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BIOSTRATIGRAPHY, PALAEOGEOGRAPHY AND PALAEOENVIRONMENTAL SIGNIFICANCE OF *SOREX RUNTONENSIS* HINTON, 1911 (MAMMALIA, SORICIDAE): FIRST RECORD FROM THE IBERIAN PENINSULA

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Abstract

Sorex runtonensis (Mammalia, Soricidae) is a well-known Pleistocene taxon with a broad distribution in Europe. However, no record of the species had been reported from the Iberian Peninsula up to now. Here we present nearly two hundred specimens of *S. runtonensis* recovered from the Lower Red Unit (levels TE7-14) of Sima del Elefante (Sierra de Atapuerca, Burgos, Spain), dated to ~1.1-1.5 Ma. Rigorous morphometrical and morphological analyses allowed the assignation of the items from Sima del Elefante confidently to this taxon, distinguishing them from the several other Pleistocene species of similar size that inhabited Europe. *Sorex runtonensis* survived all through the Pleistocene (and maybe more), but the remains from Sima del Elefante exhibit some traits that appear to be particular to the Early Pleistocene, which agrees with the pre-Jaramillo chronology inferred for the lower levels of the site. Western Palearctic *S. runtonensis* has been regarded as a proxy of patchy and relatively arid, open past biotopes due to its similarity to recent Eastern Palearctic *S. tundrensis*. In light of this fact, and given the high relative quantities of this taxon at the site, previous palaeoenvironmental reconstructions proposed for the lowermost unit of Sima del Elefante should be revised to present a more ecologically diverse scenario than previously thought.

Keywords: Soricidae; palaeontology; prehistory; Early Pleistocene; Iberian Peninsula; Sima del Elefante.

1. Introduction

Recently, some specimens of *Sorex* (*Drepanosorex*) *margaritodon* Kormos, 1930 have been indisputably identified and described at the Lower Red Unit (levels TE7-14) of Sima del Elefante (Sierra de Atapuerca, Burgos, Spain), biochronologically dated to ~1.1-1.5 Ma (Rofes and Cuenca-Bescós, 2013). Therefore, all the items provisionally called *Sorex* sp.2 in Cuenca-Bescós et al. (2013) are now regarded as *S. (D.) margaritodon*. However, there is another type of *Sorex* in the same levels, provisionally called *Sorex* sp.1 in Cuenca-Bescós et al. (2013, 2015) and Rofes and Cuenca-Bescós (2013). It is smaller in size and much more numerous than *S. (D.) margaritodon*.

The combination of characteristics such as the large and triangular internal fossa, the mandibular condyle with articular facets moderately separated and a relatively broad interarticular area, the pigmented teeth, the serrated first lower incisors, and the presence of entoconid crests in the lower molars makes it possible to assign the specimens to the genus *Sorex* (Reumer, 1998). Figuring out the specific identity of the specimens, whose size falls roughly between current representatives of *Sorex minutus* Linnaeus, 1766 and *S. araneus* Linnaeus, 1758, is not an easy task. There are several *Sorex* species from the European Pleistocene that are intermediate in size between *Sorex minutus* and *S. araneus*. Among them we have *S. hundsheimensis* Rabeder, 1972, *S. casimiri* Rzebik-Kowalska, 1991, *S. prealpinus* Heller, 1930, *S. bor* Reumer, 1984, *S. subaraneus* Heller, 1958, and *S. runtonensis* (Rzebik-Kowalska, 1998).

Primary aim of this paper is to describe the Sima del Elefante remains and assign them first to the *S. runtonensis-subaraneus* group and then specifically to *S. runtonensis* using detailed morphological and morphometrical analyses. Next, we question the status of *S. subaraneus* as a valid taxon in light of the current evidence. We then provide a comprehensive overview of the biostratigraphy and evolution of *S. runtonensis* in Europe. Finally, we follow the continental palaeogeography of the species throughout the Pleistocene and discuss the significance of its relative abundance at Sima del Elefante Lower Red Unit, which may alter previous palaeoenvironmental reconstructions made for the site.

2. The site

The Sima del Elefante site (TE from now on) is a major cave infill with a stratigraphic sequence of 16 litho-stratigraphic units, called TE7 to TE21 from lowermost to uppermost. The sequence is 25 m thick and 15 m wide in the exposed section, being located at the Trinchera del Ferrocarril (railway cutting) of the Sierra de Atapuerca (Fig. 1). A palaeomagnetic study has detected a polarity change at the base of unit TE17. The sediments below this unit, from TE7 to TE16, have reversed polarity and have been assigned to the Matuyama chron (>780 ka) (Parés et al., 2006).

The lowermost levels of Sima del Elefante (TE7 to TE14) are collectively known as the Lower Red Unit (TE-LRU), which is extremely rich in paleontological remains, providing one of the best collections of fossil vertebrates from the Early Pleistocene in Europe (Cuenca-Bescós and García, 2007; García et al., 2008; Blain et al. 2010; Cuenca-Bescós et al., 2013; Galán et al., 2015; Núñez-Lahuerta et al., 2015). Burial dating based on terrestrial cosmogenic nuclides (TCN) Al-Be measured in quartz grains yielded an age of 1.22 ± 0.16 Ma for level TE9, and 1.13 ± 0.18 Ma for level TE7, located a few meters below (Carbonell et al., 2008). These two ages are in good agreement with the Matuyama chronology and suggest a Pre-Jaramillo age for the deposits. This chronology is confirmed by the small mammal assemblage (see Cuenca-Bescós et al., 2015 for an updated list of species), key in dating the TE-LRU as the oldest one in Atapuerca (i.e., ~1.1-1.5 Ma, Cuenca-Bescós and Rofes, 2004; Rofes and Cuenca-Bescós, 2006, 2009, 2011, 2013; Cuenca-Bescós et al., 2010, 2013, 2015). The sample of fossil shrews analysed here comes from this Lower Red Unit.

The TE-LRU represents the oldest and most accurately dated record of human occupation in Europe (but see also Toro-Moyano et al. 2013). This takes the form of a hominin mandible and a proximal hand phalanx (from TE9c), 86 Mode 1 stone tools, and many large-mammal bones with clear evidence of human processing (Carbonell et al., 2008; Lorenzo et al., 2015; De Lombera-Hermida et al., 2015).

3. Material and Methods

The specimens were taken from the sedimentary materials coming from the excavations of Sima del Elefante site since 1998. All excavated sediments are water-screened using a stack of nested sieves of decreasing mesh size (5mm, 2mm and 0.5mm, respectively). The product is a concentrate of calcareous fragments from the cave walls, fossil remains of small vertebrates, and fragments of large vertebrates. These concentrates are labelled to maintain rigorous stratigraphic and spatial control. Except for the coarsest concentrate, which is separated using fine forceps without magnification, fossil extraction is done with the aid of a binocular microscope at a magnification of 10x to 20x. Afterwards, a preliminary classification of the microfossils is undertaken, and the information is recorded in the database of the microfauna of Atapuerca. The specimens studied in this paper are stored in the Palaeontology Museum of Zaragoza University.

We analyzed 189 specimens (Table S1 in the Supp. online Info.), most of them isolated mandibles, maxillae and teeth that are either loose or *in situ*. Reumer’s (1984) anatomical nomenclature is of standardized use among scholars dealing with fossil soricids from the Plio-Quaternary; we use it in this study with a few additions from Jin and Kawamura (1996).

