Hypsodont Myomiminae (Gliridae, Rodentia) from five new localities in the Lower Miocene Tudela Formation (Bardenas Reales, Ebro Basin, Spain) and their bearing on the age of the Agenian-Ramblian boundary

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ABSTRACT

The hypsodont Myomiminae Daams, 1981 (Gliridae) from the lower part of the Tudela Formation (Ebro Basin) are described. Five localities (CH1, CA2, CA3, CA4 and CC1) of this formation contain remains of the hypsodont genus *Armantomys* de Bruijn, 1966 and CC1 has also yielded *Praearmantomys* de Bruijn, 1966. Despite the poor material, we can identify the taxa *A.* cf. *bijmai, A. daamsi* (de Visser in Álvarez-Sierra, Daams, Lacomba, López Martínez, Van Der Meulen, Sesé & De Visser, 1991), *A.* cf. *parsani*, *A.* cf. *jasperi* and cf. *P. crusafonti*, which are characteristic of the Agenian and Ramblian continental stages. These data allow identification of the Agenian-Ramblian boundary in the Tudela Formation, and provide a calibration of this boundary on the basis of available magnetostratigraphic information.

KEY WORDS
Rodentia,
Gliridae,
Agenian,
Ramblian,
Lower Miocene,
Spain.

RÉSUMÉ

Myomiminae hypsodontes (Gliridae, Rodentia) de cinq gisements nouveaux du Miocène inférieur de la Formation Tudela (Bardenas Reales, bassin de L'Èbre, Espagne) et leur rapport avec l'âge de la limite Agénien-Ramblien.

Ce travail décrit la faune de gliridés hypsodontes de la sous-famille Myomiminae Daams, 1981 de la partie inférieure de la Formation Tudela (Bassin de l'Èbre). Cinq nouvelles localités de cette formation (CH1, CA2, CA3, CA4 et CC1) contiennent des restes du genre *Armantomys* de Bruijn, 1966, la dernière (CC1) contenant également des restes de *Praearmantomys* de Bruijn, 1966. Malgré la pauvreté du matériel, les taxons suivants ont pu être identifiés : *A.* cf. *bijmai*, *A. daamsi* (de Visser in Álvarez-Sierra, Daams, Lacomba, López Martínez, Van Der Meulen, Sesé & De Visser, 1991), *A.* cf. *parsani*, *A.* cf. *jasperi* et cf. *P. crusafonti*, caractéristiques de l'Agénien et du Ramblien. Ces données, qui permettent l'identification de la limite Agénien-Ramblien dans la Formation Tudela, fournissent un étalonnage préliminaire de cette limite basée sur l'information magnétostratigraphique disponible.

MOTS CLÉS
Rodentia,
Gliridae,
Agénien,
Ramblien,
Miocène inférieur,
Espagne.

INTRODUCTION

Over the last years we have been carrying out a detailed paleontological survey of the Lower and Middle Miocene continental successions of the Tudela Formation in the Bardenas Reales de Navarra region (western sector of the Ebro Basin) (see Murelaga 2000). This ongoing survey has resulted in the recovery of fossil remains that include a rich variety of vertebrates, such as small and large mammals (Murelaga *et al.* 2004a, b), amphibians and reptiles (Murelaga *et al.* 2002), and birds (Murelaga 2000). Among the small mammals, rich glirid faunas found at several localities in the Units 2 and 3 of the formation (Larrasoaña *et al.* 2006) have permitted the identification of zones Z and A of the Ramblian (Murelaga 2000; Murelaga *et al.* 2004a). The combination of small and large mammal faunas allows attribution of these localities to MN3.

Larrasoaña *et al.* (2006) provided magnetostratigraphy-based ages for the fossil bearing sediments of the Tudela Formation, ranging from chron C6r to C5Cr (19.65 to 17.5 Ma after recalibration to the ATNTS of Lourens *et al.* 2004). This chronology is coherent with the estimated age of the Tardienta mammal site, found to represent the boundary of local zones Y2 and Z, within chron C6r (Pérez-Rivarés *et al.* 2002). The first $^{39}Ar/^{40}Ar$ dates of an ash-layer found at Tardienta gave an age of 19.3 ± 0.7 Ma (Odin *et al.* 1997), which was later recalculated to 19.7 ± 0.3 (Dam *et al.* 2006), in better agreement with the magnetostratigraphic data.

Some of our localities, like CH1 and CC1, are correlated with local zones Y1 and Y2 (Upper Agenian), but unfortunately these localities are not directly related with paleomagnetic sections. If it were possible to find a mammal locality in the lowest part of the Tudela Formation or in the Lerín Fm. this would allow to define a boundary

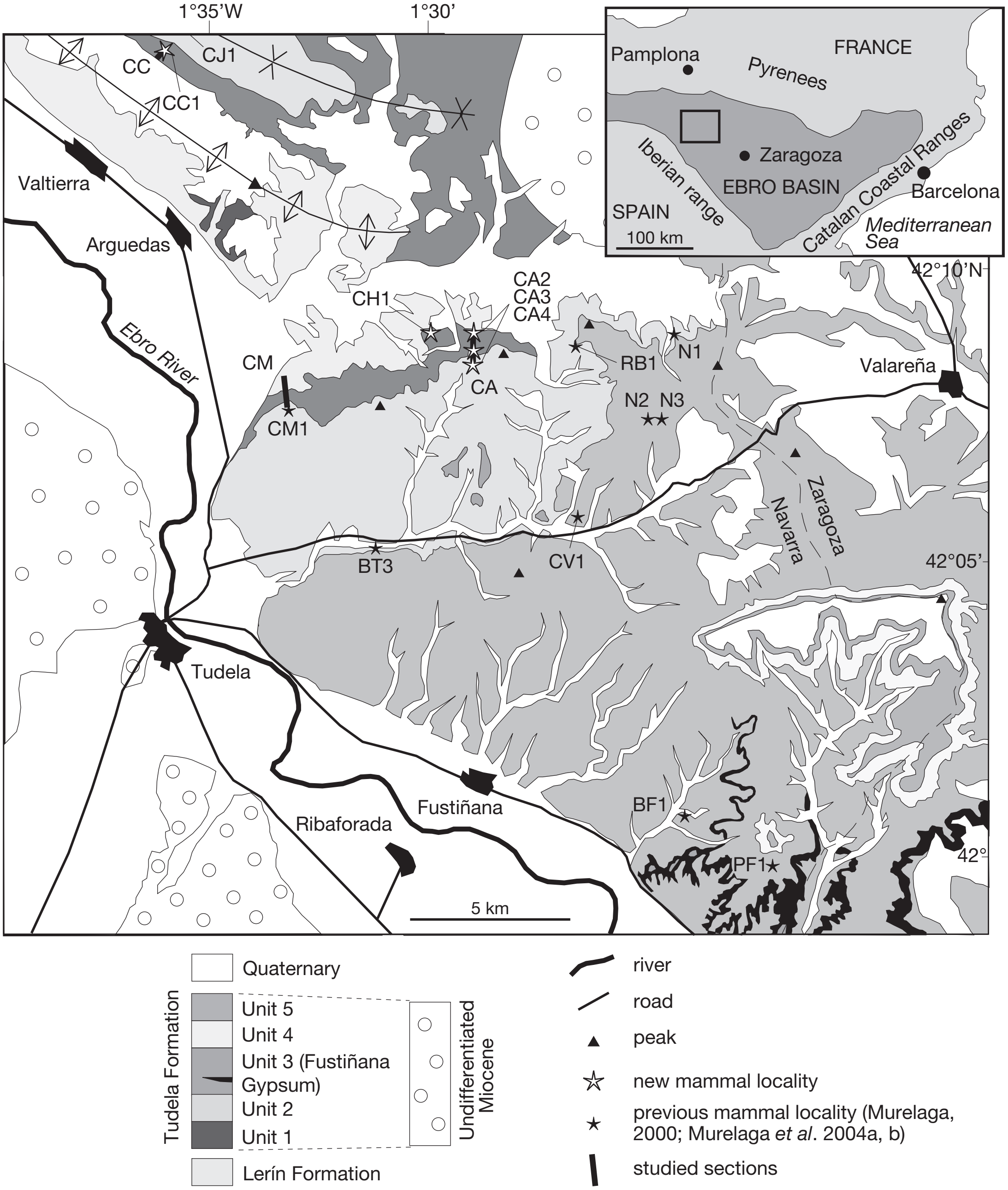

Fig. 1. — Geological map of the Lower-Middle Miocene continental sediments from the Tudela Formation at the Bardenas Reales de Navarra area, with location of the sections and fossil localities presented in this study. Abbreviations: **CA**, Cuesta Agujeros section; **CC**, Cabezo Carboneras section; **CM**, Cabezo Marijuán section. The location of other fossil localities studied previously by Murelaga (2000) and Murelaga *et al.* (2004a, b) is also shown.

