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The shrews (Soricidae, Mammalia) of the Early and Middle Pleistocene of Gran Dolina (Atapuerca, Spain): reassessing their paleontological record in the Iberian Peninsula

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ABSTRACT

Soricids are small mammals with a mainly invertebrate diet. They are generally termed insectivores and are part of the mammalian Order Eulipotyphla. Soricids of the Early-Middle Pleistocene postdating the Jaramillo subchron are poorly known in the Iberian Peninsula, except for *Dolinasorex glyphodon*, endemic to north Spain, and scattered records of *Sorex minutus*, *Crocidura russula*, *Crocidura kornfeldi* and indeterminate species of *Crocidura*, *Sorex* and *Neomys*. This is mainly due to the scarcity of sites and the fragmentary fossil remains. In contrast, the record of soricids in the rest of Europe during this period is wide: there are sites with up to ten different species in the same stratigraphic level. As Gran Dolina (Atapuerca, Spain) provides one of the best anthropological, archaeological and faunal records of the late-Early (post-Jaramillo) to early-Middle Pleistocene, and as this occurs in an excellent, well-studied stratigraphic sequence documenting terrestrial environments, we here undertake an exhaustive revision of 200 fragmentary mandibles of this group of small mammals. Nine soricid taxa were identified in this archaeo-paleontological site: *Sorex minutus*, *Sorex* ex gr. *runtonensis-subaraneus*, *Sorex* (*Drepanosorex*) ex gr. *margaritodon-savini*, *Dolinasorex glyphodon*, *Asoriculus gibberodon*, *Neomys* cf. *newtoni*, *Neomys* cf. *fodiens*, Neomyni cf. *Macroneomys* and *Crocidura kornfeldi*. This is the first record of *Neomys* cf. *newtoni* in the Iberian Peninsula, the second specimen of Neomyni cf. *Macroneomys*, and the youngest record of *A. gibberodon* worldwide. Some of these taxa exhibit particularities when compared to their counterparts in the rest of the continent, adding to the variability of the species. Relict populations of *Asoriculus gibberodon* endured in the Iberian Peninsula into post-Jaramillo times, even after they had already disappeared from the rest of Europe.

1. Introduction

The post-Jaramillo fossil record of the family Soricidae (Eulipotyphla, Mammalia) from the Early-Middle Pleistocene in the Iberian Peninsula is scant. The known post-Jaramillo taxa dated to the Early Pleistocene are: *Dolinasorex glyphodon*, *Sorex minutus*, *Sorex* sp., *Neomys* sp., Soricinae gen. et sp. indet., *Crocidura russula*, *Crocidura kornfeldi*, *Crocidura* sp., and Soricidae gen. et sp indet. (Sesé and Ruiz Bustos, 1992; Sesé, 1994; Agustí et al., 2010; Lozano-Fernández et al., 2015; Cuenca-Bescós et al., 2016; Maldonado-Garrido et al., 2017; López-Jiménez et al., 2018). The taxa documented so far at the Middle Pleistocene are: *S. minutus*, *Sorex* ex gr. *araneus-coronatus*, *Sorex* sp., *Neomys* sp., Soricinae gen. et sp. indet., *Crocidura suaveolens*, *C. russula*, *C.* cf. *russula*, *C.* aff. *russula*, *Crocidura* sp., and Soricidae gen. et sp. indet. (López-Martínez, 1980; Ruiz Bustos et al., 1982; Sevilla, 1988; Arribas, 1994; Sesé, 1994; Sesé and Soto, 2005; Sesé et al., 2011, 2016; Laplana et al., 2013; Sesé and

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López-Martínez, 2013; Cuenca-Bescós et al., 2016; López-García et al., 2016, 2018; Fagoaga et al., 2017). See Appendix A for details of the sites (data obtained from López-Martínez, 1980; Ruiz-Bustos et al., 1982; Martín-Suárez, 1988; Sevilla, 1988; Sesé, 1989, 1994; Sesé and Ruiz-Bustos, 1992; Arribas, 1994; Rzebik-Kowalska, 1998; Montoya et al., 1999; Galobart and Agustí, 2003; Furió et al., 2005; Sesé and Soto, 2005; Gibert et al., 2006; Furió, 2007a,b; García-Alix et al., 2009; Sesé et al., 2011, 2016; Minwer-Barakat et al., 2012; Laplana et al., 2013; Sesé and López Martínez, 2013; Lozano-Fernández et al., 2015; Cuenca-Bescós et al., 2016; López-García et al., 2012, 2016, 2018; Rofes et al., 2016a; Fagoaga et al., 2017; Maldonado-Garrido et al., 2017; López Jiménez et al., 2018; Piñero et al., 2020)

Dolinasorex glyphodon was first described from Gran Dolina (Burgos, Spain) (Rofes and Cuenca-Bescós, 2009b). This site is a reference in Europe due to the presence of *Homo antecessor* (Carbonell et al., 1995; Bermúdez de Castro et al., 1997) and high quantities of fossils of macro- and microvertebrates that have allowed the faunal associations, biochronology and paleoclimate to be studied (e.g., Cuenca-Bescós et al., 2005, 2011, 2015, 2016; Blain et al., 2009; Galán et al., 2019a; 2019b; Núñez-Lahuerta et al., 2021). Moreover, Gran Dolina is the best record of Pleistocene age in the Iberian Peninsula. The soricids gathered from layers Gran Dolina 4 to Gran Dolina 10 (TD3-4, TD5, TD6, TD7, TD8, TD10) are *Dolinasorex glyphodon, Sorex minutus*, *Sorex* sp., *Neomys* sp. and *Crocidura* sp. (López-Antoñanzas and Cuenca-Bescós, 2002; Cuenca-Bescós et al., 2010, 2016). In other regions of Europe, however, several species of soricids have been identified in Early-Middle Pleistocene sites, and the identification of between five and ten species in a single layer is common. Such sites include Beftia II (Rzebik-Kowalska, 2000) and Somssich Hill 2 (Botka and Mészàros, 2018).

The main object of the present work is to describe the soricids present in the stratigraphic levels of Gran Dolina, using the morphological and morphometric characters of mandibles and teeth in order to contribute to the paleontology of the Early-Middle Pleistocene transition and the fossil record of these important small mammals. Eulipotyphlans in general are key to reconstructing past environments and biostratigraphy during the Cenozoic (Furió, 2007b; Rofes, 2009). A second aim is to compare the fossil record of soricids from Gran Dolina with that of other sites in Europe and assess its biochronological relevance for the Iberian Peninsula.

2. Regional setting

Gran Dolina (42°21′6″ N, 3°31′12″ W, in visor Sigpac; Burgos, Spain) is one of the karstic cave sites of the Atapuerca Trinchera del Ferrocarril sector (Atapuerca railway trench). It is composed of inner and outer cave sediments ordered in layers up to 19 m high in a stratigraphic sequence. The field label is TD, standing for the abbreviated form of Trinchera Dolina. The Trinchera del Ferrocarril, together with the active-cave deposits of Cueva Mayor, constitute an almost complete record of the Quaternary of the Iberian Peninsula (1.5 Ma-Medieval period) (Carretero et al., 2008; Cuenca-Bescós et al., 2010, 2013; López-García et al., 2010; Rodríguez et al., 2011; Bañuls-Cardona et al., 2017; Álvarez-Posada et al., 2018). The hominin species *H. antecessor* was found in four sublayers of level TD6 (Carbonell et al., 1995; Bermúdez de Castro et al., 1997, 2017) (Fig. 1).

Gran Dolina is a large cave site that has a karstic infill dated to the post-Jaramillo Early Pleistocene (Álvarez-Posada et al., 2018) and the Middle Pleistocene (Falguères et al., 1999; Rodríguez et al., 2011). The stratigraphic sequence is 25 m thick, and within it 11 lithostratigraphic units have been identified (TD1-TD11 from bottom to top). See the literature in Parés and Pérez-González (1995, 1999), Pérez-González et al. (2001), Campaña et al. (2017) and Parés et al. (2018). The 11 lithostratigraphic units contain fossils of fauna (including hominins), flora and lithic industry (Rodríguez et al., 2011; Saladié et al., 2018). Some units are of autochthonous origin, from inside the cave (TD1, TD2, TD9), and others are allochthonous infills (TD3-4, TD5, TD6, TD7, TD8 and TD10) (Campaña et al., 2017). The allochthonous units contain fossils from outside the cave. TD11 is sterile. The lithostratigraphic units are divided into subunits by their archaeological and paleontological content (see Ollé et al., 2013).

There are numerous paleoenvironmental and biostratigraphic studies of the small vertebrates from Gran Dolina, focused on rodents, insectivores, bats, birds, herpetofauna or fish (Blain et al., 2008, 2009, 2012; Cuenca-Bescós et al., 1999; 1999, 2005, 2011, 2016, 2017; Cuenca-Bescós and García, 2007; Núñez-Lahuerta et al., 2021; Rofes and Cuenca-Bescós, 2009b; Galán, 2019; Galán et al., 2019a,b; Blanco-LaPaz et al., 2021; Estraviz-López et al., 2021). Soricids have been studied in detail only in Rofes (2009) and Rofes and Cuenca-Bescós (2009b).

3. Material and methods

3.1. Material

The material studied consists of 200 fragments of hemimandibles (mandibles from now on) and isolated lower teeth from soricids. The elements from *Dolinasorex glyphodon* are not included because Rofes and Cuenca-Bescós (2009b) have already studied numerous specimens of this taxon from the same levels. The storage code of the Museo de Ciencias Naturales de la Universidad de Zaragoza (MCNUZ) is MPZ (Museo Paleontológico de Zaragoza)-2019/1223–1423. The individual code is in Appendix B.

The material was recovered from the stratigraphic levels of Gran Dolina dated as Early Pleistocene (TD4, TD5, TD6, TD7, and lower TD8) and Middle Pleistocene (upper TD8, TD9, TD10 (former TD11)). It was recovered in field campaigns between 1991 and 2017. To obtain the fossils from the microfaunal remains, the wet-sieving method was employed, with the use of a stack of sieves of decreasing mesh sizes (10, 5 and 0.5 mm, respectively) to remove clays. This method provides a concentrate of small clasts, fragments of fossils of large vertebrates, and fossils of small vertebrates. Each sample corresponds to a volume of 1 m × 1 m x 10 cm of sediment, with information on the level, square and depth in the site. We have studied the fraction between 5 mm and 10 mm.

In the laboratory, the teeth and mandibles of shrews were sorted using pincers and an Olympus SZ61 trinocular stereomicroscope. The upper dentition is scarce, probably because upper teeth of the soricines smaller than *Dolinasorex* are usually isolated in Gran Dolina and are part of the fraction <5 mm that is not studied in this work. The few molars found in the fraction studied were not assigned to a species, so only the lower dentition and mandibles were deeply studied. The microscope has an Olympus Soft Imaging Solutions LC20 camera attached; this was used to take pictures and measurements of the mandibles and teeth (in labial, lingual, and occlusal views) and the mandibular condyle. The software used to take pictures was LCMicro, and for the measurements, TpsDig v.2.17 (Rohlf, 2013).

3.2. Taxonomic identification

3.2.1. Nomenclature and measurements

We follow the broadly accepted nomenclature proposed by Reumer (1984) for the dental and mandibular elements. For the dentition, we use “i” for the incisor; “a” for the antemolar; “p” for the premolar; and “m” for the molar. The number next to the tooth marks the position in the tooth row: i.e., i1, a1, p4, m1, m2, m3.

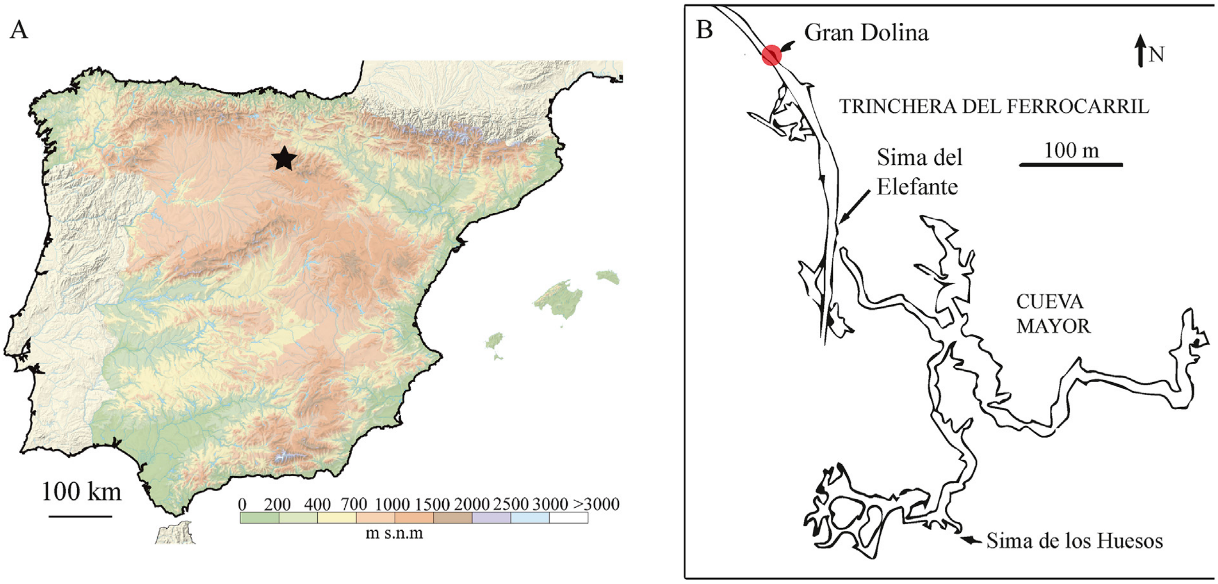

Fig. 1. **A.** Location of the sites of Sierra de Atapuerca in the Iberian Peninsula. Base of physical map of IGN: Derivate CC-BY 4.0.1:3.000.000 (Centro de Descargas del CNIG,). **B.** Map of the karstic system and location of Gran Dolina and other sites. After Martín-Merino et al. (1981).

All measurements are lineal and were taken in millimetres. Most of them are of widespread use, especially those taken from Reumer (1984). A few others, proposed by Rabeder (1972), Rofes (2009) and Rofes and Cuenca-Bescós (2009b), were also recorded. In a species with only one specimen (i.e., Neomyni cf. *Macroneomys*), moreover, the measurements of Parfitt and Harrison (2011) were used because they were the only ones available for comparison.

The measurements used in the current study are as follows:

Mandible: Lmd, length of the mandible from the mental foramen to the highest point of the base of the mandible; Hmd, height of the mandible from the highest point of the base to the tip of the coronoid process; Hmdm1, height of the mandible in lingual view below m1; Hmdm2, height of the mandible in lingual view below m2; Hmdm3 (only taken in Neomyni cf. *Macroneomys)*, height of the mandible in lingual view below m3; HmdC, height of the condyle in the direction parallel to the interarticular area; LmdUF, length of the upper facet of the condyle; LmdLF, length of the lower facet of the condyle.

Dentition: Li1, length of i1 in the direction parallel to the base and labial view; Hi1, height of i1 in the direction perpendicular to Li1, La1, Lp4, Lm1, Lm2 and Lm3, length of the crown of a1, p4, m1, m2 and m3; Wa1, Wp4, width of the crown of a1 and p4 in occlusal view; TRWm1, TRWm2, width of the trigonid of m1 and m2 in occlusal view; TAWm1, TAWm2, width of the talonid of m1 and m2 in occlusal view; Lm1-m3, length of the molar series from the anterior part of m1 to the posterior part of m3 in labial view. For more details see the figures in Moya-Costa (2020).

The results are shown in tables with the number of measurements (n), the maximum (max), minimum (min), and mean ($\overline{X}$) values, and the standard deviation (sd) for the individuals of each level. In addition, the measurements of each element are to be found in Appendix C.

