
Biochronological data for the Early Pleistocene site of Quibas (SE Spain) inferred from rodent assemblage

P. PIÑERO^{1,2} J. AGUSTÍ^{3,1,2} H. BLAIN^{1,2} M. FURIÓ⁴ C. LAPLANA⁵

¹IPHES, Institut Català de Paleoecologia Humana i Evolució Social

Zona educacional 4, Campus Sescelades URV (Edifici W3), 43007 Tarragona, Spain. Piñero E-mail: ppinero@iphes.cat
Blain E-mail: hablain@iphes.cat

²Àrea de Prehistòria, Universitat Rovira i Virgili (URV)

Avinguda de Catalunya 35, E43002 Tarragona, Spain

³ICREA, Institute of Human Paleocology

E-mail: jordi.agusti@icrea.cat

⁴Institut Català de Paleontologia, Universitat Autònoma de Barcelona

Edifici ICP, Campus de la UAB, s/n, 08193 Cerdanyola del Vallès, Barcelona, Spain
E-mail: marc.furio@icp.cat

⁵Museo Arqueológico Regional de la Comunidad de Madrid

Plaza de las Bernardas, s/n, 28801 Alcalá de Henares, Spain
E-mail: cesar.laplana@gmail.com

ABSTRACT

In this paper, the rodent fauna from the Early Pleistocene of Gruta 1 (Quibas karstic complex, Murcia, SE Spain) is described. The assemblage includes one arvicoline (*Allophaiomys* sp.), two murines (*Apodemus* ex gr. *mystacinus-epimelas*, *Castillomys rivus*) and one glirid (*Eliomys quercinus*). The rodent assemblage indicates an age very close to the age of Fuente Nueva 3 and Barranco León 5 in the Guadix-Baza Basin, and Sima del Elefante in the Atapuerca karstic complex, between ca. 1.2-1.4My.

KEYWORDS | Biochronology. Rodentia. Early Pleistocene. Iberian Peninsula.

INTRODUCTION

The karstic paleontological site of Quibas (Abanilla, Murcia) is situated on the SE slope of the Sierra de Quibas, in an area called Collado del Rey, in an abandoned limestone quarry at an altitude of 669m AMSL (Fig. 1A). The coordinates correspond to 38° 18' 51"N, 1° 4' 42"W. The fossil record provides both vertebrates and invertebrates from the Early Pleistocene. Previous faunal lists were published in

Montoya *et al.* (1999, 2001). The sample studied in the present work was collected in 2009 by A. Cuadros in order to complete her M.D. thesis (on the taphonomy of micromammals; Cuadros, 2010). This paper includes part of the M.D. thesis of P. Piñero (Piñero, 2012). As for the macrofauna from this palaeontological site, several taxonomic studies have been carried out by Carlos-Calero *et al.*, 2004, 2006a, b; Made *et al.*, 2007; Alba *et al.*, 2011. Finally, the agamid lizards have been studied by Blain *et al.* (2014).

The stratigraphic and sedimentological features of the basal part of the palaeontological site have been established in Montoya *et al.* (1999). The main interest of this site is the abundance and diversity of the faunal association identified, as well as its age (Rodríguez-Estrella *et al.*, 2004). The studied sample was collected from Gruta 1, a different point from the earlier work (Fig. 1B) because the former section is currently covered by debris.

The aim of the present paper is to identify the rodent fauna from Quibas/Gruta1 and to establish its age through the correlation with other Early Pleistocene sites from the Iberian Peninsula.

GEOLOGICAL SETTING

The Sierra de Quibas is a 6km long and 2.5km wide carbonate massif that extends in a NE-SE direction in the Middle Subbetic region. It is mainly composed of Jurassic limestone and dolomites (Rodríguez-Estrella *et al.*, 2004), which were largely affected by karstic processes during the Plio-Pleistocene, leading to numerous exokarstic and endokarstic structures. Many of these structures are infilled by chemical precipitates and/or by mixed detritic sediments. In one of these karstic structures the Quibas palaeontological site is located (Durán *et al.*, 2004).

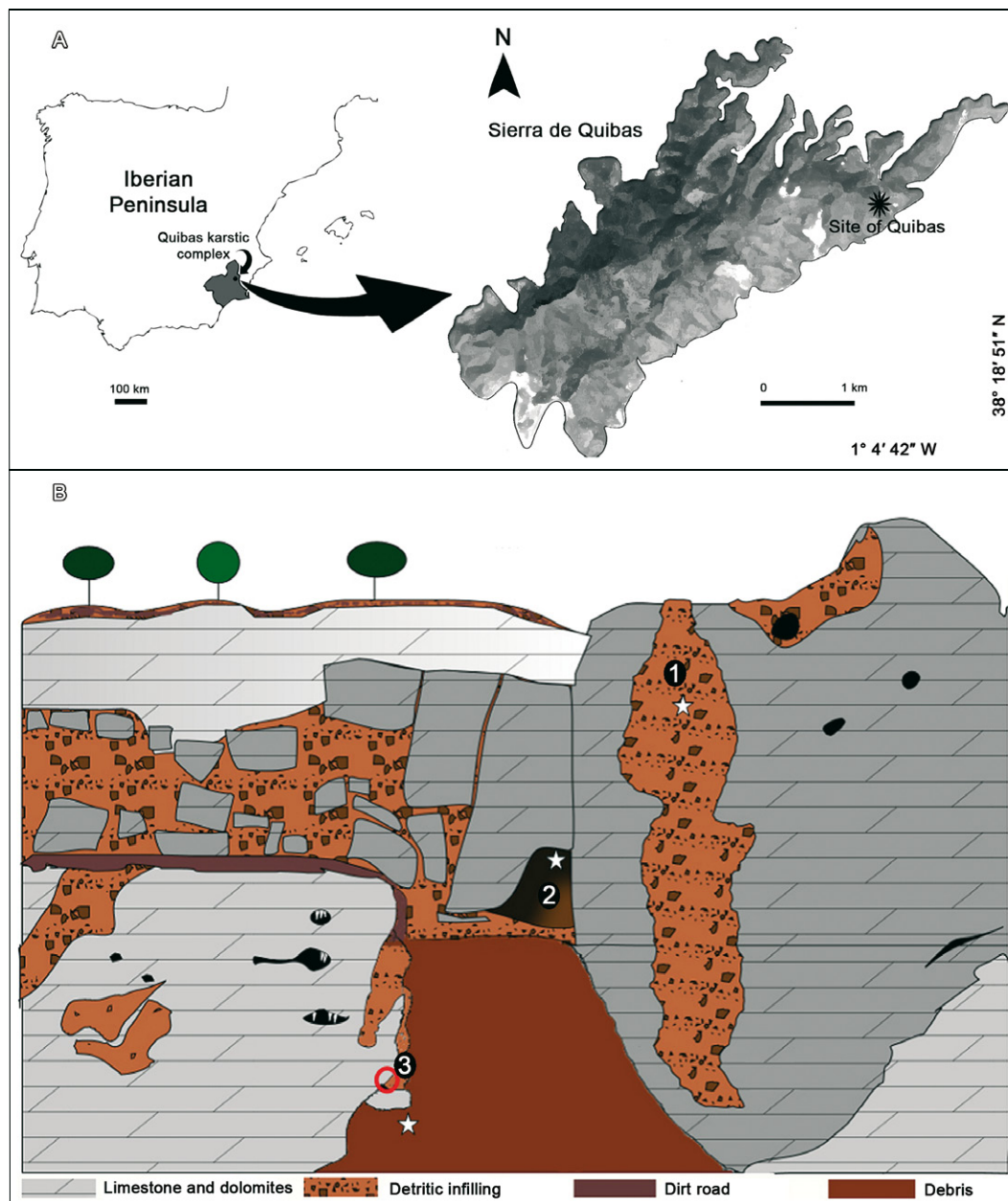


FIGURE 1. A) Geographic location of the site of Quibas (Murcia, Spain). B) Wide-angle sketch from Quibas site. 1: Sima; 2: Entrada Cueva; 3: Gruta 1; Circle: sample extraction area (modified from Cuadros, 2010).

The Quibas outcrop is mainly formed by a 5m wide and 9m high gallery (known as “Entrada Cueva”=EC on maps of the cave system) that extends laterally for more than 30m, and displays several collateral branches separated by calcitic speleothems (1 in Fig. 1B); and a 20m deep and 2m wide chasm (known as “Sima”; 2 in Fig. 1B). Although the two karstic structures are separated by 3m thick calcitic speleothems, they are likely connected (in Montoya *et al.*, 1999). Six detritic layers have been distinguished in the basal part of the site, and these are mainly composed of clays, silts, and partially cemented breccias. The studied sample is located in a detritic layer formed by limestone clasts which range between 10 and 20cm in size, and reddish silty clay matrix with carbonate crusts.

MATERIALS AND METHODS

The small mammal remains were collected from the small karst grotto known as Gruta 1 (Fig. 1B; the extraction area is marked with a red circle). All the sediment was screen-washed using superimposed 4, 1 and 0.5mm mesh screens. The specimens described are currently stored at the Institut de Paleoecologia Humana i Evolució Social (IPHES; Tarragona, Spain).

