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Fossil bats from the Late Pleistocene site of the Aguilón P7 Cave (Zaragoza, Spain)

*Assemblage fossile des chiroptères du Pléistocène supérieur de la grotte d'Aguilón P7 (Saragosse, Espagne)*Julia Galán^{a,*}, Gloria Cuenca-Bescós^a, Juan Manuel López-García^b, Víctor Sauqué^a, Carmen Núñez-Lahuerta^a^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 Sezione di Scienze Preistoriche e Antropologiche, Dipartimento di Studi Umanistici, Università degli Studi di Ferrara, C. so Ercole I d'Este 32, 44100 Ferrara, Italy

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ABSTRACT

Bats (Chiroptera, Mammalia) are a valuable and independent source of palaeoenvironmental information in Quaternary sites because bat assemblages are not necessarily produced by the same processes as those of other small mammals. Here, we report a small collection of bats (MNI 15) from a cave infill of the Aguilón P7 (AGP-7) site (Zaragoza, Spain) dated Late Pleistocene (MIS 3). This is one of the rare localities south of the Ebro River (right bank) with Neanderthal tracks; therefore, the palaeoenvironmental data provided here may help us to understand Neanderthal history. Nine bat taxa were identified, viz. *Rhinolophus ferumequinum*, *R. hipposideros*, *Myotis* gr. *myotis/blythii*, *M. cf. bechsteinii*, *M. emarginatus*, *M. daubentonii*, *Plecotus* gr. *auritus/austriacus*, *Hipsugo savii* vel. *Pipistrellus kuhlii/nathusii*, and *Miniopterus schreibersii*. The presence of a high number of yearlings of the former four species suggests the presence of breeding colonies. The surprisingly high diversity of the sample indicates a variegated vegetation cover and relatively high humidity for the MIS 3 stage in the region.

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R É S U M É

Les chauves-souris (Chiroptera, Mammalia) retrouvées dans les sites fossiles quaternaires sont une source indépendante précieuse d'information paléoenvironnementale, puisque les assemblages de chiroptères ne proviennent pas nécessairement des mêmes processus que celles d'autres petits mammifères. Ici, nous décrivons pour la première fois une petite association relativement diversifiée de chauves-souris, trouvée dans une localité d'âge Pléistocène supérieur (MIS 3), le site d'Aguilón P7 (Saragosse, Espagne). C'est l'une des rares localités du Sud de l'Èbre (rive droite) ayant des traces des Néandertaliens ; par conséquent, les données paléoenvironnementales fournies ici peuvent aider à comprendre leur histoire. Neuf taxons de chiroptères ont été identifiés : *Rhinolophus ferumequinum*, *Rhinolophus hipposideros*, *Myotis* gr. *myotis/blythii*, *M. cf. bechsteinii*, *M. emarginatus*, *M. daubentonii*, *Plecotus*

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gr. *auritus/austriacus*, *Hypsugo savii* vel. *Pipistrellus kuhlii/nathusii* et *Miniopterus schreibersii*. La présence d'un nombre élevé de jeunes individus des quatre premières espèces suggère la présence de colonies de reproduction. L'importante et surprenante diversité de l'échantillon indiquent pour le MIS 3, dans la région, une couverture végétale variée et une humidité relativement élevée.

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1. Introduction

Bat fossil remains (Chiroptera, Mammalia) are interesting palaeoenvironmental indicators in Quaternary sites mainly due to their specific habitat preferences. Bats are only occasionally preyed upon by owls and other predators, such as carnivorous mammals, snakes or lizards (García et al., 2005; Kowalski, 1995; Rosina and Shokhrin, 2011; Sommer et al., 2009), but their habit of forming roosting colonies in caves sometimes allows the formation of exceptionally well-preserved assemblages (López-García and Sevilla, 2012). Because bat assemblages are not necessarily produced by the same processes as other small mammal assemblages, they provide a valuable independent source of palaeoenvironmental information.

Here, we describe for the first time a relatively diverse association of bats found in Aguilón P7 Cave (AGP-7), a new locality dating to the Late Pleistocene (MIS 3) in the central Ebro Valley. AGP-7 is one of the rare localities of the south of the Ebro River with Neanderthal tracks, and palaeoenvironmental data provided by this site may help understanding Neanderthal history (Cuenca-Bescós et al., 2010; Sauqué et al., 2014a). We focus on the taxonomic identification of the bat remains, the origin of the accumulation, the palaeoenvironment, and the comparison with other chiropteran associations from the Iberian Late Pleistocene.

2. The locality

2.1. Geographical and geological location

AGP-7 is a palaeontological cave-site located in the north face of the Iberian Range to the south of the River Ebro. It is situated on a small hill named Cerro Pezón; the mouth of the cave is open at 683 m above sea level (masl) on the left bank of the Valdeaguilón ravine, close to the town of Aguilón and 55 km from the main city of Zaragoza (Fig. 1) (Gisbert and Pastor, 2009). The P7 cave is part of a karst system in Upper Jurassic (Malm) marine limestones that opens at the contact between the two main formations from this age in the Iberian Range: the marls and clays of Loriguilla (Kimmeridgian) and the thick limestones of Higueraulas (Tithonian) (Cuenca-Bescós et al., 2010). As with other cases of speleogenesis in the Iberian Peninsula, the karst system is expected to have developed during the Pliocene–Early Pleistocene (Ortega et al., 2013). Its geometry, orientation and karst-cavity filling were conditioned by the incision of the main rivers, such as the River Ebro, and the development and incision of their hydrological

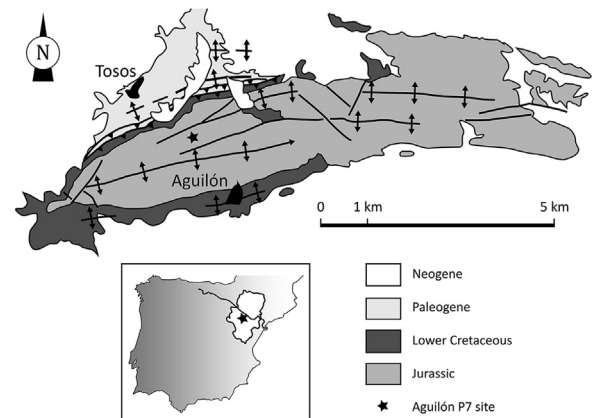


Fig. 1. Geographical and geological location of the Aguilón P7 site, modified from Cortés-Gracia and Casas-Sainz (1996).

Fig. 1. Situation géographique et géologique du site d'Aguilón P7, modifié d'après Cortés-Gracia and Casas-Sainz (1996).

basins. In the light of a preliminary geological survey made in the area in May 2010, the drainage of the karst system presumably changed from an original exit towards the River Huerva, the main river in the area, to the current discharge towards the Valdeaguilón Ravine, a secondary incision in the hydrological system of the area. The P7 cave is rather shallow and consists of an outer entrance hall and an inner gallery (Fig. 2). The cavity filling sediment of the outer entrance hall, where the main palaeontological excavation took place, consists of a single sedimentary level, 85 cm thick, comprising heterometric limestone ridges in a reddish clay matrix, probably corresponding to a single deposition event, while sediments in the inner gallery were likely deposited during a previous stage (Cuenca-Bescós et al., 2010).

2.2. Dating the sedimentary fill of the AGP-7

A bone fragment that came out of a sample of fossil remains from the surface cleaning, almost certainly from the top of the section, was dated by radiocarbon resulting in $34,760 \pm 360$ BP– $34,860 \pm 360$ BP (Beta – 222732), providing a minimum age of the reservoir in the area's known slope (P in Fig. 2). In recent years, a second radiocarbon date was provided by a bone from a roe deer *Capreolus capreolus* exhumed from the base of the section. This gave an age of just under 46.3 ka BP (OxA-27902; for the methodology employed see Bronk Ramsey et al., 2004). Thus, the faunal and lithic assemblages point to a Late Pleistocene biostratigraphic age, likely from the beginning of Marine Isotope

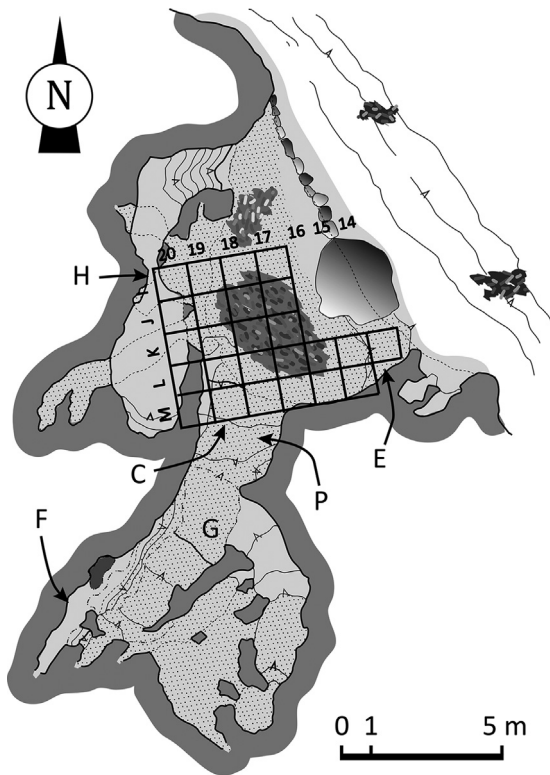


Fig. 2. Plan view of the Aguilón P7 cave and the excavation grid. The following sectors were distinguished: E: *entrada*, P: *pendiente*, C: *centro* and H: *hiedra* in the outer entrance hall; and sectors G: *galería* and F: *fondo* in the inner gallery. Modified from Gisbert and Pastor (2009); Cuenca-Bescós et al. (2010).

