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

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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 lost of mesolophs. 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.

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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.

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

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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,
France), Soblay (Ain), and Dionay (Isère), H. aguirrei from Escobosa (Soria, Spain), H. daamsi from Can Missert (Barcelona, Spain), H. dispexus 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 Lecharteriat, 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; MGISL, Museu Geológico, Lisboa, Portugal; MNCN, Museo Nacional de Ciencias Naturales, Madrid, Spain; MSNL, Centre de Conservation et d’Étude des Collections, Lyon, France; RGM, Nationalutahistorisch 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

### Table 1
Length and width measurements (mm) of the lower and upper molars of Hispanomys bijugatus from La Grive-Saint-Alban (carrière Lecharteriat, fissure L3), Isère, France.

<table>
<thead>
<tr>
<th>Tooth type</th>
<th>N</th>
<th>Length</th>
<th>Width</th>
</tr>
</thead>
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<tr>
<td></td>
<td></td>
<td>Min</td>
<td>Mean</td>
</tr>
<tr>
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<td>M1</td>
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<td>2.97</td>
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<tr>
<td>m2</td>
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<td>2.40</td>
<td>2.54</td>
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<tr>
<td>M2</td>
<td>42</td>
<td>2.30</td>
<td>2.47</td>
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<tr>
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<td>2.32</td>
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</tr>
<tr>
<td>M3</td>
<td>41</td>
<td>1.80</td>
<td>1.97</td>
</tr>
</tbody>
</table>

**Holotype**: FSL no 65478: left isolated m1 (Mein and Freudenthal, 1971: p. 37, Pl. 2, Fig. 4).

**Paratypes**: FSL 66256-66524.

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

**Age**: MN 8.

**Other localities**: Fissure L5, carrière Lecharteriat, 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. dispexus, H. thaleri, H. lavocati, H. nombrevillae, H. aragonensis, H. peralensis, H. baixasi, H. freudenthali, and H. adroveri in having a small size; differ from H. decedens, H. aguirrei, H. daamsi, H. dispexus, H. thaleri, H. lavocati, H. nombrevillae, 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 an entomesoloph on some upper molars; differ from H. decedens, H. aguirrei, H. daamsi, H. dispexus, H. thaleri, H. mediterraneus, H. peralensis, H. freudenthali, and H. adroveri in having incomplete ectolophes on the M1 and M2; differ from H. decedens, H. dispexus, H. thaleri, and H. aragonensis in lacking enamel coated valley on the M1-M2; differ from H. decedens, H. aguirrei, H. daamsi, H. dispexus, H. lavocati, H. thaleri, and H. aragonensis in having entomesoloph on the M1; differ from H. castelnovi, H. dispexus, 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.
decendens, 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.
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
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 entomesolophid; e.g., FSL 66284, 66286) or absent. The metalophulid is double. The protostylid that is joined with the anteroconid by a labial spur of the anteromesolophid, 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 anteromesolophid. The lingual anterolophid is weak (e.g., FSL 66292). These teeth show short labial and lingual posterolophs; the latter one is more developed than the former. These teeth have four roots.
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 not 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 check 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* Larret, 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 entomesolophid 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
H. dispectus Barbera (Aguilar et al., 1979) and from La Bisbal I and La 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. disjectus. 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, Gerona, Spain (Gibert et al., 1980) pertains actually to H. disjectus.

The holotype of H. disjectus (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 Conil 22 and 20 (MN 9) as well as from Ampurdá (Gerona) 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 metalophulid, 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 and 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 (MN 9, 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 than 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.

### 3.2.9.1. Historical background.

This species was originally *Hispanomys aragonensis* by Freudenthal (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).

### 3.2.8.1. Comparison with *H. bijugatus*.

None 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*.

### 3.2.10.1. Historical background.

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 \textit{H. bijugatus} have it. The m2 and m3 of \textit{H. mediterraneus} usually have the mesolophid less developed than those of \textit{H. bijugatus}.