The soricids were identified using the diagnostic characters and morphometric criteria taken from Hinton (1911), Fefjar (1966), Rabeder (1972), Hausser and Jammot (1974), Chaline et al. (1974), Jammot (1975, 1977), Malez and Rabeder (1984), Reumer (1984, 1985), Yudin (1989), Rzebik-Kowalska (1991, 1998, 2000, 2002, 2006, 2007, 2013), López-Fuster and Ventura (1996), Fanfani (1998, 1999), Maul and Rzebik-Kowalska (1998), Reumer and Hordijk (1999), Zaitsev and Baryshnikov (2002), Popov (2003), Masini et al. (2005), Rofes and Cuenca-Bescós (2006, 2009a, 2009b, 2011, 2013), Furió (2007b), Bona et al. (2008), Maul and Parfitt (2010), Parfitt and Harrison (2011), Rofes et al. (2016a,b), Botka and Mészáros (2015, 2016, 2017), Rzebik-Kowalska and Pereswiet-Soltan (2018), Mészáros et al. (2019), and Moya-Costa and Cuenca-Bescós (2019).

The references used for each species are indicated in section 4 and the data taken from previous works are compiled in Appendix D with data obtained from Hinton (1911), Sulimski (1959, 1962), Dehm (1962), Bartolomei (1964), Fefjar (1966), Mezhzherin (1972), Rabeder (1972), Jammot (1975), Reumer (1980, 1984), (Heinrich, 1983), Malez and Rabeder (1984), Yudin,(1989), Sulkava (1990), Rzebik-Kowalska (1991, 2000, 2007, 2013), Storch (1995), Maul and Rzebik-Kowalska (1998), Fanfani (1998, 1999), Reumer and Hordijk (1999), Marchetti et al. (2000), Zaitsev and Baryshnikov (2002), Masini et al. (2005), Rofes and Cuenca-Bescós (2006, 2011, 2013), Furió (2007a,b), Bona et al. (2008), Botka and Mészáros (2016, 2017), Rofes et al. (2016a), Mészáros et al. (2019), Moya-Costa (2020).

3.2.2. *Statistical analysis*

A comparison between the measurements taken here and those from previous works was undertaken. To this effect, we selected some specific measurements, as the criteria used are not always the same in different works. Additionally, some authors present the measurements of each specimen, but others only present a summary. For this reason, we compare the ranges of data from different populations to ascertain whether the specimens from Gran Dolina coincide with them.

We used the software Past v. 3.21 (Hammer et al., 2001) to analyse the measurements. Univariate and bivariate analyses were performed to determine the relations among the measurements of the soricids from Gran Dolina and those from the rest of Europe, and to support the identification of the species paired with morphological features. Different graphs were used depending on the species: univariate analysis for the most representative measurements of the mandibles and bivariate for data from the same element (e.g., Lm1 and TAWm1).

For the bivariate analysis, the data used were the maximum, minimum and mean values of each measurement in a group of individuals; these data could be, thereafter, not from real individuals as it is possible that the maximum L m1 in a group of individuals can be for a different individual that the one that have the maximum TAWm1.

3.3. *Taphonomic remarks*

The fossils of small mammals from the stratigraphic sequence of Gran Dolina have been thoroughly studied from a taphonomic point of view in previous works (Fernandez-Jalvo, 1996; Bennásar Serra, 2010). These works concluded that the assemblage was accumulated by birds of prey and that there is no reworking of the sediments. We thus consider that the levels are not mixed and that the association of soricids in each level is representative of the fauna from the area around the site.

The diagnostic elements of soricids are the teeth, the maxilla and the mandibles. Bennásar Serra (2010) points out that mandibles are significantly more abundant than maxillary remains in Gran Dolina and that mandibles preserve the teeth better, so we have chosen these elements for the present work.

4. Results

Our revision of the mandibular fossil remains of the soricids of Gran Dolina has led to the identification of nine taxa distributed as in Table 1.

The distribution of species in Gran Dolina is as in Fig. 2.

Systematic palaeontology

Class Mammalia Linnaeus, 1758
Order Eulipotyphla Waddell et al., 1999
Family Soricidae Fischer, 1817
Subfamily Soricinae Fischer, 1817
Tribe Soricini Fischer, 1817
Genus *Sorex* Linnaeus, 1758
Sorex minutus Linnaeus, 1766

The diagnosis was made following Reumer (1984). See the discussion.

Material: Nine mandibles (four right and five left) from levels TD5, TD6, TD7 and TD10. MPZ 2019/1223-1231. See Appendix B

Measurements: See Table 2. The detailed measurements for each specimen are given in Appendix C.

Description:

See Fig. 3. The complete description is in Appendix E.1.

Comparisons:

The measurements of the specimens from Gran Dolina are similar to *S. minutus* and *S. bor* (see Appendix D), especially those of the mandible (Hmd) and m1 (Lm1 and TAWm1) (Fig. 4).

Reumer (1984) describes *S. bor* and gives the diagnostic characters that differentiate it from *S. minutus*. The Gran Dolina individuals are assigned to *S. minutus* based on the presence of a longitudinal bar in the external temporal fossa and the measurements of the condyle, which are similar to *S. minutus* (Appendix D).

In addition, Reumer (1984) states that a diagnostic difference between *S. bor* and *S. minutus* is that the former has a coronoid spicule, whereas *S. minutus* does not. However, he shows some drawings of *S. minutus* from Csarnóta 2 with a coronoid spicule. In Moya-Costa and Cuenca-Bescós (2019), some recent *S. minutus* from the Pyrenees (northeastern Spain) were studied, and these present a coronoid spicule (Fig. 3). In Rzebik-Kowalska (1991), the

Table 1
Number of identified specimens (NISP) and minimum number of individuals (MNI) per level for all the soricid species identified in Gran Dolina.

	Sorex minutus		*Sorex ex* gr. *runtonensis-subaraneus*		*Sorex (Drepanosorex)* ex gr. *margaritodon-savini*		*Dolinasorex glyphodon*	*Asoriculus gibberodon*		*Neomys* cf. *newtoni*		*Neomys* cf. *fodiens*		Neomyni cf. *Macroneomys*		*Crocidura kornfeldi*	
	NISP	MNI	NISP	MNI	NISP	MNI		NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI	NISP	MNI
TD10	6	5	10	10								13	13	1	1		
TD9																	
TD8			4	4												7	4
TD7	1	1															
TD6	1	1	32	27			x	4	4	1	1					24	21
TD5	1	1	30	21	4	4	x									10	8
TD3-4			14	11			x									38	29

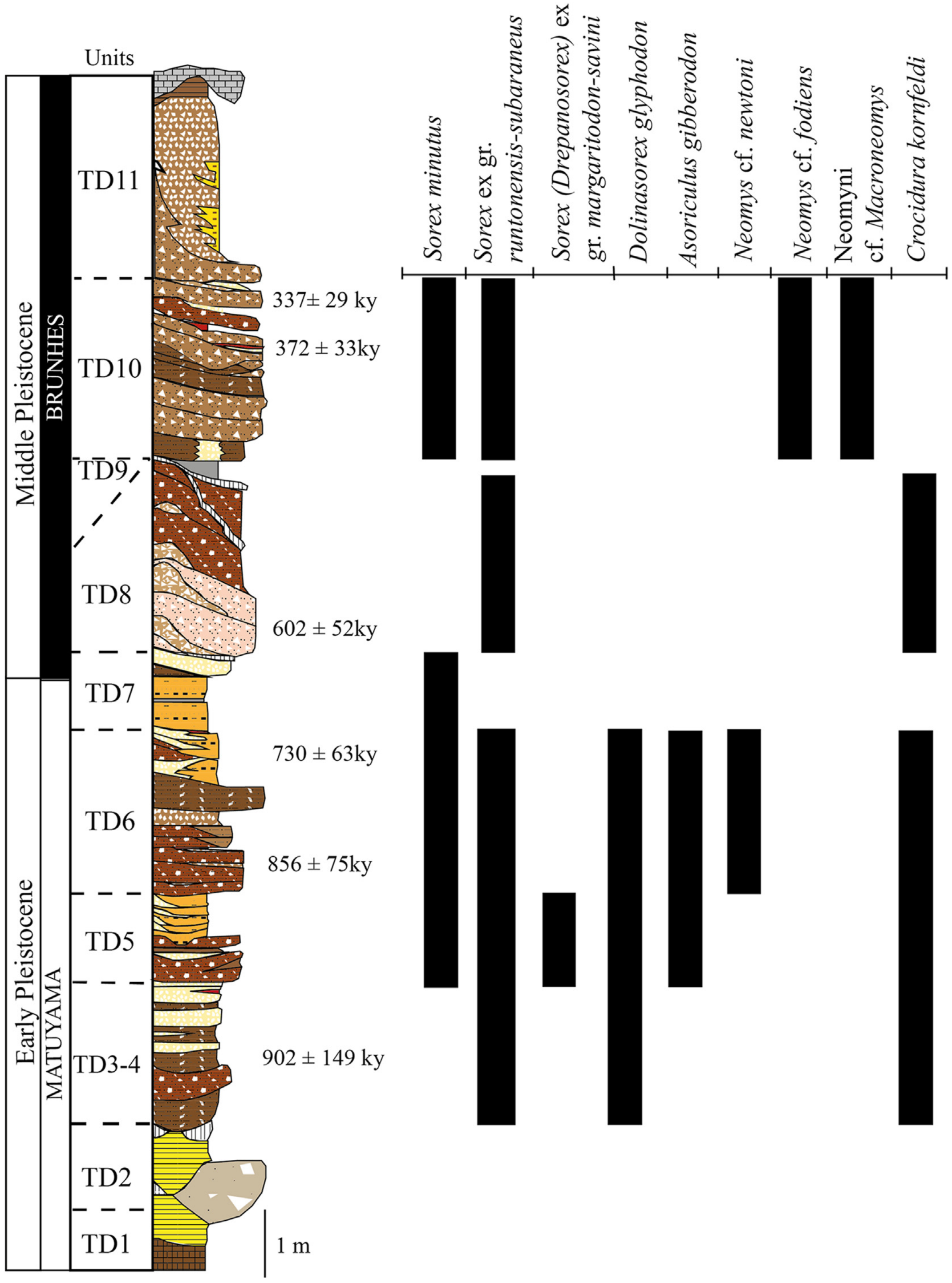

Fig. 2. Distribution of the soricid species identified along the stratigraphic sequence of Gran Dolina. Stratigraphy from Campaña et al. (2017). Dates summarized in Campaña et al. (2017) with some additions of Álvarez-Posada et al. (2018).

descriptions by Reumer (1984) are also referred to, but both species are represented with a coronoid spicule. For these reasons, we assume that the presence of a spicule is not key to the diagnosis of *S. bor*, whereas its absence is characteristic of *S. minutus.* The presence/absence of bifid upper incisors is a good diagnostic character between these taxa, but no upper incisors are identified.

The species *S. minutus* is common in Eurasia from the Pliocene to the present (Rzebik-Kowalska, 1991). The morphometric range of mandibular sizes is wide, and the individuals from Gran Dolina are among the largest (Fig. 4 and Appendix D).

Sorex ex gr. *runtonensis -subaraneus.*

The assignation follows Rzebik-Kowalska (1991, 2000), Rofes et al. (2016a,b) and Rzebik-Kowalska and Pereswiet-Soltan (2018).

Material: Ninety mandibles, (48 right and 42 left). From TD4, TD5, TD6, TD8 and TD10. MPZ 2019/1232–1321. See Appendix B.

Measurements: See Table 3. The detailed measurements for

Table 2
Summary of the measurements of the mandibles and lower molars of *S. minutus*. In mm.

Levels	TD5		TD6		TD7		TD10				
Measure	**n**		**n**		**n**		**n**	**min**	$\overline{X}$	**max**	**sd**
Lm1			1	1.29			4	1.22	1.26	1.29	0.03
TRW m1			1	0.66			4	0.61	0.64	0.66	0.02
TAW m1			1	0.68			4	0.67	0.7	0.76	0.04
L m2	1	1.24	1	1.24	1	1.21	5	1.06	1.13	1.2	0.05
TRW m2	1	0.63	1	0.66	1	0.69	5	0.6	0.63	0.68	0.03
TAW m2	1	0.69	1	0.68	1	0.73	5	0.63	0.65	0.68	0.02
L m3							5	0.82	0.9	0.97	0.06
W m3							5	0.5	0.52	0.54	0.01
L m1-m3							2	3.18	3.19	3.19	0.01
Lmd	1	4.32	1	3.87							
Hmd	1	3.7	1	3.25			1	3.24	3.24		
Hmdm1	1	1.07	1	0.95			4	0.93	1.02	1.09	0.07
Hmdm2	1	1.11	1	0.95	1	0.85	6	0.94	1.01	1.05	0.04
HmdC			1	1.46			1	1.38	1.38	1.38	
LmdUF	1	0.42	1	0.61			1	0.58	0.58	0.58	
LmdLF			1	1.02			1	0.93	0.93	0.93	

each specimen are given in Appendix C.

Description:

See Fig. 5. The complete description is in Appendix E.2.

Comparisons:

The morphology of the specimens from Gran Dolina is very similar to many European species of *Sorex*. *Sorex minutus* and *S. minutissimus* can be ruled out due to the larger size of the mandibles from Gran Dolina (Fig. 6 and Appendix D).

Other species can be ruled out as well following Rofes et al. (2013). These have restricted distributions far from the Iberian Peninsula. The species in question are from the Middle Pleistocene of North Caucasus: *S. volnuchini* Ognev, 1922; *S. satunini* Ognev, 1922; *S. raddei* Satunin, 1895; and *S. doronichevi* Zaitsev and Baryshnikov, 2002; and from the Plio-Pleistocene of Transbaikalia/Irkutsk: *S. roboratus* Hollister, 1913; *S. palaeosibiriensis* Mezhzherin, 1972; *S. erbajevae* Rzebik-Kowalska, 2007; and *S. baikalensis* Rzebik-Kowalska, 2007. Some of these species have different morphologies, such as *S. roboratus*, with a coronoid process that is very low and leaning backwards (Rzebik-Kowalska, 2007). But the measurements of the mandibles of others overlap with those from Gran Dolina, as in the case of *S. palaeosibiriensis*. Rzebik-Kowalska (2007) notes that the distribution of this species is exclusive to the east of the Palearctic region, and in the western part it is replaced by *S. runtonensis*, which has similar characteristics.

The measurements overlap partially with *S. bor*, although they are larger in general (Reumer, 1984). *S. casimiri* is not considered because has a narrower coronoid process and a bigger coronoid spicule (Rzebik-Kowalska, 1991).

The size of the mandibles from Gran Dolina falls between *S. runtonensis* and *S. subaraneus*. It overlaps with the upper extreme of *S. runtonensis* and the lower extreme of *S. subaraneus* (Fig. 6). Rofes et al. (2016a,b) propose synonymizing *S. runtonensis* and *S. subaraneus* because they are very similar, and because the characters for the diagnosis established by Rzebik-Kowalska (1991, 2000) seem to enter within the variability of each species, forming a continuity. Subsequently, Rzebik-Kowalska and Pereswiet-Soltan (2018) weighed up this possibility and then reasserted the differences.

Rzebik-Kowalska and Pereswiet-Soltan (2018) pointed out that one way to distinguish between *S. runtonensis* and *S. subaraneus* is by the shape of the interarticular surface, which is rectangular in *S. runtonensis* and trapezoidal in *S. subaraneus*. In all levels of Gran Dolina there are mandibles with trapezoidal condyles although their shape varies. In TD4, all the condyles are trapezoidal, like those shown in Rzebik-Kowalska (2000) related to *S. araneus*. In TD5, there are only trapezoidal condyles, so they should correspond to *S. subaraneus*. In TD6, TD8 and TD10, most condyles are trapezoidal too, but more stylized and narrower. Some of them are almost rectangular, so these could be *S. runtonensis*. Hence, there are two options: either both species are present, or the intraspecific variability of Gran Dolina does not allow them to be differentiated using this character.

