than the light digested remains. However, there is a shift between level 107 where the heavy digestion got the highest number and the level 105 where the moderate digestion has the highest number while the heavy digestion is the second.

The digestion modification on the teeth also varies between the taxonomical group of the assemblage (Table 6.3). In level 107, 52.5% (192) of Arvicolinae teeth show digestion marks, by which 11.7% (43) are lightly digested, 19.4% (71) are moderately digested, and 21.3% (78) are heavily digested. Within Muridae, Gliridae, and Sciuridae group, 14.9% (16) remains are observed with digestion marks: heavy digestion mark appears more frequent in 11.2% (12) while the moderate digestion mark only appears in 3.7% (4) of the remains. Moreover, in the group of Soricidae, only 5% of the remains (1) shows digestion marks and it is categorized with the moderate degree. There are no remain showing digestion evidence in the group of Chiroptera from level 107.

In level 105, 207 remains (32.5%) shows digestion marks. Arvicolinae teeth show similar pattern to the level 107 with the highest abundance of digested teeth. As much as 50.9% (110) are digested, 19% (42) of them are lightly digested, 21.3% (46) are moderately digested, and 10.2% (22) are heavily digested. However, the Soricidae is the group with the second highest percentage of digested remains, with 34.2% (13) of the assemblage are digested. Among them, 23.4% (9) are heavily digested and 10.5% (4) are moderately digested. Otherwise, the Muridae, Gliridae, and Sciuridae group shows only 23.2% (83) of the remains digested, where 12.8% (46) are moderately digested, 10.1% (36) are heavily digested, and 0.3% (1) are lightly digested. Within chiropters, only one remain 4.2% shows digestion marks and is categorized as heavy digestion.

From the comparison between the digestion marks of the taxonomical group in level 107 and level 105, some differences could be recognized (Figure 6.3). The percentage of digested remains of Arvicolinae is practically the same, with only <2% decrease in level 105. Otherwise in other taxa (Muridae, Gliridae, Sciuridae, Soricidae, and Chiroptera) the digested remains appear to increase significantly. Though it could be linked to the increases of their abundance in level 105.

Digestion category	Level 107		Level 105	
	n	%	n	%
Null	6		7	
Absent	286	57.8	429	67.5
Light	43	8.7	43	6.8
Moderate	76	15.4	96	15.1
Heavy	90	18.2	68	10.7
TOTAL	**495**	**100**	**636**	**100**

Table 6.2. Digestion marks of the remains from Cudó cave, differentiating digestion categories reached. Remains with unclear digestion marks due to poor preservation are considered as "null" and not included in the quantification.

Level 107									
Taxonomical group	**Total remains**	**Absent**	**%**	**Light**	**%**	**Moderate**	**%**	**Heavy**	**%**
Arvicolinae	366	174	47,5	43	11,7	71	19,4	78	21
Muridae, Gliridae, and Sciuridae	107	91	85	0	0	4	3,7	12	11
Soricidae	20	19	95	0	0	1	5	0	0
Chiroptera	2	2	100	0	0	0	0	0	0
Level 105									
Taxonomical group	**Total remains**	**Absent**	**%**	**Light**	**%**	**Moderate**	**%**	**Heavy**	**%**
Arvicolinae	216	106	49,1	42	19,4	46	21,3	22	10
Muridae, Gliridae, and Sciuridae	358	275	76,8	1	0,3	46	12,8	36	10
Soricidae	38	25	65,8	0	0	4	10,5	9	24
Chiroptera	24	23	95,8	0	0	0	0	1	4,2

Table 6.3. Quantification of digestion modification based on the taxonomical group of each level.

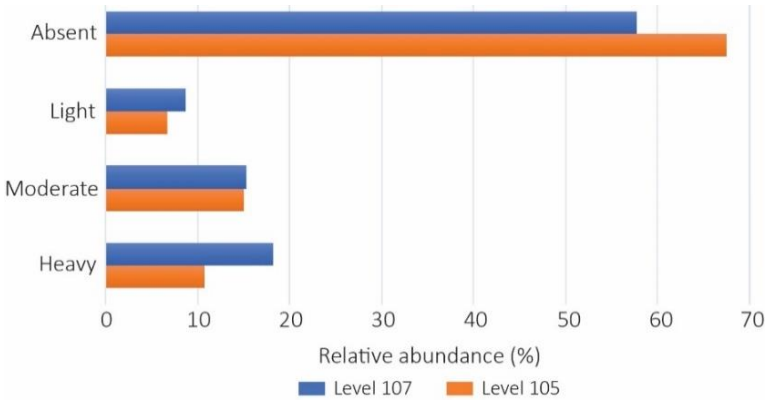

Figure 6.2. Digestion category abundances of each level.

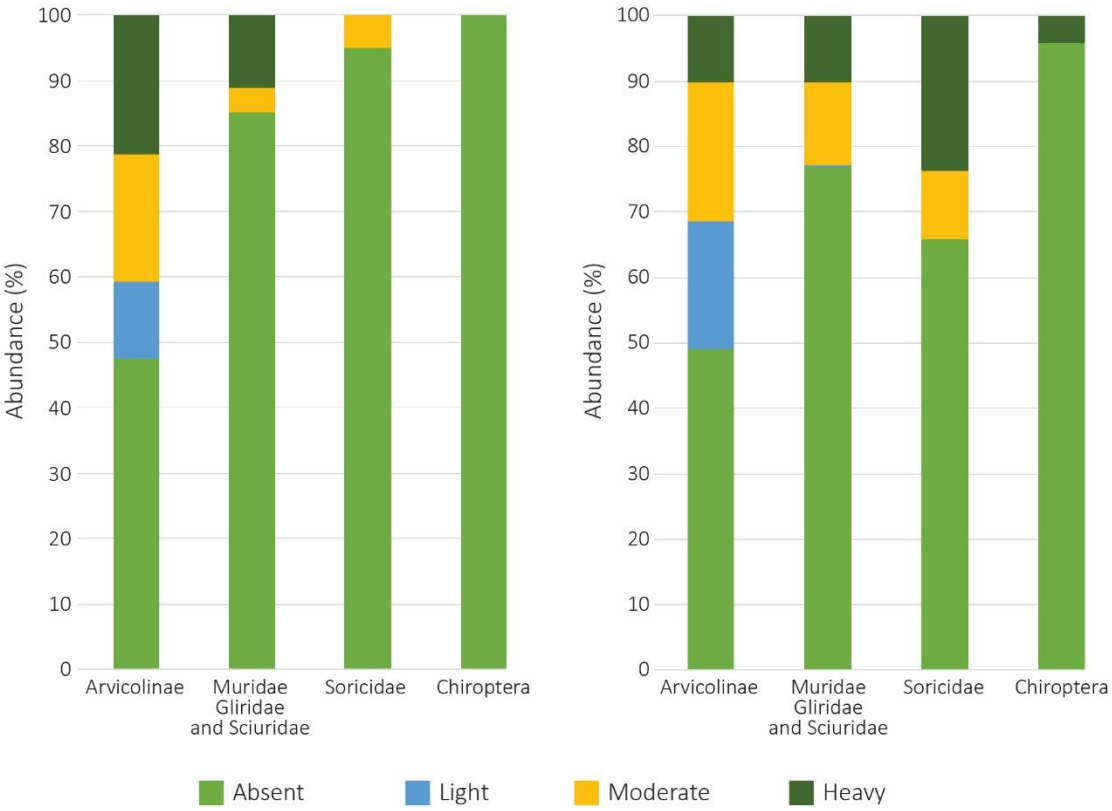

Figure 6.3. Digestion marks comparison between taxonomical group of level 107 (left) and level 105 (right).

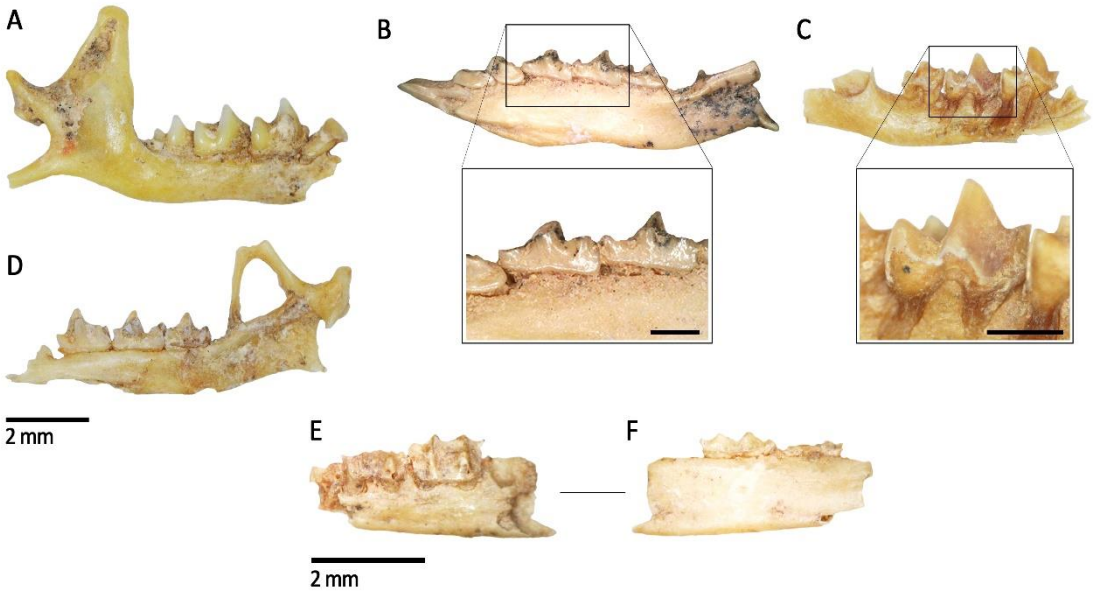

Figure 6.4. Digestion marks on the insectivores, A) light digestion; B) moderate digestion; C) heavy digestion; D) heavy digestion mark on the mandibular ramus; and E – F) heavy digestion on the chiropters. Scale in 2mm and 1mm in the detailed view (B and C).

