

Original article

First detailed description of *Hispanomys bijugatus* Mein and Freudenthal, 1971 (Rodentia, Cricetodontinae) from the Upper Aragonian of La Grive-Saint Alban (France): Biostratigraphical implications[☆]

Première description détaillée d'Hispanomys bijugatus Mein et Freudenthal, 1971 (Rodentia, Cricetodontinae) de l'Aragonien supérieur de La Grive-Saint Alban (France) : implications biostratigraphiques

Raquel López-Antoñanzas^{a,*}, Pierre Mein^b

^a Departamento de Paleobiología, Museo Nacional de Ciencias Naturales-CSIC, c/José Gutiérrez Abascal 2, Madrid 28006, Spain

^b UMR CNRS 5125 PEPS, université Lyon 1, bâtiment Géode, 2, rue Raphaël-Dubois, 69622 Villeurbanne cedex, France

Received 23 January 2009; accepted 8 April 2009

Available online 3 September 2009

Abstract

The material of *Hispanomys bijugatus* (Rodentia, Cricetodontinae) from La Grive-Saint Alban (carrière Lechartier, fissure L3) is described for the first time and compared with all species of the genus known to date. As common in the Upper Aragonian populations of *Hispanomys*, this taxon evidences a low variability. *H. bijugatus* shows some progressive characters with respect to the remaining Aragonian congeneric species, such as the absence of labial and lingual cingula surrounding the upper and lower molar valleys respectively, the increase in the number of roots on the second lower molar, and the loss of mesolophes. This suggests that *H. bijugatus*, in spite of being one of the oldest species of the genus, is relatively derived with regard to the coeval congeneric species. Because *H. bijugatus* and *H. decedens* are believed to be closely related species within the same lineage, the fact that the former shows a more progressive dental morphology than the latter suggests that the unnamed fissure-fillings from La Grive and La Grive M (with *H. decedens* only) are older than La Grive L3 (with *H. bijugatus* only). The coexistence of both species at locality L5 suggests an intermediate age.

© 2009 Elsevier Masson SAS. All rights reserved.

Keywords: *Hispanomys*; Rodentia; Cricetodontinae; Miocene; La Grive-Saint Alban; France; Systematics

Résumé

Le matériel d'*H. bijugatus* (Rodentia, Cricetodontinae) de La Grive-Saint Alban (carrière Lechartier, fissure L3) est décrit pour la première fois et comparé avec toutes les autres espèces du genre connues actuellement. Comme il a déjà été observé chez d'autres populations d'*Hispanomys* de l'Aragonien supérieur, ce taxon présente une faible variabilité. *H. bijugatus* montre des caractères dérivés par rapport au reste des espèces congénériques aragoniennes, tels que : l'absence de cingulums labiaux et linguaux sur les molaires supérieures et inférieures, respectivement ; l'augmentation du nombre de racines de la deuxième molaire inférieure ; la perte des mésolophes. *H. bijugatus*, tout en étant une des plus anciennes espèces du genre, serait donc plus évoluée que les espèces d'*Hispanomys* contemporaines. Étant donné qu'*H. bijugatus* et *H. decedens* sont considérées comme des espèces proches au sein d'une même lignée, le fait que la première montre une morphologie dentaire plus dérivée que la seconde suggère que la fissure non nommée de La Grive ainsi que La Grive M (où seul *H. decedens* a été collecté) sont plus anciennes que La Grive L3 (avec *H. bijugatus* seul). La coexistence de ces espèces à La Grive L5 suggère un âge intermédiaire.

© 2009 Elsevier Masson SAS. Tous droits réservés.

Mots clés : *Hispanomys* ; Rodentia ; Miocène ; Cricetodontinae ; La Grive-Saint Alban ; France ; Systématique

[☆] Corresponding editor: Gilles Escarguel.

* Corresponding author.

E-mail address: ralopan@mncn.csic.es (R. López-Antoñanzas).

1. Introduction

La Grive-Saint Alban is the common name used to refer to various pits located on the territory of the municipality of Saint-Alban-de-Roche (Isère, France). These pits are constituted by limestones whose fissures are filled by fossiliferous siderolithic clays. The name La Grive-Saint Alban was given by Jourdan in 1861 in his first work dealing with the fauna of this area (specifically from the Peyre et Beau quarry). Jourdan was the first to carry out field works in the Peyre et Beau pit between 1845 and 1861. During the XIXth and XXth centuries, other pits such as the Milliat or the Lechartier ones were excavated. The pits were named after their owners and, therefore, they could be re-baptized when the owner changed. Nowadays, they are known with the following names: “Chemin départemental 24” (CD24), “carrière Lechartier” (L), “carrière Milliat” (M), “carrière Peyre et Beau” (P. B.), and “carrière nouvelle” (F), which is the most recently discovered one (Fig. 1). Since 1962, one of us (P. M.) has been interested in La Grive-Saint Alban. He excavated at the Lechartier and Milliat pits, and also found some micromammal remains at the Peyre et Beau pit. P. M. was the first person to evidence that the different fissure fillings are asynchronous (Mein, 1976).

All pits have yielded micromammals, but remains of *Hispanomys* have only been recovered in La Grive L, M, P.B. (where a sole m1 was found by P. M.) as well as in an unnamed fissure-filling. L (pit Lechartier) has eight fissure-fillings numbered from L1 to L8, but the only productive ones (from a palaeontological viewpoint) are L3, L5, L6, and L7. *H. bijugatus* has been recorded from fissures L3 and L5, whereas *H. decedens* has been found in an unnamed fissure-filling as well as in fissures L5, L7, and in La Grive M (Mein and Ginsburg, 2002). Interestingly enough, almost all material of *H. decedens* from La

Grive comes from this unnamed fissure. We agree with Mein and Ginsburg (2002) who did not mention the presence of *H. decedens* in L7 because they considered that the low percentage of this taxon in the sample was possibly the result of “contamination”. The species *H. bijugatus* was originally erected as *Cricetodon (Hispanomys) bijugatus* by Mein and Freudenthal (1971) on the basis of isolated cheek teeth recorded from the locality L3 of La Grive-Saint Alban (Mein and Ginsburg, 2002). As Mein and Freudenthal’s (1971) work dealt with a whole revision and a new classification of the European tertiary cricetids, a complete description of the wealth of material of *Cricetodon (Hispanomys) bijugatus* available could not be supplied and only a brief diagnosis was provided. Additional material of this taxon has been recovered at locality L5 (Mein and Freudenthal, 1971; Mein and Ginsburg, 2002; Maridet, 2003) as well as at Lo Fournas 5, Pyrénées-Orientales, France (Aguilar et al., 1999) and Jujurieux, Ain, France (Mein, 1999), which are both MN9 localities (Mein, 1976, 1999; Montuire et al., 2006).

The aim of the present work is to offer a detailed description of *H. bijugatus* as well as comparisons with all the other species of the genus known to date. The degree of evolution of the teeth of the two species of *Hispanomys* recovered at La Grive is used to elucidate the relative infill chronology of the different localities, which is controversial.

2. Material and methods

The systematic study presented below is based on the examination of original specimens of the MNCN, RUU, IPS, and FSL collections (see abbreviations below), and data from the literature. We examined the following: original teeth of *H. bijugatus* and *H. decedens* from La Grive-Saint Alban, *H. mediterraneus* from the localities of Montredon (Hérault,

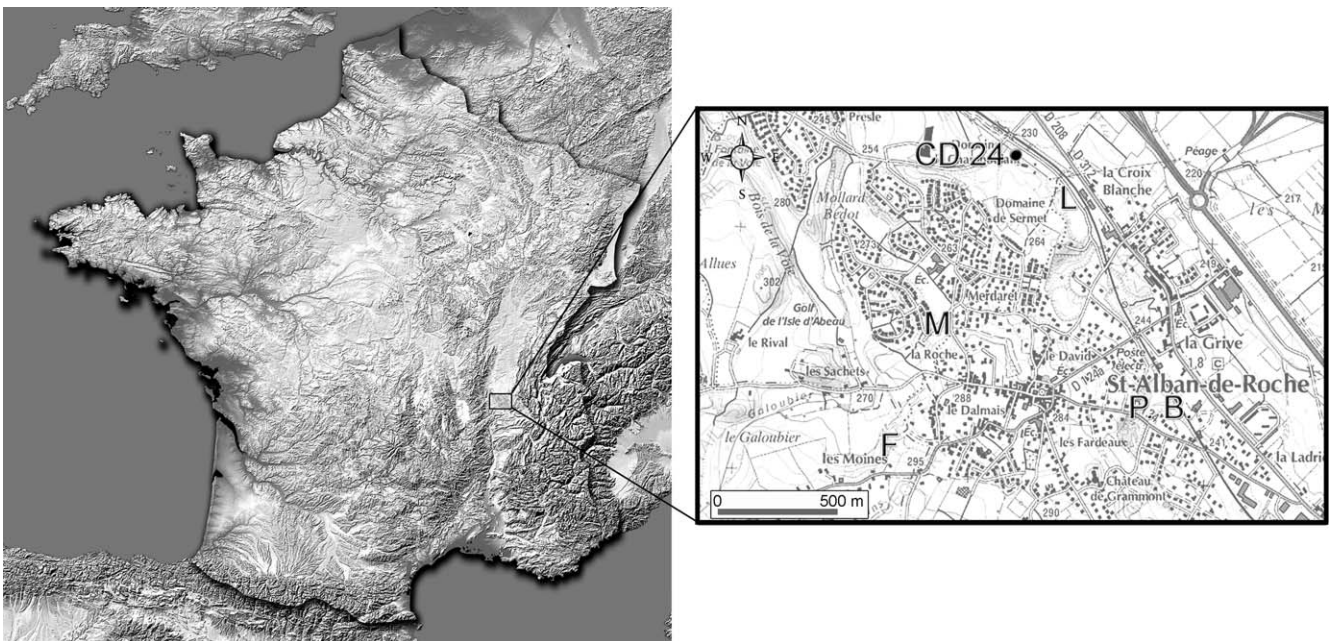


Fig. 1. Situation of the Saint-Alban-de-Roche municipality in France and close-up showing the situation of the different fossiliferous pits: CD24 “Chemin départemental 24”, L “carrière Lechartier”, M “carrière Milliat”, P. B. “carrière Peyre et Beau”, and F “carrière nouvelle”.

Table 1

Length and width measurements (mm) of the lower and upper molars of *Hispanomys bijugatus* from La Grive-Saint Alban (carrière Lechartier, fissure L3), Isère, France.

