

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	
18	Abstract The material of <i>Hispanomys decedens</i> (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 <i>H. decedens</i> shows that this taxon is a good candidate ancestor for <i>H</i> .
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 $Hispanomys \cdot Cricetodontinae \cdot La Grive-Saint Alban \cdot France \cdot Systematics$
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 synonimized C. rhodanicum with C. sansaniensis because 54 these taxa could not be differencied 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 <i>H. decedens</i> 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 differenciate 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	e biozonation giv	en 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:
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- 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).

- *All the three localities are very poor in remains of *H. decedens*. The extremely low
 proportion of this taxon in the fissure L7 has been considered to be possibly the result of
 "contamination" by Mein and Ginsburg (2002).
- 158 *Extended diagnosis Hispanomys* species of medium size with low hypsodonty;
- 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 metalophulid or a
- 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
- 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 fordward 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 fordward
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 fordward 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 <i>H. bijugatus</i> , <i>H.</i>
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

anterior side of the protoconid, closing thereby the protosinusid. The m1 have a double

204 metalophulid (e.g. FSL 67003, Fig. 1-d) or a short mesolophid (FSL 67005, FSL 67001,

Figs. 1-a, 1-c). Some teeth clearly show both structures (e.g. FSL 67002, Fig. 1-b). Even

when the mesolophid is lacking, there is a slight inflation at the end of the posterior arm

207 of the protoconid. The hypolophulid 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

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

the protoconid, whereas the other one comes out from the anterior wall of the
hypoconid. The posterolophid is short and does not join the posterior wall of the
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 fordward 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. 3-1), 253 isolating a circular valley (called enamel-coated valley), which dissapears 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 surronding 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

less worn specimens, it is possible to observe that both lingual and labial posterolophsare 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 reachs 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 surronding 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 that emerges from the anterior side of the hypocone towards the posterior side of the 287 288 protocone. These teeth show short labial and lingual posterolophs. 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 fordward 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 loca	ilities of	t
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- 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)

introduced the new subgenus *Hispanomys* and raised these subspecies to the specieslevel.

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 thought more likely that the Spanish subspecies were different from the French one, a 316 317 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 differenciated (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-

developed mesolophs are also present, but in much lesser proportion, in *H. thaleri* (a

few upper molars) and in *H. aragonensis*. Besides, *H. decedens* seems more primitive

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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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

		LENGTH			WIDTH					
Locality	Tooth type	min	mean	max	sd	Ν	min	mean	max	sd
	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
La Grive-St Alban	m2	2.27	2.48	2.69	0.09	34	1.80	1.94	2.08	0.08
2	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

443	
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 μ m.
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 $\mu m)$
465	and j-k (500 µm).
466	

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





472 Figure 1



475 Figure 2



478 Figure 3



482 Figure 4