The southwesternmost record of Sicista (Mammalia; Dipodidae) in Eurasia, with a review of the palaeogeography and palaeoecology of the genus in Europe

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Abstract

We describe the southwesternmost specimen of *Sicista betulina* (Mammalia; Dipodidae) and of the genus *Sicista* found to date in Eurasia, which comes from the early Late Pleistocene (MIS 5) site of Lezetxiki II (Arrasate, Basque Country, Spain), in the north of the Iberian Peninsula. *Sicista* is a relatively common taxon in Quaternary deposits, although not numerically abundant due to ecological and taphonomical reasons. In the light of the new discovery, we briefly but comprehensively review the palaeogeography and palaeoecology of the genus in Europe. Average colder and drier conditions during the Pleistocene allowed *Sicista* to get as far south as Chios Island in the Aegean Sea, and as far west as Lezetxiki in the Iberian Peninsula. A cold, moderately humid environment, with dominant grasslands and coniferous forests, inferred from the palaeobiological associations (including human remains) at Lezetxiki II, was ideal for *S. betulina* given its current ecological requirements.

Keywords: Lezetxiki II; Neanderthals; *Sicista betulina*; Palaeobiological associations; *Sicista subtilis*; Iberian Peninsula

1. Introduction

Sicista is the only living genus of the Sicistinae clade (Mammalia; Rodentia; Dipodidae). It has thirteen species currently living in northern parts of Eurasia (Holden and Musser, 2005), but only two of them have inhabited the European subcontinent since the Middle Pleistocene, namely, *Sicista betulina* Pallas, 1779 (northern Birch Mouse) and *Sicista subtilis* Pallas, 1773 (southern Birch Mouse). Another species, *Sicista praeloriger* Kormos, 1930, from the Early Pleistocene in Europe, is similar to *S. subtilis* and may represent its ancestral form (Kowalski, 2001).

The status of *Sicista vinogradovi* Topachevsky, 1965, from the Early and Early/Middle Pleistocene at Nogajsk (Ukraine) and neighboring sites (Rekovets and Nadachowski, 1995) needs confirmation; Kowalski (2001) does not consider it a valid taxon. *Sicista montana* Méhely, 1913, reported from a few Late Pleistocene sites in Italy, Austria, Switzerland and Germany, is a synonym of *S. betulina* (Kowalski, 2001; Holden and Musser, 2005).

Dental and bone remains of *Sicista* are relatively common but not especially abundant when found in European Quaternary sites. Their tiny dimensions together with their scarcity in owl pellets, as recently testified by the extensive fieldwork of Balciauskas et al. (2011) in Lithuania, are the main reasons why they are always recovered in small numbers, with the exception of the relatively rich sample of *S. betulina* (MNI= 14) from the Late Pleistocene locality of Vâ Tche Tchâ, in northwest Switzerland (Oppliger and Becker, 2010). This factor together with the quite problematic distinction between *S. betulina* and *S. subtilis* using dental characters, led many scholars to identify their materials as *Sicista* sp. or *Sicista* ex gr. *betulina–subtilis*.

Here we present the first record of *S. betulina* from the Iberian Peninsula, which also happens to be the southwesternmost record of the genus in the Eurasian continent. It comes from the early Late Pleistocene site of Lezetxiki II, in the Basque Country (north Spain).

The recent geographic distribution of the *Sicista* species in Europe is reasonably well known (e.g., Chaline, 1972; Pucek, 1982a, b; Kryštufek et al., 2008; Meinig et al., 2008; Balciauskas et al., 2011), but the distribution in the Pleistocene is limited to what can be inferred from isolated reports and major site compilations (e.g., Chaline, 1972; Jánossy, 1986; Maul, 1990, 2002; Nadachowski, 1990; Rekovets and Nadachowski, 1995; Koenigswald and Heinrich, 1999; Kowalski, 2001; Kalthoff et al., 2007; Oppliger and Becker, 2010). No systematic analysis of the palaeogeography of the genus has been carried out.

The aim of this paper is, through a detailed morphological and morphometrical comparison, to characterize and safely allocate the Lezetxiki II specimen to *S. betulina*, and to briefly but comprehensively review the palaeogeographic evolution of the genus during the Pleistocene in Europe in the light of the new discovery, and also discuss some significant palaeoecological points.

