



General palaeontology, systematics and evolution (Biostratigraphy)

Cricetodontini from the Calatayud–Daroca Basin (Spain): A taxonomical description and update of their stratigraphical distributions



*Les Cricetodontini du bassin de Calatayud–Daroca (Espagne):
description taxonomique et mise à jour biostratigraphique*

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ABSTRACT

The most updated stratigraphical distributions of the Cricetodontini from the Calatayud–Daroca Basin are presented. *Cricetodon sansaniensis* (local biozone F, MN6, middle Aragonian) and *Cricetodon jotae* (local biozone G1, G2 and G3, MN6–MN7/8, Middle–Upper Aragonian) from the middle Miocene are described and discussed. Generally, the genera of Cricetodontini were used to define large time intervals, whereas the species were neglected in the local biostratigraphical studies. The results presented herein show that, for the Calatayud–Daroca Basin, most of the stratigraphical distributions of the species of Cricetodontini are strongly linked with the local biozonation. That reveals that they could be used as good biostratigraphical indicators. Moreover, the unusually long local biozone G3 could be redefined and subdivided based on the distributions of the four species of Cricetodontini present in it. However, it is recommended to complete the study of the whole rodent fauna before proposing a new biozonation.

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RÉSUMÉ

Une mise à jour détaillée des distributions stratigraphiques des espèces de Cricetodontini présentes dans le bassin de Calatayud–Daroca est proposée. Les espèces *Cricetodon sansaniensis* (biozone locale F, MN6, Aragonien moyen) et *Cricetodon jotae* (biozones locales G1, G2 et G3, MN6–MN7/8, Aragonien moyen et supérieur) du Miocène moyen sont décrites et discutées. Généralement, les genres de Cricetodontini ont été utilisés dans la définition des grands intervalles de temps, tandis que les espèces ont été négligées dans les études biostratigraphiques locales. Les résultats présentés ici montrent que la plupart des distributions stratigraphiques des espèces de Cricetodontini du bassin de Calatayud–Daroca sont

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étroitement liées à la biozonation locale. En conséquence, leur importance est soulignée dans le cadre d'études biostratigraphiques à une échelle fine. De plus, la biozone locale G3, d'une durée inhabituellement longue, pourrait être redéfinie et subdivisée en fonction de la distribution des quatre espèces de *Cricetodontini* présentes. Cependant, une étude détaillée de la faune complète des rongeurs est nécessaire avant qu'on puisse proposer une nouvelle biozonation.

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1. Introduction

The tribe *Cricetodontini* is a group of large-sized rodents found in Europe, northern Africa and Asia (De Bruijn and Ünay, 1996; Jaeger et al., 1973; Rummel, 1999). Their biogeographical distribution follows a symmetrical model in which the first occurrence of the tribe is in a small area (region of Anatolia) during the Early Miocene (Álvarez-Sierra et al., 2013; De Bruijn and Ünay, 1996; Rummel, 1999). In the Middle Miocene, there is a gradual expansion into central Europe and France followed by a period of stasis in which the taxon is distributed over most Europe and Asia Minor (Álvarez-Sierra et al., 2013; De Bruijn and Ünay, 1996; Rummel, 1999). Their extinction at the end of the Pliocene was preceded by a period of fragmentation and contraction of their distribution area since the late Middle Miocene (Álvarez-Sierra et al., 2013; De Bruijn and Ünay, 1996; Rummel, 1999).

This tribe includes eight genera; three of them—*Cricetodon* Lartet, 1851, *Hispanomys* Mein and Freudenthal, 1971a, and *Ruscinomys* Depéret, 1890—are recorded in the Aragonian and Vallesian from the Calatayud–Daroca Basin.

Genera of *Cricetodontini* have been used, as biostratigraphical indicators, in many studies for the Calatayud–Daroca Basin (e.g., Álvarez Sierra et al., 2003; Daams et al., 1999; Hernández-Ballarín et al., 2011; Van der Meulen et al., 2011, 2012), although mainly to define large time intervals and limits between major continental units. For instance, the first occurrence (FO) of *Cricetodon* coincides with the beginning of the local biozone E in the Calatayud–Daroca Basin (Daams et al., 1999; Van der Meulen et al., 2012), and the relative abundance of *Cricetodon* and *Hispanomys* characterizes the faunas from the Late Aragonian and the Early Vallesian in the same basin (Daams et al., 1999).

By contrast, the species of *Cricetodontini* has been not traditionally used for local biostratigraphical subdivisions in the Calatayud–Daroca Basin. De Bruijn et al. (1993) pointed out that the mosaic morphology displayed by the species of *Cricetodontini* precludes their use for the proposal of detailed biostratigraphical scales. Nevertheless, the recently exhaustive study of the species of *Cricetodontini* has served as a source to establish biostratigraphical subdivisions. For instance, the species of *Byzantinia* and *Cricetodon* were used in the local biostratigraphy of the Neogene from Turkey (Ünay and De Bruijn, 1984; Ünay et al., 2003). Furthermore, in the workshop of the Regional Committee of Stratigraphy of the Neogene in May 2012, the biostratigraphy of the uppermost Early Badenian (Middle Aragonian) from the German Molasse were updated from those proposed by Heissig

(1997). Three species of *Cricetodon* were used to define three local biozones: *Cricetodon meini*, *Cricetodon aureus* and *Cricetodon sansaniensis* which correspond to OMS units E', F, and ?F (Böhme et al., 2012). Moreover, Kálin and Kempf (2009) also used a similar approach in the biostratigraphy of the Swiss Molasse. Therefore, it seems that a better knowledge of the species of *Cricetodontini* could reveal them as good local biostratigraphical and biochronological indicators. Furthermore, the local biozonation of Van der Meulen et al. (2012), based mainly on cricetids (e.g., *Megacricetodon* and *Democricetodon*), could be extended towards the Late Aragonian and the Early Vallesian; indeed, the most updated distribution of the *Cricetodontini* will be useful in the redefinition of the local biozonation.

Several works have recently focused in the systematics of the tribe *Cricetodontini* from the Calatayud–Daroca Basin (López-Guerrero et al., 2008, 2009, 2013a, 2014), but a number of localities and species from the earliest part of the Late Aragonian still lacked a detailed revision. Thus, the first aim of this paper is to review this material of *Cricetodon*.

The second aim is to evaluate the updated stratigraphical distributions of the *Cricetodontini* from the Calatayud–Daroca Basin and assess whether or not they are good biostratigraphical markers.

2. Material and methods

We have studied 503 upper and lower molars belonging to 18 sites. Table 1 contains all the information about the different localities. Within the total sample, 89 specimens from five localities belong to *C. sansaniensis* Lartet, 1851 and the other 414 molars correspond to *Cricetodon jotae* Mein and Freudenthal, 1971a, recovered from 13 localities (Table 1). We observed personally the material of several species summarized in Table 2. The information about the other species of *Cricetodontini* from the Calatayud–Daroca Basin has been found in López-Guerrero et al. (2008, 2009, 2013a, 2014). The numerical ages of the localities are after Daams et al. (1999), Van Dam et al. (2006) and Van Dam (in prep.). The nomenclature used follows López-Guerrero et al. (2013a). Length and width measurements for each specimen were taken (in mm) using a Nikon Measuroscope 10 microscope with digital micrometer, following the procedure suggested by López-Guerrero et al. (2013a). The photographs from Figs. 1 and 2 were taken with an environmental Scanning Electron Microscope FEI Quanta 200 at the Museo Nacional de Ciencias Naturales–CSIC, Madrid (Spain) except for those from ARM7 and VT2C, taken with a digital camera attached to a Leica Microscope at Naturalis Biodiversity Center, Leiden (The Netherlands).

Table 1

Studied material of *Cricetodon sansaniensis* and *Cricetodon jotae* from the Calatayud–Daroca Basin. Numerical ages of the localities after van Dam et al. (2006), localities, abbreviations for the localities, and institutions where the fossils are stored (see institutional abbreviations).

Tableau 1

Matériel de *Cricetodon sansaniensis* et *Cricetodon jotae* étudié dans le bassin de Calatayud–Daroca, incluant les âges numériques des localités d'après van Dam et al. (2006), les localités, les abréviations des localités et les établissements où les fossiles sont conservés (voir abréviations institutionnelles).

Age (Ma)	Locality	Abb.	Collection	M1	M2	M3	m1	m2	m3	N
<i>Cricetodon sansaniensis</i>										
13.68	Valalto 2C	VT2C	RGM	3	5	5	3	—	4	20
13.70	Valalto 2B	VT2B	RGM	—	—	—	2	1	3	6
	Armantes 7	ARM7	IAUU	5	3	5	1	1	2	17
13.75	Las Umbrias 21	LUM21	MNCN	8	8	4	5	4	5	34
13.76	Las Umbrias 22	LUM22	MNCN	—	2	2	3	2	3	12
			Total	16	18	16	14	8	17	89
<i>Cricetodon jotae</i>										
	Toril 1	TOR1	RGM	4	4	4	3	3	3	21
	Alcocer 3	AC3	RGM	—	2	—	2	—	—	4
	Alcocer 2	AC2	RGM	—	—	—	4	4	3	11
	Alcocer 1	AC1	RGM	1	—	1	—	1	—	3
	Villafeliche 9	VL9	RGM	1	2	2	2	3	2	12
	Arroyo del Val VI	ARV6	IAUU	19	10	15	19	24	22	109
13.08	Las Planas 5K	LP5K	RGM	3	5	1	5	2	—	16
13.16	Las Planas 5L	LP5L	RGM	—	2	—	3	—	1	6
	Borjas	BOR	RGM	6	4	2	5	4	3	24
	Manchones	MAN	IAUU/RGM	30	33	20	37	35	30	185
	Valalto 1	VT1	MNCN/RGM	1	—	—	1	1	2	5
13.55	Las Planas 5C	LP5C	MNCN	3	2	2	3	2	—	12
13.56	Las Planas 5B	LP5B	RGM	3	1	—	—	—	2	6
			Total	71	65	47	84	79	68	414

Abb: abbreviations for the localities; N: number of specimens.

Table 2

Information of the material personally studied for comparisons (see institutional abbreviations).

Tableau 2

Informations sur le matériel personnellement étudié pour comparaison (voir abréviations institutionnelles).

Species	Type locality	Institution
<i>C. soriae</i>	Somosaguas (Spain)	UCM
<i>C. bolligeri</i>	Petersbuch 10 (Germany)	BSPG
' <i>C. fandli</i>	Gratkorn (Austria)	BSPG
<i>C. sansaniensis</i>	Sansan (France)	MHNB
<i>C. aureus</i>	Vieux-Collonges (France)	RGM
<i>C. meini</i>	Vieux-Collonges (France)	RGM
<i>C. albanensis</i>	La Grive-Saint Alban (France)	RGM
' <i>C. klariankae</i>	Felsőtárkány-Felnémet (Hungary)	PM
<i>C. jotae</i>	Manchones (Spain)	IAUU

Institutional abbreviations: **BSPG**, Bayerische Staatssammlung für Paläontologie und Geologie, Munich (Germany); **IAUU**, Instituut voor Aardwetenschappen, Utrecht University (The Netherlands); **MNCN**, Museo Nacional de Ciencias Naturales-CSIC, Madrid (Spain); **NHNB**, Muséum d'histoire naturelle de Bâle (Switzerland); **PM**, Páztó Múzeum, Páztó (Hungary); **RGM**, Naturalis Biodiversity Center, former Rijksmuseum van Geologie en Mineralogie, Leiden (The Netherlands); **UCM**, Facultad de Geología, Universidad Complutense de Madrid (Spain).

