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FIRST EVIDENCE OF THE SORICIDAE (MAMMALIA) *ASORICULUS GIBBERODON* (PETÉNYI, 1864) IN THE PLEISTOCENE OF NORTH IBERIA

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Abstract. The paper describes thirteen specimens of the extinct red-toothed shrew *Asoriculus gibberodon* (Petényi, 1864) from the lower levels (8 to 14) of the Sima del Elefante cave (TE Lower Red Unit). These are the first bona fide examples of this taxon in the north of the Iberian peninsula. The Lower Red Unit of the Sima del Elefante dates from the early Pleistocene and contains evidence of the very first human activity in the European continent, in the form of lithic tools and large mammal bones with cutmarks.

After a detailed discussion of systematic considerations, we focus on the palaeoecological and palaeobiogeographical implications of the presence of this species in the Sima del Elefante's Lower Red Unit. In palaeoecological terms, as a member of the Neomyini, *A. gibberodon* would have had a mainly aquatic life and it is taken as an indicator of humid environments with a permanent green covering. As for its palaeobiogeographical implications, on the basis of its geographical distribution and morphometric particularities we have reconstructed the biogeography of the genus *Asoriculus* from its very first record at the end of the Miocene to its extinction shortly before the beginning of the middle Pleistocene.

Riassunto. L'articolo descrive 13 esemplari di *Asoriculus gibberodon* (Petényi, 1864), un toporagno dai denti rossi estinto derivante dai livelli inferiori (da 8 a 14) della grotta Sima del Elefante (TE "Lower Red Unit"). Questi sono i primi esemplari, a nostra conoscenza, rinvenuti nel Nord della penisola iberica. La "Lower Red Unit" della grotta Sima del Elefante viene datata al Pleistocene inferiore e contiene le più antiche evidenze di attività umana nel continente europeo, sotto forma di strumenti litici e di grandi ossa di mammiferi con incisioni.

Dopo una dettagliata discussione sistematica, vengono analizzate le implicazioni paleoecologiche e paleobiogeografiche connesse con la presenza di questa specie nella "Lower Red Unit" nella Sima del Elefante. In termini paleoecologici, quale appartenente ai Neomyini, *A. gibberodon* dovrebbe aver avuto uno stile di vita prevalentemente acquatico e viene pertanto considerato quale indicatore di ambienti umidi, con copertura vegetale permanente. Per quanto concerne la paleobiogeografia, sulla base della distribuzione geografica e delle peculiarità morfometriche, si è ricostruita la distribuzione del genere *Asoriculus*, a partire dal suo primo ritrovamento alla fine del Miocene sino alla sua estinzione prima dell'inizio del Pleistocene medio.

Introduction

In the early Pleistocene, representatives of two genera of the Neomyini tribe (subfamily Soricinae or red-toothed shrews), *Neomys* and *Asoriculus*, were present in several European localities (Rzebik-Kowalska 1998, 2000). The genus *Asoriculus* has particularly scarce records from this period in Spain. Here we present evidence of the first discovery of *A. gibberodon* in the Sierra de Atapuerca, and the first serious study on this particular insectivore species for the Iberian Peninsula.

According to Reumer (1998), there are eight genera attributed to the Neomyini tribe: *Asoriculus* Kretzoi, 1959 (†), *Chimarrogale* Anderson, 1877, *Macroneomys* Fejfar, 1966 (†), *Nectogale* Milne-Edwards, 1870, *Neomys* Kaup, 1829, *Neomysorex* Rzebik-Kowalska, 1981 (†), *Nesiotites* Bate, 1945 (†), and *Soriculus* Blyth, 1854. Hutterer (1993) considers *Chodsigoa* Kastshenko, 1907, and *Episoriculus* Ellerman and Morrison-Scott, 1951, to be subgenera of *Soriculus*. On the basis of a morphometric study, Masini & Sarà (1998) consider *Nesiotites* to be a large *Asoriculus*, and propose its inclusion in the latter genus. We are not able to support or reject their results, and maintain *Nesiotites* as a valid genus in accordance with the opinion of other authors (i.e. Reumer 1998; Rzebik-Kowalska 1998, 2000).

Hutterer (1994) transferred all fossil *Episoriculus* species known in Europe to the genus *Asoriculus*, considering that they were not congeneric with the Asiatic species *Episoriculus caudatus* Horsfield, 1851, and *E.*

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leucops Horsfield, 1855, which today inhabit south-eastern Asia (as seen above, both previously considered members of the genus *Soriculus* by Hutterer in 1993). The oldest remains of *Asoriculus* in the European continent were found at the Late Miocene localities of Santa Margarida in Portugal (Antunes & Mein 1995) and Salobreña in Spain (Crochet 1986). Rare during the Late Miocene, *Asoriculus* became common in the Pliocene and the early Pleistocene of Europe (Rzebik-Kowalska 1998, 2000, and this work).

Representatives of *Asoriculus* were also reported in Asia (Kotlia 1991) and north-western Africa (Rzebik-Kowalska 1988; Geraads 1995). However, the Asiatic species *Episoriculus repenningi* Kotlia, 1991, from the Late Pliocene of Khaigam, Kashmir (India), has never been clearly reassigned to *Asoriculus* and seems to be closer to *Soriculus* (Storch et al. 1998; Rzebik-Kowalska 2000). The African form was originally described as *Episoriculus maghrebiensis* Rzebik-Kowalska, 1988, but subsequently relocated as *Asoriculus* by the same author (Rzebik-Kowalska 2000). It was found in the localities of Irhoud Ocre (Rzebik-Kowalska 1988) and Ahl al Oughlam (Geraads 1995), both in Morocco. Butler (1998) pointed out that this *Asoriculus* is the only African shrew that does not belong to the Crocidurinae or the Crocidosoricinae. In his opinion this species was evidently an immigrant from Europe.

According to Rzebik-Kowalska (1998) and Masini & Sarà (1998), the European record of *Asoriculus* includes the following four species: *A. castellarini* (Pasa, 1947), *A. burgioi* Masini & Sarà, 1998, *A. thenii* Malez & Rabeder, 1984, and *A. gibberodon* (Petényi, 1864). The validity of *A. castellarini* has been questioned, however, since nobody has revised the poorly described and scanty materials of the original description made by Pasa (1947), and it cannot be decided whether it really belongs to a separate species or is another synonym of *A. gibberodon* (Reumer 1984; Rzebik-Kowalska 2000).

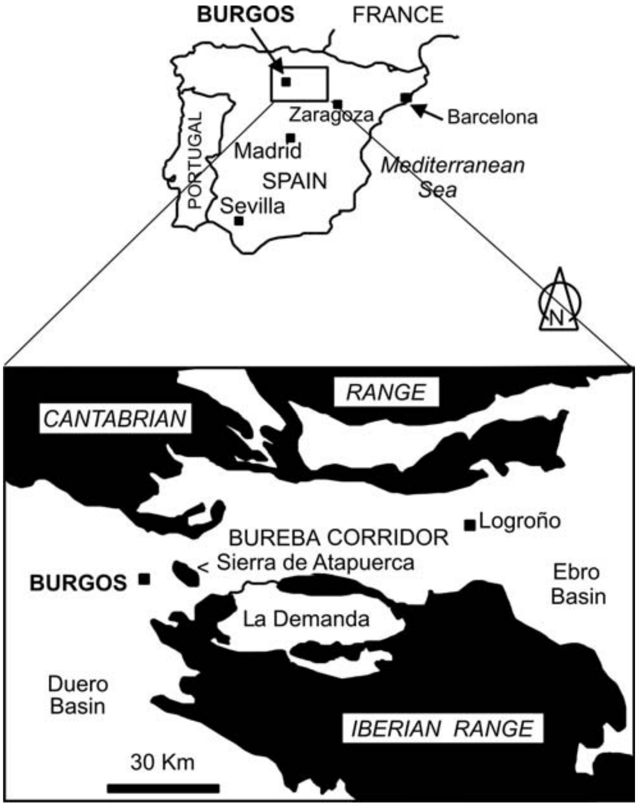

Fig. 1 - Index map of the Sierra de Atapuerca, near the city of Burgos in Spain (south-western Europe). Black squares refer to modern cities, and black areas in the lower map refer to highland systems.

