General Palaeontology, Systematics and Evolution (Palaeoenvironment)

Paleoenvironmental reconstruction of the Early Pleistocene site of Quibas (SE Spain) using a rodent assemblage

Reconstruction paléoenvironnementale du site Pléistocène inférieur de Quibas (Sud-Est de l'Espagne) à partir d'un assemblage de rongeurs

Pedro Piñero [a,b,*], Jordi Agustí [a,b,c], Hugues-Alexandre Blain [a,b], César Laplana [d]

[a] Institut Català de Paleoecologia Humana i Evolució Social (IPHES), Zona Educacional 4- Campus Sescelades URV (Edifici W3), 43007 Tarragona, Spain
[b] Àrea de Prehistòria, Universitat Rovira i Virgili (URV), Avinguda de Catalunya 35, 43002 Tarragona, Spain
[c] ICREA, Institució Catalana de Recerca i Estudis Avançats, Barcelona, Spain
[d] Museo Arqueológico Regional de la Comunidad de Madrid, Plaza de las Bernardas, s/n, 28801 Alcalá de Henares, Spain

ARTICLE INFO

ABSTRACT

In this paper we analyze the rodent assemblage from the Early Pleistocene site of Gruta1 (Quibas karstic complex, Murcia, SE Spain), providing taphonomic comments and paleoecological and paleoclimatic data. The studied assemblage includes 209 identified rodent teeth corresponding to at least four taxa. The karstic source of the site and the low presence of digested remains suggest that the accumulation is scatological in origin, with the influence of predators such as owls; the accumulation also shows certain evidence of slight hydrodynamic sorting. For the area around Quibas/Gruta1 the paleoecological study indicates a predominance of rocky areas (31.7%), forested environments (31.7%) and open dry meadows or shrublands (29.7%), which would indicate a mosaic forest environment, and to a lesser extent the presence of open humid land (5.4%) and areas along streams or ponds (1.5%). The distribution of the bioclimatic spectra yields the highest percentage for a Mediterranean climate (37.5%), while the climatic parameters calculated (MAT = 15 °C, MTW = 25.7 °C, MTC = 4.3 °C, MAP = 390 mm) suggest colder and slightly more humid conditions than today at the time of the deposition of the remains. The data also point to a relative decrease in temperature within the phase in which the site was produced, which possibly occurred during a relative cold period between MIS 36 and MIS 40 according to the age.

© 2015 Académie des sciences. Published by Elsevier Masson SAS. All rights reserved.

RÉSUMÉ

Dans cet article, nous analysons l'assemblage de rongeurs du Pléistocène inférieur de Gruta1 (complexe karstique de Quibas, Murcie, Sud-Est de l'Espagne), en ajoutant une remarque taphonomique et en fournissant des données paléoécologiques et paléoclimatiques. L'assemblage étudié comprend 209 dents de rongeurs correspondant au minimum à quatre taxons. L'origine karstique du site et le faible pourcentage de restes digérés suggèrent

* Corresponding author at: Institut Català de Paleoecologia Humana i Evolució Social, C/Marcel·lí Domingo, s/n, Campus Sescelades URV (Edifici W3), 43007 Tarragona, Spain.
E-mail address: ppinero@iphes.cat (P. Piñero).

que l'accumulation est d'origine scatologique, avec l'influence de prédateurs comme les rapaces nocturnes ; l'accumulation montre aussi une certaine évidence d'un léger tri hydrodynamique. Pour l'environnement autour de Quibas/Gruta1, l'étude paléoécologique montre une prédominance de zones rocheuses (31,5 %), d'environnements forestiers (31,5 %) et de prairies ouvertes et sèches ou de zones broussailleuses (30,3 %), qui indiquerait un environnement forestier en mosaïque et, dans une moindre mesure, la présence de territoires ouverts et humides (5,8 %) et d'aires riveraines (1 %). La distribution des spectres bioclimatiques fournit le plus haut pourcentage pour le climat méditerranéen (37,5 %), alors que les paramètres climatiques calculés (MAT = 15 °C, MTW = 25,7 °C, MTC = 4,3 °C, MAP = 390 mm) suggèrent des conditions plus froides et légèrement plus humides que l'actuel lors du dépôt des restes. Les données montrent aussi une certaine baisse des températures, suggérant que le site s'est formé probablement au cours d'une période froide, entre le SIM 36 et le SIM 40, d'après la chronologie du site.

1. Introduction

The Early Pleistocene site of Quibas (Abanilla, Murcia) is situated in an area called Collado del Rey, on the southeastern slope of the Sierra de Quibas, in an abandoned limestone quarry at an altitude of 669 meters AMSL (Fig. 1A). The location coordinates are 38° 18′ 51″ N, 1° 4′ 42″ W. The Sierra de Quibas is a 6-km-long and 2.5-km-wide calcareous massif (mainly Jurassic limestone and dolomites) that runs in a NE-SE direction in the Middle Subbetic region (Rodríguez-Estrella et al., 2004). This complex was affected by great karstic activity during the Plio-Pleistocene, resulting in many karstic structures. Some of these structures are infilled by mixed detritic sediments and/or chemical precipitates, and in one of them the Quibas site is located (Durán et al., 2004). Thus, the Quibas outcrop is formed by Pleistocene karstic infilling of several cavities situated within the dolomites of the Lower Lias (Jurassic). The main karstic structures are a gallery known as "Entrada Cueva" (5 m wide, 9 m high and more than 30 m in length; 2 on Fig. 1B) and a chasm known as "Sima" (20 m deep and 2 m wide; 1 on Fig. 1B). These two cavities are separated by 3-m-thick calcitic speleothems but are probably connected internally (Montoya et al., 1999). The stratigraphic and sedimentological features of the basal part of the Quibas site have been established by Fumanal and Blázquez in Montoya et al. (1999); nowadays they are covered by debris ("debris" on Fig. 1B). The sample was collected in 2009 (Cuadros, 2010) from Gruta1, a small karstic cavity located in the basal part of the Quibas site profile (3 on Fig. 1B). It is a detritic cavity formed by limestone clasts, which range between 10 and 20 cm in size, and a reddish silty clay matrix with carbonate crusts.

The main interest of this site lies in its chronology and the abundance and diversity of the faunal association identified (Rodríguez-Estrella et al., 2004). The fossil record provides both vertebrates and invertebrates from the Early Pleistocene. Preliminary faunal lists were published in Montoya et al. (1999, 2001), including both the vertebrate and invertebrate fossil record. As for the macrofauna, several taxonomic works have studied *Macaca sylvanus*, *Vulpes praeglacialis*, *Capra alba*, *Equus altidens* and *Equus suessenbornensis* (Alba et al., 2011; Carlos-Calero et al., 2004, 2006a, 2006b; Made van der et al., 2007; Piñero and Alberdi, 2015). Regarding the microfauna, Montoya et al. (1999, 2001) included a preliminary identification of the micromammal association; Piñero (2012); Piñero et al. (2015) described the rodent assemblage from Quibas/Gruta1; Cuadros (2010) carried out a taphonomic approach of the micromammals; and Blain et al. (2014) ascertained the latest occurrence of agamid lizards from western Europe.