The Quibas/Gruta1 assemblage includes 199 identified rodent teeth corresponding to a minimum number of 32 individuals, representing at least four taxa. All the measurements were taken on the occlusal plane of the molars with the image-treatment software Adobe Photoshop CS5, using photographs from an Infinity X camera coupled to an Olympus SZ-40 binocular microscope.

In describing and measuring the teeth of *Apodemus* and *Castillomys*, we have followed van de Weerd (1976) and, Martín Suárez and Freudenthal (1993), respectively (Fig. 2). The terminology employed for the description of the teeth of *Eliomys* is that of Daams (1981); length and width have been measured as defined by Freudenthal (2004). The nomenclature used in the descriptions of the arvicoline teeth (only lower first molars (m1) and upper third molars (M3) have been considered) is that of van der Meulen and Zagwijn (1974). To measure the different parameters of the first lower molar and the third upper molar, we have followed the criteria proposed by Agustí (1991) and Nadachowski (1991), respectively (Fig. 2). Moreover, we have carried out a principal component analysis on arvicolines in order to decrease the variables and represent them in a scatter plot. The aim is to compare the measurements of arvicoline m1s from Quibas/Gruta1 with other values from other localities (Agustí, 1991; Agustí *et al.*, 1993, 2010). The values used for the analysis are: i) ACC (anteroconid relative length) (A–A'/L–L'); ii) AC2 (anterior complex) isolation degree in relation to the

rest of the tooth (B–B'/W–W'); and iii) isolation degree between T4 and T5 (C–C'/W–W') (see Fig. 2).

Institutional Abbreviations. IPHES, Institut Català de Paleoecologia Humana i Evolució Social; QB, Quibas; G1, Gruta1.

Anatomical Abbreviations. ACC, anteroconid complex; AC2, anterior complex; AL, anterior lobe; BRA, buccal re-entrant angle; BSA, buccal salient angle; LRA, lingual re-entrant angle; LSA, lingual salient angle; PC, posterior cap; PL, posterior lobe; T1–T7, triangles 1–7; A–A', ACC length; B–B', shortest distance between BRA3 and LRA4; C–C', shortest distance between LRA3 and BRA3; L, length; L–L', occlusal surface length; W, width; W–W', distance between LSA4 and BSA3.

SYSTEMATIC PALEONTOLOGY

Family: Muridae ILLIGER, 1811

Subfamily: Arvicolinae GRAY, 1821

GENUS *Allophaiomys* (Kormos, 1932)

Allophaiomys sp. (Figure 3 A–D)

Material and measurements. Two complete m1s (IPHES QB-10-G1-R/19a, IPHES QB-10-G1-R/19b), and one partial m1 (IPHES QB-10-G1-R/19c), one complete M3 (IPHES QB-10-G1-R/20a) (Table 1).

Description. The studied m1 of *Allophaiomys* sp. has a very simple dental pattern, with three closed angles (T1–T3), and is rootless. The ACC is simple. The amount of cement in the re-entrant angles is always abundant. The AC2 is round and its leading edge does not have any enamel. The neck of AC2 is relatively wide. The lingual edge in LSA3, and particularly in LSA4, is round and slightly angular. T4 and T5 are in an alternate position but are widely confluent. The enamel differentiation of the triangles is *Miomys*-like: the enamel is wider on the posterior face than on the anterior side. In M3 the AL is continued by three angles (T2, T3 and T4). T2 is narrowly connected to AL and T3. T4 has a small size and is widely connected to PC. LSA4 is absent. The BRA3 is shallow.

Discussion. The shape of both m1 and M3 of *Allophaiomys* from Quibas/Gruta1 is in perfect accordance with *Allophaiomys* sp. from Fuente Nueva 3 and Barranco León 5 (Agustí and Madurell, 2003; Agustí *et al.*, 2010). The morphology of m1 recalls that of *Victoriamys chalinei*, which was first recognized in the Cueva Victoria site (Alcalde *et al.*, 1981) and subsequently in other Early Pleistocene karstic sites from the Iberian Peninsula (Agustí, 1982; Laplana, 1999; Cuenca-Bescós *et al.*, 2001; Minwer-

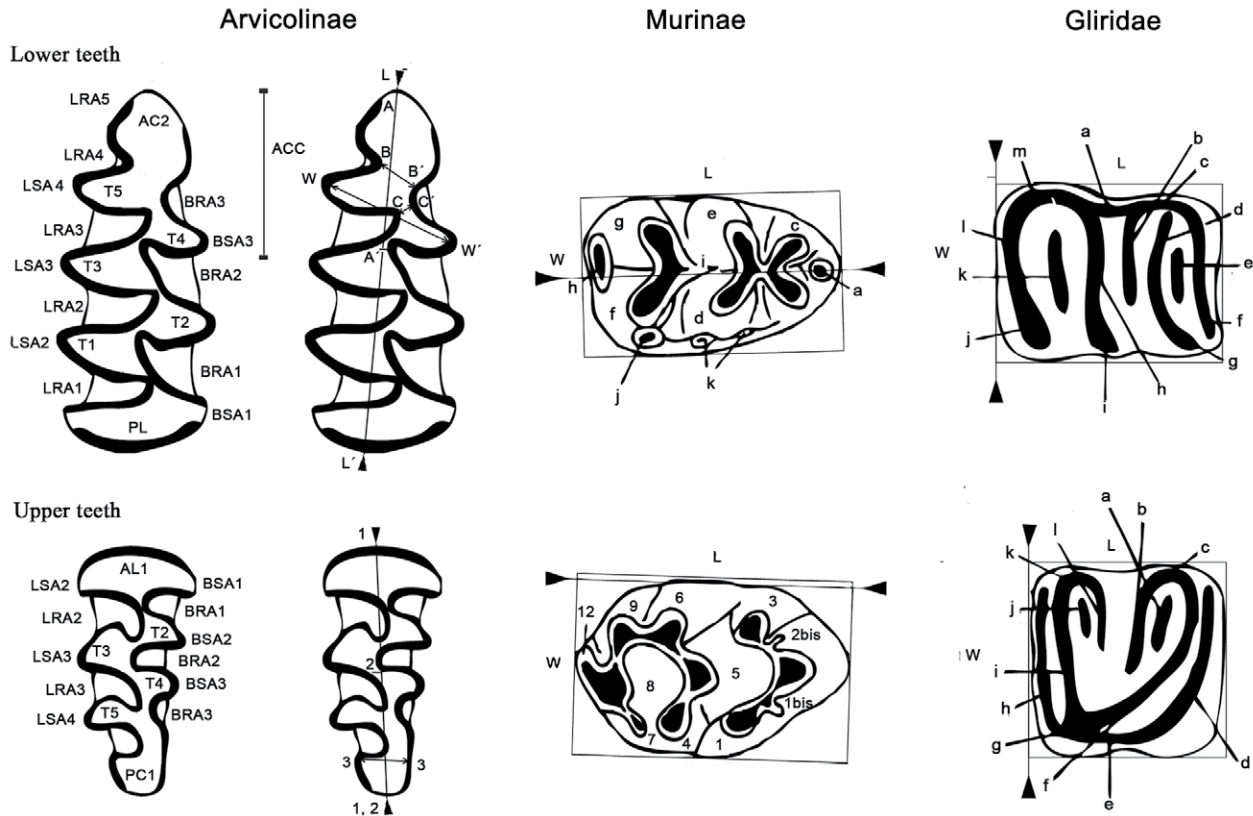


FIGURE 2. Nomenclature and measurements used in the descriptions of dental elements from the studied taxa. Arvicolinae (modified from Agustí, 1991 and Nadachowski, 1991). General abbreviations: BRA, buccal re-entrant angle; BSA, buccal salient angle; LRA, lingual re-entrant angle; LSA, lingual salient angle; T (1-5), triangle (1-5). Lower teeth: AC2, anterior complex; ACC, anteroconid complex; PL, posterior lobe. Upper teeth: AL, anterior lobe; PC, posterior complex. Murinae (modified from van de Weerd, 1976). Lower teeth: a, anteroconid cusp (=tma); b, anterolabial cusp; c, anterolingual cusp; d, protoconid; e, metaconid; f, hypoconid; g, entoconid; h, terminal heel; i, longitudinal spur; j, posterior accessory cusp (=c1); k, accessory cusps on the labial cingulum. Upper teeth: t (1-12), tubercle (1-12). Gliridae (modified from Daams, 1981). Lower teeth: a, endolophid; b, centrolophid; c, metaconid; d, metalophid; e, anterior extra ridge; f, anterolophid; g, protoconid; h, mesolophid; i, mesoconid; j, hypoconid; k, posterior extra ridge; l, posterolophid; m, entoconid. Upper teeth: a, anterior extra ridge; b, anterior centrolophid; c, paracone; d, anterolophid; e, endolophid; f, protolophid; g, protocone; h, posterolophid; i, metalophid; j, posterior extra ridge; k, metacone; l, posterior centrolophid. Measurement abbreviations: L, length; W, width. Arvicolinae. Lower teeth: L-L', occlusal surface length; W-W', distance between LSA4 and BSA3; A-A', ACC length; B-B', shortest distance between BRA3 and LRA4; C-C', shortest distance between LRA3 and BRA3. Upper teeth: 1, occlusal surface length; 2, PC length; 3, PC posterior part width.

