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Changes in the geographical distribution of *Microtus* (*Iberomys*) *cabrerae* (Thomas, 1906) from the Late Pleistocene to the Holocene

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ABSTRACT

Cabrera's vole, *Microtus* (*Iberomys*) *cabrerae*, is a currently endemic species restricted to Spain and Portugal. Its present-day distribution is fragmentary, but in the past it was broadly distributed across the Iberian Peninsula, with the exception of the northern part of the Peninsula. Various hypotheses have been expounded to explain the retraction of the species since the beginning of the Holocene: 1) the climate changes produced in the Bronze Age; 2) the human impact on the restricted habitat of the species; and 3) its direct competition with other species with similar environmental requirements, such as the southern water vole (*Arvicola sapidus*), an Iberian endemism. In this paper, we discuss these hypotheses regarding the distribution of the species fossil record in the Late Pleistocene and beginning of the Holocene, as well as its current distribution. The most plausible hypothesis for its retraction is human impact, which has destroyed the habitat of the species with the development of agriculture and road infrastructures and the increasing human population.

Keywords: *Microtus (Iberomys) cabrerae*, distribution changes, climate, human impact, competition with other species.

RESUMEN

El topillo de Cabrera, *Microtus (Iberomys) cabrerae*, es una especie actual endémica restringida a España y Portugal. Su distribución actual es fragmentaria, pero en el pasado estuvo ampliamente extendida a lo largo de la Península Ibérica, con la excepción de parte del norte peninsular. Varias hipótesis han sido formuladas para explicar la retracción de la especie desde inicios del Holoceno: 1) los cambios climáticos producidos en la Edad del Bronce; 2) el impacto humano en el hábitat restringido de la especie; y 3) la competencia directa con otras especies de requerimientos ambientales similares, como la rata de agua (*Arvicola sapidus*), un endemismo Ibérico. En este artículo se discuten estas hipótesis teniendo en cuenta la distribución del registro fósil de la especie durante el Pleistoceno superior e inicios del Holoceno, así como su distribución actual. La hipótesis más plausible para la retracción de la especie es el impacto humano, que ha destruido progresivamente el hábitat de la especie con el desarrollo de la agricultura, las infraestructuras viarias y el incremento de la población humana.

Palabras clave: *Microtus (Iberomys) cabrerae*, cambios en la distribución, clima, impacto humano, competencia con otras especies.

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1. INTRODUCTION

Microtus cabrerae (Cabrera's vole) is an endemic arvicoline restricted to the Iberian Peninsula. This vole was first described by Thomas (1906) on the basis of a specimen from the Sierra de Guadarrama (Madrid). Subsequently, Miller (1910) described the species *Microtus dentatus* on the basis of a specimen very similar to that described by Thomas (1906) as *Microtus cabrerae*. Cabrera (1914) continued to maintain the validity of the two species, whereas Niethammer *et al*. (1964) regarded *M. cabrerae* as a differentiated species and populations previously assigned to *M. dentatus* as a doubtful subspecies. Both studies of population genetic differentiation (Cabrera-Millet *et al*., 1982) and morphological studies (Ayarzagüena & López-Martínez, 1976; Ventura *et al.,* 1997) show the homogeneity of *M. cabrerae* populations and suggest that there are no reasons for a specific differentiation of *M. dentatus*. From an evolutionary point of view, *M. cabrerae* has been associated with the Middle Pleistocene fossil species *M. brecciensis*, and both species are included by Chaline (1972) in the subgenus *Iberomys*. Cabrera-Millet *et al*. (1983) considered the subgenus to be made up exclusively of *M.* (*I.*) *brecciensis* and *M.* (*I.*) *cabrerae*, which would constitute an endemic Ibero-Occitan line with more robust forms adapted to Mediterranean conditions and whose evolution would have taken place only in the Iberian Peninsula and southern France. It is possible to observe a closer relationship between these two species that suggests a linear evolution from one species to the other in the small time interval corresponding to the Late Pleistocene. On the other hand, the Cabrera vole currently shows a relict distribution, given the existence of subfossil sites outside its current range (Fig. 1). Several hypotheses have been put forward to explain the retraction of the *M.* (*I.*) *cabrerae* distribution area: 1) Cabrera-Millet *et al*. (1983) suggested that the retraction of the species took place in the Bronze Age and was provoked mainly by climatic factors; 2) another possible explanation for the retraction is the human impact on the landscape caused by agricultural development, which, as suggested by Férnandez-Salvador (1998) and Landete-Castillejos *et al*. (2000), would have caused the degradation of the species habitat; 3) another possible cause of the retraction of *M.* (*I.*) *cabrerae* is competition with other species, more specifically its direct competition with *Arvicola sapidus* (the southern water vole), which might have used very similar habitats to those used by the Cabrera vole (Pita *et al*., 2006).