Piñero (2012) and Piñero et al. (2015) identified the rodent faunal list from Quibas/Gruta1 as comprising *Allophaiomys* sp., *Apodemus* ex gr. *mystacinus-epimelas*, *Castillomys rivas*, and *Eliomys quercinus* (Fig. 2). 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). However, *A. epimelas* is likely to be present but recorded as *A. mystacinus*. Therefore Piñero (2012) and Piñero et al. (2015) classified *Apodemus* species as *A.* ex gr. *mystacinus-epimelas*. Based on the comparison with other Early Pleistocene sites, and although the arvicoline was not identified at species level, the shape of both m1 and M3 of *Allophaiomys* sp. from Quibas/Gruta1 was perfectly in accordance with *Allophaiomys* sp. from Fuente Nueva 3 and Barranco León 5 (Guadix-Baza Basin). Further comparison using principal component analysis (performed on different measurements), also indicated a great similarity with respect to the sample from Fuente Nueva 3 and Barranco León 5. Thus the chronology of Quibas/Gruta1 can be estimated as between ca. 1.2–1.4 Ma. This result is congruent with the age established for Quibas by Montoya et al. (1999, 2001) according to the faunal association (not only micromammals), which includes species that indicates an Early Pleistocene age.

The aim of the present paper is to complement the information about the rodent assemblage from Quibas/Gruta1 offered by Piñero et al. (2015), adding taphonomic information and providing paleoecological and paleoclimatic data on the "Sierra de Quibas" during the Early Pleistocene.

2. Materials and methods

The small-mammal sample was collected from the small karst cave known as Gruta1 (Piñero et al., 2015). All the sediment (around 10 kg.) was water-screening using superimposed 4, 1 and 0.5 mm mesh screens. The
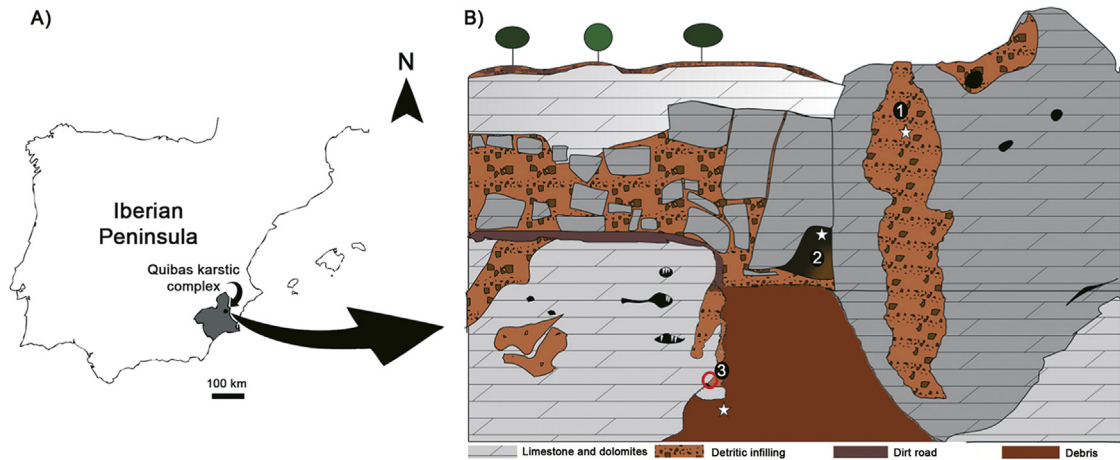
Quibas/Gruta1 assemblage includes 209 identified rodent teeth corresponding to at least four taxa (a minimum number of 32 individuals). The specimens studied are currently stored at the Institut de Paleoecologia Humana i Evolució Social (IPHES; Tarragona, Spain).

To analyze the evidence of hydrodynamic transport, the relative abundance of each type of tooth was expressed as a percentage of the recovered teeth with respect to the expected number according to the minimum number of individuals (based on the most abundant element present in the fossil sample) (Andrews, 1990; Wolff, 1973).

In order to reconstruct the ecological conditions that prevailed in the vicinity of Quibas/Gruta1, we used the Habitat Weightings Method (Blain et al., 2008; Cuenca-Bescós et al., 2005, 2009; López-García et al., 2014; among others), based on the distribution of each rodent taxon in the habitat(s) where they are found today (for extant species) or where they are assumed to have lived in the past (for extinct species). The habitats were classified into five main types: open dry meadows, open humid meadows, woodland and woodland-margin areas, water-edges, and rocky areas (Blain et al., 2008). Each taxon was rated to a maximum score of 1.00, which was divided up proportionally to its habitat preferences if the species dwelled in more than one habitat type.

To implement the Habitat Weightings Method, it was necessary to calculate the proportions of each taxon in the assemblage. There are different methods of making this calculation, one of them being the minimum number of individuals (MNI), which is normally applied to fossil assemblages without evidence of hydrodynamic transport (Avery, 2003; Chaline et al., 1995). Our sample did show
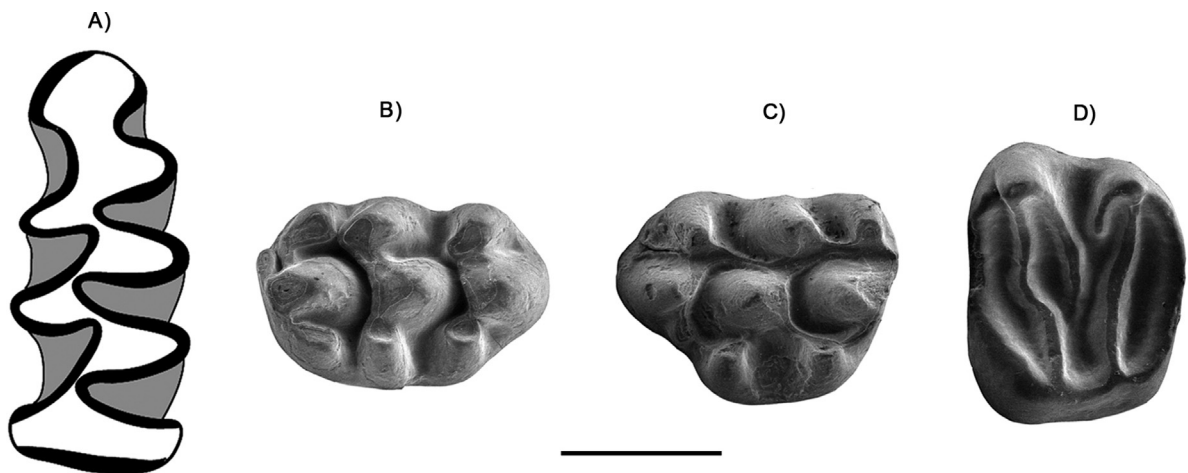
certain evidence of hydrodynamic sorting, so we calculated the quantitative composition on the basis of the relative abundance of each taxon (following Castillo, 1990; García-Alix et al., 2008, 2009; Martín-Suárez, 1988; Martín-Suárez et al., 2001; Minwer-Barakat, 2005). To avoid the over-representation of a taxon, we used the total number of teeth of each taxon, divided by its number of diagnostic elements (Murinae and Arvicolinae: 12 molars; Gliridae: 16 molars). Daams et al. (1999) proposed using rodent associations with 100 or more m1 + m2 + M1 + M2 for paleoecological studies based on micromammals. Hadly (1999) suggested that reconstructing the local mammalian community requires only a minimum sampling effort (200–250 specimens). Minwer-Barakat (2005) reduced this number to 100 because he only considered Rodentia and Insectivora. Our sample consists of 209 specimens, of which 151 are m1 + m2 + M1 + M2.