TABLE 1. — Fossil localities set of the Units 2 and 3 from the Tudela Formation containing micromammalian remains (Murelaga *et al*. 2004a; Larrasoaña *et al*. 2006). *, localities described in this paper.

Code	**Section**	**UTM (30T)**
BF1	Barranco Fraile	X = 631237; Y = 4651913
BT3	Barranco Tudela	X = 621841; Y = 4660732
CA2*	Cuesta Agujeros	X = 625012; Y = 4667147
CA3*	Cuesta Agujeros	X = 624598; Y = 4666392
CA4*	Cuesta Agujeros	X = 624726; Y = 4666596
CC1*	Cabezo Carboneras	X = 614540; Y = 4676819
CH1*	Cabezo Hermoso	X = 623670; Y = 4667338
CJ1	Cabezo de la Junta	X = 615491; Y = 4677985
CM1	Cabezo Marijuán	X = 619370; Y = 4664885
CV1	Cabezo Vaquero	X = 628833; Y = 4661506
N1	La Nasa	X = 631111; Y = 4667198
N2	La Nasa	X = 630423; Y = 4664558
N3	La Nasa	X = 630315; Y = 4664320
PF1	Pico Fraile	X = 634468; Y = 4651105
RB1	Rincón del Bu	X = 628059; Y = 4667019

stratotype for the Agenian/Ramblian, a question that is particularly important because the Agenian has never been defined properly. In this paper we use the term Agenian for the time and the corresponding sediments between the Oligocene-Miocene boundary and the base of the Ramblian.

In the past years we have located five new localities in the lower part of the Tudela Formation. In this paper we provide a detailed description of the material of *Armantomys* de Bruijn, 1966 and *Praearmantomys* de Bruijn, 1966. This new material, combined with a reevaluation of previously studied remains from the Tudela Formation (Murelaga 2000; Murelaga *et al.* 2004a, b) and from other areas in the Ebro Basin (Lacomba & Martínez-Salanova 1988; Álvarez-Sierra *et al.* 1991; Daams 1990), results in a biostratigraphic sequence of the Lower Miocene sediments of the Ebro Basin and enables a better understanding of the chronostratigraphic position of the Agenian-Ramblian boundary in the Iberian Peninsula.

GEOLOGICAL SETTING

The Ebro Basin is a triangular-shaped basin that formed during the Tertiary between the Pyrenees foreland, the Iberian Range and the Catalan Coastal Ranges fold-and-thrust belts (Fig. 1). From the late Eocene to the late Miocene, the Ebro Basin constituted an endorrheic depression where alluvial and fluvial systems originating from the Pyrenean, the Iberian and the Catalan Coastal margins converged into a central lacustrine system through a palustrine transitional zone (Alonso-Zarza *et al.* 2002; Costa *et al.* in press). The Tudela Formation is composed of 605 m of distal alluvial, fluvial, palustrine and lacustrine sediments accumulated in the western part of the central Ebro Basin during the Lower-Middle Miocene (Larrasoaña *et al.* 2006). These sediments crop out extensively at the Bardenas Reales de Navarra, a semi-arid steppe region located in the vicinity of Tudela (Fig. 1). The Tudela Formation is made up of red, brown, pink, ochre, yellow and grey mudstones with intercalations of frequent sandstones and limestones and some occasional gypsum bed. Sandstones appear either as thin (cm), sheet-like levels distributed throughout the section or as thick (dm to m) channel-like beds that are commonly associated to red and brown mudstones. Limestone beds can be up to 2 m thick, and often appear in clusters associated to pink, ochre, yellow and grey mudstones. Limestones are often massive and bioturbated, and contain abundant gastropods, ostracods, charophytes, fish teeth and other fossil fragments. Gypsum beds appear occasionally in the lowermost and upper parts of the formation. The sedimentary facies of the Tudela Formation are similar to those described elsewhere in the central Ebro Basin (see Arenas & Pardo 1999). Distal fluvial and alluvial muddy flood plains that drained the Pyrenean and Iberian Range margins are characterized by brown-red mudstones and sandstones. Transitional palustrine environments are represented by ochre, yellow, pink and grey mudstones and by intercalated thin limestone beds. Thick limestone beds and associated grey mudstones attest the lacustrine system, developed in the central sector of the basin. Palustrine and lacustrine facies are better represented in the middle and uppermost parts of the formation (i.e. Units 2, 3 and 5 in Larrasoaña *et al.* 2006) (Fig. 2), whereas distal fluvial and alluvial facies dominate in the lowermost and upper parts of the formation (Units 1 and 4 of Larrasoaña *et al.* 2006) (Fig. 2).

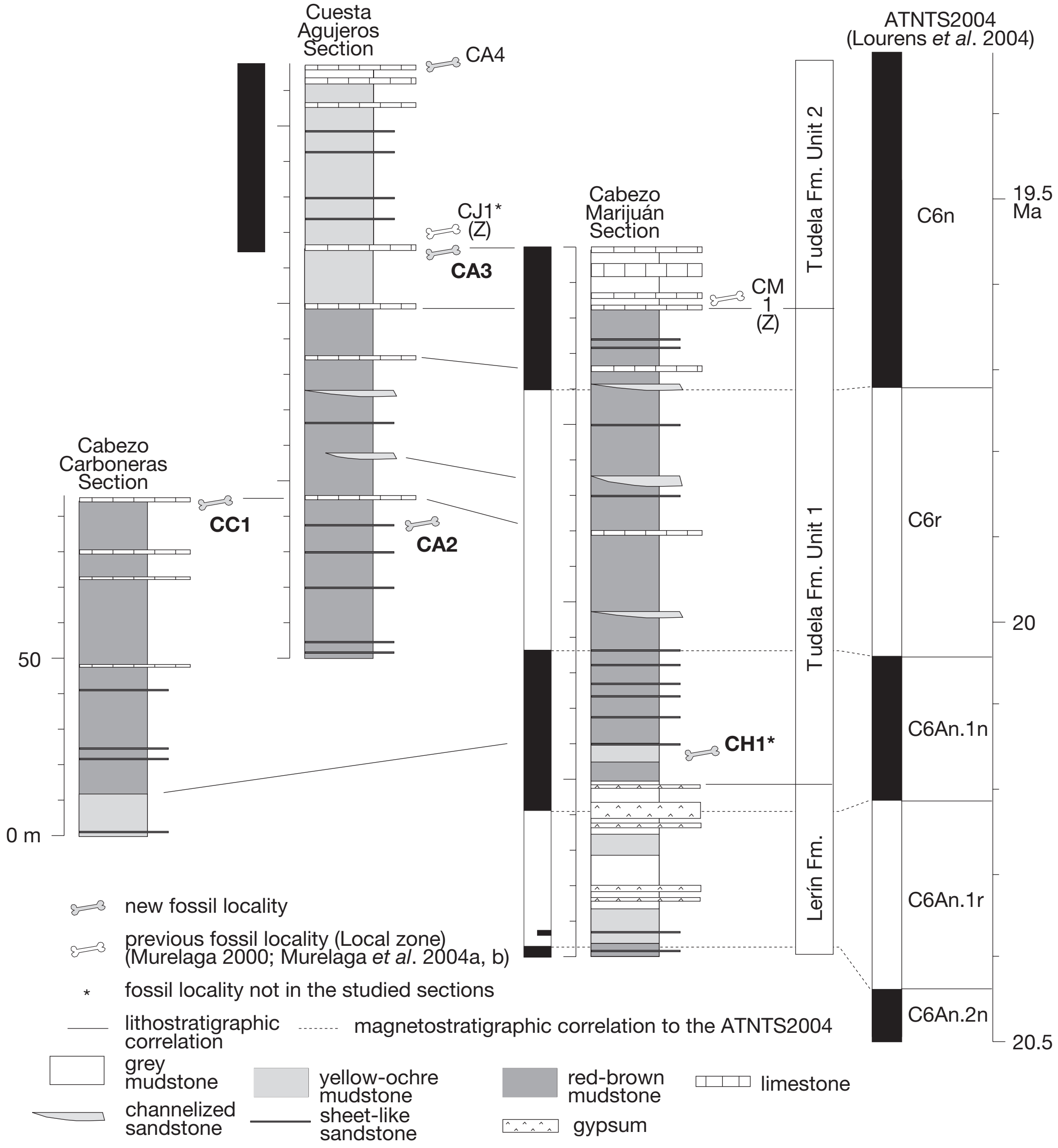

Fig. 2. — Stratigraphy of the Tudela Formation in the studied sections, with location of the new fossil localities presented here (in bold) and other localities studied previously (Murelaga 2000; Murelaga *et al.* 2004a, b). The available sequence of polarity intervals identified in the upper part of the Cuesta Agujeros section and the Cabezo Marijuán section and its correlation to the ATNTS of Lourens *et al.* (2004) is also shown (see Larrasoaña *et al.* 2006).

