Journal of
Iberian Geology
AN INTERNATIONAL PUBLICATION OF EARTH SCIENCES

Rodents and insectivores from the Lower Miocene (Agenian and Ramblian) of the Tudela Formation (Ebro Basin, Spain)

Roedores e insectívoros del Mioceno Inferior (Ageniense y Rambliense) de la Formación Tudela (Cuenca del Ebro, España)

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Abstract

The rodent and insectivore faunas of Agenian and Ramblian age from the Tudela Formation (Ebro Basin, Spain) are described. Four of the localities (CH1, CA1, CC1 and CA2) contain rodent remains of Agenian age (local zone Y), and three (CA3, CA3B and CA4) of Ramblian age (local zones Z and A). Typical Agenian taxa include *Armantomys* cf. *bijmai* (CH1), *Eucricetodon* cf. *gerandianus* (CA1), *Peridyromys turbatus*, *Simplomys* aff. *aljaphi* and *Armantomys daamsi* (CA2) and *Eucricetodon* aff. *aquitanicus* (CC1). On the other hand, some typical Ramblian taxa are *Armantomys* cf. *parsani* (CA3), *Ligerimys* aff. *magnus* and *Pseudotheridomys* sp. (CA4) and *Prodryomys* cf. *brailloni* (CA3B). The faunas are characterized by the richness and diversity of the glirids. The presence of the glirid *Altomiramys* in CA4 represents the first Upper Ramblian record of this taxon.

Keywords: Rodentia, Insectivora, Ebro Basin, Miocene, MN2, MN3

Resumen

En este trabajo se describen las faunas de roedores e insectívoros de edad Ageniense y Rambliense de la Formación Tudela (Cuenca del Ebro, España). Cuatro de las localidades (CH1, CA1, CC1 y CA2) contienen restos de edad Ageniense (zona local Y), y tres (CA3, CA3B y CA4) de edad Rambliense (zonas locales Z y A). Entre otras, las faunas Agenienses incluyen a *Armantomys* cf. *bijmai* (CH1), *Eucricetodon* cf. *gerandianus* (CA1), *Peridyromys turbatus*, *Simplomys* aff. *aljaphi* y *Armantomys daamsi* (CA2) y *Eucricetodon* aff. *aquitanicus* (CC1). Del mismo modo, entre las faunas Ramblienses se incluye a *Armantomys* cf. *parsani* (CA3), *Ligerimys* aff. *magnus* y *Pseudotheridomys* sp. (CA4) y *Prodryomys* cf. *brailloni* (CA3B). Las faunas encontradas en estos yacimientos se caracterizan por la riqueza y diversidad de glíridos. La presencia del glírido *Altomiramys* en CA4, representa el primer registro de este taxon en el Rambliense superior.

Palabras clave: Rodentia, Insectivora, Cuenca del Ebro, Mioceno, MN2, M1

1. Introduction

In the past two decades, our team has performed an extensive paleontological investigation in the Bardenas Reales of Navarra, in the western part of the central sector of the Ebro Basin (see Murelaga, 2000). This led to ample knowledge of the vertebrate fauna of Ramblian age (Lower Miocene) of the deposits of the Tudela Formation (Larrasoaña *et al*., 2006), including mammals (Murelaga *et al*., 2004a, 2004b), amphibians, reptiles (Murelaga *et al.,* 2002) and birds (Murelaga, 2000). The paleontological knowledge of the Ramblian deposits is accompanied by a magnetostratigraphical characterization (Larrasoaña *et al*., 2006), allowing to establish a detailed chronology of the fossiliferous sites.

Seven new fossiliferous levels have been found (CH1, CC1, CA1, CA2, CA3, CA3B and CA4) (Table 1) in the lower part of the Tudela Formation. Recently, Ruiz-Sánchez et al. (2012) have described the remains of hypsodont glirids of the genera *Armantomys* de Bruijn, 1966 and *Praearmantomys* de Bruijn, 1966 from several of these sites (CH1, CC1, CA2, CA3 and CA4) (Table 1). The first practical result of this work are, on the one hand, the proposal of a biostratigraphical sequence of the sediments of the Lower Miocene of the Ebro Basin and, on the other hand, the proposition of the chronostratigraphical position of the Agenian-Ramblian boundary in the Iberian Peninsula. In this contribution we present a complete study of the micromammal faunas of the seven new sites found in the basal part of the Tudela Formation, which permits a detailed biostratigraphical definition and to confirm the calibration of the Agenian-Ramblian boundary, proposed by Ruiz-Sánchez *et al.* (2012) on the basis of hypsodont glirids only.

2. Material, methods and abbreviations

The fossils were collected during the campaigns of 2004 and 2006. The samples were excavated and transported to Cenicero (La Rioja). Sieving was done in this locality with a sieve with 0.5 mm. mess. The fossils are deposited in the 'Departamento de Estratigrafía y Paleontología de la Universidad del País Vasco' (UPV/EHU). The nomenclature used in the description of the teeth and the measurement methods are taken from Fahlbusch (1970), Álvarez-Sierra (1988) (Eomyidae), Mein and Freudenthal (1971) (Cricetidae), Cuenca (1988) (Sciuridae), Hugueney (1999b) (Castoridae) and Freudenthal (2004) (Gliridae). The measurements are given in units of 0.1 mm, and were taken on a binocular microscope Leica MZ7$_5$, by means of displacement of a mechanical stage, connected to a Sony Magnescale measuring equipment.

Lower teeth are coded as p4, m1, m2, m3, upper teeth as P4, M1, M2 and M3. We use the MN units (*European*

Localities	Sediment (Kg)	Armantomys bijmai	Armantomys daamsi	Armantomys parsani	Armantomys jasperi	Altomiramys sp.	Altomiramys daamsi	Peridyromys murinus	Peridyromys turbatus	Prodryomys spp.	Simplomys aljaphi	Vasseuromys spp.	Eucricetodon spp.	Eucricetodon gerandianus	Eucricetodon aquitanicus	Rhodanomys spp.	Ritteneria spp.	Ligerimys magnus	Pseudotheridomys spp.	Heteroxerus paulhiacensis	Steneofiber spp.
CA4	340			(1)	(1)		(1)			(3)								(19)	(1)		(1)
CA3B	10									(1)											
CA3	240			(3)	(4)																
CA2	360		(14)		(5)			(21)	(2)	(18)	(1)		(8)			(1)*	(1)*		(3)		
CC1	200		(2)												(2)						
CA1	110													(1)							
CH1	920	(6)										(1)									

Table 1.- Fossil localities and number of specimens for each species. Asterisks indicate assignation of this fossil remain to *Rhodanomys* or *Ritteneria* genera.

Tabla 1.- Número de especímenes por especie y localidad. Los asteriscos indican la asignación del resto en cuestión al género *Rhodanomys* o *Ritteneria*.
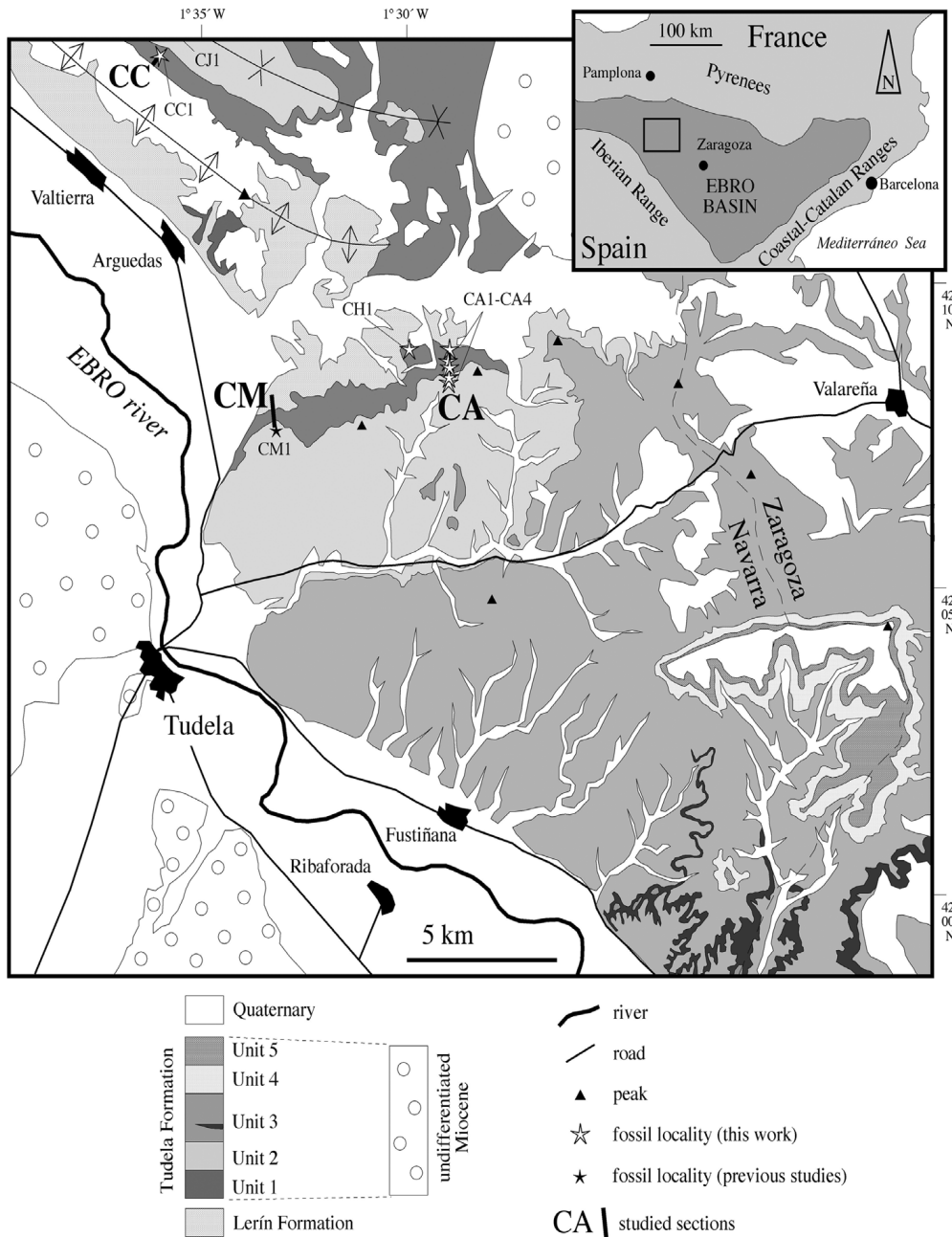
Fig. 1.- Geological map of the Tudela Formation in the Bardenas Reales of Navarra, with the situation of the localities presented in this work. CH1: Cabezo Hermoso, CC1: Cabezo Carboneras 1, CA1 to CA4: Cuesta Agujeros 1 to 4. Also shown the situation of other localities previously studied in the lower part of the Tudela Formation (Murelaga, 2000; Murelaga *et al*., 2004a,b).

Fig. 1.- Mapa geológico de la Formación Tudela en Las Bardenas Reales de Navarra, con la situación de las localidades presentadas en este trabajo. CH1: Cabezo Hermoso, CC1: Cabezo Carboneras 1, CA1 to CA4: Cuesta Agujeros 1 a 4. Así mismo se muestra la situación de las otras localidades previamente estudiadas en la parte inferior de la Formación Tudela (Murelaga, 2000; Murelaga *et al*., 2004a,b).

Neogene land mammal units) or the local zones defined by Álvarez-Sierra *et al*. (1987), Daams and Freudenthal (1988), Daams *et al*. (1999) and/or van der Meulen *et al*. (2012).

Institutional and locality abbreviations.— SCSIE(UV), Servei Central de Suport a la Investigació Experimental de la Universitat de València, Burjassot, Spain; UPV/EHU, Universidad del País Vasco/Euskal Herriko Unibertsitatea, Bilbao, Spain; CA1, Cuesta Agujeros 1; CA2, Cuesta Agujeros 2; CA3, Cuesta Agujeros 3; CA3B, Cuesta Agujeros 3B; CA4, Cuesta Agujeros 4; CC1, Cabezo Carboneras 1; CH1, Cabezo Hermoso 1; L, length; MN, European Neogene land mammal units; W, width.

3. Geological setting

The Ebro Basin developed during the Tertiary as foreland basin of the Pyrenean, Iberian and Coastal-Catalan Cordilleras (Fig. 1). From the Late Eocene onwards, when the basin lost its connection with the Atlantic (Costa *et al*., 2010), and until the Late Miocene, when it began to drain towards the Mediterranean (Urgeles *et al*., 2011), the Ebro Basin was an endorrheic depression in which the fluvial systems that drained the surrounding mountains converged. These systems flowed into the central zone of the basin, where, depending on the climatic conditions, carbonatated fresh-water lakes or evaporitic systems formed (Alonso-Zarza *et al.,* 2002).

