



ELSEVIER

Contents lists available at ScienceDirect

Comptes Rendus Palevol

www.sciencedirect.com



General Palaeontology, Systematics and Evolution (Vertebrate Palaeontology)

The fossil bat assemblage of Sima del Elefante Lower Red Unit (Atapuerca, Spain): First results and contribution to the palaeoenvironmental approach to the site



L'assemblage des chauves-souris fossiles de l'Unité inférieure rouge de Sima del Elefante (Atapuerca, Espagne) : premiers résultats et contribution à l'approche paléoenvironnementale du site

Julia Galán^{a,*}, Gloria Cuenca-Bescós^a, Juan Manuel López-García^{b,c}

^a Grupo Aragosaurus-IUCA, Área de Paleontología, Departamento de Ciencias de la Tierra, Facultad de Ciencias, Universidad de Zaragoza, C. Pedro Cerbuna 12, 50009 Zaragoza, Spain

^b IPHES, Institut Català de Paleoecologia Humana i Evolució Social, Campus Sescelades URV, edifici W3, 43007 Tarragona, Spain

^c Àrea de Prehistòria, Universitat Rovira i Virgili (URV), Avinguda de Catalunya 35, 43002 Tarragona, Spain

ARTICLE INFO

Article history:

Received 7 February 2015

Accepted after revision 3 June 2015

Available online 12 August 2015

Handled by Hugues-Alexandre Blain

Keywords:

Chiroptera

Sima del Elefante

Atapuerca karst localities

Early Pleistocene

Palaeoenvironment

Mots clés :

Chiroptera

Sima del Elefante

Localités karstiques de Atapuerca

Pléistocène inférieur

Paléoenvironnement

ABSTRACT

The fossil bat assemblage from the Lower Red Unit of Sima del Elefante (TELRU) in Atapuerca (Burgos, Spain) has been exhaustively analysed for the first time. Bat fossil assemblages are of particular relevance to palaeoenvironmental approaches to sites. Here we integrate our new data on the chiropteran fauna with the data provided previously by other authors on the basis of the small-vertebrate assemblages and the palynology of the site. Our results are consistent with the earlier results in that they indicate a generally warmer climate than at present in the area and stable environmental conditions throughout the major part of the TELRU sequence. However, fossil bat assemblages sometimes lead to problems when they are used in landscape reconstruction. These problems are discussed here and should be taken into account in future works.

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

RÉSUMÉ

L'assemblage des chauves-souris fossiles de l'Unité inférieure rouge de Sima del Elefante (TELRU), à Atapuerca, en Espagne, a été analysé de manière exhaustive pour la première fois. Les assemblages de chauves-souris fossiles sont intéressants pour les approches paléoenvironnementales. Ici, nous intégrons nos nouvelles données paléoenvironnementales à partir de la faune de chiroptères dans celles précédemment fournies par d'autres auteurs sur la base des petits assemblages de vertébrés et de la palynologie du site. Nos résultats sont cohérents avec les leurs, indiquant un climat plus chaud que le climat général actuel dans la région et des conditions environnementales

* Corresponding author.

E-mail address: galanj@unizar.es (J. Galán).

stables à travers la majeure partie de la séquence TELRU. Cependant, les assemblages fossiles de chauves-souris conduisent parfois à des problèmes quand ils sont utilisés pour la reconstruction du paysage. Ces problèmes sont abordés ici et devraient être pris en compte dans les études futures.

© 2015 Académie des sciences. Publié par Elsevier Masson SAS. Tous droits réservés.

1. Introduction

Fossil chiropteran assemblages are interesting palaeoenvironmental indicators in Quaternary sites mainly due to the specific habitat preferences of bats. Bats are only occasionally preyed upon by owls and other predators such as carnivorous mammals, snakes or lizards, which means that frequently they are hardly represented in fossil small-vertebrate assemblages (García et al., 2005; Kowalski, 1995; Rosina and Shokhrin, 2011; Sommer et al., 2009). In some circumstances, however, the formation of exceptionally abundant, well-preserved fossil bat assemblages may occur within karst-cavity fillings as the thanatocoenosis generated when the individuals of a bat colony roosting inside the cave die and accumulate *in situ* (López-García and Sevilla, 2012). Thus, as bat assemblages are not necessarily produced by the same processes as other small-vertebrate assemblages, we think that they may provide a valuable independent source of palaeoenvironmental information. This confers great importance upon the study of this group of flying mammals.

The fossil bat assemblage from the Lower Red Unit of Sima del Elefante (TELRU) in Atapuerca (Burgos, Spain) has been exhaustively analysed here for the first time.

The Sima del Elefante site in the Sierra de Atapuerca (Fig. 1), also called Trinchera Elefante (TE), is an archaeo-palaeontological locality where some of the oldest European hominine remains have been found. More specifically, an incomplete jaw bone was recovered in level TE9c, ca ~1.22 Ma, which is the oldest hominin fossil found in western Europe and was provisionally attributed to *Homo antecessor* (Carbonell et al., 2008) although it is currently under revision (Bermúdez de Castro et al., 2011). The study of this level together with the other levels that make up the Early Pleistocene stratigraphic sequence of TE, known as TELRU (Trinchera Elefante-Lower Red Unit), is of great importance in understanding the physical and ecological factors that led to the rapid occupation of Europe by hominins, as well as the evolution of these hominins. The analysis of the fossils of small vertebrates from TELRU such as insectivores, rodents, lagomorphs, amphibians and squamate reptiles has already been employed successfully as part of a palaeoenvironmental approach to the site (Blain et al., 2010; Cuenca-Bescós et al., 2013, 2015; Rodríguez et al., 2011; Cuenca-Bescós and Rofes, 2004; Rofes and Cuenca-Bescós, 2009). However, the remains of chiropters from the site have remained poorly studied to date. Here we integrate our new data on the chiropteran fauna of the site with the data provided by these previous works. In addition, this study is of particular importance since the Iberian fossil bat assemblages reported from this time period (such as those from the Guadix-Baza sites or the Almenara-Casablanca site) are rather scarce (Agustí

et al., 2011; Sesé Benito and Sevilla García, 1996; Sevilla, 1988).

2. The locality

The Sierra de Atapuerca (Burgos, Spain) rises about 1080 masl (meters above sea level), dominating the flat landscape of the Castilian plains. It comprises a set of Quaternary localities containing a very complete stratigraphic and palaeontological record (Fig. 1). The deposits – which have been studied and dated in great detail – are detritic sediments filling a complex karst system which was developed in the Cretaceous limestone of the area during the Pliocene and Early Pleistocene. The Sima del Elefante stratigraphic section (Fig. 1) comprises 16 excavated levels (from TE7 to TE21), grouped into three sedimentary phases. The lower phase of TELRU studied in the present paper ranges from TE7 to TE14. The site was an old output point for groundwater flow from the intermediate level of the Cueva Mayor Complex (Ortega et al., 2013). By the time that TELRU was deposited the opening of the pit was suspended on the mountain slope due to the fall of the base level, becoming a cave entrance which connected this intermediate level of Cueva Mayor – a vadose karst-conduit by then – with the outside. The TELRU levels are formed by detritic sediments from the immediate vicinity, displaying a marked inclination of the strata. Furthermore, they are extremely rich in faunal remains: amphibians, reptiles, birds and mammals (bats, rodents, insectivores, lagomorphs, in addition to large herbivores and carnivores).

In addition to the palaeomagnetic and cosmogenic data, which give an Early Pleistocene age for the TELRU levels, from a biostratigraphic perspective the vertebrates of the TELRU levels represent Atapuerca Faunal Unit 1 (FU 1) (Cuenca-Bescós and García, 2007; Cuenca-Bescós et al., 2010, 2013, 2015), i.e. the oldest FU of the Atapuerca record, which is also Early Pleistocene in age. No further biostratigraphic subdivisions have been identified so far within Atapuerca FU 1 because TELRU has identical small-mammal assemblages from level TE7 to level TE14 (Cuenca-Bescós et al., 2010, 2013, 2015; Rofes and Cuenca-Bescós, 2006, 2009, 2011, 2013).

