Cricetidae and Gliridae (Rodentia, Mammalia) from the Miocene and Pliocene of southern Spain

A. García-Alix, R. Minwer-Barakat, E. Martín-Suárez & M. Freudenthal

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A. García-Alix, R. Minwer-Barakat & E. Martín-Suárez, Departamento de Estratigrafía y Paleontología, Universidad de Granada, Avda. Fuentenueva s/n, 18071 Granada, Spain (agalix@ugr.es; rminwer@ugr.es; elvirams@ugr.es); M. Freudenthal, Departamento de Estratigrafía y Paleontología, Universidad de Granada, Avda. Fuentenueva s/n, 18071 Granada, Spain, and Nationaal Natuurhistorisch Museum, P.O. Box 9517, 2300 RA Leiden, The Netherlands (mfreuden@ugr.es).

Key words – Gliridae, Cricetidae, Granada basin, Guadix basin, Mio-Pliocene boundary.

Several Miocene and Pliocene continental fossiliferous localities in the Granada and Guadix basins have yielded fossil micromammals. Cricetids and glirids are known from most of these localities. This paper deals with the genera *Apocricetus*, *Ruscinomys*, *Blancomys* and *Eliomys*. The Cricetidae are important biostratigraphical markers, especially *Apocricetus*. The presence of *A. barrierei* in the locality PUR-4 indicates the beginning of the Early Ruscinian. The continuous record of *Ruscinomys* during the Late Turolian and the Early Ruscinian corroborates the lineage between *R. schaubi* and *R. lasallei*. The occurrence of a large specimen of *Blancomys* in the Granada Basin seems to indicate two phylogenetic lineages during the Late Turolian. The studied specimens of *Eliomys* allow us to confirm the relationship between *E. intermedius* and *E. quercinus*.

Contents

Introduction

The intramontane Granada and Guadix basins (southern Spain) are located in the central sector of the Betic Cordillera (Fig. 1), in which continental sedimentation began in the Late Miocene. Seven sections with Mio-Pliocene rodent faunas are situated in the Granada Basin and two in the Guadix Basin (Table 1). The locality OTU-4 is Middle Turolian, the localities in the Cantera de Pulianas section, the Arenas del Rey section, OTU-1 and PUR-3 are Upper Turolian, and PUR-4, CLC-3B, PUR-13 and YEG are Lower Ruscinian (García-Alix, 2006). The localities TCH-1 and TCH-1B are Upper Ruscinian; TCH-3 and TCH-13 are Lower Villafranchian (Minwer-Barakat, 2005).

This paper is focused on the families Gliridae (genus *Eliomys*) and Cricetidae (genera *Apocricetus*, *Ruscinomys*, *Hispanomys* and *Blancomys*). These cricetids are biostratigraphically important. The new material from the studied localities permits us to revise or establish phylogenetic relationships.

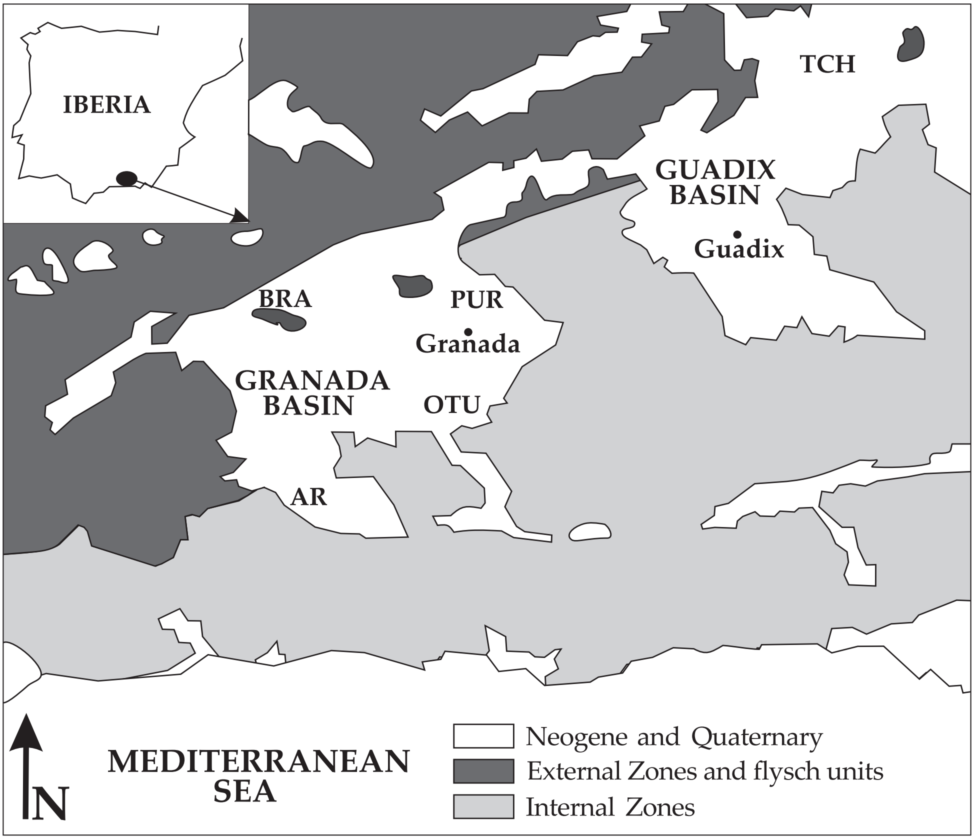


Fig. 1. Geological and geographical situation of Granada and Guadix basins (after Braga *et al*., 1990) and location of the studied sections: TCH, Tollo de Chiclana and Yeguas sections; PUR, Canteras de Jun, Cantera de Pulianas, Barranco de Purcal and Calicasas sections; OTU, Otura section; BRA, Brácana and Cerro del Águila sections; AR, Arenas del Rey section.

Table 1. Section and localities studied, chronologically arranged. Abbreviations: JUN, Canteras de Jun; OTU, Otura; PUR, Barranco del Purcal; DHS, La Dehesa; MNA, La Mina; BRA, Brácana; AGU, Cerro del Águila; CLC, Calicasas; TCH, Tollo de Chiclana.

Section	Location	Localities
Canteras de Jun	Eastern Granada Basin	JUN-2C
Otura	Eastern Granada Basin	OTU-1, OTU-4
Cantera de Pulianas	Eastern Granada Basin	PUR-23, PUR-24A, PUR-25, PUR-25A
Arenas del Rey	Western Granada Basin	DHS-1, DHS-14, DHS-15B, DHS-16, DHS-4A, DHS-4B, MNA-2, MNA-4
Brácana	Western Granada Basin	BRA-5B
Cerro del Águila	Western Granada Basin	AGU-1C
Barranco del Purcal	Eastern Granada Basin	PUR-3, PUR-4, PUR-7, PUR-13
Calicasas	Eastern Granada Basin	CLC-3, CLC-3B, CLC-4B
Yeguas	Central Guadix Basin	YEG
Tollo de Chiclana	Central Guadix Basin	TCH-1, TCH-1B, TCH-3,TCH-13

Methodology

The nomenclature used in the descriptions of the cricetid molars is that of Freudenthal *et al.* (1994); length and width have been measured as defined by Freudenthal (1966), and measured perpendicular to each other for easy orientation. The nomenclature used in the descriptions of the teeth of *Eliomys* is that of Freudenthal & Martín-Suárez (2006); length and width have been measured as defined by Freudenthal (2004). The M1 and M2 of *Eliomys* are treated together for the sake of compatibility with published data. Although m1 and m2 are similar in size, the elongate specimens that are broader posteriorly than anteriorly may be attributed to m1, and those that have parallel labial and lingual borders to m2.

Measurements were taken with a Wild M7S binocular microscope, equipped with a Sony Magnescale LM12 digital measuring device. The specimens are kept in the Departamento de Estratigrafía y Paleontología of the University of Granada. The measurement data were processed by a computer programme provided by M.F. Measurements are given in units of 1 mm. In the tables, Nt is the total number of specimens (measurable and not measurable). Photographs were made with the FEI ESEM QUANTA 400 of the Centro Andaluz de Medio Ambiente, Granada.

Only the most numerous population of each species is described, except for rare taxa, where we describe all dental elements. We have directly compared our specimens with material from the Mein collection (Lyon) and from the Departamento de Estratigrafía y Paleontología, University of Granada (Table 2).

Table 2. Material directly compared with our specimens; (c) indicates casts. Abbreviations: LG, La Gloria; LM, Los Mansuetos; VDC, Valdecebro; CR, Crevillente.

Species	Direct comparison with material in	
	Mein collection	DEPUG Collection
A. alberti	Librilla	Librilla, Venta del Moro (c), Negratín-1
A. barrierei	Alcoy, Caravaca, LG-4, Chabrier, Hautimagne	Terrats (c), La Alberca (c); Celleneuve (c), Gorafe-4, Botardo
A. angustidens		Villeneuve de la Raho (c); Serrat d'en Vacquer (c); Gorafe-3, -5
H. adroveri		Casa del Acero, CR-15
H. aff. *adroveri*		CR-17
R. schaubi	LM, Aljezar-B	LM, Aljezar-B
R. cf. *schaubi*		VDC-3 (c) and VDC-6 (c)
R. lasallei	LG-4	La Gloria-4
R. europaeus		Layna, Rambla Seca-1, -2, -6
B. sanzi		VDC-3 (c)
B. meini		Sarrión (c)
B. neglectus		Layna
E. truci	Hautimagne, LM, LG-5, VDC-6	Moreda-1A,-1B, Rambla Seca-1
E. intermedius	Balaruc-2, Sète	Casablanca-B, Galera-2, Cañada Castaño-1, -2, Gorafe-5, Moreda-1A

Systematic palaeontology

Order Rodentia Bowdich, 1821
Family Cricetidae Fischer von Waldheim, 1817
Subfamily Cricetinae Fischer von Waldheim, 1817
Genus *Apocricetus* Freudenthal, Mein & Martín Suárez, 1998

Type species – *Cricetus angustidens* Depéret, 1890.

Remarks – The majority of the available cheek teeth of *Apocricetus* were already described by Freudenthal *et al.* (1998). *Apocricetus alberti* Freudenthal *et al.*, 1998, is known from PUR-23, PUR-24A, PUR-25 and PUR-25A, and *A. barrierei* (Mein & Michaux, 1970) from PUR-4. Herein, one M3 of *A. alberti* is described from PUR-3 and two new localities with *A. barrierei* are reported, at PUR-7 and YEG. The specimens from these two new localities agree with the main features of the molars from PUR-4 described by Freudenthal *et al.* (1998).

Apocricetus alberti Freudenthal, Mein & Martín Suárez, 1998
Pl. 1, figs. 1-5.

Holotype – m1 (CR-6 111) deposited in the Instituut voor Aardwetenschappen, Utrecht, The Netherlands.

Type locality – Crevillente-6, Spain.

Occurrence in the studied localities – PUR-23, PUR-24A, PUR-25, PUR-25A and PUR-3.

Table 3. Measurements of the teeth of *Apocricetus* from the studied localities.