In spite of the fact that we focus our study in Europe, we must take into account that the origin and early dispersion of *Sicista* took place in Asia, the earliest species of birch mouse, *Sicista primus*, being recently recovered from the 17-Ma-old (late Early Miocene) locality of Gashunyinadge, in central Nei Mongol, China (Kimura, 2011). In this sense, our study could be more properly understood as one documenting the spread of the genus into Europe from a center of diversity in Asia.

2. Lezetxiki II, context and chronology

The cave site of Lezetxiki (Arrasate, Basque Country) is 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 I has been excavated in two different series of excavations: 1956–1968, under the supervision of J.M. de Barandiarán, and since 1996, by A. Arrizabalaga and M.J. Iriarte. During the first series, an extensive sequence of Late Pleistocene levels was excavated and three human fossil remains were recovered, namely, two Neanderthal teeth from Level IV and a humerus from Level VIII (Arrizabalaga et al., 2005). To provide a better context for the human fossils and other finds from this site, excavations were resumed using updated methodology (Arrizabalaga and Bernaldo de Quirós, 2006). The new research has been carried out on the southern side of the classic deposit, and also in the neighboring cave of Lezetxiki II, which is physically connected with Lezetxiki I precisely in the place where the human humerus was found and which may provide its stratigraphic context.

(INSERT HERE FIGURE 1)

The main reference to interpret the geochronology of the infill at Lezetxiki II is a Th/U date of 74 ka BP (Falguerès et al., 2005–2006), obtained for a speleothem located about 150 cm above the position of the *Sicista* molar. Two dates have also been obtained by amino acid racemisation of *Ursus* teeth found in the same stratigraphic level. The individual results are 70.0 ka and 86.8 ka, which give a mean value of 78.4 ± 8.4 ka BP. These results enable the Sicista specimen to be dated to the very last phase of MIS 5.

Evidence of human activity has been detected in both caves, in levels also attributed to MIS 5 (base of the stratigraphic sequences in Lezetxiki I and Lezetxiki II). It is scarce and consists of a few rough flakes made of raw materials other than flint, i.e., limonite, quartzite, lutite, vulcanite and even limestone (Arrizabalaga, 2005–2006).

The *Sicista* molar from Lezetxiki II was found in the sediment from the boundary between the M15 and N15 quadrats, at a depth of approximately −271 cm below the current cave datum level. This was just below a recently described macaque mandible (*Macaca sylvannus*), which is the first record of its species in the northern Iberian Peninsula, and one of the youngest macaque specimens in all Europe (Castaños et al., 2011). The first record of wolverine (*Gulo gulo*) in the Iberian Peninsula also came from Lezetxiki (Altuna, 1963).

Besides *Macaca*, the *Sicista* specimen was found in association with the following large mammal taxa (Castaños et al., 2011): Bovini (*Bos/Bison*), *Capra pyrenaica, Cervus elaphus, Capreolus capreolus, Ursus spelaeus, Ursus arctos, Vulpes vulpes* and *Mustela putorius*. The assemblage consists mainly of eurythermal species and cannot be used as an effective palaeoclimate indicator. However, the co-occurrence of large bovines and ibex indicates both open landscapes and rocky biotopes in the proximity of the site.

In addition to *Sicista*, we identified the following small mammalian taxa in the same context: *Allocricetus bursae, Arvicola sapidus, A. terrestris, Pliomys* sp., *Microtus agrestis, M. arvalis, M.* gr. *agrestis/arvalis, Terricola* sp., *Apodemus* gr. *sylvaticus-flavicolis* and *Sorex* sp. The species currently associated with grasslands (*M. agrestis* and *M. arvalis*) and water- courses (*A. sapidus*) are the most abundant, and they reflect open landscapes with flowing streams near the site. The *A. bursae* from Lezetxiki II is the first representative of this taxon to be found in the Cantabrian region.

