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First Early Pliocene micromammal faunas from the Venta del Moro area (Cabriel Basin, Spain): new data on the Messinian dispersal of *Debruijnimys*

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Abstract

The localities of La Bullana 3 and LA Bullana 2B (Valencia, E Spain) have yielded remains of *Apodemus gorafensis*, *Paraethomys* aff. *abaigari*, *Stephanomys dubari*, *Apocricetus barrierei*, Sciuridae indet. and *Asoriculus* cf. *gibberodon* the former, and *Apodemus gorafensis*, *Paraethomys* aff. *abaigari*, *Stephanomys dubari*, *Apocricetus barrierei*, Sciuridae indet., *Asoriculus* cf. *gibberodon*, *Castillomys gracilis*, *Occitanomys brailloni*, *Occitanomys* sp., *Paraethomys meini*, *Ruscinomys* sp., *Eliomys intermedius*, *Debruijnimys* cf. *julii* and *Atlantoxerus* sp. the latter. Based on the study of these micromammal assemblages, we propose an Early Pliocene age (MN14) for both sites. The presence a gerbilid related to *Debruijnimys julii* in La Bullana 2B open new questions about the phylogenetic relationship between *Debruijnimys* species from the Miocene and Pliocene of the Iberian Peninsula. Furthermore, preliminary paleomagnetic data indicate an age between 4.997 Ma and 4.896 Ma for La Bullana 2B, and between 5.235 Ma and 4.997 Ma for La Bullana 3.

Keywords: Rodentia, Neogene, Ruscinian, *Debruijnimys*, Iberian Ranges, Iberian Peninsula

Resumen

Las localidades de La Bullana 3 y La Bullana 2B (Valencia, E Spain) han cedido restos de *Apodemus gorafensis*, *Paraethomys* aff. *abaigari*, *Stephanomys dubari*, *Apocricetus barrierei*, Sciuridae indet. y *Asoriculus* cf. *gibberodon* la primera, y *Apodemus gorafensis*, *Paraethomys* aff. *abaigari*, *Stephanomys dubari*, *Apocricetus barrierei*, Sciuridae indet., *Asoriculus* cf. *gibberodon*, *Castillomys gracilis*, *Occitanomys brailloni*, *Occitanomys* sp., *Paraethomys meini*, *Ruscinomys* sp., *Eliomys intermedius*, *Debruijnimys* cf. *julii* y *Atlantoxerus* sp. la segunda. Basándonos en el estudio de estas ascociaciones de micromamíferos, proponemos una edad correspondiente al Plioceno inferior (MN14) para ambos yacimientos. La presencia de un gerbílido relacionado con *Debruijnimys julii* en La Bullana 2B plantea nuevas preguntas acerca de la relación filogenética entre las especies de *Debruijnimys* del Mioceno y Plioceno. Además, datos paleomagnéticos preliminares indican una edad entre 4.997 Ma y 4.896 Ma para La Bullana 2B, y entre 5.235 Ma y 4.997 Ma para La Bullana 3.

Palabras clave: Rodentia, Neógeno, Rusciniense, *Debruijnimys*, Cordilleras Ibéricas, Península Ibérica

1. Introduction

Near the village of Venta del Moro (Valencia, Spain) part of the youngest sediments of the Cabriel Basin crop out in La Bullana area. In this zone, the lower part of the limestone Unit that forms the uppermost deposits from this basin includes a significant proportion of detrital deposits, containing several levels with remains of freshwater gastropods and vertebrates.

In the sections of La Bullana 2 and La Bullana 3, four new localities have been located: La Bullana 2A (LB2A), La Bullana 2B (LB2B), La Bullana 3 (LB3) and La Bullana 3A (LB3A). Only two of them, La Bullana 2B and La Bullana 3, have yielded a significant number of fossil remains.

The paleontological research of the Júcar-Cabriel area has been fruitful, with two important Late Turolian (or Ventian, sensu Morales *et al*., 2013) macromammal localities, namely Venta del Moro (Morales, 1984; Montoya *et al*., 2006) and La Portera (Lacomba *et al*., 1986), along with a number of micromammal sites (see references in Montoya *et al*., 2006; Benavent *et al*., 2008; Mansino *et al*., 2009; Ruiz-Sánchez *et al*., 2011). Venta del Moro (6.23 Ma) is one of the key localities for understanding the environmental and faunal changes occurred just before the Messinian Salinity Crisis (5.96-5.33 Ma), with more than a hundred identified species, six of which have been described in this site (Montoya *et al*., 2006; Morales *et al*., 2011; Mansino *et al*., in press). The new localities of La Bullana 2B and La Bullana 3 are stratigraphically higher than the eastern localities of Venta del Moro and Los Mingos (Montoya *et al*., 2006; Benavent *et al*., 2008; Mansino *et al*., 2009) (Figs. 1–2).

In this paper we describe the fossil rodent faunas from La Bullana 2B and La Bullana 3, and discuss their chronostratigraphical, biostratigraphical and paleobiogeographical implications.

2. Material, methods and abbreviations

Field work during 2005 and 2007 provided over 1200 kg of sediment from La Bullana 2B and 1,500 kg from La Bullana 3. After sieving these sediments, the recovered fossils were kept at the Museu de Geologia de la Universitat de València (MGUV), with the field labels LB2B- and LB3-, respectively. The nomenclature used in the descriptions of the teeth and the measurement methods are those of Martín-Suárez and Freudenthal (1993) for the family Muridae, Mein and Freudenthal (1971) for the Cricetidae, Daams (1981) and Freudenthal (2004) for the Gliridae, Cuenca-Bescós (1988) and Reumer and Van de Hoek Ostende (2003) for the Sciuridae, and Reumer (1984), modified by Furió (2007), for the insectivores. Measurements (L x W) are in millimetres and were taken on a Leica MZ75 binocular microscope, by means of displacement of a mechanical stage, connected to a Sony Magnescale measuring equipment. The lower teeth are indicated as **m1**, **m2** and **m3**, the upper teeth as **M1**, **M2** and **M3**, the premolars as **p4** and **P4**, and the deciduous elements as **d4** and **D4**.

Abbreviations.- **AL2-C**, Alcoy-2C; **AL2-D**, Alcoy-2D; **CLC**, Calicasas; **L**, Length; **LB2B**, La Bullana 2B; **LB3**, La Bullana 3; **MN**, European Neogene land mammal Units; **MNA**, Mina; **PUR**, Purcal; **SCSIE (UV)**, Servei Central de Suport a la Investigació Experimental de la Universitat de València; **THC**, Tollo de Chiclana; **TLW**, talonid width; **TRW**, trigonid width; **W**, Width.

3. Geological setting

The studied sites are located in the Cabriel Basin, a Neogene basin located between the Iberian platform to the North and Betic Cordillera to the South. The sedimentary infilling of the Cabriel Basin is mostly composed of Cenozoic limestones with detrital sediments (Fig. 1). The sedimentary record of this Basin contains several mammal sites ranging from the Late Aragonian to the Villanyian (MN7/8 to MN17) (see Ruiz- Sánchez *et al*. 2011 and references therein). The sites of La Bullana 2B and La Bullana 3 are located in the upper part of the Detritic Unit of Los Isidros, within the Venta del Moro-Villatoya Formation, according the stratigraphy described by Robles (1970) (Fig. 1). They are located approximately 3 km Southwest from the classic locality of Venta del Moro, about 10 m below La Molata, the top of the stratigraphic sequence (Fig. 2). However, the dip slope of La Bullana 2B and La Bullana 3 suggests that these localities may correspond to the same carbonated unit. The cross section of La Bullana 2, from where micromammal remains have been obtained, is mainly composed of detritic deposits, although it is crowned by a decametric layer of limestone. This outcrop includes several lignite levels and abundant fluvial sands, resting on red clays with intercalations of sandy channels. One kilometer Southeast from La Bullana 2B (30SXJ6394369), La Bullana 3 is located (30SXJ6404368), which probably represents an outcrop of equivalent deposits.

4. Systematic Paleontology

Order Rodentia Bowdich, 1821
Family Muridae Illiger, 1811
Genus *Apodemus* Kaup, 1826
Apodemus gorafensis Ruiz Bustos, Sesé, Dabrio, Peña and Padial, 1984 (Fig. 3, 1-4)

Localities: LB2B, LB3.

Material: 7 m1 (LB2B-25, LB2B-88, LB2B-92, LB2B-183, LB3-2, LB3-3, LB3-30), 9 m2 (LB2B-35, LB2B-36, LB2B-41, LB2B-105, LB2B-142, LB3-10, LB3-11 to LB3-13), 8 m3 (LB2B-44, LB2B-45, LB2B-114, LB2B-115, LB2B-200, LB2B-203, LB3-17, LB3-18), 8 M1 (LB2B-9, LB2B-13, LB2B-51, LB2B-129, LB2B-250, LB2B-258, LB3-19, LB3-20), 4 M2 (LB2B-20, LB2B-21, LB2B-136, LB3-22), 4 M3 (LB2B-214, LB2B-216, LB2B-219, LB3-24).

Measurements: see Table 1.

Description:

m1: The tma is large, round and central. Symmetrical anteroconid, its labial lobe connects with the metaconid. Well-developed labial cingulid, with a big round c1 and two or three accessory cuspids. One of the specimens has a hint of longitudinal spur. Big oval posterior heel, shifted towards the lingual side of the tooth. Roots are not preserved.

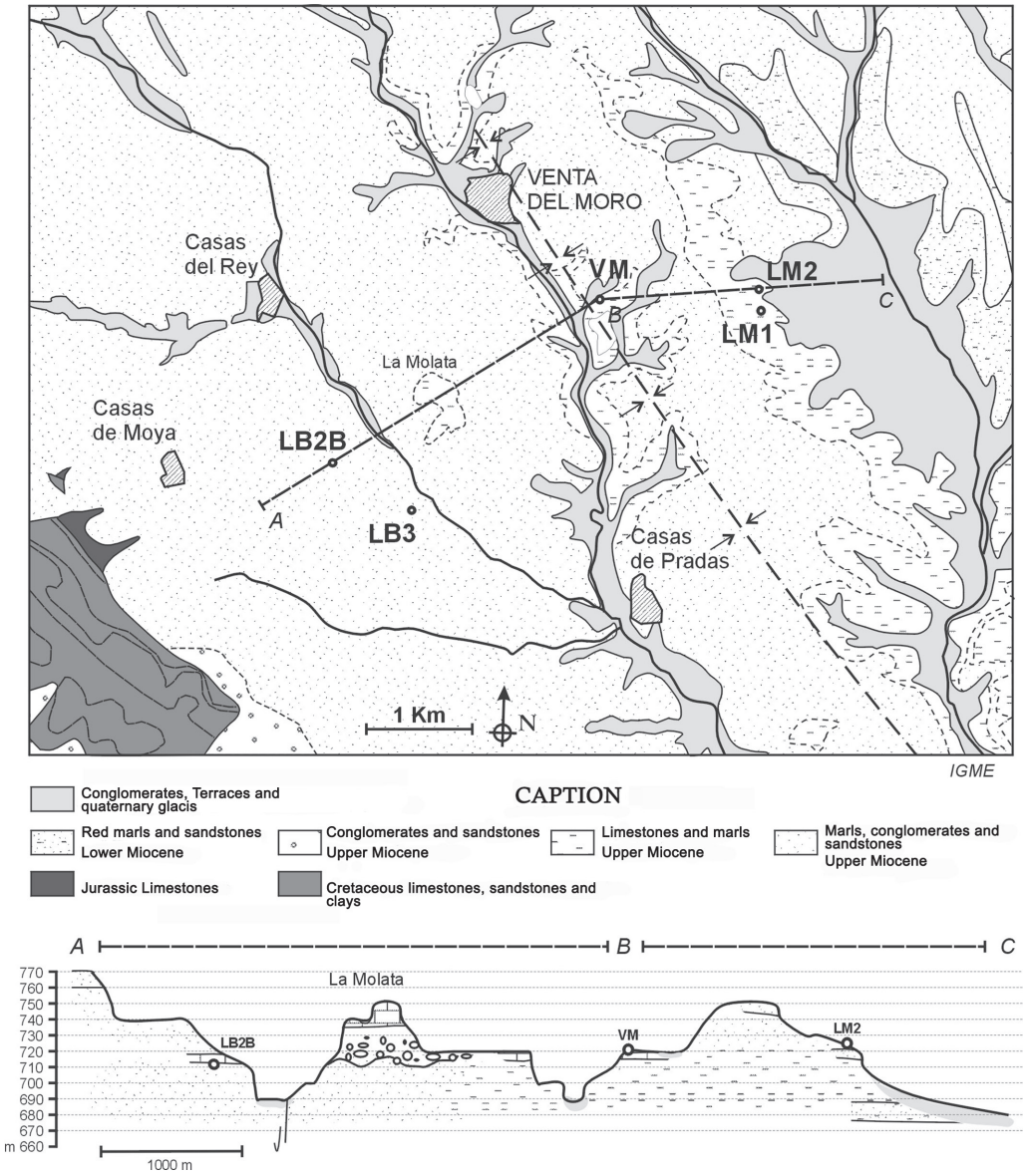


Fig. 1.- Geographic and geological setting of the surroundings of Venta del Moro (VM), showing the location of the sites Los Mingos 1 (LM1) (Benavent *et al*., 2008), Los Mingos 2 (LM2), La Bullana 2B (LB2B) and La Bullana 3 (LB3) (this paper).

m2: Big oval anterolabial cuspid. Well-developed labial cingulid, separated from the protoconid and hypoconid. There is a large round c1, except for one specimen in which this cuspid is much reduced, and one or two accessory cuspids. The posterior heel is large, round or oval. Roots are not preserved.

m3: Anterolabial cuspid reduced or absent. There is no longitudinal crest. One specimen has a small c1 connected to the labial side of the hypoconid-entoconid complex. Roots are not preserved.