Barakat et al., 2011). Nevertheless, some specimens do not closely resemble the morphology of *V. chalinei*, but rather look like *Mimomys oswaldoreigi*, which has been identified in the Early Pleistocene levels of the Guadix-Baza basin (Agustí et al., 1993). Thus, the morphology of M3 is clearly of mimomyan type, and different from that of *V. chalinei* from the Cueva Victoria site. However, the specimens from Quibas/Gruta1 do not belong to *Mimomys* because roots are absent. Even so, the relatively short length of ACC indicates that this is a primitive form of *Allophaiomys*.

Allophaiomys sp. from Quibas/Gruta1 was compared with species of arvicolines from other localities (Agustí, 1991; Agustí et al., 1993, 2010), using principal component analysis performed on the values of A-A'/L-L', B-B'/W-W', and C-C'/W-W'. The cumulative amount of variance explained by the first two components reaches

94.47%. The resulting scatter plot (Fig. 4) indicates that the greatest similarity with respect to size is between the sample from Quibas/Gruta1 and *Allophaiomys ruffoi* from Venta Micena 1, followed closely by *Allophaiomys* sp. from Fuente Nueva 3, *A. pliocaenicus* from Betfia 2, and *Allophaiomys* sp. from Barranco León 5. It is concluded that the species from Quibas/Gruta1 resembles the more archaic species of *Allophaiomys* (*A. pliocaenicus*, *A. ruffoi*, *Allophaiomys* sp.), diverging from the more derived forms (*A. vandermeuleni*, *A. burgondiae*, *A. nutiensis*). Although biometrically closer to *Allophaiomys ruffoi*, morphologically *Allophaiomys* sp. from Quibas/Gruta1 is closer to *Allophaiomys* sp. from Fuente Nueva 3 and Barranco León. In the species from Quibas/Gruta1 some derived features typical of *A. ruffoi*, such as the frequent presence of a well developed BSA 3 (*sensu* Meulen, 1973) are lacking. This is also the case of *Allophaiomys*

sp. from Fuente Nueva 3 and Barranco León. This is why we consider *Allophaiomys* sp. from Quibas/Gruta1 closer to the latter species, rather than to *A. ruffoi*. According to Agustí *et al.* (2010), the presence of an archaic *Allophaiomys* can be successfully explained by the evolution of *Mimomys oswaldoreigi* (derived *Mimomys*

with a tendency to develop hypsodont molars, according to Agustí *et al.* (1993)). Furthermore, Agustí and Madurell (2003) suggested that *Allophaiomys* sp. from Fuente Nueva 3 could possibly be an ancestor of *Victoriamys chalinei*. However, this hypothesis can be refuted in the light of both biometric and enamel differences (see Fig.

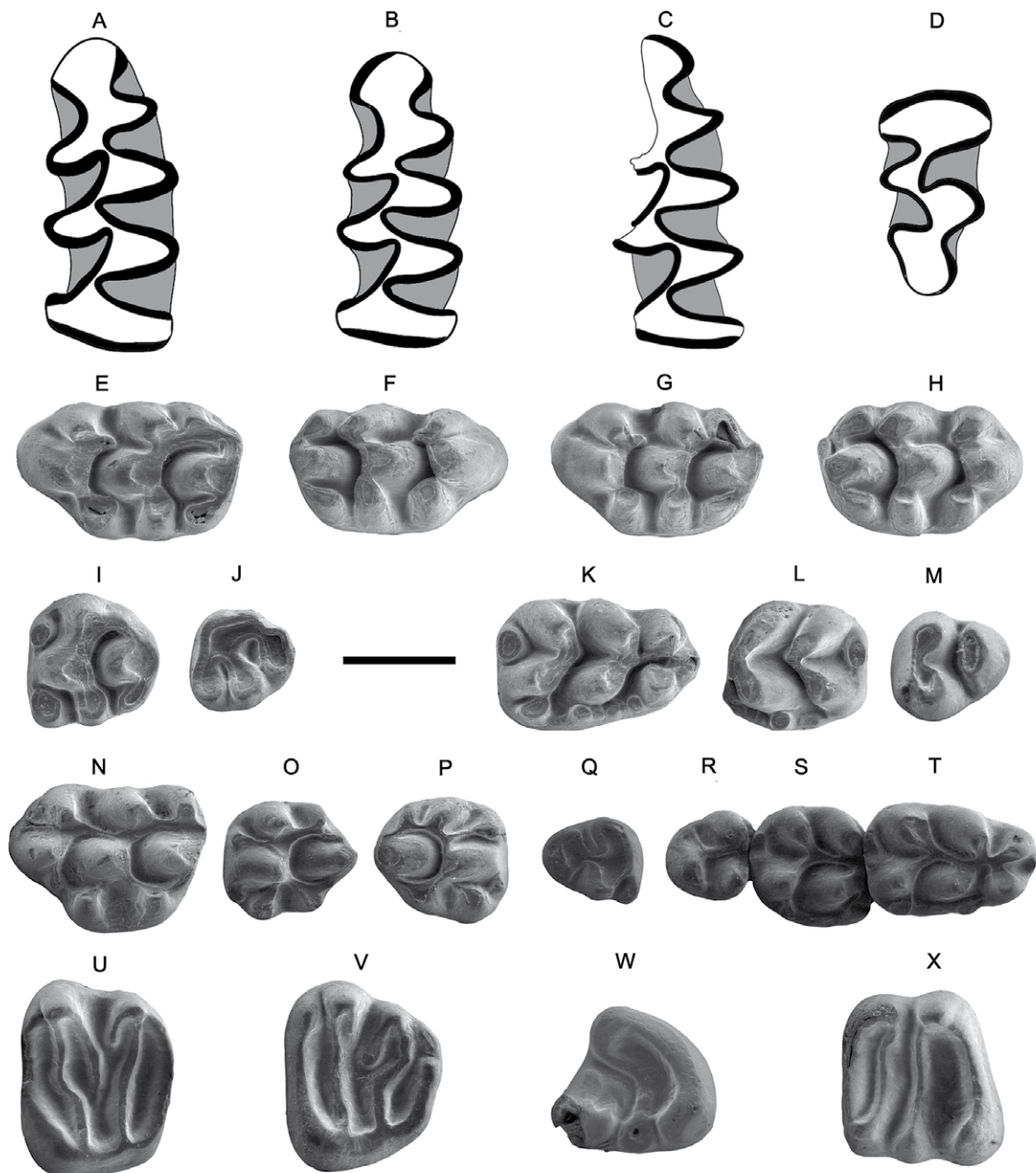


FIGURE 3. *Allophaiomys* sp. from Quibas/Gruta1: A) m1, left, QB-10-G1-R/19a; B) m1, left, QB-10-G1-R/19b; C) partial m1, left, QB-10-G1-R/19c; D) M3, right, QB-10-G1-R/20a. *Apodemus* ex gr. *mystacinus* (Danford and Alston, 1877)–*epimelas* (Nehring, 1902) from Quibas/Gruta1: E) M1 left, QB-10-G1-R/2d; F) M1, right, QB-10-G1-R/1k; G) M1, left, QB-10-G1-R/2g; H) M1, right, QB-10-G1-R/1d; I) M2, left, QB-10-G1-R/3n; J) M3, left, QB-10-G1-R/4i; K) m1, right, QB-10-G1-R/6m; L) m2, left, QB-10-G1-R/8p; M) m3, left, QB-10-G1-R/9u. *Castillomys rivas* Martín Suárez and Mein, 1991 from Quibas/Gruta1: N) M1, left, QB-10-G1-R/11a; O) M2, left, QB-10-G1-R/11e; P) M2, right, QB-10-G1-R/11g; Q) m3, left, QB-10-G1-R/11i; R) m3, right, QB-10-G1-R/11k3; S) m2, right, QB-10-G1-R/11k2; T) m1, right, QB-10-G1-R/11k1. *Eliomys quercinus* (Linnaeus, 1766) from Quibas/Gruta1: U) M1–2, left, QB-10-G1-R/13i; V) M3, right, QB-10-G1-R/14e; W) p4, left, QB-10-G1-R/15a; X) m1–2, left, QB-10-G1-R/16k. Scale bar equals 1mm.

TABLE 1. Measurements (mm) of the teeth of *Allophaiomys* sp. from Quibas Gruta1

Element	L-L'	W-W'	A-A'	B-B'	C-C'	Element	1	2	3
m1	2.825	0.974	1.068	0.236	0.201	M3	1.812	0.946	0.412
m1	2.655	1.117	1.129	0.295	0.237				

4, where *V. chalinei* and *Allophaiomys* sp. can be seen to be biometrically dissimilar). The arvicoline species from Quibas/Gruta1 probably represents a new species close to *A. ruffoi* from Fuente Nueva 3, but it is assigned as *Allophaiomys* sp. because only four teeth of *Allophaiomys* of taxonomic value have been recovered.

