

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

Première description détaillée d'*Hispanomys decedens* (Rodentia) du Miocène moyen de La Grive-Saint Alban (France)

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Abstract The material of *Hispanomys decedens* (Rodentia, Cricetodontinae) from La Grive-Saint Alban (France) is described in detail for the first time. *H. decedens*, which is one of the oldest species of the genus, shows the primitive character states that are typical of the Aragonian congeneric species, such as the mesoloph and labial cingula surrounding the upper molar valleys. The detailed examination of the teeth of *H. decedens* shows that this taxon is a good candidate ancestor for *H. aragonensis*.

Keywords *Hispanomys* · Cricetodontinae · La Grive-Saint Alban · Miocene · Systematics

Résumé Le matériel d'*Hispanomys decedens* (Rodentia, Cricetodontinae) de La Grive-Saint Alban (France) est décrit pour la première fois en détail. *H. decedens* est une des plus anciennes espèces du genre et montre des

caractères primitifs typiques des espèces congénériques aragoniennes, tels que la présence de mésolophes et de cingulums labiaux sur les molaires supérieures. L'étude détaillée d'*Hispanomys decedens* montre que ce taxon est un bon candidat au titre d'ancêtre d'*H. aragonensis*.

Mots clés · *Hispanomys* · Cricetodontinae · La Grive-Saint Alban · Miocène · Systematics

Abbreviations

FSL	Université Claude Bernard, Villeurbanne, France
IPS	Instituto Catalán de Paleontología, Sabadell, Spain
MNCN	Museo Nacional de Ciencias Naturales-CSIC, Madrid, Spain
MSNL	Centre de Conservation et d'Etude des Collections, Lyon, France
RUU	Rijksuniversiteit Utrecht, Utrecht, The Netherlands

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1 Introduction

La Grive-Saint Alban is the name used to refer to various Upper Aragonian (Middle Miocene) pits located on the territory of the municipality of Saint-Alban-de-Roche (Isère, France). These pits are constituted by fissures in Jurassic (Bajocian) oolitic limestones filled with fossiliferous siderolithic clays. Remains of *Hispanomys* have only been recovered from La Grive-Saint Alban L (quarry Lechartier), M (quarry Milliat), and P.B. (quarry Peyre et Beau, where a single m1 was found by P. Mein). La Grive-Saint Alban L has eight fissure-fillings numbered from L1 to L8, but the productive ones (from a palaeontological

viewpoint) are only L3, L5, L5', L6, and L7 (Mein & Ginsburg 2002).

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

Later on, this variety was raised to the species level (Schaub, 1944: p. 454; Schaub, 1947: p. 60). Mein & Freudenthal (1971: p. 19) introduced the subgenus *Hispanomys* for a handful of allegedly derived *Cricetodon*, such as *C. decedens*. This subgenus was elevated to the genus level by Van de Weerd (1976): p. 106 *et seq.*). The holotype of *H. decedens*, which is a left maxillary fragment with M1 and M2, is housed in the MSNL (Schaub, 1925). It seems that the original findings of *H. decedens* are not the fruits of the field works carried out by Depéret in the mid-nineteenth century, but most likely of those carried out shortly later by Gaillard, which were taken up by Ennouchi in the beginning of the twentieth century. It is believed that Ennouchi worked in the “Carrière Lechartier” (called at that time “Carrière Chemin”) at the fissures L4, L5, L5', and L7 (Ennouchi, 1930). The remains of *H. decedens* are supposedly from a now empty fissure, which is located between the fissure L5 and L7 and that is called L5'.

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

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

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

2 Materials and methods

The systematic study presented here is based on the examination of original specimens of the MNCN, RUU, IPS, and FSL collections, and data from the literature. We examined the teeth of the following species: *Hispanomys bijugatus* and *H. decedens* from La Grive-Saint Alban (Isère, France), *H. mediterraneus* from the localities of Montredon (Hérault, France), Soblay (Ain, France), and Dionay (Isère), *H. aguirrei* from Escobosa (Soria, Spain), *H. daamsi* from Can Missert (Barcelona, Spain), *H. dispectus* from Hostalets de Pierola and Castell de Barbera (Barcelona), *H. lavocati* from Hostalets de Pierola, of *H. aragonensis* from Pedregueras 2A (Saragossa, 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. moralesi* from Batallones 1, Batallones 3, Batallones 5, and Batallones 10 (Madrid, Spain), *H. thaleri* from Can Llobateres (Barcelona), *H. freudenthali* from Puente Minero (Teruel), and *H. adroveri* from Casa del Acero (Murcia, Spain).