The palynological study (included in Castaños et al., 2011) shows that the woodland biotope was well represented, consisting mainly of *Pinus* and *Tilia*. These were accompanied by *Corylus, Quercus robur* tp., *Quercus ilex* tp., and *Betula*. Gramineae and Juncaceae species predominated in the herbaceous stratum, with a discreet proportion of fern spores (particularly *Polypodium*). This association suggests a moderately humid, cold environment.

3. Material and methods

The small mammal sample from Lezetxiki II was obtained by concentrating the sediment after a process of washing and sieving the sedimentary materials acquired from the excavations. Two superimposed sieves of decreasing mesh diameter were used in the washing/sieving process: 3 mm and 0.5 mm. Subsequently, the fossils were separated from the concentrates using a stereo-microscope (magnification: 20×, 40 ×).

For the classification and nomenclature of the *Sicista* specimen, we used bibliographic support (Pucek, 1982a, b; Kalthoff et al., 2007; Oppliger and Becker, 2010). Metric values were recorded using a stereo-microscope (Nikon SMZ-U) connected to a video camera (DS-5 m).

4. Systematic palaeontology

Order RODENTIA Bowdich, 1821
Family DIPODIDAE Fischer von Waldheim, 1817 Subfamily SICISTINAE Allen, 1901
Genus *Sicista* Gray, 1827
Sicista betulina Pallas, 1779 Fig. 2
Stratigraphic range: From the Middle Pleistocene to the present. Distribution: For the geographic distribution in Europe during the Pleistocene see Fig. 3 and Table 1.
Studied locality: Lezetxiki II (Basque Country, north Spain). Material: A right first lower molar (m1).
Dimensions (mm): Length, 1.05; width, 0.74.
Description: The molar is two-rooted and moderately worn. The occlusal outline is rounded ith the hypoconid more prominent than the protoconid on the labial side. There is a distinct emargination or concavity labially at the ectoflexid. The protoconid and the hypoconid are the highest cusps. The anteroconid, metaconid and entoconid are also well developed. The mesolophid is low but clearly visible; it reaches the lingual margin of the tooth. The posterolophid is low and tenuous. The entoconid exhibits two spurs near the base, both directed away from the hypolophulid, one pointing to the mesolophid, and the other to the posterolophid.

(INSERT HERE FIGURE 2)

5. Morphology and Morphometry

The molar from Lezetxiki meets the two basic requirements or diagnostic features to be egarded as *S. betulina*, i.e., small size and relative complexity of the crown (Pucek, 1982a). The Lezetxiki m1 dimensions fall within the range of variation for recent Polish specimens of *S. betulina* reported by Pucek (1982a: 518), and clearly below the range of *S. subtilis* given by the same author (Pucek, 1982b: 506). The molar is also close to the minimum values recorded for the specimens of *S. betulina* from Vâ Tche Tchâ (Oppliger and Becker, 2010: 117). It is also smaller than the only m1 of *S. subtilis* recovered from the Late Pleistocene deposits of the Wannenköpfe volcanoes in western Germany (Kalthoff et al., 2007: 614), and those of Holocene age from two sites in the northeast of Bulgaria (Mitev, 2004: 136).

The m1 crown of *S. betulina* is more complex than that of *S. subtilis* in having anterior and posterior spurs on the entoconid, a character observed in most of the seventeen specimens from Vâ Tche Tchâ (Oppliger and Becker, 2010), and in the only one from Lezetxiki II. Kalthoff et al. (2007) proposed a new character to discriminate between the first lower molars of *S. betulina* and *S. subtilis*, namely, the general outline of the latter is not as oval and rounded as in the former. The outline of the *S. subtilis* m1 converges anteriorly markedly and exhibits a more prominent protoconid in the labial side (occlusal view), the concavity between the protoconid and the hypoconid being therefore deeper than in *S. betulina* (Kalthoff et al., 2007: Fig. 5). The Lezetxiki specimen also meets this criterion and can be safely allocated to *S. betulina*.

6. Palaeogeographic evolution of Sicista in Europe

Fig. 3 shows the distribution of the different species of *Sicista* in the European subcontinent during the Early, Middle and Late Pleistocene stages. For a detailed list of sites and countries, see Table 1.