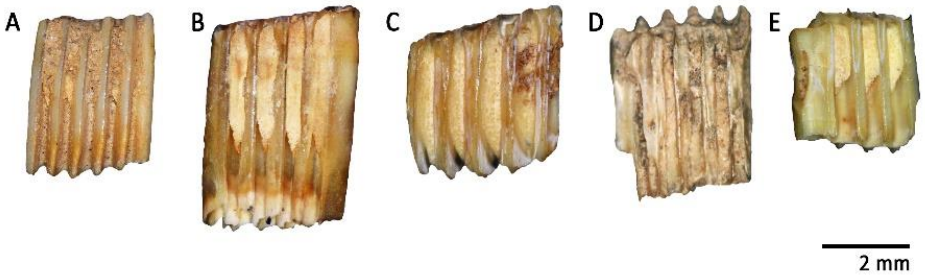

Figure 6.5. Digestion marks on the Arvicolinae lower firs molar: A) absent, B) light digestion, C) moderate digestion, D) heavy digestion, and E) intramandibular digestion. Scale in 2mm.

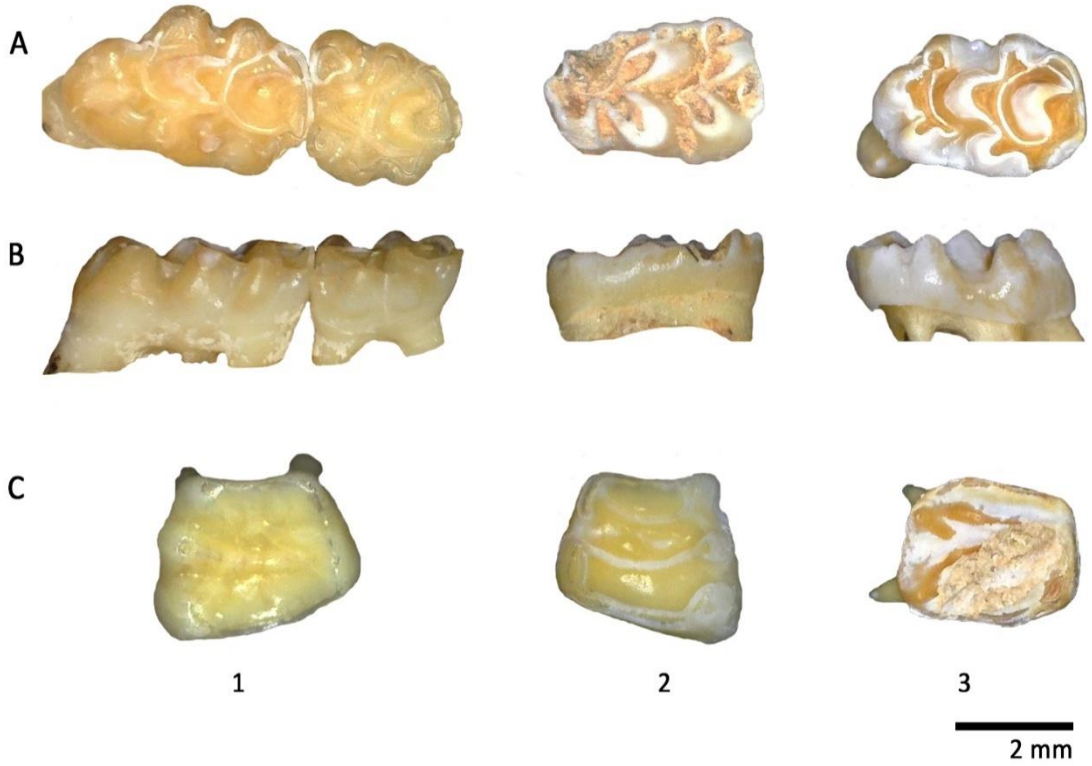

Figure 6.6. Digestion marks on the A) *Apodemus sylvaticus* molars in occlusal view, B) *Apodemus sylvaticus* molars in lateral view, and C) *Eliomys quercinus* molars in occlusal view: 1) no digestion, 2) moderate digestion, 3) heavy digestion. Scale in 2mm.

6.3 Paleoecological analysis

6.3.1 Diversity index

Simpson diversity index is applied to the species recorded in the two level of Cudó cave. In level 107, the species richness is 13 with diversity index value of 0.54. In level 105, with species richness of 15, the diversity index value is 0.78. It could be inferred that there is more domination of a particular species and less diverse environment on the level 107. In contrast, on the level 105 species are comparatively more equally represented.

These results seem to be consistent with the quantification on the relative abundance of species described before. There is strong domination of *C. nivalis* in level 107 with significantly

high abundance compared to the other species. Otherwise in level 105, even though *C. nivalis* still shows high abundance, it is not dominating the assemblage with the high abundance of *A. sylvaticus* and the relative abundance of other taxa also doubled those in level 107. Also, the appearance of two taxa in level 105 cannot be ignored in relation to the species diversity and the environmental implications. All evidence could point to more complex and diverse environment during level 105 deposition.

	Level 107	Level 105
Taxa	13	15
Individuals	265	241
Simpson Diversity index	0.54	0.78

Table 6.4. Diversity indices of the level 107 and 105.

6.3.2 Chorotype analysis

The species chorotype quantification in each of the analyzed assemblages shows quite different climatic conditions between level 107 and level 105. On level 107, chorotype 1 reaches a significantly high value (66.7%) compared to the rest of chorotypes, which are 15.2% for chorotype 2; 5,3% for chorotype 3; and 12,5% for chorotype 4. It means that the species with mid-European requirements (chorotype 1 and 2) dominate this assemblage, with more than 80%. The species related to chorotype 1 prefer environment with low mean summer temperature (<20^{o}C), low mean annual temperature (MAT) (10 – 12^{o}C), and mean annual precipitation (MAP) higher than 800mm. The chorotype 2, refers to mid-European dependent and Mediterranean-tolerant species which prefer similar ecological condition with high annual precipitation (MAP >600mm). The particular characteristic of the species within this chorotype is the wider geographic distribution to the south.

Otherwise, species belonging to chorotype 1 experienced a significant decrease to 26.9% in level 105. The decreasing value also observed on the group of the chorotype 2 to 10.1%. In contrast, the species from chorotype 4 dominate the assemblage value of 44.1%. This chorotype groups the generalist species with wide range of climatic preferences and geographical distribution and those with specific habitat requirements. Therefore, the species within this group provides little information regarding the climate. Nevertheless, the analysis shows quite remarkable increase on the species correspond to chorotype 3 (from 5.3% in level 107 to 18,9% in level 105). It could mean there is increase of Mediterranean species that prefers moderate temperature with MAT >5^{o}C and humid environment with MAP <1000mm.

	Ch1	Ch2	Ch3	Ch4
Level 107	66.7%	15.2%	5.3%	12.5%
Level 105	26.9%	10.1%	18.9%	44.1%

Table 6.5. Chorotype quantification of level 107 and level 105. Ch, chorotype.

6.3.3 Habitat weighting method

This analysis provides information related to the landscape reconstruction based on the preferred habitat of the identified species. The quantification on the assemblage from Cudó cave shows two different conditions between level 107 and 105. In level 107, rocky substratum was likely dominating the landscape represented by the abundance of species which prefers rocky landscape (67.1%). Moreover, as much as 22.1% of the remains are the species with woodland habitat requirements. Therefore, woodland environment with mature forest, woodland margin, or forest patches, with moderate ground covers could have also been present in the vicinity of Cudó cave. The open dry and open humid habitat apparently less represented in the landscape with only 5.3% corresponding to open dry habitat requirements and 5.1% corresponding to open humid dependent species.

In level 105, the landscape was likely to changed. The species with woodland habitat requirements significantly increased to 55.7%. The similar increase is also observed in the species with open humid habitat, from 5.1% in level 107 to 10.3% in level 105. Otherwise, species with rocky landscape preference decrease to 29.6%, and those which adapted to open dry habitat also decreased to 4.4%. It could be inferred that there was an increase of humidity and possibly also temperature in this region that brings more vegetation and pasture topsoil.

	Level 107	Level 105
Open dry	5.3%	4.4%
Open humid	5.1%	10.3%
Woodland	22.1%	55.7%
Rocky	67.1%	29.6%

Table 6.6. Quantification result of habitat weighting analysis.