M1: The t1 is displaced backwards. The connection between t1 and t2 is very low. There is neither t1 bis nor t2 bis. The valley between t3 and t6 is very deep and wide. The t4, t5, t6 and t9 are connected. The t7 is well developed, and there is a medium-sized t12 connected to the posterolabial side of t8. Roots are not preserved.

M2: The t1 is large, oval or round, and two specimens have a spur directed towards the t4-t5 connection. The t3 is reduced and isolated from the other cusps. The t7 is well developed and separated from t4. The t6 and t9 are connected. The t12 is small, connected to the posterolabial part of t8 and separated from t9. Roots are not preserved.

M3: The t1 is isolated. The t3 is absent. The t4, t5, t6, t8 and t9 are connected. Roots are not preserved.

Discussion:

The presence of a large tma in the m1, well-developed labial cingulid in m1 and m2 and t7 in the upper molars are typical traits of *Apodemus*. The specimens from LB2B and LB3 are larger than *Apodemus atavus* Heller, 1936 from TCH-1, 1B, 3 and 13 (Minwer-Barakar *et al*., 2005), PUR-7, PUR-13, CLC-3, CLC-3B, CLC-4B, AGU-1C and DHS-1 (García-Alix *et al*.,

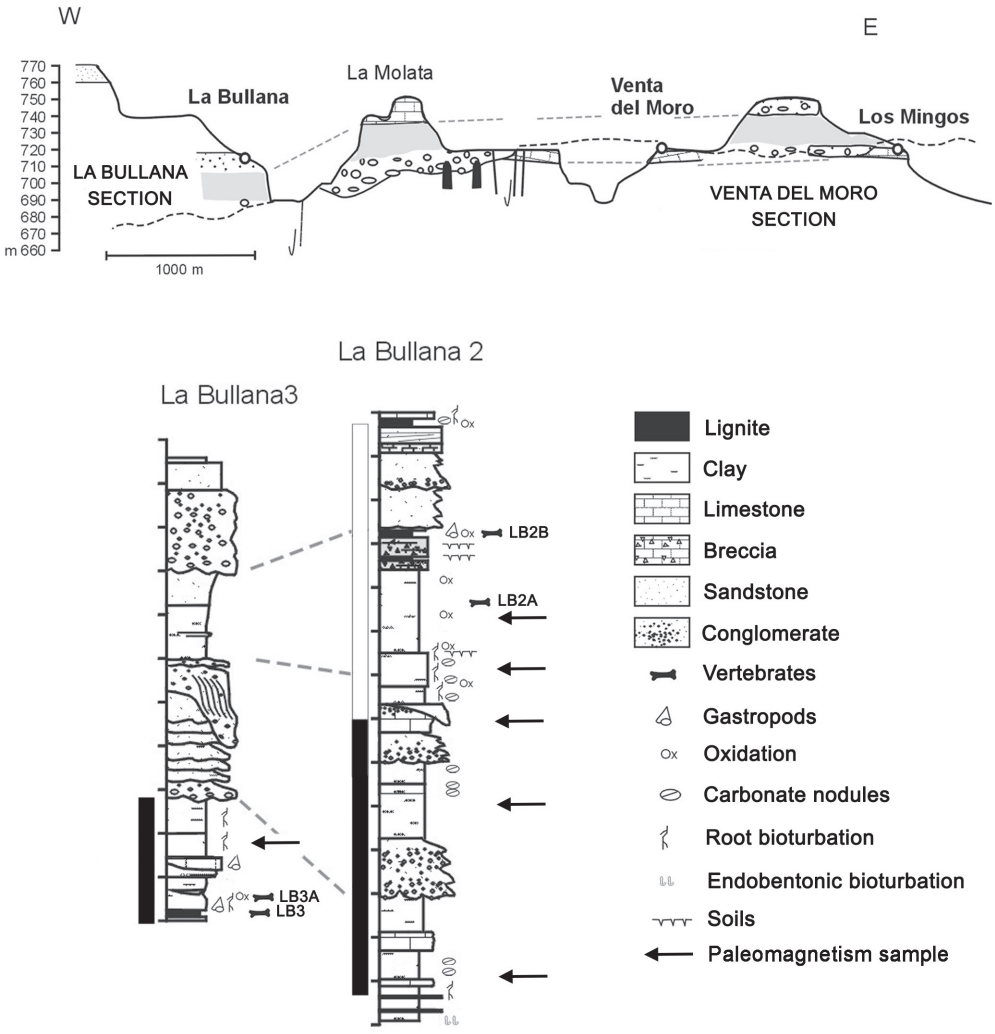


Fig. 2.- Geological sketch in the Venta del Moro area with location of the La Bullana and Venta del Moro sections, their correlation and the available paleomagnetic data: black, normal polarity; white, reversed polarity.

2008a) and smaller than *Apodemus jeanteti* Michaux, 1967 from Arquillo 3 and Villalba Alta (Adrover, 1986); this latter species further differs from *A. gorafensis* in the lack of tma in the m1. *Apodemus gorafensis* differs from its ancestor, *Apodemus gudrunae* van de Weerd, 1976, in the presence of a well-developed t7. This latter species is also slightly smaller than our specimens. In addition, *Apodemus agustii* Martín-Suárez, 1988 differs from *A. gorafensis* in the partial stephanodonty of the upper molars, less-developed tma and lack of a pit in m1 between the anteroconid, metaconid and protoconid. The size of the studied molars is consistent with *A. gorafensis* from its type locality, Gorafe A (Ruiz Bustos *et al*., 1984) and PUR-4, PUR-24A, PUR 25, PUR-25A, MNA-2 and MNA-4 (García-Alix *et al*., 2008a), Gorafe-3, Gorafe-4, Botardo-C and Huescar-1 (Martín-Suárez, 1988) and Alcoy 2C and 2D (Mansino *et al*., 2013), being also similar to *A.* aff *gorafensis* from PUR 23 (García-Alix *et al*., 2008a), Celadas 9, La Gloria 4 (Adrover *et al.,* 1993) and Peralejos E (Adrover *et al*., 1988).

The development of the tma, labial cingulid and t7 in the specimens from La Bullana 2B and La Bullana 3 agrees with *A. gorafensis*. There is a t9 (Fig. 3, 4) in two M3, while other two are much worn and this cusp cannot be observed. This cusp is absent in the fossil remains of *A. gorafensis* from the mentioned localities, with the exceptions of some specimens from PUR-23 and PUR-24A (García-Alix *et al*., 2008a).

Genus *Castillomys* Michaux, 1969
Castillomys gracilis van de Weerd, 1976 (Fig. 3, 5-7)

Locality: LB2B.

Material: 5 m1 (LB2B-90, LB2B-91, LB2B-94, LB2B-95, LB2B-188), 4 m2 (LB2B-106 to LB2B-109), 6 M1 (LB2B-14, LB2B-125, LB2B-126, LB2B-204, LB2B-205, LB2B-210) 1 M2 (LB2B-22), 1 M3 (LB2B-218).

Measurements: see Table 2.

Description:

m1: One specimen has a very small and low tma (Fig. 3, 5), absent in the rest. The anteroconid is symmetrical and connected to the protoconid-metaconid pair. There is a longitudinal spur and a narrow labial cingulid. The c1 is round

Element	Locality	Parameter	n	min.	mean	max.
m1	LB2B	L	4	2.05	2.08	2.14
		W	4	1.26	1.31	1.35
m2	LB2B	L	5	1.49	1.54	1.57
		W	5	1.27	1.36	1.41
	LB3	L	4	1.49	1.52	1.58
		W	4	1.37	1.42	1.48
m3	LB2B	L	5	1.12	1.17	1.21
		W	5	1.03	1.08	1.12
	LB3	L	1	-	1.22	-
		W	1	-	1.08	-
M1	LB2B	L	1	-	2.22	-
		W	3	1.40	1.46	1.50
	LB3	L	2	-	1.57	-
M2	LB2B	L	3	1.53	1.57	1.63
		W	3	1.37	1.42	1.45
	LB3	L	1	-	1.70	-
		W	1	-	1.50	-
M3	LB2B	L	3	1.00	1.05	1.12
		W	3	0.94	1.02	1.08
	LB3	L	1	-	0.97	-
		W	1	-	1.01	-

Table 1.- Measurements in millimeters of the teeth of *Apodemus gorafensis* from the localities La Bullana 2B and La Bullana 3. n= number of measurable specimens.

Element	Locality	Parameter	n	min.	mean	max.
m1	LB2B	L	5	1.35	1.40	1.47
		W	5	0.88	0.90	0.93
m2	LB2B	L	4	1.02	1.06	1.12
		W	4	0.93	0.95	0.98
M1	LB2B	L	6	1.44	1.52	1.61
		W	6	1.01	1.05	1.12
M2	LB2B	W	1	-	1.21	-
M3	LB2B	L	1	-	0.76	-
		W	1	-	0.69	-

Table 2.- Measurements in millimeters of the teeth of *Castillomys gracilis* from the locality La Bullana 2B. n= number of measurable specimens.

Element	Locality	Parameter	n	min.	mean	max.
m1	LB2B	L	3	1.84	1.87	1.90
		W	4	1.25	1.28	1.31
m2	LB2B	L	2	1.45	1.50	1.55
		W	2	1.39	1.40	1.40
m3	LB2B	L	5	1.05	1.09	1.15
		W	5	0.97	1.02	1.06
M1	LB2B	L	3	1.96	2.05	2.11
		W	3	1.42	1.46	1.49
M2	LB2B	L	1	-	1.48	-
		W	1	-	1.40	-

Table 3.- Measurements in millimeters of the teeth of *Occitanomys brailloni* from the locality La Bullana 2B. n= number of measurable specimens.

or oval and connected basally to the hypoconid. One molar has a small accessory cuspid. The posterior heel is small and lingually displaced. Roots are not preserved.

m2: Large anterolabial cuspid, connected to the labial cingulid. There is a small round c1. All specimens have a longitudinal spur. The posterior heel is small and oval. Roots are not preserved.

M1: The t1 is displaced backwards. All specimens have a small t1 bis. The t1 is connected to the t4-t5 junction by a longitudinal crest. There is a small distal spur in t3, directed towards the t5-t6 connection, and one specimen has a low labial longitudinal crest. The t9 is large. A small t12 is present. Roots are not preserved.

M2: The only available specimen is broken anterolabially. The t1 is connected with the t4-t5 junction by a low crest. The t3 is small and isolated. Roots are not preserved.

M3: Isolated t1. There is no t3. The connection between t4 and the t5-t6 junction is very low. The t8 is isolated. Roots are not preserved.

Discussion:

Martín-Suárez and Mein (1991) recognized an increase in size from older to younger populations in the anagenetic line *C. gracilis–C. crusafonti–C. rivas,* in which all the Iberian populations from the Pliocene and Pleistocene could be encompassed. This means that the biometrics of the molars could be used as systematic criteria along the frequency percentages of some morphological characters (Martín-Suárez and Mein, 1991). The size of *Castillomys* from La Bullana 2B is consistent with *Castillomys gracilis* van de Weerd, 1976 from its type locality (Caravaca), and Orrios-1 (Weerd, 1976), Moreda-1A and 1B, Rambla Seca-AB and Belmez-1 (Castillo, 1990), Botardo C and Gorafe 3 and 4 (Martín-Suárez, 1988), Mont-Hélène (Aguilar *et al*., 1986), Aldehuela and Villalba Alta (Adrover, 1986) and CLC-3, CLC-3B and PUR-13 (García-Alix *et al*., 2008a), but also agrees with some of the smallest measurements of *Castillomys crusafonti* Michaux, 1969 (Martín-Suárez and Mein, 1991; Minwer-Barakat *et al*., 2005).

