



## Small mammals from the early Pleistocene of the Granada Basin, southern Spain

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### ABSTRACT

The Pliocene and Pleistocene continental sedimentary records of the western sector of the Granada Basin, southern Spain, consist of alternating fluvial and lacustrine/palustrine sediments. Two Quaternary sections from this sector have been sampled: Huétor Tájar and Tojaire. They have yielded remains of rodents, insectivores and lagomorphs. The presence in the Huétor Tájar and Tojaire sections of *Mimomys*, *Apodemus atavus*, *Castillomys rivas* and two different species of *Allophaiomys*, indicates an Early Pleistocene age. These deposits, which are related to a fluvio-lacustrine system, can be differentiated from an older (Pliocene) braided fluvial system. Their dating has important repercussions on the paleogeographic reconstruction of the basin. The conditions inferred from the ecological preferences of the small mammal associations are wet and cold. These associations suggest a predominance of open herbaceous habitats, followed by forested habitats; semiaquatic habitats are the least represented.

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### Introduction

The Granada Basin is a Neogene basin located in the central sector of the Betic Cordillera of southern Spain. Its continental infilling extends from the latest Tortonian (Middle Turolian) to the present (Fig. 1).

The sediments of the northwestern sector of the basin correspond to the deposits of the “paleo-Cacín system” and recent Cacín River, with a Plio-Pleistocene or younger age, according to Fernández and Soria (1987). This paper deals with the sediments from the Huétor Tájar area, located in the northwestern sector of the basin (Fig. 1). Agustí et al. (1990) published the results of a preliminary sampling in the Quaternary deposits near the village of Huétor Tájar, which yielded five teeth of *Allophaiomys*; they proposed an Early Pleistocene age for these sediments. We have intensively sampled the area, and have obtained a large collection of Gliridae (dormice), Muridae (mice), Arvicolidae (voles), Talpidae (moles and water moles), Soricidae (shrews), and Lagomorpha (rabbits and hares). Although most localities have yielded small mammals, and even large mammal remains, we will concentrate here on those that are richer in small mammal specimens: Huétor Tájar-1 (HT-1), Huétor Tájar-8 (HT-8) and Tojaire-1 (TOJ-1). The new associations allow us to define the age of these sections, and correlate them with localities and biozonations from other basins.

We propose a paleoenvironmental interpretation of these deposits using rodents and insectivores because the combination

of both has provided useful data about the Miocene and Pliocene environmental conditions in the Granada Basin (García-Alix et al., 2008c).

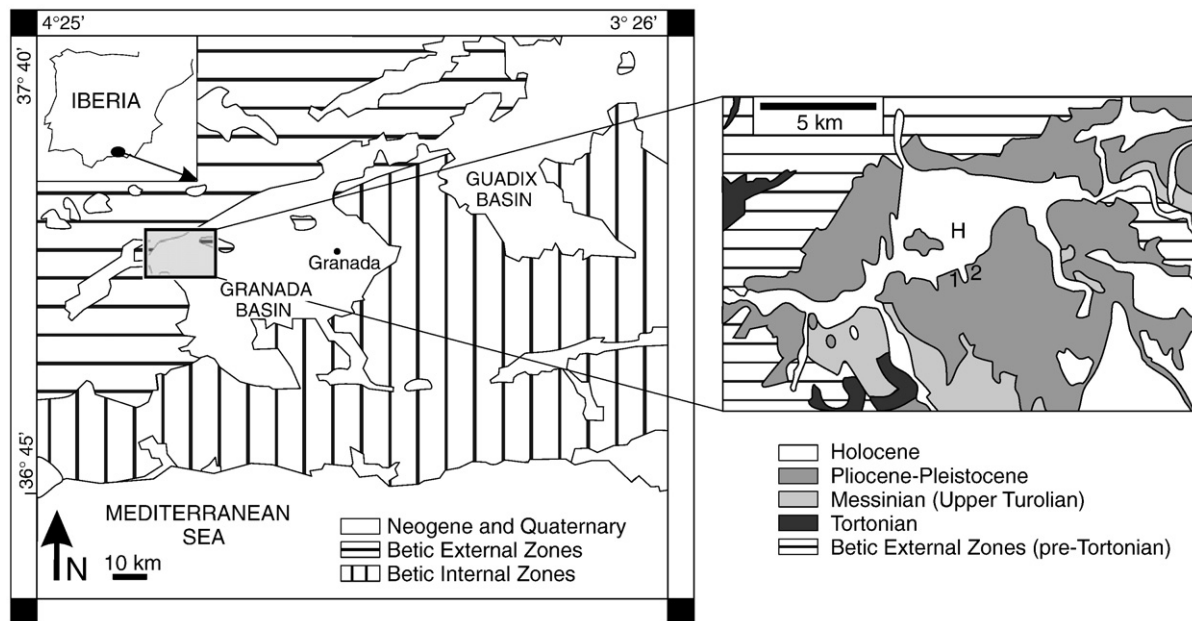
### Regional setting

The Mio-Pliocene deposits of the Granada Basin unconformably overlie older rocks from the Internal and External Zones of the Betic Cordillera. Three phases of infilling can be differentiated: one marine, one marine-continental transitional and one continental (Braga et al., 1990). The continental phase began in the latest Tortonian (middle Turolian). The Miocene continental sediments (middle and upper Turolian) are related with fluvial systems that flowed into a large central lake; this configuration changed at the Mio-Pliocene transition (Turolian-Ruscinian boundary). At that time, two independent fluvio-lacustrine systems were established: one in the east and another one in the west of the basin (García-Alix, 2006; García-Alix et al., 2008a). Nowadays the drainage of the basin consists of a large fluvial system running E–W (Genil River), and the fluvial courses of the western side of the basin are their tributaries.

The Pleistocene sediments of the western sector of the basin are related to lacustrine/palustrine and fluvial-braided systems (Fernández and Soria, 1987; García-Alix et al., 2008a, 2009). Our studied sections, Huétor Tájar and Tojaire, are located in these Pleistocene sediments near the village of Huétor Tájar, in the road-cuts of the motorway Granada-Sevilla. The Huétor Tájar section (HT) is located between UTM coordinates: 30SVG076160 and 30SVG078157. The Tojaire section (TOJ) is sited between UTM coordinates 30SVG068155 and 30SVG069156.

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**Figure 1.** Geographical and geological situation of the Granada Basin and of the studied sections (after Braga et al. (1990) and Agustí et al. (1990)). H, Huétor Tájar village; 1, Tojaire section; 2, Huétor Tájar section.

The sediments of the studied sections unconformably overlie thick Pliocene conglomerate deposits, related with a braided fluvial system (Fig. 2), which crops out near of the studied sequences (García-Alix et al., 2007a, 2009).

We have sampled several levels of those sections, but only two levels with small mammal remains have been found in the sequence of Huétor Tájar, and five in the sequence of Tojaire: HT-1 (UTM 30SVG076160) and HT-8 (UTM 30SVG076159), TOJ-1 (UTM 30SVG069156), TOJ-2 (UTM 30SVG068156), TOJ-3 (UTM 30SVG068156), TOJ-4 (UTM 30SVG068156) and TOJ-5 (UTM 30SVG068156). In this paper we refer only to those levels that have delivered the most abundant and complete small mammal record: HT-1, HT-8 and TOJ-1. The stratification of the sediments is subhorizontal, and these three localities are laterally equivalent (Fig. 2). The main lithologies of the studied sections are limestone, lutite, sand with cross-laminations and conglomerate with clasts from metamorphic rocks (marble, schist, mica schist, quartzite) and from limestone, sandstone, dolomite, and chert (Fig. 2).

