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I. García-Paredes (Israel), P. Peláez-Campomanes, M. Á. Álvarez-Sierra

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Gliridae (Rodentia, Mammalia) with a simple dental pattern: a new genus and new species from the European Early and Middle Miocene

ISRAEL GARCÍA-PAREDES^{1,2*}, PABLO PELÁEZ-CAMPOMANES² and M. ÁNGELES ÁLVAREZ-SIERRA³

¹Nationaal Natuurhistorisch Museum – Naturalis, P.O. Box 9517, 2300 RA Leiden, The Netherlands

²Museo Nacional de Ciencias Naturales – CSIC, C/ José Gutierrez Abascal 2, 28006 Madrid, Spain

³Departamento de Paleontología, Facultad de Ciencias Geológicas, Universidad Complutense de Madrid, C/ José Antonio Novais 2, 28040 Madrid, Spain

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A new genus of Gliridae, *Simplomys* gen. nov. is proposed. It contains glirids with a simplified dental pattern from the European Early and Middle Miocene. *Simplomys* gen. nov. includes several species originally described as *Pseudodryomys* such as *Simplomys simplicidens*, *Simplomys robustus*, *Simplomys julii*, and *Simplomys aljaphi*. In addition, a new species, *Simplomys meulenorum* sp. nov., is proposed from the Spanish Miocene. The species of this genus share not only a very reduced and simplified dental morphology, but also unique dental proportions that clearly separate them from any other genera of Gliridae. *Simplomys* gen. nov. is recorded in most of the fossil faunas from the Early and Middle Miocene of the Iberian Peninsula, and shows the maximum diversity in this area during Mammal Neogene Zones MN 3 and MN 4. The genus has been also recorded in other European countries such as France, Germany, and Switzerland, conferring to this very characteristic taxon an important role for biochronological correlations within the European continent.

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ADDITIONAL KEYWORDS: dental morphology – Europe – evolution – micromammals – Neogene – *Pseudodryomys* – rodents – Spain – systematics.

INTRODUCTION

The Early and Middle Miocene comprise one of the most important intervals in the evolutionary history of the ‘Old World’ family Gliridae (Rodentia, Mammalia). During this period, they reached their maximum diversity and relative abundance, becoming the most important group in European rodent faunas (Daams & de Bruijn, 1995). This maximum diversity of the family was not only related to an increase in the redundancy of existing dental morphologies but also because of evolution towards new morphological configurations that probably represented an increase in niches occupied by this family. Amongst the new

morphological configurations, the evolution towards a more simple dental morphology that occurred during the Early Miocene mainly in the Iberian Peninsula stands out. The glirids with a simple dental morphology are especially abundant in Spanish Lower and Middle Miocene micromammal assemblages, representing the most diverse group of glirids in this area. Most of the species having a simple dental pattern are included in the genera *Armantomys* De Bruijn, 1966, *Praearmantomys* De Bruijn, 1966, and *Pseudodryomys* De Bruijn, 1966. The first two genera, in addition to their trend towards dental simplification, show relatively high crowned teeth, which is a unique character amongst the glirids, and are endemic to the Iberian Peninsula, as was pointed out by Daams (1991) in his revision of these two genera (for comments about correct date of publications and

*Corresponding author. E-mail: paredes@naturalis.nl; isgarpa@mncn.csic.es

various species described in the latter paper see García-Paredes & van den Hoek Ostende, 2007). The species included in *Pseudodryomys* have more brachyodont teeth, interpreted as less specialized, and had a wider distribution through Europe.

The genus *Pseudodryomys* was defined based on material from Miocene localities of the Calatayud–Montalbán basin (Spain) and contained two different morphologies. The first morphology is represented by the type species *Pseudodryomys ibericus* De Bruijn 1966, which shows a rather conservative morphology. The second one is represented by *Pseudodryomys simplicidens* De Bruijn, 1966 which shows a derived simplified morphology and proportional reduction of the outer dental elements of the cheek teeth row.

Despite the important morphological differences shown by these two species (Daams, 1974), subsequently described species having affinities with either of these two morphologies have been assigned to *Pseudodryomys* without questioning the homogeneity of the genus (Hugueney *et al.*, 1978; Daams, 1989; Martín-Suárez, Freudenthal & Agustí, 1993; Daams & de Bruijn, 1995; Daams, 1999).

Daams (1974) gave detailed descriptions of *Pseudodryomys* from ten Lower and Middle Miocene Spanish localities. Since then, no further detailed descriptions were made until the unpublished work of García-Paredes (2006), even though the number of micromammal localities from the Spanish Lower and Middle Miocene has increased enormously. In the Gliridae assemblages, *Pseudodryomys* (*sensu* Daams & de Bruijn, 1995) is particularly abundant (García-Paredes, 2006). This increase in information and available material, which remained unstudied for a long time, allows us to define better the different species and evaluate changes in size and morphology amongst the various assemblages.

Several species of *Pseudodryomys* with a simple dental pattern form a well-defined group with particular dental proportions of premolars and third lower molars and more simplified morphology of those elements. These derived characters can be used as diagnostic criteria to propose a new genus, *Simplomys* gen. nov. from Lower and Middle Miocene localities of Spain, Portugal, France, Germany, and Switzerland. Revision of the species assigned to the new genus allows to solve taxonomic problems, to specify the stratigraphical distribution of species and the recognition of a new species of this genus, *Simplomys meulenorum* sp. nov.

MATERIAL AND METHODS

The nomenclature for the parts of the occlusal surface of the cheek teeth of Gliridae (Fig. 1) is modified after

De Bruijn (1966) and Daams (1981). P/p and M/m is used for upper/lower premolars and upper/lower molars respectively. The measurements of specimens were taken with a Nikon Measuroscope 10 microscope with digital micrometer and are given in mm units. Width represents the maximum width of the crown, taken parallel to the contact facet of the posterior wall, in the case of premolars and first molars, or the anterior wall in second and third molars. Length represents the maximum length of the crown and was measured at right angles to the width. Whenever possible, two indexes were calculated: ‘surface’ as length multiplied by width in mm², and the length: width ratio, a nondimensional index that gives an idea of the slenderness of the tooth.

Additional indices for the relative size of P4/p4 and M3/m3 were calculated by dividing the surface of P4/p4 and M3/m3 by the surface of adjacent teeth (M1/m1 and M2/m2, respectively). These indices represent the relative dental proportions. The ratios were calculated from the average values for surface (Appendix). As a rule, this was only carried out when at least five measurable specimens of each element were available. However, exceptions were made in order to include type localities of important species and/or small collections. Localities, species, and values used to calculate those indices are shown in the Appendix. Scatter diagrams presented in Figure 2A and B and Figure 3A and B show the length:width ratios of P4/p4 and M3/m3 versus their relative dental proportions. Table 1 lists the material studied, including abbreviations for fossil sites and institutions where collections are stored (see below). Descriptive statistics for measurements of the studied assemblages are given in Tables 2 and 3.

Size comparisons between *Simplomys* gen. nov. species were carried out by performing Student’s t-test in localities containing the two species to compare and at least five data per dental element of each species (Table 4).

The chronological framework and correlations used in this paper, as well as the stratigraphical distribution of species of *Simplomys* gen. nov., are shown in Table 5.

The photographs of specimens were taken on the Environmental Scanning Electron Microscope FEI Quanta 200 in environmental mode at the ‘Museo Nacional de Ciencias Naturales – CSIC’ (National Museum of Natural Sciences – CSIC) in Madrid (Spain). All specimens in Figures 4–9 are figured as if they are from the left side. If the original is from the right side its label is underlined on the plates. Holotypes are indicated by an italic character.

Lists of synonymies of species include only those references that imply a change in name in order to

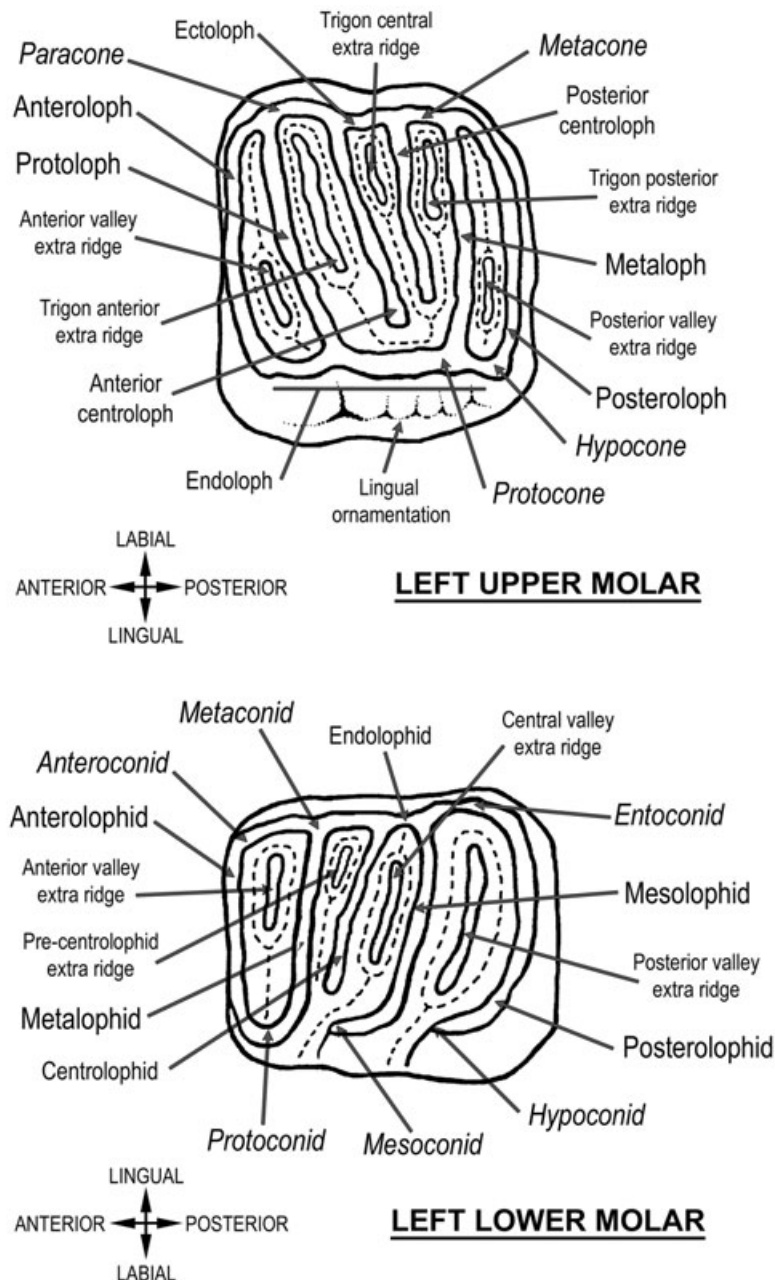


Figure 1. Nomenclature of parts of the occlusal surface of the cheek teeth of Gliridae modified after De Bruijn (1966) and Daams (1981). Drawings represent molars from the left side and names in italics indicate main cusps.

avoid very long lists of complete references, which are given in Supporting Information Appendix S1.

INSTITUTIONAL ABBREVIATIONS

MNCN, Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain; RGM, Nationaal Natuurhistorisch Museum – Naturalis, Geology Department (formerly Rijksmuseum van Geologie en Mineralogie), Leiden, The Netherlands.

SYSTEMATIC PALAEONTOLOGY

STATE OF THE ART

The genus *Pseudodryomys* was proposed by De Bruijn (1966) for Gliridae of intermediate size that have cheek teeth with concave occlusal surfaces and low crowns. Two different morphologies were included within this genus: one represented by the type species *Ps. ibericus* De Bruijn, 1966 and the other by *Ps. simplicidens* De Bruijn, 1966, both defined in Miocene

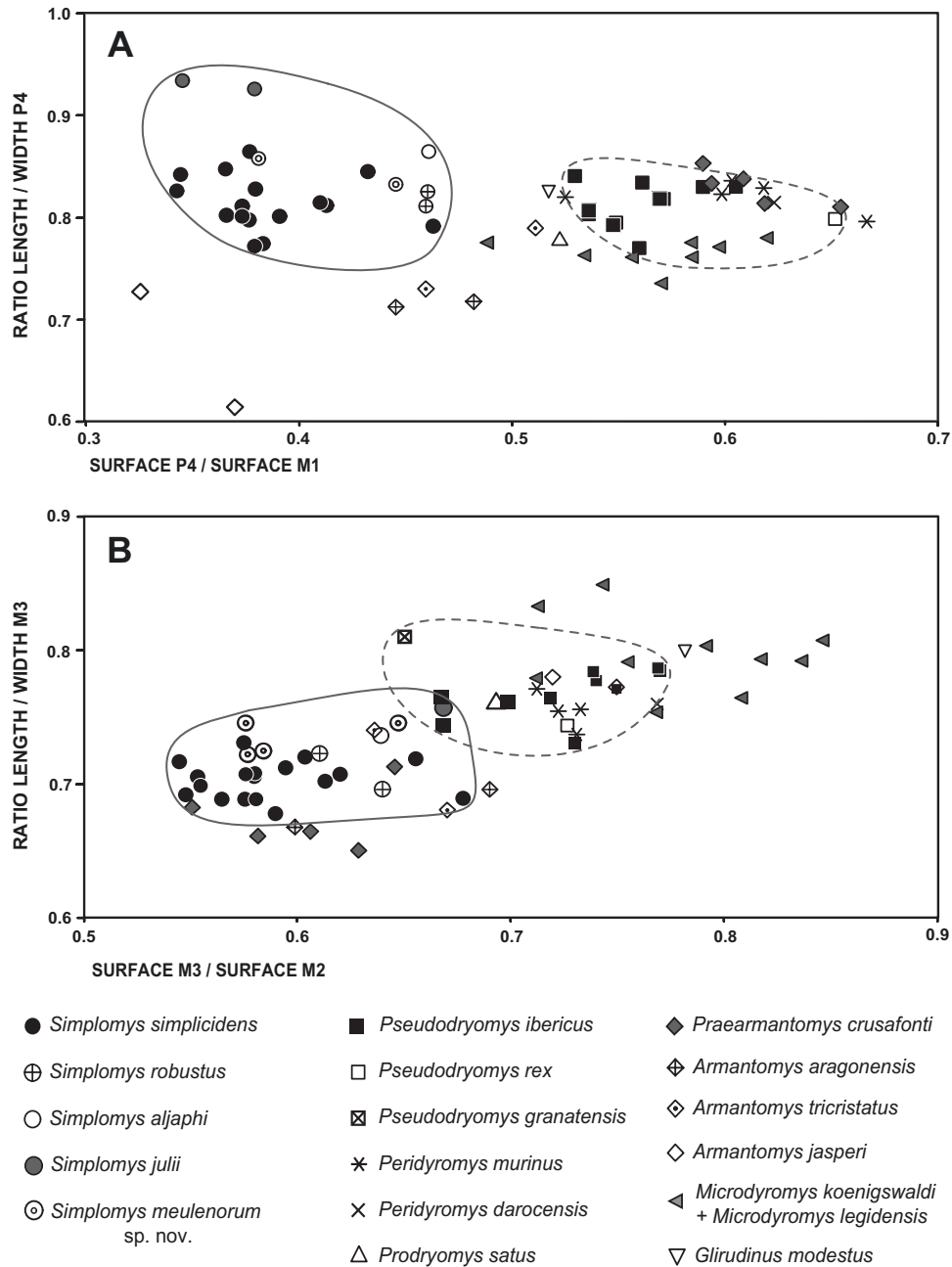


Figure 2. A, scatter diagram of the ratio of length : width of the P4 and the surface of P4/M1 in several Gliridae assemblages. B, scatter diagram of the ratio of length : width of the M3 and the surface of M3/M2 in several Gliridae assemblages (see Appendix for details). The circles denote the ranges of the *Simptomys* gen. nov. assemblages (continuous line) and the *Pseudodryomys* assemblages (discontinuous line).