3. Material and methods

3.1. Sample processing and fossil sorting

The studied material consists of disarticulated cranial and postcranial bat remains collected by water-screening the rock matrix obtained during the excavation field campaigns at the Atapuerca sites. A system of towers of superimposed sieves arranged in parallel was used to this

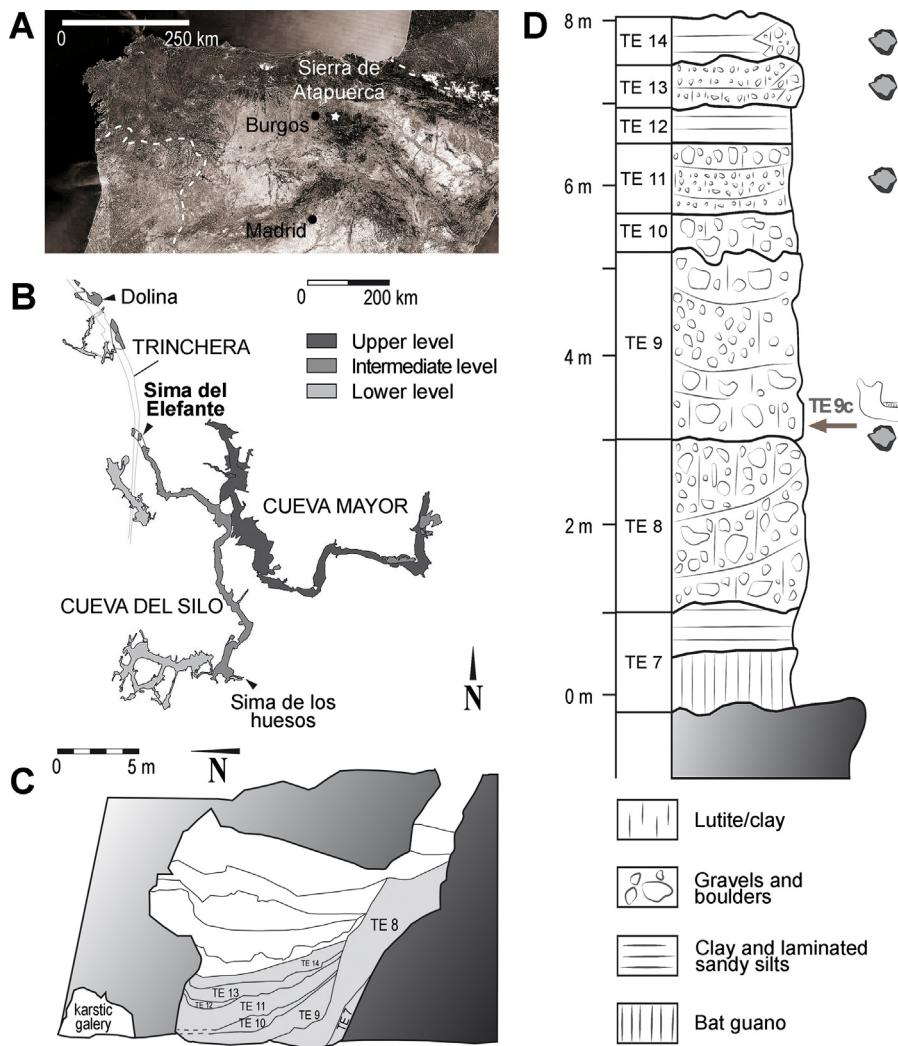


Fig. 1. A. Geographical and geological location of the Sima del Elefante site in the Sierra de Atapuerca. B. Schematic plan of the Sierra de Atapuerca karstic system (modified from Ortega et al., 2013). C. Sima del Elefante profile (modified from Cuenca et al., 2013). D. Stratigraphic sequence of TELRU (modified from Blain et al., 2010).

Fig. 1. A. Situation géographique et géologique du site de Sima del Elefante, dans la Sierra de Atapuerca. B. Plan schématique du système karstique de la Sierra de Atapuerca (modifié d'après Ortega et al., 2013). C. Profil de Sima del Elefante (modifié d'après Cuenca et al., 2013). D. Séquence stratigraphique de TELRU (modifié d'après Blain et al., 2010).

end; the sieves were provided with 10, 5 and 0.5 mm mesh. Each sample was bagged by square, layer and excavation sub-level (see a general explanation of the method in Cuenca-Bescós et al., 2015).

The sediments were excavated at the Sima del Elefante site from 1996 to 2007. The samples from each level have been studied as independent assemblages so we can compare the evolution of the fossil bat assemblages from the bottom to the top of the TELRU stratigraphic sequence.

The assemblage of fossil bat's bones recovered and studied comprise a total of 353 remains corresponding to a minimum number of 56 individuals (Table 1). These were mainly identified following the palaeontological criteria (morphological features and measurements) proposed by the following authors: for cranial remains Dupuis (1986),

Menu and Popelard (1987) and Sevilla (1988); for humeri Dupuis (1986) and Felten et al. (1973); for the other postcranial elements the remains recovered were compared with extant specimens belonging to the Doñana Biological Station-CSIC, the Aragosaurus Group-IUCA and the CIAMA-La Alfranca (International Centre for Water and Environment); the anatomical nomenclature employed here is that provided by the above-mentioned authors together with Strickler (1978). The determination of the specimens was performed to species level whenever possible. The minimum number of individuals (MNI) was calculated by counting the most abundant bone or tooth from either the left or right side of a given taxon. All the bat fossil material mentioned in this paper is housed in the University of Zaragoza.

Table 1

Presence in terms of NISP (number of identified specimens) and MNI (minimum numbers of individuals) of each identified bat taxon through the TELRU levels.

Tableau 1

Présence en termes de NISP (nombre de spécimens identifiés) et de MNI (nombre minimum d'individus) de chaque taxon de chauve-souris identifié parmi les niveaux de TELRU.

| | TE 14 | | TE 13 | | TE 12 | | TE 11 | | TE 10 | | TE 9a+ | |
|----------------------------------|-------|-----|-------|-----|-------|-----|-------|-----|-------|-----|--------|-----|
| | NISP | MNI | NISP | MNI | NISP | MNI | NISP | MNI | NISP | MNI | NISP | MNI |
| <i>Rhinolophus ferrumequinum</i> | | | | | 1 | 1 | | | | | | |
| <i>Rhinolophus mehelyii</i> | | | | | | | | | | | | |
| <i>Myotis myotis</i> | 2 | 1 | | | 1* | – | | | 40 | 4 | 15 | 2 |
| cf. <i>Eptesicus</i> | | | | | | | | | | | 1 | 1 |
| <i>Myotis</i> sp. | | | | | | | | | | | | |
| <i>Miniopterus schreibersii</i> | | | | | 3 | 1 | | | 4 | 1 | 7 | 1 |
| Chiroptera indet. | | | | | | | | | | | | |
| Total | 2 | 1 | | | 5 | 2 | | | 44 | 5 | 23 | 4 |

| | TE 9a | | TE 9b | | TE 9c | | TE 8 | | TE 7 | | Total | |
|----------------------------------|-------|-----|-------|-----|-------|-----|------|-----|------|-----|-------|-----|
| | NISP | MNI | NISP | MNI | NISP | MNI | NISP | MNI | NISP | MNI | NISP | MNI |
| <i>Rhinolophus ferrumequinum</i> | | | | | 1 | 1 | | | | | 2 | 2 |
| <i>Rhinolophus mehelyii</i> | | | | | | | | | 2 | 1 | 2 | 1 |
| <i>Myotis myotis</i> | 4 | 2 | 50 | 7 | 118 | 10 | 6 | 1 | 44 | 8 | 280 | 35 |
| cf. <i>Eptesicus</i> | 1 | 1 | | | | | | | | | 2 | 2 |
| <i>Myotis</i> sp. | | | | | | | | | 1 | 1 | 1 | 1 |
| <i>Miniopterus schreibersii</i> | 1 | 1 | 6 | 2 | 17 | 4 | 4 | 1 | 17 | 4 | 59 | 15 |
| Chiroptera indet. | 1 | – | | | | | 4 | – | 2 | – | 7 | – |
| Total | 7 | 4 | 56 | 9 | 136 | 15 | 14 | 2 | 66 | 14 | 353 | 56 |

3.2. Taphonomy

Regarding the origin of fossil bat assemblages, the most usual way for a cave-accumulation to be produced is by the natural death of the individuals forming a colony, although in some cases the accumulation may be a result of predation upon bats (Kowalski, 1995; López-García and Sevilla, 2012). For the taphonomical analysis of the fossil bat assemblage under study, the state of preservation of the remains (breakage pattern, dissolution, presence of mineral precipitation on the surface) as well as the composition of the assemblage in terms of anatomical elements (absolute presence and relative abundance of the different anatomical elements) have been considered, in accordance with Andrews (1990) and Bennàsar (2010). The sorting of the assemblage by age on the basis of the tooth-wear pattern of the fossil bats has been undertaken in accordance with Sevilla (1986).

