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# First detailed description of *Hispanomys decedens* (Rodentia) from the Middle Miocene of La Grive-Saint Alban (France)

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1 **First detailed description of *Hispanomys decedens* (Schaub,**  
2 **1925) (Rodentia) from the Middle Miocene of La Grive-Saint**  
3 **Alban (France)**

4  
5 **Première description détaillée d'*Hispanomys decedens***  
6 **(Schaub, 1925) (Rodentia) du Miocène moyen de La Grive-**  
7 **Saint Alban (France)**

8  
9 Running Title First description of *Hispanomys decedens*

10  
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17  

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18 **Abstract** The material of *Hispanomys decedens* (Rodentia, Cricetodontinae) from La  
19 Grive-Saint Alban (France) is described in detail for the first time. *Hispanomys*  
20 *decedens*, which is one of the oldest species of the genus, shows the primitive character  
21 states that are typical of the Aragonian congeneric species, such as the mesolophs and

22 labial cingula surrounding the upper molar valleys. The detailed examination of the  
23 teeth of *H. decedens* shows that this taxon is a good candidate ancestor for *H.*  
24 *aragonensis*.

25

26 **Résumé** Le matériel d'*Hispanomys decedens* (Rodentia, Cricetodontinae) de La  
27 Grive-Saint Alban (France) est décrit pour la première fois en détail. *Hispanomys*  
28 *decedens* est une des plus anciennes espèces du genre et montre des caractères primitifs  
29 typiques des espèces congénériques aragoniennes, tels que la présence de mésolophes et  
30 de cingulums labiaux sur les molaires supérieures. L'étude détaillée d'*Hispanomys*  
31 *decedens* montre que ce taxon est un bon candidat au titre d'ancêtre d'*H. aragonensis*.

32

33 **Keywords** *Hispanomys* · Cricetodontinae · La Grive-Saint Alban · France · Systematics

34 **Mots clés** *Hispanomys* · Cricetodontinae · La Grive-Saint Alban · France · Systématique

35

36

## 37 **1 Introduction**

38

39 La Grive-Saint-Alban is the name used to refer to various Upper Aragonian pits located  
40 on the territory of the municipality of Saint-Alban-de-Roche (Isère, France). These pits  
41 are constituted by fissures in limestones filled with fossiliferous siderolitic clays.

42 Remains of *Hispanomys* have only been recovered from La Grive L (quarry Lechartier),  
43 M (quarry Milliat), and P.B. (quarry Peyre et Beau, where a single m1 was found by P.  
44 M.). La Grive L has eight fissure-fillings numbered from L1 to L8, but the only

45 productive ones (from a palaeontological viewpoint) are L3, L5, L5', L6, and L7 (Mein  
46 and Ginsburg 2002).

47 In 1887, Depéret revealed the presence of two taxa of *Cricetodon* at La Grive Saint-  
48 Alban: *C. medium* and *C. rhodanicum* (Depéret 1887a, 1887b). In 1925, Schaub carried  
49 out a whole revision of the cricetine myomorph rodents. He included in the species *C.*  
50 *sansaniensis* Lartet, 1851 all the large-sized species of *Cricetodon* from Upper  
51 Aragonian localities: Sansan (Gers, France), La Grive Saint-Alban, various sites from  
52 the Swiss molasse, and the Steinberg (=Spitzberg) in the Nördlinger Ries, southern  
53 Germany. In this work, he synonymized *C. rhodanicum* with *C. sansaniensis* because  
54 these taxa could not be differentiated neither by the morphology nor by the size (Schaub  
55 1925: 9). In addition, in the course of his revision of the material of *C. sansaniensis*  
56 housed in the Museum of Lyon, he noticed the presence of two morphotypes within the  
57 material of *C. sansaniensis* from La Grive Saint-Alban: the first, slightly larger and with  
58 less developed ectolophs corresponded to *C. sansaniensis*, whereas the smaller one,  
59 with better developed ectolophs, revealed a different variety (Schaub 1925: 13), which  
60 he named *Cricetodon sansaniensis* var. *decedens*.

61 Later on, this variety was raised to the species level (Schaub 1944: 454; Schaub  
62 1947: 60). Mein and Freudenthal (1971: 19) introduced the subgenus *Hispanomys* for a  
63 handful of allegedly derived *Cricetodon*, such as *C. decedens*. This subgenus was  
64 elevated to the genus level by van de Weerd (1976: 106 *et seq.*). The holotype of *H.*  
65 *decedens*, which is a left maxillary fragment with M1 and M2, is housed in the MSNL  
66 (Schaub 1925). It seems that the original findings of *H. decedens* are not the fruits of the  
67 field works carried out by Depéret in the mid-XIXth century, but most likely of those  
68 carried out shortly later by Gaillard, which were taken up by Ennouchi in the beginning

69 of the XXth century. It is believed that Ennouchi worked in the “Carrière Lechartier”  
70 (called at that time “Carrière Chemin”) at the fissures L4, L5, L5’, and L7 (Ennouchi  
71 1930). The remains of *H. decedens* are supposedly from a now empty fissure, which is  
72 located between the fissure L5 and L7 and that is called L5’.

73 Although *H. decedens* from La Grive-Saint Alban has been mainly found in the  
74 fissure-filling L5’, it has also been recorded in fissures L5, L7, as well as in La Grive M  
75 (Mein and Ginsburg 2002). Additional material of this species has been mentioned by  
76 Alba et al. (2006) and Casanovas-Vilar (2007) from various MN7/8 sites of the Can  
77 Mata series (Barcelona, Spain).

78 The other species of *Hispanomys* found in La Grive-Saint Alban is *H. bijugatus*,  
79 which has been recorded from fissures L3 and L5 and has been described in detail in  
80 López-Antoñanzas and Mein (2009).