According to the same authors, another way to distinguish them is the position of the mental foramen with respect to the protoconid of m1, calculating the percentage of mandibles where the foramen is anterior or posterior to the cuspid. Assuming that all the mandibles are from the same species, in 75% of the mandibles with a visible foramen, it is posterior to the protocone; in accordance with this criterion, it would thus be *S. runtonensis*. By contrast, in the mandibles that can be assigned to *S. subaraneus* by the condyle, the percentage is 50%, corresponding to *S. subaraneus*. However, it should be borne in mind that there are only eight mandibles with a foramen, m1 and condyle, so the statistical value is low. Rzebik-Kowalska and Pereswiet-Soltan (2018) note that another way to differentiate between the species is by the position of a1, but we do not use this criterion, because of the scarcity of mandibles with a1.

The mandibles from Gran Dolina are in general bigger than those of *S. runtonensis* from Sima del Elefante (Rofes et al., 2016a,b). This could be because the mandibles from Gran Dolina belong to *S. subaraneus*, which is slightly larger than *S. runtonensis*, or because of the progressive increase in size that is recorded over time in the latter species according to Rzebik-Kowalska and Pereswiet-Soltan (2018).

The proportions and measurements of the specimens from Gran Dolina coincide to a great extent with data from recent specimens of *S. coronatus* from the Pyrenees (see Fig. 6 and Appendix D). Data from this species are scarce due to the similarity with *S. araneus*, which makes it difficult to differentiate them in the fossil record, and it is not clear when the species first appears (Jammot, 1977; Rzebik-Kowalska and Pereswiet-Soltan, 2018). However, it is important to keep in mind that *S. coronatus* is a species with high intraspecific variability, which presents major differences in size depending on the area of distribution (Moya-Costa and Cuenca-Bescós, 2019).

In Rzebik-Kowalska and Pereswiet-Soltan (2018), the differences and similarities among *S. subaraneus*, *S. runtonensis*, *S. araneus* and *S. coronatus* are extensively discussed. The authors suspect that these species could have been confused several times. Jammot (1977) indicates that *S. subaraneus* is the ancestor of *S. araneus* and *S. coronatus*, and that some of the populations from the Middle Pleistocene of France assigned to *S. subaraneus*, could be *S. coronatus*. In fact, the principal criterion for differentiating *S. araneus* from *S. subaraneus* and *S. runtonensis* is smaller size. However, it has not been proved that *S. coronatus* is also smaller than *S. araneus* in some areas, especially in the Iberian Peninsula, it being very difficult to differentiate the species only by their mandibles (López-Fuster and Ventura, 1996; Hausser and Jammot, 1974; Moya-Costa and Cuenca-Bescós, 2019).

In view of all of these considerations, and as the differences between the two species are not clear and there are specimens with intermediate morphology (e.g., Fig. 5), the group of specimens described in Gran Dolina is designated *S.* ex gr. *runtonensis-subaraneus.*

Sorex (Drepanosorex) ex gr. *margaritodon*–*savini.*

The diagnosis follows Reumer (1985), Rofes and Cuenca-Bescós (2013) and Rzebik-Kowalska (2013).

Material: Four left mandibles from TD5. MPZ 2019/1322–1325.

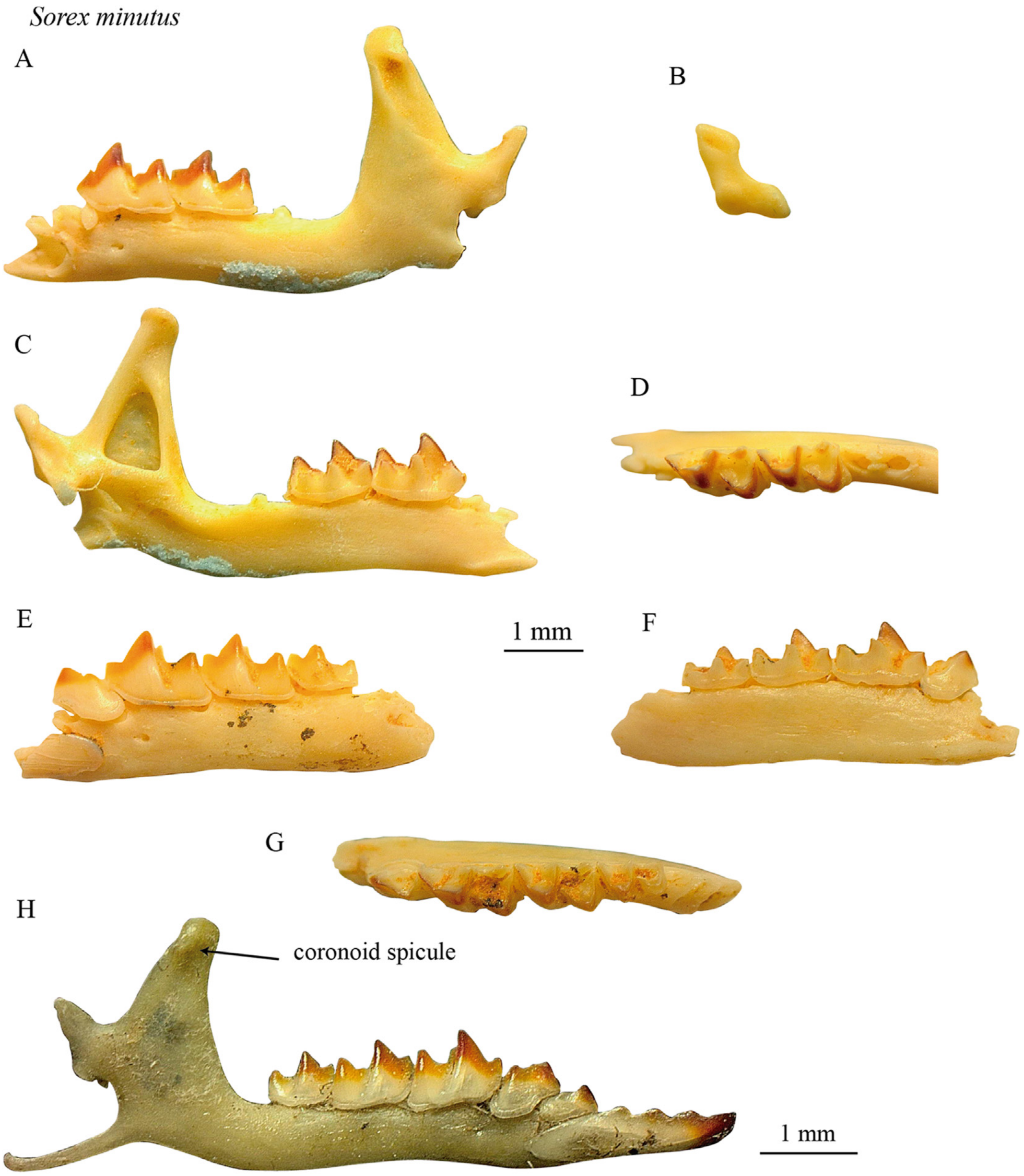

Fig. 3. *S. minutus.* **A-D.** Specimen of td6.3.6g10z840-850 (MPZ, 2019/1224); **E-G.** Specimen of td10.3n21z510-520 (MPZ, 2019/12,030). **A**. Labial view of the mandible. **B**. Condyle. **C**. Lingual view of the mandible. **D**. Occlusal view of m1 and m2. **E**. Labial view of the mandible. **F**. Lingual view of the mandible. **G**. Occlusal view of the mandible. **H**. Labial view of the mandible of a recent *S. minutus* from Aizcorbe (Navarra). MPZ 2019/1070.The shape of the coronoid spicule can be appreciated.

See Appendix B.

Measurements: See Table 4. The detailed measurements for each specimen are given in Appendix C.

Description:

See Fig. 7. The complete description is in Appendix E.3.

Comparisons:

The mandibles correspond to the subgenus *Drepanosorex* as judged by the robustness of the coronoid and condyle. They share this character with *Sorex bifidus* Rzebik-Kowalska, 2013. However, in the only mandible with teeth, these are bulbous, which rules this species out. It is also smaller in size.

Reumer (1985) reviews the species of the subgenus *Drepanosorex* and reduces them to four: *Sorex (Drepanosorex) praearaneus*, *Sorex (Drepanosorex) margaritodon*, *Sorex (Drepanosorex) savini* and *Sorex (Drepanosorex) austriacus*, Kormos, 1930. Zaitsev and Baryshnikov (2002) defined *Sorex (Drepanosorex) rupestris*.

The *Drepanosorex* from TD5 could be either *S.* (*D.*) *margaritodon* or *S.* (*D.*) *savini*, given the size of the mandible, specifically Hmd and Hm2, two of the most representative and common measurements in the literature.

Reumer (1984) states the differences between *S.* (*D.*) *praearaneus*, *S.* (*D.*) *margaritodon* and *S.* (*D.*) *savini* on the basis of the size of the mandible, the condyle, and the degree of bulbosity of the teeth. Rzebik-Kowalska (1991) shows that the sizes of *S.* (*D.*) *margaritodon* and *S.* (*D.*) *savini* overlap and unifies the two species in *S.* (*D.*) *savini.* Later, in Rzebik-Kowalska (2000), she separates the species by the degree of similarity between M1 and M2.

M1 and M2 were not found in TD, so this criterion cannot be applied. For this reason, the assignation is *S.* (*D.*) ex gr. *margaritodon-savini.*

In the description of *S. savini*, Hinton (1911) notably establishes that the pigmentation of the teeth is dark and occupies the whole

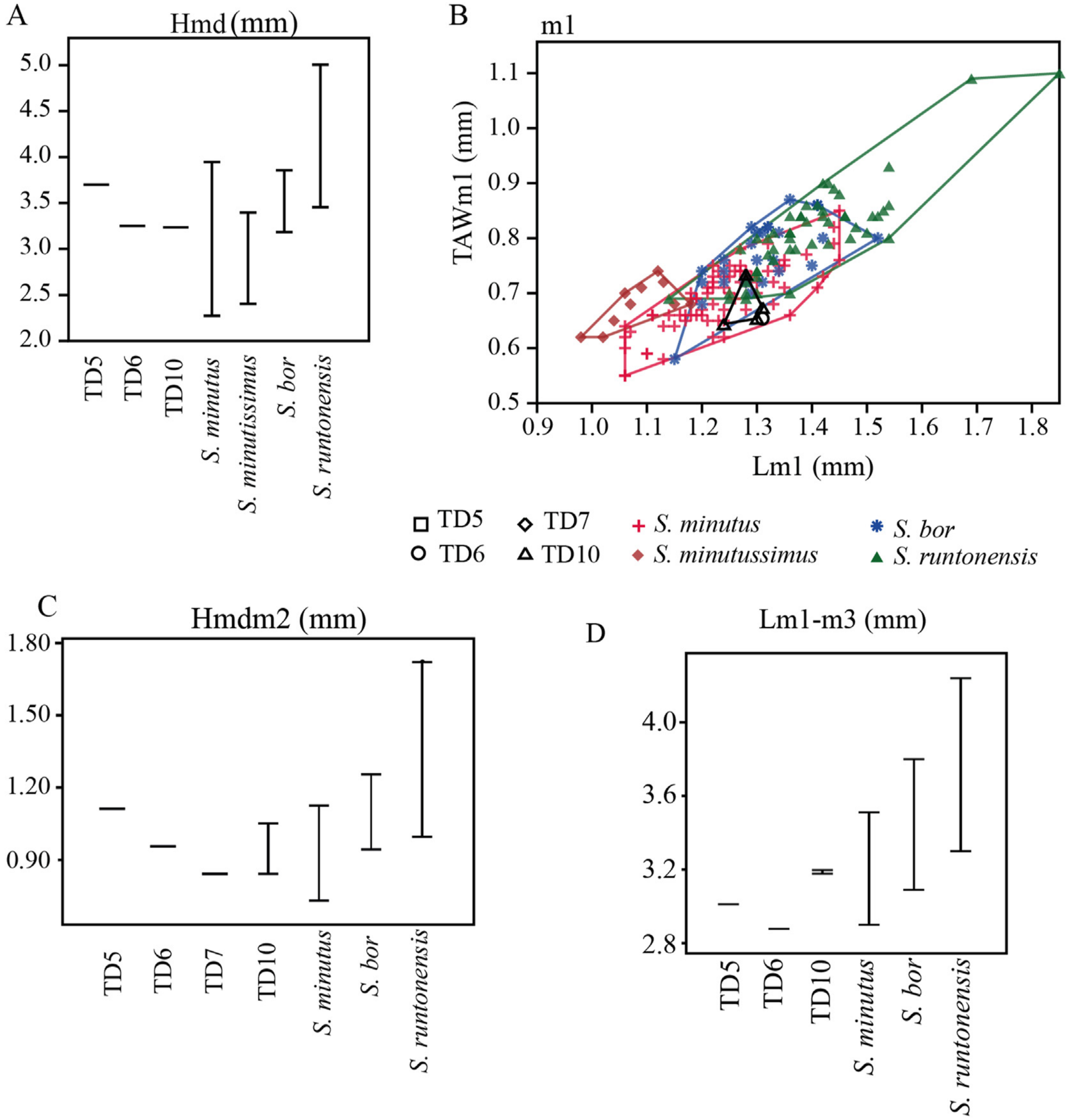

Fig. 4. A. Range of Hmd measurements of *S. minutus* from Gran Dolina compared to data of other species similar in size. **B**. Lm1/TAWm1 bivariate plot of *S. minutus* from Gran Dolina and other European species. **C**. Range of Hmdm2 measurements of *S. minutus* from Gran Dolina compared with other European *S. minutus*, *S. bor* and *S. runtonensis*. **D**. Range of Lm1-m3 measurements of *S. minutus* from Gran Dolina compared with other European *S. minutus*, *S. bor* and *S. runtonensis*. Data other than this work taken from Reumer (1984), Rzebik-Kowalska (1991, 2000, 2006, 2007 [including Yudin 1989 and Sulkava 1990], 2013, Reumer and Hordijk (1999), Furió (2007b), Rofes et al. (2016a,b), Moya-Costa and Cuenca-Bescós (2019). See the original data in Appendix D.

crown except for the cingulum. However, this criterion is not used here because no subsequent author has corroborated it. Rabeder (1972) and particularly Reumer (1985) indicate that the pigmentation of the subgenus *Drepanosorex* is not uniform, including the description of Hinton (1911).

Regardless of whether they belong to *S. (D.) margaritodon* or *S. (D.) savini*, the specimens from TD5 present clear differences with respect to *S. (D.) margaritodon* from the lower levels of TE (Rofes and Cuenca-Bescós, 2013): the mental foramen is more anterior in the mandibles of TD5, specifically below the p4, whereas in the mandibles of TE it is below the trigonid of m1. In all the mandibles from TD5 there are two mandibular foramina, whereas in those from TE there are either one or two. In the specimens from TD5, the coronoid process is more robust than in those from TE, also being wider up to the apex. In addition, the coronoid spicule is more marked. When the measurements are compared, the mandibles and condyles of the specimens from TD5 are always found to be larger than those from TE. As Rofes and Cuenca-Bescós (2013) assigned the specimens from TE to *S. (D.) margaritodon* using the criteria of Rzebik-Kowalska (2000) based on the size ratio between the upper molars, the differences observed between those specimens and the specimens from TD5 could indicate that the latter are *S.* (*D.*) *savini*. The difference in size between the *Drepanosorex* of the two sites and a possible difference in the species reasonably matches the age of the levels where they were found. The TE specimens are smaller, and dated to the pre-Jaramillo Early Pleistocene (Rofes and Cuenca-Bescós, 2013), whereas those from TD5, larger in size, are from the post-Jaramillo Early Pleistocene (Rodríguez et al., 2011).

The distinction between *S.* (*D.*) *margaritodon* and *S.* (*D.*) *savini* has been invalidated twice. The first time this was by Rzebik-Kowalska (1991), who revalidated it in Rzebik-Kowalska (2000), and then it was by Botka and Mészàros (2016). In the latter work, the authors base their rejection on the overlap between measurements demonstrated in Rzebik-Kowalska (1991). This evidence leads them to believe that the distinctions made by Rzebik-

Table 3
Summary of the measurements of *S.* ex gr. *runtonensis-subaraneus* of Gran Dolina. In mm.

