



Late Aragonian mammal sites of Cuesta del Rey (Duero Basin, Burgos, Spain)

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ABSTRACT

The Cuesta del Rey mammal sites located on the NE border of the Duero Basin are of great importance with regard to understand the general biostratigraphy of the basin, because Miocene mammal sites are extremely scarce in this area in comparison with the central part of the basin. The mammals identified in Cuesta del Rey-1 are: Eulipotyphla: cf. *Miosorex* sp.; Rodentia: *Heteroxerus* sp., *Armantomys* cf. *tricristatus*, *Megacricetodon ibericus*, *Megacricetodon minor-Megacricetodon debruijni*, *Hispanomys* sp. and *Democricetodon* sp. The Cuesta del Rey-1 rodent assemblage is characteristic of the end of the upper Aragonian (MN 7/8, end of the middle Miocene), equivalent to the local subzone G3 of the G zone. The presence of the genera *Heteroxerus* and *Armantomys*, and the predominance of *Megacricetodon* (with 80% of the total percentage of the minimum number of individuals of the micromammals) suggested an open savannah or steppe palaeoenvironment. The mammals identified in Cuesta del Rey-3 are: Rodentia: *Megacricetodon* cf. *ibericus*; Artiodactyla: *Dorcatherium* sp. and *Listriodon* cf. *splendens*. *Dorcatherium* sp. represents the first appearance of the Tragulidae family in the Duero Basin, suggesting the existence of permanent watercourses.

Keywords: Mammals, middle Miocene, upper Aragonian, Duero Basin, Cuesta del Rey sites.

RESUMEN

Los yacimientos con mamíferos de Cuesta del Rey, situados en el borde NE de la cuenca del Duero, tienen una gran importancia para el conocimiento general de la biostratigrafía de la cuenca debido a la extrema escasez de yacimientos miocenos con mamíferos en comparación con las partes centrales de la misma. Los mamíferos identificados en Cuesta del Rey-1 son: Eulipotyphla: cf. *Miosorex* sp.; Rodentia: *Heteroxerus* sp., *Armantomys* cf. *tricristatus*, *Megacricetodon ibericus*, *Megacricetodon minor-Megacricetodon debruijni*, *Hispanomys* sp. y *Democricetodon* sp. Esta asociación, principalmente por la composición de los roedores, es característica del final del Aragoniense superior (final del Mioceno medio), de la subzona G3 de la zona G, unidades MN 7/8. La presencia de los géneros *Heteroxerus*, *Armantomys*, y el predominio de *Megacricetodon* (que constituye el 80 % del porcentaje total del número mínimo de individuos de los micromamíferos), sugieren un ambiente abierto de tipo sabana o estepa. Los mamíferos identificados en Cuesta del Rey-3 son: Rodentia: *Megacricetodon* cf. *ibericus*; Artiodactyla: *Listriodon* cf. *splendens* and *Dorcatherium* sp. El tragúlido *Dorcatherium* sp. representa la primera aparición de la familia en la cuenca del Duero, y sugiere la existencia de cursos de agua permanentes.

Palabras clave: Mamíferos, Mioceno medio, Aragoniense superior, Cuenca del Duero, Yacimientos de Cuesta del Rey.

1. INTRODUCTION

The Cuesta del Rey mammal sites are located on the NE border of the Duero Basin, close to the city of Burgos. This area is near the western end of the Ebro basin; both zones are connected by the Bureba corridor. Unlike other areas of the Duero Basin, the mammal fossil record here is still quite scarce, and for a long time the only findings of remains have involved two species of mastodons near the village of Castrillo del Val, Burgos (Badillo, 1952; Bergounioux & Crouzel, 1958; Mazo Pérez, 1977). The site was dated as late Vindobonian (equivalent of the upper Aragonian). During the Geological mapping at 1:50.000 scale (Spanish “Plan Magna”) in the 1990’s, new fossil mammal sites were found including that of Cuesta del Rey-1, the object of the present research. These new sites have made it possible to accurately determine the age of the Miocene formations in this area (Morales & Sesé, 1997; Pineda, 1997). Subsequent sampling of the same area performed by Olmo *et al.* (2008) has shown the existence of other mammal sites, among these a new one in the Cuesta del Rey (CR-3) section, presenting an assemblage of small and large mammals.

2. GEOLOGICAL SETTING

The Cuesta del Rey section is located close to the village of Villarmero (Burgos). The fossiliferous levels are situated in a butte known as Cuesta del Rey (Fig. 1), which is aligned with two other partially eroded buttes between the Ubierno and Villatoro rivers. The base of the Cuesta del Rey Butte rises along the NW slope from an altitude of 894 m above sea-level; the outcrop sediments are mudstone, marls and gypsum, attributed to the Villatoro facies (Pineda, 1997). Olmo *et al.* (2008) suggest that these facies are the lateral continuation of the base of the Riocerezo Series “Marls, silts and terminal limestones” of the Dueñas facies. The Riocerezo rodent site located at the bottom of this series, with *Megacricetodon cf. crusafonti* and *Megacricetodon cf. lopezae*, enables these sediments to be dated as upper Aragonian (MN 6) (Olmo *et al.*, 2008). The Cuesta del Rey-3 site is situated at an altitude of 910 m, approximately 10 m above the contact with the Villatoro facies; the presence of the cricetid *Megacricetodon cf. ibericus* enabled Olmo *et al.* (2008) to date the site as upper Aragonian (MN 6/7), suggesting a correlation with the lower part of the Cuesta facies of the central sector of the Duero Basin, in particular with the “Intercalación Ocre”. The Cuesta del Rey-1 site, at an altitude of 930 m, approximately 20 m above Cuesta del Rey-3, is located in terrigenous sediments: yellow and ochre sand, silts and clays. The age of the rodent assemblage was

attributed by Morales & Sesé (1997) to the end of the upper Aragonian (MN 7/8). Pineda (1997) place the site in the Tierra de Campos facies, which is characterized by terrigenous sediments overlying the Villatoro facies, but in nearby areas the terrigenous sediments overlap the terminal limestones of the Dueñas facies. There is therefore an important discrepancy between the work of Pineda (1997) and Olmo *et al.* (2008) in relation to the interpretation of the sedimentary facies in this area. However, the discrepancy is not due to erroneous dating of the sites, as stated by Olmo *et al.* (2008), but rather to different interpretations of the relationships between the facies supported by the new biostratigraphic data.