The morphology of the studied specimens agrees better with *C. gracilis* than with *C. crusafonti*, showing a longitudinal spur in m1 and a posterior spur in t3 of M1 instead of full longitudinal crests. However, 1 out of 6 M1 does have a low longitudinal crest in t3, and all of them present a complete longitudinal crest connecting the t1 to the t4-t5, which is unusual in *C. gracilis* (Martín-Suárez and Mein, 1991). Moreover, the presence of a low crest in t1 of the M2 is rare in this species. However, based on the size of the specimens and the lack of longitudinal crests in the lower molars, we ascribe the sample from La Bullana 2B to *C. gracilis*.

Genus *Occitanomys* Michaux, 1969

Occitanomys brailloni Michaux, 1969 (Fig. 3, 8-13)

Locality: LB2B.

Material: 5 m1 (LB2B-53, LB2B-82, LB2B-93, LB2B-96, LB2B-184), 2 m2 (LB2B-39, LB2B-100), 5 m3 (LB2B-112, LB2B-113, LB2B-116, LB2B-119, LB2B-201), 4 M1

(LB2B-11, LB2B-123, LB2B-124, LB2B-251) 1 M2 (LB2B-135).

Measurements: see Table 3.

Description:

m1: Symmetrical anteroconid, connected to the protoconid-metaconid pair by a narrow crest. The labial cingulid is well developed. The c1 is large and round. Two specimens have a very small accessory cuspid. There is a longitudinal spur, which is reduced in two molars (Fig. 3, 8), more developed in other two, and developed into a very low longitudinal crest in one specimen (Fig. 3, 9). The posterior heel is small and oval. There are two roots.

m2: Trapezoidal outline, with the anterior side wider than the posterior one. Big round anterolabial cuspid, connected basally to the protoconid. The labial cingulid is reduced. The two available specimens have a longitudinal spur. The posterior heel is round. Roots are not preserved.

m3: There is neither anterolabial cuspid nor c1. Roots are not preserved.

M1: The connection between t1 and t2 is very low. The t1 bis is well developed. There is a small t2 bis (Fig. 3, 12), absent in one specimen. There is a low connection between t1 and the anterolingual side of t5. One specimen has a hint of distal spur in t3. The t6 and t9 are connected. The t12 is very small, barely a fold of the enamel. Roots are not preserved.

M2: The t1 is well developed, connected to the anterolingual side of t5 in one molar (Fig. 3, 13) and isolated in the other one. One specimen has a large t1 bis (Fig. 3, 13). Reduced t3, isolated from the other cusps. The t9 is well developed. Roots are not preserved.

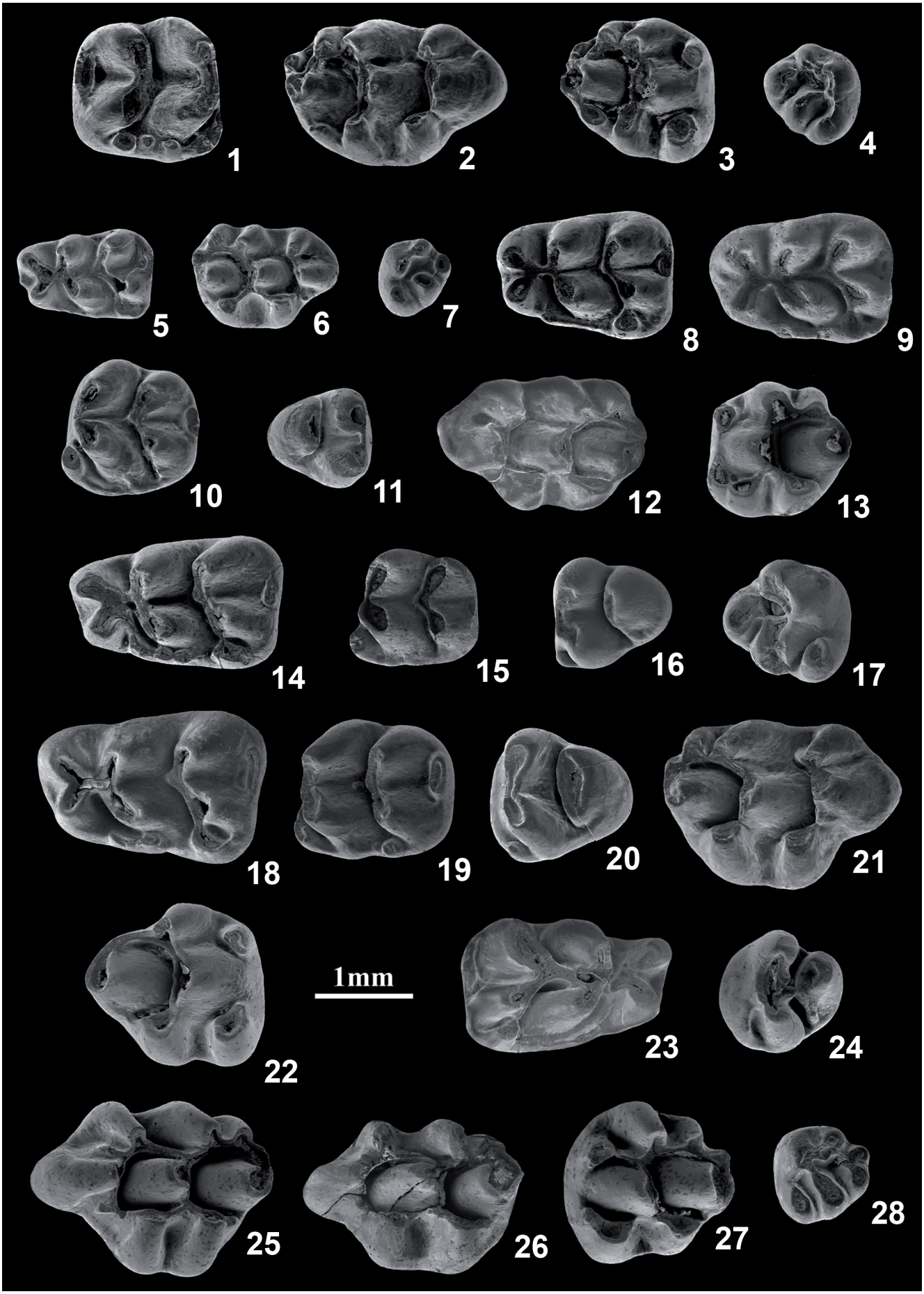
Discussion:

The specimens from La Bullana 2B largely agree with the material of *O. brailloni* from Layna (type locality) described by Michaux (1969): m1 without tma and with the accessory cuspids less developed than *Apodemus*, M1 with t1 bis, a crest that connects t1 to the posterior crown and a much reduced t12, and M2 with reduced t3 and well-developed t1 connected to the t5 by a crest. Michaux (1969) also considered diagnostic the presence of a low longitudinal crest in m1, lower than in *Stephanomys*. Regarding this character, there seems to be a great variability among populations, and Adrover (1986) suggested an increase of the longitudinal crest in m1 and m2 through time. In the localities of the MN14 the longitudinal crest of m1 is developed in 3 out of 7 molars from Kardia and Ptolemais (Weerd, 1979), absent in the single m1 from Gorafe A (Ruiz Bustos *et al*., 1984), and present in 1 out of 5 specimens from La Bullana 2B. In localities assigned to the early MN15, this crest is present in 2 out of 7 specimens from Arquillo 3 (Adrover, 1986), and absent in the two m1 from Vorio 3 (Hordijk and de Bruijn, 2009). In more recent localities, such as Layna, Nîmes (Michaux, 1969) and TCH-1B (Minwer-Barakat *et al*., 2005) there is always a low longitudinal crest.

The distal crests in M1 show also a great variability. The specimens from Kardia (Weerd, 1979) have a crest on t1, and 1 out of 4 molars have also a crest on t3, while other two have a small spur. The single M1 from Gorafe A has a weak t1-t5 connection, and no trace of t3-t5 connection (Ruiz Bustos *et al*., 1984). In the specimens from La Bullana 2B, the crest on t1 is high in one molar and much lower in the other one, while 2 out of 3 specimens have a much reduced spur on t3 (Fig. 3, 11). All specimens from Arquillo 3 have a crest on t1, and 4 out of 6 M1 have a spur on t3 (Adrover, 1986). In the Greek locality of Vorio 3 (Hordijk and de Bruijn, 2009) all M1 have a crest on t1, two molars have a spur on t3 and another one a developed crest. In Layna and Nîmes there is always a crest on t1, but the t3 has a spur (Michaux, 1969). The single M1 from TCH-1B has well-developed crests on t1 and t3 (Minwer-Barakat *et al*., 2005). The single specimen from Rambla Seca A1 also has developed crests, but lower than in the molar from TCH-1B (Minwer-Barakat, 2005). Each of the localities Cañada del Castaño 1 and Rambla Seca A2 yielded one M1, with a low crest on t3 and an isolated t1, while in the two M1 from Bélmez 1 the t1 has a low crest, and one specimen has a crest on t3, absent in the other one (Castillo, 1990; Martín-Suárez, 1988). The morphological variability of these connections is difficult to assess because of the scarcity of the remains in the localities where this species is found (Minwer-Barakat, 2005), although they seem to be slightly more developed in younger localities.

With respect to the size, the material from La Bullana 2B is similar in size to *O. brailloni* from other MN14 localities such as Ptolemais 1 and 3 and Kardia (Weerd, 1979), Gorafe A (Ruiz Bustos *et al*., 1984) and Vorio 1 (Hordijk and de Bruijn, 2009), and slightly smaller than the same taxon from MN15 localities such as Vorio 3 (Hordijk and de Bruijn, 2009), Arquillo 3 and Aldehuela (Adrover, 1986), Layna, Nîmes and Sête (Michaux, 1969), Cañada del Castaño 1 (Martín-Suárez, 1988), TCH-1B (Minwer-Barakat *et al*., 2005), Bélmez 1, Rambla Seca A1, A2 and A3, Moreda 1L-4 and the MN16 locality of Moreda 1B (Castillo, 1990). The scarce material from AL2-D (Mansino *et al*., 2013) is morphologically con-

Fig. 3.- (opposite page). Rodents from La Bullana 2B and La Bullana 3, Cabriel Basin, Spain. *Apodemus gorafensis* from LB2B and LB3. **1**, right m2, LB3-10; **2**, right M1, LB2B-9; **3**, right M2, LB2B-21; **4**, right M3, LB2B-219. *Castillomys gracilis* from LB2B. **5**, left m1, LB2B-90; **6**, right M1, LB2B-14; **7**, left M3, LB2B-214. *Occitanomys brailloni* from LB2B. **8**, left m1, LB2B-93; **9**, left m1, LB2B-82; **10**, left m2, LB2B-39 **11**, right m3, LB2B-112; **12**, left M1, LB2B-123; **13**, left M2, LB2B-135. *Paraethomys meini* from LB2B. **14**, left m1, LB2B-29; **15**, left m2, LB2B-193; **16**, left m3, LB2B-198; **17**, right M3, LB2B-138; *Paraethomys* aff. *abaigari* from LB2B. **18**, left m1, LB2B-187; **19**, left m2, LB2B-191; **20**, left m3, LB2B-3; **21**, right M1, LB2B-128; **22**, right M2, LB2B-134; *Stephanomys dubari* from LB2B and LB3. **23**, right m1, LB2B-182; **24**, left m3, LB2B-199; **25**, left M1, LB2B-127; **26**, left M1, LB2B-12; **27**, left M2, LB2B-132; **28**, left M3, LB3-24. Scale bar equals 1 mm.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sistent with *O. brailloni*, but due to its extremely large size it is not clear if these specimens should be ascribed to this taxon or to a related form.

O. brailloni differs from *O. alcalai* Adrover, Mein and Moissenet, 1988, *O. adroveri* (Thaler, 1966), *O. sondaari* van de Weerd, 1976 and *O. debruijni* Sen, Jaeger, Dalfes, Mazin and Bochernes, 1989, by its larger size. It differs from *O. montheleni* Aguilar, Calvet and Michaux, 1984, by its smaller size. Some of the specimens from La Bullana 2B are close to the smallest values of *O. brailloni*, and therefore close to the largest dimensions of *O. alcalai* and within the size range of *O. adroveri*. *O. sondaari* differs from *O. brailloni* by the weak t6-t9 junction, the lesser development of the longitudinal crest in m1, the absence of t1-t5 connection in unworn specimens and by the absence of a crest on the t3 of the M1. *O. alcalai* differs from *O. brailloni* by the lesser development of longitudinal crests in the upper and lower molars. According to Michaux (1969), the longitudinal crest of *O. adroveri* is less developed than in *O. brailloni*, but as we noted before this character shows a great variability. The m1 of *O. adroveri* may present well-developed accessory cuspids. In the upper molars, the distal crests on t1 and t3 are usually more developed in *O. brailloni* than in *O. adroveri*, and the t12 is more reduced in *O. brailloni*. *O. debruijni* differs from *O. brailloni* by the reduced or absent t3-t5 connection and absence of c1 in m2, which may be present in *O. brailloni* (see material from Layna and Vorio 3 in Hordijk and de Bruijn, 2009, plate 8).