A stereo-microscope (Olympus MSZH, objective 64x) connected to a video camera was used to record metric values. We also followed Reumer (1984) in the measurements to be taken and the PE-index, with a few additions from Rabeder (1972) and Rofes and Cuenca-Bescós (2006). The PE-index quantifies the degree of posterior emargination of the large upper teeth. This was calculated for the M1 and M2 by means of the formula: LL + BL / 2 PE – 1. The morphometric analysis was performed using the PAST v3.09 statistical programme (Hammer et al., 2001).

3.1 Dental Terminology and Measurements

A, upper antemolar; **P,** upper premolar; **M,** upper molar; **i,** lower incisor; **a,** lower antemolar; **p,** lower premolar; **m,** lower molar; **L,** length; **H,** height; **W,** width; **BL,** buccal length; **LL,** lingual length; **AW,** anterior width; **PW,** posterior width; **PE,** posterior emargination; **TRW,** trigonid width; **TAW,** talonid width; **Hm1,** height of mandible below m1 (medial side); **Hm2,** height of mandible below m2 (medial side); **HC,** height of the condyle; **WC,** width of the condyle; **LUF,** length of the upper facet (of the condyle); **LLF,** length of the lower facet (of the condyle).

4. Results

4.1. Systematic palaeontology

Class MAMMALIA Linnaeus, 1758

Order EULIPOTYPHLA Waddell, Okada, and Hasegawa, 1999

Family SORICIDAE Fischer von Waldheim, 1814

Subfamily SORICINAE Fischer von Waldheim, 1814

Genus *Sorex* Linnaeus, 1758

Sorex runtonensis Hinton, 1911

Figs. 2-3.

Selected synonyms:

S. kennardi Hinton, 1911

S. aranoides Heller, 1930

S. helleri Kretzoi, 1959

Sorex sp.1, in Cuenca-Bescós et al. (2013, 2015) and Rofes and Cuenca-Bescós (2013).

Type locality: West Runton (UK).

Studied locality: Lower Red Unit (levels TE7-14) of Sima del Elefante (Sierra de Atapuerca, Burgos, Spain).

Selected other localities: Varshets (Bulgaria; Popov, 2003), Rifreddo (Italy; Masini et al., 2005 as *S.* gr. *runtonensis-subaraneus*), Obłazowa Cave, Krucza Skała, Komarowa Cave and Żabia Cave (Poland; Rzebik-Kowalska, 2003, 2006, 2013). For the remaining sites see Rzebik-Kowalska (1998, 2000).

Geographic distribution and age: Great Britain and continental Europe (from Western Russia to the north of the Iberian Peninsula) during its maximum at the Early Pleistocene.

Diagnosis: Given by Hinton (1911), it should be complemented with detailed descriptions by Harrison (1996) and Rzebik-Kowalska (1991, 2000, and 2006).

Measurements: See Tables 1 and 2.

4.2. Description of material from TE-LRU

The dental elements are stained a dark red in the apical part of the crowns. The dental formula of the genus is: 1.5.1.3/1.1.1.3.

A3-A5 (Fig. 2): Only these three antemolars are present in the sample. They are unicuspid, with the cusps situated on the buccal side. The teeth have well-developed cingula on both sides. They decrease in size posteriorly or A4 is roughly the same size as A5.

P4 (Fig. 2): It has a prominent parastyle and well-developed paracone and protocone. The hypocone is connected to the protocone by a weak curving crest. A cingulum runs from the posterobuccal apex of the teeth progressively fading on its way down to the posterior emargination.

M1-M2 (Figs. 2): They are subquadrate in shape. The metacone, protocone, and hypocone are well developed in both teeth. The metaloph is weakly developed, as it is the hypoconal flange. There is a wide and deep valley between the metacone and the metaloph, and a narrower valley between the metaloph and the hypocone. The lingual and posterior cingula are pronounced. The PE-index of M1 is moderate (0.21), and that of M2 is also moderate (0.23).

i1: Tricuspulate. The buccal cingulum is narrow and not pronounced.

a1 (Figs. 3a, b, d): It is long and single-cusped, or with an almost indistinct second cusp in some cases. Wide and well-developed cingula on both sides.

p4 (Figs. 3a, b, d): The occlusal outline is roughly triangular, with an elongation of the posterobuccal corner of the crown. Two main cusps are present, the anterior one being slightly higher. These cusps are connected by a sharp, high ridge which encloses a posterolingual basin on its lingual side. This wide and shallow basin drains steeply posterolingually without reaching the lingual cingulum. The cingula on both sides are thick. The lingual one is more pronounced.

m1-m2 (Figs. 3a, b, d): They have a trapezoidal shape in occlusal view. The protoconid is the highest cusp of the crown, situated anterobuccally to the metaconid. The hypoflexid steeply descends buccally without reaching the buccal cingulum. The hypolophid extends lingually from the hypoconid to the entostylid, which is tiny and almost indistinct. The entostylid is separated from the entoconid by a valley more widely opened on m1. The entoconid is an isolated conical cusp which connects to the posterior base of the metaconid by the entoconid crest, the latter being moderately high. On m1 the talonid is wider than the trigonid. On m2 the talonid is equal to or slightly narrower than the trigonid. The lingual cingulum is broad but hardly pronounced. The buccal cingulum is narrow, well-projected and slightly undulated.

m3: The occlusal outline is nearly semicircular. The trigonid is smaller but basically similar to those of the first two molars. The talonid is smaller than the trigonid but well developed, with discernible hypoconid and entoconid. The entoconid crest is moderately high. The cingula are as on m1 and m2.

Mandible (Fig. 3): It is relatively stout and the coronoid process tall and narrow. The posterior margin of the coronoid process is straight and the anterior one slightly concave. The apex is rounded in lateral and medial views, and slightly curved lingually. The coronoid spicule is small but distinct, and situated close to the apex. The external temporal fossa is deep and extends downwards to the level of the upper sigmoid notch. It is provided with two longitudinal bars parallel to the posterior edge of the coronoid process, the posterior one being usually shorter and less conspicuous. The condyle is rather high with a moderately broad interarticular area. The upper sigmoid notch has a marked ventral emargination. The lower sigmoid notch is straight. The internal temporal fossa is triangular with rounded edges. It extends far upwards to halfway along the coronoid process, and may sometimes continue almost to the apex. In these cases, a trace of a horizontal bar inside the fossa is sometimes discernible. There are either one or two mandibular foramina below the posterior corner of the internal temporal fossa. The mental foramen is situated below the hypoflexid of m1.

5. Discussion

5.1. Morphometry and morphology

The elements included in the morphometric analyses were both dental and mandibular, namely M1, m2 and the horizontal ramus. The measurements used as variables were: the length (L), buccal length (BL), posterior emargination (PE), posterior width (PW), trigonid width (TRW), and the height of mandible below m2 (Hm2). We compared the sample from TE-LRU with all the specimens of valid Pleistocene taxa of *Sorex* from Europe that have these measurements available from the literature. We included an Eurasiatic species as well, i.e. *S. pseudoalpinus* Rzebik-Kowalska, 1991 (n=2), which had representatives in Central Europe during the Pliocene (Rzebik-Kowalska, 1998).

Also, we incorporated *S.* (*Drepanosorex*) *margaritodon* from TE-LRU and Central Europe (Rofes and Cuenca-Bescós, 2013) as size reference.