	TD3-4					TD5					TD6				
	n	**min**	$\bar{X}$	**max**	**sd**	**n**	**min**	$\bar{X}$	**max**	**sd**	**n**	**min**	$\bar{X}$	**max**	**sd**
Lp4						3	0.92	0.98	1.05	0.06					
Wp4						3	0.64	0.68	0.73	0.04					
Lm1	2	1.43	1.52	1.62	0.13	4	1.36	1.42	1.48	0.05	7	1.37	1.42	1.46	0.04
TRWm1	2	0.73	0.76	0.79	0.04	4	0.70	0.73	0.75	0.02	6	0.68	0.73	0.77	0.03
TAWm1	4	0.79	0.80	0.82	0.01	6	0.70	0.78	0.82	0.04	7	0.75	0.78	0.82	0.03
Lm2	7	1.26	1.31	1.37	0.04	8	1.14	1.28	1.41	0.09	6	1.18	1.24	1.30	0.05
TRWm2	7	0.72	0.75	0.78	0.02	8	0.63	0.71	0.76	0.05	6	0.68	0.72	0.76	0.03
TAWm2	7	0.73	0.77	0.81	0.03	8	0.68	0.71	0.75	0.03	6	0.68	0.72	0.76	0.03
Lm3	4	1.00	1.04	1.10	0.04	4	0.95	1.01	1.07	0.05	2	0.99	1.00	1.02	0.02
Wm3	4	0.59	0.62	0.65	0.03	4	0.53	0.56	0.58	0.02	2	0.57	0.60	0.63	0.04
L m1-m3						1	3.62	3.62	3.62		1	3.40	3.40	3.40	
Lmd	7	4.20	4.40	4.58	0.13	17	4.20	4.62	4.87	0.17	13	4.37	4.64	5.01	0.17
Hmd	11	3.70	3.94	4.14	0.13	21	3.70	3.98	4.19	0.12	22	3.79	3.93	4.23	0.10
Hmdm1	10	1.21	1.33	1.52	0.09	20	1.07	1.23	1.41	0.07	19	1.14	1.25	1.39	0.07
Hmdm2	14	1.08	1.28	1.40	0.09	25	1.11	1.22	1.39	0.06	29	1.14	1.22	1.42	0.07
HmdC	11	1.43	1.64	1.95	0.18	26	1.45	1.58	1.69	0.07	25	1.47	1.61	1.73	0.07
LmdUF	12	0.59	0.74	0.90	0.09	29	0.42	0.68	0.79	0.07	28	0.58	0.71	0.82	0.05
LmdLF	12	0.95	1.07	1.20	0.07	26	0.91	0.98	1.08	0.05	26	0.90	1.01	1.12	0.05

	TD8					**TD10**				
	n	**min**	$\bar{X}$	**max**	**sd**	**n**	**min**	$\bar{X}$	**max**	**sd**
Lm1	2	1.48	1.50	1.51	0.02	3	1.41	1.44	1.47	0.03
TRWm1	2	0.74	0.75	0.77	0.02	3	0.73	0.75	0.79	0.03
TAWm1	2	0.83	0.83	0.84	0.01	3	0.78	0.80	0.82	0.02
Lm2	2	1.32	1.33	1.35	0.02	3	1.23	1.31	1.44	0.11
TRWm2	2	0.72	0.76	0.79	0.05	3	0.68	0.73	0.78	0.05
TAWm2	2	0.76	0.78	0.80	0.03	3	0.72	0.78	0.83	0.06
Lm3	1	1.03	1.03	1.03		2	0.94	1.00	1.06	0.09
Wm3	1	0.62	0.62	0.62		2	0.54	0.59	0.64	0.07
L m1-m3	1	3.62	3.62	3.62						
Lmd	2	4.63	4.78	4.92	0.20	3	4.80	5.02	5.17	0.20
Hmd	2	3.89	4.04	4.18	0.20	5	3.96	4.02	4.10	0.05
Hmdm1	2	1.18	1.22	1.27	0.06	5	1.21	1.32	1.43	0.08
Hmdm2	4	1.15	1.21	1.35	0.10	6	1.17	1.29	1.41	0.08
HmdC	4	1.54	1.63	1.76	0.09	6	1.54	1.75	1.92	0.14
LmdUF	4	0.57	0.63	0.71	0.06	6	0.59	0.78	0.93	0.13
LmdLF	4	0.97	1.04	1.10	0.05	6	0.91	1.05	1.15	0.10

Kowalska (2000), supported in Rofes and Cuenca-Bescós (2013), are not reliable.

To demonstrate the overlap in measurements, however, Botka and Mészàros (2016) only use the length and width of m1, omitting the other lower teeth and the measurements of the mandible. As other studies such as Moncunill-Solé et al. (2016), Rofes et al. (2018), and Moya-Costa and Cuenca-Bescós (2019) have shown, the measurements of the lower molars and mandible do not always follow the same trends, the mandibular measurements being more useful in detecting microevolutionary changes in soricids. In Fig. 7, it can be observed that the mandibular and condylar measurements exhibit a progression in size, although they overlap partially. The number of individuals is small in the case of *S.* (*D.*) *margaritodon* from TE and *S.* (*D.*) ex gr. *margaritodon-savini* from TD5, sites just 200 m apart, but the differences in size are noticeable and there is no overlap. However, a comparison of Lm1 measurements gives different results. It should be borne in mind that there is only one m1 from TD5, so it is difficult to base reliable generalizations on it. Nonetheless, it can be seen in Fig. 7 that the larger dimensions correspond to the molars from TD5 and Sima del Elefante, something that does not occur with the mandibular measurements. However, the protocol used by different authors for taking the measurements can bias the results of the molars more than the mandible. Moreover, it has been proved that the width of m1 is not a good variable for comparison, due to the mixture of data for TAW, TRW and W in different works, specifying neither how the W is measured nor the exact orientation. In addition to the reduced number of variables, this can result in a high error rate in taking measurements depending on the author, compared to other, clearer parameters. The measurements of different species can be found in Appendix D.

In light of the previous discussion, we do not here support the proposals made by Botka and Mészàros (2016) and maintain the separation between *S.* (*D.*) *margaritodon* and *S.* (*D.*) *savini*.

Dolinasorex glyphodon Rofes and Cuenca-Bescós 2009b.

The detailed description and measurements are given in Rofes (2009) and in Rofes and Cuenca-Bescós (2009b). The fossil remains of *Dolinasorex glyphodon* have been found in levels TD4, TD5 and TD6.

Tribu Neomyini Matschie, 1817
Genus *Asoriculus* Kretzoi, 1959.
Asoriculus gibberodon (Petényi, 1864)

The identification follows Reumer (1984), Rzebik-Kowalska (1991), Fanfani (1999), Rzebik-Kowalska (2000), Rofes and Cuenca-Bescós (2006) and Furió (2007b).

Material: Four mandibles (two left and two right) from TD5 and TD6. MPZ 2019/1326–1329. See Appendix B.

Measurements: See Table 5. The detailed measurements for each specimen are given in Appendix C.

Description:

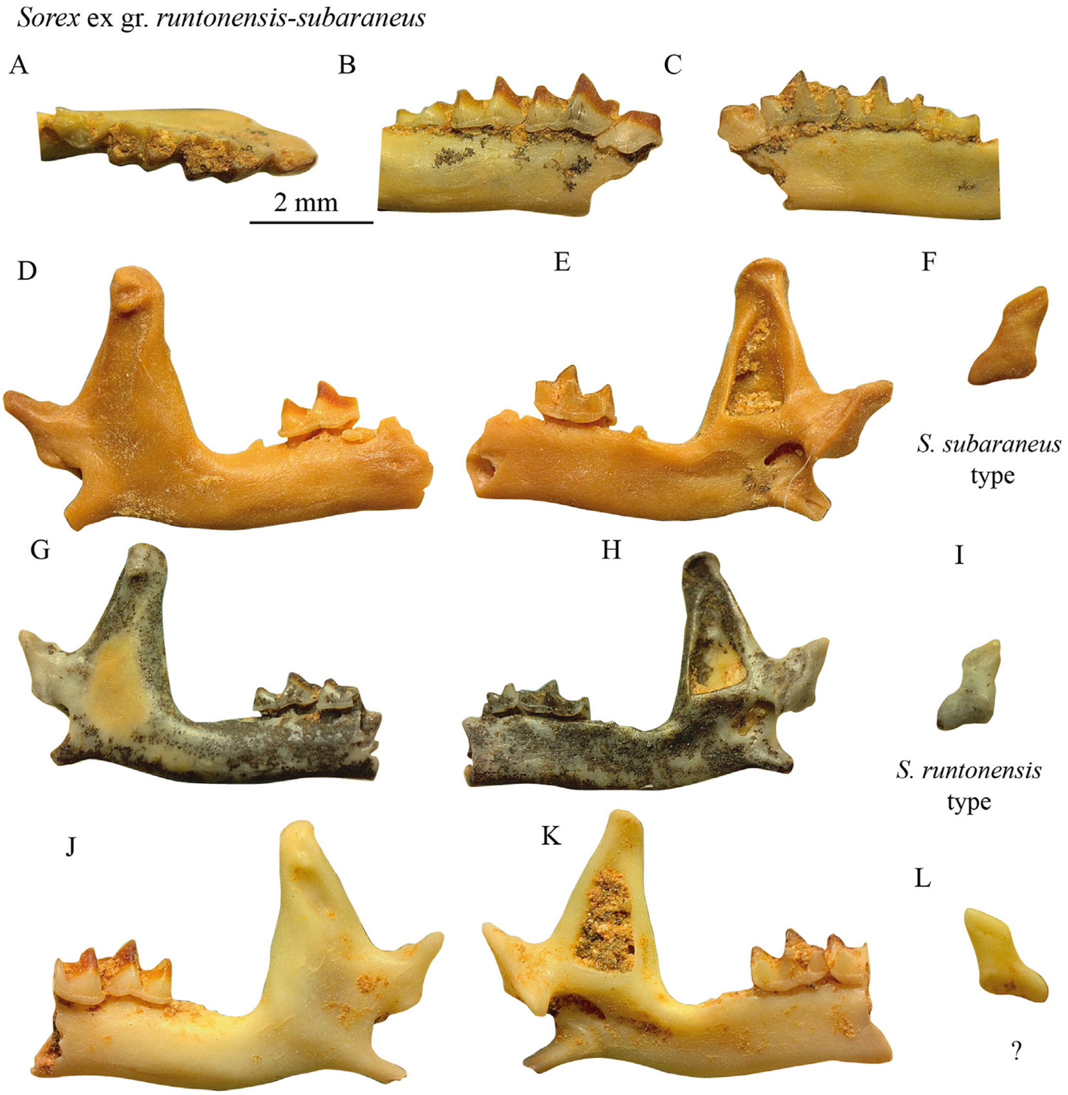

Fig. 5. *S.* ex gr. *runtonesis-subaraneus.* **A-C.** Mandible with p4-m3 of td5.2.2g13z1000-1010 (MPZ, 2019/1270). **A.** Occlusal view. **B.** Labial view. **C.** Lingual view. **D-F.** Mandible of td4.2wg09z1210-1220 with condyle as *S. subaraneus* (MPZ, 2019/1244). **D.** Labial view. **E.** Lingual view. **F.** Condyle. **G-I.** Mandible of td5-1-t5f12z980-990 with condyle as *S. runtonensis* (MPZ, 2019/1257). **G.** Labial view. **H.** Lingual view. **I.** Condyle. **J-L.** Mandible of td5.2.3e14z1000-1010 (MPZ, 2019/1272) with intermediate condyle between *S. subaraneus* and *S. runtonesis* type. **J.** Labial view, **K.** Lingual view, **L.** Condyle.

See Fig. 8. The complete description is in Appendix E.4.

Comparisons:

In the Early Pleistocene of Europe, there were several neomynines with characters similar to the specimens from Gran Dolina: i.e., *Asoriculus gibberodon*, *Asoriculus thenii*, *Neomys newtoni*, *Macroneomys* and *Nesiotites.*

In comparing the dimensions of the mandibles, there are taxa that can be ruled out due to their size, which is larger than the specimens from Gran Dolina. These are *Asoriculus thenii, Macroneomys* and *Nesiotites* (see Appendix D). This leaves *A. gibberodon* and *N. newtoni* as the remaining candidates.

The fossils are assigned to *A. gibberodon* because they exhibit most of the diagnostic criteria established by a variety of authors (i.e., Reumer, 1984; Rzebik-Kowalska, 1991; Fanfani, 1999; Rzebik-Kowalska, 2000; Rofes and Cuenca-Bescós, 2006; Furió, 2007b). These criteria are the narrow interarticular area, the coronoid spicule at the midpoint of the coronoid process, the articular facets visible in lingual view, and the robust mandible. They are almost identical in size and morphology to those from the nearby site of Sima del Elefante (Rofes and Cuenca-Bescós, 2006).

Genus *Neomys* Kaup, 1829.

Neomys cf. *newtoni* Hinton, 1911.

Material: Left mandible from level TD6, from sample td6.3.2g12z770-790. MPZ 2019/1330. See Appendix B.

Measurements: See Table 6.

Description:

See Fig. 8 The complete description is in Appendix E.5.

Comparisons:

Li1 coincides with *A. gibberodon* and *N. newtoni* (see Appendix D). The shape of the incisor is straight and thin, with the cuspule at the midpoint, which coincides with the type of incisor of *Neomys.* The concavity of the incisor coincides with the descriptions by Zaitsev and Baryshnikov (2002) for *N. newtoni*. However, the position of the cuspule does not coincide with *N. newtoni*, and Zaitsev and Baryshnikov (2002) claim that the incisor does not have a cingulum. It should be noted that although Zaitsev and Baryshnikov

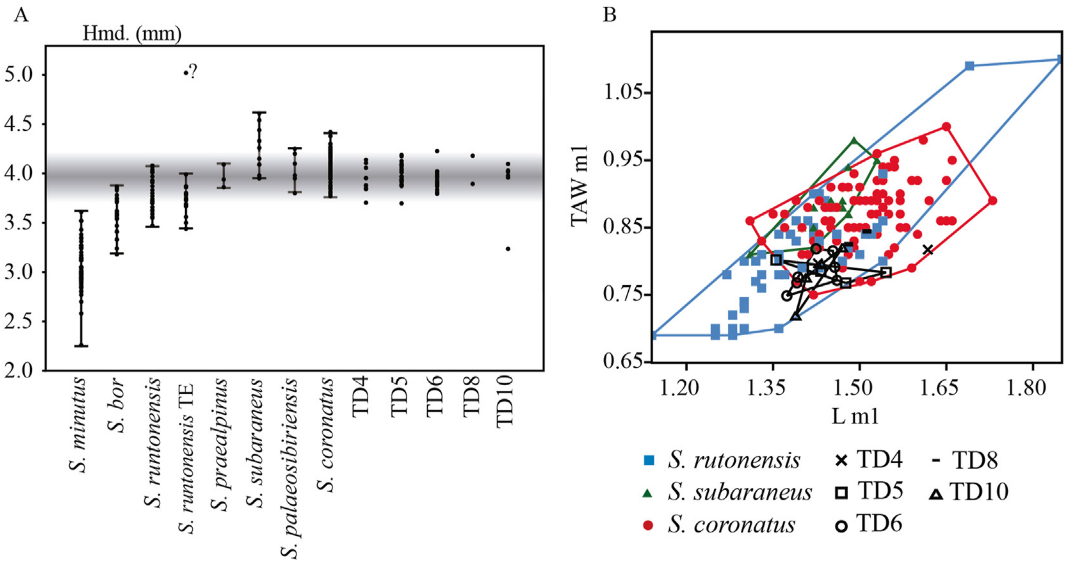

Fig. 6. A. Hmd of some species of *Sorex* of Europe. The lines indicate ranges of measurements, and the points indicate the measurements of concrete specimens. The shadow marks the zone of maximum coincidence of the measurements of Gran Dolina. **B**. Bivariant graph of Lm1 and TAWm1 of *S.* ex gr. *runtonensis-subaraneus* of Gran Dolina and other European *Sorex* of sizes very similar to them. Data other than this work taken from Reumer (1984), Rzebik-Kowalska (1991, 2000, 2006, 2007 (includes Yudin, 1989 and Sulkava, 1990), 2013), Reumer and Hordijk (1999), Furió (2007b), Rofes et al. (2016a,b), Moya-Costa and Cuenca-Bescós (2019). See Appendix D.