3. Systematic palaeontology

RODENTIA Bowdich, 1821

CRICETIDAE Fischer, 1817

CRICETODONTINAE Stehlin and Schaub, 1951

CRICETODONTINI Simpson, 1945

Cricetodon Lartet, 1851

Cricetodon soriae López Martínez, Cárdbaba, Salesa, Hernández Fernández, Cuevas González and Fesharaki, 2006 in Hernández Fernández et al., 2006.

The most important features of *C. soriae* are: medium to large size; brachydont molars without styles or stylids. The upper molars have short or absent ectolophs, the anterior ectoloph is absent on the M1; presence of split anterocone and anterior + posterior protolophule on the M1, as well as well-developed posteroloph on the M3. The lower molars often show ectomesolophids and low-developed mesolophids; the m1 possesses both metalophulid, I and II; incomplete metalophulid I and rounded anteroconid; the m3 is large and longer than the m1, and it has long and double mesolophids.

Type locality: Somosaguas N, Madrid Basin, Spain, local biozone E (MN5, Middle Aragonian, Middle Miocene).

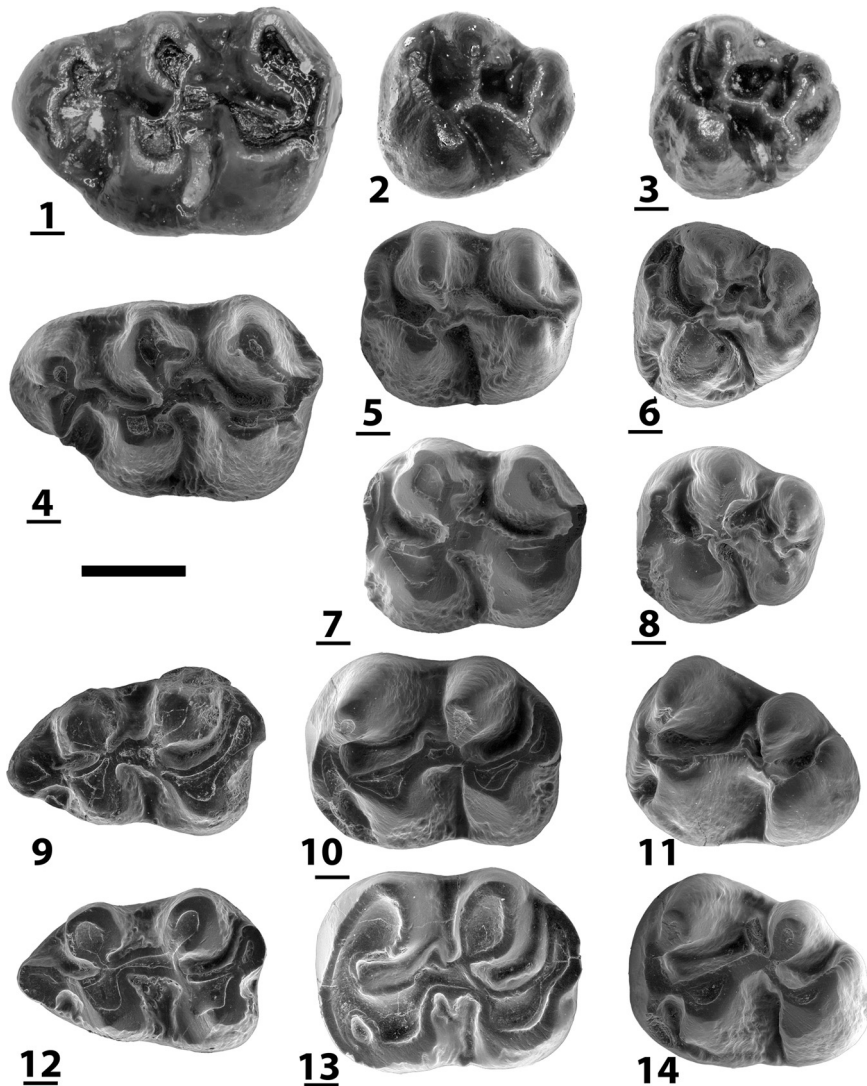


Fig. 1. *Cricetodon sansaniensis* from Calatayud–Daroca. Upper molars. Armantes 7: **1**, inverted right M1, ARM7 (58)–542; **2**, left M3, ARM7 (58)–531. Valalto 2C: **3**, inverted right M3, RGM-266419. Las Umbrías 21: **4**, inverted right M1, LUM21-179; **5**, inverted right M2, LUM21-156; **6**, inverted right M3, LUM21-69. Las Umbrías 22: **7**, inverted right M2, LUM22-115; **8**, inverted right M3, LUM22-116. Lower molars: Las Umbrías 21: **9**, left m1, LUM21-161; **10**, inverted right m2, LUM21-164; **11**, left m3, LUM21-166. Las Umbrías 22: **12**, inverted right m1, LUM22-120; **13**, inverted right m2, LUM22-122; **14**, left m3, LUM22-124. **Fig. 1.** *Cricetodon sansaniensis* de Calatayud–Daroca. Molaires supérieures : Armantes 7 : **1**, M1 droite inversée, AR-7 (58)–542, **2**, M3 gauche, AR-7(58)–531. Valalto 2C : **3**, M3 droite inversée, RGM-266419. Las Umbrías 21. **4**, M1 droite inversée, LUM21-179, **5**, M2 droite inversée, LUM21-156, **6**, M3 droite inversée, LUM21-69. Las Umbrías 22 : **7**, M2 droite inversée, LUM22-115, **8**, M3 droite inversée, molaires LUM22-116. Molaires inférieures : Las Umbrías 21 : **9**, m1 gauche, LUM21-161, **10**, m2 droite inversée, LUM21-164 ; **11**, m3 gauche, LUM21-166. Las Umbrías 22 : **12**, m1 droite inversée, LUM22-120, **13**, m2 droite inversée, LUM22-122 ; **14**, m3 gauche, LUM22-124.

Stratigraphical distribution in the Calatayud–Daroca Basin: local biozone E (MN5, Middle Aragonian, Middle Miocene). FO: LUM11 (14.06 Ma); LO: LUM20 (13.80 Ma)

Detailed morphological descriptions are in López-Guerrero et al., 2013a.

Cricetodon sansaniensis Lartet, 1851.

Figs. 1, 3; Tables 1, 3.

Type locality: Sansan, France, (MN6, Middle Miocene).

Stratigraphical distribution in the Calatayud–Daroca Basin: local biozone F (MN6, Upper Aragonian, Middle Miocene) FO: LUM22 (13.76 Ma); LO: VT2C (13.68 Ma).

Detailed description of the material from Calatayud–Daroca Basin is provided below.

Studied Material: See Table 1.

Measurements: See Table 3.

Emended diagnosis (Maridet and Sen, 2012: 30): “Large-sized *Cricetodon*; M1 with an anterocone either undivided or divided at its top, but complete on the 3/4 of the crown height. In M1, ectolophs are absent in half of the specimens, weakly developed on the posterior surface of the anterocone and/or paracone in the other half of the specimens. The mesocone presents a triangular shape with a short mesoloph in 1/4 of the M1s, slightly more frequent in

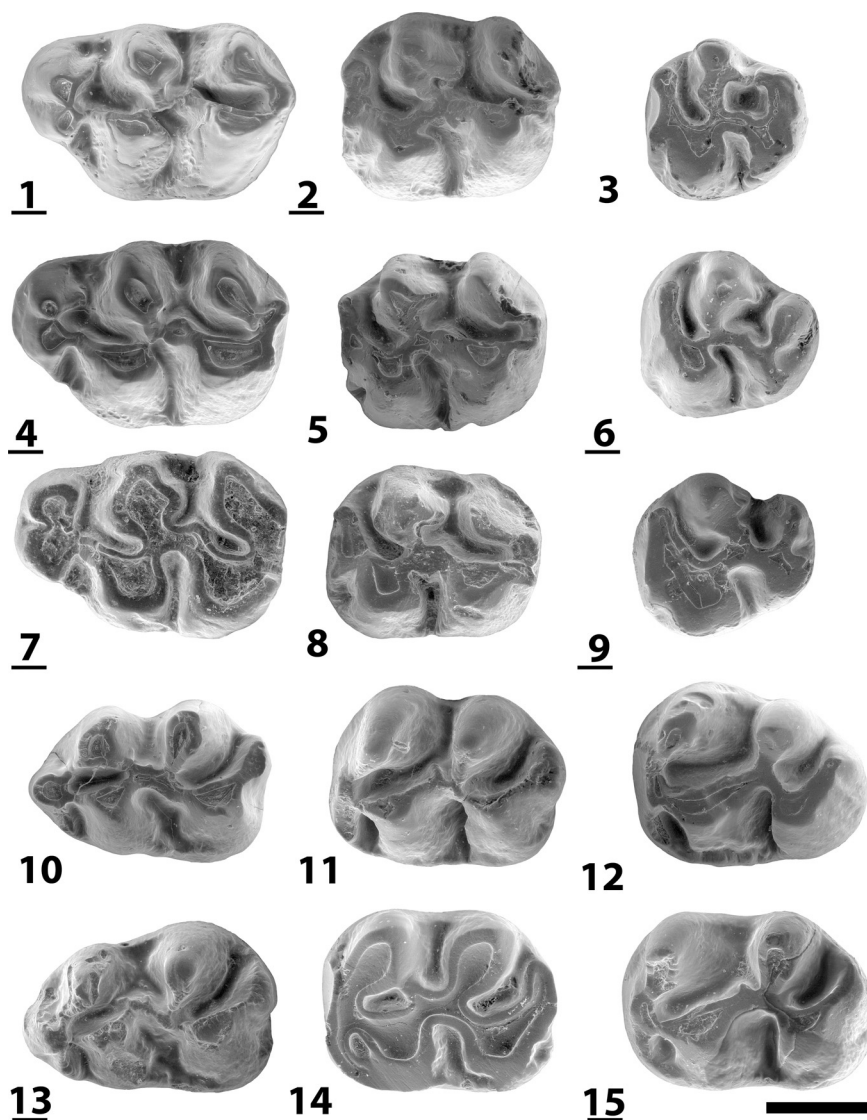


Fig. 2. *Cricetodon jotae* from Calatayud–Daroca. Upper molars. Manchones: **1**, inverted right M1, MA-2183; **2**, inverted right M2, MA-2199; **3**, left M3, MA-2213; **4**, inverted right M1, MA-2188; **5**, left M2, MA-2196; **6**, inverted right M3, MA-2220. Las Planas 5C: **7**, inverted right M1 LP5C-5; **8**, left M2, LP5C-8; **9**, inverted right M3, LP5C-11. Lower molars. Manchones: **10**, left m1, MA-2225; **11**, left m2, LP5C-2245; **12**, left m3, MA-2253. Las Planas 5C: **13**, inverted right m1, LP5C-19; **14**, left m2, LP5C-15; **15**, inverted right m2, LP5C-16.

