Ecomorphological characterization of Murinae and hypsodont "Cricetidae" (Rodentia) from the Iberian Plio-Pleistocene

Caracterización ecomorfológica de los Murinae y "Cricetidae" hipsodontos (Rodentia) del Plio-Pleistoceno ibérico

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Abstract: In order to make inferences on the climatic range of extinct rodent genera, cluster analysis using dental morphological variables is performed. The goal of this study is to obtain rodent groupings which relate extinct an extant rodent genera on the basis of the ecomorphology of the dentition. The method is applied to two rodent groups, Murinae and hypsodont "Cricetidae" from the Iberian Plio-Pleistocene. The results show that dental morphology of the Plio-Pleistocene Murinae from the Iberian Peninsula shows similar patterns to those found in extant genera inhabiting tropical forested biomes. The hypsodont "Cricetidae" show a close relationship in dental pattern to that of Phillotini genera, which are inhabitants of herbaceous biomes mainly. The coexistence of both studied groups in the Spanish Plio-Pleistocene could imply an ecological segregation between them. The Murinae would preferably occupy the forested areas and the hypsodont "Cricetidae" the areas with open landscapes. Nevertheless, both groups contain genera that could occupy both types of ecosystems (*Huerzelerimys* and *Ruscinomys*).
Key words: Paleoecology, Ecomorphology, Rodents, Muroidea, Pliocene, Pleistocene, Spain, Cluster analysis

Resumen: Resumen: Con el objetivo de inferir el rango de climas ocupados por géneros de roedores extintos, se han realizado análisis de conglomerados jerárquicos en los que se han introducido variables morfológicas dentales. Con este análisis se pretenden obtener agrupaciones que relacionen géneros fósiles con actuales sobre la base de la ecomorfología de la dentición. Esta metodología es aplicada a dos grupos de roedores, Murinae y "Cricetidae" hipsodontos, del Plio-Pleistoceno ibérico. Los resultados muestran que la morfología dental de los Murinae Plio-Pleistocenos de la Península Ibérica presenta patrones similares a los encontrados en géneros actuales habitantes principalmente de biomas forestales tropicales. Por otro lado, los "Cricetidae" hipsodontos presentan patrones más parecidos a los de habitantes de biomas predominantemente herbáceos. La coexistencia de ambos grupos en los yacimientos españoles del Plio-Pleistoceno podría implicar, posiblemente, una segregación ecológica entre ellos. Los Murinae ocuparían preferentemente las áreas forestales y los "Cricetidae" hipsodontos las áreas con medios abiertos. No obstante, en ambos grupos aparecen géneros (*Huerzelerimys* y *Ruscinomys*) que podrían ocupar ambos tipos de ecosistemas.
Palabras clave: Paleoecología, Ecomorfología, Roedores, Muroidea, Plioceno, Pleistoceno, España, Análisis de conglomerados jerárquicos

INTRODUCTION

One of the objects of mammalian paleoecology is the ecological and climatic reconstruction of the past environments based on mammal faunas recorded in fossil sites. Generally, prior to making paleoecological interpretations on the basis of extinct faunas, paleoecological studies are needed to make basic suppositions on the environmental preferences of each of the species present. Examples are the studies of van de Weerd & Daams (1978), Daams & van der Meulen (1984, 1989) and van der Meulen & Daams (1992), based on Neogene rodent faunas from the Calatayud-Teruel basin.

Hernández Fernández (2001a) proposed a new method (Bioclimatic Analysis) to infer the paleoclimatic conditions based on the mammal association recorded in fossil localities. This method needs for

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each of the taxa of the fauna the assignation to a range of climates. In some cases the assignation is relatively easy since there are close living relatives on which the whole group shows the same climatic range. The problem arises with taxa without close relatives.

The aim of this study is to infer the climatic range of extinct rodents using the morphological similarities in dentition with extant taxa and thus extrapolate the climatic range of the morphologically closer living taxa to the fossil ones. These dental analogies presumably have an ecomorphological meaning.

Ecomorphological analyses of extinct taxa depend on studies based on extant species, through comparative analysis (BRYANT & RUSSELL, 1995). In the last decades, various methodologies have been proposed to infer environmental preferences of extinct taxa (EISENMANN & GUÉRIN, 1984; KAPPELMAN, 1991; PLUMMER & BISHOP, 1994; JANIS, 1995; GUERRERO-ALBA *et al.*, 1997; KAPPELMAN *et al.*, 1997; PALMQVIST *et al.*, 1999; PALMQVIST *et al.*, 2001). Classical ecomorphological studies on fossil rodents are those of HOOPER (1952, 1957). VAN DER MEULEN & DE BRUIJN (1982) and DAAMS & VAN DER MEULEN (1984) grouped the extinct and living species of the family Gliridae on the basis of the characteristic features of the first and second upper molars and then extrapolated the ecology of the extant representatives present in each morphological group to the extinct species of the same morphological group. Similarly, COLLINSON & HOOKER (1987, 1991)

looked for modern dental analogues to interpret the diet and the habitats of Paleogene mammals. Recently, new statistical and morphometric tools have been used to analyse dental morphology of rodents (VIRIOT *et al.*, 1993; VAN DAM, 1996, 1997; RENAUD *et al.*, 1996, 1999a, 1999b; RENAUD, 1999; RENAUD & VAN DAM, 2002).

In this work a new type of analysis on the dentition of extant and extinct rodents is presented. Cluster analysis using several dental features will be applied to the Murinae and hypsodont "Cricetidae" from the Iberian Plio-Pleistocene. The climatic ranges of the extant genera allow new paleoecological interpretation for these Plio-Pleistocene genera.

For a clear exposition of the ecological preferences of extant genera, a specific climatic typology is used (Table 1). We selected the climatic classification of WALTER (1970) because it has a simple nomenclature and coincides with the traditional biomes (ODUM, 1971; LACOSTE & SALANON, 1973; LIETH, 1975; STRAHLER & STRAHLER, 1987).

MATERIAL AND METHODS

MURINAE

Although the study focuses on genera recorded in the Iberian Plio-Pleistocene, populations from other

CLIMATE		ZONOBIOME (mainly vegetation type)	
I	Equatorial	I	Evergreen tropical rain forest
II	Tropical with summer rains	II	Tropical deciduous forest
II/III	Transition tropical semiarid	II/III	Savanna
III	Subtropical arid	III	Subtropical desert
IV	Winter rain and summer drought	IV	Sclerophyllous woody plants
V	Warm-temperate	V	Temperate evergreen forest
VI	Typical temperate	VI	Nemoral broadleaf-deciduous forest
VII	Arid-temperate	VII	Steppe to cold desert
VIII	Cold-temperate (boreal)	VIII	Boreal coniferous forest (taiga)
IX	Artic	IX	Tundra

Table 1.- Climatic typology used in this paper (modified from WALTER, 1970) and its relationships with world vegetation types. WALTER considers II/III as a zonoecotone between tropical forests and deserts but we apply it as a zonobiome because is traditionally used in Paleoecology because its unique faunistic community.

