

General palaeontology (biostratigraphy)

First record of *Beremendia fissidens* (Mammalia, Soricidae) in the Pleistocene of the Iberian Peninsula, with a review of the biostratigraphy, biogeography and palaeoecology of the species

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Abstract

This paper reports the first paleontological record of *Beremendia fissidens* (Mammalia, Soricidae) in the Iberian Peninsula during the second third of the Early Pleistocene. The species is exclusively present at the lowermost levels (Lower Red Unit: TE8–14) of the Sima del Elefante site, one of the largest stratigraphic sections of the Atapuerca cave complex (Burgos, Spain). The age of Sima del Elefante shows that this large-sized type of red-toothed venomous shrew inhabited the Sierra de Atapuerca more than 1.1 Myr ago, coexisting with an extremely rich and diverse faunal association of nearly 40 small and large mammalian species, including hominines. The presence of this species in the Atapuerca locality has important palaeoecological, palaeobiogeographical and biostratigraphic implications, which are extensively discussed here, throwing light on aspects largely left aside for this important group of red-toothed shrews, previously relegated to nothing but mere faunal lists, at least in the Iberian Peninsular context. **To cite this article:** J. Rofes, G. Cuenca-Bescós, C. R. Palevol 8 (2009).

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Résumé

Première citation de *Beremendia fissidens* (Mammalia, Soricidae) dans le Pléistocène de la péninsule Ibérique, avec une révision de la biostratigraphie, biogéographie et paléocologie de l'espèce. Ce document rapporte le premier registre paléontologique de *Beremendia fissidens* (Mammalia, Soricidae) dans la péninsule Ibérique pendant le deuxième tiers du Pléistocène inférieur. Cette espèce est exclusivement présente aux niveaux les plus bas (Unité rouge inférieure : TE8–TE14) du gisement de Sima del Elefante, une des plus grandes sections stratigraphiques du complexe karstique d'Atapuerca (Burgos, Espagne). L'âge de Sima del Elefante prouve que ce grand type de musaraigne venimeuse aux dents pigmentées en rouge a habité la sierra d'Atapuerca il y a plus de 1,1 MYR, coexistant avec une association faunique extrêmement riche et diverse de presque 40 espèces de mammifères petites et grandes, y compris des hominines. La présence de cette espèce dans la localité d'Atapuerca a des implications paléocologiques, paléobiogéographiques et biostratigraphiques importantes, qui sont discutées ici en détail, jetant la lumière sur des aspects en grande partie laissés de côté pour cet important groupe de musaraignes à dents rouges, précédemment relégué à rien, si ce n'est à des listes

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fauniques, au moins dans le contexte de la péninsule ibérique. *Pour citer cet article* : J. Rofes, G. Cuenca-Bescós, C. R. Palevol 8 (2009).

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Keywords: Soricine; Systematic palaeontology; Palaeoecology; Palaeobiogeography; Atapuerca; Sima del Elefante; Spain

Mots clés : Soricine ; Paléontologie systématique ; Paléoécologie ; Paléobiogéographie ; Atapuerca ; Sima del Elefante ; Espagne

1. Abbreviations

Institutional – **MPZ**, Museo Paleontológico de Zaragoza, Zaragoza, Spain.

Fieldwork labels – **TE**, Sima del Elefante site; **TE-LRU**, Lower Red Unit of TE; **Z**, depth; **ATA**, Atapuerca.

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

2. Introduction

Insectivores are a group of mammals whose fossil record has assumed a special relevance in the Iberian Peninsula in the last few years (e.g. [10,11,21,45]). To this group belongs *Beremendia fissidens* (Mammalia, Soricidae), a kind of red-toothed shrew which inhabited Eurasia from the Early Pliocene to the beginnings of the Middle Pleistocene [30,62].

Although trustworthily described by Rzebik-Kowalska [61] and Reumer [52] in central Europe, the biostratigraphy, biogeography and morphological peculiarities of *Beremendia* are poorly known in the Iberian Peninsula. Besides, its general phylogenetic affinities urgently need a revision at the light of new challenging discoveries [30,31,57]. As if it were not enough, its precise palaeoecological preferences have remained obscure and highly speculative.

In Spain, in particular, the records of *B. fissidens* up to now are scanty and all come from the Late Pliocene [1,21,37,44]. Pleistocene records correspond to previous misidentifications, and, with the exception of the unpublished Ph.D. dissertation of Furió [21], all said references are limited to the inclusion of *B. fissidens* in general faunal lists. In this paper we present evidence of the first bona fide examples of this large-sized soricid

in the Iberian Peninsula during the Early Pleistocene (as chronologically stated by Aguirre and Pasini [3], based on the Vrica section in Calabria, Italy), which comes from the site of Sima del Elefante in Atapuerca (Burgos, Spain). We also take advantage of the opportunity to carry out a comprehensive review and updating of the current knowledge we have on the species, throwing light on such aspects as those mentioned before.

Sima del Elefante (TE labelled in stratigraphic, palaeontological and archaeological samples) is a major cave infill located in the railroad cutting (Trinchera del Ferrocarril) of the Sierra de Atapuerca (Fig. 1). It may correspond to an ancient opening to Galería Baja in the Cueva Mayor karst subsystem, and is completely full of sediments of allochthonous origin. The stratigraphic section of Sima del Elefante, including Lower and Middle Pleistocene deposits, is 25 m thick, 19 of which were exposed during the construction of the railway. This section comprises 22 levels, the lowermost of which, grouped and known as the Lower Red Unit (TE-LRU), are Early Pleistocene in age [5,8,10,38,58,59]. The sample of fossil shrews analysed here comes from the Lower Red Unit of the Sima del Elefante site (Fig. 2).

TE-LRU comprises levels TE8 to TE14 and is extremely rich in faunal remains, most of which are very well preserved; some of them were even found in anatomical connection [58,59]. The latter include (updated from Cuenca-Bescós and García [8]): (1) Eulipotyphla (Insectivores) – *Asoriculus gibberodon*, *B. fissidens*, *Crocidura kornfeldi*, *Crocidura* sp., *Sorex* cf. *minutus*, *Sorex* cf. *araneus*, *Erinaceus* cf. *praeglacialis*, *Galemys* cf. *kormosi*, *Talpa* cf. *europaea*; (2) Carnivora – *Canis* cf. *arnensis/mosbachensis*, *Vulpes* cf. *alopeoides*, *Ursus* cf. *dolinensis*, cf. *Baranogale antiqua*, *Mustela* cf. *palerminae/praeivalis*, *Pannonictis nestii*, *Panthera gombaszoegensis*, *Lynx* cf. *issiodorensis*; (3) Perissodactyla – *Stephanorhinus etruscus*, and Equidae indet.; (4) Artiodactyla – *Hippopotamus* sp., *Eucladoceros giulii*, *Megaloceros savini*, Cervidae indet., *Bison* sp., Bovidae indet., Suidae indet.; (5) Rodentia – *Sciurus* cf. *wharthae*, *Eliomys quercinus*, *Castor fiber*, *Ungaromys nanus*, *Pliomys* cf. *simplicior*, *Allophaiomys lavocati*, *A. burgondiae*, *A. nutiensis*, Arvicolinae gen. et sp. nov., *Castillomys*

