This is a preprint version of a Published Work that appeared in final form in Quaternary Science Reviews 19 : 106-115 (2015). To access the final edited and published work see https://doi.org/10.1016/j.quascirev.2015.04.017

The return to the Iberian Peninsula: first Quaternary record of *Muscardinus* and a palaeogeographical review of the genus in Europe.

Naroa GARCIA-IBAIBARRIAGA [a, b] *, *Álvaro ARRIZABALAGA* [a], *María-José IRIARTE-CHIAPUSSO* [a, c], *Juan ROFES* [d], *Xabier MURELAGA* [b]

a Dpto. Geografía, Prehistoria y Arqueología, Universidad del País Vasco UPV/EHU, C/ Tomás y Valiente s/n, 01006 Vitoria-Gasteiz, Spain.

b Dpto. Estratigrafía y Paleontología, Universidad del País Vasco UPV/EHU, Barrio Sarriena s/n, 48940 Leioa, Spain.

c IKERBASQUE, Basque Foundation for Science, 48011 Bilbao, Spain.

d) UMR 7209, CNRS, « Archéozoologie, Archéobotanique » MNHN CP56, 55 rue Buffon 75005, Paris, France.

Abstract

Although the earliest record of the genus *Muscardinus* dates from the Middle Miocene in Spain, no mention has been reported for a period since the Lower Pliocene in the Iberian Peninsula. For the first time, Quaternary fossil remains of a hazel dormouse (*Muscardinus avellanarius*) are described in the Iberian Peninsula, with this also being the westernmost record of the genus in the Eurasian continent. The fossils, two second upper molars and a first upper molar, come from Lezetxiki II Cave, an early Late Pleistocene site in northern Spain. The presence of the hazel dormouse is in agreement with the abundance of rodent species indicative of woodland, suggesting mild climatic conditions and a landscape formed by deciduous forest. This assemblage has been arguably assigned to warm and humid conditions associated with an interstadial period in MIS 5. We also present an analysis of the palaeogeography of the genus in Europe. The identification of this dormouse reinforces the idea of natural connections between western Iberia and the rest of Europe during the Pleistocene.

Corresponding author:
Naroa Garcia-Ibaibarriaga
Dpto. Geografía, Prehistoria y Arqueología, Universidad del País Vasco UPV/EHU, C/ Tomás y Valiente s/n, 01006 Vitoria-Gasteiz, Spain
naroa.garcia@ehu.eus

Keywords: *Muscardinus avellanarius*; Palaeogeography; Palaeoecology; Upper Pleistocene; Lezetxiki II; Iberian Peninsula.

1. Introduction

As pointed out by Bright et al. (1996a, p. 9), the dormouse is widely known from its appealing photographs and its occurrence in children's story books, notably *Alice's Adventures in Wonderland*. However, compared with current knowledge, little is known about the fossil record of *Muscardinus*.

The fact is that the dental remains of *Muscardinus* are somewhat rare in Pleistocene sites. Chaline (1972) proposes that its rarity, probably more apparent than real, is partly due to the smallness of the teeth, which easily go unnoticed in a sieve. Meanwhile, Hanquet (2011) argued that it can be explained by the scarcity of this species in nature. However, as noticed by Daoub (1993), the frequency of glirids found in some fossil assemblages, especially at the end of the Early Pleistocene, is often very high, although they may have suffered a decline during the Late Quaternary. Additionally, it should be borne in mind that the hazel dormouse is one of the smallest of the European dormice, with an estimated body mass of 25g (Freudenthal and Martín-Suárez, 2013a), besides being a nocturnal arboreal species rarely active on the ground and difficult to prey on (Capizzi et al., 2002).

In the present study, we describe one first upper cheek tooth (M1) and two second upper cheek teeth (M2) from the early Late Pleistocene archaeological site of Lezetxiki II (Basque Country, North Spain). This discovery represents the first Quaternary record of *Muscardinus avellanarius* in the Iberian Peninsula, and also the westernmost record of the genus in the Eurasian continent.

Lezetxiki II is an important site in the Basque Country and the Cantabrian coast. To date, it has yielded a notable amount of small vertebrate fossils that document the richness of Upper Pleistocene biomes of northern Spain. The first description of a hazel dormouse from this site contributes to the general knowledge of this taxon, and an updated review of the palaeogeographical evolution of the genus in Europe will be certainly useful for future research. This discovery also contributes to a better understanding of the palaeoecology and palaeobiogeography of the area during the Late Pleistocene, and provides information about movements of mammals between Iberia and the rest of Europe.

2. Lezetxiki II Cave

Lezetxiki (Arrasate, Basque Country) is a karst complex located in the central sector of northern Iberia (Fig. 1), in the upper valley of the River Deba, near the end of the Bay of Biscay. The classic deposit of Lezetxiki was first excavated from 1956 to 1968 by J.M. de Barandiarán, and an extensive sequence of Late Pleistocene levels was revealed. Three human fossil remains were also recovered, namely, two Neanderthal teeth from Level II and a humerus from Level VIII, provisionally dated to MIS 6 (Arrizabalaga, et al., 2005). In 1996, excavations were restarted by A. Arrizabalaga and M.J. Iriarte using updated methodology (Arrizabalaga, 2006, 2005), in order to provide a better context for the human fossils and other finds. The new research has been carried out on the southern side of the classic deposit and in the neighbouring cave of Lezetxiki II. This latter site has provided a *ca.* 3 m deep sedimentary sequence (Levels A-K) and is physically connected with Lezetxiki precisely in the place where the human humerus was found, providing its probable stratigraphic context. Scarce archaeological remains have been recorded in both caves, mainly rough flakes made of raw materials other than flint, i.e., limonite, quartzite, lutite, vulcanite and even limestone (Arrizabalaga, 2005).

(INSERT FIGURE 1 HERE)

On the contrary, the mammal materials from this locality include the first fossil record in the Cantabrian region of *Allocricetus bursae* and the south-westernmost record of *Sicista betulina* in Eurasia (Rofes et al., 2012), as well as the first fossil remain of *Macaca sylvanus* of the Cantabrian region, which is one of the most recent macaques across Europe (Castaños et al., 2011). The first record of wolverine (*Gulo gulo*) in the Iberian Peninsula also came from Lezetxiki (Altuna, 1973).

A Th/U date of 74 ka BP (Falguerès et al., 2006), obtained for a speleothem located about 100 cm above the position of the *Muscardinus* molars, is the primary reference to interpret the geochronology of the infill at Lezetxiki II. Consequently, the *Muscardinus* remains from Level G have a minimum date of the very last phase of MIS 5. This result is in accordance with the sedimentological analysis carried out by Arriolabengoa et al. (2014), which specifies that the variations in the sediment composition between levels with a predominance of allochthonous and autochthonous materials may result from repeated environmental changes in the interestadials that characterized MIS 5.

The preliminary results of the palynological study have not provided information about the vegetation in this period, due to poor spore and pollen conservation. In addition, reference deposits for MIS 5 in northern Spain are located in the western coastal area (Gómez-Orellana, 2002; Gómez-Orellana et al., 2007), and are lacustrine deposits with very different biogeographical characteristics from Lezetxiki II. Even so, there is no complete picture of the events in this isotope stage, only of certain times in Phases 5c (Longa Area, Galicia) and 5a (La Franca, Asturias). Both temperate phases are characterised by extensive forest cover (arboreal pollen >60%), with such mesophilic and thermophilic species as *Quercus robur* tp., *Corylus*, *Betula* and *Fagus*, as well as *Carpinus* and *Myrica*. In the periods of climate deterioration (MIS 5d and 5b) identified in other records in the southern Europe, the herbaceous-shrub species spread to the detriment of woodland (Pons and Reille, 1988; Burjachs i Casas, 1990).

The faunal association from the studied level is given in Table 1. Due to the scarcity and lack of identifiable remains among the large mammal association (25 identifiable remains from 134 NR) they cannot be used as a palaeoclimate indicator (Villaluenga et al., 2012). In contrast, the small vertebrate assemblage comprises at least 21 taxa, suggesting a patchy landscape dominated by wet meadows and woodland areas, with the presence of water sources in the vicinity of the cave.

(INSERT TABLE 1 HERE)

3. Material and methods

Level G at Lezetxiki II, at the entrance of the cave, yielded the *Muscardinus* molars at a depth of approximately -225cm below the current cave datum level. The sediment from at least 0.3 m^2 of all the stratigraphic units in the M13 quadrant was extracted during sampling for small vertebrate remains. The sediment was water-screened using a stack of sieves of decreasing mesh size (4 mm-0.5 mm). Subsequently, the fossils were separated from the concentrates, classified and studied with a stereoscopic microscope (Nikon SMZ-U).

The specific assignment of the fossil remains to *Muscardinus avellanarius* was based on diverse bibliographic support (Couzi, 2011; Rolland, 2008). For the nomenclature used in the description of the teeth (see Figure S1 in the Supplementary Online Information), we follow Daams (1981). The orientation of the specimens is as defined by García-Alix et al. (2008), and the method of counting series of parallel ridges, from front to back was performed after van den Hoek Ostende (2003). The taxonomic classification follows Wilson and Reeder (2005). Measurements were taken as defined by Daams (1981) (see Figure S1 in the Supplementary Online Information) using a stereoscopic microscope (Nikon SMZ-U) connected to a video camera (DS-5 m). Scanning electron microscopy was performed using a JEOL JSM-5400 Scanning Electron Microscope (SEM) at the University of the Basque Country (EHU/UPV), which belongs to the General Research Services (SGIKER).

Bivariate comparative analyses were performed by plotting the length against the width of several recent and Pleistocene hazel dormice dimensions (see Table S1 in the Supplementary Online Information). We have also used univariate plots for better characterisation of the incomplete left M2 from Lezetxiki II. Statistical analyses and graphics were performed in the R statistical environment (R Development Core Team, 2014).