Element	Species	Locality	Parameter	n	min.	mean	max.
m1	*P.* aff *abaigari*	LB2B	L	1	-	2.36	-
			W	3	1.49	1.52	1.57
	P. aff *abaigari*	LB3	L	1	-	2.36	-
			W	1	-	1.54	-
	P. meini	LB2B	L	8	2.12	2.18	2.26
			W	9	1.38	1.43	1.46
m2	*P.* aff *abaigari*	LB2B	L	7	1.65	1.71	1.76
			W	9	1.45	1.53	1.62
	P. aff *abaigari*	LB3	L	3	1.66	1.71	1.76
			W	3	1.51	1.53	1.58
	P. meini	LB2B	L	2	1.37	1.40	1.42
			W	2	1.25	1.32	1.39
m3	*P.* aff *abaigari i*	LB2B	L	7	1.43	1.47	1.51
			W	7	1.25	1.31	1.37
	P. meini	LB2B	L	5	1.29	1.31	1.35
			W	6	1.15	1.20	1.28
M1	*P.* aff *abaigari*	LB2B	L	4	2.53	2.56	2.61
			W	4	1.67	1.70	1.74
	P. meini	LB2B	W	1	-	1.50	-
M2	*P.* aff *abaigari*	LB2B	L	5	1.79	1.87	1.96
			W	6	1.60	1.67	1.73
	P. meini	LB2B	L	1	-	1.56	-
			W	2	1.47	1.48	1.49
M3	*P.* aff *abaigari*	LB2B	L	4	1.23	1.29	1.38
			W	4	1.23	1.27	1.34
	P. meini	LB2B	L	1	-	1.16	-
			W	1	-	1.18	-

Table 4.- Measurements in millimeters of the teeth of *Paraethomys* aff. *abaigari* and *P. meini* from the localities La Bullana 2B and La Bullana 3. n= number of measurable specimens.

Occitanomys sp.

Locality: LB2B.

Material: 1 M2 (LB2B-211).

Description:

M2: (1.38 x 1.32): The t1 is well developed, and connects basally with the t5. The t3 is smaller than the t1 and isolated from the other cusps. The t9 is well developed. Roots are not preserved.

Discussion:

The general morphology of the specimen resembles *Occitanomys*, but it is much smaller than the remains ascribed to *O. brailloni*. In addition, the t1-t5 connection is very low, while in *O. alcalai* it is usually higher. Because of the scarcity of the material that prevents the observation of more diagnostic features, we ascribe this molar to *Occitanomys* sp.

Genus *Paraethomys* Petter, 1968

Paraethomys aff. *abaigari* Adrover, Mein and Moissenet, 1988 (Fig. 3, 18-22)

Localities: LB2B, LB3.

Material: 5 m1 (LB2B-87, LB2B-99, LB2B-187, LB2B-189, LB3-1), 13 m2 (LB2B-2, LB2B-34, LB2B-38, LB2B-40, LB2B-42, LB2B-86, LB2B-103, LB2B-110, LB2B-191, LB3-7 to LB3-9, LB3-14), 7 m3 (LB2B-3, LB2B-47, LB2B-48, LB2B-118, LB2B-121, LB2B-195, LB2B-197), 6 M1 (LB2B-4, LB2B-15, LB2B-128, LB2B-206, LB2B-208, LB2B-209), 6 M2 (LB2B-17, LB2B-18, LB2B-130, LB2B-134, LB2B-212, LB2B-213), 4 M3 (LB2B-139, LB2B-140, LB2B-215, LB2B-217).

Measurements: see Table 4.

Description:

m1: One molar has a very small cingulid ridge between the lobes of the anteroconid (Fig. 3, 18) and another one shows a low and small tma. The anteroconid is slightly asymmetrical. The anteroconid and the protoconid-metaconid pairs are connected by a narrow crest, which has an enamel funnel in one specimen. There is a longitudinal spur. The labial cingulid is moderately developed, with a large oval c1 and one or two accessory cuspids. The posterior heel is variable in size and shape, and lingually displaced. Roots are not preserved.

m2: Well-developed anterolabial cuspid, connected basally to the protoconid and the labial cingulid. A c1 variable in size and an accessory cuspid may be present. There is a longitudinal spur in 9 out of 11 specimens. The posterior heel is reduced in some molars, while others have a medium sized cuspid. Roots are not preserved.

m3: The anterolabial cuspid is reduced in two specimens and absent in five. The hypoconid-entoconid complex is separated from the protoconid-metaconid pair. One of the specimens presents a small c1 attached to the labial side of the posterior complex. Roots are not preserved.

M1: The connection between t1 and t2 is lower than the connection between t2 and t3. The t2 and t3 are very close together. Two specimens have a very low crest connecting t1 with the posterolingual side of t5. The spur in t3 is always present, small in two specimens and more developed in other two. The t9 is well developed. The connection between t4 and t8 is low. There is a small t12. Roots are not preserved.

M2: Isolated t1 and t3. The t9 may be absent (2), reduced (2) or developed (1). A much reduced t12 is present in two specimens. Roots are not preserved.

M3: The t1 is large and isolated, while t3 is absent. The t8 is connected with the t4-t5-t6 junction. Roots are not preserved.

Discussion:

Different species of *Paraethomys* are recognized in MN14 localities from the Iberian Peninsula: the small sized *P. meini* (Michaux, 1969), and the larger *P. abaigari* and *P*. aff. *abaigari*, which have more developed distal spurs in the upper molars. Adrover *et al*. (1993) identified two species of *Paraethomys* in La Gloria 4 and Celadas 1 and 9, *P. meini* and *P. anomalus* (Bruijn, Dawson and Mein, 1970). These two species were morphologically very similar, and differed mainly in their size. Later, García-Alix *et al*. (2008a) ascribed the big-sized specimens from PUR-13 and CLC-5A to *P*. aff. *abaigari*, a form related to *P. abaigari* but slightly smaller, and considered the big-sized *Paraethomys* from La Gloria 4 and Celadas 9 to belong to the same taxon. Slightly older assemblages of *Paraethomys*, like the rich population from PUR-4, show a wide size range but, due to the impossibility to discriminate two clusters in this population, García-Alix *et al.* (2008a) ascribed that sample to *P. meini*, considering unlikely the coexistence of two *Paraethomys* species in that locality.

The specimens from La Bullana 2B and La Bullana 3 are similar in size to *P.* aff. *abaigari* from CLC-5A and PUR-13 (García-Alix *et al*., 2008a), Celadas 9 and La Gloria 4 (Adrover *et al*., 1993), slightly smaller than *P.* aff. *abaigari* from AL2-C and AL2-D (Mansino *et al*., 2013), and clearly smaller than *P. abaigari* from Villalba Alta (Adrover *et al*., 1988). These molars are larger than *P. meini* from Sète (type locality), Layna, Nîmes, La Juliana, Arquillo III, Villalba Alta, Perpignan, Aldehuela, Orrios (Adrover, 1986), Villalba Alta Río, Peralejos E (Adrover *et al*., 1988), Celadas 9 and La Gloria 4 (Adrover *et al*., 1993), PUR-3, 4, 7 and 13, CLC-3, 3A, 4A, 4B, 5A, CAC-11,BRA-5B, DHS-1, 4A, 4B, 15B, 16 and MNA-4 (García Alix *et al*., 2008b) and Rambla de Chimeneas 3 (Minwer-Barakat *et al*., 2009a), *P. anomalus* from Maritsa and *P. miocaenicus* from Khendek el Ouaich (Adrover, 1986), considered synonyms of *P. meini* by several authors (van de Weerd, 1976; Adrover, 1986; Castillo, 1990; Minwer-Barakat, 2005; García-Alix, 2006, García-Alixet *et al*., 2008a)

The development of distal spurs on the t1 and t3 of the M1 also agrees with *P. abaigari* rather than with *P. meini*. For these reasons, we ascribe the studied material to *P*. aff. *abaigari*.

Paraethomys meini (Michaux, 1969) (Fig. 3, 14-17)

Locality: LB2B.

Material: 12 m1 (LB2B-1, LB2B-26, LB2B-29 to LB2B-33, LB2B-83, LB2B-85, LB2B-89, LB2B-185, LB2B-186), 2 m2 (LB2B-100, LB2B-193), 6 m3 (LB2B-46, LB2B-50, LB2B-120, LB2B-122, LB2B-194, LB2B-198), 3 M1 (LB2B-16, LB2B-52, LB2B-84), 2 M2 (LB2B-19, LB2B-131), 1 M3 (LB2B-138).

Measurements*:* see Table 4.

Description:

m1: one specimen has a very low and small tma. The anteroconid is slightly asymmetrical. The anteroconid and the protoconid-metaconid pair are connected by a narrow crest. Three specimens have a funnel of enamel in the connection between the anteroconid and the protoconid-metaconid (Fig. 3, 14). In 8 out of 11 teeth there is a weak longitudinal spur. The labial cingulid is moderately developed, with a large oval c1 and one or two accessory cuspids, variable in size. Roots are not preserved.

m2: Well-developed anterolabial cuspid, connected basally to the protoconid and the labial cingulid. A small c1 is present in one specimen. There are no accessory cuspids. In 2 out of 3 specimens there is a longitudinal spur. The posterior heel is large in two molars and more reduced in another one. Roots are not preserved.

m3: One specimen has a small anterolabial cuspid, absent in the others. The hypoconid-entoconid complex is separated from the anterior protoconid-metaconid pair. A small crest-shaped c1 is present in two molars. Roots are not preserved.

M1: All specimens are broken posteriorly. One specimen has two small cusps attached to the anterior side of t2. The t1 has a distal spur, developed into a very low crest in one of the specimens. There is a spur on the t3. Roots are not preserved.

M2: The dentine is almost completely lost in both molars. Isolated t1 and t3. The t9 is slightly developed, and there is no t12. Roots are not preserved.

M3: The t1 is large and isolated. Absent t3. The t8 is connected to the t4-t5-t6 junction. Roots are not preserved.

Discussion:

Together with the large *P*. aff. *abaigari*, a small form of *Paraethomys* occurs in La Bullana 2B. The coexistence of two species of *Paraethomys* differing mainly in size has been recorded in several Pliocene localities from the Teruel and Granada Basins (Adrover, 1986; Adrover *et al*., 1988, 1993; García-Alix *et al*., 2008a), as well as in the French site of

Sète (type locality of *P. meini*, Michaux, 1969). When both forms appear together, the size of *P. meini* is usually very small (García-Alix, 2006). The size of the specimens from La Bullana 2B is similar to *P. meini* from Sète, Layna, Nîmes, La Juliana, Arquillo III, Villalba Alta, Perpignan, Aldehuela, Orrios (Adrover, 1986), Villalba Alta Río, Peralejos E (Adrover *et al*., 1988), Celadas 9 and La Gloria 4 (Adrover *et al*., 1993), PUR-3, 4, 7 and 13, CLC-3, 3A, 4A, 4B, 5A, CAC-11,BRA-5B, DHS-1, 4A, 4B, 15B, 16 and MNA-4 (GarcíaAlix *et al*., 2008b) and Rambla de Chimeneas 3 (Minwer-Barakat *et al*., 2009a), *P. anomalus* from Maritsa and *P. miocaenicus* from Khendek el Ouaich (Adrover, 1986).

The only morphological character used to distinguish *P. meini* from *P. abaigari* is the development of distal spurs in the upper molars, more prevalent in the latter species (Adrover *et al*., 1993). The three M1 from La Bullana 2B show spurs on the t1 and t3, which is unusual in *P. meini*, although in some localities like Peralejos E the presence of spurs in t1 and especially t3 is quite common (Adrover *et al*., 1993).

Genus *Stephanomys* Schaub, 1938

Stephanomys dubari Aguilar, Michaux, Bachelet, Calvet and Faillat, 1991 (Fig. 3, 23-28)

Localities: LB2B, LB3.

Material: 5 m1 (LB2B-27, LB2B-28, LB2B-97, LB2B-98, LB2B-182), 5 m2 (LB2B-37, LB2B-101, LB2B-102, LB2B-104, LB2B-111), 4 m3 (LB2B-49, LB2B-117, LB2B-196, LB2B-197), 4 M1 (LB2B-10, LB2B-12, LB2B-127, LB2B-207), 5 M2 (LB2B-23, LB2B-132, LB2B-133, LB2B-252, LB3-21), 3 M3 (LB2B-24, LB2B-137, LB2B-249).

Measurements: see Table 5.