			Length				Width			
Element	Localities	Nt	N	Min.	Mean	Max.	N	Min.	Mean	Max.
m1	YEG	1	1		2.64		1		1.61	
	PUR-4	5	3	2.43	2.48	2.56	4	1.42	1.48	1.56
	PUR-25A	3	2	2.33	2.35	2.36	2	1.38	1.41	1.43
	PUR-24A	2	2	2.19	2.20	2.21	2	1.35	1.36	1.36
m2	PUR-4	3	3	1.91	2.08	2.18	3	1.47	1.62	1.71
	PUR-25A	3	3	2.01	2.03	2.06	3	1.59	1.62	1.67
	PUR-23	1	1		1.81		1		1.53	
m3	YEG	1	1		2.21		1		1.72	
	PUR-4	4	4	2.07	2.14	2.25	4	1.51	1.64	1.77
	PUR-25A	2	2	2.03	2.03	2.03	2	1.58	1.60	1.61
	PUR-25	2	2	2.03	2.04	2.05	2	1.50	1.56	1.61
M1	PUR-4	5	4	2.42	2.52	2.66	4	1.57	1.67	1.81
M2	PUR-4	1	1		2.31		1		1.80	
M3	PUR-7	1					1		1.45	
	PUR-4	2	2	1.51	1.65	1.78	2	1.45	1.56	1.66
	PUR-25A	1	1		1.77		1		1.49	
	PUR-24A	2	1		1.71		1		1.51	

Material and measurements – See Table 3.

Description and discussion – The M3 from PUR-3, which is slightly damaged posteriorly, has a well developed anterior protolophule and a lingual anteroloph (in *A. barrierei* the anterior protolophule is weak or absent and the lingual anteroloph is less developed). The specimens from PUR-23, PUR-24A, PUR-25, PUR-25A and PUR-3 agree in size and morphology (the crest-shaped anteroconid with a weak superficial subdivision in some specimens, the single or double anterolophulid in m1 and the weak or absent mesoloph in the upper molars) with those of *Apocricetus alberti* from the localities Librilla, La Gloria-5, Venta del Moro, Crevillente-6, and Negratín-1 (data from Freudenthal *et al.*, 1998). They are smaller than those of *A. angustidens* (Depéret, 1890) from Mont-Hélène, Gorafe-3, Gorafe-5, Sète Serrat d'en Vacquer (data from Freudenthal *et al.*, 1998) and Villeneuve de la Raho, and those of *Apocricetus barrierei* from Vendargues (Mein & Michaux, 1970), Gorafe-4, Botardo, Hautimagne, Celleneuve, Terrats (Mein & Michaux, 1970), Alcoy, Caravaca, La Gloria-4, Chabrier, and La Alberca (data from Freudenthal *et al.*, 1998), although some parameters may overlap with *A. barrierei*.

***Apocricetus barrierei* (Mein & Michaux, 1970)**

Pl. 1, figs. 6-11.

Holotype – M1 (FSL 65356) deposited in the Faculté des Sciences, Université de Lyon, France.

Type locality – Chabrier, France.

Occurrence in the studied localities – PUR-4, PUR-7 and YEG.

Material and measurements – See Table 3.

Description and discussion – The molars from PUR-4, PUR-7 and YEG are larger than those of *A. alberti* in the populations mentioned above, and, although some values overlap, the mean values of these teeth are larger. The populations from PUR-4, PUR-7 and YEG have the principal features of *A. barrierei*, like the large size, the slightly bilobed or trilobed anteroconid in m1, the double anterolophulid, the reduced lingual anteroloph in M3 and the presence of an anterior protolophule in the upper molars. Our specimens are smaller than those of *A. angustidens*, although some values overlap slightly; our m1 have a slightly bilobed or trilobed anteroconid, whereas in those of *A. angustidens* it is crest-shaped, and our M1 do not have an anterior cingulum in front of the anterocone, which is very common in *A. angustidens*.

Remarks on the genus Apocricetus – *Apocricetus* aff. *plinii* was an immigrant in the Early Turolian (MN11) and gave rise to the phylogenetic lineage *A.* aff. *plinii* - *A. plinii* - *A. alberti* - *A. barrierei* - *A. angustidens* (Freudenthal *et al.*, 1998). *Apocricetus alberti* occurs only in Upper Turolian localities (MN13) and *A. barrierei* is Lower Ruscinian (MN14) (Mein, 1975; Martín Suárez, 1988; Ruiz Bustos, 1990, 1992; Freudenthal *et al.*, 1998; Kälin, 1999).

Subfamily Cricetodontinae Stehlin & Schaub, 1951
Genus *Hispanomys* Mein & Freudenthal, 1971

Type species – *Cricetodon decedens aragonensis* Freudenthal, 1966.

Hispanomys aff. *adroveri* Agustí, 1986
Pl. 2, figs. 1-3.

Occurrence in the studied localities – JUN-2C.

Material and measurements – See Table 4.

Description – *m2* – Worn specimen. The thick mesolophid is in contact with the metaconid and closes the mesosinusid. The posterosinusid is open. Narrow sinusid. Three roots.

m3 – The mesolophid closes the mesosinusid. The posterosinusid is open in one specimen and closed at a low level in the other one. Narrow sinusid. Three roots.

M1 – Bilobed anterocone. The very well developed protosinus and the narrow sinus reach the base of the crown. Anterosinus and mesosinus are partially closed. Four roots.

M2 – Worn specimen. Narrow and deep sinus. One of the two funnels delimited by the ectolophs has disappeared through wear. Roots cannot be observed.

M3 – Worn specimen. It is divided into two lobes (anterior and posterior) by a narrow and deep sinus, and by the mesosinus. The funnels have disappeared through wear. Roots cannot be observed.

Discussion – The specimens have a medium degree of hypsodonty, less hypsodont than *Ruscinomys*. They are smaller than *Ruscinomys schaubi* Villalta & Crusafont Pairó, 1956, from Aljezar-B and Los Mansuetos (Adrover, 1986; van de Weerd, 1976), although our maxima overlap with the minimum values of *R. schaubi*.

The specimens share the main features of *Hispanomys adroveri* Agustí, 1986, from Casa del Acero and CR15, but they are smaller, like the specimens of *Hispanomys* aff. *adroveri* from CR-17 (Freudenthal *et al.*, 1991). The size of our specimens (Table 4) is near the lowest values for CR-17.

Table 4. Measurements of the teeth of *Hispanomys* aff. *adroveri* from JUN-2C.

		Length				Width			
Element	Nt	N	Min.	Mean	Max.	N	Min.	Mean	Max.
m2	1	1		2.68		1		1.83	
m3	2	2	2.26	2.28	2.30	2	1.54	1.58	1.62
M1	2	1		3.54		2	2.19	2.22	2.24
M2	1	1		2.58		1		1.82	
M3	1	1		1.85		1		1.57	

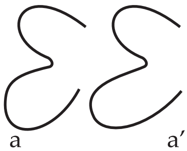
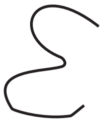
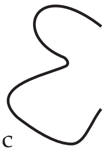
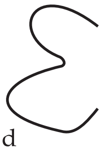
	Morpho-type / **Locality**	**N**	 a a′	 b	 c	 d
R. europaeus	LAYNA	8			3	5
R. lasallei	PUR$	12			7	5
	ALCOY	2			1	1
R. aff. *schaubi*	DHS*	3			3	
	PUR*	4		2	2	
R. schaubi	ALJ-B, LM	11	11			

Fig. 2. Morphotypes of the lingual lobe of the anterocone of *Ruscinomys*. (a, a′) oblique and rounded; (a) unworn, (a′) worn specimen. (b) forward directed with an smooth lingual angle. (c, d) forward directed with a sharp lingual angle. PUR* includes PUR-23, PUR-24A, PUR-25 and PUR-25A; DHS* includes DHS-4B and DHS-16; PUR$ includes PUR-4, PUR-13 and BRA-5B.

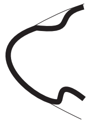
	Morphotype / **Locality**	**N**	1 	2 	3 
R. europaeus	LAYNA	14			14
R. lasallei	PUR$	14			14
	ALCOY, LG-4	4			4
R. aff. *schaubi*	DHS*	6		2	4
	PUR*	8		4	5
R. schaubi	ALJ-B, LM	8	1	6	1

Fig. 3. Morphotypes of the anteroconid of *Ruscinomys* (after van de Weerd, 1976). (1) Reduced anterolophid. (2) There is no anterolophid *sensu stricto*, but a reduced crest in the labial border of the anteroconid. (3) Rounded anteroconid. PUR* includes PUR-23, PUR-24A, PUR-25 and PUR-25A; the legend DHS* includes to DHS-4A, DHS-4B and DHS-16; the legend PUR$ includes to PUR-4 and PUR-13.

Genus *Ruscinomys* Depéret, 1890

Type species – *Ruscinomys europaeus* Depéret, 1890.

Remarks – Five morphotypes are distinguished for the lingual lobe of the anterocone in the M1 of *Ruscinomys* (Fig. 2). Morphotypes a and a′ have an oblique and rounded lingual lobe of the anterocone (a for unworn and a′ for worn specimens); in morphotype b the lingual lobe of the anterocone is directed forward with a smooth lingual angle; and in morphotypes c and d the lingual lobe of the anterocone is directed forward with a sharp lingual angle. Morphotype d has the sharp lingual angle weaker than morphotype c.

Three different morphotypes are distinguished for the anteroconid of the m1 (after van de Weerd, 1976) (Fig. 3). These are: morphotype 1, reduced anterolophid; morphotype 2, there is no anterolophid *sensu stricto*, but there is a reduced crest in the labial border of the anteroconid; and morphotype 3, rounded anteroconid.

***Ruscinomys* aff. *schaubi* Villalta & Crusafont Pairó, 1956**

Pl. 2, figs. 4-10.

Occurrence in the studied localities – PUR-23, PUR-24A, PUR-25, PUR-25A, MNA-2, MNA-4, DHS-15B, DHS-14, DHS-16, DHS-4A and DHS-4B.

Material and measurements – See Table 5.

Description of the material from DHS-16 – m1 – One specimen has a reduced labial crest in the anteroconid (morphotype 2); the others three specimens have a rounded anteroconid (morphotype 3). The mesolophid partially closes the mesosinusid and forms a funnel. The posterolophid closes the posterosinusid at a low level and it forms another funnel. Narrow and deep sinusid. Two roots (anterior and posterior).

m2 – Two funnels are formed by the mesolophid and the posterolophid, which partially close the mesosinusid and the posterosinusid, respectively; the posterolophid is lower than the mesolophid. Three roots (one anterior and two posterior).

m3 – There is an anterior funnel; in fresh specimens the posterolophid does not close the posterosinusid completely. Narrow and deep sinusid. Two roots (anterior and posterior).

M1 – The anterocone is divided into two lobes by a medium-deep groove that comes close to the base of the crown; its lingual lobe presents morphotype b (Fig. 2). The complete ectolophs delimit two funnels. The bottom of the deep and narrow sinus is at the level of the crown basis. The posteroloph is curved slightly posterolabially. There are five roots corresponding to the cusps.

M2 – Worn specimens. The complete ectolophs delimit two funnels. The posteroloph is curved slightly posterolabially. Four roots (two anterior and two posterior).

M3 – Worn specimens. The sinus and the mesosinus divide the teeth into two lobes; the posterior lobe is smaller than the anterior one. Two roots; the anterior one may be split.

Discussion – Our material is generally slightly smaller and lower crowned than that of *Ruscinomys lasallei* Adrover, 1969, from Alcoy, or La Gloria-4. *Ruscinomys lasallei* has a rounded anteroconid in m1, without labial crest (morphotype 1; Fig. 3). Our specimens are larger than those of *R. gilvosi* Adrover *et al.*, 1988, especially in the width. *Ruscinomys bravoi* Adrover & Mein, 1996, was defined for some very broad M1 of *R. schaubi* from Aljezar-B. These M1 are larger than our material. Nevertheless, the figured and described specimens of *R. bravoi* do not have the labial crest of the anteroconid in m1, nor are the lingual lobes of the anterocone in M1 like those of our specimens.

Our material agrees in size with *R. schaubi* from Los Mansuetos and Aljezar-B, among others. The labial crest of the anteroconid in m1 is variable in the specimens from Los

Table 5. Measurements of the teeth of *Ruscinomys* aff. *schaubi* from the studied localities.

