

## LATE PLEISTOCENE AND HOLOCENE BATS OF LATIUM (CENTRAL ITALY)

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ABSTRACT: Salari L. & Kotsakis T., *Late Pleistocene and Holocene bats of Latium (Central Italy)*.

In this paper the Late Pleistocene and Holocene fossil and subfossil bats collected in Latium have been examined. Seventeen taxa belonging to eight genera and to four families were reported in the list of fossil species (the presence of three additional species in the fossil assemblages is dubious). Fifteen of them are reported as living today in the region. Exceptions are the boreal species *Myotis dasycneme* and *Eptesicus nilssonii*. On the other hand the presence in Latium of *Myotis mystacinus* and *Barbastella barbastellus* after 1980 is dubious. The majority of the fossil remains of bats collected in the sites of Latium (especially in terms of number of specimens) belong to troglomorphic species, forming reproductive and/or hibernating colonies in caves (Rhinolophidae, *Myotis myotis*, *M. blythii*, *M. capaccinii* and *Miniopterus schreibersii*). Bats roosting in trees or rock fissures (*Nyctalus noctula* and *Tadarida teniotis*) or visiting the caves only during colder winters (*Myotis bechsteinii* and members of the genera *Pipistrellus* and *Hypsugo*) are quite rare. During the colder stages of the Late Pleistocene, the coastal regions of Latium must have played the role of refugia for animals and plants, as testified by several thermophilous Mediterranean *sensu stricto* species of bats, e.g. *Rhinolophus euryale*, *M. capaccinii*, *Pipistrellus kuhlii*, *M. schreibersii* and *T. teniotis*.

RIASSUNTO: Salari L. & Kotsakis T., Chiroteri del Pleistocene superiore e dell'Olocene del Lazio (Italia centrale).

In questo lavoro vengono esaminate le associazioni fossili e subfossili a chiroteri del Pleistocene superiore e dell'Olocene della regione Lazio. Sono state individuate diciassette specie appartenenti a otto generi e quattro famiglie (la presenza di ulteriori tre specie è dubbia). Quindici di queste specie vivono attualmente nella regione. Sono assenti le specie boreali *Myotis dasycneme* e *Eptesicus nilssonii*. D'altra parte la presenza nel territorio della regione Lazio di *Myotis mystacinus* e *Barbastella barbastellus* dopo il 1980, è dubbia. La maggioranza dei chiroteri raccolti nei siti fossiliferi laziali (in particolar modo se si considera il numero degli individui classificati con certezza) appartiene a specie troglomorfe che formano colonie riproduttive e/o ibernanti in grotte (Rhinolophidae, *Myotis myotis*, *M. blythii*, *M. capaccinii* e *Miniopterus schreibersii*). Specie viventi sugli alberi o in fessure (*Nyctalus noctula* e *Tadarida teniotis*) oppure che visitino le grotte solamente durante gli inverni particolarmente freddi (*Myotis bechsteinii* e i membri dei generi *Pipistrellus* e *Hypsugo*) sono piuttosto rare. Durante gli stadi freddi del Pleistocene superiore almeno due specie boreali hanno fatto la loro comparsa nel Lazio ma, d'altra parte, le regioni costiere del Lazio devono aver svolto il ruolo di area rifugio come testimonia la presenza di molte specie termofile, mediterranee *sensu stricto*, nei vari siti fossiliferi (*Rhinolophus euryale*, *M. capaccinii*, *Pipistrellus kuhlii*, *M. schreibersii* e *T. teniotis*).

Key Words: Bats, Late Pleistocene, Holocene, Central Italy.

Parole-chiave: Chiroteri, Pleistocene superiore, Olocene, Italia centrale.

### 1. INTRODUCTION

Bats are very useful for paleoecological reconstructions: they are flying insectivorous animals, and they rapidly react to climatic and environmental changes. They are also good indicators for reconstruction of hypogean microclimates. Their abundance in the cave sediments testifies the absence or sporadic presence of prehistoric humans in these sites during the same timespan. Instead, they have low value as biochronologic indicators and probably for this reason few people is interested to their systematic study.

Our aims are to point out palaeobiogeographical, palaeoecological, microclimate, human activity and, if possible, biochronological indications for the late Pleistocene and Holocene bat assemblages of Latium.

### 2. MATERIALS AND METHODS

The paper discusses the fossil and subfossil records of the Late Pleistocene and early Holocene bats of Latium (Fig. 1). It is a first attempt at a regional synthesis and it shows several uses in palaeontology of bat remains. The data were based on fossil assemblages directly investigated by the Authors (Grotta Breuil, Grotta Barbara, Grotta del Fossellone, Riparo Salvini, Grotta di Cittareale, and Grotta Mora Cavorso) or on material reported in the literature (Grotta di Sant'Agostino and Grotta Polesini).