Element	Locality	Parameter	n	min.	mean	max.
m1	LB2B	L	5	2.07	2.16	2.27
		W	5	1.29	1.31	1.44
m2	LB2B	L	5	1.51	1.62	1.70
		W	5	1.46	1.51	1.58
m3	LB2B	L	3	1.25	1.31	1.37
		W	3	1.21	1.24	1.28
M1	LB2B	L	4	2.30	2.46	2.69
		W	4	1.58	1.74	1.83
M2	LB2B	L	3	1.58	1.74	1.88
		W	3	1.70	1.73	1.76
	LB3	L	1	-	1.72	-
		W	1	-	1.63	-
M3	LB2B	L	2	1.15	1.25	1.36
		W	2	1.13	1.22	1.31

Table 5.- Measurements in millimeters of the teeth of *Stephanomys dubari* from the localities La Bullana 2B and La Bullana 3. n= number of measurable specimens.

Description:

m1: Slightly asymmetrical anteroconid, connected to the protoconid and metaconid. The labial cingulid is low and narrow. There is a well-developed longitudinal crest that connects the posterior cuspids to the connection of the protoconid-metaconid pair. There is a well-developed oval c1. The posterior heel is lingually displaced, ranging from oval to laminar. Two roots.

m2: Large and high anterolabial cuspid, connected to the protoconid and to a narrow labial cingulid. The longitudinal crest is lingually displaced towards the metaconid. There is neither c1 nor accessory cuspids. The posterior heel is large and oval. Roots are not preserved.

m3: Small and low anterolabial cuspid, connected to the protoconid. The longitudinal crest is complete (Fig. 3, 24). There are two roots.

M1: The t1 is slightly displaced backwards. There are small t1 bis and t2 bis, more developed in one of the specimens (Fig. 3, 25). The posterior crest on the t1 is high and well developed in two specimens (Fig. 3, 25), and very low in other two (Fig. 3, 26), while the posterior crest on the t3 is high in all specimens. The t12 is highly reduced. Roots are not preserved.

M2: The t1 has a small t1 bis attached to its anterior side (Fig. 3, 27). In unworn specimens, the posterior crest of t1 is complete in two molars and low in another two, while the posterior crest on the t3 is complete in two specimens, low in one and absent in another one. The t12 is reduced in one molar and well developed in another one (Fig. 3, 27). There are three roots.

M3: The t1 is connected basally to t5. The t3 is absent. The t4, t5 and t6 are connected to t8. One specimen has a t9 (Fig. 3, 28). Roots are not preserved.

Discussion:

The great height of the crown, high longitudinal crests in the lower molars (Fig. 3, 23–24) and crests or spurs in t1 and t3 of the upper molars (Fig. 3, 25–27) indicate that these specimens belong to the genus *Stephanomys*. These molars are smaller, lower crowned and have a less pronounced stephanodonty than the *Stephanomys* identified in the Pliocene and Pleistocene (see Minwer-Barakat *et al*., 2011 and references therein).

The studied specimens share some characters with *S. cordii* Ruiz Bustos, 1986, like the t1 slightly more posterior than the t3 in M1 (Fig. 3, 25–26) and one m3 with the longitudinal crest connected to the protoconid (Fig. 3, 24). However, although some molars have the size and morphology of *S. cordii* (Fig. 3, 25) most of them agree better with *S. dubari* Aguilar, Michaux, Bachelet, Calvet and Faillat, 1991, with low crests connecting t1 and t5 in M1 (Fig. 3, 26), low or absent longitudinal crests in M2 and a smaller size. The presence of specimens similar to *S. cordii* has been reported in some populations of *S. dubari*, such as in the lower Ruscinian sites of PUR-4 and PUR-13 in the Granada Basin (García-Alix *et al*., 2008a). The material from La Bullana 2B and La Bullana 3 has been directly compared with *S. cordii* from AL2-C

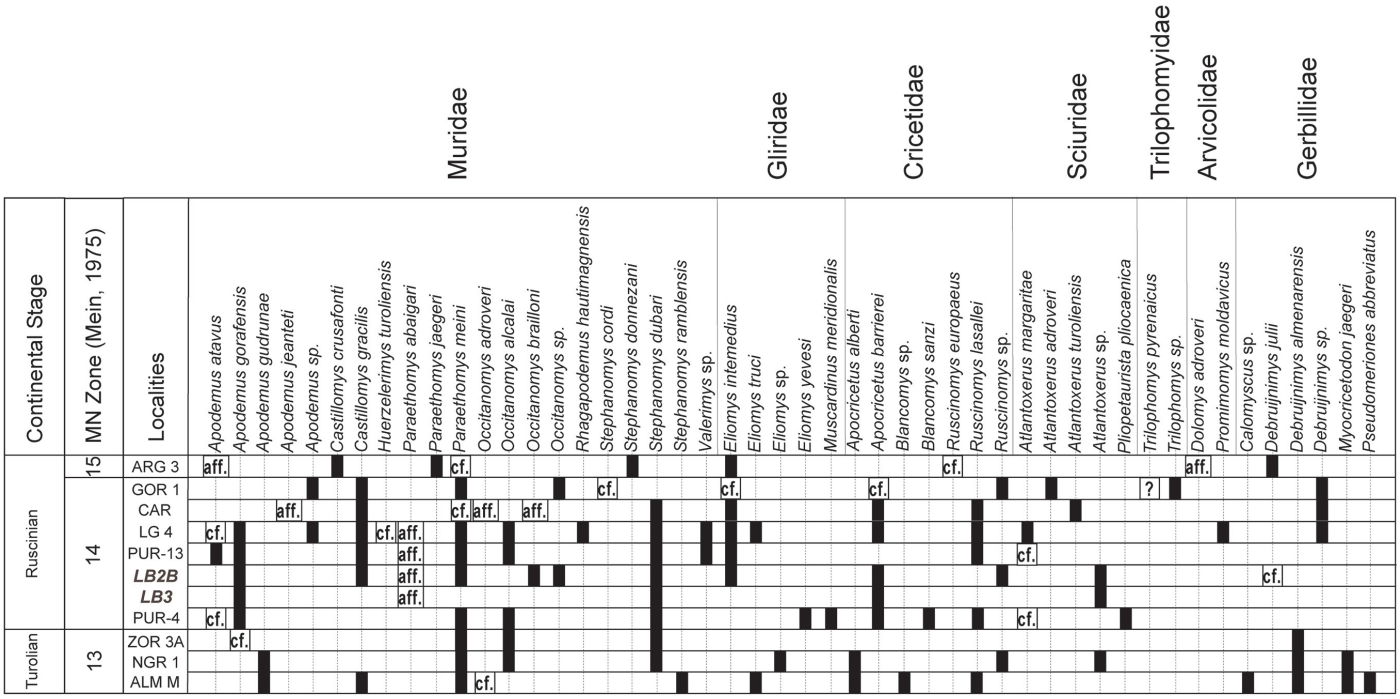

Fig. 4.- Distribution chart of the rodents studied in this paper and of related species of similar age. Abbreviations: **ARG3**, Asta Regia 3 (Castillo and Agustí, 1996); **GOR 1**, Gorafe 1 (Bruijn, 1974; Martín-Suárez and Mein, 1991; Agustí and Martín-Suárez, 1984); **CAR**, Caravaca (Freudenthal *et al*., 1998, Bruijn *et al*., 1975, Weerd 1976, Aguilar *et al*., 1991); **LG 4**, La Gloria 4 (Mein *et al*., 1990); **PUR-13**, Purcal 13 (García-Alix, 2006); **LB3**, La Bullana 3 and **LB2B**, La Bullana 2B (this paper); **PUR-4**, Purcal 4 (García-Alix *et al*., 2008c; Mansino *et al*., in press); **ZOR3 A**, Zorreras 3A (Martín-Suárez *et al*., 2000); **NGR 1**, Negratín 1 (Minwer-Barakat *et al*., 2009 and 2012); **ALM M**, Almenara M (Agustí and Galobart, 1986; Agustí *et al*., 2011). For making this figure the following synonymies have been taken in account: *Apodemus dominans* as *A. atavus*; *Castillomys crusafonti gracilis* as *C. gracilis*; *Paraethomys anomalus* as *P. meini*; *Stephanomys medius* as *S. cordii*; *Cricetus barrierei* as *Apocricetus barrierei*; *Protatera almenarensis* as *Debruijnimys almenarensis*; *Protatera* sp. as *Debruijnimys* sp.

and AL2-D (Mansino *et al*., 2013). The molars from the two latter localities are slightly larger, having usually higher longitudinal crests and are clearly higher crowned than the teeth from La Bullana 2B and La Bullana 3. For these reasons, we ascribe the material from the studied localities to *S. dubari*.

Family Gerbillidae Alston, 1876
Subfamily Taterillinae Chaline, Mein and Petter, 1977
Genus *Debruijnimys* Castillo and Agustí, 1996
Debruijnimys cf. *julii* Castillo and Agustí, 1996 (Fig. 5, 1)

Locality: LB2B.
Material: 1 M1 (LB2B-248).

Description:

M1: (2.78 x 2.03): The anterocone is sub-triangular, with a flat anterior face. An indentation on the anterior face of the anterocone subdivides this cusp into two lobes. There is a posterior spur on the lingual lobe of the anterocone, directed towards the protocone-paracone junction. The anterocone and the protocone are linked by a low longitudinal ridge. The protocone and paracone are equivalent in size, and separated from the hypocone-metacone complex by a deep valley. The posterior walls of the protocone and the paracone show low posterior spurs that connect, at medium level, to the hypocone and the metacone, respectively. The hypocone is larger than the metacone, and posteriorly displaced. There is a shallow furrow between hypocone and metacone. Roots are not preserved.

Discussion:

In the Iberian Peninsula several Late Miocene and Early Pliocene localities have yielded remains of *Debruijnimys* Castillo and Agustí, 1996 (see Agustí and Casanovas-Vilar, 2003 and Minwer-Barakat *et al*., 2009b). The record of *Debruijnimys* in Spain comprises two species: *D. almenarensis* (Agustí, 1990) from the Late Miocene (MN13) and *D. julii* Castillo and Agustí, 1996 from the middle Pliocene (MN15). *Debruijnimys almenarensis* is recorded in Salobreña, Almenara M, Zorreras 2B and 3A, and Negratín-1 (Agustí, 1990; Agustí, 1991; Martín-Suárez *et al*., 2000; Minwer-Barakat *et al*., 2009b; Agustí *et al*., 2011) and *D. julii* in Asta Regia-3 (Castillo and Agustí, 1996).

Other Spanish localities of Early Ruscinian age (MN14) with presence of the genus *Debruijnimys* are Alcoy, Caravaca, Gorafe 1, Botardo, Bacochas 1 and La Gloria 4 (Sesé, 1989; Agustí, 1991; Castillo and Agustí, 1996 and Minwer-Barakat *et al*., 2009b) (Fig. 4). The scarcity of material in these localities led the authors to determine these specimens as *Debruijnimys* sp.; Agustí and Casanovas-Vilar (2003) considered that all these samples from the Ruscinian referred to *Debruijnimys* sp. were forms related to *D. julii*.

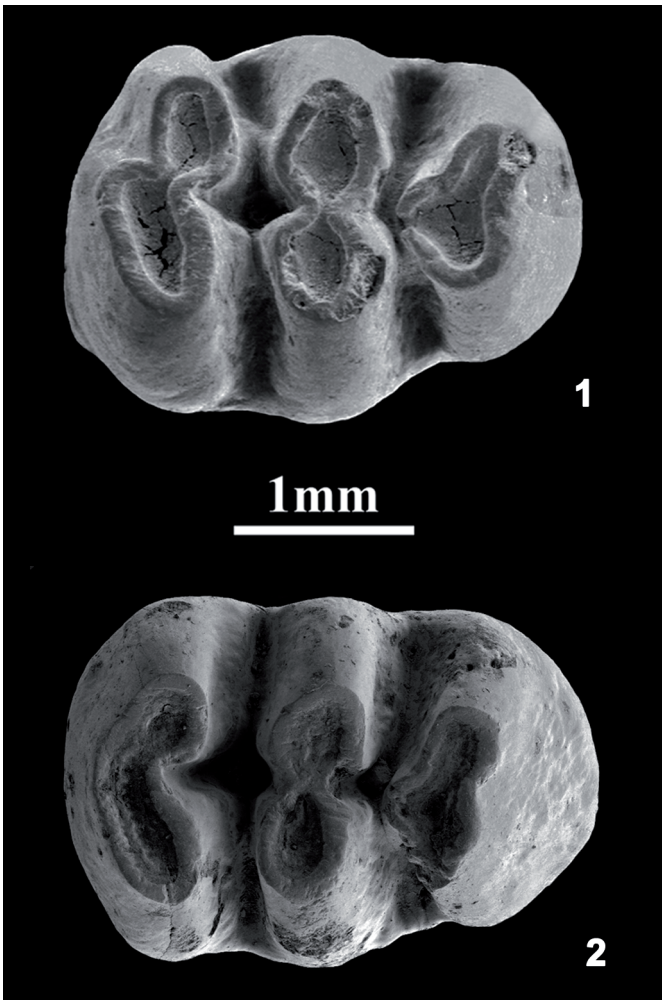

Fig. 5.- *Debruijnimys* cf. *julii* from La Bullana 2B (Cabriel Basin). **1**, right M1, LB2B-248. *Debruijnimys almenarensis* from Almenara M, **2,** right M1, MGUV-27742.