4. Systematic Palaeontology

Order RODENTIA Bowdich, 1821

Family GLIRIDAE Muirhead, 1819

Subfamily LEITHIINAE Lydekker, 1895

Genus *Muscardinus* Kaup, 1829

Muscardinus avellanarius Linnaeus, 1758

(Fig. 2)

(INSERT FIGURE 2 HERE)

Stratigraphic range of the genus

From the Middle Miocene (European Mammal Neogene Zone 6, MN6; Serravallian) to the present day.

Studied Locality and Horizon

Lezetxiki II (Arrasate, Basque Country, North Iberian Peninsula); Basque-Cantabrian Basin, early Late Pleistocene (MIS 5)

Material and Measurements

Measurements (length x width) are given in 0.1 millimetres units. See Table 2

(INSERT TABLE 2 HERE)

Distribution: For the geographic distribution in the Iberian Peninsula since the Miocene (with a few references for the Pliocene) see Fig. 3, with a detailed list of sites and countries in Table 3. Fig. 4 and Table 4 are dedicated to the distribution of the genus in the European subcontinent during the Early, Middle and Late Pleistocene.

4.1 *Description of the material*

M1: the degree of wear does not allow a precise interpretation. The molar, with a flat occlusal surface, is much longer than wide. There are five transverse enamel crests, separated by broad valleys. It is not possible to confirm if the ridges are lingually connected by an endoloph or not. No accessory ridges have been identified. The anteroloph and protoloph (first and second ridges respectively) are straight, oblique, lingually more backward than labially. The valley between the protoloph and mesoloph is wide, but it narrows towards the labial side. The metaloph and posteroloph are approximately parallel to the axis of the tooth.

M2: The dental pattern of this molar is difficult to observe due to the poor preservation of the teeth, which are fragmented. The outline of the occlusal surface is sub-square, with seven narrow transverse low ridges. The ridges, longitudinally lingually connected by an endoloph, are approximately straight. The third ridge is interrupted in both specimens.

5. Palaeogeographical evolution in Europe

The current distribution of dormice in Europe, including *M. avellanarius*, is well-known from the literature, including studies in Croatia (Tvrtković et al., 1994), Czech Republic (Anděra, 1994), Denmark (Vilhelmsen, 2003), Germany (Büchner, 2007), Great Britain (Bright et al., 1996), Hungary (Hecker et al., 2003), Italy (Amori et al., 1994), Lithuania (Juškaitis, 2003) and the Netherlands (Foppen et al., 2002), among others. In contrast, the distribution in the Pleistocene is limited to what can be inferred from isolated reports and major site compilations (e.g. Jánossy, 1986; Kowalski, 2001; Marcolini, 2003; Nadachowski, 1990; Socha, 2014; Terzea, 1994). No detailed analysis of the palaeogeography of the genus has been carried out.

In addition, the origin of the genus remains unclear. While Daams and De Bruijn (1995) proposed *Glirudinus* as the ancestor of *Muscardinus*, Aguilar and Lazzari (2006) considered that *Muscardinus* migrated from Iberian Peninsula to Europe at the MN4/MN5 transition (García-Alix et al., 2008). From the Late Miocene onwards, diverse lineages and species emerge in Europe. The *Pentaglis*, named by Kretzoi (1943) and *Eomuscardinus*, the new subgenus of *Muscardinus* described by Hartenberg in 1966, were synonymized with *Muscardinus* by Daams and Bruijn (1995). *Muscardinus avellanarius* is the only extant representative of the genus (Mammalia, Rodentia, Gliridae).

The first record of the genus (Daams, 1985), namely *Muscardinus thaleri*, is from the Middle Miocene (MN4B) in Spain. Nevertheless, according to Aguilar and Lazzari (2006) the first reliable evidence of *Muscardinu*s genus comes from MN4/5 at Blanquatère 1, described as *Muscardinus sansaniensis* (Lartet, 1851). Freudenthal and Martín-Suárez (2013b) object to this and consider that “the fauna (of Blanquetère 1) is a mixture of various ages and that the genus does not appear before MN6”. During the Miocene the genus presents a restricted distribution in the south of the Iberian Peninsula (Fig. 3), without ever going further north than the Ebro Basin (Tarazona-3; Álvarez-Sierra et al., 2006).

(INSERT FIGURE 3 HERE)
(INSERT TABLE 3 HERE)

The dormice underwent a significant radiation from the Iberian Peninsula during the Miocene (i.e., in the early Vallesian, Late Miocene according to Agustí, 1990), probably favoured by the warm climates of the epoch. Thereby, the genus was represented by *M. thaleri* in Spain and *M. sansaniensis* in France and Central Europe (Daams and De Bruijn, 1995).

In this context, according to published data (Sesé, 2006), dormice suffered a drastic reduction in the Catalan basins during the Upper Vallesian (MN 10), with only two genera surviving: *Muscardinus* and *Glis*. In the inland basins of the Iberian Peninsula, the only survivors of the loss of diversity during the Turolian (MN11-13) were *Muscardinus* and *Eliomys*. A late Miocene insular endemism, *Muscardinus cyclopaeus*, has been described on the island of Menorca (Agustí, 1990). Although the survival of the genus in the Iberian Peninsula during the Lower Pliocene should be corroborated by a more extended fossil assemblage, the latest fossil records attributed to the genus in the Iberian Peninsula are from the earliest Ruscinian (MN 14-15; Lower Pliocene) of Cantera de Pulianas Purcal-4 (where a new species, *Muscardinus meridionalis* was described; García-Alix et al., 2008), Cañada del Castaño (as *Muscardinus* cf. *pliocaenicus*; Agustí and Martín-Suárez, 1984) and Campredó (as *Muscardinus* aff. *vireti*; Agustí et al., 1983). Since then, neither living nor fossil hazel dormice have been recorded in the Iberian Peninsula, and therefore the species probably became locally extinct.

As regards the oldest reliable European finds of hazel dormouse, and in the absence of a consensus of scholars as to whether *Muscardinus dacicus* is a synonym of *Muscardinus avellanarius* (as proposed by Kowalski, 2001), we accept that they come from the Early Biharian (1.8-1.5 ma) of Kadzielnia-1 (Nadachowski, 1990a). In fact, during the Early Pleistocene the genus is concentrated in Eastern Europe (Fig.4A), although this lack of evidence could be more apparent than real. One of the few Mediterranean sites (Rivoli Veronese; Kotsakis et al. 2003) provided the single record of *Muscardinus pliocaenicus* in this period. The western limit of the expansion of the genus is marked by Vallonet (Maul, 1990), the single Early Pleistocene locality in France with remains of the genus. Meanwhile, the eastern range reached the sites of Chiscau and Subpiatra, both in Bihor Department, in Rumania (Kowalski, 2001; Maul, 1990).

(INSERT FIGURE 4 HERE)
(INSERT TABLE 4 HERE)

The situation during the Middle Pleistocene is quite different (Fig. 4B). The number of records decreases notably, from the 37 mentions in the previous period to the current 26. At the same time, the genus presents a wider distribution, expanding through central and southern Europe, although never further west than Charente Department (Fontéchevade site; Chaline, 1972). This is when the genus reaches its maximum limit of expansion eastwards, with the fossils from a cave in the Párului, in Rumania (Kowalski, 2001). Furthermore, the only finds of the genus in the United Kingdom are from the Boxgrove and Westbury-sub-Mendip sites, which are also the northernmost records for the genus. This time witnessed the extinction of other species in the genus except *Muscardinus* *avellanarius*, with a last record of *Muscardinus dadicus malvensis* from the site of Cave 10 in the Lupsa Valley (Kowalski, 2001).

According to the data, there is an underlying assumption that during the Late Pleistocene the species distribution suffered a latitudinal decline to below the 50° parallel (Fig. 4C), only surpassed by the mention of *Muscardinus avellanarius* from Pisede, in Germany (Kowalski, 2001). The increase in the number of Italian references for this period is remarkable, with the only Greek fossil from Loutraki Bear-cave (Chatzopoulou, K., 2001). There is a record of *Muscardinus malatestai* at the Italian site of Grotta Vascio ‘o Funno (Kotsakis, 2003), considered the descendant of *Muscardinus avellanarius*. However it should be treated with caution given that it is currently not an accepted species. The northernmost limit of hazel dormouse during the Late Pleistocene is Pisede; the southernmost , Cipolliane Cave (Kowalski, 2001); the westernmost, Lezetxiki II (this paper) and the easternmost Bacho Kiro (Kowalski and Nadachowski, 1982).

Nowadays, *M. avellanarius* is a widespread species, with a range that extends from Europe to northern Asia Minor, although in continental Europe it is absent from Iberia, south-west France, and northern parts of Fennoscandia and Russia (Amori et al., 2008).

6. Palaeoecological implications

The hazel dormouse, traditionally associated with hazel, occurs in a broad range of wooded habitats. Even if the majority of hazel dormouse sites include hazel, the forest composition is different in various parts of their geographic range depending on latitude and altitude; hence they can sometimes be found among other tree species, even conifers. Except for hibernation, they rarely descend to the ground and are reluctant to cross open spaces, surely due to the danger posed by owls and other predators (Bright et al., 1996). Even so, *Muscardinus avellanarius* can be regarded as a “woodland edge" animal, while they prefer to live in shrub layers full of undergrowth. A continuous shrub layer is ideal, especially where there are a few larger canopy trees. Its presence is indicative of temperate climate and humid forested environments.

From a palaeoecological point of view, the presence of the hazel dormouse in Level G in Lezetxiki II Cave, together with the abundance of rodent species indicative of deciduous forest, warmer and moist environments (such as *Apodemus sylvaticus-flavicollis, Eliomys quercinus, Pliomys lenki* and *Clethrionomys glareolus*) and the absence of strictly cold species, suggest a landscape of deciduous forest with the presence of open areas, and mild climatic conditions.

Some characteristics in common with the record from Lezetxiki II can be found at the French site of Baume Mola-Guercy (Defleur et al., 2001). The levels corresponding to the MIS 5 present a similar small mammal assemblage, with a high percentage of forest species.