## Materials and methods

We processed 2300 kg of sediments from HT-1, 4200 kg from HT-8, and 1260 kg from TOJ-1. To concentrate the fossil remains, samples were reduced using sieves and acetic acid at 10% concentration; finally small mammal remains were picked out with a binocular stereomicroscope.

The nomenclature used in the descriptions of the teeth of Gliridae is that of Freudenthal and Martín Suárez (2006); length and width have been measured as defined by Freudenthal (2004). The nomenclature used in the descriptions of the teeth of Muridae is that of van de Weerd (1976); length and width have been measured as defined by Martín Suárez and Freudenthal (1993). The nomenclature used in the descriptions of the teeth of Arvicolidae is that of van der Meulen and Zagwijn (1974), and Rabeder (1981); length and width have been measured as defined by van der Meulen (1973), and van der Meulen and Zagwijn (1974). The nomenclature used in the descriptions of the teeth of Desmaninae is that of Rümke (1985); lengths and widths have been measured as defined by Martín Suárez et al. (2001). The nomenclature used in the descriptions of the teeth of Soricidae is that of Reumer (1984). Lengths and widths have been

measured as defined by Reumer (1984). Nomenclature is synthesized in Figure 3.

Lower teeth ( $I_1$ ,  $P_1$ ,  $M_1$ : incisor, premolar, molar) are indicated by subscripts, and upper teeth ( $I^1$ ,  $P^1$ ,  $M^1$ : incisor, premolar, molar) by superscript; 1, 2, 3 or 4, indicate the order. Other nomenclature abbreviations are indicated in Figure 3.

Measurements of the teeth were taken with a Wild M7S binocular microscope, equipped with a Sony Magnescale LM12 digital measuring device. Measurements of the studied specimens are compiled in the Supplementary data of the online version. Photographs were made with the FEI ESEM QUANTA 400 in environmental mode of the 'Centro Andaluz de Medio Ambiente' (Granada). The specimens are kept in the 'Departamento de Estratigrafía y Paleontología' of the University of Granada, Spain.

## Small mammal assemblages from Huétor Tájar and Tojaire sections

The faunal lists for the studied localities are:

HT-1: *Eliomys* aff. *quercinus*, *Apodemus atavus*, *Castillomys rivas*, *Allophaiomys pliocaenicus*, *Allophaiomys chalinei*, *Mimomys oswaldoreigi*, *Galemys pyrenaicus*, *Crociodura* sp., *Sorex* sp., and *Prolagus calpensis*.

HT-8: *Eliomys* aff. *quercinus*, *A. atavus*, *C. rivas*, *A. pliocaenicus*, *A. chalinei*, *M. oswaldoreigi*, *G. pyrenaicus*, *Crociodura* sp., *Sorex* sp. and *Lepus* cf. *granatensis*.

TOJ-1: *Eliomys* aff. *quercinus*, *A. atavus*, *C. rivas*, *A. pliocaenicus*, *A. chalinei*, *M. oswaldoreigi*, *G. pyrenaicus*, *Crociodura* sp., *Sorex* sp., *P. calpensis* and *Lepus* cf. *granatensis*.

In this paper we will discuss only the taxons belonging to the orders Rodentia (murids, glirids, and arvicolids) and Lipotyphla (talpids and soricids), because of their biostratigraphical (rodents) and paleoecological (rodents and insectivores) importance.

## Family Gliridae

Only one species of Gliridae has been identified: *Eliomys* aff. *quercinus* (Fig. 4: 1–7). The main feature of the studied specimens is

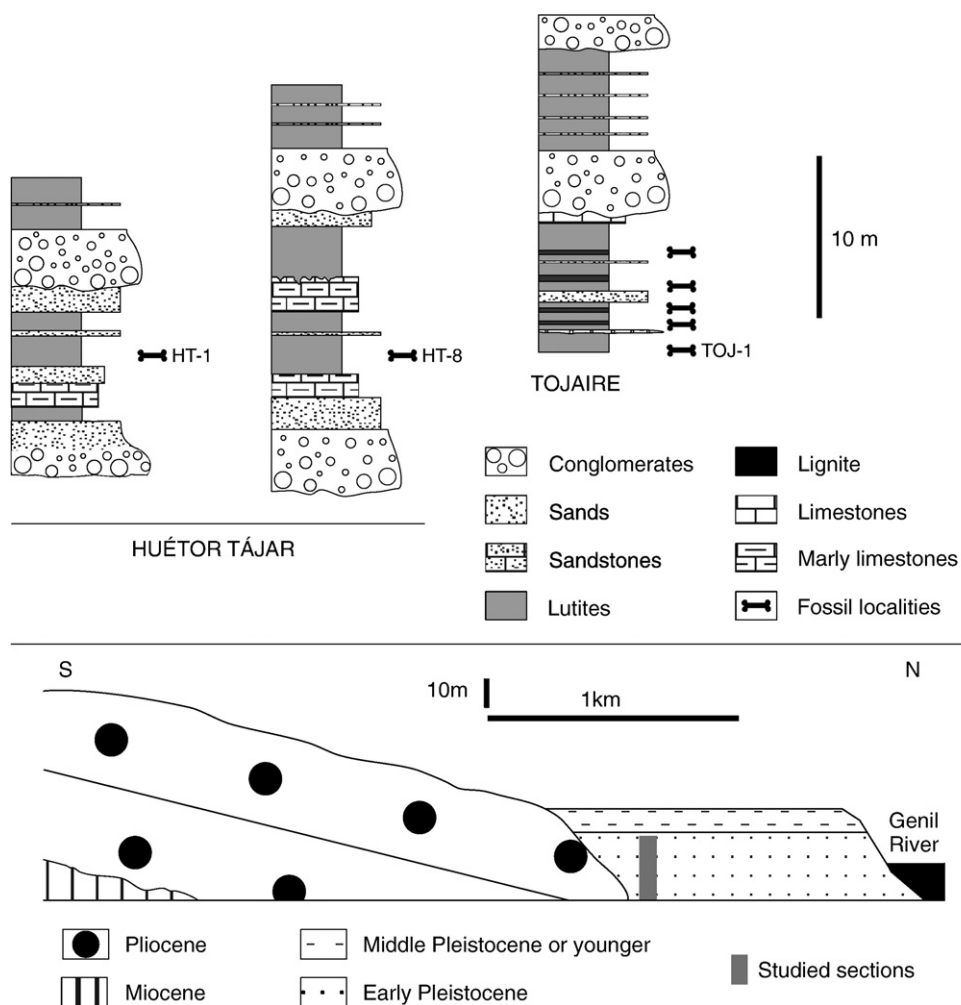


Figure 2. Stratigraphic columns and schematic relationships between the studied deposits (modified from García-Alix et al. (2009)).

the absence of accessory crests in lower and upper teeth. The  $P_4$  has a single root; the metaconid and protoconid are fused and separated from the posterior complex (mesoconid, entoconid, and hypoconid). The  $M_{1-2}$  does not have a centrolophid. The  $M_3$  does have a centrolophid, and one specimen has a curved metalophid; the protoconid and hypoconid are in contact with the anterolophid and mesoconid, respectively, in another specimen.

The  $P^4$  has three roots, a short anteroloph connected to the paracone, and an interrupted protoloph; it has no centrolophs. The  $M^{1-2}$  is shorter lingually than labially, they have two centrolophs, placed close together (the precentroloph is best developed), and three roots. The  $M^3$  always has a postcentroloph, the precentroloph is present in two specimens only; the posteroloph is in contact with the endoloph.