Geological and palaeontological settings

The localities of the Sierra de Atapuerca (Atapuerca highland) are internationally renowned for their amazing early and middle Pleistocene hominine and other vertebrate fossil records, as well as for their remarkable lithic tool complexes. The most important localities are the Gran Dolina (TD), which contains *Homo antecessor* in the TD-6 level (ca. 800 ka), and Sima de los Huesos, which has the most complete *Homo heidelbergensis* (ca. 400 ka) record in the world. However, this study focuses on a less well known locality, the Sima del Elefante cave (TE). Together with a rich vertebrate fossil record, this site yielded lithic tools from the lower levels of the cave associated with early Pleistocene fauna (MIS 37-49). These tools provide some of the oldest evidence of human activity in the European continent (Rosas et al. 2001, 2004; Cuenca Bescós & Rofes 2004). The Sierra de Atapuerca is a small highland area dominating the landscape in the Neogene flat territories of Castilla, near the city of Burgos in Spain (Fig. 1). It is composed of Late Cretaceous limestone, which is the substrate for the development of a complex karst system during the Late Miocene. The caves and galleries contain sediments dated between at least 1.5 Ma and ca. 200 ka. An old railway (currently disused) cut through the Sierra de Atapuerca, exposing cave deposits on both sides of the resulting cutting. These cave sediments contain an excellent Pleistocene record of macrofauna, microfauna and lithic tools. There are three main sites in the "Trinchera" (cutting): the Gran Dolina, the Trinchera Galeria (the Tres Simas Complex and the Cueva de los Zarpazos), and the Sima del Elefante (Fig. 2). The fissures and cavities have a phreatic-vadose origin and are mainly filled with allochthonous materials associated with the faunal and archaeological remains.

The Sierra de Atapuerca also has some active caves, such as Cueva Mayor and Cueva del Silo. In this context, the archaeo-palaeontological setting as a whole

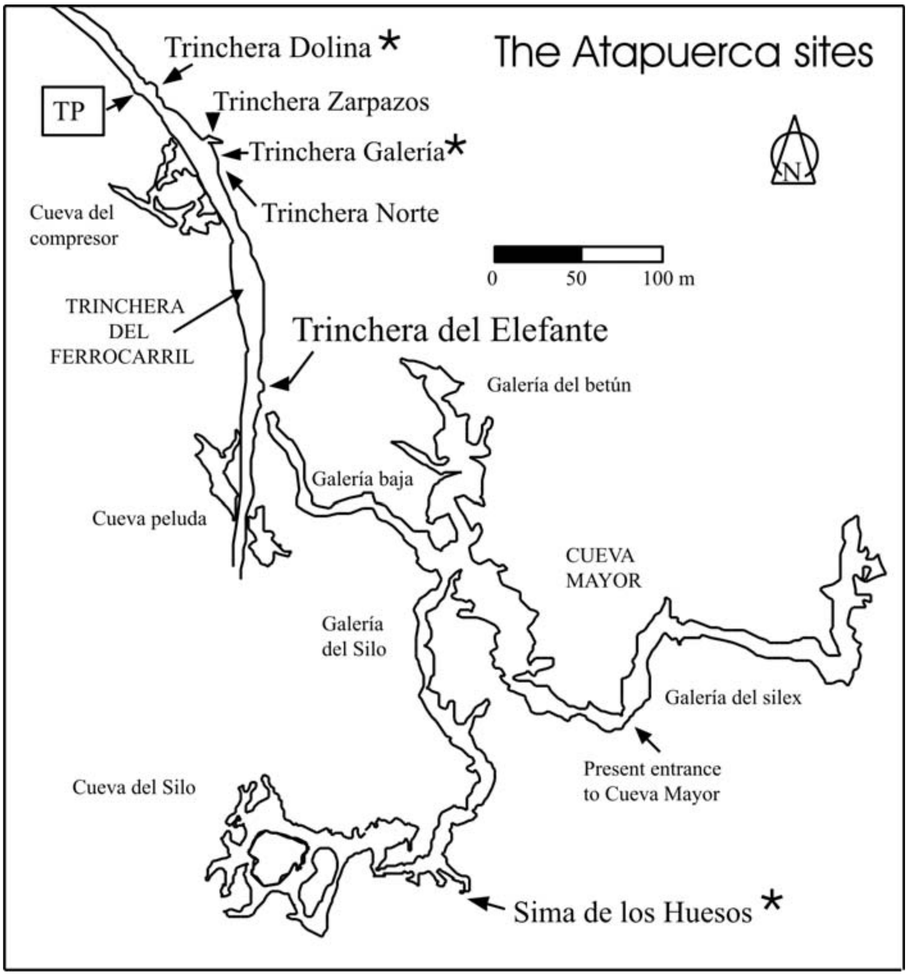

Fig. 2 - Map of the Atapuerca karst system showing the sites along the Trinchera del Ferrocarril (railway cutting), and the Cueva Mayor-Sima de los Huesos karst complex. The Trinchera del Elefante cave sediments outcrop at the south of the cutting ("Trinchera"). TP means Trinchera Penal and the asterisks refer to hominin-bearing sites.

is usually divided into two parts: the "Trinchera del Ferrocarril" sites (previously listed) and the "Sima de los Huesos" site, which is in the Cueva Mayor complex (Fig. 2). Given the richness, completeness, and antiquity of their fossil and archaeological contents, the Sierra de Atapuerca caves and fissure fillings represent one of the best Pleistocene sequences in the world.

The Sima del Elefante is a major cave infill, which may correspond to an ancient opening to the Galeria Baja in the Cueva Mayor karst subsystem (Fig. 2), and it is completely full of sediment. The section of the TE is 25 m thick, including the lower and middle Pleistocene layers (Fig. 3). A considerable portion of the cave sediments (19 m) outcropped during the construction of the railway cutting at the end of the nineteenth century. The sediments of the TE have an allochtonous origin. The deepest levels of the stratigraphic sequence remain undescribed as this section does not emerge. In 1996 a sample pit was made in order to find out the length, composition, palaeomagnetism and fossil contents of the sediments below the current ground level of the cutting. This perforation, as well as two drills made in 2001, revealed six more metres of sediments.

The TE stratigraphic section comprises 21 levels further grouped into three sedimentary phases (Fig. 3). The lower phase, i.e. the Lower Red Unit, is extremely rich in faunal remains: birds, reptiles and mammals (bats, rodents, insectivores, lagomorphs, in addition to large herbivores and carnivores). Moreover, the fossils in this unit are very well preserved, and some of them were found in anatomical connection. The Lower Red Unit comprises levels TE-8 to TE-14.

In our study of the rodents from the TE Lower Red Unit (Laplana & Cuenca-Bescós 2000), we found an assemblage older than any of the ones previously found in Atapuerca. In particular, the *Allophaiomys* (Rodentia) association is similar to that recorded in other South-European localities such as Les Valerots, Bagur 2 or Le Vallonnet, which makes the TE Lower Red Unit older than the deepest exposed levels of the Gran Dolina (TD-3 to TD-6, ca. 0.9-0.78 Ma). The insectivore assemblage (Cuenca Bescós & Rofes 2004) shows that this unit may be at least as old as the localities of Fuente Nueva 3 and Barranco Leon in the Granada basin (ca. 1.2 Ma, Martínez Navarro et al. 1997; Agustí et al. 2004). Parés et al. (2005) show that levels TE 9 to TE 16 display reverse polarity magnetization interpreted as the Matuyama magnetic age after the biostratigraphic data provided by Cuenca Bescós et al. (2004). There is a second phase comprising levels TE-15

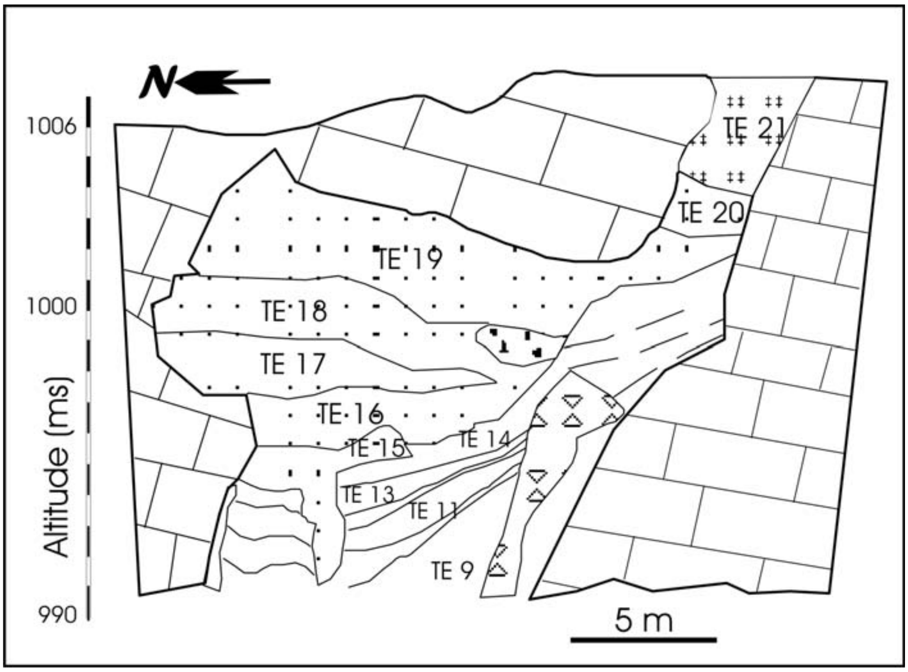

Fig. 3 - Trinchera del Elefante cave schematic stratigraphic section showing the main phases and units referred to in the text. Levels E-9 to E-13 of the first phase (Lower Red Unit) yielded the *Asoriculus gibberodon* specimens studied in this paper (redrawn from Parés et al. 2005).

to TE-20, and a third phase that comprises the uppermost infill sediments, namely level TE-21 (Rosas et al. 2004; Parés et al. 2005). This study only deals with the first phase or Lower Red Unit of the Sima del Elefante cave.