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

The first, second, and third lower molar are designed as m1, m2, and m3, respectively, whereas the first, second, and third upper molar are designed as M1, M2, and M3, respectively. The terminology used in the tooth descriptions follows that of Freudenthal, Huguency, & Moissenet (1994) and López-Antoñanzas et al. (2010).

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

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

N	Tooth type	Length (mm)				Width (mm)			
		Min	Max	Mean	Sd	Min	Max	Mean	Sd
29	m1	2.44	2.80	2.60	0.09	1.60	1.78	1.69	0.05
34	m2	2.27	2.69	2.48	0.09	1.80	2.08	1.94	0.08
25	m3	1.92	2.42	2.23	0.15	1.63	1.93	1.79	0.08
62	M1	2.74	3.59	3.16	0.18	1.76	2.31	2.05	0.10
54	M2	2.14	2.69	2.43	0.15	1.72	2.23	1.92	0.12
26	M3	1.64	2.09	1.82	0.12	1.50	1.90	1.68	0.09

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

3 Systematic paleontology

Order Rodentia BOWDICH, 1821

Subfamily Cricetodontinae SCHAUB, 1925

Genus *Hispanomys* MEIN and FREUDENTHAL, 1971

Type species *Hispanomys aragonensis* (FREUDENTHAL, 1966)

Hispanomys decedens (SCHAUB, 1925) (Figs. 1, 2, 3)

Holotype ML-Lgr 130: left maxillary fragment with M1 and M2 (Schaub 1925: fig. 2, plate III).

Referred specimens FSL67000-FSL67003, FSL67005, FSL67006, FSL67099-FSL67101, FSL67103, FSL67105-FSL67108, FSL67118, FSL67121, FSL67122, FSL67142 (mandibular ramus with m1-m3); FSL67004, FSL67021, FSL67102, FSL67120 (mandibular ramus with m1-m2); FSL67098 (mandibular ramus with m2-m3); FSL67111 (mandibular ramus with m3); FSL67093-FSL67097, FSL67104, FSL67133 (isolated m1); FSL67047-FSL67052, FSL67060-FSL67065 (isolated m2); FSL67053-FSL67059 (isolated m3); FSL67007, FSL67009-FSL67011, FSL67046, FSL67110, FSL67113, FSL67115, FSL67116, FSL67119, FSL67135, FSL67136, FSL67138, FSL67140, FSL67143, FSL67144, FSL67146 (maxilla with M1-M3); FSL67008, FSL67109, FSL67112, FSL67114, FSL67117, FSL67123, FSL67124, FSL67126, FSL67129, FSL67134, FSL67137, FSL67139, FSL67141, FSL67145, FSL67147 (fragmentary maxilla with M1-M2); FSL67125, FSL67128 (fragmentary maxilla with M1); FSL67127 (fragmentary maxilla with M2-M3); FSL67012-FSL67017, FSL67022-FSL67045, FSL67130-FSL67132 (isolated M1); FSL67018-FSL67020, FSL67066-FSL67084 (isolated M2); FSL67085-FSL67092 (isolated M3). Measurements are given in Table 1, Electronic Supplementary Material and Fig. 4.

Type locality La Grive-Saint Alban (fissure L5') (López-Antoñanzas and Mein 2009: fig. 1).

Age Probably MN 7 (see below).