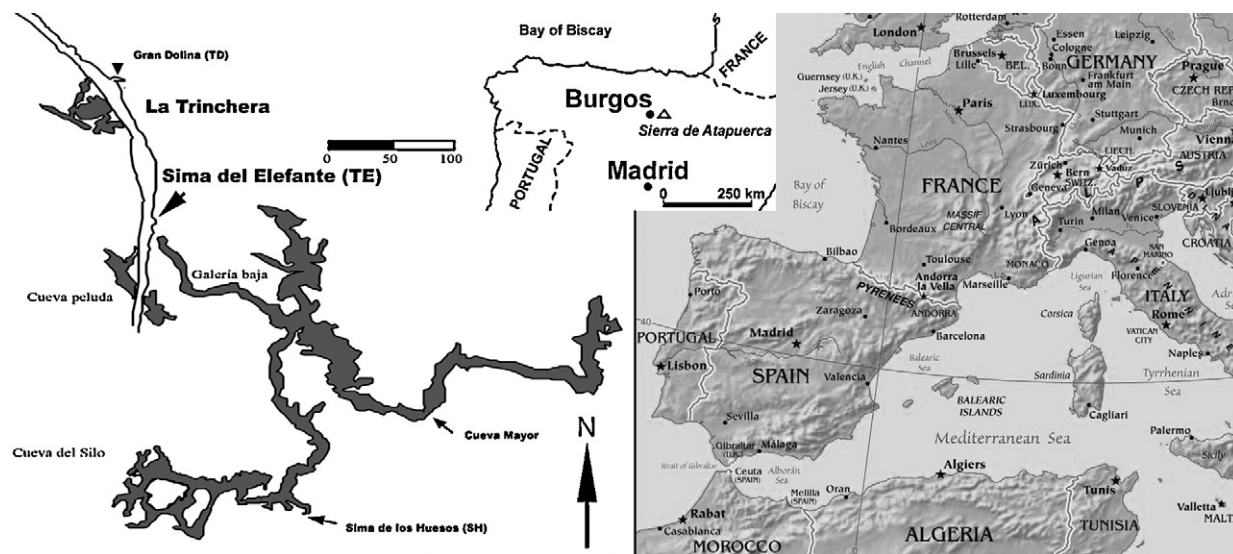


Fig. 1. Geographic situation of the Sierra de Atapuerca and a plan view of the sites and the cave system (left). The sites of La Trincheria are white. The subsurface caves are shaded.

Fig. 1. Situation géographique des gisements de la Sierra de Atapuerca et plan des emplacements et du système de cavernes (gauche). Les emplacements de La Trincheria sont blancs. Les cavernes à fleur de terre sont ombrées.

rivas, *Apodemus* sp.; (6) Lagomorpha – *Lepus* sp. and *Oryctolagus* sp.; (7) Aves – *Carduelis chloris*, *Perdix paleoperdix*, *Coturnix coturnix*, *Columba livia*, *Haliaeetus albicilla*, *Circaetus gallicus*, *Falco tinunculus*, *Falco* sp., *Turdus* sp., Alaudidae indet., *Anas* sp.; (8) Fishes, amphibians and reptiles – Salmonidae indet., *Bufo bufo*, *B. calamita*, and Chelonia indet.

Small mammals proved to be crucial in dating the TE-LRU as the oldest one in Atapuerca (i.e. more than 1 Myr old [8,10,38,56]). The arvicolid and insectivore associations, in particular, showed that this unit may be Early Pleistocene, pre-Jaramillo in age, at least as old as the localities of Fuente Nueva 3 and Barranco León in the Granada basin (ca. 1.2–1.5 Myr [55]). This is consistent with the reverse polarity of the TE9 to TE16 levels, interpreted as Matuyama Magnetochron by Parés et al. [46], and with the presence of the large-sized mustelid *Pannonictis nestii*, referable to the Early Pleistocene [22]. Recent cosmogenic nuclide analysis dated the TE9 level to ~1.2 Ma [5], thus confirming the biostratigraphically-inferred chronology.

Noteworthy is that the Lower Red Unit from Sima del Elefante (TE9) represents the oldest and most accurately dated record of human occupation in Europe. This takes the form of a hominin mandible, 32 Mode 1 stone tools, and many large-mammal bones with clear evidence of human processing [5].

We introduce here in advance the taxonomic authorities for the main genera and species of sorcids

mentioned in the text with the purpose of facilitating further reading. Those taxa are, in alphabetic order, namely as follows: *Beremendia* Kormos, 1934 [33]; *Beremendia fissidens* (Petényi, 1864) [48]; *Beremendia minor* Rzebik-Kowalska, 1976 [61]; *Beremendia pohaiensis* (Kowalski and Li, 1963) [35]; *Beremendia ucrainica* Pidoplitschka, 1956 [49]; “*Dolinasorex glyphodon*” Rofes and Cuenca-Bescós, in press [57]; *Lunanosorex* Jin and Kawamura, 1996b [31]; *Lunanosorex lii* Jin and Kawamura, 1996b [31]; *Nectogalinia altaica* Gureev, 1979 [25]; *Neomys sinensis* Zdansky, 1928 [71]; *Peisorex* Kowalski and Li, 1963 [35]; *Peisorex pliocaenicus* Flynn and Wu, 1994 [20]; *Peisorex pohaiensis* Kowalski and Li, 1963 [35].

3. Materials and methods

The specimens were obtained by concentrating the sediment after a process of washing and sieving the sedimentary materials acquired from the excavations of Sima del Elefante during the course of the Atapuerca campaigns between 1999 and 2007, plus two previous sample pits in 1995–1996 (roughly 12–15 tons of sediment each year out of 25 processed for all the Atapuerca locations). The product was a concentrate consisting fundamentally of fossil remains of small vertebrates (packed in small plastic boxes). This was duly labelled with an abbreviation indicating in order the site and stratigraphic level from which it came, the excavation

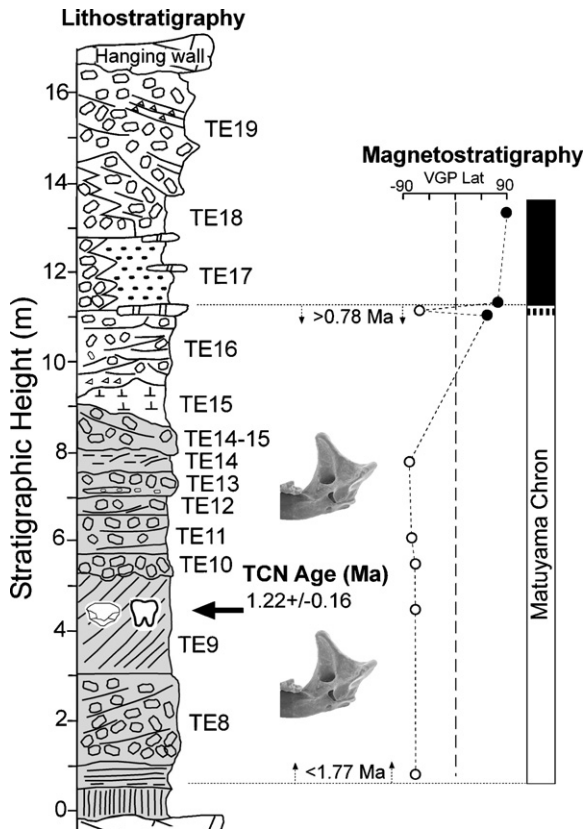


Fig. 2. Synthetic column showing the different stratigraphic units of the central-north section of the Sima del Elefante site, labelled TE (levels TE8 to TE19). Gray levels correspond to the Lower Red Unit (TE8 to TE14–15). Units TE20 to TE22 do not outcrop here but in the southern section. Black arrow points to level TE9 from which the recently discovered human remains were retrieved. Right column shows the palaeomagnetic-based chronology recorded in the section. The figure has been modified from Carbonell et al. [5].

Fig. 2. Colonne synthétique montrant les différentes unités stratigraphiques de la section nord-centrale de Sima del Elefante, marqué TE (niveaux TE8 à TE19). Les niveaux gris correspondent à l'Unité rouge inférieure (TE8 à TE14–15). Les unités TE20 à TE22 n'affleurent pas ici mais dans la section du sud. La flèche noire indique le niveau TE9 dans lequel les restes humains récemment découverts ont été recherchés. La colonne droite montre la chronologie paléomagnétique enregistrée dans la section. Modifiée de Carbonell et al. [5].

grid unit, the depth (Z) in centimeter where appropriate, and the year in which the remains were recovered (e.g. TE-9B/K-29/Z: 600-620/ATA 02), enabling us to maintain rigorous stratigraphic control throughout. Subsequently, the small fossil remains were separated from these concentrates using a hand-held or binocular magnifying glass. Afterwards, a preliminary classification of the fossils was undertaken, and these were recorded in the database and provisionally stored in the Department of Palaeontology of Zaragoza University. The specimens studied for this paper are kept in the Palaeon-

tology Museum of Zaragoza University, abbreviated as MPZ.

The 171 specimens analysed in the present study have been drawn from the enormous volume of remains gathered in the course of 11 years of continuous excavations. The sample is composed of mandibles, maxillae and teeth that are either loose or *in situ*. Here we follow Reumer's [52] anatomical nomenclature, above all for comparative purposes given its nearly standardized use among scholars dealing with fossil shrews. For a slightly different approach, particularly with reference to the so-called "unicuspid" teeth, see Hutterer [29].