6.3.4 Bioclimatic model

The bioclimatic model estimations in level 107 show that the MAT is 3.3°C lower than current MAT recorded on the nearest city, Alcover. The similar differences also appeared on the mean temperature of the coldest month (MTC), 4.9°C colder than today as well as on the mean temperature of the warmest month (MTW), 1.1°C colder. Otherwise, the MAP is remarkably higher than present-day, with 657mm difference. This bioclimatic estimation is roughly similar to what is recorded in level 105. It estimates colder and wetter conditions than present-day. The MAT is 3.9°C lower, the MTC is 6.4°C lower, the MTW is 1.1°C lower, and the MAP is 586mm higher than the current records. However, compared to level 107, data from level 105 are indicating slightly colder and dryer conditions (Table 6.7).

Species	Climatic zone			
	IV	VI	VIII	IX
107				
Microtus arvalis	0	1	0	0
Microtus agrestis	0	0.5	0.5	0
Microtus (Tericola) duodecimcostatus	0	1	0	0
Microtus (Iberomys) cabrerae	1	0	0	0
Chionomys nivalis	0.25	0.25	0.25	0.25
Apodemus sylvaticus	0.5	0.5	0	0
Eliomys quercinus	0.5	0.5	0	0
Σ CRI	2.25	3.75	0.75	0.25
Bci=(Σ CRIi)100/S	32.14	53.57	10.71	3.57

Species	Climatic zone			
	IV	VI	VIII	IX
105				
Microtus arvalis	0	1	0	0
Microtus agrestis	0	0.5	0.5	0
Microtus (Tericola) duodecimcostatus	0	1	0	0
Microtus (Iberomys) cabrerae	1	0	0	0
Chionomys nivalis	0.25	0.25	0.25	0.25
Apodemus sylvaticus	0.5	0.5	0	0
Eliomys quercinus	0.5	0.5	0	0
Sciurus vulgaris	0.33	0.33	0.33	0
Σ CRI	2.58	4.08	1.08	0.25
Bci=(Σ CRIi)100/S	32.25	51.00	13.50	3.13

Table 6.7. Climatic zone assignation and climate restriction index (CRI) calculation of each species(S) within the order of Rodentia in level 107 and 105 of Cudó cave, and the bioclimatic spectrum calculation (Bci).

	Level 107				Level 105			
	Estimation	Current data	Difference	Standard deviation	Estimation	Current data	Difference	Standard deviation
MAT (ºC)	11.4	14.7	-3.3	1.7	10.8	14.7	-3.9	2.0
MTC (ºC)	5.1	10.0	-4.9	3.7	3.7	10.0	-6.4	3.2
MTW (ºC)	18.8	20.0	-1.1	0.6	18.9	20.0	-1.1	0.5
MAP (mm)	1209.3	552.0	657.3	328.7	1138.3	552.0	586.3	293.1

Table 6.8. Quantification of climatic parameters based on the bioclimatic index. Current climatic data obtained from the climate-data.org for the region of Alcover. MAT, mean annual temperature; MTC, mean temperature of the coldest month; MTW, mean temperature of the warmest month; MAP, mean annual precipitation.

6.3.5 Mutual ecogeographic range method

From the intersection of the current geographic distribution of the analyzed taxa present in Cudó cave, equivalent taxa assemblages today are restricted to small areas different from the current location of the cave. In the case of level 107, similar set of taxa are only represented by a single point in northern Catalan Pyrenees. It corresponds to lower MAT (-7.2ºC) and higher MAP (+848mm) than the current condition in the vicinity of Cudó cave. The mean temperature of the coldest month (MTC) and mean temperature of the warmest month (MTW) are also lower than presend-day, with a difference of 10ºC for the MTC and 12.5ºC difference on the MTW. In

the vegetation aspect, it corresponds to the Eurosiberian-type habitat with mountain to sub-alpine vegetation covers, whereas the area around Cudó cave currently covered by the mesomediterranean vegetation (Figure 6.7).

In level 105 the results are slightly different. Four spots are obtained from the intersection on the present geographical distribution of analyzed species present in this level. These spots are distributed on the northern Catalan Pyrenees with one spot, two spots in the margin of western Pyrenees, and another one spot in the Iberian System. Those locations have different climatic conditions, but in all cases present lower MATs and higher MAPs than the current data recorded from Alcover region, with a difference of -4.1ºC and +273mm respectively. On the MTC and MTW, lower temperatures are also obtained, with a difference of -7.5ºC and -3.1ºC respectively. Thus, climatic conditions are less distant to current data compared to those from level 107. Furthermore, those areas also correspond to different habitat type and vegetation covers: from the Eurosiberian habitat with mountain or sub-alpine vegetation, which could be found in the northern areas and around the Pyrenees, to the Mediterranean habitat with supramediterranean vegetation is found in the Iberian System (Figure 6.8).

	Level 107				Level 105			
	MAT	**MTC**	**MTW**	**MAP**	**MAT**	**MTC**	**MTW**	**MAP**
n	1	1	1	1	4	4	4	4
Mean	7.5	0	17.5	1400	10.6	2.5	16.9	825
Min	7.5	0	17.5	1400	10	0	15	100
Max	7.5	0	17.5	1400	12.5	5	17.5	1000
SD	-	-	-	-	2.4	2.0	1.1	126
Error	-	-	-	-	1.2	1.4	1.3	63
Current data	14.7	10	30	552	14.7	10.0	20.0	552
Differences	-7.2	-10.0	-12.5	848	-4.1	-7.5	-3.1	273

Table 6.9. Mutual Ecogeographic Range method of level 107 and 105 of Cudo cave. The current climatic data obtained from the climate-data.org for the region of Alcover, Catalunya. MAT, mean annual temperature; MTC, mean temperature of the coldest month; MTW, mean temperature of the warmest month; MAP, mean annual precipitation; SD, standard deviation.

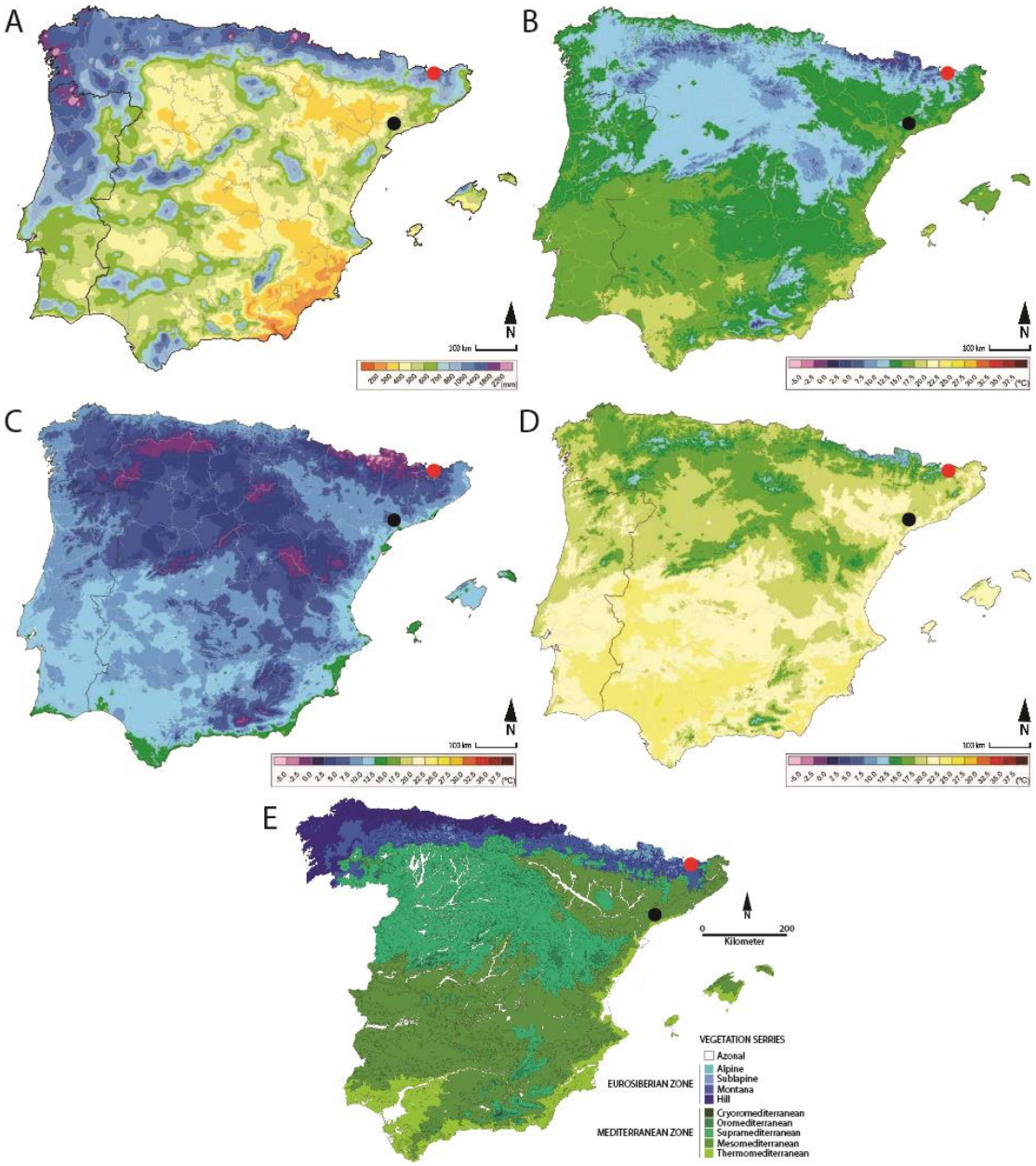

Figure 6.7. Maps show the locations with current climatic conditions (red dots) resembling the small mammal assemblage recovered from Cudó cave level 107. A) by MAP; B) by MAT; C) by MTC; D) by MTW (AEMET and IMP, 2011); and E) by the vegetation covers (Rivas Martínez, 1987). The black dots are the location of Cudó cave.