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

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 (=1.16) ratios (third lower and upper molars not reduced); lower molars usually lacking the cingula on the lingual valleys; with some m1 having a double metalophid or a short mesolophid or even both; three rooted m2 with a short, but distinct, mesolophid; 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; four-rooted M1 having one or two anterior cusps on the prelobe, with the anterior ectoloph well developed, but lacking the forward paracone spur and usually having prominent protostyles and entostyles; M2 with lingual anteroloph, having the anterosinus usually open, but having sometimes anterior ectoloph and forward paracone spur, less M2 than M1 with mesoloph and enamel-coated valley, and all of them having well-developed backward paracone spur and posterior ectoloph; M3 with distinct anteroloph and posteroloph and having backward paracone spur, but lacking the anterior ectoloph, the forward paracone spur, and the posterior ectoloph.

Differential diagnosis Differing from *Hispanomys daamsi*, *H. thaleri*, *H. freudenthali* and *H. adroveri*, in being smaller; differing from *H. bijugatus*, *H. thaleri*, *H. moralesi*, *H. peralensis*, *H. baixasi*, *H. freudenthali*, and *H. adroveri* in having strong labial cingula surrounding the valleys on the M1; differing from *H. bijugatus*, *H. aragonensis*, *H. thaleri*, *H. moralesi*, *H. peralensis*, *H. baixasi*, *H. freudenthali*, and *H. adroveri* in having strong labial cingula surrounding the valleys on the M2; differing from *H. mediterraneus*, *H. moralesi*, *H. peralensis*, *H. freudenthali*, and *H. adroveri* in having four-rooted M1; differing from *H. dispectus*, *H. thaleri*, *H. mediterraneus*, *H. moralesi*, *H. peralensis*, *H. freudenthali*, and *H. adroveri* in having incomplete ectolophs on the M1 and M2; differing from *H. castelnovi*, *H. bijugatus*, *H. daamsi*, *H. aguirrei*, *H. nombrevillae*, *H. lavocati*, *H. mediterraneus*, *H. moralesi*, *H. peralensis*, *H. freudenthali*, and *H. adroveri* in having an enamel-coated valley on many M1-M2; differing from *H. castelnovi*, *H. bijugatus*, *H. nombrevillae*, *H. mediterraneus*, *H. moralesi*, *H. peralensis*, *H. freudenthali*, and *H. adroveri* in having usually a mesoloph on the M1; differing from *H. castelnovi*, *H. dispectus*, *H. nombrevillae*, *H. thaleri*, *H. mediterraneus*, *H. moralesi*, *H. peralensis*, *H. freudenthali*, and *H. adroveri* in having the M3 less