7. Discussion

Dormice are characterized by having brachydont cheek teeth, with quite low crowns and well-developed roots. The dental crown pattern consists of a set of varying numbers of primary and secondary transverse ridges of enamel on the occlusal surface (lophodont dentition). The position, length and number of these ridges enable the classification of the species. It is also possible to distinguish between upper and lower teeth. In the upper teeth the hind wall of the ridges slopes gently down and has transverse grooves while the front slope is steep and smooth (García-Alix et al. 2008).

The teeth from Lezetxiki II Cave resemble those in various recent and Pleistocene samples in overall size and morphology. In absolute terms, the width of the first upper molar is below the range of variation of most of the comparative samples (Fig. 5a), and is especially narrower than the mean value of 26 M1 from the Upper Pleistocene site of Arma delle Manie (Paunescu, 2001). However, it is within the range of variation of the Late Biharian (Calabrian) hazel dormouse remains from Kozi Grzbiet (Hoek Ostende, 2003).

(INSERT FIGURE 5 HERE)

In the case of the bivariate analysis of M2, we can only take into account the right M2 from Lezetxiki II (Figure 5b) due to the incompleteness of the one from the left side. Even if the assemblage of recent *Muscardinus avellanarius* from France (MNHN) also presents comparable values regarding the length, the most similar specimens are those from the Lower Pleistocene at Kozi Grzbiet. The width is below the range of variation of most of the samples except for the Lower Pleistocene specimens at Kozi Grzbiet.

The results of the univariate analysis of the two M2 lengths and their comparison are shown in Fig. 6. The most remarkable feature of the left M2 is its short length, while the incompleteness of the tooth means that it cannot be determined whether a similar pattern is observed in the width. In the latter case, the values are quite close to the minimum rate obtained from the MNHN assemblage. Right M2, in contrast, is close to the mean of the modern samples and the fossil sample from Kozi Grzbiet, but its value is below the range of variation of the Upper Pleistocene sample from Arma delle Manie.

(INSERT FIGURE 6 HERE)

This noticeable difference between the right and left M2 at Lezetxiki II, which exceeds the range of variation of any of the comparative samples, could have various explanations:

- The first is a probable sexual dimorphism, although no differences have been found between modern hazel dormouse sexes with respect to the presence and morphology of the bones.
- The second interpretation is based on the possibility that the left M2 belonged to an abnormally small individual, maybe pathological. This option seems improbable due to lack of morphological differences identified in the tooth.
- Another conceivable scenario is that the M2 presented in this work belongs to a subadult. One year-old dormice are larger in size than two to three months-old individuals (Juškaitis and Büchner, 2013).
- Finally, the justification could be biogeographical. This last supposition is based on Bergmann's rule: in a warm-blooded animal species having distinct geographic populations, individuals of larger size are found in colder environments, while animals of the same species living in warm climates are of smaller size. According to some recent research, the validity of this tendency in small mammals must be considered with caution (Ashton et al., 2000; Meiri and Dayan, 2003).

It is also remarkable that the width of the Lezetxiki specimens is similar to the Lower Pleistocene samples from Kozi and very different from the Upper Pleistocene samples from Arma delle Manie. Besides the aforementioned biogeographical explanation, another factor that may account for these differences is the chronology. It is known that the phylogenetic evolution of the *Muscardinus* lineage is expressed by a size increase and by a loss in the number of ridges in the cheek teeth (García-Alix et al., 2008), although once again, this tendency would not explain the pattern presented by the Lezetxiki II teeth.

8. Conclusion

The discovery of a hazel dormouse (*Muscardinus avellanarius*) is reported. One first upper molar and two second upper molars from the early Late Pleistocene site of Lezetxiki II (Arrasate, Basque Country, Spain) are described, indisputably attributed to *M. avellanarius* on the basis of diagnostic morphological and morphometric features.

The genus *Muscardinus* was reported in the fossil record of the Iberian Peninsula during the Miocene, probably becoming locally extinct after the Lower Pleistocene. Therefore these remains, represent the first Quaternary record in the Iberian Peninsula, and constitute the westernmost reference of the genus in the Eurasian continent, expanding its range of distribution beyond the Pyrenees.

Concerning the climate conditions during deposition in Lezetxiki II, the presence of hazel dormouse would be hypothetically linked to warm and humid conditions associated with an interstadial period of MIS 5. Today, hazel dormouse inhabits a wide variety of woody environments with a substantial shrub layer. A similar landscape composition is inferred by the small vertebrate association.

The criteria of dental pattern suggest that the teeth are within the range of variation of known Pleistocene and current species. However, the most complete dormouse teeth from Lezetxiki can be described as narrow when compared to modern comparative samples but within the range of variation in the Kozi Grzbiet Lower Pleistocene specimens.

The occurrence of a new faunal element during the Late Pleistocene at Lezetxiki II, added to the previous discoveries, supports the existence of connections between western Iberia and the rest of Europe during the Pleistocene. Correspondingly, the idea of the existence of geographical barriers that hindered the interchange of mammal groups, including humans, must be dismissed.

Acknowledgments

We would like to thank A. Gómez-Olivencia for his useful insights that improved this paper and Peter Smith for his assistance with the English editing. The technical and human support provided by SGIker (UPV/EHU) is also gratefully acknowledged. N. Garcia-Ibaibarriaga has a predoctoral fellowship (BFI-2010-289) from the Basque Government, while J. Rofes has a Marie Curie Action Project (MCA-IEF Project No. 629604) from the European Commission. The archaeological work in Lezetxiki was funded by Aranzadi Science Society, Gipuzkoako Foru Aldundia, the Municipality of

Arrasate and Kobate Quarry. We also received financial support from the Research teams GIU12/35 and IT-622-13 at the Universidad del País Vasco UPV-EHU.

References

Aguilar, J.-P., Agustí, J., Gibert, J., 1979. Rongeurs, miocenes dans le Valles-Penedes. Les rongeurs de Castell de Barbera. Palaeovertebrata 9, 17–31.

Aguilar, J.-P., Crochet, J.-Y., Krivic, K., Marandat, B., Michaux, J., Mihevc, A., Sigé, B., Šebela, S., 1998. Pleistocene small mammals from some karstic fillings of Slovenia. Preliminary Results. Acta Carsologica 27, 141–150.

Aguilar, J.-P., Lazzari, V., 2006. Nouvelles espèces de gliridés du gisement karstique de Blanquatère 1 (Miocène moyen, sud de la France). Geodiversitas 28, 277–295.

Agustí, J., 1990. The Miocene Rodent succession in Eastern Spain: A Zoogeographical appraisal, in: Lindsay, E.H., Fahlbusch, V., Mein, P. (Eds.), European Neogene Mammal Chronology. Plenum Pres, New York, pp. 373–404.

Agustí, J., Anadon, P., Julià, R., 1983. Nuevos datos sobre el Plioceno del Baix Ebre. Aportación a la correlación entre las escalas marina y continental. Acta Geológica Hispánica 18, 123–130.

Agustí, J., Casanovas-Vilar, I., Furió, M., 2005. Rodents, insectivores and chiropterans (Mammalia) from the late Aragonian of Can Missert (Middle Miocene, Vallès-Penedès Basin, Spain). Geobios 38, 575–583.

Agustí, J., Gibert, J., Moyá, S., Cabrera, L., 1979. Roedores e Insectivoros (Mammalia) del Mioceno superior de la Seu d'Urgell (Cataluña, España).pdf. Acta Geológica Hispánica 14, 362–369.

Agustí, J., Martín-Suárez, E., 1984. El Plioceno continental de la depresión Guadix-Baza (Prov. Granada) y su fauna de micromamíferos. Nota preliminar. Acta Geológica Hispánica 19, 277–281.

Alba, D.M., Moyà-Solà, S., Casanovas-Vilar, I., Galindo, J., Robles, J.M., Rotgers, C., Furió, M., Angelone, C., Köhler, M., Garcés, M., Cabrera, L., Almécija, S., Obradó, P., 2006. Los vertebrados fósiles del Abocador de Can Mata (els Hostalets de Pierola, l'Anoia, Cataluña), una sucesión de localidades del Aragoniense superior (MN6 y MN7+8) de la cuenca del Vallès-Penedès. Campañas 2002-2003 , 2004 y 2005. Estud. Geológicos 62, 295–312.

Altuna, J., 1973. Primer hallazgo del glotón (Gulo gulo L.) en la Península Ibérica. Munibe 15, 128.

Álvarez-Sierra, M.A., García Paredes, I., Peláez-Campomanes, P., 2006. Middle Miocene Rodents from the Tarazona Area (Ebro Basin, Spain). Beiträge zur Paläontologie 30, 5–13.

Amori, G., Cantini, M., Rota, V., 1994. Distribution and conservation of Italian dormice. Hystrix 6, 331–336.

Amori, G., Hutterer, R., Kryštufek, B., Yigit, N., Mitsain, G., Meinig, H., Juškaitis, R., 2008. Muscardinus avellanarius. The IUCN Red List of Threatened Species. Version 2014.3.

Anděra, M., 1994. The present status of dormice in the Czech Republic. Hystrix 6, 155–160.

Andrews, P.J., 1990. Owls, Caves and Fossils, The South African Archaeological Bulletin. Natural History Museum Publications, London.

Arriolabengoa, M., Iriarte, E., Aranburu, A., Yusta, I., Arrizabalaga, A., 2014. Provenance study of endokarst fine sediments through mineralogical and geochemical data (Lezetxiki II cave, northern Iberia). Quat. Int. 1–13.

Arrizabalaga, A., 2005. Las primeras ocupaciones humanas en el Pirineo Occidental y Montes Vascos. Un estado de la cuestión en 2005. Munibe 57, 53–70.

Arrizabalaga, A., 2006. Lezetxiki (Arrasate, País Vasco). Nuevas preguntas hacerca de un antiguo yacimiento., in: Cabrera Valdés, V., Bernaldo de Quiros Guidotti, F., Maíllo Fernández, J.M. (Eds.), En El Centenario de La Cueva de El Castillo: El Ocaso de Los Neandertales. Centro Asociado de la UNED en Santoña, pp. 293–309.