The Tudela Formation is composed of 655 meters of fluvial distal, palustrine and lacustrine sediments accumulated during the Early and Middle Miocene in the central part of the Western sector of the basin (Larrasoaña *et al*., 2006) and crops out extensively in the so-called Bardenas Reales of Navarra (Fig.1). The sediments are grey, yellowish, brown and reddish lutites with frequent intercalations of sandstones and limestones, and occasionally gypsum levels. The sandstone layers vary in thickness between 10 and 300 cm, are associated with reddish and brownish lutites, and present predominantly tabular geometries. The limestones frequently show bioturbations and include abundant remains of gastropods, ostracods and charophytes, as well as other organisms. The limestone levels are up to 200 cm thick, and are frequently grouped in packets of decametric thickness. The sedimentary facies represented in the Tudela Formation are similar to those described in other sectors of the cen-
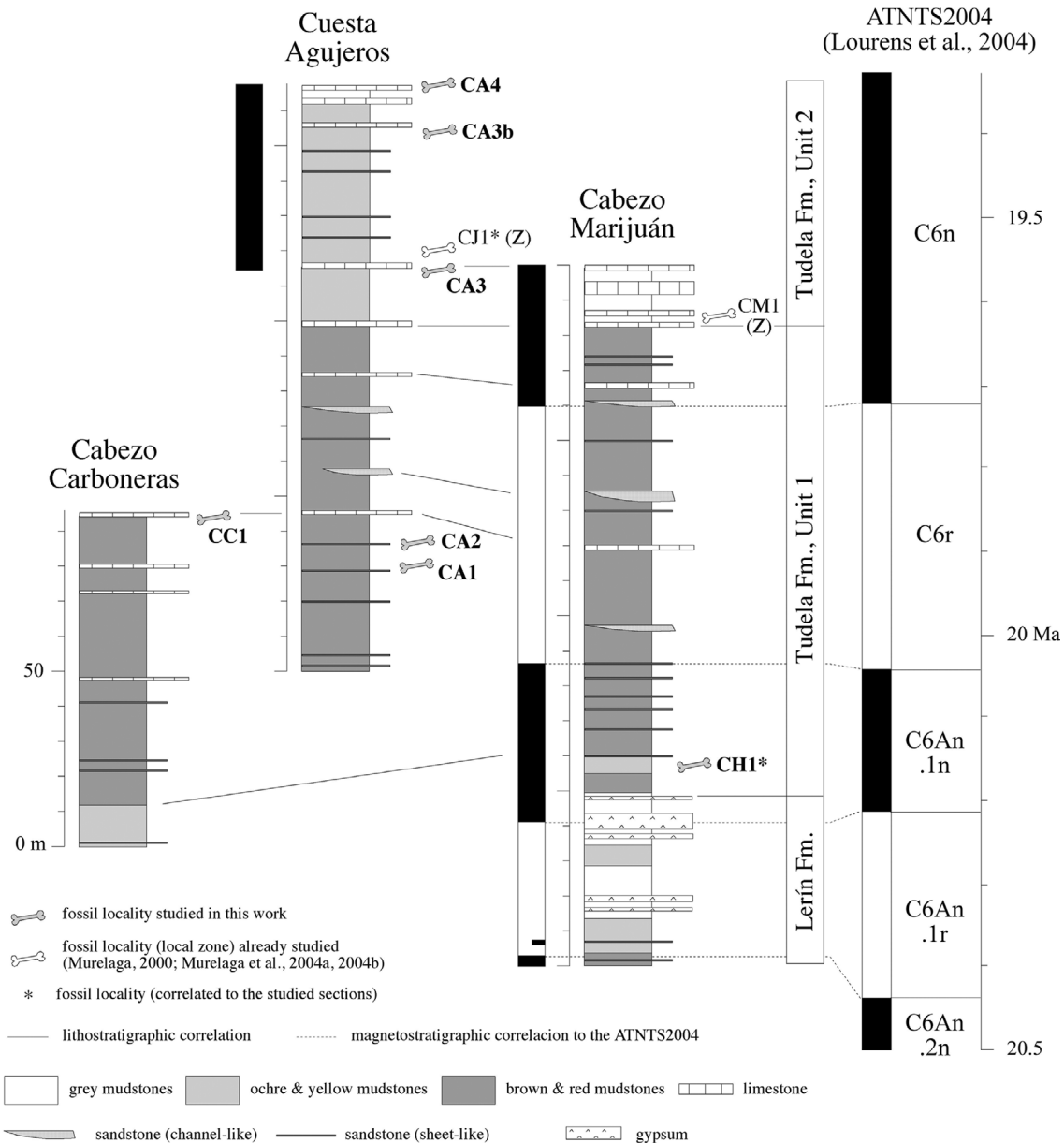

Fig. 2.- Stratigraphy of the Tudela Formation in the studied sections, with the localities presented in this work and other localities studied previously (Murelaga 2000; Murelaga et al. 2004a,b; Larrasoaña et al. 2006), and with the paleomagnetic sequence of the higher part of the section of Cuesta Agujeros and of the section of Cabezo Marijuán (see Larrasoaña *et al.* 2006), correlated with the ATNTS time scale of Lourens *et al.* (2004).

Fig. 2.- Estratigrafía de la Formación Tudela en las secciones estudiadas, con indicación de las localidades presentadas en este trabajo y en otros estudios previos (Murelaga, 2000; Murelaga *et al.,* 2004a,b; Larrasoaña *et al.,* 2006), y con la secuencia paleomagnética de la parte superior de las secciones de Cuesta Agujeros y Cabezo Marijuán (ver Larrasoaña *et al*., 2006), correlacionada con la escala de tiempo ATNTS de Lourens *et al.* (2004).

tral part of the basin (Arenas and Pardo, 1999; Alonso-Zarza *et al.*, 2002). The sandstones and the reddish and brown clays indicate the deposition in distal floodplains, whereas the sequences dominated by limestones and grey lutites indicate lacustrine zones. The palustrine transition between these zones is represented by yellowish and grey lutites that include thin intercalations of sandstones and limestones.

The fossil sites presented in this work are located in three sections that span the two lower units of the Tudela Formation (Figs. 1 and 2). Unit 1 is characterized by the predominance of fluvial distal facies with occasional intercalations of palustrine facies; unit 2 is characterized by the predominance of lacustrine and palustrine facies (Fig. 2) (Larrasoaña *et al.*, 2006). The sites studied in this work are situated in grey lutites of palustrine origin, except for CA2, which is in sandstone (Fig. 2). The lithostratigraphic correlation between the sections, together with available magnetostratigraphic data (Larrasoaña *et al.*, 2006), permit dating the fossiliferous sites between 19.65 and 17.5 Ma (Burdigalian) according to ATNTS2004 (Lourens *et al.*, 2004) (Fig. 2).

4. Systematic paleontology

Order: Rodentia Bowdich, 1821
Family: Cricetidae Fischer, 1817
Genus: *Eucricetodon* Thaler, 1966
Type species: *Cricetodon collatus* Schaub, 1925

Species: *Eucricetodon* sp.
(Fig. 3/1)

Locality: Cabezo Hermoso 1 (CH1)
Material: 1 incomplete m1 (CH1-1)
Description:

m1: Anteroconid, protoconid and metaconid are high, round cusps. The anteroconid is pointed and displaced towards the labial part of the tooth, presenting two anterolophids that connect with protoconid and metaconid. The labial anterolophid is low and connected to the base of the protoconid, whereas the lingual one is high and connected to the metaconid. The wall formed by anteroconid, lingual anterolophid and metaconid closes the anterosinusid completely. Anterolophulid absent.

Remarks: This small fragment is similar to the morphology described by Thaler (1966) for the m1 of *Eucricetodon*. The presence of inflated cusps, and the not divided anteroconid of the m1 of CH1 is characteristic of the different species of *Eucricetodon*.

Species: *Eucricetodon* cf. *gerandianus* (Schaub, 1925)
(Fig. 3/2)

Locality: Cuesta Agujeros 1 (CA1)
Material and measurements (L x W): 1 m1 (CA1-1)
(22.10 x 12.60)
Description:

m1: Anteroconid labially extended. Anterolophulid low and complete, connected to the anteroconid. Protoconid connected to the metaconid through the labial spur of the metalophulid. Metaconid connected to the anteroconid by a short crest that runs along the lingual part of the anterosinusid. Lingual wall of the metaconid moderately developed, without closing the mesosinusid. Mesoconid robust, developed towards the sinusid as well as to the mesosinusid. Mesolophid short.
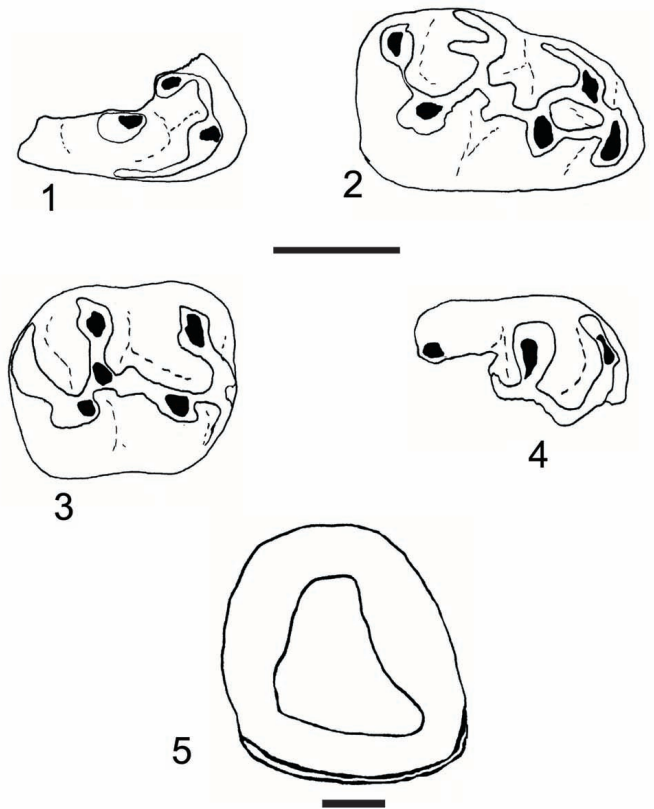

Fig. 3.- *Eucricetodon* sp. from Cabezo Hermoso 1 (CH1). 1, m1 dext. (CH1-1); *Eucricetodon* cf. *gerandianus* (Schaub, 1925) from Cuesta Agujeros 1 (CA1). 2, m1 dext. (CA1-1); *Eucricetodon* aff. *aquitanicus* Baudelot and de Bonis, 1968 from Cabezo Carboneras 1 (CC1). 3, m2 dext. (CC1-1); 4, m1,2 sin. (CC1-2); *Steneofiber* sp. from Cuesta Agujeros 4 (CA4). 5, Upper incisor (CA4-8). Scale: 1 mm.
Fig. 3.- *Eucricetodon* sp. de Cabezo Hermoso 1 (CH1). 1, m1 dext. (CH1-1); *Eucricetodon* cf. *gerandianus* (Schaub, 1925) de Cuesta Agujeros 1 (CA1). 2, m1 dext. (CA1-1); *Eucricetodon* aff. *aquitanicus* Baudelot and de Bonis, 1968 de Cabezo Carboneras 1 (CC1). 3, m2 dext. (CC1-1); 4, m1,2 sin. (CC1-2); *Steneofiber* sp. de Cuesta Agujeros 4 (CA4). 5, Incisivo superior (CA4-8). Escala: 1 mm.

Remarks: The size of the m1 of *Eucricetodon* cf. *gerandianus* from CA1 is slightly larger than in the same element of *E. gerandianus* and *E. longidens*, less than in *E. cetinensis* and within the range of *E. haslachensis, E. infralactorensis* and *E. aquitanicus*. The robust mesoconid and the short mesolophid are typical of the populations of *E. gerandianus* of unit MN2, and very different from the other species of the genus *Eucricetodon* (Hugueney, 1999a).

Species: *Eucricetodon aquitanicus* Baudelot and de Bonis, 1968 (Fig. 4/11-15)

Locality: Cuesta Agujeros 2 (CA2)
Material: 3 m1 (CA2-2/36, CA2-2/37, CA2-2/40), 2 m2 (CA2-1, CA2-2/35), 1 m3 (CA2-2/34) and 2 M3 (CA2-2/38, CA2-2/39).
Measurements: see Table 2.
Description:
m1: Two cingulums that descend from the anteroconid connect with protoconid and metaconid, closing the anterosinusid and the protosinusid. The continuous anterolophulid connects the protoconid with the anteroconid. The metalophulid is anterior and connected to the anteroconid. The posterior branch of the metalophulid is short and not connected to the protoconid. Mesoconid thick. Labial posterolophid short or absent. Mesolophid short. Ectomesolophid present in one out of three specimens. Posterior branch of protoconid and hypoconid absent.
m2: Lingual anterolophid absent. Labial anterolophid connected to the base of the protoconid, closing the pro-

tosinusid. Metalophulid slightly anterior. Sinusid directed backwards. Hypolophulid transverse or slightly anterior. Mesoconid thick. Mesolophid very short. Posterolophid high and closing the posterosinusid or descending towards the base of the entoconid, leaving the posterosinusid lingually open. In spite of the degree of wear, in one of the two specimens one can observe a short posterior branch of the hypoconid (CA2-2/35).
M3: Lingual anteroloph much reduced, almost non-existent. Labial anteroloph long and united to the base of the paracone. Protolophule slightly anterior. Sinus reduced. Neo-entoloph high and narrow. Axioloph absent or very low. Mesoloph absent. Centroloph long and connected to the labial wall.