			Length				Width			
Element	Localities	Nt	N	Min.	Mean	Max.	N	Min.	Mean	Max.
m1	DHS-4B	1	1		3.20		1		2.10	
	DHS-4A	1	1		3.09		1		2.16	
	DHS-16	4	4	3.10	3.19	3.28	4	1.90	2.02	2.10
	PUR-25A	2	2	3.20	3.23	3.26	1		2.12	
	PUR-25	2	1		3.20		2	2.13	2.15	2.17
	PUR-24A	2	1		3.08		1		2.18	
	PUR-23	5	1		3.13		1		2.08	
m2	DHS-4B	1	1		2.91		1		2.06	
	DHS-4A	1	1		2.78		1		1.81	
	DHS-16	2	2	2.96	2.99	3.02	2	1.96	1.96	1.96
	PUR-25A	2	1		3.01		1		1.95	
	PUR-25	1	1		3.12		1		2.01	
	PUR-24A	2	1		3.08		1		2.09	
	PUR-23	1	1		2.97		1		2.13	
m3	DHS-4B	1	1		2.55		1		2.02	
	DHS-4A	1	1		2.67		1		1.62	
	DHS-16	4	4	2.36	2.40	2.46	4	1.63	1.76	1.97
	DHS-14	1	1		2.47		1		1.65	
	DHS-15B	1	1		2.70		1		1.78	
	MNA-4	2	2	2.33	2.46	2.59	2	1.59	1.63	1.66
	MNA-2	1	1		2.53		1		1.67	
	PUR-25A	4	4	2.53	2.66	2.77	4	1.68	1.73	1.80
	PUR-25	2	1		2.49		2	1.77	1.81	1.85
	PUR-24A	2	2	2.43	2.50	2.56	2	1.74	1.77	1.79
	PUR-23	5	4	2.52	2.65	2.77	5	1.68	1.75	1.78
M1	DHS-4A	1								
	DHS-16	2	2	3.85	3.89	3.92	2	2.32	2.35	2.37
	PUR-25A	2	2	3.73	3.79	3.84	1		2.35	
	PUR-25	2					2	2.45	2.60	2.76
	PUR-24A	1	1		3.87		1		2.40	
	PUR-23	2	1		3.72		2	2.34	2.44	2.54
M2	DHS-4B	1	1		2.90		1		2.15	
	DHS-16	2	2	2.96	3.07	3.17	2	2.05	2.24	2.42
	PUR-25A	3	3	2.66	2.82	3.05	2	2.19	2.26	2.32
	PUR-25	1	1		3.00		1		2.29	
	PUR-24A	5	4	2.52	2.72	2.85	4	2.05	2.11	2.15
	PUR-23	3	2	2.59	2.81	3.03	2	2.00	2.06	2.12
M3	DHS-16	1	1		1.90		1		1.57	
	PUR-25A	3	3	1.95	2.07	2.20	3	1.61	1.66	1.76
	PUR-25	3	2	1.94	2.05	2.15	2	1.56	1.60	1.63
	PUR-24A	1	1		2.07		1		1.65	
	PUR-23	2	2	1.74	1.84	1.94	2	1.43	1.51	1.58

Mansuetos and Aljezar-B, but it is less developed and less frequent in our specimens (Fig. 3). The lingual lobe of the anterocone in the M1 of *R. schaubi* is oblique and rounded (morphotypes a, a'; Fig. 2), or slightly oval, whereas our specimens show morphotype b or c (Fig. 2). Morphotype c is observed in more recent *Ruscinomys* (Fig. 2).

Contemporaneous localities from Teruel (Valdecebro-3, Valdecebro-6, La Gloria-5, Arquillo-1, Celadas-2 and Arquillo-4) contain specimens of *R.* cf. *lasallei* that are slightly smaller, slightly less hypsodont and more archaic than *R. lasallei* from La Gloria-4 (Adrover *et al.*, 1993). Our specimens are classified as *Ruscinomys* aff. *schaubi* because they share features with *R. schaubi* (such as their size and the crest of the anteroconid in some specimens) and with *R. lasallei* (like the shape of the lingual lobe of the anterocone).

Ruscinomys lasallei **Adrover, 1969**

Pl. 2, figs. 11-18.

Holotype – M1 (AL 10) deposited in the Instituto de Paleontología Miquel Crusafont, Sabadell, Spain.

Type locality – Alcoy, Spain.

Occurrence in the studied localities – BRA-5B, PUR-4, CLC-3 and PUR-13.

Material and measurements – See Table 6.

Description – *m1* – There is a rounded anteroconid (morphotype 3). In fresh specimens the mesosinusid and the posterosinusid are not completely closed by the mesolophid and posterolophid. The funnels have disappeared in worn specimens. Narrow and deep sinusid. Two roots.

m2 – The mesolophid and the posterolophid partially close the mesosinusid and the posterosinusid, respectively. This last one is closed at a lower level than the mesosinusid. Narrow and deep sinusid. Three roots (one anterior and two posterior), but in one specimen from PUR-4 the anterior root is split at mid-height.

Table 6. Measurements of the teeth of *Ruscinomys lasallei* from the studied localities.

			Length				Width			
Element	Localities	Nt	N	Min.	Mean	Max.	N	Min.	Mean	Max.
m1	PUR-13	1	1		3.46		1		1.99	
	PUR-4	19	9	3.34	3.46	3.54	11	2.11	2.27	2.39
	BRA-5B	1								
m2	CLC-3	1	1		3.50		1		2.28	
	PUR-4	8	5	3.20	3.33	3.45	6	2.07	2.14	2.21
	BRA-5B	1					1		2.16	
m3	PUR-13	2	2	2.60	2.69	2.78	2	1.91	1.94	1.96
	PUR-4	14	11	2.62	2.72	2.83	11	1.81	1.94	2.09
M1	PUR-13	1	1		4.75		1		2.86	
	PUR-4	9	4	4.31	4.40	4.52	6	2.63	2.73	2.83
	BRA-5B	3	2	4.33	4.35	4.36	2	2.75	2.76	2.77
M2	PUR-4	16	12	2.93	3.10	3.34	14	2.13	2.30	2.79
	BRA-5B	1	1		3.27		1		2.31	
M3	PUR-4	14	13	1.86	2.03	2.22	13	1.56	1.67	1.74
	BRA-5B	1	1		2.05		1		1.81	

m3 – The mesosinusid is partially closed by the mesolophid. The posterosinusid is open and in only one specimen from PUR-13 the posterolophid closes the posterosinusid at a low level. Narrow and deep sinusid. Two roots (anterior and posterior).

M1 – The anterocone is split into two lobes by a strong groove (strongest in PUR-13) that almost descends to the base of the crown. The lingual lobe of the anterocone has morphotype c or d (Fig. 2). The complete ectolophs form two funnels. Narrow and deep sinus. Five roots corresponding with the cusps.

M2 – The complete ectolophs delimit two funnels (the posterior funnel is closed at a lower level than the anterior one). The posteroloph is curved slightly posterolabially. Narrow and deep sinus. Four roots.

M3 – Some specimens have two funnels. The sinus and the mesosinus divide the teeth in two lobes, and the posterior lobe is smaller than the anterior. The anterosinus is weak. Two roots (anterior and posterior).

Discussion – The studied specimens are large and hypsodont. They are higher crowned than those of *R. schaubi*. The size of our specimens (like those of *R. lasallei* from Alcoy and La Gloria-4) agrees with the maximum of *R. schaubi* or they are even larger. Our specimens are, in general, larger and higher-crowned than those of *R. gilvosi* and *R. bravoi*.

The studied specimens usually have complete ectolophs and they have no labial crest in the anteroconid of m1. One M1 from PUR-4 and another one from PUR-13 agree with the minimum size of *R. europaeus* Depéret, 1890, but in general our specimens have lower crowns and smaller sizes than *R. europaeus* from Layna. In our M1 the groove of the anterocone does not continue on the anterior root, as is the case of *R. europaeus* (see Fig. 4). The lingual lobe of the anterocone of the studied M1 is similar to those of *R. europaeus* from Layna (morphotype c or d; Fig. 2).

Ruscinomys cf. *lasallei* Adrover, 1969

Occurrence in the studied localities – AGU-1C, PUR-3 and CLC-4B.

Material and measurements – See Table 7.

	Subdivision **Locality**	**N**	Weak	Medium	Strong	Very strong	Total
R. europaeus	LAYNA	8					▨
R. lasallei	PUR-13	1				▨	
	BRA-5B and PUR	11			▨		
R. aff. *schaubi*	DHS*	3		▨			
	PUR*	4	▨				
R. schaubi	ALJEZAR-B	11	▨				

Fig. 4. Subdivision of the anterior wall of the anterocone of *Ruscinomys*. Weak is a superficial subdivision and total means that the subdivision continues on the anterior root. PUR* includes PUR-23, PUR-24A, PUR-25 and PUR-25A; DHS* includes DHS-4B and DHS-16.

Table 7. Measurements of the teeth of *Ruscinomys* cf. *lasallei* from the studied localities.

			Length				Width			
Element	Localities	Nt	N	Min.	Mean	Max.	N	Min.	Mean	Max.
m1	PUR-3	3	2	3.12	3.18	3.24	2	1.99	2.06	2.10
m3	AGU-1C	1	1		2.23		1		1.72	
M1	PUR-3	1	1		3.81		1		3.27	
M3	CLC-4B	1	1		1.95		1		1.55	

Description and discussion – Two worn and broken m1 with rounded anteroconid and two roots, and one M1 have been found in PUR-3. The two lobes of the anterocone of M1 are elongated and very marked (morphotype c, Fig. 2). There are two funnels and a deep, narrow sinus. Roots are not preserved. Their sizes agree with the maximum values of *R.* aff. *schaubi*, and they are near the minimum size of *R. lasallei* from BRA-5B, PUR-4, PUR-13, Alcoy and La Gloria-4. They are slightly more hypsodont than those of *R.* aff. *schaubi*. The anterocone has morphotype c (Fig. 2) like the more recent species of *Ruscinomys*.

In one worn m3 from AGU-1C and one worn M3 from CLC-4B without roots, only the main folds are well preserved. We ascribe this scarce and badly preserved material to *Ruscinomys* cf. *lasallei*.

Remarks on the genus Ruscinomys – Adrover (1969) defined *R. lasallei* as a species intermediate between the Miocene *R. schaubi* and the Pliocene *R. europaeus.* Mein & Freudenthal (1971) attributed these species to two different genera and two independent phylogenetic lineages: *Pseudoruscinomys*, for *R. schaubi* and *R. lavocati* (now *Cricetodon lavocati*); and *Ruscinomys*, for *R. lasallei, R. europaeus* and *R. thaleri* (now *Hispanomys thaleri*). *Pseudoruscinomys* has a labial crest in the anteroconid (not an anterolophid *sensu stricto*) and a well-developed furrow in the upper incisors (Mein & Freudenthal, 1971). Van de Weerd (1976) synonymized *Pseudoruscinomys* with *Ruscinomys* since this furrow is present in *Cricetodon, Hispanomys, Ruscinomys* and *Byzantinia*, so the taxonomic value of this feature is limited.

Mein & Freudenthal (1971) thought the origin of *Ruscinomys* and *Pseudoruscinomys* to be *Cricetodon albanensis*. Agustí (1982) suggested that the origin of the genus *Ruscinomys* is *Hispanomys peralensis*.

The position of *R. gilvosi* in the line of *Ruscinomys* is not clear and Adrover *et al.* (1988) suggested that it may be related with an immigration. *Ruscinomys bravoi* also has an indeterminate position within the genus *Ruscinomys*, maybe independent of *R. schaubi*, because both species coexist in Aljezar-B. *Ruscinomys africanus* Geraads, 1998, from Lissasfa (Casablanca, Morocco) resembles *Byzantinia* (reduced anterolophid in m1 and very well-developed spur in the lingual anterolophule of the M1), a genus unknown so far in the western Mediterranean area.