3.3. Palaeoenvironmental interpretation

To undertake a palaeoenvironmental interpretation of the site on the basis of our fossil bat assemblage, aspects of the extant ecology, habitat preferences and geographical distribution of the identified taxa have been used (in accordance with de Paz and Benzal, 1991; Palomo et al., 2007; Sevilla, 1988), as all the identified species in the site have extant representation on modern populations. The habitat weighting method (Andrews, 2006; Evans et al., 1981) has been employed here in an attempt to reconstruct the habitat. The performance of the analysis involved the following steps: firstly the habitat types of the studied region may be defined; here we followed the five habitat types established by Blain et al. (2010) who already applied this method to the analysis of the herpetofauna assemblage from the

TELRU. Secondly, for every identified taxon a habitat score or percentage was provided proportionally to its current living preferences. Then the assigned habitat scores were multiplied by the percentage that each taxon represents within the whole assemblage in terms of MNI (minimal number of individuals). Finally the summation of the values obtained to every type of habitat provided an approach of the composition of the palaeoenvironment of the site. However the results obtained here have not been satisfactory; the problems associated with using this method on our assemblage are discussed in the section 7.

4. Recorded taxa

Rhinolophus ferrumequinum (Fig. 2H) appears sporadically as an accidental species (Table 1; list of material in Table 2). The identification of this taxon is unequivocal. Its dental formula (1.1.2.3/2.1.3.3), the morphology of the mandible (particularly the mandibular ramus, which is flat and square) and the morphology of the lower molars (which are nyctalodont and present a narrow and regular cingulum) allow this genus to be distinguished from other nyctalodont bats, while the large size of the specimens clearly shows that they belong to this species, which is by far the largest horseshoe bat in the Palearctic region.

The greater horseshoe bat currently inhabits the middle latitudes of Europe from England to the Mediterranean peninsulas; it is a common species throughout Spain—including the Balearic Islands, although it is scarcer there—reaching altitudes of 1600 masl. In Spain it is a ubiquitous species although it mainly prefers transitional woodland areas; it roosts in caves forming small colonies (Palomo et al., 2007).

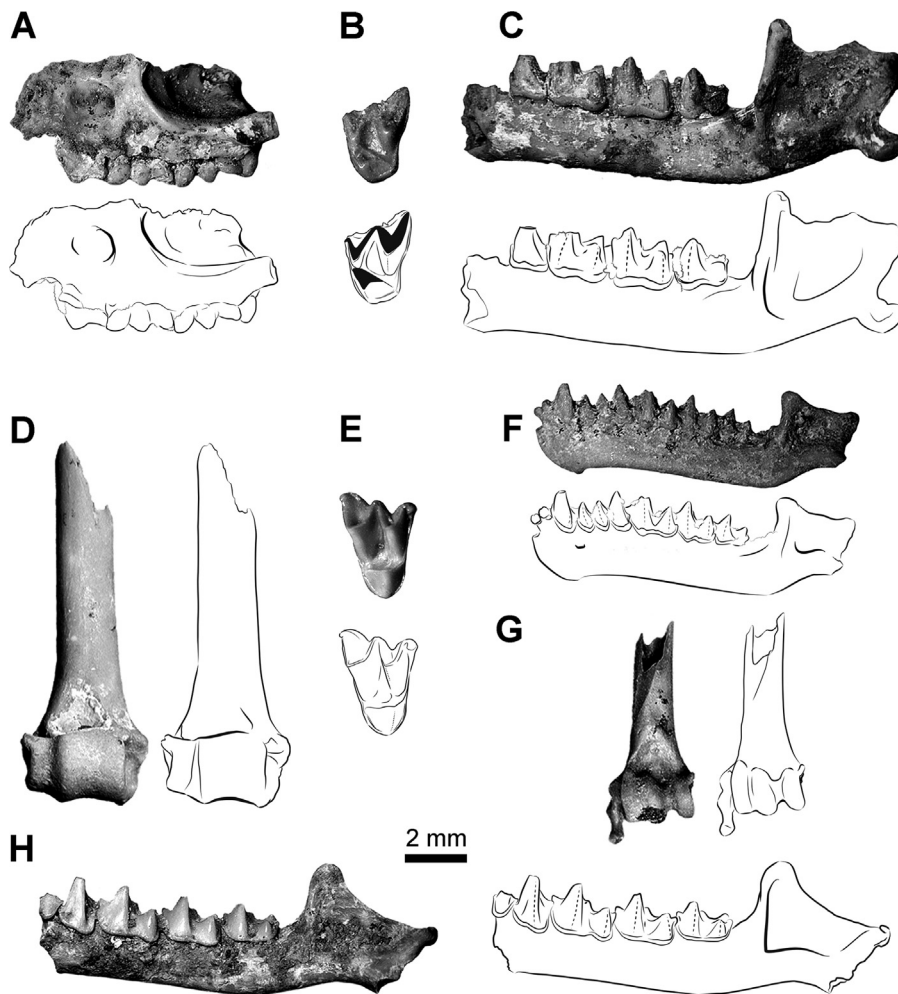


Fig. 2. Fossil bat remains from Sima del Elefante Lower Red Unit. *M. myotis*. A. Fragment of left maxilla (TE9c). B. Left M1 (TE9c). C. Fragmented left mandible (TE9c). D. Distal epiphysis of right humerus (TE9c). E. Right M2 (TE9c). *M. schreibersii*. F. Left mandible (TE9c). G. Distal epiphysis of left humerus (TE9c). *R. ferrumequinum*. H. Fragmented left mandible (TE9c).

Fig. 2. Restes fossiles de chauves-souris de l'Unité inférieure rouge de Sima del Elefante. *M. myotis*. A. Fragment de maxillaire gauche (TE9c). B. M1 gauche (TE9c). C. Mandibule gauche fragmentée (TE9c). D. Épiphyse distale d'humérus droit (TE9c). E. M2 droite (TE9c). *M. schreibersii*. F. Mandibule gauche (TE9c). G. Épiphyse distale d'humérus gauche (TE9c). *R. ferrumequinum*. H. Mandibule gauche fragmentée (TE9c).

Rhinolophus mehelyi appears sporadically as an accidental species (Table 1; list of material in Table 2). The morphology of the lower molars, which is quite similar to the previous case, allows the mandible to be assigned to this genus. The size of m2 and m3 is under the lower limit of size variation for *R. ferrumequinum* but above the upper limit of size variation for the medium-sized horseshoe bat *Rhinolophus euryale*, so we have assigned the mandible to *R. mehelyi*, which is the other medium-sized form of this genus that usually appears in the Pleistocene sites of the Iberian Peninsula (Sevilla, 1988). The proximal epiphysis of the humerus presents great development of the trochin in this genus, and both the trochin and the trochiter extend proximally to a similar level beyond the humeral head, which is triangular rather than rounded and dips towards the trochin. The size of the specimen (3.6 mm wide) and the morphology of the ventral ridge, which is flat, agree with the material used for comparison for this taxon.