Species: *Eucricetodon* aff. *aquitanicus* Baudelot and de Bonis, 1968 (Fig. 3/3-4)

Locality: Cabezo Carboneras 1 (CC1)
Material and measurements (L x W): 2 m2 (CC1-1, CC1-2) (17.51 x 14.77; x).
Description:
m2: Lingual anterolophid absent. Metalophulid transverse (1) or directed backwards (1). Mesolophid very short. Sinusid directed backwards. Posterolophid high.
Remarks: The size of the molars of *Eucricetodon* aff. *aquitanicus* from CA2 is in the range of measurements of *E. aquitanicus* from Laugnac and *E. infralactorensis* from Estrepouy, the type-localities of these species, and is larger than in *E. gerandianus*. The length of the m2 of *E.* aff. *aquitanicus* from CC1 is slightly inferior to that from Laugnac and Estrepouy, while the width coincides with the lower values in these French populations.

The morphology of *Eucricetodon* from the Navarra localities here studied is characterized by a reduced (very short) mesolophid in the lower molars and the slightly oblique orientation of the crests. In the lineage *E. collatus - E. infralactorensis* a progressive change in the orientation of the crests has been observed (Hugueney, 1999a). The younger species present oblique crests (directed backwards), whereas they are transverse in the older ones. In the lower molars from CA2 and CC1, the metalophulid is more oblique than the hypolophulid, which is almost transverse. The strongly oblique orientation of the crests is more pronounced in the populations of *E. infralactorensis* from MN3. The reduction of the length of the mesolophids of the lower molars is very similar to what has been described in the populations of *E. aquitanicus* and *E. infralactorensis* of MN2 and MN3. Therefore, we assign this material from CA2 and CC1 to *E.* aff. *aquitanicus*.

Element	Parameter	n	min.	mean	max.
m1	*L*	1	-	22.1	-
	W	2	14.6	14.6	14.7
m2	*L*	2	18.1	18.3	18.5
	W	2	15.2	15.3	15.5
m3	*L*	-	-	-	-
	W	1	-	12.6	-
M3	*L*	2	12.8	13.1	13.4
	W	2	11.8	12.4	12.9

Table 2.- Measurements (in tenths of mm) of the teeth of *Eucricetodon aquitanicus* from CA2. Abbreviations: L—Length; W—Width; m1—First lower molar; m2—Second lower molar; m3—Third lower molar; M3—Third upper molar.
Tabla 2.- Medidas (en décimas de milímetro) de los dientes de *Eucricetodon aquitanicus* de CA2. Abreviaciones: L—Longitud; W—Anchura; m1—Primer molar inferior; m2— Segundo molar inferior; m3— Tercer molar inferior; M3— Tercer molar superior.

Fig. 4.- *Ligerimys* aff. *magnus* Álvarez-Sierra, 1988 from Cuesta Agujeros 4 (CA4). 1, d4 sin. (CA4-1/22); 2, p4 sin. (CA4-1/11); 3, m1,2 dext. (CA4-1/10); 4, m3 sin. (CA4-1/16); 5, D4 dext. (CA4-1/14); 6, M1 dext. (CA4-2); 7, M2 sin. (CA4-1/15); 8, M3 sin. (CA4-1/20); Eomyidae indet. from Cuesta Agujeros 2 (CA2). 9, M1 sin. (CA2-2/31); *Pseudotheridomys* sp. from Cuesta Agujeros 4 (CA4). 10, D4 dext. (CA4-1/12); *Eucricetodon aquitanicus* Baudelot and de Bonis, 1968 from Cuesta Agujeros 2 (CA2). 11, m1 dext. (CA2-2/36); 12, m2 sin. (CA2-1); 13, m3 sin. (CA2-2/34); 14, M3 sin. (CA2-2/38); 15, M3 sin. (CA2-2/39); *Heteroxerus* cf. *paulhiacensis* Black, 1965 from Cuesta Agujeros 2 (CA2). 16, D4 sin. (CA2-3/2); 17, P4 dext. (CA2-3/1). Scale: 1 mm.

Fig. 4.- *Ligerimys* aff. *magnus* Álvarez-Sierra, 1988 de Cuesta Agujeros 4 (CA4). 1, d4 sin. (CA4-1/22); 2, p4 sin. (CA4-1/11); 3, m1,2 dext. (CA4-1/10); 4, m3 sin. (CA4-1/16); 5, D4 dext. (CA4-1/14); 6, M1 dext. (CA4-2); 7, M2 sin. (CA4-1/15); 8, M3 sin. (CA4-1/20); Eomyidae indet. de Cuesta Agujeros 2 (CA2). 9, M1 sin. (CA2-2/31); *Pseudotheridomys* sp. de Cuesta Agujeros 4 (CA4). 10, D4 dext. (CA4-1/12); *Eucricetodon aquitanicus* Baudelot and de Bonis, 1968 de Cuesta Agujeros 2 (CA2). 11, m1 dext. (CA2-2/36); 12, m2 sin. (CA2-1); 13, m3 sin. (CA2-2/34); 14, M3 sin. (CA2-2/38); 15, M3 sin. (CA2-2/39); *Heteroxerus* cf. *paulhiacensis* Black, 1965 de Cuesta Agujeros 2 (CA2). 16, D4 sin. (CA2-3/2); 17, P4 dext. (CA2-3/1). Escala: 1 mm.

Family: Gliridae Muirhead, 1819
Genus: *Altomiramys* Díaz Molina and López Martínez, 1979
Type species: *Altomiramys daamsi* Díaz Molina and López Martínez, 1979

Species: *Altomiramys* aff. *daamsi* Díaz Molina and López Martínez, 1979 (Fig. 5/1-5)

Locality: Cuesta Agujeros 2 (CA2)
Material and measurements (L x W): 2 m1 (CA2-1/26, CA2-1/27) (13.79 x 13.40; 12.11 x 12.71), 1 m2 (CA2-1/25) (13.75 x 13.88), 2 M1 (CA2-1/21, CA2-1/22) (12.53 x 13.44; 12.55 x).
Description:
m1: Low-crowned teeth, with narrow crests and broad valleys. The anterolophid is long and very narrow, connected to the protoconid or isolated from it. Lingually, the metalophid joins the metaconid; labially it curves and is connected or not with the anterolophid. Centrolophid connected to the metaconid or not connected, short, or more than half the width of the tooth. The centrolophid forms a pronounced right angle with the metaconid complex. Mesolophid and posterolophid fuse into the entoconid. The mesolophid of one of the teeth presents a small posterior spur. Posterotropid of medium length or absent.
m2: Low-crowned teeth, with narrow crests and broad valleys. Anterolophid not connected to the protoconid. The centrolophid is short (not more than ¼ of the width of the tooth) and forms a right angle with the metaconid complex. Mesolophid and posterolophid fuse into the entoconid. Accessory crests absent.
M1: Anteroloph isolated from the protocone and lower than that cusp. There is only one precentroloph, of medium length, connected to the paracone. Protoloph and metaloph connect at the lingual border to the protocone, forming an oblique Y. Posteroloph low connected to the protocone.
Remarks: The species *Altamiromys daamsi* was described on the basis of a single specimen in the locality of Loranca (upper part of unit MN2) (Díaz-Molina and López-Martínez, 1979). Daams (1989) enlarged the scarce knowledge of this species, describing a population from the locality of Ramblar 1 (Lower Ramblian). Daams (1999) cited the presence of unpublished material of this genus, which shows important similarities with *Peridyromys murinus*, in Spanish localities of unit MN1 and the lower part of MN2. Since then, no other record of this genus was published.
The size of the material from CA2 is somewhat different from the material described by Daams (1989) from Ram-

blar 1. In CA2, the length of m1,2 is somewhat smaller than in Loranca and Ramblar 1, whereas the width is similar to the m2 from Ramblar 1 and quite larger than the m1 from that locality. The size of the M1 from CA2 is clearly smaller than in Loranca and Ramblar 1.
The low crown, narrow crests and wide valleys are diagnostic characters of the genus *Altomiramys*. However, the material from CA2 shows some important differences, apart from size. One of these differences is the development of a short posterior spur on the middle of the mesolophid of one of the two m1 (Fig. 5/2). Another difference is the presence of a posterotropid in one of the two m1 (Fig. 5/1), characters not present in the population from Ramblar 1. The morphology of the m2 from CA2 is similar to the material from Ramblar 1, although the shape is more quadrate in CA2 (13.75 x 13.88) than in Ramblar 1, where it is subrectangular (14.10 x 13.10). The absence of the endoloph, the presence of an anteroloph with a lingual end that is much lower than the protocone, and the development of a precentroloph of medium length in the M1 of the *Altomiramys* from CA2 is very similar to what was described for *A. daamsi*. However, while in the M1 from CA2 the anteroloph is connected to the base of the paracone and the posteroloph to the base of the metacone, the two M1 of Ramblar 1 do not show this kind of connections.
Daams (1989) considered the material of *Pseudodryomys simplicidens* from Cetina de Aragón (Daams, 1974) to represent *Altomiramys* aff. *daamsi*. In that association, Daams (1989) observed, among other things, that 23% of the m1,2 lack accessory crests, and 23% of the M1,2 only have a precentroloph, concluding that these specimens belong to *Altomiramys* aff. *daamsi*.
The material of *Altomiramys* from CA2 differs from *A. daamsi* from Loranca and Ramblar 1 and coincides greatly with the description by Daams (1989) of *Altomiramys* aff. *daamsi* from Cetina de Aragón. Therefore, until more material is available, we classify this material as *A.* aff. *daamsi*.

Species: *Altomiramys* sp.
(Fig. 5/6)

Locality: Cuesta Agujeros 4 (CA4)
Material and measurements (L x W): 1 M2 (CA4-1/3) (x 14.93).
Description:
M2: Crests are narrow and well separated. Anteroloph long, connected to the paracone and not connected to the protocone. Protoloph continuous and connected to the paracone. The lingual portion of the protoloph is longitu-
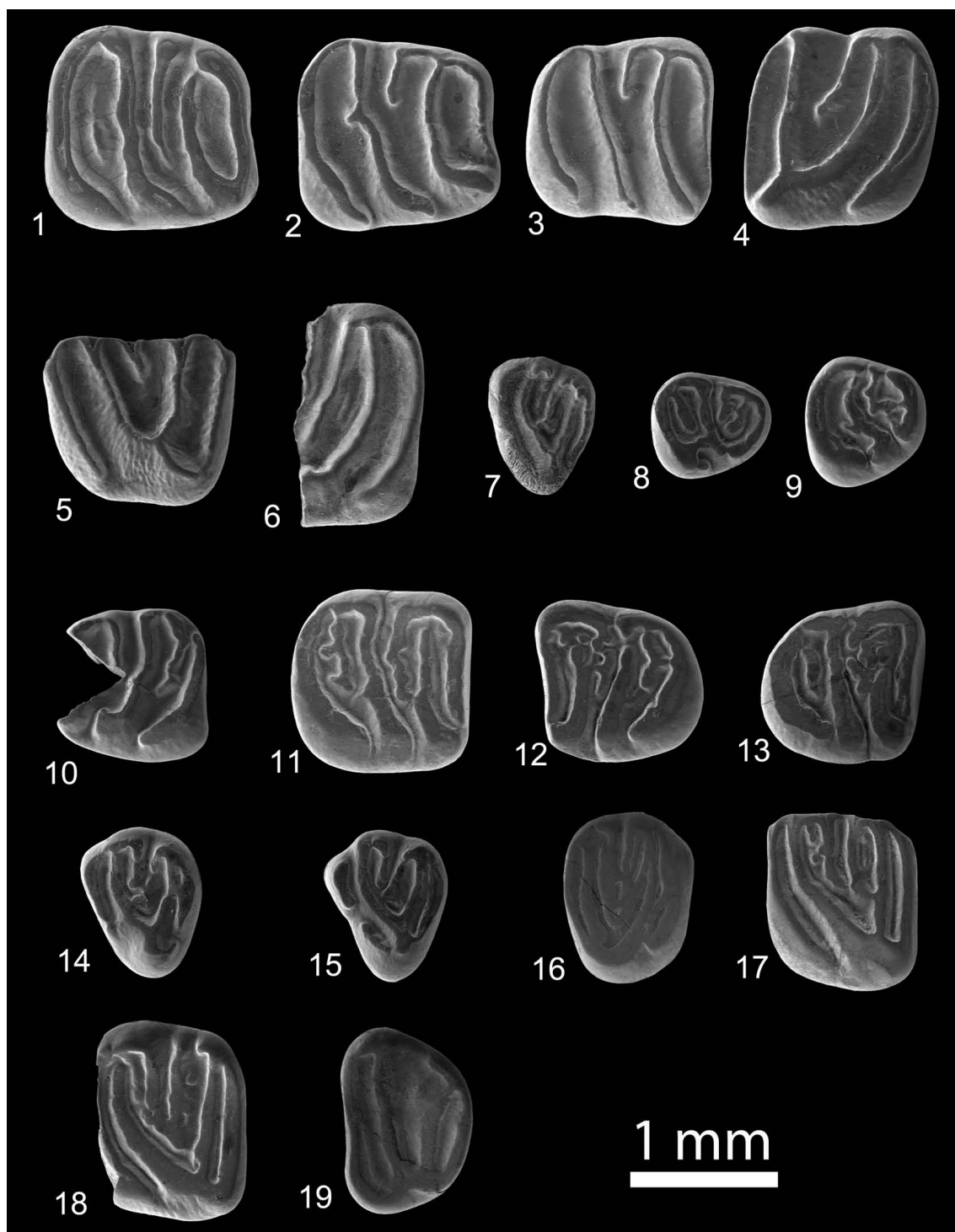
Fig. 5.- *Altomiramys* aff. *daamsi* Díaz Molina and López Martínez, 1979 from Cuesta Agujeros 2 (CA2). 1, m1 dext. (CA2-1/26); 2, m1 dext. (CA2-1/27); 3, m2 dext. (CA2-1/25); 4, M1 dext. (CA2-1/21); 5, M1 sin. (CA2-1/22); *Altomiramys* sp. from Cuesta Agujeros 4 (CA4). 6, M2 dext. (CA4-1/3); cf. *Vasseuromys* sp. from Cuesta Agujeros 2 (CA2). 7, D4 sin. (CA2-2/22); *Peridyromys turbatus* Álvarez et al., 1990 from Cuesta Agujeros 2 (CA2). 8, d4 dext. (CA2-2/21); 9, p4 dext. (CA2-2/23); 10, m1 sin. (CA2-2/30); 11, m2 dext. (CA2-1/24); 12, m3 sin. (CA2-1/30); 13, m3 dext. (CA2-1/32); 14, D4 sin. (CA2-1/17); 15, D4 sin. (CA2-2/18); 16, P4 dext. (CA2-1/19); 17, M1 sin. (CA2-1/29); 18, M2 sin. (CA2-1/23); 19, M3 sin. (CA2-1/31). Scale: 1 mm.