Fig. 2. *Cricetodon jotae* de Calatayud–Daroca. Molaires supérieures. Manchones : **1**, M1 droite inversée, MA-2183 ; **2**, M2 droite inversée, MA-2199, **3**, M3 gauche, MA-2213, **4**, M1 droite inversée, MA-2188, **5**, M2 gauche, MA-2196 ; **6**, M3 droite inversée, MA-2220. Las Planas 5C : **7**, M1 droite inversée LP5C-5, **8**, M2 gauche, LP5C-8, **9**, M3 droite inversée, LP5C-11. Molaires inférieures. Manchones : **10**, m1 gauche, MA-2225 ; **11**, m2 gauche, LP5C-2245 ; **12**, m3 gauche, MA-2253. Las Planas 5C : **13**, m1 droite inversée, LP5C-19, **14**, m2 gauche, LP5C-15, **15**, m2 droite inversée, LP5C-16.

M2 and M3. The anterior surface of both the paracone and the metacone are notched by a vertical groove. The m1 has an undivided anteroconid; the metaconid has a posterior metalophulid in more than half of the specimens, double or only anterior for the other specimens. Mesolophid absent or rare in m1, more frequent in m2 and m3, but always short. M1 with four roots, and m2 with 2 roots, with the posterior one either with a double pulp cavity or divided at its extremity for about half of the specimens”.

Description of the studied material

M1. This molar has four roots. A shallow groove on the anterior wall divides the anterocone in two parts, but not covering the entire height of the cusp (Fig. 1.1; 1.4). The

anterolophule is disconnected in two teeth from ARM7 (Fig. 1.1). The protolophule is posteriorly directed; it is anterior in two specimens (1/5 in LUM21 and 1/5 in ARM7); it is present but disconnected in one specimen from LUM21. The anterior ectoloph is frequently absent (2/3 in VT2C; 3/4 in LUM21, and 2/4 in ARM7); it is composed by the posterior ectoloph of the anterocone (Fig. 1.1) in all teeth but one from VT2C, which is double, composed by the posterior ectoloph of the anterocone and the anterior ectoloph of the paracone. The anterior ectoloph is never complete. The posterior ectoloph is frequent (Fig. 1.4); it is absent only in LUM21 (1/4). It is always composed by the posterior ectoloph of the paracone, and never complete. The

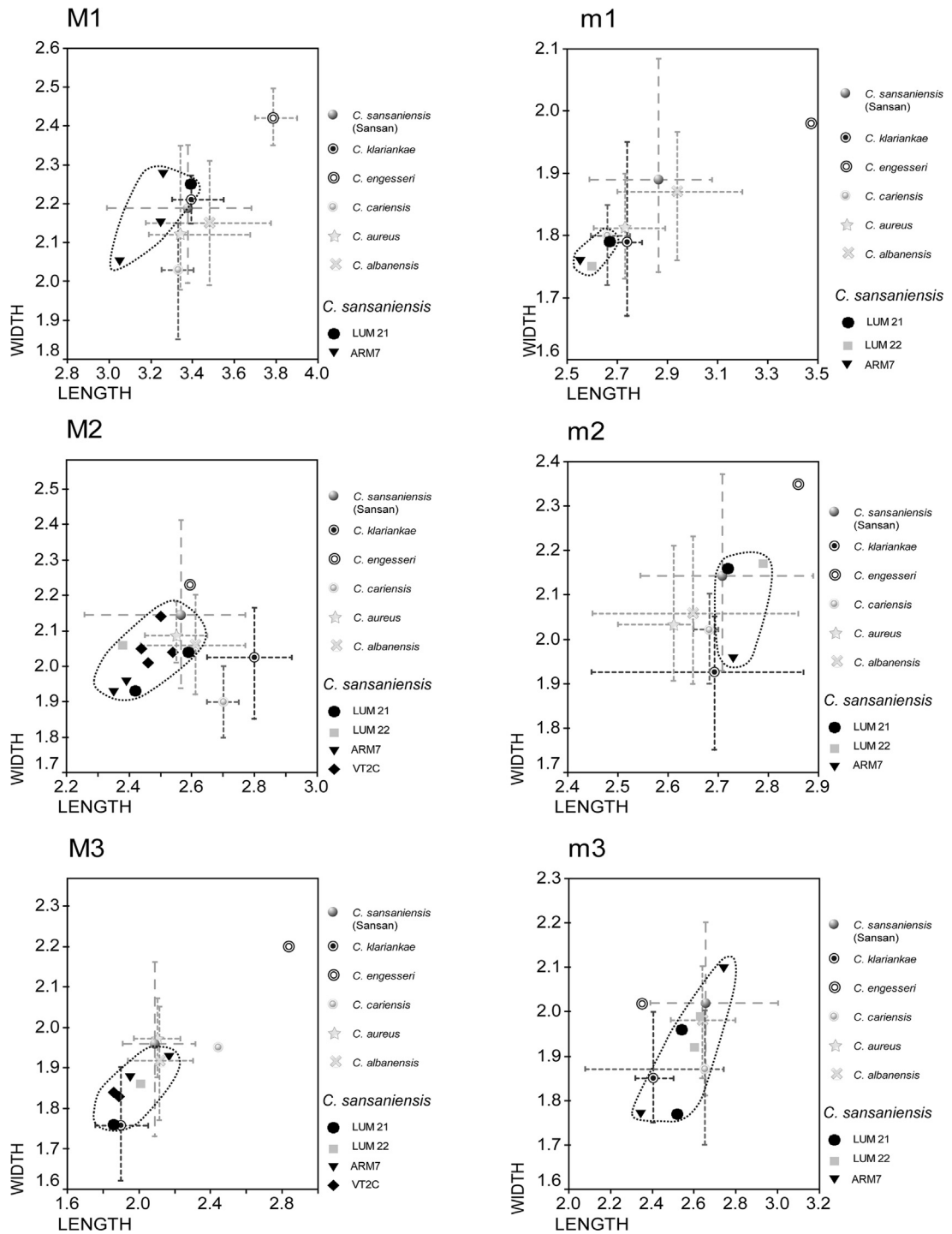


Fig. 3. Length and width scatter diagram of several large-sized species of *Cricetodon*. Dotted circles denote the range of *Cricetodon sansaniensis* from Calatayud-Daroca and dashed lines indicate the maximum and minimum values of the compared species in its type localities. Source of data: Mein and Freudenthal, 1971a (*Cricetodon albanensis*), 1971b (*Cricetodon aureus*); Sen and Ünay, 1979 (*Cricetodon cariensis*); Rummel and Kälin, 2003 (*Cricetodon engesseri*); Sen and Maridet, 2012 (*C. sansaniensis*).

Fig. 3. Diagramme de dispersion de la longueur et de la largeur de plusieurs espèces de *Cricetodon* de grande taille. Les cercles pointillés représentent la variabilité de *Cricetodon sansaniensis* de Calatayud-Daroca et les lignes en tiretés indiquent les mesures maximales et minimales des espèces par en fonction de leurs localités types. Source des données : Mein et Freudenthal, 1971a (*Cricetodon albanensis*), 1971b (*Cricetodon aureus*); Sen et Ünay, 1979 (*Cricetodon cariensis*); Rummel et Kälin, 2003 (*C. engesseri*); Sen et Maridet, 2012 (*C. sansaniensis*).

Table 3Length and width of the studied material of *Cricetodon sansaniensis*. Units are given in mm.**Tableau 3**Longueur et largeur du matériel de *Cricetodon sansaniensis* étudié. Les unités sont exprimées en mm.

	Locality	Length				Width			
		Min	Mean	Max	N	Min	Mean	Max	N
M1	ARM7	3.05	3.19	3.26	3	2.04	2.16	2.28	1
	LUM21		3.39		1	2.03	2.14	2.25	2
M2	VT2C	2.44	2.49	2.54	4	2.01	2.06	2.14	4
	ARM7	2.35	2.37	2.39	2	1.93	1.94	1.96	2
	LUM21	2.42	2.51	2.59	3	1.93	2.02	2.09	3
	LUM22		2.38		2	1.88	1.97	2.06	2
M3	VT2C	1.86	1.88	1.89	2	1.83	1.84	1.84	2
	ARM7	1.95	2.06	2.17	2	1.88	1.90	1.93	2
	LUM21	1.86	1.92	1.98	2	1.76	1.87	1.98	2
	LUM22		2.01		1		1.86		1
m1	VT2C				–		1.78		1
	VT2B				–	1.69	1.73	1.78	2
	ARM7		2.55		1		1.76		1
	LUM21		2.67		1		1.79		1
	LUM22		2.60		1		1.75		1
m2	ARM7		2.73		1		1.96		1
	LUM21		2.72		1	1.99	2.08	2.16	2
	LUM22		2.79		1		2.17		1
m3	VT2C				–		2.07		1
	VT2B				–	1.94	2.01	2.07	2
	ARM7	2.34	2.54	2.74	2	1.77	1.94	2.10	2
	LUM21	2.52	2.53	2.54	2	1.77	1.87	1.96	2
	LUM22	2.60	2.62	2.63	2	1.92	1.96	1.99	2

Min: minimum values; Max: maximum values; N: number of specimens.

mesoloph is mostly absent (Fig. 1.1); it is short (1/2 in VT2C and 1/4 in ARM7; Fig. 1.4) or reduced to an enlargement of the enamel, called incipient, (3/4 in ARM7 and 3/4 in LUM21). The anteroloph is open in one specimen from LUM21; closed by a cingulum (4/4 in ARM7; 3/4 in LUM21 and 1/3 in VT2C; Fig. 1.1; 1.4) or by a style (2/3 in VT2C). The mesoloph is open (1/4 in LUM21) or blocked by a cingulum (Fig. 1.1; 1.4). The sinus can be either open (3/4 in LUM21; 1/4 in ARM7; Fig. 1.4), closed by a cingulum (1/2 in VT2C; 1/4 in ARM7 and 1/4 in LUM21; Fig. 1.1) or blocked by a style (1/4 in ARM7 and 1/2 in VT2C).