Tooth type	N	Length				Width			
		Min	Mean	Max	sd	Min	Mean	Max	sd
m1	50	2.44	2.60	2.80	0.09	1.54	1.63	1.81	0.07
M1	49	2.97	3.23	3.50	0.11	1.92	2.05	2.18	0.06
m2	43	2.40	2.54	2.74	0.08	1.65	1.83	1.93	0.06
M2	42	2.30	2.47	2.61	0.08	1.80	1.92	2.07	0.07
m3	39	2.32	2.47	2.72	0.07	1.58	1.68	1.80	0.06
M3	41	1.80	1.97	2.18	0.08	1.57	1.70	1.93	0.07

France), Soblay (Ain), and Dionay (Isère), *H. aguirrei* from Escobosa (Soria, Spain), *H. daamsi* from Can Missert (Barcelona, Spain), *H. dispectus* from Hostalets de Pierola and Castell de Barbera (Barcelona), *H. lavocati* from Hostalets de Pierola, *H. aragonensis* from Pedregueras 2A (Zaragoza, Spain), *H. nombrevillae* from Molina de Aragón (Guadalajara, Spain), *H. peralensis* from Peralejos 4, Peralejos C, Peralejos D, Masía del Barbo 2A and Masía del Barbo 2B (Teruel, Spain), *H. thaleri* from Can Llobateres (Barcelona), *H. freudenthali* from Puente Minero (Teruel), and *H. adroveri* from Casa del Acero (Murcia, Spain).

The material of *H. bijugatus* from La Grive-Saint Alban (carrière Lechartier, fissure L3 and L5) is described for the first time and compared with the equivalent teeth of all the species of *Hispanomys* known to date. The occlusal measurements (maximum length and maximum width) were taken following Van de Weerd (1976) for all dental elements but upper second molars, where the maximum length has been taken parallel to the labial side of the tooth. Measurements have been obtained using a Microscope Leitz Ortholux with a platinum ultrapack (Table 1; Fig. 2).

First, second, and third lower molars are designed as m1, m2, and m3, respectively, whereas first, second, and third upper molars as M1, M2, and M3. The terminology used in the tooth descriptions follows that of Freudenthal et al. (1994). We use the local subzones of Van Dam et al. (2001) when relevant.

Institutional Abbreviations: FSL, Université Claude-Bernard, Villeurbanne, France; IPS, Instituto Catalán de Paleontología, Sabadell, Spain; MGISTL, Museu Geològic, Lisboa, Portugal; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; MSNL, Centre de Conservation et d'Étude des Collections, Lyon, France; RGM, Nationaal Natuurhistorisch Museum Leiden, The Netherlands; RUU, Rijksuniversiteit Utrecht, Utrecht, The Netherlands; USTL, Université des Sciences et Techniques du Languedoc, Montpellier, France.

3. Systematic paleontology

Order RODENTIA Bowdich, 1821

Subfamily CRICETODONTINAE (Stehlin and Schaub, 1951)

Genus *Hispanomys* Mein and Freudenthal, 1971

Species *Hispanomys bijugatus* Mein and Freudenthal, 1971
Figs. 3 and 4

Holotype: FSL n° 65478: left isolated m1 (Mein and Freudenthal, 1971: p. 37, Pl. 2, Fig. 4).

Paratypes: FSL 66256-66524.

Type locality: Fissure L3, carrière Lechartier, La Grive-Saint Alban.

Age: MN 8.

Other localities: Fissure L5, carrière Lechartier, La Grive-Saint Alban (Mein and Freudenthal, 1971); Lo Fournas 5 (Aguilar et al., 1999); Jujurieux (Mein, 1999).

Extended diagnosis: *Hispanomys* species of medium size, with weak or absent grooved upper incisors and low hypsodonty; having low values of the mean LM1/mean LM3 and mean Lm1/mean Lm3 ratios (unreduced third lower and upper molars); lower molars lacking cingula on the lingual valleys and having well-developed labial anterolophid; m1 having a double metalophid and lacking mesolophid, m2 and m3 with short, but distinct, mesolophid; three-rooted m2; upper molars lacking mesoloph, enamel coated valley and labial cingula, and having incomplete lingual cingula and partial anterior ectoloph; M1 with four roots, with spur of the anterolophule and prominent protostyle; upper molars with vestigial entomesoloph.

Differ from *Hispanomys daamsi*, *H. thaleri*, *H. freudenthali*, and *H. adroveri* in being smaller; differ from *H. castelnovi*, *H. aguirrei*, *H. daamsi*, *H. dispectus*, *H. thaleri*, *H. lavocati*, *H. nombrevillae*, *H. aragonensis*, *H. peralensis*, *H. baixasi*, *H. freudenthali*, and *H. adroveri* in having an entomesoloph on some upper molars; differ from *H. decedens*, *H. aguirrei*, *H. daamsi*, *H. dispectus*, *H. lavocati*, *H. nombrevillae*, and *H. aragonensis* in lacking labial cingula surrounding the valleys on the upper molars; differ from *H. mediterraneus*, *H. peralensis*, *H. freudenthali*, and *H. adroveri* in having four rooted M1; differ from *H. daamsi*, *H. dispectus*, *H. thaleri*, *H. mediterraneus*, *H. peralensis*, *H. freudenthali*, and *H. adroveri* in having incomplete ectolophs on the M1 and M2; differ from *H. decedens*, *H. dispectus*, *H. thaleri*, and *H. aragonensis* in lacking enamel coated valley on the M1-M2; differ from *H. decedens*, *H. aguirrei*, *H. daamsi*, *H. dispectus*, *H. lavocati*, *H. thaleri*, and *H. aragonensis* in lacking mesoloph on the M1; differ from *H. castelnovi*, *H. dispectus*, *H. nombrevillae*, *H. thaleri*, *H. mediterraneus*, *H. peralensis*, *H. freudenthali*, and *H. adroveri* in having the M3 much less reduced; differ from *H. peralensis*, *H. freudenthali*, and *H. adroveri* in having labial anterolophid in all m1; differ from all species of *Hispanomys* in having double metalophid on the m1 (some of them like *H.*

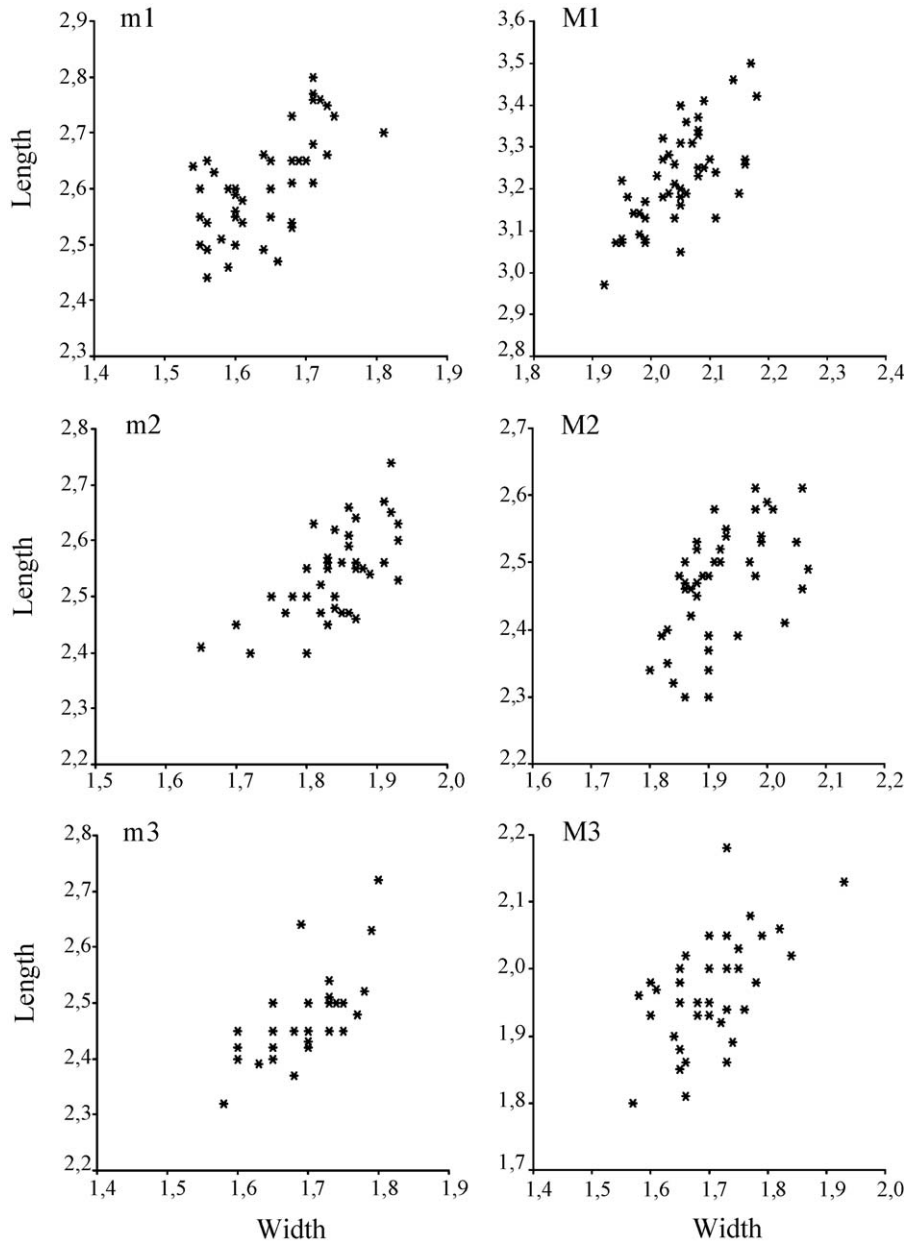


Fig. 2. Length/width scatter diagrams of the upper and lower molars of *Hispanomys bijugatus* from La Grive-Saint Alban (carrière Lechartier, fissure L3).

decedens, *H. aguirrei*, *H. lavocati*, *H. nombrevillae*, *H. mediterraneus*, and *H. baixasi* have it in a major or minor part of the specimens, whereas in the remaining species it is absent); differ from *H. adroveri* in having very short or absent mesolophid on the m1; differ from *H. aragonensis*, *H. thaleri*, *H. nombrevillae*, and *H. aguirrei* in having the m2 three-rooted; differ from *H. nombrevillae*, *H. aguirrei*, *H. peralensis*, *H. freudenthali*, and *H. adroveri* in having the m3 much more reduced.

3.1. Description

M1: These teeth show a pronounced groove between the two lobes of the anterocone. The anterolophule connects the lingual lobe of the anterocone with the protocone. There is a labial spur

of the anterolophule in some specimens. The protosinus is partially closed by a large protostyle that can be connected to the anteroloph by a ridge. The anterior ectoloph is well developed; it is as high as the anterocone, and reaches or nearly reaches the anterior wall of the paracone closing the anterosinus. The forward paracone spur is usually absent. The protolophule is anterolabially directed and it is oblique. The long and strong backward paracone spur connects to a more labially located branch (posterior ectoloph), which arises from the anterior wall of the metacone, closing the mesosinus. The backward paracone spur emerges from the midpoint of the protolophule and is generally posterolabially oriented. All specimens lack the mesoloph, but some of them have the beginning of the anterior arm of the hypocone somewhat inflated. They have no cingula surrounding the labial valleys.