In Teruel, *Ruscinomys* is very abundant in the Middle Turolian, and scarce in Upper Turolian and Ruscinian localities. This may be related to some kind of ecological control (Adrover *et al.*, 1993). At present, the oldest record of *Ruscinomys* is from Masada del Valle-2 (MN12) (Freudenthal *et al.*, 1991). Our populations of *R.* aff. *schaubi,* like those from Teruel mentioned above, share features with *R. lasallei* (degree of hypsodonty, the strong groove splitting the anterocone, the shape of the anterocone in M1, and the very well-developed ectolophs and mesolophid) and with *R. schaubi* (reduced labial crest in the anteroconid of some m1 and the weak to moderate development of the groove that divides the anterocone in M1) (Figs. 2-4).

Two phylogenetic hypotheses for the genus *Ruscinomys* are possible.

1: *Pseudoruscinomys schaubi* is a *Ruscinomys* in which some archaic features resemble those of *Hispanomys* (van de Weerd, 1976), like the reduced anterolophid in some specimens and the height of the crown (Fig. 5A).

2: *Pseudoruscinomys schaubi* represents a phylogenetic line independent of *Ruscinomys* (according to Mein & Freudenthal, 1971). The specimens of *R.* aff. *schaubi* (with the reduced labial crest in the anteroconid) are descendants of *Pseudoruscinomys schaubi* (Fig. 5B).

The data from the Granada basin agree with the first hypothesis (Fig. 5A). Figures 2-4 show a gradual evolution of the anteroconid in m1 and the anterocone of M1 from the older localities to the younger ones. However, more Upper Turolian populations of *Ruscinomys* are necessary to specify the phylogenetic relationship between *R. schaubi* and *R. lasallei* in more detail.

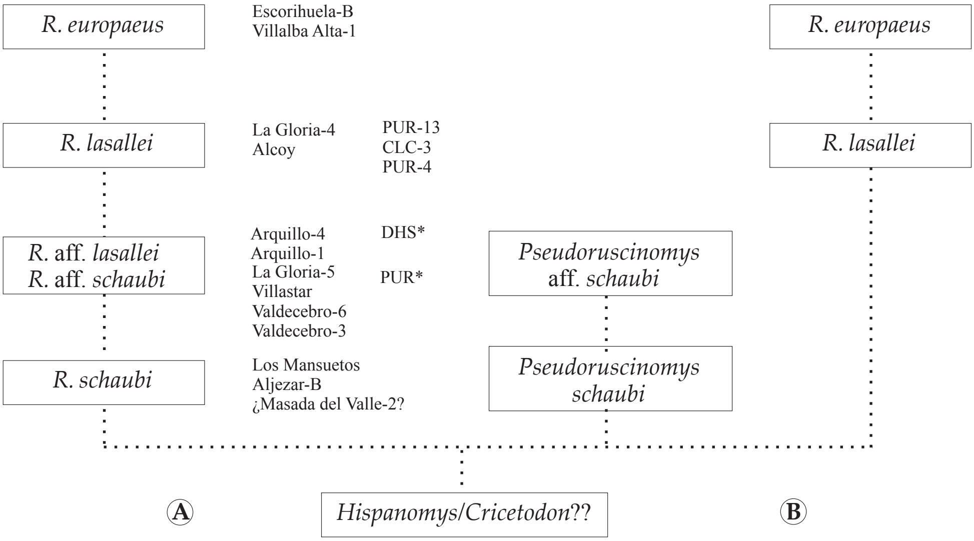


Fig. 5. Two phylogenetic hypotheses for *Ruscinomys*. (A) After van de Weerd (1976) and this paper. (B) After Mein & Freudenthal (1971). PUR* includes the populations of *Ruscinomys* from PUR-23, PUR-24A, PUR-25 and PUR-25A; DHS* includes the populations of *Ruscinomys* from the section of Arenas del Rey.

Cricetidae Incertae Subfamiliae

Blancomys van de Weerd, Adrover, Mein & Soria, 1977

Type species – *Blancomys neglectus* van de Weerd *et al.*, 1977.

Blancomys sanzi Adrover, Mein & Moissenet, 1993

Pl. 3, figs. 4-11.

Holotype – m1 (LG-5 1) deposited in the Instituto de Paleontología Miquel Crusafont, Sabadell, Spain.

Type locality – La Gloria-5, Spain.

Occurrence in the studied localities – PUR-4.

Material and measurements – See Table 8.

Description – *m3* – Bilobed tooth that is anterolingually broken. The sinusid is weak, and the mesosinusid is narrow and deep. The posterosinusid has disappeared because of wear. Roots are not preserved.

M1 – The hook-shaped anterocone is directed towards the labial border. Anterosinus, mesosinus and sinus are well developed, but the protosinus and posterosinus are weakly curved and little pronounced. Roots are not preserved.

M2 – Bilobed tooth. The sinus is narrower and deeper than the mesosinus, which is wide and weakly curved. Roots are not preserved.

M3 – Bilobed teeth, slightly compressed longitudinally. The sinus is narrow and deep. Two roots (anterior and posterior).

Discussion – These specimens are smaller than those of *B. meini* Adrover, 1986, and *B. neglectus*, and similar in size to those of *Blancomys sanzi* from the Teruel localities La Gloria-5, Valdecebro-3, Valdecebro-6, Villastar and Celadas-2 (Adrover *et al.*, 1993). The M1 presents some features similar to those of *B. neglectus*, like the wider anterosinus that penetrates only slightly in the anterocone.

Table 8. Measurements of the teeth of *Blancomys* from the studied localities.

			Length				Width			
Element	Localities	Nt	N	Min.	Mean	Max.	N	Min.	Mean	Max.
m1	TCH-1B	2	1		4.75		1		3.18	
	BRA-5B	1	1		4.54		1		2.73	
m3	PUR-4	1	1		2.30					
M1	TCH-1B	1								
	PUR-4	1	1		3.89		1		2.83	
M2	PUR-4	1	1		2.80		1		2.34	
	TCH-1B	1	1		3.17				3.19	
M3	PUR-4	3	3	2.06	2.09	2.14	3	1.76	1.91	2.02
	TCH-1B	1	1		2.95				2.81	

Blancomys meini Adrover, 1986

Pl. 3, figs. 12-14.

Holotype – m1 (SAR) deposited in the Instituto Lucas Mallada (C.S.I.C.), Madrid, Spain.

Type locality – Sarrión, Spain.

Occurrence in the studied localities – TCH-1B.

Material and measurements – See Table 8.

Description – *m1* – The weak and open anterosinusid, and a wide and deep mesosinusid, reach the level of the crown basis. The shallow posterosinusid does not reach the crown basis. The labial border is almost straight due to the wear. Two roots (anterior and posterior).

M1 – Broken posterolabially. The rounded anterosinus is less deep than the U-shaped sinus. The mesosinus is deeper than the anterosinus. The weak protosinus almost reaches the crown basis. Roots are not preserved.

M2 – The deep sinus and the mesosinus both reach the basis of the crown, and divide the teeth into two lobes; the anterior lobe is wider than the posterior one. The anterior border is almost straight and the posterior one is rounded. Roots are not preserved.

M3 – It is divided into two lobes like M2 and slightly compressed longitudinally. The anterior lobe is wider than the posterior one. Two roots (anterior and posterior).

Discussion – The lengths of our specimens agree with those of *B. meini* from its type locality (Sarrión), but the width is slightly larger in the TCH-1B molars. The size of *B. meini* from Moreda-1 (Adrover, 1986; Castillo, 1990) agrees with our specimens. The specimens from TCH-1B are larger than those of *B. neglectus* from Layna (type locality), Villalba Alta and Arquillo 3 (van de Weerd *et al.*, 1977; Adrover, 1986), and *B. sanzi* from La Gloria-5 (type locality), Valdecebro-3, Valdecebro-6, Celadas-2, Villastar (Adrover *et al.*, 1993) and PUR-4. The morphological differences between the species of *Blancomys* are few; the main diagnostic feature is size (Adrover, 1986; Adrover *et al.*, 1993).

Blancomys aff. *sanzi* Adrover, Mein & Moissenet, 1993

Pl. 3, figs. 1-3.

Occurrence in the studied localities – BRA-5B.

Material and measurements – See Table 8.

Description – A large m1 has been found with an almost straight labial border and a wide and weak sinusid. The anteroconid is rounded and there is neither an anterolophid nor a mesolophid. The large, wide and U-shaped mesosinusid reaches the level of the crown basis. Deep and narrow posterosinusid. Metaconid and entoconid are parallel and perpendicular to the longitudinal axis of the molar. Two broad and robust roots (anterior and posterior).

Discussion – The morphology of the tooth is very similar to *B. sanzi* because of the nearly straight labial border. This is not frequent in *B. neglectus* nor in *B. meini*. The posterosinusid is deep and narrow, penetrating far into the occlusal surface like in *B. sanzi*. *Blancomys meini* and *B. neglectus* usually have a shallow posterosinusid that hardly penetrates into the occlusal surface. However, our specimen is larger and presents a higher degree of hypsodonty than *B. sanzi*. The teeth of *B. sanzi* are smaller than those of *B. neglectus* and *B. meini*, whereas our specimen even exceeds the size of *B. neglectus* and comes close to the values of *B. meini*, the largest and youngest *Blancomys* known (Fig. 6).

The presence in BRA-5B of a very big *Blancomys* with *sanzi*-like morphology, while 'normal' *B. sanzi* persists in the contemporaneous locality PUR-4, suggests that we are dealing with an unknown species (Fig. 6).

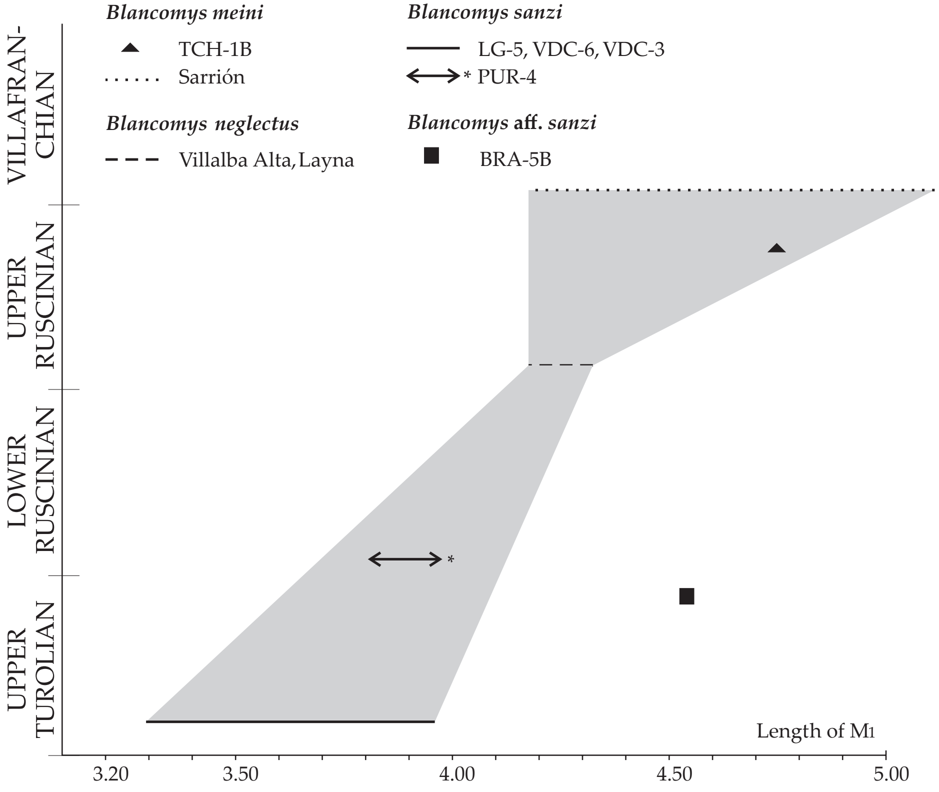


Fig. 6. Size distribution of the length of m1 of different *Blancomys* species (data from Adrover *et al.*, 1993). The length of the m1 from PUR-4 has been estimated from the length of M1.