Arrizabalaga, A., Altuna, J., Areso, P., Falguerès, C., Iriarte-Chiapusso, M.-J., Mariezkurrena, K., Pemán, E., Ruiz-Alonso, M., Tarriño, A., Uriz, A., Vallverdú, J., 2005. Retorno a Lezetxiki (Arrasate, País Vasco): nuevas perspectivas de la investigación, in: Santonja, M., Pérez-González, A., Machado, M.J. (Eds.), Geoarquelogía Y Patrimonio En La Península Ibérica Y El Entorno Mediterráneo. ADEMA, Madrid, pp. 81–91.

Ashton, K.G., Tracy, M.C., Queiroz, A. De, 2000. Is Bergmann’s Rule Valid for Mammals? Am. Nat. 156, 390–415.

Bertolini, M., Fedozzi, S., Martini, F., Sala, B., 1996. Late glacial and holocene climatic oscillations inferred from the variations in the micromammal associations at Grotta della Serratura. Quat. Ital. J. Quat. Sci. 9, 561–566.

Bogićević, K., Nenadić, D., Mihailović, D., Lazarević, Z., Milivojević, J., 2011. Late Pleistocene rodents (Mammalia: Rodentia) from the Baranica cave near Knjaževac (Eastern Serbia): systematics and palaeoecology. Riv. Ital. di Paleontol. e Stratigr. 117, 331–346.

Bon, M., Piccoli, G., Sala, B., 1991. I giacimenti quaternari di vertebrati fossili nell'Italia nord-orientale. Mem. di Sci. Geol. dell'Università di Padova 43, 185–231.

Bright, P., Morris, P., Mitchell-Jones, T., 1996a. The dormouse conservation handbook. English Nature., Peterborough.

Bright, P., Morris, P.A., Mitchell-Jones, A.J., 1996b. A new survey of the dormouse Muscardinus avellanarius in Britain, 1993–4. Mamm. Rev. 26, 189–195.

Büchner, S., 2007. Die Haselmaus in Hessen. Verbreitung, Nachweismethoden and Schutzmassnahmen. Gießen: Hessen-Forst FENA, FB Naturschutz.

Burjachs i Casas, F., 1990. Evolició de la Vegetació i paleoclimatologia desde fa més de 85.000 anys a la regió d'Olot. Anàlisi pollínica del Pla de l'Estany (Sant Joan les Fonts, la Garrotxa). Vitrina 5: 39-46.

Capizzi, D., Battistini, M., Amori, G., 2002. Analysis of the hazel dormouse, Muscardinus avellanarius , distribution in a Mediterranean fragmented woodland. Ital. J. Zool. 69, 25–31.

Casanovas-Vilar, I., Alba, D.M., Robles, J.M., Moyà-Solà, S., 2011. Registro paleontológico continental del mioceno de la cuenca del Vallès-Penedès, in: Pérez de los Ríos, M., Marigó, J., Minwer-Barakat, R., Bolet, A., DeMiguel, D. (Eds.), Guía de Campo XXVII Jornadas de La Sociedad Española de Paleontología. Institut Català de Paleontologia Miquel Crusafont, Sabadell, pp. 55–80.

Castaños, P., Murelaga, X., Arrizabalaga, A., Iriarte-Chiapusso, M.-J., 2011. First evidence of Macaca sylvanus (Primates, Cercopithecidae) from the Late Pleistocene of Lezetxiki II cave (Basque Country, Spain). J. Hum. Evol. 60, 816–20.

Chaline, J., 1972. Les Rongeurs du Pléistocène Moyen et Supérieur de France (Systématique, Biostratigraphie, Paléoclimatologie). Cahiers de Paléontologie. Ed. C.N.R.S. Paris.

Chaline, J., 1983. Les rongeurs, les paléoenvironnments et les climats du Pléistocène Moyen de Vergranne (Doubs). Géologie 5, 31–45.

Chaline, J., Brunet-Lecomte, P., Campy, M., 1995. The last glacial/interglacial record of rodent remains from the Gigny karst sequence in the French Jura used for paleoclimatico and paleoecological reconstrucions. Palaeogeogr. Palaeoclimatol. Palaeoecol. 117, 229–252.

Chatzopoulou, K., Vasileiadou, A., Koliadimou, K., Tsoukala, E., Rabeder, G., Nagel, D., 2001. Preliminary report on the Late Pleistocene small mammal fauna from the Loutraki Bear-cave (Pella, Macedonia, Greece). Cad. do Lab. Xeolóxico Laxe 26, 485–495.

Couzi, L., 2011. Identifier les petits mammifères non-volant Erinaceomorpha, Soricomorpha, Rodentia d'Aquitaine. LPO, Aquitaine/www.faune-aquitaine.org.

Daams, R., 1981. The dental pattern of the dormice Dryomys, Myomimus, Microdyromys and Peridyromys. Ultrecht Micropaleontological Bulletins.

Daams, R., 1985. Glirinae (Gliridae, Rodentia) from the type area of the Aragonian and adjacent areas (provinces of Teruel and Zaragoza, Spain). Scr. Geol. 77, 1–20.

Daams, R., De Bruijn, H., 1995. A Classification of the Gliridae (Rodentia) on the basis of the dental morphology. Hystrix 6, 3–50.

Daoub, A., 1993. Evolution of Gliridae (Rodentia, Mammalia) in the Pliocene and Quaternary of Poland. Acta Zool. cracoviensia 36, 199–231.

Defleur, A., Crégut-Bonnoure, E., Desclaux, E., Thinon, M., 2001. Présentation paléo-environnementale du remplissage de la Baume Moula-Guercy à Soyons (Ardèche): implications paléoclimatiques et chronologiques. Anthropologie. 105, 369–408.

Desclaux, E., Defleur, A., 1997. Étude préliminaire des micromammifères de la Baume Moula-Guercy à Soyons (Ardèche, France). Systématique, Biostratigraphie et Paléoécologie. Quaternaire 8, 213–223.

Dimitrijević, V., 1996. Upper Pleistocene mammals from cave deposits in Serbia. Acta Zool. cracoviensia 39, 117–120.

Falguerès, C., Yokoyama, Y., Arrizabalaga, A., 2006. La geocronología del yacimiento pleistocénico de Lezetxiki (Arrasate, País Vasco). Crítica de las dataciones existentes y algunas nuevas aportaciones. Munibe 57, 93–106.

Foppen, R., Verheggen, L., Boonman, M., 2002. Biology, status and conservation of the hazel dormouse (Muscardinus avellanarius) in the Netherlands. Lutra 45, 147–154.

Freudenthal, M., Martín-Suárez, E., 2013a. Estimating body mass of fossil rodents. Scr. Geol. 145, 1–130.

Freudenthal, M., Martín-Suárez, E., 2013b. New ideas on the systematics of Gliridae (Rodentia, Mammalia). Spanish J. Palaeontol. 28, 239.252.

García-Alix, A., Minwer-Barakat, R., Martín-suárez, E., Freudenthal, M., 2008. Muscardinus meridionalis sp. nov., a new specird of Gliridae (Rodentia, Mammalia) and its implications for the phylogeny of Muscardinus. J. Vertebr. Paleontol. 28, 568–573.

Gibbard, P.L., West, R.G., Zagwijn, W.H., Balson, P.S., Burger, A.W., Funnell, B.M., Jeffery, D.H., Kolfschoten, J.D.J.T. Van, Lister, A.M., Meijer, T., Norton, P.E.P., Preece, R.C., Rose, J., Stuart, A.J., Whiteman, C.A., Zalasiewicz, J.A., 1991. Early and Early Middle Pleistocene correlations in southern north Sea Basin. Quat. Sci. Rev. 10, 23–52.

Gómez-Orellana, L., 2002. El último Ciclo Glaciar-Interglaciar en el litoral del NW ibérico: Dinámica climática y paisajística. PhD thesis, University of Santiago de Compostela, Lugo, Spain.

Gómez-Orellana, L., Ramil-Rego, P., Muñoz Sobrino, C., 2007. The Würm in NW Iberia, a pollen record from Area Longa (Galicia). Quat. Res. 67, 438-452

Hanquet, C., 2011. Evolution des paléoenvironnements et des paléoclimats au Pléistocène moyen, en Europe méridionale, d'après les faunes de micromammifères. Université Montpellier III-Paul Valéry.

Hecker, K., Bakó, B., Csorba, G., 2003. New data on the distribution of the Hungarian dormouse species (Gliridae). Állattani Közlemények 88, 57–67.

Hernández Fernández, M., 2000. Análisis paleoecológico y paleoclimático de las sucesiones de mamíferos del Plio-Pleistoceno Ibérico.

Hoek Ostende, L.W. van den., 2003. Gliridae (Rodentia, Mammalia) from the Upper Pliocene of Tegelen (province of Limburg, The Netherlands). Scr. Geol. 126, 203–215.

Jánossy, D., 1986. Pleistocene Vertebrate faunas of Hungary. Elsevier, Amsterdam.

Juškaitis, R., 2003. New data on distribution, habitats and abundance of dormice (Gliridae) in Lithuania. Acta Zool. Acad. Sci. Hungaricae 49, 55–62.

Juškaitis R., Büchner S., 2013. The hazel dormouse Muscardinus avellanarius. NBB English edition, vol 2. Hohenwarsleben: Westarp Wissenschaften.

Kolfschoten, T. van, 1990. The evolution of the mammal faunas in the Netherlands and the Middle Rhine area (Western Germany) during the Late Middle Pleistocene. Meded. Rijks Geol. D. 43, 1–69.

Kotsakis, T., 2003. Fossil glirids of Italy: the state of the art. Coloquios Paleontol. 1, 335–343.

Kotsakis, T., Abbazzi, L., Angelone, C., Argenti, P., Fanfani, F., Marcolini, F., Masini, F., Tre, R., Firenze, U., 2003. Plio-Pleistocene biogeography of Italian mainland micromammals. Deinsea 10, 313–342.