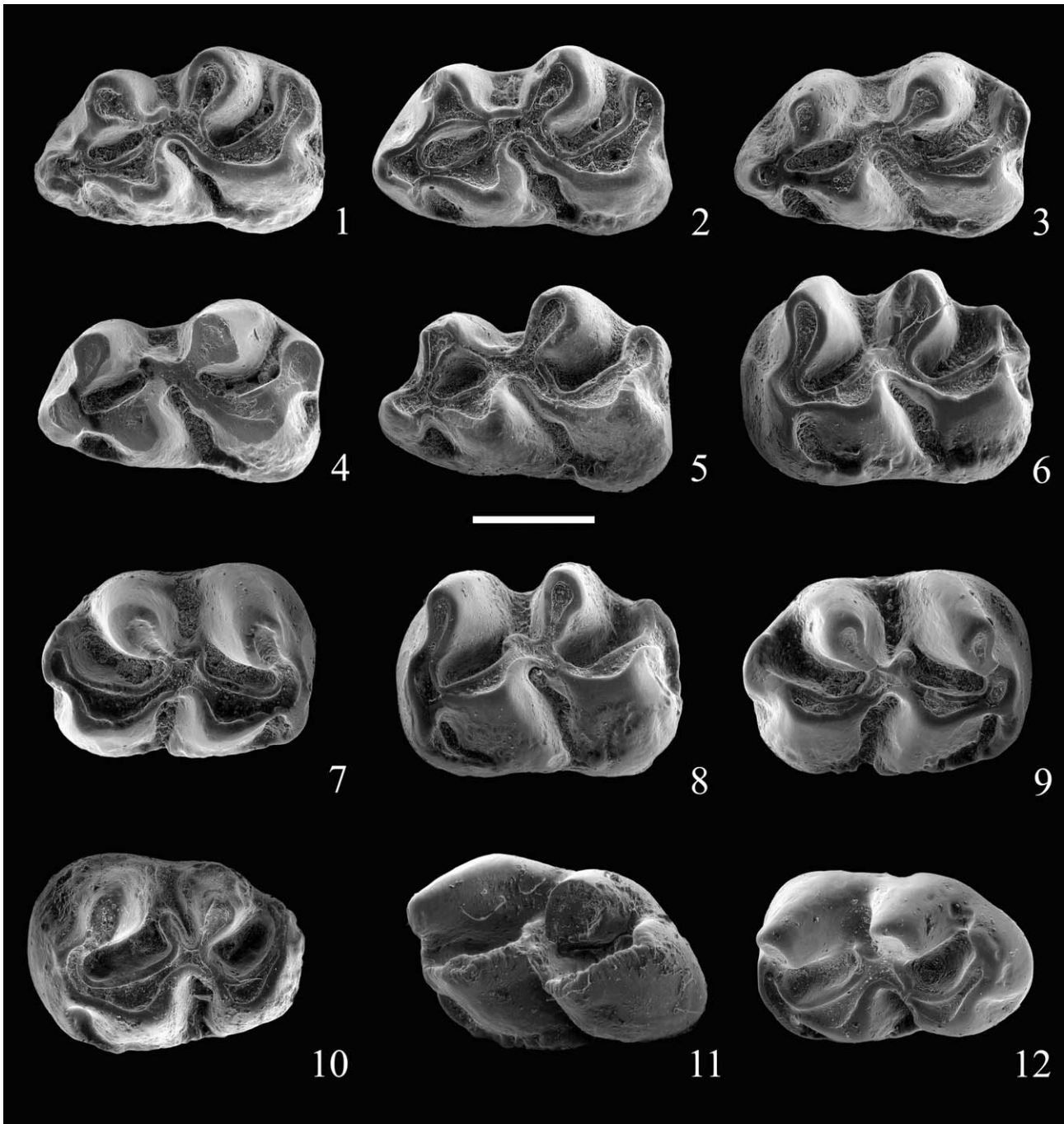


Fig. 3. Lower molars of *Hispanomys bijugatus*. 1. Left m1 (FSL 66256). 2. Left m1 (FSL 66257). 3. Left m1 (FSL 66258). 4. Left m1 (FSL 66259). 5. Left m1 (FSL 66260). 6. Left m2 (FSL 66261). 7. Right m2 (FSL 66262). 8. Left m2 (FSL 66263). 9. Right m2 (FSL 66264). 10. Left m3 (FSL 66265). 11. Left m3 (FSL 66266). 12. Left m3 (FSL 66267). Scale bar: 1 mm.

The nearly transverse sinus is almost closed by a ridge, which emerges from the hypocone. Some specimens show entostyle and a vestigial entomesoloph. These teeth have short labial and lingual posteroloph. They have four roots.

M2: The outline of these teeth in occlusal view is sub-rectangular, longer than wide, with its posterior part somewhat rounded and narrower than the anterior one. They have a well-developed lingual anteroloph and a distinct protosinus in the anterior margin of the teeth. The labial anteroloph is absent.

The anterior ectoloph and the forward paracone spur are usually absent, but they are very low and tiny on occasion. Therefore, the anterosinus is generally open except in highly worn specimens, in which it is closed. The paracone spur is long and strong, reaching a small anterior ridge of the metacone (posterior ectoloph) to entirely close the mesosinus. All teeth have the mesosinus larger than the anterosinus and they have no labial cingula surrounding the valleys. A true mesoloph is lacking, but some specimens have the beginning of the anterior

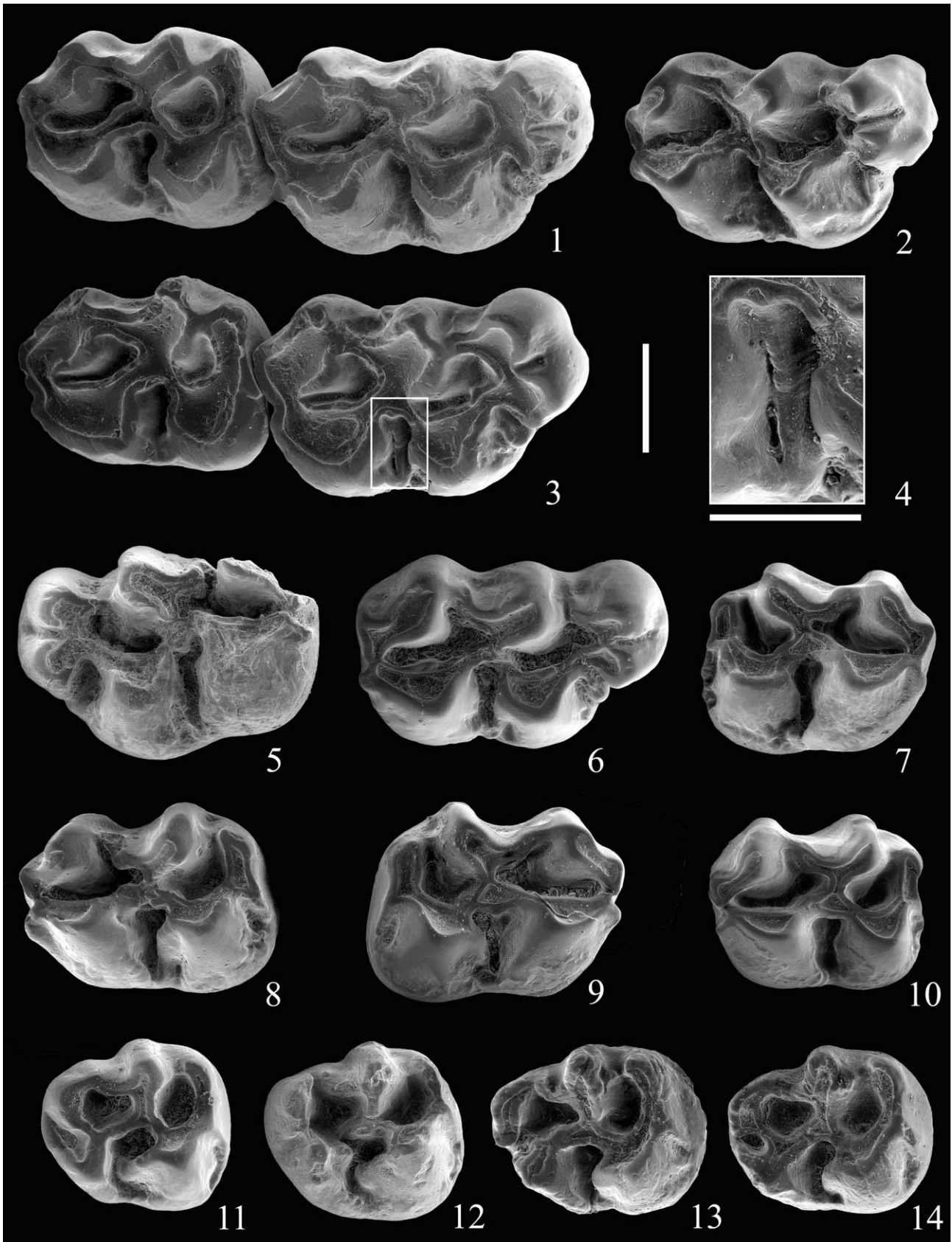


Fig. 4. Upper molars of *Hispanomys bijugatus*. 1. Right M1-M2 (FSL 66268). 2. Right M1 (FSL 66269). 3, 4. Right M1-M2 (FSL 66270) and close-up showing the entomesoloph. 5. Left M1 (FSL 66271). 6. Right M1 (FSL 66272). 7. Right M2 (FSL 66273). 8. Left M2 (FSL 66274). 9. Right M2 (FSL 66275). 10. Left M2 (FSL 66276). 11. Right M3 (FSL 66277). 12. Right M3 (FSL 66278). 13. Right M3 (FSL 66279). 14. Right M3 (FSL 66280). Scale bar: 1 mm.

Table 2

First/third molar length ratio for all species of *Hispanomys* known to date from various localities. Calculated from data in Aguilar (1982), Aguilar et al. (1994, 2007), Agustí (1977a, 1980, 1981, 1986), Agustí et al. (2005), Casanovas-Vilar (2007), Casanovas-Vilar et al. (2006), Freudenthal et al. (1991), Lacomba Andueza (1988), López Martínez et al. (1977), Mein and Freudenthal (1971), van Dam (personal data).