Paleoclimatic reconstruction was carried out following the qualitative bioclimatic method proposed by Hernández Fernández (2001). This analysis is made on the supposition of a significant correlation between climate and mammal community composition, applying multivariate discriminant analysis to modern mammal faunas and climates from throughout the world (Hernández Fernández and Peláez-Campomanes, 2003a). The approach to the past climatic conditions at Quibas/Gruta1 was based on the bioclimatic components from the rodent fauna (Hernández Fernández and Peláez-Campomanes, 2005). We used the rodent assemblage identified by Piñero et al. (2015) to apply this method. The bioclimatic characterization of the extinct rodent species and living species from Quibas/Gruta1 that was required for calculation of the bioclimatic spectra was taken from Hernández Fernández et al. (2007) and Hernández Fernández (2001), respectively.

3. Taphonomy

3.1. Scatological origin

The percentages of specimens digested, exemplified by the progressive reduction of enamel on the teeth (Fig. 3), are low (9 pieces, 4.3% of the rodent teeth). This suggests the influence of what Andrews (1990) designated a category 1 predator, such as owls, in the accumulation of the rodent assemblage in Quibas/Gruta1. Most authors consider that small-mammal remains in karstic sites are accumulated by the action of nocturnal avian predators (owls) through the rejection of pellets rich in skeletal material after digestion (Dauphin et al., 1996; Saavedra and Simonetti, 1998; Terry, 2004). Agustí and Martín-Suárez (1986) pointed out that nocturnal birds of prey are the major accumulators of micromammal remains at sites of scatological origin, above all those that are active near their nesting and roosting sites, such as current barn owls.

The faunal list of the Quibas site published in Montoya et al. (1999, 2001) includes three species of nocturnal birds of prey (which are potential predators): *Athene noctua*, *Otus scops* and *Strix aluco*. *Athene noctua* is a small predator that nests in cavities and feeds mainly on small mammals and invertebrates (Tomé et al., 2008), so it may be an important accumulator of small mammals in our karstic site. In this case, the biological bias would be reduced because *A. noctua* shows opportunistic feeding behaviour that does not reflect prey selection (Goutner and Alivizatos, 2003). *Otus scops* can incorporate small vertebrates into its diet, but it is mainly insectivorous (Latková et al., 2012). *Strix aluco* is an opportunistic bird of prey that can collect and accumulate a significant representation of the small-mammal fauna from a given area (Cuenca-Bescós et al., 2005; Pokines, 1998). These owl species are usually generalist feeders, but they are limited by their small body size and take a restricted range of prey, though one that is representative of their hunting range area (Fernandez-Jalvo et al., 1998). The opportunistic behaviour of the potential predators point out to a reduced biological bias. To a lesser degree, diurnal birds of prey and mammalian carnivores may also be involved in the scatological accumulation, but these show opportunistic behaviour (Fernandez-Jalvo et al., 1998).

3.2. Evidence of slight hydrodynamic transport

In karstic systems, fluvial activity is usually a short-lived process because transport ranges tend to be short in contrast to those of open-air sites (Gillieson, 1996; Kos, 2003a). Taking into account the rodent cranial fossils (mandibles, maxillaries and teeth), our sample shows a certain degree of evidence of slight hydrodynamic sorting:

- the number of isolated molars is ten times greater than the number of empty alveolar spaces in the maxillae
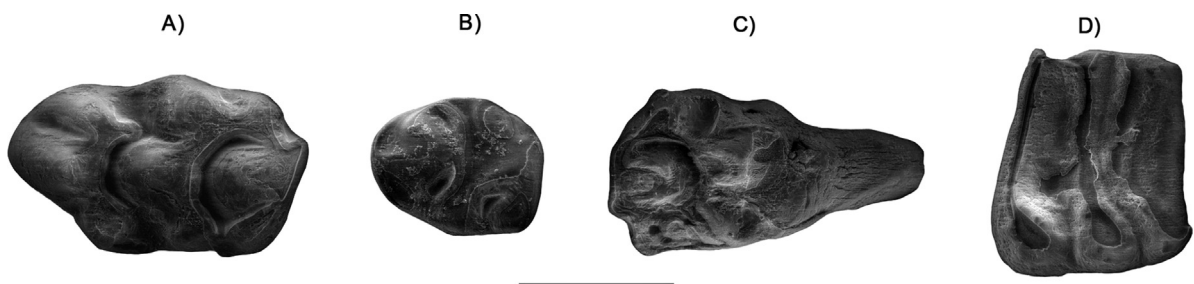
Fig. 3. Digested teeth from Quibas/Gruta1. **A**. Left M1 of *A.* ex gr. *mystacinus-epimelas*, QB-10-G1-R/2k. **B**. Right M3 of *A.* ex gr. *mystacinus-epimelas*, QB-10-G1-R/4d. **C**. Left M1 of *C. rivas*, QB-10-G1-R/11c. **D**. Right m2 of *E. quercinus*, QB-10-G1-R/16a. Scale bar equals 1 mm.
Fig. 3. Dents digérées de Quibas/Gruta1. **A**. M1 gauche d'*A.* ex gr. *mystacinus-epimelas*, QB-10-G1-R/2k. **B**. M3 droite d'*A.* ex gr. *mystacinus-epimelas*, QB-10-G1-R/4d. **C**. M1 gauche de *C. rivas*, QB-10-G1-R/11c. **D**. m2 droite d'*E. quercinus*, QB-10-G1-R/16a. Échelle = 1 mm.

Table 1

Percentage of each type of tooth for each rodent species recovered from Quibas/Gruta1 relative to the expected number according to the MNI (100% correspond to a recovery of all teeth expected in accordance with the MNI).

Tableau 1

Pourcentage de chaque type de dent pour chaque espèce de rongeurs récoltés à Quibas/Gruta1 en fonction du nombre attendu selon le NMI (100 % correspond à la récolte de toutes les dents attendues dans le gisement en accord avec le NMI).