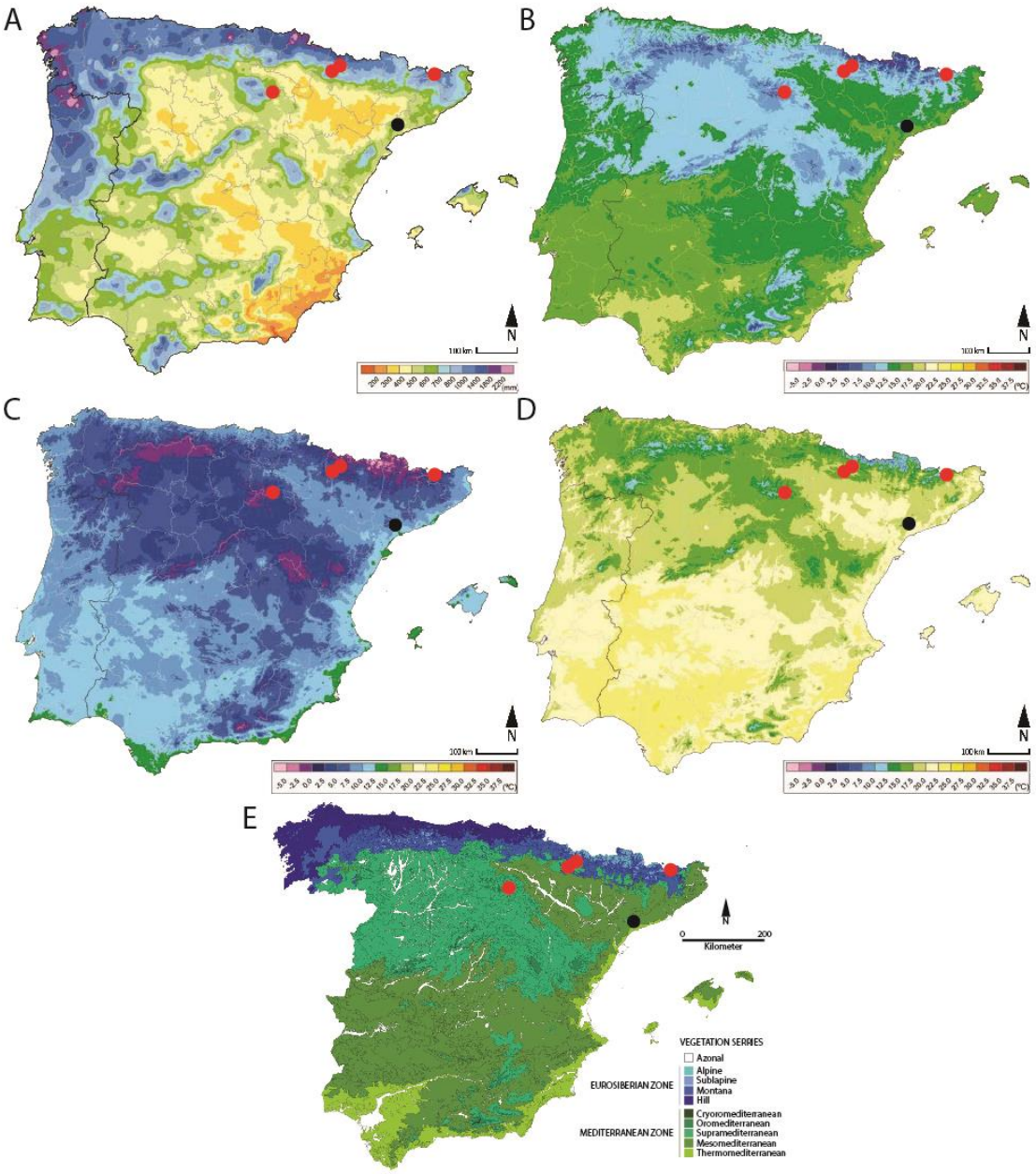

Figure 6.8. Maps show the locations with current climatic conditions (red dots) resembling the small mammal assemblage recovered from Cudó cave level 105. A) by MAP; B) by MAT; C) by MTC; D) by MTW (AEMET and IMP, 2011); and E) by the vegetation covers (Rivas Martínez, 1987). The black dots are the location of Cudó cave.

7. DISCUSSION

7.2. The origin of the assemblage of small mammals in Cudó cave

As mentioned in previous chapters, identification of the predators producing the assemblages is a clue to understand the biases and to make the paleoecological inferences more accurate. Small mammal assemblages could have different causes of accumulation and even if predation is the cause of the accumulation, it could be attributed to different predators that inhabit the same area. From the analyses performed in the identified teeth (mainly molars) from level 107 and 105, some important ideas can be presented, despite constitute just to a preliminary approach.

Remains show digestion marks, in different intensity indicating that predators were contributing to the assemblage formation. In general, it can be seen that 42.3% of the molars in level 107 and 32.5% in level 105 show digestion marks (Figure 7.1). It is indicating that predation is the main cause of accumulation in both levels. This high abundance of digested remains could point to both nocturnal and diurnal groups as the main producer group of the assemblages. The probable species contributing to such percentage are *Strix aluco, Athene noctua,* and *Circus cyaneus* (Fernández-Jalvo et al., 2016). Considering the proportion of digestion intensity, in level 107 the light digested molars appear in 8.7%, moderate digested molars in 15.4%, and heavy digested molars in 18.2%. Otherwise in level 105, light digested molars are only 6.8%, moderate digested molars are 15.1%, and heavy digested molars is 10.7% of the remains. The heavy digested molars appear in the highest portion in level 107 (18.2%), even higher than molars with light and moderate digestion marks. While in level 105, this category still remarkably high (10.7%). It is signalling that the predator groups that can produce this level of digestion marks are significantly contributing to the accumulation of the small mammal assemblage. The category 4 predators, including *S. aluco, A. noctua, C. cyaneus, Falco perregrinus* and *F. tinnunculus*, are likely to be assigned to this pattern of digestion (Fernández-Jalvo et al., 2016).

Associating the accumulation of small mammal remains in Cudó cave with those species of nocturnal and diurnal raptors is possible considering their current geographic distribution which also covering the Iberian Peninsula. Apart from that, it is also important to see the habitat preferences and the behaviour of those predators. Almost all of the species mentioned from category 4 are having similar habitat preferences for dwelling such as cliffs and natural cervices or woodland. For the hunting environment, they tend to hunt in open landscape such as grassland or woodland margins (Fernández-Jalvo et al., 2016 and references therein).

Considering the hunting behaviour, the species belong to the category 4 predator known to have different hunting range, from the smallest with 0.22km radius which corresponds to *Athene noctua* to the largest range with 6.91km radius which corresponds to *Circus cyaneus* (Figure 7.3). These ranges however, vary depending on the landscape and the abundance of the prey. The hunting range of the predators will be smaller in dense woodland compared to the open grassland. Despite of the varied ranges, it covers several kinds of ecosystem, from the riparian in the valley to arid plateau with semi woodland covering, even in the smallest hunting range of *A. noctua*. Consequently, it can increase the richness of the small mammal assemblage produced by the raptors in Cudó cave.

Most of the potential raptors contributing to the assemblage formation are considered as generalist or opportunistic predators that will get pretty much any species present within its

hunting range. Regarding the prey diversity, those predators are known to hunt relatively high rodent species diversity. It indicates that the predatory selection is minimum and the prey species represent the environmental condition within their hunting range (Andrews, 1990; Fernández-Jalvo et al., 2016). However, it is difficult to specifically assign the assemblage formation to the species of predators due to limited information with this level of observation. Complete taphonomic analysis will be helpful to confidently assign the predator species to the accumulation and to specifically identify the origin of the small mammal assemblages in this site.

In addition, the shifting pattern of the digestion marks between level 107 and level 105 by the increase of absent group and decrease of the heavy digested group cannot be barely interpreted with the change of predator composition. Instead, if detailed observation on the order groups, the significant increase of *Apodemus sylvaticus* remains (see Chapter 6) could alter the general composition of digestion marks. It is because the increase of the NISP leads to the rising number of non-digested molars. However, from the soricides and bats remains, it can be seen that the high digestion marks still remarkable in level 105. It shows that the small mammal accumulation in both levels could be linked to the same predator category. Therefore, the changes on the remains composition reflect the changes on the conditions of the surrounding environment.

It is understood that the agents contributing to the accumulation of small mammal remains are not restricted to the predatory activity. Other natural elements such as water stream or sediment movement might also contribute to the assemblage formation and other variables than the digestion marks should also be considered to obtain the whole images of the assemblage formation processes. However, this preliminary study on the small mammal isolated molars is sufficient to get the images of predatory activity as the main accumulator agent. It is in regards on the enough quantity of the remains showing digestion marks in the assemblages.