*Eliomys quercinus* is a descendant of *E. intermedius*, therefore, the younger populations of *E. intermedius* are closer to the extant *E. quercinus* (Chaline, 1972; García-Alix et al., 2008b). The presence of the centrolophid and the frequency of accessory crests (tropids) in  $M_{1-2}$  of *E. intermedius* decreases through time (García-Alix et al., 2008b), while the frequency of the connection between metalophid and metaconid increases, and the number of centrolophs increases:  $M^{1-2}$  with two centrolophs is more frequent in younger populations (García-Alix et al., 2008b). The size of the teeth agrees with that of *E. intermedius* and *E. quercinus*. The studied specimens have a simplified structure, typical for *E. quercinus*: absence of accessory crests in upper and lower teeth, and absence of centrolophids in  $M_{1-2}$ . However, our  $M_3$  and  $M^3$  are less compressed (mainly in width) than those of *E.*

*quercinus*; this compression can be observed in some specimens of *E. quercinus* of the contemporaneous locality of Cueva Victoria (Agustí, 1982). Therefore, although our specimens are closer to *E. quercinus*, they are determined as *Eliomys* aff. *quercinus*.

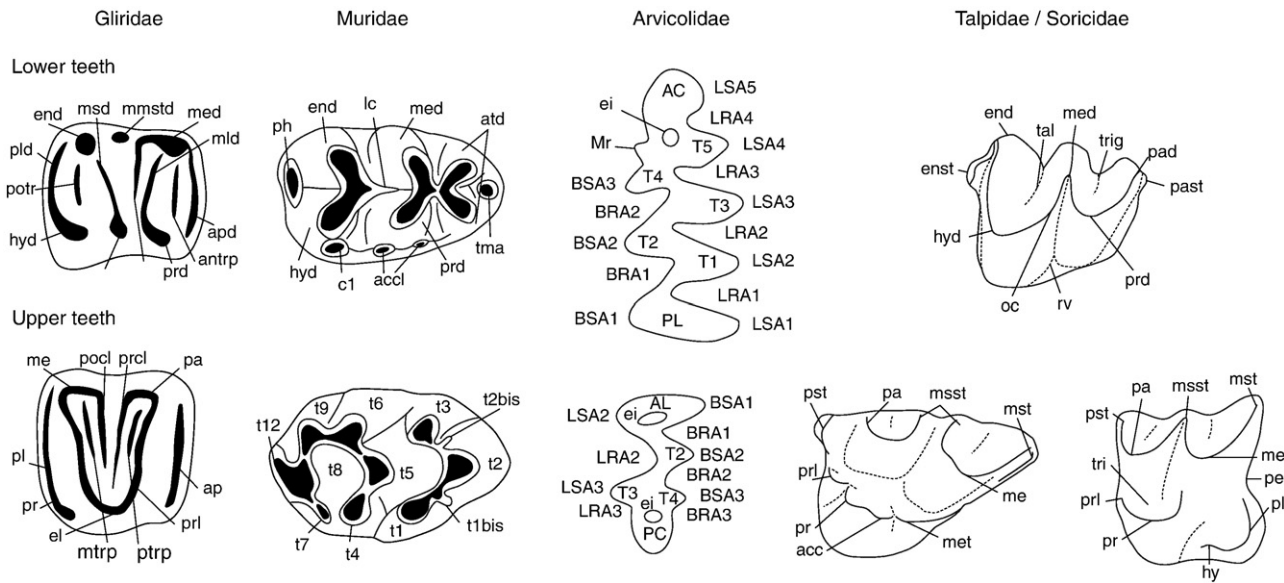
#### Family Muridae

Two species of murids may be recognized in the studied localities: *A. atavus* (Fig. 4: 8–13) and *C. rivas* (Fig. 4: 14–19).

The studied  $M_1$  of *A. atavus* has a medium-large antero-central cusp (tma), a well-developed connection between the lingual lobe of the anteroconid and the metaconid, and a broad labial cingulum (with c1 and up to two accessory cusps). The lower molars have usually an oval and voluminous posterior heel, and two roots. In the upper molars, the t7 is completely isolated from t4, and the t12 is reduced (in  $M^1$ ) or usually absent (in  $M^2$ ). They have three roots, except for some  $M^3$  that have two roots.

The morphology of the studied teeth agrees with that of *A. atavus*. The size coincides with that of other populations of *A. atavus*; however, the mean values are slightly larger than in older (Pliocene) samples. These data suggest a small increase in size from older to younger populations of *A. atavus*. According to Martín Suárez and Mein (1998), the Pleistocene *A. sylvaticus* and *A. flavicollis* are descendants of *A. atavus*.

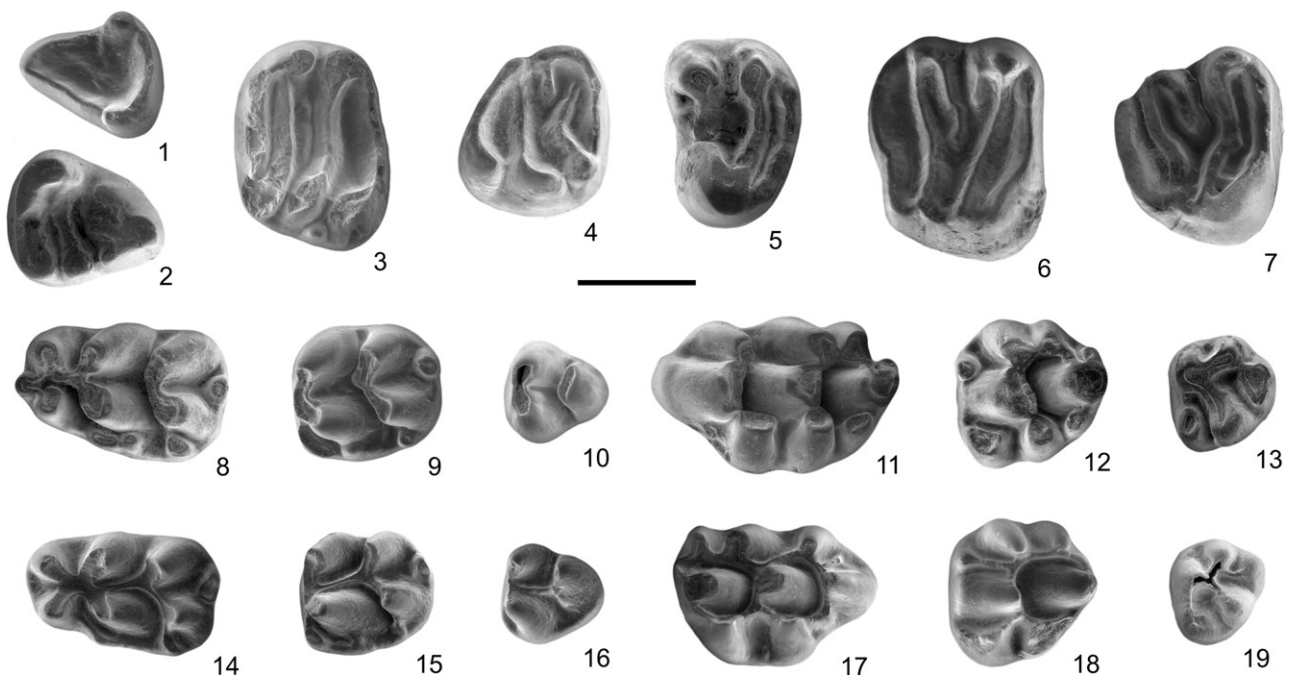
The lower molars of *C. rivas* have a well-developed longitudinal crest and a broad labial cingulum. The anterolabial cusp is large in  $M_2$  and in most of the  $M_3$ . The c1 is well-developed in  $M_1$ , reduced in  $M_2$