Table 4
Summary of the measurements of *Sorex (Drepanosorex)* ex gr. *margaritodon-savini* of Gran Dolina. In mm.

Level	TD5				
Measurement	**n**	**min**	$\bar{X}$	**max**	**sd**
L p4	1	1.37	1.37	1.37	
Wp4	1	1	1	1	
Lm1	1	1.79	1.79	1.79	
TRWm1	1	0.99	0.99	0.99	
TAWm1	1	1.06	1.06	1.06	
Lm2	1	1.67	1.67	1.67	
TRWm2	1	0.97	0.97	0.97	
TAWm2	1	0.95	0.95	0.95	
Lm3	1	1.21	1.21	1.21	
Wm3	1	0.79	0.79	0.79	
L m1-m3	1	4.18	4.18	4.18	
Lmd	3	6.04	6.17	6.28	0.12
Hmd	4	5.44	5.54	5.61	0.09
Hmdm1	3	1.74	1.77	1.78	0.02
Hmdm2	4	1.67	1.74	1.8	0.05
HmdC	2	2.72	2.75	2.78	0.04
LmdUF	3	1.05	1.19	1.34	0.15
LmdLF	4	1.47	1.57	1.63	0.07

(2002) state that there is no buccal cingulum in the molars either, they represent the cingulum in the figures.

The shape of the incisors of *A. gibberodon* is very different from that of the specimen from TD6. This may thus belong to the species *N. newtoni*, but, as there are no other diagnostic elements such as the condyle or coronoid process, we assign it to *Neomys* cf. *newtoni*.

Neomys cf. *fodiens* Pennant, 1771.

Material: Thirteen mandibles (six right and seven left) from level TD10. MPZ 2019/1331–1343. See Appendix B.

Measurements: See Table 7. The detailed measurements for each specimen are given in Appendix C.

Description:

See Fig. 9. The complete description is in Appendix E.6.

Comparisons:

Hmd of the mandibles from TD10 coincides with recent *N. fodiens* specimens from the Pyrenees and Italy (Fanfani, 1999; Moya-Costa and Cuenca-Bescós, 2019; Moya-Costa, 2020), with *A. thenii* (Malez and Rabeder, 1984) and *Macroneomys* sp. (Fanfani, 1999) and with part of the record of *A. gibberodon*, especially individuals from Fuente Nueva 3 (Furió, 2007a), whose mandibles are higher than other European specimens (Reumer, 1984; Fanfani, 1999; Rzebik-Kowalska, 2000; Rofes and Cuenca-Bescós, 2006). Hmdm2 coincides very well with *N. fodiens*, but this measurement is not usually recorded, so data from other species are scarce. The measurements of the condyle (HmdC, LmdUF and LmdLF) coincide better with *A. gibberodon*, *A.* aff. *thenii* and *N. newtoni* (Fig. 10). Other measurements, such as those taken on the teeth, overlap with all these species and others too (Fig. 10 and Appendix D).

Species such as *A. gibberodon* are ruled out because of the position of the coronoid spicule or the elongated shape of the coronoid process. It is unlikely to be *A. thenii*, because this has not been recorded outside Croatia.

In summary, the height of the coronoid process, which is typical of *N. fodiens* (Chaline et al., 1974), the shape of the condyle, the mild orange pigmentation, and the thick and wavy cingula indicate that it is a species very similar to *N. fodiens*. The mandibular measurements (Hmd) are greater than *N. anomalus* from the Pyrenees (Chaline et al., 1974). In addition, the lower incisor is elongated and acuspulate, which is typical of *Neomys* and rules out assignation to the genus *Asoriculus*.

The morphometric differences in the condyle compared to the recent specimens of *N. fodiens* raise some doubts, so the Gran Dolina specimens are assigned to *N.* cf. *fodiens*.

In general, the neomynines of the Middle Pleistocene of Atapuerca are much larger than those of the Early Pleistocene, both post-Jaramillo (Gran Dolina) and pre-Jaramillo (Sima del Elefante) (Rofes and Cuenca-Bescós, 2006).

Neomyni cf. *Macroneomys* Fefjar, 1966.

Material: Right mandible with no teeth. From the level TD10.1 of Gran Dolina. Sample: ata04td10.1g20z380-400. MPZ 2019/1344.

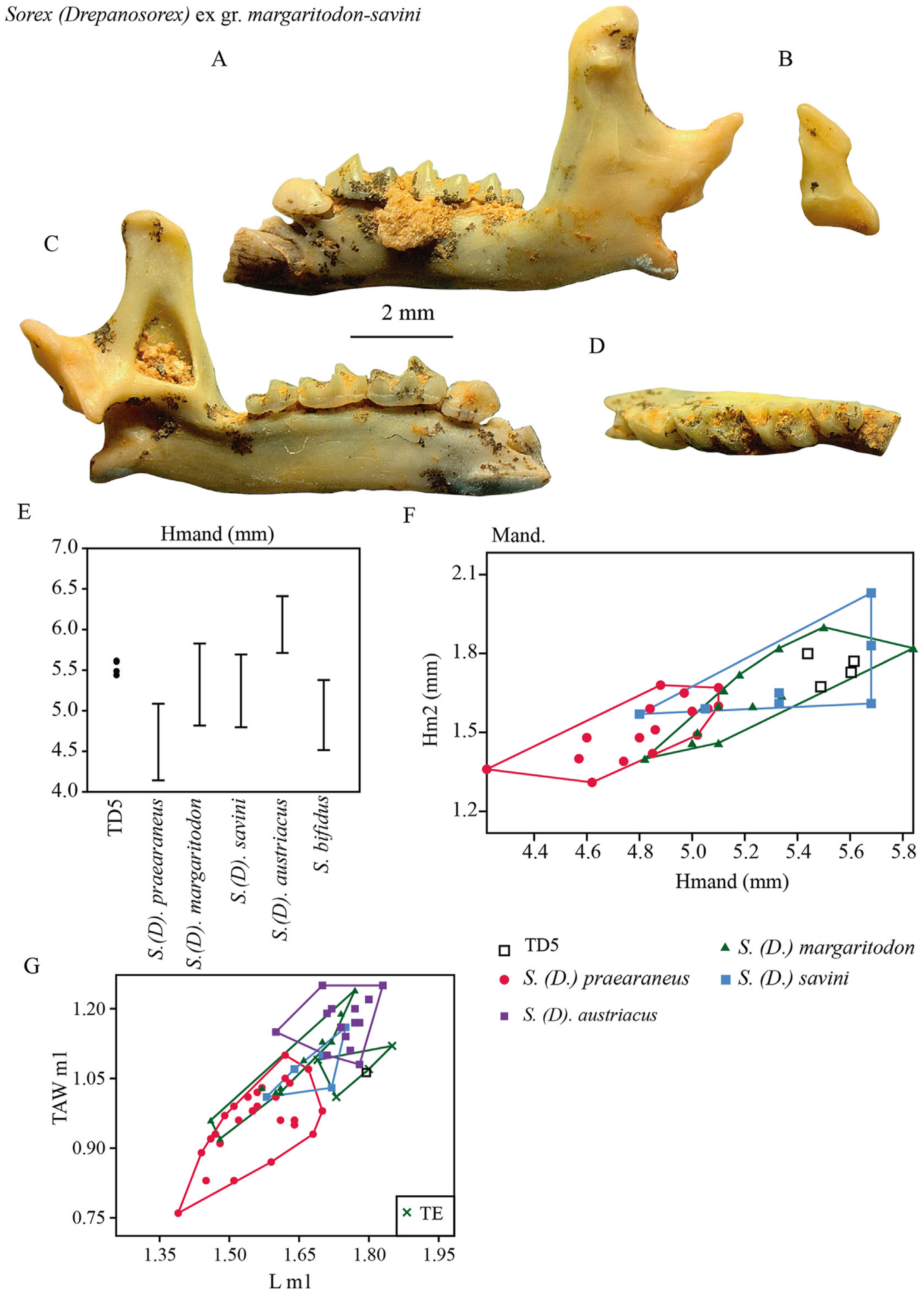

Fig. 7. A-D. Specimen of *S. (D).* ex gr. *margaritodon-savini* of td5t5f14z950-960 (MPZ, 2019/1325). **A**. Mandible in labial view. **B**. Condyle. **C**. Mandible in lingual view. **D**. Occlusal view of p4-m3. **E, F**. Hmd of the specimens of TD5 compared with European species. The specimens of TD5 overlap with *S. (D). savini* and *S. (D). margaritodon* **E**. Hmand (lines) of the specimens of Gran Dolina (dots) compared with European specimens. **F**. Hmd/Hmdm2 bivariate plot of *S.(D). margaritodon-savini* of Gran Dolina and other European specimens. **G**. Lm1/TAWm1 bivariate plot of *S.(D). margaritodon-savini* of Gran Dolina and the different species of *Drepanosorex*. Data other than this work taken from Hinton (1911), Rabeder (1972), Reumer (1984), Reumer and Hordijk (1999), Zaitsev and Baryshnikov (2002), Rzebik-Kowalska (1991, 2000, 2013), Rofes and Cuenca-Bescós (2013), Botka and Mészáros (2016). All data are in Appendix D.

See Appendix B.

Measurements: See Table 8.

Description:

See Fig. 11. The complete description is in Appendix E. 7.

Comparisons:

Fefjar (1966) and Maul and Rzebik-Kowalska (1998) do not

Table 5
Measurements of *Asoriculus gibberodon*. In mm.

Levels	TD5		TD6				
Measures	**n**		**n**	**min**	**$\overline{X}$**	**max**	**sd**
Lm1			1		1.71		
TRWm1			1		0.87		
TAWm1			1		0.97		
Lm2			1		1.5		
TRWm2			1		0.87		
TAWm2			1		0.92		
Lmd	1	4.62					
Hmd			1		4.27		
Hmdm1	1	1.59	2	1.59	1.61	1.64	0.04
Hmdm2	1	1.54	3	1.44	1.49	1.54	0.05
HmdC	1	2.12	2	2.24	2.24	2.24	0.01
LmdUF	1	0.91	2	0.95	0.96	0.98	0.02
LmdLF	1	1.49	3	1.52	1.62	1.68	0.09

Table 6
Measurements of *Neomys* cf. *newtoni*.

	TD6	
Measure	n	
Li1	1	3.95
Hi1	1	0.81
La1	1	1.13
Lp4	1	1.27
Wp4	1	0.77

specify how they took their measurements, so we cannot know with certainty whether the measurements available for *M. brachygnathus* in their works are the same as those we took for the individual from TD10 following Reumer (1984). If we assume that our Hmd, Hmdm3, HmdC, LmdUF and LmdLF are equivalent to those of the aforementioned authors, the specimen from TD10 is way smaller than the central European ones, being closer to the dimensions of *N. fodiens* (see Appendix D)

Hmd is similar to the specimen attributed to *Macroneomys* sp. by Fanfani (1998). However, it shows some differences. *Macroneomys* sp. has a wide ascending ramus, which contrasts with the individual from TD10, whose is narrow. It forms an obtuse angle with the horizontal ramus, whereas in the individual from TD10 the angle is right.

The specimen from TD10 and *Macroneomys* sp. are similar in the size of the ascending ramus, the external temporal fossa, and the long coronoid spicule. The mandibular foramen is oval in both cases and is located below the posterior part of the internal temporal fossa. In both cases, the upper segment of the horizontal ramus is located below the posterior part of the internal temporal fossa. In both cases, the upper segment of the horizontal ramus tends to be

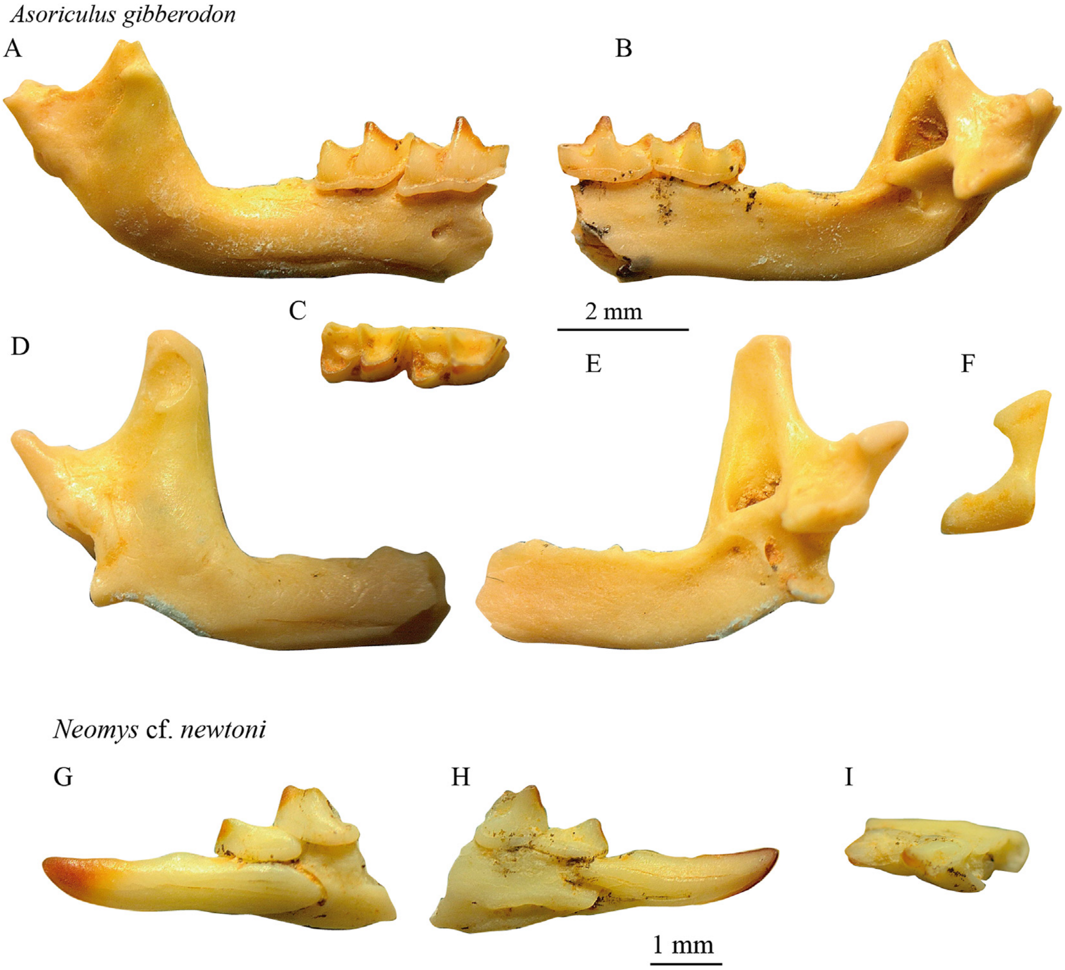

Fig. 8. A-F *Asoriculus gibberodon*. **A-C**. Mandible with m1 and m2 of td6.3.6f14z860-870 (MPZ, 2019/1327). **A**. Labial view, **B**. Lingual view, **C**. Occlusal view, **D-F**. Mandible of td636g10z850-860 (MPZ, 2019/1328). **D**. Labial view. **E**. Lingual view. **F**. Condyle. **G-I** *N.* cf. *newtoni* of td6.3.2g12z770-790 (MPZ, 2019/1330). **G**. Labial view of the anterior part of the mandible, **H**. Lingual view. **I**. Occlusal view of a1 and p4.

Table 7
Summary of the measurements of *Neomys* cf. *fodiens* of TD10. In mm.