Species	*Apodemus* ex gr. *mystacinus-epimelas*	*Castillomys rivas*	*Allophaiomys* sp.	*Eliomys quercinus*
P^4				35.7
M^1	73.7	50	0	32.2
M^2	44.8	66.6	16.7	
M^3	23.7	0	16.7	35.7
Total upper teeth	47.4	38.9	11.1	33
P_4				21.5
M_1	97.4	66.6	50	39.3
M_2	73.7	50	50	
M_3	73.7	33.3	16.7	14.3
Total lower teeth	81.6	50	38.8	28.6
Total population	64.5	44.5	25	31.3

MNI: minimum number of individuals.

and mandibles (only 26 out of 209 teeth are inserted in 14 bones, which present in total 17 empty alveolar spaces), indicating destruction either of mandibles or skulls (Andrews, 1990; Kos, 2003a);

- lower teeth are over-represented with respect to upper teeth (see Table 1). Maxillae are more fragile than jaws (Castillo et al., 2001), so during transport activity the former tend to be lost faster. In this context, element abundances indicate that more than half of the expected pieces based on the MNI are absent from the upper teeth; and only one fractured maxilla is preserved as opposed to 13 mandibles (*A.* ex gr. *mystacinus*: nine mandibles and one maxilla; *C. rivas*: three mandibles; *Allophaiomys* sp.: one mandible; *E. quercinus*: no mandible or maxilla);
- the frequency of preservation and the size of the murine teeth (*Apodemus* and *Castillomys*) decrease overall in the order: M1, M2, M3 (see Table 1). A predominance of the same type of tooth is evidence of the dispersion of the remains due to hydrodynamic sorting (Wolff, 1973). A lower 0.5 mm screen has been used in order to recover all the fossils and so avoid possible bias during the collecting process (Minwer-Barakat, 2005);
- different numbers of left and right teeth occur within the same species. Lateral selection indicates separation of the pellets before their burial (Minwer-Barakat, 2005).

Montoya et al. (1999) detected infilling of the cavities at the Quibas site by mudflow and mass displacement. Pellets produced by owls could have been transported into the cave via the entrance or moved inside the cavities. If material was regurgitated within the vicinity of the cave or even inside the cave, it could have been displaced with minimal damage (Andrews, 1990; Kos, 2003b), since most of the teeth retain their roots and show no signs of abrasion (rounding).

4. Paleoecology

Micromammals are more effective than macromammals when it comes to making paleoenvironmental inferences, since they have more specific ecological requirements, the energetic and physiological restrictions create a high degree of specialization in small species, and micromammal species are more abundant than macromammal species (Hernández Fernández, 2001). In this sense, micromammals have widely been used as paleoclimatical and paleoecological indicators; studies of rodent assemblages in particular provide useful information on paleoenvironments and paleoclimates (García-Alix et al., 2008; Martín-Suárez et al., 2001; Minwer-Barakat et al., 2005; Montuire et al., 2006, among others). The rodent association may be influenced by the ability of predators to select their prey. However, as pointed out in the previous section, the owl species in question can collect and accumulate a significant representation of the small-mammal fauna, and also in this case potential predators do not seem to have led to a significant biological bias. In this context, we attempt to analyze the environment in the vicinity of Quibas/Gruta1 at the moment of its deposition.

The main criterion used to establish the habitat(s) of an extant species is based on actualism, whereas the habitat of an extinct taxon is based on its phylogenetic relationships with extant species, on its association with taxa whose ecological requirements are known, or on biogeographical criteria (García-Alix et al., 2008; López Antoñanzas and Cuenca-Bescós, 2002). Dental patterns can also be used (Gómez Cano et al., 2013; Hernández Fernández and Peláez-Campomanes, 2003b), but this method should be taken with caution, at least in reconstructing the humidity preferences of fossil rodents (Freudenthal et al., 2014). Martín-Suárez et al. (2001) indicated that taxa within the same anagenetic evolutionary lineage have the same preferences. Nevertheless, when the speciation occurs due to a change in the physical environment (vicariant speciation) ancestor and descendant may have opposite ecological preferences. These authors also suggested that taxa with opposite frequency peaks have opposite ecological preferences, and that immigrants replacing taxa with highly similar dental patterns may have opposite preferences.

4.1. Ecological preferences

Allophaiomys is an extinct microtine genus and represents the earliest evolutionary grade of voles with

Table 2

Relative abundances of each rodent taxon from the Early Pleistocene of Quibas/Gruta1, with the distribution of their potential habitats.

Tableau 2

Abondances relatives pour chaque taxon de rongeur du Pléistocène inférieur de Quibas/Gruta1, avec leur distribution selon les habitats potentiels.

Species	Relative abundance (%)	Habitat				
		W	R	OD	OH	WE
Allophaiomys sp.	4.6	–	–	0.33	0.33	0.33
Apodemus ex gr. *mystacinus-epimelas*	73.0	0.33	0.33	0.33	–	–
Castillomys rivas	7.6	–	–	0.5	0.5	–
Eliomys quercinus	14.8	0.5	0.5	–	–	–

W: woodland and woodland-margin areas; R: rocky areas; OD: open dry meadows or shrublands; OH: open humid meadows; WE: water-edges.

rootless lower teeth and cementum in the reentrant angles. According to Cuenca-Bescós et al. (2005), the fact that *Allophaiomys* has no roots and has continuously growing molars indicates open grassland or tundra dwellers. *Allophaiomys* is believed to have been ancestral to European *Microtus* (Chaline, 1966; Martin, 1975). Nowadays *Microtus* generally prefers open meadows, but there are also species inhabiting water-edge areas. Voles in general are animals adapted to fibrous grasslands, as shown by their hypsodont molars (Cuenca-Bescós et al., 2005). During the Plio-Pleistocene, different lines of arvicolids increased their molar hypsodonty with the appearance of cementum, an evolutionary trend which is usually interpreted as an adaptation to a diet rich in abrasive food such as grasses, and therefore as indicating a spread of open meadow areas (Fejfar and Heinrich, 1990; Fejfar and Repenning, 1992; Minwer-Barakat, 2005). On the basis of this information we assume that the environment inhabited by *Allophaiomys* sp. was open dry meadows (0.33), open humid meadows (0.33) and water-edge areas (0.33).

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 shrubland in rocky areas. Their presence in fossil sites may be connected with the presence of rocky environments in the vicinity of the locality (Agustí, 1982; Minwer-Barakat, 2005; Mitchell-Jones et al., 1999; Storch, 2004). Therefore, we distribute this taxon into three habitat types: open dry meadows (0.33), woodland (0.33) and rocky areas (0.33).

Castillomys rivas is an extinct rodent. It is interpreted as a eurytopic species, i.e. it does not provide information about specific ecological conditions (García-Alix et al., 2009; Minwer-Barakat, 2005). Nevertheless, given the presence of morphological features in the dental pattern associated with stephanodonty (the development of longitudinal ridges between molar cusps), it may indicate a diet based on grass (van Dam and Weltje, 1999; Gómez Cano et al., 2013; Montoya et al., 1999; Renaud et al., 2005), so open meadows should be expected as its preferred habitat (0.5 open dry; 0.5 open humid).