The bats were collected from fossiliferous sites spanning from 55 ky BP (Grotta Sant'Agostino) to less than 7 ky BP (Grotta Mora Cavorso). Data about the first (warm) stage of the Late Pleistocene (MIS 5) are lack-



Fig. 1 - Location of the sites.  
Ubicazione dei siti.

ing. The fossil assemblages were assigned to four distinct time periods (from the oldest to the most recent one):

- 1) Grotta di Sant'Agostino (TOZZI, 1970) to the last stage of the first pleniglacial (last stage of MIS 4 and beginning of MIS 3);
- 2) Grotta Breuil (KOTSAKIS, 1991; ALHAIQUE *et al.*, 1996; SALARI & DI CANZIO, 2009), Grotta Barbara (SALARI & DI CANZIO, 2009 and unpublished data) and Grotta del Fossellone (unpublished data) to the last part of the interpleniglacial (final stages of MIS 3 and beginning of MIS 2);
- 3) Grotta Mora Cavorso (SALARI *et al.*, 2010, this volume), Riparo Salvini (ZHUOWEI & KOTSAKIS, 2008), Grotta di Cittareale (ARGENTI *et al.*, 2008) and Grotta Polesini (RADMILLI, 1974) to the late glacial (final stages of MIS 2);
- 4) Grotta Mora Cavorso to the early Holocene (ROLFO *et al.*, 2009).

In three caves, the fossil bats were associated with different lithic industries and/or cultural horizons: Grotta Barbara (Mousterian and Aurignacian), Grotta del Fossellone (Mousterian, Aurignacian and advanced upper Paleolithic), Grotta Mora Cavorso (final Epigravettian and Neolithic) (Tabs. 1 and 2). For the numerical data of micro and macro faunas and the detailed stratigraphies of the various sites, see the literature cited.

### 3. SYSTEMATIC OBSERVATIONS

The fossil remains from the investigated sites of Latium do not show major morphological and/or morphometric differences from living species. However, paleontologists are confronted with some issues raised by recent applications of modern bioacoustic and molecular biology techniques (combined with conventional ones based on morphological and morphometric cri-

teria), which identified and/or erected new species. In particular, some subspecies or geographic varieties of species belonging to the genera *Myotis*, *Pipistrellus* and *Plecotus* were elevated to the rank of good species, but the lack of sound morphometric data for their taxonomic determination did not permit to adequately assess them. The fossil remains potentially falling into the above taxa (e.g. *Pipistrellus pygmaeus*, LEACH, 1825) and supposedly having the same variability as the one of *Pipistrellus pipistrellus* (SCHREBER, 1774), or those of the cryptic species of *Myotis mystacinus* (KUHLE, 1817) were attributed to the traditionally more known species, followed by *sensu lato* (*s.l.*) in accordance with "Linee guida per il monitoraggio dei Chiropteri" (AGNELLI *et al.* 2004) for reports of these taxa prior to 1999-2000. This is the case of *M. mystacinus s.l.* of Grotta Breuil and *P. pipistrellus s.l.* of Grotta Barbara.

Also the distinction between *Hypsugo savii* and species of larger size of the genus *Pipistrellus* is problematic. The morphology and size of the distal epiphysis of the humerus are identical (see FELTEN *et al.*, 1973) and the variability of the size of the lower tooth row largely overlaps. On the other hand the morphology and position of the upper incisors suggests a clear discrimination between the cranial remains of *Pipistrellus kuhlii* (KUHLE, 1817), those of *Pipistrellus nathusii* (KEYSERLING & BLASIUS, 1839) and those of *H. savii* (see MILLER, 1912; LANZA & AGNELLI, 2002) but - as is known - incisors are rarely recovered from fossil remains. In these cases (e.g. at Riparo Salvini), the fossil remains were attributed to *Hypsugo vel Pipistrellus* (ZHUOWEI & KOTSAKIS, 2008). Conversely, at Grotta Barbara, two mandibular branches were ascribed to *P. kuhlii* (SALARI & DI CANZIO, 2009), because the size of the lower tooth row (C-M<sub>3</sub> alveolar length = 5.4 mm) lay close to the upper limit of the size range of *P. kuhlii* (MILLER, 1912; BENDA *et al.*, 2003) and was not included in the overlap range between the above three species.

The attribution of some remains of a "middle size" *Rhinolophus* collected in Grotta Breuil is uncertain, because the morphology of the fragmentary specimens not allow to assign the fossils to specific level, and the dimensions are inside the range of both *Rhinolophus euryale* BLASIUS, 1853 and *Rhinolophus mehelyi* MATSCHIE, 1901.

### 4. BIOCHRONOLOGICAL INDICATIONS

Pleistocene bats appear to have a low value as biostratigraphic indicators. Only two extinct species, both from the Early and Middle Pleistocene, were discovered in Italy (TATA & KOTSAKIS, 2005).

The species known in the Late Pleistocene are all extant and, except for *Myotis dasycneme* (BOIE, 1825), they are all currently distributed in Italy (AGNELLI *et al.*, 2004). *M. dasycneme* is reported from a few Late Pleistocene sites of north and central Italy, always in "cold" assemblages, but is not reported in any of the few known Holocene sites. Hence, based on the occurrence of *M. dasycneme* at Grotta di Cittareale, the chiropteran assemblage was ascribed to one of the last cold stages of the Late Pleistocene, probably the Younger Dryas (ARGENTI *et al.*, 2008).