Fig. 2. Plan de la grotte P7 d'Aguilón et du carroyage de fouille. Les secteurs suivants ont été distingués E: *entrada*, P: *pendiente*, C: *centro* et H: *hiedra* dans le hall d'entrée extérieur et les secteurs G: *galería* et F: *fondo* dans la galería intérieure. Modifié d'après Gisbert et Pastor (2009); Cuenca-Bescós et al. (2010).

Stage 3 (MIS3). MIS 3 was a period characterized by rapid climate changes (Sánchez-Goni and D'Errico, 2005), supporting the existence of Pleistocene communities with no present-day analogy, and that shared distributions that are currently disjunct (López-García et al., 2010; Sauqué et al., 2014b; Sommer and Nadachowski, 2006).

2.3. The faunal assemblage

Even though only a small part of AGP-7 cave has been excavated, the species richness and the number of remains are notable. The faunal list is as follows (Cuenca-Bescós et al., 2010; Galán, 2013; Núñez-Lahuerta et al., 2015): small mammals—*Crocidura* sp., *Lagomorpha* indet., *Apodemus* sp., *Microtus* sp., *Microtus (Terricola)* sp., *Iberomys cabreræ* and *Chionomys nivalis*; large mammals—*Cuon alpinus*, *Canis lupus*, *Crocota crocata*, *Panthera pardus*, *Vulpes vulpes*, *Ursus arctos*, *Lynx pardinus*, *Felis silvestris*, *Meles meles*, *Cervus elaphus*, *Capra pyrenaica*, *Capreolus capreolus*, *Rupicapra pyrenaica* and *Equus ferus*; birds—Galliformes indet., *Lagopus* sp., *Aquila chrysaetos*, *Gyps fulvus*, Passeridae indet., *Anthus trivialis*, *Prunella modularis*, *Sturnus cf. unicolor*, and *Corvus monedula*. The cave may have been used as

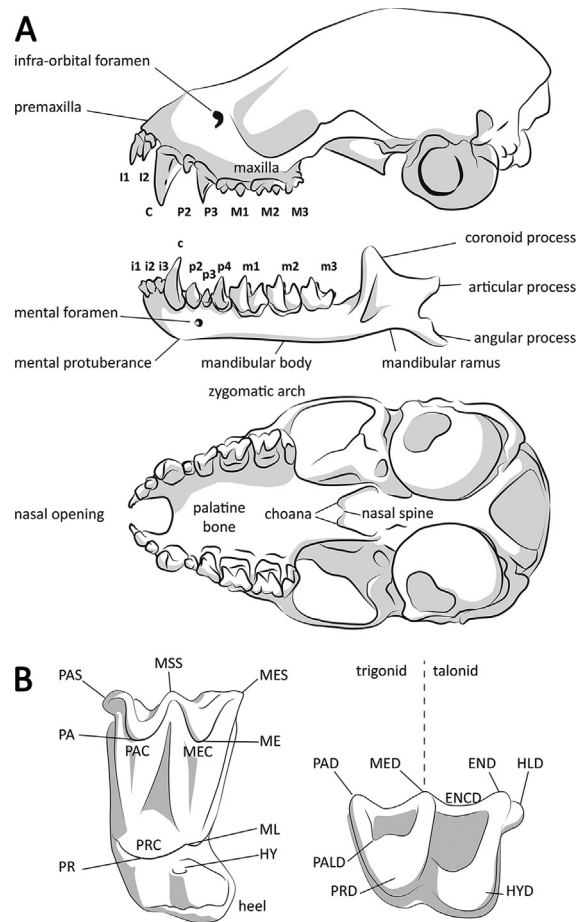


Fig. 3. Anatomy of bat cranial skeleton. A. Lateral view of skull and hemimandible, and ventral view of skull, modified from Benzal and de Paz (1990). B. Occlusal view of upper molar (left) and lower molar (right), modified from Sevilla (1988). Abbreviated names are explained in the paragraph “Abbreviations”.

Fig. 3. Anatomie du crâne d'une chauve-souris. A. Vue latérale du crâne et de la mandibule, et vue ventrale du crâne, modifié d'après Benzal et de Paz (1990). B. Vue occlusale de la molaire supérieure (à gauche) et de la molaire inférieure (à droite), modifié d'après Sevilla (1988). Les abréviations sont expliquées dans le paragraphe « Abréviations ».

a den by large carnivores, yet some Mousterian tools have been recovered, including a scraper, and tool marks in some fossils have been observed, suggesting that the cave was visited by Neanderthals, even though no human remains have been found.

3. Material and methods

3.1. Abbreviations

Institutional—MPZ: Palaeontological Museum of Zaragoza; EBD: Doñana Biological Station-CSIC; MNCN: National Museum of Natural Science-CSIC, Madrid; GA: Aragosaurus Group-IUCA, Zaragoza; CIAMA: International Centre for Water and Environment-La Alfranca, Zaragoza.

Dental terminology (Fig. 3)—I: upper incisor; C: upper canine; P: upper premolars; M: upper molars; the teeth from the lower dental series are indicated in the same way

but using lowercase letters. The anatomical parts of molars are abbreviated as follows, PA: paracone; ME: metacone; PR: protocone; PAC: paracrista; MEC: metacrista; PRC: protocrista; PAS: parastyle; MSS: mesostyle; MES: metastyle; HY: hypocone; PL: paraconule; ML: metaconule; PAD: paraconid; MED: metaconid; PRD: protoconid; END: entoconid; HYD: hypoconid; HLD: hypoconulid; ENCD: entoconid; PALD: paralophid; tg: trigonid; td: talonid.

Anatomical elements – max: maxilla; md: mandible; hu: humerus; d. e.: distal epiphysis; diap.: diaphysis; fr: fragment.

3.2. Sample processing and fossil sorting

The bat fossil remains studied here consist of disarticulated bone fragments collected by water-screening the sediment excavated at the Cave P7 during the years 2005, 2009 and 2010. Superimposed screens of 0.2 cm and 0.05 cm mesh were used. The palaeontological excavation was divided into six different sectors (Fig. 2): *Entrada* (E), *Pendiente* (P), *Centro* (C), *Galería* (G), *Fondo* (F) and *Hiedra* (H); *in situ* material was extracted from sector F and from sectors E, P, C and H. The fossils were picked out from the residues, and then the bat remains were separated and identified. They are all kept in the MPZ. To evaluate the bat representation, the number of identified specimens (NISP) and the minimum number of individuals (MNI) were calculated for each taxon in accordance with Lyman (1994). For taxonomic identification these authors have been followed: Dupuis (1986); Felten et al. (1973), Menu and Popelard (1987), Sevilla (1988). The reference collections of the EBD, MNCN, GA and CIAMA were used.

3.3. Palaeoenvironmental approach

We used the habitat weighting method (see Andrews, 2006; Evans et al., 1981) to infer palaeoenvironmental characteristics. Five types of habitat are defined according to concrete environmental features: “open dry (OD)”, meadows under seasonal climate change; “open humid (OH)”, evergreen meadows with dense pastures and suitable topsoil; “woodland (Wo)”, mature forest including woodland margins and forest patches with moderate ground cover; “rocky (Ro)”, areas with a suitable rocky or stony substratum; and “water (Wa)”, areas along streams, lakes and ponds. Bat remains from sector F (Fig. 2) were not taken into account for the palaeoenvironmental approach as they correspond to a previous accumulation event (Cuenca-Bescós et al., 2010), but they were identified and measured.

4. Recorded taxa

Order CHIROPTERA Blumenbach, 1779

Family RHINOLOPHIDAE Gray, 1825

Genus *Rhinolophus* Lacépède, 1799

Rhinolophus ferrumequinum (Schreber, 1774) – Greater horseshoe bat (present habitat and distribution in Table 1).

MATERIAL (Fig. 4A, H; Appendix A): 1 max (fr) with M1, M2; 1 max (fr) with M3; 3C; 1 P4; 1 md with p4, m1; 1 md

with p3, p4, m1, m2, m3; 1 md (fr) with p4; 1 c; 2 m1; 2 m2; 2 m3; 1 m1 (fr).