M2. The anterior ectoloph is reduced (Fig. 1.5; 1.7) and, generally, lower than the anteroloph; it can be absent (1/3 in ARM7). The posterior ectoloph is composed by the posterior ectoloph of the paracone and it is not complete (Fig. 1.5; 1.7); it is rarely absent (1/2 in LUM22 and 1/3 in ARM7). The mesoloph is mostly absent (Fig. 1.5; 1.7); it can be short (1/4 in VT2C) or incipient (2/6 in LUM21 and 1/4 in VT2C). The labial posteroloph is always present and the lingual posteroloph is absent in LUM22 (2/2) and in 1/4 in VT2C. The anteroloph is always closed by a cingulum. The protosinus is weak but distinguishable in 1/7 in LUM21 (Fig. 1.7). The mesosinus, which is well developed, can be open (1/2 in LUM22; 2/6 in LUM21, and 3/3 in ARM7) or closed by a cingulum (4/4 in VT2C, 1/2 in LUM22 and 4/6 in LUM21; Fig. 1.5; 1.7). The sinus can be open (3/4 in VT2C; 1/2 in LUM22; 2/6 in LUM21, and 1/2 in ARM7; Fig. 1.5; 1.7) or closed, either by a cingulum (1/2 in LUM22; 4/6 in LUM21, and 1/2 in ARM7) or by a style (1/4 in VT2C).

M3. Both labial and lingual anterolophs are present, but the lingual branch is weaker than the labial one (Fig. 1.3; 1.6; 1.8). The anterior ectoloph is absent (Fig. 1.3; 1.6; 1.8). All specimens, except for 2/4 from ARM7 have a posterior ectoloph; it is formed by the posterior ectoloph of the paracone (2/4 ARM7; 1/3 in LUM21; 2/2 in LUM22, and 2/4 in VT2C; Fig. 1.3; 1.6; 1.8). The posterior ectoloph is composed by both the posterior ectoloph of the paracone and the anterior ectoloph of the metacone in some cases (1/4 in LUM21 and 2/4 in VT2C); it is absent in two out of four specimens from ARM7. The posterior ectoloph is complete in two molars (1/4 in VT2C and 1/4 in LUM21). Most of the specimens have a mesoloph; it is absent in two teeth (1/5 in VT2C and 1/2 in LUM22). The length of the mesoloph is variable; it can be short (1/5 in VT2C and 3/4 in ARM7; Fig. 1.8), about half the distance between longitudinal ridge and labial border (3/5 in VT2C; 2/4 in LUM21, and 1/4 in ARM7; Fig. 1.3), or reaching the labial border (1/2 in LUM22 and 2/4 in LUM21; Fig. 1.6). An enamel-coated valley can be present (1/4 in VT2C; 1/2 in LUM22 and 2/4 in LUM21). The axioloph is disconnected (2/3 in VT2C) or continuous (Fig. 1.3; 1.6; 1.8). The labial posteroloph is well developed but short and it is never connected to the metalophule or the metacone (Fig. 1.3; 1.6; 1.8); it is absent in 2/4 specimens from LUM21.

m1. Only a metalophulid I is found in some specimens (1/2 in LUM2; 1/3 in LUM22; Fig. 1.9; 1.12); both metalophulids, I and II, are present together in the remaining teeth. The metalophulid I is incomplete in one case (LUM21; Fig. 1.9). The mesolophid is rare; only three teeth from

LUM21 have one; they are incipient (Fig. 1.9), short and medium, respectively. The ectomesolophid is present in one specimen from LUM22. The entoconid spur and the labial posterolophid are absent. The mesosinusid can be open or blocked; it is closed by a low cingular ridge (1/2 in VT2C and 1/3 in LUM22; Fig. 1.9) or by a stylid (1/2 in VT2B). The sinusid is blocked by a cingular ridge (2/2 in VT2C; 1/2 in VT2B; in ARM7 and 2/3 in LUM21) or it remains open (Fig. 1.9; 1.12). The posterosinusid is blocked by a cingular ridge in one specimen (1/2 in VT2B); it is open in the rest of the teeth.

m2. The labial branch of the anterolophid is well developed and it reaches the protoconid (Fig. 1.10; 1.13). Only the tooth from ARM7 possesses a lingual anterolophid. A short mesolophid (Fig. 1.10; 1.13) is usually present; it is absent in one tooth. In some specimens (4/5 in LUM21), the mesolophid is curved and projected towards the metaconid, reaching it. One specimen from LUM22 shows an ectomesolophid (Fig. 1.13). There is no anterosinusid and the mesosinusid is always blocked by a cingular ridge. The sinusid is blocked by a cingulid; in one out of four teeth from LUM21, this cingular ridge is split in two crests. The lingual posterosinusid is open (2/2 in LUM22 and 2/4 in LUM21), blocked by a cingular ridge (2/4 in LUM21), or by the joint of the lingual posterolophid and the entoconid (1/1 in ARM7).

m3. The labial branch of the anterolophid is long and it reaches the protoconid (Fig. 1.11; 1.14). The lingual branch of the anterolophid is present in two out of four molars from LUM21. The mesolophid can be short (1/4 in VT2C; 1/3 in VT2B; 1/2 in LUM22; 3/5 in LUM21, and 2/2 in ARM7; Fig. 1.14) or have medium length (2/4 in VT2C; 1/2 in LUM22, and 1/5 in LUM21; Fig. 1.11). In two fossils (1/3 in VT2B and 1/5 in LUM21) the mesolophid is double and short. In one tooth (1/3 in LUM22) it is connected with the metaconid, being absent in the remaining specimens (1/4 in VT2C and 1/3 in VT2B). The lingual posterolophid can be constricted behind the hypoconid (Fig. 1.11); its lingual part is cuspidate and displays a weak valley on the posterior wall. The sinusid is blocked, in most cases, by a low cingular ridge or by a stylid (1/2 in VT2B); it remains open in two specimens (1/2 in VT2B and 1/2 in LUM21; Fig. 1.11; 1.14). The mesosinusid is open or blocked by a low cingular ridge. A cingulid is also present at the end of the lingual posterosinusid (1/2 in LUM22 and 1/4 in LUM21). The lingual posterolophid projects towards the entoconid in some teeth (2/2 in VT2C; 2/2 in VT2B; 2/2 in ARM7, and 1/4 in LUM21). In the remaining specimens (1/2 in LUM22 and 2/4 in LUM21), the lingual posterosinusid is open (Fig. 1.11; 1.14).

Discussion

The described specimens fit within the size range of *C. sansaniensis* Lartet, 1851 (Fig. 4), one of the largest species of *Cricetodon* recovered until now. However, the measurements of the m1 are slightly smaller than the mean value of those from Sansan (Fig. 3). The incompletely divided anterocone, the presence of anterior ectoloph, the labially curved anterior ectoloph, and the poorly developed or absent posterior ectoloph on the M1 are characteristic traits of *C. sansaniensis* from Sansan (Baudelot, 1972; Maridet and Sen, 2012). These characters

are also found in the studied fossils. In addition, the large mesoloph of the M3 and the presence of metalophulid I and II together in the m1 are features commonly found in the specimens from Sansan (Baudelot, 1972; Maridet and Sen, 2012) and also present in the Calatayud–Daroca Basin. The studied material has no lingual spur of the anterolophule, neither two crests at the edge of the anterosinusid and mesosinusid of the M1, and the material from Sansan has both structures. Apart from that, one of the m1 from LUM22 displays ectomesolophid, whereas this feature is shown by 11 out of 29 specimens from Sansan (Maridet and Sen, 2012); nevertheless, the relative frequency of this character in both areas cannot be compared due to the small sample size of the assemblages from Calatayud–Daroca with respect to that from Sansan.

Part of the studied material were already cited in the Calatayud–Daroca Basin, that from ARM7 as *Cricetodon* cf. *sansaniensis* in Freudenthal (1966) and Mein and Freudenthal (1971a), and the molars from VT2C and VT2B as *Cricetodon* sp. in Daams and Freudenthal (1981). The fossils from LUM21 and LUM22 are described and assigned for the first time. *Cricetodon sansaniensis* is widespread across the central and southwestern European basins. Apart from Sansan and the localities of the present study, it has recorded in another five fossil sites (Bolliger, 1994; Ginsburg and Bulot, 2000; Kälin and Kempf, 2009; Sach, 1999). Besides, *Cricetodon* cf. *sansaniensis* has been reported 12 times in the literature (Bolliger, 1994; García Moreno, 1988; Ginsburg and Bulot, 2000; Kälin and Kempf, 2009; Rummel, 2000; Rummel and Kälin, 2003; Sach, 1999; Seehuber, 2008), although some of them might be not refer to *C. sansaniensis*. The type locality, Sansan, has been biostratigraphically correlated to Niderwis, Nord Alpine Foreland Basin, Switzerland (14.1 Ma; Kälin and Kempf, 2009). Apart from Niderwis, *C. sansaniensis* is recorded in other Swiss localities from the local biozone Öschgraben ranging from 14.2 Ma to 14.1 Ma (Kälin and Kempf, 2009); therefore, the oldest known record is from Switzerland. The youngest known record of the species is uncertain. The assignment to *C. sansaniensis* of the fossils described by García Moreno (1988) in the *Megacricetodon lopezae* zone from the Duero Basin (~local biozone G in Calatayud–Daroca Basin) is questionable and the specimens are under revision. Not considering the Duero record, the youngest occurrence is in the Calatayud–Daroca Basin, in which *C. sansaniensis* is present in the biozone F, between 13.76 Ma and 13.68 Ma (Daams et al., 1999; Van Dam et al., 2006).

C. sansaniensis from the Calatayud–Daroca Basin has some character states (such as weak ectolophs and both metalophulids, I and II, on the same m1, and mesolophids) which places it among the basal representatives of the tribe according to the trends described for Cricetodontini (Agustí, 1982; De Bruijn et al., 1993; Hír, 2007; Maridet and Sen, 2012).