After a detailed review of recent references (Zaitzev and Baryshnikov, 2002; Rzebik-Kowalska, 2007), we have deliberately left aside from the analyses a series of Middle Pleistocene *Sorex* species from the Northern Caucasus (i.e., *S. volnuchini* Ognev, 1922, *S. satunini* Ognev, 1922, *S. raddei* Satunin, 1895, and *S. doronichevi* Zaitsev and Baryshnikov, 2002) and Plio-Pleistocene taxa from the Transbaikalia/Irkutsk Region (i.e., *S. roboratus* Hollister, 1913, *S. palaeosibiriensis* Mezhezherin, 1972, *S. erbajevae* Rzebik-Kowalska, 2007, and *Sorex baikalensis* Rzebik-Kowalska, 2007), either because they have a geographic range so remote to the Iberian Peninsula that they are very unlikely to be the species from TE-LRU, or because their size/morphology is clearly different, or a combination of both.

Figures 4 and 5 show the results of the principal component analyses (PCA) carried out with the measurements of the upper and lower molars and the mandible (Tables 2 and 3). A closer look at the loads of PC1 and PC2 in both plots (Tables S2 and S3 in the Supp. online Info.) reveals that the load of the different variables in PC1 is roughly homogenous, a sure sign that the first axes represent size in both graphics; PC1 explains 94.39% of the total variance in Fig. 4 and 91.38% in Fig. 5. In PC2 of Fig. 4, by contrast, the contribution of PEM1 is clearly greater, as it is the contribution of Lm2 in PC2 of fig. 5, which means that these components may have a higher morphological load, although they only explain 4% of the variance in Fig. 4 and 7.29% of the variance in Fig. 5. Therefore, size plays an important role in the matrices.

The morphometric analyses of the dentition and mandible of several Pleistocene species of *Sorex* allow us to discard some European taxa for the identity of TE-LRU specimens.

In both plots it is evident that the core values of *S. minutus* and *S. araneus* fall outside the range of TE, especially on PC1 (in fact, *S. minutus* and *S. araneus* distributions roughly delimitate the range of TE in both sides of this axis), meaning that the differences are mainly in size. *Sorex hundsheimensis* (n=1) falls outside the range of TE in Fig. 5, and *S.* (*D.*) *margaritodon* distribution is far from TE's much smaller items in both plots.

More difficult is the situation with *S. bor, S. prealpinus, S. casimiri, S. subaraneus* and *S. runtonensis*: their distributions overlap with TE-LRU in different degrees. *Sorex bor* values, in particular, overlap more with those of *S. runtonensis* than with those of TE, more distinctly on PC2 of both graphics. Morphologically speaking, the hypocones of the upper premolars and molars of TE specimens are well developed while those of *S. bor* are weaker or absent. Also, the longitudinal bars, parallel to the posterior border of the coronoid process and present in all TE specimens, are missing in *S. bor* (Rzebik-Kowalska, 2000; compare TE specimens with those depicted in Plate 7 of Reumer 1984: 32-33).

According to the PCAs, the M1 (n=1) of *S. prealpinus* is morphometrically closer to *S. araneus* than to TE on PC1 (Fig. 4). However, the two individuals included in the analysis of the m2 and mandible fall inside the distribution of TE specimens on both axes (Fig. 5). Concerning morphology, there are several differences: the a1 of *S. prealpinus* is two-cusped, the interarticular area of the condyle is narrower, the posterolingual basin of p4 reaches the cingulum, and the mental foramen is situated farther anterior than in TE items (Popov, 2003; compare TE specimens with those depicted in Fig. 7 of Rzebik-Kowalska, 1991: 363).

Sorex casimiri (n=3) items fall inside the lower values of the distribution of m2/mandible TE specimens on PC2 (Fig. 5), but morphologically they differ from the latter in having a p4 posterolingual basin that reaches the cingulum, a different type of coronoid spicule that is larger and lies higher in the coronoid process, a more delicate coronoid process, and a mental foramen placed farther to the front (Popov, 2003; compare TE specimens with those depicted in Fig. 5 of Rzebik-Kowalska, 1991: 352).

The only specimen of *S. hundsheimensis* included in the analyses falls very close to the *S. araneus* distribution on PC1 and relatively far from TE in this same axis (Fig. 5). In terms of morphology, the mandible of *S. hundsheimensis* is more massive than those of TE; the interarticular area of the condyle is longer; the coronoid process is shorter and broader, the tip being undulated; and the upper premolars and molars are broader mesiodistally and therefore more rectangular shaped (compare TE specimens with those depicted in plate 5 of Rabeder, 1972).

The disparity between the values of the two individuals of *S. pseudoalpinus* included in the analysis is because one of them comes from the Late Miocene (MN13) of China (Storch, 1995) and the other from the Middle Pliocene (MN15) of Poland (Rzebik-Kowalska, 1991). The European specimen in particular is morphometrically closer to *S. subaraneus* than to TE items in both axes of Fig. 5. Morphologically, the coronoid spicule of this taxon is more conspicuous and situated much lower in the coronoid process than it is in the TE specimens. Besides, the mental foramen, as in previous cases, is placed farther to the front (Popov, 2003; compare TE specimens with those depicted in Fig. 6 of Rzebik-Kowalska, 1991: 357).

Therefore, the two candidates remaining for the identity of the specimens from TE-LRU are *S. runtonensis* and *S. subaraneus*. Rzebik-Kowalska (1991: 377) proposed a series of characters to distinguish these two taxa, i.e., *S. subaraneus* having a more massive mandible; a different shape of the coronoid process, which is wider; a shorter internal temporal fossa; a condyle that is comparatively wide and low with a trapezoidal interarticular area (not rectangular as in *S. runtonensis*); and a larger i1 with cingulum less distinct than in *S. runtonensis*. But also, the same author adds that the morphology of the processes in *S. subaraneus* is highly variable, and it is hard to discriminate this species from *S. runtonensis*. It is the case that *S. runtonensis* is polymorphic as well, Rzebik-Kowalska (2000: 9-10) recording five different morphotypes for the Early Pleistocene Romanian site of Betfia.

Given all the aforementioned, Masini et al. (2005: 83) opted for considering their fragmentary material from the Middle Pleistocene locality of Rifreddo (Italy) as belonging to *Sorex* gr. *runtonensis-subaraneus*. We provisionally followed this criteria in a recent conference abstract (Rofes et al., 2014). However, our material is much more numerous and complete than that of Rifreddo, which allowed us to perform a multivariate analysis. Both the PCAs for the M1 and those for m2/mandible (Figs. 4 and 5) show that the material from TE-LRU morphometrically fits slightly better with *S. runtonensis* than with *S. subaraneus*, being the overlapping of distributions more obvious in the upper tooth. This fact, together with an exhaustive review of many bibliographic references displaying pictures, drawings and detailed descriptions (Sulimski, 1959, 1962; Bartolomei, 1964; Van der Meulen, 1973; Bishop, 1982; Rzebik-Kowalska, 1991, 2000, 2003, 2006, 2013; Maul, 2001; Zaitzev and Baryshnikov, 2002; Popov, 2003), allows us to assign the items from TE to *S. runtonensis*. In particular, most of the specimens from TE correspond to morphotypes A and D of Rzebik-Kowalska (2000: 9) for the coronoid process, and morphotypes A and B of the same author (2000: 10) for the condyle. All the specimens provisionally called

Sorex sp.1 in Cuenca-Bescós et al. (2013), Rofes and Cuenca-Bescós (2013), and Cuenca-Bescós et al. (2015) should be regarded from now on as *S. runtonensis*.