Metric values were recorded using a stereomicroscope connected to a video camera, which sent the images to a computer programme (Matrox Inspector) that made it possible to visualize and measure the specimens with great accuracy. We also follow Reumer [52] in the choice of measurements to be taken and the PE-index, with a few additions from Rabeder [50] and Rofes and Cuenca-Bescós [56]. The PE-index quantifies the degree of posterior emargination of the large upper teeth. This has been calculated for P4, M1 and M2 by means of the formula: $LL + BL/2 PE - 1$. For the morphometric analysis we used the PAST v1.77 statistical programme [26].

There is no doubt regarding the assignation of the remains from Sima del Elefante to the Soricinae subfamily, on account of the characteristic red pigment of the teeth and the presence of a conspicuous posterolingual basin in the fourth lower premolar. Even though it lacks a formal diagnosis, the genus *Beremendia*, defined by Kormos in 1934, does have a detailed description. Repenning [51] and Reumer [52] selected a series of characters from this description as the diagnostics of the group, to which Jin and Kawamura [30] added further observations. The result of this is the version presented in the following section.

4. Systematic palaeontology

Class MAMMALIA Linnaeus, 1758 [39]

Order EULIPOTYPHILA Waddell, Okada, and Hasegawa, 1999 [69]

Family SORICIDAE Fisher von Waldheim, 1817 [19]

Subfamily SORICINAE Fisher von Waldheim, 1817 [19]

Genus *Beremendia* Kormos, 1934 [33]

Beremendia fissidens (Petényi, 1864) [48]

Figs. 3–4.

Synonyms: *Beremendia ucrainica* Pidoplitschka, 1956 [49]

Nectogalinia altaica Gureev, 1979 [25]

Table 1a

Measurements (in millimetres) of the upper dentition of *Beremendia fissidens* from Sima del Elefante. **Abbreviations:** **n**, number of specimens; **min**, minimum value; **max**, maximum value; **s.d.**, standard deviation; **TE-LRU**, Sima del Elefante–Lower Red Unit; **Europe**, *B. fissidens* specimens from European Plio-Pleistocene locations other than Sima del Elefante (sources: Dehm [16]; Rzebik-Kowalska [61,63,64]; Harrison and Clayden [27]; Dahlmann and Storch [13]; Reumer and Hordijk [54]; Marchetti, Parolin and Sara [42]; Koufos et al. [34]).

Tableau 1a

Mesures (en millimètres) de la dentition supérieure de *Beremendia fissidens* de Sima del Elefante. **Abréviations:** **n**, nombre de spécimens; **min**, valeur minimum; **max**, valeur maximum; **écart-type**, **s.d.**, écart-type; **TE-LRU**, Unité rouge inférieure de Sima del Elefante; **Europe**, spécimens de *B. fissidens* des endroits européens du Plio-Pléistocène, autres que Sima del Elefante (d'après : Dehm [16]; Rzebik-Kowalska [61,63,64]; Harrison et Clayden [27]; Dahlmann et Storch [13]; Reumer et Hordijk [54]; Marchetti, Parolin et Sara [42]; Koufos et al. [34]).

Levels	TE8	TE9						TE12	TE14	TE-LRU	Europe
Element	Measure	Mean	n	Min	Mean	Max	s.d.	Mean	Mean	Mean	Mean
I1	L	3.38	4	3.02	3.28	3.44	0.19		3	3.24	3.68
	H	2.28	4	2.18	2.24	2.31	0.06		2.11	2.22	2.32
	LT	1.52	4	1.46	1.55	1.63	0.08		1.3	1.5	1.6
P4	BL	2.53	18	2.48	2.68	2.81	0.09			2.67	2.66
	LL	2.05	19	1.76	1.89	2.05	0.08			1.9	1.84
	PE	1.89	19	1.59	1.74	1.94	0.09			1.74	1.8
	W	2.3	18	2.2	2.4	2.6	0.12			2.39	2.49
M1	BL	2.32	33	2.24	2.38	2.57	0.07	2.28		2.38	2.43
	LL	2.26	35	2.06	2.38	2.52	0.1	2.28		2.33	2.06
	PE	1.91	35	1.74	1.92	2.1	0.09	2.07		1.92	1.93
	AW		34	2.34	2.53	2.7	0.09	2.41		2.53	2.48
	PW	2.7	33	2.41	2.54	2.77	0.08	2.55		2.54	2.57
M2	BL		17	1.86	1.99	2.11	0.07	1.97		1.98	2.04
	LL		18	1.76	1.92	2.18	0.01	1.88		1.91	1.71
	PE		18	1.53	1.65	1.77	0.07	1.69		1.65	1.6
	AW		18	2.3	2.44	2.63	0.09	2.44		2.44	2.5
	PW		17	1.76	1.91	2.08	0.09	1.95		1.91	1.99
M3	L		3	0.75	0.78	0.82	0.04			0.78	0.9
	W		3	1.43	1.56	1.68	0.13			1.56	1.65

Type species: *Crossopus fissidens* Petényi, 1864 [48]

Type locality: Beremend 1 (Hungary).

Studied locality: Sima del Elefante (Lower Red Unit) in the Sierra de Atapuerca (Burgos, Spain).

Selected other localities: See reviews by Rzebik-Kowalska [62], Storch et al. [67], and Furió [21].

Geographic and stratigraphic distribution: Eurasia, from the Early Pliocene (MN 14) to the late Early Pleistocene; early Middle Pleistocene?

Diagnosis: As stated by Jin and Kawamura [30]: dental formula 1-4-3/1-2-3; teeth stained red to almost black; first upper incisor markedly bifid; upper antemolars decreasing in size from A1 to A4; A4 reduced or lacking, and invisible from the buccal side of the skull; posterior emargination in P4 and upper molars moderate; parastyle of M1 normal and not strongly developed; coronoid process leaning anteriorly to varying degrees; upper pterygoid fossa markedly or slightly depressed; upper facet narrowly elliptic to oval; interarticular area very broad, and with lingual emargination; lower facet placed greatly anteriorly, and thus invisible in buccal view; internal temporal fossa deeply pocketed; first lower incisor without cusplets on its cutting edge; its apex

markedly bent upward; p4 with two cusps and a posterolingual basin; entoconid crest with various degrees of development in lower molars.

Measurements: See Table 1a and Table 1b and the morphometric analysis below.

4.1. Description

In general, the dentition of the soricids consists of one incisor, three molars and small elements situated between the incisor and the molars, which are named, following Reumer [52], the antemolars (AA). In the upper dentition, the last antemolar is conventionally designated P4, the number of remaining antemolars varying from two to five. The antemolars of the Soricidae are often called “unicuspids”. This name is considered incorrect because quite often these teeth possess accessory cusps [52]. In the lower dentition there is only one tooth called an antemolar (a1); as in the case of its upper counterpart, the last antemolar (“a2”) is generally considered to be a premolar and is named p4. The i1 of the soricids has a single cusp, known as the apex, and a series of serrations on the dorsal edge, which may vary from nonexistent up to

Table 1b

Measurements (in millimetres) of the lower dentition of *Beremendia fissidens* from Sima del Elefante. **Abbreviations:** **n**, number of specimens; **min**, minimum value; **max**, maximum value; **s.d.**, standard deviation; **TE-LRU**, Sima del Elefante–Lower Red Unit; **Europe**, *B. fissidens* specimens from European Plio-Pleistocene locations other than Sima del Elefante (sources: Heller [28]; Pasa [47]; Dehm [16]; Rzebik-Kowalska [60,61,63,64]; Van der Meulen [68]; Storch, Franzen and Malec [66]; Malez and Rabeder [41]; Harrison and Clayden [27]; Dahlmann and Storch [13]; Reumer and Hordijk [54]; Marchetti, Parolin and Sara [52]; Koufos et al. [34]; Maul [43]).

Tableau 1b

Mesures (en millimètres) de la dentition inférieure de *Beremendia fissidens* de Sima del Elefante. **Abréviations:** **n**, nombre de spécimens; **min**, valeur minimum; **max**, valeur maximum; **s.d.**, écart-type; **TE-LRU**, Unité rouge inférieure de Sima del Elefante; **Europe**, spécimens de *B. fissidens* des gisements européens du Plio-Pléistocène autres que Sima del Elefante (d'après : Heller [28]; Pasa [47]; Dehm [16]; Rzebik-Kowalska [60,61,63,64]; Van der Meulen [68]; Storch, Franzen et Malec [66]; Malez et Rabeder [41]; Harrison et Clayden [27]; Dahlmann et Storch [13]; Reumer et Hordijk [54]; Marchetti, Parolin et Sara [52]; Koufos et al. [34]; Maul [43]).