Due to its large size, *C. sansaniensis* has been included by some authors (Mein and Freudenthal, 1971a; Maridet and Sen, 2012) in the anagenetic lineage *C. aureus*–*C. sansaniensis*–*Cricetodon albanensis*. According to Mein and Freudenthal (1971a), *Cricetodon albanensis* has been considered the descendant of *C. aureus* because it possesses

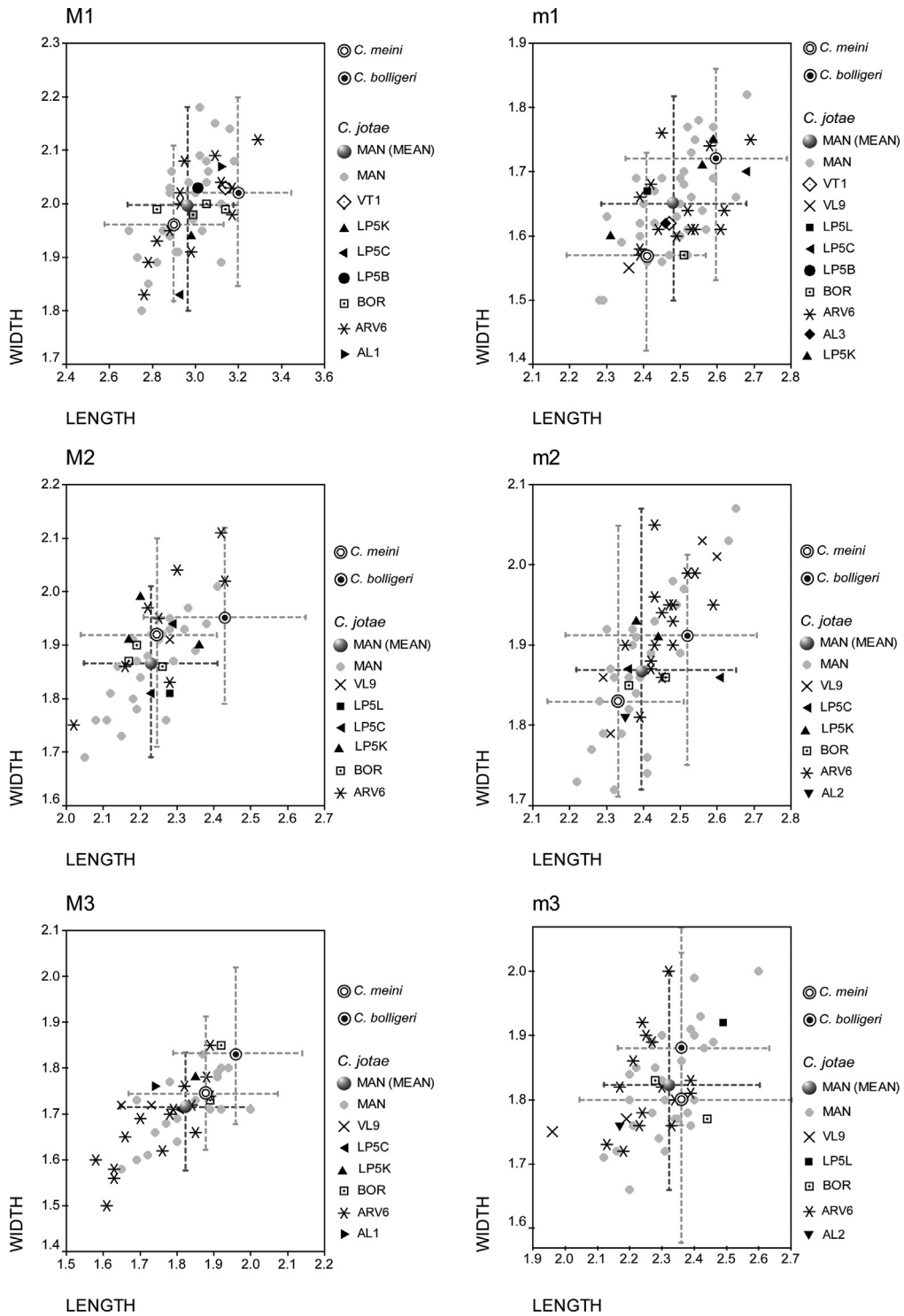


Fig. 4. Length and width scatter diagram of *Cricetodon jotae* from Calatayud–Daroca (including all specimens), *Cricetodon meini* from Vieux-Collonges and *Cricetodon bolligeri* from Petersbuch 10. Dashed lines indicate the maximum and minimum values of the compared species in its type localities. Source of data: Mein and Freudenthal, 1971b (*C. meini*), Rummel, 2001 (*C. bolligeri*).

Fig. 4. Diagramme de dispersion de la longueur et de la largeur de *Cricetodon jotae* de Calatayud–Daroca (incluant tous les échantillons), *Cricetodon meini* de Vieux-Collonges et *Cricetodon bolligeri* de Petersbuch 10. Les lignes pointillées indiquent les mesures maximales et minimales pour les espèces comparées à leurs localités types. Source des données : Mein et Freudenthal, 1971b (*C. meini*), Rummel, 2001 (*C. bolligeri*).

more developed ectolophs and has metalophulids I more frequently. Agustí (1982) proposed *C. sansaniensis* from ARM7 as the ancestor of *Hispanomys lavocati* from the Vallès-Penedès Basin (named by this author as *Cricetodon* (*Pararuscinomys*) *lavocati*). He supported this hypothesis in the large size of both species, but since then, many other large-sized species of Cricetodontini (such as *C. soriae* and *Cricetodon engesseri*) have been described and they have to be taken into consideration in any further phylogenetic analysis.

C. jotae Mein and Freudenthal, 1971

Figs. 2, 4; Tables 1, 4

Type locality: Manchones, Calatayud–Daroca Basin, Spain, local biozone G2, (MN6 Upper Aragonian, Middle Miocene).

Stratigraphical distribution in the Calatayud–Daroca Basin: local biozone G1–local biozone G3 (MN6–MN7/8, Upper Aragonian, Middle Miocene). FO: LP5B (13.56 Ma); LO: TOR1.

The morphology of the material from the Calatayud–Daroca Basin is described below.

Studied Material: See Table 1.

Measurements: See Table 4.

Original Diagnosis translated from Mein and Freudenthal (1971a:18): “[Bigger than *C. meini*; the posterior metalophulid is less frequent than in *C. meini*, the anterior metalophulid, however, is more frequent; the ectolophs are better developed, but none of them forms a complete connection]”.

Emended Diagnosis: The upper molars show poor development of the mesolophs and posterolophs. The anterior ectoloph of the M1 can be composed by the anterior ectoloph of the paracone or by the posterior ectoloph of the anterocone. The M1 always has a posterior ectoloph, composed by the posterior ectoloph of the paracone, by the anterior ectoloph of the metacone, or by both. The ectolophs are not complete. The lingual posteroloph is common, but short. The main valleys are frequently blocked by cingula and styles. The lower molars have short or absent mesolophids, ectomesolophids and lingual anterolophids. Most of the m1 display a metalophulid I and a metalophulid II together in the same specimen, but some m1 have only a metalophulid I or a metalophulid II. The m2 possesses two or three roots; the posterior root can be either partially or completely split.

Differential Diagnosis: Differs from *Cricetodon caucasicus* Argyropulo, 1938; *Cricetodon versteegi* De Bruijn et al., 1993; *Cricetodon tobieni* De Bruijn et al., 1993; *Cricetodon aliveriensis* Klein Hofmeijer and De Bruijn, 1988 and *Cricetodon kasapligili* De Bruijn et al., 1993 in the larger size of all elements. Apart from that, *C. caucasicus* has a non-divided anterocone; *C. versteegi* backwards directed sinusids; *C. tobieni* and *C. aliveriensis* more developed anterolophs on the M2 and *C. kasapligili* does not have metalophulid I in the m1.

Differs from *C. engesseri* Rummel and Kälin, 2003; *C. soriae* López Martínez et al. in Hernández Fernández et al., 2006; *Cricetodon hungaricus* (Kordos, 1986); *Cricetodon jumaensis* Rummel, 2001; *Cricetodon* *klariankae* Hír, 2007; *C. albanensis* Mein and Freudenthal, 1971a; *C. sansaniensis*

Lartet, 1851 and *C. aureus* Mein and Freudenthal, 1971b in the smaller size of all elements. Additionally, *C. engesseri* possess a developed posterolophid on the M3; *C. albanensis* does not have metalophulid II; *C. jumaensis* and *C. sansaniensis* display a more basal pattern on the m3, with larger mesolophids. *Cricetodon klariankae* was originally ascribed to *Cricetodon* but recently its generic assignation was questioned (Prieto et al., 2014); it possesses a posterior ectoloph of the M1 mostly double and it is complete; *C. aureus* has metalophulids II without metalophulid I more frequently than *C. jotae*.

Differs from *Cricetodon pasalarensis* (Tobien, 1978) in: anterocone divided by a groove that covers the entire height of the crown; presence of anterior ectoloph; absence of roughness on the basis of the hypocone and the absence of lingual anterolophid in the m3. Differs from *C. candirensis* (Tobien, 1978); *C. cariensis* (Sen and Ünay, 1979) and ‘*Cricetodon*’ *fandli* Prieto et al., 2010 in: ectolophs not complete; absence of enamel-coated valley; presence of non-interrupted metalophulid I. Differs from *C. boligeri* Rummel, 1995 in: absence of ectomesolophid and thick stylids on the m1; anterolophule always connected to the anteroconid on the m1 and the poor development of the mesolophid on the m3. Differs from *C. meini* Freudenthal, 1963 in: absence of neo-entoloph and less-developed mesoloph on the M3. Differs from *C. wanhei* Qiu, 2010 in: absence of neo-entoloph on the M3; forwards directed hypolophulid on the m1. Differs from *C. volkeri* Wu et al., 2009 in: absence of labial spur of the anterolophule; anterocone well divided and short posteroloph on the M1; absence of neo-entoloph on the M3.

Description of the material from the type locality Manchones

M1. This molar has four roots. The anterocone shows a furrow which reaches the base of the crown (Fig. 2.1; 2.4). A posterior protolophule connects the paracone with the posterior branch of the protocone. The anterior ectoloph is frequent (21/27); it is formed by the anterior ectoloph of the paracone in one tooth or by the posterior ectoloph of the anterocone (20/27; Fig. 2.1; 2.4). One specimen has a well-developed anterior ectoloph reaching the paracone. All the fossils have posterior ectoloph; the posterior spur of the paracone is always present (Fig. 2.1; 2.4) and in three out of 29 cases it is associated with the anterior spur of the metacone. None of the fossils have the posterior ectoloph complete. The mesoloph is short (9/23), highly reduced (6/23; Fig. 2.4) or absent (8/23; Fig. 2.1). A ridge-like structure is developed in the anterior wall of the protocone (14/24); it is absent in the remaining specimens (Fig. 2.1; 2.4). The labial posteroloph is quite thin but well delimited; it can be absent (4/27). Most molars possess a lingual posteroloph (18/27; Fig. 2.4). The anterosinus is closed by a cingulum (20/24), being low in one tooth (Fig. 2.1; 2.4), and remaining open in three specimens. The mesosinus is blocked by a cingulum (17/23; Fig. 2.1; 2.4), by a low cingulum (2/23) or it is open (4/23). Several specimens display an open sinus (18/24; Fig. 2.1; 2.4); it is closed by a cingulum (5/24) or by two crests (1/24). The protosinus can be blocked by a style (5/28) or by a cingulum (22/28) and it remains open in one specimen.

Table 4Length and width of the studied material of *Cricetodon jotae*. Units are given in mm.**Tableau 4**Longueur et la largeur du matériau étudié de *Cricetodon jotae*. Les unités sont exprimées en millimètres.