Having considered the similarities in shape and appearance between *S. runtonensis* and *S. subaraneus*, and the polymorphic nature of both, one can reasonably wonder if the criterion to distinguish them given by Rzebik-Kowalska (1991: 377), namely, “if they appear together in the same locality *S. subaraneus* will always be a little bigger”, is enough to consider that they are different species. When populations from different geographic locations and ages are evaluated (e.g., Rzebik-Kowalska, 1991, 2000, 2006, 2013; Maul, 2001; Popov, 1988, 2003; Masini et al., 2005; this work), the size range of the two species overlaps to some extent. In consequence, highly polymorphic *S. runtonensis* and *S. subaraneus* could be regarded as a morphometrical continuum of the same species, in which case the name *S. runtonensis* would have priority as being stated before (i.e., *S. runtonensis* Hinton, 1911 vs. *S. subaraneus* Heller, 1958). A rigorous geometric morphometric study would be required to solve the problem and possibly establish a synonymy of these two taxa.

5.2. Biostratigraphy and evolution

Unlike *S.* (*D.*) *margaritodon*, the other species of *Sorex* recently described for TE-LRU (Rofes and Cuenca-Bescós, 2013), *S. runtonensis* was very common in Europe throughout the Pleistocene. The oldest record of the species is from Varshets (Early Pleistocene, MN17) in north Bulgaria (Popov, 2003); some specific characteristics and the size of these specimens indicate that they are primitive representatives of *S. runtonensis*. There are a number of Pliocene references for *S.* cf. *runtonensis* and *S.* aff. *runtonensis* (i.e., MN15-16) compiled by Rzebik-Kowalska (1998: 64-65). However, this author states that all data on the occurrence of *S. runtonensis* previous to the Pleistocene should be treated with caution, because very likely those specimens belong to another taxon (Rzebik-Kowalska, 1998: 64).

The latest records for *S. runtonensis* come from Late Pleistocene localities in the UK, Germany and Poland (Rzebik-Kowalska, 1998, 2006). Arguably, the species could have survived into the Holocene, if we consider as reliable the 21 specimens found at the Holocene Layer-A of Komarowa Cave in Poland (Rzebik-Kowalska, 2006), which, according to the author, we have no reason to distrust.

Regarding the specimens from TE-LRU, we observe in Fig. 4 (upper teeth PCA) that, with the exception of one specimen, their distribution fits morphometrically better with that of Early Pleistocene *S. runtonensis* from Betfia than with the mean value of Late Pleistocene Komarowa items. Figure 5 (m2/mandible PCA) shows that TE-LRU specimens' distribution concentrates much more around the mean value from Varshets (Bulgaria) than around other specimens from Romania and Poland. Considering this together with the fact that the specimens from TE-LRU have two of the three characteristics (i.e., a1 with a trace of a second cusp and a relatively stoutly built mandible) interpreted as "primitive" by Popov (2003: 51), we can arguably conclude that the Spanish specimens are also morphometrically primitive.

The TE-LRU has been biostratigraphically dated as older than the Jaramillo reverse subchron, its upper boundary being at roughly 1.1 Ma (Cuenca-Bescós et al., 2010, 2013, 2015). This upper limit is marked by the last local record of some rodents (*Ungaromys nanus*, *Allophaiomys lavocati*, *A. nutiensis*, *A. burgondiae*, *Castillomys rivas*, and *Arvicola jacobeus*), one talpid (*Galemys* cf. *kormosi*), one erinaceid (*Erinaceus* cf. *praeglacialis*), and four soricids (*Crocidura kornfeldi*, *Beremendia* *fissidens*, *Asoriculus gibberodon*, and *S.* (*D.*) *margaritodon*). Now we can add *S. runtonensis* to the list of soricids, as the specimens from TE-LRU seem to correspond morphologically and morphometrically to a primitive form of the species, apparently restricted to the Early Pleistocene. We can also provisionally add this taxon to the representatives of Faunal Unit (FU) 1 (Cuenca-Bescós and García, 2007; Cuenca-Bescós et al., 2010, 2013, 2015), the oldest FU of the Atapuerca record.

The identity of the *Sorex* spp. from the neighbouring site of Gran Dolina (TD), whose Lower Pleistocene layers (TD3-6) cover the period from the Jaramillo subchron to the Matuyama-Brunhes boundary (i.e., ~0.99-0.78 Ma, Berger et al., 2008; Duval et al., 2012; Cuenca-Bescós et al., 2015), remains to be elucidated. Given the conspicuous faunal turnover that characterizes the transition from FU1 (=TE-LRU) to FU2 (Early Pleistocene layers of TD) of Atapuerca (Cuenca-Bescós et al., 2010, 2015), the local survival of *S. runtonensis* after the Jaramillo subchron seems highly unlikely. In fact, 80% of the small mammals from TE-LRU disappeared, including all other taxa of soricids (Cuenca-Bescós et al., 2015).

Finally, it is also remarkable that, according to Rzebik-Kowalska’s data (2006: 96-97), *S. runtonensis* populations from Europe increased in size during the Late Pleistocene.

5.3. Palaeogeography and palaeoecology

If we exclude the uncertain records, *S. runtonensis* was present in the current territories of Austria, Bulgaria, Croatia, Czech Republic, France, Germany, Hungary, Italy, Poland, Romania, and the UK (Rzebik-Kowalska, 1998, 2000, 2013; Popov 2003; Kotsakis et al., 2003; Sala and Masini, 2007) during the Early Pleistocene (Fig. 6). Now we can add Spain, specifically the north of the Iberian Peninsula, to the previous list.

Remains of *S.* cf. *runtonensis* from this period were also found in Slovakia (Fejfar and Horáček, 1983), and there are findings of *S. runtonensis* from Poland and Russia from the Early/Middle Pleistocene boundary (Rzebik-Kowalska, 1991; Birûkov et al., 1992).

At the Middle Pleistocene (Fig. 6), the distribution of *S. runtonensis* includes the Czech Republic, France, Germany, Italy, Romania, and the UK (Rzebik-Kowalska, 1998, 2000; Masini et al., 2005). As *S.* cf. *runtonensis* it is also reported from Austria, Greece, and Russia. This last record, from Treugolnaya Cave in the Northern Caucasus (Zaitzev and Baryshnikov, 2002: 291-293 and Fig. 5 therein) appears particularly trustworthy to us, which is not the case with the specimens vaguely identified as "*Sorex* sp. size *S. helleri*" at the Spanish site of Aridos 1 (López-Martínez, 1980). A new revision of this material is necessary to verify the identity of these remains.

During the Late Pleistocene (Fig. 6), the distribution of the species is restricted to Germany, Poland, and the UK (Rzebik-Kowalska, 1998, 2003, 2006). To this, we have to add the relict Holocene population from Komarowa Cave (Fig. 6) (Rzebik-Kowalska, 2006). As is evident from our maps, *S. runtonensis* had its peak-distribution at the European continent during the Early Pleistocene, at least in a longitudinal sense, probably spanning from Western Russia all the way to Spain. Its range diminished in Central Europe during the Middle Pleistocene. In spite of this decline, the species reached southern latitudes (i.e., Italy and Greece), and some populations became isolated, such as those from Romania, Greece and Western Russia. The Late Pleistocene witnessed the near extinction of the taxon, with the only exception being the endemic Holocene specimens from Poland. The absence of *S. runtonensis* from the Polish record during the Middle Pleistocene is surprising, especially because it is the zone where the species survived for the longest period subsequently.