81 *Hispanomys decedens* is to date the less-known species of *Hispanomys*. Actually, no  
82 complete description or photographs of this important material have been made  
83 available so far. Therefore, the aim of the present work is to offer a detailed description  
84 of this taxon, which has been neglected until now.

85

## 86 **2 Material and methods**

87

88 The systematic study presented below is based on the examination of original  
89 specimens of the MNCN, RUU, IPS, and FSL collections (see below for abbreviations),  
90 and data from the literature. We examined the following: original teeth of *Hispanomys*  
91 *bijugatus* and *H. decedens* from La Grive Saint-Alban (Isère, France), *H. mediterraneus*  
92 from the localities of Montredon (Hérault, France), Soblay (Ain, France), and Dionay

93 (Isère), *H. aguirrei* from Escobosa (Soria, Spain), *H. daamsi* from Can Missert  
94 (Barcelona, Spain), *H. dispectus* from Hostalets de Pierola and Castell de Barbera  
95 (Barcelona), *H. lavocati* from Hostalets de Pierola, *H. aragonensis* from Pedregueras  
96 2A (Saragossa, Spain), *H. nombrevillae* from Molina de Aragón (Guadalajara, Spain),  
97 *H. peralensis* from Peralejos 4, Peralejos C, Peralejos D, Masía del Barbo 2A, and  
98 Masía del Barbo 2B (Teruel, Spain), *H. moralesi* from Batallones 1, Batallones 3,  
99 Batallones 5, and Batallones 10 (Madrid, Spain), *H. thaleri* from Can Llobateres  
100 (Barcelona), *H. freudenthali* from Puente Minero (Teruel), and *H. adroveri* from Casa  
101 del Acero (Murcia, Spain).

102 Measurements of the occlusal surface of the teeth (maximum length and maximum  
103 width) have been taken following the method of van de Weerd (1976) for all dental  
104 elements except for the second upper molars, for which the maximum length has been  
105 taken parallel to the labial side of the tooth. Measurements were obtained with a Nikon  
106 digital counter CM-6S measuring device (Table 1).

107 First, second and third lower molars are designed as m1, m2, and m3, respectively,  
108 whereas first, second and third upper molars as M1, M2, and M3. The terminology used  
109 in the tooth descriptions follows that of Freudenthal et al. (1994) and López-Antoñanzas  
110 et al. (2010).

111 Since de Bruijn et al. (1992), the biozones MN7 and MN8 have been grouped into a  
112 single unit MN7/8 due to the impossibility to distinguish them. However, Mein and  
113 Ginsburg (2002), based on the different species of *Democricetodon* recorded in the  
114 different fissure-fillings of La Grive-Saint Alban, were able to differentiate them in this  
115 area. They considered La Grive M and La Grive L3 as reference sites for the biozones  
116 MN7 and MN8 respectively, a conclusion with which López-Antoñanzas and Mein

117 (2009) agreed. Thus, in this work, we apply the biozonation given by Mein and  
118 Ginsburg (2002) for the fissure fillings of La Grive-Saint Alban.

119

## 120 **Institutional Abbreviations**

121 FSL Université Claude Bernard, Villeurbanne, France

122 IPS, Instituto Catalán de Paleontología, Sabadell, Spain

123 MNCN Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain

124 MSNL Centre de Conservation et d'Etude des Collections, Lyon, France

125 RUU Rijksuniversiteit Utrecht, Utrecht, The Netherlands

126

## 127 **3 Systematic paleontology**

128

129 Order Rodentia BOWDICH, 1821

130 Subfamily Cricetodontinae SCHAUB, 1925

131 Genus *Hispanomys* MEIN ET FREUDENTHAL, 1971

132 Species *Hispanomys decedens* (SCHAUB, 1925)

133 (Figs. 1, 2, 3)

134

135 *Holotype* - ML-Lgr 130: left maxillary fragment with M1 and M2 (Schaub 1925:

136 fig. 2, plate III)

137 *Referred specimens* - FSL67000, FSL67001, FSL67002, FSL67003, FSL67005,

138 FSL67006, FSL67100, FSL67103, FSL67105, FSL67106, FSL67107, FSL67118,

139 FSL67121, FSL67122, FSL67142 (mandibular ramus with m1-m3); FSL67004,

140 FSL67021, FSL67101, FSL67120 (mandibular ramus with m1-m2); FSL67098

141 (mandibular ramus with m2-m3); FSL67093-FSL67097, FSL67104 (isolated m1);  
142 FSL67047-FSL67052, FSL67060-FSL67065 (isolated m2); FSL67053-FSL67059,  
143 FSL67111 (isolated m3); FSL67007, FSL67009-FSL67011, FSL67046, FSL67110  
144 (maxilla with M1-M3); FSL67008, FSL67109, FSL67112-FSL67117, FSL67119,  
145 FSL67123, FSL67124, FSL67126, FSL67129, FSL67134-FSL67140, FSL67143-  
146 FSL67147 (maxilla with M1-M2); FSL67125, FSL67128, FSL67130, FSL67141  
147 (maxilla with M1); FSL67127 (maxilla with M2); FSL67012-FSL67017, FSL67022-  
148 FSL67045 (isolated M1); FSL67018-FSL67020, FSL67066-FSL67084 (isolated M2);  
149 FSL67085-FSL67092 (isolated M3). Measurements are given in Table 1 and Fig. 4

150 *Type locality* - La Grive-Saint Alban (fissure L5')

151 *Age* - Probably MN 7

152 *Other localities* - La Grive-Saint Alban (Carrière Milliat « M », Carrière Lechartier,  
153 fissures L5 and L7\*), Isère, France (Mein and Ginsburg 2002); Hostalets de Pierola,  
154 Barcelona, Spain (Alba et al. 2006; Casanovas-Vilar 2007).