localities from the Calatayud–Montalbán basin. The most common dental pattern in *Ps. ibericus* consists of upper molars with four main ridges, two centrolophs and sometimes one or two extra ridges inside the trigon. Lower molars always have one posterior extra ridge and a relatively long centrolophid in addition to the four main ridges. In contrast, *Ps. simplicidens* is

characterized by a simple dental pattern. The most common morphology shows only the four main ridges in the upper molars and lower molars with a short centrolophid as the only additional crestid. Subsequent species assigned to *Pseudodryomys* have been recognized as part of the two main morphological groups: *Pseudodryomys aljaphi* Hugueney *et al.*,

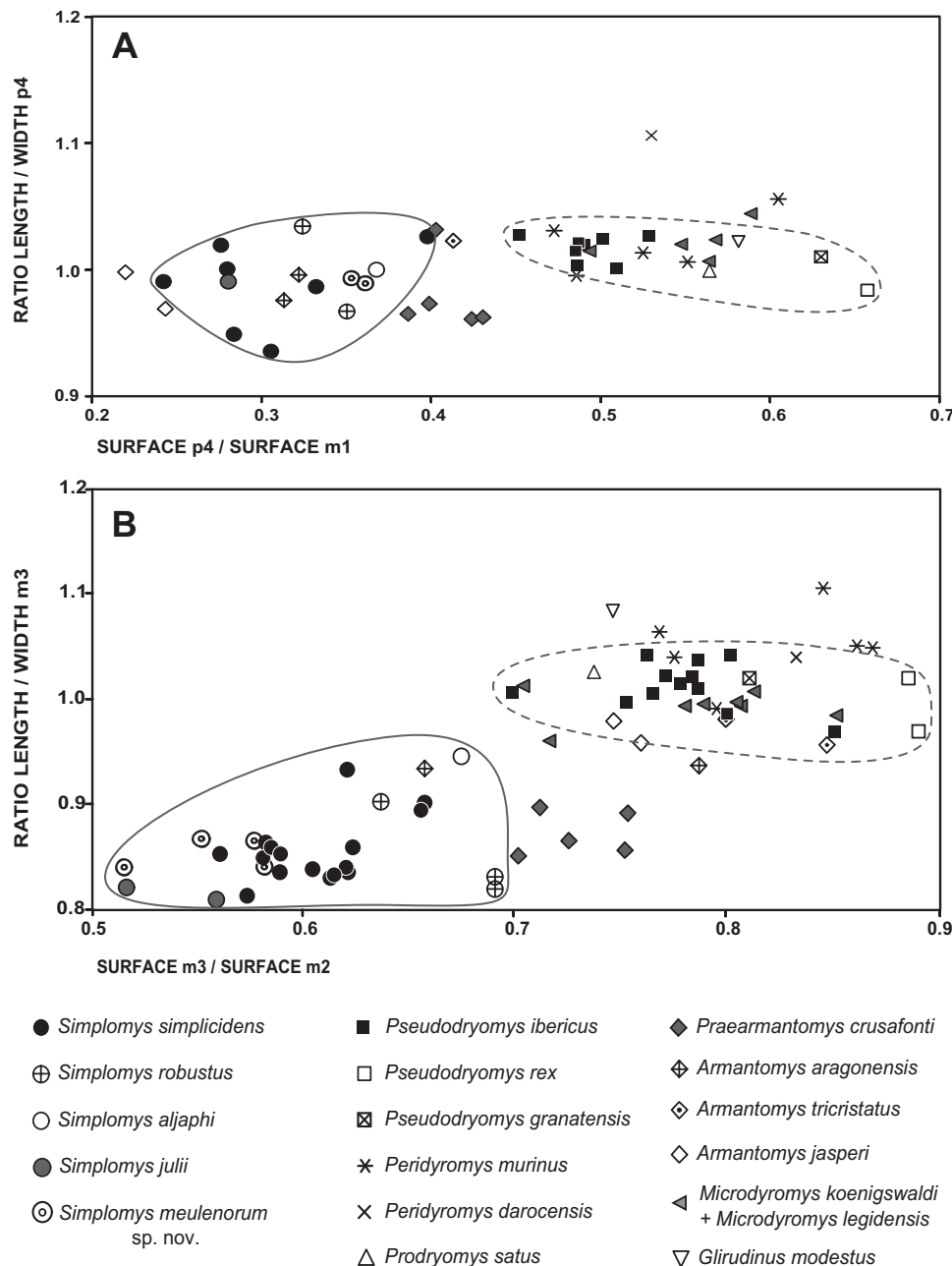


Figure 3. A, scatter diagram of the ratio of length : width of the p4 and the surface of p4/m1 in several Gliridae assemblages. B, scatter diagram of the ratio of length : width of the m3 and the surface of m3/m2 in several Gliridae assemblages (see Appendix for details). The circles denote the ranges of the *Simplomys* gen. nov. assemblages (continuous line) and the *Pseudodryomys* assemblages (discontinuous line).

1978, *Pseudodryomys rex* (García-Moreno, 1986 in Álvarez Sierra & García-Moreno, 1986), and *Pseudodryomys granatensis* Agustí, 1993 in Martín-Suárez *et al.*, 1993, are placed with *Ps. ibericus* in the more complex group (Daams & de Bruijn, 1995; Daams, 1999). *Pseudodryomys robustus* De Bruijn, 1967; *Pseudodryomys julii* Daams, 1989 and *Ps. simplicidens* are included in the simple dental pattern

group (Daams & de Bruijn, 1995; Daams, 1999). The latter group was recognized on the basis of its particular dental morphology. *Pseudodryomys simplicidens* and *Ps. robustus* were considered as morphologically identical species (De Bruijn, 1967; Daams, 1974) that differ only in size, *Ps. simplicidens* being smaller than *Ps. robustus*. This led to the use of the term ‘simplicidens – robustus’ or the term

Table 1. Material of *Simplomys meulenorum* sp. nov. from localities of the Aragonian type area (Calatayud–Montalbán basin, Spain)

<i>Simplomys meulenorum</i> sp. nov.					P4	M1	M2	M3	p4	m1	m2	m3	Total
MN 4	C	16.13	Vargas 3	VR3 (MNCN)	1	3	7	4	–	2	3	3	23
		16.14	Vargas 1A	VR1A (RGM)	3	9	22	8	4	6	4	7	63
		16.15	Vargas 4BB	VR4BB (MNCN)	1	4	8	4	–	1	4	9	31
		16.16	Vargas 4B	VR4B (MNCN)	–	–	2	–	–	–	2	1	5
		16.18	Vargas 4A	VR4A (MNCN)	–	3	1	4	–	3	5	7	23
		16.35	San Roque 3	SR3 (MNCN)	1	6	5	3	–	5	6	7	33
		16.51	Artesilla	ART (MNCN)	8	10	12	10	4	16	14	9	83
	B	16.67	San Roque 2	SR2 (RGM)	3	11	14	10	–	11	15	11	75
		16.70	San Marcos	SAM (MNCN)	2	–	2	1	–	1	1	1	8
		16.73	Olmo Redondo 2	OR2 (RGM)	3	1	6	1	–	1	–	6	18
		16.76	Olmo Redondo 1	OR1 (RGM)	–	–	–	1	–	1	–	1	3
		16.78	San Roque 1	SR1 (RGM)	3	10	21	13	2	14	12	21	96

Total number of specimens in Aragonian type area (Calatayud–Montalbán Basin) = 461. Left columns include Mammal Neogene Zones (MN), local zones and numerical ages (in My) after Daams *et al.*, 1999, as well as abbreviations for localities and institutions where collections are stored (see Material and Methods). Type locality in bold.

‘simplicidens-group’ that also included *Ps. julii* after 1989 (e.g. Daams & Freudenthal, 1981, 1988; Cuenca *et al.*, 1983; Daams & van der Meulen, 1984; Sesé, López-Martínez & Herráez, 1985; Daams, Freudenthal & Álvarez Sierra, 1987; Van der Meulen & Daams, 1992; Daams *et al.*, 1997; Daams *et al.*, 1998). Thus, the group was treated as a supraspecific entity.

Álvarez Sierra *et al.* (1991) raised the question as to whether or not *Ps. simplicidens* and *Ps. robustus* should be included in the genus *Pseudodryomys*. A discussion on that subject was not included, because it was beyond the scope of their paper (for comments about the correct date of publication of various species described in Álvarez Sierra *et al.*, 1991, see García-Paredes & van den Hoek Ostende, 2007). No further mention has been made about the option to exclude the species with a simple dental pattern from *Pseudodryomys* until the unpublished work of García-Paredes (2006), in which the designation of a new genus to include them was proposed.

In this paper we formally propose the new genus *Simplomys* gen. nov. to include all the species that show a highly simplified dental morphology and/or with a reduction in the size proportions of the upper and lower premolars and third molars relative to the first and second molars, as will be discussed below, that were previously included in the genus *Pseudodryomys*.

ORDER RODENTIA BOWDICH, 1821

FAMILY GLIRIDAE MUIRHEAD, 1819

SIMPLOMYS GARCÍA-PAREDES GEN. NOV.

Type species: *Pseudodryomys simplicidens* De Bruijn, 1966.

Diagnosis: Small to large-sized Gliridae with simple dental pattern and cheek teeth with moderately concave occlusal surface. The crowns of the cheek teeth are of medium height and the ridges are wide. Premolars are small and very simplified in morphology compared to molars. The upper molars generally consist of the four main ridges only; one centroloph may be present and in some cases even two. Centrolophs are usually not longer than half the width of the occlusal surface. In M1 and M2 the anteroloph ends freely on the lingual side. The protoloph and metaloph are connected before reaching the lingual border, forming an Y-shaped trigon. The lower molars have four or five ridges. If present, the centrolophid is small; its morphology varies from a short prolongation on the anterior lingual border to a well-developed ridge that extends diagonally into the central valley. Its length never exceeds the central axis of the occlusal surface. The mesolophid of the m3 is reduced and does not reach the labial border. The extension of the posterior valley varies from half the width of the occlusal surface to absent.

Differential diagnosis: *Simplomys* gen. nov. differs from *Pseudodryomys* De Bruijn, 1966, *Peridyromys* Stehlin & Schaub, 1951, *Miodryomys* Kretzoi, 1943, and *Prodryomys* Mayr, 1979 by its simpler dental pattern and by having relatively smaller and simplified premolars and lower third molars. In *Simplomys* gen. nov. the mesolophid of the m3 and the p4 is reduced and the posterior valley may be absent.

Simplomys gen. nov. differs from *Pseudodryomys* and *Peridyromys* by having a less concave occlusal surface in the upper molars.

Table 2. Descriptive statistics for *Simplomys meulenorum* sp. nov. upper cheek teeth from localities of the Aragonian type area (Calatayud–Montalbán basin)

	L						W						Surface area (L × W)						L / W ratio					
	N			Mean			SD			Min.			Max.			Mean			N			Min.		
P4																								
C	16.13	VR3	1		0.80					1	1.07		1.10			1	0.86		1			1	0.75	
	16.14	VR1A	3	0.80	0.86	0.90				2	1.07		1.10			2	0.94	0.97	2	0.82		2	0.82	0.82
	16.15	VR4BB	1		0.79					1	1.07					1	0.85		1			1	0.74	
	16.35	SR3	1		0.90																			
	16.51	ART	8	0.88	0.93	0.98	0.040			8	1.04	1.12	1.17	0.042		8	0.95	1.04	1.15	0.071	8	0.78	0.83	0.88
B	16.67	SR2	1		0.85					2	1.02	1.04	1.05			1	0.89		1			1	0.81	
	16.70	SAM	1		0.82					1	1.01					1	0.83					1	0.81	
	16.73	OR2	3	0.76	0.82	0.86				3	0.97	1.01	1.05			3	0.76	0.83	0.90		3	0.76	0.82	0.87
	16.78	SR1	3	0.81	0.84	0.89				3	0.95	0.99	1.01			3	0.81	0.83	0.85		3	0.81	0.86	0.94
M1																								
C	16.13	VR3	3	1.39	1.45	1.49				3	1.67	1.67	1.68			3	2.32	2.42	2.49		3	0.83	0.86	0.89
	16.14	VR1A	9	1.27	1.46	1.55	0.086			7	1.57	1.64	1.73	0.064		7	2.03	2.42	2.68	0.224	7	0.79	0.90	0.94
	16.15	VR4BB	4	1.40	1.47	1.58				4	1.57	1.65	1.76			4	2.21	2.43	2.78		4	0.87	0.89	0.90
	16.18	VR4A	1		1.40					1	1.61													
	16.35	SR3	6	1.38	1.48	1.57	0.081			5	1.57	1.64	1.70	0.050		5	2.17	2.43	2.64	0.183	5	0.82	0.90	0.95
B	16.51	ART	10	1.37	1.44	1.52	0.053			9	1.53	1.60	1.69	0.053		9	2.11	2.33	2.55	0.138	9	0.85	0.90	0.96
	16.67	SR2	8	1.32	1.39	1.45	0.043			6	1.52	1.56	1.59	0.029		6	2.04	2.17	2.31	0.112	6	0.85	0.89	0.92
	16.73	OR2	1		1.44																			
	16.78	SR1	9	1.37	1.41	1.46	0.028			10	1.52	1.57	1.62	0.030		9	2.11	2.21	2.30	0.075	9	0.88	0.90	0.94
M2																								
C	16.13	VR3	6	1.36	1.44	1.52	0.068			5	1.66	1.74	1.82	0.071		5	2.32	2.53	2.74	0.203	5	0.82	0.84	0.86
	16.14	VR1A	19	1.26	1.38	1.46	0.063			16	1.59	1.70	1.83	0.074		15	2.04	2.37	2.64	0.184	15	0.78	0.82	0.88
	16.15	VR4BB	6	1.21	1.37	1.52	0.119			7	1.62	1.71	1.85	0.086		6	1.96	2.36	2.75	0.329	6	0.75	0.80	0.84
	16.16	VR4B	2	1.39	1.40	1.41				2	1.63	1.70	1.77			2	2.30	2.38	2.46		2	0.79	0.83	0.87
	16.18	VR4A	1							1	1.77													
B	16.35	SR3	3	1.38	1.38	1.39				3	1.63	1.73	1.78			3	2.27	2.39	2.46		3	0.78	0.80	0.85
	16.51	ART	11	1.35	1.42	1.49	0.045			8	1.70	1.75	1.82	0.036		7	2.36	2.48	2.62	0.101	7	0.79	0.82	0.86
	16.67	SR2	14	1.29	1.33	1.38	0.024			11	1.55	1.64	1.75	0.068		11	2.02	2.18	2.35	0.117	11	0.77	0.81	0.85
	16.70	SAM	2	1.23	1.24	1.25				1	1.58					1	1.94				1	0.78		
	16.73	OR2	6	1.16	1.22	1.28	0.049			6	1.52	1.59	1.69	0.058		6	1.81	1.94	2.11	0.125	6	0.73	0.77	0.81
16.78	SR1	17	1.16	1.29	1.39	0.057				13	1.57	1.63	1.68	0.042		13	1.86	2.09	2.32	0.133	13	0.72	0.79	0.85