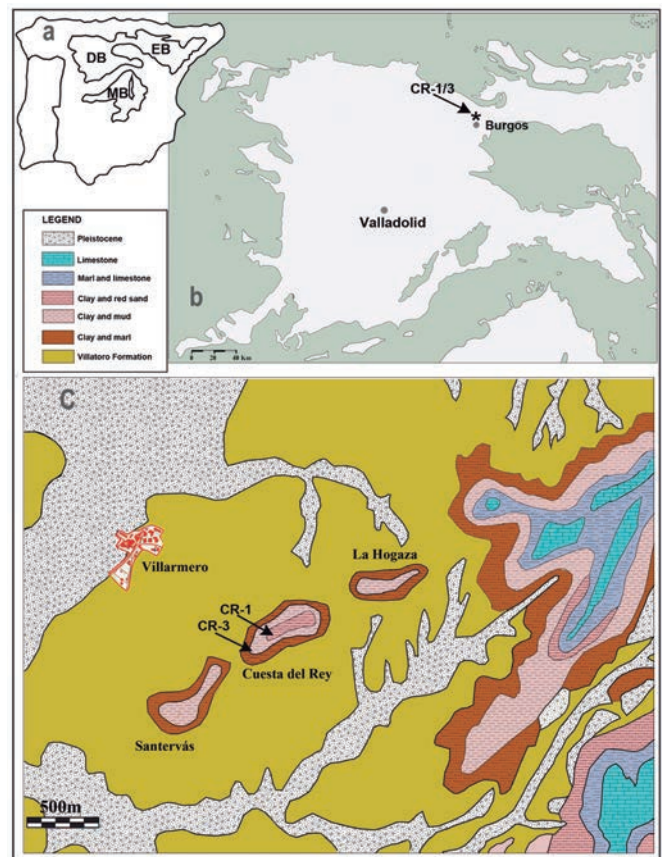


Figure 1. a) Location map of the Duero Basin (DE), Ebro Basin (EB) and Madrid Basin (MB) in the Iberian Peninsula. b) Location map of Cuesta del Rey mammal localities (CR-1 and CR-3) in the Cenozoic Duero Basin. c) The geological scheme of Cuesta del Rey area is based on the MAGNA geological map of Burgos -Sheet 200- (Pineda, 1977).

3. METHODOLOGY

In Cuesta del Rey-1, 150 kg of sediment were screen-washed with different mesh sizes, the smallest of which was 0.5 mm. The fossils were selected with the use of a stereomicroscope. Among the fossiliferous remains 140 identifiable teeth of micromammals were found. The material from Cuesta del Rey-1/3 is stored in the collections of the MNCN.

The teeth were measured with a Nikon Measuroscope 10 5x microscope with an incorporated micrometer of an accuracy of 0.025 mm. The measurements are maximum length (L) and width (W) of the occlusal surface of the tooth, and have been taken after Reumer (1984) for Soricidae, Cuenca Bescós (1988) for Sciuridae, García Paredes (2006) for Gliridae, and Daams & Freudenthal (1988) for Cricetidae; we give the maximum (Max.), medium (Med.) and minimum (Min.) in millimeters (mm) for the number of teeth measured (N).

The teeth were drawn with a Nikon SMZ-10 40x microscope with an attached light camera, and the drawings were redrawn with the Corel Drawn software.

The photographs of the micromammal teeth were taken at the Laboratory of Optical Microscopy of the Museo Nacional de Ciencias Naturales (MNCN) with the use of the FEI Quanta 200 Scanning Electronic Microscope (SEM) in mode Low Vacuum.

The nomenclature used for the teeth of the different groups of micromammals follows Sesé (1980).

To compare the relative abundance of the different micromammals, we employed the Minimal Number of Individuals (MNI) of each taxon using the most abundant piece, taking into account the highest number between lefts and rights.

4. SYSTEMATIC PALAEOONTOLOGY

Class MAMMALIA Linnaeus, 1758
 Order EULIPOTYPHILA Waddell, Okada & Hasegawa, 1999
 Family **Soricidae** Fischer, 1814
 Genus *Miosorex* Kretzoi, 1959

cf. *Miosorex* sp.
 (Figs 2a, 3a)

Locality. Cuesta del Rey-1.

Material and measurements. 1 m3: L = 1.06 mm; W = 0.68 mm.

Description and discussion. The size of this molar fits within the variability of that of *Miosorex grivensis*, and

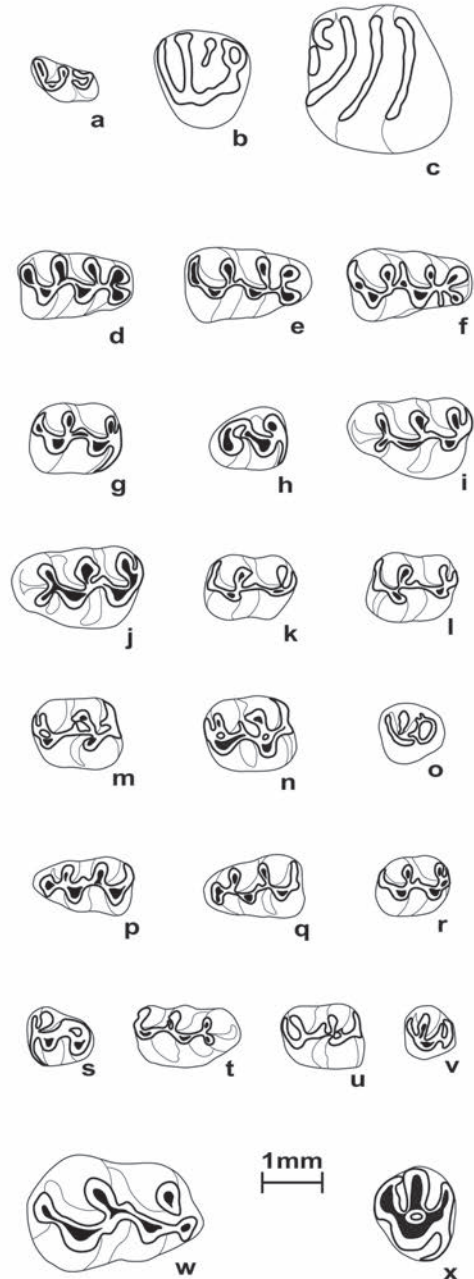


Figure 2. Drawings of the micromammal tooth in occlusal view from Cuesta del Rey-1. (a) cf. *Miosorex* sp., left m3 (CR-1: s/n 4). (b) *Heteroxerus* sp., left P4 (CR-1: s/n: 8). (c) *Armantomys* cf. *tricrostatus*, left m2 (CR-1: s/n: 1); (d-o) *Megacricetodon ibericus*, (d) right m1 (CR-1: 9); (e) right m1 (CR-1: 2); (f) right m1 (CR-1: 3); (g) right m2 (CR-1: 39); (h) right m3 (CR-1: s/n: 8); (i) left M1 (CR-1: 103); (j) left M1 (CR-1: 102); (k) left M2 (CR-1: 79); (l) left M2 (CR-1: 88); (m) right M2 (CR-1: 89); (n) right M2 (CR-1: 82); (o) left M3 (CR-1: 100). (p-v) *Megacricetodon minor*-*Megacricetodon debruijini*: (p) left m1 (CR-1: 17); (q) left m1 (CR-1: 18); (r) right m2 (CR-1: 37); (s) left m3 (CR-1: s/n: 17); (t) right M1 (CR-1: 114); (u) right M2 (CR-1: 93); (v) left M3 (CR-1: 98); (w) *Hispanomys* sp., right m1 (CR-1: s/n: 1); (x) *Democricetodon* sp., right M3 (CR-1: s/n: 3).

its morphology, with the talonid basin greatly reduced, is characteristic of this species (Sesé, 1980). Sesé (1980) defined the new subspecies of *Miosorex grivensis lopezae* Sesé 1980 at the Escobosa de Calatañazor site, based on some dental and mandibular characters that distinguish it from the subspecies *Miosorex grivensis grivensis* of the type-site of La Grive de Saint Alban, where the species was defined. Nonetheless, the material from Cuesta del Rey-1 is so scarce that we reservedly determine the Soricidae from this site as cf. *Miosorex* sp.