(INSERT HERE FIGURE 3 AND TABLE 1)

The earliest remains of *Sicista* (identified as *Sicista* sp.) in Europe come from the localities of Betfia-XIII (Romania) and Čerevičnoe-2 (Ukraine), both older than 1.8 Ma (Kowalski, 2001). Dental elements reliably assigned to *S. praeloriger* first appeared in the second third of the Early Pleistocene in both central Europe and France (Fig. 3.1) (Jánossy, 1986; Maul, 1990; Nadachowski, 1990; Kowalski, 2001). The single locality with *S. praeloriger* in France (Les Valerots) marks the western limit of the genus during this time. The eastern range reached the site of Akkulaevo in Russia (Fig. 3.1), all the specimens from the European zone of this country and from Ukraine being classified as *Sicista* sp. (Rekovets and Nadachowski, 1995; Kowalski, 2001). Also from the Early Pleistocene is the first record of *S. subtilis*, at the Bulgarian locality of Temnata Cave (Kowalski, 2001), which establishes the southern boundary of the genus (Fig. 3.1). There is another record of *S.* cf. *subtilis* from the Slovakian site of Včeláre (Kowalski, 2001), but it may be treated with caution given the presence of *S.* cf. *praeloriger* in the same location.

During the Middle Pleistocene, the population of *S. praeloriger* decreases notably, and is concentrated in central Europe (Fig. 3.2). In contrast, specimens of *S. subtilis* are to be found from the southern Netherlands (Maastricht-Belvedere) in the north, to Chios Island (Latomi-1, Greece) in the south (Mayhew, 1978; Kowalski, 2001). The record from Maastricht-Belvedere is also the westernmost for the species, and that from Demidovka in Ukraine, is the most to the east (Kowalski, 2001). The northernmost records for the genus (*Sicista* sp.) are from La Cotte St. Brelade in the United Kingdom, and Korotoâk in Russia (Kowalski, 2001). Remarkable is the appearance of a new species, *S. betulina*, at this time, its distribution being mostly concentrated to the west, especially in modern France (Fig. 3.2), with a few other records from Germany, Hungary and Romania (Jánossy, 1986; Marquet, 1989; Koenigswald and Heinrich, 1999; Kowalski, 2001). The south- and easternmost record of *S. betulina* is from Aldène in France, and the northernmost from Erkenbrechtsweiler bei Kirchheim in south Germany (Koenigswald and Heinrich, 1999; Kowalski, 2001). The westernmost record for the genus is that from La Cotte St. Brelade (Kowalski, 2001).

The Late Pleistocene witnessed the extinction of *S. praeloriger*, with a last record from the site of Zlaty Kun in the Czech Republic (Fig. 3.3) (Chaline, 1972); it was finally completely replaced by the two extant species. *S. subtilis* slightly expanded to the west, into Gigny (eastern France) (Kowalski, 2001), and *S. betulina* greatly expanded in every direction from its Middle Pleistocene core-area in southeast France (compare Fig. 3.2 and 3.3). It reached Allerød in Denmark to the north, Ferrovia Cave in Italy to the south, Scocul Scorotei in Romania to the east, and Lezetxiki II in north Spain to the west (Kowalski, 2001; this paper). In terms of the genus, the northernmost limit of *Sicista* is again Allerød; the westernmost, Lezetxiki II; the easternmost, Novgorod Seversk in north Ukraine, and the southern boundary is defined by the records in Serbia and Bulgaria (Fig. 3.3) (Kowalski, 2001; this paper).

With the arrival of the Holocene Climatic Optimum, the distribution of *Sicista* in Europe became considerably reduced and pushed eastwards in comparison with in the Pleistocene. Today, the populations of *S. betulina* are mainly located in forested areas (taigas) of the eastern Paleartic: from Lithuania, Poland and the Czech Republic to Lake Baïkal, and from the southern Arctic Circle to the Carpathians (Chaline, 1972; Pucek, 1982a; Balciauskas et al., 2011). In central Europe, few relic populations persist in restricted refuge areas of Scandinavia, northern Germany, and Austria (Pucek, 1982a; Meinig et al., 2008). Regarding *S. subtilis*, its populations inhabit rather open environments (steppes) and its geographical range spreads from Ukraine to northwestern China and Lake Baïkal (Chaline, 1972; Pucek, 1982b). Some isolated populations are present in Hungary, Romania, Bulgaria, and southeastern Poland (Kryštufek et al., 2008).