Taxa	Locality	Age	Lm1/Lm3	LM1/LM3
<i>H. adroveri</i>	Casa del Acero	MN12	1.26	2.01
<i>H. adroveri</i>	Crevillente 15	MN12	1.23	1.96
<i>H. freudenthali</i>	Masada del Valle 2	MN12	1.23	1.90
<i>H. freudenthali</i>	Vivero de Pinos	MN11	1.19	2.06
<i>H. freudenthali</i>	Aguanaces	MN10/MN11	1.18	2.05
<i>H. baixasi</i>	Lo Fournas 16-M	MN11	1.13	1.85
<i>H. baixasi</i>	Lo Fournas 6	MN11	1.13	1.77
<i>H. peralensis</i>	Crevillente 2	MN11	1.17	1.83
<i>H. peralensis</i>	Peralejos C	MN10 J3	1.22	1.79
<i>H. peralensis</i>	Masía del Barbo 2B	MN10 J2	1.06	1.93
<i>H. peralensis</i>	Masía del Barbo 2A	MN10 J1	1.11	1.90
<i>H. mediterraneus</i>	Montredon	MN10	1.16	1.92
<i>H. thaleri</i>	Can Llobateres	MN9b	1.24	1.86
<i>H. thaleri</i>	Riu Ripoll	MN9b	1.11	1.82
<i>H. thaleri</i>	Can Ponsic	MN9b	1.17	1.80
<i>H. aragonensis</i>	Pedregueras	MN9b	1.16	1.78
<i>H. nombrevillae</i>	Molina de Aragón	MN9a	1.25	1.86
<i>H. nombrevillae</i>	Nombrevilla	MN9a	1.29	2.03
<i>H. dispectus</i>	Creu Conill 22	MN9a	1.16	1.79
<i>H. dispectus</i>	Creu Conill 20	MN9a	1.13	1.80
<i>H. dispectus</i>	Hostalets de Pierola (upper levels)	MN9a	1.20	1.89
<i>H. dispectus</i>	Castell de Barbera	MN8	1.15	1.70
<i>H. dispectus</i>	Hostalets de Pierola (lower levels)	MN8	1.22	1.91
<i>H. daamsi</i>	Can Missert	MN8	1.08	1.78
<i>H. lavocati</i>	Saint Quirze	MN8	1.13	1.74
<i>H. aguirrei</i>	Escobosa	MN7/MN8	1.21	1.76
<i>H. bijugatus</i>	La Grive-Saint Alban	MN7/MN8	1.04	1.62
<i>H. decedens</i>	La Grive-Saint Alban	MN7/MN8	1.13	1.73
<i>H. castelnovi</i>	Castelnou 6	MN6?	1.17	1.83

arm of the hypocone slightly inflated. The backward paracone spur is generally posterolabially oriented; it emerges from the midpoint of the protolophule from which it rises to reach the labial side of the tooth. Some specimens show a short lingual spur emerging from the backward paracone spur. The protolophule is oblique and anterolingually directed. The sinus is usually closed by the junction of a ridge that emerges from the anterior side of the hypocone with another that descend from the posterior margin of the protocone (vestigial entomesoloph; e.g., FSL 66482, FSL 66276; Fig. 4.8). These teeth show short labial and lingual posterolophes; the latter one is more developed than the former. These teeth have four roots.

M3: The occlusal outline of these teeth is rounded, longer than wide, with its posterior part narrower than the anterior one. The labial anterolophid is long and the lingual one is less developed, but distinct. The anterosinus is somewhat smaller than the mesosinus. The anterior ectoloph is lacking and the forward paracone spur is small or even absent. The backward paracone spur is long; in some specimens it emerges from the midpoint of the protolophule from which it rises to reach the labial side of the tooth. It usually connects to the posterior ectoloph, closing the mesosinus, but in some specimens it is free because of the absence of the posterior ectoloph (e.g., FSL 66501). The nearly transverse protolophule connects to the junction between the posterior arm of the protocone and the anterior arm of the hypocone at about the centre of the tooth.

These teeth usually have a long and distinct posteroloph, but occasionally the metacone may be fused with the posteroloph, making the latter indistinct. The posterior side of the protocone generally has a strong ledge, which is directed towards the hypocone. This ledge comes into the sinus closing it partially. The sinus is very anterolabially directed. These teeth have three or four roots and they are not reduced. The value of the mean LM1/mean LM3 ratio of the teeth is indeed very low; one of the lowest ones obtained for any *Hispanomys* species known to date (Table 2).

m1: The occlusal outline of these teeth is sub-rectangular, longer than wide, with its anterior part somewhat rounded and narrower than the posterior one. The labial anterolophid is long and prominent. It reaches the anterior side of the protoconid, closing thereby the protosinusid. Specimen 66284 has a protostylid that is joined with the anteroconid by a labial spur of the anterolophulid. The lingual anterolophid is weak (e.g., 66288, 66286) or absent. The metalophulid is double. The mesolophid is usually absent with some specimens showing a slight inflation at the end of the posterior arm of the protoconid, but it can be short (e.g., 66292). These teeth have usually no lingual cingulum surrounding the valleys, but some of them (e.g., 66290, 66292, 66306, 66305) have it. Most of the teeth lack ectomesolophid, but in some of them (e.g., 66284) it is present. The sinusid is anterolingually directed. It is generally closed by the junction of two ridges; the first one emerging from

the posterior wall of the protoconid and the second one from the anterior wall of the hypoconid. This ridge can bear an ectostylid. The posterosinusid is very small, but distinct. The posterolophid is long, but does not reach the posterior wall of the entoconid. These teeth are two rooted.

m2: These teeth are rectangular in shape, though they are anteriorly and posteriorly rounded. They show a prominent labial anterolophid that reaches the anterolabial side of the protoconid, closing the protosinusid. The metalophulid and the hypolophulid are anterolabially directed. These teeth have no lingual cingula surrounding the valleys. The mesolophid is short or of medium size and usually ends free; it can join with the posterior side of the metaconid. The nearly transverse sinusid is partially closed by two ridges; the first one emerging from the posterior wall of the protoconid and the second one from the anterior wall of the hypoconid. The posterolophid is long, but does not reach the posterior side of the entoconid. These teeth are three-rooted.

m3: The occlusal outline of these teeth is rectangular, longer than wide, with its posterior part rounded and somewhat narrower than the anterior one. They show a long and strong labial anterolophid that connects to the anterior wall of the protoconid, closing the protosinusid. The lingual anterolophid is absent. The mesolophid is short or of medium size and it can be free or connected to the posterior wall of the metaconid. The posterosinusid and mesosinusid are open; there are no lingual cingula surrounding the valleys. The nearly transverse sinusid is partially closed by two ridges: the strongest emerges from the posterior wall of the protoconid, whereas the other comes out from the anterior wall of the hypoconid. An ectostylid can be present (e.g., FSL 66372). The posterolophid is long, but it does not join with the posterior wall of the entoconid, and a labial posterosinusid is very weak or lacking. These teeth are three-rooted.

3.2. Comparisons

3.2.1. *Hispanomys castelnovi* Aguilar, Calvet and Michaux, 1994

3.2.1.1. Historical background. This species was erected on the basis of several lower and upper isolated molars from the MN6 locality of Castelnou 6 (Pyrénées-Orientales, France). The holotype (CTN 6 no. 54), a single m1, is housed at the USTL (Aguilar et al., 1994). According to these authors this locality is Middle Miocene in age. However, the degree of evolution of the teeth of *Hispanomys castelnovi* may suggest a younger age.

3.2.1.2. Comparison with *H. bijugatus*. The cheek teeth of *H. bijugatus* are larger than those of *H. castelnovi*. In addition, the upper molars of this species lack the entomesoloph, whereas a vestigial entomesoloph is present in some specimens of *H. bijugatus*. Furthermore, a few upper molars of *H. castelnovi* have a low labial cingulum (Aguilar, pers. comm. 2009), whereas none of those of *H. bijugatus* has it. One of the most remarkable differences between these taxa is the absence of a

double metalophulid on the m1 of *H. castelnovi*. This structure is always present on the m1 of *H. bijugatus*.

3.2.2. *Hispanomys decedens* (Schaub, 1925)

3.2.2.1. Historical background. This species was erected by Schaub (1925: p. 13) as *Cricetodon sansaniense* Lartet, 1851 var. *decedens*. Later on, this author raised this variety to the species level (Schaub, 1944: p. 454). Mein and Freudenthal (1971: p. 19) introduced the subgenus *Hispanomys* for a handful of supposedly derived *Cricetodon*. This subgenus was elevated to the genus level by Van de Weerd (1976: p. 106 *et seq.*). The holotype of this species (Lgr130), a left maxillary fragment with M1 and M2, comes from a MN7/8 unnamed fissure-filling of La Grive-Saint Alban. It is housed in the MSNL. Alba et al. (2006) and Casanovas-Vilar (2007) mentioned the existence of additional material of *H. decedens* from various MN7/8 sites of the Can Mata series (Barcelona).

3.2.2.2. Comparison with *H. bijugatus*. The M1 and M2 of *H. decedens* show low labial cingula surrounding the valleys (absent in *H. bijugatus*). The upper molars of *H. decedens* have usually a mesoloph, which is absent on those of *H. bijugatus*, and the ectolophs are less developed than in the latter species. With regard to the lower molars, the percentage of m1 with a double metalophulid in *H. decedens* is lower than in *H. bijugatus*. In contrast, there are more m1 with ectomesolophid in *H. decedens* than in *H. bijugatus*. The lingual anterolophid is usually more developed on the m1 of *H. decedens* than in those of *H. bijugatus*. Some m3 of *H. decedens* have the mesolophid long, whereas it is short or of medium size in *H. bijugatus*.

3.2.3. *Hispanomys aguirrei* (Sesé in López-Martínez, Sesé and Sanz-García, 1977)

3.2.3.1. Historical background. This taxon was initially named *Cricetodon aguirrei* by Sesé in López-Martínez et al. (1977) and posteriorly reallocated to the genus *Hispanomys* by Agustí (1977a: p. 31). The holotype (ES-221/224) is a left maxillary fragment with M1-M2 (kept in the collections of the MNCN) from the Middle Miocene (MN 7/8) locality of Escobosa I, Escobosa de Catalañazor. Additional material of this species has been found at the coeval localities of Escobosa M and Escobosa G-2 (Sesé in López-Martínez et al., 1977) and recently at the Upper Aragonian locality of Nombrevilla 2 (Zaragoza; López Guerrero et al., 2008).