Table 2. Continued

M3	L			W			Surface area (L × W)						L / W ratio		
	N	Min.	Mean	Max.	SD	N	Min.	Mean	Max.	SD	N	Min.	Mean	Max.	SD
C	16.13	VR3	4	0.96	0.98	1.02									
	16.14	VR1A	8	1.01	1.06	1.13									
	16.15	VR4BB	4	0.98	1.00	1.01									
	16.18	VR4A	4	0.99	1.04	1.08									
	16.35	SR3	3	0.91	0.94	0.99									
B	16.51	ART	10	0.92	1.03	1.14									
	16.67	SR2	10	0.89	0.95	1.04									
	16.70	SAM	1		0.93										
	16.73	OR2	1		0.97										
	16.76	OR1	1		0.94										
	16.78	SR1	12	0.88	0.94	0.99	0.038	1.23	1.29	1.41	0.055	1.08	1.22	1.37	0.018

L, length; W, width; N, number of specimens; Min., minimum values; Max., maximum values; SD, standard deviation. First and second left columns show local zones and numerical ages (in My) for the localities after Daams *et al.*, 1999. For abbreviations of localities see Table 1. Type locality in bold.

Simplomys gen. nov. differs from *Prodryomys* by having cheek teeth with higher and thicker ridges with slanting walls, as well as narrower valleys.

Simplomys gen. nov. differs from *Armantomys* De Bruijn, 1966 and *Praearmantomys* De Bruijn, 1966 by having molars with thinner and lower ridges, by having upper molars with protoleph and metaloph always connected at the lingual half of the occlusal surface forming an Y-shaped trigon. In *Simplomys* gen. nov. the molars are not progressively smaller from M1/m1 through to M3/m3 as in *Armantomys* and *Praearmantomys*.

Simplomys gen. nov. differs from *Tempestia* Van de Weerd, 1976 by having molars with thinner and lower ridges, M1 and M2 with Y-shaped trigon, m1 and m2 longer than wider and the posterior part of the m3 more reduced and simplified.

Simplomys gen. nov. differs from *Altomiramys* Díaz Molina & López Martínez, 1979 by having cheek teeth with thicker and slanting ridges and narrower valleys, upper molars with less rounded outline and an anterior valley that does not extend along the lingual border to the protocone.

Etymology: After the simplicity of its dental pattern.

Stratigraphical distribution: Local zones X to E (MN 1, Lower Miocene – MN 5, Middle Miocene).

Geographical distribution: Spain, Portugal, France, Switzerland, and Germany.

Species included

Pseudodryomys simplicidens De Bruijn, 1966

Pseudodryomys robustus De Bruijn, 1967

Pseudodryomys aljaphi Hugueney *et al.*, 1978

Pseudodryomys julii Daams, 1989

Simplomys meulenorum sp. nov.

DISCUSSION ON *SIMPLOMYS* GEN. NOV. AND COMPARISON WITH OTHER GENERA

The particular characteristics used to define *Simplomys* gen. nov. are the combination of a simplified dental morphology with unusual dental proportions amongst the different elements of the tooth row. In our opinion, the dentition should be understood as a complete organ and hence a functional entity. It is important to study the variability of all cheek teeth. The importance of premolars and third molars for taxonomy has usually been underestimated. Several works pointed out the difficulties in their specific or even generic assignation (Daams, 1974, 1981, 1999b). In our experience, most of the premolars and third molars can be assigned and provide useful systematic characters.

Table 3. Descriptive statistics for *Simptomys meulendorum* sp. nov. lower cheek teeth from localities of the Aragonian type area (Calatayud–Montalbán basin)

	L			W			Surface area (L × W)						L / W ratio								
	N	Min.	Mean	Max.	SD	N	Min.	Mean	Max.	SD	N	Min.	Mean	Max.	SD	N	Min.	Mean	Max.	SD	
p4																					
C	16.14	VR1A	4	0.85	0.89	0.92		0.87	0.90	0.94		4	0.74	0.80	0.86		4	0.98	0.99	1.00	
	16.51	ART	4	0.76	0.88	0.96		0.86	0.88	0.89		4	0.65	0.77	0.85		4	0.88	0.99	1.08	
B	16.78	SR1	1		0.84			2	0.82	0.85	0.88	0.042	1	0.74			1	0.95			
m1			L				W														
	N	Min.	Mean	Max.	SD	N	Min.	Mean	Max.	SD	N	Min.	Mean	Max.	SD	N	Min.	Mean	Max.	SD	
C	16.13	VR3	1		1.65			5	1.41	1.46	1.55	0.056	5	2.07	2.21	2.54	0.193	5	0.99	1.04	1.06
	16.14	VR1A	6	1.44	1.52	1.64	0.070	1	1.38				1	2.11			1	1.11		0.033	
	16.15	VR4BB	1	1.53	1.53	1.53		2	1.41	1.44	1.46		2	2.20	2.24	2.28	2	1.07	1.09	1.11	
	16.18	VR4A	2	1.56	1.56	1.56		5	1.29	1.34	1.38	0.048	5	1.82	1.97	2.14	0.121	5	1.04	1.10	1.15
	16.35	SR3	5	1.41	1.47	1.55	0.054	15	1.30	1.41	1.53	0.069	14	1.89	2.19	2.51	0.164	14	1.00	1.09	1.19
B	16.51	ART	15	1.43	1.54	1.64	0.062	10	1.21	1.34	1.42	0.066	10	1.63	1.91	2.23	0.162	10	1.01	1.07	1.12
	16.67	SR2	11	1.35	1.42	1.57	0.058													0.036	
	16.73	OR2	1		1.36			1	1.34				1	1.85			1	1.03			
	16.76	OR1	1		1.38			12	1.21	1.31	1.44	0.075	11	1.62	1.83	2.20	0.192	11	1.05	1.08	1.14
	16.78	SR1	13	1.33	1.40	1.53	0.069													0.028	
m2			L				W														
	N	Min.	Mean	Max.	SD	N	Min.	Mean	Max.	SD	N	Min.	Mean	Max.	SD	N	Min.	Mean	Max.	SD	
C	16.13	VR3	1		1.53			3	1.54	1.57	1.60		1	2.36			1	0.99			
	16.14	VR1A	4	1.48	1.56	1.67		4	1.53	1.62	1.70		4	2.26	2.53	2.79	4	0.92	0.96	1.00	
	16.15	VR4BB	4	1.57	1.60	1.62		4	1.50	1.56	1.59		4	2.39	2.48	2.56	4	0.99	1.03	1.06	
	16.16	VR4B	2	1.54	1.55	1.56		2	1.58	1.59	1.60		2	2.46	2.46	2.46	2	0.96	0.97	0.99	
	16.18	VR4A	4	1.50	1.60	1.69		4	1.56	1.64	1.79		4	2.34	2.63	3.03	4	0.94	0.97	1.00	
B	16.35	SR3	6	1.53	1.57	1.63	0.042	6	1.44	1.53	1.62	0.073	6	2.20	2.40	2.61	0.157	6	0.95	1.03	1.06
	16.51	ART	14	1.48	1.60	1.71	0.072	12	1.53	1.62	1.73	0.060	12	2.32	2.60	2.89	0.181	12	0.94	0.99	1.06
	16.67	SR2	14	1.40	1.45	1.54	0.047	13	1.41	1.45	1.50	0.032	13	1.97	2.11	2.28	0.097	13	0.93	1.00	1.05
	16.70	SAM	1		1.44			1	1.45				1	2.09			1	0.99		0.033	
	16.78	SR1	11	1.41	1.47	1.55	0.048	10	1.39	1.48	1.59	0.063	10	2.02	2.16	2.46	0.129	10	0.94	0.99	1.07

Table 3. *Continued*

m3	L				W				Surface area (L × W)				L / W ratio			
	N	Min.	Mean	Max.	SD	N	Min.	Mean	Max.	SD	N	Min.	Mean	Max.	SD	
C	3	1.04	1.11	1.20		3	1.32	1.35	1.41		3	1.38	1.50	1.69		
16.13 VR3	6	1.04	1.08	1.13	0.040	6	1.16	1.24	1.31	0.069	6	1.21	1.33	1.48	0.119	0.85
16.14 VR1A	8	1.00	1.08	1.18	0.065	8	1.20	1.26	1.33	0.047	8	1.24	1.37	1.53	0.109	0.90
16.15 VR4BB	1	1.11				1	1.28				1	1.42				0.053
16.16 VR4B	7	0.99	1.06	1.13	0.056	6	1.17	1.27	1.41	0.083	6	1.17	1.33	1.55	0.136	0.87
16.18 VR4A	7	0.94	1.08	1.13	0.068	7	1.18	1.29	1.40	0.083	7	1.11	1.39	1.54	0.162	0.88
16.35 SR3	8	1.01	1.11	1.21	0.058	8	1.18	1.29	1.41	0.083	8	1.19	1.43	1.71	0.159	0.89
16.51 ART	8	0.89	1.05	1.20	0.097	7	1.07	1.18	1.27	0.082	7	0.96	1.21	1.44	0.170	0.034
B	8	0.89	1.05	1.20	0.097	7	1.07	1.18	1.27	0.082	7	0.96	1.21	1.44	0.170	0.031
16.67 SR2	1	1.02				1	1.20				1	1.22				0.89
16.70 SAM	5	0.90	0.94	0.97	0.027	5	1.06	1.13	1.19	0.047	4	1.07	1.07	1.08		0.85
16.73 OR2	1	1.11				1	1.23				1	1.37				0.82
16.76 OR1	19	0.89	0.97	1.02	0.045	17	1.06	1.15	1.26	0.047	17	0.98	1.11	1.26	0.077	0.90
16.78 SR1																0.84
																0.91
																0.041

L, length; W, width; N, number of specimens; Min., minimum values; Max., maximum values; SD, standard deviation. First and second left columns show local zones and numerical ages (in My) for the localities after Daams *et al.*, 1999. For abbreviations of localities see Table 1. Type locality in bold.

Table 4. Results of Student's t-test comparing size variables in localities containing both *Simplomys simplicidens* and *Simplomys meulenorum* sp. nov. and with at least five data points for each species

<i>S. meulenorum</i> sp. nov. / <i>S. simplicidens</i>	M1				M2				M3			
	SR1	ART	SR3	VR1A	SR1	VR1A	SR2	ART	VR4BB	SR1	VR1A	ART
L	••	••	••	••	••	••	••	••	••	••	••	••
W	••	••	••	••	••	••	••	••	••	••	••	••
Surface area (L × W)	••	••	••	••	••	••	••	••	••	••	••	••
Ratio L / W	NS	NS	NS	NS	NS	NS	•	NS	NS	••	••	•
<i>S. meulenorum</i> sp. nov. / <i>S. simplicidens</i>	m1				m2				m3			
	SR1	ART	SR3	VR1A	SR1	VR1A	SR2	ART	VR4BB	SR1	VR1A	ART
L	••	••	••	••	••	••	••	••	••	NS	••	••
W	••	••	••	••	••	••	••	••	••	••	••	••
Surface area (L × W)	••	••	••	••	••	••	••	••	••	NS	••	••
Ratio L / W	••	•	NS	NS	NS	NS	•	•	NS	••	NS	NS

L, length; W, width; NS, not significant; •, significant ($P < 0.05$); ••, highly significant ($P < 0.01$). For abbreviations of localities see Table 1.

Table 5. Stratigraphical distribution of the species of *Simplomys* **gen. nov.** Series; continental stages; Mammal Neogene Zones (MN zones) proposed for Europe by Mein (1975, 1990) and revised by De Bruijn *et al.* (1992); and local biostratigraphical scale after Daams *et al.* (1999)

MIOCENE																			
(LOWER)					(MIDDLE)														
					ARAGONIAN														
(LOWER)					(MIDDLE)														
‘AEGENIAN’		(LOWER) (UPPER)		RAMBLIAN		(LOWER)		(MIDDLE)											
MN 1		MN 2		MN 3		MN 4		MN 5											
X		Y		Z		A		C											
						B		Da											
								Db											
								Dc											
								Dd											
								E											
LOCAL BIOZONE																			
SPECIES																			
<i>Simplomys aljaphi</i>																			
										<i>Simplomys simplicidens</i>									
										<i>Simplomys robustus</i>									
										<i>Simplomys neulenorum</i> sp. nov.									
<i>Simplomys julii</i>																			

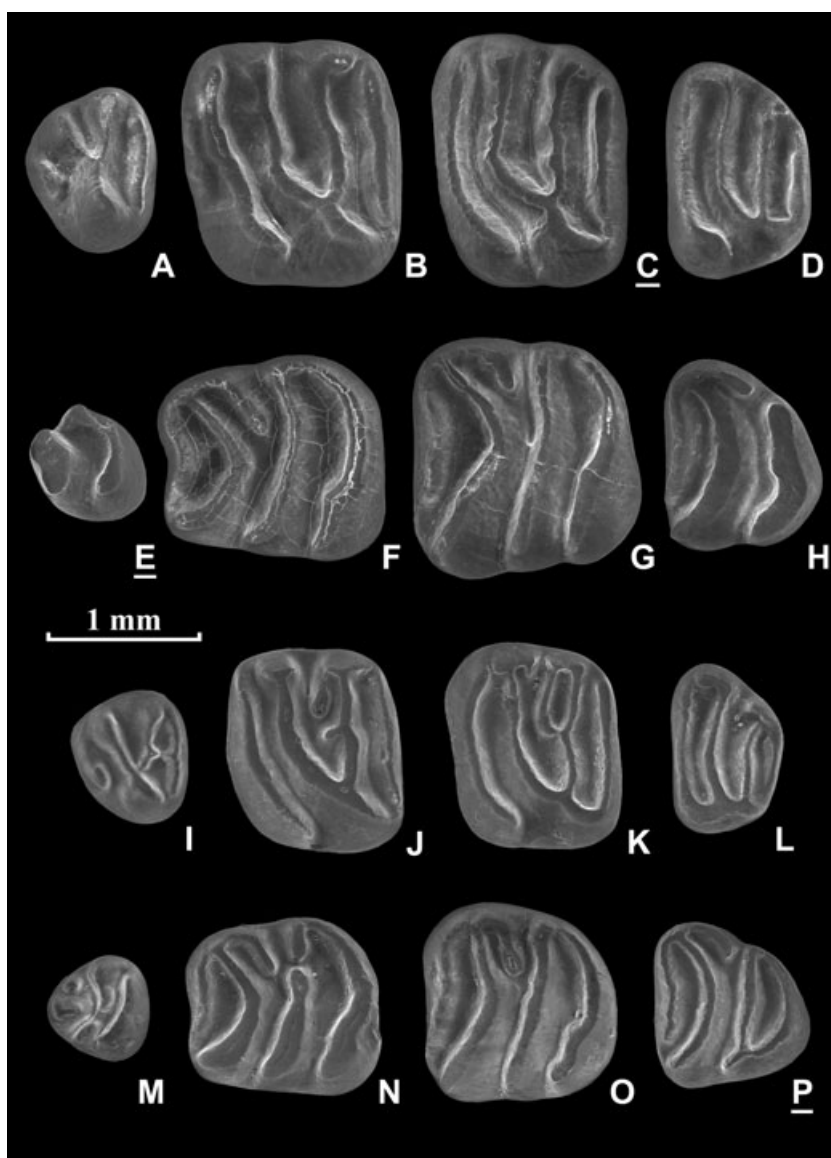


Figure 4. *Simptomys simplicidens* (De Bruijn, 1966) from Valdemoros 3F (Fig. 4A–H) and Artesilla (Fig. 4I–P) (collection MNCN). A, P4 VA3F-27. B, M1 VA3F-39. C, M2 VA3F-52. D, M3 VA3F-62. E, p4 VA3F-342. F, m1 VA3F-73. G, m2 VA3F-76. H, m3 VA3F-95. I, P4 ART-1134. J, M1 ART-931. K, M2 ART-943. L, M3 ART-1173. M, p4 ART-2455. N, m1 ART-966. O, m2 ART-990. P, m3 ART-1186. Right side specimens underlined.