3.2.11. Hispanomys peralensis \textit{Van de Weerd, 1976}

3.2.11.1. Historical background. \textit{Van de Weerd} (1976) erected the species \textit{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 (\textit{Van de Weerd, 1976}), which is correlated to the local subzone J3 (MN 10) of \textit{Van Dam et al.} (2001). It is stored in the collection of the RUU. According to \textit{Van de Weerd} (1976), the two species of \textit{Cricetodon} from Masía del Barbo 2A and 2B described by Freudenthal (1966: pp. 308–310), but not named, also pertain to \textit{H. peralensis}. \textit{Antunes and Mein} (1979: p. 916) mentioned the presence of \textit{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 \textit{H. freudenthali} by \textit{Van de Weerd} (1976), as well as that from the MN 11 localities of Crevillente 1, 3 and 4 (Alicante, Spain) described by \textit{De Bruijn et al.} (1975: p. 297) as \textit{H. sp. A}, also correspond to \textit{H. peralensis}. More material of \textit{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 \textit{H. peralensis} at the MN10 (J3) localities MR604-A and B, and \textit{H. cf. peralensis} at MR604-B, Masía de la Roma, Teruel, Spain. Furthermore, \textit{Van Dam et al.} (2001) listed \textit{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 Ruea, and Peralejos C). In addition, they mentioned the co-occurrence of this species and \textit{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, \textit{Van Dam et al.} (2001) mentioned other localities where either \textit{H. peralensis} or \textit{H. aff. peralensis} is present (Masía de la Roma 4B, 6, 8, 9, La Salle, Masía de la Roma 11, and Los Aguanares 5A). Besides, two m1 identified as \textit{H. cf. peralensis} have been recovered from two MN10 localities (CRS2A and CRS2B) of the Cortasogas site, Calatayud Basin, Spain (\textit{Van Dam and Sanz Rubio, 2003}). On the basis of very poor material (two isolated teeth and three fragments), Calvo et al. (1978) recognized \textit{H. cf. peralensis} at the MN10 locality of Hijar-1, Albacete, Spain. \textit{H. cf. peralensis} has also been cited from the MN11 site of Lobrieu, Vaucluse, France (\textit{Mein, 1999}).

3.2.11.2. Comparison with \textit{H. bijugatus}. The M1 of \textit{H. peralensis} are four or five-rooted, whereas those of \textit{H. bijugatus} are four-rooted. In addition, none of the M1 of \textit{H. peralensis} has either labial spur on the anterolophule or entomesoloph, and all of them have a distinct forward paracnon spur and a weak lingual cingulum. In contrast, some of the M1 of \textit{H. bijugatus} have a labial spur on the anterolophule and an entomesoloph; they usually lack the forward paracnon spur and have a strong lingual cingulum. Furthermore, the M2 of \textit{H. peralensis} have the lingual cingulum less developed than those of \textit{H. bijugatus} and none of them have entomesoloph, whereas some of the M2 of \textit{H. bijugatus} show a vestigial entomesoloph. The M3 of \textit{H. peralensis} are much more reduced than those of \textit{H. bijugatus} (Table 2) and they lack the posterior cingulum. This posterior cingulum is well developed and almost always present on the M3 of \textit{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 \textit{H. peralensis} has the double metalophulid, which is always present on the m1 of \textit{H. bijugatus}. Finally, the m2 and m3 of \textit{H. peralensis} have the mesolophid usually less developed than those of \textit{H. bijugatus}.


3.2.12.1. Historical background. This species has been erected on the basis of mandibles, maxillae, and numerous isolated cheek teeth from the Turopolian locality of Lo Fournes 16-M, Pyrénées-Oriantales. 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 Fournes 6, Castelnou 1 and 3, Pyrénées-Oriantales (\textit{Aguilar et al., 2007}).

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

3.2.13. Hispanomys freudenthali \textit{Van de Weerd, 1976}

3.2.13.1. Historical background. The validity of the species \textit{H. freudenthali} from the MN12 locality of Masada del Valle 2 (Teruel-Alfambra region) was discussed by \textit{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 \textit{Pseudoruscinomys schaubi}. Consequently, according to \textit{Freudenthal et al.} (1991), the nominal taxon \textit{H. freudenthali} should be considered a junior synonym of \textit{P. schaubi}. \textit{Freudenthal et al.} (1991) pointed out that the specimen MDV2-1212, one m2, should be also attributed to \textit{P. schaubi}. Incidentally, \textit{Pseudoruscinomys} is considered a synonym of \textit{Ruscinomys} by \textit{Agusti} (1980), who judged that \textit{H. freudenthali} should be accommodated into the genus \textit{Ruscinomys}. According to \textit{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 Aguanaes 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 Tuorlionic (MN 11) locality of Puente Minero (Teruel, Spain). Furthermore, Van Dam et al. (2001) listed H. freudenthali at various MN12 (Masada Rueba 4, 3, Masada del Valle 2, Los Mansuetos 2, Tortajada B) and MN11 (Valdecebro 4, Vivero de Pinos, Tortajada A, Los Aguanaes 3, Los Aguanaes, Regajo 2, Puente Minero 3, La Gloria 10, Masada Rueba 2, Puente Minero, Peralesjos D) and MN10 (33) (Los Aguanaes 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.


3.2.14.1. Historical background. The holotype of this species (F-CA 180) is an isolated M1 from the Middle Tuorlionic (MN 12) locality of Casa del Acero, Fortuna Basin, Murcia. It is housed in the IPS. This species has also been recorded in the coeval locality of Crevillente 15 (Freudenthal et al., 1991). Additional material of this taxon has been recovered from the Late Tuorlionic (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 also be 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 ectolophs 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 protoloph (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 protoloph 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. dissectus, 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.

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