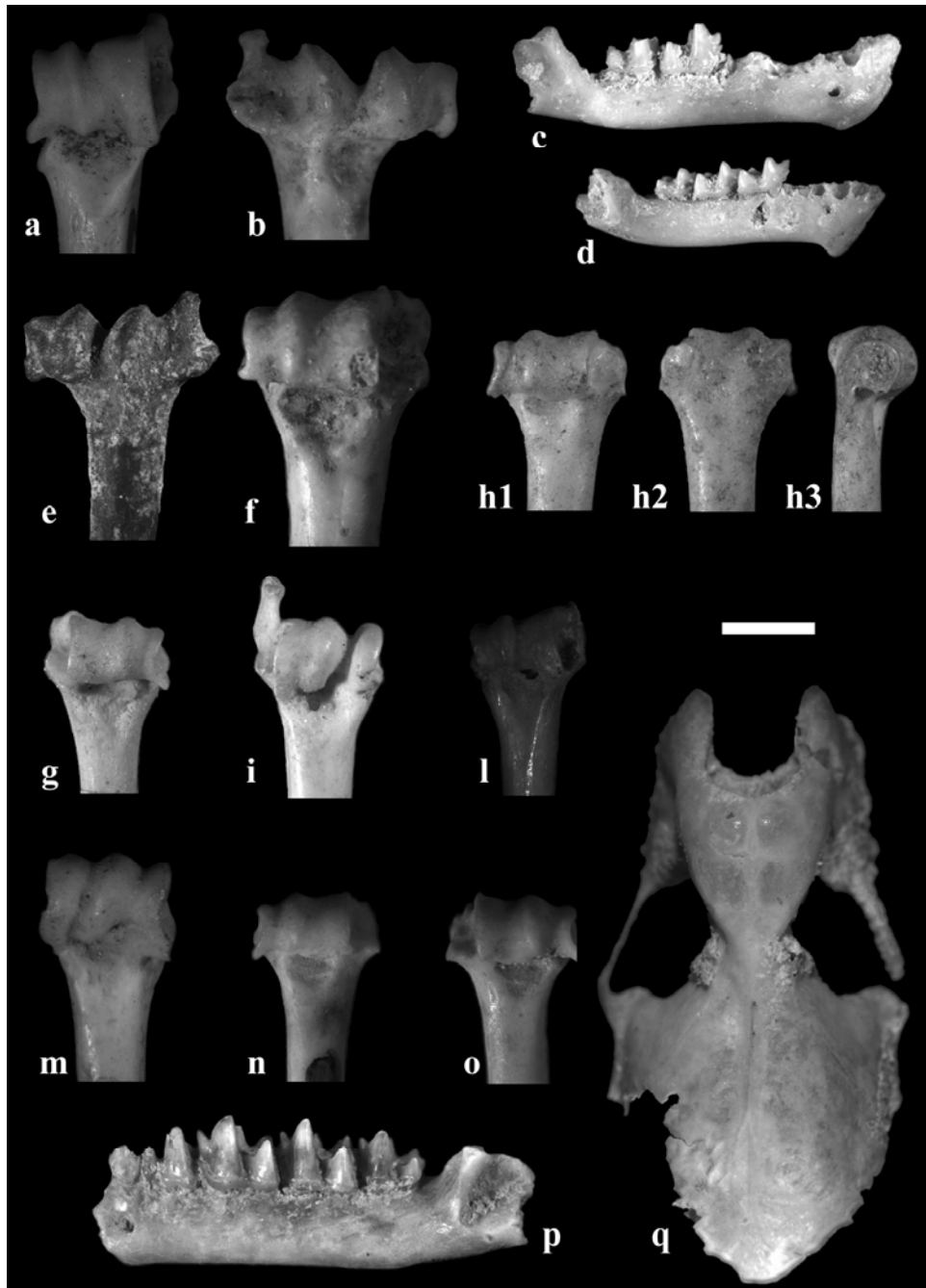


Fig. 2 - Grotta Breuil: a) *Nyctalus noctula*, distal epiphysis of left humerus; Grotta Barbara: b) *Rhinolophus ferrumequinum*, distal epiphysis of right humerus; c) *Pipistrellus kuhlii*, fragment of right mandibular ramus, labial view; d) *Pipistrellus pipistrellus* s.l., fragment of right mandibular ramus, labial view; Grotta del Fossellone: e) *Rhinolophus euryale*, distal epiphysis of left humerus; f) *Myotis blythii*, distal epiphysis of left humerus; g) *Myotis capaccinii*, distal epiphysis of right humerus; h) *Eptesicus nilssonii*, distal epiphysis of left humerus (h1 external, h2 internal, h3 dorsal views); i) *Miniopterus schreibersii*, distal epiphysis of right humerus; Riparo Salvini: l) *Hypsugo* vel *Pipistrellus*, distal epiphysis of left humerus, *processus styloideus* broken; Grotta di Cittareale: n) *Myotis dasycneme*, distal epiphysis of left humerus; o) *Myotis bechsteinii*, distal epiphysis of right humerus; Grotta Mora Cavorso: p) *Myotis bechsteinii*, fragment of left mandibular ramus, labial view; q) *Rhinolophus hipposideros*, skull, dorsal view. All the humeri are illustrated in external view. Scale bar = 2 mm.