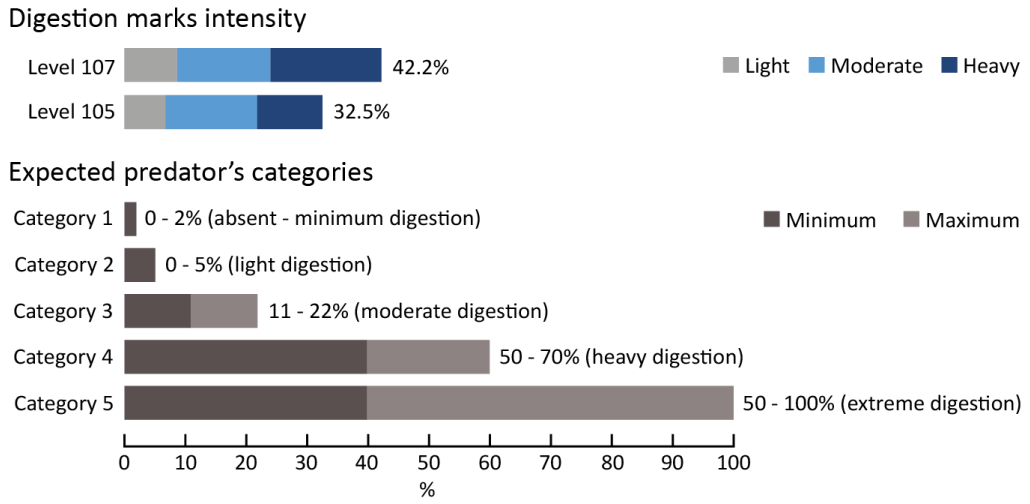

Figure 7.1. Percentage of digested remains observed in the assemblage of level 107 and 105 of Cudó cave and the expected digested molars per predator's category (after Fernández-Jalvo et al., (2016).

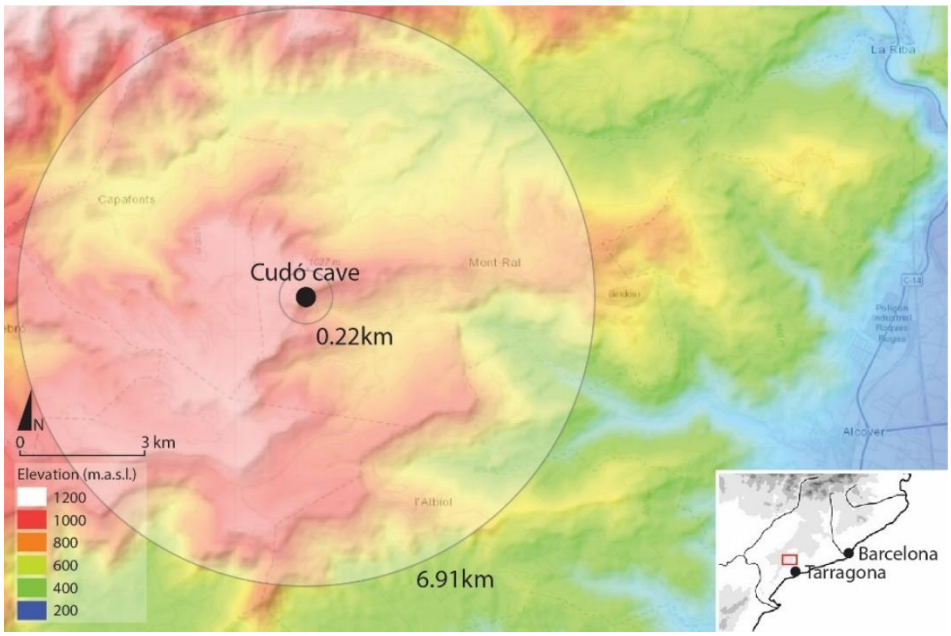

Figure 7.2. The approximation of hunting radius of the predators contributing on the assemblage formation in Cudó cave based on the present-day records (https://animaldiversity.org/): the smallest radius, 0.22km corresponds to *Athene noctua* and the largest radius, 6.91km corresponds to *Circus cyaneus* (map source: https://www.geamap.com/en/spain).

7.3. Paleoenvironmental reconstruction of Cudó cave

Initial observation on the two archaeostratigraphic levels, level 107 and 105, indicate that these could be the result of several short-term occupation in this cave during the Late Pleistocene. From the archaeological point of view, it could be assigned to the Upper Palaeolithic culture, particularly coinciding to the Magdalenian techno-culture complex, considering the malacological artefacts as well as the lithic artefacts (Vergès, 2017). In fact, these two layers are only separated by a thin layer of ash, labelled as level 106, but chronologically level 107 and 105 are separated by about 9000 years, where level 107 dated to 31.2 – 24.4 ka cal BP and level 105 to 15.5 – 10.2 ka cal BP. It makes these levels interesting in term of paleoenvironmental understanding considering chronologically it lies around the LGM and the end of the Late Glacial Period.

7.3.1. Landscape in the vicinity of Cudó cave

The results of the analysis show that level 107 and 105 have notably different environmental conditions. It can be seen in the Simpson's diversity index value of 0.54 for level 107 and 0.78 for level 105 (Figure 7.3). It is a signal that level 107 has significantly less diverse ecosystem with a certain species domination compared to level 105. The increase of the value from level 107 to 105 indicating an increase of the diversity in the small mammal assemblage in level 105. This means that there was no significant domination of a certain taxa in this level, and all of the taxa are well represented in the ecosystem. It is indicating that the ecosystem was more favorable in level 105 compared to level 107. The ecosystem could have been increase its capacity to support more species, for example with the increase of vegetation complexity in the arboreal ecosystem (e.g., Williams et al., 2002)

The signal of landscape change is supported with the data from the habitat weighting method. In level 107 the rocky habitat prevails (67.1%) and only a small proportion of woodland habitat (22.1%). On contrast, in level 105 there was predominance of woodland habitat (55.7%) and smaller proportion of rocky habitat (29.6%). The increasing proportion of woodland and decreasing rocky habitat in level 105 (Figure 7.3) could be an indicator that there was a climatic amelioration that boost the development of more closed vegetation cover. The increase also could be seen in the proportion of open humid landscape of level 105. It could also signaling to the increase of humidity or precipitation in this area during 15.5 – 10.2 ka cal BP, consistent to the palynological data extracted from Banyoles Lake which shows increases on the trees taxa after 15 ka BP compared to the period between 31 to 24 ka BP (Pèrez-Obiol and Julià, 1994). However, despite of decreasing proportion, the presence of rocky habitat cannot be ignored as it still has considerable portion in the landscape (29.6%).

Furthermore, the result displayed from chorotype analysis indicating a consistent trend of environmental change. The mid-European faunal taxa notably dominate the assemblage of level 107 (81.9%) shifted to the Mediterranean and generalist species (chorotype 3 and 4) in level 105 (63%) (Figure 7.3). By the climatic aspect, the increases of chorotype 3 and 4 taxa signaling the increase of temperature and humidity (Sans-Fuentes and Ventura, 2000). This could provide a better condition of the flourishing woodland habitat and increasing small mammal diversity in level 105.

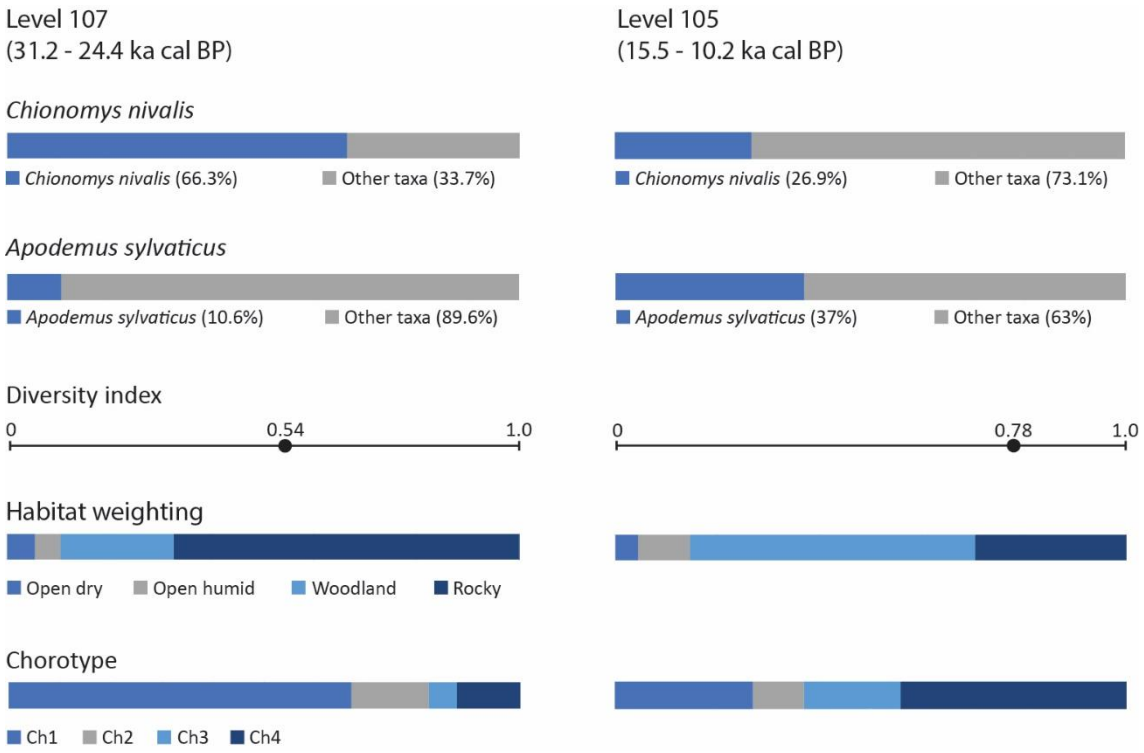

Figure 7.3. Comparison of some ecological indicators extracted from the assemblages of level 107 and 105 of Cudó cave. Comparison between *Chionomys nivalis* and *Apodemus sylvaticus* with the other taxa are being presented here as these two taxa become the most abundant taxa among the assemblages and it shows significant information about the environment.