Tabla 1.- Clasificación climática usada en este trabajo (modificada de WALTER, 1970) y su relación con los tipos de vegetación mundial. WALTER considera II/III como un zonoecotono entre los bosques tropicales deciduos y los desiertos pero nosotros lo utilizamos como zonobioma porque es tradicionalmente usado en Paleoecología debido a su comunidad faunística única.

Plio-Pleistocene European localities have been also included in order to incorporate in the analysis all the possible morphologic variability attained by the studied genera (Table 2).

The morphological characteristics of the upper first molar (M1) of the studied fossil genera allow their inclusion into the "*Parapodemus*" group as defined by MISONNE (1969). This author considered the "*Parapodemus*" group and the "*Lenothrix*" one parallel groups, joining them in the "*Lenothrix-Parapodemus*" division. Representatives of this division have been included in the analysis (Table 3), based on the morphological similarities shown by the fossil

taxa with extant members of this division. However, genera belonging to the "*Mesembriomys*" series of Australian origin, and to the "*Lophuromys-Colomys-Zelotomys*" series of African origin, have been excluded since they present advanced characters (MISONNE, 1969) not closely related with the studied fossil forms.

Analysed variables

The morphometric variables used in the analysis are all related to the upper first molar (M1). This element is chosen because it is the most diagnostic dental element (VAN DAM, 1997). The variables included in the study are the following (see Fig. 1):

1. Total length (LM1): the maximum length of the M1 measured in mm.

2. M1 vs. M2 length ratio (%M1): represents the relative length of M1 in relation to M2 (100*length of M1/length of M2; MISONNE, 1969).

3. Percentage of the M1 length vs. total row length (%M1tot): represents the relative length of the M1 with respect to the total row length (100*length of M1/length of total cheek teeth length).

4. Length/width ratio of the M1 (L/W).

5. Angle t1-t2-t3: this measure indicates the alignment degree of these three molar cusps (Fig. 2).

6. Stephanodonty (Ste): It is a particular development, or hypertrophy, of some longitudinal crests at particular points, connecting the molar cusps lengthways (SCHAUB, 1938). Original definition by SCHAUB (1938) was extended by MISONNE (1969), to include species with a prolongation backwards of crests although there is no connection between cusps. The latter definition is the one used here. This structure increases the abrasion surface of the molar. This feature is just distinguished by their presence or absence.
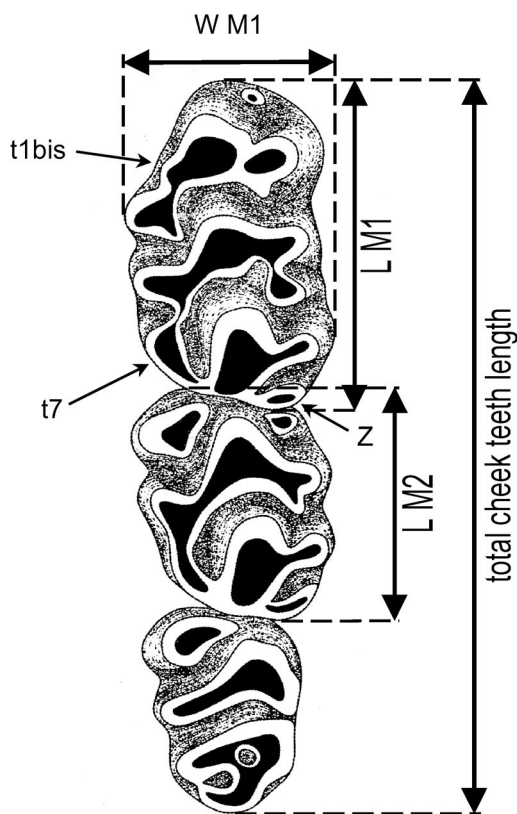

Figure 1.- Terminology of the dental elements of the Murinae used in this work, shown in drawings of the right upper tooth row. Length (L) and width (W) are measured as indicated. Explanation in the text (analysed variables).
Figura 1.- Terminología de los elementos dentales de los Murinae usada en este trabajo, sobre un dibujo de la serie molar superior derecha. Longitud (L) y anchura (W) son medidas como se indica. Explicación en el texto (analysed variables).
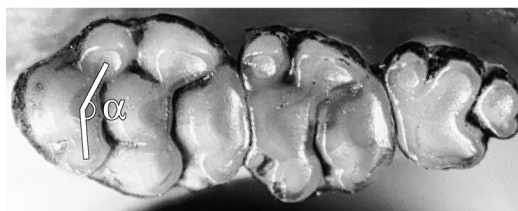

Figure 2.- Angle t1-t2-t3 (α) in Murinae M1. Image source: CHIMIMBA *et al.* (1999).
Figura 2-. Ángulo t1-t2-t3 (α) en el M1 de Murinae. Procedencia de la imagen: CHIMIMBA et al. (1999).