To evaluate relative dental proportions in '*Pseudodryomys*' (*sensu* Daams & de Bruijn, 1995), various assemblages of Miocene species included in that genus and other common species assigned to different genera have been analysed (Appendix).

Several indices have been calculated to evaluate relative dental proportions: (1) the length : width ratios of upper and lower premolars and third molars; (2) the ratios between the surface of the upper and lower premolars and the first molar per species; and (3) the ratios between the surface of the upper and lower third molars and the second molar per species.

The results are shown in scatter diagrams (Figs 2A–B, 3A–B) that represent the slenderness of premolars and third molars (length : width ratio) versus their relative size to adjacent teeth.

In the case of P4 (Fig. 2A), most assemblages fall within a well-defined range of length : width ratio (0.7–0.9) showing small differences amongst most analysed species of Gliridae. Lower values of P4 length : width ratio are for species of *Armantomys*, *Armantomys jasperi* being the lowest, also for the surface P4 : surface M1 ratio. Similar values of surface P4 : surface M1 ratio are occupied by species



Figure 5. *Simplomys robustus* (De Bruijn, 1967) from San Roque 4A (collection MNCN). A, P4 SR4A-895. B, M1 SR4A-754. C, M2 SR4A-778. D, M3 SR4A-787. E, p4 SR4A-921. F, m1 SR4A-801. G, m2 SR4A-804. H, m3 SR4A-918. Right side specimens underlined.

of *Simplomys* gen. nov. but with higher P4 length : width ratios, being clearly separated from the other species and particularly from the species of *Pseudodryomys*. The highest values of P4 length : width ratio are for *Simplomys julii*, which, with the most rounded P4 of all studied species, is outside of the abovementioned Gliridae range.

For the M3 length : width ratio and surface M3 : surface M2 ratio (Fig. 2B), lower values for both indices are for species of *Simplomys* gen. nov., species of *Armantomys*, and *Praearmantomys crusafonti*. They form a clearly differentiated group from the rest of species despite the small overlap between higher values of species of *Simplomys* gen. nov. (*S. julii*) and lower values of *Pseudodryomys ibericus*.

In the case of the p4 (Fig. 3A), there is a similar situation as in the P4 (Fig. 2A). Most analysed species of Gliridae have a p4 length : width ratio of approximately 1.0. The lowest values of the p4 length : width ratio are for *Simplomys simplicidens*. For the p4 : m1 surface ratio there is a clear low values group including species of *Simplomys* gen. nov. and species of *Armantomys*. This group is clearly separated from *Pseudodryomys ibericus* and other *Pseudodryomys* species.

Figure 3B shows the m3 length : width ratio and surface m3 : surface m2 ratio. The lowest values for both indexes are only for species of *Simplomys* gen. nov. with a small overlap between the highest values of species of *Simplomys* gen. nov. (*Simplomys aljaphi*)

and the lowest values of *Armantomys aragonensis*. Two *Simplomys robustus* assemblages with low values of the m3 length : width ratio and medium values of the surface ratio are slightly out of the main *Simplomys* gen. nov. area being near to those of *Praearmantomys crusafonti*.

Based on the obtained results there is a clear differentiation in relative dental proportions amongst the genera with a very simple dental morphology (*Armantomys*, *Praearmantomys*, and *Simplomys* gen. nov.) and those with a somewhat conservative dental morphology (*Pseudodryomys*, *Peridyromys*, *Prodryomys*) or the more complicated ones (*Microdryomys* De Bruijn, 1966 and *Glirudinus* De Bruijn, 1966). All simple-patterned species have relatively small and slender upper and lower premolars and third molars compared to the more complicated species. The differences amongst the three genera with simple dental morphology are the following: *Praearmantomys* has in general less reduced premolars and third molars than *Simplomys* gen. nov. and *Armantomys*. *Simplomys* gen. nov. and *Armantomys* differ mainly by the length : width ratio of the P4, being in general on average smaller in *Simplomys* gen. nov. than in *Armantomys* (Fig. 2A) and the relatively more reduced m3 in *Simplomys* gen. nov. (Fig. 3B). In addition, there is a clear difference in hypsodonty amongst these genera, *Simplomys* gen. nov. being significantly lower crowned than *Armantomys* and *Praearmantomys*.

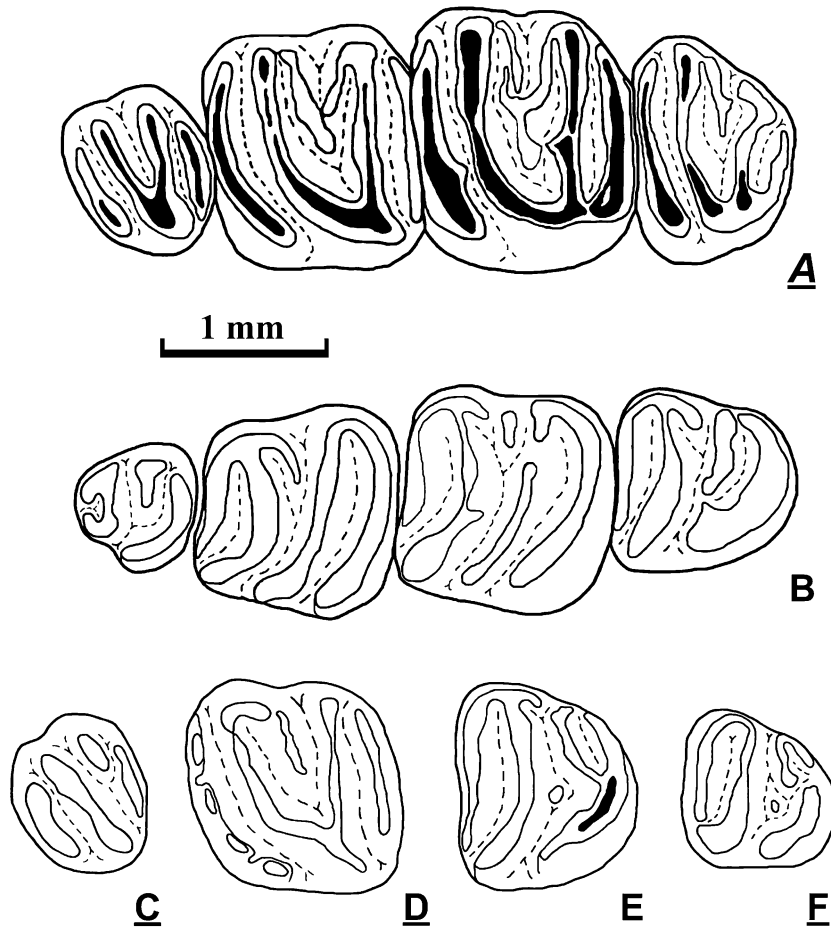


Figure 6. *Simplomys aljaphi* (Hugueneu *et al.*, 1978) from Montaignu-le-Blin (modified after Hugueneu *et al.*, 1978). A, P4-M3 AC. MB 191 holotype. B, p4-m3 P.O. C, P4 AC. MB 103. D, M1 F.S.L. 97 461. E, m3 AC. MB 706. F, m3 F.S.L. 97 464. Right side specimens underlined. Holotype in italics.

The clear differences between the dental proportions of *Simplomys* gen. nov. species and those of *Pseudodryomys* are remarkable. The species assigned to the latter genus show dental proportions closer to the genera *Peridyromys*, *Prodryomys*, and even *Microdryomys* and *Glirudinus* than to *Simplomys* gen. nov.

The morphology of *Simplomys aljaphi* is intermediate in complexity between *S. simplicidens* and *Pseudodryomys ibericus*, as will be discussed below, but it already shows a high degree of reduction in the upper and lower premolars and third molars, and therefore has been included in *Simplomys* gen. nov.

SIMPLOMYS SIMPLICIDENS (DE BRUIJN, 1966)
(FIG. 4)

Synonymy

Pseudodryomys ibericus pro-parte in De Bruijn, 1967
Pseudodryomys cf. *robustus* from Armantes 3 in De Bruijn, 1967: 210

Pseudodryomys robustus from Armantes 3 in Daams, 1974

Pseudodryomys robustus from Armantes 3 in Daams, Freudenthal & van de Weerd, 1977

Pseudodryomys meini Adrover, 1978

Pseudodryomys robustus in Alberdi, Morales & Sesé, 1980

Pseudodryomys robustus in Alberdi *et al.*, 1981

Pseudodryomys robustus in Alberdi *et al.*, 1984

Pseudodryomys robustus in Alberdi *et al.*, 1985

Pseudodryomys robustus in Sesé *et al.*, 1985

Pseudodryomys robustus in Antunes *et al.*, 1987

Pseudodryomys robustus in López Martínez, Sesé & Herráez, 1987

Pseudodryomys robustus in Herráez, 1993

Pseudodryomys robustus in Cerdeño & Íñigo, 1997

Original diagnosis (De Bruijn, 1966: 10): 'Pseudodryomys with cheek teeth that are slightly larger than those of the previous species [*Pseudodryomys iberi-*

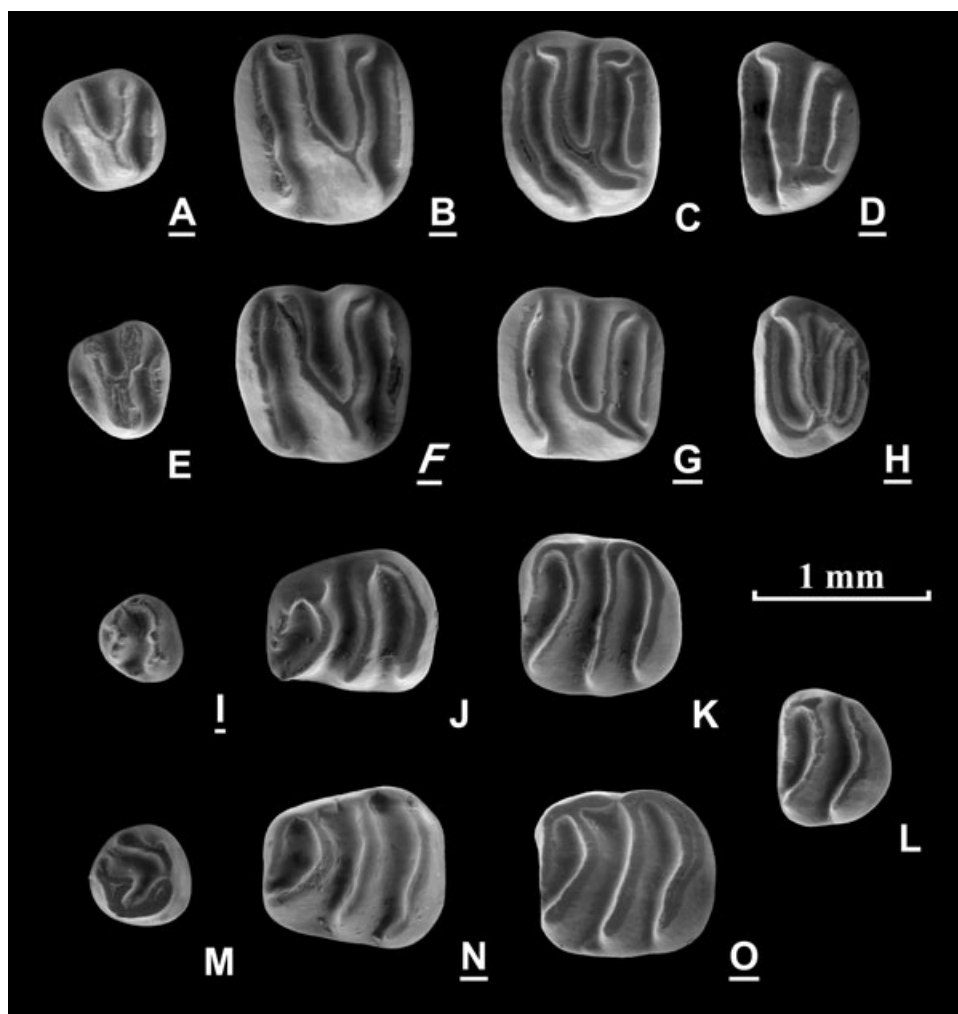


Figure 7. *Simplomys julii* (Daams, 1989) from Artesilla (Fig. 7A–H; J–L; N–O) and San Roque 3 (Fig. 7I, M) (collection MNCN). A, P4 ART-2444. B, M1 ART-3. C, M2 ART-28. D, M3 ART-21. E, P4 ART-2447. F, M1 ART-4 holotype. G, M2 ART-13. H, M3 ART-1176. I, p4 SR3-803. J, m1 ART-16. K, m2 ART-14. L, m3 ART-1036. M, p4 SR3-604. N, m1 ART-22. O, m2 ART-27. Right side specimens underlined. Holotype in italics.

cus]. The dental pattern is very simple. The M1–2 have neither centrolophs nor extra ridges. The m3 is reduced. M1/m1 smaller than M2/m2.’