Eliomys quercinus underwent a great expansion throughout Europe during the entire Pleistocene. Nowadays, it is generally found in low-density deciduous and conifer woodland (0.5), and also in stony or rocky areas (0.5) with some vegetation at forest edges from Spain to the Ural Mountains. Areas with abundant herbaceous vegetation seem to be a limiting factor on its presence (López-García et al., 2011). Its identification in fossil sites has been considered indicative of forest areas and a temperate climate (Chaline, 1972; López-García et al., 2011; Sesé and Villa, 2008).

4.2. Paleoecological reconstruction

The rodent assemblage from Quibas/Gruta1 is clearly dominated by *Apodemus* ex gr. *mystacinus-epimelas*, with a relative abundance of 73%, followed by *Eliomys quercinus* with a prevalence of 14.8%, *Castillomys rivas* with 7.6% and *Allophaiomys* sp. with 4.6% (Table 2). The distribution of the relative abundances of rodent taxa and their habitat preferences (Table 2; Fig. 4) indicates a dominance of rocky habitats (31.7%), woodland and woodland-margin areas (31.7%), and open dry meadows (29.7%). The mixture of inhabitants of dry meadows or shrublands and forested environments is consistent with a mosaic forest scenario in the vicinity of Quibas/Gruta1, while rocky areas probably reflect the proximity of the cave. The existence of open habitats with a predominance of shrublands and rocky environments is supported by the appearance of certain macromammal taxa in Quibas, such as *Lynx pardinus* and *Capra alba*, and gastropods such as *Pomatias sulcatus* and *Chondrina farinesii*, while the presence of cervids (Cervidae indet.) suggests the occurrence of forested areas (Montoya et al., 1999, 2001). Our rodent assemblage also indicates open herbaceous habitats with some humidity requirements (5.4%) and areas surrounding water such as
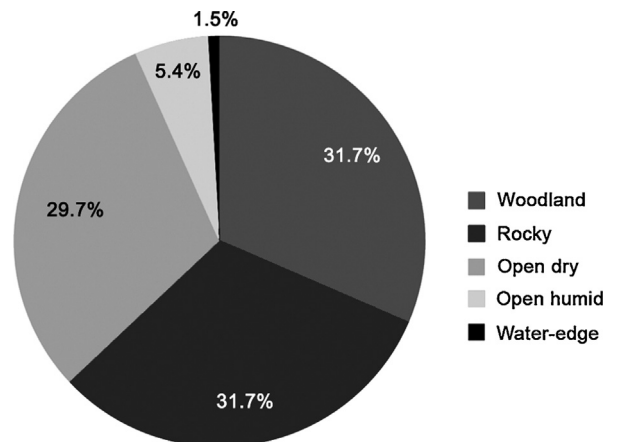
Fig. 4. Distribution of the habitats at Quibas/Gruta1 according to the ecological preferences of the rodent species.
Fig. 4. Distribution des rongeurs de Quibas/Gruta1 par habitat, en accord avec leurs préférences écologiques.

Table 3

Climatic parameters for Quibas/Gruta1 calculated according to the bioclimatic analysis based on rodent associations proposed by Hernández Fernández (2001), present climate data from Abanilla (Rivas-Martínez and Rivas-Sáenz, 1996–2009), and climatic parameters from Quibas obtained by Agustí et al. (2009) and Hernández Fernández et al. (2007).

Tableau 3

Paramètres climatiques pour Quibas/Gruta1, calculés selon l'analyse bioclimatique basée sur les associations de rongeurs proposée par Hernández Fernández (2001), les données climatiques actuelles d'Abanilla (Rivas-Martínez et Rivas-Sáenz, 1996–2009) et les paramètres climatiques de Quibas obtenus par Agustí et al. (2009) et Hernández Fernández et al. (2007).

	Quibas/Gruta1			Current data in Abanilla	Difference between results and current data	Agustí et al. (2009)	Hernández Fernández et al. (2007)
	Results	r^2	ES				
MAT	15.1	0.930	3.6	19.6	−4.5	15.0 ± 2.3	15.378
MTW	25.7	0.746	4.7	33.6	−7.9	24.2 ± 1.5	26.074
MTC	4.3	0.932	5.1	8.8	−4.5	7.0 ± 2.9	4.307
MATA	21.4	0.779	6.4	24.8	−3.4	–	21.76
MAP	390.6	0.746	470.6	303	+87.6	723 ± 233	417.217
AD	4.5	0.926	1.3	5	−0.5	–	4.94

MAT: mean annual temperature (in °C); MTW: mean temperature of the warmest month (in °C); MTC: mean temperature of the coldest month (in °C); MATA: mean annual thermal amplitude (in °C); MAP: mean annual precipitation (in mm); AD: aridity duration (months); ES: standard error for the estimation; r^2: coefficient of determination.

areas along streams, lakes or ponds (1.5%). The presence of humid areas at Quibas is well supported by the occurrence of *Anthus pratensis*, *Geronticus eremita* and *Saxicola torquata* (Montoya et al., 1999, 2001), avian species that dwell in wet meadows and at pond edges. Large herbivores such as *Praeovibos mediterraneus* as well as *Equus altidens* and *Equus suessenbornensis* (Piñero and Alberdi, in press) also provide evidence of the presence of wet and open meadows.

5. Paleoclimatology

Nowadays, the climate around the Sierra de Quibas is characterized by a strong tendency towards aridity due to the low and irregular rainfall distribution shared by all Mediterranean basins. The great variability of rainfall together with elevated temperatures results in high evapotranspiration, reaching a maximum in the months of extreme drought, i.e. June, July and August. Abanilla has a mean annual precipitation (MAP) that ranges between 250–300 mm and a mean annual temperature (MAT) of 19.6 °C (Manzano Garro, 1987; Rivas-Martínez and Rivas-Sáenz, 1996–2009).

On the basis of the rodent association from Quibas/Gruta1 we have calculated climatic parameters (Table 3) following the bioclimatic model proposed by Hernández Fernández (2001) for rodent assemblages. The distribution of the bioclimatic spectra yields the highest percentage for a Mediterranean climate (37.5%), followed by tropical with summer rains (25%), typical temperate (12.5%), arid-temperate (12.5%), and cold-temperate (12.5%). The Mediterranean climate at Quibas/Gruta1 is supported by the resulting climatic parameters, such as low mean annual precipitation ($MAP_{Quibas/Gruta1}$ = 390 mm) and the aridity duration ($AD_{Quibas/Gruta1}$ = 4.5 months). Our results indicate a colder and slightly more humid climate than today in the Sierra de Quibas. The mean annual temperature ($MAT_{Quibas/Gruta1}$ = 15.1 °C) was 4.5 °C lower, and the mean annual precipitation 87 mm higher than current values. The mean temperature of the coldest month (MTC) was 4.3 °C, and the mean temperature of the warmest month (MTW) was 25.7 °C, whereas today in Abanilla MTC = 8.8 °C and MTW = 33.6 °C.