Mehely's horseshoe bat currently inhabits Mediterranean Europe, albeit only discontinuously; it occurs in the Mediterranean margin and the southern half of Spain but does not usually reach altitudes above 500 masl, although some isolated citations exist at altitudes as great as 1200 masl. In Spain, it mainly prefers transitional woodland areas where the trees are more scattered; it roosts in caves, forming colonies of variable size (Palomo et al., 2007). This is one of the few species classified nowadays as Vulnerable by the IUCN in Spain, with decreasing trends in populations which has been estimated as 10% in the last 10 years in Andalusia while the datum remains unquantified in other regions of the country but still appears to have been considerable (Hutson et al., 2008).

Myotis myotis (Fig. 2A–E) appears frequently throughout the TELRU sequence, being present in all levels except TE11, TE12 (where a fragmented mandible was recovered though this seems more likely to be a reworked specimen from

Table 2

List of the recovered material for each bat taxon.

Tableau 2

Liste des ossements récupérés pour chaque taxon de chauve-souris.

| Taxon | n | Element | n | Element |
|----------------------------------|----|--------------------------|----|-----------------------|
| <i>Rhinolophus ferrumequinum</i> | 1 | md with p3 - m3 | 1 | md (fr) with m1 and c |
| <i>Rhinolophus mehelyi</i> | 1 | md (fr) with m2 - m3 | 1 | hu (p. e. + diap.) |
| | 1 | max (fr) with M1 | 1 | md (fr) with p4 - m3 |
| | 2 | max (fr) with M2 | 3 | md (fr) with p4 |
| | 1 | max (fr) with M2 - M3 | 2 | md (fr) with m1 - m2 |
| | 1 | max (fr) with P4 - M1 | 2 | md (fr) with m1 |
| | 1 | max (fr) with P4 and M2 | 3 | md (fr) with m2 - m3 |
| | 1 | max (fr) with M1 - M3 | 9 | md (fr) with m2 |
| | 2 | max (fr) with P4 | 9 | md (fr) with m3 |
| | 3 | max (fr) with P4 - M3 | 3 | i3 |
| | 3 | I2 | 5 | c |
| | 13 | C | 7 | p2 |
| | 8 | P4 | 8 | p3 |
| | 17 | M1 | 15 | p4 |
| | 11 | M2 | 21 | m1 |
| <i>Myotis myotis</i> | 5 | M3 | 10 | m2 |
| | 7 | M (fr) | 7 | m3 |
| | 1 | md with p3 - m3 | 21 | m (fg) |
| | 2 | md with p4 - m3 | 3 | hu (p. e.) |
| | 1 | md with m1 - m3 | 9 | hu (p. e. + diap.) |
| | 1 | md with m1 - m2 | 6 | hu (d. e.) |
| | 2 | md with m2 - m3 | 16 | hu (d. e. + diap.) |
| | 2 | md with m2 | 2 | hu (diap.) |
| | 0 | md with m3 | 1 | rad (d. e. + diap.) |
| | 1 | md | 6 | rad (p. e.) |
| | 7 | md (fr) | 6 | rad (p. e. + diap.) |
| | 1 | md (fr) with c - p3 | 1 | fem |
| | 1 | md (fr) with c-p2 and m1 | 6 | fem (p. e.) |
| | 1 | md (fr) with p3 | 2 | fem (d. e. + diap.) |
| cf. <i>Eptesicus</i> | 1 | md (fr) | 1 | hu (d. e. + diap.) |
| <i>Myotis</i> sp. | 1 | hu (d. e. + diap.) | | |
| | 1 | max (fr) with M2 - M3 | | |
| | 4 | C | 3 | md (fr) with m2 - m3 |
| | 2 | P4 | 1 | c |
| | 2 | M1 | 2 | p4 |
| | 2 | M3 | 9 | m1 |
| <i>Miniopterus schreibersii</i> | 1 | M (fr) | 1 | m3 |
| | 1 | md with i2 - m3 | 6 | m (fr) |
| | 2 | md with m2 - m3 | 7 | hu (d. e.) |
| | 1 | md (fr) | 3 | hu (d. e. + diap.) |
| | 2 | md (fr) with p4 - m3 | 3 | hu (p. e.) |
| | 1 | md (fr) with p4 and m3 | 2 | hu (p. e. + diap.) |
| | 1 | md (fr) with m2 | 2 | rad (p. e. + diap.) |
| Chiroptera indet. | 4 | md (fr) | 1 | fem (d. e.) |
| | 1 | P4 (fr) | 1 | diap |

I: upper incisor; C: upper canine; P: upper premolar; M: upper molar; i: lower incisor; c: lower canine; p: lower premolar; m: lower molar; md: mandible; max: maxilla; hu: humerus; rad: radius; fem: femur; fr: fragment; p. e., proximal epiphysis; d. e.: distal epiphysis; diap.: diaphysis.

lower levels) and TE13 (Table 1; list of material in Table 2). Identification of the cranial remains as a large-sized form of the genus *Myotis* is straightforward on the basis of the dental formula (2.1.2.3/3.1.3.3), the morphology of the mandible (particularly the mandibular ramus, which is wide and presents a considerably higher coronoid process in relation to the articular process), the myotodont lower molars, the thick and quite irregular cingulum present on all teeth, and the large size of the specimens. The proximal epiphysis of the humerus presents a rounded head and a rather small trochin ridge, but lacks any trochiter ridge; the trochin and the proximal edges of the head reach a similar height while the proximal edge of the trochiter extends above the other two. The distal epiphysis of the humerus lacks a styloid process and the epicondylar spine

is rather reduced; in external view, the proximal edges of the trochlea and condyle reach a similar height. The femur (L = 19.93 mm) presents trochanters similar in size to each other, the head is almost spherical and the whole proximal epiphysis is more lateromedially symmetrical than it is in other genera. The proximal end of the radius presents a not very pointed proximal process; the articular surface is somewhat trilobed in shape but lacks any crossing ridge, and the biceps insertion fossa is open. The distal end of the radius presents two knob-like anterior processes and a posterior, longitudinal crest.

The two large-sized Eurasian forms of this genus, *M. myotis* and *Myotis blythii* (which are accepted as different species even though recent genetic studies have demonstrated that they may have fertile hybrid offspring; see

Bogdanowicz et al. (2009)), are difficult to distinguish from each other due to the extreme similarity of their morphology. The former species is generally larger although both species share an overlapping range of size variation. The measured molars are of a size above the upper limit for *M. blythii*, except for the specimens from level TE9, where the lower molars mostly lie within the range of overlap between the two taxa while the upper molars are above the upper limit of size variation for *M. blythii*. As it has previously been indicated by some authors, the sympatric presence of the two sibling species in Europe did not occur until the Holocene; previously, the western region of Europe had been occupied by the *M. myotis* group while *M. blythii* was an Asian species (Berthier et al., 2006; Bogdanowicz et al., 2009). However, the moment of separation of the two taxa is not clear. Work based on molecular data gives a date of about 0.56 Ma for the split, but according to Sevilla (1988) *M. myotis* has been identified in the Iberian Lower Pleistocene site of La Unión. As no different characters have been observed allowing us to attribute our remains to any other species, here we have decided to assign them to the taxon *M. myotis*.