Order RODENTIA Bowdich, 1821
Family **Sciuridae** Fischer de Waldheim, 1817
Genus *Heteroxerus* Stehlin & Schaub, 1951

Heteroxerus sp.
(Figs 2b, 3b)

Locality. Cuesta del Rey-1.

Material and measurements. 1 P4: L = 1.47 mm; W = 1.56 mm.

Description and discussion. The morphology of this tooth is characteristic of the genus *Heteroxerus*. Its size is greater than or close to the maximum values of the different populations of *Heteroxerus rubricati* Crusafont, Villalta & Truyols, 1955. It is somewhat smaller or close to the minimum values of *Heteroxerus grivensis* (Forsyth Major, 1893), mainly in relation to length (Cuenca Bescós, 1988), and is also smaller than the values of the population of the latter species from Escobosa de Calatañazor (Sesé, 1980). As this tooth exhibits no characters to distinguish between both species, and its size is not differential, because it fits within the variability of both species, it cannot be assigned to either of them.

Family **Gliridae** Muirhead, 1819
Genus *Armantomys* de Bruijn, 1966

Armantomys cf. *tricristatus* López Martínez, 1977, in:
López Martínez, Sesé Benito & Sanz García, 1977
(Figs 2c, 3c-d)

Locality. Cuesta del Rey-1.

Material and measurements. 1 m2: L = 2.24 mm; W = 2.16 mm; 1 P4: L = 1.0 mm; W = 1.49 mm.

Description.

m2. In the m2 of Cuesta del Rey-1, the ridge curvature is greater than that of *Armantomys aragonensis* de Bruijn, 1966, and is similar to that of *Armantomys tricristatus*. The anterolophid is shorter than in *Armantomys aragonensis* and similar to that of *Armantomys tricristatus*. These two

characters enable both species to be distinguished (López Martínez *et al.*, 1977; Daams, 1990). The size of the m2 is bigger than that of *Armantomys aragonensis* (Bruijn 1966, 1967; Daams, 1990; García Paredes, 2006), and fits within the variability of *Armantomys tricristatus* (López Martínez *et al.*, 1977; Sesé, 1980; Daams, 1990; García Paredes, 2006).

P4. In the P4 of Cuesta del Rey-1, there is no anterocone or anteroloph, as occurs in *Armantomys tricristatus*, a character that allows it to be distinguished from that of *Armantomys aragonensis*, which generally presents an anterocone (Daams, 1990; García Paredes, 2006). The size of the P4 is more similar to that of *Armantomys aragonensis*, although García Paredes (2006) points out that there are no notable differences in the size of this tooth between both species.

Discussion. Although the material from Cuesta del Rey-1 fits well in *Armantomys tricristatus*, its size and morphology are less evolved than those of the population of Escobosa de Calatañazor, the site where the species was described (López Martínez *et al.*, 1977; Sesé, 1980), in which the curvature of the ridges is even more marked than in the material of Cuesta del Rey-1. Daams (1990) considers *A. aragonensis* - *A. tricristatus* to constitute a different lineage, bigger than that of the small-to-medium size of *A. bijmai* (Lacomba & Martínez Salanova, 1988) - *A. daamsi* (de Visser, 1990, in: Álvarez Sierra *et al.*, 1990a) - *A. parsani* Daams, 1990 - *A. jasperi* Daams, 1990. The *A. aragonensis* - *A. tricristatus* lineage is characterized by a tendency towards increased molar size, greater inclination of the ridges, shortening of the anteroloph in the lower molars and the loss of the anterocone in the P4 (Daams, 1990). Based upon all these data, and due to the scarcity of the material in Cuesta del Rey-1, we reservedly identify it as *Armantomys* cf. *tricristatus*.

Family **Cricetidae** Fischer de Waldheim, 1817
Genus *Megacricetodon* Fahlbusch, 1964

Megacricetodon ibericus (Schaub, 1944)
(Figs 2d-o, 3e-r)

Locality. Cuesta del Rey-1.

Material. 32 m1; 31 m2; 9 m3; 15 M1; 21 M2; 4 M3.

Measurements. See Table 1.

Description. For the morphological description of the molars we follow the morphotypes distinguished by Daams & Freudenthal (1988) for the lineage *Megacricetodon primitivus* (Freudenthal, 1963) - *Megacricetodon collongensis* (Mein, 1958) - *Megacricetodon collongensis-crusafonti* - *Megacricetodon crusafonti* (Freudenthal, 1963)

– *Megacricetodon crusafonti-ibericus* - *Megacricetodon ibericus*. Oliver Pérez (2015) recently reviewed this lineage, of which she retains the lineage of *Megacricetodon crusafonti* – *Megacricetodon crusafonti-ibericus* - *Megacricetodon ibericus*, which due to its morphology is the most interesting one with regard to the taxonomic determination of the material of Cuesta del Rey-1.

m1. There are four morphotypes for the anteroconid in the genus *Megacricetodon*, from rounded or bean-shaped (first morphotype) to deeply split, forming an X pattern with the protoconid and metaconid (fourth morphotype). In Cuesta del Rey-1 the latter morphotype is the only one present, at least in the 23 specimens presenting no wear that could affect the morphology, as occurs in *Megacricetodon ibericus*. One specimen (Fig. 2f) presents a long labial spur of the anterolophid, a character that was pointed out by Daams & Freudenthal (1988) in a few specimens of *M. primitivus* and *M. collongensis*.

In the genus *Megacricetodon* the mesolophid presents four morphotypes from long to absent. In Cuesta del Rey-1, its variation is the following: of the 29 specimens in which this character is observable, only 3 (10%) exhibit a medium-sized mesolophid (second morphotype), 16 (55%) present a short mesolophid developed as a small protuberance of the ectolophid (third morphotype), and 10 (35%) have no mesolophid (fourth morphotype). In the *Megacricetodon crusafonti* - *Megacricetodon ibericus* lineage, there is a trend towards the reduction of the mesolophid, which practically disappears in the latter species, as occurs in the material of Cuesta del Rey-1 where it is generally absent.

m2. There are three morphotypes for the lingual anterolophid of the genus *Megacricetodon*, from long and well developed to absent. Of the 26 specimens of Cuesta del Rey-1 in which this character is observable, 6 (23%) display a short or weakly defined lingual anterolophid (second morphotype), and 20 (77%), most of the population, present no lingual anterolophid at all (third morphotype). In the *Megacricetodon crusafonti* - *Megacricetodon ibericus* lineage, the lingual anterolophid tends become reduced. In *Megacricetodon ibericus* the third morphotype is the most abundant one, the second

morphotype is present in a few specimens, and none of them exhibit the first one, as occurs in the Cuesta del Rey-1 population.