155 \*All the three localities are very poor in remains of *H. decedens*. The extremely low  
156 proportion of this taxon in the fissure L7 has been considered to be possibly the result of  
157 "contamination" by Mein and Ginsburg (2002).

158 *Extended diagnosis* - *Hispanomys* species of medium size with low hypsodonty;  
159 having low values of the mean LM1/mean LM3 (=1.74) and mean Lm1/mean Lm3  
160 (=1.16) ratios (third lower and upper molars not reduced); lower molars usually lacking  
161 the cingula on the lingual valleys; with some m1 having a double metalophid or a  
162 short mesolophid or even both; three rooted m2 with a short, but distinct, mesolophid;  
163 m3 having a long or short, but distinct, mesolophid; M1 and M2 having labial cingula  
164 surrounding their valleys and usually having a mesoloph and an enamel-coated valley;



165 four-rooted M1 having one or two anterior cusps on the prelobe, with the anterior  
166 ectoloph well developed, but lacking the forward paracone spur and usually having  
167 prominent protostyles and entostyles; M2 with lingual anteroloph, having the  
168 anterosinus usually open, but having sometimes anterior ectoloph and forward  
169 paracone spur, less M2 than M1 with mesoloph and enamel-coated valley, and all of  
170 them having well-developed backward paracone spur and posterior ectoloph; M3 with  
171 distinct anteroloph and posteroloph and having backward paracone spur, but lacking the  
172 anterior ectoloph, the forward paracone spur, and the posterior ectoloph.

173 *Differential diagnosis* - Differing from *Hispanomys daamsi*, *H. thaleri*, *H.*  
174 *freudenthali* and *H. adroveri*, in being smaller; differing from *H. bijugatus*, *H. thaleri*,  
175 *H. moralesi*, *H. peralensis*, *H. baixasi*, *H. freudenthali*, and *H. adroveri* in having strong  
176 labial cingula surrounding the valleys on the M1; differing from *H. bijugatus*, *H.*  
177 *aragonensis*, *H. thaleri*, *H. moralesi*, *H. peralensis*, *H. baixasi*, *H. freudenthali*, and *H.*  
178 *adroveri* in having strong labial cingula surrounding the valleys on the M2; differing  
179 from *H. mediterraneus*, *H. moralesi*, *H. peralensis*, *H. freudenthali*, and *H. adroveri* in  
180 having four-rooted M1; differing from *H. dispectus*, *H. thaleri*, *H. mediterraneus*, *H.*  
181 *moralesi*, *H. peralensis*, *H. freudenthali*, and *H. adroveri* in having incomplete  
182 ectolophs on the M1 and M2; differing from *H. castelnovi*, *H. bijugatus*, *H. daamsi*, *H.*  
183 *aguirrei*, *H. nombrevillae*, *H. lavocati*, *H. mediterraneus*, *H. moralesi*, *H. peralensis*, *H.*  
184 *freudenthali*, and *H. adroveri* in having an enamel-coated valley on many M1-M2;  
185 differing from *H. castelnovi*, *H. bijugatus*, *H. nombrevillae*, *H. mediterraneus*, *H.*  
186 *moralesi*, *H. peralensis*, *H. freudenthali*, and *H. adroveri* in having usually a mesoloph  
187 on the M1; differing from *H. castelnovi*, *H. dispectus*, *H. nombrevillae*, *H. thaleri*, *H.*  
188 *mediterraneus*, *H. moralesi*, *H. peralensis*, *H. freudenthali*, and *H. adroveri* in having

189 the M3 less reduced; differing from *H. moralesi*, *H. peralensis*, *H. freudenthali*, and *H.*  
190 *adroveri* in having labial anterolophid in all m1; differing from *H. castelnovi*, *H.*  
191 *daamsi*, *H. dispectus*, *H. thaleri*, *H. baixasi*, *H. aragonensis*, *H. moralesi*, *H. peralensis*,  
192 *H. freudenthali*, and *H. adroveri* in having a double metalophid on some m1; differing  
193 from *H. thaleri*, *H. nombrevillae*, and *H. aguirrei* in having three-rooted m2; differing  
194 from *H. nombrevillae*, *H. aguirrei*, *H. moralesi*, *H. peralensis*, *H. freudenthali*, and *H.*  
195 *adroveri* in having the m3 less reduced.

196

### 197 3. 1 Description

198 i: The incisor enamel bears in its labial side two feeble longitudinal ridges.

199 m1: The outline of these teeth in occlusal view is sub-rectangular, longer than wide,  
200 with its anterior part somewhat rounded and narrower than the posterior one. The  
201 lingual anterolophid is usually lacking, but in few specimens (e.g. FSL 67005) it is  
202 present, but weak. The labial anterolophid is long and prominent and can even reach the  
203 anterior side of the protoconid, closing thereby the protosinusid. The m1 have a double  
204 metalophid (e.g. FSL 67003, Fig. 1-d) or a short mesolophid (FSL 67005, FSL 67001,  
205 Figs. 1-a, 1-c). Some teeth clearly show both structures (e.g. FSL 67002, Fig. 1-b). Even  
206 when the mesolophid is lacking, there is a slight inflation at the end of the posterior arm  
207 of the protoconid. The hypolophid is transverse. A few teeth have an ectomesolophid  
208 (FSL 67000, Fig. 2). All the specimens have a labial cingulum surrounding the sinusid.  
209 This cingulum is constituted by the junction of two ridges: the first emerging from the  
210 posterior wall of the protoconid and the second from the anterior wall of the hypoconid.  
211 It can bear an ectostylid. Some m1 also show a thin, low ridge surrounding the lingual  
212 valley. The sinusid is antero-lingually directed. The posterolophid is short and

213 constricted behind the hypoconid; it does not reach the posterior wall of the entoconid.

