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Holocene bats (Mammalia, Chiroptera) from five caves of Central Apennines (Italy)

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Spanish title: Murciélagos (Mammalia, Chiroptera) del Holoceno de cinco cuevas de los Apeninos Centrales (Italia)

Abstract: Sixteen taxa divided into three families (Rhinolophidae, Vespertilionidae and Miniopteridae) and seven genera (*Rhinolophus*, *Myotis, Nyctalus, Plecotus, Barbastella, Miniopterus* and *Hypsugo* vel *Pipistrellus*) have been recorded among the microvertebrate remains from five caves of the Central Apennines (Italy). Archaeological excavations were carried out in the caves Grotta Bella in Umbria, Grotta Continenza in Abruzzi, Grotta Mora Cavorso, Grotta Regina Margherita and Grotta di Pastena in Latium, over the last decades. The chronology of the sites spans from the early to middle Holocene (Mesolithic to the Bronze Age).

Taphonomic observations suggest that the majority of the bat assemblages examined are autochthonous thanatocoenoses. The microclimate of the caves and the surrounding paleoenvironments can be reconstructed on the basis of ecological attributes of these taxa. The relative abundance of bat remains in the cave sediments testifies to the absence or the sporadic presence of humans in these sites during the corresponding time spans. The occurrence of *Rhinolophus mehelyi* in Central Italy during the early and middle Holocene adds new information on the geographical distribution of this species in the past.

Keywords: Chiroptera, Holocene, Italy, ecology, microclimate, biogeography, human activities.

Resumen: En cinco cuevas de los Apeninos Centrales (Italia) han sido encontrados, entre los restos de microvertebrados, dieciséis taxones agrupados en 3 familias (Rhinolophidae, Vespertilionidae y Miniopteridae) y 7 géneros (*Rhinolophus*, *Myotis*, *Nyctalus*, *Plecotus*, *Barbastella*, *Miniopterus* y *Hypsugo* vel *Pipistrellus*). En estas cuevas (Grotta Bella en Umbría, Grotta Continenza en Abruzos, Grotta Mora Cavorso, Grotta Regina Margherita y Grotta di Pastena en Lazio) se llevaron a cabo excavaciones arqueológicas en las últimas décadas. Los yacimientos se extendien desde el Holoceno antiguo y medio (Mesolítico hasta la Edad del Bronce).

Las observaciones tafonómicas sugieren que la mayoría de las comunidades de murciélagos analizadas son tanatocenosis autóctonas. Considerando las características ecológicas de estos taxones es posible reconstruir el microclima de las cuevas y el ambiente que constituye el entorno de los yacimientos. La abundancia relativa de los restos de murciélago hallados en el sedimento de las cuevas evidencia la ausencia o la esporádica presencia humana en estos sitios en los correspondientes intervalos de tiempo. La presencia de *Rhinolophus mehelyi* en Italia central durante el Holoceno antiguo y medio proporciona nueva información sobre la distribución geográfica de esta especie en el pasado.

Palabras clave: Chiroptera, Holoceno, Italia, ecología, microclima, biogeografía, actividades humanas.

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Introduction

European Chiroptera are flying insectivorous animals that react rapidly to climatic and environmental changes (Kowalski 1995, Rebello et al. 2010, Lanza 2012). Therefore, they are very useful for paleoecological reconstructions, and they are also good indicators for reconstruction of hypogean microclimates. Their abundance in the cave sediments testifies to the absence or the sporadic presence of prehistoric humans in these sites during the same time spans (Guillem Calatayud 1997, Rossina, 2006, Rossina et al. 2006, Salari & Kotsakis 2011, López-García & Sevilla 2012). On the other hand, they do not provide significant biochronological indications, and probably for this reason few people are interested in their systematic study (Salari & Kotsakis 2011), particularly for the more recent past, the Holocene.

This paper aims to explore the environmental, microclimate and biogeographic information provided by the bat remains recovered from five caves of Central Italy (Fig. 1), as well as their interactions with humans. The caves are: Grotta Bella in Umbria, Grotta Continenza in Abruzzi, Grotta Mora Cavorso, Grotta Regina Margherita and Grotta di Pastena in Latium. The archaeological investigations carried out over the last decades allowed to recover lithic, bone and pottery finds referred to a time interval spanning the early and middle Holocene (between the Mesolithic and the Middle Bronze Age), from Preboreal to Subboreal chronozones (Mangerud et al. 1974, Orombelli & Ravazzi 1996). Stratigraphic sequences of these caves also include Upper Palaeolithic and/or historical layers that are not considered in this work.

Stratigraphic notes

Grotta Bella

The cave is located on the slopes of Mount Aiola, in the Amerini Mountains, at 530 m a.s.l., about 2 km from Santa Restituta in Avigliano Umbro (Terni, Umbria).

The cave consists of a vast, almost semi-circular chamber (about 25 x 30 m) with a floor sloping towards the bottom with a gradient of about 32%. The analysed material was recovered during archaeological excavations carried out by the "Soprintendenza per i Beni Archeologici dell'Umbria" in collaboration with the Palaethnology Institute of the University of Milan between 1970 and 1973. The excavations have shown evidence of human presence from the Neolithic to the Roman age. After a preliminary survey, three trenches (I, II and III) were opened; of these, the third (III) has revealed the best preserved stratigraphy. Below a remarkably thick layer of approximately 3 m (which contained archaeological and faunal finds related to the Imperial and Republican Age, the Iron Age and the Bronze Age), Neolithic levels were recognised, sealed by a thin soil layer concretioned and reddened by fire. The Neolithic levels are characterized by a first layer (about 1.65 m thick) of compact soil reddened by fire, followed by a crumbly gray soil with abundant sharp-edged debris, large charcoal fragments and trichromatic painted pottery; finally, a dark layer (about 1.25 m thick) with charcoal fragments, increasingly abundant stones and linear pottery was identified (Guerreschi et al. 1992, Curci et al. 2010, 2014).

In the Stratigraphic Units (SSUU; Harris 1979) referred to the Neolithic and the Bronze Age, remains of *Erinaceus europaeus*, *Lepus europaeus*, *Glis glis*, *Eliomys quercinus*, *Arvicola amphibius*, *Microtus (Terricola) savii*, *Clethrionomys glareolus*, *Apodemus sylvaticus* vel *flavicollis*, *Vulpes vulpes*, *Ursus arctos*, *Martes martes*, *Meles meles*, *Felis silvestris*, *Lynx linx*, *Cervus elaphus*, *Capreolus capreolus*, *Sus scrofa*, *S. domesticus*, *Bos taurus*, *Ovis aries* vel *Capra hircus*, undetermined amphibians, reptiles and birds (Curci et al. 2010, 2014, Salari 2014, in press) and also of *Myotis bechsteini*, *M. capaccinii* and *Miniopterus schreibersii* (Tables 1 and 2) were recovered. The minimum number of individuals (MNI) of the non-volant micromammals from the Bronze Age SSUU is 46 (Salari 2014), therefore bats make 11.5% of the total of micromammals from these SSUU.