3.2.3.2. Comparison with *H. bijugatus*. About a quarter of the m1 of *H. aguirrei* shows a double metalophulid, whereas all m1 of *H. bijugatus* have it. Most of the m2 of *H. aguirrei* have two double roots, whereas those of *H. bijugatus* already are three-rooted. The m3 of *H. aguirrei* from Escobosa are smaller than those of *H. bijugatus*. With regard to the upper molars, most of the M1 and M2 of *H. aguirrei* have well-developed low cingula closing the labial valleys; some of them have mesoloph and lack entomesoloph. In contrast, both the labial cingula and the mesoloph are always missing on the M1 and M2 of *H. bijugatus* and some of them have an entomesoloph. Even though the M3 of *H. aguirrei* are not much reduced, the value of the mean

LM1/mean LM3 ratio is higher in this species than in *H. bijugatus* (Table 2). In addition, some M3 of *H. aguirrei* have a mesoloph, whereas the mesoloph is missing on all M3 of *H. bijugatus*.

3.2.4. *Hispanomys daamsi* Agustí, Casanovas-Vilar and Furió, 2005

3.2.4.1. Historical background. The holotype of this species (IPS 16444), a left mandible with m1-m3, is housed at the IPS. This species was erected on the basis of several teeth recovered from the late Aragonian (MN 8) locality of Can Missert (Agustí et al., 2005). Further material of this taxon has been recently reported from MN7/8 levels at Hostalets de Pierola (Alba et al., 2006; Casanovas-Vilar, 2007).

3.2.4.2. Comparison with *H. bijugatus*. The cheek teeth of *H. daamsi* are larger than those of *H. bijugatus*. The M1 and M2 of *H. daamsi* show small cingula at the base of the labial valleys and lack the entomesoloph, whereas the labial cingula are missing in the M1 and M2 of *H. bijugatus* and some of them have the entomesoloph. Even if the M3 are not much reduced in *H. daamsi*, this taxon has a mean LM1/mean LM3 ratio higher than *H. bijugatus* (Table 2). In addition, all the M3 of *H. daamsi* lack a vestigial entomesoloph, whereas it is present on some M3 of *H. bijugatus*. With respect to the lower molars, the m1 of *H. bijugatus* have a double metalophid, which is single on those of *H. daamsi*.

3.2.5. *Hispanomys dispectus* Agustí, 1980

3.2.5.1. Historical background. This species was first cited by Agustí and Gibert (1979: pp. 17–18), but in a way that does not fulfill the requirements for the name to be considered as available (ICZN, 1999, article 13.1). In particular, the short description does not provide characters purported to differentiate the taxon. The valid description of this taxon is provided by Agustí (1980), as explicitly mentioned by Agustí and Gibert (1979: p. 17).

According to Agustí (1980: p. 56), the material from Hostalets de Pierola described by Schaub (1944, 1947) and listed by Crusafont and Casanovas (1973) as *Cricetodon decedens* would pertain to *H. dispectus*. In addition, in the same work, this author stated that *H. cf. thaleri* from Castell de Barbera (Aguilar et al., 1979) and from La Bisbal I and La Bisbal II, Girona, Spain (Gibert et al., 1980) pertains actually to *H. dispectus*.

The holotype of *H. dispectus* (IPS VP 610) is a complete left maxilla from a lower level (MN 8) of the Hostalets de Pierola locality. Additional material of this species has been also recovered from the Vallès Penedès at the sites of Hostalets de Pierola (upper levels, MN 9), Can Feliu (MN 7/8), Castell de Barbera (MN 8), and Creu Conill 22 and 20 (MN 9) as well as from Ampurdá (Girona) at the MN 9 locality of La Bisbal II (Agustí, 1980, 1981; Gibert et al., 1980; Casanovas-Vilar et al., 2006).

3.2.5.2. Comparison with *H. bijugatus*. This species differs from *H. bijugatus* in having labial valleys surrounded by low

cingula on the upper molars and, in some specimens, quite well-developed mesolophs, which are absent on the upper molars of *H. bijugatus*. The value of the mean LM1/mean LM3 ratio of the teeth of *H. dispectus* is higher than that calculated for *H. bijugatus*, which has therefore the M3 less reduced (Table 2). With regard to the lower molars, the m1 of *H. dispectus* lacks the double metalophid, which is present in all m1 of *H. bijugatus*.

3.2.6. *Hispanomys lavocati* (Freudenthal, 1966)

3.2.6.1. Historical background. This taxon was erected by Freudenthal (1966) as a species of *Cricetodon*. Subsequent authors (Agustí, 1977a: p. 31 *et seq.*) reallocated it to the genus *Hispanomys*, an act with which we agree. The holotype of this species (VP 536), a complete left maxilla from the lower levels (MN 8) of the Hostalets de Pierola locality, is housed in the IPS. Additional material of this taxon has been also recovered in the coeval locality of Sant Quirze, Barcelona, Spain (Agustí, 1977b) and Nombrevilla 2 (López-Guerrero et al., 2008). The material from Viladecavalls (Barcelona) described by Schaub (1947: p. 62) as *C. decedens* and reallocated to *H. lavocati* by Freudenthal (1966: p. 313), actually belongs to *H. thaleri* (Agustí, 1980: p. 59).

3.2.6.2. Comparison with *H. bijugatus*. *H. lavocati* is larger than *H. bijugatus*. With regard to the upper molars, the M1 and M2 of *H. lavocati* have labial cingula surrounding the valleys and, on occasion, a short mesoloph, both of which are absent on the upper molars of *H. bijugatus*. In addition, some M3 of *H. lavocati* have a moderately long mesoloph, which is lacking in *H. bijugatus*. With regard to the lower molars, those of *H. lavocati* have the mesolophids well developed, whereas *H. bijugatus* have them short or even absent. Furthermore, the m1 of *H. lavocati* have a single metalophid, whereas it is double in those of *H. bijugatus*. Most m2 of *H. lavocati* have two double roots, whereas those of *H. bijugatus* are three-rooted.

3.2.7. *Hispanomys nombrevillae* (Freudenthal, 1966)

3.2.7.1. Historical background. Freudenthal (1966) created the subspecies *Cricetodon decedens nombrevillae*. Later on, in their classification of the Cricetidae, Mein and Freudenthal (1971) reallocated it to the subgenus *Hispanomys*. According to them, most of the Can Llobateres material assigned to *Ruscinomys thaleri* by Hartenberger (1965) would pertain to that taxon (see discussion below). The holotype of *H. nombrevillae* (NO 258) is a single M1 from the lower Vallesian site (MN9, H) of Nombrevilla. It is housed in the IPS. Additional material of this species has been recovered from a MN 9 locality near Molina de Aragón (Lacomba Andueza, 1988).

3.2.7.2. Comparison with *H. bijugatus*. The size of the cheek teeth of *H. nombrevillae* is smaller to *H. bijugatus*. In addition, the M1 and M2 of *H. nombrevillae* have low labial cingula surrounding the valleys; these cingula are absent on the upper molars of *H. bijugatus*. The M3 of *H. nombrevillae* are much reduced, the values of the mean LM1/mean LM3 ratio of

its teeth being very high, whereas it is very low in *H. bijugatus*, which has not the third upper molars reduced (Table 2). With regard to the lower molars, none of the m1 of *H. nombrevillae* has a double metalophulid, whereas it is present in all m1 of *H. bijugatus*. The m2 of *H. nombrevillae* have two double roots, whereas those of *H. bijugatus* are three-rooted.

3.2.8. *Hispanomys thaleri* (Hartenberger, 1965)

3.2.8.1. Historical background. Hartenberger (1965) erected the new species *Ruscinomys thaleri* on the basis of cheek teeth from the MN 9b locality of Can Llobateres. Later on, Mein and Freudenthal (1971) discussed the status of *R. thaleri*. According to them, the holotype of this species would be a true *Ruscinomys*, but most of its paratypes would correspond to *Cricetodon Hispanomys* cf. *nombrevillae*. The comparison of the Vallesian material of Can Ponsic with that of Can Llobateres by Agustí (1984) led him to consider *H. thaleri* a homogeneous population, to which an emended diagnosis was given. This species has been also recovered from the MN 9 localities of Rubí Terrassa-6E, Can Ponsic, and Riu Ripoll (Barcelona, Spain), and the MN 10 localities of Can Casablanques, Camí de Can Tarumbot-2, Rubí Terrassa-7, Viladecavalls, Torrent de Febulines, Trinxera Sur Autopista II, Trinxera Nord Autopista II, and Can Jofresa, Barcelona, Spain (Agustí, 1981; Agustí and Gibert, 1982; Agustí et al., 1997). The holotype of *H. thaleri* (CL3630) is a single M1 housed at the IPS (Hartenberger, 1965).

3.2.8.2. Comparison with *H. bijugatus*. One of the differences between the two taxa is the presence of the enamel-coated valley. Even if only few upper molars of *H. thaleri* have it, none of *H. bijugatus* show this structure. In addition, the M3 of *H. thaleri* are noticeably less reduced than those of *H. bijugatus* (Table 2). None of the m1 of *H. thaleri* has a double metalophulid, whereas it is present in all m1 of *H. bijugatus*. The m2 of *H. thaleri* have two roots, whereas those of *H. bijugatus* are three-rooted. Finally, the m3 of *H. thaleri* are less reduced than those of *H. bijugatus*.

3.2.9. *Hispanomys aragonensis* (Freudenthal, 1966)

3.2.9.1. Historical background. This species was originally erected as *Cricetodon decedens aragonensis* by Freudenthal (1966). Subsequently, Mein and Freudenthal (1971) reallocated it to the subgenus *Hispanomys*. The holotype of this species (PEC 1164), an isolated M1 from the lower Vallesian (MN9, I) locality of Pedregueras IIC, is housed in the IPS. Additional material has been recovered from the MN 9 (I) localities of Pedregueras 1A and 2A (Freudenthal, 1966). Two teeth of this species have been also reported from the MN9 (H) locality of Los Valles de Fuentidueña, Segovia, Spain (Agustí, 1978: p. 139).

3.2.9.2. Comparison with *H. bijugatus*. The upper molars of *H. aragonensis* have labial cingula surrounding the valleys, which are lacking on the upper molars of *H. bijugatus*. Some of the M1 and M2 of *H. aragonensis* have a small enamel-coated valley in the occlusal surface of the paracone, whereas it is

absent in all M1 and M2 of *H. bijugatus*. The M3 of *H. aragonensis* are less reduced than those of *H. bijugatus* (Table 2). With regard to the lower molars, some of those of *H. aragonensis* have a lingual cingulum surrounding the valley, whereas it is lacking on those of *H. bijugatus*. With regard to the lower molars, some m1 of *H. aragonensis* show two short mesolophids, whereas there is only one or none on the m1 of *H. bijugatus*. The metalophulid is single in *H. aragonensis*, whereas it is double on all m1 of *H. bijugatus*. In addition, some m1 of *H. aragonensis* have a lingual anterolophid, which is lacking on the m1 of *H. bijugatus*. Finally, the m2 of *H. aragonensis* have two roots (the posterior one being splitted), whereas those of *H. bijugatus* are three-rooted.