Up to now, ten fossil-bearing localities, located in the lower part of the Tudela Formation have been reported and studied in detail (Fig. 2; Table 1) (Murelaga *et al.* 2004a; Larrasoaña *et al.* 2006). These localities are found in grey mudstones formed in either palustrine or lacustrine environments. The association of small and large mammals allows attribution of these localities to local zones Z and A that constitute the Ramblian stage (Daams *et al.* 1987), and to European mammal unit MN3 (Agustí *et al.* 2001). Magnetostratigraphic dating brackets the age of these fossil localities between 19.65 and 17.5 Ma (Burdigalian, see Larrasoaña *et al.* 2006) (Fig. 2) according to ATNTS2004 (Lourens *et al.* 2004).

Three of these localities are in the Cuesta Agujeros section and one in the Cabezo Carboneras section, whereas a fifth locality has been found in an isolated outcrop halfway between the Cuesta Agujeros and Cabezo Marijuán sections (Figs 1; 2). Of these sites, only one lies in sediments for which magnetostratigraphic data are available, namely the uppermost part of the Cuesta Agujeros section (Larrasoaña *et al.* 2006). The other localities have been placed in the magnetostratigraphic scheme developed by Larrasoaña *et al.* (2006) on the basis of detailed lithostratigraphic correlation between sections (Fig. 2). The localities containing the new *Armantomys* material presented here partly overlap stratigraphically with the localities with *Armantomys* remains previously reported from Units 2 and 3 (Murelaga 2000; Murelaga *et al.* 2004a, b; Larrasoaña *et al.* 2006).

MATERIAL AND METHODS

The new *Armantomys* and *Praearmantomys* material has been described following the nomenclature of Freudenthal (2004) for the cheek teeth, and has been compared with previously studied material from other localities in the Tudela Formation (Murelaga 2000; Murelaga *et al.* 2004a, b) and elsewhere in the Ebro Basin (Lacomba & Martínez-Salanova 1988; Álvarez-Sierra *et al.* 1991; Daams 1990). All these faunas have been placed in the biochronostratigraphic scheme of local zones developed by Daams (1990). Measurements are given in units of 0.1 mm. All the studied specimens are provisionally stored in the Department of Stratigraphy and Paleontology of University of the Basque Country.

Because of the scarcity of the material we have estimated hypsodonty through visual comparison and we have made no attempt to measure hypsodonty.

ABBREVIATIONS

BARD	Bardenas;
BARG	Bargota;
BF1	Barranco del Fraile 1;
BT3	Barranco de Tudela 3;
CA2	Cuesta Agujeros 2;
CA3	Cuesta Agujeros 3;
CA4	Cuesta Agujeros 4;
CC1	Cabezo Carboneras 1;
CH1	Cabezo Hermoso 1;
CJ1	Cabezo de la Junta 1;
CM1	Cabezo Marijuán 1;
CV1	Cabezo Vaquero 1;
FM2	Fuenmayor 2;
L, W	length and width, respectively;
MN	European Neogene land mammal units;
N1	Nasa 1;
N2	Nasa 2;
N3	Nasa 3;
NAVAL	Navalón;
PF1	Pico del Fraile 1;
QU1	Quel 1;
RAMBL1	Ramblar 1;
RB1	Rincón del Bu 1;
RGM	Rijksmuseum van Geologie en Mineralogie, Leiden;
SJ	San Juan;
STC	Santa Cilia;
SCSIE (UV)	Servei Central de Suport a la Investigació Experimental, University of Valencia, Valencia;
UPV/EHU	University of Basque Country/Euskal Herriko Unibertsitatea, Bilbao.

SYSTEMATIC PALEONTOLOGY

The genus *Armantomys* comprises six species (Daams 1990): *A. bijmai* (Lacomba & Martínez-Salanova, 1988), *A. daamsi* (de Visser *in* Álvarez-Sierra, Daams, Lacomba, López Martínez, Van Der Meulen, Sesé & De Visser, 1991), *A. aragonensis* de Bruijn, 1966, *A. parsani* Daams, 1990, *A. jasperi* Daams, 1990 and *A. tricristatus* López, 1977. These species appear in sediments from the interval between the Late Agenian (local subzone Y1; Álvarez-Sierra *et al.* 1987) and the Late Aragonian (zone G3) (Daams 1990). They are excellent biochronological markers, particularly in the lower part of their range (Agenian and Lower Ramblian). *Armantomys bijmai* and *A. daamsi* are restricted to subzones Y1 and Y2, respectively, *A. parsani* is found from subzone Y2 till zone A, and *A. jasperi* is found from zone A till

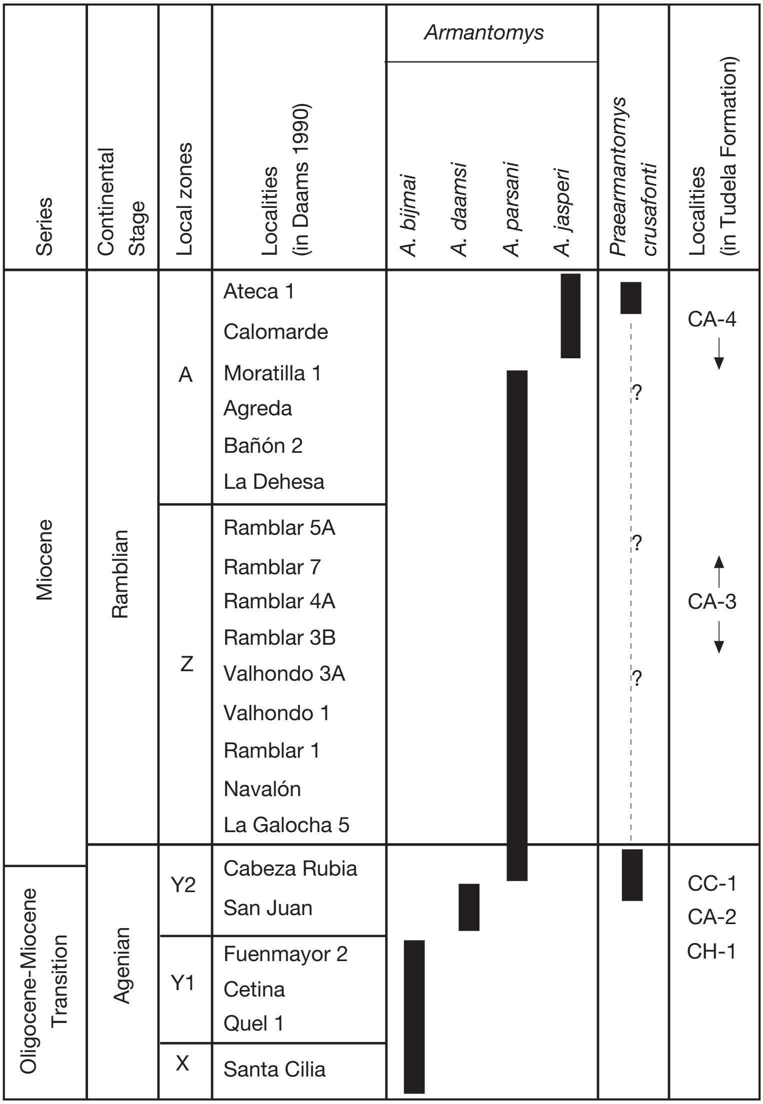

FIG. 3. — Distribution chart of the Myomiminae species studied in this paper and in Daams (1990). The succession of the localities from Daams (1990) is, though in stratigraphical order, not calibrated.

the lower part of subzone Dd (Daams 1990; Daams *et al.* 1999; Fig. 3). Therefore, finding a continuous fossil record of different species of *Armantomys* can be used for establishing detailed biostratigraphic schemes for Lower-Middle Miocene sediments.