Level	TD10				
Measurement	**n**	**min**	$\bar{X}$	**max**	**sd**
Li1	1	4.2	4.2	4.2	
Lm1	2	1.72	1.77	1.82	0.07
TRWm1	2	1	1.04	1.09	0.06
TAWm1	2	0.93	0.97	1.01	0.05
Lm2	3	1.57	1.6	1.62	0.03
TRWm2	3	0.86	0.92	0.97	0.05
TAWm2	3	0.87	0.93	0.97	0.05
Lm3	2	1.16	1.17	1.18	0.01
Wm3	2	0.7	0.73	0.76	0.04
L m1-m3	2	4.37	4.45	4.53	0.11
Lmd	2	4.86	4.91	4.95	0.06
Hmd	3	4.6	5.02	5.4	0.4
Hmdm1	3	1.7	1.86	2	0.15
Hmdm2	4	1.71	1.81	1.9	0.1
HmdC	6	2.01	2.27	2.64	0.21
LmdUF	7	0.72	0.9	1.04	0.12
LmdLF	8	1.43	1.58	1.81	0.12

higher in its posterior part.

In summary, the specimen from TD10 shows some differences with respect to *Macroneomys* sp. of Fanfani (1998), but its main dimensions are similar. This opens up the possibility of there being several species of *Macroneomys* coexisting in the Middle Pleistocene.

In its coronoid process Neomyni cf. *Macroneomys* resembles the specimens from Koněprusy (Fefjar, 1966), la Fage (Jammot, 1975) and Voigtstedt (Maul and Rzebik-Kowalska, 1998). It also has characters in common with *M.* cf. *brachygnathus* of Fontana Marella cave (Bona et al., 2008), although the ascending ramus is relatively taller and narrower in the lower part.

Macroneomys is a very scarce genus in the European fossil record, but with a relatively wide area of dispersion. Therefore, it is important as a biostratigraphic marker. It can be found in Great Britain, Germany, the Czech Republic, Poland, Italy, France and Spain (Fefjar, 1966; Jammot, 1975; Malez and Rabeder, 1984; Rzebik-Kowalska, 1991; Maul and Rzebik-Kowalska, 1998; Fanfani, 1998, 1999; Masini et al., 2005; Harrison et al., 2006; Bona et al., 2008; Maul and Parfitt, 2010; Parfitt and Harrison, 2011). In Spain there is a reference in Galicia (Parfitt and Harrison, 2011), but without a description. In Parfitt and Harrison (2011) there is also another citation in the south of France, but with no additional data.

Subfamily Crocidurinae Milne-Edwards, 1874

Genus Crocidura Wagler, 1832.
Crocidura kornfeldi Kormos, 1934.

The identification follows Reumer (1984), Rzebik-Kowalska (1991), and Rofes and Cuenca-Bescós (2011).

Material: 79 mandibles (37 left and 42 right) from levels TD3, TD4, TD5, TD6 and TD8 of the site of Gran Dolina. MPZ 2019/1345–1423. See Appendix B.

Measurements: See Table 9. The detailed measurements for each specimen are given in Appendix C.

Description:

See Fig. 12. The complete description is in Appendix E.8.

Comparisons:

From the Early Pleistocene of Europe four species of the genus

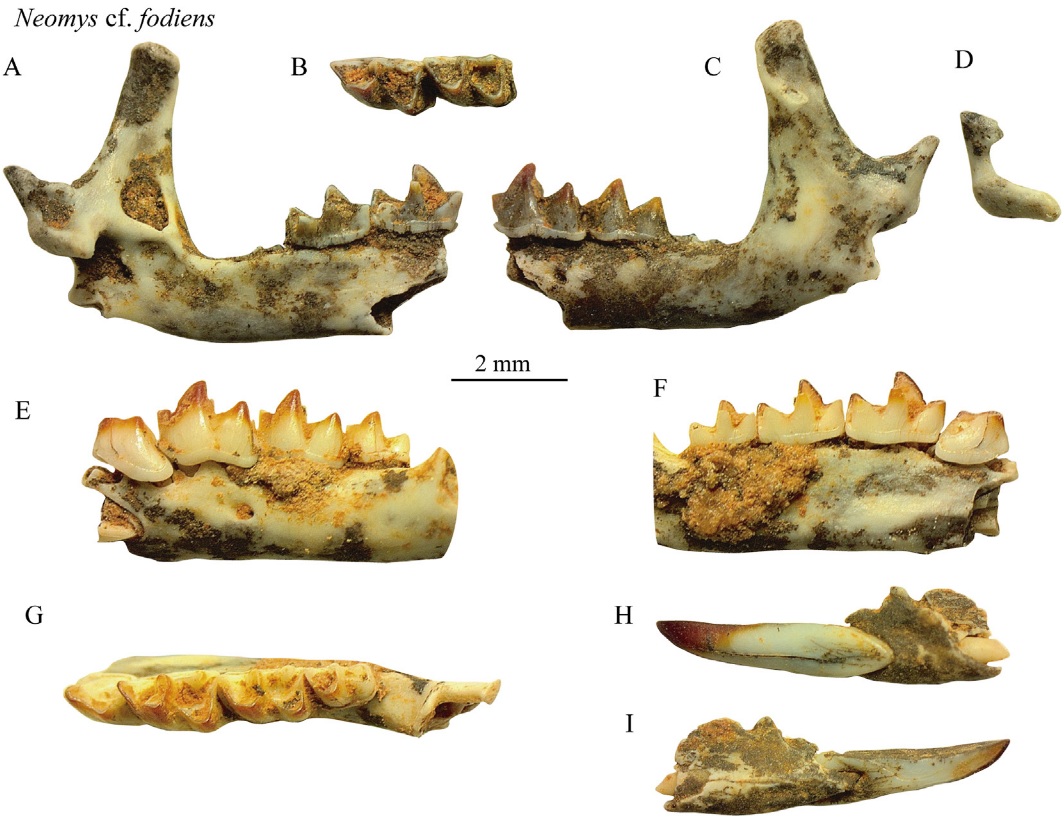

Fig. 9. *Neomys* cf. *fodiens*. **A-D.** Mandible of td10.2n19z430-440 (MPZ, 2019/1337). **A**. Lingual view. **B**. m1 and m2 in occlusal view. **C**. Labial view. **D**. Condyle. **E-G** Fragment of mandible with p4-m3 of td10.2n18z405-415 (MPZ, 2019/1336). **E**. Labial view, **F**. Lingual view. **G**. Occlusal view. **H–I**. Incisor of td10-2n21z410420 (MPZ, 2019/1333). **H** Labial view. **I**. Lingual view.

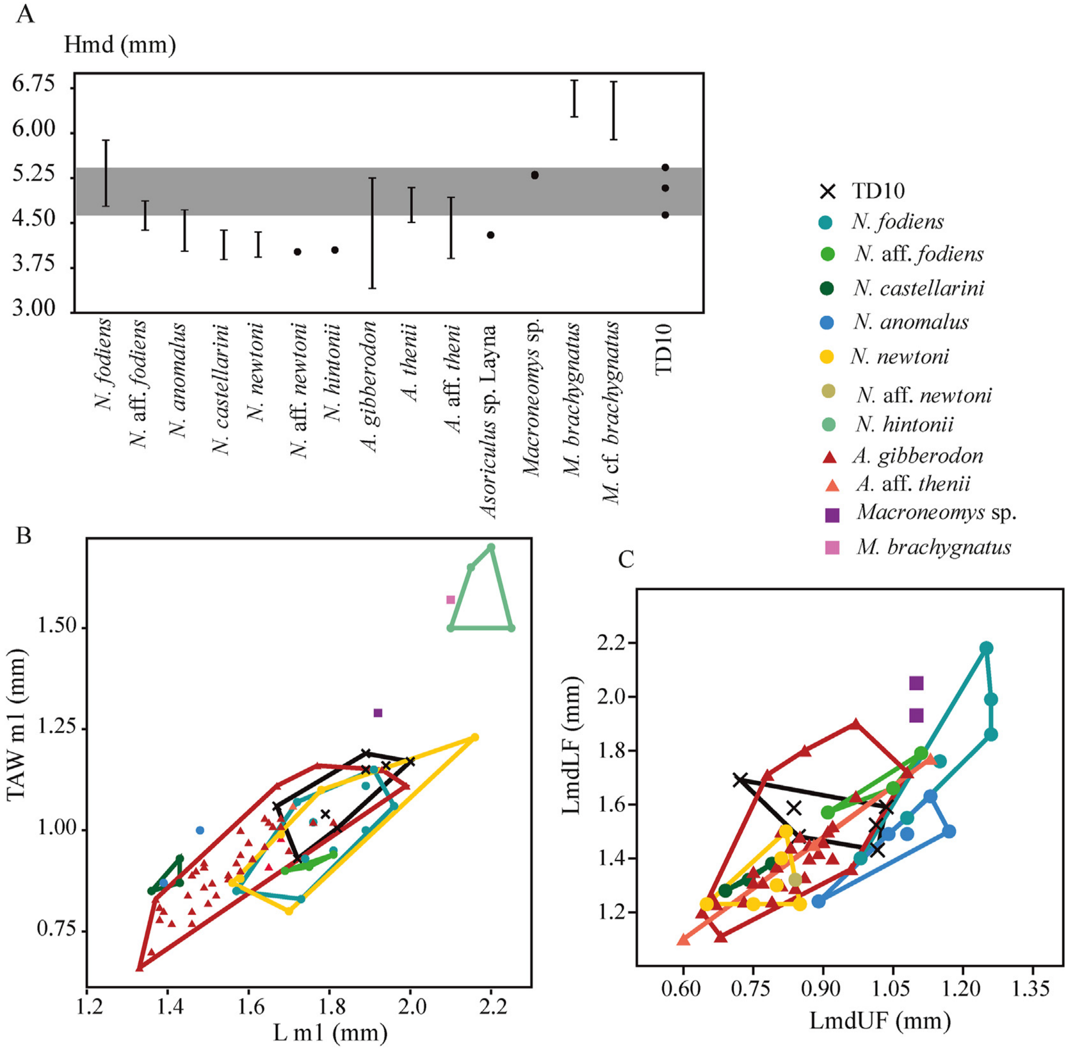

Fig. 10. A. Hmd measurements of *Neomys* cf. *fodiens* of TD10 compared with other european neomynines. **B.** Lm1/TAWm1 bivariate plot of N. cf. fodiens of TD10 compared with other European species. **C.** LmdUF/LmdLF bivariate plot of *N.* cf. *fodiens* of TD10 compared with other European species. Data other than is work taken from Hinton (1911), Fefjar (1966), Jammot (1975), Malez and Rabeder (1984), Reumer (1984), Rzebik-Kowalska (1991, 2000, 2007, 2013), Maul and Rzebik-Kowalska (1998), Fanfani (1998, 1999), Zaitsev and Baryshnikov (2002), Masini et al. (2005), Rofes and Cuenca-Bescós (2006), Furió (2007b), Bona et al. (2008), Botka and Mészàros (2017) and Moya-Costa (2020). See Appendix D to know all the data.

Table 8
Measurements of Neomyni cf. *Macroneomys*. In mm.

Level	TD10	
Measure	n	
Hmd	1	5.57
Hmdm3	1	1.66
HmdC	1	2.51
LmdUF	1	0.75
LmdLF	1	1.51

Crocidura have been found: *C. kornfeldi*, *C. obtusa*, *C. sicula* and *C. zorzii*. From the Middle Pleistocene onwards *C. leucodon* and *C. russula* also appear (Rzebik-Kowalska, 1998; Fanfani, 1999; Rofes and Cuenca-Bescós, 2011).

The species that we can expect in the Early Pleistocene levels of Gran Dolina are: *C. kornfeldi*, *C. obtusa* and/or *C. zorzii*, because *C. sicula* is an endemism from the island of Sicily (Kotsakis, 1986). Here we compare them with other species of similar chronologies.

Rofes and Cuenca-Bescós (2011) describe more than 200 specimens of *C. kornfeldi* in Sima del Elefante. The images of the mandibles included in that study show morphological variability in the coronoid process like that in Gran Dolina.

The scarce data available for *C. zorzii* (Fanfani, 1999) indicate that it is a species of larger size than *Crocidura* from Gran Dolina, its measurements lying outside the range of Gran Dolina in Hmd, HmdC and Lm1 (Fig. 12).

In general, the measurements of *C. obtusa* overlap with the upper extreme of the ranges of the specimens from Gran Dolina. The same occurs with *C. leucodon*. The measurements of *C. suaveolens* are slightly lower (See Fig. 12 I).

Mészàros et al. (2019) establish a neotype for *C. obtusa* and redefine this species because the holotype is lost and Kretzoi (1938) did not establish clear differences with respect to other species of *Crocidura*. These authors also set a series of criteria for diagnosis to differentiate it from *C. kornfeldi*. These relate to the size of the mandibular ramus, the inclination of the coronoid process, the height of the condyle and the interarticular area. However, the authors do not give measurements or specific differences. They give data for the molars while stating that they are not diagnostic

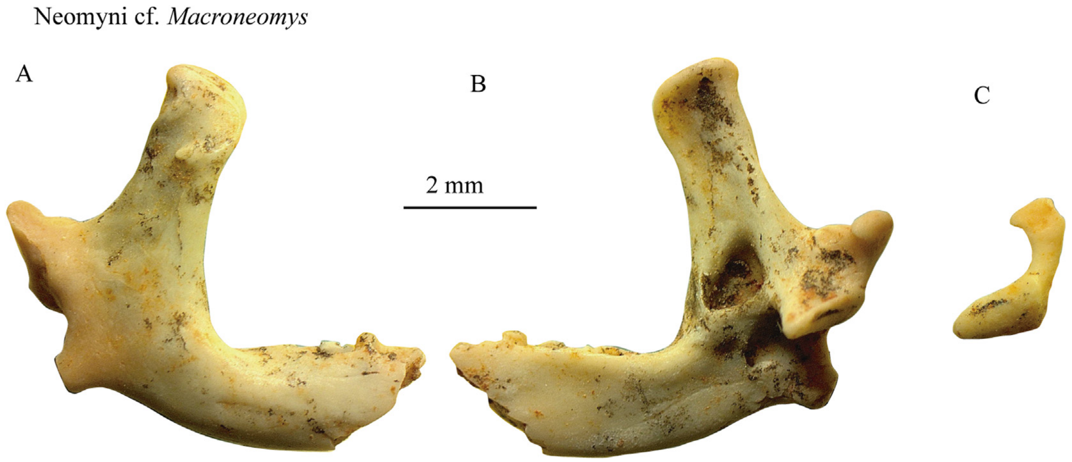

Fig. 11. Neomyni cf. *Macroneomys* of td10.1g20z380-400 (MPZ 2019/1344). **A.** Labial view of the mandible. **B.** Lingual view of the mandible. **C.** Condyle.

Table 9
Measurements of *Crocidura kornfeldi* of Gran Dolina. In mm.