In the Amerini Mountains area, *Rhinolophus ferrumequinum* and *R. hipposideros* have been currently reported (Natura 2000 Database IT5220008).

Grotta Continenza

The cave is situated on the slopes of Mount Labbrone, 710 m a.s.l., along the southern slope of the Fucino basin, next to the village of Trasacco (L'Aquila, Abruzzi).

Archaeological digs, started in 1978 and directed by the Archaeology Department of the University of Pisa, uncovered several human remains, as well as one of the most complete stratigraphic sequences ranging from final Epigravettian and the Neolithic (Barra et al. 1990, Bevilacqua 1994).

In the Mesolithic and Neolithic layers *Erinaceus europaeus*, *Crocidura suaveolens*, *C. leucodon*, *Sorex* gr. *arenaus-samniticus*, *Lepus europaeus*, *Marmota marmota*, *Glis glis*, *Eliomys quercinus*, *Microtus (Terricola) savii*, *Clethrionomys glareolus*, *Apodemus (Sylvaemus)* sp., *A. (S.) sylvaticus*, *A. (S.) flavicollis*, *Canis lupus*, *C. familiaris*, *Vulpes vulpes*, *Martes* sp., *Meles meles*, *Lutra lutra*, *Felis silvestris*, *Ursus arctos*, *Sus scrofa*, *S. domesticus*, *Cervus elaphus*, *Capreolus capreolus*, *Bos primigenius*, *B. taurus*, *Rupicapra* sp., *Capra ibex*, *C. hircus*, *Ovis aries* and various bird, fish and mollusc species were found (Barra et al. 1990; Bevilacqua 1994, Di Canzio 2004), along with *Rhinolophus ferrumequinum*, *R. mehelyi*, *R. euryale*, *R. hipposideros*, *Myotis myotis*, *M. blythii*, *M. capaccinii*, *M. emarginatus*, *Myotis* sp., *Hypsugo* vel *Pipistrellus*, *Nyctalus noctula*, *Barbastella barbastellus* and *Miniopterus schreibersii* (Tables 1 and 2). In the Mesolithic spits, the remains of 230 individuals were found belonging to rodents and soricomorphs, and in the Neolithic spits, 89 individuals were counted (Di Canzio 2004); hence the bats make 15.1 and 17.6% of the micromammal individuals respectively.

Currently, several bat species, such as *R. ferrumequinum*, *R. hipposideros*, *M. myotis*, *M. brandtii*, *B. barbastellus* and *M. schreibersii* are recorded in the neighbouring Abruzzi National Park (Natura 2000 Database IT7110205; Agnelli et al. 2006).

Fig. 1 - Location of the sites. GB: Grotta Bella; GC: Grotta Continenza; GMC: Grotta Mora Cavorso; GRM: Grotta Regina Margherita; GP: Grotta di Pastena.

Grotta Mora Cavorso

The cave is located at 715 m a.s.l., in Palo Montano locality, near Jenne (Rome, Latium) and faces the right side of the upper Aniene River valley in the Regional Natural Park of the Simbruini Mountains.

The cave presents a succession of chambers and passages. At the end of the chamber 1 (about 20 x 10 m) a narrow passage leads to a natural duct with a 20° gradient. At the end of the duct the first inner room (about 6 x 4 m) is found, covered by stalagmite crusts. On the north wall, a second, horizontal natural duct is present, strongly concreted, and about 20 m long. At the end of it, two chambers (Upper and Lower) containing human remains were found. Archaeological investigations started in 2006 by the University of Rome "Tor Vergata", in agreement with the "Soprintendenza per i Beni Archeologici del Lazio", and focused initially on the areas with the human remains (at least 21 individuals spread over about 10 sq m) referred to the early Neolithic, fully incorporated into stalagmite crusts. Subsequently, several digs were opened with the purpose of investigating the stratigraphical sequence of

Table 1 - Number of identified specimens (NISP) of taxa identified and their percentage reports. GC: Grotta Continenza; GMC: Grotta Mora Cavorso; GB: Grotta Bella; GRM: Grotta Regina Margherita; GP: Grotta di Pastena. M: Mesolithic; N: Neolithic; B: Bronze Age.

Species/NISP	GC	GC	GC	GC	GMC	GMC	GMC	GMC	GB	GB	GRM	GRM	GP	GP
	M	M	N	N	N	N	NB	NB	B	B	B	B	B	B
	n.	%	n.	%	n.	%	n.	%	n.	%	n.	%	n.	%
Rhinolophus ferrumequinum	17	20,7	15	35,7	2	28,6	8	61,5			15	42,9		
Rhinolophus euryale	1	1,2	1	2,4							2	5,7		
Rhinolophus mehelyi	1	1,2												
Rhinolophus euryale/mehelyi			1	2,4										
Rhinolophus hipposideros	1	1,2			2	28,6	1	7,7			1	2,9		
Myotis myotis	1	1,2					1	7,7			7	20,0		
Myotis blythii	30	36,6	11	26,2	2	28,6	1	7,7			6	17,1	3	100
Myotis myotis/blythi	1	1,2	1	2,4	1	14,3								
Myotis bechsteini									4	40,0				
Myotis capaccinii	15	18,3	10	23,8					5	50,0				
Myotis emarginatus	1	1,2												
Myotis mystacinus s.l.											1	2,9		
Myotis sp.	6	7,3												
Hypsugo vel Pipistrellus	1	1,2												
Nyctalus noctula			1	2,4										
Plecotus auritus s.l.							1	7,7						
Barbastella barbastellus	2	2,4												
Miniopterus schreibersii	5	6,1	2	4,8			1	7,7	1	10,0	3	8,6		
total NISP	82		42		7		13		10		35		3	
total taxa	12		8		4		6		3		7		1	

Table 2 - Minimum number of individuals (MNI) of taxa identified and their percentage reports. For abbreviations see Tab.1 caption.