In the Upper Agenian and Aragonian, an additional large Myomiminae with simple dental pattern and concave occlusal surface is present. This glirid was first described and assigned to the genus *Praearmantomys* by de Bruijn (1966). *Praearmantomys* differs from *Armantomys* in several features (Daams 1990: 28): *Praearmantomys* is characterized by a larger size, lower hypsodonty, more or less vertical ridges in the lower molars and a strong reduction of the posterolingual side of m3 compared with the smaller-sized *Armantomys*. The record of *Praearmantomys* starts at subzone Y2

(Upper Agenian) and extends to zone C of the Lower Aragonian, although it is absent in most of the Ramblian (zone Z and lower and middle parts of zone A) (Fig. 3). *Praearmantomys* is a dominant component of rodent faunas in the Upper Agenian and around the Ramblian/Aragonian boundary (Daams 1990).

Order RODENTIA Bodwich, 1821
Family GLIRIDAE Thomas, 1987
Genus *Armantomys* de Bruijn, 1966

Armantomys cf. ***bijmai***
(Lacomba & Martínez-Salanova, 1988)
(Fig. 4A-E)

HOLOTYPE. — QU1-165, left M1 (Lacomba & Martínez-Salanova 1988: pl. 1, fig. 8).

TYPE LOCALITY. — Quel 1, Ebro Basin, Spain.

LOCALITY AND AGE. — Cabezo Hermoso 1 (CH1), province of Navarre, Spain. Agenian (Local subzone Y1, MN2).

MATERIAL AND MEASUREMENTS (L×W). — CH1-3 (13.04 ×), incomplete right m1; CH1-5 (6.83 × 7.56), right D4; CH1-4 (7.96 × 9.61), right P4; CH1-6 (12.84 × 17.11), left M2; CH1-7 (14.50 ×), incomplete right M1,2; CH1-8 (8.77 × 13.32), incomplete right M3.

DESCRIPTION

m1
Anterolophid separated from the protoconid by a deep furrow. Metalophid short and oblique, separated from the metaconid. Centrolophid short. Between metalophid and mesolophid there is a short isolated accessory ridge. Mesolophid and posterolophid separated at the entoconid by a deep furrow and without other connections among the ridges.

D4
Anteroloph reaching the labial tooth border and connected to the paracone. Protoloph long and continuous. Precentroloph absent. The metaloph is a transverse ridge, directed to the protoloph, with a posterior connection to the posteroloph. Postcentroloph short. The posteroloph has a narrow furrow halfway its length. Posteroloph not connected to protocone.

P4
Anteroloph reaching the labial tooth border and connected to the paracone. The lingual end does not reach the protocone. Protoloph and metaloph continuous and connected to the protocone, forming a composite Y-shaped ridge. Posteroloph lingually and labially elongated, connected to protocone and metacone.

M1
Tooth labially broken. The metaloph joins the protoloph. The posteroloph joins the protocone lingually.

M2
The anteroloph is labially separated from the paracone. Protoloph continuous. A medium-sized precentroloph is connected to the protoloph. A tiny postcentroloph is present. The metaloph is a continuous ridge, connected with the short postcentroloph. Posteroloph labially separated from the metacone and lingually connected to protocone.

M3
Anteroloph labially connected to the paracone at medium height and lingually high connected to the protocone. Protoloph and metaloph continuous and connected to the protocone, forming a composite Y-shaped ridge. No centrolophs. Posteroloph continuous, not connected to metacone and with a narrow furrow just in front of the protocone.

REMARKS

The morphology of the material of *Armantomys* from CH1 is similar to *A. bijmai* and *A. daamsi*. *A. bijmai* is characterized by its hypsodonty, medium size, the constant presence in M1,2 of a metaloph-protoloph connection and the variable presence of centrolophs and centrolophids. On the other hand, the M1,2 of *A. daamsi* may have one or two short centrolophs and the m1,2 may have a short centrolophid.

The hypsodonty of the material from CH1 is very similar to what Lacomba & Martínez-Salanova (1988: 116, fig. 5) described for *A. bijmai*, and much

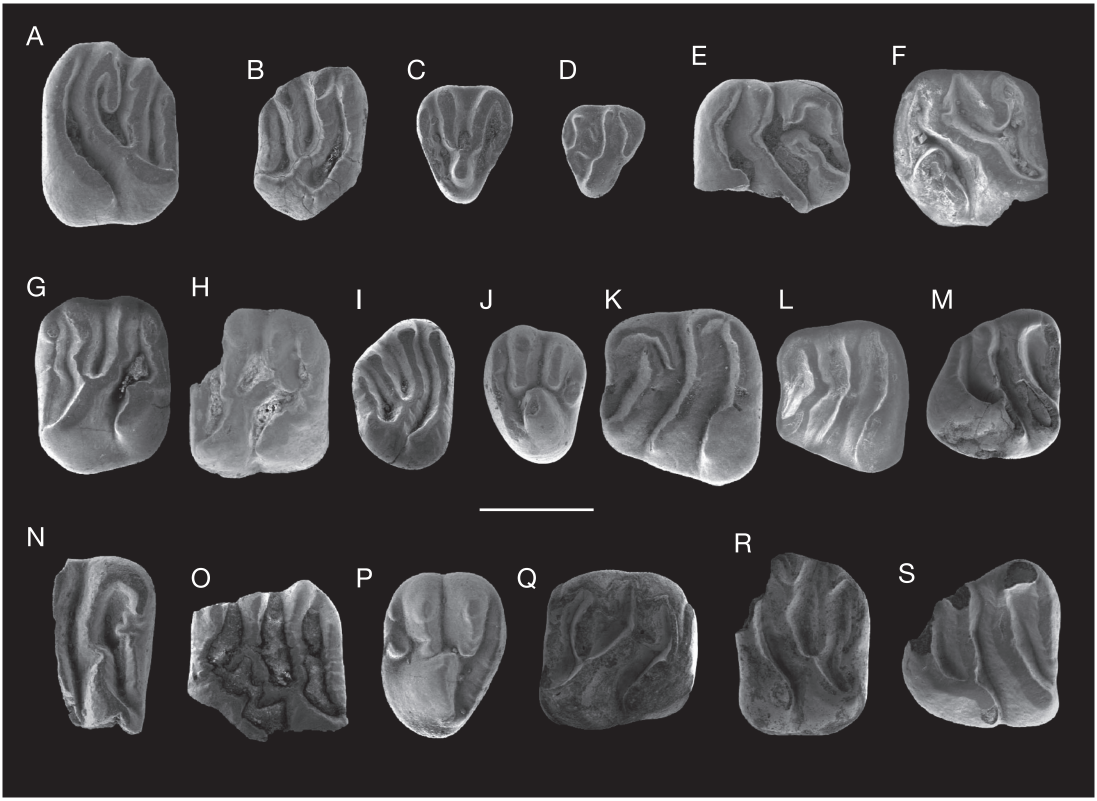

FIG. 4. — **A**-**E**, *Armantomys* cf. *bijmai* from Cabezo Hermoso 1 (CH1): **A**, left M2, CH1-6; **B**, right M3, CH1-8; **C**, right P4, CH1-4; **D**, right D4, CH1-5; **E**, right m1, CH1-3; **F**-**M**, *Armantomys daamsi* from Cuesta Agujeros 2 (CA2): **F**, left M1, CA2/1-6; **G**, right M2, CA2/1-5; **H**, right M2, CA2/2-6; **I**, right M3, CA2/1-15; **J**, right P4, CA2/1-12; **K**, left m1, CA2/1-8; **L**, left m1, CA2/1-10; **M**, right m3, CA2/2-5; **N**, *Armantomys* cf. *jasperi* from Cuesta Agujeros 4 (CA4), fragmentary right m2, CA4/1-27; **O**, **P**, *Armantomys* cf. *parsani* from Cuesta Agujeros 3 (CA3): **O**, left M2, CA3-1; **P**, left P4, CA3-2; **Q**, **R**, *Armantomys* cf. *daamsi* from Cabezo Carboneras 1 (CC1): **Q**, right M1, CC1-31; **R**, left M2, CC1-38; **S**, cf. *Praearmantomys crusafonti* from Cabezo Carboneras 1 (CC1), right m3, CC1-22. Scale bar:1 mm.

weaker than that of the large species of *Armantomys* (*A. aragonensis* from the Ramblian-Lower and Middle Aragonian, and *A. tricristatus* from Middle-Upper Aragonian), and of the contemporary genera *Praearmantomys* and *Pseudodryomys*.

The development of a connection between protoloph and precentroloph in *A. bijmai* is variable. This connection looks like a shepherd's crook (see Lacomba & Martínez-Salanova [1988: fig. 2, morphotype C]) or a Greek "Tau" (*op. cit.*, morphotype T), but other morphologies exist too. A shepherd's crook shape is common in Santa Cilia (29%) and Quel 1 (52%). A Greek letter "Tau" shape appears in 53% of the specimens from Santa Cilia, 48% from Quel 1 and 20% from Fuenmayor 2. The only M2 recovered in CH1 (CH1-6) presents a precentroloph of medium length with an intermediate morphology between these two morphotypes (Fig. 4A) and a tiny postcentroloph. The presence of precentroloph and postcentroloph is known in the M2 of *A. bijmai* from Quel 1 (QU1-164; Lacomba & Martínez-Salanova 1988: pls 1, 10) and in some specimens of *A. daamsi* from San Juan (Álvarez-Sierra *et al.* 1991).