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

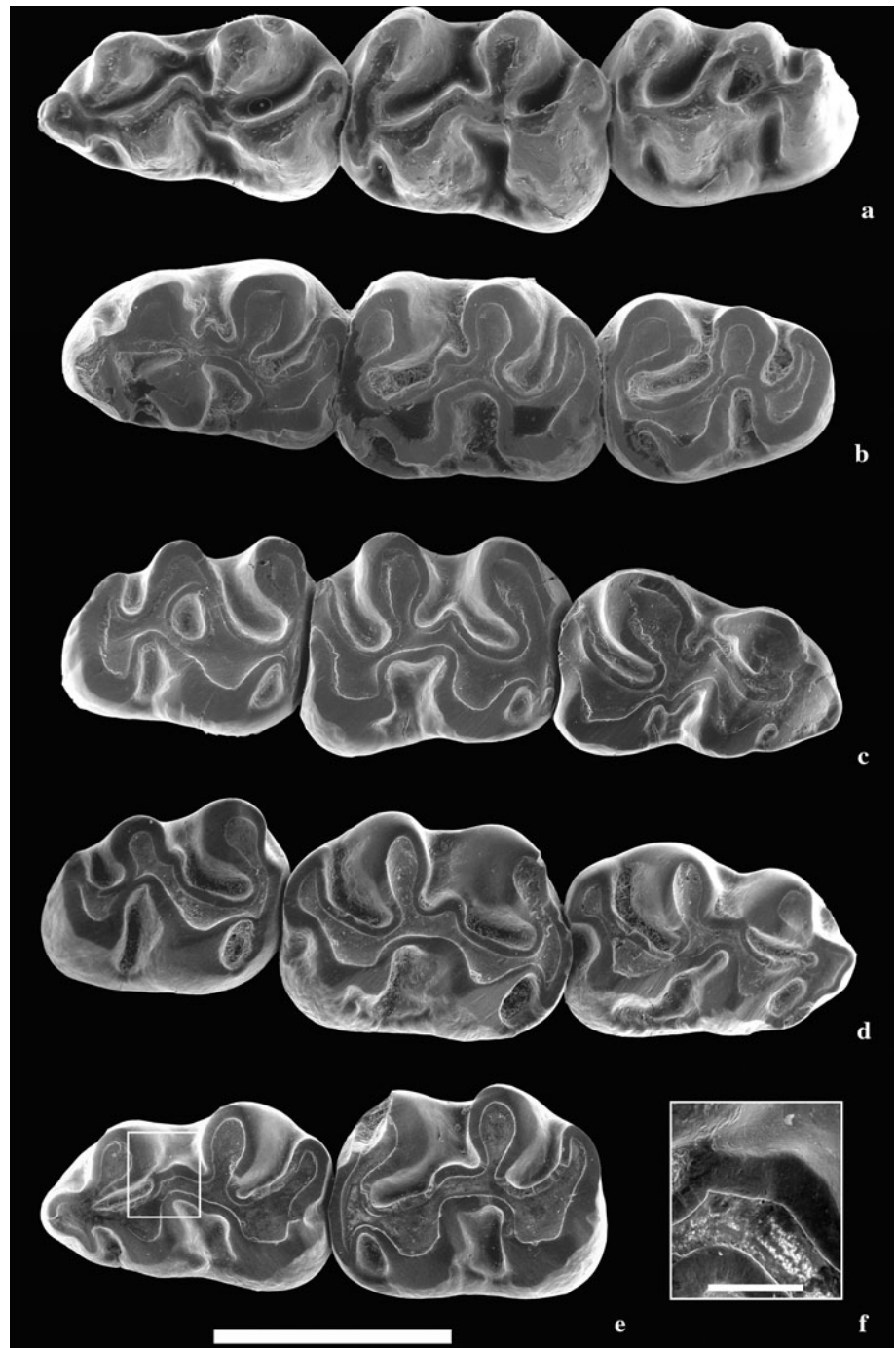
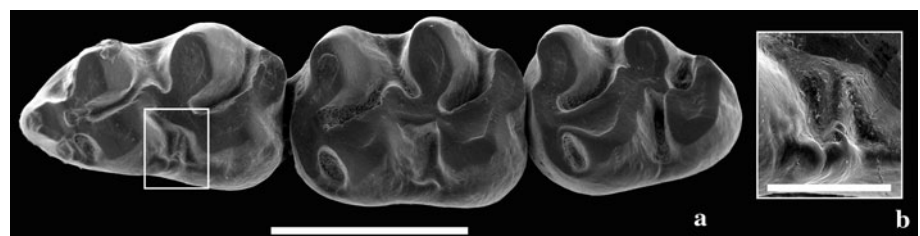


Fig. 2 *Hispanomys decedens* from La Grive-Saint Alban (fissure L5'). **a** Left mandible with m1–m3 (FSL 67000). *Scale bar* represents 2 mm. **b** Close-up of the ectomesolophid of the m1 of specimen FSL 67000. *Scale bar* represents 500 μ m