DESCRIPTION: *R. ferrumequinum* is the most abundant species in AGP-7 and one of the largest. The **C** has a trapezoidal occlusal outline with a strong crown with three sides and a distally bent apex. The lingual side is the widest; it is flat and presents a small heel. The cingulum thickness is variable and has a zigzag morphology, inflexions pointing alternately to apex and root. The **P4** has a rectangular occlusal outline, a wide, well-developed heel and a narrow cingulum, which disappears distally. The upper molars present a parastyle forming an angle, though only the M1 has a (straight) metastyle. The **M1** and **M2** have a rectangular occlusal outline and a well-developed parastyle and heel. The protocone is on the mesial margin and its base lacks a cingulum. The **M3** has a subtriangular occlusal outline and presents a small parastyle. The metacone is smaller than the protocone, and there is a slightly developed metaconule on the post-protocrista. The **maxilla** fragments present the infra-orbital foramen located over the alveolus of the M2, and the alveolus of the M3 is located on the zygomatic arch root. The **c** has a semicircular occlusal outline in the base but the cusp has two sides, its apex and root are aligned and the cingulum is narrow and forms a small projection at posterior side. The **p3** is very small – sometimes even absent – and appears out of the dental series. The **p4** has a trapezoidal occlusal outline with three sides and a narrow cingulum, which is slightly thicker at the distal margin. The lower molars are of the nyctalodont type and present a narrow and regular labial cingulum. The **m1** and **m2** have an open trigonid, which is narrower in m2, and their lingual cusplets are not aligned, the hypoconulid having a labial position. The **m3** presents a narrow trigonid and a reduced talonid due to the labial migration of the entoconid. The **mandibles** have a long and flat horizontal body and an almost rectangular mandibular ramus with flat and low coronoid process. The mental protuberance appears well-developed; the mental foramen is circular and located under the p2 alveolus, or under the junction of the alveoli of c and p2.

DISCUSSION: The morphological features and the size (Appendix A) of the teeth and bones of this fossil material conform to the specimens of *R. ferrumequinum* described in Sevilla (1988).

Rhinolophus hipposideros (Bechstein, 1800) – Lesser horseshoe bat (present habitat and distribution in Table 1).

MATERIAL (Fig. 4E; Appendix A): 1 max (fr) with P4, M1, M2.

DESCRIPTION: This is the smallest species of this genus in the Palaearctic region. The **P4** has a rectangular occlusal outline and a wide, well-developed heel. The thickness of the cingulum is constant along the heel. The upper molars present a parastyle forming an angle, a straight metastyle and a comparatively wide heel. The **M1** has a square occlusal outline, while the **M2** is narrower. The base of the protocone lacks a cingulum and in the M1, it advances beyond the heel. Although the studied **maxilla** is fragmented, the bulging-out nasal region can be appreciated, and also the huge palatine incision caused by the

Table 1

Synthetic notes on current distribution, habitat preferences and roosting habits for the bat species considered in this work. Masl: meters above sea level. Data obtained from [Palomo et al. \(2007\)](#).

Tableau 1

Notes synthétiques sur la distribution actuelle, préférences d'habitat et modes de gîte pour les espèces de chiroptères considérées dans ce travail. Masl : mètres au-dessus du niveau de la mer. Les données ont été extraites de [Palomo et al. \(2007\)](#).

Taxon	Geographic range in Europe	Distribution (Spain)	Alt. range (Spain)	Habitat preferences (Spain)	Roosting habits (Spain)
<i>Rhinolophus ferrumequinum</i>	From England to the Mediterranean peninsulas	All Spain (with the Balears); scarcer in the internal areas	0–1600 masl	Ubiquitous; mainly prefer transitional woodland areas	Mainly caves. Small colonies
<i>Rhinolophus hipposideros</i>	From the southern Germany and Poland to the Medit. peninsulas	All Spain (with the Balears); scarcer in the internal areas	0–2000 masl	Woodland and transitional woodland; water bodies	Caves. Nursery colonies; solitary hibernation
<i>Myotis myotis</i>	Western, central and southern Europe	All Spain (with the Balears); scarcer in the central Ebro Valley and the South Submeseta	0–2060 masl	Woodland, transitional woodland and woodland margins	Caves. Massive nursery colonies; smaller hibernating colonies
<i>Myotis blythii</i>	Southern Europe and southern parts of central Europe	All Spain (with the Balears), except the Northwest margin; very scarce	0–100 masl	Open areas, seasonal meadows	Caves. Massive nursery colonies; smaller hibernating colonies
<i>Myotis bechsteinii</i>	Across central and southern Europe (including islands)	Mainly in the Cantabrian margin and the Central Range; very scarce	0–500 masl	Woodland	Mainly caves. Small nursery colonies; solitary hibernation
<i>Myotis emarginatus</i>	From the South of the Netherlands and Germany across southern Europe	All Spain (with the Balears); very scarce, especially in the most internal areas	0–1700 masl	Woodlands; frequently avoiding the most closed areas	Caves. Nursery colonies
<i>Myotis daubentonii</i>	Almost all Europe; scarcer at the southern margins of the Medit. peninsulas	Across the north-western Peninsula, sporadically in the Medit. margin	0–1600 masl	Always linked to water bodies	Caves, tree-holes. Small nursery colonies; solitary hibernation
<i>Plecotus auritus</i>	All the palaeartic region	Mountain ranges of the northern Peninsula	0–1600 masl	Mature woodlands	Caves, tree-holes. Nursery colonies; solitary hibernation
<i>Plecotus austriacus</i>	Middle latitudes, from England to southern Europe	All Spain (with the Balears); not very abundant but frequent	0–2100 masl	Woodland, transitional woodland and dry, seasonal meadows	Caves, tree-holes. Nursery colonies; solitary hibernation
<i>Pipistrellus kuhlii</i>	Across southern Europe	All Spain (with the Balears and the Canaries); except north-western margin	0–1500 masl	Mainly open woodland; but high synanthropy	Tree-holes and crevices. Small to medium nursery colonies
<i>Pipistrellus nathusii</i>	All Europe from Scandinavia to the Medit. peninsulas	Mainly limited to northern Peninsula; very scarce	0–900 masl	Woodland	Tree-holes, crevices. Small to medium nursery colonies
<i>Hypsugo savii</i>	Across the Medit. Europe	Almost all Spain (with the Canaries); scarce	0–3300 masl	All type of habitats	Tree-holes, crevices. Small to medium nursery colonies
<i>Miniopterus schreibersii</i>	Across the southern Europe	All Spain (with the Balears)	0–1400 masl	Open and woodland areas; rocky habitats where caves or crevices occur	Caves, crevices. Massive nursery and hibernation colonies

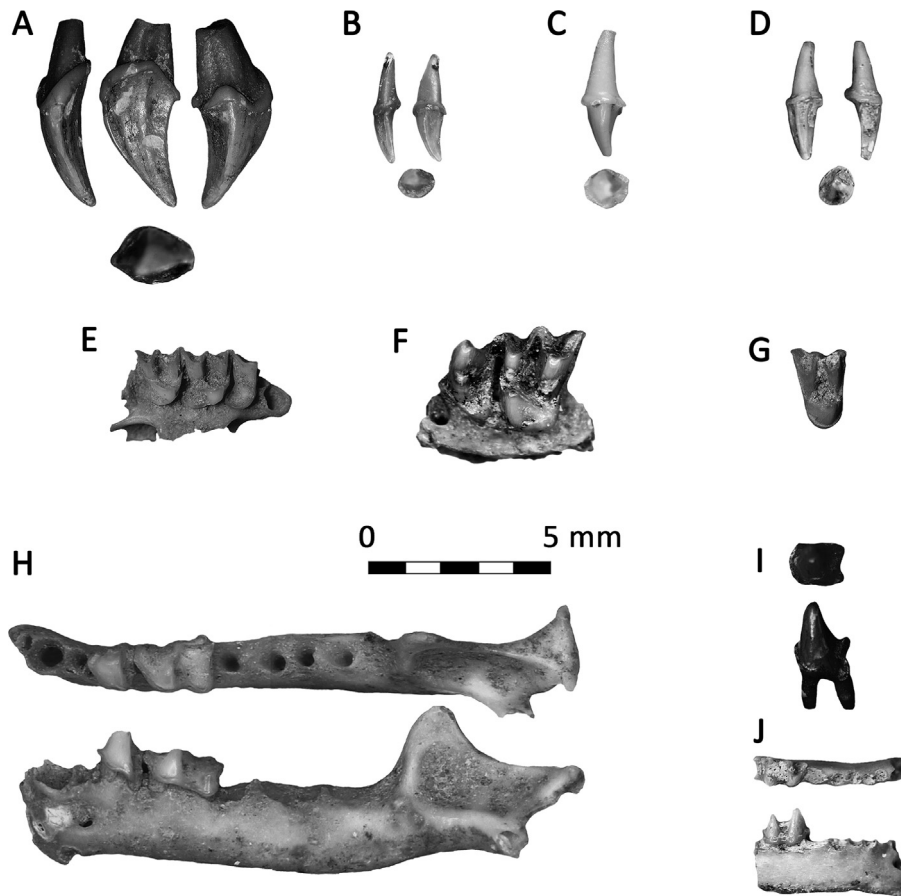


Fig. 4. Fossil cranial bat remains from the Aguilón P7 site. A. Right C of *Rhinolophus ferrumequinum* (MPZ 2014/257). B. Left C of *Myotis emarginatus* (MPZ 2014/278). C. Left C of *Plecotus* gr. *auritus/austriacus* (MPZ 2014/286). D. Right C of *Miniopterus schreibersii* (MPZ 2014/290). E. Fragment of right maxilla of *Rhinolophus hipposideros* (MPZ 2014/240). F. Fragment of left maxilla of *Myotis* gr. *myotis/blythii* (MPZ 2014/271). G. Right M2 of *Plecotus* gr. *auritus/austriacus* (MPZ 2014/285). H. Left mandible of *Rhinolophus ferrumequinum* (MPZ 2014/241). I. Left p4 of *Myotis* gr. *myotis/blythii* (MPZ 2014/265). J. Fragment of left mandible of *Myotis daubentonii* (MPZ 2014/279).