***Blancomys*? sp.**

Occurrence in the studied localities – MNA-4.

Description and discussion – A single specimen (2.15 × 2.01 mm) only preserves the external wall of the crown. Its determination is very difficult. It may be a m3 or M3. It has two lobes separated by the sinus(id). The posterior lobe is smaller than the anterior one. We attribute it to *Blancomys*? sp.

Remarks on the genus Blancomys – *Blancomys* is characterized by its large size, high crowns, thick enamel, opposed lingual and labial folds, and reduced M3. The main difference between the species of the genus is the size; there is an increase in size through time (Fig. 6) (Adrover, 1986; Adrover *et al.*, 1993).

The taxonomic position of this genus is not clear. Adrover *et al.* (1993) proposed that it belongs to the family Cricetidae. McKenna & Bell (1997) placed it in the family Muridae, but outside their subfamily Cricetinae (which is equivalent to our family Cricetidae). Mazo *et al.* (1985) suggested a relation with the family Ctenodactylidae. Fejfar (1999) included it in the microtoid cricetids (*sensu* Schaub, 1934; Stehlin & Schaub, 1951), an informal taxonomical category that groups some cricetids with pronounced hypsodonty. The genus is poorly known, its record is very discontinuous and the material is scarce.

Blancomys is very rare in the south of the Iberian Peninsula. *Blancomys neglectus* is known from Huéscar-3 (Mazo *et al.*, 1985) and Barranco de Quebradas-1 (Sesé, 1989), and *Blancomys meini* only from Moreda (Castillo, 1990).

Until now, *B. sanzi* was only known from Upper Turolian localities in Teruel (Mein *et al.*, 1990), but now it is known from the Early Ruscinian (PUR-4), too. There is a reference of two specimens and a fragment of *B. sanzi* in Alcoy by Adrover *et al.* (1993), but the measurement data appear to be erroneous and we prefer not to use this record. *Blancomys neglectus* occurs in latest Early Ruscinian localities (Mein *et al.*, 1990). *Blancomys meini* occurs in the latest Ruscinian and lowest Villafranchian. The genus disappeared in the Villafranchian.

Blancomys aff. *sanzi* from BRA-5B (latest Turolian) is larger than *B. sanzi* from PUR-4 (earliest Ruscinian) and its size is close to *B. meini*. It may represent an unknown lineage of large-sized *Blancomys*.

Family Gliridae Muirhead, 1819
Subfamily Dryomyinae de Bruijn, 1967
Genus *Eliomys* Wagner, 1840

Type species – *Eliomys melanurus* Wagner, 1840.

***Eliomys truci* Mein & Michaux, 1970**

Pl. 4, figs. 1-8.

Holotype – Unnumbered M1-2 deposited in the University of Lyon, France.

Type locality – Hautimagne, France.

Occurrence in the studied localities – OTU-1, OTU-4, PUR-23, PUR-24A, PUR-25, PUR-25A, DHS-1, DHS-16, TCH-1B and TCH-13.

Material and measurements – See Table 9.

Description – *p4* – Subtriangular outline with rounded anterior and posterior borders. The protoconid, anterolophid and metaconid are fused, and they form a rounded-triangular complex with a central depression, posterolingually open in the figured specimen from PUR-23 (Pl. 4, fig. 1). This complex is separated from the mesolophid by a deep valley. There is no centrolophid. Mesoconid and hypoconid are separated. There is a posterotropid. One broad and robust central root.

m1-2 – Rectangular outline. The anterolophid is separated from the protoconid (except in the specimens from PUR-25A) and from the metalophid. There is no anterotropid. The metalophid and the metaconid have a weak contact in one specimen from each of the localities OTU-1 (Pl. 4, fig. 2), PUR-25A and THC-13. The centrolophid is long (except in the specimens from THC-13) and may be in contact with the middle of the metalophid. The metaconid and the large entoconid are separated by a deep valley. There is a well-developed posterotropid, except in one specimen from TCH-13. Three roots (two anterior and one posterior).

Table 9. Measurements of the teeth of *Eliomys truci* from the studied localities.

			Length				Width			
Element	Localities	Nt	N	Min.	Mean	Max.	N	Min.	Mean	Max.
p4	PUR-23	2	1		0.92		2	0.86	0.87	0.88
	OTU-1	1								
m1-2	TCH-13	2	1		0.98					
	TCH-1B	1	1		1.03		1		1.15	
	PUR-25A	2	2	1.19	1.19	1.19	2	1.20	1.23	1.26
	PUR-24A	1	1		1.18		1		1.32	
	PUR-23	2	1		1.22		1		1.27	
	OTU-1	4	3	1.07	1.13	1.18	2	1.26	1.30	1.34
m3	TCH-13	1								
	OTU-1	2	1		0.93		1		1.09	
D4	TCH-13	1	1		0.63		1		0.79	
P4	TCH-13	2					1		1.23	
	DHS-1	1	1		0.94		1		1.33	
	PUR-25	1								
	OTU-4	1	1		0.73		1		1.00	
M1-2	TCH-13	1	1		1.02		1		1.28	
	TCH-1B	2	2	1.08	1.09	1.10	2	1.41	1.43	1.45
	DHS-1	1	1		1.06		1		1.39	
	DHS-16	1	1		1.01		1		1.31	
	PUR-23	1								
	OTU-1	2								
M3	TCH-13	1	1		0.90		1		1.19	
	TCH-1B	1	1		0.96		1		1.31	

m3 – The labial face is longer than the lingual one; the posterior border is rounded. The anterolophid is separated from protoconid and metalophid by a groove. There is a weak centrolophid in the specimen from TCH-13. The metalophid and the mesolophid, which may be slightly sinuous, are separated by a valley, as are the metaconid and the entoconid. There are no accessory crests (anterotropid or posterotropid). The posterolophid is continuous and very much curved. Three roots (two anterior and one posterior).

D4 – Triangular outline. The protocone is higher than the paracone and the metacone. The low and curved anteroloph is in contact with the paracone. There is no centroloph. The low posteroloph is isolated. Roots are not preserved.

P4 – Sub-triangular or trapezoidal outline. The metacone is higher than the paracone. The short and low anteroloph is united to the paracone. There is a precentroloph, except in one specimen from TCH-13. The metacone of the specimen from DHS-1 seems to bear an incipient postcentroloph. The low posteroloph is separated from the metacone, and only in the specimens from OTU-4 and DHS-1 is it connected to the protocone. There are no accessory crests (anterotrope or posterotrope). Roots are not preserved.

M1-2 – Sub-rectangular outline. The anteroloph is separated from protoloph and paracone by a deep valley. The protoloph is sinuous in the specimens from TCH-13 and TCH-1B. There is a well developed precentroloph and, in the specimens from DHS-1, PUR-23 and OTU-1, there an incipient postcentroloph. There are no accessory crests. The metacone is separated from the protoloph. All crests (except for the centroloph and, in the specimen from TCH-13, the posteroloph) are sub-perpendicularly connected to the endoloph. Three roots (one lingual and two labial)

M3 – Trapezoidal outline, with the posterior border narrower. The paracone is larger than the metacone. The protoloph and metaloph are slightly sinuous, and are separated by a deep and wide valley. The specimen from TCH-13 has no centrolophs, but the specimen from TCH-1B has a small and isolated postcentroloph. The posteroloph is straight, short and separated from the metacone. Roots are not preserved.

Discussion – The main features of the studied populations are summarized in Tables 10-12. The outline of the molars tends to be slightly angular and the crests are usually straight, as in *Eliomys truci* Mein & Michaux, 1970, from Hautimagne (Mein & Michaux, 1970; Adrover, 1986), Los Mansuetos, Concud-3 (van de Weerd, 1976), Moreda-1A,-1B, Rambla Seca-1 (Castillo, 1990), Aljezar-B, Orrios (Adrover, 1986), Valdecebro-6 and La Gloria-5 (Adrover *et al.*, 1993), among others. In contrast, the teeth of *E. intermedius* Friant, 1953, from Sète (Friant, 1953), Galera-2, Cañada del Castaño-1, 2, Gorafe-5 (Martín Suárez, 1988), Moreda-1A (Castillo, 1990), La Gloria-4 (Adrover *et al.*, 1993), Arquillo-III, Villalba Alta (Adrover, 1986), Orrios 3 (Adrover, 1986) and Casablanca-B, among others, are larger and have a more rounded outline, as well as more sinuous crests than our specimens. The small size and the simple structure of our specimens agree with *E. truci*. The extant species *Eliomys quercinus* is larger, the teeth have a more rounded contour (especially in the upper molars), and the cusps are higher and more voluminous than in *E. truci.*

Table 10. Summary of the principal features observed in the lower molars of *Eliomys truci.*

						Centrolophid				
		Connection anterolophid-protoconid		Connection metalophid-metaconid		Absent	Connected to metalophid	Without connection to metalophid	Postero-tropid	
		Yes	No	Yes	No				Yes	No
m1-2	TCH-13	0	2	1	1	0	0	2	1	1
	TCH-1B	?	?	0	1	0	0	1	1	0
	PUR-25A	2	0	0	2	0	0	2	2	0
	PUR-25	0	1	1	0	0	0	1	1	0
	PUR-24A	0	1	0	1	0	1	0	1	0
	PUR-23	0	2	0	2	0	1	1	2	0
	OTU-1	0	3	1	2	0	0	3	3	0
m3	TCH-13	0	1	0	1	0	0	1	0	1
	OTU-1	0	2	0	2	2	2	2	0	2

Table 11. Summary of the principal features of the M1-2 of *Eliomys truci.*

	Centrolophs				Connection posteroloph-endoloph	
M1-2	Precentroloph	Postcentroloph	Both	Absent		
					Yes	No
TCH-13	1	0	0	0	0	1
TCH-1B	2	0	0	0	2	0
DHS-1	1?	0	1?	0	1	0
PUR-23	0	0	1	0	1	0
OTU-1	0	0	1	0	1	0

Table 12. Summary of the main features of the M3 of *Eliomys truci*.

M3	Centrolophs						
		Precentroloph		Postcentroloph			
	Absent	Connected to paracone		Connected to metacone		Connection posteroloph-endoloph	
		Yes	No	Yes	No	Yes	No
TCH-13	1	0	0	0	0	1	0
TCH-1B	0	0	0	0	1	1	0

Eliomys intermedius Friant, 1953

Pl. 4, figs. 9-19.

Original reference – *Eliomys quercinus l. intermedius* Friant, 1953.

Holotype – Unnumbered M1, deposit unknown.

Type locality – Sète, France.

Occurrence in the studied localities – PUR-13, TCH-3, TCH-1B and TCH-1.

Table 13. Measurements of the teeth of *Eliomys intermedius* from the studied localities.