The cave sediments of the TE Lower Red Unit contain a rich and diverse vertebrate assemblage characterized by warm and wet elements, as well as inhabitants of forested areas and open lands. This vertebrate association comprises: (1) Rodentia – *Allophaiomys lavocati*, *A. nutiensis*, *Ungaromys nanus*, *Pliomys episcopalis*, *Mimomys* sp., *Castillomys rivas*, *Apodemus* sp., *Glis* sp., *Castor* sp., and *Sciurus* sp. (Laplana & Cuenca Bescós 2000); (2) Lipotyphla – *Asoriculus gibberodon, Beremendia fissidens, Sorex* sp., *Crocidura* aff. *kornfeldi*, *Crocidura* cf. *russula*, *Talpa* cf. *europaea*, Desmaninae indet., and *Erinaceus* cf. *europaeus* (Cuenca Bescós & Rofes 2004); (3) Lagomorpha - *Lepus* sp. and *Oryctolagus* sp.; (4) Artiodactyla - *Hippopotamus* sp., Cervidae indet., *Eucladoceros giulli*, *Megaloceros savini*, Bovidae indet., *Bison* sp., and Suidae indet.; (5) Perissodactyla - *Stephanorhinus etruscus*, and Equidae indet.; (6) Carnivora – cf. *Baranogale antiqua*, cf. *Mustela palerminea/ praenivalis*, Felidae indet. (leopard size), cf. *Lynx issiodorensis*, cf. *Canis arnensis/mosbachensis*, cf. *Pannonictis* sp., cf. *Vulpes alopecoides*, and *Ursus* sp.; (7) Aves - *Carduelis chloris*, *Falco* sp., *Perdix paleoperdix*, *Coturnix coturnix*, *Columba livia*, *Haliaethus albicilla*, *Circaetus gallicus, Falco tinunculus, Turdus* sp., Alaudidae indet., and *Anas* sp.; (8) Other vertebrates – Salmonidae indet., *Bufo bufo*, *B. calamita*, and Chelonia indet. (3 to 8 taken from Rosas et al. 2004).

Even though no human fossil remains older than the 0.8 Ma of *Homo antecessor* in Atapuerca have been found so far in Western Europe, the Sima del Elefante cave is providing essential information on human activity in Europe from more than 1.1 Ma. An early migration to western Europe, probably during the Waalian warm period, is supported by the lithic tools recorded in the TE Lower Red Unit (Rosas et al. 2001, 2004; Cuenca Bescós & Rofes 2004), as well as in two other localities in Spain: Barranco Leon and Fuente Nueva 3 in Orce (Martínez Navarro et al. 1997). Both the TE and Orce lithic assemblages technologically belong to the Olduvayan or Mode 1 style. In addition, TE has yielded several large herbivore bones with cutmarks on the surface, which may indicate a human agent responsible for part of this mammalian accumulation (Rosas et al. 2004).

Identification Code (excavation label)	Elements
MPZ 2005 / 353 (TE-13 / ATA 99)	Mand D
MPZ 2005 / 352 (TE-10 / Z: 190-210 / ATA 98)	Mand D
MPZ 2005 / 351 (TE-10 / Z: 190-210 / ATA 98)	Mand D
MPZ 2005 / 350 (TE-10 (South) / ATA 96)	Mand D
MPZ 2005 / 349 (TE-10 (South) / ATA 96)	I_1 S
MPZ 2005 / 348 (TE-10 (South) / ATA 96)	Mand D
MPZ 2005 / 347 (TE-9B / K-30 / Z: 600-620 / ATA 02)	Mand D
MPZ 2005 / 346 (TE-9B / K-29 / Z: 620-630 / ATA 02)	Mand D
MPZ 2005 /345 (TE-9C / L-29, 30, 31 / Z: 1280-1290 / ATA 03)	Mand D
MPZ 2005 / 344 (TE-9C / K-31, L-31 / Z: 1330-1340 / ATA 03)	Mand S
MPZ 2005 / 343 (TE-8 (North) / ATA 96)	I_1 D
MPZ 2005 / 342 (TE-8 (North) / ATA 96)	Mand S
MPZ 2005 / 341 (TE-8 (North) / ATA 96)	Mand S

Tab. 1 - Stratigraphic distribution of *Asoriculus gibberodon* in the Lower Red Unit section of the Sima del Elefante cave. Abbreviations: TE, Sima del Elefante; ATA, Atapuerca; Z, depth in cm; Mand, mandible; D, dextral (right); S, sinistral (left).