	MN zone	Local biozone	Locality	Length				Width			
				Min	Mean	Max	N	Min	Mean	Max	N
M1	MN7/8	G3	TOR1	2.62	2.80	2.89	3	1.82	1.87	1.92	3
	MN7/8	G3	AC1		3.12		1		2.07		1
	MN7/8	G3	VL9		2.95		1				–
	MN6	G2	ARV6	2.76	2.99	3.29	13	1.83	1.98	2.12	16
	MN6	G2	LP5K		2.98		1	1.94	2.01	2.07	2
	MN6	G2	BOR	2.82	3.00	3.14	4	1.98	1.99	2.00	4
	MN6	G2	MAN	2.69	2.94	3.18	19	1.80	1.99	2.18	19
	MN6	G1	VT1		3.14		1		2.03		1
	MN6	G1	LP5C		2.93		1	1.82	1.87	1.97	3
MN6	G1	LP5B		3.01		1	1.83	1.93	2.03	2	
M2	MN7/8	G3	TOR1	2.19	2.23	2.27	2	1.95	1.96	1.97	2
	MN7/8	G3	VL9		2.28		1		1.91		1
	MN6	G2	ARV6	2.02	2.26	2.43	8	1.71	1.92	2.11	9
	MN6	G2	LP5K	2.17	2.24	2.36	3	1.90	1.93	1.99	3
	MN6	G2	LP5L		2.28		1		1.81		1
	MN6	G2	BOR	2.17	2.21	2.26	3	1.86	1.88	1.90	3
	MN6	G2	MAN	2.05	2.23	2.41	8	1.69	1.87	2.01	8
	MN6	G1	LP5C	2.23	2.26	2.29	2	1.81	1.88	1.94	2
M3	MN7/8	G3	TOR1		2.55		1		1.73		1
	MN7/8	G3	AC1		1.74		1		1.76		1
	MN7/8	G3	VL9	1.65	1.69	1.73	2		1.72		2
	MN6	G2	ARV6	1.58	1.75	1.89	15	1.50	1.67	1.85	15
	MN6	G2	LP5K		1.85		1		1.78		1
	MN6	G2	BOR	1.89	1.90	1.92	2	1.73	1.79	1.85	2
	MN6	G2	MAN	1.65	1.83	2	18	1.58	1.71	1.83	18
	MN6	G1	LP5C		1.81		1		1.71		1
m1	MN7/8	G3	TOR1	1.67	1.76	1.86	3	1.68	1.73	1.80	3
	MN7/8	G3	AC3		2.46		1		1.62		1
	MN7/8	G3	AC2				–		1.66		1
	MN7/8	G3	VL9		2.36		1		1.55		1
	MN6	G2	ARV6	2.39	2.50	2.69	14	1.57	1.65	1.76	15
	MN6	G2	LP5K	2.31	2.49	2.59	3	1.60	1.69	1.75	4
	MN6	G2	LP5L		2.41		1		1.67		1
	MN6	G2	BOR	2.45	2.48	2.51	2	1.57	1.64	1.71	3
	MN6	G2	MAN	2.28	2.48	2.68	35	1.50	1.65	1.82	35
	MN6	G1	VT1		2.47		1		1.62		1
	MN6	G1	LP5C		2.68		1		1.70		1
	m2	MN7/8	G3	TOR1		2.46		1		1.83	
MN7/8		G3	AC2		2.35		1	1.81	1.88	1.95	2
MN7/8		G3	AC1				–		2.02		1
MN7/8		G3	VL9	2.29	2.44	2.60	4	1.79	1.92	2.03	4
MN6		G2	ARV6	2.35	2.46	2.59	17	1.78	1.92	2.05	18
MN6		G2	LP5K	2.38	2.41	2.44	2	1.91	1.92	1.93	2
MN6		G2	BOR	2.36	2.41	2.46	2	1.85	1.86	1.86	2
MN6		G2	MAN	2.22	2.39	2.65	27	1.71	1.87	2.07	28
MN6		G1	LP5C	2.36	2.49	2.61	2	1.86	1.87	1.87	2
m3		MN7/8	G3	TOR1	2.24	2.32	2.39	2	1.76	1.83	1.89
	MN7/8	G3	AC2		2.17		1		1.76		1
	MN7/8	G3	VL9	1.96	2.08	2.19	2	1.75	1.76	1.77	2
	MN6	G2	ARV6	2.13	2.27	2.39	15	1.69	1.82	2.00	16
	MN6	G2	LP5L		2.49		1		1.92		1
	MN6	G2	BOR	2.28	2.36	2.44	2	1.77	1.80	1.83	2
MN6	G2	MAN	2.12	2.32	2.60	10	1.66	1.82	2.00	10	

Min: minimum values; Max: maximum values; N: number of specimens.

M2. The anterior ectoloph is reduced and generally lower than the anteroloph; it is absent in 12 out of 31 teeth (Fig. 2.2; 2.5). The posterior ectoloph is always present; it is simple and not connected to the metacone (Fig. 2.2; 2.5). The mesoloph is frequently absent (17/28; Fig. 2.2; 2.5), but it can be incipient (11/28). The protocone bears a spine in

most molars (18/20). The entomesoloph is found in only one out of eleven cases. The labial posteroloph is common (26/27; Fig. 2.2; 2.5), as well as the lingual posteroloph (18/23; Fig. 2.5). The well-developed mesosinus is closed by a cingulum in 21 out of 25 specimens (Fig. 2.2; 2.5); it is open in four. The sinus is open in 23 out of 33 specimens

(Fig. 2.2; 2.5). The protosinus is always weak but distinguishable (Fig. 2.2; 2.5).

M3. It has reduced hypocone. The lingual anteroloph is distinguishable but weak in 13 out of 18 cases (Fig. 2.3). A well-developed labial anteroloph is displayed in 15/18 molars. The anterior ectoloph is absent. The posterior ectoloph is always present; it is formed by both posterior ectoloph of the paracone and anterior ectoloph of the metacone (9/16; Fig. 2.3) or only by the posterior ectoloph of the paracone (Fig. 2.6). In six specimens the posterior ectoloph is complete (Fig. 2.3). Six out of nine teeth have mesoloph; it is short in five teeth and long, reaching the labial border, in one. The axioloph is continuous. Most M3 possess a posteroloph (14/18); it is usually weak and short (Fig. 2.6), and ends free. The sinus is long, curved and mostly directed forwards, although it is transversal in one specimen.

m1. The labial anterolophid is a well-developed ridge displayed by most m1 (30/33); it can be connected to the protoconid (10/33), or not (20/33; Fig. 2.10). Metalophulid I is found in eight out of 37 teeth, and metalophulid II in five. Twenty-three out of 37 specimens show both metalophulids, I and II (Fig. 2.10). Only one incipient mesolophid is observed. The ectomesolophid is barely present (2/23); one of them is incipient and the other one is a long crest. Some protoconids bear a spur. The entoconid spur and the labial posterolophid are absent. The hypolophulid is directed forwards (Fig. 2.10). The mesosinusid is closed by a cingular ridge (11/35), by a stylid (1/35), or it remains open (23/35; Fig. 2.10). The sinusid is wide and short and it is slightly directed forwards (Fig. 2.10); it can be blocked by a low cingular ridge (26/34), by two crests attached to the hypoconid and the protoconid (3/34), or by a stylid (2/34). The sinusid remains open in three teeth. The posterosinusid is blocked by a cingular ridge (4/27) or it is open (Fig. 2.10).

m2. This molar shows two (3/9) or three roots (4/9), the posterior one being partially split in two out of four specimens, and completely split in the other two. The lingual anterolophid is found in only three teeth (3/31); it is short and does not reach the metaconid in two of them. The mesolophid is present in 20 out of 33 fossils and it is mostly short (13/20; Fig. 2.11); it can be curved and projected towards the metaconid, reaching it in two out of twenty specimens. A short and isolated crest is placed near the mesolophid in five out of twenty molars. There is no anterosinusid and the mesosinusid is blocked by a cingular ridge (9/32) or it remains open (Fig. 2.11). In most of the teeth, the sinusid is closed by a cingulid (19/31); it can be blocked by two crests attached to the hypoconid and the protoconid (2/31), by a stylid (1/31), or it can remain open (9/31; Fig. 2.11). The lingual posterosinusid can be blocked by a cingular ridge (5/25) or the lingual posterolophid can be directly connected to the entoconid (7/25); it is open in 13 out of 25 specimens (Fig. 2.11).

m3. The labial branch of the anterolophid is long and it reaches the protoconid (25/27). In two teeth, the anterolophid is extended through the basis of the protoconid towards the sinusid. The lingual branch of the anterolophid is mostly absent (Fig. 2.12); two out of ten specimens have it, but without reaching the metaconid. The mesolophid is barely present (8/28; Fig. 2.12); it is short (7/28) or long (1/28), but it does not exceed the half length

of the mesosinusid (medium). The lingual posterolophid is large and extends towards the entoconid. The anteriorly directed hypolophulid is connected to the anterior branch of the hypoconid (Fig. 2.12). The sinusid is open (17/27) or blocked by a cingulum (10/27; Fig. 2.12). The mesosinusid is mostly open (27/29), but it is closed by a cingulum in two teeth. The lingual posterosinusid is open (20/28; Fig. 2.12) or blocked by the lingual posterolophid that projects towards the entoconid closing it.

***Cricetodon jotae* from other sites in the Calatayud–Daroca Basin**

C. jotae is a species commonly present in the Calatayud–Daroca Basin but despite the abundance of fossils of this species, detailed morphometric descriptions have been never presented in a systematic study. Here we offer the morphology of the rest of the assemblages of *C. jotae* found in the Calatayud–Daroca Basin in order to know all the intraspecific variability of the species. The fossils of *C. jotae* are homogeneous in morphology and size (Fig. 4; Table 4). However, there is certain degree of variability in several features that are absent in the type locality, which are the following grouped by element:

- M1: The anterior ectoloph is composed by the posterior ectoloph of the anterocone and the anterior ectoloph of the paracone in ARV6 (2/15). Three localities have molars without a posterior ectoloph of the paracone: BOR (1/5), ARV6 (8/17) and TOR1 (1/4). A labial spur of the anterolophule is shown in LP5B (1/2) and TOR1 (1/3). The mesoloph is short in all the localities except for LP5K, where it can be long (1/2). A style is present at the edge of the mesosinus in BOR (2/5), ARV6 (1/17) and TOR1 (1/3), and at the sinus in BOR (1/5), LP5K (1/2), ARV6 (4/6), VILL9, ALC1 and TOR1 (1/3). The protosinus is blocked by two crests in LP5K (1/2) and ARV6 (1/16);
- M2: The posterior ectoloph is absent in BOR (1/3) and ALC3, and a style is blocking the mesosinus in LP5C (1/2);
- M3: The posterior ectoloph of the paracone is absent in a specimen from ARV6 (1/13). The mesoloph exceeds the half of the length of the mesosinus, but it does not reach the labial border in ARV6 (2/13). The mesoloph and ectoloph can be connected in BOR (1/2), and the neo-entoloph is found in ARV6 (1/13) and in the only M3 from ALC1;
- m1: The lingual anterolophid is present and reaches the metaconid in LP5K (1/4), ARV6 (1/15), and ALC3. The mesolophid is short in specimens from BOR (1/4), ALC2 (2/3) and TOR1 (1/2);
- m2: The labial anterolophid is short or absent in two out of twenty m2 from ARV6; rarely, the mesolophid exceeds the half of the length of the mesosinusid, but without reaching the labial border, in ARV6 (2/21); the ectomesolophid is present but incipient in ARV6 (2/21) and VILL9 (1/4). The sinusid is closed by a stylid and a crest attached to the hypoconid in ARV6 (1/20);
- m3: The lingual anterolophid is present in one out of 17 cases from ARV6. The mesolophid is connected to the metaconid in ARV6 (1/20) and is double in BOR (1/20). The sinusid is closed by a cingulid in LP5B (1/2), BOR (1/2), LP5L, ARV6 (1/19) and in ALC2 (1/2); closed by two crests

in ARV6 (1/19) and in VILL9 (1/2); and a stylid is shown in ARV6 (1/19) and in TOR1 (1/3).