Fig. 5.- *Altomiramys* aff. *daamsi* Díaz Molina and López Martínez, 1979 de Cuesta Agujeros 2 (CA2). 1, m1 dext. (CA2-1/26); 2, m1 dext. (CA2-1/27); 3, m2 dext. (CA2-1/25); 4, M1 dext. (CA2-1/21); 5, M1 sin. (CA2-1/22); *Altomiramys* sp. de Cuesta Agujeros 4 (CA4). 6, M2 dext. (CA4-1/3); cf. *Vasseuromys* sp. de Cuesta Agujeros 2 (CA2). 7, D4 sin. (CA2-2/22); *Peridyromys turbatus* Álvarez et al., 1990 de Cuesta Agujeros 2 (CA2). 8, d4 dext. (CA2-2/21); 9, p4 dext. (CA2-2/23); 10, m1 sin. (CA2-2/30); 11, m2 dext. (CA2-1/24); 12, m3 sin. (CA2-1/30); 13, m3 dext. (CA2-1/32); 14, D4 sin. (CA2-1/17); 15, D4 sin. (CA2-2/18); 16, P4 dext. (CA2-1/19); 17, M1 sin. (CA2-1/29); 18, M2 sin. (CA2-1/23); 19, M3 sin. (CA2-1/31). Escala: 1 mm.

dinal, parallel to the lingual border. Precentroloph long. Between protoloph and precentroloph a short prototrope is present.

Remarks: One of the striking morphological characters of this specimen is the small width of the crests, a morphology that is typical of the genus *Altomiramys* (Díaz Molina and López-Martínez, 1979; Daams, 1989; Daams, 1999). The original diagnosis of the genus gives as diagnostic character the presence of a single centroloph (precentroloph). In Ramblar 1, Daams (1989) confirmed this character in the M1 and described a second centroloph (postcentroloph) in the M2. Apart from the presence of this second centroloph, Daams (1989) described in some of the M2 from Ramblar 1 the existence of a small accessory crest, which would be the prototrope according to the nomenclature of Freudenthal (2004), used in this work.

The specimen CA4-1/3 is broken. Therefore, it is difficult to know whether it is a M1 or a M2. However, the lingual end of the protoloph shows a change of orientation, from oblique to longitudinal (Fig. 5/6), which is typical of the M2 of the majority of representatives of the family Gliridae. In the posterior part of this specimen a short postcentroloph seems to be present (Fig. 5/6).

The presence of widely separated narrow crests, of a long precentroloph, a short prototrope and of a possible postcentroloph in this M2 permit to refer this fragment to the genus *Altomiramys*.

Until now, the genus *Altomiramys* had been recognized in localities of the Iberian Peninsula in the interval between unit MN1 and the lower part of unit MN3 (local zone Z). The accompanying fauna in CA4 (*Pseudotheridomys* sp., *Ligerimys* aff. *magnus* and *Armantomys* cf. *jasperi*) permits to attribute this locality to the Upper Ramblian (local zone A, MN3), which constitutes an upward extension of its range.

Genus: *Peridyromys* Stehlin and Schaub, 1951
Type species: *Peridyromys murinus* (Pomel, 1853)

Species: *Peridyromys murinus* (Pomel, 1853)
(Fig. 6/1)

Locality: Cuesta Agujeros 3 (CA3)
Material and measurements (L x W): 1 d4 (CA3-1/8) (7.33 x 6.18), 3 M1,2 (CA3-1/3, CA3-1/5, CA3-1/6) (9.78 x 10.82; 9.18 x 9.80; 9.39 x).
Description:
d4: Narrower anteriorly than posteriorly. The anterior valley presents two parallel crests. The posterior valley is closed. Posterotropid absent.

M1,2: Anteroloph long and not connected to protocone or paracone. Protoloph long and oblique, connected to the metaloph in Y-pattern. Pre- and postcentroloph present. Precentroloph longer than postcentroloph. Metaloph transverse. Posteroloph connected to the metacone or not connected.

Remarks: In size, the material of *Peridyromys murinus* from CA3 is very similar to other populations (Álvarez-Sierra *et al.*, 1990; Murelaga, 2000; Murelaga *et al.*, 2004a). The development of a complete pre- and postcentroloph in the M1,2 from CA3 coincides with morphotype C described by Daams (1981). This morphotype is dominant (between 60% in La Galocha 5 and 76% in Santa Cilia) in the M1,2 of Iberian populations of *P. murinus*.

Species: cf. *Peridyromys murinus* (Pomel, 1853)
(Fig. 6/2)

Locality: Cuesta Agujeros 4 (CA4)
Material and measurements (L x W): 1 M3 (CA4-1/2) (6.86 x 8.85).
Description:
M3: Endoloph continuous. Anteroloph and protoloph connected to the paracone. Precentroloph of medium length. Postcentroloph absent. Posteroloph short and separated from the metacone by a narrow groove.
Remarks: The small size of this specimen, the presence of a single centroloph (precentroloph) of medium length and the degree of connection between anteroloph and protocone in the M3 of CA4 are characteristic of *P. murinus* from the Lower Miocene.

Species: *Peridyromys turbatus* Álvarez et al., 1990
(Fig. 5/8-19)

Locality: Cuesta Agujeros 2 (CA2)
Material: 3 d4 (CA2-6, CA2-2/21, CA2-2/26), 3 p4 (CA2-1/44, CA2-2/23, CA2-2/29), 1 m1 (CA2-2/30), 2 m2 (CA2-1/24, CA2-2/14), 3 m3 (CA2-1/30, CA2-1/32, CA2-2/11), 3 D4 (CA2-1/16, CA2-1/17, CA2-2/18), 1 P4 (CA2-1/19), 2 M1 (CA2-1/29, CA2-2/7), 1 M2 (CA2-1/23), 2 M3 (CA2-1/31, CA2-2/17).
Measurements: see Table 3.
Description:
d4: Narrower anteriorly than posteriorly. The anterior valley presents two small parallel crests that run from the lingual border almost to the labial border, and which are connected halfway. The posterior valley is closed and presents a long posterotropid, connected to the entoconid.
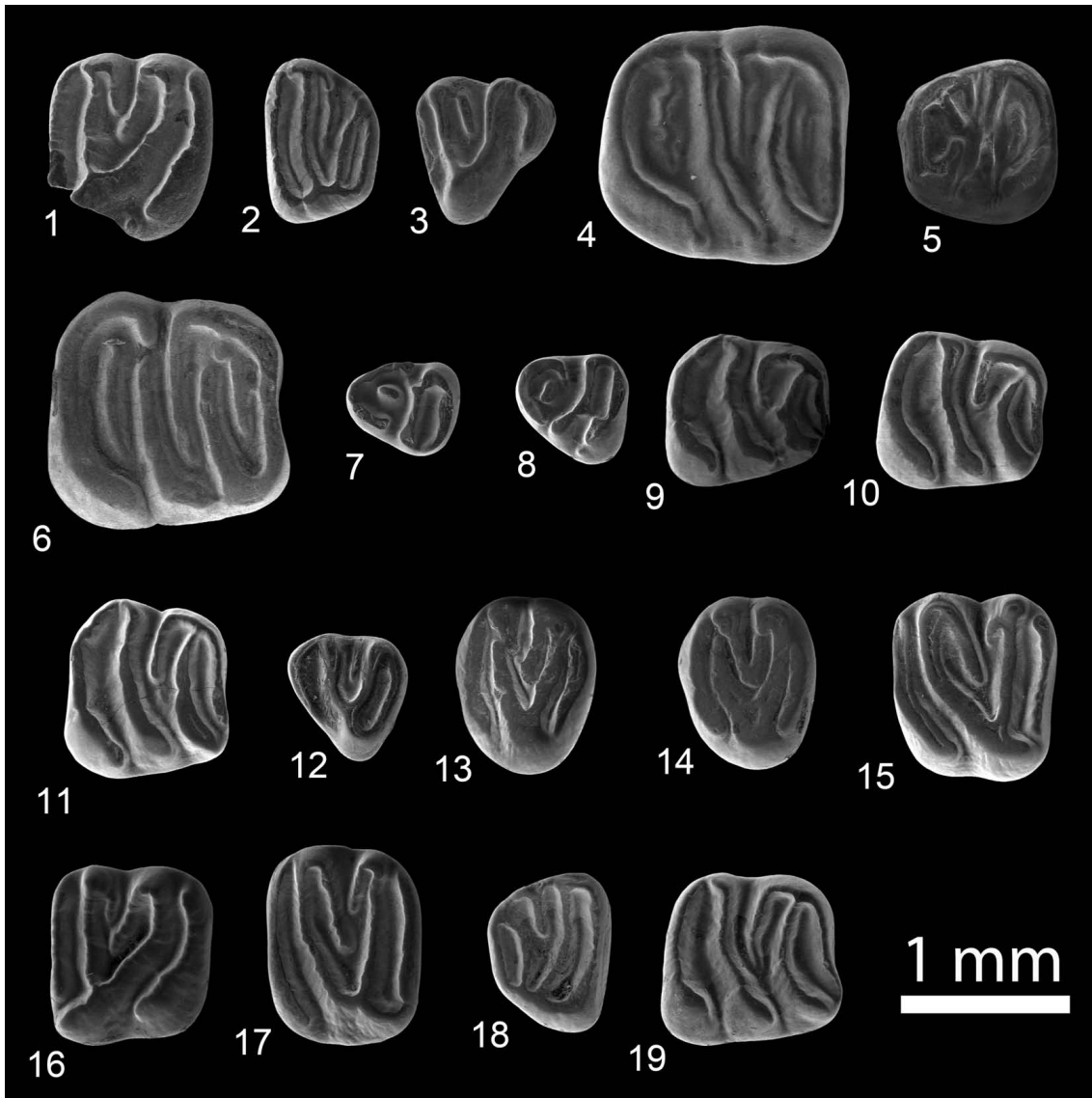
Fig. 6.- *Peridyromys murinus* (Pomel, 1853) from Cuesta Agujeros 3 (CA3). 1, M1 dext. (CA3-1/3); cf. *Peridyromys murinus* from Cuesta Aguje-
ros 4 (CA4). 2, M3 sin. (CA4-1/2); cf. *Prodryomys* sp. from Cuesta Agujeros 2 (CA2). 3, D4 dext. (CA2-2/19); *Prodryomys* cf. *brailloni* (Thaler,
1966) from Cuesta Agujeros 3B (CA3B). 4, m2 dext. (CA3B-1); *Prodryomys* cf. *brailloni* from Cuesta Agujeros 4 (CA4). 5, p4 sin. (CA4-4);
6, m1 dext. (CA4-1/1); *Simplomys* aff. *aljaphi* Hugueney et al. 1978 from Cuesta Agujeros 2 (CA2). 7, d4 dext. (CA2-2/28); 8, p4 sin. (CA2-
2/25); 9, m1 dext. (CA2-1/36); 10, m1 dext. (CA2-1/37); 11, m2 dext. (CA2-1/40); 12, D4 sin. (CA2-2/20); 13, P4 sin. (CA2-1/18); 14, P4 sin.
(CA2-1/20); 15, M1 sin. (CA2-1/34); 16, M1 dext. (CA2-1/35); 17, M2 sin. (CA2-1/33); 18, M3 dext. (CA2-2/16); 19, m2 dext. (CA2-1/39).
Scale: 1 mm.
Fig. 6.- *Peridyromys murinus* (Pomel, 1853) de Cuesta Agujeros 3 (CA3). 1, M1 dext. (CA3-1/3); cf. *Peridyromys murinus* de Cuesta Agujeros 4
(CA4). 2, M3 sin. (CA4-1/2); cf. *Prodryomys* sp. de Cuesta Agujeros 2 (CA2). 3, D4 dext. (CA2-2/19); *Prodryomys* cf. *brailloni* (Thaler, 1966)
de Cuesta Agujeros 3B (CA3B). 4, m2 dext. (CA3B-1); *Prodryomys* cf. *brailloni* de Cuesta Agujeros 4 (CA4). 5, p4 sin. (CA4-4); 6, m1 dext.
(CA4-1/1); *Simplomys* aff. *aljaphi* Hugueney et al., 1978 de Cuesta Agujeros 2 (CA2). 7, d4 dext. (CA2-2/28); 8, p4 sin. (CA2-2/25); 9, m1
dext. (CA2-1/36); 10, m1 dext. (CA2-1/37); 11, m2 dext. (CA2-1/40); 12, D4 sin. (CA2-2/20); 13, P4 sin. (CA2-1/18); 14, P4 sin. (CA2-1/20);
15, M1 sin. (CA2-1/34); 16, M1 dext. (CA2-1/35); 17, M2 sin. (CA2-1/33); 18, M3 dext. (CA2-2/16); 19, m2 dext. (CA2-1/39). Escala: 1 mm.

p4: The configuration of the crests in the anterior part is chaotic. The posterior part is formed by the mesolophid and the posterolophid that close the posterior valley lingually. In two of the three specimens, the middle part of the mesolophid develops a short posterior spur, possibly related with the posterotropid. In two of the three specimens, a posterotropid, which is continuous or formed by two smalls cusps, is present in the posterior valley.

m1: The only specimen is broken anteriorly. Centrolophid of medium length. There is no connection of the metalophid with the metaconid. Mesolophid somewhat sinuous. Mesolophid and posterolophid connected to the entoconid. From the entoconid a sinuous posterotropid reaches the middle of the tooth.