Emended diagnosis by Daams (1974: 234): ‘*Pseudodryomys*–assemblages with a simple dental pattern. The M1,2 has the posterior centroloph only, or no centroloph at all. The main ridges are wide. In the lower molars extra ridges are absent. The m3 is reduced.’

Emended diagnosis: *Simplomys* species with a simple dental pattern, but the posterior centroloph may be present. In some cases, mainly in M2, posterior and anterior centrolophs are present, the posterior one being usually longer. Centrolophs are at right angles to the labial border and not longer than half the width

of the occlusal surface. The dental pattern of m1 and m2 shows the four main ridges and a well-developed centrolophid extending diagonally into the central valley and never reaching more than half way along the occlusal surface. The m3 has the posterior part small and simplified in morphology and the posterior valley may be completely absent in the younger occurrences.

Type locality: Valdemoros 3B, Calatayud–Montalbán basin, Spain (local zone Dc, MN 5, Middle Miocene).

Stratigraphical distribution: Local zones Y to E (MN 2, Lower Miocene–MN 5, Middle Miocene).

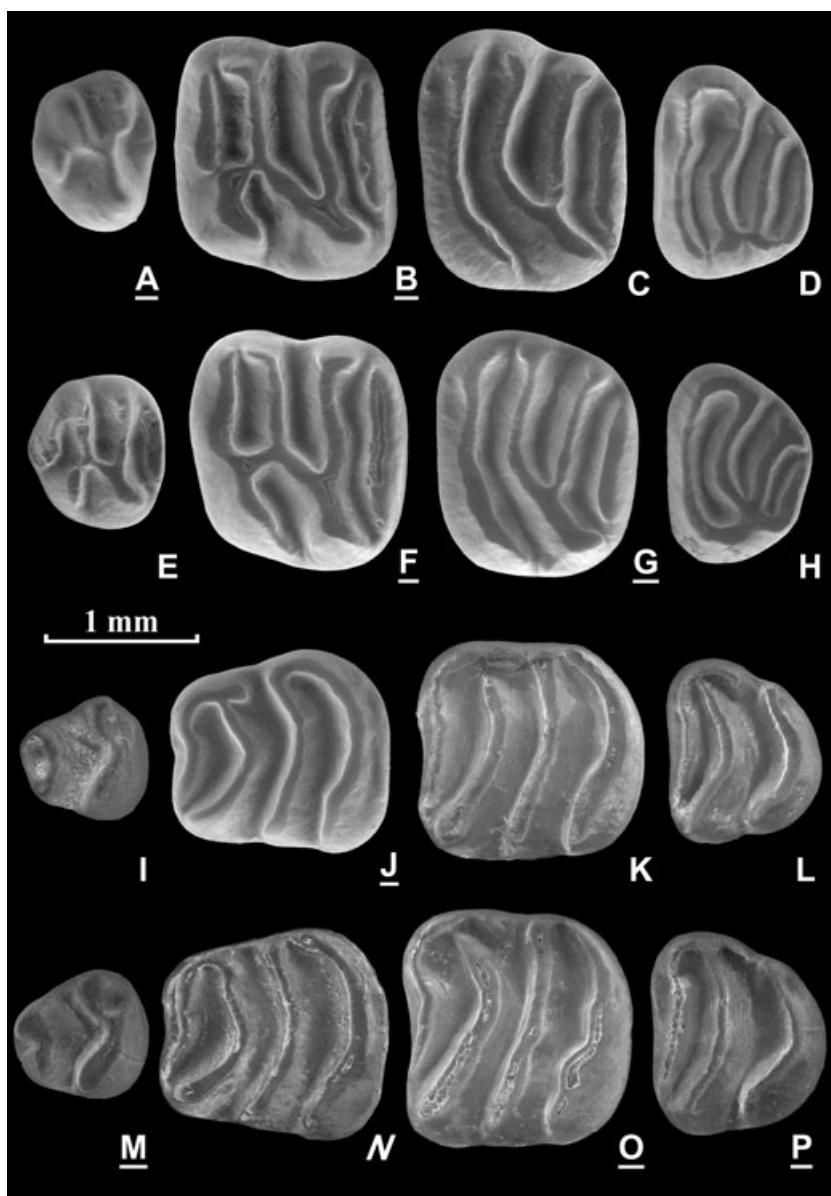


Figure 8. *Simptomys meulenorum* sp. nov. from Artesilla (collection MNCN). A, P4 ART-1142. B, M1 ART-874. C, M2 ART-882. D, M3 ART-1164. E, P4 ART-1227. F, M1 ART-873. G, M2 ART-886. H, M3 ART-1163. I, p4 ART-2498. J, m1 ART-901. K, m2 ART-910. L, m3 ART-1156. M, p4 ART-2499. N, m1 ART-894 holotype. O, m2 ART-918. P, m3 ART-1158. Right side specimens underlined. Holotype in italics.

Geographical distribution: *Simptomys simplicidens* is widely known from Spain and is also present in Portugal, France, Switzerland and Germany (see Supporting Information Appendix S1).

REMARKS ON *SIMPTOMYS SIMPLICIDENS*

Simptomys simplicidens was proposed by De Bruijn (1966) for glirid material with a rather simple dental pattern from Miocene localities of the Calatayud–Montalbán basin. This author named an assemblage

Ps. ibericus if more than 75% out of at least ten M1-2 had the ‘*ibericus* – morphotype’ and *Ps. simplicidens* if more than 75% of at least ten M1-2 had the ‘*simplicidens* – morphotype’. If one of the two patterns did not exceed 75% of the total number of M1-2 or if the assemblage consisted of fewer than ten specimens, the indication *Ps. ibericus* – *simplicidens* was used (De Bruijn, 1967). According to De Bruijn & Moltzer (1974) it was not clear whether the specimens with ‘*ibericus*’ morphology and those with ‘*simplicidens*’ morphology were morphotypes occurring in one

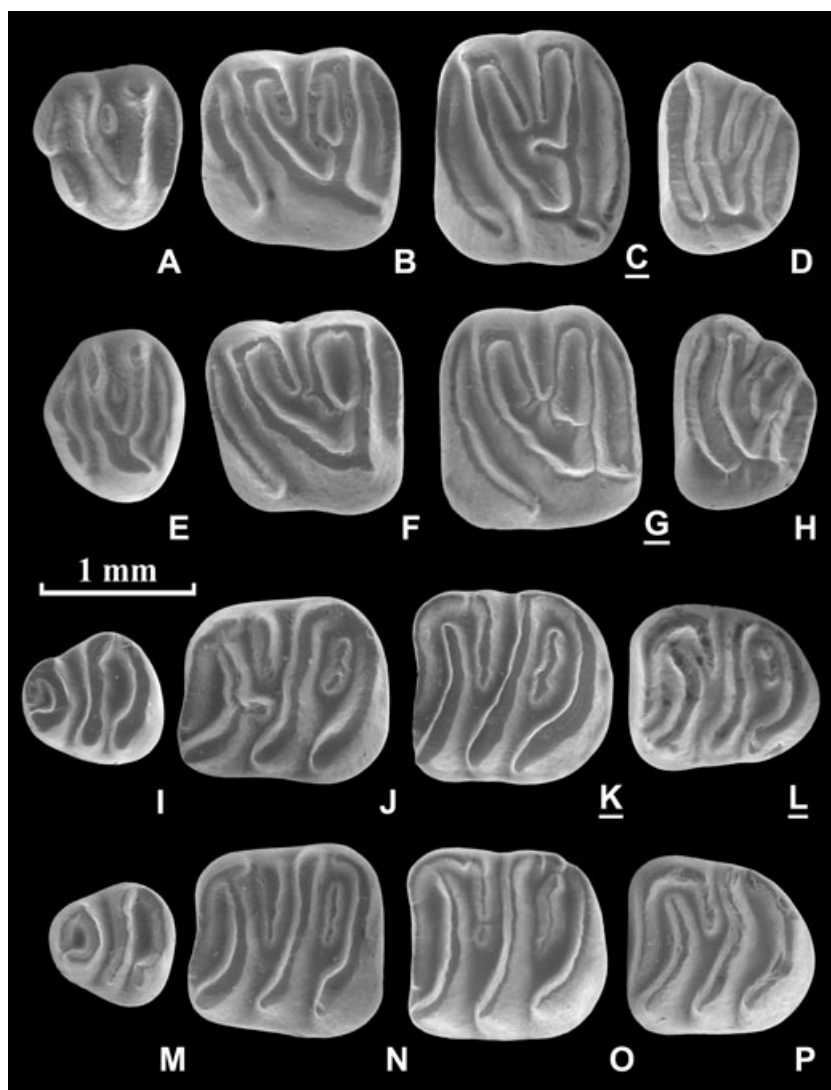


Figure 9. *Pseudodryomys ibericus* De Bruijn, 1966 from La Col C (collection MNCN). A, P4 COL C-2178. B, M1 COL C-1986. C, M2 COL C-2021. D, M3 COL C-2040. E, P4 COL C-2205. F, M1 COL C-2096. G, M2 COL C-2064. H, M3 COL C-2123. I, p4 COL C-2181. J, m1 COL C-1989. K, m2 COL C-2024. L, m3 COL C-2042. M, p4 COL C-2206. N, m1 COL C-2068. O, m2 COL C-2108. P, m3 COL C-2138. Right side specimens underlined.

natural population, or represented two species. In fact, there are several specimens belonging to *S. simplicidens* amongst *Ps. ibericus* paratypes, such as paratype number 60–422, figured in plate IV, figure 7 in De Bruijn (1967).

Daams (1974) studied *Pseudodryomys* material from ten Miocene localities of Spain, analysing the distribution of standard morphotypes of the cheek teeth. The results show that *Ps. ibericus* and *Ps. simplicidens* are separated species and the original diagnoses were emended. Later field campaigns, mainly in the Aragonian and Ramblian type areas (Calatayud–Montalbán basin), have increased the

number of localities with *Pseudodryomys* and *Simplomys* gen. nov. enormously (see Supporting Information Appendix S1).

Based on more than 2700 specimens from 59 localities of the type area of the Aragonian, García-Paredes (2006) demonstrated trends toward size increase of the cheek teeth (Fig. 10), toward simplification of the p4 and toward simplification of the posterior part in the m3 of *S. simplicidens*. This study also demonstrated that morphological features, such as simplification degree of the m3, can be used to distinguish *S. simplicidens* from *S. robustus*, even though size ranges of *S. simplicidens* and *S. robustus* overlap (Fig. 10).

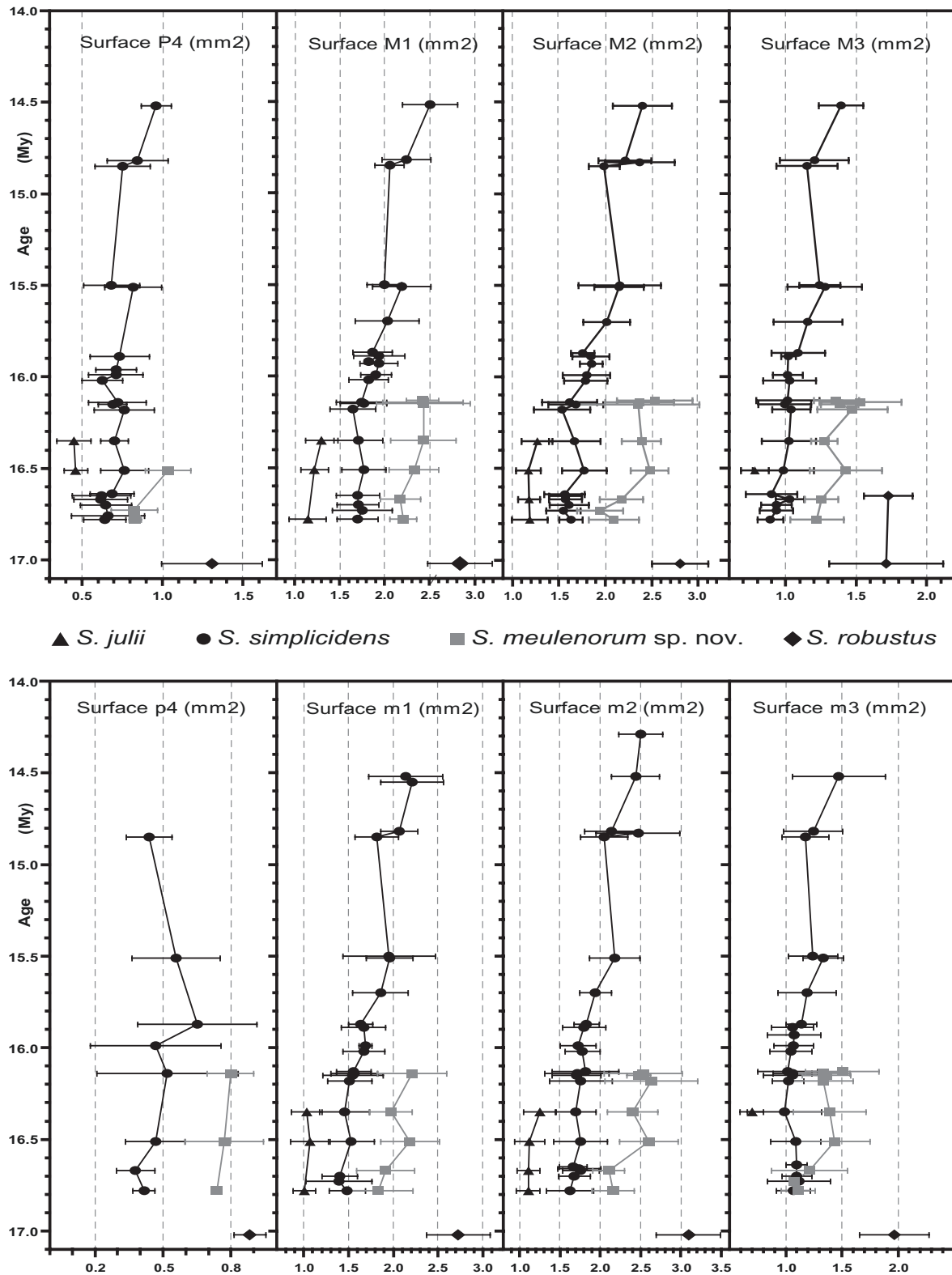


Figure 10. Temporal distribution of average surface of the upper and lower cheek teeth in species of *Simptomys* gen. nov. from the Aragonian type area (Calatayud–Montalbán basin, Spain). Only localities with at least five measurable specimens of each element are included. Horizontal bars represent two times the standard deviation. Modified after García-Paredes, 2006.

However, when these species occur in the same locality, *S. robustus* is always larger than *S. simplicidens*.