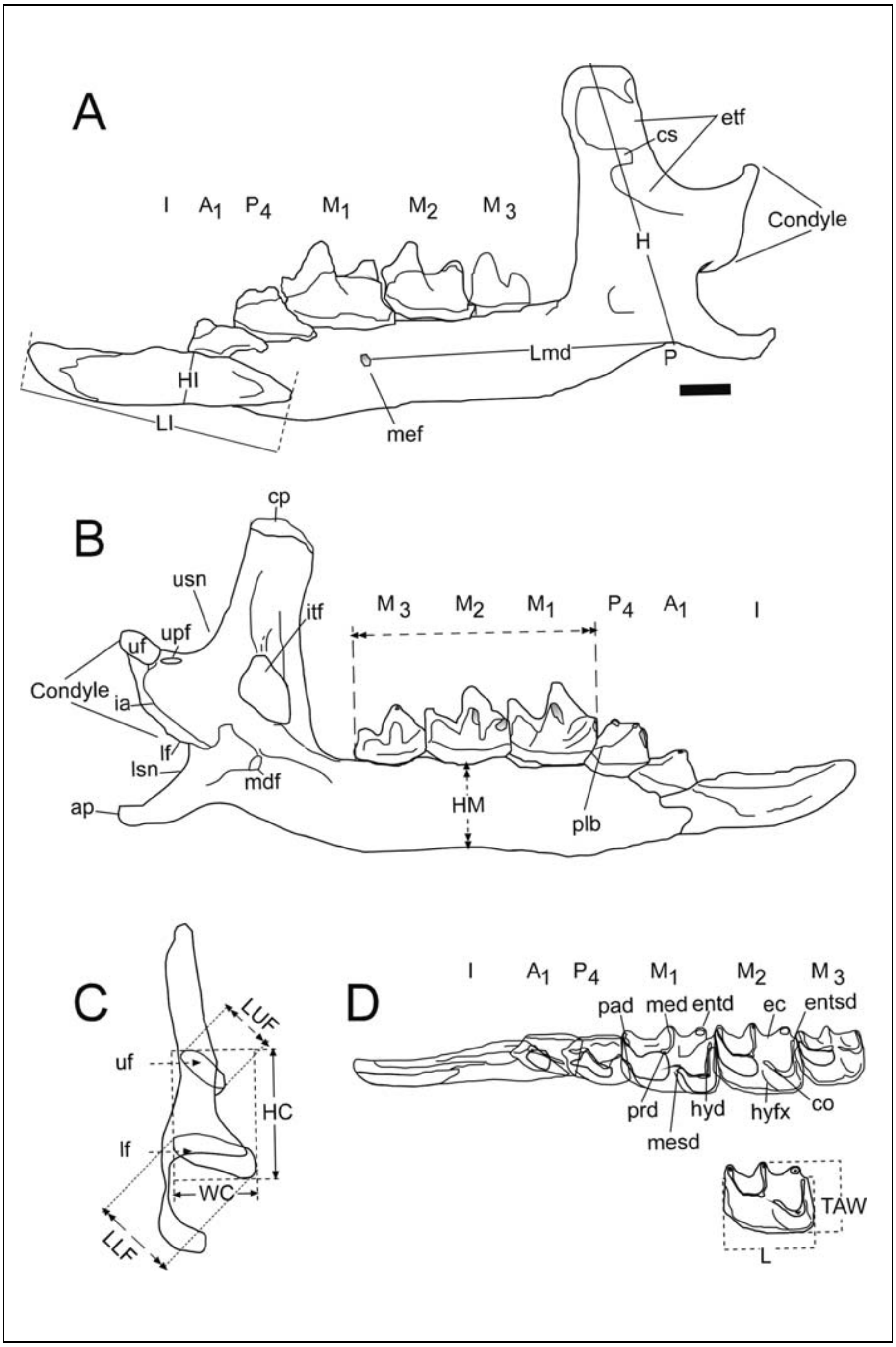

Fig. 4 - Generalized Neomyini mandible and teeth based on extant *Neomys fodiens*, MNCM 1979, in (A) buccal, (B) lingual, (C) posterior, and (D) occlusal views. Anatomical abbreviations: A$_1$, first lower antemolar; ap, angular process; co, crista obliqua; cp, coronoid process; cs, coronoid spicule; ec, entoconid crest; entd, entoconid; entsd, entostylid; etf, external temporal fossa; hyd, hypoconid; hyfx, hypoflexid; I, lower incisor; ia, interarticular area; itf, internal temporal fossa; lf, lower facet; lsn, lower sigmoid notch; M$_1$, first lower molar; M$_2$, second lower molar; M$_3$, third lower molar; mdf, mandibular foramen; med, metaconid; mef, mental foramen; P$_4$, fourth lower premolar; pad, paraconid; plb, postero-lingual basin; prd, protoconid; uf, upper facet; upf, upper pterygoid fossa; usn, upper sigmoid notch. Metrical abbreviations: H, height from P to the tip of the coronoid process; HC, height of the condyle; HI, height of the lower incisor; HM, height of the mandible below M$_2$; L, length of the molars; LI, length of the lower incisor; LM$_{1-3}$, overall length of M$_1$-M$_3$; Lmd, length from the uppermost point P of the arch in front of the angular process to the posterior rim of the mental foramen; LLF, length of the condylar lower facet; LUF, length of the condylar upper facet; TAW, talonid width of the molars; WC, width of the condyle. Scale bar equals 1 mm.

Methods

The specimens were obtained by washing-screening the cave sediments in the nearby River Arlanzón. Ever since the very first systematic excavation in 1996, the sediment removed from the TE has been processed using a screen and washing method, which has resulted in an enormous accumulation of small fossil vertebrates recovered from the cave. These comprise thousands of cranial fragments, isolated teeth and postcranial bones. The samples are stratigraphically ordered following Rosas et al. (2001, 2004; Fig. 3). Each sample comes from a specific stratigraphic level, which is horizontally divided into a multiple square metre grid. Some levels are subdivided into smaller units (i.e. TE9a, TE9b) according to different factors such as the lithology, granulometry or fossil content. Finally, the sample is labelled as appropriate with the initials TE for the Sima del Elefante (or "Trinchera del Elefante"), followed by the stratigraphical level, and the coordinates (given by letter and number) of the corresponding 1m^2 segment. This is followed by the initials ATA (for Atapuerca), and a number indicating the year of collection. An example of a label for a Lower Red Unit sample would be expressed as follows: TE-9c M-31 ATA03. Sometimes, the depth (Z) is added between the coordinates and the ATA initials. As the specimens are stored in the Museo Paleontológico de Zaragoza (MPZ), moreover, the label is preceded by the museum's identification code (as seen in Tab. 1).

The nomenclature of the dental pattern, parts of the lower teeth, and the components of the mandible, as well as the anatomical orientation and measurements, have been taken mainly from Reumer (1984) and Jin & Kawamura (1996). Metric values were recorded using a stereo-microscope connected to a video camera, which sent the images to a computer programme (Matrox Inspector) that makes it possible to visualize and measure the specimens with great accuracy. The main features and measurements are shown in an extant *Neomys fodiens* mandible reproduced in Fig. 4. For the taxonomical identification, the TE material was compared with a fossil *Beremendia*, an extant and fossil *Neomys*, and other Soricidae stored in the theriological collections of the Palaeontological Department of Zaragoza University, the Museo Nacional de Ciencias Naturales (MNCN), and the Universidad Autónoma de Madrid. Here we use the most recent revision of the systematic classification of extant and fossil shrews, carried out by Reumer (1998).

Age	Biozone	Ma	Location	Geographic situation
Late Miocene	MN 13	6.8	Brisighella, Monticino	Italy
Late Mi-early Pli	MN 13-14		Maramena	Greece
Early Pliocene	MN 14	4.9	Mont Hélène	France
			Osztramos 1, 9, 13	Hungary
			Podlesice, Zamkowa Dolna Cave B	Poland
			La Gloria 4, Peralejos E, Villalba Alta Rio 1	Spain
	MN 14-15		Zalesiaki 1B	Poland
	MN 15	4.2	Muselievo	Bulgaria
			Csarnóta 2	Hungary
			Weze 1	Poland
			Ivanovce	Slovakia
			El Arquillo 3, Layna, Lomas de Casares 1, Orrios 7	Spain
	?		Nimes, Serrat-d'en-Vacquer, Sète	France
			Maritsa, Apolakkia	Rhodes
Early-Late Pliocene	MN 15-16		Dunaalmás 4	Hungary
Late Pliocene	MN 16	3.2	Deutsch-Altenburg 9, 20	Austria
			Balaruc 2, Seynes	France
			Tourkobounia 1	Greece
			Beremend 5, Osztramos 7	Hungary
			Rebielice Krolewskie 1A, 2	Poland
	MN 17	2.5	Montoussé 5	France
			Villány 3	Hungary
			Kielniki 3B, Zamkowa Dolna Cave A	Poland
			Kolinany 1, Plesivec, Vcelare 3	Slovakia
	?		Nuraghe Su Casteddu	Sardinia
Early Pleistocene		1.8	Les Valerots, Mas Rambault	France
			Beremend 1-3, 17, Somssichhegy 1, Villány 5	Hungary
			Monte Peglia, Pirro Nord, Soave	Italy
			Zabia Cave	Poland
			Betfia 10, 11	Romania
			Vcelare 4A/5	Slovakia
			Barranco León, Fuente Nueva 3	Spain

Tab. 2 - European localities with *A. gibberodon* other than the Sima del Elefante. Data on age, biozone, location and geographical situation were taken from Rzebik-Kowalska (1998), with the exception of Marathoussa (Koufos et al. 2001), Monte La Mesa (Marchetti et al. 2000), and Gundersheim 4 (Dahlmann & Storch 1996). Ma dates correspond to the lower limit of each MN (Mammal Neogene) biozone (after Agustí et al. 2001).

Systematic palaeontology

Class **Mammalia** Linnaeus, 1758

Order **Eulipotyphla** Waddel, Okada and Hasegawa, 1999

Family Soricidae Fischer, 1817

Subfamily Soricinae Fischer, 1817

Tribe Neomyini Matschie, 1817

Genus *Asoriculus* Kretzoi, 1959

Type species: *Crocidura gibberodon* Petényi, 1864

Asoriculus gibberodon (Petényi, 1864)

Fig. 5A-H

Stratigraphic range. From the late Turolian (MN 13) to the early Biharian (MQ 1).

Distribution. For the biostratigraphic and geographic distribution of the species see Table 2.

Occurrence. Sima del Elefante levels: TE 8, 9B, 9C, 10, and 13 of the Lower Red Unit of the Sima del Elefante cave (Fig. 3), Sierra de Atapuerca, Burgos, Spain.

Material. Two lower incisors, one right and one left, as well as eleven fragmentary mandibles, eight right and three left, which in general have all the dental and mandibular elements preserved, with the exception of the third molar and the angular process (Tab. 1).

Measurements. The dental and mandibular measurements are shown in Tables 3 and 4.

Description. In general, the dentition of the soricids consists of one incisor (I), three molars (M) and small elements situated between the incisor and the molars, which are named, following Reumer (1984), the antemolars (A). In the lower dentition, there is only one tooth called an antemolar (A_1); the A_2 is generally considered to be a premolar and is called P_4 (Fig. 4). The I_1 of the soricids has a single cusp, known as the apex, and a series of serrations on the dorsal edge that may vary from one to four or may not exist at all. Reumer (1984) called these serrations "cuspules" to distinguish them from the true cusps of the rest of the teeth. According to Reumer (1984) and our own observations, the dental elements of *Asoriculus* are lightly pigmented. Just the tip of the cusps has a light orange colour.

I_1. This extends straight forward in occlusal view. It is short and has a single serration. Between this posterior cuspule and the apex, there is only a slight undulation of the dorsal margin. The apex is short and strongly upturned. A lingual cingulum is present along the posterior part of the tooth, not only dorsally, but also reaching the ventral margin. An almost indistinct buccal cingulum is also present. The crown reaches below the posterior margin of P_4 on the buccal side, and below the middle part of A_1 in the lingual face (Fig. 5F-G).

A_1. The occlusal outline is triangular. The crown has a single cusp in an anterior position, and for about half its length lies imbricated between the incisor and the fourth premolar. It has a shallow posterolingual basin, and a cingulum is moderately well developed on both sides. (Fig. 5F-H).