In the genus *Megacricetodon* the mesolophid presents four morphotypes from long to absent. In Cuesta del Rey-1, its variation is the following: of 31 specimens, 9 (29%) have a short mesolophid developed as a small protuberance of the ectolophid (third morphotype), and 22 (71%) have no mesolophid (fourth morphotype). In the *Megacricetodon crusafonti* - *Megacricetodon ibericus* lineage, the mesolophid shows a tendency to become reduced, totally disappearing in the latter species as occurs with most of the Cuesta del Rey-1 material.

M1. The anterocone presents four morphotypes in the genus *Megacricetodon*, from a simple cusp (very scarce even in primitive species such as *Megacricetodon primitivus* and *Megacricetodon collongensis*) to deeply split and with a small cingulum ridge at its anterior edge in front of the anterocone (fourth morphotype). The latter morphotype is the only one in *Megacricetodon ibericus*, as occurs in the whole Cuesta del Rey-1 population.

With respect to the development of the labial spur on the anterolophule, of the three morphotypes distinguished in the genus *Megacricetodon* (from well-developed to absent) none exist in the Cuesta del Rey-1 specimens, as occurs in *Megacricetodon ibericus*.

In relation to the three morphotypes of the development of the paracone ectoloph, from absent (first morphotype) to well developed (third morphotype), the 15 specimens of Cuesta del Rey-1 present a short ectoloph (second morphotype), a similar development to what occurs in *Megacricetodon ibericus*.

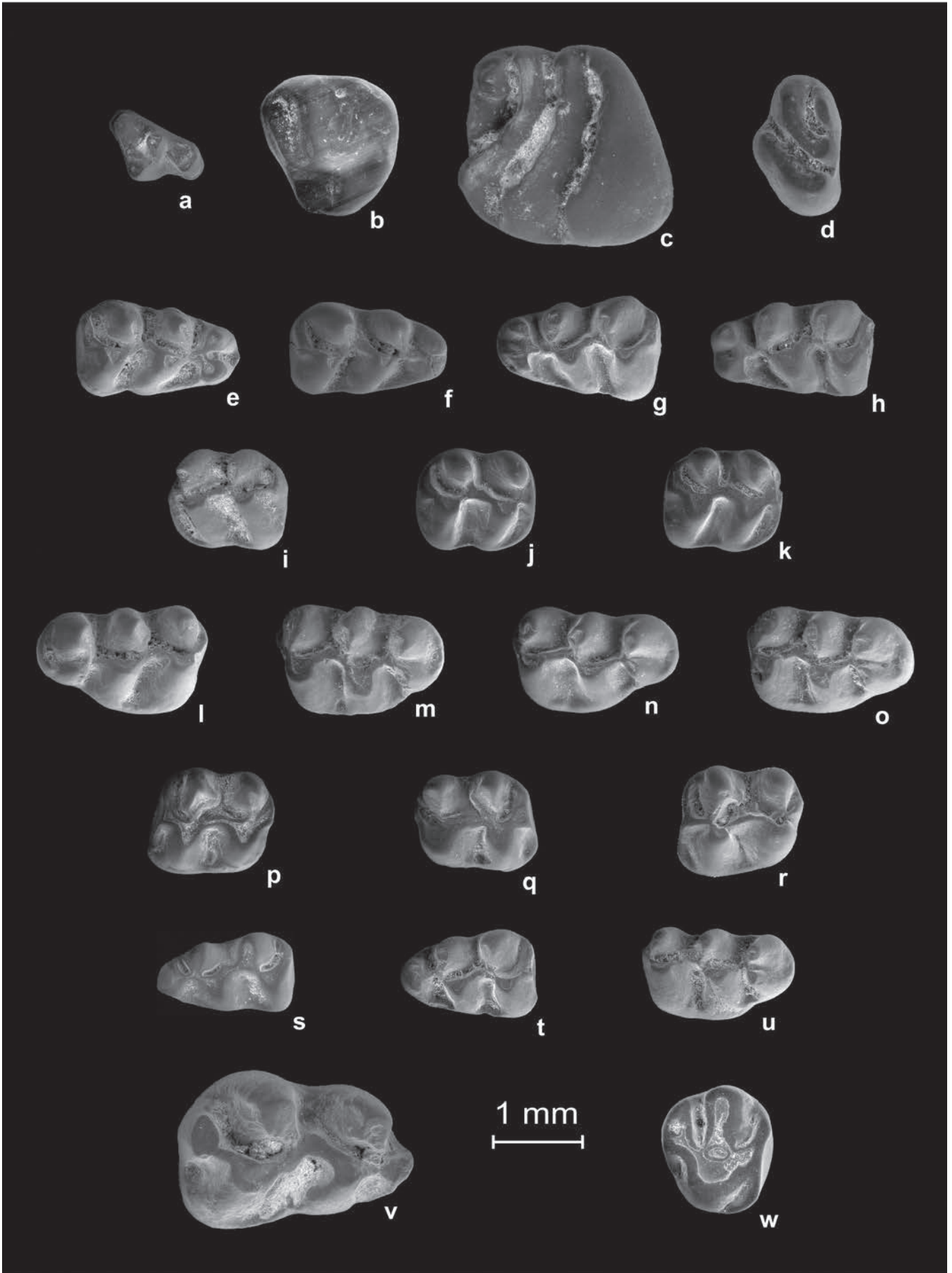
The mesoloph presents four morphotypes in the genus *Megacricetodon*, from long to absent. The variation of the 15 Cuesta del Rey-1 specimens is the following: in the vast majority (12 specimens; 80%) it does not exist (fourth morphotype), and only 3 specimens (20 %) develop a very short mesoloph, as a small protuberance of the entoloph (third morphotype), as occurs in *Megacricetodon ibericus*.

The posterosinus displays four morphotypes in the genus *Megacricetodon*, from well developed to absent. Its variation in the 15 Cuesta del Rey-1 specimens is the following: in the vast majority (12 specimens; 80%), the posteroloph is very short and encloses a small posterosinus (third morphotype), and in 3 specimens (20%) no posteroloph or posterosinus exist, as occurs in *Megacricetodon ibericus*.

M2. The protolophule variation presents five morphotypes in the genus *Megacricetodon*. In the 20 Cuesta del Rey-1 specimens, its variation is the following: in 7 specimens (35%) the protolophule is transverse to the protocone (second morphotype), in 3 (15%) the protolophule is transverse to the entoloph behind the protocone (third morphotype), in 7 (35%) the protolophule connects with the entoloph and the sinus is strongly curved

Table 1. Measurements of the molars of *Megacricetodon ibericus* from Cuesta del Rey-1.