214 These teeth are two-rooted.

215 m2: These teeth are rectangular in shape, though they are anteriorly and posteriorly

216 slightly rounded. They show a prominent labial anterolophid that reaches the

217 anterolabial side of the protoconid, closing thereby the protosinusid. The metalophulid

218 is anterolabially directed and the hypolophulid is transverse. The mesolophid is usually

219 short and ends free. The m2 have rarely lingual cingula surrounding the valleys (e.g.

220 FSL 67006), but all of them have strong labial cingula closing the sinusid. These

221 cingula are constituted by two ridges; the first (which is stronger) emerging from the

222 posterior wall of the protoconid and the second from the anterior wall of the hypoconid.

223 The sinusid is transverse. The posterolophid is short and constricted behind the

224 hypoconid; it does not reach the posterior side of the entoconid. The posterior root splits

225 into two and, therefore, these teeth are three-rooted. The posterolabial root is stronger

226 than the posterolingual one.

227 m3: The occlusal outline of these teeth is rounded, longer than wide, with its

228 posterior part narrower than the anterior one. They show a long and strong labial

229 anterolophid that connects with the anterior wall of the protoconid, closing the

230 protosinusid. The lingual anterolophid is absent. Most of the specimens have a short

231 mesolophid (FSL 67002, FSL 67003, Figs. 1-b, 1-d). However, 4 out of 27 have it long

232 (e.g. FSL 67001, FSL 67005, FSL 67054, FSL 67057 Figs 1-a, 1-c). From these, three

233 specimens (FSL 67001, FSL 67005, FSL 67054) have the mesolophid connected to the

234 anterior side of the entoconid. The posterosinusid and mesosinusid are open; there are

235 no lingual cingula surrounding the valleys. The sinusid is slightly posteriorly directed; it

236 may be partially closed by two ridges: the strongest emerges from the posterior wall of

237 the protoconid, whereas the other one comes out from the anterior wall of the  
238 hypoconid. The posterolophid is short and does not join the posterior wall of the  
239 entoconid. These teeth are three-rooted.

240 M1: These teeth show a pronounced groove between the two lobes of the anterocone.  
241 Most of the specimens show either a strong cusp (even two) in the prelobe or a low  
242 anterior ridge in front of the anterocone (e.g. Fig. 3-h). The anterolophule connects the  
243 lingual lobe of the anterocone with the protocone. The protosinus is closed by a large  
244 protostyle (Figs. 3-d, 3-h, 3-i, 3-l) or by a low and strong ridge (Fig. 3-a). The  
245 protolophule is anterolabially directed. The anterior ectoloph is well developed and ends  
246 free most of the time. It can be parallel to the longitudinal axis of the tooth or postero-  
247 lingually directed. The forward paracone spur is usually absent. The long and strong  
248 backward paracone spur connects to the posterior ectoloph closing the mesosinus, but it  
249 ends free in some specimens. The backward paracone spur emerges at about the  
250 midpoint between the labial side of the tooth and the entoloph. Most of the specimens  
251 have a short or medium mesoloph. In some of them, the mesoloph connects labially to a  
252 lingual spur of the backward paracone spur that points towards the mesoloph (Fig. 3-l),  
253 isolating a circular valley (called enamel-coated valley), which disappears through wear.  
254 Otherwise these structures are too short to be connected (Fig. 3-h, 3-i, 3-k). The M1 of  
255 *Hispanomys decedens* have strong, low cingula surrounding the labial valleys; some of  
256 which bears a mesostyle. The anteriorly directed sinus is usually partially closed by a  
257 strong entostyle or by a ridge, which emerges from the hypocone towards the  
258 posteriolabial side of the protocone. Some specimens (e.g. FSL 67015, Figs. 3-i, 3-j)  
259 and FSL 67017 (Fig. 3-h) show a vertical ridge emerging from the posterior wall of the  
260 protocone towards the lingual side of the tooth (a sort of vestigial entomesoloph). In the

261 less worn specimens, it is possible to observe that both lingual and labial posterolophs  
262 are short, but distinct. These teeth are four-rooted.

263 M2: The outline of these teeth in occlusal view is sub-rectangular, longer than wide,  
264 with its posterior part somewhat rounded and narrower than the anterior one. They have  
265 quite developed lingual anteroloph and a small, but distinct, protosinus in the anterior  
266 margin of the teeth. The labial anteroloph is well developed. The anterosinus is usually  
267 open due to the absence of anterior ectoloph, forward paracone spur or both (e.g. Figs.  
268 3-e, 3-g, 3-m). However, some of the M2 have the anterior ectoloph connected to the  
269 forward paracone spur, closing the anterosinus (e.g. Figs. 3-d, 3-f). The backward  
270 paracone spur is long and strong and usually reaches the posterior ectoloph (a small  
271 anterior ridge of the metacone) and, in so doing, entirely closes the mesosinus.  
272 Nevertheless, some specimens lack the posterior ectoloph and, therefore, have a  
273 backward paracone spur that ends free (e.g. Fig. 3-m) or the two crests are not  
274 connected (e.g. Fig. 3-f). All teeth have the mesosinus much larger than the anterosinus  
275 and they have a cingulum surrounding the main labial valley. A lesser number of M2  
276 than M1 shows the mesoloph. When present, it is short or of medium length; in some  
277 specimens it reaches the backward paracone spur forming an enamel-coated valley (e.g.  
278 Fig. 3-m). The enamel-coated valley is formed by the connection of the mesoloph with  
279 a lingual spur emerging from the backward paracone spur. In some specimens, the  
280 mesoloph and the backward paracone spur are too short and, therefore, they are  
281 disconnected (Fig. 3-e). The presence of a mesoloph on the M2 is related to the  
282 presence of a mesoloph on the M1. Every M2 that lacks the mesoloph shows a slight  
283 inflation at the beginning of the anterior arm of the hypocone (Figs. 3-d, 3-f). The  
284 backward paracone spur is long and usually posterolabially oriented; in some specimens