Element	Parameter	n	min.	mean	max.
d4	L	1	-	7.11	-
	W	2	6.14		6.84
p4	L	3	7.99	8.29	8.83
	W	3	7.53	8.20	8.61
m1	L	0	-	-	-
	W	1	-	9.96	-
m2	L	2	11.75	11.79	11.82
	W	1	-	12.03	-
m3	L	3	10.56	10.84	11.24
	W	3	10.24	10.38	10.67
D4	L	3	8.18	8.69	9.09
	W	3	9.63	9.81	10.06
P4	L	1	-	7.93	-
	W	1	-	11.23	-
M1	L	2	9.87	10.10	10.32
	W	2	12.06	12.71	13.35
M2	L	0	-	-	-
	W	1	-	13.20	-
M3	L	2	6.77	7.41	8.05
	W	2	9.37	10.48	11.58

Table 3.- Measurements (in tenths of mm) of the teeth of *Peridyromys turbatus* Álvarez *et al.,* 1990 from CA2. Abbreviations: L—Length; W—Width; d4—Fourth lower decidual; p4—Fourth lower premolar; m1—First lower molar; m2—Second lower molar; m3—Third lower molar; D4—Fourth upper decidual; P4—Fourth upper premolar; M1—First upper molar; M2—Second upper molar; M3—Third upper molar.

Tabla 3.- Medidas (en décimas de milímetro) de los dientes de *Peridyromys turbatus* Álvarez *et al*., 1990 de CA2. Abreviaciones: L—Longitud; W—Anchura; d4—Cuarto decidual inferior; p4—Cuarto premolar inferior; m1—Primer molar inferior; m2— Segundo molar inferior; m3— Tercer molar inferior; D4—Cuarto decidual superior; P4—Cuarto premolar superior; M1—Primer molar superior; M2— Segundo molar superior; M3— Tercer molar superior.

m2: Anterolophid and metalophid not connected to protoconid and entoconid, respectively. Centrolophid sinuous, medium-long, not reaching the labial border. One specimen has a small accessory crest in the central valley. In the other specimen, two small accessory crests in the central valley are connected to the centrolophid. Mesolophid and posterolophid connected to the entoconid. In one of the specimens, the mesolophid has a small posterior spur (Fig. 5/11). Posterotropid sinuous and of medium length, not connected to the entoconid or connected (Fig. 5/11). In this latter specimen the posterotropid presents two short posterior spurs, one of which is low connected to the posterolophid.

m3: Anterolophid not connected to the protoconid. Metalophid not connected to the metaconid and with a chaotic configuration. In all the specimens, the centrolophid is of medium length with several connections to the chaotic lingual part of the metalophid and to its continuous labial part. Mesolophid sinuous, continuous (1) (Fig. 5/13) or interrupted (2) (Fig. 5/12), and generally connected to the entoconid. Posterolophid connected to the entoconid. Posterotropid sinuous and medium-long. In one of the three specimens, the posterotropid is connected labially to the mesolophid and has a posterolingual spur, connected to the posterolophid (Fig. 5/12).

D4: Anteroloph of medium length or long, continuous (Fig. 5/14) or interrupted (Fig. 5/15), connected or not to paracone and protocone. Pre- and postcentroloph present in all specimens; the postcentroloph is longer than the precentroloph, connected to the protoloph. The precentroloph in two of the three specimens is connected to the postcentroloph. Posteroloph continuous (1) (Fig. 5/15) or interrupted (2) (Fig. 5/14), connected (2) to the metacone or not connected (1), and isolated (2) (Fig. 5/14) or not (1) (Fig. 5/15) from the protocone.

P4: Anteroloph long, separated from protocone and paracone by a narrow groove. Pre- and postcentroloph present and connected to paracone and metacone, respectively. The postcentroloph is longer than the precentroloph and these crests are interconnected in two points. Posteroloph well developed.

M1: Endoloph absent. Protocone strongly displaced towards the posterolingual border. Pre- and postcentroloph present. Prototrope present in both specimens; metatrope present in one of the two. The centrolophs connect at their lingual end. The postcentroloph is curved and connected to the completely transverse metaloph. Posteroloph high and connected to the protocone.

M2: Endoloph absent. Protoloph not connected to the paracone. Pre- and postcentroloph present. The precentroloph is connected to the paracone and the postcentroloph not connected to the metacone. Prototrope of medium length. Metatrope medium-long, with several connections to the postcentroloph, in a chaotic way. Metaloph slightly oblique. Posteroloph connected to the protocone and separated from the metacone by a narrow groove.

M3: Endoloph present. Anteroloph and protoloph connected to the paracone. Precentroloph short. Postcentroloph long, with a curved lingual end and connected to the metaloph. Posteroloph of medium length, connected to the metaloph.

Remarks: The species *Peridyromys turbatus* was first described from the locality of San Juan (Álvarez-Sierra *et al*., 1990). The size of *P. turbatus* from CA2 is very simi-

lar to that from the type-locality, and clearly larger than *P. murinus*. Only the M3 from CA2 is somewhat smaller than that of *P. murinus*.

The lower dentition of *Peridyromys turbatus* from CA2 is very similar to that from the type-locality, San Juan. Some morphological characters, however, are different: The centrolophid of the m3 from CA2 is more continuous than in the material from San Juan. In *P. turbatus* from San Juan, the metalophid and centrolophid are discontinuous; in CA2 that morphology is only present in the metalophid, whereas the centrolophid is continuous.

The upper molars from CA2 are very similar to those from the type-locality. Only the M3 from CA2 has a more simple pattern than in San Juan. In San Juan more than 90% of the specimens have an accessory crest, the single specimen from CA2 does not have one.

The only differences between the populations of *Peridyromys turbatus* from San Juan and CA2 are observed in the D4 and P4: the D4 from CA2 has pre- and postcentroloph connected, and a posteroloph not connected to the protocone in two out of three specimens; in the P4 from CA2 there are two connections between the centrolophs, whereas there is only one connection in D4 and P4 from San Juan.

The chaotic pattern of the crests, the oblique trigone of the M1 and the absence of accessory crests between the centrolophs of the upper molars of the population from CA2, distinguish this material clearly from *Peridyromys jaegeri* and *P. aquatilis*. The size and general morphology of the material from CA2 is clearly distinct from *P. murinus*.

The slight differences observed between the populations from CA2 and San Juan don't appear to be relevant at species level. We refer this material to *P. turbatus*.

Genus: *Prodryomys* Mayr, 1979
Type species: *Prodryomys satus* Mayr, 1979

Species: cf. *Prodryomys* sp.
(Fig. 6/3)

Locality: Cuesta Agujeros 2 (CA2)
Material and measurements (L x W): 2 D4 (CA2-2/19, CA2-2/27) (7.49 x 8.63;x).
Description:
D4: Anteroloph of medium length, isolated from the protocone and connected to the paracone. Postcentroloph of medium length and connected to the metacone. Posteroloph long, lingually low, connected to the metacone and the protocone at low or high level.
Remarks: The morphology of the anteroloph and the degree of development of the centrolophs is similar to the

D4 of *Peridyromys* (*Prodryomys*) *brailloni* from La Galocha 5 (Álvarez-Sierra *et al.*, 1990). On the other hand, the general morphology of this specimen is very different from the other D4 from CA2.

Species: *Prodryomys* cf. *brailloni* (Thaler, 1966)
(Fig. 6/4-6)

Locality: Cuesta Agujeros 3B (CA3B)
Material and measurements (L x W): 1 m2 (CA3B-1) (14.31 x 13.40).
Description:
m2: Anterolophid connected to the protoconid. Metalophid connected to the protoconid and to the base of the metaconid. The metalophid surpasses the middle of the tooth. Mesolophid and posterolophid continuous and connected to the entoconid. Two accessory crests are present, an anterotropid of medium length and a medium-long posterotropid.
Remarks: The general morphology and the size of the m2 from CA3B-1 are very similar to those of the populations of *Prodryomys brailloni* from MN3. The size of this scarce material is clearly smaller than that of other species of the genus (*P. gregarius* and *P. remmerti*) and larger than *P. satus*.

Morphologically, the single available molar from CA3B presents broad and shallow valleys and two accessory crests, one in the anterior valley (anterotropid) and one in the posterior valley (posterotropid). The development of these accessory crests is very similar to those described from Bouzigues, type-locality of *P. brailloni* (Thaler, 1966; Aguilar, 1974) and La Galocha 5 (Ebro Basin, MN3; Álvarez-Sierra *et al.*, 1990).

Locality: Cuesta Agujeros 4 (CA4)
Material and measurements (L x W): 1 p4 (CA4-4) (9.45 x 9.36), 1 m1 (CA4-1/1) (14.05 x 13.38), 1 M1,2 (CA4-1/5) (x).
Description:
p4: Anterolophid connected to the protoconid. Metalophid not continuous and connected to protoconid and metaconid. The metaconid gives rise to a short centrolophid. Mesolophid and posterolophid continuous and connected to the entoconid. Posterotropid long.
m1: Anterolophid connected to the protoconid. Metalophid connected to the protoconid and separated from the metaconid. Anterotropid long and connected to the metalophid at its lingual end. Centrolophid long and free, not reaching the labial border. Mesolophid interrupted near the lingual border. Posterolophid thick and connected to the entoconid. Posterotropid long.

M1,2: Only the anterolabial part is preserved. The anterior valley is wide and shallow. Anteroloph connected to the paracone at medium height. In the central valley there are two centrolophs.

Remarks: The general morphology and the size of this material is very similar to *Prodryomys brailloni*, described by Álvarez-Sierra *et al.* (1990) from the localities of La Galocha 5 and San Juan.

Prodryomys from CA4 has brachyodont molars with broad and shallow valleys, and thick crests. The presence in m1 of a metalophid that is not connected to the metaconid reminds one of *Peridyromys*, but the much larger size of the material from CA4 distinguishes it clearly from the species of that genus from the Lower Miocene.

The scarce material available of this taxon impedes a precise determination.

Genus: *Simplomys* García-Paredes, 2009 (in García-Paredes *et al.* 2009)
Type species: *Pseudodryomys simplicidens* de Bruijn, 1966

Species: *Simplomys* aff. *aljaphi* (Hugueney *et al.* 1978) (Fig. 6/7-19)

Locality: Cuesta Agujeros 2 (CA2)
Material: 1 d4 (CA2-2/28), 1 p4 (CA2-2/25), 3 m1 (CA2-1/36, CA2-1/37, CA2-1/38), 3 m2 (CA2-1/39, CA2-1/40, CA2-1/41), 1 D4 (CA2-2/20), 2 P4 (CA2-1/18, CA2-1/20), 4 M1 (CA2-2, CA2-1/34, CA2-1/35, CA2-2/12), 2 M2 (CA2-1/33, CA2-2/13), 1 M3 (CA2-2/16).

Measurements: see Table 4.
Description:

d4: Tooth with suboval outline and a very simple crest pattern. The anterior part is formed by a continuous crest that runs from the lingual border, near the base of the entoconid to close to the mesoconid. In the center of the anterior valley a small crest/cusp is present. Mesolophid and posterolophid enclose a posterior valley without accessory crests.

p4: Tooth with suboval contour and a little concave. The reduced anterior part is formed by a curved crest with a labial spur that appears to be the metalophid. The mesolophid is longer than the posterolophid, connected to the latter near the labial border, thus dividing the posterior valley into a large lingual part and a smaller labial part.

m1: Teeth with subrectangular outline. Anterolophid short and not connected to the protoconid. Centrolophid curved and long; in two specimens it reaches the middle of the tooth (Fig. 6/10), and in one it is longer (Fig. 6/9),

Element	Parameter	n	min.	mean	max.
d4	*L*	1	-	6.02	-
	W	1	-	5.46	-
p4	*L*	1	-	6.25	-
	W	1	-	6.16	-
m1	*L*	3	8.83	9.30	9.55
	W	3	8.32	8.74	8.96
m2	*L*	3	9.59	9.75	9.84
	W	3	8.97	9.65	10.36
D4	*L*	1	-	6.71	-
	W	1	-	7.12	-
P4	*L*	2	8.27	8.46	8.64
	W	2	9.82	9.92	10.01
M1	*L*	4	8.50	9.04	9.27
	W	4	10.24	10.47	10.68
M2	*L*	1	-	8.92	-
	W	1	-	11.40	-
M3	*L*	1	-	6.54	-
	W	1	-	9.01	-

Table 4.- Measurements (in tenths of mm) of the teeth of *Simplomys* aff. *aljaphi* Hugueney *et al.* 1978 from CA2. Abbreviations: L—Length; W—Width; d4—Fourth lower decidual; p4—Fourth lower premolar; m1—First lower molar; m2—Second lower molar; D4—Fourth upper decidual; P4—Fourth upper premolar; M1—First upper molar; M2—Second upper molar; M3—Third upper molar.