**Figure 3.** Terminology used in the descriptions of teeth of the studied taxa. General nomenclature: lower teeth: ac, accessory crest; end, entoconid; hyd, hypoconid; med, metaconid; pad, paraconid; prd, protoconid. Upper teeth: ac, accessory crest; en, entocone; hy, hypocone; me, metacone; pa, paracone; pr: protocone. Gliroidae (modified from Freudenthal and Martín Suárez (2006)). Lower teeth: antrp, anterotripid; apd, anterolophid; cld, centrolophid; mld, metalophid; msd, mesolophid; msstd, mesostylid; pld, posterolophid; potr, posterotripid; prld, protolophid. Upper teeth: ap, anteroloph; el, endoloph; ei, enamel islet; LRA, lingual re-entrant angle; LSA, lingual salient angle; T (1–5), triangle (1–5). Lower teeth: AC, anteroconid complex or anterior complex; Mr, *Miomys*-ridge; PL, posterior lobe. Upper teeth: AL, anterior lobe; PC, posterior complex. Talpidae (modified from Rümke (1985)) and Soricidae (modified from Reumer (1984)). Lower teeth: enst, entostylid; hyd, hypolophid; oc, oblique crest; past, parastylid; prld, paralophid; rv, re-entrant valley; tal, talonid; trig, trigonid. Upper: acc, accessory cusp; mel, metaconule; msst, mesostyle; mst, metastyle; pe, posterior emargination; pl, posteroloph; prl, protoconule; pst, parastyle; tri, trigone.

and very rare in  $M_3$ . They have two roots. In  $M^1$  and  $M^2$ , the posterior crests of t1 and t3 are well-developed and the t12 is reduced. In most  $M^3$  the t3 is absent and the t8 is completely isolated. The  $M^1$  has three roots and a small protuberance in the centre of the molar, the  $M^3$  has two roots; the roots of  $M^2$  are not preserved.

The large size, the very well-developed longitudinal crest in the lower teeth and the very well-developed posterior crests of t1 and t3 in upper teeth, agree with *C. rivas* from Loma Quemada (Martín Suárez and Mein, 1991), Tollo de Chiclana-10, 10B (Minwer-Barakat et al., 2005), Orce-2, 3, 7, Valdeganga-7, Bagur-II, Mas Rambault, and



**Figure 4.** *Eliomys* aff. *quercinus*: 1. HT-8 121 left  $D_4$ ; 2. HT-8 125 right  $P_4$ ; 3. HT-8 126 left  $M_{1-2}$ ; 4. HT-8 122 right  $M_3$ ; 5. HT-8 128 left  $P^4$ ; 6. HT-1 122 left  $M^{1-2}$ ; 7. HT-1 123 right  $M^3$ ; *Apodemus atavus*: 8. HT-8 59 left  $M_1$ ; 9. HT-8 64 left  $M_2$ ; 10. HT-1 32 left  $M_3$ ; 11. HT-8 74 left  $M^1$ ; 12. HT-8 81 left  $M^2$ ; 13. TOJ-1 81 left  $M^3$ ; *Castillomys rivas*: 14. HT-8 94 left  $M_1$ ; 15. HT-8 98 left  $M_2$ ; 16. HT-8 103 left  $M_3$ ; 17. TOJ-1 60 right  $M^1$ ; 18. HT-8 115 left  $M^2$ ; 19. HT-1 113 left  $M^3$ . Scale bar equals 1 mm. Modified from García-Alix et al. (2009).

Cueva Victoria (data from Martín Suárez and Mein (1991)). The studied specimens are larger and have more developed crests in lower and upper teeth than those of *C. gracilis* and *C. crusafonti*.

#### Family Arvicolidae

Three representatives of this family have been found in the studied localities: *A. chalinei* (Fig. 5: 1, 2, 7, 8), *A. pliocaenicus* (Fig. 5: 3, 4, 9, 10), and *M. oswaldoreigi* (Fig. 5: 5, 6, 11, 12).

The  $M_1$  of *A. chalinei* has a short and wide anteroconid complex (AC), with a narrow neck (in comparison with the AC) that is in contact with T5 and T4; it has a reduced BSA4. The T4 and T5 are broadly confluent. The T1, T2 and T3 are non-confluent or slightly confluent. The cement is very abundant in the re-entrant folds. The enamel is undifferentiated: it has approximately the same thickness on the anterior (leading edge) and posterior side (trailing edge) of the triangles. In  $M^3$  the anterior lobe-T2, and T3–T4 are non-confluent or slightly confluent; the T2–T3 are usually confluent. The T3 is well-delimited, and there is a deep LRA3 and a shallow LRA4 that delimitate an incipient T5.

The material of *A. chalinei* is very similar in the three studied localities; however, the length of the anteroconid complex, compared to the total length of the tooth is slightly larger in HT-1. The enamel structure of the lower teeth is undifferentiated (not *Mimomys*-type nor *Microtus*-type). The AC is short, wide and rounded, with a very narrow neck (low rate  $b/w$ , see van der Meulen and Zagwijn (1974)), the T3 is well-individualized, and there is an incipient T5 delimited by a deep LRA3 and a shallow LRA4 in the  $M^3$ . These morphological characters are typical of *A. chalinei*.

The  $M_1$  of *A. pliocaenicus* has a non-confluent or slightly confluent posterior lobe-T1, and T2–T3. The T1–T2 are weakly confluent; however, the T3–T4, T4–T5, T5–AC are confluent, especially T4–T5, T5–AC, which are broadly confluent. Some specimens have a shallow LSA5, typical of the “morphotype *pliocaenicus*”; other specimens have a more marked LSA5. The cement is abundant in the re-entrant folds. The BRA3 is usually shallow. The enamel is wider in the leading edge than in the trailing one. The T2–T3 are slightly confluent in  $M^3$ . In

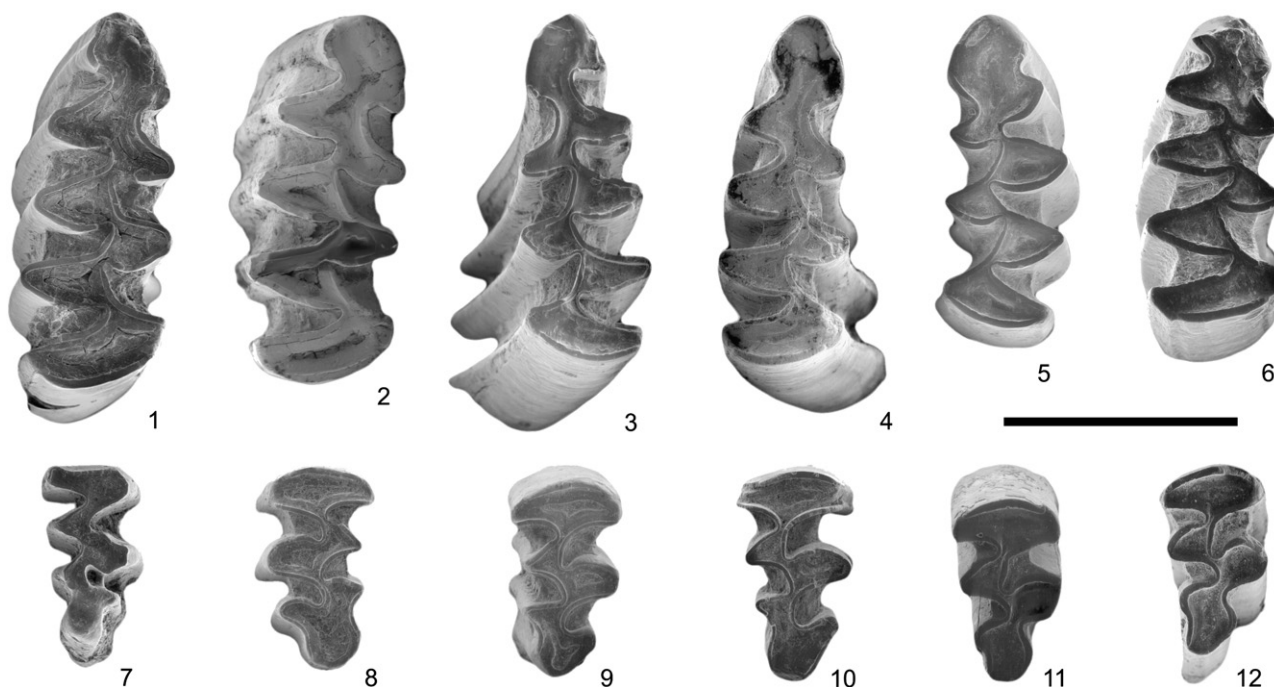
contrast to the specimens of *A. chalinei* the LRA4 is not developed and the T5 is absent in  $M^3$ .