Taking into account this background, the principal aim of this paper is to discuss the different hypotheses for the changes in distribution of the species *M.* (*I.*) *cabrerae* from the Late Pleistocene and beginning of the Holocene to the present and to try to ascertain which of these hypotheses is most tenable.

2. MATERIAL AND METHODS

In order to discuss the geographical changes undergone by *M.* (*I.) cabrerae* we used the current distribution of the species taken from Shenbrot & Krasnov (2005) (Fig. 1), together with data from previously published archaeo-palaeontological sites of the Late Pleistocene and beginning of the Holocene where *M.* (*I.*) *cabrerae* occurs (Table 1; Fig. 1). The nomenclature used in the descriptions of the *M.* (*I.) cabrerae* teeth (first lower molars only) is that of van der Meulen (1973) (Fig. 2).

A description of the species *M.* (*I.) cabrerae* is not the objective of this paper, but we consider it is important to point out the main morphological features of the teeth that allow the species to be identified, as well as to highlight the geographical and stratigraphical distribution of the species. The lineage of the subgenus *Iberomys* has only one present-day representative, *M.* (*I.*) *cabrerae*. The first citations of the species stem from the beginnings of the Late Pleistocene, around 90 ka (López- García *et al*., 2008; Arsuaga *et al*., 2010). *M.* (*I.*) *cabrerae* descended from *Microtus* (*I.*) *brecciensis*, which is represented in the Middle Pleistocene of the Iberian Peninsula at various sites, such as Galeria, Gran Dolina (TD10) and Sima del Elefante (TE18-19) in Atapuerca, province of Burgos (Cuenca-Bescós *et al*., 1999, 2010b; López-García *et al*., 2011a), Ambrona in Soria (Sesé & Soto, 2005), Bolomor in Valencia (Guillem-Calatayud, 2001), Valdocarros in Madrid (Sesé *et al*., 2011) and Mollet in Girona (Maroto *et al*., 2012). According to Ayarzagüena & López-Martínez (1976), the species *M.* (*I.*) *cabrerae* is characterized in general by having a large, wide m1; reduction of the triangles of the anteroconid complex (ACC); a long, narrow fifth lingual salient angle (LSA5), which according to Cuenca-Bescós *et al*. (1995) is a measure of its lateromedial asymmetry; a fourth buccal salient angle (BSA4) that is triangular-quadrangular in shape; and enamel that covers virtually all the labial wall of the ACC (Figs 2-3).

M. (*I.*) *cabrerae* is endemic to the Iberian Peninsula. Its current distribution is fragmentary, occupying various main nuclei in the foothills of the Pyrenees, the southern Iberian System, the Betic Sierras, and the Central System. The species is also present in the southern half of Portugal (Fig. 1). It inhabits exclusively Mediterranean areas. The species requires grassy cover all year round, with a high water table. Its altitudinal range is from 250 to 1500 m. The species is broadly distributed in the Late Pleistocene and at the beginning of the Holocene of the Iberian Peninsula (Fig. 1), with the exception of the northern part of the Peninsula (López-García, 2011).