Given these new insights, the material from several middle Aragonian localities in the area of Madrid (Spain), described as *Pseudodryomys robustus* (Alberdi *et al.*, 1980, 1981, 1984, 1985; Sesé *et al.*, 1985; López Martínez *et al.*, 1987; Herráez, 1993; Cerdeño & Íñigo, 1997), could be revised. The measurements of this material fit within the size ranges of *Simplomys simplicidens* from biochronologically similar localities in the Calatayud–Montalbán basin (Fig. 10). Furthermore, the m3 from Madrid show the same degree of simplification as *S. simplicidens* (Fig. 4H). As a consequence, the *Ps. robustus* assemblages from middle Aragonian localities of Madrid (Moratines; Estación Imperial; Paseo de las Acacias; O'Donnell; Henares 2; Arroyo del Olivar) are now assigned to *S. simplicidens*. This change in the specific determination was already suggested by Amezua *et al.* (2000), Peláez-Campomanes & Herráez (2000), Soria *et al.* (2000) and Peláez-Campomanes *et al.* (2003), without, however, justification or mention of the previous specific status of the aforementioned material.

The situation with the material from Middle Miocene locality Armantes 3 in the Calatayud–Montalbán basin described as *Pseudodryomys* cf. *simplicidens* by De Bruijn (1967) and assigned to *Pseudodryomys robustus* by Daams (1974) and Daams *et al.* (1977) is similar and is here assigned to *Simplomys simplicidens*.

Pseudodryomys meini Adrover, 1978 described from Navarrete del Río (local biozone Z, MN1, Lower Miocene) was considered a junior synonym of *Ps. simplicidens* by Agustí (1983) as well as by Daams & de Bruijn (1995). However, these authors did not give any argument to justify this decision. The morphology of the specimens described as *Ps. meini* fits the diagnosis of *Simplomys simplicidens*. Adrover (1978) noted that the Navarrete del Río material is smaller than the type material of *Pseudodryomys* [= *Simplomys*] *simplicidens*. Because of the trend toward size increase in *S. simplicidens*, this species is smaller in older than younger localities (Fig. 10). Therefore, *Ps. meini* Adrover (1978) is considered a subjective synonym of *S. simplicidens*.

Simplomys simplicidens has been reported from localities of Portugal (e.g. Antunes & Mein, 1986), France (e.g. Baudelot & Collier, 1982; Aguilar, Escarguel & Michaux, 1999), Germany (e.g. Mayr, 1979; Wu, 1990, 1993), and Switzerland (e.g. Kálin, 1997) (see Supporting Information Appendix S1 for details on localities and references).

The material from the Lower and Middle Miocene fissure fillings in southern France listed by Aguilar *et al.* (1999) is of special interest. Several of these

localities (Ste. Catherine 3, Ste. Catherine 4, Ste. Catherine 5, and Ste. Catherine 9) contain both *S. simplicidens* and *S. robustus*. As a result of the nature of these fossil sites, the material assigned to *S. simplicidens* and to *S. robustus* in Aguilar *et al.* (1999), may represent the same species at different stages of evolution (Fig. 10). Therefore, further analysis is needed in order to establish whether this material belongs to *S. robustus*, *S. simplicidens*, or to *Simplomys meulenorum* sp. nov.

SIMPLOMYS ROBUSTUS (DE BRUIJN, 1967) (FIG. 5)

Original diagnosis (De Bruijn, 1967: 259, translated from Spanish): '[Large *Pseudodryomys* with simple dental pattern. The upper molars have neither centrolophs nor extra ridges. The m1 and m2 have a small centrolophid. The m3 is reduced]'.

Emended diagnosis by Daams (1974: 236): '*Pseudodryomys*-assemblages consisting of large teeth which differ from *P. simplicidens* in size and in the less reduced m3. The dental patterns of the other molars are identical of those of *P. simplicidens*'.

Emended diagnosis: Large *Simplomys* in which the dental pattern in m1 and m2 is formed by the four main ridges and a well-developed centrolophid. The latter extends diagonally into the central valley but never exceeds the middle part of the occlusal surface. The m3 always has a posterior valley and shows little reduction in its posterior part. The M1 may rarely present a small anterior centroloph.

Differential diagnosis: *Simplomys robustus* differs from *S. simplicidens* by having the premolars and the m3 less reduced in size and less simplified in morphology. The posterior valley of m3 is, in contrast to *S. simplicidens*, always present. When both species occur in the same assemblage, *S. robustus* is always larger than *S. simplicidens*.

Type locality: Ateca 3, Calatayud–Montalbán basin, Spain (local zone Z, MN 3, Lower Miocene).

Stratigraphical distribution: Local zones Z to C (MN 3–MN 4, Lower Miocene).

Geographical distribution: Spain, Portugal, and France.

REMARKS ON *SIMPLOMYS ROBUSTUS*

Simplomys robustus is rare in the fossil record. Its stratigraphical distribution is restricted to the Ramblian and lowest Aragonian (Lower Miocene). In

Spain it is present in the Calatayud–Montalbán basin and in the Vallès–Penedès basin (Agustí, 1981). Ginsburg, Morales & Soria (1987) cited *Ps. robustus* from the locality Valquemado (Tagus basin, local zone Y1). However, in later papers (Álvarez Sierra, Daams & Peláez-Campomanes, 1994; Morales *et al.*, 1999) this material is referred to as *Pseudodryomys* [= *Simplomys*?] sp. *Simplomys robustus* is also present in Portugal (Antunes, 1984) and France (e.g. Aguilar *et al.*, 1999) (see Supporting Information Appendix S1 for details on localities and references).

SIMPLOMYS ALJAPHI (HUGUENEY *ET AL.*, 1978)
(FIG. 6)

Original diagnosis (Hugueney *et al.*, 1978: 28, translated from French): '[*Pseudodryomys* similar in size to *P. ibericus* and *P. simplicidens*, close to *P. ibericus* by the evolutionary degree of its M1-2, which also possesses centrolophs and sometimes accessory ridges, but with a protoloph almost parallel to the metaloph, which gives a quite less pointed trigon on the upper molars; this new species on the whole has more simple molars than *P. ibericus*, with P4 and M3 much more reduced and very simplified. The reduction of the P4 and M3 is not as extreme as in *P. simplicidens*, which, in addition, has upper molars without centrolophs]’.

Emended diagnosis: Medium-sized *Simplomys*. The dental pattern of the upper molars is formed by the four main ridges. Centrolophs may be present. Sometimes tiny extra ridges are present inside the trigon. The M1 and M2 show a protoloph almost parallel to the metaloph; both ridges are joined near the lingual border. The dental pattern of m1 and m2 consists of the four main ridges and a well-developed centrolophid. The centrolophid does not exceed the central axis of the occlusal surface. The m1 and m2 also may possess tiny and low extra ridges in variable positions. The premolars and the m3 show the lowest degree of reduction and simplification amongst species of *Simplomys* gen. nov.

Differential diagnosis: *Simplomys aljaphi* differs from *S. simplicidens* by its less reduced and simplified premolars and m3. When centrolophs are present in the M1 and M2, they extend diagonally into the central valley. The anterior one is always present and longer than the posterior one in *S. aljaphi*, whereas in *S. simplicidens* the centrolophs are closer to being parallel to protoloph and/or metaloph and the posterior one is longer. *Simplomys aljaphi* differs from *S. simplicidens* by having, in general, a more complicated dental pattern in the lower molars that may include tiny and low extra ridges.

Simplomys aljaphi differs from *S. robustus* by its smaller size and its more complicated dental pattern.

Type locality: Montaigu-le-Blin, Allier, Central Massif basin, France (MN 2, Lower Miocene).

Stratigraphical distribution: Local zones X to Y (MN 1–MN 2, Lower Miocene).

Geographical distribution: Spain, France, and Switzerland.

REMARKS ON *SIMPLOMYS ALJAPHI*

This species is included in *Simplomys* gen. nov. because of its degree of reduction and simplification of the premolars and m3. The morphology of the premolars and the m3 of *S. aljaphi*, and their size relative to the molars are more similar to *S. simplicidens* than to *Ps. ibericus*. The morphology of m1 and m2 is also close to that of *S. simplicidens*. Most specimens from Montaigu-le-Blin described by Hugueney *et al.* (1978) have a relatively simple morphology and a similar number of ridges as in the most complicated *S. simplicidens* upper molars. The complicated ones are, however, more similar to *Ps. ibericus* than to *S. simplicidens*.

Other than the type locality, this species has been reported from Autol (Cuenca, 1983, 1985) and Moncalvillo (Daams, Lacomba & López Martínez, 1986) in central Spain and from the Upper Freshwater Molasse in Switzerland (Kälin, 1997) (see Supporting Information Appendix S1 for details on localities and references).

SIMPLOMYS JULII (DAAMS, 1989) (FIG. 7)

Synonymy: Pro-parte *Peridyromys murinus* from Vilafeliche 2A in Daams (1981).

Original diagnosis (Daams, 1989: 16): ‘A small *Pseudodryomys* species with a flat to slightly convex occlusal surface. The M1,2 have a subquadrate circumference. Simple dental pattern. Centrolophs are absent, and centrolophids are short or absent. Protoloph and metaloph form a Y – pattern in M1,2’.

Emended diagnosis: Small *Simplomys* species with molars that have a flat to slightly convex occlusal surface and simple pattern. Anteroloph and posteroloph are situated slightly below the plane of the trigon (protoloph–metaloph). The protoloph and metaloph form a composite ‘Y’ shape with a bent connection. A line connecting the labial end of the metaloph and the lingual end of the protoloph is aligned at right angles to the anteroposterior axis of the tooth. The occlusal

surface of the M1 and M2 has a square outline. In M1 the anteroloph and the anterior valley are straight and parallel to the anterior border of the tooth. In the lower molars, the centrolophid is absent or poorly developed and it does not extend into the central valley. The m3 has the posterior part reduced in size and in most cases the posterior valley is absent.

Differential diagnosis: *Simplomys julii* differs from *S. simplicidens*, *S. robustus*, and *S. aljaphi* in its smaller size, less concave cheek teeth, and by having the centrolophid less developed.

Type locality: Artesilla, Calatayud–Montalbán basin, Spain (local zone C, MN 4, Lower Miocene).

Stratigraphical distribution: Local zones A to Db (MN 3–MN 4, Lower and Middle Miocene).

Geographical distribution: Spain and France (see Supporting Information Appendix S1).

REMARKS ON *SIMPLOMYS JULII*

Simplomys julii is a rare species in the fossil record. It has not been studied since Daams (1989). Material from other than the type locality was not described until the revision of *S. julii* from the Aragonian type area by García-Paredes (2006). This study demonstrated a trend toward size increase of the cheek teeth (Fig. 10) and gives for the first time detailed descriptions of the premolars and lower third molars of this species, showing its high degree of simplification and reduction (Fig. 7).

Simplomys julii has been considered to have a short stratigraphical distribution restricted to the lower Aragonian (Lower Miocene) (Daams & de Bruijn, 1995; Daams, 1999). García-Paredes (2006) extended the stratigraphical distribution of this species to the upper Ramblian (Lower Miocene) and part of the middle Aragonian (Middle Miocene) (Table 5). *Simplomys julii* has been found only in Spain and France (see Supporting Information Appendix S1 for details on localities and references).

***SIMPLOMYS MEULENORUM* GARCÍA-PAREDES SP. NOV. (FIG. 8)**

Synonymy

Pseudodryomys robustus in Díaz Molina & López Martínez, 1979.

Pseudodryomys robustus in Alférez *et al.*, 1982.

Pseudodryomys robustus in Álvarez Sierra *et al.*, 1994.

Pseudodryomys robustus in Alférez *et al.*, 1999.

Pseudodryomys robustus in Morales *et al.*, 1999.

Pseudodryomys robustus pro-parte in Van Dam *et al.*, 2006.

Pseudodryomys robustus pro-parte in Van der Meulen *et al.*, 2005.

Pseudodryomys robustus pro-parte in Van der Meulen & Peláez-Campomanes, 2007.

Diagnosis: Medium to large-sized *Simplomys* with simple dental pattern. Centrolophs are absent. The anteroloph is interrupted in the middle in half of the M1 and may be connected medially to the protoloph. The centrolophid is absent or poorly developed and does not extend into the central valley. The mesolophid of the m3 is reduced and limited to the lingual part (entoconid). In most cases the mesolophid and posterolophid are fused as a unique ridge and the posterior valley is absent.

Differential diagnosis: *Simplomys meulenorum* sp. nov. differs from *S. simplicidens* by having a less developed centrolophid and by its less reduced and simplified premolars. When these species occur in the same association, *S. meulenorum* sp. nov. is larger, and the m3 is more reduced and simplified. When the mesolophid and posterolophid of the m3 are fused in a single ridge, in *S. meulenorum* sp. nov. the last ridge is mainly composed of the posterolophid and the mesolophid is almost completely reduced (Fig. 8L, P), whereas in *S. simplicidens* the last ridge is equally composed of the lingual part of the mesolophid and the labial part of the posterolophid (Fig. 4H).

Simplomys meulenorum sp. nov. differs from *S. robustus* by having a less-developed centrolophid and by the simpler morphology of the posterior part of the m3. When both species co-occur in the same locality *S. meulenorum* sp. nov. is smaller than *S. robustus*.

Simplomys meulenorum sp. nov. differs from *S. aljaphi* by its larger cheek teeth and by having in general a less complicated dental pattern, less developed centrolophid, and by having the posterior part of the m3 more reduced and simplified.

Simplomys meulenorum sp. nov. differs from *S. julii* by its larger cheek teeth and by having a more concave occlusal surface. In *S. meulenorum* sp. nov. the central valley of M1 and M2 is narrower and its protoloph–metaloph connection is more pointed than in *S. julii*. In *S. meulenorum* sp. nov. the anteroloph and the anterior valley of M1 are not straight as in *S. julii*.

Etymology: After our friend and colleague Dr Albert J. van der Meulen (Utrecht University, The Netherlands) and his family.

Type locality: Artesilla, Calatayud–Montalbán basin, Spain (local zone C, MN 4, Lower Miocene).

Holotype: m1 left (ART-894 stored at MNCN) Figure 8N.

Paratypes (stored at MNCN)

P4: ART-1142; ART-1148 to ART-1152; ART-1227; ART-1228

M1: ART-870 to ART-876; ART-922; ART-929; ART-1035

M2: ART-878; ART-879; ART-881 to ART-886; ART-888; ART-890; ART-950

M3: ART-524; ART-1160; ART-1162 to ART-1168; ART-1217

p4: ART-1225; ART-2426; ART-2498; ART-2499

m1: ART-891 to ART-898; ART-900 to ART-907

m2: ART-908 to ART-920; ART-984

m3: ART-1154 to ART-1159; ART-1222; ART-1224

Stratigraphical distribution: Local zones A to C (MN 3–MN 4, Lower Miocene).

Material and measurements from localities in the Aragonian type area: Tables 1–3.