285 (Fig. 3-d) it emerges practically at the midpoint of the protolophule. The protolophule is  
286 slightly oblique and anterolabially directed. The sinus is nearly closed by a low ridge  
287 that emerges from the anterior side of the hypocone towards the posterior side of the  
288 protocone. These teeth show short labial and lingual posteroloph. They have four roots.

289 M3: The outline of these teeth in occlusal view is rounded, longer than wide, with  
290 the posterior part narrower than the anterior one. The labial anteroloph is long; the  
291 lingual one is much less developed, but distinct (except in worn specimens). The  
292 anterior ectoloph and the forward paracone spur are lacking and the anterosinus is  
293 open. A true mesoloph is lacking in all M3 of *Hispanomys decedens*, but some show a  
294 small inflation corresponding to this ridge (Fig. 4-d). The teeth have a short, but  
295 distinct, posteroloph and a posterosinus. The well-developed backward paracone spur  
296 ends usually free due to the absence of the posterior ectoloph. The posterolabial side of  
297 the protocone generally has a strong ledge, which is directed towards the hypocone.  
298 This ledge closes the sinus partially. The sinus is directed backwards. These teeth are  
299 not reduced; actually, the value of the ratio mean LM1/mean LM3 of the teeth is very  
300 low (=1.736), one of the lowest ones obtained for any *Hispanomys* species known to  
301 date (López Antoñanzas and Mein 2009). These molars are three-rooted.

302

#### 303 **4 Discussion**

304

305 In 1966, Freudenthal based on the cricetodontine material from the localities of  
306 Nombrevilla and Pedregueras 2C (Zaragoza, Spain) he studied to coin two new  
307 subspecies of *Cricetodon decedens* in addition to *C. decedens decedens*: *C. decedens*  
308 *aragonensis* and *C. decedens nombrevillae*. Later on, Mein and Freudenthal (1971: 19)

309 introduced the new subgenus *Hispanomys* and raised these subspecies to the species  
310 level.

311 Freudenthal's (1966) decision of regarding the two taxa as subspecies of *C. decedens*  
312 was the result of the lack of information available at that time about the "typical"  
313 *decedens* from La Grive-Saint Alban. Actually, Freudenthal (1966) did not discard the  
314 possibility that, once the material from La Grive-Saint Alban is studied in detail, one of  
315 the two subspecies he named could turn out to be a synonym of *decedens*. However, he  
316 thought more likely that the Spanish subspecies were different from the French one, a  
317 conclusion that the present work supports.

318 The detailed study of *Hispanomys decedens* from La Grive-Saint Alban shows that  
319 this taxon is, in fact, very different from *H. nombrevillae* and, even though it seems  
320 closely related to *H. aragonensis* from Pedregueras, both species can be easily  
321 differentiated (see below).

322 The main characters usually used to establish the evolutionary stage of the  
323 *Hispanomys* species are: 1) the different development of the ectolophs; 2) the degree of  
324 reduction of the mesolophs and mesolophids; 3) the presence or loss of labial  
325 anterolophids; 4) the presence or loss of cingular structures; 5) the acquisition or not of  
326 extra roots; 6) the degree of reduction of the third molars; and 7) the degree of  
327 hypsodonty (van de Weerd 1976; Agustí 1981, 1982, López-Antoñanzas and Mein  
328 2009; López-Antoñanzas et al. 2010). The most archaic morphologies of *Hispanomys*  
329 would be characterized by having lower molars with well-developed labial  
330 anterolophids, lingual anterolophids, lingual cingula surrounding the valleys, two-rooted  
331 m2, and unreduced m3. Besides, the most primitive upper molars would be  
332 characterized by having mesolophs, labial cingula surrounding the valleys, quite

333 incomplete ectolophs, four-rooted M1, and unreduced M3 (van de Weerd, 1976; Agustí  
334 1981, 1982; López-Antoñanzas and Mein 2009; López-Antoñanzas et al. 2010)

335 *H. decedens* and *H. aragonensis* share some primitive character states as the  
336 presence of a mesoloph forming an enamel-coated valley on the M1 and M2 and the  
337 presence of labial cingula surrounding the M1 as well as some derived ones like the  
338 absence of a mesoloph on the M3 and the splited posterior root on the m2. However,  
339 there are also differences between these species that makes *H. decedens* a reasonable  
340 forerunner of *H. aragonensis*. In the latter species, there is a trend towards the decrease  
341 in the proportion of M1 and M2 with the mesoloph and in that of M1 with either  
342 anterior cingulum or anterostyle in the prelobe. Besides, another progressive character  
343 distinguishing *H. aragonensis* from *H. decedens* is the lack of the labial cingulum  
344 surrounding the valley on M2. Therefore, *H. aragonensis* shows a trend to lose archaic  
345 characters so characteristic of *H. decedens*.

346 Moreover, if we compare the dental evolutionary stage of *Hispanomys decedens* and  
347 the Upper Aragonian and Lower Vallesian species of *Hispanomys*, it appears that the  
348 former shows a quite primitive morphology.