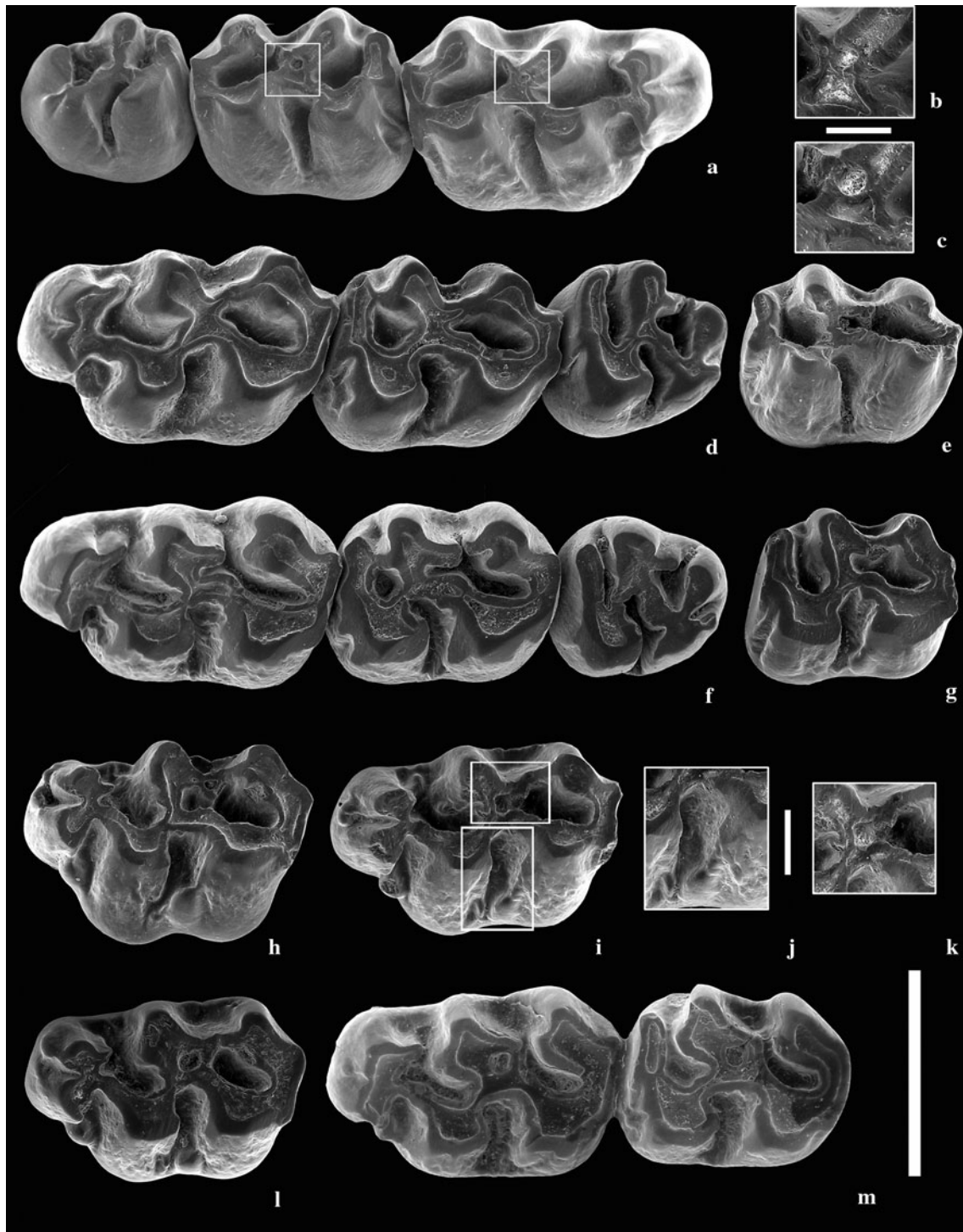