Subfamily: Murinae ILLIGER, 1811

GENUS *Apodemus* Kaup, 1829

Apodemus ex gr. *mystacinus* (Danford and Alston, 1877)–*epimelas* (Nehring, 1902). (Figure 3 E–M)

Material and measurements. 28 M1s (IPHES QB-10-G1-R/1a–1m, 2a–2n, 5a1), 17 M2s (IPHES QB-10-G1-R/3a–3p, 5a2), 9 M3s (IPHES QB-10-G1-R/4a–4i); 37 m1s (IPHES QB-10-G1-R/6a–6o, 7a–7n, 10a1, 10c1, 10d1, 10e1, 10f1, 10g1, 10h1, 10i1), 28 m2s (IPHES QB-10-G1-R/8a–8u, 10a2, 10b2, 10c2, 10d2, 10e2, 10g2, 10h2.), 28 m3s (IPHES QB-10-G1-R/9a–9z, 9aa, 10d3) (Table 2).

Description. The m1s have a round and well-developed anterocentral cuspid, which is isolated in 35% of cases. The anterolabial and anterolingual cusps are symmetric. The protoconid is slightly larger than the metaconid. The hypoconid-entoconid complex is isolated. The labial cingulum is well developed (with a large and isolated c1 and up to three accessory cusps). The terminal heel is oval, large and isolated (except IPHES QB-10-G1-R/6c, 7b, 7i). The m2s usually present an oval and isolated anterolabial cuspid. The protoconid and the metaconid are not connected to the hypoconid and the entoconid. The c1 is absent (in ten specimens). When it is present, it is round and reduced, with one to no accessory cusp. IPHES QB-10-G1-R/8l has a reduced round tuber attached to the labial edge of the terminal heel. In m3, the anterolabial cusp is weakly represented in four specimens (IPHES QB-10-G1-R/9m, 9n, 9d, 9e). The c1 is absent. The lower molars have no longitudinal crests. In M1, t1 is round and separated from t5. Only IPHES QB-10-G1-R/1a has t2bis. In 18 out of 28 recovered specimens, t1 is connected to t2 forming a ridge to t3 (in the other specimens t1 is isolated). The t3 has a spur in a posterior direction that does not contact t5 or t6. The anterior tubercles (t1, t2 and t3) are not connected to the middle tubercles (t4, t5 and t6), but the latter do connect with t9. The t4 is completely separated from t7 (except in four out of 28 specimens in an advanced stage of wear). In most specimens, t12 is laterally compressed, forming a

curved lamellar structure toward t9, which may present a t12 connection both with t8 and t9 (38% of the studied M1; see Fig. 3E, F), or a t12 connection just with t8, excluding the t12-t9 connection (62% of the studied M1; see Fig. 3G, H). In M2, t1 and t3 are round and isolated, t1 being larger than t3. The t4 is oval and generally smaller than t6. The t4, t5, t6, t9 and t8 are connected to form a single ridge, even reaching t7 (in 70% of cases). The t7 is oval and separated from t4. The t6 is larger than t9, and they are connected. The t9 is well developed in 60% of the sample. The t12 is absent or weak. The M3s have a large and oval t1. The t3 is absent. The t4 is fused to t5, t6 and t8 to form a continuous ridge.

Discussion. The morphology of the studied teeth agrees with that of *A. ex gr. mystacinus-epimelas*. The species from Quibas/Gruta1 differs from *A. sylvaticus* because the latter is smaller and characterized by great development of t7 in M1 (Arrizabalaga et al., 1999) and a frequent t7-t4 connection (Nores, 1988), while none of the teeth from Quibas/Gruta1 have those features (except four specimens in an advanced stage of wear). Moreover, 60% of the teeth studied have the t9 in M2 poorly developed or absent, a lack of connection between hypoconid-entoconid and protoconid-metaconid, tma in m2 is attached to only one of the anteroconids, and the t12 in M1 laterally compressed toward t9. All these characteristics allow *A. ex gr. mystacinus-epimelas* to be distinguished also from *A. flavicollis* which is morphologically more similar to *A. sylvaticus* (Agustí et al., 2010).

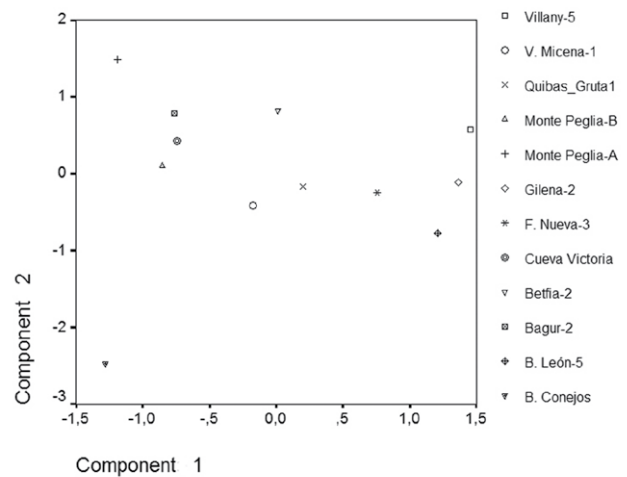


FIGURE 4. Scatter plot with the two principal components (Component 1 = 0.316xL + 0.243xA/L + 0.322xB/W + 0.358xC/W; Component 2 = 0.090xL + 0.877xA/L - 0.605xB/W - 0.132xC/W) for A-A'/L-L', B-B'/W-W' and C-C'/W-W' values of m1 from Gruta1, and different arvicolines from other localities previously studied: *Allophaiomys* sp. (Fuente Nueva 3 and Barranco León 5), *Mimomys oswaldoreigi* (Gilena 2), *Allophaiomys deucalion* (Villany-5), *A. pliocaenicus* (Betfia-2, Bagur-2), *A. ruffoi* (Venta Micena-1), *A. vandermeuleni* (Barranco de los Conejos), *V. chalinei* (Cueva Victoria), *A. nutiensis* (Monte Peglia-A), *A. burgondiae* (Monte Peglia-B).

TABLE 2. Measurements (mm) of the teeth of *Apodemus* ex gr. *mystacinus-epimelas* from Quibas Gruta1

Element	Length				Width			
	N	min	mean	max	N	min	mean	max
M1	28	1.94	2.05	2.22	26	1.21	1.30	1.39
M2	17	1.22	1.35	1.50	17	1.18	1.28	1.34
M3	9	0.87	0.97	1.13	9	0.87	0.93	0.97
m1	33	1.67	1.90	2.09	35	0.88	1.14	1.25
m2	28	1.19	1.29	1.36	28	1.01	1.16	1.27
m3	28	0.88	1.08	1.19	27	0.78	0.96	1.04

The mean length and width of the sample from Quibas/Gruta1 was compared with *A. mystacinus* from Cueva Victoria (Agustí, 1982), *A. mystacinus* from Orce-7 (Agustí *et al.*, 1987a), *A. atavus* from Tollo de Chiclana (Minwer-Barakat, 2005), *A. flavicollis* from Fuente Nueva 3 (Agustí *et al.*, 2010) and *Apodemus sylvaticus* from Torrent de Vallparadís (Minwer-Barakat *et al.*, 2011). In all cases, the species from Quibas/Gruta1 is larger than *A. atavus* and *A. flavicollis*, being more similar to *A. mystacinus* from Orce-7 and Cueva Victoria. The mean values of *A. ex gr. mystacinus-epimelas* from Quibas/Gruta1 are slightly smaller than *A. mystacinus* from Cueva Victoria, but larger than those from Fuente Nueva 3 (Agustí *et al.*, 2010), and very close to those from Orce-7 (Agustí *et al.*, 1987a). Besides, the values fit the range of *A. mystacinus* from Fuente Nueva 3 (Agustí *et al.*, 2010), Orce-2, and Barranco León 2-3 (Agustí *et al.*, 1987a).

Until recently, *A. mystacinus* included two subspecies: *A. mystacinus mystacinus* and *A. mystacinus epimelas*. Nowadays these subspecies are ranked as separate species, *A. mystacinus* and *A. epimelas* (Krystufek and Vohralik, 2009; Wilson and Reeder, 2005). Hitherto *A. epimelas* has not been identified in Early Pleistocene sites from the Iberian Peninsula. However, this species is likely to be present but recorded as *A. mystacinus*. Thus a revision of all specimens of *A. mystacinus* from the Iberian Peninsula is required. In this context, 62% of the M1 from Quibas/Gruta1, according to Storch (1977), have features typical of *A. epimelas* (t12 is only connected to t8, the t12-t9 connection is absent, see Fig. 3G, H and Fig. 5B), while the remaining 38% present features of *A. mystacinus* (t12 is usually connected directly both with t8 and t9, see Fig. 3E, F and Fig. 5C). Accordingly, the species from Gruta1 is identified as *A. ex gr. mystacinus-epimelas*.