The enamel differentiation is *Microtus*-type: the enamel is wider on the anterior side than on the posterior faces of the triangles in the lower molars. The AC is rounded in  $M_1$ , usually longer than wide; however, some specimens may have AC with approximately the same length and width. These morphological features and the size agree with those of *A. pliocaenicus* from the Guadix-Baza Basin (Agustí et al., 1987; Agustí, 1991; among others), Bektia-2 (van der Meulen and Zagwijn, 1974), and the localities from the Russian Plain and Taman Peninsula, like Litvin, Shamin, Kari-Dubina and Colle Curti (Markova, 2005), where *A. pliocaenicus* is very abundant; however some of our specimens are slightly larger than those described by Markova (2005).

The main differences between our specimens of *A. pliocaenicus* and those of *A. chalinei* are the enamel structure in lower teeth (undifferentiated in *A. chalinei* and *Microtus*-type in *A. pliocaenicus*), the structure of the anteroconid in  $M_1$  (wider in *A. chalinei* and slender in *A. pliocaenicus*), and the morphology of the  $M^3$  (with a marked LRA4 and an incipient T5 in *A. chalinei*, which are absent in *A. pliocaenicus*).

The  $M_1$  of *M. oswaldoreigi* has a very simple dental pattern and has no roots. The AC is wide. The *Mimomys*-ridge and the enamel ring are absent. The neck connecting AC with T4–T5 is wide. The posterior lobe (PL)-T1, T1–T2, T2–T3 and T3–T4 are usually non-confluent. The T4 and T5 are strongly confluent. The enamel is thicker on the posterior side of the triangles than on the anterior side. The  $M^3$  has no posterior enamel ring, nor T5; the BRA3 and the LSA4 are reduced, and the T3 is oval or rounded.

The simplified structure, characteristic of the *Mimomys* from the latest Pliocene, the absence of roots in most specimens, except for some  $M_3$  (although true roots have not been observed, the shape of the base of the crown, insinuates roots in some  $M_3$ ), agree with the main features of *M. oswaldoreigi*. The large reduction of the roots in  $M_3$ , indicates an early stage of *M. oswaldoreigi*, near the rootless species of arvicolids of the Early Pleistocene. The specimens of *M. oswaldoreigi* are smaller than those of *Allophaiomys* from the studied localities. The enamel structure is *Mimomys*-type, which contrasts



**Figure 5.** *Allophaiomys chalinei*: 1. HT-1 10 right  $M_1$ ; 2. HT-1 8 right  $M_1$ ; 7. HT-8 37 right  $M^3$ ; 8. TOJ-1 25 left  $M^3$ ; *Allophaiomys pliocaenicus*: 3. HT-8 1 left  $M_1$ ; 4. TOJ-1 115 right  $M_1$ ; 9. HT-8 43 right  $M^3$ ; 10. HT-8 38 right  $M^3$ ; *Mimomys oswaldoreigi*: 5. HT-8 3 left  $M_1$ ; 6. HT-8 27 right  $M_1$ ; 11. TOJ-1 18 right  $M^3$ ; 12. HT-8 42 right  $M^3$ . Scale bar equals 2 mm. Modified from García-Alix et al. (2009).

with that of the studied *Allophaiomys* (*Microtus*-type and undifferentiated), and the structure of the teeth is more simplified in the specimens of *M. oswaldoreigi* than in the studied *Allophaiomys*, especially in  $M^3$ .

#### Enamel structure of the studied arvicolid

The three species of Arvicolidae from the studied localities have different enamel structures. *M. oswaldoreigi* has a *Mimomys*-type enamel differentiation: the enamel of the trailing edge is thicker than that of the leading one; *A. pliocaenicus* has a *Microtus*-type differentiation: the enamel of the leading edge is thicker than that of the trailing one; *A. chalinei* has an undifferentiated structure: the enamel has approximately the same thickness in the trailing and in the leading edge.

The reduction of the trailing edge in the evolved species of *Allophaiomys* is related with morphological changes in the phylogenetic lineage between *Mimomys* and *Microtus* (Koenigswald, 1980). Although it is commonly accepted that the *Allophaiomys* species with *Mimomys*-type differentiation are archaic, those with *Microtus*-type differentiation (like *A. pliocaenicus*) are close to *Microtus*, and those with an undifferentiated enamel structure (like *A. chalinei*) are intermediate between both; the relationships between the different species of *Allophaiomys* are very complex (Agustí, 1991).

According to Koenigswald (1980) three main types of enamel can be identified in arvicolid teeth: lamellar, radial and tangential. In the anterior part of the triangles of the lower teeth (leading edge), one can differentiate two types of enamel: radial (parallel prisms) on the outer side, and lamellar (prisms organized in layers) on the inner side. The microphotographs of the chewing surface of the studied lower teeth show differences between *Mimomys* and *Allophaiomys* species (Fig. 6): in *M. oswaldoreigi* the outer radial enamel is wider than in the two studied *Allophaiomys*. The enamel structure of *A. chalinei* is more diffuse: one cannot identify clearly the radial enamel, the structure of the lamellar enamel is apparently more chaotic, and it is less marked than in the other two arvicolid species.

#### Family Talpidae

Only one representative has been found: *G. pyrenaicus* (Fig. 7: 1–7). The lower premolars ( $P_2$ ,  $P_3$  and  $P_4$ ) have sharp anterocristids and posterocristids, and small paraconids. In the  $P_4$ , the posterocristid closes the talonid basin posteriorly, and thickens forming an incipient entoconid. The lower molars have wide parastylids. The entostylid is very prominent in  $M_1$  and  $M_2$ , and minuscule in  $M_3$ . The  $M_2$  has a narrow anterolabial cingulum and another weak cingulum at the base of the re-entrant valley.

The  $P^2$  has two protrusions, in anterior and posterior positions; it has no lingual extension. The  $P^4$  has no individualized metacone; the

protocone is low and separated from the paracone, and the parastyle is more developed than the metastyle. In the  $M^2$ , the protoconule is well-individualized and connected to the protocone. There is no well-differentiated accessory cusp, but a posterior crest on the protocone directed to the metaconule. The metaconule is lower than the protoconule and isolated.