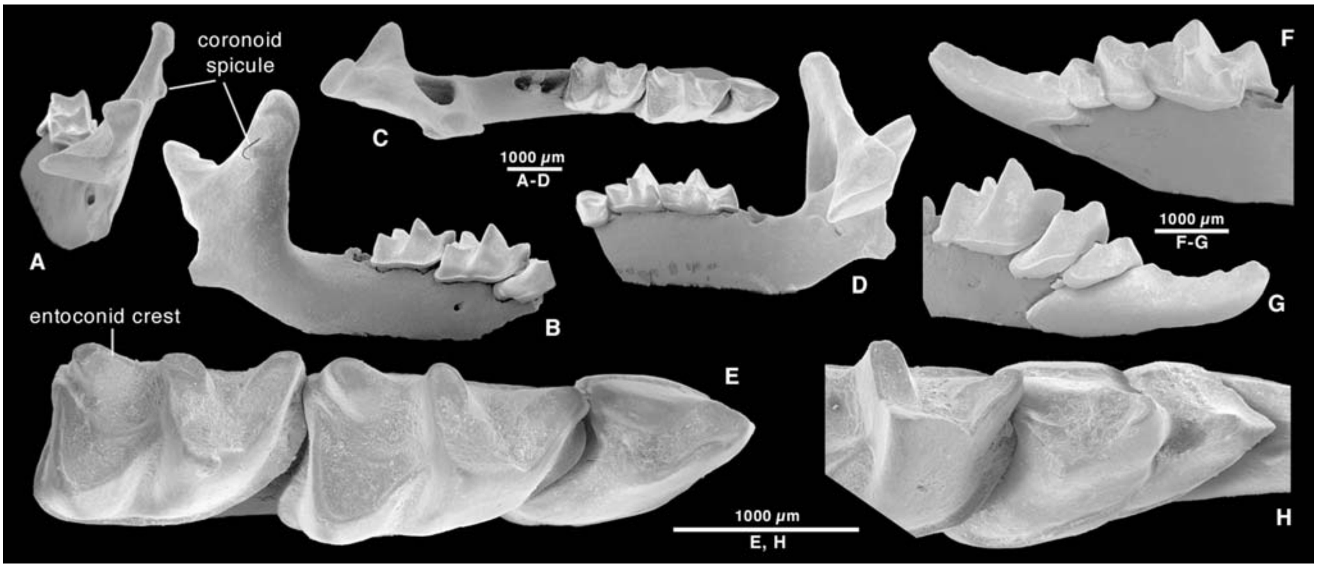

Fig. 5 - Mandibles of *Asoriculus gibberodon* from the Lower Red Unit of the Trinchera del Elefante cave: A-E, right, MPZ 2005 / 350 (TE-10 / ATA 96), in (A) posterior, (B) buccal, (C) dorsal, (D) lingual, and (E) occlusal views; F-H, right, MPZ 2005 / 348 (TE-10 / ATA 96), in (F) lingual, (G) buccal, and (H) occlusal views.

Element	L	TAW	H
I	3,8		1
A_1	0,9	0,87	
P_4	1,3	0,76	
	1,3	1,01	
M_1	1,55	0,89	
	1,55	0,94	
	1,56	1	
	1,65	0,97	
	1,68	0,96	
	1,63	1,03	
M_2	1,39	0,94	
	1,48	0,93	
	1,48	0,91	
M_1-M_3	3,75		
	3,89		
	4		
	4		
	3,95		

Tab. 3 - Measurements of the teeth of *A. gibberodon* from the Lower Red Unit of the Sima del Elefante cave. Tooth and measurement abbreviations in Fig. 4.

Lmd	H	HM	HC	WC	LUF	LLF
		1,35	1,82	1,63		1,32
4,47	4,06	1,29	1,86	1,88	0,8	1,37
4,16		1,52	1,93	1,73	0,81	1,5
4,72	4,28	1,44	1,51	2,02	0,89	1,42
4,98	4,3	1,35	1,78	1,6	0,85	1,48
4,68	3,97	1,43	1,95	1,65	0,86	1,33
4,51	4,05	1,54			0,78	1,29
4,56	4,16	1,41	1,85	1,62		
			1,56	1,68	0,79	1,24
					0,75	1,31

Tab. 4 - Measurements of the mandibles of *A. gibberodon* from the Lower Red Unit of the Trinchera del Elefante cave. Measurement abbreviations in Fig. 4.

P_4. The occlusal outline is roughly triangular, although the posterior face is remarkably incurvated due to the elongation of the posterobuccal corner of the crown. Two main cusps are present on the crown. The anterior one is higher, and lingually oriented in occlusal view. These two cusps are connected by a high sharp ridge which encloses a posterolingual basin on its lingual side. This basin is shallow and drains steeply posterolingually. A well developed cingulum is present on both sides of the tooth (Fig. 5E-H).

M_1-M_2. These have a trapezoidal shape in occlusal view and present five main cusps: paraconid, protoconid, metaconid, entoconid and hypoconid. They also have an accessory cusp, the entostylid. The three anterior cusps (para-, proto- and metaconid) are connected by crests or ridges and form the trigonid, which is V-shaped. The buccal vertex of the "V" is the protoconid, which is connected to the paraconid by the paralophid and to the metaconid by the protolophid. The paralophid is much longer than the protolophid. Each crest has a notch at its middle part. The protoconid is the highest cusp of the crown, and is anterobuccal in relation to the metaconid. The inner surface of the trigonid is the trigonid basin. The union of the posterior cusps (hypoconid and entostylid) and ridges forms the talonid, which is also V-shaped. The buccal vertex is the hypoconid. From this cusp, the crista obliqua descends anterolingually toward the protoconid and attaches to its posterior face forming the hypoflexid, which steeply

descends buccally as far as the buccal cingulum. Another ridge, the hypolophid, extends lingually from the hypoconid to the entostylid. The latter is an indistinct cusplet at the lingual end of the hypolophid. The entostylid is separated from the entoconid by a marked valley. Unlike the other main cusps, the entoconid is a conical isolated cusp, which connects to the posterior base of the metaconid by a ridge known as the entoconid crest. The entoconid crest is short and very shallow. The inner surface between the hypoconid and the entoconid crest is the talonid basin. Generally, in M_1 the talonid is wider than the trigonid, and in M_2 the trigonid is wider or equal. Together, the trigonid and the talonid form the ectolophid, which is nearly W-shaped. The lingual cingulum is only slightly developed and is almost missing below the metaconid. The buccal cingulum is well developed and sometimes slightly undulated (Fig. 5B-E).

Mandible. This has two regions, the horizontal ramus or mandibular body that houses the teeth, and the ascending ramus that has the coronoid process, the mandibular condyle and the angular process as its main components (Fig. 4). The coronoid process and the articular condyle are usually well preserved in the fossil record and are of great systematic value. Below there follows a detailed description of our specimens' mandible components: (1) Mandibular body. This is thin and narrow with the teeth overhanging buccally. The horizontal ramus is ventrally straight (Fig. 5B-D); (2) Coronoid process. The anterior and posterior margins are slightly concave. The tip is rounded. A coronoid spicule is present at the lateral side of the mandible. This is moderately to

Element	Species	Age	Location	L	W	H
I_1	*A. gibberodon*	Early Pliocene	Osztramos 9	3,18		
			Osztramos 1	2,97		
			Csarnóta 2	3,37		
		Late Pliocene	Osztramos 7	3,62		
			Villány 3	3,06		
		Early Pleistocene	Betfia-X			0,76
			Betfia-XI	3,28		0,83
			Betfia-IX			0,82
			Betfia-VII/1	3,27		0,84
			Monte La Mesa	3,71		0,95
	A. thenii	Early Pleistocene	Podumci 1	4,9		
			Tatinja Draga	4,9		
	N. newtoni	Latest Early/earliest Middle Pleistocene	Kozi Grzbiet	4,03		0,96
A_1	*A. gibberodon*	Early Pleistocene	Betfia-XI	0,89		
	A. thenii	Early Pleistocene	Tatinja Draga	1,29	0,9	
P_4	*A. gibberodon*	Early Pleistocene	Betfia-XI	1,31	0,79	
			Betfia-IX	1,16	0,79	
	A. thenii	Early Pleistocene	Tatinja Draga	1,61	1,08	
	N. newtoni	Latest Early/earliest Middle Pleistocene	Kozi Grzbiet		0,9	
M_1	*A. gibberodon*	Early Pliocene	Osztramos 9	1,49	0,86	
			Osztramos 1	1,46	0,8	
			Csarnóta 2	1,57	0,92	
		Late Pliocene	Osztramos 7	1,64	0,96	
			Villány 3	1,51	0,87	
			Vceláre 3/1	1,42	0,9	
		Early Pleistocene	Betfia-X	1,48	1	
			Betfia-XI	1,39	0,87	
			Betfia-IX	1,43	0,87	
			Betfia-VII/1	1,44	0,87	
			Monte La Mesa	1,58	1,02	
	A. thenii	Early Pleistocene	Podumci 1	1,71	1,08	
			Tatinja Draga	1,86	1,12	
	A. maghrebiensis	Late Pliocene	Ahl Al Oughlam	1,72		
	N. newtoni	Latest Early/earliest Middle Pleistocene	Kozi Grzbiet	1,68	0,98	
M_2	*A. gibberodon*	Early Pliocene	Osztramos 9	1,39	0,79	
			Osztramos 1	1,38	0,72	
			Csarnóta 2	1,44	0,83	
		Late Pliocene	Osztramos 7	1,5	0,83	
			Villány 3	1,36	0,79	
			Vceláre 3/1	1,31	0,78	
		Early Pleistocene	Vceláre 4 A/5	1,32	0,88	
			Betfia-X	1,3	0,89	
			Betfia-XI	1,27	0,79	
			Betfia-IX	1,35	0,84	
			Betfia-VII/1	1,24	0,8	
			Monte La Mesa	1,51	0,94	
	A. thenii	Early Pleistocene	Podumci 1	1,58		
			Tatinja Draga	1,65	1,01	
	A. maghrebiensis	Late Pliocene	Ahl Al Oughlam	1,56		
	N. newtoni	Latest Early/earliest Middle Pleistocene	Kozi Grzbiet	1,54	0,99	
M_1-M_3	*A. gibberodon*	Early Pliocene	Osztramos 9	3,78		
			Csarnóta 2	3,85		
		Late Pliocene	Villány 3	3,56		
			Vceláre 3/1	3,7		
			Monte La Mesa	3,64		
	A. thenii	Early Pleistocene	Podumci 1	4,19		
			Tatinja Draga	4,46		
	N. newtoni	Early Pleistocene	West Runton	3,85		
		Middle Pleistocene	Westbury	4,35		
			Monte Peglia	3,93		
	N. browni	Late Pleistocene	Grays Thurrock	4,29		