Levels		TE9					TE10					TE14	TE-LRU	Europe
Element	Measure	n	Min	Mean	Max	s.d.	n	Min	Mean	Max	s.d.	Mean	Mean	Mean
i1	L	10	5.51	5.59	5.84	0.13						5.4	5.66	6.28
	H	4	1.34	1.38	1.45	0.05						1.43	1.39	1.41
a1	L	7	1.14	1.2	1.25	0.04							1.2	1.47
	W	7	0.98	1.14	1.21	0.08							1.13	1
p4	L	18	1.66	1.79	1.92	0.07							1.79	1.93
	W	18	1.26	1.41	1.49	0.07							1.4	1.3
m1	L	58	2.38	2.64	2.88	0.1						2.64	2.64	2.54
	TRW	58	1.36	1.48	1.67	0.06						1.45	1.48	1.45
	TAW	59	1.45	1.57	1.75	0.06						1.46	1.57	1.56
m2	L	44	2.07	2.23	2.46	0.09							2.23	2.2
	TRW	45	1.2	1.34	1.47	0.06							1.34	1.35
	TAW	44	1.16	1.28	1.51	0.01							1.28	1.34
m3	L	14	1.39	1.57	1.93	0.14							1.57	1.63
	W	14	0.82	0.91	0.97	0.04							0.9	0.93
m1-m3	L	41	5.41	5.71	6.11	0.19						5.55	5.72	6.15
Ramus	L	23	6.05	6.58	6.94	0.25						6.53	6.57	7.43
	H	28	5.51	6.01	6.64	0.26						5.91	6	6.28
	Hm1	33	2.27	2.5	2.77	0.11							2.5	2.74
	Hm2	60	2.01	2.38	2.77	0.16							2.37	2.57
	HC	40	3.32	3.64	4.03	0.16	3	3.47	3.69	3.86	0.2		3.63	3.35
	LUF	39	1.51	1.82	2.05	0.13	2	1.86	1.96	2.05	0.13		1.82	1.84

four. Reumer [52] named these serrations “cuspules” to distinguish them from the true cusps (e.g. cuspules have no connection with the pulp cavity). As in other soricines, all the dental elements of *B. fissidens* are stained a dark red in the apical part of the crowns.

4.1.1. II

This is strongly bifid, namely with a supplementary cusplet on the medial side, slightly divergent and separated from the main cusp by a wide, deep groove on the apical part of the tooth. The talon is broad mesiodistally, and is trapezoidal to square-shaped in lateral view. The lateral root-crown junction line is nearly perpendicular to the dorsal edge of the tooth, or slightly inclines to the front. This line is either slightly or markedly undulated. The cingulum along the posterior buccal edge is only present behind the talon. The root is robust with a deep, longitudinal groove on the lateral face. The posterior part of the root is notably bent ventrally (Fig. 3a and b).

4.1.2. AA

According to Rzebik-Kowalska [61] and Reumer [52], the four antemolars decrease in size successively; the second is slightly smaller than the first, the third is half the size of the first, and the fourth is tiny and not visible in buccal view. Unfortunately, we do not have any A3 or A4 preserved in the sample, but only the alveoli corresponding to these teeth. Our description therefore focuses on the first two antemolars. A1 and A2 are unicuspid, with a rounded triangular outline in occlusal view. In both cases, the cusp is placed somewhat anteriorly, the one in A1 being the higher. From the cusp, a short, thick ridge runs to the anterior tip of the crown, and another longer but thinner ridge extends to the posterior margin of the crown. These ridges form a somewhat S-shaped line. The basal part of the crown is surrounded by a cingulum, which is thickest in the posterobuccal side. This corner protrudes markedly to posterior.

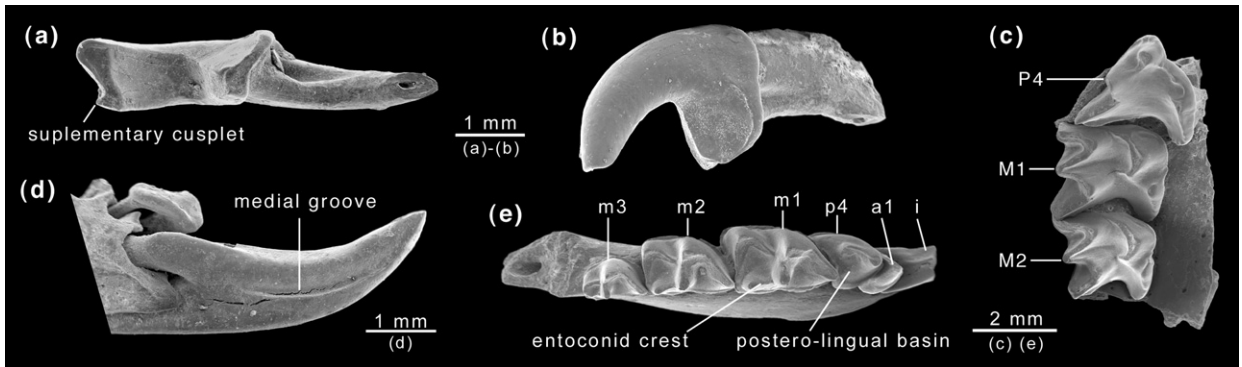


Fig. 3. Selected specimens of *Beremendia fissidens* from the Lower Red Unit of Sima del Elefante: (a)–(b), left upper incisor, MPZ 2005/511 (TE14/Z: 190-210/ATA 98), in (a) ventral and (b) lateral views; (c), fragmentary maxilla, MPZ 2005/437 (TE9B/K-29/Z: 620-630/ATA 02), in ventral view; (d), left lower incisor, MPZ 2005/374 (TE9C/K-31, L-31/Z: 1330-1340/ATA 03), in medial view; (e), incomplete left mandible, MPZ 2005/471 (TE9A/L-30/Z: 580-590/ATA 01), in dorsal view.

Fig. 3. Spécimens choisis de *Beremendia fissidens* de l'Unité rouge inférieure de Sima del Elefante: (a)–(b), incisive supérieure gauche, MPZ 2005/511 (TE14/Z: 190-210/ATA 98), en (a) vue ventrale et (b) vue latérale; (c), maxillaire supérieur fragmentaire, MPZ 2005/437 (TE9B/K-29/Z: 620-630/ATA 02), en vue ventrale; (d), incisive inférieure gauche, MPZ 2005/374 (TE9C/K-31, L-31/Z: 1330-1340/ATA 03), en vue médiale; (e), fragment de mâchoire inférieure gauche, MPZ 2005/471 (TE9A/L-30/Z: 580-590/ATA 01), en vue dorsale.

4.1.3. P4

The occlusal outline is nearly triangular owing to the strong posterior emargination of the crown. The parastyle is a high conical cusp at the anterobuccal tip of the crown. A weak cingulum runs from the parastyle to the paracone, progressively decreasing in width. A deep parastylar crest extends from the parastyle to the anterior face of the paracone. The paracone is the highest cusp and is placed somewhat anterior to the middle part of the crown and therefore closer to the parastyle than to the posterobuccal tip of the tooth. A sharp, high ridge runs from the paracone to the posterobuccal corner of the crown. The lingual part of the crown, including the protocone and the hypocone, is very low. The protocone is a small indistinct cusp placed on the anterolingual margin of the crown near the lingual base of the parastyle. A broad but shallow valley separates this cusp from the hypocone, which is much higher. A low ridge extends from the hypocone to the posterolingual corner of the crown, which is slightly elevated. The hypoconal flange is moderately broad (Fig. 3c).