Levels	TD3-4					TD5					TD6					TD8				
Measurement	**n**	**min**	$\overline{X}$	**max**	**sd**	**n**	**min**	$\overline{X}$	**max**	**sd**	**n**	**min**	$\overline{X}$	**max**	**sd**	**n**	**min**	$\overline{X}$	**max**	**sd**
Li1	1	3.22	3.22	3.22							2	2.77	2.91	3.05	0.2					
Hi1											2	0.78	0.78	0.79	0.01					
La1	1	1.12	1.12	1.12																
Lp4	6	0.98	1.13	1.19	0.08	2	1.18	1.21	1.23	0.04	1	1.05	1.05	1.05		1	1.17	1.17	1.17	
Wp4	6	0.8	0.87	0.99	0.06	2	0.82	0.87	0.92	0.07	1	1.09	1.09	1.09		1	0.77	0.77	0.77	
Lm1	18	1.41	1.55	1.69	0.07	6	1.45	1.53	1.58	0.05	8	1.35	1.45	1.53	0.07	5	1.45	1.52	1.63	0.07
TRWm1	18	0.86	0.95	1.04	0.05	6	0.88	0.93	0.99	0.04	8	0.8	0.9	0.99	0.05	5	0.86	0.92	1.02	0.06
TAWm1	18	0.95	1.07	1.15	0.05	6	0.98	1.06	1.12	0.06	8	0.9	1.02	1.14	0.07	5	1	1.04	1.13	0.05
Lm2	23	1.34	1.51	1.63	0.08	5	1.35	1.50	1.67	0.14	10	1.25	1.4	1.46	0.07	3	1.37	1.52	1.61	0.13
TRWm2	23	0.84	0.91	0.99	0.04	5	0.80	0.89	0.99	0.07	10	0.81	0.89	0.92	0.04	3	0.84	0.89	0.96	0.06
TAWm2	23	0.88	0.95	1.03	0.05	5	0.87	0.95	0.99	0.05	10	0.84	0.91	1	0.05	3	0.86	0.92	0.96	0.05
Lm3	13	1.13	1.2	1.28	0.04	5	1.04	1.17	1.25	0.10	6	1.07	1.13	1.16	0.04	2	1.1	1.13	1.17	0.05
Wm3	13	0.63	0.67	0.73	0.03	5	0.64	0.68	0.73	0.04	6	0.59	0.62	0.66	0.03	2	0.61	0.64	0.67	0.05
L m1-m3	10	0.43	3.52	4.08	1.1	2	3.74	3.89	4.03	0.21	4	3.38	3.65	3.81	0.19	1	3.66	3.66	3.66	
Lmd	10	5	5.35	5.82	0.28	2	4.95	5.19	5.43	0.34	5	5.09	5.33	5.67	0.24					
Hmd	13	4.36	4.59	4.83	0.16	5	4.35	4.65	5.17	0.33	4	4.31	4.48	4.68	0.16	1	4.31	4.31	4.31	
Hmdm1	29	1.35	1.64	1.95	0.13	7	1.41	1.55	1.63	0.09	13	1.41	1.55	1.73	0.09	4	1.31	1.47	1.6	0.12
Hmdm2	33	1.33	1.56	1.83	0.13	7	1.35	1.50	1.67	0.10	17	1.34	1.44	1.71	0.09	6	1.1	1.41	1.6	0.17
HmdC	14	1.39	1.61	1.79	0.13	5	1.32	1.52	1.66	0.14	10	1.32	1.52	1.72	0.13	1	1.6	1.6	1.6	
LmdUF	13	0.58	0.71	0.82	0.07	5	0.63	0.71	0.79	0.06	12	0.63	0.76	0.87	0.06	1	0.7	0.7	0.7	
LmdLF	16	1.02	1.25	1.41	0.1	6	1.13	1.25	1.50	0.13	11	1.11	1.25	1.4	0.09	1	1.29	1.29	1.29	

because they overlap with *C. kornfeldi*. One diagnostic character that they introduce is the coronoid spicule, which is well developed in *C. obtusa*, but not in *C. kornfeldi*. In previous works such as Fanfani (1999), Rofes and Cuenca-Bescós (2011) and Botka and Mészàros (2016), *C. kornfeldi* presents a coronoid spicule that is fainter in appearance than the only drawing in Mészáros et al. (2019) and the neotype of *C. obtusa*. The mandibles of *C. kornfeldi* from Gran Dolina have a small coronoid spicule, unlike those illustrated by Rzebik-Kowalska (2000) for *C. obtusa*.

The range of measurements of these specimens, both mandibular and dental, coincides totally with *C. kornfeldi* (Fig. 12). Compared to the measurements from Sima del Elefante, it is ascertained that the mandibles from Gran Dolina are slightly above the mean, although they mostly overlap.

Hmd or HmdC also coincides with *C. russula*, but in general the height of the mandible is lower in the latter.

5. Discussion

As well as *D. glyphodon*, the soricid assemblage from Gran Dolina contributes the first post-Jaramillo Early Pleistocene records in the Iberian Peninsula of *Sorex* ex gr. *runtonensis-subaraneus*, *Sorex* (*Drepanosorex*) ex gr. *margaritodon-savini*, *Asoriculus gibberodon* and *Neomys* cf. *newtoni*. It also yields the second record of *S.* ex gr. *runtonensis-subaraneus* in the Middle Pleistocene of the Iberian Peninsula, which might actually be the first if we dismiss the dubious “*Sorex* sp. size *helleri*” of López-Martínez (1980), interpreted as *Sorex* cf. *runtonensis* by Rzebik-Kowalska (1998). In addition, there are several sites with unidentified *Sorex* specimens (see Appendix A and Moya-Costa, 2020) that may potentially belong to this group. In the rest of Europe, the group is present in many sites both in the post-Jaramillo Early Pleistocene and in the Middle Pleistocene (Van der Meulen, 1973; Terzea, 1995; Paunović and JambreŠić, 1997; Rzebik-Kowalska, 1998, 2000; Fanfani, 1999; Zaitsev and Baryshnikov, 2002; Bona et al., 2008; Botka and Mészáros, 2018).

Neomys cf. *newtoni* has not previously been found in the Iberian Peninsula, although there are records of *Neomys* sp. in the Early Pleistocene, e.g., at Almenara-Casablanca 3 (Furió, 2007b), Cueva Negra del Estrecho del Río Quípar (López-Jiménez et al., 2018),

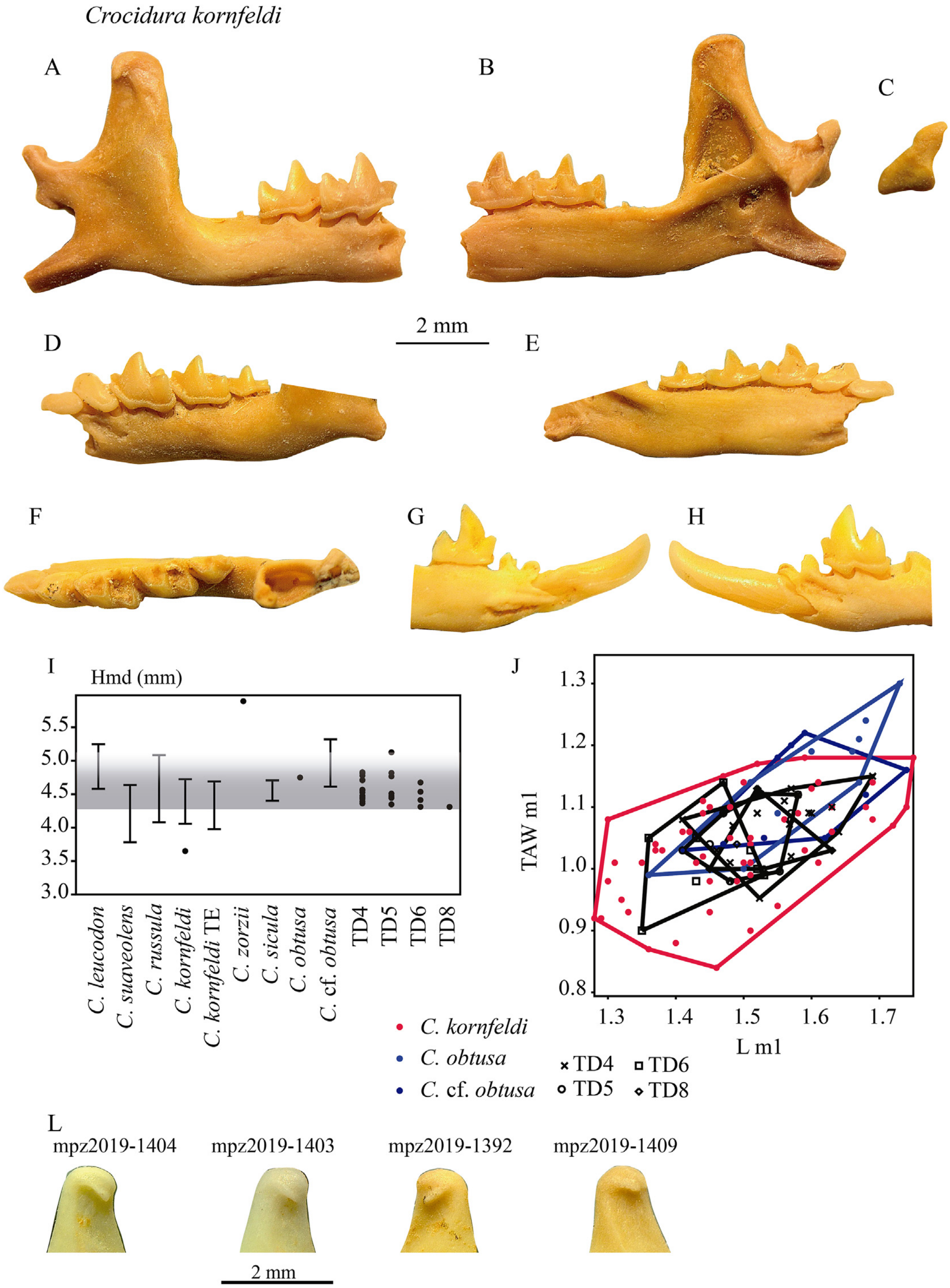

Fig. 12. *C. kornfeldi*. **A-C.** Mandible of td4.2wh09z1220-1230 (MPZ, 2019/1380). **A**. Labial view. **B**. Lingual view. **C**. Condyle. **D-F.** Mandible with a1-m3 of td4.2wg09z1210-1220 (MPZ, 2019/1372). **D**. Labial view. **E**. Lingual view. **F.** Occlusal view. **G** and **H.** Anterior fragment of mandible with incisive of td4.2wg09z1210-1220 (MPZ, 2019/1375). **G**. Lingual view. **H**. Labial view. **I** Hmand of the *Crocidura* of the different levels of Gran Dolina compared with European *C. kornfeldi* and other species of *Crocidura*. **J**. Lm1/TAWm1 bivariate plot of *C. kornfeldi* of Gran Dolina with the rest of Europe and with *C. obtusa*. Data other than this work taken from Reumer (1984), Fanfani (1999), Rzebik-Kowalska (2000, 2007), Rofes and Cuenca-Bescós (2011), Botka and Mészáros (2016), Mészáros et al. (2019) and recent *Crocidura* from the Pyrenees (Moya-Costa, 2020) See Appendix D for the full data. **L.** Different coronoid spicules of *C. kornfeldi* from Gran Dolina.

Loma Quemada 2 (Maldonado-Garrido et al., 2017), and Cúllar Baza 1 (Agustí et al., 2010). However, its presence is rather common in the late Early Pleistocene and Middle Pleistocene sites of the rest of Europe (Rzebik-Kowalska, 2009, 2000, 2013; Kotsakis et al., 2003; Pazonyi et al., 2016; Botka and Mészáros, 2018).

Gran Dolina contributes the youngest record of *A. gibberodon* worldwide, as late as the end of the Early Pleistocene. Other fossil records are older. These are the Pleistocene sites of Somssich Hill 2, Hungary, which is older than 1 Ma (Botka and Mészáros, 2017; Pazonyi et al., 2018), and Deutsch-Altenburg DA4, Austria, with an

Table 10

European sites containing soricid species present in Sima del Elefante and Gran Dolina (Atapuerca), distributed by chronologic range either as Early Pleistocene pre-Jaramillo, post-Jaramillo or Middle Pleistocene. Particular taxonomic assignations are indicated in brackets. Austria: Deutsch-Altenburg (DA), Hundsheim (Hund), Bulgaria: Cave 15 –I Temnata-Prohodna Cave System (TP15), Morovitsa Cave 1 (MorC), Temnata Cave (TemC), Varbeshnitsa (Varb); Croatia: Dubci Cave (DubC), Marjan, Rava (Marj), Razvode (R), Tatinja Draga (TaDa), Podumci (P), Ugljan (Ugl); Czech Republic: Cervený Kopec (CerK), Chlum 4 (Chl), Dobrkovice 2 (Dob2), Holstejn (Hols), Koneprusy C718 and JK (Kon), Mladecská Cave (Mlad), Prezletice (Prez), Stránska Skála (StrS), Turold (Tur); France: Aldène and Gerde (AlGe), Grotte de la Carriére and Grotte du Cap de la Bielle (GCCB), La Fage (Fag), Les Valerots Caves (ValC), Montoussé (Mont), Mas Rambault (Mram), Nestier (Nest), Sant Esteve Janson (SEJ); Germany: Breitenberghöle (Breit), Erpfingen (Erpf), Genkingen 2 (Genk), Heppenloch (Hepp), Hohensülzen (Hohe), Hunas (Hunas), Husarenhof 4 (Husa), Kärlich (Karl), Miesenheim 1 (Mies), Plaidter-Hummerich (Pl-Hu), Petersbuch (Pete), Sackdilling Cave (Sack), Sudmer-Berg 2 (SudB), Untermassfeld (Unt), Voigtstedt (Voig), Westhofen (West), Windloch (Wind); Greece: Marathoussa (M), Petralona (Pet), Ravin Voulgarakis (RV), Tourkobounia (T); Hungary: Beremend (Ber), Horvögly Cave (HorC), Kövesvárad (Kov), Nagyharsanyhegi (Nag), Somssich Hill 2 (SH2), Ostrazmos 3/2 (O3/2), Pongor -lyuk Cave (PIC), Tarko (Tark), Uppony 1 (Upp), Várhegy-Buda (Va-Bu), Vértesszolos 2 (Vert), Villány 3 (V3) ; Italy: Bosco Chiesanova (BC), Cala Cave -Sicily (CCS), Cava dell'Erba (CE), Cave Minore di San Benardino (CMSB), Fontana Marella (FontM), Loara (Loa), Montagnola (Mtg), Monte Peglia (MP), Pirro Nord (PN), Rifreddo (Rif), San Agostino (Ago), Sant'Arcangelo (SA)), San Giovanni di Duino (SGD), Soave- Cava Sud (S-CS), Soave-Cengelle (SC), Soave-Viatelle (SV), Spessa 2 (Spe), Tre Fossi (TF), Valdemino (Val), Visogliano (Vis), Netherlands: Maastricht-Belvédeère 3 and 4 (MaBe); Poland: Kielniki (Kiel), Kozi Grzbiet (KoGr), Nietoperzowa Cave (Niet), Rebielice Królewskie 4 (ReKr), Żabia Cave (ZC), Zalesiaki 1A (Zal), Zamkowa Dolna Cave C (ZDC); Romania: Betfia (Bef), Cave in the Parului Valley (CPV), Feldioara-Cariera (FeCa), Gesprengberg Cave (Gesp), Gura Dobrogei Cave 1 (GuDo), Rotbav-Dealul Tiganilor (RDT), Sindominic 1 (Sind); Russia: Konachovka 1 and 2 (Kona), Ilinka 1 and 2 (Ilin), Treugolnaya cave (TC); Slovakia: Gombasek (Gomb), Vceláre (Vce), Zirany (Zir); Spain: Almenara-Casablanca (ACB), Aridos (Ari), Barranco de los Conejos (BCN), Barranco León (BL), Cueva del Camino (CuCa), Cueva Victoria (CV), Cúllar Baza (CB), Fuente Nueva 3 (FN), Gran Dolina (TD), Incarcal (Inc),Orce 3 (Orc), Quibas (Q) , Sima del Elefante (TE), Somiedo (So) Venta Micena (VM); Ukraine: Cherevichnoe 1(Che), Medzhybozh (Med); United Kingdom: Beeches Pit (Bee), Box-groove (Box), East Farm (EF), Little Oakley Channel (LOC), Ostend (Ost), Pakefield (Pak), Sugworth (Sug), Westbury-Sub-Mendip (WSM), West Runton (WR)(Van der Meulen, 1973; Reumer, 1984; Reumer and Doukas, 1985; Jánnossy, 1986; Terzea, 1995; Paunović and JambreŠić, 1997; Maul and Rzebik-Kowalska, 1998; Rzebik-Kowalska, 1998, 2000; Fanfani, 1999; Koufos et al., 2001; Zaitsev and Baryshnikov, 2002; Furió, 2007b, 2015; Galobart and Agustí, 2003; Kotsakis et al., 2003; Rofes and Cuenca-Bescós, 2006, 2009a, 2009b, 2011, 2013; Bona et al., 2008; Agustí et al., 2010, 2011; Nadachowski et al., 2011; Parfitt and Harrison, 2011; Laplana et al., 2013; Rzebik-Kowalska, 2013; Pazonyi et al., 2016; Rofes et al., 2016a,b; Rzebik-Kowalska and Rekoveks, 2016; Maldonado-Garrido et al., 2017; Botka and Mészáros, 2018; Piñero et al., 2020 and this work). The Atapuerca sites are in bold. "?" means the chronometric age is unknown and here it is correlated with the possible ages.