Species/MNI	GC	GC	GC	GC	GMC	GMC	GMC	GMC	GB	GB	GRM	GRM	GP	GP
	M	M	N	N	N	N	NB	NB	B	B	B	B	B	B
	n.	%	n.	%	n.	%	n.	%	n.	%	n.	%	n.	%
Rhinolophus ferrumequinum	8	19,5	6	31,6	1	25,0	5	50,0			8	36,4		
Rhinolophus euryale	1	2,4	1	5,3							1	4,5		
Rhinolophus mehelyi	1	2,4												
Rhinolophus euryale/mehelyi			1	5,3										
Rhinolophus hipposideros	1	2,4			1	25,0	1	10,0			1	4,5		
Myotis myotis	1	2,4					1	10,0			5	22,7		
Myotis blythii	12	29,3	5	26,3	1	25,0	1	10,0			4	18,2	2	100
Myotis myotis/blythi					1	25,0								
Myotis bechsteini									2	33,3				
Myotis capaccinii	7	17,1	5	26,3					3	50,0				
Myotis emarginatus	1	2,4												
Myotis mystacinus s.l.											1	4,5		
Myotis sp.	3	7,3												
Hypsugo vel Pipistrellus	1	2,4												
Nyctalus noctula			1	5,3										
Plecotus auritus s.l.							1	10,0						
Barbastella barbastellus	1	2,4												
Miniopterus schreibersii	4	9,8	1	5,3			1	10,0	1	16,7	2	9,1		
total MNI	41		19		4		10		6		22		2	

the deposit. In particular, Digs B, C and D (in chamber 1, in chamber 2 and in the duct that connects them) held, with some discontinuities, archaeological findings from the Upper Palaeolithic to the historical age. In some layers of compact silty ground, intercalated with thin stalagmite concretions and containing, in places, limestone clasts with sharp edges, lithic artefacts were found (from Upper Paleolithic to middle Bronze Age), pottery (from Neolithic to the historical age), disarticulated human bones (only in the middle Bronze Age), faunal remains, charcoal fragments and ash (in all layers) (Rolfo et al. 2012a, 2013, Salari et al. 2011, 2012, Silvestri et al., in press). The Neolithic finds from Digs B, C and D were attributed to the early Neolithic and late Neolithic, but study of the stratigraphic sequence is still in progress.

The SSUU related to the Neolithic and the Bronze Age held the remains of *Talpa caeca*, *Lepus* sp., *Glis glis*, *Eliomys quercinus*, *Arvicola amphibius*, *Microtus* (*Microtus*) *arvalis*, *M.* (*Terricola*) *savii*, *Clethrionomys glareolus*, *Apodemus sylvaticus* vel *flavicollis*, *Canis lupus*, *C. familiaris*, *Vulpes vulpes*, *Martes martes* vel *foina*, *Meles meles*, *Lutra lutra*, *Felis silvestris*, *Cervus elaphus*, *Capreolus capreolus*, *Sus scrofa*, *S. domesticus*, *Bos taurus*, *Ovis aries*, *Capra hircus*, undetermined amphibians, reptiles and birds (Rolfo et al. 2012a, 2013, Salari et al. 2012, Salari 2014) and also of *Rhinolophus ferrumequinum*, *R. hipposideros*, *Myotis myotis* vel *blythii*, *M. blythii*, *M. myotis*, *Plecotus auritus s.l.* and *Miniopterus schreibersii* (microvertebrates found from 2006 to 2008 only) (Tables 1 and 2). The MNI of the non-volant micromammals is 18 in the burial area and 15 in Digs B, C and D (Salari 2014), therefore the bats represent 18.2 and 40.0% of the micromammal individuals found in the various areas investigated.

Today, in the different karstic caves of the Regional Natural Park of Simbruini Mountains, *R. euryale*, *R. ferrumequinum*, *R. hipposideros*, *M. myotis*, *Eptesicus serotinus* and *M. schreibersii* occur (Papi 2004); Grotta Mora Cavorso is frequented by a small colony of *R. hipposideros*.

Grotta Regina Margherita

The cave is located on the southern side of the cliff on top of which is the village of Collepardo (Frosinone, Latium), in the Ernici Mountains, about 30 m above Fiume creek, a tributary of the Cosa River.

The cave consists of a large chamber of about 90 x 60 m that reaches 20 m in height, and is divided into three sectors of increasingly higher level, delimitated by impressive stalagmite columns; to the east of the entrance is a branch with a length of about 20 m. This karst cave, recorded at the end of the 19th Century under the name "Grotta dei Bambocci", is known in the literature for the excavations by Ponzi, for the Pleistocene faunal remains found by Segre in the last century and, later, for the pottery referred to the beginning of the Middle Bronze Age published by Biddittu and Guidi (Angle et al. 2010b, with references). The material examined comes from five test pits dug in different areas of the cave by the "Soprintendenza per i Beni Archeologici del Lazio" in 2008. Digs A (8 sq m), B (3 sq m), C (1 sq m), D (9 sq m) and E (1 sq m) held human bones referred to 31 individuals and several archaeological and faunal finds that testify to intense human frequentation during the early Middle Bronze Age (Angle et al. 2010b). A joint collaboration between the "Soprintendenza per i Beni Archeologici del Lazio" and the University of Durham has resumed the investigations in 2014.

Preliminary analysis of the faunal remains recovered in 2008 has documented the presence of *Ovis aries* vel *Capra hircus*, *Bos* sp., *Equus* sp., *Canis* sp., *Lepus* sp., *Vulpes* sp., undetermined amphibians and birds (Angle et al. 2010b), *Crocidura leucodon*, *Talpa caeca*, *Glis glis*, *Eliomys quercinus*, *Muscardinus avellanarius*, *Arvicola amphibius*, *M.* (*Terricola*) *savii*, *Microtus* sp., *Clethrionomys glareolus*, *Apodemus sylvaticus* vel *flavicollis* and *Rattus rattus* (Salari 2014) and also of *Rhinolophus ferrumequinum*, *R. euryale*, *R. hipposideros*, *Myotis myotis*, *M. blythii*, *M. mystacinus s.l.* and *Miniopterus schreibersii* (Tables 1 and 2). The MNI of rodents and soricomorphs is 93 (Salari 2014), therefore bats in this cave make 19.1% of micromammal individuals.

Presently, *R. ferrumequinum*, *R. euryale*, *R. hipposideros*, *Myotis capaccinii*, *M. myotis* e *M. schreibersii* occur in the cave (Natura 2000 Database IT6050006).

Grotta di Pastena

The cave is located 310 m a.s.l., in the Cretaceous limestones of the S. Cataldo Mount, in the Ausoni Mountains, adjacent to the Province Road that leads from Castro dei Volsci to Pastena (Frosinone, Latium).