The change patterns of diversity, landscape, and the chorotype are apparently suited to the change of the abundance of two most common species in the assemblage from Cudó cave, which are *Chionomys nivalis* and *Apodemus sylvaticus* (Figure 7.3). *Chionomys nivalis* fills 66.3% (MNI: 175) of the level 107 and decreased to 26.9% (MNI: 64) in level 105. As it requires specific rocky habitat and colder climate, the significant change of its abundance in between levels show a remarkable change on the reconstructed ecosystem, indicating a decreasing rocky landscape and improvement of the climate. Considering the current geographic distribution, *Chionomys nivalis* are not any longer live in the vicinity of Cudó cave. Instead, its current distribution is restricted to the high altitude of eastern Pyrenees, northward from Cudó cave. It shows that during the level 107 the periglacial condition and subalpine ecosystem exist in the lower latitude than today. It points to the less herbaceous and reduced tree covers in favor to rocky environment in Prades Mountains during the H3 and the beginning of H2 or LGM. In addition, the shift of *Apodemus sylvaticus* abundance from 10.6% (MNI: 28) in level 107 to 37% (MNI: 88) in level 105 also signaling an increase of woodland covers, considering that it strongly depends on this type of landscape. These environmental changes apparently lead to the increasing small mammal diversity in the area which indicating the more favorable environment.

The high diversity seen in the species, habitat, and chorotype composition both from level 107 and 105 is also interesting apart from the shifting pattern between those two levels. In case of habitat composition for instance, four types of habitats are present in both levels regardless the proportion. It could be understood considering the varied terrain around Cudó cave. As mentioned in a previous chapter, Cudó cave is located in a limestone cliff on the elevation of 987 ma.a.s.l, with various terrain in vicinity, from the lowland to plateau and from riparian landscape in the lower elevation to arid wood and scrubland on the higher elevation. This wide range of altitude variation inducing the diversity of vegetation covers from grassland, shrubland, to woodland, and consequently leads to the diversity of small mammal assemblage. Not to forget, this high variation occurs within the hunting range of the predators contributing to the small mammal assemblage formation in level 107 and 105 of Cudó cave (Figure 7.2).

Talking about vegetation covers, however, it could be distinguished that there was two vegetation serries inferred from the assemblages using the MER analysis. In level 107 the co-occurrence area of the taxa could be found in the eastern Pyrenees, where currently covered with Eurosiberian vegetation, including subalpine and mountain vegetation (see Chapter 6, Figure 6.7). This is consistent to the domination of rocky environment in this level. Otherwise, in level 105 some points referring to the area currently covered by Mediterranean vegetation zone appears as the co-occurrence area of the taxa. It is including the supramediterranean and oromediterranean vegetation which related to warmer and more humid environment (see Chapter 6, Figure 6.8).

7.3.2. Paleoclimatic context of Cudó cave

The result of the bioclimatic model and mutual ecogeographic range analysis suggest that the conditions during the formation of small mammal assemblages both in level 107 and 105 were colder and wetter than current condition in Cudó cave. In level 107 the MAT has difference ranging from -3.3 (BM) to -7.2^{o}C (MER) and the MAP from +657 (BM) to +848mm (MER) in respect to the current data. In level 105, the MAT difference spans between -3.9 (BM) and -4.1^{o}C (MER) and for the MAP, from +373 (BM) to +586mm (MER). In addition, the inferences of MTC and MTW of both levels also displayed lower temperature than current

condition. In level 107 the MTC are 5.1°C (BM) and 0°C (MER) while the MTW are 18.8°C (BM) and 17.5°C (MER). Otherwise, in level 105 the MTC are 3.7°C (BM) and 2.5°C (MER) while the MTW are 18.9°C (BM) and 16.9°C (MER) (Figure 7.4). Lower temperatures and higher precipitation rates are suited to some proposals about the paleoclimatic condition of Iberian Peninsula for the last 35000 years (e.g., Badal et al., 2012; Fletcher et al., 2010; Fletcher & Sánchez Goñi, 2008; Moreno et al., 2012; Pèrez-Obiol & Julià, 1994) and currently showed by other small vertebrate studies (e.g., López-García et al., 2014a; 2014b). The lower MTW and higher precipitation also indicating the colder summers and more wet winters that could be linked to the Heinrich Events (e.g., Sanchez Goñi and d'Errico, 2005; Fletcher and Sánchez Goñi, 2008), in this case, it could be related to the HE3 and the beginning of HE2.

However, some different shifting trends appear when comparing the level 107 and 105 in detail between the result from bioclimatic model and mutual ecogeographic range analysis. The estimated MAT of level 107 is slightly higher compared to level 105 based on bioclimatic model result. In contrast, the mutual ecogeographic range shows significantly colder temperature in level 107 than in level 105. This pattern also can be seen for the MTC and MTW. Otherwise, for the MAP, level 107 has slightly higher precipitation compared to level 105 based on bioclimatic model analysis. Whilst from the mutual ecogeographic range analysis the gap is wider, with the level 105 is significantly dryer than level 107 (Figure 7.5).

The difference of the result from these analysis methods is possible to happen considering that are qualitative methods based on the presence or absence of the taxa, but treated in different ways. It is also possibly related to the numbers of taxa included in the analysis. Only rodents are used for the bioclimatic model analysis while in mutual ecogeographic range insectivores are also included. However, when the results are compared to other data, the result of habitat weighting and chorotype analysis for instance, the result of mutual ecogeographic range analysis fit better than of the bioclimatic model. Moreover, by the comparison to palynological data from Banyoles Lake where there were increases on the tree taxa after 15 ka BP (Pèrez-Obiol and Julià, 1994), the result from mutual ecogeographic range analysis also shows better consistency. Unfortunately, until the moment there are no other climatic or environmental proxies in the site to compare this work results, by which palynological and large mammal studies will probably provide interesting new information for the site.

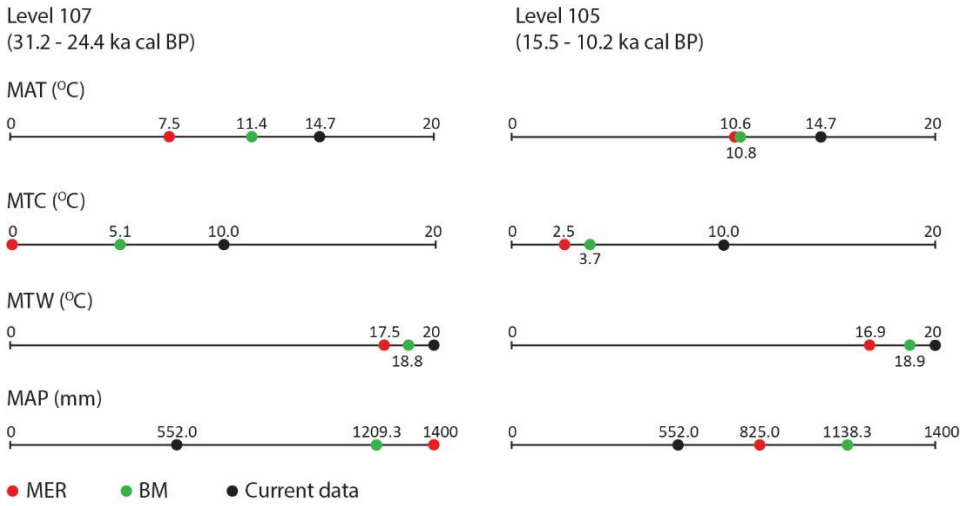

Figure 7.4. Comparison of the climatic variable on level 107 and 105 to the current condition of Cudó cave.

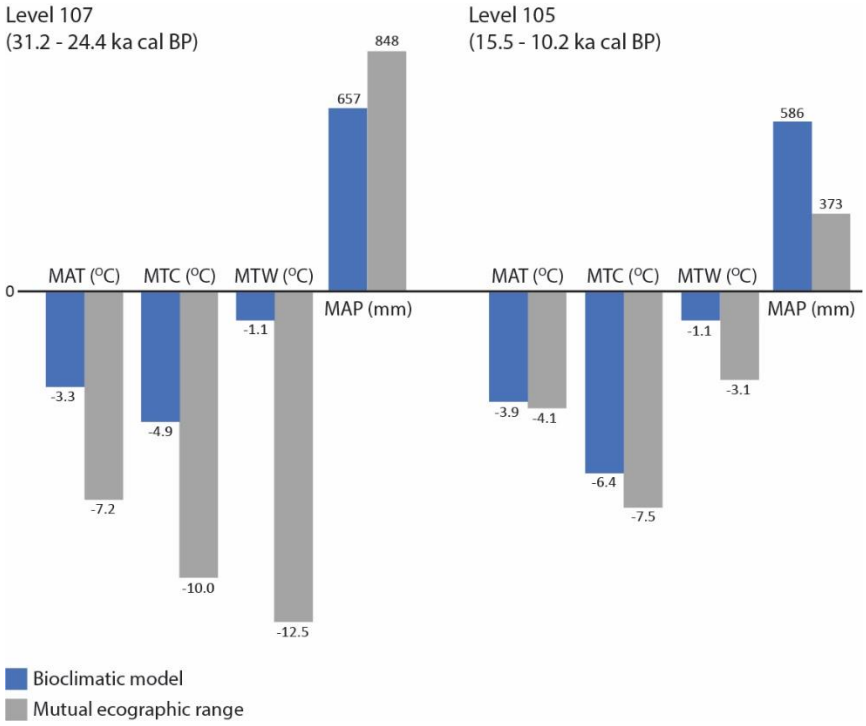

Figure 7.5. Comparison between the differences of some climatic variables during the archaeo-paleontological deposit formation acquired from the bioclimatic model and mutual ecogeographic range methods to the current data of both level 107 and 105 from Cudó cave. MAT, mean annual temperature; MTC, mean temperature on the coldest month; MTW, mean temperature on the warmest month; MAP, mean annual precipitation.