Genus	Species	Fossil site		References
Castillomys	*C. crusafonti* Michaux, 1969	Balaruc 6	MN 17	Bachelet, 1990
		Huélago 5	MN 17	Sesé, 1989
		Lo Fournas 4	MN 17	Bachelet, 1990
		Mas Rambault 2	MN 17	Bachelet, 1990
		Trassanel	MN 17	Bachelet, 1990
		Balaruc 2	MN 16	Bachelet, 1990
		Escorihuela	MN 16	van de Weerd, 1976; Adrover, 1986
		Moreda 1	MN 16	Martín Suárez & Mein, 1991
		Pla de la Ville	MN 16	Bachelet, 1990
		Sarrión	MN 16	Adrover, 1986
		Seynes	MN 16	Bachelet, 1990
		Arquillo III	MN 15	Adrover, 1986
		Layna	MN 15	Martín Suárez & Mein, 1991
		Sete	MN 15	Bachelet, 1990
		Villalba Alta 1	MN 15	Adrover, 1986
		Mont Helene	MN 14	Bachelet, 1990
	C. gracilis van de Weerd, 1976	Lo Fournas 13	MN 16	Bachelet, 1990
		Aldehuela	MN 15	Adrover, 1986
		Orrios 1	MN 15	Adrover, 1986
		Caravaca 1	MN 14	Adrover, 1986
		La Gloria 4	MN 14	Adrover *et al.*, 1993
	C. rivas Martín Suárez & Mein, 1991	Bagur 2	Pl.	Martín Suárez & Mein, 1991
		Huéscar 1	Pl.	Sesé, 1989
		Mas Rambault 1	Pl.	Martín Suárez & Mein, 1991
		Quibas	Pl.	Montoya *et al.* 1999
		Casablanca 1	MN 17	Gil & Sesé, 1984
		Valdeganga III	MN 17	Martín Suárez & Mein, 1991
Huerzelerimys	*H. turolensis* (Michaux, 1969)	La Gloria 4	MN 14	Adrover *et al.*, 1993
Occitanomys	*O. alcalai* Adrover *et al.*, 1983	La Gloria 4	MN 14	Adrover *et al.* 1993
		Peralejos E	MN 14	Adrover *et al.* 1988
	O. brailloni Michaux, 1969	Balaruc 6	MN 17	Bachelet, 1990
		Balaruc 2	MN 16	Bachelet, 1990
		Lo Fournas 13	MN 16	Bachelet, 1990
		Pla de la Ville	MN 16	Bachelet, 1990
		Aldehuela	MN 15	Adrover, 1986
		Arquillo III	MN 15	Adrover, 1986
		Layna	MN 15	Michaux, 1969
		Orrios 1	MN 15	van de Weerd, 1976
		Sete	MN 15	Bachelet, 1990
		Villalba Alta 1	MN 15	Adrover, 1986
		Kardia	MN 14	van de Weerd, 1979
Paraethomys	*P. abaigari* Adrover *et al.*, 1988	La Gloria 4	MN 14	Adrover *et al.*, 1993
	P. anomalus (de Bruijn *et al.*), 1970	Maritsa	MN 14	de Bruijn *et al.*, 1970
		Peralejos E	MN 14	Adrover *et al.*, 1988
	P. jaegeri Montenat & de Bruijn, 1976	Lo Fournas 13	MN 16	Bachelet, 1990
		Perpignan	MN 15	Bachelet, 1990
		Mont Helene	MN 14	Bachelet, 1990
	P. meini (Michaux), 1969	Lo Fournas 13	MN 16	Bachelet, 1990
		Aldehuela	MN 15	Adrover, 1986
		Arquillo III	MN 15	Adrover, 1986
		Layna	MN 15	Adrover, 1986
		Orrios 1	MN 15	Adrover, 1986
		Perpignan	MN 15	Bachelet, 1990
		Villalba Alta 1	MN 15	Adrover, 1986
		La Gloria 4	MN 14	Adrover *et al.*, 1993
		Mont Helene	MN 14	Bachelet, 1990

Table 2.- Species and localities of extinct genera of Murinae recorded in the Iberian Plio-Pleistocene.
Tabla 2.- Especies de Murinae extintos del Plio-Pleistoceno ibérico analizados y yacimientos en los que se han registrado.

Rhagapodemus	*R. frequens* KRETZOI, 1959	Lo Fournas 4	MN 17	BACHELET, 1990
		Balaruc 2	MN 16	BACHELET, 1990
		Pla de la Ville	MN 16	BACHELET, 1990
		Seynes	MN 16	BACHELET, 1990
		Tourkobounia 1	MN 16	DE BRUIJN & VAN DER MEULEN, 1975
		Gundersheim 4	MN 15	FEJFAR & STORCH, 1990
	R. hautimagnensis MEIN & MICHAUX, 1970	Ptolemais 3	MN 15	VAN DE WEERD, 1979
		Kardia	MN 14	VAN DE WEERD, 1979
		La Gloria 4	MN 14	ADROVER *et al.*, 1988
		Mont Helene	MN 14	AGUILAR *et al.*, 1986
		Peralejos E	MN 14	ADROVER *et al.*, 1988
		Ptolemais 1	MN 14	VAN DE WEERD, 1979
Stephanomys	*S. balcellsi* GMELING MEYLING & MICHAUX, 1973	Casablanca 1	MN 17	GIL & SESÉ, 1984
		Casablanca B	MN 17	GIL & SESÉ, 1985
	S. donnezani DÉPERET, 1890	Lo Fournas 13	MN 16	BACHELET, 1990
		Perpignan	MN 15	BACHELET, 1990
		Sete	MN 15	BACHELET, 1990
		Mont Helene	MN 14	BACHELET, 1990
		Peralejos E	MN 14	ADROVER *et al.* 1988
	S. dubari AGUILAR *et al.*, 1991	La Gloria 4	MN 14	ADROVER *et al.*, 1993
	S. margaritae ADROVER, 1986	Aldehuela	MN 15	ADROVER, 1986
		Arquillo III	MN 15	ADROVER, 1986
		Villalba Alta 1	MN 15	ADROVER, 1986
	S. minor GMELING MEYLING & MICHAUX, 1973	Escorihuela	MN 16	VAN DE WEERD, 1976
		Escorihuela A	MN 16	VAN DE WEERD, 1976
		Sarrión	MN 16	ADROVER, 1986
	S. thaleri LÓPEZ MARTÍNEZ *et al.*, 1998	Balaruc 6	MN 17	BACHELET, 1990
		Lo Fournas 4	MN 17	BACHELET, 1990
		Mas Rambault 2	MN 17	BACHELET, 1990
		Seynes	MN 16	BACHELET, 1990
		Barranco Quebradas	MN 15	SESÉ, 1989

Table 2.- (cont.).

7. Presence/absence of t7: when present, a more complete dental occlusion is produced (MISONNE, 1969).

8. Presence/absence of t1bis: this cusp is usually small although, when present, it changes the cusp pattern of the tooth, such that the t1 is located more distally (MISONNE, 1969).

9. Presence/absence of Z: it is not a true cone but only a short crest being projected labially.

10. Relative importance of the labial cusps compared to the lingual ones (lab): two stages are distinguished; (1) labial cusps better developed than lingual cusps; (0) labial cusps less developed than lingual cusps.

Each variable was calculated for every extant genus as the mean value of the included species. Those of the fossil genera were calculated as the mean value of the fossil populations recorded from the analysed sites (Table 2). For presence/absence of cusps we take as present when the frequency of the studied character is higher than 25% in any species of the genus. For characters varying with wear we used unworn material. Data on extant genera have been obtained from MISONNE (1969) and data on extinct ones have been obtained from the references in Table 2. The values for all variables and all genera are shown in Table 3.

HYPSODONT "CRICETIDAE"

The genera *Blancomys*, *Celadensia*, *Ruscinomys* and *Trilophomys* from the Iberian Pliocene, included in the particular group of "microtoid Cricetidae" (*sensu* FEJFAR, 1999) are ecomorphologically analysed. Similarly to the Murinae, populations from Pliocene European localities have been included to incorporate the total morphologic variability of the studied fossil genera, (Table 4).