Archaeological interest in this site has been known since the earliest investigations carried out in the 1980s (Angle et al., 2010a with references). Remains of *Ovis aries* vel *Capra hircus*, *Bos* sp., *Sus* sp., *Felis* sp. *Emys* sp., undetermined birds and molluscs come from the various test pits dug in 2008 by the "Soprintendenza per i Beni Archeologici del Lazio" (Angle et al. 2010a). A joint collaboration between the "Soprintendenza per i Beni Archeologici del Lazio" and the University of Rome "Tor Vergata" has resumed the investigations at the site in 2013 (Angle et al. 2014).

Among the micromammal remains found in 2008 in the sediments of the niche "E10", referred to the Middle Bronze Age, the only specimens taxonomically identified are an upper incisor of a medium-large sized rodent, along with an intact humerus and two distal portions of humerus attributed to *M. blythii* (Tables 1 and 2).

Currently, *R. ferrumequinum*, *R. euryale*, *R. hipposideros*, *M. myotis*, *M. blythii* and *Miniopterus schreibersii* live in this karst cave (Natura 2000 Database IT6050022).

Materials and methods

The material from Grotta Regina Margherita, Grotta di Pastena and Grotta Mora Cavorso (Digs B, C and D) was sieved with a 2-mm mesh in the field (smaller screens require the use of water, which was absent or scarce at the sites) and relatively good samples of bat remains were obtained. Because of difficulty separating the bones from the stalagmite crusts, only selected elements (mainly humeri) were recovered from the burial area of Grotta Mora Cavorso. The collection methods for the microvertebrate remains from Grotta Bella and Grotta Continenza are not known.

The bat remains were compared with osteological material, both fossil and recent, stored in the Department of Earth Sciences of the University of Rome "Sapienza", in the Department of Geological Sciences of the "Roma Tre" University and in the Laboratory of Archaeozoology of the National Museum of Prehistory and Ethnography "Luigi Pigorini" of Rome. The morphological and morphometric observations and the dichotomous keys given by Miller (1912), Lanza (1959, 2012), Felten et al. (1973), Sevilla García (1986; 1988), Ruedi et al. (1990), Niethammer & Krapp (2001), Benda et al. (2003), Csorba et al. (2003) and Salari (2004) were also consulted. The analyses were performed with a stereoscopic microscope Nikon SMZ-U in the Department of Geological Sciences of the "Roma Tre" University.

For the taphonomic observations, the samples were considered *in toto*, while for the taxonomic determinations the analyzed material was chosen on the basis of its systematic importance (skull, maxilla, mandible and humerus). Other skeletal parts (e.g., scapula, radius, metacarpal bones, coxal) that enable identification at family or genus level or even species level, were not considered in order to minimize the statistical bias for small-bodied species. Their fragile skeletal elements are more frequently subject to the processes of differential destruction than those of larger species, or can be lost during collection. The minimum number of individuals (MNI) was calculated using the most represented side (right or left) of maxillae, mandibles and humeri; this result was integrated with the analysis of the age and the dimensional characters of the other skeletal elements.

The environmental reconstructions are based on actual studies on the ecology and biogeography of the taxa found in the different levels of the caves (Lanza 1959, 2012, Horáček et al. 2000, Niethammer & Krapp 2001; Lanza & Agnelli 2002, Agnelli et al. 2006). Holocene chronostratigraphy follows Orombelli & Ravazzi (1996), supplemented by Ravazzi (2003).

Systematic notes

In this work we follow the taxonomic and geographic synthesis by Simmons (2005), with the following exceptions.

- Family Miniopteridae is considered distinct from Vespertilionidae, according to Mein & Tupinier (1977), Lanza & Agnelli (2002), Agnelli et al. (2006), Miller-Butterworth et al. (2007) and Lanza (2012).

- We use the taxon *M. blythii* instead of *M. oxygnathus*. According to Simmons (2005), the extant European and Near-Eastern populations, up to North and West Iran, should be ascribed to *M. oxygnathus* as opposed to *M. blythii oxygnathus* or to *M. blythii* (Lanza 2012). However, the vast majority of the paleontological works examined identifies the remains of large-sized *Myotis*, distinct from *M. myotis*, as *M. blythii* (not as *M. oxygnathus*). In the Western Paleartic, *M. blythii* fossils date back to Pliocene (Salari et al. 2013 with references).

With respect to the distinction between the large-bodied *Myotis* (excluding *M. punicus* for palaeobiogeographic reasons), *M. myotis* is larger in size, but the dimensions of large *M. blythii* and small *M. myotis* overlap (Sevilla 1988, Niethammer & Krapp 2001, Ghazali 2009). The only certain morphological difference between the teeth of *M. myotis* and *M. blythii* occurs on the talonid of m3, which is more reduced in *M. myotis* (Topál & Tusnadi 1963, Sevilla 1986, 1988). Therefore we calculated the talonid reduction index (TRI = talonid width x 100/tooth length) and we assigned the specimens with the TRI less to 0.45 to *M. myotis*, and those with TRI close to 0.50 to *M. blythii* (Mein 1975). The dimensions of other specimens (Table 4) support our attribution (Ruedi et al. 1990, Niethammer & Krapp 2001, Benda et al. 2003, Lanza 2012).

Concerning the humeri of identical morphology (Felten et al. 1973), discrimination between the two species mainly relied on the distal epiphysis, ascribing only the larger ones and those of more robust aspect to *M. myotis*, with all remaining material being assigned to *M. blythii*.

In Tables 1 and 2, percentages of the number of identified specimens (NISP) and of the minimum number of individuals (MNI) from the different caves are recorded; in Table 1 the number of identified taxa is also recorded. It can be immediately noted that the data differ considerably from site to site: some caves, such as Grotta Continenza and partly Grotta Regina Margherita, held a large number of remains, whereas others, such as Grotta di Pastena, held a rather limited number of bones.

The bat remains from the investigated caves do not show major morphological or morphometric differences from other Holocene and living species (Tables 3 and 4). However, the recent applications of modern bioacoustic and molecular biology techniques (combined with conventional approaches based on morphological and morphometric criteria), have allowed identification of new species. In particular, some subspecies or geographic varieties of species belonging to the genera *Pipistrellus*, *Myotis* and *Plecotus* (e.g., *Pipistrellus pygmaeus*, *Myotis alcathoe*, *M. aurascens*, *M. punicus*, *Plecotus gaisleri*, *P. kolombatovici*, *P. macrobullaris*, *P. sardus*) were elevated to the rank of full species (Agnelli et al. 2006, Lanza 2012), but the lack of sound morphometric data for their taxonomic determination did not permit adequate assessment of them. The fossil remains potentially falling into the above taxa were attributed to the traditionally recognised species, followed by *s.l.* (= *sensu lato*) in accordance with Agnelli et al. (2006) for reports of these taxa prior to 2000. This is the case of humeri of *M. mystacinus s.l.* (i.e. *M. mystacinus* or *M. brandtii* or *M. alcathoe*) from Grotta Regina Margherita and of *Plecotus auritus s.l.* (i.e. *P. auritus* or *P. macrobullaris*) from Grotta Mora Cavorso.