4.1.4. M1

The occlusal outline is roughly a square with rounded corners and a concave posterior side due to the different degrees of emargination. The whole W-shaped ectoloph is a sharp, high ridge. The parastyle is poorly developed. The paracone is situated very near the anterior margin of the crown. The metacone is the highest cusp of the crown. The metastyle is a ridge-like elongate cusp, which protrudes posterobuccally beyond the level of the parastyle and mesostyle, so that the post-ectoflexus is larger than

the pre-ectoflexus. No cingulum is present on the buccal face of the crown. In the lingual part of the crown, the protocone is a distinct cusp, but generally lower than the ectoloph. From the protocone, a low ridge extends along the anterior margin of the crown to the lingual base of the paracone. Another ridge extends posteriorly, becoming indistinct at the central part of the crown. A broad, shallow valley separates this ridge from the hypocone, which is placed near to the middle of the lingual margin of the crown. The hypocone is much lower and less developed than the protocone. A low ridge runs from the hypocone to the posterolingual corner of the crown. This corner protrudes greatly posteriorly, so that the talon basin is much larger than the trigon basin. The PE-index is moderate (0.23) (Fig. 3c).

4.1.5. M2

The basic construction is the same as in M1, but there are a few differences: the parastyle is better developed than in M1, and protrudes buccally beyond the level of the mesostyle and the metastyle, whereas the metastyle is much less developed than in M1. Consequently, the occlusal outline of this tooth is sometimes slightly trapezoidal. The PE-index is also moderate (0.18) (Fig. 3c).

4.1.6. M3

This is b-shaped and notably reduced with respect to the first two molars. The buccal part of the crown has a single straight ridge. In the anteromedial part of the crown this ridge turns at a nearly perpendicular angle, reaching the posterior side. The lingual basin is

sometimes surrounded by a near-circular ridge, but in other cases this ridge is split up into several individual cusps.

4.1.7. *i1*

This robust and elongated tooth extends straight forward in dorsal view. The apical part is strongly upturned and sharply pointed. The dorsal edge is acuspluate. No cingulum is visible along the posterior margin of the crown. On the medial face of the crown, a narrow but conspicuous groove runs from the tip to the root-crown junction of the tooth. The surface of the groove is enamel-covered, and it is almost uniformly C-shaped in cross section [11]. The crown reaches below the posterior margin of p4 on the buccal face, and below the middle part of a1 on the lingual face (Figs. 3d and 4a).

4.1.8. *a1*

The occlusal outline is triangular. The crown has a single cusp anteriorly placed, 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 the lingual side and well developed on the buccal side (Figs. 3e and 4a–b).

4.1.9. *p4*

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 sharp, high ridge, which encloses a posterolingual basin on its lingual side. This basin is shallow and drains steeply posterolingually. A very thick cingulum is observed on the buccal base of the crown, where the crown hangs over the root. The cingulum on the lingual side is also well developed but weaker than the buccal one (Figs. 3e and 4a–b).

4.1.10. *m1-m2*

These have a trapezoidal shape in occlusal view and present five main cusps: the 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, forming the trigonid which is V-shaped. The paralophid is longer than the protolophid. Each crest has a notch at its middle part. The protoconid is the highest cusp of the crown, and is situated anterobuccally to the metaconid. From the hypoconid, the oblique crest descends anterolingually toward the protoconid,

and attaches to its posterior face forming the hypoflexid, which steeply descends buccally and reaches 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 an isolated conical cusp, which connects to the posterior base of the metaconid by a ridge known as the entoconid crest. The entoconid crest is short and moderately high. Generally, in m1 the talonid is more widely developed than the trigonid, and in m2 the trigonid is wider. The lingual cingulum is broad but hardly pronounced, and is almost missing below the metaconid. The buccal cingulum is well developed and sometimes slightly undulated (Figs. 3e and 4a–b).

4.1.11. *m3*

The occlusal outline is semicircular. The trigonid is smaller but basically similar to those of the first two molars. The talonid is markedly reduced, so that the talonid basin is much smaller and shallower than the trigonid basin. A ridge extends backwards from the posterior face of the protolophid (below the notch), and then curves lingually to form a small indistinct cusp at its lingual end. This cusplet adjoins the entoconid, which is also small. The entoconid crest is lacking, so that the talonid basin opens lingually between the entoconid and the metaconid. The cingulum on the buccal base of the crown is well developed and undulated, while that on the lingual base is weaker, and interrupted below the metaconid (Figs. 3e and 4a–b).

4.1.12. *Mandible*

For descriptive purposes, the mandible is generally divided up into two regions: the horizontal ramus or mandibular body that houses the teeth, and the ascending ramus, which has the coronoid process, the mandibular condyle and the angular process as its main components. The coronoid process and the articular condyle are usually preserved well in the fossil record, and are of great systematic value (Fig. 4a–f).

4.1.12.1. *Mandibular body.* This is stoutly built and attains its maximum height below the talonid of the first molar. The symphysis comprises upper and lower antero-posteriorly elongated ridges (to which the symphyseal cartilage would have been attached in the life of the animal [11]), and a broad fossa between them. Of the two ridges, the upper one is more prominent. The symphysis terminates below the posterior root of the first molar.

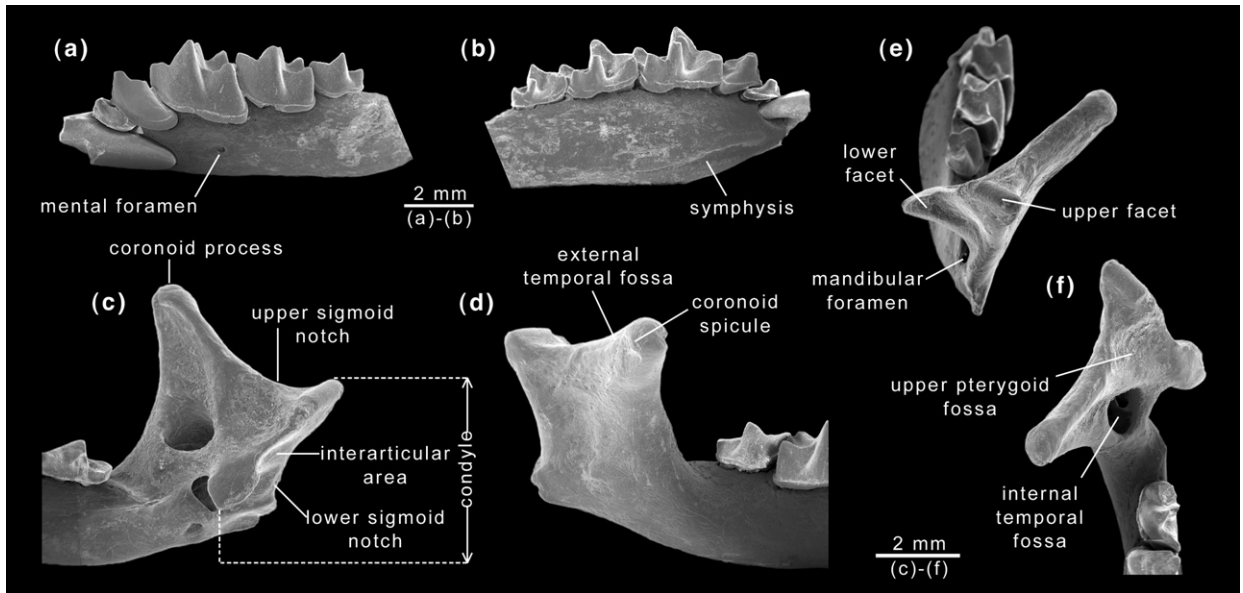


Fig. 4. Selected specimens of *Beremendia fissidens* from the Lower Red Unit of Sima del Elefante: (a)–(b), incomplete left mandible, MPZ 2005/471 (TE9A/L-30/Z: 580-590/ATA 01), in (a) lateral and (b) medial views; (c)–(f), right mandible, MPZ 2005/449 (TE9B/K-30/Z: 600-620/ATA 02), in (c) medial, (d) lateral, (e) posterior, and (f) dorsal views.

Fig. 4. Spécimens choisis de *Beremendia fissidens* à partir de l'Unité rouge inférieure de Sima del Elefante : (a)–(b), fragment de mâchoire inférieure gauche, MPZ 2005/471 (TE9A/L-30/Z: 580-590/ATA 01), en vue (a) latérale et (b) médiale ; (c)–(f), mâchoire inférieure droite, MPZ 2005/449 (TE9B/K-30/Z: 600-620/ATA 02), en (c) vue médiale, (d) latérale, (e) postérieure, et (f) dorsale.