The constant metaloph-protoloph connection is characteristic for *A. bijmai*. It is the exclusive morphology in the upper molars from CH1. It also appears in *A. daamsi*, although not exclusively like in *A. bijmai*.

TABLE 2. — Measurements (in tenths of millimetres) of the teeth of *Armantomys daamsi* (de Visser, 1991) from CA2.

Element	Parameter	n	min.	mean	max.
m1	L	2	11.31	12.24	13.16
	W	2	12.54	13.50	14.45
m2	L	1		12.51	
	W	2	12.43	12.54	12.64
m3	L	1		11.59	
	W	2	12.45	12.63	12.80
P4	L	3	8.62	8.96	9.28
	W	3	10.66	11.32	11.66
M1	L	1		13.70	
	W	1		13.64	
M2	L	3	12.39	12.91	13.19
	W	2	16.23	16.59	16.95
M3	L	1		8.70	
	W	1		12.60	

Among the remains from CH1 there is a m1 (CH1-3; Fig. 4E) with the postero-labial side broken off. This specimen shows a metalophid disconnected from the metaconid, a short centrolophid, a short accessory ridge between metalophid and mesolophid and a mesolophid-posterolophid not connected at the lingual border. The first two morphologies appear in *A. bijmai* and a few specimens of *A. daamsi* and *A. parsani*, but the accessory ridge between metalophid and mesolophid has only been found in *A. bijmai* from Santa Cilia (STC-56) (Lacomba & Martínez-Salanova 1988). According to size and morphology the material of CH1 can be assigned to *A. bijmai*. We call it *A.* cf. *bijmai* because of the scarcity of material.

Armantomys daamsi
(de Visser *in* Álvarez-Sierra, Daams, Lacomba,
López Martínez, Van Der Meulen, Sesé &
De Visser, 1991)
(Fig. 4F-M)

HOLOTYPE. — SJ-193, right M1 (*in* Álvarez-Sierra *et al.* 1991: pl. 8, fig. 3).

TYPE LOCALITY. — San Juan, Ebro Basin, Spain.

LOCALITY AND AGE. — Cuesta Agujeros 2 (CA2), Province of Navarre, Spain. Agenian (Local subzone Y2, MN2).

MATERIAL AND MEASUREMENTS. — See Table 2.

DESCRIPTION

m1

Anterolophid separated from the protoconid by a narrow furrow. Metalophid connected to metaconid. Centrolophid short (1) or absent (4). Mesolophid and posterolophid separated at the entoconid by a shallow furrow (2), or connected (2). The mesolophid is not connected to the mesoconid in one specimen. In the rest it is continuous and connected to the mesoconid.

m2

Anterolophid separated from the protoconid by a deep furrow. Metalophid connected to metaconid. One out of three m2 has a short centrolophid. Mesolophid and posterolophid separated at the entoconid by a shallow furrow. Mesolophid continuous and connected to mesoconid.

m3

The anterolophid is separated from the protoconid by a deep furrow. Metalophid connected to metaconid. Centrolophid absent. In one specimen the mesolophid is connected to the labial end of the posterolophid. In another specimen the mesolophid is of medium length, ending labially free. Mesolophid and posterolophid separated at the entoconid by a deep furrow.

P4

The anteroloph is reduced to an isolated, very short and low cusp. Protoloph continuous with a shallow and narrow furrow halfway (2) or transverse, free and not connected to protocone. Metaloph transverse and not connected to protocone (2) or continuous with a deep furrow near the protocone. Posteroloph long and curved, low connected to protocone and metacone.

M1

The anteroloph joins the paracone and lingually it is separated from the protocone by a shallow furrow. Protoloph oblique and continuous. The metaloph is short and ends free, neither connected to protoloph nor to protocone. No centroloph ridges. Posteroloph connected to protocone and metacone.

M2

Anteroloph transverse and separated from the paracone by a deep furrow. The anteroloph is not connected to the protocone. Protoloph continuous. One out of two specimens has an anterior spur directed towards to the anteroloph and separated from it by a narrow and deep furrow. Metaloph connected to protoloph, forming a Y-pattern. Posteroloph transverse, low or high connected to protocone.

M3

The anteroloph is low connected to the protocone and it is separated from the paracone by a shallow furrow. Protoloph and metaloph form a Y-pattern. Posteroloph connected to protocone and metacone.

REMARKS

The material of *Armantomys* from CA2 is similar to *A. daamsi*, described by Álvarez-Sierra *et al.* (1991) from San Juan. Some differences may be observed. The diagnosis of this species says it is of medium size with an M1,2 that may have one or two short centrolophs and an m1,2 with a short centrolophid (Álvarez-Sierra *et al.* 1991).

Like in *Armantomys* from CH1, the hypsodonty of the upper molars from CA2 is very similar to *A. bijmai* (Lacomba & Martínez-Salanova 1988: 116, fig. 5), and clearly distinct from the species of large size (*A. aragonensis* from the Ramblian and Lower-Middle Aragonian and *A. tricristatus* from the Middle-Upper Aragonian).

The three P4 from CA2 also have a very similar morphology. These specimens have a very short anteroloph, not connected to protocone and paracone, protoloph continuous or interrupted, transverse metaloph, not connected to protocone and a long posteroloph, joined to protocone and metacone.

The M1,2 from CA2 do not have centroloph ridges. In *A. daamsi* from San Juan, 4 out of 10 M1 present precentroloph only, three present both centrolophs and three have no centroloph at all. In that locality five out of 15 M2 have a precentroloph. The connection between metaloph and protoloph is an important character to distinguish small-medium sized *Armantomys* species. Álvarez-Sierra *et al.* (1991) do not specify the connections between metaloph and protoloph. Nevertheless, the holotype M1 of *A. daamsi* has a free-ending metaloph, not connected to the protoloph (SJ-G 193). The connection between metaloph and protoloph is constant in the M2 from San Juan (Álvarez-Sierra *et al.* 1991). In CA2 there is an almost complete M1 (Fig. 4F) with a short metaloph not connected to the protoloph. On the other hand, all M2 from CA2 have a metaloph connected to the protoloph. The M3 from CA2 also presents a forward directed metaloph, connected to the protoloph. In *A. bijmai* from the localities of the Ebro Basin (Lacomba & Martínez-Salanova 1988) the connection between metaloph and protoloph is characteristic in all upper molars. On the contrary, in several M1 of *A. daamsi* from the type locality the metaloph is not connected to the protoloph and in the rest of the upper molars (M2,3) this connection is constant. This is identical to the upper molars of *Armantomys* from CA2. On the other hand, the distinction between *A. daamsi* and *A. jasperi* is based on the metaloph-protoloph connection in M3. This connection is constant in *A. daamsi* and variable in *A. jasperi* (Daams 1990).

The m3 from San Juan have an anterior side very similar to m1,2 (Álvarez-Sierra *et al.* 1991). In the majority of the m3 from San Juan (72%) mesolophid and posterolophid form a Y. In the rest of the material, mesolophid and posterolophid form a composite ridge (14%) or the mesolophid ends labially free (14%). The morphology and size of the m3 from CA2 is very similar to the material of *A. daamsi* from San Juan described by Álvarez-Sierra *et al.* (1991) and with a more complicated dental pattern than described by Daams (1990) for *A. parsani*.

Armantomys cf. *daamsi*

(de Visser *in* Álvarez-Sierra, Daams, Lacomba,
López Martínez, Van Der Meulen, Sesé &
De Visser, 1991)
(Fig. 4Q-R)

LOCALITY AND AGE. — Cabezo Carboneras 1 (CC1), Province of Navarre, Spain. Agenian (Local subzone Y2, MN2).

MATERIAL AND MEASUREMENTS (L×W). — CC1-31 (13.76 estimated × 14.04), right M1; CC1-38 (11.71 × 15.80), left M2.

DESCRIPTION

M1

Anteroloph joined to paracone and separated from the protocone by a deep furrow. Protoloph oblique and continuous. Near the paracone the protoloph presents a short, forward directed, spur. Metaloph low connected to protoloph. Postcentroloph short. Posteroloph connected to protocone and metacone.