Phylogenetically speaking, the origin of *S. runtonensis* is unclear, but according to Osipova et al. (2006) it is very similar in morphology to the widely distributed extant Eastern Palearctic species *S. tundrensis* Meriam, 1900. Based on this, Rzebik-Kowalska (2006) suggested that these two forms may be conspecific. However, there is a considerable spatial gap between the distributions of Western Palearctic *S. runtonensis* and Eastern Palearctic *S. tundrensis* (compare Fig. 6 with the map at http://www.iucnredlist.org/details/41422/0). This fact together with the high intraspecific variability of *S. tundrensis* (eight subspecies described for East Siberia; Yudin, 1989) makes it very hard to argue for a synonymyzation (Osipova et al., 2006; Rzebik-Kowalska, 2013).

Sorex tundrensis inhabits different biotopes from arctic tundra to steppe, and tolerates more open and dry environments than other species of the genus. It is therefore one of the most eurytopic species of *Sorex*. Given the great similarity between fossil *S. runtonensis* and recent *S. tundrensis*, it is plausible to assume that they have similar ecological preferences, and *S. runtonensis* may be regarded as a proxy of either patchy or relatively arid, open (i.e., tundra, steppe forest) past biotopes (Osipova et al., 2006; Rzebik-Kowalska, 2006, 2013).

Taxonomically and quantitatively, the TE-LRU has been regarded as representing a relatively stable climatic period of predominant warm-temperate and humid conditions (Blain et al., 2010; Rodríguez et al., 2011; Cuenca-Bescós et al., 2013; Galán et al., 2015). Moreover, a palaeoenvironmental reconstruction of the TE-LRU, based on the distribution of Eulipotyphla throughout the sequence (Cuenca-Bescós and Rofes, 2004; Rofes and Cuenca-Bescós, 2006, 2009, 2011), reflects a succession of three phases: warm-cold-warm (w-c-w). These were correlated with the Waalian pollen episode of northern central Europe (Zagwijn, 1998), the only one that contains the same w-c-w phases, and the chronology of which (1.25-1.5 Ma) concurs with the period of inverse magnetic polarity prior to the positive Jaramillo subchron proposed for this period (Carbonell et al., 2008; Cuenca-Bescós et al., 2010, 2013, 2015).

In that reconstruction, *Sorex* spp. (now *S.* (*D.*) *margaritodon* and *S. runtonensis*) were tentatively taken as proxies of cold and humid conditions based on actualistic assumptions. This characterization is likely correct for the large *S.* (*D.*) *margaritodon* (Rofes and Cuenca-Bescós, 2013), but not entirely accurate for the smaller *S. runtonensis*, which, as seen above, is representative of patchy landscapes with a bias towards arid and steppe conditions. Given the high numbers of this taxon in TE-LRU (n=189), which makes them proportionally significant, the interpretation of the degree of humidity and forestation of these levels should be reconsidered and probably adjusted. Moreover, if we consider the presence of other taxa representative of open-dry landscapes, such as the arvicolines (*Allophaiomys*, *Ungaromys*, *Pliomys*) or the anuran *Epidalea calamita*, the habitats in the vicinity of Atapuerca during TE-LRU should be regarded as much more diverse than previously assumed.

6. Conclusions

Nearly 200 specimens of *Sorex runtonensis* have been retrieved from the Lower Red Unit (levels TE7-14) of Sima del Elefante (Sierra de Atapuerca, Burgos, Spain), dated to the second third of the Early Pleistocene (~1.1-1.5 Ma). This is the first record of this species ever reported for the Iberian Peninsula.

A combined set of morphometrical and morphological traits has allowed us to confidently assign the specimens from TE-LRU, first to the group *runtonensis-subaraneus*, and then to the species *S. runtonensis*, distinguishing them from the several other Pleistocene *Sorex* species of Europe that are similar in size, i.e., *S. bor*, *S. prealpinus*, *S. casimiri*, *S. hundsheimensis*, and the Pliocene *S. pseudoalpinus*. The polymorphic nature of both *S. runtonensis* and *S. subaraneus* does not allow a reliable distinction between them. A detailed geometric morphometric study would be necessary to establish or reject a synonymy, in which positive case the name *S. runtonensis* would have priority as being older.

Sorex runtonensis inhabited Europe throughout the Pleistocene (since MN17), and possibly during the beginning of the Holocene as a relict population in Poland. It reached its maximum geographical distribution at the Early Pleistocene, spanning from Western Russia to the north of the Iberian Peninsula. The TE-LRU assemblage is from this period, and the specimens appear to have some primitive traits restricted to the Early Pleistocene. This is consistent with the pre-Jaramillo subchron (i.e. >1.1 Ma) small-mammal fauna that dominate FU1 (=TE-LRU), the oldest fauna of the Atapuerca record.

Fossil Western Palearctic *S. runtonensis* is very similar to recent Eastern Palearctic *S. tundrensis*, the latter currently inhabiting Siberian plains. Despite the fact that a synonymy between the two species appears difficult to support, it makes sense to infer similar ecological requirements, therefore making *S. runtonensis* a proxy of patchy and relatively open past biotopes. In light of this fact, and given the high proportions of this taxon and the presence of other representatives of arid biotopes in TE-LRU, the palaeoenvironmental reconstructions proposed for this unit up to now should be revised.

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Figure captions

Fig. 1. Geographic location of the Sierra de Atapuerca (Burgos, Spain) and a plan view of the sites and the cave system (left). The underground galleries are shaded.

Fig. 2. Incomplete right maxilla of *Sorex runtonensis* (MPZ 2015/1624) from the Lower Red Unit of Sima del Elefante, in occlusal view.

Fig. 3. Incomplete left mandible of *Sorex runtonensis* (MPZ 2015/1746) from the Lower Red Unit of Sima del Elefante, in **a** lateral, **b** occlusal, **c** posterior, and **d** medial views.

Fig. 4. Principal component analysis (PCA) of the upper dentition showing plots of components 1 against 2. Measurements other than those of *Sorex runtonensis* from Sima del Elefante were taken from Furió (2007), Koufos et al. (2001), Popov (2003), Reumer (1984), Reumer and Hordijk (1999), Rofes and Cuenca-Bescós (2013), and Rzebik-Kowalska (1991, 2000, 2006). Measurements: BLM1, PEM1 and PWM1. Details are to be found in Table S2 of the Supp. online Info.

Fig. 5. Principal component analysis (PCA) of the lower dentition and mandible showing plots of components 1 against 2. Measurements other than those of *Sorex runtonensis* from Sima del Elefante were taken from Furió (2007), Harrison and Clayden (1993), Heinrich (1983), Marchetti et al. (2000), Popov (2003), Rabeder (1972), Rofes and Cuenca-Bescós (2013), Rzebik-Kowalska (1991, 2000, 2006, 2007), and Storch (1995). Measurements: Lm2, TRWm2, and Hm2. Details are to be found in Table S3 of the Supp. online Info.

Fig. 6. Pleistocene and early Holocene (relict) distributions of *Sorex runtonensis* in Europe. Data compiled from Birûkov et al. (1992), Fejfar and Horáček (1983), Masini et al. (2005), Popov (2003), Rzebik-Kowalska (1991, 1998, 2000, 2006, 2013), and Zaitzev and Baryshnikov (2002).