Fig. 4. Restes crâniens fossiles de chauve-souris du site d'Aguilón P7. A. C droite de *Rhinolophus ferrumequinum* (MPZ 2014/257). B. C gauche de *Myotis emarginatus* (MPZ 2014/278). C. C gauche de *Plecotus* gr. *auritus/austriacus* (MPZ 2014/286). D. C droite de *Miniopterus schreibersii* (MPZ 2014/290). E. Fragment de maxillaire droit de *Rhinolophus hipposideros* (MPZ 2014/240). F. Fragment de maxillaire gauche de *Myotis* gr. *myotis/blythii* (MPZ 2014/271). G. M2 droite de *Plecotus* gr. *auritus/austriacus* (MPZ 2014/285). H. Mandibule gauche de *Rhinolophus ferrumequinum* (MPZ 2014/241). I. p4 gauche de *Myotis* gr. *myotis/blythii* (MPZ 2014/265). J. Fragment du mandibule gauche de *Myotis daubentonii* (MPZ 2014/279).

disarticulation of the premaxilla, typical in this genus. The posterior rim of the horizontal plate of the palatine presents a square outline, a well-developed posterior nasal spine and a choanal line anteriorly displaced in comparison with other members of the genus.

DISCUSSION: The wide heel of the upper teeth and the size of the remains (Appendix A) indicate that the remains belong to *R. hipposideros* according to Sevilla (1988). The features of the palatine posterior rim have been also observed in the *R. hipposideros* specimens from the EBD collection.

Family VESPERTILIONIDAE Gray, 1821

Genus *Myotis* Kaup, 1829

Myotis myotis (Borkhausen, 1797) – Greater mouse-eared bat (present habitat and distribution in Table 1).

Myotis blythii (Tomes, 1857) – Lesser mouse-eared bat (present habitat and distribution in Table 1).

Myotis gr. *myotis/blythii*

MATERIAL (Fig. 4F, I; Appendix A): 1 max (fr) with P4, M1; 1 P2; 2 P4; 1 M1; 2 c; 3 p4; 5 m1 (fr); 1 m2 (fr).

DESCRIPTION: The **P2** has an oval occlusal outline, while **P4** is triangular with a very strong crown; both have a thick cingulum. The **M1** has a square occlusal outline. It presents a well-developed parastyle forming an angle, and a smaller bent metastyle. The cingulum is thick, but it is not present at the base of the protocone and the lingual. There is a metaconule. The **maxilla** fragment presents the infra-orbital foramen located above the junction of the P4 and M1 alveoli; the bone bar between the foramen and the orbit is rather thick. The **c** has a semicircular occlusal outline in the base but the cusp has three sides, apex and root being aligned. In the distal side, the thick cingulum is slightly projected backwards and also forms an inflexion upwards; it disappears in the anterior side. The **p4** has a rectangular occlusal outline and a three-faced crown; the distal side is strongly concave. The cingulum is thick, irregular and continuous. The lower molars are of the myotodont type,

with a thick and slightly irregular cingulum. The trigonid is rather closed in **m1** and **m2**, and narrower in the latter. The lingual cusplets are not aligned; the hypoconulid has a more labial position. The entocristid is almost straight.

DISCUSSION: These two species (*M. myotis* and *M. blythii*) are difficult to distinguish from one another as their bones and teeth are very similar in morphology and size, although *M. myotis* is in general terms slightly larger than *M. blythii* (López-García, 2008; Sevilla, 1988). The morphological features and the size (Appendix A) of the remains indicate that they belong to a large species of the genus *Myotis* (*M. myotis* or *M. blythii*) based on the data provided by Sevilla (1988). Some biometric methods allow the two species to be distinguished, but these are hard to use when the sample is composed of isolated teeth. The measurements of the **m3** are a good diagnostic element (Sevilla, 1988), but this molar has not been found in the assemblage. A biometric analysis has been performed on the M1 specimens (after López-García, 2008), comparing them with current specimens from the collections at the EBD, GA, MNCN and CIAMA suggests that they probably belong to *M. myotis*. However, as the remaining elements cannot be assigned to either of the two species either by biometric or morphological criteria, the whole sample has been classified as *M. gr. myotis/blythii*.

Myotis bechsteinii (Kuhl, 1817)–Bechstein's bat (present habitat and distribution in Table 1).

Myotis cf. bechsteinii

MATERIAL (Fig. 5A; Appendix A): 1 hu (d. e. + diap.).

DESCRIPTION: The **distal humeral epiphysis** presents a rather shallow antecubital fossa. In external view, the trochlea and the condyle dip slightly to the epicondyle and there is a shallow furrow between them. The distal ends of the trochlea and the condyle have a similar height. The posterior epicondyle outline presents a concave–convex morphology with a pointed but not sharp edge.

DISCUSSION: The specimen presents typical *Myotis* features – a reduced epitrochlea and a styloid process. The morphology coincides with the fossil specimens of *M. bechsteinii* reported by Sevilla (1990); the epiphysis length (Appendix A) agrees with data for that species provided by Felten et al. (1973). However, a single humeral fragment does not allow unequivocal identification in the case of *M. bechsteinii* so we determined it as *M. cf. bechsteinii*.

Myotis emarginatus (Geoffroy, 1806). Geoffroy's bat (present habitat and distribution in Table 1).

MATERIAL (Fig. 4B; Appendix A): 1C; 1 **m3**; 2 **m2**.

DESCRIPTION: The **C** has an oval occlusal outline with two sides; apex and root are aligned. The labial side presents a longitudinal furrow in the distal margin. The cingulum is thicker in the anterolabial margin. The **m2** has a closed trigonid and its cingulum is thick and almost regular. The lingual cusplets are almost aligned, except for the hypoconulid, which is slightly labial. The paraconid and metaconid cusplets are similar in height, while the

entoconid is slightly lower. The paralophid is concave and the entocristid is almost straight. The **m3** has a closed trigonid and a medium-thick cingulum, which is thinner in the mesial and distal margins. The paralophid is concave and not angular. The talonid appears reduced due to the labial displacement of the hypoconulid.

DISCUSSION: The main morphological features and the size (Appendix A) of the specimens described above coincide with the data reported by Sevilla (1990) for *M. emarginatus*. According to this author, the occlusal outline and the furrow in the C, and the disposition of the talonid cusplets in the lower molars, are diagnostic elements for distinguishing this taxon from other similarly sized species of *Myotis*, such as *M. nattereri*. The development of the entoconid in the **m2** differs somewhat from that observed in the material used for comparison, where this is the highest and strongest labial cusp. However, this was not considered reason enough to assign the specimens to another taxon, but was regarded as intraspecific variability.

Myotis daubentonii (Kuhl, 1817)–Daubenton's bat (present habitat and distribution in Table 1).

MATERIAL (Fig. 4J; Appendix A): 1 M1; 1 md (fr) with **m2**; 1 **m1**.

DESCRIPTION: *M. daubentonii* is small in comparison with other members of the genus *Myotis*. The **M1** has a subtriangular occlusal outline. It presents a well-developed parastyle forming an angle, and a slightly bent metastyle. The metacone is markedly stronger than the paracone and somewhat higher. The base of the protocone presents a strong cingulum in its distal margin. There is a well-developed metaconule and also a paraconule is present. The **mandible** fragment shows a circular mental foramen located under the p2 alveolus. The lower molars present a thick and irregular cingulum. The trigonid is rather closed in **m1** and **m2**, being narrower in **m2**. The lingual cusplets are almost aligned except for the hypoconulid, which is slightly labial. It is notable that the entoconid is the strongest lingual cusp, as high as the metaconid. The paralophid has a shallow concavity.

DISCUSSION: The size (Appendix A) and morphological features of the described specimens agree with data for *Myotis daubentonii* from Sevilla (1990). The presence of a paraconule in the M1 allows distinguishing this taxon from *M. mystacinus* according to Menu and Popelard (1987). Regarding the lower molars, the entoconid in lingual view is remarkably strong in both teeth, which is a feature that only has been observed in extant *M. daubentonii* from the reference collection but not in other small *Myotis*, such as *M. mystacinus*.

Myotis emarginatus/daubentonii

MATERIAL (Fig. 5B; Appendix A): 1 hu (d. e. + diap.).

DESCRIPTION: The **distal humeral epiphysis** presents a well-marked antecubital fossa. In external view, the trochlea and the condyle dip slightly to the epitrochlea and there is a shallow but somewhat angular furrow between them. The distal end of the trochlea is higher than the condyle. The epitrochlea has an angular contour.