			Length				Width			
Element	Localities	Nt	N	Min.	Mean	Max.	N	Min.	Mean	Max.
d4	TCH-3	2	2	1.04	1.05	1.05	2	0.95	0.97	0.98
	TCH-1B	3	3	1.18	1.24	1.29	3	1.11	1.13	1.14
	TCH-1	1	1		1.22		1		1.05	
p4	TCH-3	5	5	1.26	1.38	1.51	5	1.11	1.30	1.43
	TCH-1B	6	5	1.36	1.45	1.59	6	1.24	1.31	1.43
	PUR-13	1					1		1.10	
m1-2	TCH-3	10	10	1.33	1.55	1.60	10	1.69	1.84	1.95
	TCH-1B	12	7	1.49	1.62	1.69	8	1.78	1.91	1.99
	PUR-13	5	5	1.30	1.37	1.48	4	1.45	1.51	1.54
m3	TCH-3	6	6	1.30	1.43	1.49	6	1.50	1.59	1.72
	TCH-1B	6	6	1.28	1.40	1.46	6	1.52	1.61	1.67
	PUR-13	1	1		1.26		1		1.45	
D4	TCH-3	4	3	0.91	0.95	0.98	3	1.23	1.29	1.39
	TCH-1B	2	2	0.80	0.82	0.84	2	1.19	1.21	1.23
P4	TCH-3	6	6	1.13	1.20	1.27	6	1.55	1.61	1.70
	TCH-1B	1	1		1.09		1		1.48	
M1-2	TCH-3	14	13	1.38	1.46	1.62	13	1.77	2.01	2.25
	TCH-1B	13	8	1.36	1.50	1.62	8	1.80	1.95	2.15
	PUR-13	1	1		1.25		1		1.67	
M3	TCH-3	6	6	1.38	1.40	1.43	6	1.68	1.77	1.86
	TCH-1B	4	4	1.36	1.45	1.56	4	1.65	1.74	1.81
	PUR-13	1	1		1.13		1		1.49	

Material and measurements – See Table 13.

Description of the material from TCH-3 – d4: Worn specimens with subtriangular outline, with a slightly convex posterior border. There is a wide lingual valley that separates the metaconid from the high entoconid. The metalophid and the accessory crests are not visible due to the wear. The high and continuous posterolophid is connected to hypoconid and entoconid. Roots are not preserved.

p4 – Subtriangular outline, with a slightly convex posterior border. The fused protoconid and metaconid form a high, triangular complex, which is separated from the mesolophid, mesoconid and entoconid by a deep groove. The mesolophid may be continuous or interrupted (two specimens). Mesoconid and hypoconid are separated. There is no posterotropid. The posterolophid is high and curved. One root with triangular section.

m1-2 – Trapezoidal outline. The anterolophid may be in contact with the protoconid or separated. There is no anterotropid. The metalophid is usually in contact with the metaconid. The centrolophid is present, except in two specimens, and variable in length; it is short, long or discontinuous, and its labial end may be connected to the metalophid or not. The metaconid and the entoconid are separated. There is no endolophid. The mesolophid is continuous except in one specimen. Some specimens have a posterotropid. Large hypoconid. Three roots (two anterior and one posterior).

m3 – The labial face is longer than the lingual one. The anterolophid is usually separated from the protoconid. The metalophid may be in contact with the metaconid. There are no accessory crests. When present, the centrolophid is short. The metaconid and the entoconid are separated by a narrow valley. The posterolophid is continuous. The mesolophid is usually sinuous. Three roots (two anterior and one posterior).

D4 – Triangular outline. Protocone, paracone and metacone are high. The low and short anteroloph is connected labially to the paracone. Protoloph and metaloph are high and continuous. One specimen has a precentroloph, two have a postcentroloph and the other specimen has no centroloph (Pl. 4, fig. 15). The low posteroloph is separated from the metacone. It is connected to the protocone in two specimens. Three roots (one lingual and two labial).

P4 – Triangular outline. Paracone and metacone are usually higher than the protocone. The low and short anteroloph is connected labially to the paracone. In two specimens it is connected lingually to the protoloph. Four specimens have a discontinuous protoloph. Two specimens have a small precentroloph, two have a large precentroloph and a reduced postcentroloph, and the other specimens have no centrolophs. The metaloph is high and continuous. The posteroloph is low and connected lingually to the protocone, and, in one specimen only, it is connected to the metacone. Three roots (one lingual and two labial).

M1-2 – Subrectangular or trapezoidal outline. The anteroloph is separated from the protoloph and from the paracone, except in one case. Paracone and metacone are high and separated. The protoloph and the metaloph are continuous. There is usually a precentroloph and, frequently, the two centrolophs are present; one specimen has only the postcentroloph and in another one both centrolophs are absent. In two specimens the posteroloph is separated from the endoloph. Three roots (one lingual and two labial).

M3 – Trapezoidal outline. The anteroloph is separated from the protoloph and in one specimen it is united labially to the high paracone. The postcentroloph is always present; it may be connected to the metacone. Some specimens have a precentroloph, attached to the paracone. The posteroloph may be connected to the endoloph. Three roots (one lingual and two labial).

Discussion – The occlusal surface is strongly concave, the crests are high and continuous, and the outline of the teeth is rounded. The studied populations show a large variability (Tables 14-16). The specimens are larger than those of *E. truci.* The size and

Table 14. Summary of the principal features of the lower molars of *Eliomys intermedius.*

						Centrolophid				
		Connection anterolophid-protoconid		Connection metalophid-metaconid		Absent	Connected to metalophid	Without connection to metalophid	Postero-tropid	
		Yes	No	Yes	No				Yes	No
m1-2	TCH-3	5	5	6	4	2	3	5	2	8
	TCH-1B	4	6	7	5	0	2	10	6	6
	PUR-13	0	5	4	1	0	2	3	5	0
m3	TCH-3	2	4	3	3	2	1	3	0	6
	TCH-1B	1	4	2	5	2	0	4	1	5
	PUR-13	0	1	0	1	0	0	1		

Table 15. Summary of the principal features of the M1-2 of *Eliomys intermedius*.

M1-2	Centrolophs				Connection posteroloph-endoloph	
	Precentroloph	Postcentroloph	Both	Absent	Yes	No
TCH-3	7	1	5	1	12	2
TCH-1B	8	1	3	0	10	3
PUR-13	0	0	1	0	1	0

Table 16. Summary of the principal features of the M3 of *Eliomys intermedius*.

M3	Centrolophs						Connection posteroloph-endoloph	
	Precentroloph			Postcentroloph				
	Absent	Connected to paracone		Absent	Connected to metacone			
		Yes	No		Yes	No	Yes	No
TCH-3	2	4	0	0	3	3	4	2
TCH-1B	3	1	0	0	3	1	3	1
PUR-13	0	0	0	0	0	1	1	0

morphology (sinuous crests in the upper cheek teeth, especially in M3; connection between metalophid and metaconid in m1-2; well-developed centrolophs in the upper teeth) of our specimens are similar to those of *E. intermedius*. The specimens from PUR-13 are small-sized *E. intermedius*.

Castillo (1990) argued that the presence of the centrolophid in *E. intermedius* decreases through time, while the frequency of the connection between metalophid and metaconid increases. The same author pointed out that in the upper teeth the number of centrolophs increases; M1-2 with two centrolophs are more frequent in younger populations. Our populations corroborate these trends and we also observe a decrease in the frequency of accessory crests (tropids) in m1-2. In Casablanca-B (latest Pliocene), there is a decrease in the presence of accessory crests in m1-2 in comparison with our specimens and two centrolophs are present in all M1-2. Therefore, these younger populations of *E. intermedius* are closer to the extant *E. quercinus* than the older populations.

Table 17. Measurements of the teeth of *Eliomys* aff. *intermedius* from the studied localities.

			Length				Width			
Element	Localities	Nt	N	Min.	Mean	Max.	N	Min.	Mean	Max.
p4	PUR-4	1	1		1.29		1		1.18	
m1-2	PUR-4	12	12	1.19	1.27	1.37	12	1.26	1.42	1.57
m3	CLC-3B	1	1		1.23		1		1.36	
	PUR-4	3	3	1.10	1.19	1.23	3	1.29	1.33	1.39
D4	PUR-4	1	1		0.71		1		0.84	
P4	PUR-4	1	1		0.98		1		1.37	
M1-2	CLC-3B	2	2	1.24	1.25	1.26	2	1.42	1.53	1.64
	PUR-4	2	2	1.17	1.120	1.22	1		1.51	
M3	CLC-3B	1	1		1.20		1		1.45	
	PUR-4	3	2	1.11	1.11	1.11	2	1.37	1.38	1.38

***Eliomys* aff. *intermedius* Friant, 1953**

Occurrence in the studied localities – PUR-4 and CLC-3B.

Material and measurements – See Table 17.

Description of the material from PUR-4 – *p4* – Subtriangular outline, with a curved posterior border. The anterolophid is in contact with the protoconid, thus defining a rounded complex with a posterolabially open central depression. This complex is separated from the mesolophid. The centrolophid is discontinuous. There are no accessory crests. Roots are not preserved.

m1-2 – The anterolophid is united to the protoconid in five out of eleven specimens. The centrolophid is in contact with the midpoint of the metalophid. The metaconid and the entoconid are separated by a valley. In three cases the metalophid is connected to the metaconid. The posterotropid is discontinuous in one specimen. Three roots; two small anterior roots that may be fused at the base, and one broad and robust posterior root.

m3 – The anterolophid is separated from protoconid. There are no accessory crests. There is a centrolophid in two specimens. Two or three roots, depending on whether the anterior root is split or not.

D4 – Subtriangular outline. There is a small anteroloph, an oblique protoloph, a precentroloph and a metaloph that departs from the metacone although it does not reach the protocone. Three roots (one lingual and two labial).

P4 – Subtriangular outline. Small anteroloph united to the paracone. There is a precentroloph. The posteroloph is discontinuous. Roots are not preserved.

M1-2 – The precentroloph extends to the midpoint of the molar and one specimen has a short postcentroloph. One specimen has a short posterotrope. Three roots (one lingual and two labial)

M3 – Trapezoidal outline. One specimen has a sinuous protoloph. The postcentroloph is long in one specimen; the precentroloph is absent. Three roots (one lingual and two labial).

Discussion – The size range in PUR-4 and CLC-3B is intermediate between *Eliomys truci* and *E. intermedius*, and it may overlap the maximum values of *E. truci* and the minima of *E. intermedius*. The morphology of these teeth agrees with *E. intermedius*, because they have a rounded outline, high crests and more developed postcentrolophs as compared to *E. truci*. Most of the m1-2 have a posterotropid; we have already discussed that the presence of the posterotropid in the cheek teeth of *E. intermedius* decreases through time. The postcentrolophs are very well developed in some of the M3, which is characteristic of *E. intermedius*; even the specimen from CLC-3B has two very well-developed centrolophs. Three m1-2 have a metalophid-metaconid connection, which is frequent in *E. intermedius* (Castillo, 1990; Minwer-Barakat, 2005). Because of the size, which is intermediate between *E. truci* and *E. intermedius*, and the morphological resemblance to *E. intermedius*, we ascribe this material to *Eliomys* aff. *intermedius*.

Eliomys sp.

Occurrence in the studied localities – PUR-3 and PUR-7.

Description and discussion – In PUR-3 we found only one worn and digested m3, which presents a very much curved metalophid as well as a centrolophid. There is a broken M1-2 in PUR-7, with the anteroloph separated from the protoloph, a very well developed precentroloph that is in contact with the short postcentroloph and three roots (one lingual and two labial). The material does not allow a specific determination.

Remarks on the genus Eliomys – In the studied localities, three groups of *Eliomys* have been found, *E. truci, E. intermedius* and *E.* aff. *intermedius*. According to Daams & de Bruijn (1995, p. 16), "the oldest record of *Eliomys* is *E. truci* from the Middle Miocene (MN4) of Spain (Daams & Freudenthal, 1988)." However, Daams & Freudenthal (1988) give Solera (MN7-8) as the oldest record. The specimen from Solera, described by Daams (1989) as *E.* cf. *truci*, may be an *Eliomys*, but it is not fully convincing. The first doubtless record of *E. truci* may be from MN9 (Pedregueras 2A, Daams & Freudenthal, 1988). The youngest record of *E. truci* is in TCH-13 (Early Villafranchian). The temporal range of *E. intermedius* is from the Early Ruscinian (PUR-13 or La Gloria-4; Adrover *et al.*, 1993) to the Early Pleistocene (Venta Micena 1, Agustí *et al.*, 1987; Sierra de Quibas, Montoya *et al.*, 2001). Its geographical range is broad, including Europe and western Asia.