MOLAR	N	LENGTH in mm			N	WIDTH in mm		
		Min.	Med.	Max.		Min.	Med.	Max.
m1	19	1.63	1.72	1.82	19	0.97	1.05	1.12
m2	21	1.21	1.30	1.42	22	0.90	1.07	1.16
m3	9	1.01	1.11	1.23	9	0.80	0.90	0.98
M1	14	1.67	1.79	1.93	14	1.04	1.14	1.23
M2	18	1.26	1.33	1.40	19	0.98	1.08	1.16
M3	4	0.83	0.88	0.94	4	0.81	0.88	0.93



forward (fourth morphotype), and in 3 (15%) there is a double protolophule (fifth morphotype). This development is similar to what occurs in *Megacricetodon ibericus*.

As it happens in the M1, in relation to the three morphotypes presented by the development of the ectoloph of the paracone in the genus *Megacricetodon*, from absent (first morphotype) to well developed (third morphotype), the 21 Cuesta del Rey-1 specimens exhibit a short ectoloph (second morphotype).

In the Cuesta del Rey-1 population, the representation of the three morphotypes of the sinus in the genus *Megacricetodon* is the following: in 3 specimens (14%) the sinus is transverse (first morphotype), in 9 (43%) the sinus is slightly curved forward (second morphotype), and in the other 9 (43%) it is strongly curved forward (third morphotype). The latter two morphotypes, the most frequent ones in the Cuesta del Rey-1 population, are also the most frequent in *Megacricetodon crusafonti* and *Megacricetodon ibericus*.

Discussion. The population of Cuesta del Rey-1 presents the characteristics of *Megacricetodon ibericus* according to Daams & Freudenthal (1988): m1 with a deeply split anteroconid and a greatly reduced or absent mesolophid; m2 with a very reduced lingual anterolophid, which is generally absent, and a greatly reduced mesolophid which in most of the population does not exist and in the rest is very short and developed as a small protuberance of the ectolophid; M1 with the anterocone deeply split and with a small cingulum at its anterior border, absence of a labial spur on the anterolophule, ectoloph of the paracone always present, mesoloph absent in the vast majority and very reduced in the rest, developed as a small protuberance of the entoloph, and a greatly reduced or absent posteroloph and posterosinus; M2 with the protolophule generally connected to the protocone and to the entoloph, ectoloph of the paracone always present, and the sinus curved forward in the majority of the specimens. The morphology and size of the material from Cuesta del Rey-1 are similar to those of the populations of *Megacricetodon ibericus* from several sites in the Calatayud-Teruel basin (Daams & Freudenthal, 1988; Oliver Pérez, 2015) and of the Escobosa de Calatañazor site in the Duero Basin (Sesé, 1977, 1980).

Megacricetodon minor (Lartet, 1851) - *Megacricetodon debruijini* Freudenthal, 1968
(Figs 2p-v, 3s-u)

Locality. Cuesta del Rey-1.

Material. 2 m1; 3 m2; 4 m3; 2 M1; 2 M2; 2 M3.

Measurements. See Table 2.

Table 2. Measurements of the molars of *Megacricetodon minor*-*Megacricetodon debruijini* from Cuesta del Rey-1.

MOLAR	L in mm	W in mm
m1 (CR-1: 17)	1.47	0.86
m1 (CR-1: 18)	1.44	0.95
m2 (CR-1: 36)	1.05	0.86
m2 (CR-1: 37)	1.05	0.85
m2 (CR-1: 60)	1.10	0.96
m3 (CR-1: s/n: 7)	0.95	0.79
m3 (CR-1: s/n: 13)	0.95	0.81
m3 (CR-1: s/n: 15)	0.97	0.83
m3 (CR-1: s/n: 17)	1.00	0.84
M1 (CR-1: 114)	1.56	0.92
M1 fr. (CR-1: 119)	----	----
M2 (CR-1: 92)	1.18	0.97
M2 (CR-1: 93)	1.20	1.00
M3 (CR-1: 98)	0.74	0.80
M3 (CR-1: 99)	0.78	0.81

Description. The size of this material, especially m1 and M1, is generally close to the maximum values of some populations of *Megacricetodon minor* (Las Planas 5H) and *Megacricetodon debruijini* (Carrilanga) according to the data of Daams & Freudenthal (1988).

For morphological description of the material we used the emended diagnosis of *Megacricetodon minor*

Figure 3. Scanning electronic microscope photographs of the micromammal tooth in occlusal view from Cuesta del Rey-1. (a) cf. *Miosorex* sp., left m3 (CR-1: s/n: 4). (b) *Heteroxerus* sp.: left P4 (CR-1: s/n: 8). (c-d) *Armantomys* cf. *tricristatus*, (c) left M₂ (CR-1: s/n: 1); (d) left P4 (CR-1: s/n: 2). (e-r) *Megacricetodon ibericus*, (e) right m1 (CR-1: 4); (f) right m1 (CR-1: 6); (g) left m1 (CR-1: 7); (h) left m1 (CR-1: 10); (i) left m2 (CR-1: 44); (j) right m2 (CR-1: 52); (k) right m2 (CR-1: 42); (l) left M1 (CR-1: 105); (m) right M1 (CR-1: 108); (n) right M1 (CR-1: 110); (o) right M1 (CR-1: 112); (p) left M2 (CR-1: 72); (q) right M2 (CR-1: 75); (r) left M2 (CR-1: 81). (s-u) *Megacricetodon minor*-*Megacricetodon debruijini*, (s) left m1 (CR-1: 17); (t) left m1 (CR-1: 18); (u) right M1 (CR-1: 114). (v) *Hispanomys* sp., right m1 (CR-1). (w) *Democricetodon* sp., right M3 (CR-1).

and *Megacricetodon debruijni* performed by Daams & Freudenthal (1988).

m1. One of the two specimens has a simple anteroconid as occurs in *Megacricetodon minor*, and the other one presents a slightly subdivided anteroconid as in *Megacricetodon debruijni*, although in the latter species the anteroconid is divided into two separated cusps by a deep split, according to Daams & Freudenthal (1988). The mesolophid is very reduced and barely outlined, as occurs in *Megacricetodon debruijni*, where it is short or absent, whereas in *Megacricetodon minor* it is generally well developed (long, medium length or short).

m2. The mesolophid is very reduced: it is absent in 2 of 3 specimens and in another one it is barely outlined.

M1. The anterocone is completely divided, as occurs in *Megacricetodon debruijni* and in 70 % of *Megacricetodon minor* according to Daams & Freudenthal (1988). They display a short mesoloph and a simple protolophule.

M2. One of the two specimens presents a short mesoloph, which is absent in the other. In one of the two specimens, there is a simple metalophule and in the other, this is double. In one specimen, the sinus is transverse (the most frequent morphotype in *Megacricetodon minor*), whilst in the other it is strongly curved forwards, as occurs in *Megacricetodon debruijni*.

Discussion. The principal character enabling *Megacricetodon minor* and *Megacricetodon debruijni* to be distinguished involves the presence of a simple m1 anteroconid in the former species, and a divided anteroconid in the latter one, according to Freudenthal (1968). In one of the two m1 of Cuesta del Rey-1 the anteroconid is simple, as in *Megacricetodon minor* and in the other specimen the anteroconid is subdivided, although in *Megacricetodon debruijni* the anteroconid is completely divided into two cusps. The reduction of the mesolophids in m1 and m2 and mesolophs in M1 and M2 from Cuesta del Rey-1 is similar to what occurs in *Megacricetodon debruijni*.