The Atapuerca sites
FRANCE
BURGOS
Atlantic Ocean
Zaragoza
Barcelona
Madrid
PORTUGAL
SPAIN
Mediterranean Sea
Sevilla
0
50
100 m
GranDolina
Trinchera Zarpazos
Trinchera Galería
Trinchera Norte
Cueva del compresor
TRINCHERA DEL FERROCARRIL
Sima del Elefante
Galería del betún
Galería baja
Cueva peluda
CUEVA MAYOR
Galería del Silo
Galería del silex
Present entrance to Cueva Mayor
Cueva del Silo
N
Sima de los Huesos

Figure 1

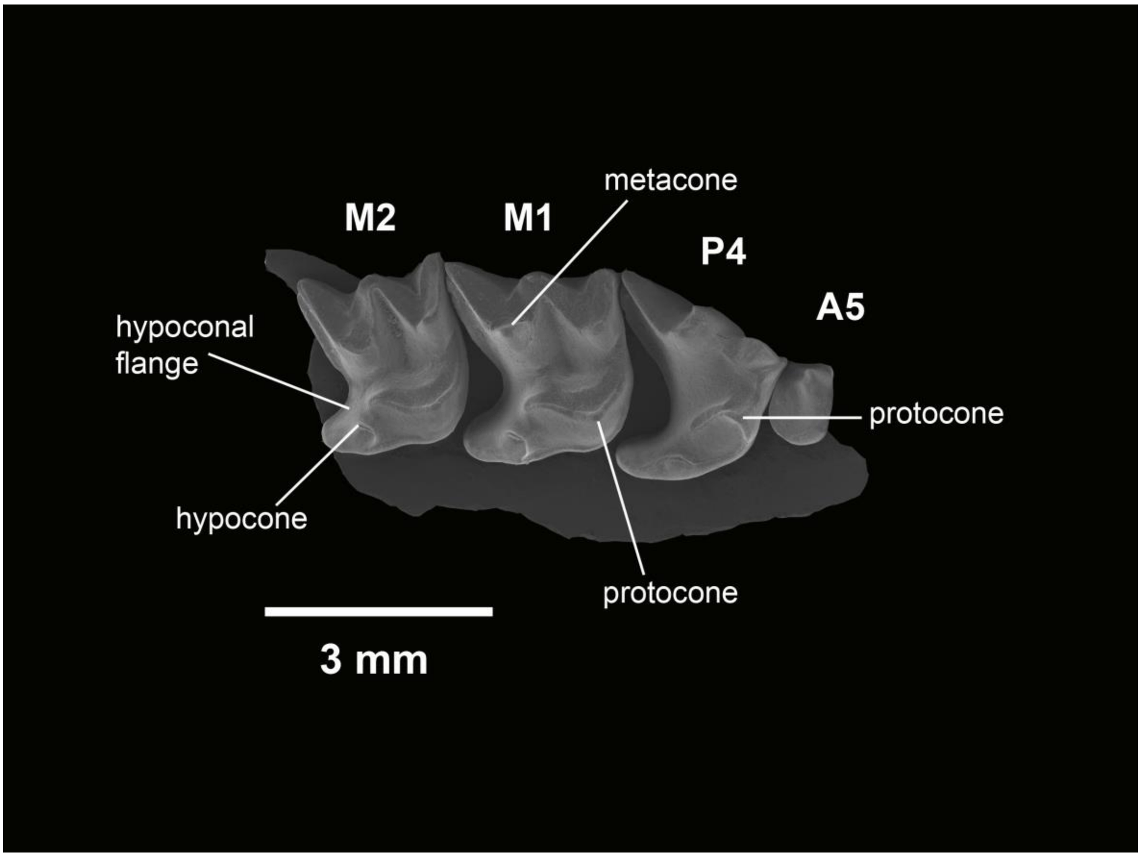
M2
M1
metacone
P4
A5
hypoconal flange
protocone
hypocone
protocone
3 mm

Figure 2

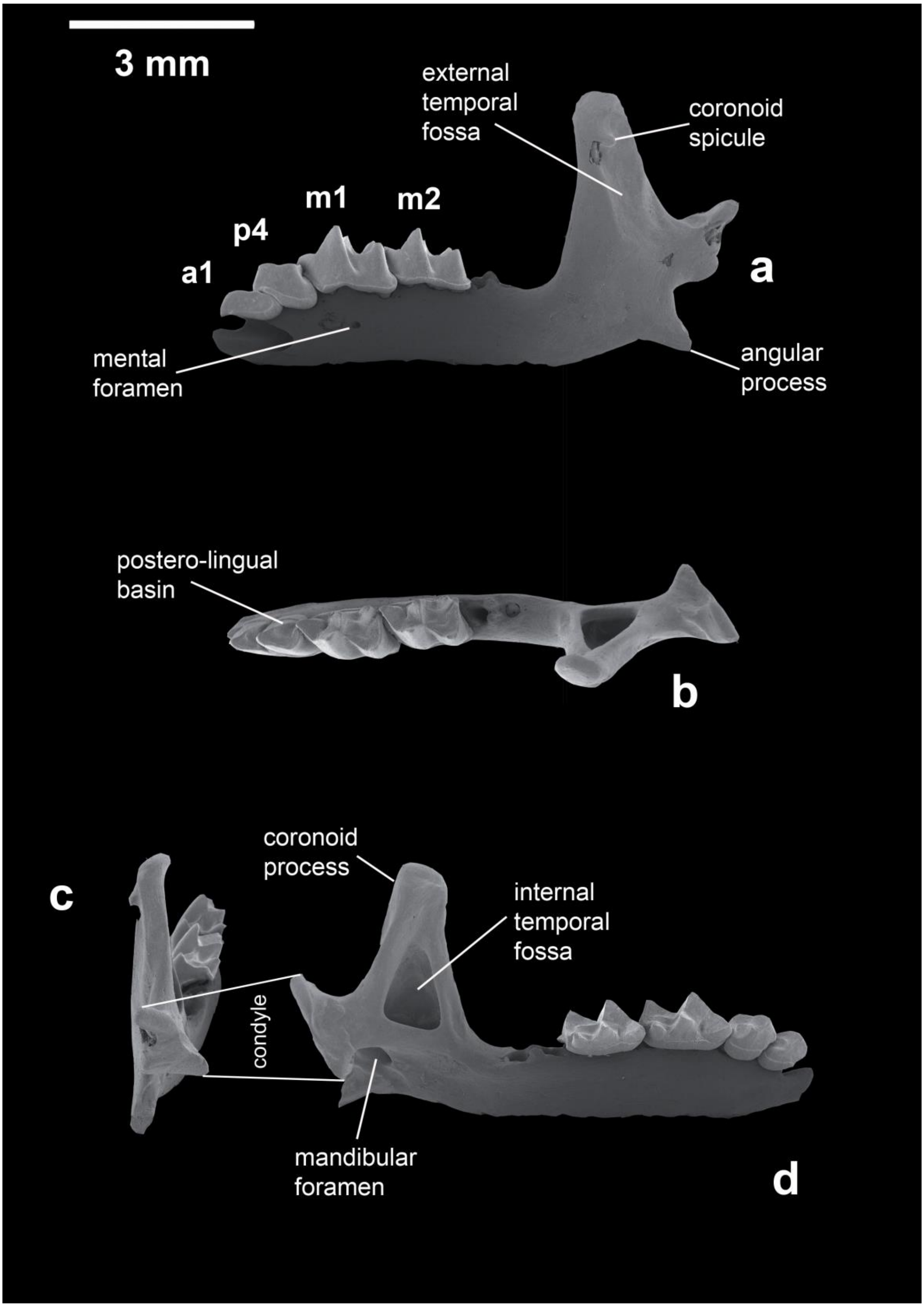
3 mm
external temporal fossa
coronoid spicule
m1
m2
p4
a1
a
mental foramen
angular process
postero-lingual basin
b
coronoid process
c
internal temporal fossa
condyle
mandibular foramen
d