There are some localities where *E. truci* and *E. intermedius* co-occur, including Orrios-3, Sète (Adrover, 1986), La Gloria-4, Villalba Alta-1, Escorihuela (Mein *et al.*, 1990), Moreda-1A, -1B, Rambla Seca-1 (Castillo, 1990) and TCH-1B, amongst others. The most abundant *Eliomys* species in Late Ruscinian and Early Villafranchian localities is *E. intermedius*. However, *E. truci* is the only species found in the locality TCH-13 (the youngest locality, Early Villafranchian). This may be due to a climate change in the Villafranchian (Minwer-Barakat, 2005) which favoured the habitats of *E. truci*.

The relationship of *E. assimilis* Mayr, 1979, and *E. reductus* Mayr, 1979, from the Early Vallesian of Germany to *E. truci* and *E. intermedius* is unknown (Daams & de Bruijn, 1995). However, Nadachoswki & Aoud (1995) related these species to *E. quercinus*. Daams & de Bruijn (1995) considered the insular Plio-Pleistocene subgenera of *Eliomys*, such as *Hypnomys, Eivissia* (Balearic Islands), *Tyrrhenoglis* (Sardinia) and *Maltamys* (Malta), as independent genera, because of their more complex dental pattern than in *Eliomys*.

Adrover (1986) proposed a model of cladogenetic evolution for *Eliomys* with an initial division into three groups (Fig. 7). The coexistence of two different species of *Eliomys* in some localities is evidence of the initial cladogenetic evolution of these species (Adrover, 1986). According to Chaline (1972) and Castillo (1990), there is an anagenetic evolution during the latest Pliocene and the Pleistocene in the *E. intermedius - E. quercinus* lineage, because of the increasing dominance of morphotype *quercinus* over morphotype *intermedius*, together with a decrease in size.

Our data of *E. intermedius* from TCH-1B and TCH-3 corroborate the ancestor-descendant relationship between *E. intermedius* and the recent species, *E. quercinus*. Furthermore, *E. intermedius* is the single representative of the genus in the latest Pliocene and Early Pleistocene, until the apparition of *E. quercinus*.

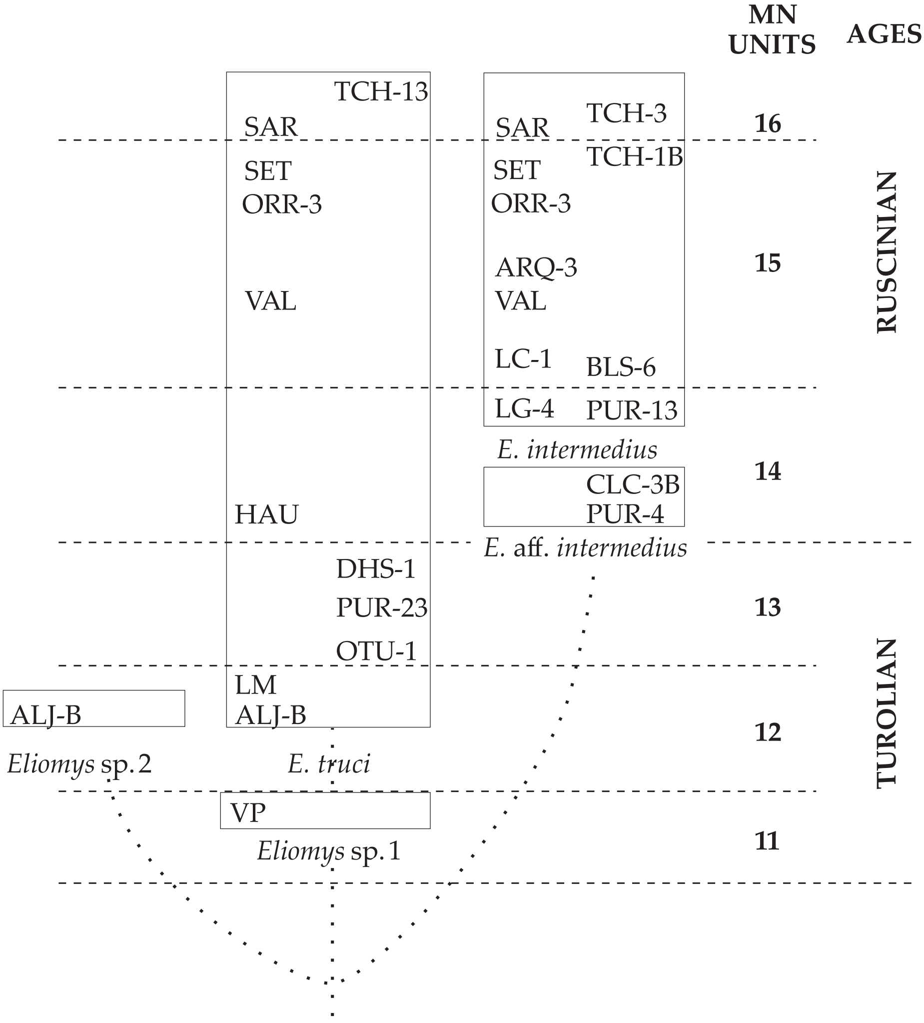


Fig. 7. Hypothesis of the phylogeny of the genus *Eliomys* after Adrover (1986), revised with data from Mein *et al.* (1990) and Mein (1990). The localities in the Granada and Guadix basins are represented on the right. Abbreviations: VP, Viveros de Pino; SET, Sète; HAU, Hautimagne; SAR, Sarrión; ORR, Orrios; VAL, Villaba Alta; LM, Los Mansuelos; ALJ, Aljezar (data from Adrover, 1986); LC, Lomas de Casares (Mein *et al.*, 1990); LG, La Gloria (Mein *et al.*, 1990; Adrover *et al.*, 1993); BLS, Barranco de Blas (García-Alix, 2006).

On the basis of the presence of two recent subspecies of *Eliomys* in the Iberian Peninsula (*E. quercinus quercinus* and *E. quercinus lusitanicus*), Martín Suárez (1988), suggested that *Eliomys quercinus* and *E. intermedius* would have been two subspecies. The two recent subspecies present different dental patterns, different body-size (Moreno Garrido, 1984) and different geographical distributions with some geographic overlap, where intermediate forms exist (ecotypes according to Moreno Garrido, 1984), but they have no significant chromosome differences (Díaz de la Guardia & Ruiz Girela, 1979).

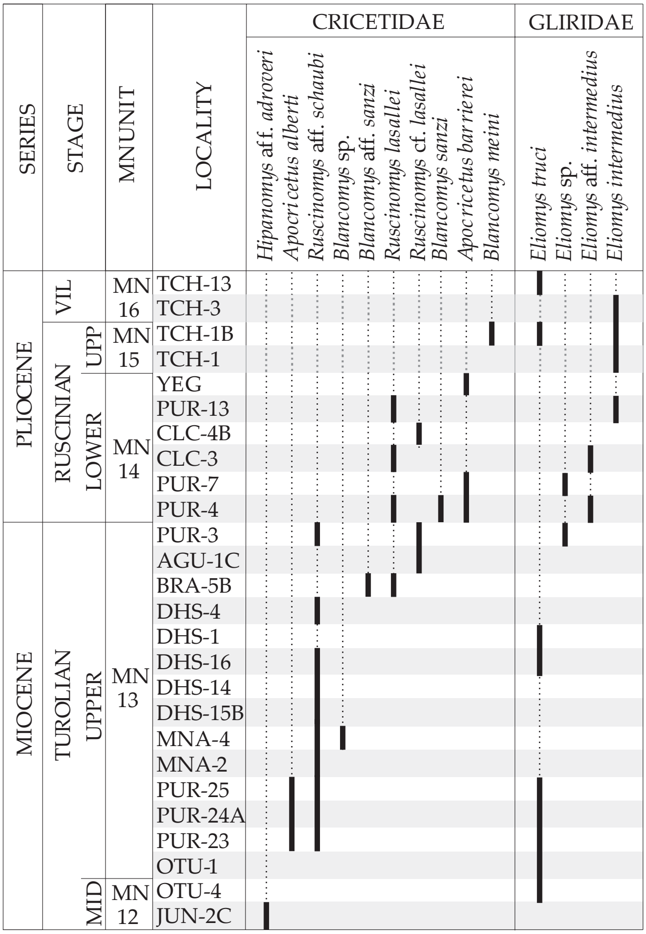


Fig. 8. Distribution range of the studied Cricetidae and Gliridae from the Granada and Guadix basins. The localities are chronologically arranged. Localities from the same stratigraphic level (lateral equivalents) PUR-25 (25+25A), DHS-4 (A+B), and CLC- 3 (3+3B) have been lumped together.

Conclusions

The studied taxa have been recorded in a broad time range. *Hispanomys* is only known in the oldest sedimentary rocks from Granada Basin (Middle Turolian). *Apocricetus barrierei* is a fundamental guide taxon for the Lower Ruscinian. Its presence in the localities PUR-4, PUR-7 and YEG suggest an Early Ruscinian age (Fig. 8).

Ruscinomys aff. *schaubi* is known from the Late Turolian, and *R. lasallei* from the latest Turolain and the Early Ruscinian from the Granada Basin (Fig. 8). Our new data allow us to corroborate the phylogenetic line *Ruscinomys schaubi – R. lasallei – R. europaeus*.

Blancomys aff. *sanzi* from BRA-5B may represent an unknown phylogenetic lineage related to the large-sized *Blancomys*. The record of *Blancomys sanzi* from PUR-4 confirms the presence of this species in the earliest Ruscinian and in the south of Spain; *B. meini* is only known in one studied Late Ruscinian locality from the Guadix Basin (Fig. 8).

The last occurrence of *Eliomys truci* is recorded in TCH-13 (Early Villafranchian). *Eliomys intermedius* from PUR-13 (Granada Basin) and Gloria-4 (Teruel) represent the oldest record of this species (Fig. 8). We agree with the initial cladogenetic evolution of the species of the genus *Eliomys*, and our data of *E. intermedius* from the Ruscinian and Villafranchian corroborate the posterior anagenetic evolution from *E. intermedius* towards *E. quercinus*.

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Plate 1

Figs. 1-5. *Apocricetus alberti* Freudenthal, Mein & Martín Suárez, 1998.
Fig. 1. PUR-25A 81 right m1.
Fig. 2. PUR-25A 84 right m2.
Fig. 3. PUR-25A 87 right m3.
Fig. 4. PUR-25A 88 right M3.
Fig. 5. PUR-24A 98 left M3.

Figs. 6-11. *Apocricetus barrierei* (Mein & Michaux, 1970).
Fig. 6. PUR-4 1 left m1.
Fig. 7. PUR-4 5 right m2.
Fig. 8. PUR-4 10 right m3.
Fig. 9. PUR-4 4 right M1.
Fig. 10. PUR-4 17 left M2.
Fig. 11. PUR-4 19 right M3.