Tabla 4.- Medidas (en décimas de milímetro) de los dientes de *Simplomys* aff. *aljaphi* Hugueney *et al.*, 1978 de CA2. Abreviaciones: L—Longitud; W—Anchura; d4—Cuarto decidual inferior; p4—Cuarto premolar inferior; m1—Primer molar inferior; m2— Segundo molar inferior; D4—Cuarto decidual superior; P4—Cuarto premolar superior; M1—Primer molar superior; M2— Segundo molar superior; M3— Tercer molar superior.

connecting to the metalophid near the labial border of the tooth. Mesolophid and posterolophid long and connected to the entoconid.

m2: Subquadrangular. Anterolophid not connected to the protoconid. Centrolophid curved and long, reaching beyond the middle of the tooth. In two of the three specimens the labial end of the centrolophid is low connected to the metalophid. Mesolophid long and connected to the entoconid. Posterolophid long and connected to the entoconid at mid-height. In one of the three specimens, there are two tiny, low accessory crests, one between centrolophid and mesolophid and another one (posterotropid) in the posterior valley.

D4: Anteroloph of medium length, connected to the paracone. Protoloph and metaloph of equal length, united

in a Y-shape. Postcentroloph low and of medium length. Posteroloph long and connected to protocone and paracone.

P4: Teeth of suboval contour. Anteroloph long and not connected to protocone or paracone. Protoloph and metaloph united to the protocone in a V-shape. In one specimen (Fig. 6/15), pre- and postcentroloph are large and united in the central valley. In the other one (Fig. 6/14), the precentroloph is short and the postcentroloph long and they are not connected. Posteroloph of medium length to long, somewhat shorter than the anteroloph.

M1: Anteroloph medium-long, not connected to protocone or paracone. The lingual part of the anteroloph is very much separated from the protocone. Protoloph strongly oblique, directed towards posterior, where it connects to the protocone, together with the metaloph near the posterolingual border. Precentroloph long. Postcentroloph absent (1), very short (1) or short (2). The centrolophs are not interconnected. Posteroloph transverse, not connected to paracone or protocone (3) (Fig. 6/17) or to the protocone only (1) (Fig. 6/16). No accessory crests neither inside nor outside the trigone.

M2: Subrectangular, broader than long. Anteroloph not connected to the protocone nor to the paracone. The lingual portion of the anteroloph is separated from the protocone, but not as much as in M1. Protoloph oblique, connected to the protocone near the transverse metaloph. Precentroloph very long. Postcentroloph of medium length, not connected to the precentroloph. Posteroloph not connected to the protocone nor to the paracone (1) or to the protocone only (1).

M3: Subtrapezoidal. The anterior part is quite broader than the posterior part. Endoloph continuous. The cusps and crests of the labial wall are connected. The labial and lingual ends of the anteroloph are curved backwards. Protoloph curved posterolingually. Precentroloph of medium length. No accessory crests.

Remarks: The sizes of the specimens from CA2 are, in general, slightly smaller than those from the localities of the Upper Agenian (San Juan) and Lower Ramblian (La Galocha 5) from the Ebro basin, where *Peridyromys murinus* (Álvarez-Sierra *et al.*, 1990) is found, and much smaller than that of *Pseudodryomys ibericus* from the same basin. The development of the accessory crests in the m1,2 from CA2 is very different from *P. ibericus*, and not exactly the same as in *P. murinus*. Although *Simplomys* is not abundant in CA2, the presence of one among three m2 with accessory crests in the central and posterior valley is clearly different from what happens in *P. murinus*, and very similar to what is said in the emended diagnosis (García-Paredes *et al.*, 2009) of *Simplomys aljaphi*.

The M1,2 of *S. aljaphi* from the type-locality, Montaigu-le-Blin (France), are characterized by having almost parallel protoloph and metaloph, connected to the protocone at the lingual border. The M1,2 of *S.* aff. *aljaphi* from CA2 have a morphology of these crests (especially of the protoloph) which is quite different from the French population. In the M1 from CA2 that difference is more notable than in the M2. In the M2 from CA2, the protoloph is not as oblique as in the M1. The disposition of the trigone of *S.* aff. *aljaphi* from CA2 reminds one very much of *Peridyromys*.

Simplomys is characterized by a reduction of the length of the mesolophid in the p4 and m3, which tends to reduce the extension of the posterior valley (García-Paredes *et al.*, 2009). The mesolophid is reduced, and may be connected to the posterolophid at variable height, reducing the posterior valley, as occurs in *S. aljaphi* from Montaigu-le-Blin, or obliterating it completely, as occurs in many specimens of *S. julii* from the Spanish and French localities of MN3-MN4. In the single p4 from CA2, the mesolophid and the posterolophid are united towards the middle of the tooth, subdividing the posterior valley in two parts. In the process of reduction of the posterior valley that morphology may be interpreted as more primitive, even more so than in the oldest species of the genus, *S. aljaphi*.

Another primitive morphology observed in the lower molars of *Simplomys* in CA2 is the development of the centrolophid. According to García-Paredes *et al.* (2009), the centrolophid in the species of the genus varies from a short prolongation to a well-developed crest that extends in the central valley and that never continues beyond the central axis of the occlusal surface. In this respect, according to these authors, the more derived dental morphology is observed in some of the younger forms of the genus, e.g., *S. meulenorum* and *S. julii*. The more primitive morphology corresponds to *S. aljaphi*, the species that conserves the longest centrolophids. In CA2, the length of the centrolophid is even larger than in *S. aljaphi*, with specimens in which the centrolophid is long, curved and occasionally united to the metalophid, surpassing the middle of the tooth in more than 50% of the lower molars. According to García-Paredes *et al.* (2009), that morphology would be the most primitive of the genus.

Genus: *Vasseuromys* Baudelot and de Bonis, 1966
Type species: *Vasseuromys rugosus* Baudelot and de Bonis, 1966

Species: cf. *Vasseuromys* sp.
(Fig. 5/7)

Locality: Cuesta Agujeros 2 (CA2)
Material and measurements (L x W): 1 D4 (CA2-2/22) (6.64 x 9.15).
Description:
D4: Subtriangular outline. Anteroloph long, low in its lingual part and connected to protocone and paracone. Protoloph oblique, connected lingually in a Y-shape to the slightly oblique metaloph. Postcentroloph longer than the precentroloph. Precentroloph long and interrupted. Postcentroloph connected to the protoloph. No accessory crests between the centrolophs. Metatrope short and lingually united to the postcentroloph. Posteroloph low in its lingual part and connected to protocone and metacone.
Remarks: Only a few D4 of the genus *Vasseuromys* are known. However, the subtriangular outline of the specimen from CA2 reminds one of the populations from Lower Miocene localities (MN1 and upper part of MN2) of the Ebro basin (Cuenca, 1985; Martínez-Salanova, 1987). The dental pattern of the D4 from CA2 is not as complicated as in *V. bacchius* from Fuenmayor 2 described by Martínez-Salanova (1987), and it is somewhat more complicated than that of *V. autolensis* from the locality Autol 1 (Cuenca, 1985).

Family: Eomyidae Winge, 1887
Eomyidae indet.
(Fig. 4/9)

Locality: Cuesta Agujeros 2 (CA2)
Material and measurements (L x W): 1 M1 (CA2-2/31) (6.49 x 6.63)
Description:
M1: Subrectangular-rounded outline. Anteroloph absent. Protoloph curved and low. The mesoloph is long, reaches the labial border and is connected with the protoloph, whereas the posterolingual end is not connected to the metaloph. Longitudinal crest absent. Metaloph connected to the hypocone. Posteroloph curved and connected to the hypocone and to the posterolabial end of the metaloph. Labial and lingual sinus communicate, forming a continuous valley, narrowed in the center by the mesoloph.
Remarks: The specimen in question is difficult to assign to a known species. However, the general morphology is similar to some morphotypes of M1 of the genus *Rhodanomys*, and to a lesser extent *Ritteneria*. Among other characters, its long mesoloph reaches the labial border but is not connected to the hypocone. A long mesoloph is common in *Rhodanomys transiens* from Bergasa and *R. schlosseri* from Autol 1 and Moncalvillo, but the morphology of the anterior part of the mesoloph is quite dif-

ferent from these populations, where the mesoloph is always connected to the hypocone (Álvarez-Sierra, 1988). The presence of long mesolophs is uncommon in the species of the genus *Ritteneria*.

The size of the specimen from CA2 is significantly smaller than any M1 of the species of *Rhodanomys* and *Ritteneria*. Its size (0.649 x 0.663 mm) is at the limit of the material recovered by the usual screenwashing with 0.5 mm mesh. It would not be surprising if a large part of the material of this species had been lost in screening.

In the Iberian Peninsula, the last record of the genus *Rhodanomys* is in MN1 (local zone X) (Álvarez-Sierra, 1988). The accompanying rodent fauna in CA2 (*Armantomys daamsi* and *Eucricetodon aquitanicus*, among others) permits to place this locality in the upper part of the Agenian (local zone Y2). The general morphology and the size of the specimen lead us to classify it as Eomyidae indet.

Genus: *Ligerimys* Stehlin and Schaub, 1951
Type species: *Ligerimys florancei* Stehlin and Schaub, 1951

Species: *Ligerimys* aff. *magnus* Álvarez-Sierra, 1988
(Fig. 4/1-8)

Locality: Cuesta Agujeros 4 (CA4)
Material: 2 d4 (CA4-1/22, CA4-1/23), 1 p4 (CA4-1/11), 4 m1,2 (CA4-1, CA4-1/8, CA4-1/9, CA4-1/10), 3 m3 (CA4-1/16, CA4-1/17, CA4-1/21), 3 D4 (CA4-1/14, CA4-1/18, CA4-1/19), 2 M1 (CA4-2, CA4-1/6), 3 M2 (CA4-1/7, CA4-1/13, CA4-1/15) and 1 M3 (CA4-1/20).
Measurements: see Table 5.
Description:
d4: Anterolophid well developed, united to the lingual and labial end of an oblique metalophid. In one case, at the anterior border, there is a relatively large anterior sinusid. Mesolophid long and complete in one specimen and partially interrupted in the other one.
p4: Anterolophid present, smaller than the metalophid to which it is connected at the lingual and labial end. Mesolophid partially interrupted in the middle of the crest. Hypolophid and posterolophid lingually united, closing the posterosinusid.
m1,2: Anterolophid of small to medium length, connected to the lingual and labial end of the transverse metalophid. Mesolophid complete. Hypolophid and posterolophid lingually united.
m3: Anterolophid short, lingually and labially connected to the metalophid. Mesolophid completely developed and united to the metalophid through the metaconid.

Mesosinusid lingually open or partially blocked by a low lingual wall. Hypolophid lingually connected to the posterolophid in two of the three specimens. In the third one, these crests are not connected and the hypolophid is connected longitudinally to the posterolophid by a short crest.

D4: The crests are relatively thin and the valleys broad. Anteroloph and protoloph are isolated labially and connected lingually to the protocone. Mesoloph absent. Longitudinal crest present in the three specimens. Metaloph and posteroloph separated labially. Sinus reduced, strongly directed anteriorly, or almost transverse.

M1: The lingual part of the anteroloph curves slightly backward. Anteroloph and protoloph separated labially. Mesoloph absent. Wall of the mesosinus of medium height or low. Metaloph transverse. Metaloph and posteroloph connected to the metacone. Posteroloph curved in its labial part and lingually transverse. Sinus relatively deep and narrow, partially orientated towards anterior.

M2: The anterolabial part is slightly or much higher than the posterior part. Anteroloph and protoloph labially connected at medium height. The lingual part of the anteroloph is slightly (1) or strongly (2) directed backwards, leaving the lingual sinus open (1) or almost closing it (2). In the latter two specimens the opening of the lingual sinus is displaced backwards. Protoloph slightly (1) or strongly (2) oblique. Mesoloph very short and labial (1) or absent (2). Metaloph transverse (1) or strongly oblique (2). In the latter two specimens, it forms an oblique Y. Posteroloph slightly (1) or strongly (2) curved labially and united to the metacone.

M3: Anteroloph and posteroloph form a circular crest. Protoloph and metaloph parallel, connected labially and lingually with the circular crest, and interconnected by a longitudinal crest somewhat lingually of the tooth axis. No lingual sinus. The labial sinuses are parallel and not connected.

Remarks: The population of *Ligerimys* found in CA4 is characterized by a much smaller size than *Ligerimys magnus* from Bañón 2 and 5 and, in general, smaller than *Ligerimys* aff. *magnus* from Ramblar 3B and 4A.