Kowalski, K., 1958. An Early Pleistocene fauna of small mammals from the Kadzielnia Hill in Kielce (Poland). Acta Paleontol. Pol. 3, 1–47.

Kowalski, K., 2001. Pleistocene rodents of europe. Folia Quat. 72, 3–389.

Kowalski, K., Nadachowski, A., 1982. Rodentia (Bacho Kiro, Bulgaria), in: Excavation in the Bacho Kiro Cave (Bulgaria). Fianl Report. pp. 45–51.

Kunst, K., Nagel, D., Rabeder, G., 1989. Erste grabungsergebnisse vom Nixloch bei Losenstein-Ternberg. Jahrb. des Oberösterreichischen Musealvereines Gesellschaft für Landeskd. 134, 199–212.

López-García, J.M., Berto, C., Colamussi, V., Valle, C.D., Vetro, D. Lo, Luzi, E., Malavasi, G., Martini, F., Sala, B., 2014. Palaeoenvironmental and palaeoclimatic reconstruction of the latest Pleistocene–Holocene sequence from Grotta del Romito (Calabria, southern Italy) using the small-mammal assemblages. Palaeogeogr. Palaeoclimatol. Palaeoecol. 409, 169–179.

Mais, K., Rabeder, G., 1984. Das große Höhlensystem im Pfaffenberg bei Bad Deutsch-Altenburg (Niederösterreich) und seine fossilen Faunen. Die Höhle 35, 213–230.

Marchetti, M., Parolin, K., Sala, B., 2000. The Biharian fauna from Monte La Mesa (Verona, northeastern Italy). Acta Zool. cracoviensia 43, 79–105.

Marcolini, F., 2003. Continental Lower Valdarno rodent biochronology and two new methods for the systematics of Mimomys (Arvicolidae, Rodentia). Atti della Soc. Toscana Sci. Nat. di Pisa 108, 129–136.

Marković, Z., 2008. Small mammals (Rodentia and Lagomorpha) from Gradašnica Cave (East Serbia). Bull. Nat. Hist. Museum Belgrade 1, 65–77.

Marquet, J.C., 1989. Paléoenvironnement et chronologie des sites du domaine atlantique français d'âge Pléistocène moyen et supérieur d'après l'étude des rongeurs. Thesis. Univ. Bourgogne, 637 pp.

Martín-Suárez, E., Freudenthal, M., 1998. Biostratigraphy of the continental Upper Miocene of Crevillente (Alicante, SE Spain). Geobios 31, 839–847.

Maul, L., 1990. Überblick über die unterpleistozänen KleinsÄugerfaunen Europas. Quartärpaläontologie 8, 153–191.

Meiri, S., Dayan, T., 2003. On the validity of Bergmann ’ s rule. J. Biogeogr. 30, 331–351.

Nadachowski, A., 1990a. Review of fosil Rodentia from Poland (Mammalia). Senckenb. Biol. 70, 229–250.

Nadachowski, A., 1990b. Lower Pleistocene rodents of Poland: faunal succession and biostratigraphy. Quartärpaläontologie 8, 215–223.

Nadachowski, A., Stefaniak, K., Szynkiewicz, A., Marciszak, A., Socha, P., Schick, P., August, C., 2011. Biostratigraphic importance of the Early Pleistocene fauna from Żabia Cave (Poland) in Central Europe. Quat. Int. 243, 204–218.

Paunescu, A.C., 2001. Les rongeurs du Pléistocène inférieur et moyen de trois grottes du Sud-Est de la France (Vallonnet, Caune de l'Arago, Baume Bonne). Implications systématiques, biostrati- graphiques et paléoenvironnementales. 2001. Thèse de Doctorat, Muséum national d'Histoire naturelle, Paris.

Pons, A., Reille, M., 1988. The Holocene- and Upper Pleistocene pollen record from Padul (Granada, Spain): a new estudy. Palaeogeogr. Palaeoclimatol. Palaeoecol. 66: 243-263.

Popov, V. V., 1989. Middle Pleistocene small mammals (Insectivora, Lagomorpha, Rodentia) from Morovitsa Cave (North Bulgaria). Acta Zool. cracoviensia 32, 561–588.

R Developement Core Team, 2014. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Radulescu, C., Samson, P., 1985. Pliocene and Pleistocene mammalian biostraligraphy in South-eastern Transylvania. Traveaux de l'Institut de Spéologie "Emille Racovitza" 24.

Roebroeks, W., Conard, N., Kolfschoten, T. van, 1992. Dense Forests, cold Steppes and the palaeolithic Settlement of Northern Europe. Curr. Anthropol. 33, 551–586.

Rofes, J., Garcia-Ibaibarriaga, N., Murelaga, X., Arrizabalaga, A., Iriarte-Chiapusso, M.-J., Cuenca-Bescós, G., Villaluenga, A., 2012. The southwesternmost record of Sicista (Mammalia; Dipodidae) in Eurasia, with a review of the palaeogeography and palaeoecology of the genus in Europe. Palaeogeogr. Palaeoclimatol. Palaeoecol. 348-349, 67–73.

Rolland, C., 2008. Clé d'identification des micro-mammifères de Rhône Alpes. CORA Faune Sauvage.

Ronchitelli, A., Boscato, P., Surdi, G., Masini, F., Petruso, D., Accorsi, C.A., Torri, P., 2011. The Grotta Grande of Scario (Salerno, Italy): Archaeology and environment during the last interglacial (MIS 5) of the Mediterranean region. Quat. Int. 231, 95–109.

Ruiz-Sánchez, F.J., Santisteban, C., Crespo-Roures, V.D., Freudenthal, M., 2011. New rodent faunas from Middle Miocene and Mio- Pliocene in the Cabriel Basin (Valencia, Spain). J. Iber. Geol. 37, 161–172.

Sesé, C., 2003. Paleontología y bioestratigrafía del Mioceno continental de la cuenca de Calatayud (Zaragoza): Nuevos yacimientos de Micromamíferos. Estud. Geológicos 59, 249–264.

Sesé, C., 2006. Los roedores y lagomorfos del Neógeno de España. Estud. Geológicos 62, 429–480.

Socha, P., 2014. Rodent palaeofaunas from Biśnik Cave (Kraków-Częstochowa Upland, Poland): Palaeoecological, palaeoclimatic and biostratigraphic reconstruction. Quat. Int. 326-327, 64–81.

Terzea, E., 1994. Fossiliferous sites and the chronology of mammal faunas at Beftia (Bihor, Romania). Trav. du Muséum Natl. d'Histoire Nat. "Grigore Antipa". 34, 467–485.

Tvrtković, N., Dulić, B., Grubešić, M., 1994. Distribution and habitats of dormice in Croatia. Hystrix 6, 199–208.

Valensi, P., Abbassi, M., 1998. Reconstitution de paléoenvironnements quaternaires par l ’ utilisation de diverses méthodes sur une communauté de mammifères - Application à la grotte du Lazaret. Quaternaire 9, 291–302.

Van Dam, J.A., Alcalá, L., Alonso Zarza, A., Calvo, J.P., Garcés, M., Krijgsman, W., 2001. The Upper Miocene mammal record from the Teruel-Alfambra Region (Spain). The MN system and continental stage/age concepts discussed. J. Vertebr. Paleontol. 21, 367–385.

Vilhelmsen, H., 2003. Status of dormice (Muscardinus avellanarius) in Denmark. Acta Zool. Acad. Sci. Hungaricae 49, 139–145.

Villaluenga, A., Monrepos, S., Castaños, P., Alustiza Mujika, J.A., 2012. Cave Bear (Ursus spelaeus Rosenmüller Heinroth, 1794) and Humans During the Early Upper Pleistocene (Lower and Middle Palaeolithic) in Lezetxiki , Lezetxiki II and Astigarragako Kobea. J. Taphon. 10, 521–543.

Wilson, D.E., Reeder, D.M., 2005. Mammal Species of the World. A Taxonomic and Geographic Reference. John Hopkins University Press, Baltimore.

Table

Table 1

Vertebrate faunal list from Level G in Lezetxiki II cave (Arrasate, Basque Country, northern Iberian Peninsula).

Artiodactyla	**Rodentia**	**Erinaceomorpha**	**Anura**
Bovidae	*Apodemussylvaticus-flavicollis*	*Erinaceus europaeus*	*Bufo* sp.
	Muscardinus avellanarius		*Rana temporaria-iberica*
Carnivora	*Eliomys quercinus*	**Eulipotyphla**	*Salamandra salamandra*
Ursus spelaeus	*Arvicola amphibius*	*Talpa* sp.	
	Microtus agrestis	*Sorex araneus-coronatus*	**Squamata**
Lagomorpha	*Microtus arvalis*	*Crocidura* sp.	*Anguis fragilis*
Oryctolagus cuniculus	*Microtus (Terricola)* sp.		Colubridae indet.
	Clethrionomys glareolus		Viperidae indet.
Chiroptera	*Pliomys lenki*		
Chiroptera indet.			

Data source: artiodactyls and carnivores (Villaluenga et al., 2012); small vertebrates (this paper)

Table 2

Measurements (in mm) of the teeth of *Muscardinus avellanarius* Linnaeus, 1758 from Lezetxiki II Cave (Arrasate, Basque Country, northern Iberian Peninsula)

Dental element	Lenght	Width
right M1	18,2	11,4
right M2	13,3	11,9
left M2	10,5	

Table 3

Detailed list of Iberian locations with different *Muscardinus* species during the Miocene and Pliocene.