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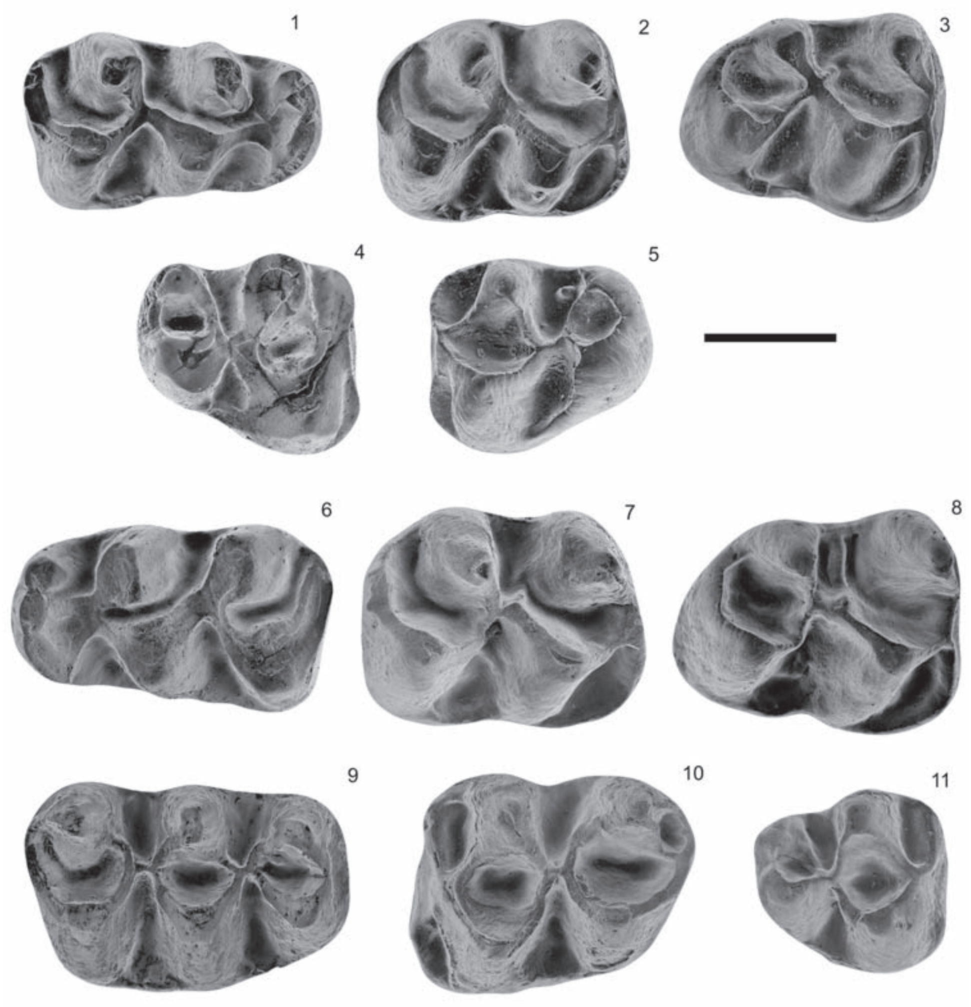
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Plate 2

Figs. 1-3. *Hispanomys* aff. *adroveri* Agustí, 1986.
Fig. 1. JUN-2C 16 right m2.
Fig. 2. JUN-2C 18 right m3.
Fig. 3. JUN-2C 21 right M2-3.

Figs. 4-10. *Ruscinomys* aff. *schaubi* Villalta & Crusafont Pairó, 1956.
Fig. 4. DHS-4B 31 left m1.
Fig. 5. DHS-16 189 right m1.
Fig. 6. DHS-16 191 right m2.
Fig. 7. PUR-25 66 right m3.
Fig. 8. DHS-16 197 right M1.
Fig. 9. DHS-4B 33 left M2.
Fig. 10. PUR-25A 102 left M3.

Figs. 11-18. *Ruscinomys lasallei* Adrover, 1969.
Fig. 11. PUR-4 824 right m3.
Fig. 12. PUR-4 810 right m2.
Fig. 13. PUR-4 794 right m1.
Fig. 14. PUR-4 865 right M3.
Fig. 15. PUR-4 851 right M2.
Fig. 16. PUR-4 832 right M1.
Fig. 17. PUR-13 190 left M1.
Fig. 18. PUR-13 192 left m3.

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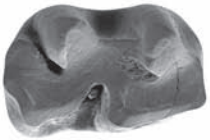
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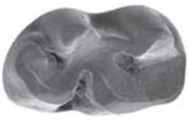
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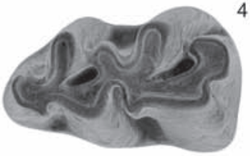
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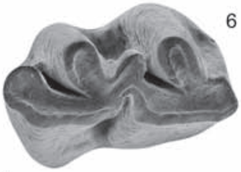
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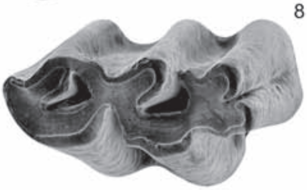
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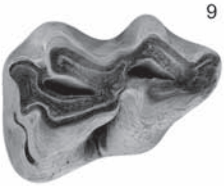
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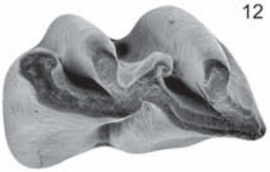
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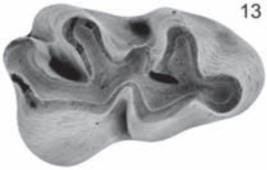
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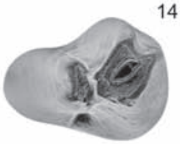
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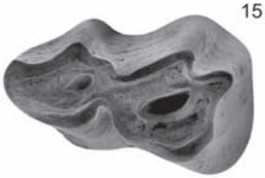
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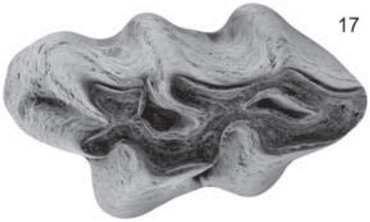
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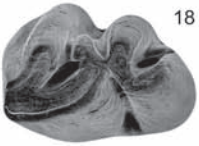
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Plate 3

Figs. 1-3. *Blancomys* aff. *sanzi* Adrover, Mein & Moissenet, 1993.
Fig. 1. BRA-5B 1 left m1 occlusal view.
Fig. 2. BRA-5B 1 left m1 labial view.
Fig. 3. BRA-5B 1 left m1 lingual view.

Figs. 4-11. *Blancomys sanzi* Adrover, Mein & Moissenet, 1993.
Fig. 4. PUR-4 781 left M1 occlusal view.
Fig. 5. PUR-4 781 left M1 labial view.
Fig. 6. PUR-4 781 left M1 lingual view.
Fig. 7. PUR-4 779 left m3.
Fig. 8. PUR-4 782 left M2 occlusal view
Fig. 9. PUR-4 782 left M2 labial view.
Fig. 10. PUR-4 782 left M2 lingual view.
Fig. 11. PUR-4 784 right M3.

Figs. 12-14. *Blancomys meini* Adrover, 1986.
Fig. 12. TCH-1B 620 left m1.
Fig 13 TCH-1B 623 right M2.
Fig 14 TCH-1B 624 left M3.

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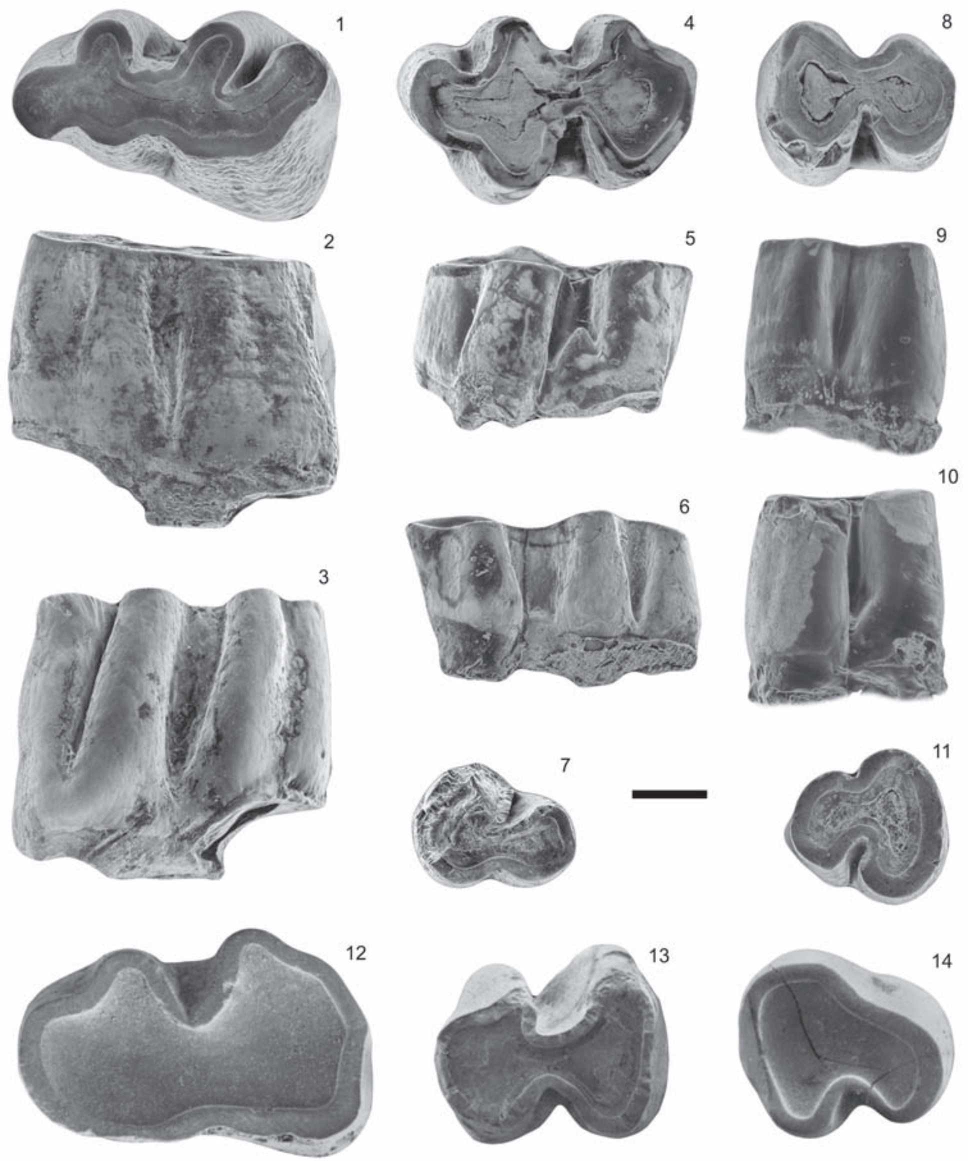
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Plate 4

Figs. 1-8. *Eliomys truci* Mein & Michaux, 1970.
Fig. 1. PUR-23 174 right p4.
Fig. 2. PUR-23 148 right m1-2.
Fig. 3. OTU-1 96 left m1-2.
Fig. 4. OTU-1 97 right m3.
Fig. 5. OTU-4 20 right P4.
Fig. 6. DHS-16 185 right M1-2.
Fig. 7. DHS-1 35 left M1-2.
Fig. 8. TCH-1B 563 right M3.

Figs. 9-19. *Eliomys intermedius* Friant, 1953.
Fig. 9. TCH-1B 590 right m3.
Fig. 10. TCH-1B 582 right m1-2.
Fig. 11. TCH-1B 577 right m1-2.
Fig. 12. TCH-1B 565 right d4.
Fig. 13. TCH-1B 571 right p4.
Fig. 14. PUR-13 200 left m3.
Fig. 15. TCH-1B 591 left D4.
Fig. 16. TCH-1B 593 15 right P4.
Fig. 17. TCH-1B 595 left M1-2.
Fig. 18. PUR-13 201 left M1-2.
Fig. 19. TCH-1B 609 right M3.

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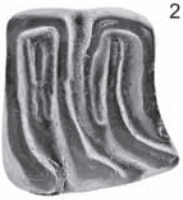
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