The d4 from CA4 is characterized by the complete or almost complete mesolophid, a morphology that is very similar to that in the localities Ramblar 3B and 4A and different from the reduced mesolophid of the d4 from Bañón 2 and 5 (Álvarez-Sierra, 1988).

An outstanding feature of the p4 is the presence of a mesolophid that is complete, but interrupted in the middle, a morphology that is present in *L.* aff. *magnus* from Ramblar 3B and 4A and absent in *L. magnus*.

All the m1,2 from CA4 present a complete mesolophid, like in *L.* aff. *magnus* from Ramblar 3B and 4A, where between 78% and the 80% of the specimens show this morphology (Álvarez-Sierra, 1988); this morphology is less frequent in *L. magnus*: from Bañón 2 (42%) and Bañón 5 (0%) (Álvarez-Sierra, 1988).

The M2 from CA4 show two different morphotypes. In the two smaller specimens the strongly backward development of anteroloph, protoloph and metaloph, forms a valley between anteroloph and protoloph that is directed backwards. That morphology is very similar to what is seen in the material of *L. magnus* from Bañón 2 (Álvarez-Sierra, 1988). The size, especially the width, of the material from CA4 is much smaller than in Bañón 2. The second morphotype of the M2 from CA4 (no. CA4-1/7) does not possess this morphology of the first valley nor the strong backward shift of the lingual sinus. That pattern is very similar to the only morphotype that has been described by Álvarez-Sierra (1988) in *L. magnus* from the locality of Bañón 5 (Ramblian, zone A) and in *L.* aff. *magnus* from the localities Ramblar 3B and 4A (Ramblian, zone Z). The size of the specimen CA4-1/7 is comparable to that of *L.* aff. *magnus* from Ramblar 3B and 4A (Álvarez-Sierra, 1988).

Element	Parameter	n	min.	mean	max.
d4	L	1	-	11.43	-
	W	2	7.62	7.81	8.00
p4	L	1	-	12.72	-
	W	1	-	11.46	-
m1.2	L	4	11.91	12.59	13.37
	W	4	11.50	11.87	12.17
D4	L	3	11.22	11.55	11.79
	W	3	10.53	10.65	10.73
M1	L	2	10.22	11.47	12.71
	W	2	12.56	13.47	14.38
M2	L	3	8.96	9.99	11.30
	W	3	11.60	12.52	13.99
M3	L	1	-	8.46	-
	W	1	-	9.80	-

Table 5.- Measurements (in tenths of mm) of the teeth of *Ligerimys* aff. *magnus* Álvarez-Sierra, 1988 from CA4. Abbreviations: L—Length; W—Width; d4—Fourth lower decidual; p4—Fourth lower premolar; m1,2—First or Second lower molar; D4—Fourth upper decidual; M1—First upper molar; M2—Second upper molar; M3—Third upper molar.

Tabla 5.- Medidas (en décimas de milímetro) de los dientes de *Ligerimys* aff. *magnus* Álvarez-Sierra, 1988 de CA4. Abreviaciones: L—Longitud; W—Anchura; d4— Cuarto decidual inferior; p4—Cuarto premolar inferior;; m1,2—Primer o segundo molar inferior; D4—Cuarto decidual superior; M1—Primer molar superior; M2—Segundo molar superior; M3—Tercer molar superior.

In Álvarez-Sierra (1988; fig. 75), the chronological sequence of the localities is: Ramblar 4A, Ramblar 3B (local zone Z), Bañón 5 and Bañón 2 (local zone A). The morphological and biometrical comparison of the material of the genus *Ligerimys* from Ramblar 4A, Ramblar 3B, Bañón 5, Bañón 2 and CA4 lead us to place CA4 in an age range close to the base of the local zone A of the Ramblian.

The two different morphologies of the M2 from CA4 pose the question of the presence of two species of the genus *Ligerimys* in CA4, as did Álvarez-Sierra (1988) by distinguishing *L. magnus* (Bañón 2 and 5) and *L.* aff. *magnus* (Ramblar 3B and 4A). The diagnosis of *L. magnus* characterized the species as being of large size and having an M2 with a backward directed anteroloph that almost closes the lingual sinus. The measurements of the M2 from Bañón 2 and CA4 with this morphology are very different. Moreover, this typical morphology of the M2 is not unique in CA4, nor in Bañón 2 (Álvarez-Sierra, 1988, pl. 23, figs. 7 and 9). Until more material from CA4 is available we classify these specimens as *Ligerimys* aff. *magnus*, though different from *Ligerimys* aff. *magnus* from the localities Ramblar 3B and 4A as described by Álvarez-Sierra (1988).

Genus: *Pseudotheridomys* Schlosser, 1926
Type species: *Pseudotheridomys parvulus* (Schlosser, 1884)

Species: *Pseudotheridomys* sp.
(Fig. 4/10)

Locality: Cuesta Agujeros 4 (CA4)
Material and measurements (L x W): 1 D4 (CA4-1/12) (x 10.48).
Description:
D4: Tooth with five lophs. The anteroloph low connected to the protoloph at the labial border. Labial end of the protoloph not connected to the labial end of the mesoloph. The second valley is labially open. Mesoloph, metaloph and posteroloph connected at the labial border. The third valley is the largest of the four. The posteroloph is a small crest from the middle of the metaloph curving at its labial end and connecting to the metaloph. The posterosinus is very narrow, being the smallest valley of the tooth.
Remarks: The most outstanding morphological character of this specimen is the presence of five crests, a feature only cited in the genus *Pseudotheridomys* (Álvarez-Sierra, 1988). The other specimens of eomyids from CA4 do not have five crests.
The posteroloph of CA4-1/12 is much reduced. The lingual and labial ends of that crest are fused to the

metaloph. This morphology has not been cited in any population of the genus *Pseudotheridomys* from the Lower Miocene. The accompanying fauna in CA4 indicates an Upper Ramblian age, for which the only species known in the Iberian Peninsula is *P. fejfari* (Álvarez-Sierra and Daams, 1987). That species has been found in the localities Bañón 11A and Moratilla 1, and in Rubielos de Mora 2, where de Bruijn and Moltzer (1974) described an eomyid as transitional between *Pseudotheridomys* and *Ligerimys*, which was later partially classified as *P. fejfari* by Álvarez-Sierra and Daams (1987) and Álvarez-Sierra (1988). The D4 is only known from Rubielos of Mora 2. De Bruijn and Moltzer (1974) described it as having five lophs (crests), interconnected at the labial border. That morphology is similar to the specimen from CA4-1/12, though the second syncline in CA4 is open at the labial border, or, in other words, the labial ends of protoloph and mesoloph are not connected.

We classify this specimen as *Pseudotheridomys* sp. The scarce material impedes a more precise determination.

Family: Sciuridae Fischer, 1817
Genus: *Heteroxerus* Stehlin and Schaub, 1951
Type species: *Xerus grivensis* Forsyth Major, 1893

Species: *Heteroxerus* cf. *paulhiacensis* Black, 1965
(Fig. 4/16-17)

Locality: Cuesta Agujeros 2 (CA2)
Material and measurements (L x W): 1 D4 (CA2-3/2) (15.14 x 15.00), 1 P4 (CA2-3/1) (14.88 x 16.49), 1 m1,2 (CA2-3/3) (14.16 x 12.77).
Description:
D4: Anteroloph low. Protoloph low, connected to paracone and protocone. Metacone and metaconule of equal size. A low crest connects the metaconule with the protocone. Hypocone high. Posteroloph low, connected to hypocone and metacone.
P4: Anteroloph low. The protoloph is connected to paracone and protocone. Metacone and metaconule of equal size. A low crest connects the metaconule with the protocone. Hypocone high. Posteroloph connected to hypocone and metacone.
m1,2: Very much worn. No anterior cingulum. Mesoconid absent. There is a weak entolophid.
Remarks: The size of the material of *Heteroxerus paulhiacensis* from CA2 is the same as in the localities Coderet (Hugueney, 1969) and Santa Cilia (Álvarez-Sierra et al., 1990); *H. rubricati* (Cuenca, 1988) is of the same size too. Morphologically, the scarce material from CA2 is characterized by the presence of a connection between

metaconule and protocone in D4 and P4. That connection is not very frequent, neither in *H. rubricati* nor in *H. lavocati* (Cuenca, 1988; Cuenca, 1991), and more frequent in *H. paulhiacensis* (Black, 1965; Álvarez-Sierra *et al.*, 1990). The scarce material of this taxon from CA2 impedes a more precise determination.

Family: Castoridae Hemprich, 1820
Genus: *Steneofiber* Geoffroy-Saint-Hilaire, 1833
Type species: *Steneofiber eseri* (Von Meyer, 1846)

Species: *Steneofiber* sp.
(Fig. 3/5)

Locality: Cuesta Agujeros 4 (CA4)
Material: 1 I (CA4-8).
Description:
I sup: The transverse section of the base of the incisor is subtriangular with the labial part flattened and covered by a fine enamel layer.
Remarks: The size and the morphology of the transverse section of the incisor are very similar to what, according to Hugueney (1999b), characterizes the genera *Steneofiber*, *Chalicomys* and *Castor*. However, *Castor* is significantly larger.
Mörs and Stefen (2010) and Casanovas-Vilar and Alba (2011) questioned the presence of *Chalicomys* in MN4 - MN6. Both papers consider this presence as doubtful (Casanovas-Vilar and Alba, 2011), or as result of a mistaken identity with *Steneofiber deperei* or *S. subpyrenaicus*.
Therefore, the temporal distribution of castorids in the Early Miocene and the presence of a flattened transverse section in CA4-8 seem to indicate a representative of the genus *Steneofiber* in CA4. We assign it to *Steneofiber* sp.

Order: Erinaceomorpha Gregory, 1910
Family: Erinaceidae Fischer, 1814
Genus: *Galerix* Pomel, 1848
Type species: *Galerix exilis* (de Blainville, 1839)

Species: *Galerix* sp.
(Fig. 7/1)

Locality: Cuesta Agujeros 4 (CA4)
Material and measurements (L x W): 1 M3 (CA4-6) (1.34 x 1.86)
Description:
M3: The occlusal outline of the tooth is triangular. The protocone and the paracone are the highest cusps. The metacone is the lowest main cusp. There is a small and thin cingulum at the base of the anterior margin, connect-

ed to the base of the parastyle. The parastyle is low, but it protrudes anterolabially in occlusal view. The central basin is closed.
Remarks: The tooth corresponds to an M3 of a Galericini erinaceid. Yet the species cannot be identified, the only genus of Galericini present in the Early Miocene of Spain is *Galerix* (Van den Hoek Ostende, 2001). Other than general size, the p4, P3, and M1/M2 are diagnostic elements to distinguish between species of *Galerix* (Van den Hoek Ostende, 2003). Unfortunately, an isolated M3 is insufficient to determine the species from this locality.

Order: Soricomorpha Gregory, 1910
Family: Soricidae Fischer, 1814

Soricidae indet.
(Fig. 7/2)

Locality: Cabezo Carboneras 1 (CC1)
Material and measurements (L x TRW): 1 trigonid of a lower molar (m2?) (CC1-5) (- x 0.70)
Description:
Lower molar (m2?): Only the trigonid is preserved. The protoconid is the highest cusp of the trigonid. The metaconid is a bit lower than the protoconid. The protolophid is short. The paraconid is the lowest cusp of the trigonid. There is a small cingulid at the base of the paralophid. The fragment does not show any pigmented part.
Remarks: This fragment of lower molar does not display any significant trait to identify the taxon further than the family level. This specimen could correspond either to an m1 or an m2, but its aspect (rather anteroposteriorly compressed) fits better within the most frequent morphology of an m2.

Order: Chiroptera Blumenbach, 1779
Chiroptera indet. (Fig. 7/3-4)

Locality: Cuesta Agujeros 4 (CA4)
Material and measurements (L x W): 1 M2 (CA4-5) (1.52 x -), 1 lower molar (CA4-7) (- x 0.98)
Description:
M1/2: Only the labial half of the tooth is preserved. The metacone is the highest cusp. The paracone is somewhat lower than the metacone. The ectoloph is continuous and the mesostyle is not divided. The parastyle is characteristically curved, oriented anterolingually in occlusal view. The metastyle is rather straight. Although the lingual half is not preserved, it seems that the distal margin had a softly pronounced posterior emargination.
Lower molar: Only the talonid is preserved. The talonid displays a myotodont pattern, where the hypoconulid
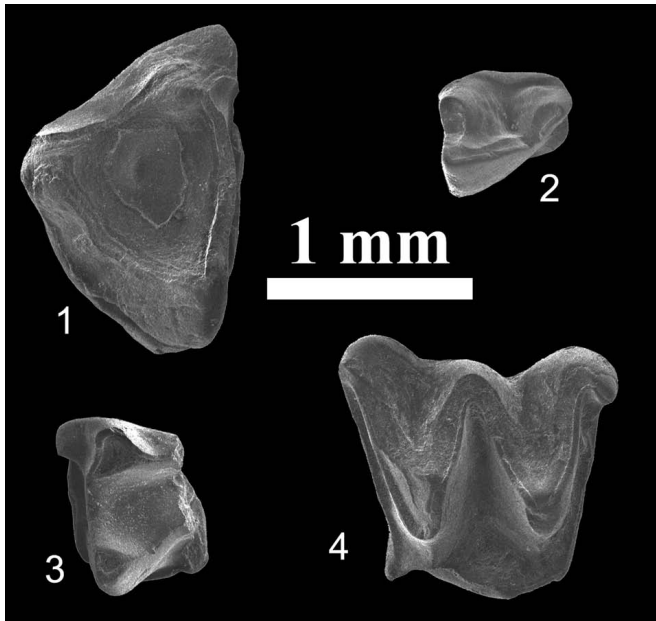
Fig. 7.- *Galerix* sp. from Cuesta Agujeros 4 (CA4). 1, M3 dext. (CA4-6); Soricidae indet. from Cabezo Carboneras 1 (CC1). 2, lower molar dext. (CC-5); Chiroptera indet. from Cuesta Agujeros 4 (CA4). 3, lower molar dext. (CA4-7); 4, upper molar dext. (CA4-5). Scale: 1 mm.