The greater mouse-eared bat currently inhabits western, central and southern Europe. It occurs throughout Spain—where it reaches altitudes of 2060 masl—including the Balearic Islands, though it is scarcer in the central Ebro Valley and the South Submeseta. Its usual foraging habitats are woodland, transitional woodland and woodland margins, and it roosts in caves, forming massive nursery colonies and smaller hibernating colonies (Palomo et al., 2007).

cf. *Eptesicus* appears sporadically as an accidental species (Table 1; list of material in Table 2). The recovered mandible presents a dental formula of 3.1.2.3 corresponding to 13 alveoli, which coincides with the genera *Eptesicus*, *Vespertilio*, *Barbastella*, *Pipistrellus*, *Hypsugo* and *Nyctalus*. However, it lacks any teeth, and the mandibular ramus is also absent. The size corresponds to a small-medium-sized bat slightly larger than the extant *Hypsugo savii* and *Pipistrellus*. The mental foramen lies between the c and the p3 alveoli, approximately at the mid-height of the mandible body, and it is circular and rather small. The mandibular body is quite robust and presents neither a narrowing towards the posterior side nor a marked mental bulge, which points to it belonging to *Eptesicus* as opposed to the other mentioned genera. Due to the lack of any other distinctive feature, we have preferred to maintain the identification as indicated. The distal epiphysis of the humerus (2.5 mm wide) presents a relatively well-developed styloid process and a rather long epicondylar spine, excluding the possibility of it being a small-sized *Myotis* or a *Plecotus*. The former feature can be observed despite the loss of the tip of the styloid process. The olecranon fossa forms a semicircle in internal view, and the union between the trochlea and the condyle is flatter than in *Pipistrellus*, *Hypsugo* and *Vespertilio*, where the furrow between the two structures is deeper. The remnant corresponds to a form of serotine bat that is definitely smaller than the two species of the genus that currently inhabit Spain: *Eptesicus serotinus* and *Eptesicus isabellinus* (Palomo et al., 2007). Three other species inhabit Europe at present: *Eptesicus bottae* (which is

larger than the Iberian ones), *Eptesicus nilssonii* and *Eptesicus anatolicus* (these two being small-sized forms). One more fossil species has been described in the Lower Pleistocene of Europe: *Eptesicus praeglacialis*, which is also a large-sized form (Sevilla, 1988). Our remains are close to those of the species *Eptesicus nilssonii* but our specimen is slightly smaller, and given the lack of any other distinctive feature we have preferred to maintain the identification as indicated.

Myotis sp. appears sporadically as an accidental species (Table 1; list of material in Table 2). The humerus is partially fragmented, but the following distinctive features of the *Myotis* genus can be observed: the styloid process is reduced, the proximal edge of the trochlea does not reach the epiphyseal border; it differs from *Plecotus* in that the proximal edge of the union between the trochlea and the condyle does not form a bulge in external view. The specimen corresponds to a small-sized form of *Myotis* such as *Myotis daubentonii*, *Myotis emarginatus* or *Myotis nattereri*. As the ventral edge of the trochlea does not reach the edge of the epiphysis, assignment to the taxon *Myotis capaccinii* can be ruled out, but a more precise identification is not possible due to its fragmentation.

Miniopterus schreibersii (Fig. 2F, G) appears frequently throughout the TELRU sequence, being present in all levels except TE11, TE13 and TE14 (Table 1; list of material in Table 2). The assignment of the items to this taxon is unequivocal: the species is characterized by the dental formula of 2.1.2.3/3.1.3.3 and the long, narrow and slender cusps of the teeth; another specific characteristic is its large p3 with two roots, which adds an extra alveolus to the mandible. The C has an oval occlusal section and deep longitudinal furrows on both the labial and lingual surfaces. P4, M1 and M2 present well-developed heels where the cingulum becomes relatively thicker; the former presents a mesiolingual longitudinal arris which ends as an extra cusp at the contact with the cingulum. The lower molars are of a nyctalodont type with a narrow but irregular cingulum, and p4 has a triangular occlusal outline. The mandible body is quite slender and shows a well-developed and angulated mental bulge; the mental foramen is large and is located close under and between the alveoli of p2 and c. The mandibular ramus is square-shaped and joins the body forming a well-marked angle; the coronoid and the articular processes reach a similar height. The distal epiphysis of the humerus is diagnostic due to the long and flattened blade-shaped styloid process, the marked olecranon fossa and the deep furrow between condyle and epicondyle. The proximal epiphysis is characterized by a wide, ear-shaped trochin and a diagonally oriented oval head, which dips towards the trochiter and extends slightly above the trochin; the ventral ridge is not very prominent and joins the trochin forming a depression, whereas there is no dorsal ridge. The proximal end of the radius is diagnostic due to the long, pointed proximal process, the two articular surfaces separated by a well-developed ridge which arises from the tip of the proximal process, and the deep, kidney-shaped biceps insertion fossa, which has an almost closed contour.

Schreibers' bat currently inhabits southern Europe. It occurs throughout Spain—where it reaches altitudes of

1400 masl—including the Balearic Islands. Its foraging habitats are both open lands and forest. This is a species linked to rocky areas where caves or crevices may occur (not necessarily close to the feeding areas since it is able to fly along great distances), as *M. schreibersii* uses them for roosting, forming massive nursery and hibernation colonies (Palomo et al., 2007).

5. Taphonomic remarks

Two levels in the sequence lack bat remains: TE 11 and TE 13, while their presence in levels TE 8, TE 12 and TE 14 is rather scarce. This absence or scarcity of bat remains has no parallelism in other groups of small vertebrates such as the herpetofauna studied by Blain et al. (2010), where a significant descent in the number of remains is only noted for level TE12. Regarding the horizontal distribution of the bat remains in each bat-fossil-bearing level, no differential distribution patterns have been observed; specifically in sublevel TE 9c, which has been excavated extensively, the bat remains occur in almost all the squares.

The abundance of bat remains within the TELRU levels (Table 1) is very low in comparison with other groups of small vertebrates such as rodents, insectivores, amphibians or reptiles (Blain et al., 2010; Rodríguez et al., 2011), but it is still remarkable when compared with the amount of bat remains recovered from other Pleistocene Iberian cave-sites, such as AGP7 in Zaragoza (Galán et al., 2015), La Unión in Murcia, Las Yedras and Cueva del Agua in Granada, Prádenas in Segovia, Guardo in Palencia, El Higerón and Las Grajas in Malaga and El Reguerillo in Madrid (Sevilla, 1988).

The bat assemblage is composed of disarticulated cranial and postcranial remains, and the occurrence of teeth attached to bone is notable. The presence of complete long bones and cranial bones is very scarce, if not non-existent, in all the levels, but the breakage pattern generally observed consists of angulated fractures rather than rounded surfaces and is not linked to dissolution surfaces; in some cases the identification of fragments belonging to the same specimen is even possible within a sample. In our opinion, this corresponds to trampling as the origin of the breakage rather than to predation or a long process of transport. The presence of isolated teeth is generally high in terms of their percentage within the total bat NISP of every level, but when the relative abundance of each element is taken into account (after Andrews, 1990) the most abundant elements are mandibles in all levels except TE 9b, where they are molars.

Only a few bones present clear marks of dissolution where digestion is the origin: specifically, a couple of humeral distal epiphyses from TE 7 (one from a *M. myotis*, the other from a *M. schreibersii*) and the mandible of cf. *Eptesicus* from TE 9a (this last is not a typical cave-dwelling bat so it seems logical that the agent of accumulation was a predator in this case). This is a small amount considering the size of the TELRU bat sample as a whole.

Carbonate precipitation has been observed in some bat specimens. In the majority of cases, the presence of carbonates is linked to a better state of conservation of the remains, such as the complete preservation of the teeth

attached to a mandible or maxilla bone; in some cases the identification of different anatomical remains belonging to the same individual and affected by superficial carbonate precipitation is even possible within a sample. This precipitation must thus have occurred in the early stages of deposition; it could have been favoured by the decomposition of the organic tissues attached to bone, which produces a local increase in pH.

The specimens forming the bat assemblage are mainly yearlings according to their tooth wear, but interesting exceptions to the age distribution may be found in some levels. In levels TE 10, TE 9c and TE 7, yearlings, adults and even old individuals are represented by the *M. myotis* group; *M. schreibersii* specimens are yearlings in almost all the levels except TE 8 and TE 9c, where adult individuals have also been found, and the two individuals of *R. ferrumequinum* from levels TE 9c and TE 12 respectively were also adults.