3.2.10. *Hispanomys mediterraneus* Aguilar, 1982

3.2.10.1. Historical background. Aguilar (1982) created this species on the basis of isolated cheek teeth from the Late Miocene (MN 10) site of Montredon. He gave a list of chresonyms, in which he states that (at least) a part of the material studied by Hartenberger (1965) and attributed to the species *Ruscinomys thaleri* and, thereby (see discussion above on *H. thaleri* above) *Hispanomys* cf. *nombrevillae* (incorrectly mentioned in the text as *H. cf. aragonensis*) discussed by Mein and Freudenthal (1971), pertained in fact to *H. mediterraneus*. However, the comparison of the Vallesian material of *H. thaleri* from Can Ponsic with that from Can Llobateres carried out by Agustí (1984) led him to consider *H. thaleri* a homogeneous population and invalidate this supposition. In addition, in the same list of chresonyms, Aguilar (1982) stated that the material from Montredon described by Thaler (1966: p. 151, Fig. 21E) as *Cricetodon (Cricetodon)* cf. *decedens* (and later on listed by Guérin and Mein (1971: p. 149) and figured by Engesser (1972: pp. 288, 292)) as well as that described and figured as *Cricetodon* sp. 1 by Hartenberger and Thaler (1963: pp. 3333–3335) would also belong to *H. mediterraneus*.

The holotype of this species (MTN no. 1509) is a single left M1 housed at the USTL. Additional material of this species has been recovered from the Upper Vallesian locality of Lo Fournas 7 (Aguilar et al., 1999). The Turolien material of *H. mediterraneus* from Lo Fournas 6, as well as that of *H. cf. mediterraneus* from Castelnou 1 and Castelnou 3 has been recently attributed to *H. baixasi* (Aguilar et al., 2007). Mein (1999) mentioned the presence of *H. mediterraneus* at the MN 10 French localities of Soblay and Dionay, as well as *H. cf. mediterraneus* at the coeval localities of Ambérieux 1 and 2 (Ain).

3.2.10.2. Comparison with *H. bijugatus*. The M1 and M2 of *H. mediterraneus* have the ectolophs more developed than those of *H. bijugatus*. In addition, all M1 of the former species lack a labial spur of the anterolophule, which is present on some specimens of *H. bijugatus*. The M2 of *H. mediterraneus* have a much less developed lingual cingulum than those of *H. bijugatus*. With respect to the M3, those of *H. mediterraneus* are much reduced, whereas those of *H. bijugatus* are not that lessened (Table 2). With regard to the lower molars, none but one of the m1 of *H. mediterraneus*, has a double metalophulid,

whereas all m1 of *H. bijugatus* have it. The m2 and m3 of *H. mediterraneus* usually have the mesolophid less developed than those of *H. bijugatus*.

3.2.11. *Hispanomys peralensis* Van de Weerd, 1976

3.2.11.1. Historical background. Van de Weerd (1976) erected the species *Hispanomys peralensis* based on material from the MN 10 locality of Peralejos C and assigned to this species material from other MN 10–11 localities of the Teruel-Alfambra region: Masía del Barbo 2A, Masía del Barbo 2B, Peralejos B, Peralejos D, and Peralejos 4. The holotype (PERC 351) is an isolated M1 from the locality of Peralejos C (Van de Weerd, 1976), which is correlated to the local subzone J3 (MN 10) of Van Dam et al. (2001). It is stored in the collection of the RUU. According to Van de Weerd (1976), the two species of *Cricetodon* from Masía del Barbo 2A and 2B described by Freudenthal (1966: pp. 308–310), but not named, also pertain to *H. peralensis*. Antunes and Mein (1979: p. 916) mentioned the presence of *H. peralensis* from the lower MN 10 site of Freiria de Rio Maior, Portugal. Freudenthal et al. (1991: p. 11) pointed out that the material from the MN 11 locality of Tortajada A (Teruel-Alfambra region) described as *H. freudenthali* by Van de Weerd (1976), as well as that from the MN 11 localities of Crevillente 1, 3 and 4 (Alicante, Spain) described by De Bruijn et al. (1975: p. 297) as *H. sp. A*, also correspond to *H. peralensis*. More material of *H. peralensis* from this zone has been recovered at the localities of Crevillente 2 and Crevillente 4B (Freudenthal et al., 1991). Alcalá et al. (2005: p. 201, Fig. 3) reported *H. peralensis* at the MN10 (J3) localities MR604-A and B, and *H. cf. peralensis* at MR604-B, Masía de la Roma, Teruel, Spain. Furthermore, van Dam et al. (2001) listed *H. peralensis* at various MN9 (I) and MN 10 localities of the Teruel-Alfambra region (Peralejos 5, Masía de la Roma 3, 4B, 4C, 6, 7, Masía del Barbo A, Masía de la Roma 9, Peralejos 4, Masía del Barbo B, Puente Minero 8, 10, Masada Rueda, and Peralejos C). In addition, they mentioned the co-occurrence of this species and *H. aff. peralensis* at some of them (Peralejos 5, Masía de la Roma 3, 4C, 7, Masía del Barbo A, Peralejos 4, and Masía del Barbo B). Finally, van Dam et al. (2001) mentioned other localities where either *H. peralensis* or *H. aff. peralensis* is present (Masía de la Roma 4B, 6, 8, 9, La Salle, Masía de la Roma 11, and Los Aguanaces 5A). Besides, two m1 identified as *H. cf. peralensis* have been recovered from two MN10 localities (CRS2A and CRS2B) of the Cortasogas site, Calatayud Basin, Spain (Van Dam and Sanz Rubio, 2003). On the basis of very poor material (two isolated teeth and three fragments), Calvo et al. (1978) recognized *H. cf. peralensis* at the MN10 locality of Hajar-1, Albacete, Spain. *H. cf. peralensis* has also been cited from the MN11 site of Lobrieu, Vaucluse, France (Mein, 1999).

3.2.11.2. Comparison with *H. bijugatus*. The M1 of *H. peralensis* are four or five-rooted, whereas those of *H. bijugatus* are four-rooted. In addition, none of the M1 of *H. peralensis* has either labial spur on the anterolophule or entomesoloph, and all of them have a distinct forward paracone spur and a weak lingual cingulum. In contrast, some of the M1

of *H. bijugatus* have a labial spur on the anterolophule and an entomesoloph; they usually lack the forward paracone spur and have a strong lingual cingulum. Furthermore, the M2 of *H. peralensis* have the lingual cingulum less developed than those of *H. bijugatus* and none of them have entomesoloph, whereas some of the M2 of *H. bijugatus* show a vestigial entomesoloph. The M3 of *H. peralensis* are much more reduced than those of *H. bijugatus* (Table 2) and they lack the posterior cingulum. This posterior cingulum is well developed and almost always present on the M3 of *H. bijugatus*, in which it emerges from the protocone reaching the posterior wall of the metacone. With regard to the lower molars, none of the m1 of *H. peralensis* has the double metalophid, which is always present on the m1 of *H. bijugatus*. Finally, the m2 and m3 of *H. peralensis* have the mesolophid usually less developed than those of *H. bijugatus*.

3.2.12. *Hispanomys baixasi* Aguilar, Michaux and Lazzari, 2007

3.2.12.1. Historical background. This species has been erected on the basis of mandibles, maxillae, and numerous isolated cheek teeth from the Turolian locality of Lo Fournas 16-M, Pyrénées-Orientales. Its holotype (Fou 16-M no. 193) is a left M1 housed at the USTL. Further material of this species has been recovered at the coeval localities of Lo Fournas 6, Castelnou 1 and 3, Pyrénées-Orientales (Aguilar et al., 2007).

3.2.12.2. Comparison with *H. bijugatus*. Only few m1 of *H. baixasi* show a double metalophid, whereas it is always present on the m1 of *H. bijugatus*. The m2 of *H. baixasi* show a less developed mesolophid than those of *H. bijugatus*. In addition, the m3 of *H. baixasi* are more reduced than those of *H. bijugatus*. With regard to the upper molars, those of *H. baixasi* have the ectoloph usually more developed than those of *H. bijugatus* and they lack the entomesoloph, which is present on some M1–M2 of *H. bijugatus*. The M3 of *H. baixasi* are much more reduced than those of *H. bijugatus* and they lack the posteroloph, which is well developed on the M3 of *H. bijugatus*.

3.2.13. *Hispanomys freudenthali* Van de Weerd, 1976

3.2.13.1. Historical background. The validity of the species *H. freudenthali* from the MN12 locality of Masada del Valle 2 (Teruel-Alfambra region) was discussed by Freudenthal et al. (1991). According to these authors, the holotype of this species (MDV2-1241), one M1 housed in the RUU, can be distinguished neither by the morphology nor by the size from a M1 of *Pseudoruscinomys schaubi*. Consequently, according to Freudenthal et al. (1991), the nominal taxon *H. freudenthali* should be considered a junior synonym of *P. schaubi*. Freudenthal et al. (1991) pointed out that the specimen MDV2-1212, one m2, should be also attributed to *P. schaubi*. Incidentally, *Pseudoruscinomys* is considered a synonym of *Ruscinomys* by Agustí (1980), who judged that *H. freudenthali* should be accommodated into the genus *Ruscinomys*. According to Freudenthal et al. (1991), the specimen (MDV2-1217), one m2, together with some m3 from the same locality, would

pertain in fact to *H. adroveri*. The remaining material considered as *H. freudenthali* by Van de Weerd (1976) should be allocated to a new species, to which would also belong the material from the MN 11 localities of Los Aguanaces and Vivero de Pinos described as *H. freudenthali* by Adrover (1986). The presence of this taxon has been mentioned by Alcalá et al. (1991) at the early Turolian (MN 11) locality of Puente Minero (Teruel, Spain). Furthermore, Van Dam et al. (2001) listed *H. freudenthali* at various MN12 (Masada Rueda 4, 3, Masada del Valle 2, Los Mansuetos 2, Tortajada B) and MN11 (Valdecebro 4, Vivero de Pinos, Tortajada A, Los Aguanaces 3, Los Aguanaces, Regajo 2, Puente Minero 3, La Gloria 10, Masada Rueda 2, Puente Minero, Peralejos D) and MN10 (J3) (Los Aguanaces 6) localities from this area.

3.2.13.2. Comparison with *H. bijugatus*. The teeth of *H. freudenthali* are larger and more hypsodont than those of *H. bijugatus*. The M1 of the former species have usually five roots, whereas those of *H. bijugatus* always are four-rooted. In addition, the lingual cingulum is much less strong on the M1 of *H. freudenthali* than on those of *H. bijugatus* and they lack the entomesoloph, which is present on some M1 and M2 of *H. bijugatus*. The M3 of *H. freudenthali* are much reduced, the mean LM1/mean LM3 ratios being very high, whereas it is very low in *H. bijugatus*, which has not the third upper molars reduced at all (Table 2). Therefore, on the M3 of *H. freudenthali*, the anteroloph, anterior ectoloph, and forward paracone spur are totally fused with the protocone and paracone, the sinus is usually very small or absent, and the posteroloph is lacking. In contrast, the M3 of *H. bijugatus* have a long anteroloph not connecting with the paracone, a quite large sinus, and a well-developed posteroloph. With regard to the lower molars, the m1 of *H. freudenthali* have a single metalophid, which is double in *H. bijugatus*; about half the individuals lack the anterolophid on the lower molars, which is always present in *H. bijugatus*.