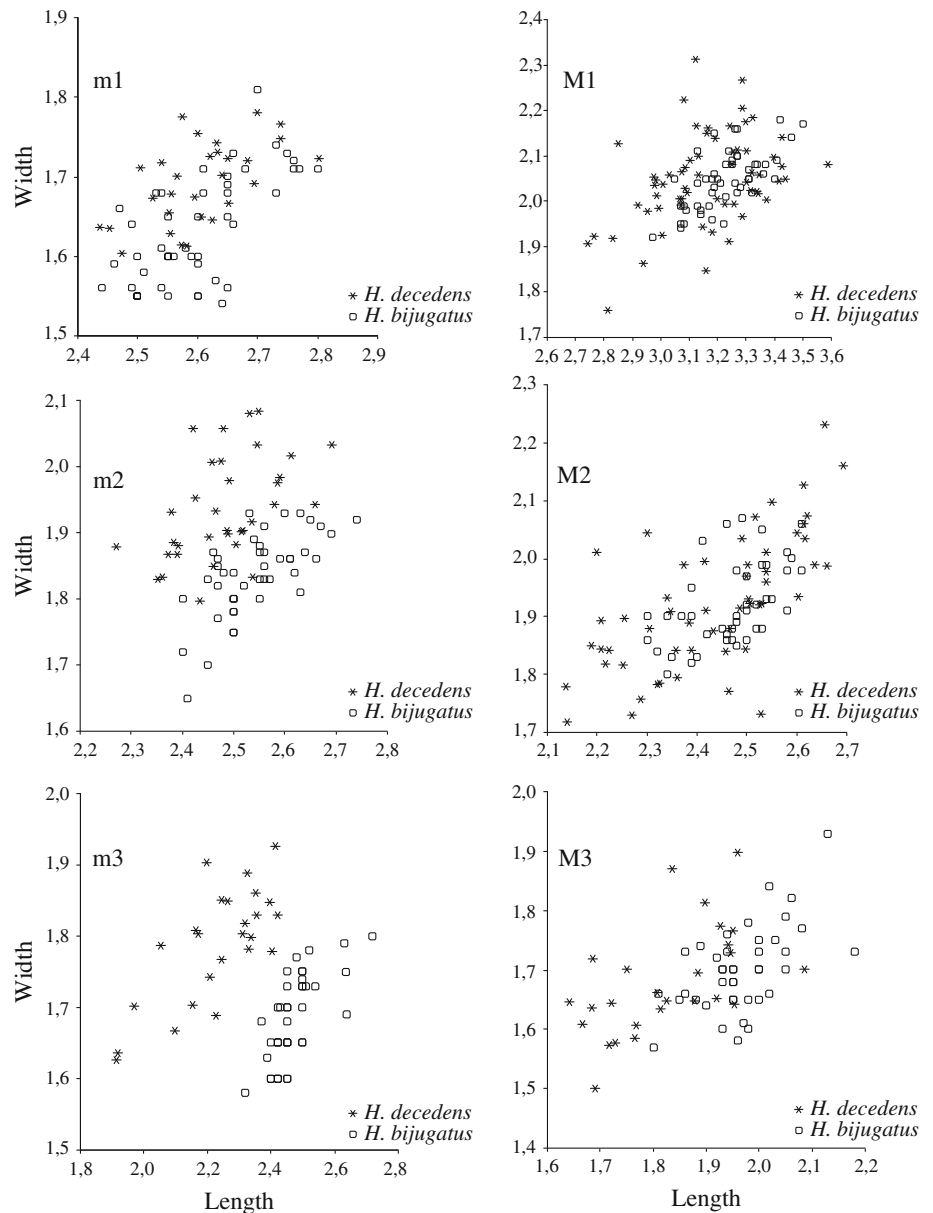