Grotta Breuil: a) *Nyctalus noctula*, omero sinistro, epifisi distale; Grotta Barbara: b) *Rhinolophus ferrumequinum*, omero destro, epifisi distale; c) *Pipistrellus kuhlii*, frammento di ramo mandibolare destro, norma labiale; d) *Pipistrellus pipistrellus* s.l., frammento di ramo mandibolare destro, norma labiale; Grotta del Fossellone: e) *Rhinolophus euryale*, omero sinistro, epifisi distale; f) *Myotis blythii*, omero sinistro, epifisi distale; g) *Myotis capaccinii*, omero destro, epifisi distale; h) *Eptesicus nilssonii*, omero sinistro, epifisi distale (h1 norma esterna, h2 norma interna, h3 norma dorsale); i) *Miniopterus schreibersii*, omero destro, epifisi distale; Riparo Salvini: l) *Hypsugo* vel *Pipistrellus*, omero sinistro, epifisi distale; Grotta di Cittareale: n) *Myotis dasycneme*, omero sinistro, epifisi distale; o) *Myotis bechsteinii*, omero destro, epifisi distale; Grotta Mora Cavorso: p) *Myotis bechsteinii*, frammento di ramo mandibolare sinistro, norma labiale; q) *Rhinolophus hipposideros*, cranio, norma dorsale. Tutti gli omeri sono illustrati in norma esterna. Scala della barra = 2 mm.

Site	Geographic ubication	Cultural chronology	Radiometric dating (years BP)	References
Grotta Mora Cavorso 2 (burial rooms)	Upper Aniene river valley, Jenne (RM)	Neolithic	6,275 ± 45 6,405 ± 35	Rolfo <i>et al.</i> , 2009; 2010
Grotta Polesini (cuts 12-7)	Lower Aniene river valley, Tivoli (RM)	final Epigravettian	10,090 ± 90	Radmilli, 1974; Alhaique & Bietti 2007
Grotta di Cittareale	San Rufo valley, Cittareale (RI)			Argenti <i>et al.</i> , 2008
Riparo Salvini (cuts 24-7)	Cliff of Giove Mount, Terracina (LT)	final Epigravettian	12,400 ± 170 13,365 ± 190	Alessio <i>et al.</i> , 1993
Grotta Mora Cavorso 1 ("Dig B2")	Upper Aniene river valley, Jenne (RM)	final Epigravettian	13,460 ± 50	Salari <i>et al.</i> , this volume
Grotta del Fossellone 3 (layers 19-1)	Circeo promontory, San Felice Circeo (LT)	Gravettian ?		Alhaique & Tagliacozzo 2000
Grotta del Fossellone 2 (layer 21)	Circeo promontory, San Felice Circeo (LT)	Aurignacian		Alhaique & Tagliacozzo 2000; Mussi <i>et al.</i> , 2006
Grotta Barbara 2 (upper level)	Circeo promontory, San Felice Circeo (LT)	Aurignacian		Mussi <i>et al.</i> , 2006
Grotta del Fossellone 1 (layers 41-23)	Circeo promontory, San Felice Circeo (LT)	Musterian		Alhaique & Tagliacozzo 2000; Alhaique & Bietti 2007
Grotta Barbara 1 (lower levels)	Circeo promontory, San Felice Circeo (LT)	Musterian		Caloi & Palombo 1989
Grotta Breuil (layers 7-3)	Circeo promontory, San Felice Circeo (LT)	Musterian	33,000 ± 2,500 39,600 ± 5,700	Schwarcz <i>et al.</i> , 1991; Alhaique <i>et al.</i> , 1996
Grotta di Sant'Agostino (strata A4-A1)	Sant'Agostino promontory, Gaeta (LT)	Musterian	39,000 ± 9,000 54,000 ± 11,000	Tozzi 1970; Schwarcz <i>et al.</i> , 1991

Tab. 1 - Schematic synthesis of stratigraphy and chronology of the sites.

Schema stratigrafico e cronologico dei siti considerati.

## 5. PALAEOBIOGEOGRAPHICAL INDICATIONS

From the end of the Pleistocene to the present, various animal species changed their home ranges. The majority of the bat species identified in the Pleistocene horizons are still present in Latium, except for *M. dasycneme*, *M. mystacinus s.l.*, *Eptesicus nilssonii* (KEYSERLING & BLASIUS, 1839), *Barbastella barbastellus* (SCHREBER, 1774) and possibly *R. mehelyi* (Tabs. 2 and 3).

Today, *M. dasycneme* has its southernmost limit of distribution in north-eastern Croatia and is regarded as an "accidental species" in Italy: the only reported specimen - likely erratic - was captured in Trento in 1881 (LANZA & AGNELLI, 2002; AGNELLI *et al.*, 2004). *M. dasycneme* fossils are known since the Early Pleistocene (Gelasian = late Villányian = middle Villafranchian) in central-eastern Europe (HORÁČEK & HANÁK, 1989) and signalled in some Middle and Late Pleistocene and Holocene sites of Asia and central-eastern Europe (HORÁČEK & HANÁK, 1989 with references; PIKSA & WOŁOSZYN, 2001; OCHMAN, 2003; OCHMAN & WOŁOSZYN, 2003; POSTAWA, 2004; ROSSINA, 2006). In Italy, it is known in the late Middle and Late Pleistocene of Grotta del Broion (Veneto, PASA, 1953), Riparo Mezzena (Veneto, BARTOLOMEI & PASA, 1980), Grotta del Vento (Marche, ESU *et al.*, 1990), and (as we have seen in the previous paragraph) in the Grotta di Cittareale (Latium, ARGENTI *et al.*, 2008). This locality is the southernmost limit of this species, even considering its distribution in the Pleistocene.