3.2.14. *Hispanomys adroveri* Agustí, 1986

3.2.14.1. Historical background. The holotype of this species (F-CA 180) is an isolated M1 from the Middle Turolian (MN 12) locality of Casa del Acero, Fortuna Basin, Murcia. It is housed in the IPS. This species has been also recorded in the coeval locality of Crevillente 15 (Freudenthal et al., 1991). Additional material of this taxon has been recovered from the Late Turolian (MN 13) Librilla section (BS-141), Fortuna Basin (Agustí et al., 1999, 2006). In addition, material attributed to *Hispanomys* aff. *adroveri* has been recovered from other Late Miocene localities of Crevillente (5, 8, 14, 17; Freudenthal et al., 1991) and from the coeval locality of Canteras de Jun, Granada, Spain (García-Alix et al., 2008). According to Freudenthal et al. (1991), this taxon would be also represented in the MN 12 locality of Masada del Valle 2 (see § on 3.2.13).

3.2.14.2. Comparison with *H. bijugatus*. This species is much larger and hypsodont than *H. bijugatus*. The M1 of *H. adroveri* are five-rooted, whereas they are four-rooted in *H. bijugatus*.

Other differences between the two taxa include the more marked development of the ectoloph on the upper molars of *H. adroveri*, particularly on the M2, in which both labial valleys are closed (the anterosinus remains usually open on the M2 of *H. bijugatus*, due to the absence of the forward paracone spur). The M3 of *H. adroveri* are much reduced; they lack the posteroloph, have the sinus connected to the anterosinus and mesosinus, and about half the specimens lack the protolophule (the paracone is isolated). In contrast, the M3 of *H. bijugatus* are not reduced, the posteroloph is well developed, the three sinuses are unconnected, and the protolophule is well developed. With regard to the lower molars, those of *H. adroveri* lack a double metalophid and they show a well-developed mesolophid that normally joins with the metaconid, whereas in *H. bijugatus* the metalophid is always double and the mesolophid usually absent. In addition, the m2 of *H. adroveri* lack the protosinusid, whereas it is present on the m1 of *H. bijugatus*.

3.2.15. *Hispanomys lusitanicus* (Schaub, 1925)

This species was originally attributed to the genus *Cricetodon* by Schaub (1925) and reallocated to the subgenus *Hispanomys* by Mein and Freudenthal (1971). This taxon is based on one incomplete mandible with m1-m2 (unnumbered, MGISTL), which is supposed to come from the late Miocene (MN 10) of Carvalhal Novo (Azambujeira, Portugal). According to Antunes (1984), the holotype is damaged, not characteristic enough, and the taxon is badly defined so that its validity is questionable. Pending a revision, this taxon is not considered in the present study.

4. Discussion

Seven species of the genus *Hispanomys* are known from Upper Aragonian strata: *H. castelnovi*, *H. decedens*, *H. bijugatus*, *H. aguirrei*, *H. daamsi*, *H. dispectus*, and *H. lavocati*. During the Late Aragonian and Early Vallesian, the main source of morphological variability are the different development of the ectolophs, the presence or absence of the mesoloph and mesolophid, the existence of cingular structures in the upper and lower molars, and the increase in the number of roots in second molars (Agustí, 1981, 1982). Despite these morphological differences, the general pattern of the cheek teeth is rather homogeneous within each population. The most primitive morphologies are characterized by having lower molars with well-developed labial anterolophids, with lingual anterolophids, lingual cingula surrounding the valleys, vestigial ectomesolophid on the m1, two-rooted m2, and unreduced m3. On the other hand, the most primitive upper molars are characterized by having mesolophs, labial cingula surrounding the valleys, quite incomplete ectolophs, vestigial entomesoloph, four-rooted M1, and unreduced M3.

From La Grive-Saint Alban, two species of *Hispanomys* have been recovered: *H. bijugatus* and *H. decedens*. The first taxon has been found in La Grive-Saint Alban at localities L3 and L5, whereas *H. decedens* has been recovered at localities L5, M, and at the unnamed fissure-filling.

The age of the different fissure-fillings of La Grive-Saint Alban is controversial. According to Mein and Ginsburg (2002), the oldest localities would be La Grive M and L7, which were correlated to the MN7, whereas the youngest ones would be La Grive L3 and L5, which they correlated with MN8. On the contrary, Maridet (2003: p. 197) pointed out that La Grive L3 and L5 would be actually the oldest of La Grive localities, being followed by L7 and finally by M, which would be the youngest one.

If we compare the degree of evolution of the teeth in *H. bijugatus* and in *H. decedens*, it appears that the former shows a more progressive dental morphology. *H. bijugatus* has indeed the following derived characters, which are lacking in *H. decedens*:

- absence of labial and lingual cingula surrounding the upper and lower molar valleys, respectively;
- absence of mesoloph on the upper molars;
- ectolophs more developed;
- lower percentage of m1 showing vestigial ectomesolophid;
- less important development of the lingual anterolophid on the m1;
- less marked development of the mesolophid on the m3.

All these differences suggest that *H. bijugatus* is more derived than *H. decedens*. Because these species are believed to be closely related species within the same lineage (Mein and Freudenthal, 1971: Fig. 1; Chaline and Mein, 1979: Fig. 33; Agustí, 1980: Fig. 4; Aguilar, 1982: Fig. 6), La Grive M (with *H. decedens* only) may be older than La Grive L3 and L5 (with *H. bijugatus*), as suggested by Mein and Ginsburg (2002). The same is true for the unnamed fissure-filling. The coexistence of the two species at La Grive L5 may indicate an older age for this locality than for L3, from which only *H. bijugatus* has been recovered. As mentioned above, Mein and Ginsburg (2002) did not take into account the two M3 of *H. decedens* found in L7. Interestingly enough, if the presence of *H. decedens* in L7 is not due to “contamination”, this locality (as La Grive M) may be older than La Grive L3 and L5, as also suggested by Mein and Ginsburg (2002).

5. Conclusion

The species *H. bijugatus* from La Grive-Saint Alban shows a low variability as common in the populations of *Hispanomys* from the Upper Aragonian. Even though *H. bijugatus* has some of the typically primitive dental characters of the Aragonian species of *Hispanomys*, such as the not reduced M3, it shows a lot of progressive characters: the absence of labial and lingual cingula surrounding the upper and lower molar valleys, respectively, the increase of the number of roots on the second lower molar, and the lost of mesolophs on the upper molars. This suggests that *H. bijugatus* is relatively derived with respect to the coeval congeneric species. For that reason, a younger age is inferred for the localities of La Grive L3 and L5, where this taxon has been recovered, than for La Grive M and for the unnamed fissure-filling, in which *H. decedens* has not been found.

Acknowledgements

J. van Dam and W. Wessels (Rijksuniversiteit Utrecht, Utrecht) kindly lent material of *Hispanomys* kept in their institution. Various aspects of this paper were improved thanks to the critical reading of J.-P. Aguilar (Université Montpellier 2, Montpellier) and M.A. Álvarez-Sierra (Universidad Complutense, Madrid). L. Celià Gelabert and J. Galindo Torres (Instituto Catalán de Paleontología, Sabadell) allowed the examination of material under their care. This study has been partly funded by research project CGL2008-05813-CO2-01 conducted by J. Morales. R.L.A. holds a Ramón y Cajal contract. Publication UMR 5125.

References

- Adrover, R., 1986. Nuevas faunas de roedores en el Mio-Plioceno continental de la región de Teruel (España). Interés bioestratigráfico y paleoecológico. Instituto de Estudios Turolenses: Teruel.
- Aguilar, J.-P., 1982. Contributions à l'étude des micromammifères du gisement miocène supérieur de Montredon (Hérault-2). Les rongeurs. Palaeovertebrata 12, 75–140.
- Aguilar, J.-P., Agustí, J., Gibert, J., 1979. Rongeurs miocènes dans le Vallès-Penedès-2. Les rongeurs de Castell de Barbera. Palaeovertebrata 9, 17–31.
- Aguilar, J.-P., Calvet, M., Michaux, J., 1994. Les rongeurs de Castelnou 6 (Pyrénées Orientales, France) et les corrélations entre faunes ibériques et françaises au Miocène moyen. Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 192, 109–131.
- Aguilar, J.-P., Escarguel, G., Michaux, J., 1999. A succession of Miocene rodent assemblages from fissure fillings in southern France, palaeoenvironmental interpretation and comparison with Spain. Palaeogeography, Palaeoclimatology, Palaeoecology 145, 215–230.
- Aguilar, J.-P., Michaux, J., Lazzari, V., 2007. Lo Fournas 16-M (Miocène supérieur) et Lo Fournas 16-P (Pliocène moyen), deux nouvelles localités karstiques à Baixas, Sud de la France. Géologie de la France 1, 63–81.
- Agustí, J., 1977a. Contribución al conocimiento del género *Hispanomys* (Cricetidae, Rodentia, Mammalia) en la cuenca miocénica del Vallès-Penedès. Boletín Informativo del Instituto de Paleontología de Sabadell 9, 30–32.
- Agustí, J., 1977b. Descripción de *Cricetodon lavocati* Freudenthal, 1966, de Sant Quirze (Trinxera). Paleontologia y Evolución 12, 65–67.
- Agustí, J., 1978. El Vallesien inferior de la Península Ibérica y su fauna de roedores (Mammalia). Acta Geológica Hispánica 13, 137–141.
- Agustí, J., 1980. La asociación de *Hispanomys* y *Cricetodon* (Rodentia, Mammalia) en el Mioceno Superior del Vallès-Penedès (Cataluña, España). Acta Geológica Hispánica 15, 51–60.
- Agustí, J., 1981. Roedores miomorfos del Neógeno de Cataluña. Ph.D. Dissertation Universidad de Barcelona, Barcelona.
- Agustí, J., 1982. Tendencias evolutivas de la línea *Cricetodon-Ruscinomys* (Rodentia, Mammalia) en la Península Ibérica. Acta Geológica Hispánica 17, 103–111.
- Agustí, J., 1984. Contribución al conocimiento de los Cricétidos (Rodentia, Mammalia) de Can Llobateres (Mioceno superior del Vallès, España). In: Anonymous (Eds.), Volume d'hommage au géologue Georges Zbyszewski. Recherche sur les Civilisations, Paris, pp. 257–267.
- Agustí, J., 1986. Nouvelles espèces de cricétidés vicariantes dans le Turolien moyen de Fortuna (Prov. Murcia, Espagne). Geobios 19, 5–11.
- Agustí, J., Cabrera, L., Garcés, M., Parés Josep, M., 1997. The Vallesian mammal succession in the Vallès-Penedès basin (northeast Spain): paleomagnetic calibration and correlation with global events. Palaeogeography, Palaeoclimatology, Palaeoecology 133, 149–180.
- Agustí, J., Casanovas-Vilar, I., Furió, M., 2005. Rodents, insectivores and chiropterans (Mammalia) from the late Aragonian of Can Missert (Middle Miocene, Vallès-Penedès Basin, Spain). Geobios 38, 575–583.