Apodemus mystacinus has been identified at many Early Pleistocene sites in southwestern Europe such as

Mas Rambault, Bourgade, Le Vallonet or Bagur-2 (Agustí, 1982). In these localities, the molars are slightly smaller than the specimens from Gruta1 (López-Martínez *et al.*, 1976). Measurements of *A. mystacinus* from eastern Europe are larger than the ones of *A. mystacinus* from Quibas/Gruta1. The smaller size of western representatives of *A. mystacinus* in relation to the eastern populations is a constant in all sites from southwestern Europe (Agustí, 1982). Today, *A. mystacinus* and *A. epimelas* (recorded as *A. mystacinus*) are found in areas with a relatively warm climate in the Balkan Peninsula and Middle East. They are associated with dry forest and shrub land in rocky areas. Their presence in fossil sites can be related to the occurrence of rocky environments in the vicinity of the locality (Agustí, 1982; Storch, 2004; Minwer-Barakat, 2005; Mitchell-Jones *et al.*, 1999).

GENUS *Castillomys* Michaux, 1969

Castillomys rivas Martín Suárez and Mein, 1991. (Figure 3 N–T)

Material and measurements. 3 M1s (IPHES QB-10-G1-R/11a–11c), 4 M2s (IPHES QB-10-G1-R/11d–11g), 4 m1s (IPHES QB-10-G1-R/11k1, 11l1, 11h, 11j1), 3 m2s (IPHES QB-10-G1-R/11k2, 11l2, 11j2), 2 m3s (IPHES QB-10-G1-R/11i, 11k3). Table 3.

Description. The lower molars have a well-developed longitudinal crest which connects the hypoconid-entoconid with the protoconid-metaconid. In m1, the anterolingual and anterolabial cusps are connected with the metaconid through a ridge. The labial cingulum is very broad and is separated from the protoconid by a valley. The c1 is

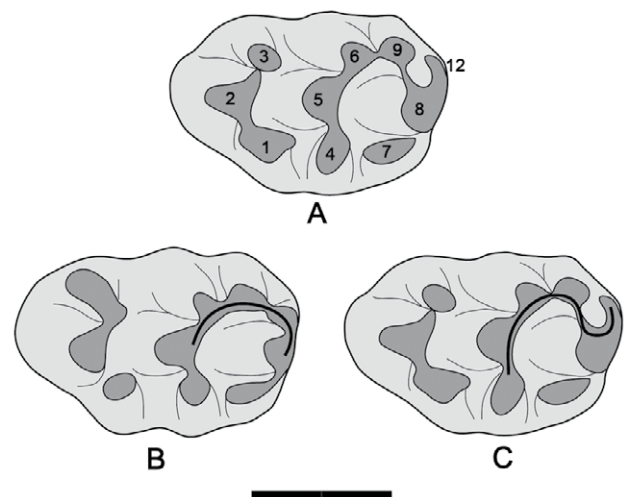


FIGURE 5. Occlusal pattern of the first upper molar of *A. mystacinus* and *A. epimelas*. A) numbering of cusps; B) QB-10-G1-R/2g, left, cusp connections typical of *Apodemus epimelas*; C) QB-10-G1-R/2i, left, cusp connections typical of *Apodemus mystacinus*. Scale bar equals 1mm. Modified from Storch, 1977.

either oval or round and it is connected to the hypoconid. Accessory cusps are absent. The anteroconid cusp is weak. The terminal heel is oval, large and isolated. The m2s have a large and oval or subtriangular anterolabial cusp, which is connected to the protoconid by a ridge in two of the three specimens (IPHES QB-10-G1-R/11j2, 11i2). The labial cingulum is wide and forms a valley with the protoconid. The c1 is small, round, and it is connected to the hypoconid. The terminal heel is oval. In m3, the anterolabial cusp may be either oval, large and connected to the protoconid (IPHES QB-10-G1-R/11i), or absent (QB-10-G1-R/k3). The upper molars have well-developed longitudinal crests. Even t4 is connected to t8 by a ridge, completing the join of the crown. Moreover, both the labial longitudinal crest (t3–t5 connection) and the lingual longitudinal crest (t1–t5 connection, except in IPHES QB-10-G1-R/11g) are present. The M1s and M2s have a small and round t1bis. In M1, the t2bis and t12 are well developed. In M2, t12 appears as a thickening from the crest that connects t8 and t9.

Discussion. The morphology of the studied molars agrees with that of *C. rivas*. To differentiate *C. rivas* from *C. crusafonti*, Martín Suárez and Mein (1991) established a set of criteria, some of them based on the percentage of appearance of certain features. *C. rivas* differs from *C. crusafonti* in that its cusps are completely connected by ridges. In the studied specimens, both upper and lower molars have well-developed longitudinal crests, completing the crown connection. Other differences between *C. rivas* and *C. crusafonti* are discernible, such as the presence in the lower molars of a very broad labial cingulum and its separation from the protoconid by a valley. Another difference is the general presence in the upper molars of t1bis and t2bis, and the large size in *C. rivas* (Martín Suárez and Mein, 1991).

The measurements of *Castillomys* from Quibas/Gruta1 were compared with the mean values of *C. crusafonti* and *C. rivas* from Tollo de Chiclana reported by Minwer-

Barakat (2005). The result was a great similarity of the studied sample with *C. rivas*, *C. crusafonti* being smaller. Additionally, the size values fit the range of *C. rivas* from Venta Micena (Agustí *et al.*, 1987b), Fuente Nueva 3 and Barranco León 5 (Agustí *et al.*, 2010), Orce-2, Orce-3, Orce-7 and Barranco León 2-3 (Agustí *et al.*, 1987a). Populations of *C. rivas* from Fuente Nueva 3 and Barranco León 5 are slightly smaller than those of Quibas/Gruta1. *C. rivas* has also been recognized in other Early Pleistocene sites such as the lower unit of Sima del Elefante (Cuenca-Bescós *et al.*, 2001) and Loma Quemada-1 (Martín Suárez, 1988). The mean values from the latter are comparable with those from Quibas/Gruta1.

Castillomys rivas is an extinct rodent. It is interpreted as an eurytopic species, *i.e.* it does not provide information about specific ecological conditions (Minwer-Barakat, 2005). Nevertheless, the development of wall-shaped ridges on the teeth suggests a diet based on grains, so open meadows should be expected as a preferred habitat (Montoya *et al.*, 1999).

Family: Gliridae THOMAS, 1897

GENUS *Eliomys* Wagner, 1840

Eliomys quercinus (Linnaeus, 1766). (Figure 3 U–X)

Material and measurements. 5 P4s (IPHES QB-10-G1-R/12a–12e), 9 M1–2s (IPHES QB-10-G1-R/13a–13i), 5 M3s (IPHES QB-10-G1-R/14a–14e), 2 d4s (IPHES QB-10-G1-R/18a, 18b), 4 p4s (IPHES QB-10-G1-R/15a–15d), 11 m1–2s (IPHES QB-10-G1-R/16a–16k), 1 m3 (IPHES QB-10-G1-R/17a). Table 4.

Description. The p4 has a triangular outline. The protoconid and metaconid are fused at the anterior end of the tooth, forming a high and robust cusp. The mesoconid and the entoconid are connected by a continuous mesolophid (but in IPHES QB-10-G1-R/15d this is interrupted). The hypoconid and the entoconid are connected by a high, curved and continuous posterolophid. There is no posterior extra ridge. The lower molars have a simple dental pattern. The m1 and m2 have five main cusps: protoconid and metaconid on the lingual border, and mesoconid, hypoconid and entoconid on the labial border. These cusps are connected by continuous crests: anterolophid, metalophid, mesolophid and posterolophid. The endolophid and accessory ridges are absent. The centrolophid may be weak or absent. The entoconid and the metaconid are separated by a wide and deep valley. In P4, the paracone and the metacone are stronger than the protocone, but this is higher than the metacone. The anteroloph is poorly developed (except in IPHES QB-10-G1-R/12c). The protoloph is long and continuous, and is connected with the endoloph. The posterior and anterior

TABLE 3. Measurements (mm) of the teeth of *Castillomys rivas* from Quibas Gruta1

Element	Length			Width				
	N	min	mean	max	N	min	mean	max
M1	1		1.95		1		1.39	
M2	4	1.14	1.21	1.24	4	1.14	1.18	1.22
M3								
m1	3	1.57	1.58	1.59	4	0.96	1.00	1.04
m2	3	1.08	1.12	1.17	3	0.99	1.03	1.09
m3	2	0.87	0.91	0.96	2	0.76	0.80	0.96

TABLE 4. Measurements (mm) of the teeth of *Eliomys quercinus* from Quibas Gruta1

Element	Length				Width			
	N	min	mean	max	N	Min	mean	max
P4	5	0.94	1.03	1.13	5	1.43	1.55	1.64
M1-2	9	1.12	1.29	1.39	9	1.56	1.76	1.99
M3	4	1.33	1.44	1.50	4	1.46	1.57	1.67
D4	2	1.04	1.045	1.05	2	0.85	0.93	1.02
p4	4	1.34	1.44	1.51	4	1.17	1.23	1.29
m1-2	11	1.25	1.38	1.53	11	1.46	1.65	1.75
m3	1		1.24		1		1.53	

centrolophids are weak or absent. The paracone and the metacone are separated by a wide and deep valley. The metaloph is continuous. The posteroloph is curved at its lingual edge and is connected to the protocone. The M1 and M2 have continuous anterolophids, protolophids, metalophids and posterolophids. There are no accessory ridges. The paracone is larger than the metacone. The anterior and posterior centrolophids are well developed. The metaloph and posteroloph are straight. In M3, the metaloph, posteroloph, anteroloph and protoloph are continuous, and the latter two are separated by a wide and deep valley. The paracone is the highest cusp. Accessory ridges are absent. The posterior centroloph is more developed than the anterior centroloph. The metacone is lower than the paracone and they are separated by a deep furrow.