The material from Cuesta del Rey-1 is very scarce and shows, as has previously been stated, some characters of *Megacricetodon minor*, on the one hand, and of *Megacricetodon debruijni* on the other. For this reason we denominate the material of this site *Megacricetodon minor-Megacricetodon debruijni*, in a similar way as in the Escobosa de Calatañazor site, where it constitutes a transitional form of both species (Sesé, 1980).

Genus *Hispanomys* (Mein & Freudenthal, 1971)

Hispanomys sp.
(Figs 2w, 3v)

Locality. Cuesta del Rey-1.

Material and measurements. 1 m1: L = 2.51 mm; W = 1.74 mm; 1 fr. M2.

Description.

m1. The anterior metalophulid is interrupted, and the metaconid therefore remains as an independent cusp disconnected from the anteroconid. The anteroconid does not display a cingular ridge. The mesolophid is very short and barely outlined.

M2. Only the anterior part of the tooth is preserved, which reveals that the ectoloph of the paracone is short and incomplete.

Discussion. The measurements of this material fit within the variability of the size of *Cricetodon jotae* (Mein & Freudenthal, 1971) from Manchones (Freudenthal, 1963, 1966) and *Hispanomys aguirrei* (Sesé 1977, in: López Martínez *et al.*, 1977) from Escobosa de Calatañazor (López Martínez *et al.*, 1977; Sesé, 1980) and Nombrevilla-2 (López Guerrero *et al.*, 2008). Due to the great morphological variability of these species and to the scarce material from Cuesta del Rey-1, it cannot be assigned to either of them. Nonetheless, it presents the advanced characters that are most frequent in the genus *Hispanomys* in general and in the species *Hispanomys aguirrei* in particular: anterior metalophulid in m1 (interrupted in Cuesta del Rey-1) and a developed but incomplete ectoloph in M2.

Genus *Democricetodon* Fahlbusch, 1964

Democricetodon sp.
(Figs 2x, 3w)

Locality. Cuesta del Rey-1.

Material and measurements. 1 M3: L = 1.25 mm; W = 1.38 mm.

Description and discussion. This specimen exhibits the characteristic morphology and size of the genus *Democricetodon*. It presents a very simplified morphology, which is similar to morphotype D (mesoloph absent) of the genus *Democricetodon* according to Freudenthal & Daams (1988; Fig. 2D, p. 139), and is also similar to morphotype S (centroloph connecting the hypocone with the postero-labial border of the molar) of Freudenthal & Daams (1988; Fig. 1s, p. 136). Its relatively large size fits with the variability of that of *Democricetodon freudenthali* (Antunes & Mein, 1981) and *Democricetodon darocensis* (Freudenthal, 1963) according to the data of Freudenthal & Daams (1988), and it is smaller than the populations of *Democricetodon crusafonti* (Agustí, 1978) from Escobosa de Calatañazor (Sesé, 1980) and of the Calatayud-Teruel Basin (Meulen *et al.*, 2003). However, as there is only

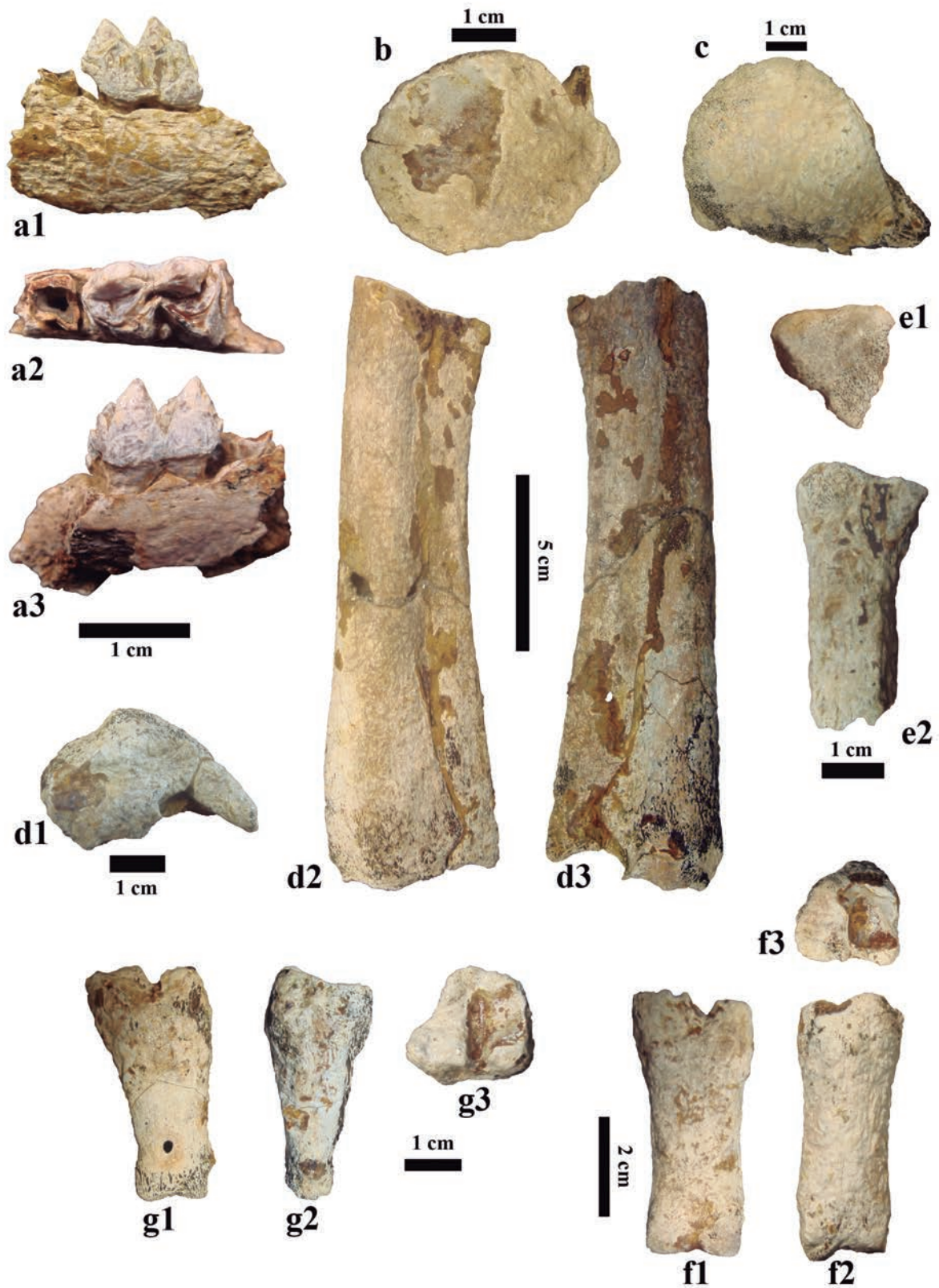


Figure 4. Large mammals from Cuesta del Rey-3. (a) *Dorcatherium* sp. CR-3-7, left fragment of mandible with m1; **a1**) buccal view, **a2**) occlusal view, **a3**) lingual view. (b-g) *Listriodon* cf. *splendens*; **b**) CR-3-1, left proximal epiphysis of scapula (glenoid cavity) in proximal view. **c**) CR-3-2, left proximal humerus epiphysis in proximal view. **d**) CR-3-3, left distal epiphysis of radius-ulna; **d1**) dorsal view, **d2**) palmar view, **d3**) distal view. **e**) CR-3-4, left proximal central metacarpal; **e1**) proximal view, **e2**) lateral view. **f**) CR-3-5, left first central phalanx; **f1**) palmar view, **f2**) dorsal view, **f3**) proximal view. **g**) CR-3-6, left first central phalanx; **g1**) palmar view, **g2**) lateral view, **g3**) proximal view.

one non-diagnostic tooth, which displays a highly variable morphology, it cannot be assigned taxonomically to any species.