Tab. 5 - Means of the measurements of the lower teeth of *Asoriculus* and *Neomys* species from European localities other than the Sima del Elefante. All the locations from which the metrical data have been taken are fully referenced in Rzebik-Kowalska (1998), with the exception of Marathoussa (Koufos et al. 2001), Monte La Mesa (Marchetti et al. 2000), and Ahl Al Oughlam (Geraads 1995). Tooth and measurement abbreviations in Fig. 4.

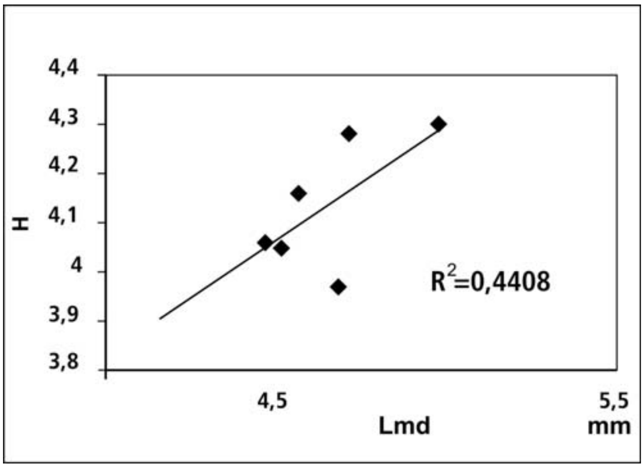

Fig. 6 - Scatter diagram of length/height (◆) of the mandibles of *A. gibberodon* from the Lower Red Unit of the Trinchera del Elefante cave (data in Table 4). All values are close to the regression line, which means that all specimens belong to a single species. Abbreviations: R^2, square of the regression index; for H and Lmd see figure 4.

well developed and located half-way between the upper sigmoid notch and the tip of the coronoid process. The whole ascending ramus is almost in the same axis as the mandibular body and does not present lateral deflection (Fig. 5A-D); (3) Mandibular condyle. The upper facet is narrow, long and cylinder-shaped. The lower facet is strongly elongated medially, pointing downwards. The interarticular area is narrow, elongated and concave in its medial side. The condylar facets are nearly parallel to each other (Fig. 5A, C-D). In buccal view, the lower facet is partially hidden behind the lower sigmoid notch. The upper sigmoid notch presents a very marked ventral emargination. (Fig. 5B); (4) Fossae. The external temporal fossa is shallow and tenuously reaches half-way down the condyle. The spicule partially divides this fossa into two parts. The walls of the external temporal fossa together with the spicule are "E"-shaped (Fig. 5A-B). The internal temporal fossa is relatively small, narrow and deep in its lower part, but it continues upwards as a shallow groove to just below the tip of the coronoid process (Fig. 5C-D); (5) Foramina. The mandibular foramen is located below the horizontal bar separating the internal temporal fossa from the depressed ventral area of the ascending ramus. It is small and elliptic, and is of variable size (Figs. 5A, D). The mental foramen is usually located below the hypoflexid or the hypoconid of the first lower molar (Fig. 5B).

Discussion. The assignment of the specimens to the subfamily Soricinae is determined by the characteristic red pigment of the preserved teeth. On the basis of the key given by Reumer (1984, 1998), a combination of the following characters diagnoses the remains from the Sima del Elefante (TE) as belonging to the Neomyini tribe: a mandibular condyle with its articular facets strongly separated by a narrow interarticular area only present at the lateral side, a lower facet elongated medially and offset from the lower sigmoid notch at its lateral side (Fig. 5A-D), a lower incisor that is never tricuspulate (Fig. 5F-G), and m1-m2 that have entoconid crests (Fig. 5E). As noted above, the light red pigment of the teeth is a diagnostic character, but we should evaluate it with caution due to the potential loss of the colour in the case of this particular group.

Despite being scarce and fragmentary, the specimens from the TE have been clearly assigned to the genus *Asoriculus*. Two representatives of the Neomyini, *Neomys* and *Asoriculus* (Rzebik-Kowalska 1998, 2000), were present in Europe during the Early Pleistocene. Rzebik-Kowalska (2000) proposed a series of morphological diagnostic characters to distinguish these two genera, of which the following are useful with respect to the remains from the TE: in *Neomys* the coronoid process slightly deflects laterally in relation to the axis of the mandibular body; in *Asoriculus* such a deflection does not exist. The coronoid spicule in *Asoriculus* is located about half-way between the upper sigmoid notch and the tip of the process; in *Neomys* it always lies higher. The angle of the upper sigmoid notch is more closed in *Asoriculus* and more open in *Neomys*. The interarticular area of the condyle is wider in *Asoriculus* than in *Neomys*.

The consistency in the results of the bivariate analysis of a series of mandibular and dental measurements suggests that all the remains from the stratigraphic sequence assigned here to the genus *Asoriculus* belong to a single species (Fig. 6). Comparison with the measurements published for other European localities that have *Asoriculus* and *Neomys* specimens (Tabs. 5-6) places those from the TE (Tabs. 3-4) in the size range of three species: *Neomys browni* Hinton, 1911, *Neomys newtoni* Hinton, 1911, and *Asoriculus gibberodon*. As previously demonstrated, the genus *Neomys* is clearly ruled out.

At the moment, the *Asoriculus* species accepted as valid are *A. gibberodon, A. thenii* and *A. bourgioi* in Europe, and *A. maghrebiensis* in Africa (see the discussion on the topic in Rzebik-Kowalska 2000; and above). If compared with the dimensions of the specimens from the TE, both *A. thenii* and *A. maghrebiensis* are considerably bigger and more massive (Fig. 7). The holotype and only described specimen of *A. burgioi* is a partial skull that has the whole upper dentition with the exception of the incisor (Masini & Sarà 1998). This makes it impossible to draw a comparison between its dimensions and those from the TE, given that the latter were measured on mandibles and lower teeth. However, *A. burgioi* is much bigger than *A. gibberodon* if compared with the specimens measured by other authors (i.e. Reumer 1984; Rzebik-Kowalska 2000). Therefore