These "microtoid Cricetidae" resemble some representatives of the tribe Phyllotini (Sigmodontinae). Therefore, we have selected representatives of the latter tribe to perform our comparative analysis. Data on

Genus	LM1 (mm)	%M1	%M1tot	L/W	t1-t2-t3	Ste	t7	t1bis	Z	lab
Anisomys	4,3	114	41	1,5	145	0	1	0	1	0
Apodemus	2,0	140	45	1,6	140	1	1	0	1	1
Batomys	2,8	138	43	1,8	140	0	1	0	0	0
Carpomys	4,7	130	42	1,3	130	0	1	0	1	0
Crateromys	5,7	110	37	1,6	150	1	1	0	0	0
Chiropodomys	2,0	130	44	1,6	125	1	1	0	1	0
Eropeplus	3,9	124	40	1,3	140	0	0	0	0	1
Grammomys	2,1	133	47	1,5	155	1	0	0	0	1
Hapalomys	3,6	138	44	1,4	145	1	1	0	0	0
Hyomys	7,4	137	41	1,5	135	1	1	0	0	0
Lenomys	4,6	133	41	1,5	140	1	1	0	1	0
Lenothrix	4,5	136	43	1,6	125	1	1	1	1	0
Mallomys	6,2	111	36	1,2	130	1	0	0	0	0
Micromys	2,1	155	46	1,3	140	1	1	0	0	0
Oenomys	2,6	150	43	1,4	130	1	0	0	1	1
Papagomys	7,0	152	44	1,5	135	0	0	0	0	1
Phloeomys	8,7	156	46	1,6	170	0	1	0	0	0
Pitecheir	4,8	138	44	1,6	125	1	1	0	0	0
Pogonomys	2,5	118	41	1,3	120	0	1	0	1	1
Stenocephalemys	2,5	148	46	1,7	150	1	0	0	0	1
Thallomys	3,1	133	42	1,3	140	1	0	0	0	1
Thamnomys	3,0	132	43	1,5	145	1	1	0	1	0
Tokudaia	2,8	142	46	1,5	140	1	0	1	1	1
Vandeleuria	1,5	146	47	1,7	105	1	1	0	1	1
Vernaya	3,5	134	45	1,3	140	1	1	0	1	0
Castillomys	1,7	146	46	1,4	105	1	0	1	1	0
Huerzelerimys	3,0	136	44	1,6	140	1	0	0	0	1
Occitanomys	2,1	137	44	1,5	120	1	0	1	1	1
Paraethomys	2,6	142	46	1,5	140	1	0	0	1	0
Rhagapodemus	2,3	149	45	1,6	130	1	1	0	1	0
Stephanomys	3,0	146	45	1,4	100	1	0	1	1	1

Table 3.- Values for morphological variables of extinct Iberian Plio-Pleistocene Murinae and extant Murinae genera. Taxonomy on extant taxa according to WILSON & REEDER (1993). For explanation of variables see the text. 1, presence; 0, absence.
Tabla 3.- Valores de las diferentes variables morfológicas en Murinae extintos del Plio-Pleistoceno de la Península Ibérica y géneros actuales de Murinae. La taxonomía de los taxones actuales sigue a WILSON & REEDER (1993). Para la explicación de las variables analizadas véase el texto. 1, presencia; 0, ausencia.

the Phyllotini genera are from HERSHKOVITZ, (1962) and the Animal Diversity Web page from the University of Michigan Museum of Zoology (http://www.nmhm.si.edu/tol/ muridae/phyllotini/dental.html). They are shown in the Table 5.

Analysed variables
As for the Murinae, the morphometric variables used in the analysis are all related to the upper first molar (M1), because it is the most diagnostic dental element. The variables included are the following (see Fig. 3):

1. Total length (LM1): the maximum length of the M1 measured in mm.

2. M1 vs. M2 length ratio (%M1): represents the relative length of the M1 respects to the M2 (100*length of M1/length of M2; MISONNE, 1969).

3. Percentage of M1 length vs. total row length (%M1tot): represents the relative length ratio of M1 respects to the total row length (100*length of M1/length of total cheek teeth length).

4. Length/width ratio of the M1 (L/W).

5. Quotient between the length of the M1 occlusal surface (LO) and the total length of the M1 (LO/LM1): this measure gives an indication of the overlapping between dental pieces (VAN DE WEERD, 1976).

6. Compression of the enamel folds (HERSHKOVITZ, 1962) (com): proportion that represents the

Genus	Species	Fossil site		References
Blancomys	*B. meini* ADROVER, 1986	Sarrión	MN 16	ADROVER, 1986
	B. neglectus VAN DE WEERD *et al.*, 1977	Moreda 1	MN 16	VAN DE WEERD *et al.*, 1977
		Arquillo III	MN 15	ADROVER, 1986
		Layna	MN 15	VAN DE WEERD *et al.*, 1977
		Villalba Alta 1	MN 15	ADROVER, 1986
		Mont Helene	MN 14	AGUILAR *et al.*, 1986
Celadensia	*C. nicolae* MEIN *et al.*, 1983	Peralejos E	MN 14	ADROVER *et al.* 1988
Ruscinomys	*R. europaeus* DEPÉRET, 1890	Lo Fournas 13	MN 16	BACHELET, 1990
		Aldehuela	MN 15	ADROVER, 1986
		Arquillo III	MN 15	ADROVER, 1986
		Sete	MN 15	BACHELET, 1990
		Villalba Alta 1	MN 15	ADROVER, 1986
		Peralejos E	MN 14	ADROVER *et al.*, 1988
	R. gilvosi ADROVER *et al.*, 1988	Peralejos E	MN 14	ADROVER *et al.* 1988
	R. lasallei ADROVER, 1969	La Gloria 4	MN 14	ADROVER *et al.* 1993
Trilophomys	*T. castroi* ADROVER, 1986	Aldehuela	MN 15	ADROVER, 1986
		Arquillo III	MN 15	ADROVER, 1986
		Villalba Alta 1	MN 15	ADROVER, 1986
	T. pyrenaicus (DEPÉRET), 1890	Lo Fournas 13	MN 16	BACHELET, 1990
		Sarrión	MN 16	ADROVER, 1986
		Orrios 1	MN 15	ADROVER, 1986
		Perpignan	MN 15	ADROVER, 1986
		Sete	MN 15	ADROVER, 1986
		Mont Helene	MN 14	AGUILAR *et al.*, 1986
	T. vandeweerdi BRANDY, 1979	Balaruc 6	MN 17	ADROVER, 1986
		Balaruc 2	MN 16	ADROVER, 1986
		Escorihuela	MN 16	VAN DE WEERD, 1976
		Escorihuela A	MN 16	VAN DE WEERD, 1976
		Pla de la Ville	MN 16	BACHELET, 1990
		Layna	MN 15	ADROVER, 1986

Table 4.- Species and localities of hypsodont "Cricetidae" genera recorded in the Iberian Plio-Pleistocene.
Tabla 4.- Especies pertenecientes a los géneros de "Cricetidae" hipsodontos registrados en el Plio-Pleistoceno ibérico y yacimientos analizados en este trabajo.

mean width of the "triangles" (Wt) regarding the M1 occlusal length (LO). This variable, as the two following ones, is an index of the available active occlusal surface.