Figure 3

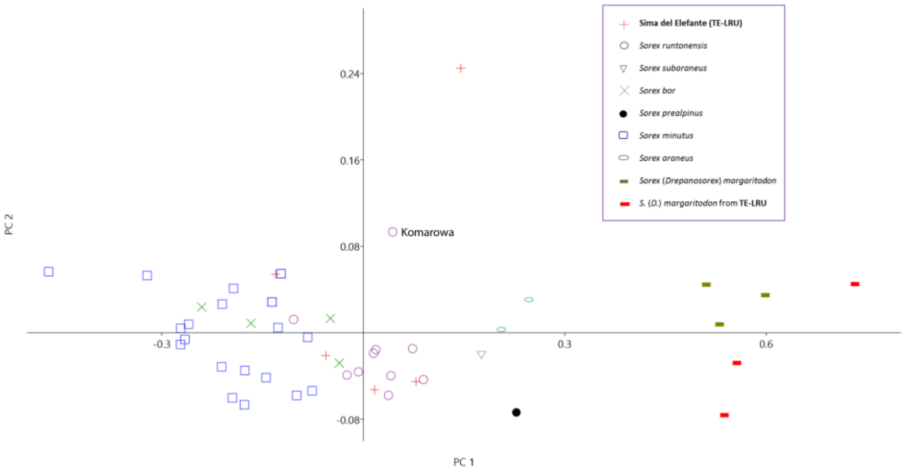
Sima del Elefante (TE-LRU)
Sorex runtonensis
Sorex subaraneus
Sorex bor
Sorex prealpinus
Sorex minutus
Sorex araneus
Sorex (Drepanosorex) margaritodon
S. (D.) margaritodon from TE-LRU
Komarowa
0.24
0.16
0.08
-0.08
-0.3
0.3
0.6
PC 2
PC 1

Figure 4

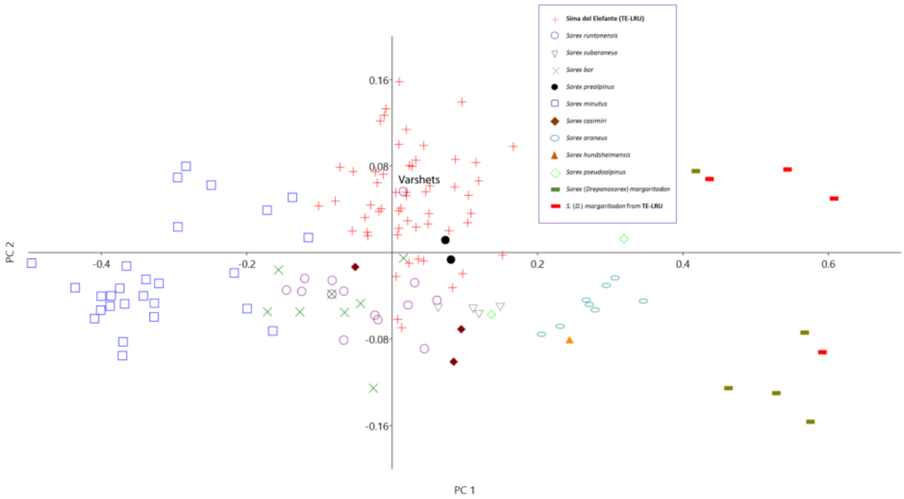
Sima del Elefante (TE-LRU)
Sorex runtonensis
Sorex subaraneus
Sorex bor
Sorex prealpinus
Sorex minutus
Sorex casimiri
Sorex araneus
Sorex hundsheimensis
Sorex pseudoalpinus
Sorex (Drepanosorex) margaritodon
S. (D.) margaritodon from TE-LRU
Varshets
0.16
0.08
-0.08
-0.16
-0.4
-0.2
0.2
0.4
0.6
PC 2
PC 1

Figure 5

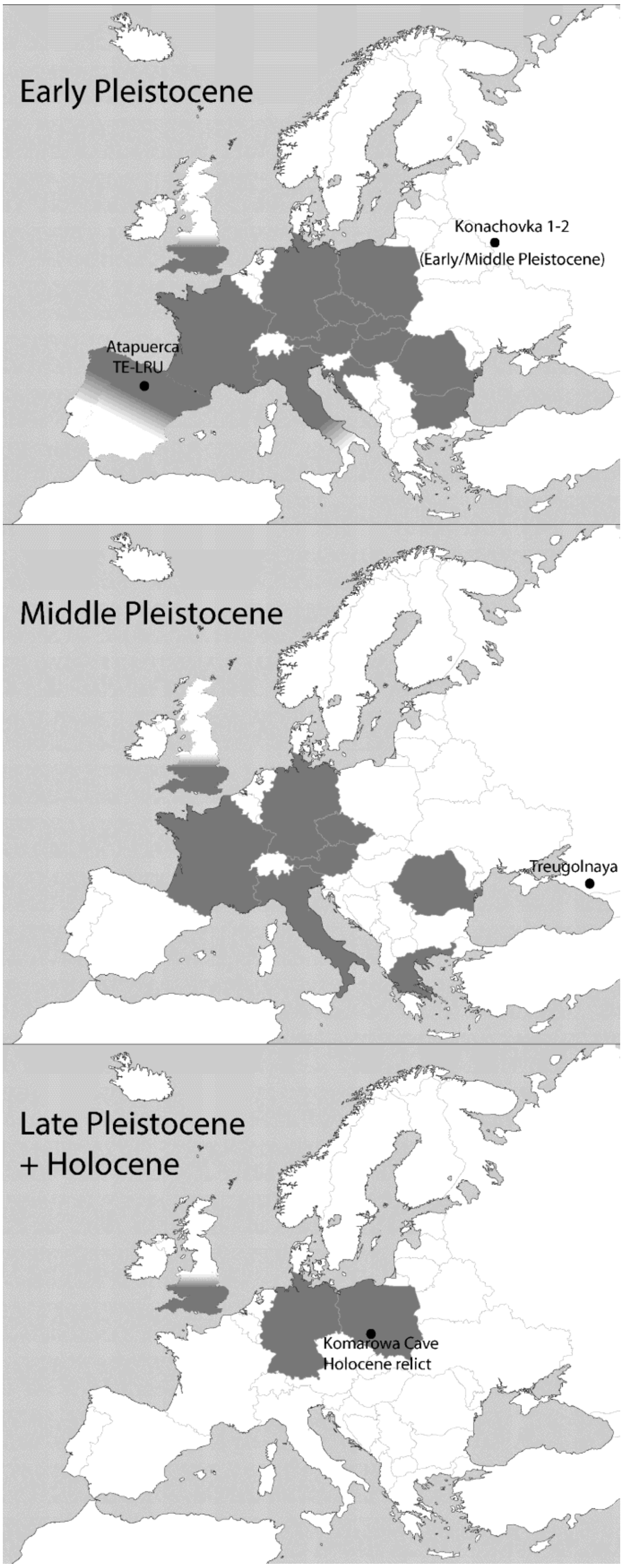
Early Pleistocene
Konachovka 1-2
(Early/Middle Pleistocene)
Atapuerca
TE-LRU
Middle Pleistocene
Treugolnaya
Late Pleistocene
+ Holocene
Komarowa Cave
Holocene relict

Figure 6

Table captions

Table 1. Measurements (in mm) of the upper dentition of *Sorex runtonensis* from the Lower Red Unit of Sima del Elefante. *n*, number of specimens; *min*, minimum value; *max*, maximum value.