4.1.12.2. Coronoid process. This is narrow, short and leans forward in lateral view. Both the anterior and the posterior margins are slightly concave, and the posterior is thicker than the anterior one. The tip is rounded. A low and almost indistinct coronoid spicule is present, and this is directed nearly vertically. The whole ascending ramus is broad anteroposteriorly, and leans markedly toward the lateral side.

4.1.12.3. Mandibular condyle. The upper facet is narrowly elliptic transversally. Its axis is set obliquely to that of the mandible in dorsal and posterior views. The interarticular area is very broad and diverges toward the lower facet. The lower part of the condyle with the lower facet on its ventral side is broad, protrudes strongly ventrolingually, and is placed far anteriorly of the lower sigmoid notch. Its anterior margin is placed on the same straight line as the posterior margin of the internal temporal fossa in lingual view. Due to its anterior position, the lower facet is invisible in buccal view. The upper sigmoid notch does not present ventral emargination, so that its posterior part is nearly horizontal in lateral view. The lower sigmoid notch forms a nearly straight line extending diagonally from the upper facet to the base of the angular process in lateral view.

4.1.12.4. Fossae. The symphyseal fossa opens only posteriorly, because the ridges that define it are confluent in the anterior side, enclosing a smooth basin with a large number of nutrient foramina. The resulting cavity formed by the union of the fossae in each half of the mandible would have been likely to contain large amounts of connective tissue in life, reinforcing the architecture of an already strongly built mandible itself [11]. The external temporal fossa is not clearly delineated. On the lateral side of the ascending ramus, below the external temporal fossa, a broad but shallow depression can be observed. The upper pterygoid fossa is a relatively large depression with a nearly circular outline on the dorso-medial face of the condyle. The internal temporal fossa is a low-positioned, large, and deeply pocketed depression with an oval outline in dorsal and lingual views.

4.1.12.5. Foramina. The mandibular foramen is very large and broadly elliptic. This foramen is connected to the internal temporal fossa inside the bony bridge, which separates them superficially, and also occasionally connects to another small foramen that is randomly present. The latter, when present, is anteroventrally placed with respect to the mandibular one. The mental foramen is

located below the hypoflexid or below the talonid of the first molar.

4.2. Morphometric analysis

The elements included in the analysis are exclusively dental, namely: P4, M1, m1 and m2; and the measurements used as variables were: BL, LL, PE and W for P4; BL, LL, PE, AW and PW for M1; L, TRW and TAW for m1 and m2.

We compared the Sima del Elefante sample with the southern and central European specimens *B. fissidens* and *B. minor* [61], as well as with the Asian *B. pohaiensis* [30]. The comparison was also with the two groups that prove to be most closely related to *B. fissidens* according to the phylogenetic analysis carried out by Rofes and Cuenca-Bescós [57]: *Lunanosorex lii* [31] and *Dolinasorex glyphodon* [57]. In every case, except for two mandibles of *B. pohaiensis* and the only one of *Lunanosorex*, as well as the TE specimens, we took the average values of the measurements published for the various specimens (see legend of Figs. 5a and b).

Fig. 5a shows the results of the principal components analysis (PCA) carried out with the dimensions of the upper teeth (Table 1a). The distributions of the specimens from Sima del Elefante, of *B. fissidens* from various European sites and the only specimen of *B. pohaiensis* are clearly grouped on PC1. On PC2, however, TE shows a tendency towards somewhat greater dimensions. The 95% confidence ellipses of TE and the European *B. fissidens* clearly overlap, although the overlap is above all with the smaller-sized TE specimens. *B. minor* falls just outside the 95% confidence ellipse of the European *B. fissidens*, whereas *Dolinasorex* falls within it. A study of the different weights of the PC1 variables reveals the uniform contribution of the chosen measurements to the general variability, whereas PC2 reflects the greater contribution of the variables LLP4 and PEP4 (Appendix 1a).

In the PCA carried out with the lower teeth (Table 1b, Fig. 5b), the overlap between the distributions of Sima del Elefante, *B. fissidens* and *B. pohaiensis* is more marked than in the previous case, as is that of the 95% confidence ellipses of TE and the European *B. fissidens*, both on PC1 and on PC2. The distributions of *B. minor* and the specimen of *Lunanosorex* fall outside the 95% confidence ellipses of TE and *B. fissidens*. *Dolinasorex*, however, falls within the 95% confidence ellipse of the European *B. fissidens*. The observed contribution to the general variability is uniform for the measurements included in PC1, but falls significantly more upon the m2 measurements in PC2 (Appendix 1b). We can see,

therefore, that the results of the PCA are consistent with the assignment of the TE specimens to the species *B. fissidens*.

4.3. Discussion

According to the most recent classification of soricids proposed by Reumer [53], the genus that is closest to *Beremendia* is *Lunanosorex*, a monospecific group (i.e. *L. lii*) of which the only remains found to date come from Yinan, a site located in the province of Shandong in northern China [31,67]. In comparison to *Beremendia*, *Lunanosorex* differs in having a longer and broader coronoid process whose apical part protrudes strongly anteriorly, a stronger coronoid spicule, a deeply excavated external temporal fossa, a much weaker upper pterygoid fossa, and a slight ventral emargination of the upper sigmoid notch [31].

A recent tentative phylogeny for the soricines [57], however, groups *Lunanosorex* with the new Iberian genus *Dolinasorex*, and both of these in turn with *Beremendia*. The differences between *Dolinasorex* and *Beremendia* are rather greater, for the former exhibits a well-developed hypocone in P4, M1 that is smaller in *Beremendia*; the posterior emargination of M1 and M2 is weaker in *Dolinasorex*; the lingual cingulum of a1 and p4 is scarcely pronounced in *Dolinasorex* but broad in *Beremendia*; the entoconid crest is absent in *Dolinasorex*'s m1; the coronoid process is long, broad, robust, not leaning forward, and with a large and strongly pronounced coronoid spicule in *Dolinasorex*, contrasting with the more slender, markedly leaning forward process, and very weak spicule of *Beremendia*; the external temporal fossa is deeply excavated in *Dolinasorex* but inconspicuous in *Beremendia* [57]. The Sima del Elefante specimens clearly differ from *Lunanosorex* and *Dolinasorex*, instead fitting perfectly with the description made by Kormos [33] and Jin and Kawamura [30]: they are therefore undoubtedly allocated to *Beremendia*. Morphometric data strongly support this assumption (see Figs. 5a and b).

Reumer [52] established Beremendiini as an initially monogeneric tribe, subsequently also including within it *Lunanosorex* and *Peisorex* [35], as well as *Beremendia* itself [53]. However, the validity of *Peisorex* was called into question by Jin and Kawamura [30], who did not find significant morphological differences between this genus from northern China and *Beremendia*. Accordingly, in their opinion the species *P. pohaiensis* would become *Beremendia*. Although Storch et al. [67] disagree with this reallocation; we follow Jin and Kawamura [30], both in this respect and in their