7.4. Paleoenvironment of northeastern Iberia and Prades Mountains during Late Pleistocene

Cudó cave is not the only site providing small mammal assemblage for the paleoenvironment inference in northeastern Iberia dated within the last 35000 years. Two other sites lie in the same mountain system and could add complementary information about the paleoenvironment of this region, which are Xaragalls cave and Galls Carboners. These sites are not exactly contemporaneous to Cudó cave. However, they provide additional information just before the Cudó cave assemblage.

Two layers that interesting from Xaragalls cave for its chronologically close to Cudó level 107 are C4 and C3, with 48.2 – 45.1 ka BP for layer C4 and possibly younger than 45 ka BP for layer C3 (López-García et al., 2011; Vallverdú et al., 2012). Paleoenvironmental inferences from these two layers shows domination of woodland covers and mid-European climatic condition (chorotype 1 and 2) (López-García et al., 2011). From the small mammal remains, it is indicated by a considerable amount of *Microtus agrestis* and also a noticeably high abundance of *Apodemus sylvaticus*. Compared to the Cudó assemblages, both layer C4 and C3 shows higher proportion of woodland landscape compared to level 107 and roughly similar to 105 of Cudó cave. Otherwise, the climatic inference shows that the proportion of species from chorotype 1 and 2 of Xaragalls cave is lower than in Cudó level 107 (Figure 7.6). In addition, by the MAT, Xaragalls layer C4 was likely warmer than Cudó level 107 but still colder than Cudó level 105, while Xaragalls layer C3 was warmer than Cudó level 105 (Figure 7.7).

Moreover, the assemblage from Galls Carboners, dated to ca. 31.3 – 31.1 ka cal BP (López-García et al., 2014a) could be even more interesting as it contemporaneous to the early stage of Cudó level 107, apart from the close geographic proximity. However, the habitat and

chorotype inferences show different pattern than what it inferred from Cudó level 107. This level represents an exceptional cold and wet event with the lowest woodland habitat and highest proportion of rocky habitat, contrast to the condition in Galls Carboners which dominated by woodland. In the species composition, Cudó level 107 shows strong dominance of mid-European species (81.9%) with the lowest Mediterranean taxa (17.8%), while in Galls Carboners only 55% of the assemblage composed by mid-European species and 45% of the assemblage are Mediterranean taxa. The big difference also can be seen in the MAT and MAP data where Cudó level 107 has lower temperature (3.5°C difference) and significantly higher precipitation (411mm difference) than Galls Carboners (Figure 7.7).

The difference between the MAT and MAP of Cudó level 107 and Galls Carboners is interesting since these two sites are located in very close proximity, in similar elevation (around 1000 m.a.s.l), and chronologically overlapping. Taphonomical biases cannot be rejected as the cause of this differences, although the opportunistic predators are considered as the main accumulator of the assemblages from both sites, but further research is recommended to evaluated the real influence. Nevertheless, even if the predatory selection played a major role during the accumulation, the significant difference of mid-European taxa of both assemblages become clear evidence of different environmental conditions. Also, the ecological changes between level 107 to 105 are not accompanied by the change of taphonomical pattern, thus these changes can be significant.

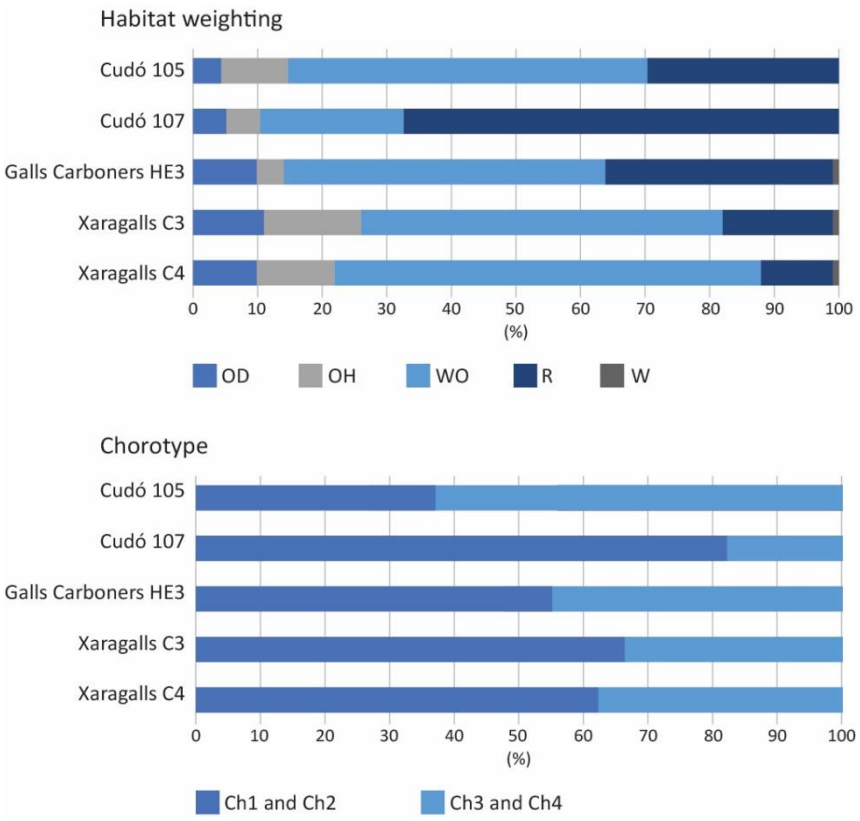

Figure 7.6. Chorotype and habitat comparison between Cudó level 107 and 105 with Galls Carboners (López-García et al., 2014a) and Xaragalls level C4 and C3 (López-García et al., 2011).

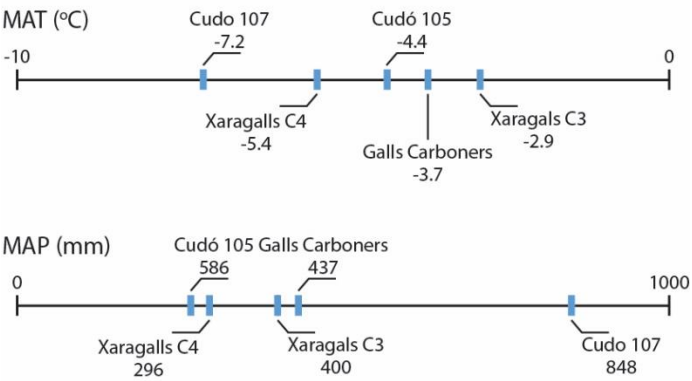

Figure 7.7. Comparison of the difference of mean annual temperature (MAT) and mean annual precipitation (MAP) between Cudó level 107 and 105 with Galls Carboners (López-García et al., 2014a) and Xaragalls level C4 and C3 (López-García et al., 2011). The data based on mutual ecogeographic range (MER) analysis result and in respect to current data from the nearest climatic station of each site.