Number	Site	Species	Number	Site	Species
1	Canteras de Jun	*Muscardinus* cf. *vireti*	17	Castell de Barbera	1 *Muscardinus* cf. *vallesiensis*
2	PUR-24A	*Muscardinus meridionalis*	17	Castell de Barbera	2 *Muscardinus hispanicus*
2	PUR-4*	*Muscardinus meridionalis*	18	Pedregueras IIC	2 *Muscardinus hispanicus*
3	Cañada del Castaño*	*Muscardinus* cf. *pliocaenicus*	19	Can Almirall	*Muscardinus hispanicus*
4	Moreda 1*	*Muscardinus* sp.	20	Can Missert	*Muscardinus hispanicus*
5	Concud 3	*Muscardinus* aff. *hispanicus*	21	Els Casots	*Muscardinus* sp.
6	Masía de la Roma 6, 7, 9, 11	*Muscardinus hispanicus*	22	T. N. & S.2 Au	*Muscardinus* sp.
7	Masía del Barbo A, B	*Muscardinus hispanicus*	23	Can Petit	2 *Muscardinus hispanicus*
8	Peralejos 4	*Muscardinus hispanicus*	24	Can Vilella	*Muscardinus vireti*
9	Puente Minero 2, 8	*Muscardinus hispanicus*	25	CR-2, 4B, 6, 8, 14, 15, 17	*Muscardinus* sp.
10	Armantes 14	*Muscardinus thaleri*	26	Juan Vich 2	*Muscardinus* cf. *thaleri*
11	Carrilanga 1	*Muscardinus hispanicus*	27	La Hornera	*Muscardinus vireti*
12	Manchones	*Muscardinus thaleri*	28	Tarazona 3	*Muscardinus* sp.
13	Abocador de Can Mata	*Muscardinus sansaniensis*	29	Sant Quirze	*Muscardinus hispanicus*
14	Barranc de Can Vila 1	*Muscardinus sansaniensis*	30	Belmonte	*Muscardinus* sp.
15	Can Llobaretes	1 *Muscardinus* cf. *vallesiensis*	31	Campredó	*Muscardinus* aff. *vireti*
15	Can Llobaretes	2 *Muscardinus hispanicus*	32	Cala Es Pou	*Muscardinus cyclopeus*
16	Can Ponsic I	2 *Muscardinus hispanicus*			

[1] Originally defined as *Eomuscardinus* cf. *vallesiensis*; [2] Originally defined as *Muscardinus crusafonti* ; *Pliocene site. The data were taken from Aguilar et al. (1979), Agustí (1990), Agustí et al. (2005, 1979), Alba et al. (2006), Álvarez-Sierra et al. (2006), Casanovas-Vilar et al. (2011), Daams (1985), García-Alix et al. (2008), Martín-Suárez and Freudenthal (1998), Ruiz-Sánchez et al. (2011), Sesé (2003), Van Dam et al. (2001). Abbreviations: CR, Crevillente; PUR, Canteras de Pulianas Purcal; T. N. & S.2 Au, Trinchera Norte & S.2 Autopista.

Table 4

Detailed list of European locations with different *Muscardinus* species during the Early, Middle and Late Pleistocene.

Stage	Number	Country	Site	Species	Stage	Number	Country	Site	Species
Early Pleistocene	36	Austria	Deutsch Altenburg 2C1, 4B	*Muscardinus dacicus*	Middle Pleistocene	75	Italy	Grotta Grande of Scario	*Muscardinus avellanarius*
	37	Czech Rep	Chlum 6	*Muscardinus* sp.		76	Poland	Biśnik Cave	*Muscardinus avellanarius*
	38	Czech Rep	Holštejn	*Muscardinus* sp.		77	Romania	Cave 10 in the Lupsa Valley	*Muscardinus dacicus malvensis*
	39	Czech Rep	Koněprusy C718	*Muscardinus* sp.		77	Romania	Cave 13 in the Lupsa Valley	*Muscardinus* cf. *avellanarius*
	39	Czech Rep	Koněprusy C718	*Muscardinus avellanarius*		78	Romania	Cave in the Párului Valley	Pleistoceno Medio (Late)
	40	Czech Rep	Skalka	*Muscardinus avellanarius*		79	Romania	Magura V	*Muscardinus avellanarius*
	42	France	Vallonet	*Muscardinus* cf. *avellanarius*		80	Romania	Sîndominic-1	*Muscardinus avellanarius*
	33	Germany	Sackdilling	*Muscardinus* aff.	Late	83	Austria	Nixloch	*Muscardinus avellanarius*

			avellanarius
34	Germany	Scbernfeld	*Muscardinus* sp.
35	Germany	Schambach near Treuchtlingen	*Muscardinus* sp.
43	Hungary	Csarnóta locality no. 2	*Muscardinus* sp.
44	Hungary	Kövesvárad	*Muscardinus dacicus*
45	Hungary	Osztramos 2	*Muscardinus* cf. *dacicus*
46	Hungary	Somssich-hegy 2	*Muscardinus* sp.
61	Hungary	Uppony Layer no. 10	*Muscardinus* cf. *avellanarius*
47	Italy	Montagnola Senese	*Muscardinus* sp.
48	Italy	Monte La Mesa	*Muscardinus* cf. *dacicus*
49	Italy	Pirro Nord	*Muscardinus* cf. *avellanarius*
50	Italy	Rivoli Veronese	*Muscardinus pliocaenicus*
51	Netherland	Tegelen	*Muscardinus* cf. *avellanarius*
52	Netherland	Zuurland Faunas 7-9	*Muscardinus* sp.
53	Poland	Kadzielnia-1	*Muscardinus* cf. *avellanarius*
54	Poland	Kielniki-3A	*Muscardinus* sp.
55	Poland	Kozi Grzbiet	*Muscardinus* cf. *avellanarius*

Pleistocene				
	84	Bulgary	Bacho Kiro	*Muscardinus avellanarius*
	85	Bulgary	Mecha Cave	*Muscardinus avellanarius*
	86	Bulgary	Temnata Cave-3	*Muscardinus avellanarius*
	89	France	Combe-Grenal	*Muscardinus avellanarius*
	90	France	Baume de Gigny	*Muscardinus avellanarius*
	91	France	Régourdou	*Muscardinus avellanarius*
	92	France	Santenay	*Muscardinus avellanarius*
	81	Germany	Genkingen-2	*Muscardinus avellanarius*
	82	Germany	Pisede	*Muscardinus avellanarius*
	93	Greece	Loutraki Bear-cave	*Muscardinus* sp.
	94	Hungary	Porlyuk (layer 1)	*Muscardinus avellanarius*
	95	Hungary	Poroslyuk of Ballavölgy (layer 3)	*Muscardinus avellanarius*
	96	Hungary	Rejtek rock shelter 1	*Muscardinus avellanarius*
	97	Italy	Arma del Manie	*Muscardinus avellanarius*
	98	Italy	Cipolliane Cave	*Muscardinus* sp.
	99	Italy	Ferrovia Cave	*Muscardinus* sp.

	56	Poland	Zabia Cave	*Muscardinus* cf. *avellanarius*
	57	Poland	Zalesiaki 1A	*Muscardinus* sp.
	58	Romania	Betfia IX	*Muscardinus* sp.
	58	Romania	Betfia XIII, X, XI, VII-1b-e, VII-3, II	*Muscardinus dacicus*
	59	Romania	Chiscau	*Muscardinus* sp.
	60	Romania	Subpiatra	*Muscardinus* sp.
	41	Slovakia	Včeláre 5	*Muscardinus* sp.
	41	Slovakia	Včeláre 6/3.7.8.9	*Muscardinus* cf. *avellanarius*
Middle Pleistocene	63	Belgium	La Belle-Roche Cave	*Muscardinus* sp.
	64	Bulgary	Morovitsa Cave	Muscardinus cf. *avellanarius*
	65	France	Baume Moula Guercy (couche XVII, XV)	Muscardinus avellanarius
	66	France	Fontéchevade	Muscardinus avellanarius
	67	France	Lazaret	Muscardinus avellanarius
	68	France	Vergranne	Muscardinus sp.
	72	Germany	Miesenheim I	Muscardinus avellanarius
	62	Germany	Sudmer-Berg-2	Muscardinus avellanarius

100	Italy	Grota del Romito	*Muscardinus avellanarius*
101	Italy	Grota Paglicci, Inner levels	*Muscardinus avellanarius*
102	Italy	Grotta “Vascio ‘o Funno”	*Muscardinus malatestai*
103	Italy	Praia a Mare	*Muscardinus avellanarius*
104	Italy	Grotta Cala	*Muscardinus avellanarius*
105	Italy	Grotta del Broion	*Muscardinus avellanarius*
106	Italy	Grotta della Serratura	*Muscardinus avellanarius*
107	Italy	Grotta di Castelcivita	*Muscardinus avellanarius*
108	Italy	Grotta Averla	*Muscardinus avellanarius*
109	Italy	Riparo Mezzena	*Muscardinus avellanarius*
110	Italy	Valdiporro	*Muscardinus avellanarius*
76	Poland	Biśnik Cave	*Muscardinus avellanarius*
111	Poland	Cioarei Cave	*Muscardinus avellanarius*
112	Poland	Hotilor Cave	*Muscardinus avellanarius*
113	Serbia	Baranica Pécina	*Muscardinus avellanarius*
114	Serbia	Gradašnica Pécina	*Muscardinus avellanarius*

69	Great Britain	Boxgrove	Muscardinus avellanarius
70	Great Britain	Westbury-sub-Mendip	Muscardinus avellanarius
71	Hungary	Tarko	*Muscardinus* cf. *avellanarius*
61	Hungary	Uppony (layer 6, 7)	*Muscardinus* cf. *avellanarius*
49	Italy	Pirro Nord	*Muscardinus* cf. *avellanarius*
73	Italy	Campani Cave	*Muscardinus avellanarius*
74	Italy	Fornace di Cornedo	*Muscardinus avellanarius*
115	Serbia	Petnička Pécina	*Muscardinus avellanarius*
116	Serbia	Smolucka Pécina	*Muscardinus avellanarius*
117	Serbia	Vasiljska Pécina	*Muscardinus avellanarius*
118	Serbia	Vrelska Pećina cave	*Muscardinus avellanarius*
87	Slovenia	Črni kal 2	*Muscardinus* sp.
88	Slovenia	Potočka Zijalka	*Muscardinus avellanarius*
119	Switzerland	Ettingen	*Muscardinus avellanarius*

The data were taken from Andrews (1990), Aguilar et al. (1998), Bertolini et al. (1996), Bogićević et al., (2011), Bon et al. (1991), Chaline (1983, 1972), Chaline et al. (1995), Chatzopoulou et al. (2001), Desclaux and Defleur (1997), Dimitrijević (1996), Gibbard et al. (1991), Hernández-Fernández (2000), Jánossy (1986), Kolfschoten (1990), Kotsakis (2003), Kotsakis et al. (2003), Kowalski (2001), Kowalski and Nadachowski (1982), Kunst (1989), López-García et al. (2014), Mais and Rabeder (1984), Marchetti et al. (2000), Marcolini (2003), Marković (2008), Marquet (1989), Maul (1990), Nadachowski (1990a, 1990b), Nadachowski et al. (2011), Paunescu (2001), Popov (1989), Radulescu and Samson (1985), Roebroeks et al. (1992), Ronchitelli et al. (2011), Socha (2014), Terzea (1994), Valensi and Abbassi (1998).