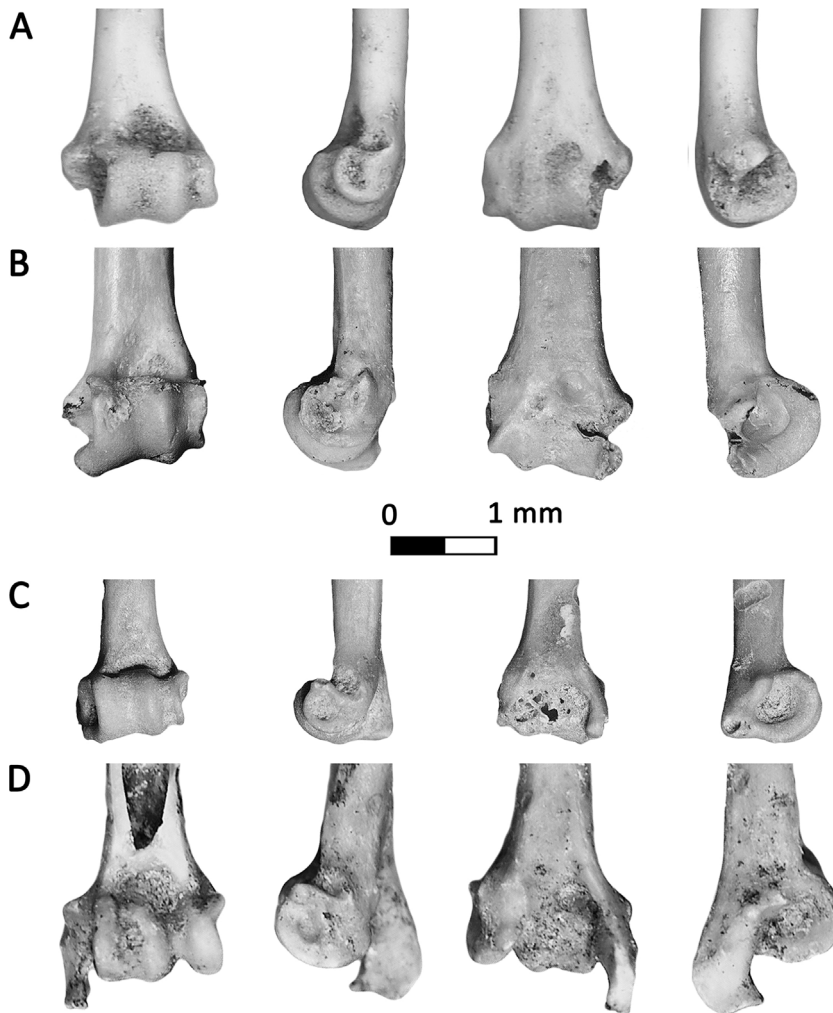


Fig. 5. Distal humeral epiphysis of fossil bat remains from the Aguilón P7 site. A. Left distal humeral epiphysis of *M. cf. bechsteini* (MPZ 2014/282). B. Left distal humeral epiphysis of *M. emarginatus/daubentonii* (MPZ 2014/281). C. Left distal humeral epiphysis of *H. savii* vel. *P. gr. kuhlii/nathusii* (MPZ 2014/287). D. Left distal humeral epiphysis of *M. schreibersii* (MPZ 2014/288).

Fig. 5. Restes postcrâniens fossiles de chauve-souris du site d'Aguilón P7. A. Épiphyse distale gauche de *M. cf. bechsteini* (MPZ 2014/282). B. Épiphyse distale gauche de *M. emarginatus/daubentonii* (MPZ 2014/281). C. Épiphyse distale gauche de *H. savii* vel. *P. gr. kuhlii/nathusii* (MPZ 2014/287). D. Épiphyse distale gauche de *M. schreibersii* (MPZ 2014/288).

DISCUSSION: The size (Appendix A) as well as the morphology of the specimens agrees with *M. emarginatus*, *M. nattereri* and *M. daubentonii* (Dupuis, 1986) (Felten et al., 1973). The length of the epitrochlea is shorter than in *M. nattereri*, which is a character indicated by Dupuis (1986) for distinguishing this taxon from *M. emarginatus* and *M. daubentonii*. Another diagnostic character is the size of the styloid process, but this part of the bone is broken in the studied specimen.

Genus *Plecotus* Geoffroy, 1818

Plecotus auritus (Linnaeus, 1758) – Brown long-eared bat (present habitat and distribution in Table 1).

Plecotus austriacus (Fischer, 1829) – Grey long-eared bat (present habitat and distribution in Table 1).

Plecotus gr. auritus/austriacus

MATERIAL (Fig. 4C, G; Appendix A): 1C; 1 M2; 1 m1; 1 m1 (fr).

DESCRIPTION: The C has an almost circular occlusal outline. The crown has two sides (labial and lingual), both of which have a longitudinal furrow in the distal half, the junction between the two sides forming a blunt edge. The cingulum is thick and almost regular. The M2 has an elongated, rectangular occlusal outline, and the base of the protocone has a circular outline and presents a thick cingulum, which continues along the distal and mesial sides. The M2 has a well-developed parastyle forming an angle, and a smaller bent metastyle. The metacone is markedly stronger and higher than the paracone. The lower molars are of the myotodont type and have a thick and very irregular cingulum. The m1 trigonid is open, and the lingual cusplets are almost aligned except for the hypoconulid, which

is slightly labial. The paraconid, metaconid and entoconid have a similar height and are somewhat short and wide. The union between the paraconid and metaconid shows a deep depression.

DISCUSSION: The material has been assigned to the genus *Plecotus* on the basis of the occlusal outline of the M2, the geometry and disposition of the trigonid and hypoconulid of the lower molars, and the occlusal outline and furrow of C, which are diagnostic characters of the two Iberian species of the genus according to the fossil and present-day specimens described by Sevilla (1988, 1990). However, distinguishing between *P. auritus* and *P. austriacus* is hard when the sample is composed of isolated teeth. According to Sevilla (1988), C and P4 are diagnostic elements. The junction between the two sides of the upper canines forming a blunted edge is characteristic of *P. auritus*, as this edge is sharper and the cusp is longer in *P. austriacus*. The upper canine probably belongs to *P. auritus*, but as there are no clear criteria applicable for distinguishing the remaining specimens, the whole sample has been classified as *P. gr. auritus/austriacus*.

Genus *Hypsugo* Kolenati, 1856 vel Genus *Pipistrellus* Kaup, 1829

Hypsugo savii (Bonaparte, 1837) – Savi's pipistrelle (present habitat and distribution in Table 1).

P. kuhlii (Kuhl, 1817) – Kuhl's pipistrelle (present habitat and distribution in Table 1).

P. nathusii (Keyserling and Blasius, 1839) – Nathusius's pipistrelle (present habitat and distribution in Table 1).

Hypsugo savii vel *Pipistrellus* gr. *kuhlii/nathusii*

MATERIAL (Fig. 5C; Appendix A): 1 hu (d. e. + diap.).

DESCRIPTION: The distal humeral epiphysis has an internally projected delta-shaped styloid process. The antecubital fossa is rather deep. In external view, the trochlea and the condyle dip slightly to the epitrochlea and there is a shallow furrow between them; the epicondyle is hidden by the condyle. The posterior epicondyle outline presents a concave-convex morphology with a bulge at the edge. The distal margin of the trochlea goes slightly beyond that of the condyle, and the distal margin of the condyle goes slightly beyond that of the epicondyle.

DISCUSSION: Based on the general morphology and the size (Appendix A) of the specimen, it can belong to the taxa *H. savii*, *P. kuhlii* or *P. nathusii* based on Dupuis (1986) and Felten et al. (1973).

Genus *Miniopterus* Bonaparte, 1837

Miniopterus schreibersii (Kuhl, 1817) – Schreibers' bat (present habitat and distribution in Table 1).

MATERIAL (Fig. 4D; Fig. 5D; Appendix A): 1 hu. (d. e. + diap.); 1 C; 1 m2.

DESCRIPTION: This is a medium-sized bat in relation to other cave-dwelling bats. The C has a nearly oval occlusal outline. The apex and the root are aligned. The cingulum is continuous, slightly irregular and not very thick. The crown has four deep longitudinal furrows, one of them in the distolabial margin, the others on the lingual side. The lower molars are of the nyctalodont type and present a thin and regular cingulum. The m2 trigonid is open and

shows a small lingual cingulum. The lingual cusplets are almost aligned except for the hypoconulid, which has a labial position. The metaconid is the highest lingual cusp; the unions between the cusplets are deep depressions. The entocristid forms a marked angle with the entoconid. The paralophid is concave. The distal humeral epiphysis presents a long, flattened blade-shaped styloid process. The antecubital fossa is well-developed. In external view, the condyle dips slightly to the trochlea. The furrows separating the condyle, trochlea and epicondyle are rather deep, the furrow between the latter two being the deepest.

DISCUSSION: According to Sevilla (1988), the deep longitudinal furrows of the C and the morphology and disposition of the m2 cusplets described above are diagnostic for the species *M. schreibersii*, as is the distal humeral epiphysis, which presents a blade-shaped styloid process and deep external furrows.

5. Results and discussion

All chiropteran fossil remains were recovered from the AGP-7 assemblage totaling 51 specimens. Every specimen has been described and assigned to a taxon. Nine taxa of the order Chiroptera have been identified (Table 2).

5.1. Taphonomy. The origin of the accumulation

The post-cranial remains in the bat fossil assemblage of AGP-7 represent less than 8% of the total, the dominant elements are isolated teeth while complete bones are scarce (Table 3). Teeth show different colours from white to dark brown (e.g., Fig. 4C, I). Clear evidence of digestion is only observed in one humerus affecting its olecranon fossa (Fig. 5C). Around 25% of the remains are partially affected by manganese oxide mineralization (e.g., Fig. 4A, F; Fig. 5D), which is a common post-burial alteration in cave-sediments (Bennàsar-Serra, 2010); only one isolated tooth is affected by carbonate concretion. Notably, 85% of dental remains belonged to yearlings showing no teeth-wear; only a few dental specimens of *R. ferrumequinum* (e.g., Fig. 4H) and *M. gr. myotis/blythii* belonged adult individuals.