Table 2. Measurements (in mm) of the lower dentition and mandible of *Sorex runtonensis* from the Lower Red Unit of Sima del Elefante. *n*, number of specimens; *min*, minimum value; *max*, maximum value.

Table 1

Levels		**TE7**				**TE9**				**TE10**	**TE12**				**TE14**
Element	**Measure**	n	min	mean	max	n	min	mean	max		n	min	mean	max	
I1	L							1.44							
	H							0.95							
	LT							0.75							
P4	BL	2	1.42	1.50	1.57	5	1.32	1.39	1.44				1.43		1.66
	LL	2	1.10	1.17	1.23	5	1.07	1.11	1.14				1.05		1.24
	PE	2	0.91	0.98	1.05	5	0.88	0.93	1				0.79		1.1
	W	2	1.43	1.54	1.65	5	1.32	1.37	1.42				1.48		1.68
M1	BL	2	1.36	1.50	1.63	3	1.27	1.49	1.77	1.37			1.35		1.54
	LL	2	1.21	1.44	1.67	3	1.23	1.39	1.64	1.34	2	1.26	1.31	1.36	1.58
	PE	2	1.29	1.32	1.35	3	1.05	1.17	1.42	1.02	2	1.01	1.02	1.03	1.26
	AW	2	1.35	1.44	1.53	3	1.32	1.51	1.81	1.38	2	1.34	1.37	1.39	1.76
	PW	2	1.48	1.69	1.89	3	1.35	1.61	1.95	1.5			1.42		1.95
M2	BL	2	1.18	1.19	1.2	2	1.16	1.33	1.5	1.19					1.15
	LL	3	1.12	1.14	1.15	2	1.1	1.28	1.45	1.17					1.13
	PE	3	0.89	0.94	1	2	0.92	1.10	1.28	0.97					0.95
	AW	3	1.34	1.37	1.41	2	1.43	1.67	1.9	1.41					1.4
	PW	2	1.37	1.38	1.39	2	1.36	1.57	1.77	1.4					1.21

Table 2

Levels		**TE7**				**TE8**				**TE9**				**TE10**				**TE12**				**TE13**				**TE14**			
Element	**Measure**	n	min	mean	max	n	min	mean	max	n	min	mean	max	n	min	mean	max	n	min	mean	max	n	min	mean	max	n	min	mean	max
I1	L			3.23		6	3.01	3.13	3.23	5	3.11	3.21	3.32	3	3.13	3.25	3.38			3.17									
	H			0.83		10	0.71	0.79	0.88	5	0.67	0.85	0.89	3	0.78	0.81	0.84			0.86									
p4	L			0.95		3	0.89	0.96	1.04	10	0.95	1.03	1.34	2	0.99	1.03	1.07			1.05		2	1.01	1.05	1.09				
	W			0.68		3	0.5	0.63	0.71	10	0.64	0.7	0.92	2	0.69	0.72	0.74			0.66		2	0.69	0.73	0.77				
m1	L	5	1.32	1.46	1.54	21	1.14	1.43	1.69	33	1.3	1.51	1.85	3	1.4	1.47	1.54	3	1.43	1.48	1.53	2	1.5	1.52	1.54				
	TRW	5	0.72	0.78	0.85	21	0.63	0.76	1.01	34	0.72	0.81	1.01	3	0.78	0.78	0.79	4	0.78	0.81	0.83	2	0.68	0.79	0.8				
	TAW	5	0.8	0.84	0.93	21	0.69	0.83	1.09	34	0.74	0.84	1.1	3	0.79	0.8	0.8	4	0.79	0.82	0.85	2	0.81	0.84	0.86				
m2	L	7	1.25	1.34	1.39	18	1.25	1.32	1.53	31	1.21	1.34	1.6	6	1.21	1.34	1.44	7	1.2	1.28	1.32	4	1.31	1.34	1.36	2	1.21	1.28	1.34
	TRW	7	0.7	0.76	0.85	18	0.71	0.78	1	32	0.69	0.78	1	6	0.71	0.76	0.79	7	0.74	0.77	0.84	4	0.7	0.76	0.8	3	0.75	0.76	0.76
	TAW	7	0.69	0.75	0.82	18	0.65	0.73	0.95	31	0.66	0.74	1	6	0.68	0.71	0.75	7	0.7	0.73	0.76	4	0.7	0.73	0.76	2	0.72	0.73	0.73
m3	L	2	0.99	1.03	1.06	6	0.94	1.01	1.13	14	0.98	1.02	1.14	4	0.99	1.03	1.07	3	1.02	1.03	1.05			1.02				1.05	
	W	2	0.59	0.61	0.62	6	0.55	0.62	0.77	15	0.56	0.6	0.67	4	0.59	0.61	0.62	3	0.56	0.59	0.62			0.64				0.64	
m1-m3	L	4	3.54	3.63	3.76	15	3.35	3.58	4.13	22	3.37	3.58	4.24			3.54		2	3.44	3.45	3.46			3.63					
Ramus	L	5	4.09	4.27	4.48	3	4.11	4.21	4.35	12	4.05	4.19	4.41	2	4.41	4.42	4.42			4.26		3	4.23	4.24	4.25				
	H			3.86		3	3.67	3.73	3.8	17	3.44	3.8	5.02	6	3.75	3.87	3.99	3	3.67	3.74	3.78	4	3.56	3.73	3.87	4	3.5	3.69	3.79
	Hm1	6	1.06	1.22	1.45	12	1.02	1.16	1.24	35	1.03	1.2	1.76	3	1.19	1.24	1.31	4	1.18	1.21	1.23	4	1.13	1.19	1.23				
	Hm2	9	1.01	1.18	1.42	26	1.07	1.18	1.68	48	1.07	1.21	1.72	10	1.16	1.22	1.31	12	1.14	1.21	1.34	4	1.17	1.18	1.2	3	1.17	1.18	1.19
	HC			1.62		5	1.55	1.62	1.69	14	1.32	1.62	2.15	7	1.52	1.63	1.7	2	1.62	1.64	1.65	6	1.5	1.62	1.69	3	1.49	1.54	1.59
	WC			1.07		5	0.92	0.95	0.99	16	0.87	1	1.3	7	0.93	1.01	1.1	3	0.91	0.98	1.03	6	0.94	0.99	1.06	3	0.92	0.93	0.96
	LUF			0.71		5	0.6	0.69	0.8	1	0.4	0.72	1.0	7	0.6	0.71	0.7	3	0.7	0.75	0.8	6	0.6	0.74	0.8	3	0.7	0.73	0.7

			1		5	4	4		6		6		6		2				4		3		2		5
			0.9		1.0	1	0.8		1.3		0.9		1.1		0.9		1.0		0.9		1.1		0.9		
LLF	1.09	5	5	0.98	5	7	8	1.04	2	7	9	1.05	4	4	3	1	8	7	5	1.05	2	3	3	0.96	1

Highlights

First record of *Sorex runtonensis* in Iberia is from Sima del Elefante (Burgos, Spain).

Morphological and morphometrical data support the assignation.

The specimens of Sima del Elefante display some particular Early Pleistocene traits.

S. runtonensis is regarded as representative of tundra and steppe biotopes.

Previous palaeoenvironmental reconstructions should be revised according to this.