Fig. 3 Upper molars of *Hispanomys decedens* from La Grive-Saint Alban (fissure L5'). **a** Right maxilla with M1–M3 (FSL 67007). **b** Close-up of the mesoloph of the M1 of specimen FSL 67007. **c** Close-up of the mesoloph of the M2 of specimen FSL 67007. **d** Left maxilla with M1–M3 (FSL 67009). **e** Left M2 (FSL 67019). **f** Left maxilla with M1–M3 (FSL 67011). **g** Left M2 (FSL 67020).

h Left M1 (FSL 67012). **i** Left M1 (FSL 67015). **j** Close-up of the entomesoloph of specimen FSL 67015. **k** Close-up of the mesoloph of specimen FSL 67015. **l** Left M1 (FSL 67017). **m** Left maxilla with M1–M2 (FSL 67008). *Scale bar* represents 2 mm, except for **b–c** (300 μm) and **j–k** (500 μm)

Fig. 4 Length/width scatter diagrams of the upper and lower molars of *Hispanomys decedens* and *H. bijugatus* from La Grive-Saint Alban (Isère, France). Except for one m1 (from Carrière M) and two M3 (from Carrière L, fissure L7), all the specimens come from fissure L5'



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

3.1 Description

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

m1: The outline of these teeth in occlusal view is sub-rectangular, longer than wide, with its anterior part somewhat rounded and narrower than the posterior one. The lingual anterolophid is usually lacking, but in few specimens (e.g. FSL 67005) it is present, but weak. The labial anterolophid is long and prominent and can even reach the anterior side of the protoconid, closing thereby the proto-sinusid. The m1 have a double metalophid (e.g. FSL 67003, Fig. 1d) or a short mesolophid (FSL 67005, FSL 67001, Fig. 1a, c). Some teeth clearly show both structures (e.g. FSL 67002, Fig. 1b). Even when the mesolophid is lacking, there is a slight inflation at the end of the posterior arm of the protoconid. The hypolophid is transverse. A few teeth have an ectomesolophid (FSL 67000, Fig. 2). All the specimens have a labial cingulum surrounding the

sinusid. This cingulum is constituted by the junction of two ridges: the first emerging from the posterior wall of the protoconid and the second from the anterior wall of the hypoconid. It can bear an ectostylid. Some m1 also show a thin, low ridge surrounding the lingual 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.

m2: These teeth are rectangular in shape, though they are anteriorly and posteriorly slightly rounded. They show a prominent labial anterolophid that reaches the anterolabial side of the protoconid, closing thereby the protosinusid. The metalophulid is anterolabially directed and the hypolophulid is transverse. The mesolophid is usually short and ends free. The m2 have rarely lingual cingula surrounding the valleys (e.g. FSL 67006), but all of them have strong labial cingula closing the sinusid. These cingula are constituted by two ridges; the first (which is stronger) emerging from the posterior wall of the protoconid and the second from the anterior wall of the hypoconid. The sinusid is transverse. The posterolophid is short and constricted behind the hypoconid; it does not reach the posterior side of the entoconid. The posterior root splits into two and, therefore, these teeth are three-rooted. The posterolabial root is stronger than the posterolingual one.

m3: The occlusal outline of these teeth is rounded, longer than wide, with its posterior part narrower than the anterior one. They show a long and strong labial anterolophid that connects with the anterior wall of the protoconid, closing the protosinusid. The lingual anterolophid is absent. Most of the specimens have a short mesolophid (FSL 67002, FSL 67003, Fig. 1b, d). However, 4 out of 27 have it long (e.g. FSL 67001, FSL 67005, FSL 67054, FSL 67057 Fig. 1a, c). From these, three specimens (FSL 67001, FSL 67005, FSL 67054) have the mesolophid connected to the anterior side of the entoconid. The posterosinusid and mesosinusid are open; there are no lingual cingula surrounding the valleys. The sinusid is slightly posteriorly directed; it 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.

M1: These teeth show a pronounced groove between the two lobes of the anterocone. Most of the specimens show either a strong cusp (even two) in the prelobe or a low anterior ridge in front of the anterocone (e.g. Fig. 3h). The anterolophule connects the lingual lobe of the anterocone with the protocone. The protosinus is closed by a large protostyle (Fig. 3d, h, i, l) or by a low and strong ridge (Fig. 3a). The protolophule is anterolabially directed. The

anterior ectoloph is well developed and ends free most of the time. It can be parallel to the longitudinal axis of the tooth or postero-lingually directed. The forward paracone spur is usually absent. The long and strong backward paracone spur connects to the posterior ectoloph closing the mesosinus, but it ends free in some specimens. The backward paracone spur emerges at about the midpoint between the labial side of the tooth and the entoloph. Most of the specimens have a short or medium mesoloph. In some of them, the mesoloph connects labially to a lingual spur of the backward paracone spur that points towards the mesoloph (Fig. 3l), isolating a circular valley (called enamel-coated valley), which disappears through wear. Otherwise these structures are too short to be connected (Fig. 3h, i, k). The M1 of *Hispanomys decedens* have strong, low cingula surrounding the labial valleys; some of which bears a mesostyle. The anteriorly directed sinus is usually partially closed by a strong entostyle or by a ridge, which emerges from the hypocone towards the posterolabial side of the protocone. Some specimens (e.g. FSL 67015, Fig. 3i, j) and FSL 67017 (Fig. 3h) show a vertical ridge emerging from the posterior wall of the 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 posterolophs are short, but distinct. These teeth are four-rooted.