Species	Age	Location	Lmd	H	HM	HC	LUF	LLF
A. gibberodon	Early Pliocene	Osztramos 9		4,14		2,18	0,75	1,35
		Osztramos 1	4,35	3,92		2,24	0,92	1,4
		Csarnóta 2	4,62	4,24		2,26	0,9	1,46
	Late Pliocene	Osztramos 7	4,48	4,06		2,24	0,92	1,52
		Villány 3	4,15	3,91		2,1	0,84	1,29
		Kolinany				1,98	0,87	1,6
		Vceláre 3/1		3,97	1,35	1,88	0,88	1,38
		Vceláre 3/2		4,01		1,76	0,77	1,3
		Vceláre 3/3			1,28	1,84	0,78	1,22
	Early Pleistocene	Vceláre 4 A/5			1,6			
		Betfia-XIII		3,87		1,9		
		Betfia-X		3,55	1,25			
		Betfia-XI			1,22	1,89		
		Betfia-IX		3,89	1,32	1,94		
		Betfia-VII/1			1,43			
		Monte La Mesa		4,45	1,54	2.15		
A. thenii	Early Pleistocene	Podumci 1		4,6				
		Tatinja Draga		4,76				
A. maghrebiensis	Late Pliocene	Ahl Al Oughlam		4,96		2,55	1,01	1,81
N. newtoni	Early Pleistocene	Zalesiaki 1A		4,08	1,2			
	Early Pleistocene	West Runton		4,07				
	Latest Early/earliest Middle Pleistocene	Kozi Grzbiet		4,28	1,49	2,03		
	Middle Pleistocene	Westbury		4,2				
		Monte Peglia		4,52				
N. browni	Late Pleistocene	Grays Thurrock		4,29				
N. anomalus	Middle Pleistocene	Hundsheim		4,5	1,6			
	Late Pleistocene-Recent	Pisede		4	1,22			
	Recent	Auma, Stelzen, Bahren		4,23				
N. fodiens	Middle Pleistocene	Belvédère 3, 4		4,55				
		Grotte du Cap de la Bielle		4,75				
	Late Pleistocene-Recent	Pisede		4,95	1,82			
	Latest Pleistocene-Recent	Grotte du Malorade 1		4,85				
	Holocene	Grotte de l'Ours		4,8				
	Recent	Auma, Stelzen, Krölpa		5,04				

Tab. 6 - Means of the measurements of the mandibles of *Asoriculus* and *Neomys* species from European localities other than the Sima del Elefante. All the locations from which the metrical data have been taken are fully referenced in Rzebik-Kowalska (1998), with the exception of Monte La Mesa (Marchetti et al. 2000), Ahl Al Oughlam (Geraads 1995), and Belvédère 3-4 (Kolfschoten 1985). Measurement abbreviations in Fig. 4.

we can safely allocate the Sima del Elefante material to *A. gibberodon*.

Palaeoecological implications

Many of the soricid species identified for the Pleistocene period have survived through to the present or have very close relatives today. In these cases, the current ecological requirements can be extrapolated to their fossil representatives.

According to this actualistic approach, *Asoriculus*, as a member of the Neomyini, would have led a mainly aquatic life or at least have preferred humid habitats, as suggested by Reumer (1984). This has been deduced by observing the preferences of the modern genera *Neomys*, *Soriculus*, *Chimarrogale* and *Nectogale*. The two current species of the Neomyini that inhabit the Iberian Peninsula (*Neomys fodiens* (Pennant, 1711) and *N. anomalus* Cabrera, 1907) have aquatic habits. In consequence, and despite being extinct, the species *A. gibberodon* is taken as an indicator of humid environments with a permanent green covering, or even of the presence of permanent water streams.

Besides the moderate representation of *Asoriculus* in almost the whole stratigraphic sequence corresponding to the Early Pleistocene of the TE, there is further evidence to support humid conditions in the Sierra de Atapuerca at this time, namely the presence of *Hippopotamus*, *Castor*, the large otter-like *Pannonictis*, the duck *Anas*, and the white-tailed eagle *Haliaethus albicilla* in the same levels (Rosas et al. 2004). This vertebrate assemblage indicates an ecosystem with nearby water sources sufficient, at least, to sustain the aquatic habits of such species, all of them characteristic of humid environments. The arvicoline assemblage (*Allophaiomys*), however, suggests the presence of open lands, whereas *Sciurus, Apodemus, Glis, Eliomys*, and an indeterminate kind of felid and suid indicate a more forested area. Together, all these bio-indicators form a complex image of the landscape surrounding the TE cave during the Lower Red Unit phase.

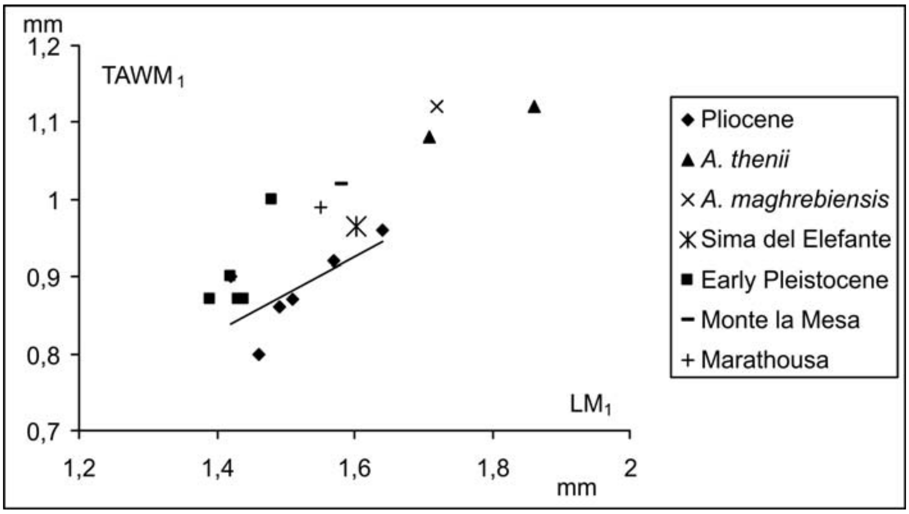

Fig. 7 - Scatter diagram of length/width of the M_1 of *A. gibberodon* and *A. thenii* from Europe, and *A. maghrebiensis* from north-western Africa (data in Tables 3, 5). The width values for *A. maghrebiensis*, lacking in the original source (Geraads 1995), have been extrapolated. The Pliocene, Early Pleistocene, Sima del Elefante, Monte la Mesa and Marathoussa items are *Asoriculus gibberodon* specimens. The line shows the tendency of the Pliocene dimensions. Abbreviations: LM_1, length of M_1; $TAWM_1$, talonid width of M_1.

Moreover, in a previous palaeoenvironmental reconstruction of this Lower Red Unit (Cuenca Bescós & Rofes 2004), we showed that the insectivore distribution seems to document a wet and temperate period with three successive warm-cold-warm phases, tentatively correlated with the Waalian (1.25-1.5 Ma), given that this warm episode of the Early Pleistocene in north-central Europe comprises the same A, B, C (w-c-w) phases (Zagwijn 1998). The Waalian phase in Spain came shortly after the arid Eburonian (1.5-1.78 Ma), which would have allowed the distribution of *Allophaiomys* throughout the Holarctic region. The next temperate period, the Bavelian (0.86-1.2 Ma), falls inside the positive Jaramillo subchron, which is in contradiction with the TE Lower Red Unit reverse magnetic polarity (Rosas et al. 2001, 2004). The next stage, the Cromerian complex (0.48-0.86 Ma), is characterized by its derived arvicoline faunas (*Microtus*) and the extinction of *Castillomys*, which makes it very difficult to correlate the TE Red Lower Unit's faunal assemblage with this period.

Palaeobiogeographical implications

Generally speaking, the dispersal of land mammals depends on the availability of geographical connections, which may or may not be related to climatic changes, as well as the presence of adequate habitats that support viable populations. In this sense Reumer (1984) and Rzebik-Kowalska (1995) document a progressive latitudinal retreat of *Asoriculus* towards the south of Europe during the Plio-Pleistocene due to the climatic deterioration recorded in the latest Miocene and all through the Pliocene.

However, we found a somewhat different scenario (Fig. 8A-D): there is a general dispersal of the species from the south to the north of Europe at the beginning of the Pliocene, followed by a slight spread to the north at the end of the same age; and finally, a progressive retreat from the north and a reoccupation of the south-western part of the continent during the early Pleistocene.

The oldest remains of *A. gibberodon,* from the Late Miocene, were found in the Mediterranean region, namely at Brisighella in Italy (De Giuli 1989), Santa Margarida and Salobreña on the Iberian Peninsula (Crochet 1986), and Maramena in Greece (Doukas et al. 1995). There are also two more records from south-central Europe, Tardosbánya and Polgárdi 4 in the Pannonian Basin (Mészáros 2000) (Fig. 8A).

In the Early Pliocene *A. gibberodon* was present from Layna in Spain to Muselievo in Bulgaria and Wéze 1 in Poland. The Early Pliocene distribution suggests a vicariant evolution of the European *Asoriculus* populations, which were mainly concentrated in two core areas: western and east-central Europe (Fig. 8B). In Spain in particular, besides Layna they have been identified at the localities of La Gloria 4, Peralejos, Villalba Alta Río 1, Lomas de Casares 1, Orrios 7, and El Arquillo 3 (Sp1 in Fig. 8B, Crochet 1986; Mein et al. 1990).

During the Late Pliocene, the species temporarily left the Mediterranean peninsulas, with the exception of the Greek locality of Tourkobounia, and we find it as far north as Rebielice K in Poland, probably meaning that central Europe had the optimal environmental conditions for *Asoriculus* at this time. The separated histories in east and west continue (Fig. 8C). The Late Pliocene North-African species, *A. maghrebiensis*, may have its origin in a previous migration either during the Late Miocene or the Early Pliocene.