As for other Desmaninae, the diagnosis of the fossil species of *Galemys* is based exclusively on biometrical characters (Rümke, 1985). The studied specimens are clearly smaller than those of *Galemys kormosi* from Beremend (type locality), Rebielice Krolewskie, Tegelen, Baza (Rümke, 1985), Galera-2 and Alquería (Martín Suárez, 1988). Their size is similar to that of the extant *G. pyrenaicus* from Spain and France (see data in Rümke (1985)), and also similar to the same species from the Pleistocene sites of Venta Micena-1, Orce and Loma Quemada-1 (Martín Suárez, 1988). In addition, some morphological features of our material (the small protocone in the  $P^4$  and paraconid in the  $P_4$ , and the lack of lingual extension in the  $P^2$ ) resemble those of *G. pyrenaicus* and differ from *G. kormosi*.

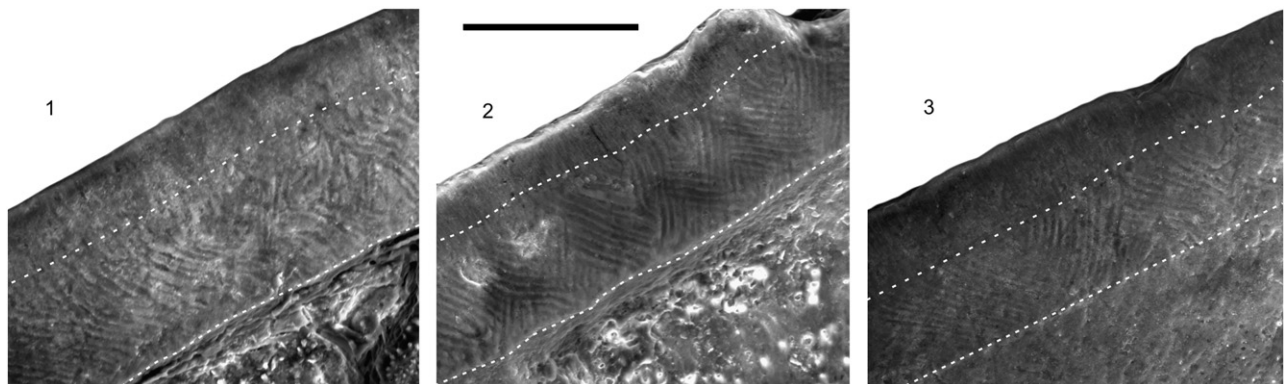
#### Family Soricidae

Two soricids have been identified in the studied localities: the crocidurine *Crocidura* sp. (Fig. 7: 8, 9), and the soricine *Sorex* sp. (Fig. 7: 10–14).

In the lower teeth of *Crocidura* sp. (three  $M_1$  and a damaged  $M_2$ ) the talonid is very short. They have a very low entoconid crest. The re-entrant valley opens very high on the labial cingulum. There is a low entostylid. The labial cingulum is well-marked and low; the lingual cingulum is weak and high. The  $M_1$  has the protoconid and metaconid higher than the paraconid; the oblique crest, low and short, reaches the base of the protoconid.

The single upper tooth of *Crocidura* sp. is a wide and short  $M^1$ . The metacone is notably higher than the paracone and has a very long posterior arm. The metastyle protrudes over the labial border. There is a minuscule parastyle. There is no metaloph, so the trigon basin is posteriorly open. The reduced hypocone is not connected to the protocone. The posteroloph is narrow and well-marked. The posterior emargination is pronounced. There is a short and weak lingual cingulum between protocone and hypocone. A well-marked cingulum occupies the entire posterior border, broadening towards the posterolabial end.

Our few specimens show the typical characters of *Crocidura*: lower molars with a very short talonid, re-entrant valley opened very high on the labial cingulum and very low entoconid crest; upper molars markedly short and wide, with pronounced posterior emargination, protruding metastyle and without metaloph. The size fits the ranges of *C. kornfeldi* from its type locality, Villany 3 (Reumer, 1984), and is also similar to the few specimens of this species from the southern Spanish



**Figure 6.** Enamel structure of the leading edges of each species from the studied Arvicolidae. 1. *Allophaiomys chalinei* HT-1 10; 2. *Allophaiomys pliocaenicus* HT-8 1; 3. *Mimomys oswaldoreigi* HT-8 3. Scale bar equals 50  $\mu$ m.

sites of Galera-2 and Orce-3 (Martín Suárez, 1988); the morphology also resembles that of this species. However, the scarcity of material does not allow us to observe the diagnostic characters of any species of *Crociodura*, and we cannot determine the studied material at the specific level.

The material of *Sorex* sp. in the studied localities is very scarce. In TOJ-1 one fragmented lower incisor with three cusps has been found; it may be tricuspluate or tetracuspluate. The labial cingulum is weak. In the lower molars, the trigonid is notably narrower than the talonid (less accentuated in  $M_2$ ). The entoconid is high, and the entoconid crest is well-developed. The re-entrant valley opens close to the labial cingulum, which is low and narrow, but well-marked. The lingual cingulum is higher and weaker than the labial one. In  $M_3$  the hypoconid and entoconid are individualized, so there exists a talonid basin.

Only one fissident upper incisor of *Sorex* sp. has been identified. It has a slightly marked labial cingulum, a well-developed talon and an almost straight dorsal border.

Three upper molars have been found. The  $M^1$  has the metacone notably higher than the paracone, and the metastyle protrudes markedly on the labial border. The protocone is separated from the hypocone by a wide valley, which is bordered by a narrow cingulum. The metaloph is absent, so the trigon basin is open. The hypocone is low, but distinct, and connected to a well-marked posteroloph. The  $M^1$  and  $M^2$  from TOJ-1 lack an individualized hypocone, contrary to the  $M^1$  from HT-8. The hypoconal flange is broad, and the posterior emargination is pronounced. The posterior cingulum is very narrow at the posterior emargination, and widens towards the labial side.

The combination of several morphological characters (upper incisor fissident, lower incisor tricuspluate or tetracuspluate, ento-