Discussion. *Eliomys quercinus* is considered a descendant of the Pliocene *E. intermedius*, from which it differs in its more simple dental pattern, with accessory ridges absent in both upper and lower teeth, and reduced centrolophids in the lower teeth (García-Alix *et al.*, 2009). All the elements described in this paper fit the morphology of *E. quercinus*. Although *E. intermedius* was quoted in the faunal list of Montoya *et al.* (1999; 2001), the sample from Gruta1 shows no morphological evidence of the presence of this species.

The measures are similar to those of *E. quercinus* from other Early Pleistocene sites such as Torrent de Vallparadís (Minwer-Barakat *et al.*, 2011), Cueva Victoria (Agustí, 1982) and Huétor-Tájar and Tojaire (García-Alix *et al.*, 2009). This species is also described in Sima del Elefante (Cuenca-Bescós and Laplana, 1997), Gran Dolina (Cuenca-Bescós *et al.*, 2011) and Almenara-Casablanca-1 and Almenara-Casablanca-3 (Agustí and Galobart, 1986). Overall, *E. quercinus* from Quibas/Gruta1 shows great biometric variability. The centrolophids of the

lower molars are present but poorly developed (as in the specimens from Cueva Victoria), which indicates a more archaic morphology than the specimens from layers EVT7 and EVT12 of Torrent de Vallparadís (Minwer-Barakat *et al.*, 2011).

Eliomys quercinus underwent a great expansion throughout Europe during the entire Pleistocene. Nowadays, it is generally found in deciduous and conifer forests, and also in stony or rocky areas with some vegetation, from Spain to the Ural Mountains. Its presence in fossil sites has been considered indicative of forest areas and a temperate climate (Chaline, 1972; Sesé and Villa, 2008).

DISCUSSION AND CONCLUSIONS

The rodent assemblage from Quibas/Gruta1 includes *Allophaiomys* sp., *Apodemus* ex gr. *mystacinus-epimelas*, *Castillomys rivas* and *Eliomys quercinus*. This association is comparable to that described by Montoya *et al.* (1999): *Allophaiomys* sp. (= *Arvicola deucalion* according to Montoya *et al.* (1999)), *Apodemus* sp., *Castillomys rivas*, *Eliomys intermedius* and *Hystrix refossa*. The presence of an archaic representative of *Allophaiomys* places both sites in the Biharian mammal age (Early Pleistocene).

The association from Quibas/Gruta1 is very similar to those from Fuente Nueva 3 and Barranco León 5 (Guadix-Baza Basin, SE Spain), with a number of common species such as *Allophaiomys* sp., *Castillomys rivas* (Agustí and Madurell, 2003; Agustí *et al.*, 2010) and *Apodemus mystacinus*. According to Duval *et al.* (2013) Fuente Nueva 3 and Barranco León 5 are dated *ca.* 1.2My and according to Toro-Moyano *et al.* (2013) *ca.* 1.4My. Assuming a trend in this species to increase its size during the Early Pleistocene, as suggested by Agustí (1982) and Martín-Suárez and Mein (1991) the morphometric data of *Castillomys rivas* could be taken to suggest a younger age for Quibas/Gruta1 than Barranco León 5 and older than Fuente Nueva 3. However, Laplana and Blain (2008) established by data analysis that this trend may not exist; rather, there is a size gap between the populations of *C. crusafonti* and *C. rivas*, and the size within each population is stable with fluctuations. Due to the presence of *Allophaiomys* sp., an age close to the Barranco León and Fuente Nueva 3 is proposed for Quibas/Gruta1, between *ca.* 1.2–1.4My.

The rodent association from Quibas can also be compared with that from Sima del Elefante (Atapuerca karstic complex), in which *Castillomys rivas* and *Eliomys quercinus* are also present (Cuenca-Bescós *et al.*, 2001; 2013) and the LAD of *Castillomys rivas* has been established at 1.1My (Cuenca Bescós *et al.*, 2010). However, the presence in Sima del Elefante of more derived forms of *Allophaiomys*

than *Allophaiomys* sp. of Quibas/Gruta1 such as *A. lavocati* suggests an older age for the latter site.

Another site close in age to Quibas in the same region (Murcia) is Cueva Victoria. This locality shares with Quibas/Gruta1 *Castillomys rivas* and *Eliomys quercinus* (Agustí, 1982), and perhaps *Apodemus mystacinus* (a review is required). However, the presence in Cueva Victoria of a species more derived such as *V. chalinei* indicates an older age for Quibas/Gruta1.

The sites of Barranco León 5, Fuente Nueva 3 and Sima del Elefante are characterized by the first occurrence of a human presence in the Iberian Peninsula (Carbonell et al., 2008; Oms et al., 2000; Toro-Moyano et al., 2013). Thus the site of Quibas, although without human evidences, coincides in time and space with the first human occupation in Iberia, as recorded in the Guadix-Baza Basin and the Atapuerca karstic complex (Fig. 6).

ACKNOWLEDGMENTS

This paper is part of projects CGL2012-38358 and CGL2011-28681 of the Spanish Ministry of Economy and Competitiveness,

AGAUR of the Generalitat de Catalunya (PIPH- 2009 SGR 754), and PI-676-04 (7507) of the Seneca Foundation (Murcia). P.P. is supported by a FPU Predoctoral Fellowship (FPU12/02668) with the financial sponsorship of the Spanish Ministry of Education, Culture and Sports. We are especially grateful to M.A. Mancheño and G. Romero, who collaborated in the fieldwork and made this paper possible. The Quibas excavation team helped with the extraction, sieving and washing of sediments, particularly P. Sevilla and A. Cuadros. The authors thank to the editor G. Arratia, and J.M. López García and an anonymous reviewer for their comments and suggestions on the manuscript.

REFERENCES

Agustí, J., 1982. Los roedores (Mammalia) del Pleistoceno Inferior de la “Cueva Victoria” (Murcia, España). *Endins*, 9, 49-55.
 Agustí, J., 1991. The *Allophaiomys* complex in Southern Europe. *Geobios*, 25, 133-144.
 Agustí, J., Galobart, A., 1986. La sucesión de micromamíferos en el complejo cárstico de Casablanca (Almenara, Castellón): problemática biogeográfica. *Paleontologia i Evolució*, 20, 57-62.
 Agustí, J., Madurell, J., 2003. Los arvicólidos (Muroidea, Rodentia, Mammalia) del Pleistoceno inferior de Barranco

Chronology	MA	Guadix-Baza Basin	Continental Biochronology (Fejfar et al., 1998)			Localities
		RODENT SEQUENCE (Oms et al., 2000)	Rodent Zones	RODENT SUPERZONES	LAND MAMMAL AGES	
Early Pleistocene	~0.78	<i>Terricola arvalidens</i> <i>Stenocranius gregaloides</i>	<i>Mimomys savini</i>	<i>Microtus-Mimomys</i>	BIHARIAN	Atapuerca TD7
	~0.9					Atapuerca TD6
	~1.0	<i>Iberomys huescarensis</i> <i>Mimomys savini</i> (large)				Huéscar 1
	~1.1		Puerto Lobo			
	~1.2		Vallparadis EVT7			
	~1.3		El Chaparral			
~1.4		<i>Allophaiomys</i> aff. <i>lavocati</i> <i>Mimomys savini</i> (small)	<i>Mimomys savini-pusillus</i>		Cueva Victoria	
						Atapuerca TE-LRU
						QUIBAS
						Barranco León 5

FIGURE 6. Correlation of the European chronology with the principal early Pleistocene archaeo-paleontological sites in the Iberian Peninsula, placing the Quibas site in its context. Atapuerca TE-LRU refers to Lower Red Unit of the Sima del Elefante; Atapuerca TD refers to Gran Dolina.