7. Presence/absence of triangulation (HERSHKOVITZ, 1962) (trg): presence of circular or oval lophs (0) or more or less triangular shaped elements with apices at crown border (1).

8. Presence/absence of involution (HERSHKOVITZ, 1962) (inv): interpenetration of the enamel folds, overlapping between internal and external folds (Fig. 4).

9. Presence/absence of lamination (HERSHKOVITZ, 1962) (lam): confluence of the folds of one side of the tooth with those of the opposite side (Fig. 4).

Each variable was calculated for every extant genus as the mean value of the constituent species. Those of the fossil genera have been calculated as the mean value of the fossil populations from the studied sites (Table 4). Data on extinct taxa have been obtained from references in Table 4. The values for all variables and all genera are shown in Table 5.

CLUSTER ANALYSIS

We have used cluster analysis techniques in order to group rodent genera based on dental similarities. Two cluster analyses have been performed, one for the Murinae and another for the hypsodont "Cricetidae". In each case, the variables have been standardized in order to eliminate differences in magnitude among them. For the similarity analysis we have used the euclidean distance since it is not dependent of magnitude character and it is sensitive to proportional and absolute differences (SNEATH & SOKAL, 1973).
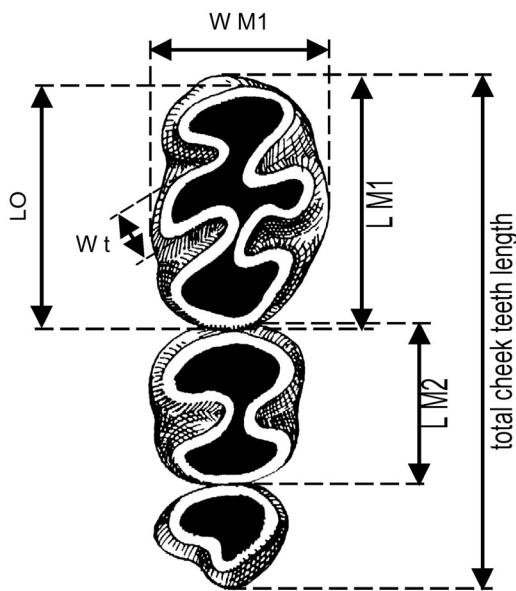
Figure 3.- Terminology of the dental elements of the hypsodont "Cricetidae" used in this work, demonstrated in drawings of the right upper tooth row. Length (L) and width (W) are measured as indicated. Explanation in the text (analysed variables).
Figura 3.- Terminología de los elementos dentales de los "Cricetidae" hipsodontos usada en este trabajo, sobre un dibujo de la serie molar superior derecha. Longitud (L) y anchura (W) son medidas como se indica. Explicación en el texto (analysed variables).

The method used to generate the similarity dendrogram has been the unweighted pair-group method using arithmetic average (UPGMA). Data analysis has been carried out using the computer program NTSYS-pc version 1.80 (ROHLF, 1993).

RESULTS

MURINAE

The similarity dendrogram obtained for studied Murinae is shown in Fig. 5. The tree shows a significant consistency regarding the distance matrix from which has been generated (Mantel test; t = 7,388; p = 1,000). The value of the Pearson's cophenetic correlation coefficient (CCC) is 0,721.

The studied genera of Murinae can be differentiated in seven main groups (Fig. 5).

The first group (A) shows an angle with regard to the cusps t1-t2-t3 with values near to 100º, a marked stephanodonty and it has the cusps Z and t1bis, being the only group that presents the latter stucture. The genus *Lenothrix* (subgroup A1) shows a set of characters that differentiate it from the other members of the group (*Tokudaia*, *Occitanomys*, *Stephanomys* and *Castillomys*; subgroup A2), such as the presence of t7, high length/width ratio, a large M1, and a relative small length of the M1 with respect to the M2 and the total length of the molar row.

Group B is characterised by the presence of stephanodonty and cusp t7. Nevertheless it exhibits a great variability, being subdivided in several smaller groups. Members of B1 (*Lenomys*, *Thamnomys*, *Ver-*
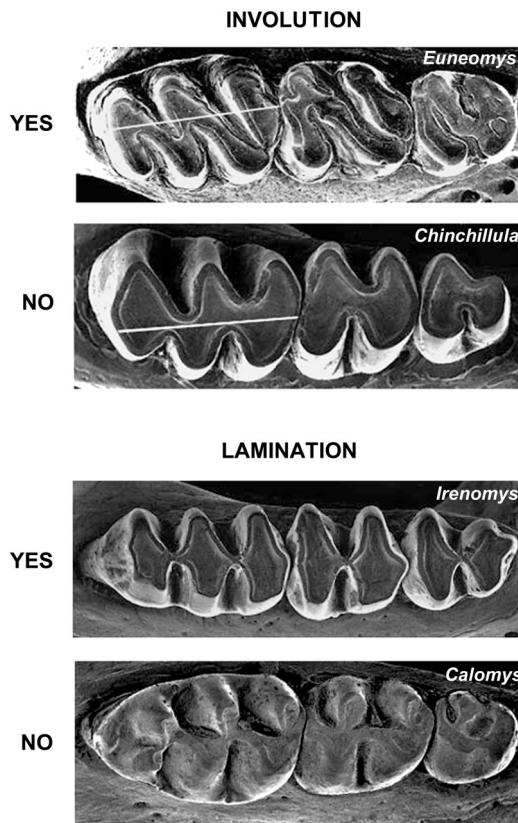

Figure 4.- M1 occlusal morphology of some Phyllotini showing the morphological patterns associated to the involution and lamination processes. Images source: http://www.nmhm.si.edu/tol/muridae/phyllotini/dental.html.
Figura 4.- Morfología oclusal del M1 de algunos Phyllotini mostrando los patrones morfológicos asociados a los procesos de involución y de laminación. Procedencia de las imágenes: http://www.nmhm.si.edu/tol/muridae/phyllotini/dental.html.