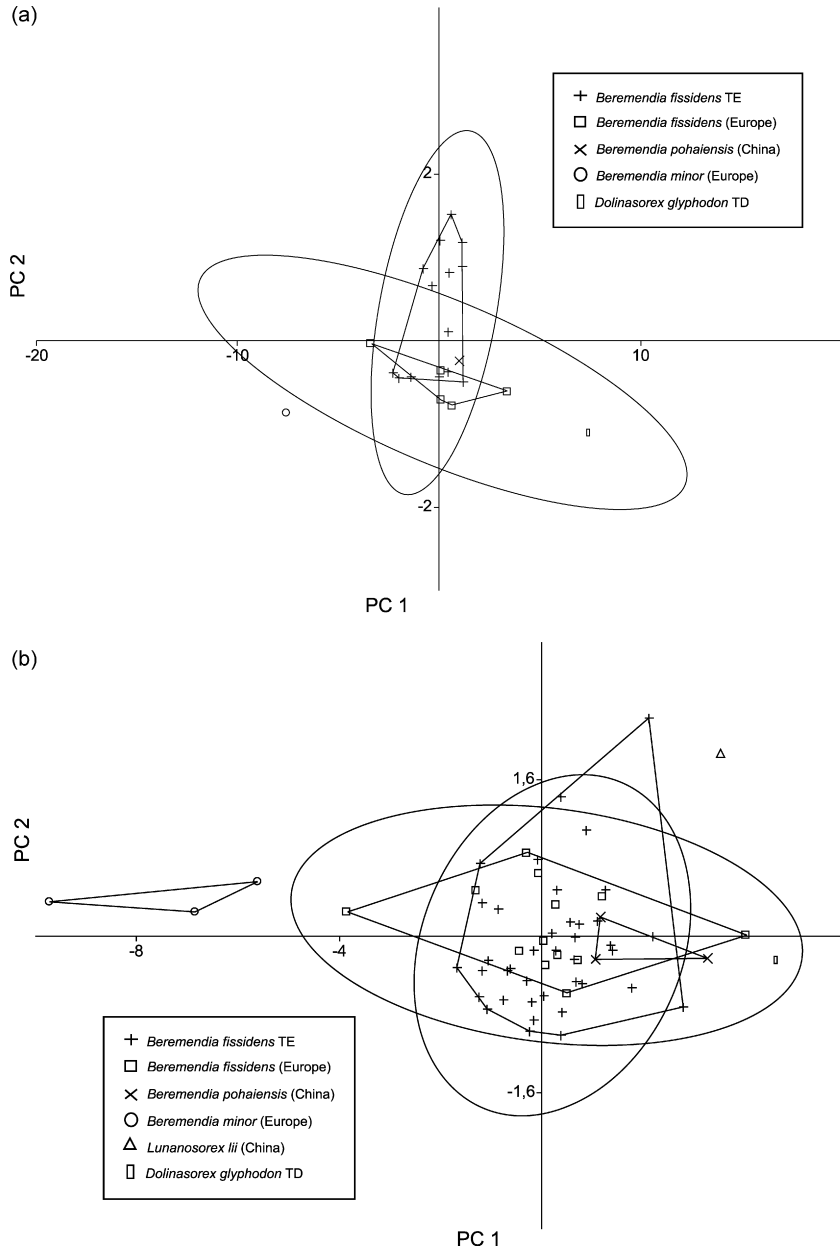


Fig. 5. Principal component analysis (PCA) showing plots of components 1 against 2. (a), PCA of the upper dentition; measurements other than those of *Beremendia fissidens* taken from Reumer [52], Jin and Kawamura [30], Koufos et al. [34], and Rofes and Cuenca-Bescós [57]. (b), PCA of the lower dentition; measurements other than those of *B. fissidens* taken from the same sources as the upper one plus Kowalski and Li [35], Rzebiak-Kowalska [61,63], Malez and Rabeder [41], Flynn and Wu [20], Jin and Kawamura [31], Reumer and Hordijk [54], and Marchetti, Parolin and Sala [42]. **Convex hulls**, distribution; **Ellipses**, 95% confidence; **TE**, Sima del Elefante; **TD**, Gran Dolina. Details can be found in Appendices 1a and 1b.

Fig. 5. Analyse en composantes principales (ACP), des composantes principales 1 en regard des composantes principales 2. (a), ACP de la dentition supérieure ; mesures autres que celles de *Beremendia fissidens* sont extraites de Reumer [52], Jin et Kawamura [30], Koufos et al. [34], et de Rofes et Cuenca-Bescós [57]. (b), ACP de la dentition inférieure ; mesures autres que celles de *B. fissidens* extraites des mêmes sources et en outre, de Kowalski et Li [35], Rzebiak-Kowalska [61,63], Malez et Rabeder [41], Flynn et Wu [20], Jin et Kawamura [31], Reumer et Hordijk [54], et Marchetti, Parolin et Sala [42]. **Convex hulls**, distribution ; **Ellipses**, confiance de 95 % ; **TE**, Sima del Elefante ; **TD**, Gran Dolina. Des détails peuvent être trouvés dans les annexes 1a et 1b.

proposal to put the species *Peisorex pliocaenicus* [20] in synonymy with *B. pohaiensis*. On a suprageneric level, however, the tribe Beremendiini proves to be paraphyletic [57], at least as it is currently defined.

In Europe three species of *Beremendia* have been described up to now: *B. fissidens*, *B. minor* and *B. ucrainica*. From this continent come the oldest specimens of the group [62]. The species *B. ucrainica* was put in synonymy with *B. fissidens* by Rzebik-Kowalska [61].

In Asia, as well as *B. fissidens* and *B. minor*, which are much less represented than in Europe, two other species have been described: *B. pohaiensis*, as mentioned above, and *B. sinensis* [36], both in China. This latter was originally described as *Neomys sinensis* [71] and then reassigned to *Beremendia* by Kretzoi [36]. Kowalski and Li [35] consider that it belongs neither to *Neomys* nor *Beremendia* and as such should be treated as a separate genus. Jin and Kawamura [30] agree with this latter point of view, as we do. Storch et al. [67], by contrast, regard the species as still valid.

Which of the valid species of *Beremendia* would the Sima del Elefante specimens thus belong to? In general terms, *B. pohaiensis* is very similar to *B. fissidens* in the morphology of the cranium, the mandible and the dentition. Jin and Kawamura [30], however, regard the following differences as important: in *B. fissidens*, the external naris is more slender, the depression behind the first upper incisor terminates more posteriorly on the lateral wall of the rostrum, the fourth upper antemolar is always present, the buccal cingula of the lower molars are generally thicker and less undulated, and the mandibular foramen is more variable in size. It is impossible to evaluate the first two characters in the TE sample, owing to the fragmentary state of the crania in general. The third difference, by contrast, proves crucial, since in *B. pohaiensis* the A4 is completely absent. Although no A4 has been recovered from among the TE specimens, the alveolus of this tooth is present in every case, which would constitute evidence enough to rule out the Asian species.

As was established by Rzebik-Kowalska [61], the morphology of *B. minor* is identical to that of *B. fissidens*, apart only from the fact that *B. minor* is significantly smaller in size. Bearing this in mind, the morphometric analysis of the dentition that we carried out (see above) would clearly exclude *B. minor*. Without any doubt, indeed, both from a morphological and a morphometrical point of view, the specimens from Sima del Elefante would correspond to the species *B. fissidens*. A detailed examination of the measurements of the TE specimens, in comparison with those published for other sites (see

the averages in Table 1a and Table 1b), shows certain particularities with respect to other populations from central and southern Europe, in particular the reduced mandibular body, reduced upper and lower incisors, and lower antemolars/premolars that are flattened mesiodistally.

The obvious compression of the TE mandibles affected the total length of the molar series, which falls below the average for the other European *B. fissidens*, even though the individual size of each tooth keeps within the standard values (Table 1b). This means that the molars have been “compressed” against one another to occupy less room. The flattening of the lower antemolars and premolars would have the same origin. Unfortunately, the fragmentary state of the crania does not allow us to establish whether the small size of the upper incisors is also related to a compression of the maxillae.

In general terms, it seems that *B. fissidens* was morphologically conservative throughout its period of existence, both structurally and in size. However, it has been shown that the *B. fissidens* from Poland grew slightly larger in the course of time, and the opposite tendency was recorded in the specimens from Romania [61,63]. These slight variations in size may be due to particular environmental conditions in each place. A similar explanation could be claimed for the *B. fissidens* from Sima del Elefante, the reduction of whose mandible size may be related to some kind of environmental and/or geographical constraints.

5. Palaeoecological considerations

On the basis of a comparison between diverse fossil associations, Reumer [52] proposed that *B. fissidens* was an ecological opportunist, a ubiquitous species which apparently did not have narrow preferences. Nonetheless, the high metabolic rate of the soricids in general and of the red-toothed shrews in particular [7] would have made the consumption of vast quantities of food essential for these enormous shrews (i.e. with a body mass of 40–45 g [11]), whose development would not have been feasible but for a favourable ecological environment. We consider, therefore, that the abundance of *Beremendia* in the Lower Pleistocene levels of Sima del Elefante (TE8 to TE14) was linked with a temperate, humid and relatively stable climate, which is in accordance with the panorama inferred on the basis of previous studies of faunal associations [10,22,56,58,59].

A tentative palaeoenvironmental reconstruction of the TE-LRU, based on the distribution of insectivores throughout the stratigraphic sequence [10], reflects a succession of three phases: warm–cold–warm (w–c–w),

correlated with the Waalian pollen episode of northern-central Europe [70], the only one that contains the same phases w–c–w, and the chronology of which (1.25–1.5 Myr) concurs with the period of inverse magnetic polarity prior to the positive Jaramillo Subchron pinpointed for this period [5].