- León y Fuente Nueva 3 (Orce, Granada). Datos preliminares. In: Toro, I., Agustí, J., Martínez-Navarro, B. (eds.). El Pleistoceno inferior de Barranco León y Fuente Nueva 3, Orce (Granada). Consejería de Cultura, Andalucía, Spain, 137-146.
- Agustí, J., Moyà-Solà, S., Martín-Suárez, E., Marín, M., 1987a. Faunas de mamíferos en el Pleistoceno inferior de la región de Orce (Granada, España). *Paleontologia i evolució Memoria Especial*, 1, 73-86.
- Agustí, J., Arbiol, S., Martín-Suárez, E., 1987b. Roedores y lagomorfos (Mammalia) del Pleistoceno inferior de Venta Micena (Guadix-Baza, Granada). *Paleontologia i Evolució Memoria Especial*, 1, 95-107.
- Agustí, J., Castillo, C., Galobart, A., 1993. Heterochronic evolution in the Late Pliocene Early Pleistocene arvicolines in the Mediterranean area. *Quaternary International*, 19, 51-56.
- Agustí, J., De Marfà, R., Santos-Cubedos, A., 2010. Roedores y lagomorfos (Mammalia) del Pleistoceno inferior de Barranco León 5 y Fuente Nueva 3 (Orce, Granada). In: Toro, I., Martínez-Navarro, B., Agustí, J. (eds.). *Ocupaciones humanas en el Pleistoceno inferior y medio de la cuenca de Guadix-Baza*. Consejería de Cultura, Andalucía, Spain, 121-140.
- Alba, D.M., Carlos-Calero, J.A., Mancheño, M.A., Montoya, P., Morales, J., Rook, L., 2011. Fossil remains of *Macaca sylvanus florentina* (Cocchi, 1872) (Primates, Cercopithecidae) from the Early Pleistocene of Quibas (Murcia, Spain). *Journal of Human Evolution*, 61(6), 703-718.
- Alcalde, G., Agustí, J., Villalta, J.F., 1981. Un nuevo *Allophaiomys* (Arvicolinae, Rodentia, Mammalia) en el Pleistoceno inferior del sur de España. *Acta Geologica Hispanica*, 16(4), 203-205.
- Arrizabalaga, A., Torre, I., Catzefflis, F., Renaud, F., Santalla, F., 1999. Primera citació d'*Apodemus flavicollis* (Melchior, 1834) al Montseny. Determinació morfològica i genètica. III i IV trobades d'estudiosos del Montseny. *Monografies*, 27, 193-195.
- Blain, H.A., Bailón, S., Agustí, J., Piñero-García, P., Lozano-Fernández, I., Laplana, C., Sevilla, P., López-García, J.M., Romero, G., Mancheño, M.A., 2014. Youngest agamid lizards from Western Europe (Sierra de Quibas, Spain, late Early Pleistocene). *Acta Palaeontologica Polonica*, 59(4), 873-878.
- Carbonell, E., Bermúdez de Castro, J.M., Parés, J.M., Pérez-González, A., Cuenca-Bescós, G., Ollé, A., Mosquera, M., Huguet, R., Made, J. Van der, Rosas, A., Sala, R., Vallverdú, J., García, N., Granger, D.E., Martín-Torres, M., Rodríguez, X.P., Stock, G.M., Vergès, J.M., Allué, E., Burjachs, F., Cáceres, I., Canals, A., Benito, A., Díez, C., Lozano, M., Mateos, A., Navazo, M., Rodríguez, J., Rosell, J., Arsuaga, J.L., 2008. The first hominin of Europe. *Nature*, 452, 465-469.
- Carlos-Calero, J.A., Mancheño, M.A., Montoya, P., Ruiz Bustos, A., 2004. El yacimiento pleistoceno de la Sierra de Quibas (Abanilla, Murcia). *Nuevas Aportaciones*. In: Calonge, A., Gozalo, R., López Carrillo, M.D., Pardo, M.V. (eds.). *Libro de Resúmenes de las XX Jornadas de la Sociedad Española de Paleontología*, Universidad de Alcalá de Henares, Madrid, Spain, 40-41.
- Carlos-Calero, J.A., Montoya, P., Mancheño, M.A., Morales, J., 2006a. Presencia de *Vulpes praeglacialis* en el yacimiento pleistoceno de la sierra de Quibas (Murcia, España). *Estudios Geológicos*, 62(1), 395-400.
- Carlos-Calero, J.A., Made, J. Van der, A., Mancheño, M.A., Montoya, P., Romero, G., 2006b. *Capra alba* Moyà-Solà, 1987 del Pleistoceno inferior de la Sierra de Quibas (Murcia, España). *Estudios Geológicos*, 62(1-2), 571-578.
- Chaline, J., 1972. Les Rongeurs du Pléistocène Moyen et Supérieur de France (Systématique, Biostratigraphie, Paléoclimatologie). *Cahiers de Paléontologie*, C.N.R.S., Paris, 410pp.
- Cuadros, I.A. 2010. Aproximación tafonómica de los micromamíferos del yacimiento paleontológico de Quibas: Evidencias de digestión, fracturas y procesos diagenéticos. M.D. Thesis. Complutense University of Madrid, Spain, 55pp.
- Cuenca-Bescós, G., Laplana, C., Canudo, J.I., Arsuaga, J.L. 1997. Small mammals from Sima de los Huesos. *Journal of Human Evolution*, 33(2), 175-190.
- Cuenca-Bescós, G., Canudo, J.I., Laplana, C., 2001. La séquence des rongeurs (Mammalia) des sites du Pléistocène inférieur et moyen d'Atapuerca (Burgos, Espagne). *L'Anthropologie*, 105(1), 115-130.
- Cuenca-Bescós, G., Agustí, J., Lira, J., Melero-Rubio, M., Rofes, J., 2010. A new species of water vole from the Early Pleistocene of Southern Europe. *Acta Palaeontologica Polonica*, 55(4), 565-580.
- Cuenca-Bescós, G., Rofes, J., López-García, J.M., Blain, H., De Marfà, R.M., Galindo-Pellicena, M.A., Bennásar-Serra, M.L., Melero-Rubio, M., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2010. Biochronology of Spanish Quaternary small vertebrate faunas. *Quaternary International*, 212(2), 109-119.
- Cuenca-Bescós, G., Melero-Rubio, M., Rofes, F., Martínez, I., Arsuaga, J.L., Blain, H.A., López-García, J.M., Carbonell, E., Bermúdez de Castro, J.M., 2011. The Early Middle Pleistocene environmental and climatic change and the human expansion in Western Europe: A case study with small vertebrates (Gran Dolina, Atapuerca, Spain). *Journal of Human Evolution*, 60(4), 481-491.
- Cuenca-Bescós, G., Rofes, J., López-García, J.M., Blain, H., Rabal-Garcés, R., Sauqué, V., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2013. The small mammals of Sima del Elefante (Atapuerca, Spain) and the first entrance of *Homo* in Western Europe. *Quaternary International*, 295, 28-35.
- Daams, R. 1981. The dental pattern of the dormice *Dryomys*, *Myomimus*, *Microdryomys* and *Peridyromys*. *Utrecht Micropaleontological Bulletin*, Special publication, 3, 1-115.