Genus	LM1 (mm)	%M1	%M1tot	L/W	LO/LM1	com	trg	inv	lam
Andinomys	3,0	124	40	1,4	0,9	9	1	1	0
Auliscomys	2,6	139	44	1,6	0,8	10	0	1	0
Calomys	1,8	147	46	2,3	0,7	4	0	0	0
Chinchillula	3,6	164	48	1,4	0,9	10	1	0	1
Eligmodontia	1,8	143	46	1,4	0,8	10	1	1	0
Euneomys	2,5	137	43	1,4	0,8	13	0	1	0
Galenomys	2,9	147	45	1,2	0,9	13	0	0	1
Graomys	2,6	160	48	1,7	0,6	10	0	1	0
Irenomys	2,9	153	44	1,7	0,8	11	1	0	1
Neotomys	3,0	147	42	1,2	0,8	8	1	1	0
Phyllotis	2,7	158	46	1,5	0,8	11	1	0	0
Reithrodon	2,5	157	45	1,7	0,7	14	1	1	0
Blancomys	4,4	149	46	1,4	0,9	12	0	0	1
Celadensia	2,6	147	46	1,7	0,6	9	1	1	0
Ruscinomys	4,4	150	49	1,6	0,8	11	1	1	0
Trilophomys	3,2	152	48	1,8	0,7	13	1	1	0

Table 5.- Values for morphological variables of extinct Iberian Plio-Pleistocene hypsodont "Cricetidae" and extant Phyllotini genera. Taxonomy on extant taxa according to Wilson & Reeder (1993). Explanation of variables in the text. 1, presence; 0, absence.

Tabla 5.- Valores de las diferentes variables morfológicas en "Cricetidae" hipsodontos del Plioceno de la Península Ibérica y Phyllotini actuales. La taxonomía de los taxones actuales sigue a Wilson & Reeder (1993). Para la explicación de las variables analizadas véase el texto. 1, presencia; 0, ausencia.

naya, *Chiropodomys* and *Rhagapodemus*) present a relatively small M1/M2 ratio, maintain Z and their labial cusps are less developed that the lingual ones. The genera included in B2 (*Pitecheir*, *Hapalomys* and *Hyomys*) have the longest M1 among the representatives of group B, Z is absent and the labial cusps are less developed than the lingual ones. *Micromys* (subgroup B3) has a large %M1 ratio compared to group B, Z is absent and the labial cusps are smaller than the lingual ones. The subgroup B4 (*Vandeleuria* and *Apodemus*) is the most differed subgroup inside B, presenting a very small M1, with a Z present and the labial cusps better developed than the lingual ones.

Group C includes genera with stephanodont M1 (except *Eropeplus*), t7 absent, labial cusps better developed than lingual ones (except *Paraethomys*), and large angle t1-t2-t3. Three clearly differentiated subgroups are observed. Subgroup C1 (*Eropeplus* and *Thallomys*) shows M1 with a small length/width ratio and Z absent. In subgroup C2 (*Grammomys*, *Stenocephalemys* and *Huerzelerimys*) Z is absent as well, but their length/width ratio is high. The subgroup C3 (*Oenomys* and *Paraethomys*) has a Z.

Batomys constitutes the group D. It has the highest length/width ratio among all the studied genera, it is not stephanodont, cusp t7 is present, while Z is absent. Its labial cusps are smaller than the lingual ones.

Group E consists of genera *Pogonomys*, *Carpomys* and *Anisomys*. Their M1 has about the same length of M2, they are not stephanodont and they have cusp Z.

Papagomys and *Phloeomys* form group F. Their M1 are larger than in the other groups, and the %M1 is among the largest. They are not stephanodont and Z is absent.

The group G (*Crateromys* and *Mallomys*) has M1 intermediate in size between group F and the rest of groups. The M1 size is similar to that of the M2 and is relatively small with respect to the total tooth row length (compared to other groups). It is stephanodont, and the labial cusps are larger than the lingual ones.

"Cricetidae"

The similarity dendrogram for Phyllotini and extinct hypsodont "Cricetidae" is shown in Fig. 6.
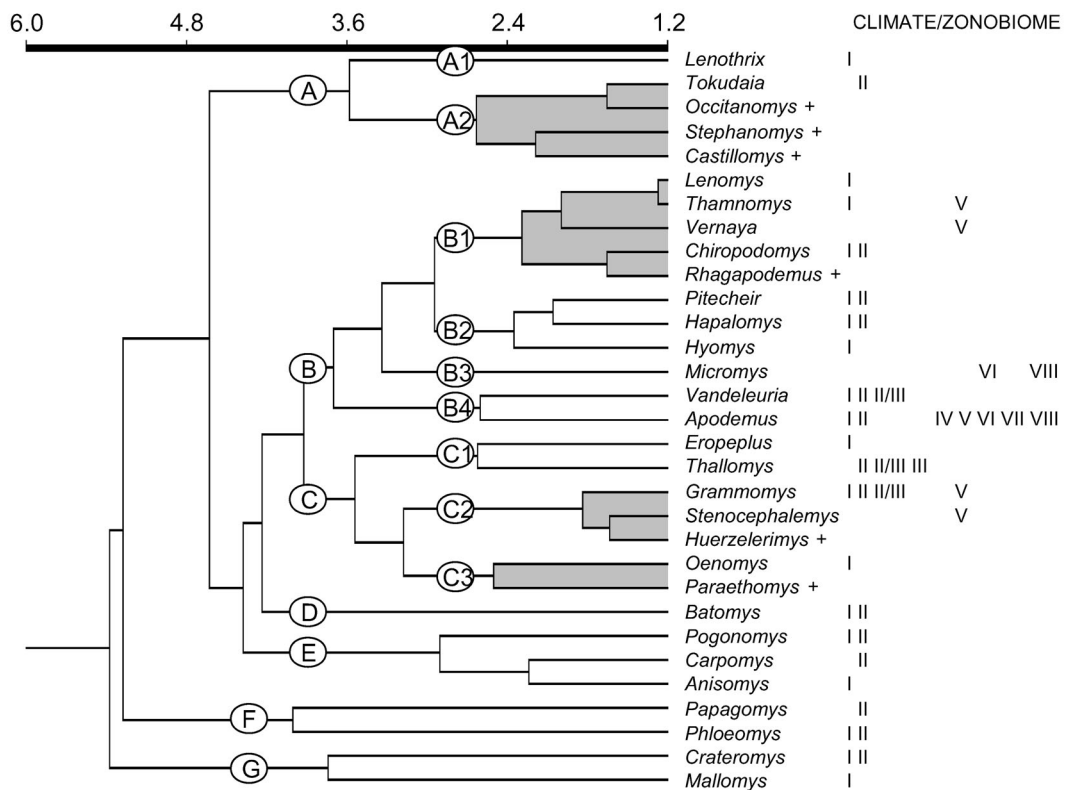
Figure 5.- M1 morphological similarity dendrogram of studied extinct and extant Murinae genera (euclidean distance). Cophenetic correlation coefficient = 0,721. The climate types occupied by the extant genera have been included, see Table 1. Groupings of genera containing fossil genera are shaded. Taxonomy of extant genera according to WILSON & REEDER (1993).