349 Thus, *Hispanomys decedens* is more primitive than *H. castelnovi*, *H. bijugatus*, *H.*  
350 *aguirrei*, *H. daamsi*, *H. lavocati*, and *H. nombrevillae* in having well-developed  
351 mesolophs on M1 and M2, which tend to form an enamel-coated valley. Well-  
352 developed mesolophs are also present, but in much lesser proportion, in *H. thaleri* (a  
353 few upper molars) and in *H. aragonensis*. Besides, *H. decedens* seems more primitive  
354 than *H. castelnovi*, *H. bijugatus*, and *H. thaleri* in having strong cingula surrounding the  
355 labial valleys of the first and second upper molars. Regarding the reduction of the third  
356 molars, this taxon is also quite primitive: *H. decedens* appears more primitive than *H.*



357 *castelnovi*, *H. dispectus*, *H. nombrevillae*, and *H. thaleri* in having the M3 much less  
358 reduced (López-Antoñanzas et al., 2010, table 2). This character is shared with the other  
359 species of *Hispanomys* from La Grive-Saint Alban: *H. bijugatus*.

360

## 361 **5 Conclusion**

362

363 So far, *Hispanomys* includes 17 species with a stratigraphical distribution that  
364 encompasses nearly 10 m.y. Among them, ten taxa are known from the Upper  
365 Aragonian and Lower Vallesian: *Hispanomys castelnovi*, *H. decedens*, *H. bijugatus*, *H.*  
366 *aguirrei*, *H. daamsi*, *H. dispectus*, *H. thaleri*, *H. lavocati*, *H. nombrevillae*, and *H.*  
367 *aragonensis*.

368 *Hispanomys decedens* from La Grive-Saint Alban has most of the typically primitive  
369 dental characters of the Aragonian species of *Hispanomys*, such as the not reduced M3,  
370 the labial cingula surrounding the first and second molar valleys, and the presence of  
371 mesolophs on the upper molars forming an enamel-coated valley. This suggests that *H.*  
372 *decedens* is a quite primitive species with respect to the coeval congeneric taxa. In  
373 addition, the detailed study of *H. decedens* from La Grive-Saint Alban shows that this  
374 taxon could be an ancestor of *H. aragonensis*.

375

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385

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- 434

435

## TABLE

436 **Table 1.** Length and width measurements (mm) of the lower and upper molars of  
 437 *Hispanomys decedens* from La Grive-Saint Alban, Isère, France. Except for one m1  
 438 (from Carrière M) and two M3 (from Carrière L, fissure L7), all the specimens are  
 439 supposed to come from fissure L5’.

440

Locality	Tooth type	LENGTH					WIDTH			
		min	mean	max	sd	N	min	mean	max	sd
La Grive-St Alban	m1	2.44	2.60	2.80	0.09	29	1.60	1.69	1.78	0.05
	M1	2.74	3.16	3.59	0.18	62	1.76	2.05	2.31	0.10
	m2	2.27	2.48	2.69	0.09	34	1.80	1.94	2.08	0.08
	M2	2.14	2.43	2.69	0.15	54	1.72	1.92	2.23	0.12
	m3	1.92	2.23	2.42	0.15	25	1.63	1.79	1.93	0.08
	M3	1.64	1.82	2.09	0.12	26	1.50	1.68	1.90	0.09

441

442

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444

## FIGURE LEGENDS

445

446 Fig. 1. Lower molars of *Hispanomys decedens* from La Grive Saint-Alban (fissure  
447 L5'). **a.** Left mandible with m1-m3 (FSL 67005). **b.** Left mandible with m1-m3 (FSL  
448 67002). **c.** Right mandible with m1-m3 (FSL 67001). **d.** Right mandible with m1-m3  
449 (FSL 67003). **e.** Left mandibular fragment with m1-m2 (FSL 67004). **f.** Close-up of the  
450 metalophulid II of specimen FSL 67004. Scale bar represents 2mm, except for f  
451 (200µm).