Grotta del Fossellone 3 (advanced upper Palaeolithic) was attended by *E. nilssonii*, a northern species and the only one - among all the bats in the world - which reproduces even beyond the Arctic Circle (as far as 70° 25' N) (RYDELL *et al.*, 1994). Its current range of distribution includes central and northern Europe, extending from the northern Balkans through the Palearctic Asia to Sahalin, Korea and Japan (AGNELLI *et al.*, 2004). Currently, its southernmost limit of distribution in Europe is the south-eastern Alpine arch and the northern Balkans, with isolated colonies in the Rila Mountains in Bulgaria (HANÁK & HORÁČEK, 1986; AGNELLI *et al.*, 2004). *E. nilssonii* fossils are known since the early Middle Pleistocene in Poland (WOŁOSZYN, 1987). During the Late Pleistocene and early Holocene, this species settled in various sites of central Europe and of the former Soviet Union (Crimea, Siberia, Russian Far East) (RYDELL, 1993 with references; HORÁČEK, 1995; POPOV, 2000; PIKSA & WOŁOSZYN, 2001; OCHMAN, 2003; OCHMAN & WOŁOSZYN, 2003; ROSSINA, 2006) and only at Grotta del Broion (Veneto) in Italy (PASA, 1953). Grotta del Fossellone represents the southernmost limit of this species in Europe, even considering its distribution in the Pleistocene.

Boreal species, e.g. *M. dasycneme* and *E. nilssonii* presumably deserted the region and the peninsula owing to climate warming in the Holocene. Conversely, the absence of nemoral species, such as *M. mystacinus* and *B. barbastellus*, both distributed in most part of Italy, is relatively recent (after 1980); this absence (if con-

firmed) is likely to be due to progressive deforestation and intense urbanisation of the region in the last century.

Another interesting paleogeographic issue is the recent settlement of animal and plant species in central-northern Europe. During the coldest periods of the Late Pleistocene and, namely, the Last Glacial Maximum (LGM), the Iberian and Italian peninsulas and the Balkans played the role of main glacial refugia for many “temperate” or “warm” animal and plant species, which then repopulated the rest of Europe (STEWART & LISTER, 2001; SOMMER & NADACHOWSKI, 2006; TRÍSKA, 2009). This phenomenon certainly involved the majority of European bats.

Considering only the stratigraphic successions supported by estimated radiometric dates, FAHLKE (2009) reported that: i) bats deserted the area north of the Alps in the LGM; and ii) it was only in the first stages of the late glacial, during the Bølling-Allerød temperate oscillations, that *Eptesicus serotinus* (Schreber, 1774) timidly returned to the area, followed by *Plecotus auritus* (LINNAEUS, 1758) and *B. barbastellus*. In effect, few other species, including *Myotis bechsteinii* (KÜHL, 1817), *Myotis nattereri* (KÜHL, 1817), *Myotis brandtii* (Eversmann, 1845), *Myotis daubentonii* (KÜHL, 1817), *E. nilssonii* and *P. nathusii*, are reported in the late glacial successions (HORÁČEK, 1995; OCHMAN, 2003), while the other species now present in central-northern Europe must have returned there only in the Holocene (HORÁČEK, 1995; BLANT *et al.*, 2008; RUEDI *et al.*, 2008; FAHLKE, 2009). Even in some regions south of the Alps (e.g. Canton Ticino), repopulation took place in the Holocene (BLANT *et al.*, 2008).

In the Late Pleistocene, Latium, and generally central-southern Italy, hosted many species which are now largely distributed in central-northern Europe, including *Rhinolophus hipposideros* (BECHSTEIN, 1800), *Myotis myotis* (BORKHAUSEN, 1797), *M. bechsteinii*, *M. dasycneme*, *M. mystacinus*, *Nyctalus noctula* (SCHREBER, 1774), *E. nilssonii* and *B. barbastellus*. Additionally, especially in the coastal sites of Latium, various species of Mediterranean s.s. thermophilous bats, e.g. *P. kuhlii*, *R. euryale*, *Myotis capaccinii* (Bonaparte, 1837), *Miniopterus schreibersii* (KÜHL, 1817) and *Tadarida teniotis* (RAFINESQUE, 1814), cohabited with “cold” species, e.g. marmot, hamster, wolverine, ermine and steinbock, even in the relatively colder stages of the Late Pleistocene.