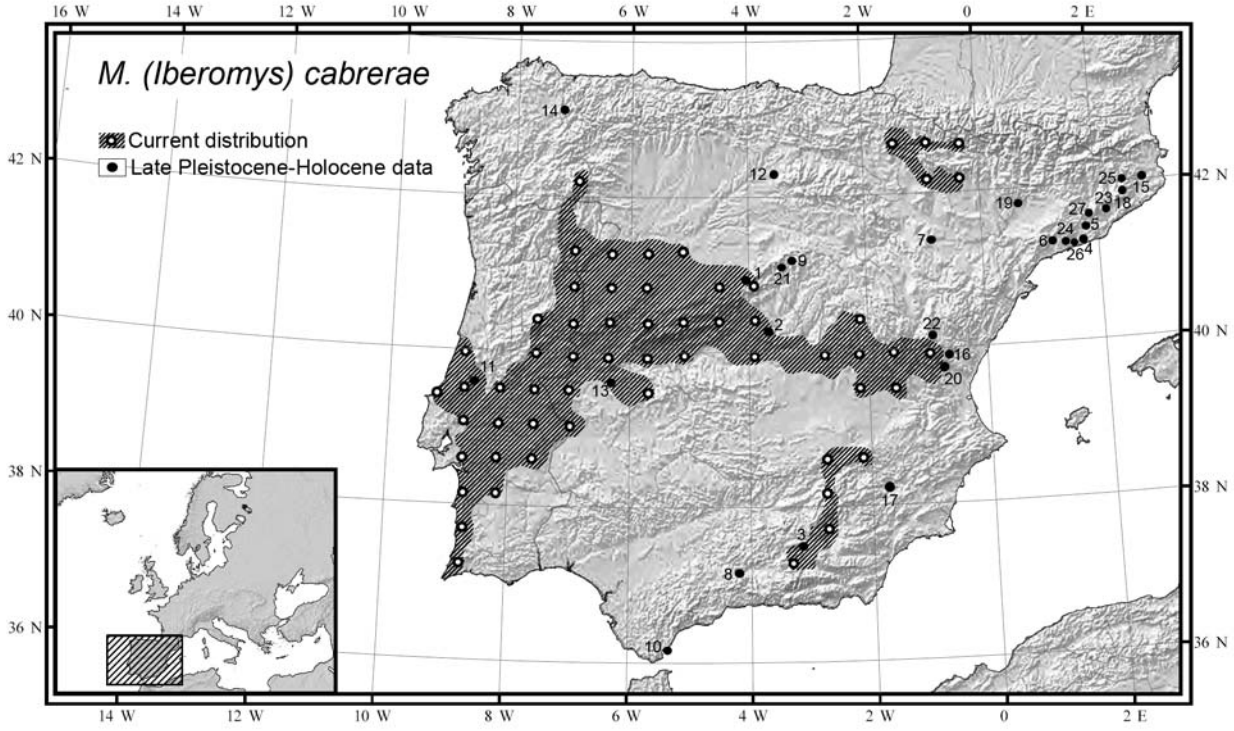

Figure 1. Current and Late Pleistocene-Holocene distribution of *Microtus* (*Iberomys*) *cabrerae*. **1.** Camino; **2.** HAT; **3.** C. Horá; **4.** C. Gegant; **5.** A. Romaní; **6.** Xaragalls; **7.** Aguilón; **8.** Zafarraya; **9.** Zarzamora; **10.** Gorham's; **11.** Caldeirao; **12.** El Portalón; **13.** Chimeneas; **14.**Valdavara-1; **15.** l'Arbreda; **16.** Cendres; **17.** Baños de Mula; **18.** Cingle Vermell; **19.** C. Colomera; **20.** La Sarsa; **21.** La Ventana; **22.** Bolumini; **23.** El Frare; **24.** Cova Foradada; **25.** Cova 120; **26.** Alorda Park; **27.** Coves del Toll (Teixoneres and Toll caves).

3. RESULTS AND DISCUSSION

As noted above, the species *M*. (*I.*) *cabrerae* is broadly distributed in the Late Pleistocene and beginning of the Holocene outside its current distribution range (Fig. 1). The species has been recovered from several sites in Catalonia from the Late Pleistocene to the beginning of the Holocene, and in southeastern, south, central and northwestern Iberia during the Late Pleistocene (Fig. 1; Table 1). In this section we discuss the possible causes that have led to these changes in geographical distribution.