452

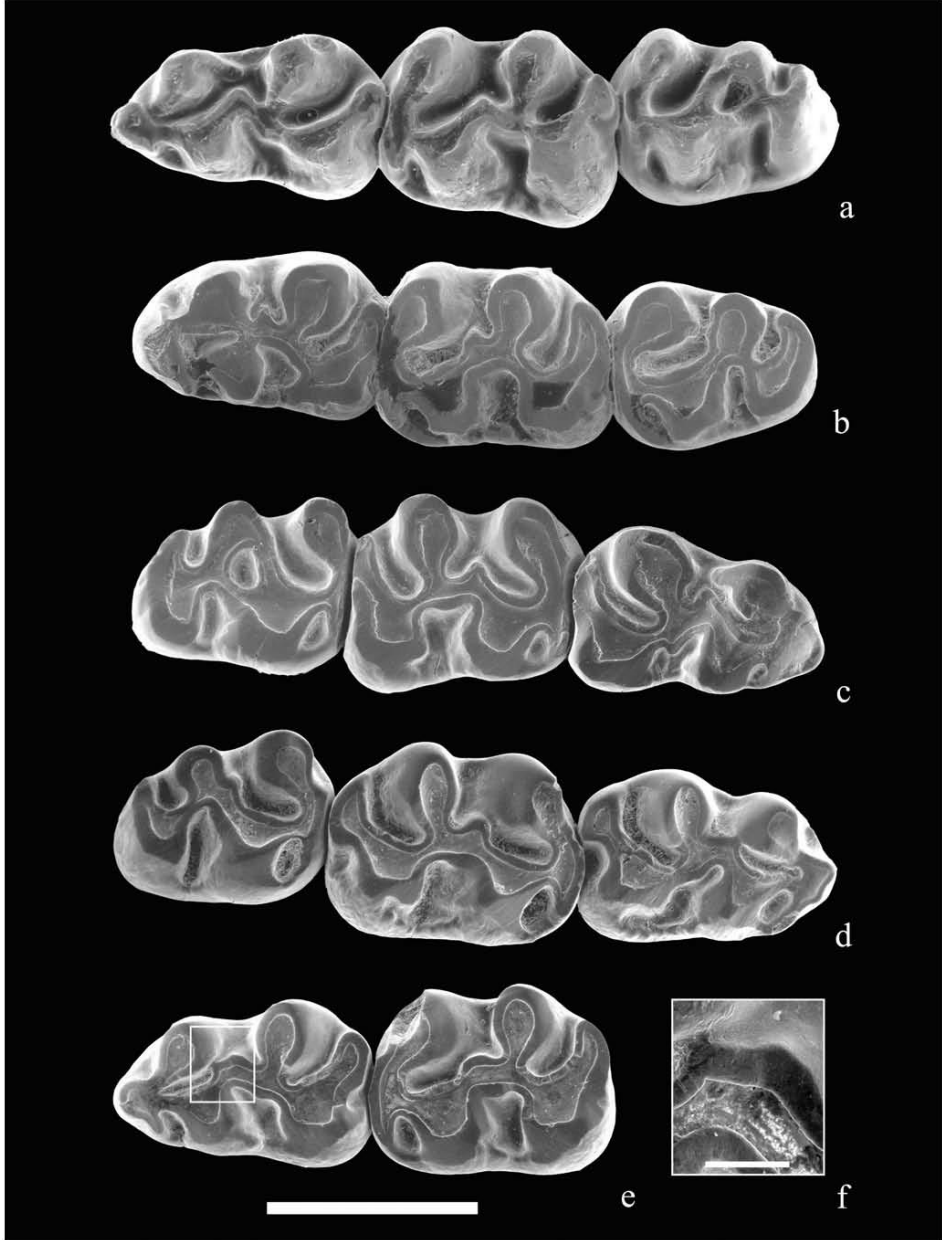
453 Fig. 2. *Hispanomys decedens* from La Grive Saint-Alban (fissure L5'). **a.** Left  
454 mandible with m1-m3 (FSL 67000). Scale bar represents 2mm. **b.** Close-up of the  
455 ectomesolophid of the m1 of specimen FSL 67000. Scale bar represents 500 µm.

456

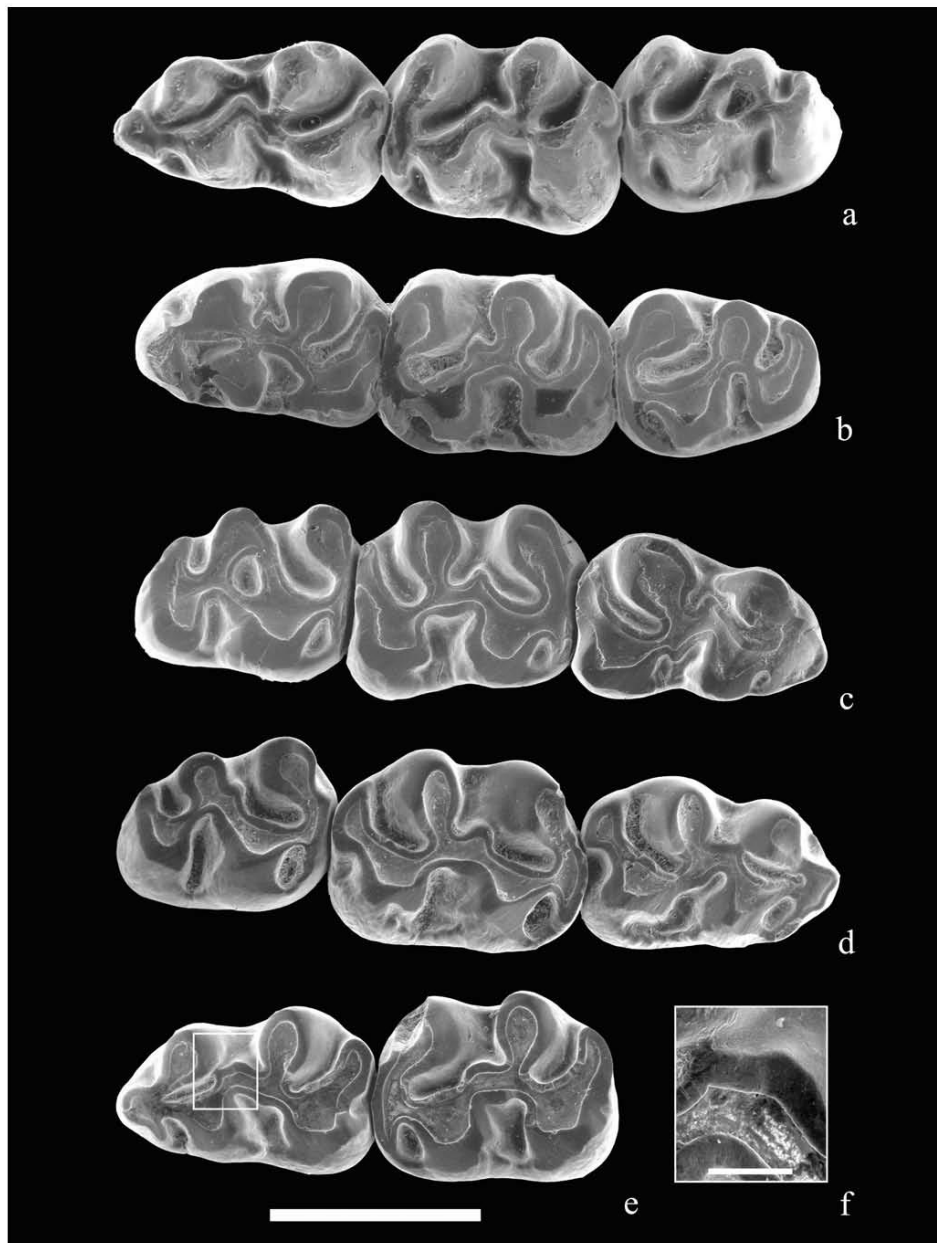
457 Fig. 3. Upper molars of *Hispanomys decedens* from La Grive Saint-Alban (fissure  
458 L5'). **a.** Right maxilla with M1-M3 (FSL 67007). **b.** Close-up of the mesoloph of the M1  
459 of specimen FSL 67007. **c.** Close-up of the mesoloph of the M2 of specimen FSL  
460 67007. **d.** Left maxilla with M1-M3 (FSL 67009). **e.** Left M2 (FSL 67019). **f.** Left  
461 maxilla with M1-M3 (FSL 67011). **7.** Left M2 (FSL 67020). **g.** Left M1 (FSL 67012).  
462 **h.** Left M1 (FSL 67015). **i.** Close-up of the entomesoloph of specimen FSL 67015. **j.**  
463 Close-up of the mesoloph of specimen FSL 67015. **k.** Left M1 (FSL 67017). **l.** Left  
464 maxilla with M1-M2 (FSL 67008). Scale bar represents 2mm, except for b-c (300 µm)  
465 and j-k (500 µm).