Distinction between *Hypsugo savii* and the species of larger size of the genus *Pipistrellus* is also problematic: the morphology and size of the distal epiphysis of the humeri are identical (Felten et al. 1973) and the humerus from Grotta Continenza was attributed to *Hypsugo* vel *Pipistrellus* (i.e. *H. savii* or *P. kuhlii* or *P. nathusii*). The attribution of a distal humerus of a medium-sized *Rhinolophus* species collected in Grotta Continenza is uncertain because the morphology of the specimen missing the styloid process does not allow assignment the bone to species level, and the dimensions fall inside the range of both *Rhinolophus euryale* and *R. mehelyi* (Felten et al. 1973). The attribution of some distal humeri of medium/small-sized *Myotis* from Grotta Continenza is also uncertain, because the morphology and breadth (2.6 - 2.7 mm) of the distal epiphysis of the humerus of *Myotis daubentonii*, *M. emarginatus* and *M. nattereri* are identical (Felten et al. 1973), and these remains are reported as "*Myotis* sp." in Tables 1 and 2; instead, a complete humerus was attributed to *M. emarginatus*. Finally, a few, highly fragmented bones of large-sized *Myotis* from Grotta Mora Cavorso and Grotta Continenza were attributed to *Myotis myotis* vel *blythii*, and a few toothless fragmented mandibles of medium/small-sized *Myotis* from Grotta Continenza is reported as "*Myotis* sp.".

Taphonomy

Bats are nocturnal animals and can be occasional prey of nocturnal birds of prey (Strigiformes), such as the long-eared owl, *Asio otus*, the tawny owl, *Strix aluco*, the little owl, *Athene noctua*, the Eurasian eagle-owl, *Bubo bubo* and

Table 3 - Rhinolophidae: osteometric measurements (mm). Abbreviations for skull, mandible and humerus dimensions: L. = maximum length; ZB = zygomatic breadth; IcB = breadth of interorbital constriction; C-C = rostral width between upper canines (incl.); M3-M3 = rostral width between third upper molars (incl.); C-M3 = length of upper tooth-row between C and M3 (incl.); M1-M3 = length of upper molars (incl.); c-m3 = length of lower tooth-row between c and m3 (incl.); m1-m3 = length of lower molars; Bd = distal breadth of humerus. Other abbreviations: min = minimum; max = maximum; mea = mean; s.d. = standard deviation. Only humerus measurements were taken by Felten et al. (1973).

Species/measurements	early and middle Holocene bats of Italy							European extant bats				
	Five caves of Central Appennine (this work)					Salari 2011		Niethammer & Krapp 2001		Benda et al 2003		Lanza 2012; Felten et al 1973
	n.	min	max	mea	s.d.	n.	min - max	n.	min - max	n.	min - max	min - max
Rhinolophus ferrumequinum												
C-M3	1			8,5		3	8,4 - 8,6	27	8,4 - 8,7	93	8,31 - 9,08	8,4 - 8,6
M1-M3	2	5,1	5,2	5,15	0,071	6	4,9 - 5,3					
L. mandible	11	15,0	15,4	15,13	0,135	4	14,4 - 15,5	27	14,9 - 15,9	94	14,94 - 16,48	15,0 - 16,3
c-m3	17	8,7	9,3	9,07	0,193	13	8,7 - 9,6	27	9,0 - 9,3	94	8,72 - 9,73	8,8 - 9,3
m1-m3	18	6,0	6,4	6,15	0,142	20	5,8 - 6,5					
L. humerus	10	32,4	35,0	33,74	1,075	2	33,2					
Bd humerus	33	5,0	5,2	5,16	0,056	13	4,9 - 5,2	27	4,8 - 5,3			~5,1
Rhinolophus euryale												
L. mandible	1			11,4		4	11,2 - 12,0	29	11,5 - 12,2	165	10,82 - 12,22	11,5 - 12,2
c-m3	2	6,4	6,8	6,60	0,283	14	6,2 - 7,0	29	6,5 - 6,9	168	5,91 - 6,92	6,6 - 6,9
m1-m3	2	4,2	4,6	4,40	0,283	22	4,2 - 4,7					
L. humerus	1			27,0		10	25,9 - 28,2					
Bd humerus	1			4,3		38	4,1 - 4,4					~4,3
Rhinolophus mehelyi												
Bd humerus	1			4,6		4	4,4 - 4,7					~4,5
Rhinolophus hipposideros												
L. skull	1			15,3				25	14,8 - 15,8	45	15,25 - 16,76	14,8 - 15,8
ZB	1			7,4				25	7,0 - 7,8	53	7,23 - 8,10	7,3 - 7,8
IcB	1			1,6				25	1,7 - 2,0	62	1,38 - 2,00	1,8 - 1,9
C-C	1			3,2				25		58	2,98 - 3,88	
M3-M3	1			5,3				25		62	4,93 - 5,64	
C-M3	2			5,4				25	5,0 - 5,5	61	5,08 - 5,53	5,4 - 5,5
M1-M3	2			3,4								
L. humerus	2	22,1	23,0	22,55	0,636	1	23,1					
Bd humerus	4	3,0	3,1	3,05	0,058	4	3,0 - 3,3					~3,1

especially the barn owl, *Tyto alba* (Andrews 1990, Lanza 2012); the last two species are the main, if not the exclusive, agents of accumulation of the non-volant micromammal remains from some of the caves examined (Salari 2014). Bats can also be occasionally preyed on by diurnal birds of prey (Falconiformes), reptiles and amphibians, as well as some mammalian carnivores (domestic dogs and cats, mustelids and foxes) and infrequently by the edible dormouse, *Glis glis* (Agnelli & Guaita 2009, Lanza 2012).