Previous paleoclimatic inferences from Quibas have been drawn using both the bioclimatic model proposed by Hernández Fernández (2001) for rodent assemblages (Hernández Fernández and Peláez-Campomanes, 2003a; Hernández Fernández et al., 2007) and the Mutual Climate Range method (Blain et al., 2009) for amphibian and squamate reptile assemblages (Agustí et al., 2009). Both studies are based on the faunal list of Quibas published in Montoya et al. (1999, 2001). The data published by Agustí et al. (2009) (Table 3) resemble ours but with differences in the MTC (7 °C) and MAP (723 mm), Quibas/Gruta1 being colder and dryer. Otherwise, the climatic parameters proposed by Hernández Fernández et al. (2007) (Table 3) fit very well with the results of this work. In any case, all of them corroborate the prevalence of colder and wetter conditions than at present.

Agustí et al. (2009) recognize five alternating climatic phases in the Early Pleistocene. Phase 3 includes the sites of Barranco León 5, Fuente Nueva 3, Sima del Elefante, Cueva Victoria and Quibas, and is characterized by a sharp increase in temperature and precipitation in relation to the previous phase, which explains the early human occupation at that time (Agustí et al., 2009). However, within this context the site of Quibas represents a moment of relative decline in temperature, particularly the mean temperature of the coldest month (Agustí et al., 2009), which also occurs in Quibas/Gruta1. García-Alix et al. (2009) indicated relative cold and wet conditions for Huétor Tájar and Tojaire sections (Granada Basin), which are coeval of Quibas/Gruta1. These localities would be included into the same phase according to the time interval and the climatic interpretation.

In conclusion, the data obtained in this work suggest a colder and slightly wetter climate than today during the formation of Quibas/Gruta1 between ca. 1.4 and 1.2 Ma (Piñero et al., 2015). This interpretation is concordant with the progressive general cooling detected by Shackleton (1995) during the Early Pleistocene. One of the characteristics of the latest Early Pleistocene of the southeast of the Iberian Peninsula was the slightly colder climate than

nowadays and the change in the rainfall regime with more rainy winters and slightly drier summers, as is displayed at Barranco León and Fuente Nueva 3 (Blain et al., 2011) and Cueva Victoria (Blain, 2015). As shown by Lisiecki and Raymo (2005) using the benthic δ^{18}O record, the period between 1.2 and 1.4 Ma manifested various cold stages, which include Marine Isotope Stages (MIS) 36, 38, and 40. The accumulation of remains at Quibas/Gruta1 could have occurred during a relative cold period between MIS 36 and MIS 40.

6. Conclusions

The analysis of the rodent assemblage from the Early Pleistocene of Gruta1 establishes the following conclusions:

- the very low percentage of digested teeth in the rodent assemblage from Quibas/Gruta1 and the karstic origin of the site suggest that the sample was accumulated by the action of nocturnal avian predators. The main accumulators are likely to have been generalist feeders, whose accumulations would represent the rodent association from their hunting area;
- the remains display evidence of a certain degree of hydrodynamic transport, such as a great abundance of isolated molars, distinct proportions of lower and upper teeth, different numbers of left and right teeth within the same species, and a decrease in the preservation of murine teeth by size in the order M1, M2, M3;
- the distribution of the species according to their potential habitat(s) indicates a mixture of dry meadows or shrublands, woodland and woodland-margin zones and rocky habitats with the presence of open herbaceous meadows and water-edges, which is consistent with a mosaic forest scenario in the vicinity of Quibas/Gruta1 during the formation of the site;
- paleoclimatic data suggest a Mediterranean climate for the Sierra de Quibas during the Early Pleistocene, with colder temperatures and slightly higher rainfall than today. They also point to a relative decrease in temperature within the phase in which it was produced. The accumulation of remains may have occurred during a relative cold period between MIS 36 and MIS 40 according to the age of the site.

Acknowledgments

References

Agustí, J., 1982. Los roedores (Mammalia) del Pleistoceno Inferior de la "Cueva Victoria" (Murcia, España). Endins 9, 49–55.

Agustí, J., Martín-Suárez, E., 1986. Un proyecto de análisis ecoestratigráfico en el Plio-Pleistoceno de la depresión de Guadix-Baza. In: E. Villas (Coord.). Memorias I Jornadas de Paleontología. Diputación General de Aragón, Departamento de Cultura, Educación, Zaragoza, pp. 21–32.

Agustí, J., Blain, H.A., Cuenca-Bescós, G., Bailón, S., 2009. Climate forcing of first hominid dispersal in Western Europe. J. Hum. Evol. 57, 815–821.

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). J. Hum. Evol. 61 (6), 703–718.

Andrews, P., 1990. Owl, Caves and Fossils. Natural History Museum Publications, London (231 p.).

Avery, D.M., 2003. Early and Middle Pleistocene environments and hominid biogeography; micromammalian evidence from Kabwe, Twin Rivers and Mumbwa Caves in central Zambia. Palaeogeogr. Palaeoclimatol. Palaeoecol. 189 (1), 55–69.

Blain, H.A., 2015. Anfibios y escamosos de Cueva Victoria. In: Gibert, L., Ferràndez-Cañadell, E. (Eds.), Geología y Paleontología de Cueva Victoria. Mastia (11-12-13), 2012–14. Museo Arqueológico Municipal de Cartagena, Cartagena, pp. 175–197.

Blain, H.A., Bailon, S., Cuenca-Bescós, G., 2008. The Early–Middle Pleistocene palaeoenvironmental change based on the squamate reptile and amphibian proxies at the Gran Dolina site, Atapuerca, Spain. Palaeogeogr. Palaeoclimatol. Palaeoecol. 261 (1), 177–192.

Blain, H.A., Bailon, S., Cuenca-Bescós, G., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2009. Long-term climate record inferred from Early-Middle Pleistocene amphibian and squamate reptile assemblages at the Gran Dolina Cave, Atapuerca. Spain. J. Hum. Evol. 56 (1), 55–75.

Blain, H.A., Bailon, S., Agustí, J., Martínez-Navarro, B., Toro, I., 2011. Paleoenvironmental and paleoclimatic proxies to the Early Pleistocene hominids of Barranco León D and Fuente Nueva 3 (Granada, Spain) by means of their amphibian and reptile assemblages. Quat. Internat. 243, 44–53.

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 Palaeontol. Pol. 59 (4), 873–878.

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. Universitiy of Alcalá de Henares, Madrid, Spain, pp. 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). Estud. Geol. 62 (1), 395–400.

Carlos-Calero, J.A., Made van der, J., Mancheño, M.A., Montoya, P., Romero, G., 2006b. Capra alba Moyà-Solà, 1987 del Pleistoceno inferior de la Sierra de Quibas (Murcia, España). Estud. Geol. 62 (1–2), 571–578.