7. Discussion

Given the current distribution of *Sicista*, from Eastern Europe to Lake Baïkal (a zone mostly associated with taigas and steppes), during the warm global conditions of the Holocene, it is not difficult to infer a harsher environmental scenario for Europe during the Pleistocene, at least during the periods of southwestern expansion of the genus. Little is known about the climatic and ecological requirements of *S. praeloriger*, but if Kowalski (2001) is right in suggesting a close relation with *S. subtilis*, then wide distribution during the Early Pleistocene in Europe (Fig. 3.1) reflects colder and drier conditions than today, but not as pronounced as in the next two stages.

During the Middle Pleistocene, *Sicista* arrived as far south as Chios Island in the Aegean Sea, and, during the Late Pleistocene, as far west as Lezetxiki in the north Iberian Peninsula. The distribution of *S. subtilis* and *S. betulina* in these stages, despite overlapping in central Europe, evidences some degree of polarization, namely, *S. betulina* occurring more to the northwest and *S. subtilis* more to the southeast (Fig. 3.2–3). This tendency continued into the Holocene, although both species have been pushed north- and eastward due to environmental factors.

Today, the northern birch mouse (*S. betulina*) inhabits cold steppes adjoining the Arctic seas which merge southward with the coniferous forest zone (taiga). These conditions are roughly similar to those inferred from the faunal and botanical associations of Lezetxiki II, where the westernmost Eurasiatic specimen of *S. betulina* has been discovered. The latter site includes a mixture of woodland and open landscapes which indicate moderately humid, cold environment.

Climatic constraints could be responsible for the northern birch mouse not spreading further south than the Cantabrian Cordillera in the Iberian Peninsula.

8. Conclusions

The southwesternmost specimen of *S. betulina* and of the genus *Sicista* in Eurasia has been discovered in the early Late Pleistocene site of Lezetxiki II (Arrasate, Basque Country, Spain), in the north of the Iberian Peninsula. It is a right first lower molar indisputably attributed to *S. betulina* on the basis of diagnostic morphological and morphometrical features.

There are three valid species of *Sicista* that inhabited the European subcontinent since the Early Pleistocene, two living, *S. betulina* and *S. subtilis*, and one extinct, *S. praeloriger*. Current Paleartic distribution of the genus, from Eastern Europe to Lake Baïkal, evidences its preference for taigas and steppes.

Average colder and drier conditions during the Pleistocene allowed *Sicista* to get as far south as Chios Island in the Aegean Sea (Middle Pleistocene), and as far west as Lezetxiki in the Iberian Peninsula (Late Pleistocene). Cold, moderately humid environmental conditions, with dominant grasslands and coniferous forests, inferred from the palaeobiological associations (including human remains) at Lezetxiki II, were ideal for *S. betulina*, which inhabited the Basque Country during the last phase of MIS 5.

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Figure

Figure 1

Location of Lezetxiki I and II caves (star) near the village of Arrasate (Basque Country, Spain). Black areas in the right picture represent small towns.

Figure 2

Right first lower molar (m1) of Sicista betulina from Lezetxiki II (Arrasate, Basque Country, Spain).

Figure 3

Palaeogeographic distribution of the different species of Sicista in Europe during the Early, Middle and Late Pleistocene. The data were taken from the same sources as in Table 1. Early/Middle Pleistocene boundary locations (see Table 1) were included in both Early and Middle Pleistocene maps.

Table

Table 1

Detailed list of European locations with the different Sicista species during the Early, Middle and Late Pleistocene. The data were taken from Chaline (1972), Mayhew (1978), Jánossy (1986), Marquet (1989), Nadachowski (1990), Maul (1990, 2002), Rekovets and Nadachowski (1995), Koenigswald and Heinrich (1999), Kowalski (2001), Kalthoff et al. (2007), and Oppliger and Becker (2010).

a Originally defined as *Sicista vinogradovi*.
b Originally defined as *Sicista montana*.