In the boluses or pellets of the Strigiformes, bats make rarely more than 1% of prey, as their regurgitations are mainly consist of rodents, small birds and soricomorphs (Sevilla 1988, Andrews 1990, Vernier 1993, Kowalski 1995, García et al. 2005). Among the material from these caves of Central Italy (leaving out the small sample from Grotta di Pastena), even where the number of remains is relatively low, percentages of bat individuals range from 11.5 to 40% of the micromammal total. These percentages can be correlated to anomalous behaviours of the predators or they can indicate autochthonous thanatocoenoses. In order to investigate what, and in which sites, were the agents of accumulation of the bat remains examined, taphonomic observations were undertaken following the methodologies proposed by Andrews (1990) and Fernández-Jalvo & Andrews (1992). These include observations about the relative abundance of bones and their fragmentation, and analysis of the material for evidence of digestion and patterns leading to the identification of the possible predators.

Table 5 shows the different skeletal elements represented in the samples. Only in the sample from Grotta Regina Margherita are almost all the skeletal elements represented. The humerus is the most abundant skeletal element from Grotta Bella, Grotta Mora Cavorso (burial area), Grotta di Pastena and Grotta Regina Margherita, whereas the most abundant elements from Grotta Continenza are the mandibles and from Grotta Mora Cavorso (Digs B, C and D) the radii (Table 5). The hindlimb bones and the smallest bones, such as phalanges, tarsal or metatarsal bones, together with isolated teeth, are absent or scarce in all the samples, especially when compared to the relative abundance of these elements expected for the respective estimated individuals (Table 5). Postcranial elements other than the humerus (not reported in Tables 1 and 2) are referable to the large-sized bats (*R. ferrumequinum*, *M. myotis*, *M. blythii*), except for two radii of medium-sized *Rhinolophus* and a radius referable to *M. schreibersii* from Grotta Continenza, and a radius of small-sized *Myotis* from Grotta Regina Margherita.

Skulls and skull fragments are missing or are very scarce in all the samples. Several maxillae were found, but only a sub-entire skull of *R. hipposideros* embedded in the stalagmite crust from Grotta Mora Cavorso (burial area), 4 splancnocrania of *M. blythii* from Grotta Continenza and a splancnocranium of *M. myotis* from Grotta Regina Margherita. Mandibles are more numerous, often with the ascending ramus missing. In all the samples, about half of the postcranial bones are intact, and recent breakage is observed in several bones (humerus, radius and metacarpal bones). However, it is difficult to estimate the extent to which the aforementioned absence and/or destructive processes are related to ingestion, digestion and deposition by possible predators or selection caused by water transport

Table 4 - Vespertilionidae and Miniopteridae: osteometric measurements (mm). For abbreviations see Tab. 3 caption. By Rabeder (1972) only *N. noctula* measurements were taken; by Felten et al. (1973) only humerus measurements were taken. Of the data of *M. blythii* taken by Niethammer & Krapp (2001), we have considered only *M. blythii oxygnathus*.

Species/measurements	early and middle Holocene bats of Italy							European extant bats				
	Five caves of Central Appennine (this work)					Salari 2011		Niethammer & Krapp 2001; Rabeder 1972		Benda et al 2003		Lanza 2012; Felten et al 1973
	n.	min	max	mea	s.d.	n.	min - max	n.	min - max	n.	min - max	min - max
Myotis myotis												
C-C	1			6,2		1	6,1	19	5,99 - 6,59	71	5,35 - 6,55	
M3-M3	1			10,0		1	9,7			68	9,28 - 10,38	
C-M3	2			10,1		2	9,8	20	9,65 - 10,24	71	9,52 - 10,42	9,8 - 10,0
M1-M3	4	5,4	5,6	5,55	0,100	2	5,6					
L. mandible	1			17,6		2	17,4	20	17,79 - 19,14	72	17,32 - 18,87	17,5 - 18,0
c-m3	1			11,4		5	10,5 - 11,1	20	10,15 - 11,11	72	10,33 - 11,90	10,5 - 10,8
m1-m3	2			6,8		7	6,2 - 6,6					
L. humerus	2	33,3	33,8	33,55	0,354	4	34,2 - 34,6					
Bd humerus	2	4,3	4,4	4,35	0,071	15	4,4 - 4,6					4,0 - 4,6
Myotis blythii												
C-C	4	5,8	6,1	5,95	0,173	1	6,2	19	5,36 - 5,89	37	5,22 - 6,17	
M3-M3	4	8,6	9,2	8,90	0,346	2	9,2	19	8,41 - 9,13	36	8,05 - 9,27	
C-M3	8	8,8	9,2	8,97	0,138	3	8,9 - 9,2	19	8,21 - 9,03	38	8,06 - 9,13	8,6 - 8,8
M1-M3	10	5,0	5,2	5,16	0,088	6	5,0 - 5,4	19	4,82 - 5,29			
L. mandible	9	16,0	16,8	16,29	0,247	12	14,7 - 17,0	19	15,35 - 16,78	39	15,30 - 17,15	15,0 - 15,5
c-m3	20	9,2	10,2	9,55	0,260	21	9,8 - 10,2	19	8,83 - 9,68	39	8,85 - 9,80	9,0 - 9,5
m1-m3	28	5,4	6,1	5,84	0,221	32	5,4 - 6,1	19	5,26 - 5,86			
L. humerus	5	31,6	32,6	32,16	0,434	12	31,9 - 32,4					
Bd humerus	13	4,0	4,2	4,13	0,095	36	3,9 - 4,3					4,0 - 4,6
Myotis bechsteini												
L. humerus	2			24,0								
Bd humerus	4			3,0								2,9 - 3,1
Myotis capaccinii												
C-M3	2			5,8				28	5,2 - 5,8	29	5,35 - 5,91	5,4 - 6,0
M1-M3	2			3,0								
L. mandible	7	10,4	11,2	10,80	0,383			28	10,0 - 11,7	28	10,38 - 11,38	10,4 - 11,7
c-m3	12	5,8	6,2	6,10	0,135	1	6,2	28	5,7 - 6,4	28	5,69 - 6,53	5,7 - 7,0
m1-m3	13	3,8	4,0	3,83	0,075	1	3,7					
L. humerus	3	21,2	22,0	21,73	0,462	2	23,5					
Bd humerus	14	2,7	3,0	2,79	0,077	11	2,7 - 3,0					~2,7
Myotis emarginatus												
L. humerus	1			22,2								
Bd humerus	1			2,6								2,6 - 2,7
Myotis mystacinus s.l.												
Bd humerus	1			2,4								2,2 - 2,4
Hypsugo vel Pipistrellus												
L. humerus	1			22,8								
Bd humerus	1			2,4								2,2 - 2,4
Nyctalus noctula												
c-m3	1			7,5					7,6	12	7,53 - 8,17	7,2 - 8,29
m1-m3	1			5,2					5,3			
Plecotus auritus s.l.												
L. humerus	1			23,8								
Bd humerus	1			2,8		1	2,8					2,7 - 2,9
Barbastella barbastellus												
Bd humerus	2	2,7	2,8	2,75	0,071							2,7 - 2,8
Miniopterus schreibersii												
L. mandible	1			10,8		3	10,9 - 11,2			66	10,41 - 11,08	10,7 - 10,9
c-m3	1			6,2		4	6,2 -6,4			66	6,13 - 6,48	6,3 - 6,4
m1-m3	1			3,6		5	3,6 - 3,9					
L. humerus	4	24,6	26,0	25,40	0,632	11	25,2 - 26,4					
Bd humerus	8	2,7	2,8	2,78	0,046	21	2,6 - 2,8					~2,7