Figura 5.- Dendrograma de similitud morfológica en el M1 de los géneros de Murinae actuales y extintos estudiados (distancia euclidea). Coeficiente de correlación cofenética = 0,721. Se han incluido los tipos de clima ocupados por los géneros actuales, véase Tabla 1. Las zonas sombreadas representan las agrupaciones que contienen géneros fósiles. La taxonomía de los géneros actuales sigue a WILSON & REEDER (1993).

The Mantel test indicate that the tree maintains a significant consistency regarding the distance matrix from which it has been generated (t = 5,520; p = 1,000). The value of the Pearson's cophenetic coefficient of correlation (CCC) is 0,768.

Calomys shows a very primitive and different morphology from the rest of the studied genera. The other genera have been grouped in three large groups.

The first of these groups (A) is characterised by the absence of involution in the M1 and by tooth lamination (except *Phyllotis*). This group combines genera with large M1, M1 relatively long compared to M2, and with high LO/LM1. Two subgroups can be distinguished: A1 (*Blancomys* and *Galenomys*) characterized by the absence of triangulation in the M1, and A2 (*Phyllotis*, *Irenomys* and *Chinchillula*) which

has M1 with triangulation and a higher compression degree than A2. In this second subgroup, the %M1 ratio is higher than in A1.

The other two groups show involution in the M1 and do not contain lamination. They differ from group A by size and proportions of the M1 (L/W).

Group B gathers genera with M1 proportionally large compared both to M2 and to the total length of the molar series, a high length/width ratio and a very low occlusal length/total ratio. *Ruscinomys* constitutes the subgroup B1 and it differs from the other genera by its large size and by its high occlusal length/total length ratio of the M1. The subgroup B2 includes *Celadensia*, *Trilophomys*, *Reithrodon* and *Graomys*.

The group C combines genera with M1 of small size, proportionally small compared to M2 and the

tooth row length and having an occlusal length similar to the maximal one. The subgroup C1 is constituted by the genera *Eligmodontia*, *Neotomys*, *Auliscomys* and *Euneomys*. *Andinomys* form the subgroup C2 that differs from the previous one by its smaller %M1 and %M1/tot ratio, and a higher LO/LM1 ratio.

DISCUSSION

Assignment of climatic ranges to fossil taxa has been conservative. The range of each of them includes all the climates where similar extant taxa are distributed. In Bioclimatic Analysis (HERNÁNDEZ FERNÁNDEZ, 2001a) stenoic species have a greater influence in climatic inference for a locality than euryoic species. If climatic range assignation is

doubtful a more conservative assignation is better for a reliable application of the method.

MURINAE

Occitanomys, *Stephanomys* and *Castillomys* show great morphologic similarity, constituting a group very different from the rest of the Murinae. Diverse authors have verified the phylogenetic proximity of these genera that constitute a monophyletic group with *Occitanomys* being the root of the other two genera (VAN DE WEERD 1976; VAN DAM, 1996; FREUDENTHAL & MARTÍN SUAREZ, 1999). This lineage has been recorded in the Iberian Peninsula since the latest Vallesian (VAN DE WEERD 1976; VAN DAM, 1997; FREUDENTHAL & MARTÍN SUÁREZ, 1999). In our analyses based on morphometric characters,
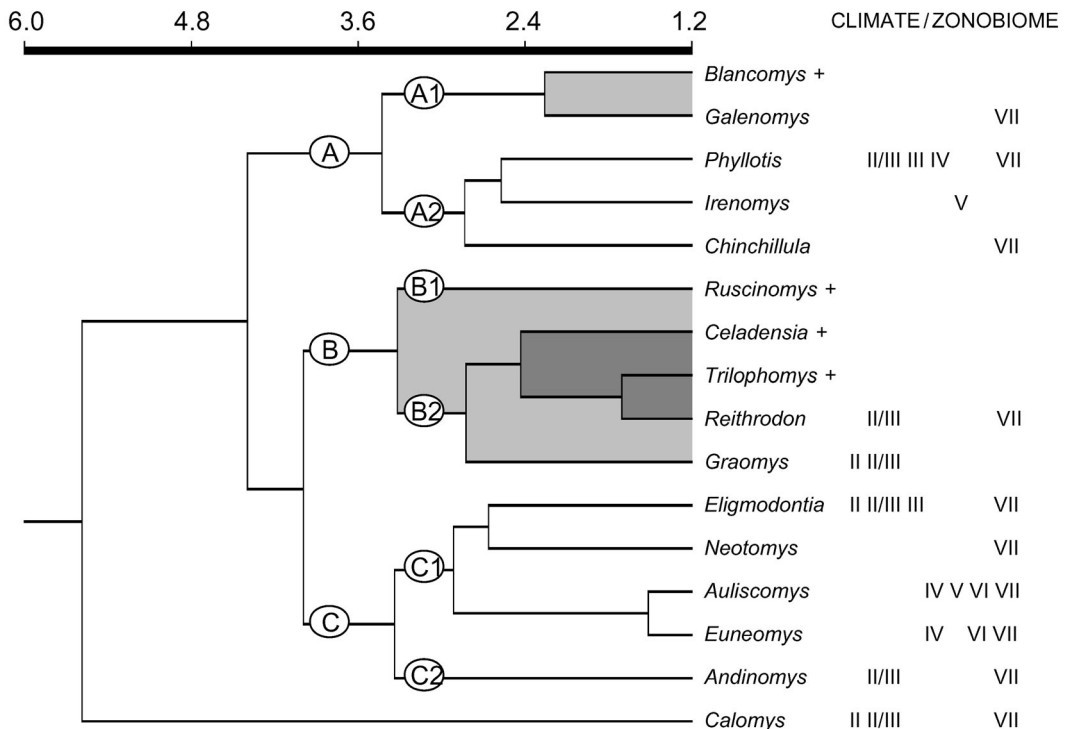

Figure 6.- M1 morphological similarity dendrogram of studied extinct "Cricetidae" and the extant Phyllotini genera (euclidean distance). Cophenetic correlation coefficient = 0,768. The climate types occupied by the extant genera have been included, see Table 1. Groupings of genera containing fossil genera are shaded. Taxonomy of extant genera according to WILSON & REEDER (1993).