Table 3. Measurements in mm of the postcranial bones of *Listriodon* cf. *splendens* from Cuesta del Rey-3. L. P-D = Length proximal-distal; L.L-M PE = Length lateral-medial proximal epiphysis; L.D-P PE = Length dorsal-palmar proximal epiphysis; L.L-M DE = Length lateral-medial distal epiphysis; L.D-P DE = Length dorsal-palmar DE epiphysis.

	Scapula	Radius/Ulna	Metacarpal	Phalanx I	Phalanx I
L. P-D				48.8.	
L.L-M PE	33		20.9	21.4	22
L.D-P PE	45		21.5	21	20
L.L-M DE		48		18	
L.D-P DE		38		15	

Order ARTIODACTYLA Owen, 1848
 Family **Suidae** Gray, 1821
 Genus *Listriodon* von Meyer, 1846

Listriodon cf. *splendens* von Meyer 1846
 (Figs 4b-g)

Locality. Cuesta del Rey-3.

Material. Left forelimb association; CR-3-1, proximal epiphysis of scapula (glenoid cavity), CR-3-2, proximal epiphysis of humerus, CR-3-3, distal fragment of radius; CR-3-4, proximal fragment of central metacarpal, CR-3-5, CR-3-6, two phalanx I.

Measurements. Table 3.

Description and discussion. This fossil assemblage was found on the surface; all bones were eroded, presenting root marks. The size of the two first phalanges is close to the undescribed homologous material from the locality of Toril-3, whose dentition was determined as *Listriodon splendens* by Pickford & Morales (2003).

Family **Tragulidae** Milne-Edwards, 1864
 Genus *Dorcatherium* Kaup & Scholl, 1834

Dorcatherium sp.
 (Fig. 4a)

Locality. Cuesta del Rey-3.

Material and measurements. CR-3-7, left m1: L= 11.5 mm; W = 7.3 mm.

Description and discussion. The m1 presents a well-marked “*Dorcatherium* fold” and the absence of a stylid in the buccal wall both constitute diagnostic features of

Dorcatherium lower dentition (Morales *et al.*, 2012). The size is close to both *D. crassum* and *D. naui*. Consequently, a more accurate determination is not feasible. Tragulidae species are characteristic of riparian habitats, and this tooth is the oldest record of the family in the Duero Basin.

5. RESULTS AND DISCUSSION

In the present paper, the following mammals are identified in the new Cuesta del Rey-1 site: Eulipotyphla: Soricidae: cf. *Miosorex* sp.; Rodentia: Sciuridae: *Heteroxerus* sp.; Gliridae: *Armantomys* cf. *tricrostus*; Cricetidae: *Megacricetodon ibericus*, *Megacricetodon minor-Megacricetodon debruijini*, *Hispanomys* sp. and *Democricetodon* sp.; the following ones are identified in Cuesta del Rey-3: Artiodactyla: *Dorcatherium* sp. and *Listriodon* cf. *splendens*.

This micromammal assemblage is characteristic of the end of the upper Aragonian (end of the middle Miocene), in subzone G3 of the G zone according to Daams & Freudenthal (1988), units MN 7/8 of Mein (1975). The species *Megacricetodon ibericus* appears in this subzone, continuing in zone H of the lower Vallesian (Sesé, 1980; Álvarez Sierra *et al.*, 2003; Dam *et al.*, 2014). The population of *Megacricetodon minor-Megacricetodon debruijini* from Cuesta del Rey, with a morphology between both species, is similar to the populations of this taxa of some sites of the final of the upper Aragonian (subzone G3), whereas de more evolved species of both, *Megacricetodon debruijini*, is characteristic of the early Vallesian. The genus *Armantomys*, a characteristic taxon mainly recorded in the early and middle Miocene of the central basins of the Iberian Peninsula (Duero, Tagus, Calatayud-Teruel, Ebro) and the Levant, but not in the Vallès-Penedès Basin (Sesé, 1988), was last recorded in subzone G3 at the end of the Aragonian (Daams, 1990; Sesé, 2006). Outside Spain Baudelot & Collier (1982) have cited an unique tooth as *Armantomys aragonensis* from Liet (Gers, France).

The Cuesta del Rey-1 site can be also situated in the cenozoone of *Megacricetodon ibericus* (Álvarez Sierra *et al.*, 1990b) by the record of this species and its association with *Megacricetodon minor-Megacricetodon debruijini*. This cenozoone also contains the sites from the Duero Basin of La Parrilla, Casasola 2, Torrelatón-1 and 2, Buenaventura-4 and 5, Torremormojón-5 and Ampudia-10 (Álvarez Sierra *et al.*, 1990b). Cuesta del Rey-1 also has all the taxa in common with Escobosa de Calatañazor, from the Duero Basin, a karstic site from the end of the upper Aragonian (Sesé, 1980), and with other sites from the Duero, Tagus and Daroca-Nombrevilla basins of this age (Fig. 5).

Continental Stage	MN Zone	Local Zone	LOCALITIES	TAXA																	
				<i>Heteroxerus</i> spp.	<i>Atlantoxerus adroveri</i>	<i>Spermophilinus</i> spp.	<i>Armantomys</i> spp.	<i>Myomimus delimi</i>	<i>Tempestia hartenbergeri</i>	<i>Microdromys</i> spp.	<i>Muscardinus hispanicus</i>	<i>Megacricetodon crusafonti</i>	<i>Megacricetodon ibericus</i>	<i>Megacricetodon minor/debruijni</i>	<i>Cricetodon / Hispanomys</i> spp.	<i>Democricetodon</i> spp.	Castoridae	<i>Listriodon splendens</i>	<i>Dorcatherium</i> sp.	<i>Hipparion</i> spp.	
LOWER VALLESIAN	9	I H	Los Valles de F. Torremormojón 5	X	X	cf.	cf.					X		X		X	X	X	X		
			Casasola 2						X		X	X	X	X		X					
			Molina de A. Nombrevilla 1	X			X	X	X	X	X	X	X	X	X		X				X
			Cendejas-2	X							X	X									
			Ledanca				X					X	X	X	cf.						
			Nombrevilla 10				X		X	X	X	X	X	X							
UPPER ARAGONIAN	7/8	G3	Escobosa	X	X	X	X			X	X	X	X								
			Cuesta del R.-1	X	X					X	X	X	X								
			Cuesta del R.-3																		cf. X
			Parrilla					X		X	X	X									
			Lupiana	X	X	X	X			X		X	cf.	X	X						
			Manchones 1	X				X	X	X	X	X	X	X	X						X
UPPER ARAGONIAN	6	G2	Otero-2					X	X	X											
			Duredos-1					X			X	X									
			Simancas-2				X				X	X	X								
			Paracuellos 3	X	X	X	X							X	X						