The abundance of such typical cave-dwelling bats as *R. ferrumequinum* and *M. gr. myotis/blythii* suggests that both taxa were accumulated by *in situ* death within the cave. However, the scarce complete bones, the differential loss of post-cranial remains and the dominance of isolated teeth indicate some grade of transport. We propose a process of dragging-out of the remains from an inner hall of the cave where the *in situ* accumulation actually took place. Both taxa show a mixed age composition with yearlings and old individuals, which is the typical pattern of hibernating colonies thanatocenosis (López-García and Sevilla, 2012). Some minority taxa in AGP-7 assemblage are also typical cave-dwelling species, such as *R. hipposideros*, *M. bechsteinii*, *M. emarginatus* or *Miniopterus schreibersii*. On the other hand, some others rarely roost in Iberian caves: *M. daubentonii*, *P. gr. auritus/austriacus*, *H. avii* and *P. gr. kuhlii/nathusii* (Palomo et al., 2007), from which at least one specimen shows marks of digestion. A relatively high diversity of the bat assemblage together with a low proportion

Table 2

Quantitative presence indices for the taxa making up the total bat assemblage of Aguilón P7, Zaragoza, Spain, and distribution by habitat (according to Palomo et al., 2007). NISP: number of identified specimens; MNI: minimum number of individuals; OD: open dry; OH: open humid; Wo: woodland/woodland margins; Ro: rocky; Wa: water.

Tableau 2

Indices de présence quantitative pour les taxons de la totalité de l'assemblage de chiroptères d'Aguilón P7, Saragosse, Espagne, et distribution par habitat (selon Palomo et al., 2007). NISP: nombre de spécimens identifiés; MNI: nombre minimum d'individus; OD: ouvert et sec; OH: ouvert et humide; Wo: forêt/bordures de forêt; Ro: rocheux; Wa: aquatique.

Taxon	NISP	MNI	%	Habitat				
				OD	OH	Wo	Ro	Wa
<i>R. ferrumequinum</i>	17	5	33.3			0.8	0.2	
<i>R. hipposideros</i>	1	1	6.7			0.6	0.2	0.2
<i>M. gr. myotis/blythii</i>	16	2	13.3	0.2		0.6	0.2	
<i>M. cf. bechsteinii</i>	1	1	6.7			0.9	0.1	
<i>M. daubentonii</i>	3	1	6.7			0.2	0.2	0.6
<i>M. emarginatus</i>	4	1	6.7	0.4		0.4	0.2	
<i>M. emarginatus/daubentonii</i>	1	–	–	–	–	–	–	–
<i>P. gr. auritus/austriacus</i>	4	2	13.3	0.2		0.7	0.1	
<i>H. savii</i> vel <i>P. gr. kuhlii/nathusii</i>	1	1	6.7	0.2	0.2	0.5	0.1	
<i>M. schreibersii</i>	3	1	6.7	0.2	0.2	0.4	0.2	
Total	51	15	100					

Table 3

Quantitative data for the osteological composition of the total bat assemblage of Aguilón P7 (Zaragoza, Spain). *n*: number of elements; %: percentage of the whole bat assemblage constituted by each element.

Tableau 3

Données quantitatives pour la composition ostéologique de l'assemblage total de chiroptères d'Aguilón P7 (Saragosse, Espagne). *n*: nombre d'éléments; %: pourcentage de chaque élément dans tout l'assemblage de chauves-souris.

Element	<i>n</i>	%
max (fr)	3	5.9
M	4	7.8
C	6	11.8
P2	1	2
P4	3	5.9
md	2	3.9
md (fr)	2	3.9
c	3	5.9
p4	3	5.9
m	12	23.5
m (fr)	8	15.7
hu (d. e. + diap.)	4	7.8
Total	51	100

of bat fossils in the entire small vertebrate sample (bat remains represent less of the 5% of the total recovered remains of small vertebrates) is the characteristic pattern of an owl-accumulated assemblage (Kowalski, 1995; López-García and Sevilla, 2012). Our proposal for this group is that probably both processes (owl-predation and death within the cave) contributed to the accumulation. The near-exclusive presence of yearlings could be explained as the typical pattern of nursery colonies thanatocenosis (López-García and Sevilla, 2012) or as a higher vulnerability to predation for young bats (Petrželková et al., 2004; Rosina and Shokhrin, 2011).

5.2. Palaeoenvironmental approach

The results of our habitat weighting analysis suggest a patched landscape where woodland and transitional

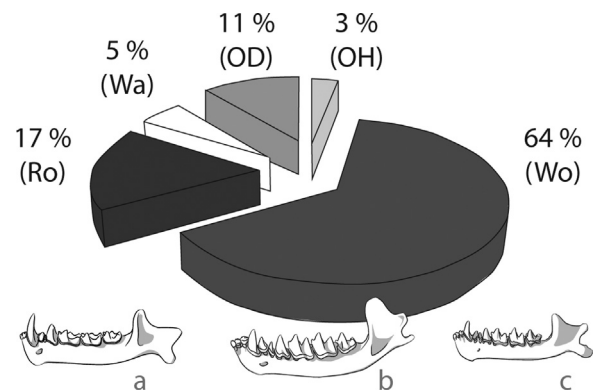


Fig. 6. Habitat composition percentages inferred from the bat fossil assemblage of Aguilón P7 (excluding the material from sector F). OD: open dry; OH: open humid; Wo: woodland/woodland margins; Ro: rocky; Wa: water. The most abundant taxa in the assemblage are A: *R. ferrumequinum*; B: *M. gr. myotis/blythii*; C: *P. gr. auritus/austriacus*.

Fig. 6. Pourcentages de composition par habitat, déduits de l'assemblage fossile de chiroptères d'Aguilón P7 excepté le matériel du secteur F. OD: ouvert et sec; OH: ouvert et humide; Wo: forêt/bordures de forêt; Ro: rocheux; Wa: aquatique. Les taxons les plus abondants dans l'assemblage sont A: *R. ferrumequinum*; B: *M. gr. myotis/blythii*; C: *P. gr. auritus/austriacus*.

woodland areas would dominate, alternating with seasonal meadows (Fig. 6). The occurrence of the typical cave-bats *R. ferrumequinum*, *R. hipposideros*, *M. gr. myotis/blythii* and *M. schreibersii* indicates the presence of exposed rock areas with cavities and/or fissures where they would roost. The existence of some surface water bodies is a limiting factor for the taxa *M. daubentonii* and *R. hipposideros*. Although all the species identified in the bat assemblage from AGP-7 currently inhabit the Iberian Peninsula, no similar community has been reported in the central Ebro Valley. However, similar communities are known in other Iberian regions: the eastern Cantabrian margin, the Sierra de Guadarrama (central Iberia) and the Sierra de Francia (central-western

Iberia) (Palomo et al., 2007); all these localities are under the influence of an oceanic climate. However, the lack of studies of present-day bat communities in the area of the central Ebro Valley must also be taken into account. Our proposal, based on the analysis of the bat assemblage from AGP-7, is that the area surrounding the locality was characterized by a mosaic of forest and meadows habitats with transitional areas, where the water supply was great enough to support a rich vegetation cover and to maintain a generally wetter, more oceanic-influenced climate than nowadays in the area.

The other fossil mammals from AGP-7 consist of taxa with highly diverse habitat preferences, which is consistent with the patched landscape obtained with bats. The dominant small mammal at AGP-7 is *Iberomys cabreræ*, an endemic Iberian species adapted to a Mediterranean climate and evergreen meadows (Cuenca-Bescós et al., 2010; López-García and Cuenca-Bescós, 2012); other small mammals with a lower presence show preferences for woodland (*Apodemus* sp.) or rocky, snow areas, such as *Chionomys nivalis*. The large mammals are eurythermal species with preference for temperate climate. The herbivorous mammals of the association, of which *Cervus elaphus* is the dominant taxon, points to a landscape characterized by a mosaic of forest and open habitats with transitional areas as the chiropteran association does.

5.3. Comparison with other Iberian Late Pleistocene bat assemblages

Several Late Pleistocene bat assemblages have been studied all along Spain (Appendix B) although this is the first report from the Ebro Valley region. The dominant taxon in AGP-7 site is *R. ferrumequinum*, which is a common species in Pleistocene Iberian sites; regarding the two following taxa in terms of abundance, *M. gr. myotis/blythii* is also a common species, but *P. gr. auritus/austriacus* is rather uncommon (López-García, 2008; Sevilla, 1988). Besides, other common species in Quaternary sites, such as *R. gr. euryale/mehelyi* and *M. schreibersii* are respectively absent or poorly represented in AGP-7; both of them are markedly thermophilic (Sevilla, 1988). The assemblage includes a rare species in the Iberian Pleistocene: *M. daubentonii*, which has only been reported in one other Iberian locality: Quibas (Lower Pleistocene, Murcia, Spain), a cool-period site (Agustí et al., 2009). Finally, a remarkable characteristic of the AGP-7 site is its high bat diversity despite of the small amount of remains recovered. Considering other Iberian sites aged MIS 3 (Appendix B), only La Carihuela (Granada) has a more diverse bat association than AGP-7, having been identified 14 taxa in there (Sevilla, 1988) among which are all the taxa identified in AGP-7. Another relatively diverse site is El Reguerillo (Madrid) where seven bat taxa have been identified although this assemblage rather differs from the one in Aguilón in terms of taxonomic composition (Sevilla, 1988; Appendix B).