Figura 6.- Dendrograma de similitud morfológica en el M1 de los géneros extintos de "Cricetidae" estudiados y los Phyllotini actuales (distancia euclidea). Coeficiente de correlación cofenética = 0,768. Se han incluido los tipos de clima ocupados por los géneros actuales, véase Tabla 1. Las zonas sombreadas representan las agrupaciones que contienen géneros fósiles. La taxonomía de los géneros actuales sigue a WILSON & REEDER (1993).

these three genera are grouped with *Tokudaia*, an endemic taxon from the tropical deciduous forests of the archipelago of Ryukyu (South of Japan). They are also close to *Lenothrix*, inhabitant of the evergreen tropical rain forests of Malaysia and Western Indonesia. Both extant genera inhabit forested biomes of tropical type. Then we could suppose for the three Iberian Plio-Pleistocene genera the occupation of similar ecosystems, probably with a higher affinity to the tropical deciduous forests, indicative of the existence of a winter dry season, as we can deduce from their higher similarity to *Tokudaia*.

Rhagapodemus clusters with *Chiropodomys* (Southeastern Asia), *Vernaya* (mountains of the South of China and North of Burma), *Thamnomys* (mountains of central Africa) and *Lenomys* (Sulawesi). This group of extant genera shows preferences for humid tropical and subtropical biomes (evergreen tropical rainforests, tropical deciduous forests and higher altitude temperate evergreen forests). Therefore, in our opinion, *Rhagapodemus* could have occupied similar biomes in Western Europe during the Plio-Pleistocene.

In the ecomorphological analysis *Huerzelerimys* clusters with *Stenocephalemys*, from the mountains of Ethiopia, and *Grammomys*, from the sub-Saharan Africa. These genera show a wide climatic distribution including evergreen tropical rainforest, tropical deciduous forest, temperate evergreen forest and savannas. Therefore, *Huerzelerimys* could have shown a higher climatic tolerance (at least, regarding the pluviometric conditions) than the other Iberian Plio-Pleistocene Murinae.

Paraethomys is close to *Oenomys*, with which it has already been compared by other authors (Renaud *et al*., 1999). This latter extant genus inhabits the African evergreen tropical rainforests. Therefore, *Paraethomys* could have been an inhabitant of the most humid, warm or non-seasonally areas of the Iberian Peninsula during the Pliocene.

"Cricetidae"

Blancomys is clustered with *Galenomys*, which occupies exclusively the Puna areas in central Andes, which could be considered as a "mountain variety" of the steppe biome (*sensu* Walter, 1970). Therefore, *Blancomys* shows a dental morphology characteristic of an inhabitant of open and probably fresh environments.

Celadensia and *Trilophomys* show the highest similarity to *Reithrodon*. This extant genus is distributed in the steppe and savanna biomes of the Southern South America. Therefore, *Celadensia* and *Trilophomys* could have occupied ecosystems whose vegetation consisted mainly of herbaceous plants, but probably they had a broader thermal niche than *Blancomys*.

Ruscinomys forms a group with the previously mentioned genera (*Reithrodon*, *Celadensia* and *Trilophomys*) and *Graomys*. This last genus inhabits steppes and savannas of Patagonia and Pampa as well as the tropical deciduous forests of El Chaco. The similarity of *Ruscinomys* with this last genus could indicate a stronger preference for forested habitats in the former than in the other Iberian hypsodont "Cricetidae".

Paleoecology of Iberian Plio-Pleistocene Murinae and hypsodont "Cricetidae"

The extinct genera of hypsodont "Cricetidae" have shown a marked preference to cluster with extant genera inhabitants of biomes in which the open landscapes prevail (steppes and savannas) although *Ruscinomys* could also occupy tropical deciduous forests. The studied fossil Murinae have dentitions morphologically closer to extant genera inhabiting forested environments (evergreen tropical rainforests, tropical deciduous forests, and temperate evergreen forests) although in some case (*Huerzelerimys*) they could also occupy savannas.

However, species of both subfamilies appear jointly in the fossil sites of the Iberian Plio-Pleistocene. The results presented in this work could indicate a possible ecological segregation among these species (Table 6). The hypsodont "Cricetidae" could have occupied those more open environments (forest gaps, prairies of edaphic origin, etc.) while the Murinae would have occupied forested habitats (forests, riversides, etc). Nevertheless, the genera *Huerzelerimys* and *Ruscinomys* could have been more catholic given the fact that they cluster with extant genera that occupy both forested and open environments.

Problems derived from actualism force us to be cautious. Correlation between dental morphology and climatic ranges could be different in fossil taxa, and climatic ranges of extinct taxa could be unlike those of extant taxa. Thus we have preferred a conservative approach to the study of climatic ranges of fossil taxa.

Forested environments	Catholic	Open environments
Castillomys	*Huerzelerimys*	*Blancomys*
Occitanomys	*Ruscinomys*	*Celadensia*
Paraethomys		*Trilophomys*
Rhagapodemus		
Stephanomys		

Table 6. Ecological segregation of the Iberian Plio-Pleistocene Murinae and "microtoid" Cricetinae.
Tabla 6. Segregación ecológica de los géneros de Murinae y Cricetinae "microtoides" del Plio-Pleistoceno ibérico.

Other source for error is the existence of unknown biomes in the past or that modern biomes have different characteristics than in the past. This problem is stronger when the age of taxa or localities increases. This possibility must be kept in mind although we think that Plio-Pleistocene biomes have been substantially equal to modern ones (CLIMAP, 1976; PRISM, 1995).

Therefore, we admit that some climatic range assignation may be wrong. However, our intention is not to define species as key climatic indicators, thus they must not be used directly as evidences for the climate of localities that contain those taxa. This work is a necessary methodological step for the Bioclimatic Analysis. This methodology is robust against a limited number of errors in the assignations. Influence of small errors associated to wrong assignation of species is weak because the whole fauna (or the rodent fauna) is used for the climatic inference for a locality.

Nevertheless, the climatic range assignations inferred in this work for Iberian Plio-Pleistocene Murinae and hypsodont "Cricetidae" would be contrasted in studies based on other groups (e.g. large mammals). The results will be used to infer climatic conditions on fossil localities based on complete faunas (HERNÁNDEZ FERNÁNDEZ, 2001b).

ACKNOWLEDGEMENTS

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