466

467 Fig. 4. Length/width scatter diagrams of the upper and lower molars of *Hispanomys*  
468 *decedens* and *H. bijugatus* from La Grive-Saint Alban (France).  
469







471

472 Figure 1

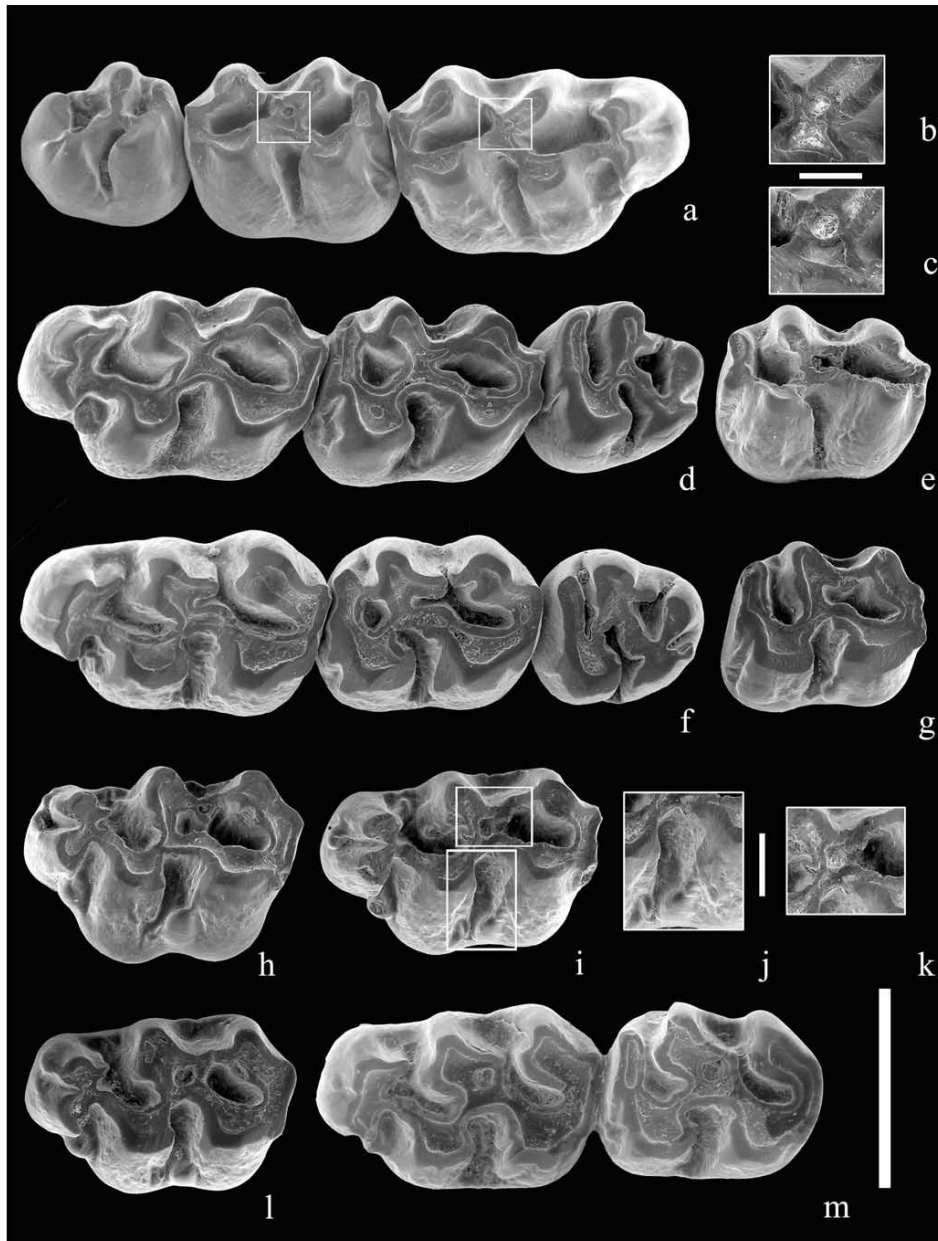
473



474

475 Figure 2

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477

478 Figure 3

479