The phylogenetic relationship of the Spanish forms of *Debruijnimys* is not clear. Thus, the larger size and the presence of derived characters in *D. almenarensis* (MN13), like the very large anteroconid, led Agustí and Casanovas-Vilar (2003) to refuse an ancestor-descendant relationship between *D. almenarensis* and the Spanish material of *Debruijnimys* from the Early Ruscinian (MN14). According to these authors, the forms of *Debruijnimys* of Early Ruscinian age would be an intermediate step in a phylogenetic lineage comprising *D. davidi* from Lissafa (Morocco) (Late Turolian, MN13, 5.5 Ma) (Raynal *et al*., 1999) and *D. julii* from Asta Regia 3 (Late Ruscinian, MN15).

The upper molars of *D. julii* differ from those of *D. almenarensis* by several characters, like the presence of a weak indentation on the anterior face of the anterocone that creates two confluent lobes and the degree of separation between the protocone-paracone and hypocone-metacone pairs. While in *D. almenarensis* there is a wide valley, without posterior spurs (Fig. 5, 2), in *D. julii* there is a low connection between the posterior walls of the protocone and paracone and the anterior sides of the hypocone and metacone, respectively (Fig. 5, 1) (Castillo and Agustí, 1996, Plate 1, Fig. 4-5). Moreover, the shape of the M1, sub-rectangular in the M1 of *D. almenarensis* (Fig. 5, 2) and more rounded in *D. julii* (Fig. 5, 1) is another difference between both species.

Minwer-Barakat *et al*. (2009b) observed an increase in size from *D. davidi* from Lissasfa to *D. julii* from Asta Regia. The size of the material of the Early Ruscinian Spanish populations of *Debruijnimys* is similar to that of *D. julii* (Castillo and Agustí, 1996) and much larger than that of *D. davidi* from Lissasfa (Geraads, 1998). The M1 from La Bullana 2B is much larger than those of *D. davidi* from Lissasfa and very similar in size to those of *D. almenarensis* and *D. julii* (Agustí, 1990; Martín Suárez *et al*.; 2000; Minwer-Barakat *et al.* 2009b).

Moreover, the M1 from La Bullana 2B clearly differs from those of Lissasfa in the morphology of hypocone-metacone pair. While in Lissasfa the metacone is placed posteriorly with respect to the hypocone, in La Bullana 2B the metacone is placed anteriorly. In the single M1 from La Bullana 2B, the metacone is placed in a more anterior position with respect to the hypocone than in *D. almenarensis* from its type locality, Almenara M (Fig. 5, 2), and similar to that of *D. julii* (Castillo and Agustí, 1996).

The morphology of the anterocone of the M1 from La Bullana 2B is more similar to *D. almenarensis* and *D. julii* than to *D. davidi*. The presence of a weak indentation on the anterior face of the anterocone, that creates two confluent lobes, is present in *D. julii* and, in a lesser degree, also in *D. almenarensis* from Almenara M (Fig. 5, 2), and in *Debruijnimys* from La Bullana 2B, being absent in the M1 of *D. davidi* from Lissasfa. The absence of lower dentition and other elements of the upper dentition in La Bullana 2B do not allow going further in the comparison between the African and the Spanish forms of *Debruijnimys* of Late Miocene-Early Pliocene age.

Based on the size, the less elongated shape of this specimen, the presence of low posterior spurs connecting the protocone-hypocone and paracone-metacone pairs and the more accentuated asymmetry in the position of metacone and hypocone in the M1 of *Debruijnimys* from La Bullana 2B, we distinguish this tooth from *D. almenarensis* and assign it to a form related with *D. julii*.

Family Gliridae Muirhead, 1819
Subfamily Dryomyinae de Bruijn, 1967
Genus *Eliomys* Wagner, 1840
Eliomys intermedius Friant, 1953 (Fig. 6, 8-10)

Locality: LB2B.

Material: 4 m1-2 **(**LB2B-6, LB2B-176, LB2B-242, LB2B-243), 1 m3 (LB2B-179), 1 P4 (LB2B-178), 1 M1-2 (LB2B-241), 1 M3 (LB2B-177).

Description:

m1-2: (1.42 x 1.77; 1.51 x -; - x 1.50; broken specimen): The anterolophid is connected to the protoconid in 1 out of 4 specimens. There is no anterotropid. There is a low connection between metalophid and metaconid. The centrolophid is

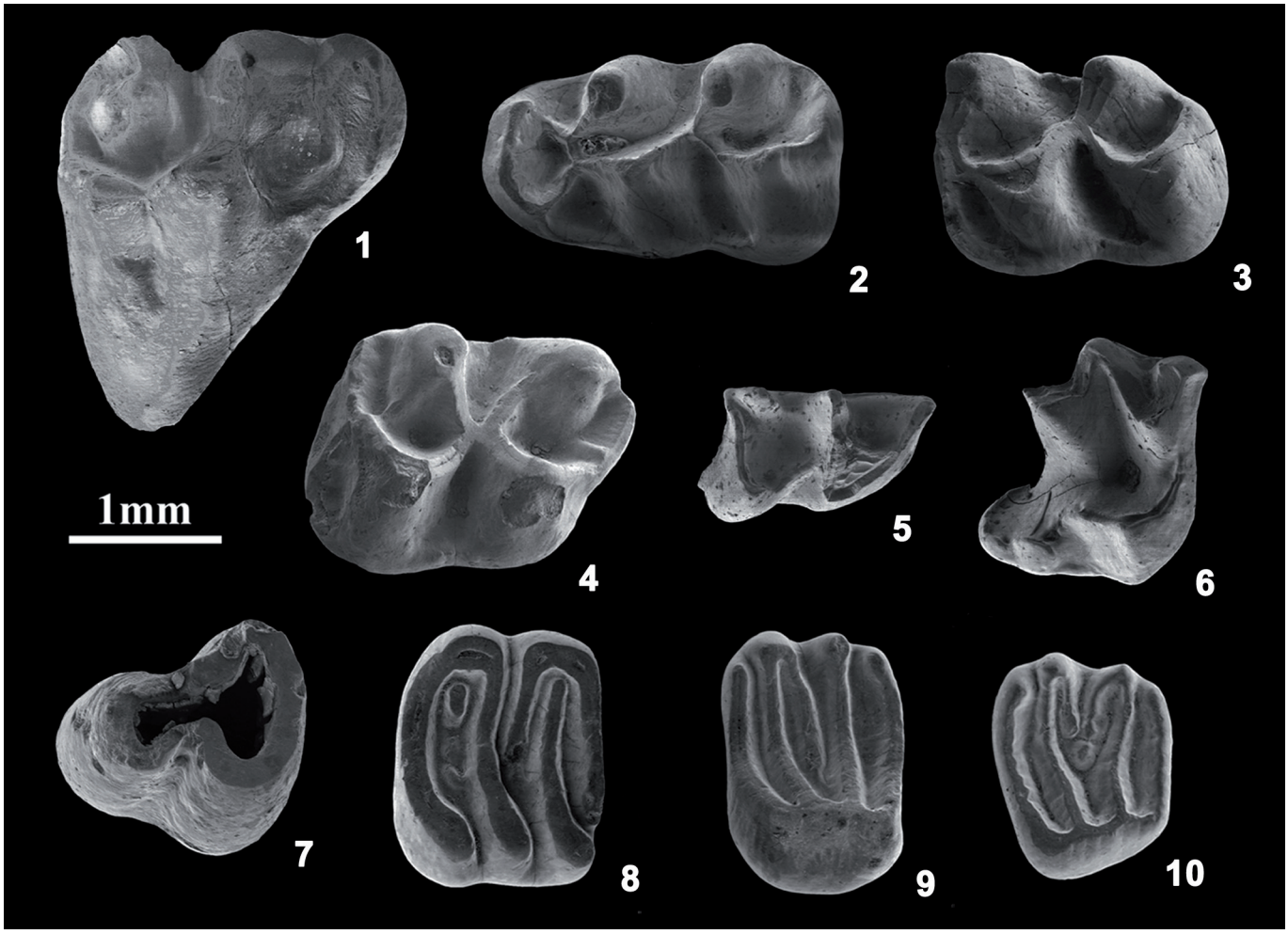

Fig. 6.- Rodents and insectivores from La Bullana 2B and La Bullana 3, Cabriel Basin, Spain. *Atlantoxerus* sp. from LB2B. **1**, right D4, LB2B-244. *Apocricetus barrierei* from LB2B. **2**, left m1, LB2B-141; **3**, left m3, LB2B-232; **4**, left M2, LB2B-220. *Asoriculus* cf. *gibberodon* from LB2B and LB3. **5**, right m1, LB2B-245; **6**, right M1, LB3-31. *Ruscinomys* sp. from LB2B. **7**, right m3, LB2B-175. *Eliomys intermedius* from LB2B. **8**, right m1-2, LB2B-176; **9**, left M1-2, LB2B-241; **10**, left M3, LB2B-177. Scale bar equals 1 mm.

long and not connected to the metalophid but in one specimen. There is no endolophid. The mesolophid is connected to entoconid. The posterotropids are well developed. Roots are not preserved.

m3: The only available tooth is broken anteriorly. The posterotropid is absent. The centrolophid is shorter than in the m1-2. There is no endolophid. The posterolophid is continuous. Roots are not preserved.

P4: (1.08 x 1.48): Subtriangular outline. There is no anteroloph, and the protoloph is discontinuous. The paracone and metacone are higher than the protocone. There is a well-developed precentroloph and a short postcentroloph. The endoloph is continuous. Roots are not preserved.

M1-2: (1.25 x 1.79): The anteroloph is separated from both protoloph and paracone by a deep valley. There is neither anterotrope nor posterotrope. Paracone and metacone are high and separated from each other. The protoloph and metaloph are continuous. In the only complete specimen the precentroloph is long, and the postcentroloph absent (Fig. 6, 8). The endoloph and posteroloph are connected and continuous. Roots are not preserved.

M3: (1.27 x 1.52): Trapezoidal outline, with the anterior part notably wider than the posterior side. The anteroloph is separated from protoloph, but closer to paracone than in M1-2. Both anterotrope and posterotrope are absent. The paracone and metacone are high and separated, and attached to a continuous protoloph and metaloph, respectively. Both centrolophs are present and well developed, being the postcentroloph longer and interrupted near its lingual end (Fig. 6, 9). The endoloph and posteroloph are connected and continuous. Roots are not preserved.

Discussion:

The specimens from La Bullana 2B are larger, more concave and have a more rounded outline than those of *Eliomys truci* Mein and Michaux 1970 and *Eliomys yevesi* Mansino, García-Alix, Ruiz-Sánchez and Montoya, 2014. Their size is similar to *Eliomys intermedius* Friant, 1953 from Sète and Orrios 3 (Adrover, 1986), PUR-13, TCH-3, TCH-1B and TCH-13 (García-Alix *et al.,* 2008b) and *Eliomys* cf. *intermedius* from Arquillo 3, Villalba Alta (Adrover, 1986) and Mont Hélène (Aguilar *et al*., 1986). The presence of two centro-

lophs, being the postcentroloph well-developed (Fig. 6, 9), in the single M3 from La Bullana 2B agree with the species *Eliomys intermedius*.

Family Sciuridae Fisher, 1817
Subfamily Pteromyinae Brandt, 1855
Genus *Atlantoxerus* Forsyth Major, 1893
Atlantoxerus sp. (Fig. 6, 1)

Localities: LB2B, LB3
Material: 1 D4 (LB2B-244), 1 m1-2 (LB3-47)

Description:

D4: (2.36 x -): Tooth broken posterolabially. Sub-triangular outline. The parastyle is connected to the anteroloph, and separated from the protoloph by a wide and deep valley. The protocone is well developed, very high and connected to the paracone by the protoloph. The metacone is partially broken, and connected to the metaconule by a narrow crest. Both cusps are very close to each other and connected basally to the posteroloph. The metaconule is separated from the hypocone and protocone by a deep valley. Roots are not preserved.

m1-2: Molar broken anteriorly. The posterolophid bears a small hypoconulid, and connects the entoconid to the hypoconid. Roots are not preserved.