3.1. Climatic factors

One of the first hypotheses postulated by Cabrera-Millet *et al*. (1983) is that the retraction of the species to form its current geographical distribution took place in the Bronze Age and was caused mainly by climatic factors. Six rapid-cooling climatic fluctuations during the Holocene have been detected, principally associated with orbital variations and solar variability (Mayewski *et al*., 2004). One of these fluctuations, occurring between 6,000-5,000 yr BP, coincided in the Northern Hemisphere with the beginning of the Bronze Age (ca. 5,000 yr BP). The Cabrera vole is typically from Mesomediterranean bioclimatic zones in Iberia (Rivas-Martínez, 1981) and is a habitat specialist with very demanding ecological requirements, the most important of which concerns humidity (Pita *et al*., 2006). Despite its strict ecological requirements, *M.* (*I.) cabrerae* survived the extremely cold climatic conditions of the Late Pleistocene (Last Glacial Maximum), during which it is represented at some sites within its current geographical range, such as Chimeneas (Extremadura) (Bañuls *et al*., 2012), and at some sites outside its present range, such as El Portalón (Burgos), Valdavara-1 (Lugo) (López-García *et al*., 2010a, 2011b) and Cova del Toll level 3 (Fernández-García & López-García, 2012). Furthermore, taking into account the subfossil data, the species *M*. (*I.*) *cabrerae* persists outside its current geographical range through to the cold interval of the Bronze Age (6,000-5,000 yr BP) and is represented at the Iron Age site of Alorda Park (Catalonia). It seems to disappear from this region in the course of the 20th century (Valenzuela *et al*., 2009) (Fig. 1; Table 1).

Table 1. Chronology and position of the principal sites with presence of *Microtus* (*Iberomys*) *cabrerae*.

Series	Cultural Age	Ka BP	Sites	Layers	Authors
Holocene	Iron Age	2.1	Alorda Park		Valenzuela *et al*., 2009
	Bronze Age	3.1	Cova 120	II-I	Alcalde, 1986
		3.9-3.4	Colomera	EE1-Asup	López-García *et al*., 2010b
		4.4-3.9	El Frare	4-3	Alcalde, 1986
		4.4	Valdavara-1	UU	López-García *et al*., 2011b
		4.7	Cendres	III-I	Guillem-Calatayud, 1999
			C. Foradada		Allué *et al*., 2012
	Neolithic	6.3-5.8	El Frare	6-5	Alcalde, 1986
		7.5-6	Cendres	VII-IV	Guillem-Calatayud, 1999
			Bolumini	V-IV	Guillem-Calatayud, 1999
			La Ventana		Sánchez *et al*., 2005
		6.9	La Sarsa		Sevilla, 1988
		7	Colomera	CE13-14/12	López-García *et al*., 2010b
Late Pleistocene		9.7	Cingle Vermell		Alcalde, 1986
		9.7-13	Toll	2	Fernández-García & López-García 2012
			Baños de Mula		Agustí *et al*., 1990
			Cendres	XIIb-IX	Guillem-Calatayud 1999
			L'Arbreda	A	Alcalde, 1986
		15-13	Valdavara-1	LU	López-García *et al*., 2011b
		18-10	Gorham's	III	López-García *et al*., 2011c
		18	Chimeneas	A	Bañuls *et al*., 2012
		30-16	Portalón	P16-P1	López-García *et al*., 2010a
		30-18	Caldeirao	K-Eb	Povoas *et al*., 1992
		33-23	Gorham's	IV	López-García *et al*., 2011c
		33	Zarzamora	1-3	Sala *et al*., 2011
		35-13	Toll	3	Fernández-García & López-García 2012
			Zafarraya		Barroso Ruiz *et al*., 2003
		41	Aguilón		Cuenca-Bescós *et al*., 2010a
		45-48	Xaragalls	C6-C4	López-Garcia *et al*., 2012b
		58-44	A. Romaní	D-O	López-García & Cuenca-Bescós 2010
		60-50	C. Gegant	III-V	López-García *et al*., 2012a
			Horá	XVIII-XII	García 1979
		74	HAT		Sesé *et al*., 2011
		90-60	Teixoneres	III	López-García *et al*., 2012c
		98.8	Camino	5	Arsuaga *et al*., 2010