*Description of **Simplomys meulenorum** sp. nov. from Artesilla*

P4: The occlusal surface is slightly concave and it has an oval or subtriangular outline. It is small in comparison to the molars. The dental pattern is simple and all specimens have four ridges. The anteroloph is usually short and situated in the middle part of the anterior border. Its labial and lingual parts end free in all the specimens. The anteroloph may be interrupted in its medial part and shows a medial connection with the protoloph in three out of eight specimens. The protoloph is oblique and its lingual end shows a cusp-like shape (protocone). The metaloph is short and its lingual end extends just to the centre of the occlusal surface. Protoloph and metaloph are connected in seven out of eight specimens forming a composite Y-shape. The short isolated posteroloph is situated medially and reaches neither the lingual nor the labial border.

M1: The occlusal surface of the M1 is concave and has a square outline with rounded corners. The most common morphotype shows four main ridges, with the metaloph connected to the protoloph, forming an asymmetric Y-shape, and the anteroloph interrupted and medially connected to the protoloph. The anteroloph is well developed and its labial and lingual parts end free in all specimens. The anteroloph is interrupted in seven out of nine specimens. There is a longitudinal connection between the anteroloph and

protoloph in six out of nine specimens. The protoloph is the longest ridge; its lingual part is more oblique than the anteroloph and reaches the posterolingual corner of the occlusal surface. The labial end of the protoloph is curved anteriorly near the border of the tooth. There are no centrolophs. The lingual end of the metaloph shows a slight bend and its labial end is curved backwards. The isolated posteroloph is relatively straight, it reaches neither the lingual nor the labial border.

M2: The occlusal surface of the M2 has a more rectangular outline than the M1. The anteroloph is not divided and there is no longitudinal connection with the protoloph. The anteroloph ends free lingually and it is connected labially to the protoloph in one out of ten specimens. As in the M1, the protoloph is the longest ridge. Its lingual end reaches the posterolingual corner of the occlusal surface. The metaloph is relatively straight. The protoloph and metaloph are connected, forming an asymmetrical Y-shape. Centrolophs are absent. The posteroloph is relatively straight; it reaches neither the lingual nor the labial border. It is labially connected to the metaloph in one out of ten specimens and it is lingually connected to the protoloph in four out of 11 specimens.

M3: The M3 has a concave occlusal surface and trapezoidal outline. The posterior part is narrower than the anterior one and it is slightly rounded. All specimens have four ridges. The labial and lingual ends of the anteroloph are curved backwards, and all specimens have the anteroloph connected labially to the protoloph. The anteroloph and protoloph are always connected labially, whereas they are lingually connected in only four out of ten specimens. As in the M2, the anteroloph is neither divided nor medially connected to the protoloph. The protoloph is curved posterolingually. Its lingual and labial ends are aligned at right angles to the anteroposterior axis of the tooth. Most specimens (eight out of ten) show a strongly asymmetric Y-shaped trigon but in two specimens the protoloph and metaloph are joined on the lingual border and the trigon shows an asymmetric V-shape. Centrolophs are absent. The curve of the metaloph is variable. Its labial part may be directed backwards. The posteroloph is the shortest ridge and ends free labially. The lingual end of the posteroloph reaches the border of the occlusal surface. It is lingually connected to the protoloph in seven out of ten specimens (forming an asymmetric Y-shaped trigon) and to the metaloph in two out of ten specimens (forming a V-shaped trigon). Only in one specimen is the posteroloph lingually free-ending.

p4: The outline of the occlusal surface is oval and slightly concave. The *p4* is small compared to the molars and its morphology is simpler than these. The anterior part is occupied by a curved ridge which is assumed to be formed by the union of the anterolophid and metalophid. The mesolophid is very short and connected to the posterolophid near the lingual border in three out of four specimens. There is a narrow trace of the posterior valley.

m1: The occlusal surface is slightly concave, with a subrectangular outline. The anterior part is narrower than the posterior one. The short anterolophid is slightly curved. Its labial part ends free in all specimens and does not reach the labial border of the tooth. The metalophid is sharply bent and its isolated labial end constitutes the anterolabial corner of the tooth, whereas its lingual border does not reach the anterolingual corner, but is connected to the anterolophid in 11 out of 14 specimens. The centrolophid is absent (three out of 14 specimens) or is poorly developed. This ridge, interpreted as a residual centrolophid, extends along the lingual border instead of into the central valley. The centrolophid, metalophid, and anterolophid are connected at the lingual border of the tooth in six out of 14 specimens. Only two specimens show a short isolated centrolophid. The mesolophid is bent and its lingual part is directed anteriorly. The posterolophid is the longest ridge and is more curved than the mesolophid. These ridges are connected lingually in eight out of 14 specimens.

m2: The *m2* differs from *m1* in having a more rectangular outline, but its morphology is very similar. In general, the anterolophid is not as short as the *m1* and its labial end neither reaches the border of the tooth nor joins the metalophid. The angle of the metalophid, situated in its middle part, is less acute than in the *m1*. The metalophid ends behind the anterolingual corner of the tooth and is connected to the anterolophid in eight out of 12 specimens. In 11 out of 12 specimens a small ridge, interpreted as a residual centrolophid, extends along the lingual border, sometimes almost reaching the mesolophid. In one specimen this structure is absent. The centrolophid, metalophid, and anterolophid are connected at the lingual border in four out of 12 specimens. In the remaining specimen, the centrolophid is connected to the metalophid. The centrolophid is isolated in four out of 12 specimens but connected to the lingual border of the anterolophid in three out of 12 specimens. The mesolophid is less bent than in the *m1* and is lingually connected to the posterolophid in six out of 12 specimens. The posterolophid is as described in the *m1*.

m3: The occlusal surface is not very concave and its outline forms a half-ellipse. The anterolophid and metalophid are connected lingually in eight out of nine specimens. The centrolophid is more variable than in *m1* and *m2* and it is absent in five out of nine specimens. The centrolophid is isolated in one specimen; in the remaining specimens with a centrolophid (three out of nine) it is connected to the metalophid and the anterolophid at the lingual border of the tooth. The posterior part of the *m3* is rounded, narrow, and very simplified in all specimens. The mesolophid and posterolophid are fused, forming a single composite posterior ridge and the posterior valley is absent in eight out of nine specimens. In the remaining specimen, the mesolophid is a very small, cusp-like, ridge connected to the posterolophid, but separated from it by a narrow trace of the posterior valley.

REMARKS ON *SIMPLOMYS MEULENORUM* SP. NOV.

In the localities of the Aragonian type area, *S. meulenorum* sp. nov. does not show much morphological variation but does show morphological simplification of the *m3*. In the older localities of zone B, the *m3* is already quite reduced and most specimens develop a single posterior ridge and full reduction of the posterior valley. In localities from the middle part of zone B until the end of zone C, only this completely reduced morphology is found.

Ongoing research shows the presence of this species in the Ramblian. These assemblages will allow us to get a better understanding of the primitive character state of the *m3*.

The *m3* of *S. meulenorum* sp. nov. and *S. simplicidens* have the mesolophid and posterolophid fused into a single ridge, but this union is achieved in different ways in both species. In *S. meulenorum* sp. nov. the mesolophid is almost completely reduced so the last ridge is mainly composed of the posterolophid (Fig. 8L, P). In *S. simplicidens* the labial part of the mesolophid and the lingual part of the posterolophid are short as is shown in specimens with intermediate simplification; thus, the last ridge is equally composed of the lingual part of the mesolophid and the labial part of the posterolophid separated by an inflexion (Fig. 4H). This inflexion is interpreted as a narrow trace of the posterior valley and is situated medially, whereas in *S. meulenorum* sp. nov. it is near the lingual border. Other morphological differences between the *m3* of these species have been observed. In *S. meulenorum* sp. nov. the central valley is deeper than in *S. simplicidens*. In *S. meulenorum* sp. nov. the posterior part is lower than the anterior one and the posterior wall of the ridges is more inclined than in *S. simplicidens*.

In the P4 of *Simplomys meulenorum* sp. nov. the main cusps are less distinguishable than in *S. simplicidens*.

An unusual morphological feature in Gliridae is found in *S. meulenorum* sp. nov. In the M1, the anteroloph may be interrupted and connected medially to the protoleph (Fig. 8B, F). The taxonomical or functional value of this particular morphology is not clear, but it is present in half of the M1 of *S. meulenorum* sp. nov. from all localities, whereas it is much less common in the M1 of *S. simplicidens*.

Simplomys meulenorum sp. nov. and *S. simplicidens* show statistically significant differences in length, width, and surface for all dental elements when these two species occur in the same locality (Table 4); *S. meulenorum* sp. nov. is the larger one.

Simplomys meulenorum sp. nov. shows a trend to size increase through time in the studied area (García-Paredes, 2006) (Fig. 10). As a result of this trend, size ranges of *S. meulenorum* sp. nov. may overlap with *S. robustus*. However, different morphologies allow us to distinguish them.

The material originally described as *Pseudodryomys robustus* from the Spanish locality Córcoles (zone C, Tagus basin) (Díaz Molina & López Martínez, 1979; Alférez *et al.*, 1982; Álvarez Sierra *et al.*, 1994; Alférez *et al.*, 1999; Morales *et al.*, 1999) has been revised and is assigned to *S. meulenorum* sp. nov.

PSEUDODRYOMYS DE BRUIJN, 1966

Type species: Pseudodryomys ibericus De Bruijn, 1966 (Fig. 9).

Original diagnosis (De Bruijn, 1966: 7): 'Gliridae of intermediate size. Occlusal surface of cheek teeth concave. Crowns of cheek teeth low. P4/p4 small relative to M1/m1 and rounded; M1/m1 smaller than M2/m2. The Spanish representatives of the genus *Pseudodryomys* are characterized by a gradual simplification of the dental pattern through time'.

Emended diagnosis: Medium to large-sized Gliridae, which have cheek teeth with a concave occlusal surface. The dental pattern is formed by the four main ridges and a variable number of extra ridges, usually between two and eight, including centrolophs and centrolophids. The ridges are relatively high, thick, and slanting and the valleys are narrow. In P4, M1, and M2 the trigon is very asymmetric forming a composite Y-shape. The upper molars generally have both centrolophs, the anterior one usually being longer. The lingual parts of the centrolophs may be joined to each other and/or also to the metaloph. The P4 has an oval outline; it is not very simplified and may present one or even two short centrolophs. Lower

molars have a relatively long centrolophid and in m1 and m2 there is at least one extra ridge in the posterior valley. The mesolophid of the m3 is not reduced and labially is not connected to the posterolophid.

Stratigraphical distribution: Local zones X to E (MN 1, Lower Miocene – MN 5, Middle Miocene).

Geographical distribution: Central and south-western Europe.

Species included

Pseudodryomys ibericus De Bruijn, 1966

Pseudodryomys rex (García Moreno, 1986 in Álvarez Sierra & García-Moreno, 1986)

Pseudodryomys granatensis Agustí, 1993 in Martín-Suárez *et al.*, 1993

REMARKS ON *PSEUDODRYOMYS*

After proposing the genus *Simplomys* gen. nov., *Pseudodryomys* is restricted to species having a complex dental pattern and fully developed third molars and premolars.

The differences between *Pseudodryomys* and *Miodryomys*, *Prodryomys*, and *Peridyromys* are not clear. Possible synonymy of these genera has been suggested by Daams & de Bruijn (1995) and Daams (1999). Several examples showing this problem can be cited. The species '*Dryomys*' *braillon* originally described by Thaler, 1966 has been included in *Pseudodryomys* (e.g. Flandrin, Mein & Truc, 1968; Daams, 1974; Adrover, 1978; Hugueney *et al.*, 1992), in *Peridyromys* (e.g. Baudelot & de Bonis, 1966; Aguilar, 1974; Agustí, 1981; Tobien, Fahlbusch & Mayr, 1987; Hugueney & Ringeade, 1990; Sigé *et al.*, 1991), and finally placed in *Prodryomys* (e.g. Wu, 1993; Daams & de Bruijn, 1995; Daams, 1999). Wu (1990) discussed the problems in distinguishing *Peridyromys* from *Prodryomys*.

We consider *Prodryomys* a genus with clear distinctive features that can be used to distinguish it from *Pseudodryomys* as has been pointed out by García-Paredes (2006). In *Pseudodryomys* the ridges are higher, thicker, more slanting, and the valleys are narrower than in *Prodryomys*. The upper molars of *Pseudodryomys* show a more asymmetrical trigon and centrolophs than *Prodryomys*. In the latter genus, the P4 is relatively larger and its morphology is more similar to that of the molars than in *Pseudodryomys*.

Therefore, we agree with Freudenthal & Martín-Suárez (2006) in excluding *Prodryomys* from the possible synonymy of *Pseudodryomys*, *Peridyromys*, *Miodryomys*, and *Prodryomys* suggested by Daams & de Bruijn (1995) and Daams (1999).

There are more difficulties in differentiating *Pseudodryomys* and *Miodryomys* because of the possible invalidity of *Miodryomys* as explained by Daams (1999). Some features have been used to distinguish species of *Miodryomys* from *Ps.* [= *Simplomys*] *simplicidens* and *Ps.* [= *Simplomys*] *robustus* but not from *Ps. ibericus*, the type species of the genus (De Bruijn & Moltzer, 1974). This problem has not been solved yet, and according to Heissig (2006), *Miodryomys* and *Pseudodryomys* can be distinguished by the more simple teeth and higher ridges of the latter genus. Although this distinction is applicable to the 'simplicidens-group', it does not hold true for the type species of *Pseudodryomys*, *Ps. ibericus*.

Concerning *Pseudodryomys* and *Peridyromys*, Álvarez Sierra *et al.* (1991) considered *Peridyromys* to apply to those species with relatively small size, wide ridges, and relatively hypsodont teeth, and assigned to *Pseudodryomys* those species with wide and robust ridges and relatively deep valleys. In addition, De Bruijn (in De Bruijn *et al.*, 2003) proposed the synonymy of *Peridyromys* and *Myomimus* Ognev, 1924, trying to solve an old controversy involving both genera (De Bruijn, Dawson & Mein, 1970; De Bruijn & Moltzer, 1974; Adrover, 1978; Agustí, 1981; Daams, 1981).

The situation involving the genera *Pseudodryomys*, *Peridyromys*, *Miodryomys*, and also *Myomimus* is a complex problem not yet solved. A separate study is necessary to establish uniform and clear diagnostic criteria for these problematic genera, but this question is out of the scope of this paper. However, the proposal of *Simplomys* gen. nov. makes this problem a bit less complicated.

CONCLUDING REMARKS

In general, the dental patterns of the different species of *Simplomys* gen. nov. are very similar because of the limited variations in their simple morphology. Nevertheless, they show different dental proportions as well as particular features in the morphology of the lower cheek teeth, and especially of the m3.

Simplomys aljaphi is the oldest species within the genus (Table 5) and it represents a primitive morphological stage. The information available indicates that *Simplomys* gen. nov. originated either in France or in the Iberian Peninsula. Because of the morphological similarities, *S. simplicidens* is probably directly related to *S. aljaphi*. The more primitive dental pattern shown by the latter suggests an ancestor-descendant relationship. *Simplomys robustus* and *S. simplicidens* are very similar and may therefore be directly related. The timing of the morphological simplification and reduction of the premolars and third molars is different but they share the presence of a

centrolophid in the lower molars that is less reduced than in the other more modern species. *Simplomys meulenorum* sp. nov. and *S. julii* show the more derived dental morphology.