Grotta Barbara 1 (Mousterian) was inhabited by *P. kuhlii*, a thermophilous species which is very anthropophilous today (LANZA & AGNELLI, 2002; AGNELLI *et al.*, 2004). Fossils of *P. kuhlii* are rare, with a few records in the late Middle and Late Pleistocene and Holocene in Germany, Russia and Turkey (SALARI & DI CANZIO, 2009 with references). *P. kuhlii* of Grotta Barbara is the first and, for the time being, the only occurrence in Italy.

taxon / sites	Grotta di S. Agostino	Grotta Breuil	Grotta Barbara 1	Grotta del Fossellone 1	Grotta Barbara 2	Grotta del Fossellone 2	Grotta del Fossellone 3	Grotta Mora Cavorso 1	Riparo Salvini	Grotta di Cittareale	Grotta Polesini	Grotta Mora Cavorso 2
<i>Rhinolophus ferrumequinum</i>	X	X			X		X	X	X	X	X	X
<i>Rhinolophus hipposideros</i>		X								X		X
<i>Rhinolophus euryale</i>		X					X				X	
<i>Rhinolophus euryale/mehelyi</i>		X										
<i>Myotis myotis</i>		X								X		
<i>Myotis blythii</i>	X	X	X	X	X	X	X		X			X
<i>Myotis myotis/ blythii</i>		X										X
<i>Myotis capaccinii</i>		X					X		X			
<i>Myotis dasycneme</i>										X		
<i>Myotis bechsteinii</i>								X		X		
<i>Myotis emarginatus</i>			X								X	
<i>Myotis mystacinus s.l.</i>		X										
<i>Myotis sp.</i>		X										
<i>Pipistrellus pipistrellus s.l.</i>			X									
<i>Pipistrellus kuhlii</i>			X									
<i>Hypsugo vel Pipistrellus</i>									X			
<i>Eptesicus nilssonii</i>							X					
<i>Nyctalus noctula</i>		X							X			
<i>Barbastella barbastellus</i>											X	
<i>Miniopterus schreibersii</i>		X					X		X		X	
<i>Tadarida teniotis</i>		X	X						X			
<b>Total taxa</b>	<b>2</b>	<b>12</b>	<b>5</b>	<b>1</b>	<b>2</b>	<b>1</b>	<b>6</b>	<b>2</b>	<b>7</b>	<b>5</b>	<b>5</b>	<b>4</b>

Tab. 2 - Late Pleistocene and early Holocene bats of Latium. (For the spelling of the species names see SIMMONS, 2005).

Quadro riepilogativo dei taxa del Pleistocene superiore e Olocene antico del Lazio. (Per l'ortografia dei nomi delle specie cf. SIMMONS, 2005).

## 6. PALAEOECOLOGICAL INDICATIONS

The favourite foraging environments of the identified species shed more light on the environment surrounding the investigated sites (Tab. 3). Moreover, settlements of species usually hibernating in hollow trees or rock fissures (*N. noctula*, *E. nilssonii* e *T. teniotis*) or, rarely, in caves (*M. bechsteinii* and members of the genera *Pipistrellus* and *Hypsugo*) may indicate periods of more adverse climate or particularly harsh winters. These climatic and environmental indications are usually consistent with those provided by the other identified taxa, especially ungulates and rodents, and may complement and/or extend the data provided by the other animal and/or plant taxa.

For instance, in the most ancient strata (cuts 24-16) of Riparo Salvini, *Myotis blythii* (TOMES, 1857) is dominant and followed by *M. capaccinii* and *M. schreibersii*. This infers that the surrounding environment was fairly open, with prairies alternating with sparse woods and wetlands. In the other cuts 15-7, *M. blythii* is still dominant and followed by *Rhinolophus ferrumequinum* (SCHREBER, 1774), *Hypsugo vel Pipistrellus* and *N. noctula*, suggesting similar but less humid environments and climatic transition from conditions similar to present ones to colder conditions. The paleoenvironmental clues given by bats match those provided by rodents. The latter passed from an assemblage with dominant *Microtus (Terricola) savii* (DE SELYS-LONGCHAMPS, 1838), followed by *Apodemus sylvaticus* (LINNAEUS, 1758), *Arvi-*