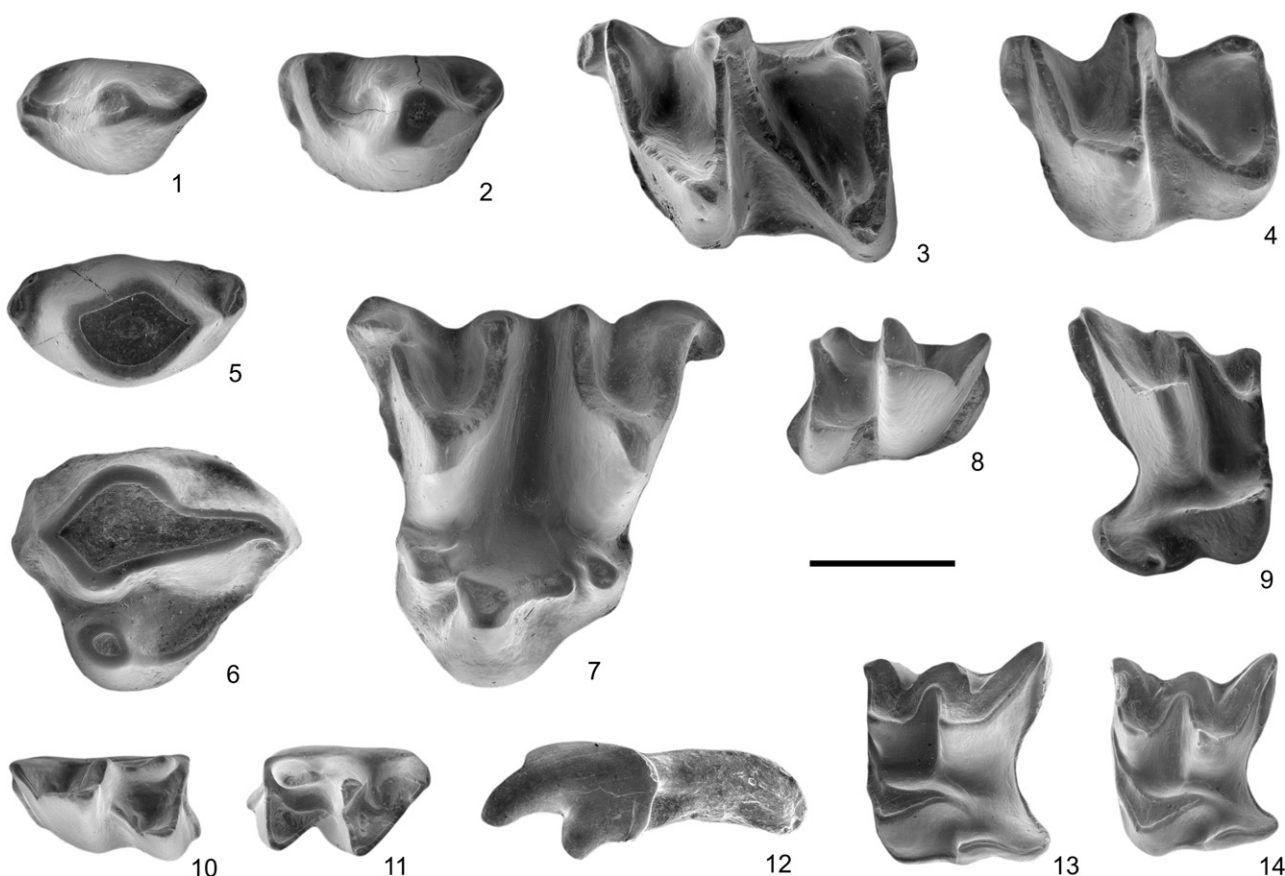
conid crest in the lower molars, upper molars without entoloph and with pronounced posterior emargination) allows us to ascribe the soricine from HT-1, HT-8 and TOJ-1 to the genus *Sorex*. Nevertheless, the assignation to one of the more than 30 species of this genus recognized in the Pleistocene of Europe is impossible due to the scarcity of the material.

## Discussion

### Biostratigraphy

Fejfar et al. (1998) proposed the Neogene and Quaternary Rodent Zones with some European reference localities, but it is very difficult to correlate them with Spanish localities because they belong to different faunistic provinces, and the rodent associations differ. However, we propose a plausible correlation between both (Fig. 8).

We have compared our data with the local biostratigraphy established in the neighbouring Guadix-Baza Basin (Agustí, 1986; Agustí et al., 1999; Oms et al., 2000a; among others), where a very complete record of the latest Pliocene and Early Pleistocene (biostratigraphically and magnetostratigraphically calibrated) exists (Fig. 8). The options about the Plio-Pleistocene boundary in the Guadix-Baza Basin are very controversial and, according to different authors, the Zone of *M. oswaldoreigi* (previously defined as Zone of *M. ostromosensis*) may indicate the latest Pliocene–earliest Pleistocene transition, or the beginning of the Pleistocene epoch (Agustí, 1986; Agustí et al., 1999; Oms et al., 2000a; Gibert et al., 2006; among others). However, we do not discuss this problem, because it does not affect our interpretations (Fig. 8).



**Figure 7.** *Galemys pyrenaicus*: 1. HT-8 132 right  $P_3$ ; 2. TOJ-1 92 right  $P_4$ ; 3. TOJ-1 93 left  $M_2$ ; 4. HT-134 8 left  $M_3$ ; 5. TOJ-1 94 right  $P^2$ ; 6. HT-8 135 left  $P^4$ ; 7. HT-8 136 left  $M^2$ ; *Crociodura* sp.: 8. HT-8 130 right  $M^1$ ; 9. HT-8 131 right  $M^2$ ; *Sorex* sp.: 10. HT-8 140 left  $M^1$ ; 11. HT-8 144 right  $M^2$ ; 12. HT-8 137 left upper I; 13. TOJ-1 88 left  $M^1$ ; 14. TOJ-1 89 left  $M^2$ . Scale bar equals 1 mm.

SERIES	STAGE	MN/MQ UNITS	RODENT ZONES	GUADIX ZONES	Taxon Distribution										SPANISH LOCALITIES	EUROPEAN LOCALITIES				
					<i>Castillomys rivas</i>	<i>Apodemus atavus</i>	<i>Eliomys quercinus</i>	<i>Mimomys oswaldoreigi</i>	<i>Allophaiomys pliocaenicus</i>	<i>Allophaiomys chalinei</i>	<i>Galemys pyrenaicus</i>	<i>Sorex sp.</i>	<i>Crocidura sp.</i>							
PLEISTOCENE	BIHARIAN	MQ 1	<i>Mimomys savini</i>	Mm	<i>Terricola arvalidens</i>	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	TD-6	Slivia (Italy)			
				Q3	<i>Allophaiomys burgondiae</i>	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	CV	Vallonnet (France)	
			<i>Mimomys pusillus + savini</i>	Mm	<i>Allophaiomys pliocaenicus</i>	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	VM	Beftia IX (Romania)
				Mm	<i>Mimomys oswaldoreigi</i>	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	OR-D	Tasso (Italy) Dmanisi (Georgia)
VILLANYAN	MN17		<i>Mimomys pliocaenicus</i>		<i>Mimomys cf. reidi</i>	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	GA-H	Tegelen (Netherland)		
					<i>Kislangia gusii</i>	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	AL	Saint Vallier (France)
						.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	GA-G	Villany-3 (Hungary)		
						.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	.....	TCH-10		

**Figure 8.** Range of distribution of the studied taxa found in HT-1, HT-8 and TOJ-1, and correlation with other Spanish and European localities (data from Agustí, 1982; Mein, 1990; Fejfar and Heinrich, 1990; Agustí, 1991; Martínez-Navarro et al., 1997, 2009; Oms et al., 2000a; Cuenca-Bescós et al., 2001; Vekua et al., 2002; Minwer-Barakat et al., 2005; Sala and Masini, 2007), with Rodent Zones (Fejfar et al., 1998), and with the updated biozonation of the Guadix-Baza Basin according to Oms et al. (2000a). Abbreviations: AL, Alquería (Guadix-Baza Basin, Spain); CV, Cueva Victoria (Murcia, Spain); FN, Fuente Nueva (Guadix-Baza Basin, Spain); GA, Galera (Guadix-Baza Basin, Spain); OR, Orce (Guadix-Baza Basin, Spain); TCH, Tollo de Chiclana (Guadix-Baza Basin, Spain); TD, Trincheras Dolina (Atapuerca, Spain); VM, Venta del Moro (Valencia, Spain).

The presence of *C. rivas* and *M. oswaldoreigi* in the studied localities indicates the latest Pliocene–earliest Pleistocene age (Martín Suárez and Mein, 1991; Agustí et al., 1993; Agustí, 1998; Oms et al., 2000a). This interval agrees with the range of *A. atavus*, whose last record is found in the earliest Pleistocene (Martín Suárez and Mein, 1998). The association of two species of *Allophaiomys*, *A. chalinei* and *A. pliocaenicus*, also indicates an Early Pleistocene age (Agustí et al., 1993; Agustí, 1998; Oms et al., 2000a).