Castillo, C., (Ph. D. dissertation) 1990. Paleocomunidades de micromamíferos de los yacimientos kársticos del Neógeno Superior de Andalucía Oriental. Universidad de Granada, Spain (225 p.).

Castillo, C., Martın-González, E., Coello, J.J., 2001. Small vertebrate taphonomy of La Cueva del Llano, a volcanic cave on Fuerteventura (Canary Islands, Spain). Palaeoecological implications. Palaeogeogr. Palaeoclimatol. Palaeoecol. 166 (3), 277–291.

Chaline, J., 1966. Un exemple d'évolution chez les Arvicolidés (Rodentia) : les lignées *Allophaiomys-Pitymys* et *Microtus*. C.R. Acad. Sci. Paris, Ser. D 263, 1202–1204.

Chaline, J., 1972. Les rongeurs du Pléistocène moyen et supérieur de France (systématique-biostratigraphie-paléoclimatologie). Cahiers de paléontologie, CNRS, Paris (410 p.).

Chaline, J., Brunet-Lecomte, P., Campy, M., 1995. The last glacial/interglacial record of rodent remains from the Gigny karst sequence in the French Jura used for palaeoclimatic and palaeoecological reconstructions. Palaeogeogr. Palaeoclimatol. Palaeoecol. 117 (3), 229–252.

Cuadros, A., (M.D. thesis) 2010. Aproximación tafonómica de los micromamíferos del yacimiento paleontológico de Quibas: Evidencias de digestión, fracturas y procesos diagenéticos. Complutense University of Madrid, Madrid, Spain (55 p.).

Cuenca-Bescós, G., Rofes, J., García-Pimienta, J., 2005. Environmental change across the Early-Middle Pleistocene transition: small mammalian evidence from the Trinchera Dolina cave, Atapuerca, Spain. Geol. Soc. London Spec. Publ. 247 (1), 277–286.

Cuenca-Bescós, G., Straus, L.G., González Morales, M.R., García-Pimienta, J.C., 2009. The reconstruction of past environments through small mammals: from the Mousterian to the Bronze Age in El Mirón Cave (Cantabria, Spain). J. Archaeol. Sci. 36 (4), 947–955.

Daams, R., van der Meulen, A.J., Peláez-Campomanes, P., Álvarez-Sierra, M.A., 1999. Trends in rodent assemblages from the Aragonian (Early-Middle Miocene) of the Calatayud-Daroca Basin, Aragon, Spain. Hominoid Evol. Climatic Change Europe 1, 127–139.

Dauphin, Y., Denys, C., Kowalski, K., Rzebik-Kowalska, B., 1996. Taphonomic study of Algerian owl pellet assemblages and differential preservation of some rodents: palaeontological implications. Acta Zool. Cracov. 39, 103–116.

van Dam, J.A., Weltje, G.J., 1999. Reconstruction of the Late Miocene climate of Spain using rodent palaeocommunity successions: an application of end-member modelling. Palaeogeogr. Palaeoclimatol. Palaeoecol. 151 (4), 267–305.

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. Bol. Geol. Minero 115, 265–270.

Fejfar, O., Heinrich, W.D., 1990. International symposium "Evolution, phylogeny and biostratigraphy of fossil arvicolids (Rodentia, Mammalia)", Rohanov, May 20–29, 1987: Topics of the meeting and results of the discussions. In: Fejfar, O., Heinrich, W.D. (Eds). In: International Symposium on the Evolution, Phylogeny, Biostratigraphy of Arvicolids (Rodentia, Mammalia), Geological Survey, Praha, pp. 443–448.

Fejfar, O., Repenning, C.A., 1992. Holarctic dispersal of the arvicolids (Rodentia, Cricetidae). Mammalian Migration and Dispersal Events in the European Quaternary. Cour. Forsch. Senckenb. 153, 205–212.

Fernandez-Jalvo, Y., Denys, C., Andrews, P., Williams, T., Dauphin, Y., Humphrey, L., 1998. Taphonomy and palaeoecology of Olduvai Bed-I (Pleistocene, Tanzania). J. Hum. Evol. 34 (2), 137–172.

Freudenthal, M., García-Alix, A., Rios, M., Ruiz-Sánchez, F., Martín-Suárez, E., Delgado Huertas, A., 2014. Review of paleo-humidity parameters in fossil rodents (Mammalia): isotopic vs. tooth morphology approach. Palaeogeogr. Palaeoclimatol. Palaeoecol. 395, 122–130.

García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E., Freudenthal, M., Martín, J.M., 2008. Late Miocene–Early Pliocene climatic evolution of the Granada Basin (southern Spain) deduced from the paleoecology of the micromammal associations. Palaeogeogr. Palaeoclimatol. Palaeoecol. 265 (3), 214–225.

García-Alix, A., Minwer-Barakat, R., Martín-Suárez, E., Freudenthal, M., 2009. Small mammals from the Early Pliocene of the Granada Basin, southern Spain. Quat. Res. 72 (2), 265–274.

Gillieson, D., 1996. Caves: Processes, Development and Management. John Wiley & Sons, Oxford, UK (315 p.).

Gómez Cano, A.R., Hernández Fernández, M., Álvarez-Sierra, M.A., 2013. Dietary ecology of Murinae (Muridae, Rodentia): a geometric morphometric approach. PloS One 8 (11), e79080.

Goutner, V., Alivizatos, H., 2003. Diet of the Barn Owl (*Tyto alba*) and Little Owl (*Athene noctua*) in wetlands of northeastern Greece. Belg. J. Zool. 133 (1), 15–22.

Hadly, E.A., 1999. Fidelity of terrestrial vertebrate fossils to a modern ecosystem. Palaeogeogr. Palaeoclimatol. Palaeoecol. 149 (1), 389–409.

Hernández Fernández, M., 2001. Análisis paleoecológico y paleoclimático de las sucesiones de mamíferos del Plio-Pleistoceno ibérico. Universidad Complutense de Madrid, Madrid (379 p.).

Hernández Fernández, M., Peláez-Campomanes, P., 2003a. The bioclimatic model: a method of palaeoclimatic qualitative inference based on mammal associations. Glob. Ecol. Biogeogr. 12, 507–517.

Hernández Fernández, M., Peláez-Campomanes, P., 2003b. Ecomorphological characterization of Murinae and hypsodont "Cricetidae" (Rodentia) from the Iberian Plio-Pleistocene. Coloq. Paleontol. 1, 237–251.

Hernández Fernández, M., Peláez-Campomanes, P., 2005. Quantitative palaeoclimatic inference based on mammal faunas. Glob. Ecol. Biogeogr. 14, 39–59.

Hernández Fernández, M., Álvarez-Sierra, M.A., Peláez-Campomanes, P., 2007. Bioclimatic analysis of rodent palaeofaunas reveals severe climatic changes in southwestern Europe during the Plio-Pleistocene. Palaeogeogr. Palaeoclimatol. Palaeoecol. 251, 500–526.