taxon	Latium fossil	Latium today	Hibernacula	Temperatures of hibernation	Foraging environment	Zoogeographical patterns
<i>Rhinolophus ferrumequinum</i>	X	X	caves	7 - 12 °C	mixed	Mediterranean s.l.
<i>Rhinolophus euryale</i>	X	X	caves	10 - 12 °C	woods	Mediterranean s.s.
<i>Rhinolophus mehelyi</i>	?		caves	11 - 13 °C	woods	Mediterranean s.s.
<i>Rhinolophus hipposideros</i>	X	X	caves	4 - 12 °C	mixed	Mediterranean s.l.
<i>Myotis myotis</i>	X	X	caves	2 - 12 °C	woods	Mediterranean s.l.
<i>Myotis blythii</i>	X	X	caves	4 - 14 °C	open	Mediterranean s.l.
<i>Myotis capaccinii</i>	X	X	caves	4 - 15 °C	woods	Mediterranean s.s.
<i>Myotis dasycneme</i>	X		caves, hollow trees	0 - 7 °C	forests	Boreal
<i>Myotis daubentonii</i>		X	caves	0 - 10 °C	forests	Boreal
<i>Myotis bechsteinii</i>	X	X	hollow trees, caves	1 - 10 °C	woods	Nemoral
<i>Myotis emarginatus</i>	X	X	caves	5 - 9 °C	miscellaneous	Mediterranean s.l.
<i>Myotis mystacinus s.l.</i>	X	?	caves	2 - 8 °C	miscellaneous	Nemoral
<i>Myotis nattereri</i>		X	caves	2 - 8 °C	woods	Nemoral
<i>Pipistrellus kuhlii</i>	X	X	buildings, rock fissures	?	miscellaneous, anthropophilous	Mediterranean s.s.
<i>Pipistrellus nathusii</i>	?	X	rock fissures, buildings	?	Woods	Nemoral
<i>Pipistrellus pipistrellus s.l.</i>	X	X	buildings, hollow trees	0 - 6 °C	woods, anthropophilous	Mediterranean s.l.
<i>Pipistrellus pygmaeus</i>	?	X	hollow trees, buildings	?	miscellaneous, anthropophilous	Nemoral ?
<i>Hypsugo savii</i>	?	X	buildings, caves	?	miscellaneous, anthropophilous	Mediterranean s.s.
<i>Eptesicus nilssonii</i>	X		rock fissures, buildings	-6 - 7 °C	forests	Boreal
<i>Eptesicus serotinus</i>		X	buildings, caves	2 - 4 °C	miscellaneous	Mediterranean s.l.
<i>Nyctalus lasiopterus</i>		?	hollow trees	-6 - 6 °C	forests	Nemoral
<i>Nyctalus leisleri</i>		X	hollow trees	?	woods	Nemoral
<i>Nyctalus noctula</i>	X	X	hollow trees	> -7 °C	forests	Nemoral
<i>Barbastella barbastellus</i>	X	?	caves	0 - 8 °C	forests	Nemoral
<i>Plecotus auritus</i>		X	hollow trees, caves	2 - 5 °C	forests	Boreal
<i>Plecotus austriacus</i>		X	caves, hollow trees	2 - 12 °C	woods	Mediterranean s.l.
<i>Miniopterus schreibersii</i>	X	X	caves	4 - 12 °C	miscellaneous	Mediterranean s.s.
<i>Tadarida teniotis</i>	X	X	rock fissures	0 - 10 °C	rocky	Mediterranean s.s.

Tab. 3 - Late Pleistocene and early Holocene chiropteran taxa, extant bat fauna of Latium and key ecological features (data from HORÁČEK *et al.*, 2000; LANZA & AGNELLI, 2002; AGNELLI *et al.*, 2004; AMORI *et al.*, 2009). (For the spelling of the species names see SIMMONS, 2005).

Confronto tra i taxa del Pleistocene Superiore e Olocene antico con l'attuale chiropterofauna del Lazio, e schema sintetico di alcune caratteristiche ecologiche (dati da HORÁČEK *et al.*, 2000; LANZA & AGNELLI, 2002; AGNELLI *et al.*, 2004; AMORI *et al.*, 2009). (Per l'ortografia dei nomi delle specie cf. SIMMONS, 2005).

*cola amphibius* (LINNAEUS, 1758) and *Eliomys quercinus* (LINNAEUS, 1766), to an assemblage with dominant *M. (T.) savii* and *Microtus (Microtus) arvalis* (Pallas, 1778), followed by *A. sylvaticus*, *E. quercinus* and *A. amphibius* together with *Chionomys nivalis* (MARTINS, 1842) (ZHUO-WEI & KOTSAKIS, 2008).

The species haunting woods and forests are always associated with cervids and/or glirids. *T. teniotis* (rupicolous species) is associated with the steinbock at Grotta Breuil, Grotta Barbara and Riparo Salvini. It is worth noting that: i) in the late glacial succession of Grotta Polesini (RADMILLI, 1974), in spite of difficulties in correlating the various trenches (ALHAIQUE & BIETTI, 2007), *R. ferrumequinum* and *M. schreibersii* disappears and *B. barbastellus* gradually increases upon the appearance of the marmot and of the wolverine; or ii) at Grotta S. Agostino (TOZZI, 1970), upon the appearance of the rhinoceros (stratum A2), only *M. blythii*

remains, accompanied by *R. ferrumequinum* in the underlying strata.

In other instances, the paleoenvironmental indications given by bats are the only ones (e.g. at Grotta di Cittareale) or improve the understanding of available data, e.g. at Grotta Barbara and Grotta Mora Cavorso. At Grotta Barbara 1 (Mousterian), the percentage ratios between the identified cervids (red deer, fallow deer, roe deer) point to two different possible scenarios in the Pontina plain: a relatively open environment with scarce or localised forest cover or diffuse Mediterranean "macchia" (CALOI & PALOMBO, 1989). The dominance of *M. blythii* validates the former assumption. At Grotta Mora Cavorso 2 (Neolithic), ungulates include the red deer and domestic ruminants; only *M. blythii* shows that the upper Aniene river valley and the Simbruini Mountains, too, were in part covered by prairies.