6. Conclusions

The following species were identified in a small set of bat remains obtained from AGP-7 (MNI=15): *R. ferrumequinum*, *R. hipposideros*, *M. gr. myotis/blythii*, *M. cf. bechsteinii*, *M. emarginatus*, *M. daubentonii*, *P. gr. auritus/austriacus*, *H. savii* vel. *P. gr. kuhlii/nathusii* and *M. schreibersii*. All the identified bat taxa from AGP-7 presently inhabit the Iberian Peninsula, but the association is more typical of regions with an oceanic climate and woodland environments than the extant conditions in the Aguilón surrounding area. Our conclusion is that the area surrounding the AGP-7 locality presented a heterogeneous vegetation structure composed of an alternation of forest and meadow zones, where the water supply was great enough to support a rich vegetation cover and to maintain generally wetter, rather more oceanic-influenced climate conditions than nowadays. Further studies on Late Pleistocene sites in the region of the Ebro Valley will be of interest in order to obtain a complete overview of the state of chiropters in this area and period; for the moment only one Iberian site with this age, La Carihuela, is comparable with AGP-7 in terms of diversity and taxonomic composition.

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Appendix A. Measurements of bat specimens from Aguilón P7 site. The measures are expressed in millimeters.

Taxon	Element	n		Min.	Max.	Average	Sd
<i>R. ferrumequinum</i>	C	3	L	1.44	1.57	1.48	0.071
			W	2.16	2.29	2.2	0.073
	P4	1	L			1.6	
			W			2.22	
	M1	1	L			2.11	
			W			2.66	
	M2	1	L			1.92	
			W			2.53	
	M3	1	L			1.47	
			W			2.01	
	c	1	L			1.2	
			W			1.65	
	p4	3	L	1.25	1.31	1.3	0.032
			W	1.25	1.37	1.31	0.061
	m1	4	L	2.12	2.25	2.21	0.063
			W1	1.14	1.31	1.21	0.073
			W2	1.23	1.64	1.4	0.179
	m2	3	L	2.23	2.35	2.29	0.061
			W1	1.34	1.4	1.36	0.035
		W2	1.37	1.55	1.46	0.090	
m3	2	L	1.96	2.17			
		W1	1.29	1.29			
		W2	0.84	0.89			
<i>R. hipposideros</i>	P4	1	L			0.9	
			W			1.36	
	M1	1	L			1.45	
			W			1.6	
<i>M. gr. myotis/blythii</i>	M2	1	L			1.34	
			W			1.58	
<i>M. gr. myotis/blythii</i>	P2	1	L			0.8	
			W			0.99	
	P4	3	L	1.55	1.95	1.75	0.199
			W	1.39	1.83	1.68	0.254
	M1	2	L	2.52	2.64		
			W	2.65	2.77		
	c	2	L	1.05	1.18		
			W	1.4	1.4		
	p4	3	L	1.39	1.43	1.41	0.02
			W	0.98	1.12	1.05	0.07
<i>M. cf. bechsteini</i>	hu (e.d.)	1	L			2.95	
<i>M. emarginatus</i>	c	1	L			1.02	
			W			0.81	
	m2	2	L	1.49	1.55		
			W1	0.8	0.83		
			W2	0.96	0.99		
<i>M. daubentonii</i>	m3	1	L			1.35	
			W1			0.93	
			W2			0.76	
	M1	1	L			1.35	
			W			1.52	
	m1	1	L			1.24	
		W1			-		
		W2			0.78		
m2	1	L			1.27		
		W1			0.73		
		W2			0.78		
<i>M. emarg/dauben</i>	hu (e.d.)	1	L			2.76	
<i>P. gr. auritus/austriacus</i>	C	1	L			1.19	
			W			1.1	
	M2	1	L			1.53	
			W			2.18	
	m1	1	L			1.7	
		W1			0.93		
		W2			1.14		
<i>H. savii</i> vel <i>P. gr. ku/nat</i>	hu (e.d.)	1	L			2.19	
<i>M. schreibersii</i>	hu (e.d.)	1	L			3.11	
	C	1	L			1.13	
			W			0.94	
	m2	1	L			1.58	
			W1			0.82	
		W2			0.86		

Appendix B. Iberian Late Pleistocene (MIS 3) bat assemblages. Data obtained from Burjachs et al. (2012), López-García (2008), López-García et al. (2012a, b, 2014), Sevilla (1988)

		<i>Rhinolophus ferreumequinum</i>	<i>Rhinolophus mehelyi</i>	<i>Rhinolophus euryale</i>	<i>Rhinolophus euryale-mehelyi</i>	<i>Rhinolophus hipposideros</i>	<i>Rhinolophus sp.</i>	<i>Myotis myotis</i>	<i>Myotis bythii (oxignathus)</i>	<i>Myotis myotis blythii</i>	<i>Myotis bechsteini</i>	<i>Myotis nattereri</i>	<i>Myotis emarginatus</i>						
North	Aguilón	x				x				x	cf.		x						
	Cueva de Covalejos	x																	
Center	Lezetxiki							x											
	Labeko Koba							x											
	Cueva Millán							x											
North-east	El Reguerillo	x		x	x			x		x	x								
	Cueva de la Buena Pinta (U2)	x	x				x	x											
North-east	Gabasa	x		x		x		x											
	Cova de l'Arbreda (G-H)							x											
	Cova de l'Arbreda (I)							x		x									
	Cova de Teixonerres (II-III)	x			x				x										
	Olopte B	x						x					x						
	Galls Carboners					x				x									
	Abric Romaní (E-O)							x											
	Cova dels Xaragalls (C3-C8)					x							x						
	Cova Negra							x											
	La Carihuela	x	x	x	x	x	x	x		x	x	x	x						
E. South	Ibex Cave							cf.											
	Zafarraya																		
		<i>Myotis daubentonii</i>	<i>Myotis capaccinii</i>	<i>Myotis sp.</i>	<i>Eptesicus serotinus</i>	<i>Eptesicus sp.</i>	<i>Plecotus auritus</i>	<i>Plecotus austriacus</i>	<i>Plecotus auritus-austriacus</i>	<i>Barbastella barbastellus</i>	<i>Nyctalus lasiopterus</i>	<i>Nyctalus leisleri</i>	<i>Pipistrellus pipistrellus</i>	<i>Pipistrellus sp.</i>	<i>Hypsugo savii</i>	<i>Pipistrellus kuhlii-nathusii</i>	<i>Miniopterus nattereri</i>	<i>Miniopterus sp.</i>	<i>Tadarida teniotis</i>
North	Aguilón	x						x						x					
	Cueva de Covalejos																		
Center	Lezetxiki																		
	Labeko Koba																		
	Cueva Millán																		
North-east	El Reguerillo																		x
	Cueva de la Buena Pinta (U2)							x											
North-east	Gabasa																		
	Cova de l'Arbreda (G-H)								x										x
	Cova de l'Arbreda (I)																		
	Cova de Teixonerres (II-III)												x						x
	Olopte B					x													
	Galls Carboners		x					x											
	Abric Romaní (E-O)									x									x
	Cova dels Xaragalls (C3-C8)							x		x									x
	Cova Negra																		x
	La Carihuela						x	x	x										x
E. South	Ibex Cave												x						
	Zafarraya																		