The scatter diagrams (Fig. 4) show a large overlap in the distributions of the measurements among the studied sites, suggesting a similar size of the fossils of *C. jotae* in the Calatayud–Daroca Basin.

Discussion

Cricetodon from Manchones was firstly described by Freudenthal (1963) as *C. meini*. A few years later, in 1966, he improved this study providing new measurements and descriptions of the fossils from that locality. The last study of the type assemblage is presented in the revision of the rodent faunas of the Caenozoic made by Mein and Freudenthal (1971a). They described a new species, *C. jotae* Mein and Freudenthal, 1971a in the material from Manchones and Arroyo de Val 6. The authors refer to Freudenthal's studies (1963 and 1966) for the metrical information and the comparison with other species is shortly described.

Outside the Calatayud–Daroca Basin, *C. jotae* is also registered in two Portuguese localities, Povóia do Santarem and Chloes (MN6; Antunes and Mein, 1977), as well as in the French locality of La Grive L7 (MN7; Mein and Freudenthal, 1971a). It is nowhere else recorded, thus the geographical range of *C. jotae* is restricted to the southwestern Europe.

Morphologically, *C. jotae* displays characters, such as the metalophulid II, which are considered basal for the tribe Cricetodontini (Mein and Freudenthal, 1971a), and also has features such as: absence of mesolophids; presence of double ectolophids; low-developed or absent mesolophids; absence of ectomesolophid and weak or absent labial anterolophid of the m1, defined as derived by many authors (Agustí, 1982; López-Antoñanzas and Mein, 2009). This mosaic distribution of the characters, combining derived and basal traits, was described in other species of Cricetodontini from the late Aragonian like *Hispanomys aguirrei* (Sesé Benito, 1977) and *Cricetodon nievei* López-Guerrero et al., 2014.

Only few authors have discussed the phylogenetic relationships of *C. jotae*. Mein and Freudenthal (1971a) suggested that *C. jotae* could be related with *C. meini*. The evolutionary trends that they described are: an increase of the hypsodonty and the development of the ectolophids. On the other hand, according to Agustí (1982), *Hispanomys aguirrei* could be the descendant of *C. jotae*, assuming a development which resulted in more-developed ectolophids, increased hypsodonty and the reduction of the cingular formations (Agustí, 1982).

Due to the above referred mosaic-type morphology of *C. jotae* and *H. aguirrei*, it is difficult to establish their phylogenetic relationships. A cladistic analysis could be used to evaluate them, but is considered outside the scope of the present paper.

C. nievei López-Guerrero, Álvarez-Sierra, García-Paredes and Peláez-Campomanes, 2014.

The most important features of *C. nievei* are: the thick enamel; the presence of styles on the protosinus of the M1; the moderate development of the ectolophids—being incomplete in most specimens—; the moderately simple

pattern of the M3; the presence of metalophulid I on the m1 and absence of metalophulid II; the presence of ectomesolophid, and the moderately reduced m3

Type locality: Toril 3A, Calatayud–Daroca Basin, Spain local biozone G3 (MN7/8, Upper Aragonian, Middle Miocene).

Stratigraphical distribution in the Calatayud–Daroca Basin: Local biozone G3 (MN7/8, Upper Aragonian, Middle Miocene). FO: TOR3A/3B (12.65 Ma); LO: LP5H (12.60 Ma)

Detailed morphological descriptions are in López-Guerrero et al., 2014

Hispanomys Mein and Freudenthal, 1971

Hispanomys aguirrei (Sesé Benito, 1977) in López-Martínez et al., 1977.

H. aguirrei presents features such as: anterior ectoloph frequently double and complete, but also there are ectolophs simple and not complete; posterior ectoloph frequently complete and composed by both anterior ectoloph of the metacone and posterior ectoloph of the paracone; mesoloph in the upper molars almost absent; frequently presence of posteroloph in the M3, which is well developed in some specimens; presence of metalophulid I and II together in the same m1 or only the metalophulid I; mesolophid and ectomesolophid highly reduced or absent, and three-rooted m2.

Type locality: Escobosa de Calatañazor, Duero Basin, Spain (MN7/8, Upper Aragonian, Middle Miocene).

Stratigraphical distribution in the Calatayud–Daroca Basin: Local biozone G3 (MN7/8, Upper Aragonian, Middle Miocene). FO: PJE1 (12.39 Ma); LO: CARR (11.33 Ma).

Morphological descriptions of the material from Calatayud–Daroca Basin are in López-Guerrero et al., 2008.

Hispanomys lavocati (Freudenthal, 1966)

The most important features of *H. lavocati* are: well-developed ectolophids; frequently composed by both anterior and posterior ectolophids and connected; posterior ectoloph on the M3 usually starting from the protolophule instead of from the paracone; axioloph interrupted in several M3; absent metalophulid II in the m1, and m2 always three-rooted.

Type locality: Hostalets de Pierola, Vallés-Penedés Basin, Spain (MN7/8, Upper Aragonian, Middle Miocene).

Stratigraphical distribution in the Calatayud–Daroca Basin: local biozone G3, (MN7/8, Upper Aragonian, Middle Miocene). FO: NOM2 (11.87 Ma); LO: NOM4 (11.80 Ma).

Morphological descriptions of the material from Calatayud–Daroca Basin are in López-Guerrero et al., 2008.

Hispanomys nombrevillae (Freudenthal, 1966)

The most important features of *H. nombrevillae* are: four-rooted M1; anterior ectoloph always present, always complete and mainly composed by the posterior ectoloph of the anterocone; anterior ectoloph composed mainly by the anterior ectoloph of the paracone; posterior ectoloph is always present and composed mainly by the posterior ectoloph of the paracone and the anterior ectoloph of the metacone, and it is always complete; mesoloph absent; main valleys open or closed by a low cingulum; M3 highly

Table 5

List of the localities from the Calatayud–Daroca Basin with Cricetodontini. The abbreviations used, local biozone and the species present in each locality are also presented. Calibration according with Daams et al. (1999), Van Dam et al. (2006) and Van Dam et al., in prep.

Tableau 5

Liste des localités de Calatayud–Daroca avec Cricetodontini. Les abréviations utilisées, les biozones locales et les espèces présentes dans chaque localité sont également présentées. Calibration d'après avec Daams et al. (1999), Van Dam et al. (2006) et Van Dam et al., en prép.

Locality	Abb.	Biozone	Age	Species
Nombrevilla 19	NOM19	I	9.98	<i>H. cf. aragonensis</i>
Pedregueras 2C	PED2C	I	10.38	<i>H. aragonensis</i>
Pedregueras 2A	PED2A	I	10.62	<i>H. aragonensis</i>
Pedregueras 1A	PDA	I	—	<i>H. aragonensis</i>
Nombrevilla 14	NOM14	I	10.68	<i>H. cf. aragonensis</i>
Nombrevilla 13	NOM13	I	10.72	<i>H. cf. aragonensis</i>
Nombrevilla 22	NOM22	I	—	<i>H. cf. aragonensis</i>
Cañada 11	CAÑ11	H	—	<i>H. cf. nombrevillae</i>
Cañada 10	CAÑ10	H	—	<i>H. cf. nombrevillae</i>
Cañada 9	CAÑ9	H	—	<i>H. cf. nombrevillae</i>
Cañada 8	CAÑ8	H	—	<i>H. cf. nombrevillae</i>
Nombrevilla 1	NOM1	H	10.77	<i>H. nombrevillae</i>
Nombrevilla 10	NOM10	H	11.18	<i>H. cf. nombrevillae</i>
Nombrevilla 9	NOM9	H	11.20	<i>H. nombrevillae</i>
Carrilanga 1	CARR1	G3	11.33	<i>H. aguirrei</i>
Nombrevilla 4	NOM4	G3	11.80	<i>H. aguirrei/H. lavocati</i>
Nombrevilla 3	NOM3	G3	11.84	<i>H. aguirrei/H. lavocati</i>
Nombrevilla 2	NOM2	G3	11.87	<i>H. aguirrei/H. lavocati</i>
Solera	SOL	G3	12.01	<i>H. cf. aguirrei</i>
Paje 2	PJE2	G3	12.26	<i>H. cf. aguirrei</i>
Paje 1	PJE1	G3	12.39	<i>H. cf. aguirrei</i>
Las Planas 5H	LP5H	G3	12.60	<i>C. nievei</i>
Toril 3B	TOR3B	G3	12.65	<i>C. nievei</i>
Toril 3A	TOR3A	G3	12.65	<i>C. nievei</i>
Toril 2	TOR2	G3	—	<i>C. nievei</i>
Toril 1	TOR1	G3	—	<i>C. jotae</i>
Alcocer 3	AC3	G3	—	<i>C. jotae</i>
Alcocer 2	AC2	G3	—	<i>C. jotae</i>
Alcocer 1	AC1	G3	—	<i>C. jotae</i>
Villafeliche 9	VL9	G3	—	<i>C. jotae</i>
Arroyo del Val VI	ARV6	G2	—	<i>C. jotae</i>
Las Planas 5K	LP5K	G2	13.08	<i>C. jotae</i>
Las Planas 5L	LP5L	G2	13.16	<i>C. jotae</i>
Borjas	BOR	G2	—	<i>C. jotae</i>
Manchones	MAN	G2	—	<i>C. jotae</i>
Valtalto 1	VT1	G1	—	<i>C. jotae</i>
Las Planas 5C	LP5C	G1	13.55	<i>C. jotae</i>
Las Planas 5B	LP5B	G1	13.56	<i>C. jotae</i>
Valalto 2C	VT2C	F	13.68	<i>C. sansaniensis</i>
Valtalto 2B	VT2B	F	13.70	<i>C. sansaniensis</i>
Armantes 7	ARM7	F	—	<i>C. sansaniensis</i>
Las Umbrías 21	LUM21	F	13.75	<i>C. sansaniensis</i>
Las Umbrías 22	LUM22	F	13.76	<i>C. sansaniensis</i>
Las Umbrías 20	LUM20	E	13.80	<i>C. soriae</i>
Las Planas 4C	LP4C	E	13.88	<i>C. soriae</i>
Las Umbrías 19	LUM19	E	13.95	<i>C. soriae</i>
Las Planas 4B	LP4B	E	13.96	<i>C. soriae</i>
Las Planas 4BA	LP4BA	E	—	<i>C. soriae</i>
Las Planas 4A	LP4A	E	13.98	<i>C. soriae</i>
Las Umbrías 16	LUM16	E	14.04	<i>C. soriae</i>
Las Umbrías 11	LUM11	E	14.06	<i>C. soriae</i>

reduced; mesolophid presents in half of the lower molars; metalophulid I is always present, some also have metalophulid II, and most m2 display three roots completely split.