Considering that only the lesser mouse-eared bat is indicative of open spaces and that various species populate miscellaneous or mixed environments, the only inconsistency concerns the most recent part of the Mousterian succession of Grotta Breuil. Among the ungulates of stratum 3, the steinbock prevails over the red deer, implying drier and colder conditions than in the underlying strata where the red deer prevails over the steinbock (ALHAIQUE & BIETTI, 2007). Among bats, *R. euryale* is dominant, testifying a good forest cover and a temperate climate, more or less as in the underlying strata. This inconsistency may be redressed by: i) assuming that the fossil remains are not coeval (bats must have colonised the cave only after the Mousterians deserted it, see later on); or ii) recalling the previous points made about the role of the coastal sites of Latium as glacial refugia for various species of thermophilous bats.

## 7. MICROCLIMATIC INDICATIONS

The microclimate of caves has a paramount importance in the selection of diurnal roosts or reproductive and hibernating environments. Each species has its own tolerability to narrow ranges of temperature and humidity (generally low temperature and high humidity). Nonetheless, the temperature and humidity of a cave may vary depending on its size and morphology, as well as on the number and orientation of its openings. Large-sized caves may have a variety of microclimates (more or less constant temperatures but variable humidity, owing above all to draughts of air) and each species selects the sites which best suit its preferences.

Usually, bats have not been hunted by prehistoric humans for food or other purposes, but may be occasional preys of nocturnal raptors (Strigiforms): in the pellets regurgitated by these raptors, bats account for as little as 1% of the preys, including rodents, small birds and insectivores (KOWALSKI, 1990, 1995; SEVILLA GARCÍA, 1998). Hence, most of the fossil remains in the investigated sites are naturally accumulated bones of bats which died in their caves. The lack of juvenile remnants (suggestive of attendance in the spring or summer reproductive period), except for an immature specimen found at Grotta Breuil, suggests that the bats are died for poor subcutaneous fat reserve or other causes during hibernation. This is why the investigated thanatocoenoses can give further insight into the winter microclimate, at least around the excavated area.

For instance, it may be assumed that: at Grotta Breuil (strata 6-3), the winter microclimate remained fairly constant (on average around 10-12° C) and with high humidity; the winter temperature fluctuated around 5-6° C at Grotta Barbara 1 (Mousterian), around 7° C at Grotta di Cittareale and rose slightly at Grotta Mora Cavorso (from roughly 7-10° C to 7-12° C) between the final stages of the Late Pleistocene and Holocene (Neolithic).

## 8. HUMAN ACTIVITY INDICATIONS

Today some species of bats, particularly of the genera *Pipistrellus* and *Hypsugo* are anthropophilous,

living in the urban areas and roosting in the buildings (MILLER, 1912; LANZA & AGNELLI 2002; AGNELLI *et al.*, 2004). However the troglophilous bats are wild and are not commensal to humans and, usually, the occurrence of bat remains in the sediments of caves evidences the absence or sporadic presence of prehistoric humans in the time interval during which the sediments were deposited (ROSSINA, 2006; SALARI & DI CANZIO, 2009; SALARI, 2010). Noise, light and heat from human attendance change hypogean environments. A particular source of disturbance to bats is the smoke from human fires, which may also alter the microclimate of caves. The disturbance is higher in winter or during the reproductive period and may cause the bats to desert the caves in search of more suitable ones (MARSICO, 2003; AGNELLI *et al.*, 2004).

It is perhaps not by chance that the percentage of bats at Grotta Breuil is almost specular to the percentages of traces of human activity left on the bones of large mammals (ALHAIQUE & BIETTI, 2007; ALHAIQUE, *in litteris*): peak of human activity corresponds to low bat attendance (stratum 7); a sharp drop in human activity is associated with a strong increase in bat attendance (stratum 6); scarce remains of bats and equally scarce human activity characterise strata 5 and 4; minimum of human activity in stratum 3 is indicative of peak of bat attendance (Tab. 4). In stratum 3 can not be excluded that bats may have settled in the cave only after the Mousterians abandoned it.

	L. 3	L. 4	L. 5	L. 6	L. 7
Large Mammals	11.6	14.1	16.1	31.6	26.5
Human activity traces	0.9	6.9	5.6	32.4	54.1
Bats	48.4	5.7	2.6	42.7	0.5

Tab. 4 - Percentages of the number of identified remains of large mammals, number of large mammals with traces of human activity and number of identified bat remains at Grotta Breuil (data from ALHAIQUE & BIETTI, 2007; SALARI & DI CANZIO, 2009; ALHAIQUE *in litteris*).

*Confronto tra il numero dei resti determinati dei grandi mammiferi, il numero di tracce di attività umana sui resti di grandi mammiferi ed il numero dei resti determinati di chiroteri di Grotta Breuil (in percentuale)(dati da ALHAIQUE & BIETTI, 2007; SALARI & DI CANZIO, 2009; ALHAIQUE in litteris).*

The alternating attendance of caves by bats and humans may have been multi-year cyclical or seasonal (late spring-early autumn for humans, late autumn-early spring for bats). Based on available data on seasonal human attendance of Grotta S. Agostino, Grotta Breuil, Grotta del Fossellone 2 (Aurignacian), Riparo Salvini and Grotta Polesini (ALHAIQUE & BIETTI, 2007) multi-year cycles seem more likely.

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