In more detail, the latest record of *M. oswaldoreigi* is found in Fuente Nueva-3 (*Allophaiomys burgondiae* Zone; Oms et al., 2000a), and the association between *M. oswaldoreigi*, *A. chalinei* and *A. pliocaenicus* is restricted to the lower part of the *A. burgondiae* Zone, according to the nomenclature of the zones of Oms et al. (2000a). Our localities may be attributed to the end of the *Mimomys pusillus/savini* Zone of Fejfar et al. (1998). They are contemporaneous with the Spanish localities of Cueva Victoria (where remains of the African primate *Theropithecus* has been described; Martínez-Navarro et al., 2005), and Fuente Nueva-3 (where lithic industry indicating a human occupation has been found; Martínez-Navarro et al., 1997; Oms et al., 2000a,b). They are older than Trincheras Dolina-6 (Spain), where *Mimomys savini* and *Terricola arvalidens* are present (Cuenca-Bescós et al., 2001), belonging to the *M. savini* Zone of Fejfar et al. (1998).

**Table 1**  
Relative abundances and ecological preferences of the studied taxa from the Pleistocene localities TOJ-1, HT-1, and HT-8 of the Granada Basin.

Taxon	Ecological preferences	Abundance (%)			
		TOJ-1	HT-1	HT-8	TOJ-1 + HT-1 + HT-8
<i>Apodemus atavus</i>	Wet, forested	24.8	18.8	11.3	17.0
<i>Castillomys rivas</i>	Eurytopic	7.2	38.1	8.8	16.2
<i>Eliomys quercinus</i>	Wet, forested	0.4	2.5	1.9	1.7
Arvicolidae*	Wet, cold, open herbaceous	64.5	39.2	75.2	62.6
<i>Galemys pyrenaicus</i>	Wet, semiaquatic	0.8	0.5	0.4	0.5
<i>Crocidura sp.</i>	Open herbaceous	0.3	0.3	0.6	0.4
<i>Sorex sp.</i>	Wet	2.0	0.7	1.8	1.5

Arvicolidae\* includes *A. pliocaenicus*, *A. chalinei*, and *M. oswaldoreigi*.

According to the data from Oms et al. (2000a), the locality of Venta Micena (Spain) may be slightly older than our studied deposits (Fig. 8).

Oms et al. (2000b) assigned an age older than 1.07 Ma to Fuente Nueva-3. Gibert et al. (2007) proposed an age of 1.2 Ma for Fuente Nueva-3 (contemporaneous with our localities), and of 1.3 Ma for Venta Micena (slightly older than our localities). According to Blain et al. (2008), the age of Cueva Victoria (contemporaneous with our localities) is around 1.1 Ma. Therefore, the approximated age of the studied sites is 1.1 Ma, it ranging between 1.07 and 1.2 Ma.

*Paleoclimatical and paleoecological approach*

The faunistic association allows us to make an approach of the past climatic and environmental conditions. The methodology used to quantify the taxa and their ecological preferences is described in García-Alix et al. (2008c): to calculate the relative abundances of each taxon, we have used the total number of specimens (teeth) of each taxon in each locality, divided by its number of diagnostic elements (no taxon is over-represented). Identifiable fragments larger than half a tooth were counted too. The number of diagnostic elements of each family is: Muridae and Arvicolidae: 12 (molars); Gliridae: 16 (P<sup>4</sup> and molars); Soricidae: 20 (incisors, P<sup>4</sup> and molars); Talpidae: 44 (all dental elements). The relative abundances and ecological preferences of the studied taxa are summarized in Table 1. We propose one interpretation for each locality, and a combined interpretation of the three localities, because all localities are situated in the same stratigraphic level (Table 2).

**Table 2**  
Paleoclimatic interpretation deduced from the ecological preferences of the studied taxon from the Pleistocene localities TOJ-1, HT-1, and HT-8 of the Granada Basin.

Localities	Cold (%)	Wet (%)	Herbaceous (%)	Forested (%)	Semiaquatic (%)
TOJ-1	64.5	92.5	64.9	25.2	0.8
HT-1	39.2	61.6	39.5	21.3	0.5
HT-8	75.2	90.7	75.8	13.3	0.4
TOJ-1 + HT-1 + HT-8	62.6	83.3	63.0	18.7	0.5



In general, the climatic interpretation derived from the ecological preferences of the taxons suggests the existence of relative cold and wet conditions, and the predominance of open herbaceous habitats, followed by forested habitats; semiaquatic taxons are scarce (Table 2).

Semiaquatic taxons like Desmaninae and Castoridae, require the existence of constant water courses. They are present during the late Turolian-earliest Ruscinian (Messinian and earliest Pliocene) in the Granada Basin, when lacustrine and very wet conditions prevailed (García-Alix et al., 2007b, 2008c). The conditions in the middle Turolian (latest Tortonian) and in the late Ruscinian (Pliocene) were drier, and although fluvio-lacustrine systems were present, these taxons are not recorded. *G. pyrenaicus*, found in the Huétor Tájar and Tojaire sections, indicates the presence of large and constant water courses in the Early Pleistocene. The humidity and the semiaquatic conditions were optimum for the presence of *Galemys*, because two main drainage systems joined in this sector: the Genil system, which drained the eastern sector of the basin, and the “paleo-Cacín system,” which drained the southwestern sector, and associated lacustrine/palustrine environments were developed.

This climatic interpretation agrees with several global and local interpretations. Agustí et al. (2001) pointed out that in the Early Pleistocene there was an expansion of steppe and cooler conditions from 1.8 to 1.6 Ma, coinciding with the expansion of *Allophaiomys plicaenicus* and other taxons from cold regions, to southern Spain. Shackleton (1995) indicated a progressive general cooling in the Early Pleistocene. Hernández Fernández et al. (2007) proposed a thermal minimum around 1.1 Ma in south western Europe; which is near the estimated age of our localities, 1.1 Ma, ranging between 1.07 and 1.2 Ma.

## Conclusions

Three fossiliferous localities have been found in the area of Huétor Tájar, in the northwestern sector of the Granada Basin. The faunal assemblage is mainly composed of *Eliomys* aff. *quercinus*, *A. atavus*, *C. rivas*, *A. pliocaenicus*, *A. chalinei*, *M. oswaldoreigi*, *G. pyrenaicus*, *Crociodura* sp., *Sorex* sp. They indicate an Early Pleistocene age, which contrasts with the late Ruscinian (Pliocene) and Middle Pleistocene or later age of the neighbouring sediments.

The faunal assemblage is slightly different from those used to define the Rodent Zones of Fejfar et al. (1998). Comparing with a precise biozonation from the Guadix-Baza Basin, our localities may be correlated with the beginning of the *A. burgondiae* Zone (Oms et al., 2000a). The studied sites are contemporaneous with the locality Fuente Nueva-3, in the neighbour Guadix-Baza Basin, where lithic industry has been found; therefore future investigations in the studied sector may be of interest for the field of human paleontology. Other contemporaneous locality with our deposits is Cueva Victoria (Spain).

The dating of these deposits will have large importance in future analysis of the evolution of the paleogeography and the drainage systems of the basin, due to their privileged stratigraphic and geographic situation (near the confluence of the Cacín and Genil rivers). These rivers belonged to two different systems during the Pliocene, and nowadays constitute one single drainage system in Granada Basin.

The ecological preferences of the studied taxons suggest wet and cold conditions, with a predominance of open herbaceous and forested habitats. Although the semiaquatic habitats were occupied by *G. pyrenaicus*, they are scarcely represented.

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## Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.yqres.2009.06.004.

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