This leads us to conclude that the origin of the main TELRU bat assemblage was as a thanatocoenosis generated by the death of the individuals that formed colonies in the ancient cave. The colonies had been mainly of the nursery-type judging by the predominance of yearlings except for the afore-mentioned cases where adult individuals have been found. On the other hand, the few isolated remains that show evidence of digestion could have been deposited by opportunistic predators such as owls, as is the case with the majority of the small-vertebrate remains within the sequence (Blain et al., 2010; Cuenca-Bescós and Rofes, 2004; Cuenca-Bescós et al., 2013, 2015; Rodríguez et al., 2011; Rofes and Cuenca-Bescós, 2009).

6. Results

6.1. Species composition

A total of 353 bat remains have been recovered from TELRU, 346 of which could be identified at least to genus level (MNI = 56). Six bat taxa have been identified within the sequence: *R. ferrumequinum*, *R. mehelyi*, *M. myotis*, *Myotis* sp., cf. *Eptesicus* and *M. schreibersii*. All the identified species currently inhabit Europe. The vertical distribution of these taxa through the sequence as a whole is characterized by the almost constant presence of *M. myotis* and *M. schreibersii*, which are also the most abundant species in each level (Table 1). Both of them are typical cave-dwelling bats and appear frequently in Iberian Pleistocene and extant bat communities; the *Rhinolophus* species recorded are also among the typical cave-dwelling species in the Iberian Peninsula and frequently occur in the Iberian Pleistocene record too (de Paz and Benzal, 1991; Galán et al., 2015; Palomo et al., 2007; Sevilla, 1988), although their presence in the studied locality is a minority.

6.2. Palaeoenvironmental interpretation

There are two dominant bat taxa, *M. myotis* and *M. schreibersii*, which appear together throughout almost the whole sequence, constituting an association typical of warm, Mediterranean climate conditions (de Paz and Benzal, 1991; Palomo et al., 2007; Sevilla, 1988).

Table 3

Habitat preferences of each identified species of bat.

Tableau 3

Préférences d'habitat pour chaque espèce identifiée de chauve-souris.

| | OD | OH | Wo | Ro | Wa |
|---------------------------------|-----|-----|-----|-----|----|
| <i>Rhinolophus ferrumquinum</i> | | | 0.8 | 0.2 | |
| <i>Rhinolophus mehelyi</i> | | | 0.8 | 0.2 | |
| <i>Myotis myotis</i> | | | 0.8 | 0.2 | |
| <i>Miniopterus schreibersii</i> | 0.2 | 0.2 | 0.4 | 0.2 | |

OD: open dry habitat; OH: open humid habitat; Wo: woodland/woodland margin habitat; Ro: rocky habitat.

The landscape inferred from our analysis of the chiropteran faunal assemblages and taking the habitat preferences of each taxon into account (see Table 3) comprises a predominantly woodland habitat, which includes mature forest, transitional areas, and woodland margins and forest patches with moderate ground cover. Areas of open land or meadows and rocky dwellings including caves, fissures and bare rock substrates would be present to a lesser extent (Fig. 3). The habitat composition presents little variation throughout the levels analysed; it should also be borne in mind that the small amount of remains recovered in levels TE 8, TE 9a, TE 9a+, TE 12 and TE 14 (Table 1) may bias the results for these levels.

7. Discussion

Of the two constant taxa in the assemblage, *M. schreibersii* is a markedly thermophilic species, as is *R. mehelyi* (Palomo et al., 2007; Sevilla, 1988), whose sporadic presence in level TE 7 reinforces this general idea of warm climatic conditions previously expounded by Blain et al. (2010), Cuenca-Bescós et al. (2013, 2015), Rodríguez et al. (2011), and Cuenca-Bescós and Rofes (2004, 2009). It is also notable that the current occurrence of *M. myotis* in

natural cave-roosts within the central and eastern Iberian regions is rather accidental, whereas this species is very frequent in the cave-roosts of southern Iberian regions (de Paz and Benzal, 1991). In this sense the chiropteran fauna from TELRU is consistent with the above-mentioned results of previous studies of small vertebrates and the palynological record from this sequence, which reported warmer conditions than at present.

Regarding the habitat composition, previous results pointed to a mixed landscape with little variation throughout the sequence, but the extent of the woodland areas indicated by analyses of other groups of small vertebrates is clearly less than in our results (Blain et al., 2010; Cuenca-Bescós et al., 2013; Rodríguez et al., 2011). Three possible causes for this disagreement may be considered and expounded here. Firstly, as woodland areas are the most important foraging habitat for European bats (Cel'uch and Kropil, 2008), a palaeoecological approach based only on the bat assemblage separately from other small-vertebrate groups may result in an overrepresentation of this type of habitat that would not occur if the fossil community as a whole were considered. Secondly, the use of the habitat weighting method—or any other method of habitat reconstruction which considers the abundance of a taxon in terms of its MNI to be a reflection of the abundance of this taxon in the palaeocommunity—may also lead to problems when working with cave-dwelling animal assemblages characterized by the *in situ* mortality of the individuals as in this case, since the abundance of one taxon in the association may be caused by a combination of ethological and taphonomic factors. The use of a cave-roost by different bat species simultaneously is quite common; many present-day examples of *M. myotis* and *M. schreibersii* sharing caves have been reported and it might occur either that they form interspecific clusters, or that each taxon occupies a different hall in the cave depending on the environmental conditions (e.g. Borda et al., 2004; de Paz and Benzal, 1991; Vincent et al., 2011). The greater presence of one taxon as opposed to another in the Sima del Elefante site, which corresponds to a quite external area of this ancient cave, could be due to the different locations of the past bat colonies within the cave instead of a dominance of a given species. Furthermore, another issue should be taken into account when interpreting a landscape on the basis of this type of assemblage: the different spatial scale of influence of each group of animals. The main bat taxa identified here are known to cover distances of about 25–29 km away from their roosts for hunting (Arlettaz, 1996; Vincent et al., 2011), while owls—a typical agent of accumulation of small-vertebrate assemblages—limit their range of action to distances of 1–5 km from their nests (e.g. Martínez and Zuberogoitia, 2004). Thus a bat assemblage produced by the death of the individuals within the cave would be providing us with palaeoecological data from an area at least ten times larger than a small-vertebrate assemblage accumulated by the action of owls; the same applies to other predators.

Finally, the changes in the bat association observed in the upper levels of the sequence (from TE 11 to TE 14) should also be discussed. Noteworthy is the decrease in the

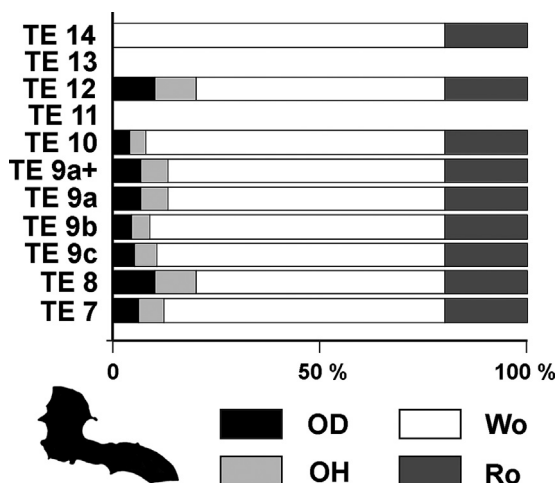


Fig. 3. Habitat weighting results. OD: open dry habitat; OH: open humid habitat; Wo: woodland/woodland margin habitat; Ro: rocky habitat.