- Danford, C.G., Alston, E.R., 1877. On the mammals of Asia Minor. Proceedings of the Zoological Society of London, 1877, 270-281.
- Durán, J.J., López-Martínez, J., Mancheño, M.A., 2004. Dos registros de espeleotemas pleistocenos de gran potencia en la Península Ibérica: primeros resultados isotópicos. Boletín Geológico y Minero, 115, 265-270.
- Duval, M., Falguères, C., Bahain, J.J., Grun, R., Shao, Q., Aubert, M., Dolo, J.M., Agustí, J., Martínez-Navarro, B., Palmqvist, P., Toro, I., 2012. On the limits of using combined U-series/ESR method to date fossil teeth from two Early Pleistocene archaeological sites of the Orce area (Guadix-Baza basin, Spain). Quaternary Research, 77(3), 482-491.
- Fejfar, O., Heinrich, W.D., Lindsay, E.H., 1998. Updating the Neogene rodent biochronology in Europe. In: Van Kolfshoten, T., Gibbard, P.L. (Eds.). The Dawn of the Quaternary. Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen, 60, 533-554.
- Freudenthal, M. 2004. Gliridae (Rodentia, Mammalia) from the Eocene and Oligocene of the Sierra Palomera (Teruel, Spain). Treballs del Museu de Geologia de Barcelona, 12, 97-173.
- García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E., Freudenthal, M., 2009. Small mammals from the early Pleistocene of the Granada Basin, southern Spain. Quaternary Research, 72, 265-274.
- Gray, J.E., 1821. On the natural arrangement of vertebrate animals. London Medical Repository, 15, 296-310.
- Illiger, C., 1811. Prodromus systematis mammalium et avium additis terminis zoographicis utriusque classis, eorumque versione germanica. Sumptibus C. Salfeld, Berlin, 302pp.
- Kaup, J., 1829. Skizzierte Entwicklungsgeschichte und Natürliches System der Europäischen Thierwelt. C.W. Leske, Darmstadt/Leipzig, 203pp.
- Kormos, T., 1932. Neue Wühlmause aus dem Oberpliozän von Püspökfürdo. Neues Jahrbuch für Mineralogie, Geologie und Paläontologie, 69, 323-346.
- Krystufek, B., Vohralik, V., 2009. Mammals of Turkey and Cyprus. Rodentia II: Cricetidae, Muridae, Spalacidae, Calomyscidae, Capromyidae, Hystricidae, Castoridae. Knjinica Annales Majora, 372pp.
- Laplana, C., 1999. Presencia de *Microtus (Allophaiomys) chalinei* Alcalde, Agustí y Villalta, 1981 (Arvicolinae, Rodentia) en el yacimiento de Bagur-2 (Pleistoceno inferior, Girona, España). Treballs del Museu de Geologia de Barcelona, 8, 25-32.
- Laplana, C., Blain, H.A., 2008. Microvertebrados (Squamata, Lagomorpha, Erinaceomorpha y Rodentia) de Fonelas P-1 (Cuenca de Guadix, Granada). In: Arribas, A., (ed.). Vertebrados del Plioceno Superior terminal en el suroeste de Europa: Fonelas P-1 y el Proyecto Fonelas. Instituto Geológico y Minero de España, Madrid, Spain, 65-83.
- Linnaeus, C., 1766. Systema naturae sive regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis Tomus 1. Editio duodecima, reformata. Laurentii Salvii, Stockholm, 532pp.
- López-Martínez, N., Michaux, J., de Villalta, J.F., 1976. Rongeurs et Lagomorphes de Bagur-2 (Province de Gérone, Espagne) nouveau remplissage de fissure du début du Pléistocène Moyen. Acta Geologica Hispanica, 11(2), 46-54.
- López-García, J.M., Cuenca-Bescós, G., Blain, H.A., Cáceres, I., García, N., van der Made, J., Gutierrez, J.M., Santiago, A., Giles Pacheco, F., 2012. Biochronological data inferred from the early Pleistocene Arvicolinae (Rodentia, Mammalia) of the El Chaparral site (Sierra del Chaparral, Cádiz, southwestern Spain). Journal of Vertebrate Paleontology, 32, 1149-1156.
- Made, J. van der., Carlos-Calero, J.A., Mancheño, M.A., 2007. New material of the goat *Capra alba* from the Lower Pleistocene of Quibas and Huéscar (Spain). Notes on sexual dimorphism, stratigraphic distribution and systematic. Bolletino della Società Italiana de Paleontología, 47(1), 13-23.
- Martín-Suárez, E., 1988. Sucesiones de micromamíferos en la Depresión de Guadix-Baza (Granada, España). PhD Thesis. University of Granada University, Granada, Spain, 241pp.
- Martín Suárez, E., Mein, P., 1991. Revision of the genus *Castillomys* (Muridae, Rodentia). Scripta Geologica, 96, 47-81.
- Martín-Suárez, E., Freudenthal, M., 1993. Muridae (Rodentia) from the lower Turolian of Crevillente (Alicante, Spain). Scripta Geologica, 103, 65-118.
- Meulen, A.J. van der., Zagwijn, W.H., 1974. *Microtus (Allophaiomys) pliocaenicus* from the Lower Pleistocene near Brielle, The Netherlands. Scripta Geologica, 21, 1-12.
- Michaux, J., 1969. Muridae (Rodentia) du Pliocène supérieur d'Europe et du Midi de la France. Palaeovertebrata, 3, 1-25.
- Minwer-Barakat, R., 2005. Roedores e insectívoros del Turoliense Superior y el Plioceno del sector central de la cuenca de Guadix. PhD Thesis. University of Granada, Spain, 535pp.
- Minwer-Barakat, R., Madurell-Malapeira, J., Alba, D., Aurell-Garrido, J., De Esteban-Trivigno, S., Moyà-Solà, S., 2011. Pleistocene rodents from the Torrent de Vallparadís section (Terrassa, northeastern Spain) and biochronological implications. Journal of Vertebrate Paleontology, 31(4), 849-865.
- Mitchell-Jones, A.J., Amori, G., Bogdanowicz, W., Krystufek, B., Reijnders, P.H.J., Spitzenberger, F., Stubbe, M., Thissen, J.B.M., Vohralik, V., Zima, J., 1999. The Atlas of European Mammals. Poyser Societas Europaea Mammalogica, Hong Kong, 484pp.
- Montoya, P., Alberdi, M.T., Blázquez, A.M., Barbadillo, L.J., Fumanal, M.P., Made, J. Van Der., Marín, M., Molina, A., Morales, J., Murelaga, X., Peñalver, E., Robles, F., Ruiz Bustos, A., Sánchez, A., Sanchiz, B., Soria, S., Szyndlar, Z., 1999. La fauna del Pleistoceno Inferior de la Sierra de Quibas (Abanilla, Murcia). Estudios Geológicos, 55(3-4), 127-161.
- Montoya, P., Alberdi, M.T., Barbadillo, L.J., Made, J. van Der., Morales, J., Murelaga, X., Peñalver, E., Robles, F., Ruiz Bustos, A., Sánchez, A., Sanchiz, B., Soria, S., Szyndlar, Z., 2001. Une faune très diversifiée du Pléistocène inférieur de la Sierra de Quibas (provincia de Murcia, Espagne). Comptes Rendus de l'Académie des sciences, 332, 387-393.

- Nadachowski, A., 1991. Systematics, geographic variation, and evolution of snow voles (*Chionomys*) based on dental characters. *Acta Theriologica*, 36(1-2), 1-45.
- Nehring, A., 1902. Ueber einige griechische Nager: *Mus epimelas* n. sp., *Cricetulus atticus* n. sp. und *Myoxus nitidula wingei* n. subsp. *Sitzungsberichte der Gesellschaft Naturforschender Freunde zu Berlin*, 1902, 1-7.
- Nores, C., 1988. Diferenciación biométrica de *Apodemus sylvaticus* y *Apodemus flavicollis* en la Cordillera Cantábrica. Primeros resultados. *Revista de Biología de la Universidad de Oviedo*, 6, 109-116.
- Oms, O., Agustí, J., Gabàs, M., Anadón, P., 2000. Lithostratigraphical correlation of micromammal sites and biostratigraphy of the Upper Pliocene to Lower Pleistocene in the Northeast Guadix-Baza Basin (southern Spain). *Journal of Quaternary Science*, 15(1), 43-50.
- Piñero, P., 2012. Los roedores del Pleistoceno inferior de la Gruta del Complejo kárstico de Quibas. M.D. Thesis. Universitat Autònoma de Barcelona and Universitat de Barcelona, Barcelona, Spain, 100pp.
- Rochebrune, A.T., 1883. Faune de la Sénégambie. Mammifères. *Actes de la Société Linnéenne de Bordeaux*, 37, 49-203.
- Rodríguez-Estrella, T., Mancheño, M.A., Romero, G., Hernández, J.M., 2004. Características geológicas de la Sierra de Quibas (Abanilla, Murcia). Su relación con un yacimiento paleontológico pleistoceno. *Geogaceta*, 35, 115-118.
- Sesé, C., Villa, P., 2008. Micromammals (rodents and insectivores) from the early Late Pleistocene cave site of Bois Roche (Charente, France): systematics and paleoclimatology. *Geobios*, 41(3), 399-414.
- Storch, G., 1977. Die Ausbreitung der Felsenmaus (*Apodemus mystacinus*): Zur Problematik der Inselbesiedlung und Tiergeographie in der Ägäis. *Natur und Museum*, 107, 174-182.
- Storch, G., 2004. Late Pleistocene rodent dispersal in the Balkans. In: Griffiths, H.I., Krystufek, B., Reed, J.M. (eds.). *Balkan Biodiversity: Pattern and Process in the European Hotspot*. Kluwer Academic Publishers, 135-145.
- Thomas, O., 1897. On the genera of rodents: an attempt to bring up to date the current arrangement of the order. *Proceedings of the Zoological Society of London 1897*, 1012-1028.
- Toro-Moyano, I., Martínez-Navarro, B., Agustí, J., Souday, C., Bermúdez de Castro, J.M., Martín-Torres, M., Fajardo, B., Duval, M., Falguères, C., Oms, O., Parés, J.M., Anadón, P., Julià, R., García-Aguilar, J.M., Moigne, A.M., Espigares, M.P., Ros-Montoya, S., Palmqvist, P., 2013. The oldest human fossil in Europe, from Orce (Spain). *Journal of Human Evolution*, 65(1), 1-9.
- Wagner, J.A., 1840. Beschreibung einiger neuer Nager. *Abhandlungen mathematisch-physische Classe, Königliche Bayerische Akademie der Wissenschaften München*, 3, 173-218.
- Weerd, A. van de, 1976. Rodent faunas of the Mio-Pliocene continental sediments of the Teruel-Alfambra region, Spain. *Utrecht Micropaleontological Bulletin, Special publication*, 2, 1-217.
- Wilson, D.E., Reeder, D.M., 2005. *Mammal species of the world: A taxonomic and geographic reference*. 3rd ed. John Hopkins University Press, Baltimore, 2142pp.

Manuscript received February 2014;
revision accepted February 2015;
published Online July 2015.