Type locality: Nombrevilla 1, Calatayud–Daroca Basin, Spain, local biozone H (MN9, Lower Vallesian, Upper Miocene).

Stratigraphical distribution in the Calatayud–Daroca Basin: local biozone H (MN7/8–MN9, Upper Aragonian–Lower Vallesian, Middle–Upper Miocene). FO: NOM9 (11.20 Ma); LO: NOM4 (10.77 Ma).

Morphological descriptions are in [Freudenthal, 1966](#).

Hispanomys aragonensis ([Freudenthal, 1966](#))

The most important features of *H. aragonensis* are: relative small size; M1 with four roots; well-developed ectolophs, mainly double and always complete; the posterior ectoloph of the M2 is oblique and connects the metacone at the point where the posterior protolophule reaches the longitudinal crest; mesoloph and enamel-coated valley frequent on the M3; weak

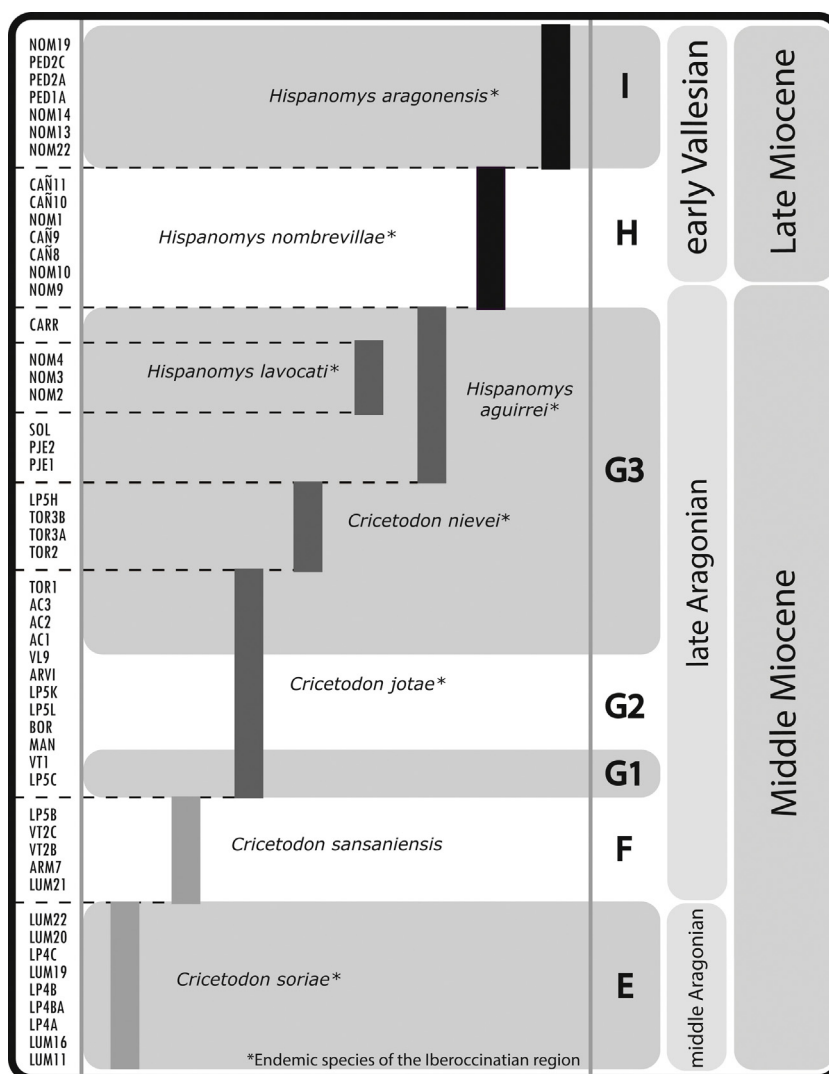


Fig. 5. Stratigraphical distributions of the species of Cricetodontini in the Calatayud–Daroca Basin. Their correlations with local biozones, the MN system, continental stages and epochs are also presented. Data acquired from López-Guerrero et al., 2008, 2009, 2013a, 2013b, 2014.

Fig. 5. Distributions stratigraphiques des espèces de Cricetodontini dans le bassin de Calatayud–Daroca. Leurs corrélations avec les biozones locales, le système de MN, les étapes continentales et les époques sont également présentées. Les données sont issues de López-Guerrero et al., 2013a, 2013b, 2014.

lingual and labial posteroloph; valleys mainly blocked by low cingula; weak posteroloph on the M3; well-developed labial anterolophid; mesolophid present in most of the lower molars, it can be double or connected with the metacone; valleys closed by low cingulids; m1 frequently shows a metalophulid I, and in some specimens, the metalophulid II is also present.

Type locality: Pedregueras 2C, Calatayud–Daroca Basin, Spain, local biozone I (MN9, Lower Vallesian, Upper Miocene).

Stratigraphical distribution in the Calatayud–Daroca Basin: local biozone H–local biozone I, (MN9, Lower Vallesian, Upper Miocene). FO: NOM13 (10.72 Ma); LO: NOM19 (9.98 Ma).

Morphological descriptions are in Freudenthal, 1966.

4. Discussion

All the material of Cricetodontini from Calatayud–Daroca Basin is now taxonomically assigned, including the most recently recovered specimens (Table 5). Eight species of Cricetodontini split in two genera have been recognized; four belong to *Cricetodon* and the other four to *Hispanomys*. The stratigraphical distribution of Cricetodontini in the Calatayud–Daroca Basin (Fig. 5) ranges from the local biozone E to I for the Middle–Upper Aragonian and Lower Vallesian (Middle–Upper Miocene). The oldest species is *C. soriae* and the youngest is *H. aragonensis*. *Hispanomys* replaced *Cricetodon* in the middle of the local biozone G3, around 12.6 and 12.39 Ma.

The stratigraphical distributions of the studied species (Fig. 5) generally fit well with the local biozonation; those

of *Cricetodon soriae*, *C. sansaniensis*, *H. nombrevillae* and *H. aragonensis* coincide with the local biozones E, F, I and H, respectively and therefore these species could be used as good biostratigraphical markers. On the other hand, the distribution of *Cricetodon jotae* is longer and it ranges about 1 my, covering several local biozones (G1, G2 and partly G3). As it shown in Fig. 5, four species of Cricetodontini are present in local biozone G3 (*C. jotae*, *C. nievei*, *H. aguirrei* and *H. lavocati*). On the light of the distribution of this species and the unusually long duration of the G3 (1 my) the redefinition and subdivision of this biozone is recommended. Nevertheless, we suggest a study of the complete rodent fauna before proposing a new biozonation. The local biozonation built for the Calatayud–Daroca Basin (Daams et al., 1999; Van der Meulen et al., 2012) uses mainly species of Cricetids (*Megacricetodon*, *Democricetodon* and *Eumyarion*), Eomyids (*Ligerimys*), Sciurids (*Heteroxerus*) and Insectivores (*Galerix*). Nonetheless, such redefinition is out of the scope of this paper.

The evolutionary patterns observed in the Cricetodontini from Calatayud–Daroca Basin agree with the following model: basal morphology in the first registered taxa (*C. soriae*, *C. sansaniensis*), mosaic configuration in most part of the Late Aragonian (*C. jotae*, *C. nievei*, *H. aguirrei* and *H. lavocati*) and, finally, derived forms starting in *H. nombrevillae*. Most of the species from the Calatayud–Daroca Basin are endemic and therefore not found elsewhere. However, this morphological patterns are also recognized in the rest of the European Cricetodontini faunas, although not synchronously (Álvarez-Sierra et al., 2013; Kálin and Kempf, 2009; López-Guerrero et al., 2013b, 2014). In line with this, Van der Meulen et al. (2011, 2012) detected several asynchronies studying the rodent bioevents sequence between from the Calatayud–Daroca Basin and Central Europe during the Early and Middle Aragonian. The asynchrony in the evolutionary patterns of the Cricetodontini between Iberian and Central Europe Basins provides new criteria that support the asynchronies noted in the works of Van der Meulen et al. (2011, 2012).

The estimated age of the localities containing these species of Cricetodontini spans a time range from 14.06 to 9.98 Ma (Daams et al., 1999; Van Dam et al., 2006, Van Dam et al., in prep.). Several important paleoclimatic changes have been detected within this interval; firstly, the Miocene Climatic Optimum (MCO), a period with high temperatures and humid tropical and subtropical conditions, is recorded worldwide (Shevenell et al., 2004; Zachos et al., 2001). The MCO predates the first occurrence of *Cricetodon* in the Calatayud–Daroca Basin. The MCO was followed by the Middle Miocene Climatic Transition (MMCT), a period characterized by Antarctic ice growth and gradual global cooling. The MMCT ends in a short-term drop in sea surface temperatures called the Middle Miocene Cooling (MMC). The MMC was triggered by the reestablishment of the eastern Antarctica ice sheet; it has been recognized also in some continental deposits from the Iberian Peninsula (Domingo et al., 2012) and represents the beginning of the cold climatic regime of the Neogene (Lear et al., 2000; Shevenell et al., 2004; Zachos et al., 2001).

Hordijk (2010) noted that these climatic phases (MCO, MMCT and MMC) agreed well with the timing of

the main changes in the mammal succession in the Calatayud–Daroca Basin. He pointed out that the gradual cooling of the MMCT is correlated with a prolonged immigration phase which produced an increase of the richness in the small mammal faunas. According to Hordijk (2010) the major turnover in the Calatayud–Daroca Basin took place during local biozones E to G2; consequently the FO of *Cricetodon* in the Calatayud–Daroca Basin (local Biozone E) is part of this event.

5. Conclusions

After this study, all the material of *Cricetodon* from the Calatayud–Daroca Basin has been taxonomically assigned at species level. The material described here belongs to two species. *Cricetodon sansaniensis* from the F local biozone of Calatayud–Daroca Basin has basal traits. *Cricetodon jotae*, found in the local biozones G1, G2 and partly G3, displays a combination of basal and derivate characters.

The stratigraphical distribution of some Cricetodontini from the Calatayud–Daroca Basin (*C. soriae*, *C. sansaniensis*, *H. nombrevillae* and *H. aragonensis*) demonstrates their suitability as biostratigraphical markers for the Calatayud–Daroca Basin. Moreover, we have been able to precise the distribution of the species of Cricetodontini belonging to the long G3. We have recognized the possibility of redefinition and subdivision of this local biozone. However, it is necessary to complete the study of the rest of fauna before proposing a new biozonation.

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