Fig. 3. Résultats de la méthode de pondération de l'habitat. OD : habitat ouvert et sec ; OH : habitat ouvert et humide ; Wo : habitat forestier et de bordure de forêt ; Ro : habitat rocheux.

number of bat remains, if not their total absence as in TE 11 and TE 13 (Table 1), which may be due to taphonomic processes that exclusively affect the chiropteran fauna since the other small-vertebrate groups do not show a similar pattern, as pointed out above in the Taphonomic remarks paragraph. However, changes in the composition of the association can also be observed: TE 12 lacks remains of *M. myotis* and TE 14 lacks remains of *M. schreibersii*. This could be related to changes in the general environmental conditions, such as the woodland regression registered for levels TE 11 and TE 12 and the climate deterioration registered for levels TE 13 and TE 14 (Blain et al., 2010). Besides, an interesting point is the life-span and reproductive strategy of bats and the implications that this biological condition could have in their fossil record. Bats are incredibly long-lived comparing to other mammals of similar size—in Central Europe the life-span average among the different species is between 25 and 30 years (Dietz et al., 2009), while concerning the two main species of TELRU record, *M. myotis* maximum life-time recorded is 25 years (Kulzer, 2003) while *M. schreibersii* is known to live at least 16 years (Spitzenberger, 1981)—and they have also a low ratio of offspring per year, from one to two breedings (Dietz et al., 2009; Palomo et al., 2007). This definitely determines the recovery of a bat population within a region after a decrease process due to an unfavorable environmental situation since it is much slower than in most other small mammals with more opportunistic strategies, and eventually can lead into a different pattern of record throughout the same stratigraphic sequence as occurs in TELRU.

8. Conclusions

The fossil bat assemblage from TELRU has been exhaustively analysed for the first time, and the following six taxa have been identified: *R. ferrumequinum*, *R. mehelyi*, *M. myotis*, *Myotis* sp., cf. *Eptesicus* and *M. schreibersii*. The origin of the accumulation is the death within the cave of the members of fossil bat colonies roosting in it. The sequence is characterized by the (almost) constant presence of two taxa: *M. myotis* and *M. schreibersii*. This is a typical Mediterranean association and would point to warmer climate conditions in the region of Atapuerca during this period than at present, as reported by previous work from the site. We have found that fossil bat assemblages are useful for drawing palaeoclimatic inferences and also as indicators of palaeoenvironmental stability when associations of taxa rather than abundances of taxa are taken into account. However, the use of fossil bat assemblages whose origin is the *in situ* death of the individuals as palaeoecological indicators leads to certain problems that may call for consideration in further papers. Indeed, the habitat weighting method is not very appropriate in such cases. The habitat preferences shown by extant bats can be used to provide an approximate, qualitative description of the past landscape, but establishing quantitative percentages of the abundance of each habitat on the basis of the abundance of each taxon would probably not yield representative results.

Acknowledgements

This work has been supported by the MICINN Project CGL2009-12703-C03-03, CGL2012-38434-C03-01, Fundación Atapuerca, H54.Grupos consolidados del Gobierno de Aragón y Fondo Social Europeo (European Social Fund). J. Galán is the recipient of a PhD fellowship from the Gobierno de Aragón. J.M. López-García is a beneficiary of a Beatriu de Pinós postdoctoral fellowship (2011BP-A200001) from the Generalitat de Catalunya, a grant co-funded by the European Union through the Marie Curie Actions of the 7th Framework Program for R+D. R. Glasgow has revised the English grammar and redaction, and H.-A. Blain has revised the French. The comments and suggestions provided by Dr. C. Berto and the other anonymous reviewer have greatly improved this work. Finally, we would like to thank our colleague C. Núñez-Lahuerta for her comments on the ethology of nocturnal birds of prey.

References

- Agustí, J., Santos-Cubedo, A., Furió, M., De Marfá, R., Blain, H.-A., Oms, O., Sevilla, P., 2011. The Late Neogene–Early Quaternary small vertebrate succession from the Almenara-Casablanca karst complex (Castellón, Eastern Spain): chronologic and paleoclimatic context. *Quat. Internat.* 243 (1), 183–191.
- Andrews, P., 1990. Owls, caves and fossils. Predation, preservation and accumulation of small mammal bones in caves, with an analysis of the Pleistocene Cave faunas from Westbury-sub-Mendip, Somerset, UK. Natural History Museum, London (239 p.).
- Andrews, P., 2006. Taphonomic effects of faunal impoverishment and faunal mixing. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 241, 572–589.
- Arlettaz, R., 1996. Feeding behaviour and foraging strategy of free-living mouse-eared bats, *Myotis myotis* and *Myotis blythii*. *Anim Behav* 51 (1), 1–11.
- Bennàsar, M.L., 2010. Tafonomía de micromamíferos del Pleistoceno Inferior de la Sierra de Atapuerca (Burgos): Sima del Elefante y Gran Dolina. Departament d'Història i Història de l'art, Universitat Rovira i Virgili, Tarragona, Spain (Ph.D. thesis, 535 p.).
- Bermúdez de Castro, J.M., Martínón-Torres, M., Gómez-Robles, A., Prado-Simón, L., Martín-Francés, L., Lapresa, M., Olejniczak, A., Carbonell, E., 2011. Early Pleistocene human mandible from Sima del Elefante (TE) cave site in Sierra de Atapuerca (Spain): a comparative morphological study. *J Hum Evol* 61, 12–25.
- Berthier, P., Excoffier, L., Ruedi, M., 2006. Recurrent replacement of mtDNA and cryptic hybridization between two sibling bat species *Myotis myotis* and *Myotis blythii*. *Proc. Royal Soc. B Biol. Sci.* 273 (1605), 3101–3123.
- Blain, H.-A., Bailon, S., Cuenca-Bescós, G., Bennàsar, M., Rofes, J., López-García, J.M., Hugué, R., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2010. Climate and environment of the earliest West European hominins inferred from amphibian and squamate reptile assemblages: Sima del Elefante Lower Red Unit, Atapuerca, Spain. *Quat. Sci. Rev.* 29 (23), 3034–3044.
- Bogdanowicz, W., Van Den Bussche, R.A., Gajewska, M., Postawa, T., Harutyunyan, M., 2009. Ancient and contemporary DNA sheds light on the history of mouse-eared bats in Europe and the Caucasus. *Acta Chiropterologica* 11 (2), 289–305.
- Borda, D., Borda, C., Tâmaş, T., 2004. Bats, climate, and air microorganisms in a Romanian cave. *Mammalia* 68 (4), 337–343.
- Carbonell, E., Bermúdez de Castro, J.M., Parés, J.M., Pérez-González, A., Cuenca-Bescós, G., Ollé, A., Mosquera, M., Hugué, R., van der Made, J., Rosas, A., Sala, R., Vallverdú, J., García, N., Granger, E.D., Martínón-Torres, M., Rodríguez, X.P., Stock, G.M., Vergès, J.M., Allué, E., Burjach, F., Cáceres, I., Canals, A., Benito, A., Díez, C., Lozano, M., Mateos, A., Navazo, M., Rodríguez, J., Rosell, J., Arsuaga, J.L., 2008. The first hominin of Europe. *Nature* 452 (7186), 465–469.
- Cel'uch, M., Kropil, R., 2008. Bats in a Carpathian beech-oak forest (Central Europe): habitat use, foraging assemblages and activity patterns. *Folia Zoologica* 57 (4), 358–372.