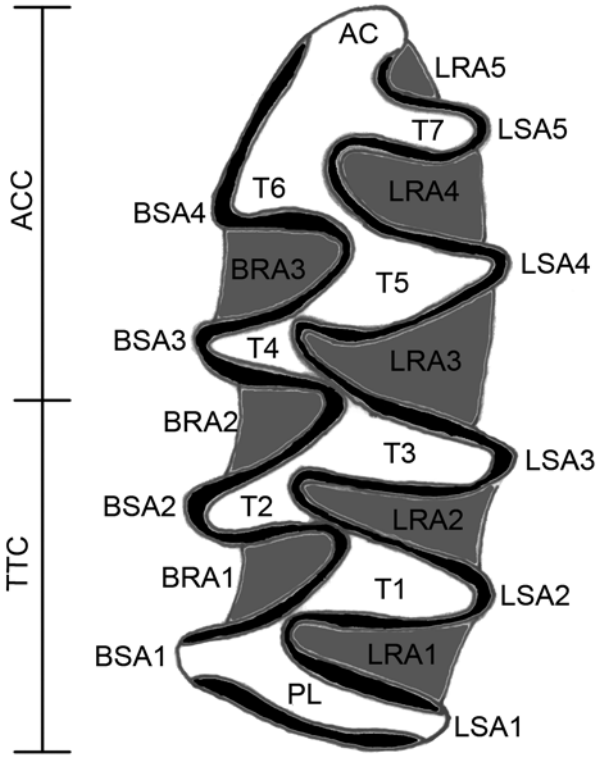

Figure 2. Nomenclature for the first lower molars (taken from van der Meulen 1973) in the description of *Microtus* (*Iberomys*) *cabrerae*. **ACC**, anteroconid complex; **AC**, anterior cap; **BRA**, buccal re-entrant angle; **BSA**, buccal salient angle; **LRA**, lingual re-entrant angle; **LSA**, lingual salient angle; **PL**, posterior lobe; **TTC**, trigonid-talonid complex, **T1-T7**, triangles.

3.2 Human impact

As noted above, *M.* (*I.*) *cabrerae* is an endemic habitat specialist with very demanding ecological requirements; it requires a type of vegetation that remains green all year round (within Mediterranean conditions) and is sufficiently tall enough to provide effective protection against predators. These environmental requirements lead the Cabrera vole to establish its colonies in biotopes characterized by well-developed soils with a high degree of humidity and located mainly on plain zones. These biotopes are at the same time sites that are potentially suitable for agriculture (Fernández-Salvador, 1998). As suggested by Landete-Castillejos *et al*. (2000), the developments in agriculture over the last 30 years, along with the increase in road infrastructures and human population, may well have destroyed the potential habitats of the species. This is the cause pinpointed by Valenzuela *et al*. (2009) for the disappearance of the species from Catalonia over the course of the 20th century.