The best modern candidate for an actualistic approach to *Beremendia* could be the North American short-tailed shrew *Blarina brevicauda*, which is the typical opportunist: it lives in forests, grasslands, marshes and brushy areas and is not restricted to any habitat [4]. This moderately large species of soricine also possesses another singular characteristic: its saliva is one of the most toxic forms described for any mammal to date [32], even though it does not have such a specialized injection mechanism (i.e. grooved lower incisors) as the Caribbean solenodon, a very close relative of the shrew [17]. A recent study [11] shows that *B. fissidens* not only possessed incisors with a medial channel in the manner of the solenodons, but also a buccal architecture specially designed to increase the power of its bite upon possible prey.

The typical diet of soricids includes insects, worms, molluscs and other invertebrates [7]. However, the venomous saliva of *B. brevicauda* (and a few other shrew species) enables the animal to deal with relatively large prey, which is immobilized by the fluid, thereby reducing its struggling [14]. This also enables *Blarina* to store food that is living but comatose, paralyzed by the toxin [17]. We assume similar behaviour in *Beremendia*. It is possible that the great size reached by *B. fissidens* was an adaptation to the hunting and handling of increasingly large prey (e.g. fish, amphibians, reptiles, small birds and mammals, including other shrews). The need to immobilize such prey would have led to the selection and subsequent development of a sophisticated mechanism, the first of its kind among soricids, for injecting them with venomous saliva in a quick and efficient way, details of which are laid out in Cuenca-Bescós and Rofes [11].

6. Palaeobiogeographical and biostratigraphic considerations

Beremendia is a Plio-Pleistocene genus with a broad European distribution and a moderate presence in the Asiatic continent [62,67]. Following the biogeographical approach of Jin and Kawamura [30], we can construct a scenario in which *Beremendia* first appeared in the Early Pliocene of Europe and then expanded eastward to East Asia by the Middle Pliocene, becoming extinct there by the end of the Early Pleistocene while pur-

portedly surviving until the early Middle Pleistocene in Europe.

The oldest records of *B. fissidens*, in particular, come from Hungary and Poland in Europe (MN 14 [62]) and from West Siberia in Asia (MN 15 [67]). In Europe, remains of the species have been recovered from more than a 100 sites, distributed over 17 countries, including Russia, the Ukraine, Hungary, Romania, Bulgaria, Poland, Germany, the Netherlands, Slovakia, Croatia, the Czech Republic, Switzerland, Austria, France, Greece, Italy, Spain and the United Kingdom [6,34,54,62,63], and covering a time period that ranges from the Early Pliocene to the beginnings of the Middle Pleistocene. However, the remains of *B. fissidens* from this latter time are very scarce and restricted to just a few specimens from Hungary, Romania, France and the United Kingdom [62]. As it will be shown below, the reliability of said references should be reconsidered at the light of new challenging discoveries [57].

In Asia there are remains of *B. fissidens* in western Siberia and Mongolia dating from the middle to the end of the Pliocene (i.e. MN 15–17 [67]), with the sole exception of the fragmentary mandible described as “*Nectogalinia altaica*” by Gureev [25] and recognized as *B. fissidens* by Storch et al. [67], which comes from an Early Pleistocene site (i.e. Razdolye in western Siberia).

B. minor, whose presence is restricted to the Pliocene, was a species with a very limited distribution both in Europe and in Asia [62,67], while *B. pohaiensis* was an endemic species that inhabited the North of China during the Early Pleistocene [30]. It is possible that both species derived from *B. fissidens*, albeit in distinct circumstances and contexts: following a sympatric speciation model in the centre of Europe in the case of *B. minor*, and possibly an allopatric model in the case of *B. pohaiensis*, due to the geographical isolation of populations in the Far East of Asia. Another possibility, pointed out by Rofes and Cuenca-Bescós [57], is that the difference in size between *B. fissidens* and *B. minor*, groups that are otherwise identical [61], is a reflection not of specific diversity but merely sexual dimorphism.

In the Iberian Peninsular all the specimens of *Beremendia* found to date correspond to the species *B. fissidens* and all the references are from the Late Pliocene. We thus have Valdeganga 2 in Albacete (MN 16 [44]), Orrios 3 and Barranco del Monte 1 in Teruel (MN 16 [1,37]) and Almenara-Casablanca 1 in Castellón (MN 17 [21]). As *Beremendia* sp. it is cited by De Bruijn [15] in Moreda (Granada, MN 16).

There is also a series of references for the Early Pleistocene [2,9,12,18,23,24,40,65], all of which refer with-

out exception to specimens identified as *B. fissidens* in levels TD4–6 of Gran Dolina, the site adjacent to Sima del Elefante in the Sierra de Atapuerca. However, Rofes and Cuenca-Bescós [57] have demonstrated that this material in fact corresponds to *Dolinasorex glyphodon*, a new species of larger soricine with certain features similar to *B. fissidens*, but phylogenetically closer to Asiatic forms (i.e. *Luanosorex lii*). If we take into consideration the previous ignorance on this new *Beremendia*-like species, potential misidentifications throughout Europe included, together with some degree of stratigraphic uncertainty, particularly in the Middle Pleistocene records of the species (e.g. Kozi Grzbiet and Betfia [61,63]), we cannot be sure if *B. fissidens* really made it beyond the Early Pleistocene.

The Sima del Elefante specimens constitute by far the most recent population of *B. fissidens* recorded in the Iberian Peninsula to date, and the only one from after the Pliocene in this geographical area, which, on account of its particular environmental features, played the role of a “last redoubt” for a significant number of species in addition to the one that concerns us here. Examples of this from the group of insectivores include *Asoriculus gibberodon*, *Crocidura kornfeldi*, *Dolinasorex glyphodon*, *Galemys kormosi* and *Erinaceus praeglacialis* [21,56,57].

7. Conclusions

The 171 specimens analysed from the Lower Red Unit (levels TE8–TE14) of the Sima del Elefante site would correspond, without any doubt, both from a morphological and a morphometric point of view, to the species *Beremendia fissidens*. It constitutes by far the most recent population of *B. fissidens* recorded in the Iberian Peninsula to date, and the only one from the sec-

ond third of the Early Pleistocene in this geographical area. Slight variations in size, in comparison to other populations from central and southern Europe, may be due to particular environmental conditions in the Iberian Peninsula. The abundance of *Beremendia* in the Lower Pleistocene levels of Sima del Elefante was undoubtedly linked with a temperate, humid and relatively stable climate, which is in accordance with the panorama inferred on the basis of previous studies of faunal associations.

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Appendix A. Results of the PCA performed with the measurements of the upper dentition. Jolliffe cut-off: 0.7.

(See Table 1.A).

Table 1.A

	PC1	PC2	PC3	PC4	PC5	PC6
Eigenvalue	7.315	0.599	0.372	0.300	0.179	0.098
% variance	81.279	6.655	4.137	3.329	1.988	1.093
Loadings						
BL P4	0.329	−0.213	0.413	−0.350	0.642	−0.131
LL P4	0.335	−0.441	−0.125	0.317	−0.165	0.411
PE P4	0.324	−0.452	−0.375	0.316	0.023	−0.433
W P4	0.329	0.376	0.150	0.479	0.234	−0.004
BL M1	0.338	−0.332	0.353	−0.260	−0.235	0.282
LL M1	0.335	0.289	−0.379	−0.380	−0.105	0.453
PE M1	0.337	0.164	−0.501	−0.345	0.130	−0.310
AW M1	0.336	0.386	0.113	0.330	0.133	0.179
PW M1	0.337	0.210	0.345	−0.091	−0.636	−0.462

Appendix B. Results of the PCA performed with the measurements of the lower dentition. Jolliffe cut-off: 0.7.

(See Table 1.B).

Table 1.B

	PC1	PC2	PC3	PC4	PC5	PC6
Eigenvalue	5.064	0.408	0.246	0.138	0.090	0.054
% variance	84.4	6.797	4.106	2.302	1.503	0.892
Loadings						
L m1	0.404	−0.501	0.099	−0.566	0.499	0.081
TRW m1	0.415	0.231	−0.582	−0.086	0.018	−0.655
TAW m1	0.425	0.085	−0.404	−0.133	−0.437	0.664
L m2	0.396	−0.599	0.228	0.441	−0.429	−0.233
TRW m2	0.419	0.257	0.063	0.615	0.567	0.234
TAW m2	0.390	0.514	0.658	−0.285	−0.234	−0.125

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