At the beginning of the Pleistocene, *Asoriculus* regains and increases its former south-western range, returning to the Iberian and Italian Peninsulas. However, it is still present to the north of the Carpathians, in Zabia cave, Poland (Bosák et al. 1982), as well as in the high Saone and Rhone valleys at Les Valerots, France (Jammot 1977) (Fig. 8D).

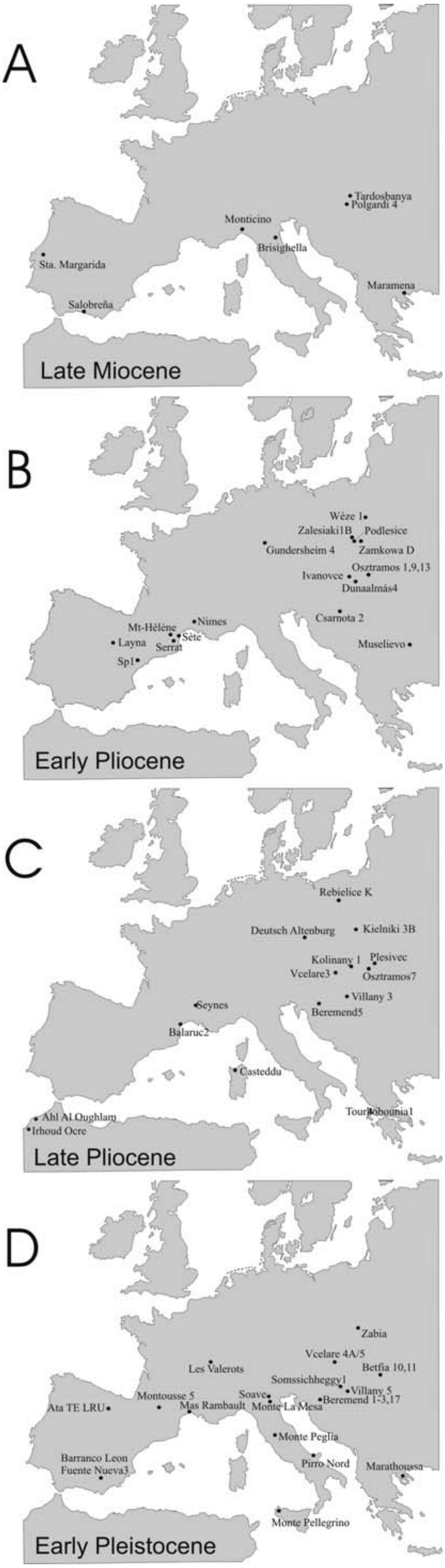

Fig. 8 - Reconstructed biogeography of the currently extinct *Asoriculus* based on the available palaeontological record (see table 1). The geographical distribution was taken mainly from Maul (1990). Black dots refer to reported localities with fossil *Asoriculus*. Sp1 in 8B correspond to the group of localities from the Teruel basin in Spain: La Gloria 4, Peralejos, Villalba Alta Río 1, Lomas de Casares 1, Orrios 7, and El Arquillo 3.

Besides the above-mentioned localities, remains of *A. gibberodon* have been found at Mas Rambault in France (Jammot 1977); Marathoussa in Greece (Koufos et al. 2001); Beremend (Jánossy 1986, 1996), Somssichhegy (Reumer 1984), and Villány (Jánossy 1986) in Hungary; Soave (Pasa 1947), Pirro Nord (De Giuli et al. 1990), Monte Peglia (Meulen 1973), and Monte La Mesa (Marchetti et al. 2000) in Italy; Betfia in Rumania (Terzea 1994; Rzebik-Kowalska 2000); Vceláre in Slovakia (Fejfar & Horácek 1983); Fuente Nueva 3-Barranco León (Furió 2003), and the Trinchera del Elefante (this paper) in Spain. *Asoriculus* diversified in southern Europe during this time and a couple of new species emerged: *A. thenii* (Podumci 1 and Tatinja Draga in Croatia, Malez & Rabeder 1984), and *A. burgioi* (Monte Pellegrino in Italy, Masini & Sarà 1998).

There is no evidence to support the persistence of *Asoriculus* into the Middle Pleistocene, with the exception of a few poorly determined cases of *Asoriculus* sp. or *Soriculus* sp. scattered across France (Montoussé 3, Clot et al. 1976), Germany (Mosbach 2 and 3, Koenigswald & Tobien 1987), and the Czech Republic (Chiscau, Maul 1990). The extinction of the species at the end of the Early Pleistocene could be explained by the marked deterioration of the unstable climatic conditions after the Jaramillo subchron event (0.99-1.07 Ma) during the last part of this time.

According to Reumer (1984), the genus *Nesiotites*, which lived in Corsica, Sardinia and the Balearic Islands from the Late Pliocene to the Holocene, is a close relative or direct descendant of *Asoriculus* (see also the discussion of the two genera in Masini & Sarà 1998). However, Maul & Rzebik-Kowalska (1998) suggest that *Asoriculus* is the ancestor of the genus *Neomys*.

As seen before, the preference of *Asoriculus* for humid and relatively warm habitats corroborates both its Mediterranean origin and its first southern distribution. After the remarkable Pliocene continental spread, there is a temporary decrease and south-western-ward retreat at the Plio-Pleistocene boundary, maybe related to drier conditions in Europe during this period (Eburonian phase). During the second third of the Early Pleistocene, the climate temporarily becomes warmer and wetter (Waalian phase), optimal conditions for the genus to re-enter its old south-western territories and diversify. The climatic conditions at the end of the Early

Pleistocene were cold and dry again, seemingly reducing the available habitats preferred by *Asoriculus*, and driving the species to its eventual extinction, after nearly three million years of history.

In conclusion, *Asoriculus* is a genus of Mediterranean origin, which appeared at the end of the Miocene and lived in south-central Europe from this time to the end of the Early Pleistocene, increasing its distribution during warmer periods and even reaching north-west Africa. There seem to have existed two bio-provinces (east and west) during the Pliocene, the eastern population being better represented than the occidental one in terms of the number of localities. The separation between the two areas seems to be sharp, the Alps being the most likely geographical barrier dividing them.

The dimensions recorded in the locality of Betfia during the early Pleistocene attest to a tendency to a reduction in size in the *A. gibberodon* populations of east Europe, possibly an adaptive character developed in groups that are progressively becoming marginal. In the Mediterranean environment (i.e. the Trinchera del Elefante, Monte la Mesa, Marathoussa), by contrast, the dimensions remain at the level of the highest recorded during the Pliocene in central Europe (Fig. 7). The lack of measurements from the Pliocene sites of the west and south of the continent makes it impossible to know whether the greater size of the specimens from this area is a primitive character or derivative with respect to previous populations. The appearance of new species such as *A. thenii* and *A. burgioi* is a clearly Mediterranean phenomenon. These new forms, much greater in size than *A. gibberodon*, probably evolved from the biggest examples of the species in areas where they were geographically and genetically isolated (i.e. Croatia, Sicily), following a model of allopatric evolution, just as would have happened previously with *A. maghrebiensis* in the north-westernmost part of Africa.

Conclusions

The remains of the red-toothed shrew (Soricinae) of the Neomyini tribe identified in the Sima del Elefante levels TE 8-14, corresponding to the early Pleistocene of the Sierra de Atapuerca, have been assigned to the species *Asoriculus gibberodon* (Petényi, 1864).

Although it is now extinct, from an actualistic perspective the *Neomys* related species *A. gibberodon* is taken as an indicator of humid environments with a good green covering, or even of the presence of permanent water sources. The moderate record of *Asoriculus* in almost all the early Pleistocene levels from the TE, together with the associated vertebrate assemblage (i.e. *Castor*, otter relatives, aquatic birds, etc), shows that the ancient landscape of the Sima del Elefante Lower Red Unit had a water component sufficient to sustain the presence and habits of a limited number of *Asoriculus* and other aquatic species during this period. Moreover, the whole faunal assemblage indicates a warm period that could be correlated with the north European Waalian, an interglacial roughly dated between 1.25 and 1.5 Ma.

Both the remains of *A. gibberodon* identified in Atapuerca and the ones from Barranco León and Fuente Nueva 3 belong to the moment when this species returned to southern European peninsulas after the brief northern retreat episode at the Plio-Pleistocene boundary. This southward dispersal of *Asoriculus* may be related to the Waalian warm phase of the Early Pleistocene, after which the species underwent a progressive path to extinction, finally disappearing at the end of this time. The distribution of the species points to the existence of two bio-provinces (east and west) during the Pliocene. However, in the Early Pleistocene there is a tendency of the remaining eastern population to reduce its body dimensions while the Mediterranean ones maintain their large size. From this latter group the much bigger new forms, *A. thenii* and *A. burgioi*, would have evolved, probably due to geographical and genetic isolation in places such as Croatia and Sicily.

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