or to destructive post-depositional processes. In the caves occupied by humans, trampling can also be responsible for dispersal, breakage and burial of bones (Andrews 1990). The weight of the sediments and the continuous trampling in confined spaces can cause bone fragmentation and the smaller fragments (together with isolated teeth and smaller bones) can be overlooked during collection. In the sites where it was used, the large mesh (2 mm) for sieving is most likely a cause of such loss. This has not strongly affected the intact long bones, the fragments of larger size, skull fragments, maxillae and mandibles, because their shape and size makes them more easily retained in the mesh.

Ascertained traces of digestion were found only on two distal epiphyses of humerus from Grotta di Pastena, but the material is too poor to identify the probable predator. Therefore it is very likely that the finds from the other caves consisted mainly of the natural accumulation of animals that lived and died there. The taxa identified were mostly troglophilous species in all the sites, whereas species that usually roost in hollow trees, or rock crevices, as well as those today distinctly anthropophilous, were lacking or missing. These data suggest that the non-troglophilous species may really be underrepresented, but they tend to confirm that the vast majority of the bat remains examined (except for Pastena) represent autochthonous thanatocoenoses (Sevilla 1988, Kowalski 1995, López-García & Sevilla 2012).

Table 5 - Skeletal elements represented in the bat assemblages.The percentage is calculated versus the theoretical frequency of the anatomical element considered (2 maxillae, 2 mandibles, 2 scapulae, 2 humeri, 2 radii, 2 ulnas, 10 metacarpal bones, 2 pelves, 2 femora, 2 tibias, 2 astragals, 2 calcanei, 10 metatarsal bones and 56 phalanges); each skull or splanchnocranium was counted as 2 maxillae. For abbreviations see Tab. 1 caption.

Skeletal elements	GC	GC	GC	GC	GMC	GMC	GMC	GMC	GB	GB	GRM	GRM	GP	GP
	M	M	N	N	N	N	NB	NB	B	B	B	B	B	B
	n.	%	n.	%	n.	%	n.	%	n.	%	n.	%	n.	%
Maxilla	6		12	31,6	2	25,0					6	13,6		
Mandible	40	48,8	22	57,9	1	12,5	1	5,0			17	38,6		
Scapula											2	4,5		
Humerus	39	47,6	16	42,1	5	62,5	15	75,0	11	91,7	22	50,0	3	75,0
Radius	3	3,7	6	15,8			18	90,0	8	66,7	16	36,4	3	75,0
Ulna														
Carpal bones														
Metacarpal bones	5	1,2	5	2,6			8	8,0	4	6,7	36	16,4	14	70,0
Pelvis											1	2,3		
Femur							2	10,0	3	25,0	4	9,1	3	75,0
Tibia											2	4,5		
Tarsal bones														
Metatarsal bones														
Phalanges							7	1,3	1	0,3	14	1,1	7	6,3
MNI	41		19		4		10		6		22		2	

Table 6 - Comparison between early and middle Holocene bats (data from Taliana et al. 1996, Wilkens 1996, Salari & Di Canzio 2009, Salari 2011, and this work) and the current bat fauna from Umbria, Abruzzi and Latium (data from Agnelli et al. 2006, Russo et al. 2010, Biscardi et al. 2012), and schematic synthesis of some ecological attributes of the bats (Horáček et al. 2000, Lanza & Agnelli 2002, Agnelli et al. 2006, Salari & Di Canzio 2009, Lanza 2012). e.m.H.: early and middle Holocene; s.s.: *sensu stricto*; s.l.: *sensu lato*.

Species	Umbria, Abruzzi and Latium		hibernacula	temperatures of hibernation	foraging environment	zoogeographical patterns
	e.m.H.	today				
Rhinolophus ferrumequinum	X	X	caves	7 to 12 °C	mixed	Mediterranean s.l.
Rhinolophus euryale	X	X	caves	10 to 12 °C	woods	Mediterranean s.s.
Rhinolophus mehelyi	X		caves	11 to 13 °C	woods	Mediterranean s.s.
Rhinolophus hipposideros	X	X	caves	4 to 12 °C	woods	Mediterranean s.l.
Myotis myotis	X	X	caves	2 to 12 °C	woods	Mediterranean s.l.
Myotis blythii	X	X	caves	4 to 14 °C	open	Mediterranean s.l.
Myotis bechsteini	X	X	hollow trees, caves	1 to 10 °C	woods	Nemoral
Myotis capaccinii	X	X	caves	4 to 15 °C	woods	Mediterranean s.s.
Myotis daubentoni	?	X	caves	0 to 10 °C	forests	Boreal
Myotis emarginatus	X	X	caves	5 to 9 °C	various	mediterranea s.l.
Myotis nattereri	?	X	caves	2 to 8 °C	woods	Nemoral
Myotis mystacinus	X?	X	caves	2 to 8 °C	various	Nemoral
Myotis brandtii	?	X	caves, building	0 to 8 °C	forests	Boreal
Myotis alcathoe	?	X	caves	?	forests	Nemoral?
Pipistrellus kuhlii	?	X	building, rock fissures	?	various, anthropophilous	Mediterranean s.s.
Pipistrellus nathusii	?	X	rock fissures, building	?	woods	Nemoral
Pipistrellus pipistrellus s.l.		X	building, hollow trees	0 to 6 °C	woods, anthropophilous	Mediterranean s.l.
Hypsugo savii	?	X	building, caves	~12 °C	various, anthropophilous	Mediterranean s.s.
Eptesicus serotinus		X	building, caves	2 to 4 °C	various	Mediterranean s.l.
Nyctalus leisleri		X	hollow trees	?	woods	Nemoral
Nyctalus noctula	X	X	hollow trees	> -7 °C	forests	Nemoral
Barbastella barbastellus	X	X	caves	0 to 8 °C	forests	Nemoral
Plecotus auritus	X?	X	hollow trees, caves	2 to 5 °C	forests	Boreal
Plecotus austriacus		X	grotte, hollow trees	2 to 12 °C	woods	Mediterranean s.l.
Miniopterus schreibersii	X	X	caves	4 to 12 °C	various	Mediterranean s.s.
Tadarida teniotis		X	rock fissures	0 to 10 °C	rocky	Mediterranean s.s.