Kos, A.M., 2003a. Characterisation of post-depositional taphonomic processes in the accumulation of mammals in a pitfall cave deposit from southeastern Australia. J. Archaeol. Sci. 30 (6), 781–796.

Kos, A.M., 2003b. Pre-burial taphonomic characterisation of a vertebrate assemblage from a pitfall cave fossil deposit in southeastern Australia. J. Archaeol. Sci. 30 (6), 769–779.

Krystufek, B., Vohralik, V., 2009. Mammals of Turkey and Cyprus. Rodentia II: Cricetidae, Muridae, Spalacidae, Calomyscidae, Capromyidae, Hystricidae, Castoridae. Knjznica Annales Majora. Koper, Slovenia (372 p.).

Latková, H., Sándor, A.K., Kraštín, A., 2012. Diet composition of the scops owl (*Otus scops*) in central Romania. Slovak Raptor J. 6, 17–26.

Lisiecki, L.E., Raymo, M.E., 2005. A Pliocene-Pleistocene stack of 57 globally distributed benthic δ^{18}O records. Paleoceanography 20 (1), PA1003.

López Antoñanzas, R., Cuenca-Bescós, G., 2002. The Gran Dolina site (Lower to Middle Pleistocene, Atapuerca, Burgos, Spain): new palaeoenvironmental data based on the distribution of small mammals. Palaeogeogr. Palaeoclimatol. Palaeoecol 186 (3), 311–334.

López-García, J.M., Blain, H.A., De Marfà, R., García, A., Martinell, J., Cuenca-Bescós, G., 2011. Small mammals from the Middle Pleistocene layers of the Sima del Elefante (Sierra de Atapuerca, Burgos, northwestern Spain). Geol. Acta 9 (1), 29–43.

López-García, J.M., Blain, H.A., Julià, R., Maroto, J., 2014. Environment and climate during MIS 7 and their implications for the late Middle Pleistocene hominins: the contribution of Mollet cave, Serinyà, Girona, northeastern Iberian Peninsula. Quat. Internat. 337, 4–10.

Made van der, J., 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. Boll. Soc. Paleontol. Ital. 47 (1), 13–23.

Manzano Garro, T., 1987. Características morfométricas del río Chicamo: cuenca Abanilla-Fortuna (sureste de España). Paralelo 37 (11), 107–112.

Martin, R.A., 1975. *Allophaiomys* Kormos from the Pleistocene of North America. Studies on Cenozoic Paleontology and Stratigraphy. CW Hibbard Memorial 3, 97–100.

Martín-Suárez, E., (PhD Thesis) 1988. Sucesiones de micromamíferos en la Depresión de Guadix-Baza (Granada, España). University of Granada, Granada, Spain (241 p.).

Martín-Suárez, E., Freudenthal, M., Civis, J., 2001. Rodent palaeoecology of the continental Upper Miocene of Crevillente (Alicante, SE Spain). Palaeogeogr. Palaeoclimatol. Palaeoecol. 165 (3), 349–356.

Minwer-Barakat, R., (PhD Thesis) 2005. Roedores e insectívoros del Turoliense Superior y el Plioceno del sector central de la cuenca de Guadix. University of Granada, Granada, Spain (535 p.).

Minwer-Barakat, R., García-Alix, A., Martín-Suárez, E., Freudenthal, M., 2005. Muridae (Rodentia) from the Pliocene of Tollo de Chiclana (Granada, southeastern Spain). J. Vertebr. Paleontol. 25 (2), 426–441.

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 (484 p.).

Montoya, P., Alberdi, M.T., Barbadillo, L.J., Made van der, J., 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). C. R. Acad. Sci. Paris, Ser. IIa 332, 387–393.

Montoya, P., Alberdi, M.T., Blázquez, A.M., Barbadillo, L.J., Fumanal, M.P., Made van der, J., 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). Estud. Geol. 55 (3–4), 127–161.

Montuire, S., Maridet, O., Legendre, S., 2006. Late Miocene–Early Pliocene temperature estimates in Europe using rodents. Palaeogeogr. Palaeoclimatol. Palaeoecol. 238 (1), 247–262.

Piñero, P., (M.D. thesis) 2012. Los roedores del Pleistoceno inferior de la Gruta1 del Complejo kárstico de Quibas. Universitat Autònoma de Barcelona and Universitat de Barcelona, Barcelona, Spain (100 p.).

Piñero, P., Alberdi, M.T., in press. Estudio de los caballos del yacimiento de Quibas, Pleistoceno Inferior final (Abanilla, Murcia, España). Estud. Geol.

Piñero, P., Agustí, J., Blain, H.A., Furió, M., Laplana, C., 2015. Biochronological data for the Early Pleistocene site of Quibas (SE Spain) inferred from rodents assemblage. Geol. Acta. 13 (3), 229–241.

Pokines, J.T., 1998. The Paleoecology of Lower Magdalenian Cantabrian Spain. BAR International Series 713, pp. 1–189.

Renaud, S., Michaux, J., Schmidt, D.N., Aguilar, J.P., Mein, P., Auffray, J.C., 2005. Morphological evolution, ecological diversification and climate change in rodents. Proc. R. Soc. B. 272, 609–617.

Rivas-Martínez, S., Rivas-Sáenz, S., 1996–2009. Sistema de Clasificación Bioclimática Mundial. Centro de Investigaciones Fitosociológicas, España http://www.ucm.es/info/cif.

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.

Saavedra, B., Simonetti, J.A., 1998. Small mammal taphonomy: intraspecific bone assemblage comparison between South and North American Barn Owl, *Tyto alba*, Populations. J. Archaeol. Sci 25 (2), 165–170.

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.

Shackleton, N.J., 1995. New data on the evolution of Pliocene climatic variability. In: Vrba, E.S., Denton, G.H., Partridge, T.C., Burckle, L.H. (Eds.), Paleoclimate and Evolution, with Emphasis on Human Origins. Yale University Press, New Have, pp. 242–248.

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. Springer Netherlands, pp. 135–145.

Terry, R.C., 2004. Owl pellet taphonomy: a preliminary study of the post-regurgitation taphonomic history of pellets in a temperate forest. Palaios 19 (5), 497–506.

Tomé, R., Catry, P., Bloise, C., Koipiméiki, E., 2008. Breeding density and success, and diet composition of Little Owls *Athene noctua* in steppe-like habitats. Ornis Fenn. 85, 22–32.

Wilson, D.E., Reeder, D.M., 2005. Mammal Species of the World. A Taxonomic and Geographic Reference, third ed. John Hopkins University Press, Baltimore (2142 p.).

Wolff, R.G., 1973. Hydrodynamic sorting and ecology of a Pleistocene mammalian assemblage from California (USA). Palaeogeogr. Palaeoclimatol. Palaeoecol. 13 (2), 91–101.