Discussion:

Heteroxerus and *Atlantoxerus* differ mainly in size, but *Atlantoxerus* has also higher crowns and cusps, more rounded conules and wider crests (Cuenca-Bescós, 1988). The studied specimens are larger than those of *Heteroxerus*, *Atlantoxerus cuencae* Aguilar, Calvet and Michaux, 1995, *A. martini* Aguilar, 2002 and *A. idubedensis* Cuenca, 1988, They are clearly smaller than those of *Atlantoxerus tadlae* (Lavocat, 1961), slightly smaller than *A*. cf. *margaritae* from La Gloria-2 and Villalba Alta, and slightly larger than the same taxon from Aldehuela (Adrover *et al*., 1993). The D4 is shorter but wider than that of *A*. cf. *margaritae* from Purcal-4 (García-Alix *et al*., 2007). *Atlantoxerus adroveri* de Bruijn and Mein, 1968, from Concud 3 (Weerd, 1976), and *A. rhodius* De Bruijn, Dawson and Mein, 1970 are slightly smaller than our specimens. Due to the scarcity and bad preservation of the recovered specimens we cannot confirm whether the *Atlantoxerus* from La Bullana 2B is a form related to *A. margaritae* or to *A. adroveri*, so we ascribe these molars to *Atlantoxerus* sp.

Sciuridae indet.?

Locality: LB2B.
Material: 1 m1,2 (LB2B-254).

Description:

m1-2: The molar is broken posterolingually. The protoconid is large, and connected to a well-developed anteroconulid. There is a weak anterior cingulid. The crest that connects the protoconid and the hypoconid is slightly swollen, forming a weak mesoconid. Roots are not preserved.

Discussion:

The specimen from La Bullana 2B certainly corresponds to a sciurid, but it is much smaller than the other remains of sciurids found in this locality ascribed to *Atlantoxerus*. The presence of an anterior cingulid is characteristic of some species of *Heteroxerus*, although a reduced cingulid may be present in some species of *Atlantoxerus*, like *Atlantoxerus blacki* (Cuenca-Bescós, 1988). Therefore, a more precise determination of this tooth is not possible.

Family Cricetidae Fischer, 1817
Subfamily Cricetinae Fischer, 1817
Genus *Apocricetus* Freudenthal, Mein and Martín-Suárez, 1998
Apocricetus barrierei (Mein and Michaux, 1970)

Localities: LB2B, LB3.
Material, descriptions and Measurements: in Ruiz-Sánchez *et al*., 2014.

Discussion:

The assemblages from La Bullana 2B and La Bullana 3 have an intermediate size between *A. angustidens* and *A. alberti*. The m1 from La Bullana 2B have a crest-like anteroconid, with a weak subdivision, with two anterolophulids arising from a prelophid. In 2 out of 12 specimens there is a third crest pointing backwards from the middle of the anteroconid. The mesolophids are generally absent in m1 and m2. The m3 is generally longer than the m2, having a complete mesolophid in 3 out of 13 specimens. In the m3 from La Bullana 3 the mesolophid is absent.

In La Bullana 2B, the cingulum ridge on the base of the anterocone of M1 is absent (5) or weak (1). Of the seven M1, two have a complete anterior protolophule, one has a weakly developed crest and four have no crest at all. The posterior metalophule is very scarce in M1. 16 out of 20 M2 from La Bullana 2B have an anterior protolophule, whereas the only complete M2 from La Bullana 3 lacks this ridge. 4 out of 17 M2 from La Bullana 2B and 1 out of 3 from La Bullana 3 have a hint of metalophule. In the M3 an anterior protolophule is always present, being complete in 9 out of 13 specimens from La Bullana 2B and in 1 out of 2 from La Bullana 3.

The size of the *Apocricetus* assemblages from La Bullana 2B and La Bullana 3 agrees with that of *A. barrierei* (Freudenthal *et al*., 1998; Ruiz-Sánchez *et al*., 2014).

The lower molars of *A. barrierei* from La Bullana 2B and La Bullana 3 differ from those of *A.* aff. *plinii* and *A. plinii* in the weakly split anteroconid in m1, the more pronounced enlargement of m3 and the absence of mesolophids in most m1-2. The prelophid is present in some specimens of *A. alberti*, but is less developed than in *A. barrierei* (Mansino *et al*., 2014).

The M1-2 of *A. barrierei* from La Bullana 2B and La Bullana 3 differ from those of *A.* aff. *plinii* and *A. plinii* by the

bifid anterolophule in the M1 and the absence of mesoloph in the M1-2. Some specimens of *A. alberti* and *A. barrierei* develop a weak cingulum ridge on the base of the anterocone of M1 (Mansino *et al*., 2014). This ridge is well-developed in *A. angustidens*.

The anterior protolophule of the upper molars is less developed in *A. barrierei* from La Bullana 2B and La Bullana 3 than in *A.* aff. *plinii*, *A. plinii* and *A. alberti*, and higher than in *A. angustidens*. In addition, the presence of posterior metalophule, complete or hinted, in *A. barrierei* from La Bullana 2B and La Bullana 3 differs from those of *A. angustidens*.

Therefore, on the basis of metric and morphological features, the material of the genus *Apocricetus* from La Bullana 2B and La Bullana 3 may be assigned to *A. barrierei*.

Subfamily Cricetodontinae Stehlin and Schaub, 1951
Genus *Ruscinomys* Depéret, 1890
Ruscinomys sp.

Locality: LB2B.
Material: 1 M3 (LB2B-175).

Description:

M3: (1.80 x 1.54): The dentine is completely lost. This molar has two lobes delimited by the sinus and mesosinus. The posterior lobe is smaller than the anterior one. Roots are not preserved.

Discussion:

Because of its general morphology and hypsodonty, we can ascribe the unique cricetodontine tooth from LB2B to the genus *Ruscinomys*, although a specific determination is not possible. The only available is an M3, an element which lacks most diagnostic characters. Adrover (1969) noted that the M3 of *Ruscinomys lasallei* Adrover, 1969, and *R. schaubi* Villalta and Crusafont Pairó, 1956, are less reduced than those of *R. europaeus* Déperet, 1890. The M3 from La Bullana 2B differs from the latter species by the presence of two well-developed lobes. However, distinguishing between *R. lasallei* and *R. schaubi* is difficult. The size of the M3 from La Bullana 2B is consistent with the lower measurements of *R. lasallei* and *R. schaubi* and even with smallest values of *R. europaeus*. For all these reasons, we ascribe the specimen from La Bullana 2B to *Ruscinomys* sp.

Order Soricomorpha Gregory, 1910
Family Soricidae Fischer von Waldheim, 1817
Subfamily Soricinae Fischer von Waldheim, 1817
Tribe Nectogalini Anderson, 1879
Genus *Asoriculus* Kretzoi, 1959
Asoriculus cf. *gibberodon* (Petényi, 1864) (Fig. 6, 5-6)

Localities: LB2B, LB3.
Material: 1 m1 (LB2B-245), 1 M1 (LB3-31).

Description:

m1: (L: 1.44; TRW: 0.77; TLW: 0.91): The talonid is wider than the trigonid. The hypolophid is well developed and does not reach the entoconid. There is a well-developed oblique crest, which connects the hypoconid with the trigonid. The metaconid is slightly higher than the paraconid. The depression of the trigonid is open and 'V' shaped. The protoconid is broken. The lingual cingulid is low and narrow. The labial cingulid is reduced. Roots are not preserved.

M1: (LL: 1.57; AW: 1.68): The metaloph does not reach the hypocone. There is a well-developed hypoconal flange and a pronounced posterior emargination. The basal connection between the hypocone and posteroloph agrees with the morphotype B described by Reumer (1984). The preprotocrista is in contact with the paracone. The parastyle is short. The paracrista is the shortest crest in the ectoloph. The paramesocrista is longer than the postmesocrista. The metastyle is broken. The metacone is higher than the paracone. The ectoloph is asymmetric. Roots are not preserved.

Discussion:

Asoriculus gibberodon is the smallest species of the genus, and very common in the Pliocene of Europe (Minwer-Barakat *et al*., 2010; Furió and Angelone, 2010). The presence of a large protoconid and a complete basal cingulid in lower molars are typical features of *A. gibberodon* (Furió, 2007). The hypocone attached to the posteroloph in the M1 agree with the morphotype B of Reumer (1984). The size of the m1 is consistent with the minimum values of the molars from Villany 3, Csarnota 2, Ostrazmos 1 and 9 (Reumer, 1984), Varshets (Popov, 2003), Fuente Nueva 3 (Furió, 2007), TCH-1 and TCH-3 (Minwer-Barakat *et al*., 2010) and Capo Mannu D1 (Furió and Angelone, 2010). The size of the M1 matches the largest values of the specimens from the mentioned localities. This great biometrical variability is usual in *A. gibberodon* (Reumer, 1984; Minwer-Barakat *et al*., 2010).

5. Discussion

5.1. Biostratigraphy

Figure 4 contains information on the stratigraphical distribution of the rodent faunas described in La Bullana 2B and La Bullana 3, besides other of Spanish localities from MN13 to MN15. The locality of La Bullana 2B contains *Apodemus gorafensis*, *Castillomys gracilis*, *Paraethomys* aff. *abaigari*, *Paraethomys meini*, *Occitanomys brailloni*, *Occitanomys* sp., *Stephanomys dubari*, *Eliomys intermedius*, *Apocricetus barrierei*, *Ruscinomys* sp., *Atlantoxerus* sp., Sciuridae indet., *Debruijnimys* cf. *julii* and *Asoriculus* cf. *gibberodon*. On the other hand, the locality La Bullana 3 contains *Apodemus gorafensis*, *Paraethomys* aff. *abaigari*, *Stephanomys dubari, Apocricetus barrierei*, *Atlantoxerus* sp., and *Asoriculus* cf. *gibberodon*. The coexistence of *Apodemus gorafensis*, *Paraethomys meini*, *Castillomys gracilis* and *Stephanomys dubari*

is considered typical of the latest Turolian-earliest Ruscinian (García-Alix *et al*., 2008a). The size and morphology of *Stephanomys* present in La Bullana 2B and La Bullana 3, with some specimens close to *S. cordii*, are similar to the molars from the lower Ruscinian (MN14) sites of PUR-4, PUR-7 and PUR-13 (García-Alix *et al*., 2008a).

Other species of biostratigraphic relevance in La Bullana 2B are *Occitanomys brailloni* and *Paraethomys* aff. *abaigari*. *Occitanomys brailloni* appears in MN14, extending its range to MN16 (Weerd, 1979; Ruiz Bustos *et al*., 1984; Castillo, 1990; Minwer-Barakat, 2005). *Paraethomys* aff. *abaigari* is found together with the smaller *P. meini* in some localities of the MN14, like PUR-13, CLC-5A, Celadas-14, Celadas-5, Celadas-5A, La Gloria 4 and Celadas 9 (García-Alix *et al*., 2008c). In older localities, closer to the MN13-MN14 boundary like PUR-4, *P. meini* shows a wide size range, which may indicate that the lineage of *P. abaigari* is already present in those assemblages, and in Peralejos E two specimens are close to *P.* aff. *abaigari* (García-Alix *et al*., 2008a).

Regarding the cricetids, the presence of *Apocricetus barrierei* in La Bullana 2B and La Bullana 3 clearly indicates a lower Ruscinian age for these localities (Freudenthal *et al*., 1998; García-Alix *et al*., 2008b).

In La Bullana 2B, glirids are represented by *Eliomys intermedius*. This species appears in MN14 (Sesé, 2006), being La Gloria 4 in the Teruel basin (Mein *et al.*, 1990), and PUR-13 in the Granada Basin (García-Alix *et al*., 2008b), the oldest records of this taxon. The faunal assemblage of La Bullana 2B indicates a similar age for the three localities (see Fig. 4).

Debruijnimys julii was described in the middle Pliocene (MN15) locality of Asta Regia (Castillo and Agustí, 1996), where *Stephanomys donnezani*, *Paraethomys jaegeri* and *Paraethomys* cf. *meini* are also present. This assemblage is clearly younger than that from LB2B.

Debruijnimys sp. has been cited in the lower Ruscinian sites of Gorafe 1, La Gloria 4, Alcoy 4B and Caravaca (Minwer-Barakat *et al*., 2009b). Gorafe 1, from the latest MN14 is included by Minwer-Barakat *et al*. (2012) in the *Trilophomys* Assemblage Zone of the Guadix basin, characterized by the association of *Apocricetus barrierei*, *Stephanomys cordii*, *Castillomys gracilis*, *Apodemus gorafensis*, *Paraethomys meini* and *Trilophomys*.

With respect to La Gloria 4, this locality belongs to the *Promimomys* and *Paraethomys* Assemblage Zone of the Teruel basin, within the MN14, where two species of *Paraethomys*, *P. meini* and *P. abaigari*, coexist (Mein *et al*., 1990). The presence of *Stephanomys dubari*, two *Paraethomys* species and *Apocricetus barrierei* suggest a similar age for La Gloria 4 and La Bullana 2B and La Bullana 3 (Fig. 4). In Caravaca, the presence of *S. dubari*, *Apocricetus barrierei*, *Castillomys gracilis* and a big-sized *Apodemus* indicate a similar age to that of La Bullana 2B and La Bullana 3 (Freudenthal *et al*., 1998; Bruijn *et al*., 1975; Weerd, 1976; Aguilar *et al.*, 1991).