Figure 1

Click here to download high resolution image

Figure 2
Click here to download high resolution image

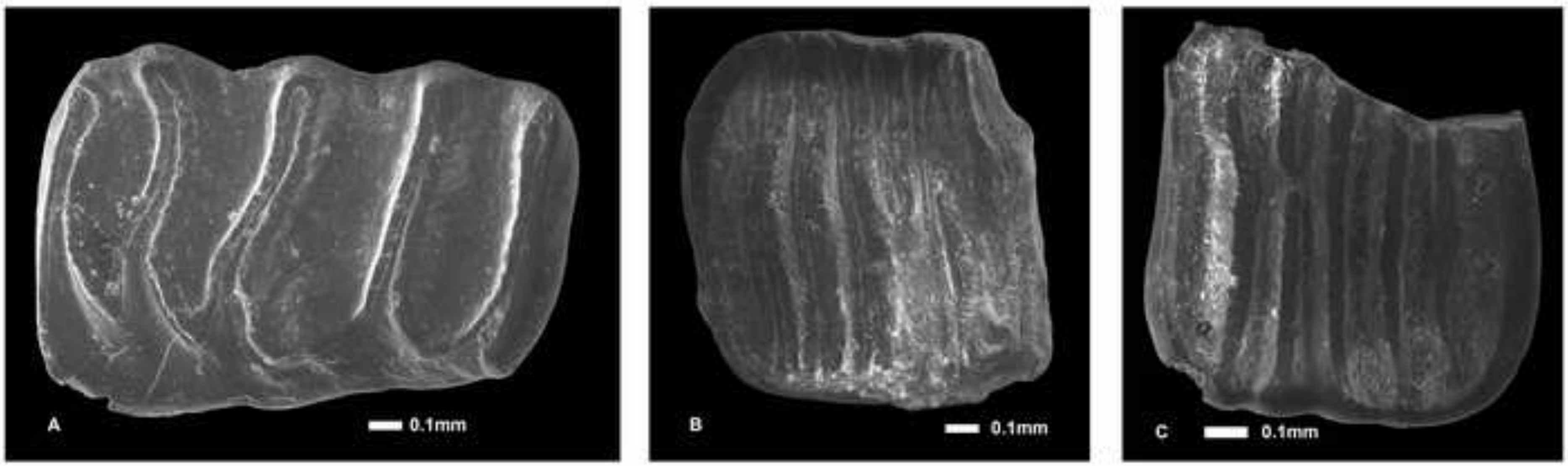

Figure 3
Click here to download high resolution image

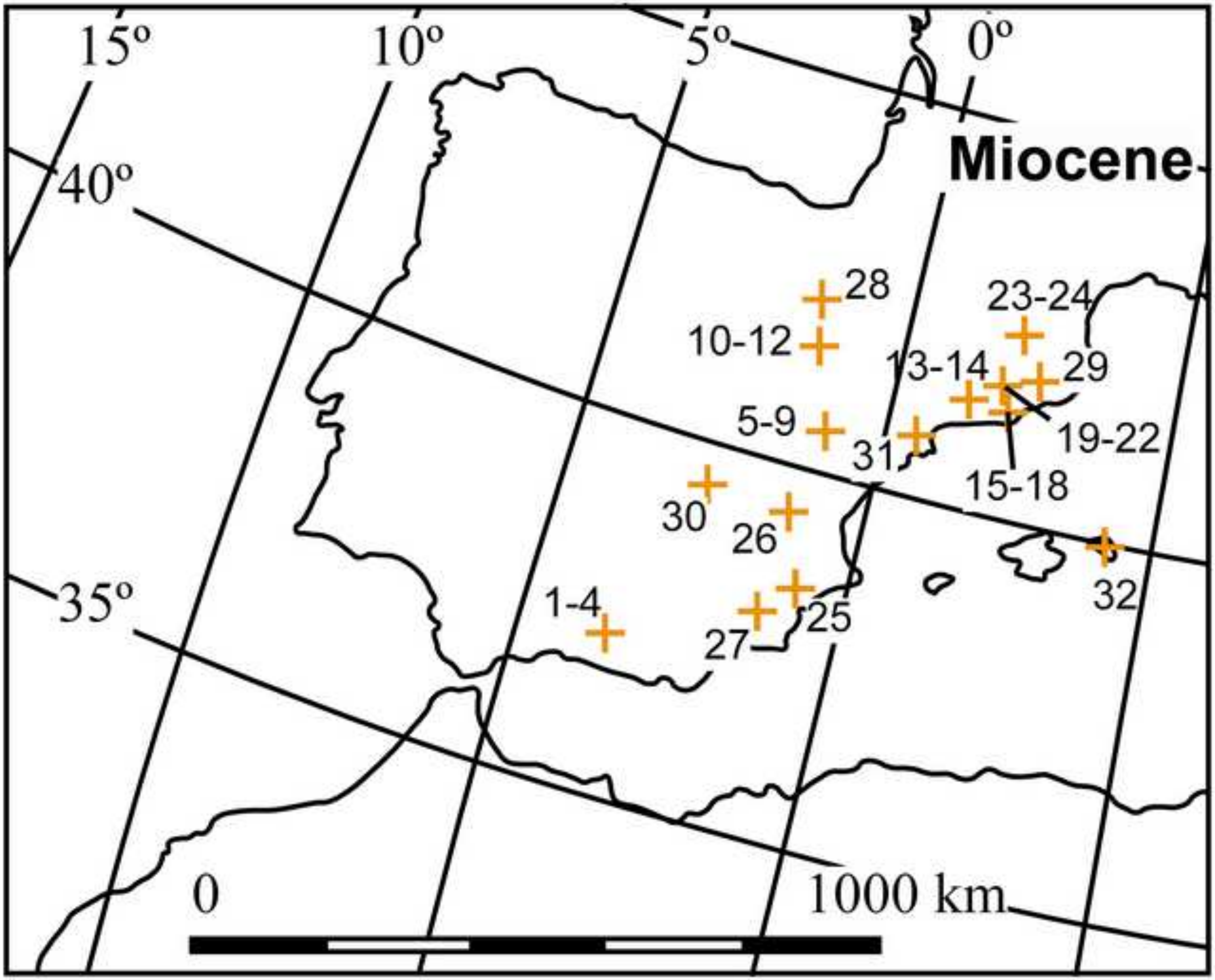

Figure 4
Click here to download high resolution image

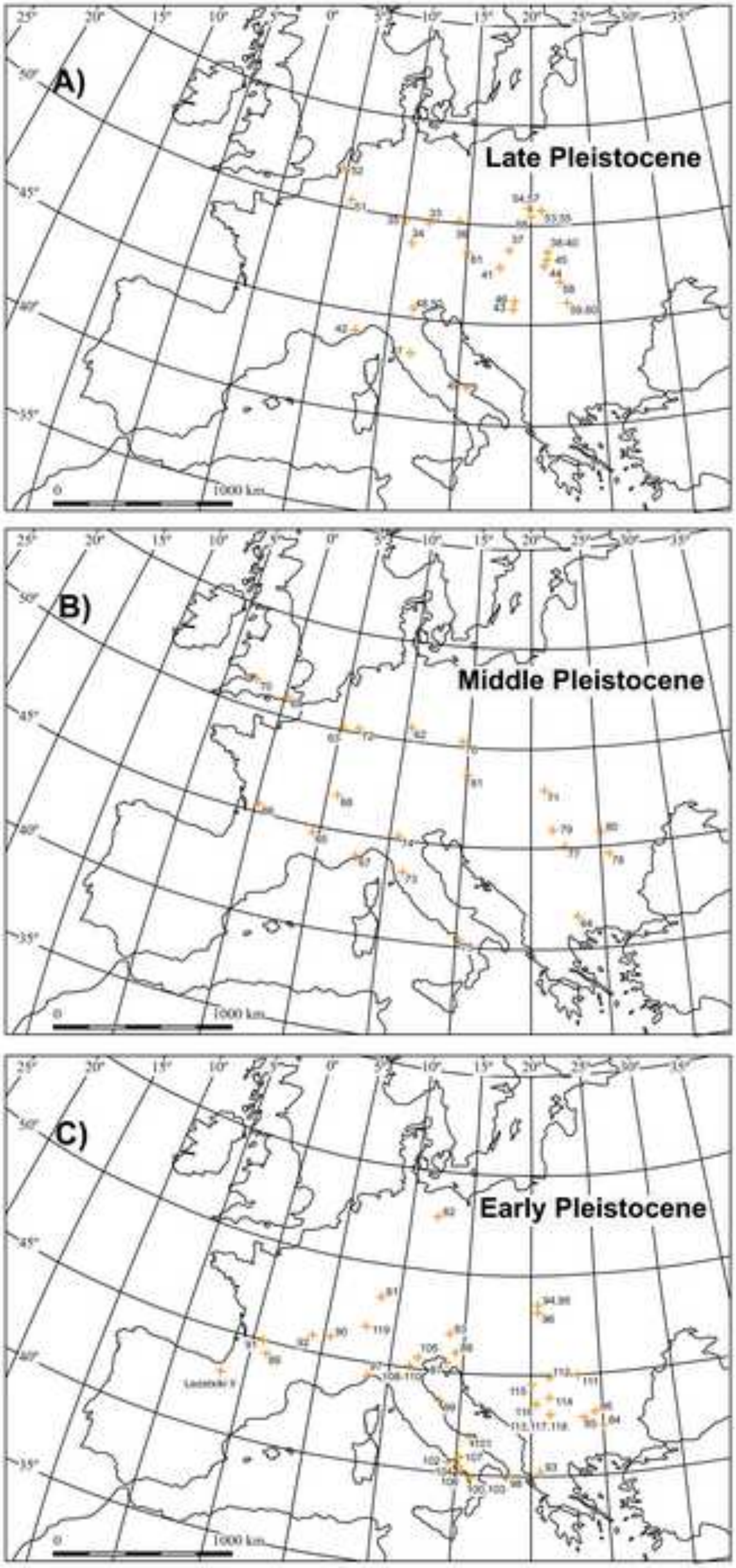

Figure 5

Click here to download high resolution image

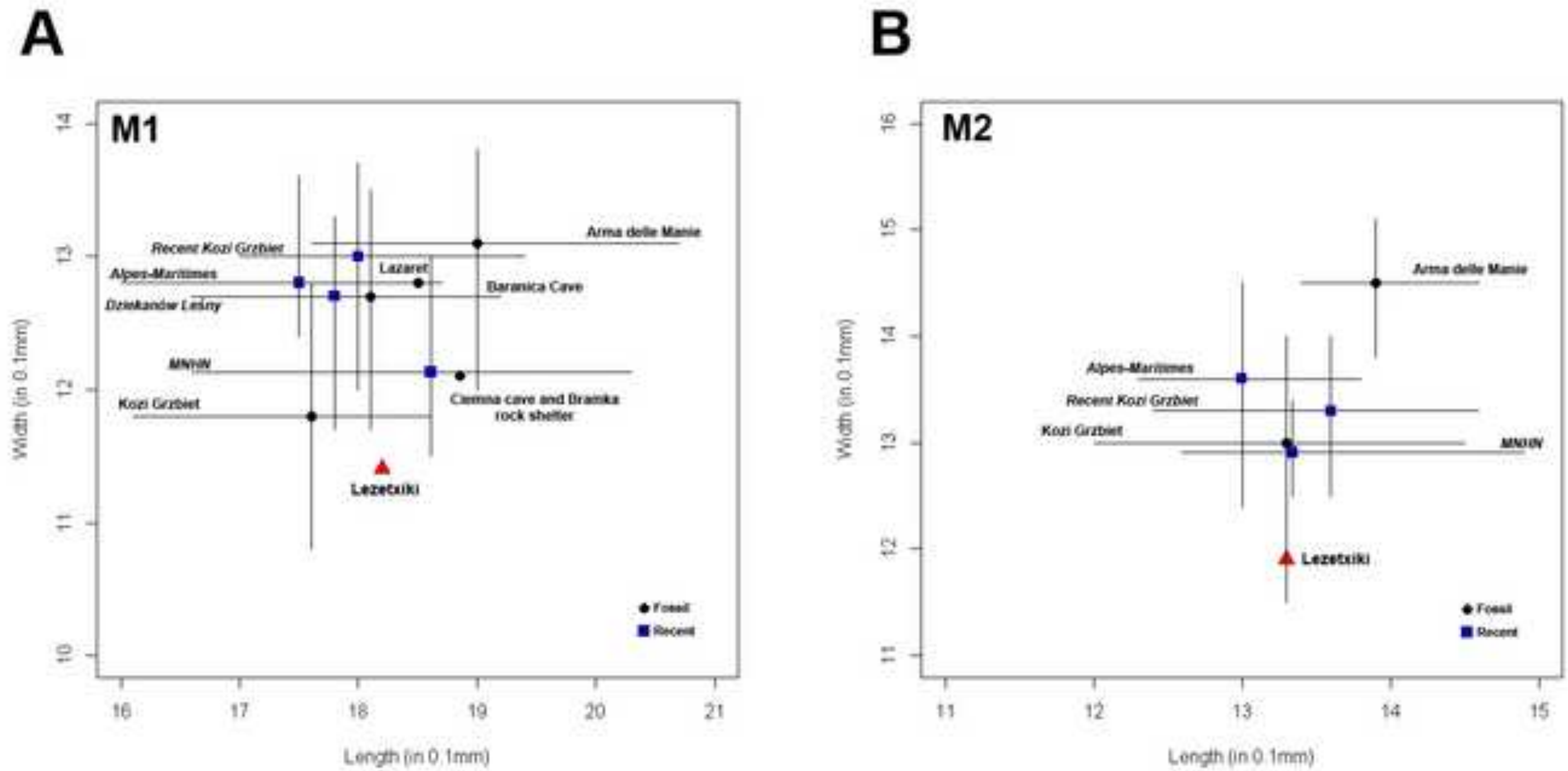

Figure 6
Click here to download high resolution image

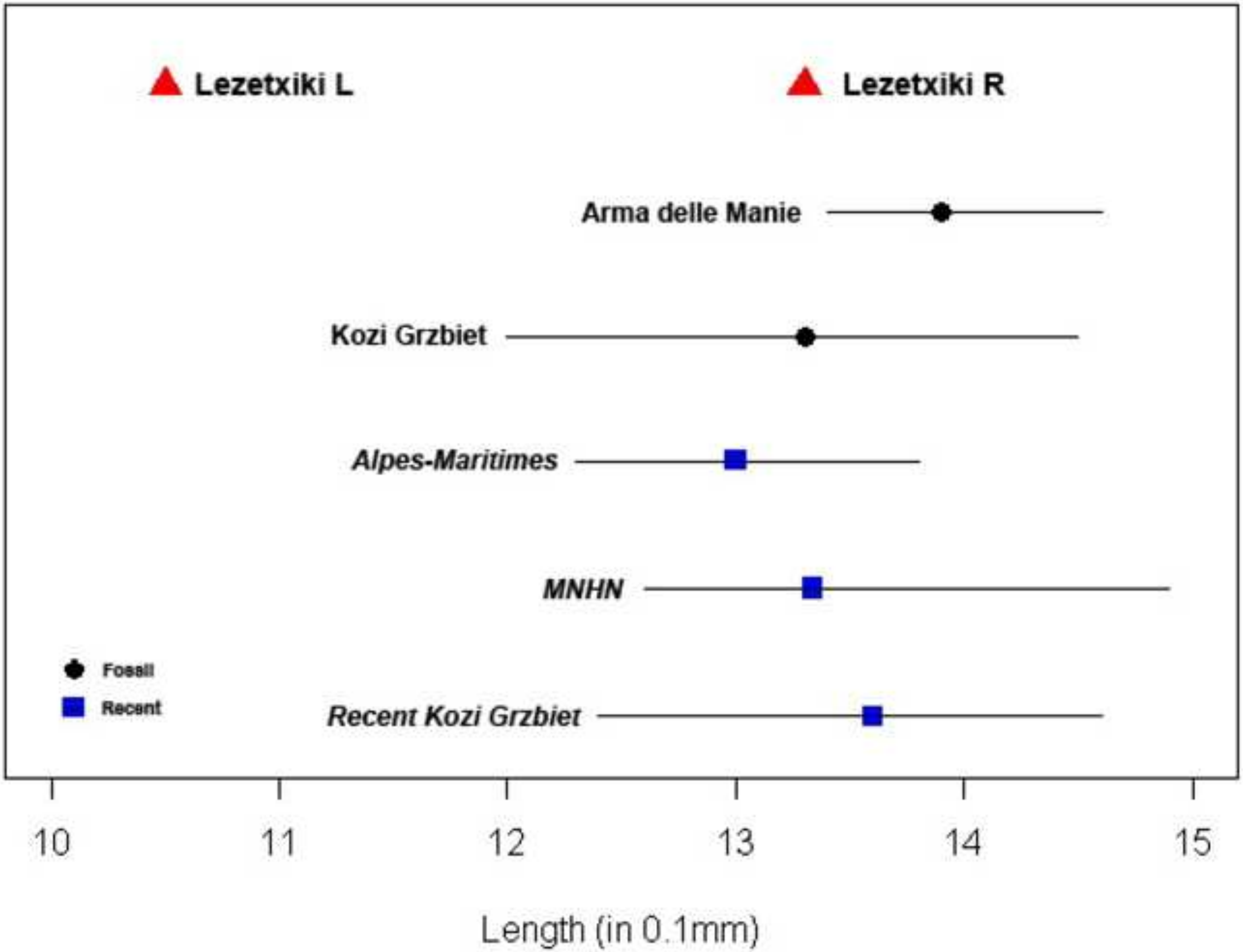

Figure Legends

Figure 1. Geographical location of Lezetxiki II Cave (Arrasate, Gipuzkoa, Spain) and the approximate location of other archaeological sites (Mdt 25 obtained from the IGN).

Figure 2. Right first upper molar (M1), right second upper molar (M2) and left second upper molar (M2) of *Muscardinus avellanarius* from Lezetxiki II (Arrasate, Basque Country, Spain).

Figure 3. Palaeogeographic distribution of the different species of *Muscardinus* in Spain during the Miocene and Pliocene. The data were taken from the same sources as in Table 3.

Figure 4. Palaeogeographic distribution of the different species of *Muscardinus* in Europe during the Early (A), Middle (B) and Late (C) Pleistocene. The data were taken from the same sources as in Table 3.

Figure 5. A and B. Bivariate analyses of the length and width values for the first and second upper molar of several *Muscardinus avellanarius* populations (fossil and modern), respectively. Variables are given in mm. For the row data and references see Table S1 in the Supplementary Online Information

Figure 6. Univariate analysis of the length values for the second upper molar of several *Muscardinus avellanarius* populations (fossil and modern). Variables are given in mm.

Lezetxiki L = Lezetxiki Left M2 and Lezetxiki R= Lezetxiki Right M2. For the row data and references see Table S1 in the Supplementary Online Information

Supplementary Data

Click here to download Supplementary Data: Supplementary information.docx