- Agustí, J., Garcés, M., Krijgsman, W., 1999. Investigaciones bioestratigráficas y magnetoestratigráficas en la Cuenca de Fortuna (Murcia) y sus implicaciones para la evolución de la cuenca mediterránea durante el Messiniense (Mioceno superior). *Memorias de Arqueología* 14, 27–36.
- Agustí, J., Garcés, M., Krijgsman, W., 2006. Evidence for African-Iberian exchanges during the Messinian in the Spanish mammalian record. *Palaeogeography, Palaeoclimatology, Palaeoecology* 238, 5–14.
- Agustí, J., Gibert, J., 1979. Nuevos datos sobre los roedores e insectívoros (Mammalia) del Mioceno superior del Vallès (Cataluña, España). *Paleontologia i Evolució* 14, 17–20.
- Agustí, J., Gibert, J., 1982. Roedores e insectívoros (Mammalia) del Mioceno Superior de Can Jofresa y Can Perellada (Vallès-Penedès, Cataluña). *Paleontologia i Evolució* 17, 29–41.
- Alba, D.M., Moyà-Solà, S., Casanovas-Vilar, I., Galindo, J., Robles, J.M., Rotgers, C., Furió, M., Angelone, C., Köhler, M., Garcés, M., Cabrera, L., Almécija, S., Obradó, P., 2006. Los vertebrados fósiles del Abocador de Can Mata (els Hostalets de Pierola, l'Anoia, Cataluña). *Estudios Geológicos* 62, 295–312.
- Alcalá, L., Sesé, C., Herráez, E., Adrover, R., 1991. Mamíferos del Turoliense inferior de Puente Minero (Teruel, España). *Boletín de la Real Sociedad Española de Historia Natural Sección Geológica* 86, 205–251.
- Alcalá, L., Van Dam, J., Luque, L., Montoya, P., Abella, J., 2005. Nuevos mamíferos vallesianos en Masía de La Roma (Cuenca de Teruel). *Geogaceta* 37, 199–202.
- Antunes, M., 1984. Essai de synthèse sur les Mammifères du Miocène du Portugal. In: Anonymous (Eds.), *Volume d'hommage au géologue Georges Zbyszewski. Recherche sur les Civilisations*, Paris, pp. 301–323.
- Antunes, M., Mein, P., 1979. Le gisement de Freiria de Rio Maior, Portugal, et sa faune de mammifères ; nouvelle espèce de *Rotundomys*, conséquences stratigraphiques. *Geobios* 12, 913–919.
- De Bruijn, H., Mein, P., Montenat, C., Van De Weerd, A., 1975. Corrélations entre les gisements de rongeurs et les formations marines du Miocène terminal d'Espagne méridional (I. Provinces d'Alicante et de Murcia). In: *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B* 78. pp. 282–313.
- Calvo, J.P., Elizaga, E., López Martínez, N., Robles, F., Usera, J., 1978. El Mioceno superior continental del Prebético Externo: Evolución del Estrecho Nordbético. *Boletín Geológico y Minero* 89, 407–426.
- Casanovas-Vilar, I., 2007. The rodent assemblages from the Late Aragonian and the Vallesian (Middle to Late Miocene) of the Vallès-Penedès basin (Catalonia, Spain). Ph.D. dissertation, Universidad de Barcelona, Barcelona.
- Casanovas-Vilar, I., Furió, M., Agustí, J., 2006. Rodents, insectivores and paleoenvironment associated to the first-appearing Hipparionine horses in the Vallès-Penedès Basin (Northeastern Spain). *Beiträge zur Paläontologie* 30, 1–19.
- Chaline, J., Mein, P., 1979. Les rongeurs et l'évolution. Doin, Paris.
- Crusafont, M., Casanovas, L., 1973. *Mammalia Tertiaria Hispaniae*. In: *Fossilium Catalogus. I. Animalia, pars. 121*, Kluwer Academic Publishers, Den Haag.
- Engesser, B., 1972. Die obermiozäne Säugetierfauna von Anwil (Baselland). *Tätigkeitsbericht Naturforschende Gesellschaft Baselland* 28, 37–363.
- Freudenthal, M., 1966. On the mammalian fauna of the *Hipparion* beds in the Calatayud-Teruel basin (province of Zaragoza, Spain). Part I: The genera *Cricetodon* and *Ruscinomys* (Rodentia). In: *Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen B* 69. pp. 296–317.
- Freudenthal, M., Huguency, M., Moissenet, E., 1994. The genus *Pseudocricetodon* (Cricetidae, Mammalia) in the Upper Oligocene of the province of Teruel (Spain). *Scripta Geologica* 104, 57–114.
- Freudenthal, M., Lacombe Andueza, J.I., Martín-Suárez, E., 1991. The Cricetidae (Mammalia, Rodentia) from the Late Miocene of Crevillente (prov. Alicante, Spain). *Scripta Geologica* 96, 9–46.
- García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E., Freudenthal, M., 2008. Cricetidae and Gliridae (Rodentia, Mammalia) from the Miocene and Pliocene of southern Spain. *Scripta Geologica* 136, 1–37.
- Gibert, J., Agustí, J., Moyà-Solà, S., 1980. Nuevos datos sobre la bioestratigrafía del Ampurdan. *Boletín Geológico y Minero* 91, 705–712.
- Guérin, C., Mein, P., 1971. Les principaux gisements de mammifères miocènes et pliocènes du domaine rhodanien. *Documents des Laboratoires de Géologie de l'Université de Lyon HS*, 131–170.
- Hartenberger, J.L., 1965. Les Cricetidae (Rodentia) de Can Llobateres (Néogène d'Espagne). *Bulletin de la Société géologique de France* 7, 487–498.
- Hartenberger, J.L., Thaler, L., 1963. Sur les Rongeurs fossiles du Vallésien de Can Llobateres (Sabadell, Espagne). *Comptes Rendus de l'Académie des Sciences de Paris* 256, 3333–3336.
- ICZN (International Commission on Zoological Nomenclature), 1999. *International Code of Zoological Nomenclature*. The International Trust for Zoological Nomenclature and The Natural History Museum, London.
- Lacombe Andueza, J.I., 1988. Rodents and lagomorphs from a lower Vallesian fissure filling near Molina de Aragón (prov. Guadalajara, Spain). *Scripta Geologica Special Issue* 1, 19–38.
- López Martínez, N., Sesé Benito, C., Sanz García, J.L., 1977. La microfauna (Rodentia, Insecta, Lagomorpha y Reptilia) de las fissuras del Mioceno medio de Escobosa de Calatañazor (Soria, España). *Acta Geologica Hispanica* 12, 47–73.
- López Guerrero, P., Álvarez-Sierra, M.A., López-Antoñanzas, R., Oliver Pérez, A., Peláez-Campomanes, P., 2008. Cricetodontini (Cricetidae, Rodentia) del Aragonense superior (Mioceno medio) de Nombrevilla 2, (Zaragoza, España). *Publicaciones del Seminario de Paleontología de Zaragoza* 8, 259–271.
- Maridet, O., 2003. Révision du genre *Democricetodon* (Mammalia, Rodentia, Cricetinae) et dynamique des faunes de rongeurs du Néogène d'Europe occidentale : évolution, paléobiodiversité et paléobiogéographie. Ph. D. dissertation, Université Claude Bernard Lyon 1 (inédit).
- Mein, P., 1976. Biozonation du Néogène méditerranéen à partir des mammifères. *Proceedings of the VIth Congress of the Regional Committee on Mediterranean Neogene Stratigraphy, Bratislava (September 4–7, 1975)*, 2, 18.
- Mein, P., 1999. The late Miocene small mammal succession from France, with emphasis on the Rhone Valley localities. In: Agustí, J., Rook, L., Andrews, P. (Eds.), *The Evolution of Neogene Terrestrial Ecosystems in Europe*. Cambridge University Press, Cambridge, pp. 140–164.
- Mein, P., Freudenthal, M., 1971. Une nouvelle classification des Cricetidae (Mammalia, Rodentia) du Tertiaire de l'Europe. *Scripta Geologica* 2, 1–37.
- Mein, P., Ginsburg, L., 2002. Sur l'âge relatif des différents dépôts karstiques miocènes de La Grive-Saint Alban (Isère). *Cahiers scientifiques du Muséum d'Histoire naturelle de Lyon* 2, 7–47.
- Montuire, S., Maridet, O., Legendre, S., 2006. Late Miocene-Early Pliocene temperature estimates in Europe using rodents. *Palaeogeography, Palaeoclimatology, Palaeoecology* 238, 247–262.
- Schaub, S., 1925. Die Hamsterartigen Nagetiere des Tertiärs und ihre lebenden Verwandten. *Abhandlungen der Schweizerischen paläontologische Gesellschaft* 45, 1–114.
- Schaub, S., 1944. Cricetodontiden der Spanischen Halbinsel. *Eclogae Geologicae Helvetiae* 37, 453–457.
- Schaub, S., 1947. Los Cricetodontidos del Vallés-Panadés. *Estudios Geológicos* 6, 55–67.
- Thaler, L., 1966. Les rongeurs fossiles du Bas Languedoc. *Mémoires du Muséum National d'Histoire Naturelle C* 17, 1–295.
- Van Dam, J., Alcalá, L., Alonso Zarza, A., Calvo, J.P., Garcés, G., Krijgsman, W., 2001. The Upper Miocene Mammal record from the Teruel-Alfambra region (Spain): The MN system and continental stage/age concepts discussed. *Journal of Vertebrate Paleontology* 21, 367–385.
- Van Dam, J., Sanz Rubio, E., 2003. Late Miocene and Pliocene small mammals from the Calatayud Basin (Central Spain). *Coloquios de Paleontología Vol. Ext. 1*, 115–126.
- Van de Weerd, A., 1976. Rodents fauna of the Mio-Pliocene continental sediments of the Teruel-Alfambra region, Spain. *Utrecht micropaleontological bulletins, Special publication* 2, 1–185.