- Cuenca-Bescós, G., Rofes, J., 2004. Insectívoros (Mammalia), clima y paisaje de los niveles inferiores de Trinchera Elefante (Pleistoceno Inferior, Atapuerca). In: Baquedano, E., Rubio Jara, S. (Eds.), *Miscelánea en homenaje a Emiliano Aguirre. Zona Arqueológica, Alcalá de Henares. II: Paleontología, Zona Arqueológica 4*, Museo Arqueológico Regional, Alcalá de Henares, pp. 150–156.
- Cuenca-Bescós, G., García, N., 2007. Biostratigraphic succession of the Early and Middle Pleistocene mammal faunas of the Atapuerca cave sites (Burgos, Spain). *Courier Forschungsinstitut Senckenberg* 259, 99–110.
- Cuenca-Bescós, G., Rofes, J., López-García, J.M., Blain, H.-A., De Marfá, R.J., Galindo-Pellicena, M.A., Bennàsar-Serra, M.L., Melero-Rubio, M., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2010. Biochronology of Spanish Quaternary small vertebrate faunas. *Quatern. Int.* 212 (2), 109–119.
- Cuenca-Bescós, G., Rofes, J., López-García, J.M., Blain, H.-A., Rabal-Garcés, R., Sauqué, V., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2013. The small mammals of Sima del Elefante (Atapuerca, Spain) and the first entrance of *Homo* in Western Europe. *Quat. Internat.* 295, 28–35.
- Cuenca-Bescós, G., Blain, H.A., Rofes, J., Lozano-Fernández, I., López-García, J.M., Duval, M., Galán, J., Núñez-Lahuerta, C., 2015. Comparing two different Early Pleistocene microfaunal sequences from the caves of Atapuerca, Sima del Elefante and Gran Dolina (Spain): biochronological implications and significance of the Jaramillo subchron. *Quat. Internat.*, <http://dx.doi.org/10.1016/j.quaint.2014.12.059>.
- de Paz, O.D., Benzal, J., 1991. Los refugios importantes y su valoración ecológica para los murciélagos españoles. In: Benzal, J., de Paz, O. (Eds.), *Los murciélagos de España y Portugal*. ICONA, Madrid, pp. 3–140.
- Dietz, C., von Helversen, O., Nill, D., 2009. L'encyclopédie des chauves-souris d'Europe et d'Afrique du Nord : biologie, caractéristiques, protection. Delachaux et Niestlé, Paris (400 p.).
- Dupuis, I., 1986. Les chiroptères du Quaternaire en France. Univ. de Paris I, Paris (Mémoire de Maîtrise, 561 p.).
- Evans, E.M.N., Van Couvering, J.A.H., Andrews, P., 1981. Palaeoecology of Miocene sites in western Kenya. *J. Human Evol.* 10, 99–116.
- Felten, H., Helfricht, A., Storch, G., 1973. Die Bestimmung der europäischen Fledermäuse nach der distalen Epiphyse des Humerus. *Senckenbergiana Biologica* 54 (4/6), 291–297.
- Galán, J., Cuenca-Bescós, G., López-García, J.M., Sauqué, V., Núñez-Lahuerta, C., 2015. Fossil bats from the Late Pleistocene site of the Aguilón P7 Cave (Zaragoza, Spain). *C. R. Palevol*, <http://dx.doi.org/10.1016/j.crpv.2014.12.003>.
- García, A.M., Cervera, F., Rodríguez, A., 2005. Bat predation by long-eared Owls in Mediterranean and temperate regions of southern Europe. *J. Raptor. Res.* 34 (4), 445–453.
- Hutson, A.M., Spitzenberger, F., Juste, J., Aulagnier, S., Alcaldé, J.T., Palmeirim, J., Paunovic, M., Benda, P., Karataş, A., 2008. *Rhinolophus mehelyi*. The IUCN Red List of Threatened Species. Version 2014.3. (www.iucnredlist.org).
- Kowalski, K., 1995. Taphonomy of bats (Chiroptera). *Geobios* 18, 251–256.
- Kulzer, E., 2003. Großes Mausohr *Myotis myotis*. In: Braun, M., Dieterlen, F. (Eds.), *Die Säugetiere Baden-Württembergs I*, Ulmer-Verlag, pp. 357–377.
- López-García, J.M., Sevilla, P., 2012. La contribución de los fósiles a la reconstrucción de las dinámicas de población de murciélagos. *Barbastella* 5 (1), 12–18.
- Martínez, J.A., Zuberogoitia, I., 2004. Habitat preferences for Long-eared Owls *Asio otus* and Little Owls *Athene noctua* in semi-arid environments at three spatial scales: capsule there is a relationship between owl numbers and the availability of the agri-forest patchwork. *Bird Study* 51 (2), 163–169.
- Menu, H., Popelard, J.-B., 1987. Utilisation des caractères dentaires pour la détermination des Vespertilioninés de l'Ouest européen. *Le Rhinolophe* 4, 1–88.
- Ortega, A.I., Benito-Calvo, A., Pérez-González, A., Martín-Merino, M.A., Pérez-Martínez, R., Parés, J.M., Aramburu, A., Arsuaga, J.L., Bermúdez de Castro, J.M., Carbonell, E., 2013. Evolution of multilevel caves in the Sierra de Atapuerca (1 Burgos, Spain) and its relation to human occupation. *Geomorphology* 196, 122–137.
- Palomo, L.J., Gisbert, J., Blanco, J.C., 2007. *Atlas y Libro Rojo de los Mamíferos Terrestres de España*. Dirección General para la Biodiversidad-SECEM-SECEMU, Madrid (588 p.).
- Rodríguez, J., Burjachs, F., Cuenca-Bescós, G., García, N., Van der Made, J., Pérez González, A., Blain, H.-A., Expósito, I., López-García, J.M., García Antón, M., Allué, E., Cáceres, I., Huguet, R., Mosquera, M., Ollé, A., Rosell, J., Parés, J.M., Rodríguez, X.P., Díez, C., Rofes, J., Sala, R., Saladié, P., Vallverdú, J., Bennasar, M.L., Blasco, R., Bermúdez de Castro, J.M., Carbonell, E., 2011. One million years of cultural evolution in a stable environment at Atapuerca (Burgos, Spain). *Quat. Sci. Rev.* 30 (11), 1396–1412.
- Rofes, J., Cuenca-Bescós, G., 2006. First evidence of the Soricidae (Mammalia) *Asoriculus gibberodon* (Petényi, 1864) in the Pleistocene of North Iberia. *Rivista Italiana di Paleontologia e Stratigrafia* 112, 301–315.
- Rofes, J., Cuenca-Bescós, G., 2009. First record of *Beremendia fissidens* (Mammalia Soricidae) in the Pleistocene of the Iberian Peninsula, with a review of the biostratigraphy, biogeography and palaeoecology of the species. *C. R. Palevol* 8 (1), 21–37.
- Rofes, J., Cuenca-Bescós, G., 2011. Evolutionary history and biogeography of the genus *Crociodura* (Mammalia, Soricidae) in Europe, with emphasis on *Crociodura kornfeldi*. *Mamm. Biol.* 76, 64–78.
- Rofes, J., Cuenca-Bescós, G., 2013. First record of *Sorex (Drepanosorex) margaritodon* (Mammalia, Soricidae) in western Europe: biostratigraphy, biogeography and evolution of the species. *Paläontologische Zeitschrift* 87, 529–541.
- Rosina, V.V., Shokhrin, V.P., 2011. Bats in the diet of owls from the Russian Far East, southern Sikhote Alin. *Hystrix Ital. J. Mammal.* 22 (1), 205–213.
- Sesé Benito, C., Sevilla García, P., 1996. Los micromamíferos del Cuaternario peninsular español: cronoestratigrafía e implicaciones bioestratigráficas. *Revista Española de Paleontología (Extraordinario)*, pp. 278–287.
- Sevilla, P., 1986. Identificación de los principales quirópteros ibéricos a partir de sus dientes aislados. Valor sistemático de los caracteres morfológicos y métricos dentarios. *Doñana Acta Vert.* 13, 111–130.
- Sevilla, P., 1988. Estudio Paleontológico de los Quirópteros del Cuaternario español. *Paleontología i Evolució* 22, 113–233.
- Sommer, R.S., Niederle, M., Labes, R., Zoller, H., 2009. Bat predation by the barn owl *Tyto alba* in a hibernation site of bats. *Folia Zoologica* 58 (1), 98–103.
- Spitzenberger, F., 1981. Die Langflügel-Fledermaus (*Miniopterus schreibersii*) in Österreich. *Mammalia austriaca* 5. Mitt. Abt. Zool. Landesmus. Joanneu 10 (2), 139–156.
- Strickler, T.L., 1978. Functional osteology and myology of the shoulder in the chiroptera. contributions to vertebrate evolution, vol. 4. S. Karger, New York (198 p.).
- Vincent, S., Nemoz, M., Aulagnier, S., 2011. Activity and foraging habits of *Miniopterus schreibersii* (Chiroptera: Miniopteridae) in southern France: implications for its conservation. *Hystrix Ital. J. Mammal* 22 (1), 52–72.