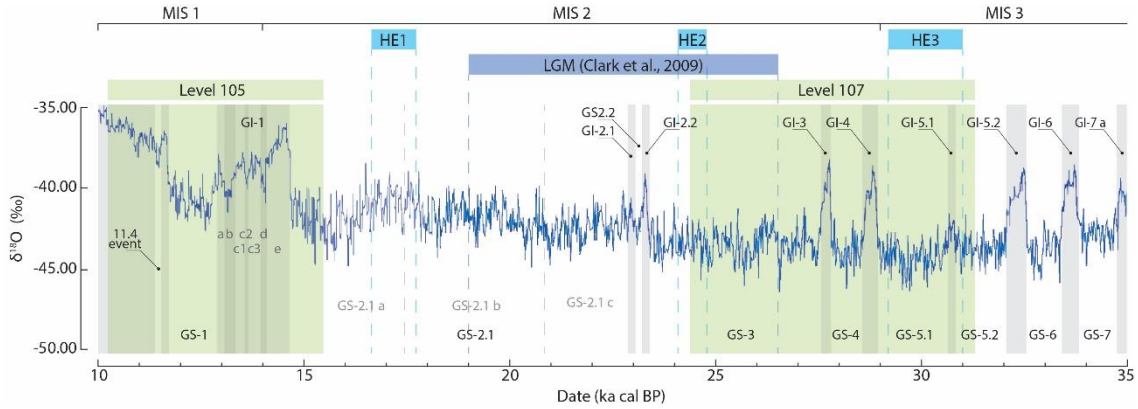

Figure 7.8. Chronological position of level 107 and 105 of Cudó cave among the global climatic events (modified from Maier et al., 2021 and Rasmussen et al., 2014)

The probable reason is that the Galls Carboners assemblages are only correspond to the short chronological period, which are coinciding to the beginning of the HE3. Despite the Heinrich Events known to have severe climatic conditions, most of these events could be divided into three stages based on the different climatic conditions, which are the early, main, and late stage. During the HE3, the early stage was not so severe, indicated by the at least the sea surface temperature (e.g., Cacho et al., 2001; 2006) and the palynological records (e.g., Fletcher and Sánchez Goñi, 2008). The less harsh climate maintains the higher proportion of Mediterranean taxa with woodland habitat preferences. In contrast, level 107 of Cudó cave, which represent the coldest yet most humid period, spans longer chronological period, including the whole HE3 and the beginning of HE2 and LGM (Figure 7.8). The later stage of level 107 might also coincide with the early stage of glaciers expansion in the southern latitude (e.g., Lewis et al., 2009; Moreno et al., 2012). With this expansion and considering the high altitude, snow covers could possibly present in the vicinity of Cudó during the major part of the year. Which consequently increase the abundance of mid-European taxa with rocky habitat preferences and demonstrate the importance of glacial deposit extension in high altitudes even in Mediterranean-affected environments that generally were experiencing milder conditions.

The exceptionally cold and wet condition of level 107 which probably related to HE3 or HE2 when the cold summer and humid winter conditions was experienced are apparently different with the previous HE4 event. The HE4 event, which recorded in Xaragalls C4 also in Els Canyars level MLU, are distinctively warmer and drier than what recorded in Cudó level 107, even though in all these three sites located in the Mediterranean-affected region. Furthermore, if Cudó level 107 compared to Arbreda level C (23.5 – 22.9 ka cal BP), Cudó level 107 still colder and significantly wetter than Arbreda level C. These discrepancies could be linked to the geographic condition where Cudó cave situated. The mountainous relief with elevation reaching 1000 m.a.s.l. could give this colder condition in level 107. Even though, the domination of mid-European taxa in Arbreda level C become evidence of the cold and humid climate after the HE2 and during the LGM.

Otherwise, the Cudó level 105 is in line if compared to the other site in Northeastern Iberia. It is roughly similar to level CE-15 of Colomera cave (ca. 13 ka BP), where the mid-European taxa become the important group of the assemblage. The inferred habitat also dominated with woodland (54%) and a quite high proportion of rocky habitat (24%). The climatic improvement also observed in Toll cave, from roughly equal proportion of mid-European and Mediterranean taxa in level 3 (ca. 47.1 – 45.5 ka cal BP) become dominated by Mediterranean taxa in level 2. Unfortunately, there is no absolute date assigned to this level to build a better correlation.

Thus, the small mammal assemblage of level 105 clearly indicates a climatic improvement compared to level 107. This is particularly showed by the decreasing mid-European taxa and the increasing woodland habitat. However, this improvement is not exceptional if the older assemblages from Muntanyes Prades are considered. The increasing Mediterranean taxa is not so much different from the Xaragalls C4, C3, and particularly the Galls Carboners assemblage. The woodland and open humid habitat composition even shows more similarities. Interestingly, the rocky habitat appears with bigger proportion in Cudó level 105 than the Xaragalls C4 and C3 assemblages. This pattern could be related to several abrupt climatic events such as Older Dryas (GI-1d) and Inter-Allerød Cold Period (GI-1b) (Figure 7.8).

8. CONCLUSIONS

Terrestrial proxies and records add knowledge of our understanding on how the climatic fluctuation in the past affects the continental environment. Despite its importance, the continental paleoenvironmental records are sparsely distributed and rarely provide a long continuous record. Particularly on northeastern Iberia during the Late Pleistocene, specifically around the LGM, there are few continental records identified yet. In this term, small mammal assemblage from Cudó cave which are presented in this work could add information and knowledge to understand on the climatic fluctuation around LGM in northeastern Iberia.

Cudó cave that belongs to the Prades Mountains system yielded two archaeo-paleontological stratigraphic levels, which are level 107 and 105. These two levels dated between 31.2 – 24.4 ka cal BP (level 107) and 15.5 – 10.2 ka cal BP (level 105), which coinciding to several climatic events of the Late Pleistocene. These two levels contain archaeological remains associated to Upper Paleolithic period, including lithic and faunal artefacts. Moreover, level 107 and 105 of Cudó cave are especially rich in small mammal remains. 1185 specimens were identified in this work corresponding to a minimum of 502 individuals have been analyzed, and 14 species have been identified, including *Crocidura russula*, *Sorex* gr. *araneus-coronatus*, *Rhinolophus* cf. *ferrumequinum*, *Myotis* gr. *myotis-blythii*, *Pipistrellus* cf. *pipistrellus*, *Microtus arvalis*, *Microtus agrestis*, *Microtus* gr. *arvalis*-agrestis, Microtus (*Terricola*) *duodecimcostatus*, *Microtus* (*Iberomys*) *cabrerae*, *Chionomys nivalis*, *Apodemus sylvaticus*, *Eliomys quercinus*, *Sciurus vulgaris*.

From the taphonomic analysis of Cudó cave assemblages, predatory activity has been identified as the main factor of the accumulation process. It is based on the traces left by this process such as digestive corrosion caused by the predator's digestive acid. This digestion marks appears in 42% of the remains in level 107 and 32.6% in level 105. Several species of predators could be linked to this considerable amount of digested remains, such as *Strix aluco, Athene noctua, Falco tinnunculus,* and *Circus cyaneus*. By considering the intensity digestion, by which heavy digestion remains appear with significant amount, it could be inferred that category 4 predators are the main accumulator agent to both levels. This includes as possible predators, all species previously mentioned in addition to *Falco tinnunculus and Falco perregrinus*.

Considering the hunting range of the predators, the small mammal assemblage could have been originating within the radius approximately 6.91km from the cave. Even inside this group of predators, opportunistic hunters prevailed, some tend to preferentially hunt in open landscape, and it should be taken into consideration. From the inspection on the digestion pattern in relation to the predator's categories of both levels, it is deduced that the climatic factors prevailed the taphonomic explanation. Apparently, the same type of predators was involved in the small mammal remains accumulation in both levels. Nevertheless, further research to reach the specific identification of the predatory group using complementary taphonomic analyses and other variables could give more information regarding the taphonomic history of the assemblages and the degree of environmental bias.

From the small mammal taxonomic identification, the paleoenvironmental condition surrounding of Cudó cave has been inferred. The level 107 shows a moderate level of diversity compromise by the predominance of *Chionomys nivalis*, a species which belongs to the mid-European requirements group (chorotype 1). The high abundance of this species also indicates

the predominance of rocky habitat as well as cool mean annual temperatures and high precipitation rates. This mean temperature and precipitation rate are significantly different from the current condition in the area. Such environmental pattern, together with the chronology proposed for this level, could be linked to the HE3 or HE2 as well as the beginning of LGM. It is contrast to the level 105, where the environment could have been more diverse with relatively low proportion of mid-European requirements taxa compared to Mediterranean taxa. The habitat also seems to be improved with the significant increase of woodland habitat following the decrease of rocky habitat. Furthermore, the mean annual temperatures and the precipitation rates also differs from the current condition. It could be an indicator of an environmental improvement in respect to the level 107.

In a regional perspective, the level 107 of Cudó cave appears to be the coldest and wettest compared to the neighboring and chronologically overlapping sites such as Galls Carboners as well as the chronologically older sites such as Toll cave level 3 and 4; Xaragalls level C4 and C3; Els canyars MLU; as well as Arbreda level B-C. Despite of the climatic improvement, level 105 shows that the environmental conditions were not exceptionally different compared to the other sites such as Colomera cave level CE-15, the upper level of Toll cave, as well to the older level of Xaragalls C4 and C3. It is indicated by the remarkable proportion of rocky habitat, the low temperature, and the high precipitation rates that are still maintained in this level. This pattern might correspond to several abrupt climatic events during the period of 15.5 – 10.2 ka cal BP, such as Older Dryas (GI-1d) and Inter-Allerød Cold Period (GI-1b).

Finally, those patterns observed in Cudó cave small mammal assemblages indicates several things. First, consistent to previously published works, the HE3 and HE2 was cold and humid period in northeastern Iberia, with several climatic condition than the HE4. Second, the environmental condition in this area could have been more diverse despite of the similar Mediterranean affected climate. Moreover, the environmental improvement after 15 ka as it seen in many studies does not appears so significant in all areas in all proxies. Instead, the climatic changes were responded differently depending on the proxies and the geographic area.

As final remarks, this work advice to enlarge the taphonomic study in order to complete the taphonomic characterization on the small mammal assemblages from this site and finally evaluate the ecological biases. With a similar goal, studies on other environmental proxies of Cudó cave, such as pollen, charcoal, or phytoliths analysis, large vertebrate studies, and the sedimentological analysis will be helpful to characterize the site. A better understanding on this site will be useful in a larger geographic scope than local studies, considering the scarcity of environmental data linked to LGM context in northeastern Iberia.

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