References

- Agustí, J., Blain, H.-A., Cuenca-Bescós, G., Bailon, S., 2009. Climate forcing of first hominid dispersal in Western Europe. *J. Hum. Evol.* 57 (6), 815–821.
- Andrews, P., 2006. Taphonomic effects of faunal impoverishment and faunal mixing. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 241, 572–589.
- Bechstein, M.B., 1800. *Pennant, Allgemeine Ueber. Vierfüß. Thiere*, 2.
- Bennàsar-Serra, M., (Ph. D. Thesis) 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.
- Benzal, J., de Paz, O., 1990. Clave para la Identificación de los Murciélagos en la Península Ibérica (Mammalia, Chiroptera). *Miscelánea zool.* 13, 153–156.
- Blumenbach, J.F., 1779. *Handbuch der Naturgeschichte: mit Kupfern, Vol. 1. Erster Theil*. Dieterich, Göttingen.
- Borkhausen, M.B., 1797. *Deutsche Fauna, oder kurzgefaste Naturgeschichte der Thiere Deutschlands 1*. Barrentrapp und Menner. Frankfurt am Main.
- Bonaparte, C.L., 1837. *Iconografia della Fauna Italica 1*. Mammiferi. Tipogr. Salviucci, Roma 20.
- Bronk Ramsey, C., Higham, T., Leach, P., 2004. Towards High-Precision AMS: Progress and limitations. *Radiocarbon* 46 (1), 17–24.
- Burjachs, F., López-García, J.M., Allué, E., Blain, H.-A., Rivals, F., Bennàsar, M., Expósito, I., 2012. Palaeoecology of Neanderthals during Dansgaard-Oeschger cycles in northeastern Iberia (Abric Romaní): from regional to global scale. *Quat. Int.* 247, 26–37.
- Cortés-Gracia, A.L., Casas-Sainz, A.M., 1996. On the transition from detachment folds to fault-propagation folds: example from the Aguilón anticline (Iberian Chain). *Geogaceta* 19, 7–10.
- Cuenca-Bescós, G., Martínez, I., Mazo, C., Sauqué, V., Ramón-del Río, D., Rabal-Garcés, R., Canudo, J.J., 2010. Nuevo yacimiento de vertebrados del Cuaternario del Sur del Ebro en Aguilón, Zaragoza, España. In: XXVI Jornadas de la Sociedad Española de Paleontología, pp. 106–108.
- Dupuis, I., (Mémoire de Maîtrise) 1986. *Les Chiroptères du Quaternaire en France*. Université de Paris I, Paris.
- Evans, E.M.N., van Couvering, J.A.H., Andrews, P., 1981. Palaeoecology of Miocene sites in western Kenya. *J. Hum. Evol.* 10, 99–116.
- Felten, H., Helfricht, A., Storch, G., 1973. Die Bestimmung der europäischen Fledermäuse nach der distalen Epiphyse des Humerus. *Senckenb. Biol.* 54 (4/6), 291–297.
- Fischer, J.B., 1829. In: Cotta, S.J.G. (Ed.), *Synopsis Mammalium*. Oxford University, Oxford.
- Galán, J., (Master Thesis. (unpublished)) 2013. *Análisis taxonómico del Orden Chiroptera (MAMMALIA) del Pleistoceno del relleno del complejo kárstico de Aguilón*. Universidad de Zaragoza, Zaragoza.
- 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.
- Geoffroy, E., 1806. *Ann. Mus. Natn. Hist. Nat. Paris* 8.
- Geoffroy, E., 1818. Description des Mammifères qui se trouvent en Egypte 2, 112., pp. 118–119.
- Gisbert, M., Pastor, M. (Eds.), 2009. *Cuevas y Simas de la provincia de Zaragoza*. Centro de Espeleología de Aragón, Zaragoza.
- Gray, J.E., 1821. On the natural arrangement of vertebrate animals. *London Med. Repos.* 15 (1), 296–310.
- Gray, J.E., 1825. An outline of an attempt at the disposition of Mammalia into Tribes and Families, with a list of genera apparently appertaining to each Tribe. In: *The Annals of Philosophy, new series (Vol 10)*. C. Baldwin, New Bridge-street, London, pp. 337–344.
- Kaup, J.J., 1829. Skizzirte Entwickelungs Geschichte und natürliches System der Europäischen Thierwelt (Vogelsäugethiere Vögel, Entstehung d. Vögel aus Amphibien). In: Commission bei Carl Wilhelm Leske, Darmstadt und Leipzig 1.
- Keyserling, A., Blasius, J.H., 1839. *Arch. Naturgesch.* 5 (1), 320.
- Kolenati, F., 1856. Eine neue österreichische Fledermaus. *Sitzungsberichte-Bayerische Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Klasse Wien* 29, 250–256.
- Kowalski, K., 1995. Taphonomy of bats (Chiroptera). *Geobios* 18, 251–256.
- Kuhl, H., 1817. Die Deutschen Fledermäuse. Hanau.
- Lacépède, B.G.É., 1799. *Discours d'Ouverture et de Clôture du Cours d'Histoire Naturelle Donnée dans le Muséum National d'Histoire Naturelle, l'an VII de la République, et tableaux méthodiques des mammifères et des oiseaux*. Plassan, Paris.
- Linnaeus, C.N., 1758. *Systema Naturae per Regna Tria Naturae, secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis, Tomis I*. Laurentii Salvii, Holmiae, Stockholm.
- López-García, J.M., (Ph. D. Thesis) 2008. *Evolución de la diversidad taxonómica de los micromamíferos en la Península Ibérica y cambio Paleambientales durante el Pleistoceno Superior*. Universitat Rovira i Virgili, Tarragona.
- López-García, J.M., Cuenca-Bescós, G., 2012. Changes in the geographical distribution of *Microtus (Iberomys) cabreræ* (Thomas, 1906) from the Late Pleistocene to the Holocene. *Spanish J. Palaeontol.* 27 (2), 117–124.
- 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.
- López-García, J.M., Blain, H.-A., Allué, E., Bañuls, S., Bargalló, A., Martín, P., Morales, J.I., Pedro, M., Rodríguez, A., Solé, A., Oms, F.X., 2010. First fossil evidence of an "interglacial refugium" in the Pyrenean region. *Naturwissenschaften* 97 (8), 753–761.
- López-García, J.M., Blain, H.-A., Bennàsar, M., Alcover, J.A., Bañuls-Cardona, S., Fernández-García, M., Fontanals, M., Martín, P., Morales, J.I., Muñoz, L., Pedro, M., Vergés, J., 2014. Climate and landscape during Heinrich Event 3 in south-western Europe: the small-vertebrate association from Galls Carboners cave (Mont-ràl, Tarragona, north-eastern Iberia). *J. Quat. Sci.* 29 (2), 130–140.
- López-García, J.M., Blain, H.-A., Bennàsar, M., Euba, I., Bañuls, S., Bischoff, J., López-Ortega, E., Saladié, P., Uzquiano, P., Vallverdú, J., 2012a. A multiproxy reconstruction of the palaeoenvironment and palaeoclimate of the Late Pleistocene in northeastern Iberia: Cova dels Xaragalls, Vimbodí-Poblet, Paratge Natural de Poblet, Catalonia. *Boreas* 4 (2), 235–249.
- López-García, J.M., Blain, H.A., Burjachs, F., Ballesteros, A., Allué, E., Cuevas-Ruiz, G.E., Rivals, F., Blasco, R., Morales, J.I., Rodríguez-Hidalgo, A., Carbonell, E., Serrat, D., Rosell, J., 2012b. A multidisciplinary approach to reconstructing the chronology and environment of southwestern European Neanderthals: the contribution of Teixoneres cave (Moià, Barcelona, Spain). *Quat. Sci. Rev.* 43, 33–44.
- Lyman, R.L., 1994. *Vertebrate Taphonomy*. Cambridge University Press, Cambridge.
- Menu, H., Popelard, J.-B., 1987. Utilisation des caractères dentaires pour la détermination des Vespertilionines de l'Ouest européen. *Le Rhinologie* 4, 1–88.
- Núñez-Lahuerta, C., Cuenca-Bescós, G., Sauqué, V., Galán, J., 2015. Avian remains from the Upper Pleistocene (MIS3) site of Aguilón P-7, south of the Ebro River, Spain. *Historical Biology* (In press).
- 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 (Burgos, Spain) and its relation to human occupation. *Geomorphology* 196, 122–137.
- Palomo, L.J., Gisbert, J., Blanco, J.C. (Eds.), 2007. *Atlas y Libro Rojo de los Mamíferos Terrestres de España*. Dirección General para la Biodiversidad-SECEM-SECEMU, Madrid.
- Petrželková, K.J., Obuch, J., Zukal, J., 2004. Does the barn owl (*Tyto alba*) selectively predate individual great mouse-eared bats (*Myotis myotis*). *Lynx (Praha)* 35, 123–132.
- Rosina, V.V., Shokhrin, V.P., 2011. Bats in the diet of owls from the Russian Far East, southern Sikhote Alin. *Hystrix* 22 (1), 205–213.
- Sánchez-Goñi, M.F., D'Errico, F., 2005. La historia de la vegetación y el clima del último ciclo climático (OIS5-OIS1, 140.000–10.000 años BP) en la Península Ibérica y su posible impacto sobre los grupos paleolíticos. *Museo y Centro de investigación de Altamira Monografías* 20, 115–129.
- Sauqué, V., Galán, J., Núñez-Lahuerta, C., Sola-Almagro, C., Rabal-Garcés, R., Martínez, I., Mazo, C., Cuenca-Bescós, G., 2014a. Neandertales en el Pleistoceno Superior del valle del Ebro, paleoambiente y evidencias tafonómicas en Aguilón P-7. *Fundamental*, 223–226.
- Sauqué, V., García-González, R., Cuenca-Bescós, G., 2014b. A Late Pleistocene (MIS3) ungulate mammal assemblage (Los Rincones, Zaragoza, Spain) in the Eurosiberian-Mediterranean boundary. *Hist. Biol. Int. J. Paleobiol.*, <http://dx.doi.org/10.1080/08912963.2014.945926>.
- Schreber, J.C.D., 1774. *Die Säugethiere in Abbildungen nach der Natur mit Beschreibungen 1*.
- Sevilla, P., 1988. Estudio Paleontológico de los Quirópteros del Cuaternario español. *Paleontología i Evolució* 22, 113–233.
- Sevilla, P., 1990. The fauna of bats from the Upper Pleistocene locality of Santenay (Côte-d'Or, France). *Quat.* 1 (2), 101–110.
- Sommer, R.S., Nadachowski, A., 2006. Glacial refugia of mammals in Europe: evidence from fossil records. *Mammal Rev.* 36 (4), 251–265.
- 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 Zool.* 58 (1), 98–103.
- Tomes, R.F., 1857. Descriptions of four undescribed species of bats. *Proc. Zool. Soc. Lond.*, 50–54.