M2

Anteroloph slightly oblique, connected to the protocone and separated from the paracone by a deep furrow. Protoloph continuous without spurs. Metaloph connected to protoloph, forming a Y-pattern. No centroloph ridges. Posteroloph slightly oblique and high connected to the protocone.

REMARKS

Two specimens from Cabezo Carboneras 1 (CC1) (Fig. 4Q, R) have been assigned to *A.* cf. *daamsi* on the basis of size, the presence of a posterior centroloph in M1 and the kind of connections between metaloph and protoloph in M1,2. The presence of an anterior and/or posterior centroloph is dominant in populations of *Armantomys* from the Upper Agenian and Lower Ramblian (Daams 1990). On the other hand, in CC1-31 (Fig. 4Q), a short spur on the anterior side of the protoloph is present. This feature appears in populations of *Armantomys* from Upper Agenian to Middle Aragonian. The presence of spurs on the protoloph of M1,2 is frequent in *A. parsani* and dominant in *A. jasperi* from the Lower Ramblian; it has been cited in some specimens of *A. daamsi* from the Upper Agenian (Daams 1990). Therefore, on the basis of morphology, size and the scarcity of the material we assign these specimens to *A.* cf. *daamsi*.

Armantomys cf. ***parsani*** Daams, 1990
(Fig. 4O-P)

HOLOTYPE. — RGM 337 724, left M1 (*in* Daams 1990: pl. 1; fig. 4).

TYPE LOCALITY. — Ramblar 1, Calatayud-Teruel Basin, Spain.

LOCALITY AND AGE. — Cuesta Agujeros 3 (CA3), Province of Navarre, Spain. Ramblian (Local zone Z, MN3).

MATERIAL AND MEASUREMENTS (L×W). — CA3-2 (10.53 × 13.86), left P4; CA3-1 (13.58 ×), 1 fragmentary left M2; CA3-7, 1 fragmentary and not measurable left M3.

DESCRIPTION

P4

The anteroloph is reduced to two cusps, a short and low labial cusp and a medium-low central cusp. Protoloph continuous, low connected to the protocone. Metaloph transverse and separated from the protocone by a narrow and deep furrow near the protocone. Posteroloph long, low connected to the protocone and separated from the metacone.

M2

Anteroloph continuous with a short posterior spur, directed to the protoloph. The protoloph has two anterior spurs, directed towards the anteroloph but not connected to it. The metaloph joins the protoloph, forming a Y-pattern shape. Posteroloph transverse and low connected to the protocone.

M3

Anteroloph connected to the paracone and separated from the protocone by a narrow and deep furrow. Protoloph and metaloph form a Y-pattern. The middle of the protoloph has a short anterior spur directed towards the anteroloph.

REMARKS

In the upper portion of the Cuesta Agujeros section, the locality CA3 has provided a small collection of *Armantomys* remains. The large anterocone of P4, the absence of centrolophs in M2 and the presence of spurs in the anteroloph of M2 and the protoloph of M3 are very similar to what Daams (1990) described for *A. parsani* from its type locality and other sites that contain this species.

Armantomys cf. ***jasperi*** Daams, 1990 (Fig. 4N)

HOLOTYPE. — COR 70, left M2 (in Daams 1990: pl. 2; fig. 17).

Type locality. — Córcoles, Loranca Basin, Spain.

Locality and age. — Cuesta Agujeros 4 (CA4), Province of Navarre, Spain. Ramblian (Local zone A, MN3).

Material and measurements. — CA4-1/27, incomplete right m2.

Description

m2

Anterolophid long and separated from the protoconid by a narrow and deep furrow. Near the metaconid, the anterolophid is partially interrupted, thus forming a short posterior spur. Metalophid high connected to the metaconid. The metalophid is continuous with a short fold directed towards the anterolophid, but not connected to that ridge. Centrolophid absent.

Remarks

The presence of a short longitudinal spur on the posterior wall of the anterolophid is described in the m2 of *A. jasperi* from its type locality, Córcoles (Daams 1990). This morphology has not been mentioned in other populations of medium-sized *Armantomys* species. Therefore, the presence of a short spur on the posterior wall of the anterolophid and the width of the specimen indicate that it belongs to *A. jasperi*. Nevertheless, the scarcity of material and its fragmentary state do not allow a certain assignment.

Genus *Praearmantomys* de Bruijn, 1966

cf. ***Praearmantomys crusafonti*** de Bruijn, 1966
(Fig. 4S)

Holotype. — Ateca 1, fragment mandible and maxila with incomplete dentition (Nr. 72, 73, 74 and 75; de Bruijn 1966: pl. I; figs 1-4).

Type locality. — Ateca 1, Ebro Basin, Spain.

Locality and age. — Cabezo Carboneras 1 (CC1), Province of Navarre, Spain. Agenian (Local subzone Y2, MN2).

Material and measurements (L×W). — CC1-22 (13.92 × 14.31), right m3.

Description

m3

Posterolingual side very reduced with a subtriangular shape. Anterolophid separated from the protoconid by a deep furrow. Metalophid connected to metaconid. Centrolophid absent. Mesolophid transverse and connected to the labial end of the posterolophid. Mesolophid and posterolophid separated at the entoconid.

In CC1 a m3 of large size has been recovered. Its size and above all its hypsodonty are very similar to *Praearmantomys*. The ridges are vertical. The size is larger than *A. bijmai* and *A. daamsi* and similar to the populations of *A. parsani*. The hypsodonty is very different from these latter species.

The shape of this molar is characterized by the strong reduction of posterolingual side. This morphology has been cited in populations of *P. crusafonti* (Daams 1990) and seems to be characteristic of this genus.

For the mesolophid of m3 of *P. crusafonti* from Cabeza Rubia two morphotypes have been figured (Daams 1990). The first (2 out of 3 specimens), with a transverse mesolophid not connected to the posterolophid and the second with a mesolophid connected to the posterolophid forming a Y-shape. In the rest of the populations of *P. crusafonti* the first morphotype is very poorly represented. In the m3 from CC1 the mesolophid is transverse and connected to the posterolophid on the labial side of the tooth. The mesolophid from CC1 is similar but not identical to the first morphotype described by Daams, because the mesolophid is connected on the labial border.

The fossil record of *P. crusafonti* ranges from uppermost Agenian to Lower Aragonian (Fig. 3). In Cabeza Rubia (Upper Agenian, zone Y2) *P. crusafonti* has been cited together with *A. parsani* (Daams 1990). Cabezo Carboneras 1 (CC1) contains an unknown glirid association of *P. crusafonti* with *A. daamsi*. This implies an older age for CC1 and may explain the presence of a morphotype that is not known in Cabeza Rubia. The material is too poor to draw solid conclusions.

DISCUSSION AND CONCLUSIONS

Several forms of *Armantomys* are recognized in the localities studied in this paper. These taxa are characteristic of the Upper Agenian (zones Y1 and