The phylogenetic relationships of *Simplomys* gen. nov. with other genera are not clear yet. The dental morphology of *S. aljaphi*, the oldest species within the genus, is similar to that of *Peridyromys murinus*, which is considered to be the ancestor of a number of other genera of Gliridae such as *Armantomys*, *Praearmantomys*, *Pseudodryomys*, etc. (Daams, 1991; Daams & de Bruijn, 1995). The genera of Gliridae with simple dental morphology form a peculiar group within this family. As *Armantomys* and *Praearmantomys* presumably originated on the Iberian Peninsula, a close relationship with *Simplomys* gen. nov. is expected, but morphological similarities can be the result of convergent evolution as a result of living in a similar environment. The change in the morphology of the m3 of *Armantomys* shows a different trend than in *Simplomys* gen. nov. Except for its simple morphology, *Armantomys* looks like a group clearly separated from *Simplomys* gen. nov. *Praearmantomys* shows a reduction in the m3 more similar to *Simplomys* gen. nov. but their possible phylogenetic relationships are not clear at the moment.

The morphological characterization of the species assigned to the new genus allows us to solve taxonomical problems and to specify their stratigraphical distribution. This study also shows the systematic value of the outer elements of the teeth row (premolars and third molars) and its interest concerning the study of evolutionary patterns.

Simplomys gen. nov. is very common in Lower and Middle Miocene localities of the Iberian Peninsula, but it has been also recorded in other European countries such as France, Germany, and Switzerland. As we noted in this paper, there has been considerable taxonomic confusion regarding the species of the 'simplicidens-group' (i.e. *Simplomys* gen. nov.). Therefore, a review of the 'simplicidens-group' material from localities outside Spain is needed, using the taxonomic framework proposed in this paper and in García-Paredes (2006). This is a worthwhile exercise because *Simplomys* gen. nov. is a very characteristic taxon, which, in combination with its wide distribution, makes it a promising tool for biochronological correlations within Europe.

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APPENDIX

Species, localities, number of specimens, and values used in the scatter diagrams of Figures 2 and 3. Ratios of length : width (L/W) of premolars and third molars and their relative dental proportions are shown. The indices for the relative size of P4/p4 and M3/m3 have been calculated by dividing the surface area of P4/p4 and M3/m3 by the surface area of adjacent teeth (M1/m1 and M2/m2, respectively). As a rule, this was only carried out when at least five measurable specimens of each element were available. However, exceptions were made (grey shaded cells) for material from type localities (bold text) and/or small collections. Abbreviations: MC, F, Massif Central basin; France; C-M, S, Calatayud-Montalbán basin, Spain; T, S, Tagus basin, Spain; D, S, Duero basin, Spain; G, S, Granada basin, Spain. For details on localities see Supporting Information Appendix S1.

Species		P4		M1		M3		M2		p4		m1		m3		m2		
Localities	Basin	N	L/W	N	Surface P4/M1	N	L/W	N	Surface M3/M2	N	L/W	N	Surface p4/m1	N	L/W	N	Surface m3/m2	
<i>Simplomys aljaphi</i> Montaigu le Blin	MC, F	18	0.86	44	0.46	13	0.74	47	0.64	14	1.00	52	0.37	30	0.82	39	0.67	(1)
<i>Simplomys julii</i> Artesilla	C-M, S	4	0.93	8	0.38	3	0.76	14	0.67					1	0.82	9	0.52	
San Roque 3	C-M, S	4	0.93	18	0.35					2	0.99	13	0.28	4	0.81	14	0.56	
<i>Simplomys robustus</i> Ágreda	C-M, S													8	0.83	7	0.69	
Ateca 3	C-M, S	7	0.81	26	0.46	15	0.70	26	0.64	6	0.97	15	0.35	11	0.82	14	0.69	(2)
San Roque 4A	C-M, S	6	0.83	9	0.46	9	0.72	9	0.61	6	1.03	9	0.32	5	0.90	4	0.64	
<i>Simplomys simplicidens</i> Artesilla	C-M, S	27	0.84	14	0.43	12	0.70	16	0.55	9	0.94	19	0.31	9	0.93	24	0.62	
La Col C	C-M, S	8	0.77	18	0.38	7	0.71	14	0.55					18	0.85	19	0.59	
La Col D	C-M, S					11	0.71	13	0.62	6	1.03	10	0.40	7	0.86	6	0.62	
Olmo Redondo 2	C-M, S					8	0.72	5	0.60									
Olmo Redondo 3	C-M, S	8	0.85	5	0.37													
Olmo Redondo 5	C-M, S	10	0.84	16	0.34	10	0.71	12	0.58					17	0.84	19	0.59	
Olmo Redondo 8	C-M, S	9	0.80	12	0.37	10	0.69	15	0.56	7	1.02	6	0.28					
San Marcos	C-M, S	8	0.83	18	0.38	7	0.71	22	0.58					6	0.90	22	0.66	
San Roque 1	C-M, S	9	0.86	12	0.38	7	0.69	7	0.55	5	1.00	11	0.28	6	0.90	9	0.66	
San Roque 2	C-M, S					5	0.72	6	0.66									
San Roque 3	C-M, S	8	0.82	16	0.41	11	0.70	16	0.61					6	0.86	27	0.58	
Valdemoros 3B	C-M, S	5	0.80	8	0.37	12	0.71	8	0.58	5	0.99	7	0.24	10	0.81	7	0.57	
Valdemoros 3F	C-M, S	9	0.77	7	0.38	8	0.69	9	0.58					11	0.84	6	0.60	
Valdemoros 8A	C-M, S					9	0.73	11	0.57					14	0.83	8	0.61	
Villafeliche 2A	C-M, S					6	0.69	6	0.58									
Villafeliche 4A	C-M, S	34	0.81	51	0.37	28	0.71	65	0.59	13	0.95	44	0.28	36	0.83	44	0.61	
Villafeliche 4B	C-M, S	8	0.83	6	0.34	6	0.71	9	0.58									
Vargas 1A	C-M, S	15	0.81	10	0.41					8	0.99	15	0.33	18	0.84	10	0.62	
Vargas 3	C-M, S													8	0.85	6	0.56	
Vargas 4A	C-M, S	5	0.79	10	0.46	5	0.69	13	0.68					12	0.85	7	0.58	
Vargas 4BB	C-M, S	7	0.80	22	0.39	14	0.68	19	0.59					22	0.84	36	0.62	
Vargas 7	C-M, S	9	0.80	15	0.38	10	0.72	9	0.54					9	0.86	11	0.58	
<i>Simplomys meulenorum</i> sp. nov. Artesilla	C-M, S	8	0.83	9	0.45	10	0.75	7	0.58	4	0.99	14	0.35	8	0.87	12	0.55	
San Roque 1	C-M, S	3	0.86	9	0.38	12	0.72	13	0.58					17	0.84	10	0.51	
San Roque 2	C-M, S					10	0.72	11	0.58					7	0.87	13	0.58	
San Roque 3	C-M, S													7	0.84	6	0.58	
Vargas 1A	C-M, S					7	0.75	15	0.65	4	0.99	5	0.36					
<i>Armantomys aragonensis</i> San Roque 3	C-M, S									13	1.00	8	0.32					
San Roque 4A	C-M, S					6	0.67	5	0.60									
Valdemoros 8A	C-M, S	5	0.71	5	0.45	5	0.70	7	0.69									
Villafeliche 2A	C-M, S													2	0.93	2	0.66	
Vargas 7	C-M, S	7	0.72	6	0.48					6	0.98	7	0.31	12	0.94	9	0.79	

APPENDIX *Continued*

Species		P4		M1		M3		M2		p4		m1		m3		m2	
Localities	Basin	N	L/W	N	Surface P4/M1	N	L/W	N	Surface M3/M2	N	L/W	N	Surface p4/m1	N	L/W	N	Surface m3/m2
<i>Armantomys jasperi</i>																	
Artesilla	C-M, S													4	0.96	11	0.54
Córcoles	T, S	1	0.73	6	0.46	5	0.74	6	0.64					4	0.98	8	0.75
San Roque 1	C-M, S	7	0.79	3	0.51	5	0.68	4	0.67	2	1.02	4	0.41				
<i>Armantomys tricristatus</i>																	
Escobosa de Calatañazor	D, S	7	0.73	38	0.33	22	0.77	13	0.75	5	1.00	16	0.22	25	0.96	24	0.85
Las Umbrias 20	C-M, S	3	0.61	2	0.37	3	0.78	5	0.72	2	0.97	2	0.24	1	0.98	1	0.80
<i>Glirudinus modestus</i>																	
Olmo Redondo 2	C-M, S	1	0.83	6	0.52					2	1.02	1	0.58				
Villafeliche 2A	C-M, S					9	0.80	8	0.78					11	1.09	7	0.75
<i>Microdyromys koenigsuvaldi</i> / <i>Microdyromys legidensis</i>																	
La Col C	C-M, S	7	1.04	50	0.58	5	0.85	53	0.74					10	0.99	52	0.78
La Col D	C-M, S					6	0.75	34	0.77	5	1.04	26	0.59	7	0.98	34	0.85
Fuente Sierra 2	C-M, S					5	0.79	10	0.84								
Fuente Sierra 3	C-M, S													5	1.01	17	0.81
Las Umbrias 3	C-M, S	6	0.76	5	0.53												
Olmo Redondo 8	C-M, S	8	0.76	15	0.59	10	0.80	18	0.79	5	1.02	18	0.57	11	1.00	24	0.80
San Roque 2	C-M, S					5	0.81	10	0.85								
Valdemoros 1A	C-M, S									5	1.02	5	0.49				
Valdemoros 3B	C-M, S					11	0.83	14	0.71					8	1.01	12	0.70
Valdemoros 6A	C-M, S	5	0.78	21	0.49					7	1.01	16	0.56	7	1.00	10	0.79
Valdemoros 7B	C-M, S					7	0.78	8	0.71					8	0.96	11	0.72
Villafeliche 2A	C-M, S					12	0.79	5	0.82								
Vargas 11	C-M, S	5	0.76	16	0.56												
Vargas 1A	C-M, S	13	0.74	53	0.57	7	0.76	48	0.81	6	1.02	62	0.55	14	0.99	75	0.81
Vargas 4A	C-M, S	5	0.77	54	0.60												
Vargas 4BB	C-M, S	5	0.78	48	0.62												
<i>Peridyromys darocensis</i>																	
San Roque 4A	C-M, S	7	0.81	33	0.62	7	0.76	33	0.77	5	1.11	16	0.53	5	1.04	8	0.83
<i>Peridyromys murinus</i>																	
Artesilla	C-M, S	31	0.84	##	0.60	6	0.74	##	0.73	22	1.01	53	0.53	24	0.99	66	0.79
San Marcos	C-M, S	6	0.82	37	0.53					6	1.01	20	0.55	14	1.05	23	0.87
San Roque 1	C-M, S	20	0.82	85	0.60	7	0.76	85	0.73	9	1.00	28	0.49	27	1.04	36	0.77
San Roque 2	C-M, S	17	0.83	47	0.62	8	0.77	47	0.71	11	1.03	22	0.47	17	1.06	30	0.77
San Roque 4A	C-M, S	5	0.80	15	0.67					7	1.06	6	0.60	5	1.11	9	0.84
Villafeliche 2A	C-M, S					9	0.75	43	0.72					9	1.05	23	0.86
<i>Praearmantomys crusafonti</i>																	
Artesilla	C-M, S	89	0.81	65	0.62	57	0.71	89	0.65	65	0.96	45	0.43	70	0.85	47	0.70
Ateca 1	C-M, S	15	0.81	11	0.65	19	0.65	19	0.63	14	1.03	19	0.40	22	0.86	17	0.75
Olmo Redondo 1	C-M, S	11	0.83	7	0.59	11	0.68	13	0.55	12	0.96	9	0.42	12	0.89	10	0.75
San Roque 1	C-M, S	27	0.84	19	0.61	24	0.66	19	0.58	22	0.96	22	0.39	24	0.90	37	0.71
San Roque 2	C-M, S	22	0.85	35	0.59	35	0.66	38	0.61	30	0.97	39	0.40	33	0.87	45	0.72
<i>Prodyromys satus</i>																	
La Col C	C-M, S	8	0.78	16	0.52	6	0.76	15	0.69	5	1.00	13	0.56	6	1.03	8	0.74
<i>Pseudodryomys granatensis</i>																	
Murchas	G, S					3	0.81	1	0.65	1	1.01	1	0.63	2	1.02	1	0.81
<i>Pseudodryomys ibericus</i>																	
Artesilla	C-M, S	29	0.83	33	0.56	26	0.78	35	0.74	22	1.01	38	0.49	30	1.01	29	0.79
Ateca 1	C-M, S	5	0.83	20	0.59	15	0.73	20	0.73	5	1.02	12	0.49	14	0.97	14	0.85
La Col C	C-M, S	17	0.81	25	0.54	23	0.74	20	0.67	19	1.03	24	0.45	20	1.04	26	0.79
La Col D	C-M, S	16	0.84	24	0.53	23	0.76	27	0.70	22	1.02	22	0.49	22	1.02	21	0.77
San Marcos	C-M, S	7	0.80	8	0.54												
San Roque 1	C-M, S	11	0.83	15	0.61	14	0.79	12	0.77	15	1.00	18	0.51	14	0.99	17	0.80
San Roque 2	C-M, S	9	0.82	18	0.57	18	0.76	12	0.72	5	1.00	14	0.49	19	1.02	10	0.78
San Roque 3	C-M, S					6	0.77	9	0.75								
San Roque 4A	C-M, S	26	0.82	17	0.57	18	0.78	15	0.77	17	1.03	19	0.53	31	1.00	29	0.75
Valdemoros 8A	C-M, S									7	1.02	5	0.50	5	1.01	7	0.70
Vargas 1A	C-M, S	7	0.79	16	0.55	11	0.77	13	0.67					13	1.04	16	0.76
Vargas 3	C-M, S													6	1.04	5	0.80
Vargas 4A	C-M, S													5	1.01	7	0.76
Vargas 4BB	C-M, S	16	0.80	17	0.55	9	0.78	13	0.74					15	1.02	13	0.78
<i>Pseudodryomys rex</i>																	
Las Planas 4B	C-M, S					1	0.74	1	0.73								
Las Umbrias 8	C-M, S	2	0.80	1	0.65					1	0.98	2	0.66	1	1.02	1	0.88
Torreormojón 6B	D, S	1	0.77	2	0.56									1	0.97	1	0.89

(1) After Huguency *et al.* (1978); (2) after De Bruijn (1967); (3) after Daams (1991); (4) after Martín-Suarez *et al.*, 1993; (5) after De Bruijn (1966); (6) after Álvarez Sierra & García-Moreno, 1986.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Review of the cited localities in literature for the species of *Simplomys* **gen. nov.**

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