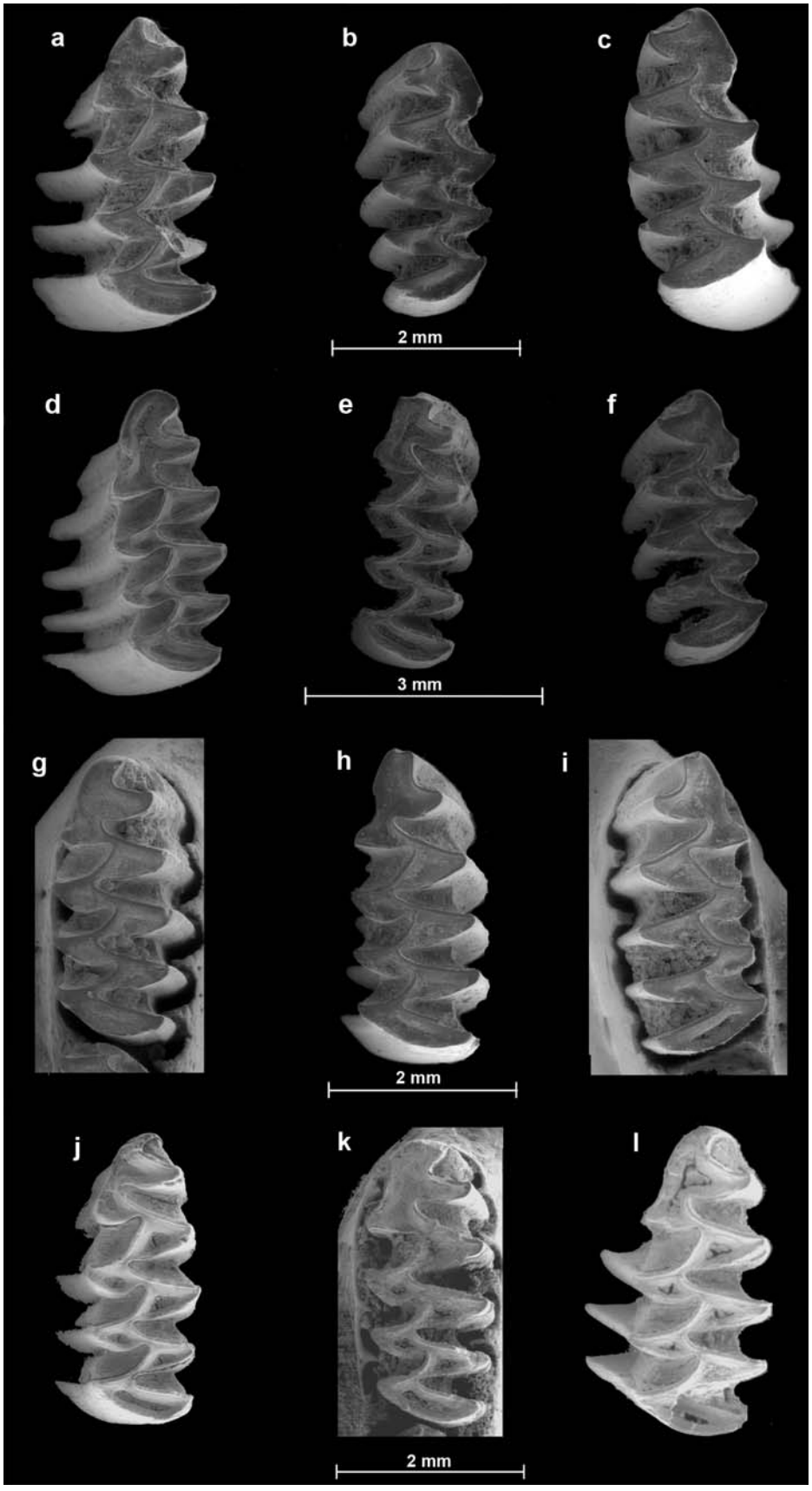

Figure 3. Some *Microtus* (*Iberomys*) *cabrerae* teeth from the sites mentioned in text. **a-c)** first lower molars (m1) from the C. Gegant. **a:** m1 left. **b-c:** m1 right. **d-f)** m1 from Gorham's cave; **d-e:** m1 left; **f:** m1 right. **g-l)** m1 from A. Romaní; **g-h:** m1 left; **i:** m1 right; **j-l:** m1 left. All teeth are in occlusal view.

3.3 Competition with other species

Finally, studies of current populations of the Cabrera vole support the possibility of competition between this species and the southern water vole (*Arvicola sapidus*). Pita *et al*. (2006) show that at sites where one species is present, the other is always absent. Findings by Fedriani *et al*. (2002) on the habitat requirements for the southern water vole suggest that this species might use very similar habitats to those used by the Cabrera vole. Regarding the subfossil data, however, there does not seem to be direct competition between the Cabrera vole and the southern water vole, given that the two species appear together at 17 (Camino, HAT, Horá, Romaní, Xaragalls, Zarzamora, Gorham's, Caldeirao, Portalón, Chimeneas, Valdavara-1, l'Arbreda, Cendres, Baños de Mula, Cingle Vermell, Bolumini and Cova 120) of the 26 Late Pleistocene and Holocene sites exposed (Table 1). These results seem to lend support to Fernández-Salvador's (1998) hypothesis that southern water voles would occupy the banks of rivers and other water bodies, while the Cabrera vole would be established in the vicinity of ditches and creek margins, but without going into the banks that *Arvicola sapidus* occupy.

4. CONCLUDING REMARKS

This study of the geographical changes undergone by the species *M.* (*I.*) *cabrerae* allows us to establish that the most plausible hypothesis for the retraction of its distribution during the Late Pleistocene and beginning of the Holocene is the human impact, which has destroyed the habitat of the species with the development of agriculture, road infrastructures and increasing human population.

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