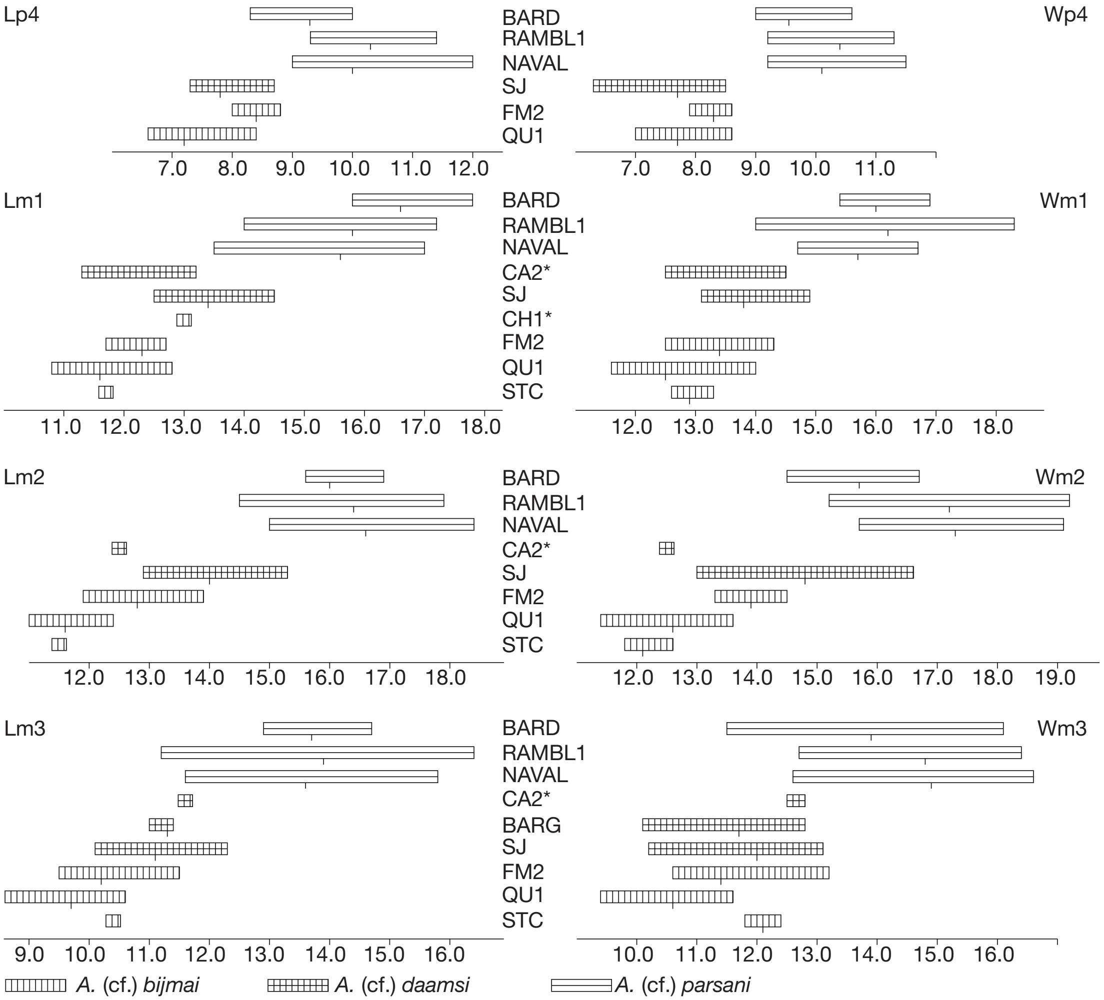

FIG. 5. — Ranges of variation and number of specimens for length and width of the lower (pre)molars of *Armantomys* de Bruijn, 1966 populations of Agenian and Ramblian localities from Spain. BARD (Bardenas) is a combination of the localities published by Murelaga *et al.* (2004a, b). *, localities described in this paper.

Y2; *A.* cf. *bijmai* and *A. daamsi*), Upper Agenian to Ramblian (Y2, Z and A; *A. parsani*) and Upper Ramblian to Middle Aragonian (A, B, C and D; *A. jasperi*) (Fig. 3).

Figures 5 and 6 show a comparison of measurements of material from several localities with *A. bijmai*, *A. daamsi* and *A. parsani* from the Lower Miocene of Spain. According to these data the size of P4 from CH1 overlaps with the minimum values of *A. bijmai* from Quel 1 and it is smaller than *A. bijmai* from Fuenmayor 2 and *A. daamsi* from the type locality San Juan. D4 from CH1 is clearly smaller (6.83 × 7.56) than the only specimen of *A. bijmai* in the three localities of the Ebro Basin where this species is cited (Quel 1, Santa Cilia and Fuenmayor 2) (8.40 × 10.00). The length of M1 (14.50) and size of M2 from CH1 is bigger than *A. bijmai* and overlaps with the maximum values of *A. daamsi* from San Juan. Finally, the length of M3 and m1 from CH1 is a bit larger than that of

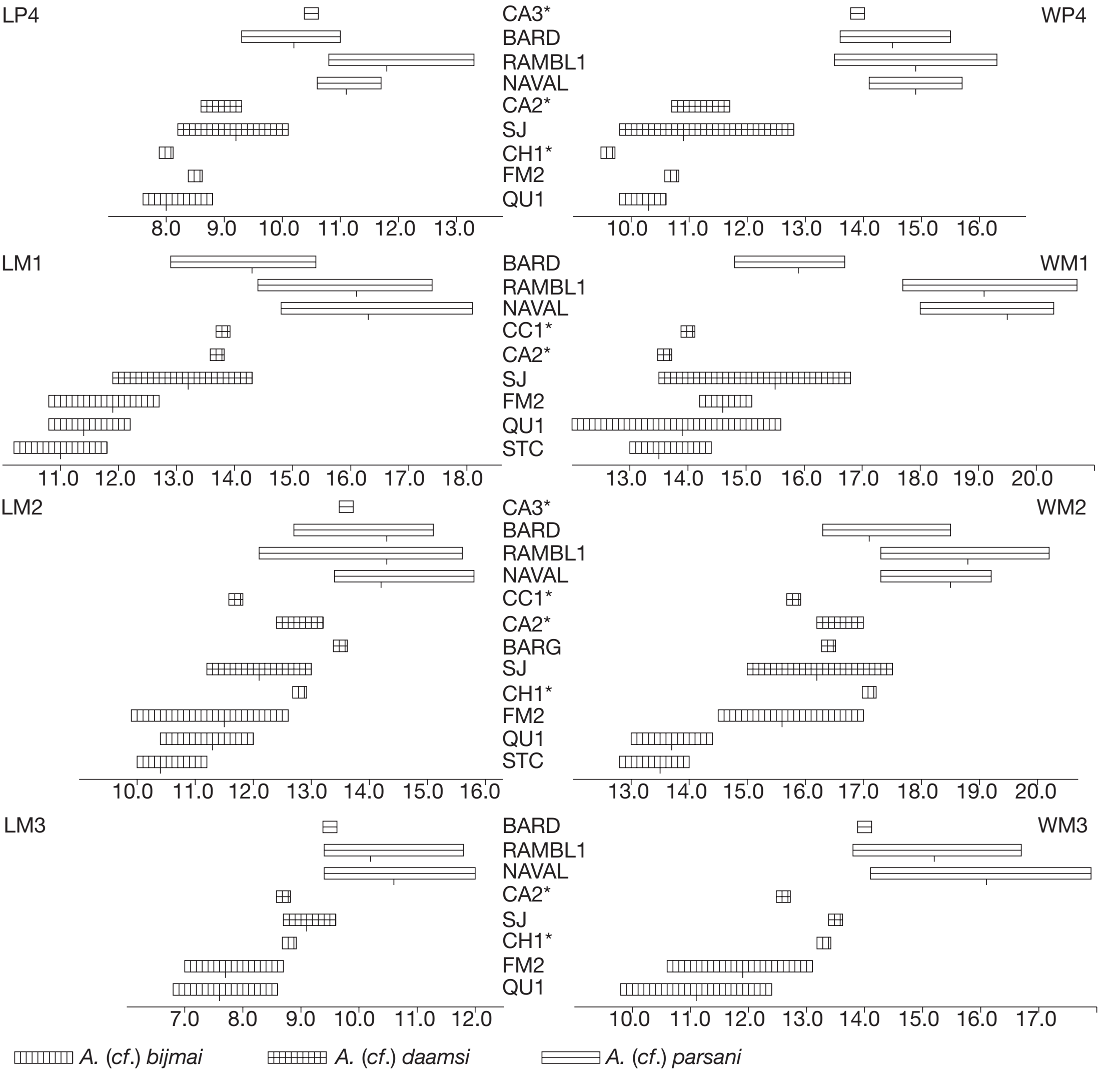

FIG. 6. — Ranges of variation and number of specimens for length and width of the upper (pre) molars of *Armantomys* de Bruijn, 1966 populations of Agenian and Ramblian localities from Spain. BARD (Bardenas) is a combination of the localities published by Murelaga *et al.* (2004a, b). *, localities described in this paper.

A. bijmai and overlaps with the minimum values of *A. daamsi* from its type locality. In general, the size of the material from CH1 overlaps with the values of *A. bijmai* and *A. daamsi* (Figs 5; 6). Only the length of M1 (Fig. 6) is somewhat bigger than in *A. daamsi* from its type locality.

The material from CC1 is smaller than that from the type locality of *A. parsani* (Ramblar 1) and overlaps with *A. daamsi* (Figs 5; 6). Only the length of M1 of CC1 overlaps the minimum values of populations of *A. parsani* from Bardenas. In Cabeza Rubia the size of M1 and M2 assigned to *A. parsani* are: 14.9 × 17.8 for M1 and 14.5 × 19.3 for M2 (Daams 1990). These values are clearly bigger than the teeth of *Armantomys* from CC1 (Figs 5; 6).

The size of *Armantomys* from CA2 is very close to *A. daamsi* from San Juan (Figs 5; 6). *Armantomys* from CA2 is larger than *A. bijmai* from Quel 1, Fuenmayor 2 and Santa Cilia (Lacomba & Martínez-Salanova 1988), and clearly smaller that the rest of the species of small-medium size of this genus (*A. parsani* and *A. jasperi*). The size of P4 from CA2 is intermediate between *A. bijmai* and *A. daamsi*, whereas it is smaller than *A. jasperi* (Daams 1990) and *A. parsani*.