	Early Pleistocene pre-Jaramillo	Early Pleistocene post-Jaramillo	Middle Pleistocene
Crocidura kornfeldi	PN, CE, R, TaDa, M (?), RV (?), T (?), Ber (?), O3/2, V3, Bef, BL, Q, **TE**	DA, P, M (?), RV (?), T(?), SH2, Bef, Nag, **TD**, CV	SA, Rif, Vis, TF, CB, **TD**
Beremendia fissidens	TP15(?), TemC(?), Hols, Hohe (?), Sack (?),Unt (?),Wind (?), S-CS, R, TaDa, M(?), RV (?), T, Ber (?), O3/2, Kiel, Bef, Gomb (?) ACB, **TE**	DA, TP15(?), TemC(?), Chl, Mlad, P, StrS, ValC, Mram, Hohe (?), Sack (?), Unt (?), Wind (?), Nag, SH2, KoGr,Zal, Bef, ZDC, Gomb (?), Zir, WR	Mont, MP, SV, Bef, KoGr, Gesp, Sug (cf.)
Dolinasorex glyphodon		**TD**	
Sorex minutus	TemC (?), Hohe (?), Sack (?), M (?), RV (? cf.), Ber (aff., ?), Kov (?), O3/2, V3, Mtg, Kiel, ZC, Bef, Gomb (?), Vce (cf.), ACB, BCN, BL, FN, Inc	DA (cf.), TemC (?), Varb (cf.), Chl, Kon, Mlad (cf.), Prez, StrS, ValC, Hohe (?), Sack (?), Kov (?), SH2, Upp, Bef, Mtg, Zal, ZDC, Gomb (?), **TD**, Zir, WR	Hund, MorC (+cf.), Dob2, Kon (cf.), Tur (cf.), AlGe, Fag, Genk, Hunas, Husa, Mies, Pl-hu, Pete, SudB, West, HorC, Val, Nag, PIC, Tark, Upp, Vert, CCS, FontM, Loa, Spe, Niet, Bef, GuDo (cf.), Sind, TC (aff.), **TD,** Bee, EF, LOC (cf.), WSM
Sorex ex gr. *runtonensis-subaraneus*	TP15 (runt.,?), DubC (cf. runt., ?), Marj (runt.,?), TaDa (runt.), Ugl (runt,?), Hols (runt.), Hohe (runt., ?), Sack (cf. runt. and sub., ?), Unt (runt., ?), Wind (runt., ?), CE (bor-runt.), R (runt.), Ber (aff. runt., ?), Kov (aff. runt.,?), Kiel (runt.), ZC (runt.), Bef (runt. and cf.sub.), Ilin (runt., ?), Vce (cf. run.t), Che (aff. runt., ?), **TE** (runt.),	DA (runt.), TP15(runt., ?), Varb (sub.), DubC (cf. runt.,?), Marj (runt,?), P (runt.), Ugl (runt,?), Chl (cf. runt.), Kon (runt.), Mlad (runt.+ cf.runt.), Prez (runt.), StrS (runt.), ValC (runt.), Mram (runt.), Hohe (runt.,?), Sack (cf. runt. and sub., ?), Unt (runt., ?), SH2 (runt.), Upp (sub.+cf. sub.), Wind (runt., ?), Kov (aff. runt., ?), KoGr (both), Zal (runt.), Bef (runt. and cf. sub), Kona (runt.), Ilin (runt.,?), Che (aff. runt., ?), **TD**, WR (runt.)	Hund (cf. runt.), MorC (sub.), CerK (runt.), Tur (sub.), AlGe (sub.), Fag (both), Mont (runt.), Nest (sub.), SEJ (runt.), Erpf (cf. runt., sub.), Hepp (cf. runt.), Hunas (aff.runt., cf. sub.), Husa (cf. runt.), Karl (cf. runt.), Mies (runt.), Pet (cf. runt.), Tark (sub.), Upp (sub.+ cf. sub.), Va-Bu (cf. runt. and aff. sub., Vert (sub.), SA, FontM (cf. runt.), Loa (runt.), MP (runt.), Rif, Ago (runt.), SC, SV, SGD (runt.), Spe (runt.), Val, Vis, KoGr (both), ReKr (sub.), BC, Bef (runt.), FeCa (sub), Gesp (sub.), RDT (sub.), Kona (runt.),TC (cf. runt.), Ari (cf. runt.), **TD**, Box (runt.), Ost (runt.), WSM (runt.)
Sorex (Drepanosorex) ex gr. *margaritodon-savini*	Hols (marg.), Hohe (sav.,?), Sack (cf. Sav., ?), Wind (sav., ?), Bef (marg.), Gomb (sav., ?), Vce (marg.), **TE** (marg.)	DA (marg.), Kon (sav.), Mlad (marg.), Prez (sav.), ValC, (sav.), Hohe (sav.,?), Sack (cf. Sav., ?), Nag (marg.), SH2 (sav.), Upp (sav.), Wind (sav., ?), KoGr (sav.), Zal (sav.), Bef (marg.), ZDC(sav.), Gomb (sav., ?),**TD**, WR (sav.)	Breit (sav.), Erpf (sav.), Husa (sav.), Mies (sav.), Pete (marg.), SudB (sav.), West (cf. sav.), Tark (sav.), Upp (sav.),KoGr (sav.), DA (marg.), Bef (marg.), Bee (sav.), Ost (sav.), Sug (sav.), WSM (sav.)
Asoriculus gibberodon	PN (aff.), M(?), T, Ber (?), V3, ZC, Bef,BL, FN, Orc, **TE**, VM	DA (cf.), SH2, **TD**	
Neomys fodiens			GCCB, Fag, CMSB, Spe (+cf.), CPV, **TD (cf.)**
Neomys newtoni	S-CS (cf.), ZC	Kon, SH2, Zal, Bef (cf.), **TD (cf.)**, WR	Fag (cf.), Mies (cf.), MP(cf.), TC, Med, WSM (cf.)
Neomyni cf. *Macroneomys*		Kon, Voig, Kov, Vis, KoGr, Pak, Sug, WR	Fag (cf. Brachignatus), Mont, SA(brachignatus),FontM (cf. Brachignatus), Voig (brachignatus), Rif (brachignatus),Vis, BC (sp.), So, **TD**

age of 1–1.1 Ma (Rabeder et al., 2010). The remains from Gran Dolina, recorded in TD6, date to ~846 ± 57 ka (Álvarez-Posada et al., 2018).

The youngest record of *S. (D.)* ex gr. *margaritodon-savini* in the Iberian Peninsula is from Gran Dolina as well. This is the only one from the Middle Pleistocene of this region, whereas it is very common in the rest of Europe (Rzebik-Kowalska, 1998; Botka and Mészáros, 2018).

There is a single previous Middle Pleistocene record of cf. *Macroneomys* in the Iberian Peninsula, namely from Somiedo (Parfitt and Harrison, 2011). However, the one from Gran Dolina is the first one to be properly documented and described. In the rest of Europe, it is widely distributed but scant in numbers, appearing in 18 sites in the late Early Pleistocene and the Middle Pleistocene (Maul and Rzebik-Kowalska, 1998; Fanfani, 1999; Kotsakis et al., 2003; Bona et al., 2008).

Sorex minutus is a common species in the Pleistocene of Europe (Reumer, 1984; Jánnossy, 1986; Terzea, 1995; Rzebik-Kowalska, 1998, 2000, 2013; Fanfani, 1999; Koufos et al., 2001; Zaitsev and Baryshnikov, 2002; Galobart and Agustí, 2003; Furió, 2003; 2007; Bona et al., 2008; Agustí et al., 2010, 2011; Nadachowski et al., 2011; Pazonyi et al., 2016; Botka and Mészáros, 2018), but rare in the Iberian Peninsula, with a few Early Pleistocene records and only one from the Middle Pleistocene (Furió, 2003, 2007; Galobart and Agustí, 2003; Laplana et al., 2013; see Appendix A). The specimens from Gran Dolina are slightly larger than others, as inferred from the size of their mandibles, increasing the morphometric range of the species.

The oldest record of *N.* cf. *fodiens* in the Iberian Peninsula is from TD10, the species being scarce in the rest of Europe at this time, with only six Middle Pleistocene sites with *N. fodiens* or *N.* cf. *fodiens* spread over France, Italy and Romania (Rzebik-Kowalska, 1998).

Crocidura kornfeldi endured the Jaramillo threshold and persisted even into the Middle Pleistocene of Gran Dolina (TD8), although larger in average size than the pre-Jaramillo specimens of Sima del Elefante (Rofes and Cuenca-Bescós, 2011). As well as at Atapuerca, the species is also present at Cúllar Baza (Agustí et al., 2010) in the south of the Iberian Peninsula. In the rest of Europe, it is a common Early Pleistocene species, but it appears in only six sites in the Middle Pleistocene (Reumer, 1984; Reumer and Doukas, 1985; Jánnossy, 1986; Terzea, 1995; Paunović and JambreŠić, 1997; Rzebik-Kowalska, 1998, 2000; Fanfani, 1999; Koufos et al., 2001 Kotsakis et al., 2003; Agustí et al., 2010; Furió et al., 2015; Pazonyi et al., 2016; Botka and Mészáros, 2018; Piñero et al., 2020).

Dolinasorex glyphodon is a species that was likely endemic to the Iberian Peninsula, although there are other taxa with similar features (large size, robustness and skull morphology) in Europe, such as *Beremendia* and *Blarinoides* (Rofes and Cuenca-Bescós, 2009a). These may have occupied a similar ecological niche elsewhere.

Table 10 displays an updated synthesis of the European distribution and chronology of the soricid species identified so far in the Early (pre- and post-Jaramillo) and Middle Pleistocene of Atapuerca, organized by localities and countries. Remarkably, and aside from the endemism of *D. glyphodon*, the table brings to light that the Iberian Peninsula was a refugium for certain species, seemingly the last stand for relict populations of *A. gibberodon*, and one of the last for *S.* ex gr. *runtonensis-subaraneus*, *S.* (*D.*) ex gr. *margaritodon-savini* and *Neomys* cf. *newtoni*..

Cuenca-Bescós et al. (2007, 2010, 2016) proposed a series of biozones (based on faunal successions) for the different sites of the Atapuerca archaeo-paleontological complex, namely, Atapuerca Faunal Units (ATU) 1 to 9. The soricids from Gran Dolina described here are present in the stratigraphic layers corresponding to ATU 2-6a (Cuenca-Bescós al., 2016). Their presence is as follows: *S. minutus* in ATU 2–8, except 6b, c.; *S.* ex gr. *runtonensis-subaraneus* in ATU 1-6a; *S. (D.)* ex gr. *margaritodon-savini* in ATU 1–2; *A. gibberodon* in ATU 1–3; *N.* cf. *newtoni* in ATU 3; *N.* cf. *fodiens* in ATU 6a and 7; cf. *Macroneomys* in ATU 6a; and *C. kornfeldi* in ATU 1-6a. *Dolinasorex glyphodon* is present in ATU 2–4.

Comparison of the post-Jaramillo soricid assemblage from Gran Dolina with the pre-Jaramillo record of Sima del Elefante reveals that.

- *Asoriculus gibberodon* and *C. kornfeldi* persist beyond Jaramillo in the Gran Dolina stratigraphic section, with some morphometric variations especially conspicuous in *C. kornfeldi*, whose size increases.
- *Beremendia fissidens* does not persist beyond the Jaramillo threshold.
- *Dolinasorex glyphodon* appears to be a post-Jaramillo Early Pleistocene endemism so far.
- *Sorex runtonensis* persists beyond the Jaramillo limit or is replaced by *S.* ex gr. *runtonensis-subaraneus*, which is larger in size.
- *Sorex (D.) margaritodon* persists as well or is replaced by *S. (D.)* ex gr. *margaritodon-savini.*
- *S. minutus* appears only in post-Jaramillo times.

There are several sites in Europe with soricid assemblages similar to the Early and Middle Pleistocene layers of Gran Dolina, the best-known instances being Somssich Hill 2 (Botka and Mészàros, 2014, 2015, 2016), Betfia VII/3 (Terzea, 1995; Rzebik-Kowalska, 2000), and Kozi Grzbiet (Rzebik-Kowalska, 1976, 1991). It is noteworthy that in other regions, especially in eastern Europe, it is common to have stratigraphic layers with up to ten different contemporaneous soricid species during this period (e.g., Somssich Hill 2), whereas in the Iberian Peninsula only levels TD5 and TD6 of Gran Dolina have more than four species present at the same time (six each) (see Appendix A). The numbers in Italian sites (e.g., Pirro Nord, Dell'Erba, Soave, and Visogliano) are close to those in the Iberian Peninsula (Fanfani, 1999). From this we may infer that the general environmental conditions were optimal for soricids in eastern Europe at this time, or at least better than in the southern peninsulas.

In regard to the paleoclimate, we observe that the soricid taxa found in the different levels of Gran Dolina match previous palaeoenvironmental and paleoclimatic inferences done with small mammals, particularly rodents (Cuenca-Bescós et al., 2005, 2010; Moya-Costa, 2020) and bats (Galán et al., 2019a,b), amphibian and squamate reptile assemblages (Blain et al., 2009), pollen (García-Antón, 1989), non-pollen palynomorphs (Expósito et al., 2017) and combinate works (Rodríguez et al., 2011). The studies of herpetofauna (Blain et al., 2009) provide estimations of rainfall and temperatures, two factors remarkably conditioning the distribution of soricids as well (Reumer, 2001; Furió et al., 2011, 2018). Data from herpetofauna and soricids are in agreement. During the deposition of the levels of Gran Dolina humidity was high, creating optimal conditions to sustain several species of shrews. Water bodies and currents, where *Asoriculus* and *Neomys* lived, were also important. The most notorious environmental event inferred from soricids is the change to cooler conditions during the period represented by TD10: *Crocidura*, more resilient to warmer and dryer environments than *Sorex* (Churchfield, 1990; Mittermeier and Wilson, 2018) is not present in these layers, as also detected with other proxies (Galán et al., 2019).

6. Conclusions

Nine soricid taxa are present in the Early-Middle Pleistocene sequence of Gran Dolina: *Sorex minutus*, *Sorex* ex gr. *runtonensis-*

subaraneus, *Sorex* (*Drepanosorex*) ex gr. *margaritodon-savini*, *Dolinasorex glyphodon*, *Asoriculus gibberodon*, *Neomys* cf. *newtoni*, *Neomys fodiens*, Neomyni cf. *Macroneomys* and *Crocidura kornfeldi*.

Aside from the previously described *D. glyphodon*, the identification and description of this assemblage adds notably to the previously known biochronology and biogeography of the abovementioned taxa, contributing: a) the first Iberian post-Jaramillo Early Pleistocene record of *S.* ex gr. *runtonensis-subaraneus*, *S. (D.)* ex gr. *margaritodon-savini*, *A. gibberodon* and *N.* cf. *newtoni*; b) arguably the first and the youngest record of *S.* ex gr. *runtonensis-subaraneus* in the Middle Pleistocene of the Iberian Peninsula; c) the second record of cf. *Macroneomys* in the Iberian Peninsula, the first with data and a description; d) the first account of *N.* cf. *newtoni* in the Iberian Peninsula; e) the youngest record of *Asoriculus gibberodon* in the world; f) the youngest record of *S. (D.) margaritodon-savini* in the Iberian Peninsula.

Our morphometric study shows that the Gran Dolina specimens of *S. minutus* and *C. kornfeldi* are among the largest in Europe, whereas those of *N.* cf. *fodiens* and Neomyni cf. *Macroneomys* are among the smallest from the continent, which is likely due to the particular eco-geographical conditions in the Iberian Peninsula.

Relict populations of *A. gibberodon*, which had otherwise vanished from Europe in post-Jaramillo times, persisted and were gradually driven into extinction in the Iberian Peninsula.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The research data are in the Supplementary information.

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Appendices. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.quascirev.2023.108093.

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