Fig. 7.- *Galerix* sp. de Cuesta Agujeros 4 (CA4). 1, M3 dext. (CA4-6); Soricidae indet. de Cabezo Carboneras 1 (CC1). 2, molar inferior dext. (CC-5); Chiroptera indet. de Cuesta Agujeros 4 (CA4). 3, molar inferior dext. (CA4-7); 4, molar superior dext. (CA4-5). Escala: 1 mm.

is completely separated from the entoconid in a basal posterior position. The hypoconid is the highest cusp of the part talonid. The entoconid is not as high as the hypoconid. There is a thin crest anteriorly connected to the entoconid. There is a continuous well-defined cingulum covering the posterior and the labial bases of the talonid. The oblique cristid descends to half the height from the hypoconid.

Remarks: The two dental elements are broken. The diagnostic traits in isolated upper molars of fossil bats are usually found in the lingual half (Sevilla, 1988), which unfortunately is the missing part in the only M available. The relative development of the ectoloph crests and the curved parastyle resembles the morphology of *Rhinolophus*.

The myotodont pattern of the lower molar fragment precludes its attribution to the genus *Rhinolophus*. However, this element could also correspond to a different species. A generic identification based on such scarce elements would be highly speculative.

5. Biostratigraphy

Figure 8 gives the distribution of the taxons in the localities studied in this paper. The localities CH1 and CA1 contain, among other taxons, *Eucricetodon* cf. *gerandi-*

anus and *Armantomys* cf. *bijmai*, an association that is typical for local zone Y1 of the Agenian (Álvarez-Sierra *et al*., 1987; Daams, 1990; Hugueney, 1999a). CA2 and CC1 contain *Eucricetodon aquitanicus* and *Armantomys daamsi*, characteristic elements of zone Y2 of the Agenian (Álvarez-Sierra *et al.,* 1987; Daams, 1990).

In the upper part of the Agenian the record of eomyids is rather scarce (Álvarez-Sierra *et al*., 1990; Mein, 1999). In the locality San Juan, assigned to local zone Y2 by Álvarez-Sierra *et al*. (1990), those authors cited the presence of 10 specimens of eomyids in a collection of ca 320 rodent remains (3% of the total). The very scarce representation of eomyids in the upper part of zone Y, and the fact that our collections contain less then 30 specimens per locality, might explain the absence of eomyids in most of them. In the described faunas, remains of eomyids are only present in the locality CA2, where a doubtful specimen of *Rhodanomys* or *Ritteneria* has been found (Fig. 8).

The localities CA3 and CA3B contain a scarce fauna, composed by glirids only. The only biostratigraphically relevant taxon is *Armantomys* cf. *parsani* from CA3. According to Daams (1990), this taxon is present throughout the upper part of the Agenian (local zone Y2) and the Ramblian (local zones Z and A). The locality is stratigraphically intermediate between CM1 and CJ1, both belonging to local zone Z (Murelaga *et al.,* 2004a), and therefore placed in the same zone. On the other hand, CA3B is only 13 meters below CA4, attributed to local zone A. This means that the limit between zones Z and A is situated in the higher part of the section of Cuesta Agujeros, and has an age of ca. 19.45 Ma (Figs. 2 and 8).

Stratigraphically, CA4 is the highest of the studied localities. It contains *Pseudotheridomys* sp., *Ligerimys* aff. *magnus* and *Armantomys* cf. *jasperi*. *Pseudotheridomys* is represented by a single specimen, not classified at species level. The genus has a stratigraphic distribution from the upper part of the Oligocene (local zone W) to the Lower Aragonian (local zone B) (Fig. 8). In the Iberian Peninsula, Álvarez-Sierra (1988) cited the presence of *Pseudotheridomys* in the age range between local zones W and Y2 and in the localities Bañón 11A and Moratilla 1, of the local zone A. Other Iberian localities of zone A that contain a member of the genus *Pseudotheridomys* are Rubielos de Mora 2 (transitional association between *Pseudothyeridomys-Ligerimys* in de Bruijn and Moltzer, 1974; Álvarez-Sierra and Daams, 1987) and Alto de Ballester (Ruiz-Sánchez, 1992; Montoya *et al*., 1996), both situated in the basin of Rubielos de Mora. There is no record of *Pseudotheridomys* in localities of the Lower Ramblian (local zone Z) in the Iberian Peninsula. In Central Europe, Engesser (1999) and Pippèrr *et al*. (2007), cite the presence of *Pseudoth-*
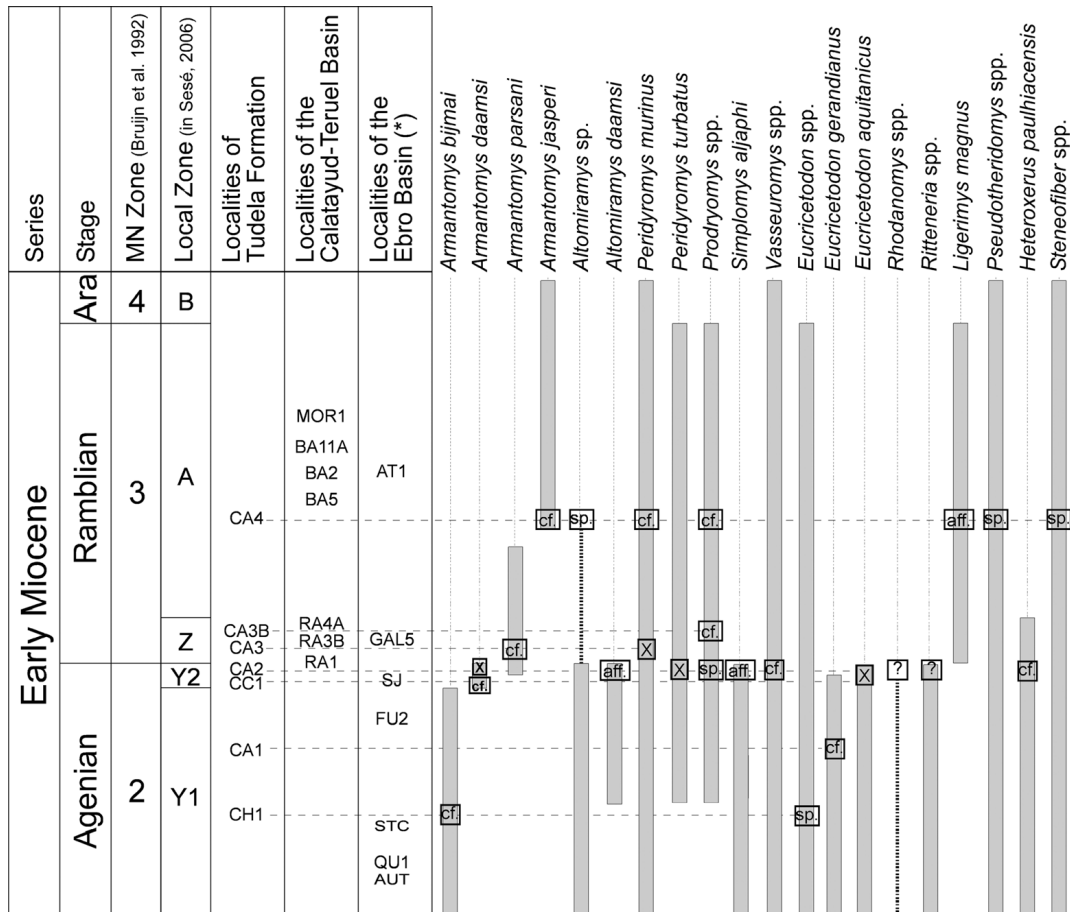
Fig. 8.- Distribution of the rodents species studied in this work and in Daams and Freudenthal (1988), Lacomba and Martínez-Salanova (1988), Álvarez-Sierra *et al*. (1990), and Daams (1990). The succession of localities is in stratigraphic order, but not on scale. **Abbreviations**: CH1—Cabezo Hermoso 1; CA1—Cuesta Agujeros 1; CC1—Cabezo Carboneras 1; CA2—Cuesta Agujeros 2; CA3—Cuesta Agujeros 3; CA3B—Cuesta Agujeros 3B; CA4—Cuesta Agujeros 4; RA1—Ramblar 1; RA3B—Ramblar 3B; RA4A—Ramblar 4A; BA5—Bañón 5; BA2—Bañón 2; BA11A—Bañón 11A; MOR1—Moratilla 1; AUT—Autol 1; STC—Santa Cilia; QU1—Quel 1; FU2—Fuenmayor 2; SJ—San Juan; GAL5—La Galocha 5; AT1—Ateca 1. Ara—Aragonian. (*)— Localities of the Tudela Formation not included.

Fig. 8.- Distribución de las especies de roedores estudiadas en este trabajo y en Daams and Freudenthal (1988), Lacomba and Martínez-Salanova (1988), Álvarez-Sierra et al. (1990), y Daams (1990). La sucesión de localidades se presenta en orden estratigráfico pero no a escala. Abbreviations: CH1—Cabezo Hermoso 1; CA1—Cuesta Agujeros 1; CC1—Cabezo Carboneras 1; CA2—Cuesta Agujeros 2; CA3—Cuesta Agujeros 3; CA3B—Cuesta Agujeros 3B; CA4—Cuesta Agujeros 4; RA1—Ramblar 1; RA3B—Ramblar 3B; RA4A—Ramblar 4A; BA5—Bañón 5; BA2—Bañón 2; BA11A—Bañón 11A; MOR1—Moratilla 1; AUT—Autol 1; STC—Santa Cilia; QU1—Quel 1; FU2—Fuenmayor 2; SJ—San Juan; GAL5—La Galocha 5; AT1—Ateca 1. Ara—Aragonian. (*)— No incluidas las localidades de la Formación Tudela.

eridomys n. sp. in the lower part of the MN4.

As far as *Ligerimys* aff. *magnus* is concerned, Álvarez-Sierra (1988) cited the presence of a similar form, but slightly smaller than *Ligerimys magnus*, in the localities Ramblar 3B and Ramblar 4A of zone Z of the Ramblian and in the localities Bañón 2 and Bañón 5 of zone A, also Ramblian. The morphology of *Ligerimys* aff. *magnus* from CA4 is very similar to *Ligerimys magnus* of zone A, though its size is clearly smaller.

The stratigraphic distribution of *Armantomys* cf. *jasperi* covers the Upper Ramblian (local zone A) through the Middle Aragonian (local zone D2 in Daams, 1990; Dc in van der Meulen *et al*., 2012). The co-occurrence

of *Pseudotheridomys* sp., *Ligerimys* aff. *magnus* and *Armantomys* cf. *jasperi* leads us to place the locality CA4 in local zone A of the Ramblian.

The data of the rodent faunas from the localities of the Tudela Formation studied in the present work corroborate the biostratigraphical results of Ruiz-Sánchez *et al.* (2012), based exclusively on the hypsodont Gliridae from the same localities.

6. Conclusions

Seven new localities have been found in the Tudela Formation (CH1, CA1, CA2, CC1, CA3, CA3B and

CA4), covering the time interval between the Middle-Late Agenian (MN2) and the Late Ramblian (upper part of MN3).

In the faunas from the localities of the Agenian four forms of Cricetidae are represented, eight Gliridae, one Sciuridae and one Eomyidae. The faunas from the localities of the Early Ramblian are restricted to three forms of Gliridae. Finally, in the single fauna of the Late Ramblian (CA4) are represented four forms of Gliridae, two Eomyidae and one Castoridae.

The relative abundance and high species diversity of the Gliridae in both the Agenian and the Ramblian are important features, as well as the absence of Cricetidae in the localities of the Ramblian.

The discovery of an eomyid (*Rhodanomys* or *Ritteneria*) in the locality CA2 constitutes the first record of this taxon in the Iberian Peninsula in deposits of Late Agenian age.

The record of *Altomiramys* sp. in CA4 is the first one of this taxon in the Upper Ramblian.

The morphology of *Simplomys* aff. *aljaphi* from CA2 represents an evolutionary stage a slighty different to the oldest described forms of the genus and probably demonstrates close phylogenetic relationship with the genus *Peridyromys*.

Unfortunately, the record of insectivores and bats in the Tudela Formation is rather anecdotic, and they cannot refine the information provided by rodents.

The distribution of the species studied permits to assign the localities CH1 and CA1 to local zone Y1 (lower part of zone MN2), CA2 and CC1 to local zone Y2 (upper part of zone MN2), CA3 and CA3B presumably to local zone Z (lower part of zone MN3), and finally, CA4 to local zone A (upper part of zone MN3).

Acknowledgements

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