The scarce remains of *Armantomys* from CA3 are clearly bigger than *A. bijmai* and *A. daamsi*, and overlap with minimum and medium values of *A. parsani* (Fig. 5).

On the other hand, the width value of the fragmentary m2 from CA4 is 15.45. This is bigger than *A. bijmai* and matches the mean values of *A. daamsi* from San Juan; it is a bit smaller than the minimum value of *A. parsani* and it matches with the medium values of *A. jasperi*.

Lastly, the locality Cabezo Carboneras 1 (CC1) has yielded a m3 which is clearly bigger than *A. bijmai* and *A. daamsi*, it matches the mean values of *A. parsani* and it is somewhat smaller than the m3 of *Praearmantomys crusafonti* from Cabeza Rubia.

The combined presence of *A. parsani* and *P. crusafonti* has been cited in Cabeza Rubia (zone Y2, Upper Agenian, Daams 1990). In this paper, a single specimen of the latter species is cited in the locality CC1. Therefore one might consider that the material of *Armantomys* from CC1 belong to *A. parsani* and not to *A.* cf. *daamsi* as we describe here. However, the remains of *Armantomys* from CC1 are clearly smaller than *A. parsani* from Cabeza Rubia, and their morphology is very similar to *A. daamsi*.

The presence of *A. bijmai* in CH1 and *A. daamsi* in CA2 and CC1 dates Unit 1 of the Tudela Formation unambiguously as Agenian (Fig. 2). The lack of magnetostratigraphic data for the Cabezo Carboneras section and the middle-lower part of the Cuesta Agujeros section, where these localities are found, impedes a direct dating of these Agenian faunas. However, lithostratigraphic correlation between these sections and those for which magnetostratigraphic data are available (Larrasoaña *et al.* 2006) allows a dating to be proposed. This correlation, combined with the presence of Ramblian faunas in the same sections (Fig. 2) and with radiometric data of other relevant fossil localities allows a calibration of the Agenian/Ramblian boundary (Fig. 7). Magnetostratigraphic data of the neighbouring Cabezo Marijuán section indicate that the Agenian localities CH1, CA2 and CC1 are located within chrons C6An.1n and the lower middle part of chron C6r, so that they range between *c.* 20.15 and 19.9 Ma according to ATNTS2004 (Figs 2; 7). On the other hand, the Ramblian faunas of CA3 and CA4 studied here, together with those of CM1 and CJ1 studied previously (Murelaga 2000; Murelaga *et al.* 2004a, b; Larrasoaña *et al.* 2006), are found in the lower part of chron C6n so that they range between 19.3 Ma and 19.6 Ma in age in the ATNTS2004 (Lourens *et al.* 2004) (Figs 2; 7). These data indicate that the Agenian/Ramblian boundary must be located somewhere between 19.6 and 19.9 Ma, which is entirely consistent with the recalibrated age of the original ^{40}Ar/^{39}Ar dating of 19.7 ± 0.3 Ma for the Tardienta fossil locality (van Dam *et al.* 2006). Tardienta is interpreted as being located at the boundary between zones Y and Z (Odin *et al.* 1997) (Fig. 7). Van Dam *et al.* (2006: Supplementary fig. 1), however, place this boundary in the middle of C6n at 19.1 Ma, 0.8 Ma younger than Tardienta. We propose an age of 19.88 Ma for the Agenian/Ramblian boundary, based on the revised radiometric age of Tardienta (Van Dam *et al.* 2006), its positions within the middle part of chron C6r (Pérez-Rivarés *et al.* 2002), and the position of the youngest Y2 locality (CC1) in the Tudela Formation (Fig. 7). The proposed chronostratigraphic scheme also allows a tentative dating of other zonal boundaries. The boundary between Agenian subzones Y1 and Y2 lies between the localities CH1 (Y1) and CA2 (Y2) and has an approximate age of 20.05 Ma, roughly coinciding with the boundary between chrons C6An.1n and C6r (Fig. 7). Moreover, the boundary between the lower (zone Z) and upper (zone A) Ramblian can be placed within the lower part of chron C6n at an approximate age of *c.* 19.45 Ma (Fig. 7). New magnetostratigraphic data from the Cabezo Carboneras and Cuesta Agujeros sections are necessary, along with ongoing biostratigraphic studies

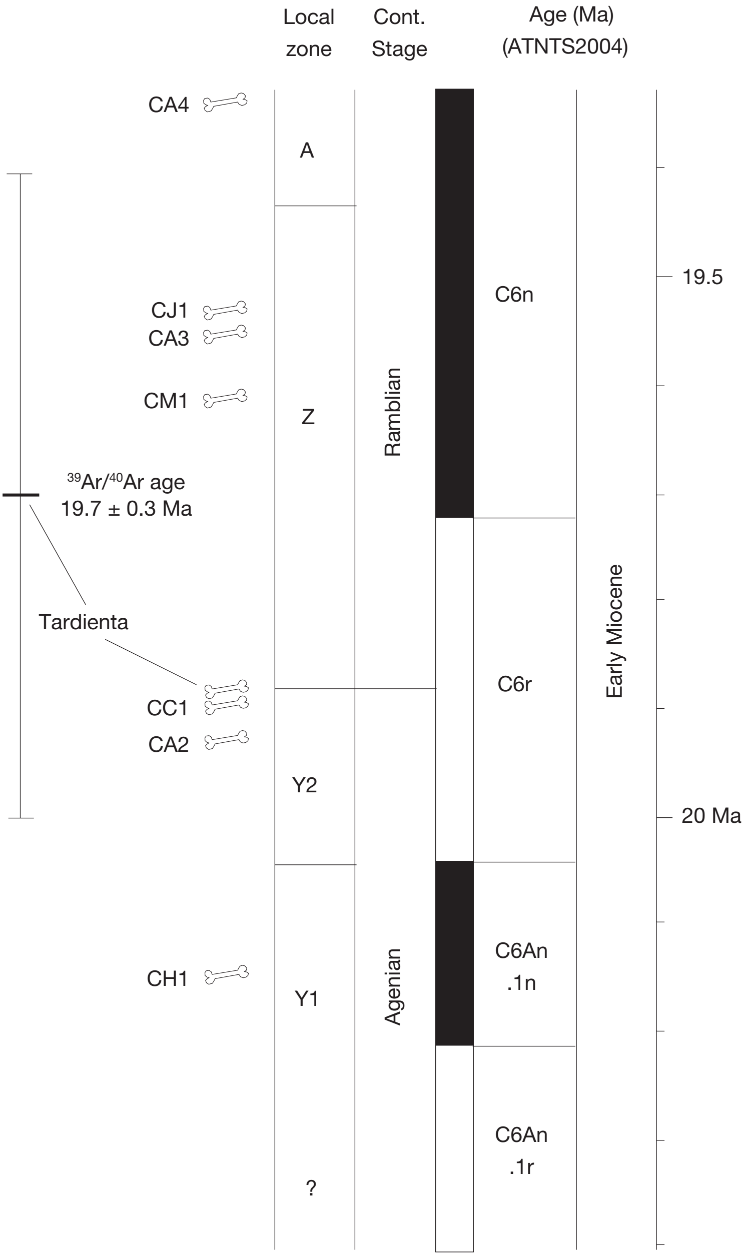

FIG. 7. — Calibration of the Agenian/Ramblian boundary proposed in this study on the basis of the new material from the Tudela Formation and on the recalibrated radiometric age of the Tardienta fossil locality (Van Dam *et al.* 2006), placed in the ATNTS of Lourens *et al.* (2004). The vertical bar indicates the error associated to the ^{39}Ar/^{40}Ar age of the Tardienta fossil locality.

based on other fossil rodents, to validate the new calibration of the Agenian/Ramblian boundary proposed here.

The presence of *A.* cf. *daamsi* and cf. *P. crusafonti* in locality CC1 represents the first record of this faunal association and extends the temporal distribution of *A. daamsi* to the upper part of Agenian zone Y2.

On the other hand, preliminary data indicate the presence of *Eucricetodon* cf. *gerandianus* in CA1 (a new fossiliferous level, stratigraphically situated between CH1 and CA2), *Peridyromys turbatus* and *Simplomys* aff. *aljaphi* in CA2 and *Eucricetodon* aff. *aquitanicus* in CC1, which reinforces the assumption of their Agenian age (Álvarez-Sierra *et al.* 1987; Daams 1999) inferred from their glirid faunas. The occurrence of *Ligerimys* aff. *magnus* and *Pseudotheridomys* sp. at locality CA4 is also consistent with the Ramblian age (Álvarez-Sierra *et al.* 1991) suggested by the glirid faunas.

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