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 quite developed lingual anteroloph and a small, but distinct, protosinus in the anterior margin of the teeth. The labial anteroloph is well developed. The anterosinus is usually open due to the absence of anterior ectoloph, forward paracone spur or both (e.g. Fig. 3e, g, m). However, some of the M2 have the anterior ectoloph connected to the forward paracone spur, closing the anterosinus (e.g. Fig. 3d, f). The backward paracone spur is long and strong and usually reaches the posterior ectoloph (a small anterior ridge of the metacone) and, in so doing, entirely closes the mesosinus. Nevertheless, some specimens lack the posterior ectoloph and, therefore, have a backward paracone spur that ends free (e.g. Fig. 3m) or the two crests are not connected (e.g. Fig. 3f). All teeth have the mesosinus much larger than the anterosinus and they have a cingulum surrounding the main labial valley. A lesser number of M2 than M1 shows the mesoloph. When present, it is short or of medium length; in some specimens it reaches the backward paracone spur forming an enamel-coated valley (e.g. Fig. 3m). The enamel-coated valley is formed by the connection of the mesoloph with a lingual spur emerging from the backward paracone spur. In some specimens, the mesoloph and the backward paracone spur are too short and, therefore, they are disconnected (Fig. 3e). The

presence of a mesoloph on the M2 is related to the presence of a mesoloph on the M1. Every M2 that lacks the mesoloph shows a slight inflation at the beginning of the anterior arm of the hypocone (Fig. 3d, f). The backward paracone spur is long and usually posterolabially oriented; in some specimens (Fig. 3d) it emerges practically at the midpoint of the protolophule. The protolophule is 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 protocone. These teeth show short labial and lingual posterolophids. They have four roots.

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

4 Discussion

In 1966, Freudenthal based on his studies of the cricetid material from the localities of Nombrevilla and Pedregueras 2C (Zaragoza, Spain) established two new subspecies of *Cricetodon decedens* in addition to *C. decedens decedens*: *C. decedens aragonensis* and *C. decedens nombrevillae*. Later on, Mein and Freudenthal (1971: 19) introduced the new subgenus *Hispanomys* and raised these subspecies to the species level.

Freudenthal's (1966) decision of regarding the two taxa as subspecies of *C. decedens* was the result of the lack of information available at that time about the "typical" *decedens* from La Grive-Saint Alban. Actually, Freudenthal (1966) did not discard the possibility that, once the material from La Grive-Saint Alban is studied in detail, one of 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 conclusion that the present work supports.

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

The main characters usually used to establish the evolutionary stage of the *Hispanomys* species are: (1) the different development of the ectolophids; (2) the degree of reduction of the mesolophids and mesolophids; (3) the presence or loss of labial anterolophids; (4) the presence or loss of cingular structures; (5) the acquisition or not of extra roots; (6) the degree of reduction of the third molars; and (7) the degree of hypsodonty (van de Weerd 1976; Agustí 1981, 1982; López-Antoñanzas and Mein 2009; López-Antoñanzas et al. 2010). The most archaic morphologies of *Hispanomys* would be characterized by having lower molars with well-developed labial anterolophids, lingual anterolophids, lingual cingula surrounding the valleys, two-rooted m2, and unreduced m3. Besides, the most primitive upper molars would be characterized by having mesolophids, labial cingula surrounding the valleys, quite incomplete ectolophids, four-rooted M1, and unreduced M3 (van de Weerd, 1976; Agustí 1981, 1982; López-Antoñanzas and Mein 2009; López-Antoñanzas et al. 2010).

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

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

Thus, *Hispanomys decedens* is more primitive than *H. castelnavi*, *H. bijugatus*, *H. aguirrei*, *H. daamsi*, *H. lavocati*, and *H. nombrevillae* in having well-developed mesolophids on M1 and M2, which tend to form an enamel-coated valley. Well-developed mesolophids 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. castelnavi*, *H. bijugatus*, and *H. thaleri* in having strong cingula surrounding the labial

valleys of the first and second upper molars. Regarding the reduction of the third molars, this taxon is also quite primitive: *H. decedens* appears more primitive than *H. castelnovi*, *H. dispectus*, *H. nombrevillae*, and *H. thaleri* in having the M3 much less reduced (López-Antoñanzas et al., 2010: table 2). This character is shared with the other species of *Hispanomys* from La Grive-Saint Alban: *H. bijugatus*.

5 Concluding remarks

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

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

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