Figure 5. Distribution of selected rodent taxa from the upper Aragonian and lower Vallesian localities: Simancas-2, Duredos-1, Otero-2, La Parrilla, Casasola 2, Torremormojón 5 (García Moreno, 1988), Escobosa de Calatañazor (Sesé, 1980), Los Valles de Fuentidueña (Sesé & López Martínez, 1981) and Cuesta del Rey-1/3 from the Duero Basin; Paracuellos 3 (Sesé *et al.*, 1985; Alberdi *et al.*, 1985), Lupiana, Ledanca, Cendejas-2 (Sesé *et al.*, 1990) and Molina de Aragón (Lacomba, 1988) from the Tagus Basin; Manchones 1 (Daams & Freudenthal, 1988), Nombrevilla 2 and Nombrevilla 1 (classical site) from the Calatayud- Daroca-Nombrevilla (Teruel and Zaragoza) Basin (Álvarez Sierra *et al.*, 2003).

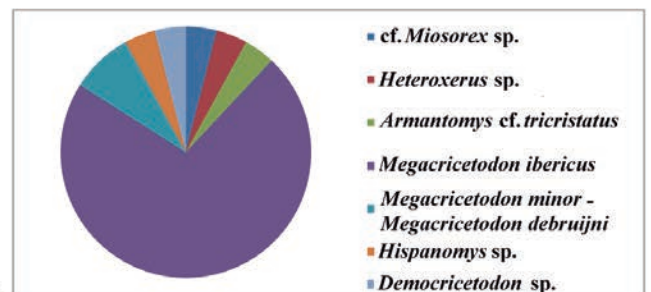
The rodent assemblages from the upper Aragonian and the early Vallesian (zone H) sites, generally display a great continuity in relation to most of the taxa, except for the last record of the genus *Armantomys* in the upper Aragonian (Sesé, 2006). *Megacricetodon ibericus* and *Megacricetodon minor-Megacricetodon debruijni*, two very characteristic taxa due to represent the stages of evolution of two different lineages of the genus *Megacricetodon*, are common in these assemblages and also are present in some sites of the Vallès-Penedès (Catalonia), (Agustí, 1982; Casanovas-Vilar *et al.*, 2016), the second represented by *Megacricetodon debruijni* in the Vallesian. The interior basins of the Iberian Peninsula also present great continuity in the record of the other species of cricetids, glirids, and castorids between the Aragonian/Vallesian transition. The

castorids, which were absent during the Ramblian, and lower and middle Aragonian, reappear at the end of the upper Aragonian, and they have since been recorded until the end of the Neogene (Sesé, 2006).

From the paleoenvironmental perspective, the genera *Heteroxerus* and *Armantomys* suggest a dry and open environment with savannahs and meadows, whereas *Megacricetodon* might have lived in different types of environments that could be dry and open with savannahs and meadows, or in moist and wooded ones (Weerd & Daams, 1978; Daams *et al.*, 1988). The genus *Megacricetodon* is the most abundant micromammal taxon in Cuesta del Rey-1, with an MNI of 20 of the total MNI of 25 (80% of the total percentage of the MNI) (Fig. 6). In the rodent assemblages from the end of the Aragonian

TAXONES	/	NMI - % NMI	NMI	% NMI
cf. <i>Miosorex</i> sp.			1	4
<i>Heteroxerus</i> sp.			1	4
<i>Armantomys</i> cf. <i>tricristatus</i>			1	4
<i>Megacricetodon ibericus</i>			18	72
<i>Megacricetodon minor - Megacricetodon debruijni</i>			2	8
<i>Hispanomys</i> sp.			1	4
<i>Democricetodon</i> sp.			1	4
TOTAL			25	100

a



b

Figure 6. a) Abundance of micromammal taxa from Cuesta del Rey-1 according to the MNI, and to percentage of the MNI. b) Representation of the percentage abundance (% of the MNI) of the micromammal taxa from Cuesta del Rey-1.

in the central basins of the Iberian Peninsula, the genus *Megacricetodon* is also the most abundant taxon in general terms (Meulen & Daams, 1992; Oliver Pérez, 2015). López Martínez *et al.* (2000) also highlight the great abundance of the genus *Megacricetodon* in the micromammal assemblages of the upper Aragonian in the central basins, which suggests an open savannah or steppe habitat, as it could happen in Cuesta del Rey-1 by the great abundance of *Megacricetodon ibericus*. With regard to climate, Meulen & Daams (1992) suggest that in the upper Aragonian there was a cooling event, with some oscillations of humidity. Additionally, the presence of *Dorcatherium* at Cuesta del Rey-3 suggests the existence in this area of permanent watercourses, which is consistent with the sedimentary change observed in the Cuesta del Rey section. Moreover, independently from the relationship between the Villatoro facies, located at the base of Cuesta del Rey Butte, and the Riocerezo “Marls, clays and limestones” facies, the Cuesta del Rey terrigenous sediments represent alluvial environments prograding on the marsh/lacustrine sediments of the lower facies. The terrigenous sedimentation in this area ends with the deposition of marls and limestones (Pineda, 1997). This sequence is comparable in age and general characteristics with the Paramo Superior sequence described by Nozal & Herrero (2005) on the SE border of the Duero Basin. It is testimony to a general change in the environment towards wetter conditions in the Iberian central basins (Calvo *et al.*, 1993).

6. CONCLUSIONS

The study of the mammal fauna of the Cuesta del Rey sites represents an important contribution to a better understanding of the Neogene faunas and biostratigraphy of the Duero Basin. Unfortunately, despite the great palaeontological potential of this area, no other studies have been conducted since the prospection of Olmo *et al.* (2008). Moreover, the mammal assemblages of the Aragonian/Vallesian transit deserve particular attention in different basins: García Moreno (1988) and Álvarez Sierra *et al.* (1990b) in the Duero Basin; Álvarez Sierra *et al.* (2003) and Dam *et al.* (2014) in the area of Daroca-Nombrevilla; García-Paredes *et al.* (2016) in the area of Calatayud-Montalbán; and Casanovas-Vilar *et al.* (2016) in the Vallès-Penedès Basin (Catalonia). The rodent assemblage of Cuesta del Rey-1 confirms the fact that no significant change clearly marks the boundary between the late Aragonian (middle Miocene) and the early Vallesian (upper Miocene) in Iberian continental environments.

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