According to these observations, *Debruijnimys* sp. from Gorafe 1 and Alcoy 4B are younger than the form present in La Bullana 2B, and *Debruijnimys* sp. from Caravaca and La Gloria 4 may be of a similar age. The sites where *D. almenarensis* is present, Negratín-1 and Almenara M, correspond to the Late Turolian and are clearly older than La Bullana 2B and La Bullana 3.

5.2. Paleomagnetism

A preliminary paleomagnetic study was carried out in the localities La Bullana 2B and La Bullana 3. We collected five samples to produce a preliminary paleomagnetic study around La Bullana sites, which are stratigraphically above the classical site of Venta del Moro, dated at 6.23 Ma (Gibert *et al*., 2013). The samples from La Bullana 3 show normal polarity, like the two lower samples from La Bullana 2B, while the two upper samples from this locality show reverse or ambiguous polarities, indicating a normal-reverse polarity sequence (Fig. 2). The presence of a basal normal zone, the differences with Venta del Moro fauna and the similarities with sites located in the latest Miocene or earliest Pliocene suggest that the identified normal zone should be correlated with chron C3n.4n in the earliest Pliocene, dated between 5.235 Ma and 4.997 Ma (Lourens *et al*., 2005). Therefore, the fauna of La Bullana 3 can be constrained to the age of this chron and the site La Bullana 2B, placed a few meters above its upper boundary, should be constrained between the age of this boundary (4.997 Ma) and the next magnetic reversal at 4.896 Ma.

5.3. Paleoecology

The analysis of micromammal assemblages has been widely used as a paleoclimatic indicator (Weerd, 1976; Daams *et al*., 1988; Casanovas-Vilar and Agustí, 2007; García-Alix *et al*., 2008; Furió *et al*., 2011).

Some authors have proposed a minimum sample size of at least 100 specimens when dealing with fossil assemblages (Daams *et al*., 1999; García-Alix *et al*., 2008d), while others used a minimum of 50 specimens (Casanovas-Vilar and Agustí, 2007), arguing that in most cases larger samples only add one or two species to the assemblage, with an abundance of less than 1 %. According to this, the sample from La Bullana 3 is too scarce to carry out any paleoecologic inference, having yielded just 32 specimens. For this reason we only present here the data from La Bullana 2B.

To interpret the paleoecologic requirements of each taxon found in La Bullana 2B, we have used mainly the climatic and habitat preferences proposed by García Alix *et al.* (2008d). According to that work, a number of taxa are considered as warm weather indicators (*Apodemus gorafensis*, *Paraethomys meini*, *Apocricetus*, *Atlantoxerus* and *Asoriculus gibberodon*), whereas *Ruscinomys*, of which a single element has been found, indicates cold conditions. Regarding the humidity, the presence of *P. meini*, *Ruscinomys* and *Atlantoxerus* has been associated with dry conditions, while *A.*

	N	DE	N/DE	RA	Temperature	Humidity	Habitat
Apodemus gorafensis	26	12	2.17	10.43	W	H	E
Castillomys gracilis	17	12	1.42	6.81	E	E	E
Occitanomys brailloni	17	12	1.42	6.81	U	U	U
Occitanomys sp.	1	12	0.08	0.40	U	U	U
Paraethomys aff. *abaigari*	36	12	3.00	14.43	U	U	U
Paraethomys meini	27	12	2.25	10.82	W	D	E
Stephanomys dubari	25	12	2.08	10.02	E	E	E
Apocricetus barrierei	89	12	7.42	35.68	W	E	O
Ruscinomys sp.	1	12	0.08	0.40	C	D	O
Debruijnimys cf. julii	1	12	0.63	3.01	U	D	U
Eliomys intermedius	10	16	0.08	0.40	E	E	E
Atlantoxerus sp.	1	16	0.06	0.30	W	D	O
Sciuridae indet.	1	16	0.05	0.24	U	U	U
Asoriculus cf. *gibberodon*	1	20	0.05	0.24	W	H	F
TOTALS					Warm: 57.87 % Cold: 0.40 % Eurytopic: 19.84 % Unknown: 21.89 %	Humid:10.66 % Dry: 11.93 % Eurytopic: 55.52 % Unknown: 21.89 %	Open: 36.78 % Forested: 0.25 % Eurytopic: 41.09 % Unknown: 21.88 %

Table 6.- Paleoecological affinities of the taxa from the studied localities. The relative abundance (RA) of each taxon is calculated following Martín-Suárez (1988), dividing the number of specimens (N) by the number of diagnostic elements (DE) of each group. Abbreviations: **C**, cold; **DE**, diagnostic elements; **D**, dry; **E**, eurytopic; **F**, forested; **H**, humid; **N**, number of specimens; **O**, open; **RA**, relative abundance; **U**, unknown; **W**, warm.

gorafensis, *Eliomys intermedius* and *A. gibberodon* would indicate a wet environment. The presence of *Apocricetus*, *Ruscinomys* and *Atlantoxerus* indicates open habitats, whereas *Eliomys intermedius* and *Asoriculus gibberodon* would suggest the presence of forested zones in the area (García-Alix *et al.*, 2008d). However, Freudenthal *et al*., (2014) point out that the genus *Eliomys* cannot be considered a humid environment indicator based on the ecological affinities of extant *E. quercinus*, which is a habitat generalist, and the distribution of *E. munbyanus* and *E. melanurus*, restricted to semidesert environments. Therefore, we consider *E. intermedius*, probable ancestor of *E. quercinus* (García-Alix *et al*., 2008b), and eurytopic taxon regarding both habitat and humidity. The presence of the gerbilid *Debruijnimys* suggests a dry and arid environment (Minwer-Barakat *et al*., 2009b), and the affinities of *P*. aff. *abaigari*, *Occitanomys brailloni* and *Occitanomys* sp. are unknown (García-Alix *et al*., 2008d).

The proportions of the taxa within each ecological category are shown in table 6. Regarding the humidity, most of the taxa recorded in La Bullana 2B are eurytopic (55.52 %) or with unknown affinities (*P*. aff. *abaigari* and *Occitanomys brailloni* and sp. 21.89 %). Because of that, the relative proportion of humid (10.66 %) and dry (11.93 %) environment indicators does not seem very representative. However, most of the taxa studied in this work are considered as typical to warm environments (57.87 %), and the abundance of *Apocricetus* together with *Ruscinomys* and *Atlantoxerus* and the presence of *Debruijnimys* suggest an open environment (36.78 % of the assemblage). Therefore, we consider that the faunas from La Bullana 2B indicate warm conditions and probably an open environment with some patches of vegetation.

5.4. Considerations on the "gerbil event" in Europe according to the presence of Debruijnimys in La Bullana 2B

The Messinian Salinity Crisis (MSC) is the main event in the evolution of the Mediterranean during the Neogene. The beginning of the MSC took place about 5.96 Ma ago, with the closure of the Betic and Rifian seaways, which connected the Atlantic and Mediterranean domains. The Mediterranean was reflooded at the base of the Pliocene after the opening of a new seaway, the Gibraltar strait (Hsü *et al*., 1973). The effects of this event on the faunal exchanges between Africa and Europe during this time interval have been widely discussed in the literature, and several authors have accepted the creation of new migration routes for terrestrial organisms (Brandy and Jaeger, 1980; Agustí and Casanovas-Vilar, 2003; Aguirre, 2003; Made *et al*., 2006; Agustí *et al*., 2006; Minwer-Barakat *et al*., 2009b; Gibert *et al*., 2013, among others).

One of the taxa of African origin that colonised the Iberian Peninsula during the MSC is the gerbil *Debruijnimys*. Until now, only two species of this genus have been recorded in Europe, *D. almenarensis*, identified in some MN13 localities, and *D. julii*, only known from the type locality, Asta Regia (MN15).

The origin of *D. almenarensis* and *D. julii* has been discussed in several papers (Castillo and Agustí, 1996; Agustí and Casanovas-Vilar, 2003; Minwer-Barakat *et al*., 2009b), which has important paleobiogeographic implications. While *D. almenarensis* (MN13) has a clear African origin, related to the MSC Event, the origin of *D. julii* (MN15) is more difficult to establish. Thus, the dispersion processes which explain the presence of gerbils in Western Europe have proven to be

very complicated. According to Agustí and Casanovas-Vilar (2003), there are, at least, two different waves of gerbil colonisation from northern Africa recorded in the Iberian basins. The first wave, of Late Turolian age (Late Miocene), involved *D. almenarensis*, whereas the second one corresponds to the representatives of *Debruijnimys* (*Debruijnimys* sp.) found in the Lower Pliocene (lower Ruscinian, MN14) localities of Alcoy, Gorafe, Caravaca and La Gloria 4. The presence of *A. barrierei* in Botardo, Alcoy 4B, Caravaca, La Gloria 4 (Freudenthal *et al*., 1998) and La Bullana 2B, confirm an Early Pliocene age (early Ruscinian, MN14) for these localities. La Bullana 2B is older than Alcoy 4B, probably slightly older than La Gloria 4 and similar in age to Caravaca and Botardo.

If *D. julii* is not the direct descendant of *D. almenarensis*, the presence of *D. julii* in the MN15 implies, necessarily, a second migration event from Africa to Europe in the span interval between MN13 and MN15 (Agustí and Casanovas-Vilar, 2003). Thus, according to Agustí and Casanovas-Vilar (2003), *Debruijnimys* sp. from the lower Ruscinian localities of Alcoy, Gorafe, Caravaca and La Gloria 4 (MN14) would be the descendant of *D. davidi*, and the ancestor of *D. julii*, known from the Late Ruscinian (MN15) site of Asta Regia 3.

However, there is a great similarity between *D. almenarensis* and the subsequent forms of *Debruijnimys* (see Fig. 5), and a direct ancestor-descendant relationship cannot be discarded. Still, if the presence of *D. julii* in MN14 is confirmed, it would expand the range of this taxon, until now recorded only in MN15. This would make the phylogeny of *Debruijnimys* even more complex, since the relationship between *Debruijnimys* sp. from MN14 and *D. julii* is not clear, and they may even be the same species. Another option would be a process of cladogenetic speciation along the Early Pliocene, resulting in two different lineages of *Debruijnimys*, and unnamed species and *D. julii*, but the relationship between this latter species and the forms present in MN14 is not clear, and they may be indeed the same taxon.

Nevertheless, any hypothesis on the phylogenetic relationships of *Debruijnimys* is difficult to test because of the scarce material of *Debruijnimys* sp. from the early Pliocene of the Iberian Peninsula. Only Alcoy 4B yielded a rich sample, but nowadays it is a lost locality. Therefore, until new material from Ruscinian sites becomes available, little more can be said in this regard.

The new data from La Bullana 2B contribute to improve the knowledge on the status of this lineage of African rodents in the Iberian Peninsula after the colonisation processes during the Messinian Salinity Crisis, but open new questions around the evolution of this group, too.

6. Conclusions

The faunal list of La Bullana 3 comprises *Apodemus gorafensis*, *Paraethomys* aff. *abaigari*, *Stephanomys dubari*, *Apocricetus barrierei*, Sciuridae indet. and *Asoriculus* cf. *gibberodon*. In addition to these taxa, La Bullana 2B has yielded remains of *Castillomys gracilis*, *Occitanomys brailloni*, *Occitanomys* sp., *Paraethomys meini*, *Ruscinomys* sp., *Eliomys intermedius*, *Debruijnimys* cf. *julii* and *Atlantoxerus* sp. Based on these faunal assemblages, we propose a lower Ruscinian age (MN14) for both localities.

The preliminary paleomagnetic analysis indicates an earliest Pliocene age for La Bullana 3 and La Bullana 2B. The age of La Bullana 3 lies probably within the C3n.4n chron, dated between 5.235 Ma and 4.997 Ma. The age of La Bullana 2B should be constrained between the top of this chron (4.997 Ma) and the next magnetic reversal at 4.896 Ma.

The presence of *Eliomys intermedius* in La Bullana 2B constitutes one of the oldest records of this taxon, probably equivalent to la Gloria 4 and PUR-13. The presence in La Bullana 2B of *Apodemus gorafensis*, *Paraethomys meini*, *Apocricetus barrierei*, *Atlantoxerus* and *Asoriculus* cf. *gibberodon* suggest warm conditions, and the relative abundance of *Apocricetus*, *Ruscinomys* and *Atlantoxerus* is consistent with an open environment.

The Early Ruscinian locality of LB2B constitutes the first record of a form related to *Debruijnimys julii* in MN14. However, the scarcity of the available material of *Debruijnimys* from Early Pliocene sites prevents any proper analysis, and its phylogenetic relationships remain controversial.

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