Elements of juvenile bats were not identified in any sample, whereas in Grotta Bella, Grotta Mora Cavorso and Grotta Regina Margherita juvenile remains of *Glis glis*, *Apodemus sylvaticus* vel *flavicollis* and other rodents were found (Salari 2014, in press), along with perinatal remains of domestic animals from Grotta Continenza and Grotta Mora Cavorso (Barra et al. 1990, Salari et al. 2012, Silvestri et al. in press). This suggests that the absence of juvenile bat remains is not simply attributable to processes of differential destruction, and therefore we hypothesize that the examined remains were accumulated mainly during hibernation, during the winter semester.

Microclimate and environment

For bats, the choice of diurnal roosts, as well as of reproduction and hibernation environments, is strongly influenced by the microclimate of the cave. Every species has a specific level of tolerance to limited ranges of temperature and humidity (generally, low temperature with high hygrometric rate) (Niethammer & Krapp 2001, Lanza & Agnelli 2002, Lanza 2012). However, temperature and humidity in caves can vary according to cave size, its morphology, the number of openings and their orientation. Larger caves can have different microclimates (with more or less constant temperatures but variable humidity, owing above all to draughts of air) and each species selects the spots that best suit their preferences (Sevilla 1988, Lanza & Agnelli 2002, Lanza 2012).

With the only exception of Pastena, taphonomical observations suggest that the remains examined accumulated prevalently during the winter semester. By evaluating the hibernation requirements of the taxa identified (Table 6), inferences can be drawn about the winter microclimate of the caves (at least related to the areas close to the excavation areas) in the time intervals considered.

At Grotta Mora Cavorso, in the inner chambers that held the human remains of at least 21 individuals, the Neolithic's microclimate was probably characterised by a high humidity (close to saturation) and a temperature ranging between 7 and 12°C. The hypothesis, already formulated by Salari & Kotsakis (2011), has recently been confirmed by both the study of the stalagmite formations and the monitoring of the current physical parameters of the karst cave. In fact, in the winter semester of 2007-2008, temperatures between 10 and 12°C were recorded, with a relative humidity close to 80% in the inner chambers of the cave (Rolfo et al. 2012c). The temperature values, estimated on the basis of the assumed needs of the identified taxa, are thus compliant with the physical parameters recorded. With regards to the humidity, instead, it has to be noted that calcite precipitation in the Neolithic required a higher hygrometric rate than at present (Rolfo et al. 2012b).

Supported by these experimental results, we can hypothesize that in the chronological intervals considered, at Grotta Continenza the winter microclimate remained rather constant, with average temperatures ranging from 8 to 12°C and a high humidity; moreover, we can assume that the winter temperature ranged between 4 and 12°C in Grotta Bella, and between 10 and 12°C in Grotta Regina Margherita. The occurrence of some taxa that usually roost in hollow trees (*Nyctalus noctula*, *Plecotus auritus s.l.*), in addition, might indicate periods of climatic deterioration or at least particularly cold winters.

Bats have a foraging range of several kilometres from their roosts (Niethammer & Krapp 2001, Lanza & Agnelli 2002, Lanza 2012). Therefore, by analysing the actual distribution areas and foraging environments of the taxa identified (Table 6), the study of the bones found in the archaeological digs provides interesting information on the surroundings of the caves at the time of their deposition.

For refined quantitative analyses, significantly numerous samples are required, taking into account that some species form large colonies (monospecific or mixed), even of thousands of individuals (e.g., *Myotis myotis*, *M. blythii*, *M. capaccinii*, *Miniopterus schreibersii*), others form smaller colonies, from a few individuals to several hundred (e.g., *Rhinolophus ferrumequinum*, *R. hipposideros*, *M. mystacinus*) or have more solitary behaviours (e.g., *M. bechsteini*, *M. emarginatus*, *Barbastella barbastellus*). However, despite the limited numerical significance of some samples, these can still provide useful environmental information.

For example, species found at Grotta Bella suggest that, in the Bronze Age, the slopes of Mount Aiola were mostly covered by woodland near wetland areas and they were frequented by *Myotis bechsteinii* and *M. capaccinii*, whereas the presence of *Miniopterus schreibersii* indicates the existence of a more varied environment, both rich in woodlands and clearings. The bat taxa found at Grotta Mora Cavorso show that in the chronological interval considered in the Upper Aniene Valley both woodlands, frequented by *Myotis myotis*, *Plecotus auritus s.l.* and *Rhinolophus hipposideros*, and open spaces were present, as suggested by *Myotis blythii*, which prefers rich grasslands as foraging areas, avoiding both arid or denuded areas and any type of woodland and forest. At the same time, *R. ferrumequinum* indicates the presence of different environments, both forested and open, close to waterways. Although the individuals of the species that prefer mixed environments are relatively numerous (*R. ferrumequinum*, *Myotis mystacinus s.l.* and *Miniopterus schreibersii*), the surroundings of the Grotta Regina Margherita, in Collepardo, were likely to be covered by woodlands in the Middle Bronze Age, and frequented by the other rhinolophids and by *M. myotis*, whereas the presence of *M. blythii* indicates the existence also of open spaces (Fig. 2).

The ratio of the taxa recovered from the stratigraphic sequence of Grotta Continenza, finally, shows that from the Mesolithic (layer 27) to the Neolithic (layer 23), along the Fucino basin and the slopes of Mount Labbrone, the tree crown cover increased at the expense of open spaces (Fig. 3). In effect, this coincides with an increase in the woodland-adapted species, with some fluctuations, from 36.4 to 55.6%.

The aforementioned environmental indications provided by bats are generally compliant with those derived from the study of the non-volant micromammals, i.e. rodents and soricomorphs (Di Canzio 2004, Salari 2014).

Biogeography

All the taxa identified are still part of the extant Italian bat fauna. With regards to the species recognised through the use of modern bioacustic and biomolecular analyses (see "Systematic notes"), in Italy *P. pygmaeus* seems to be found along the entire pensinsula, *M. punicus* and *P. sardus* in Sardinia, *M. alcathoe* in central and southern Italy, *P. macrobullaris* in the Alpine regions, *P. kolombatovici* in the extreme North-East, *P. gaisleri* in the island of Pantelleria, whereas the presence of *M. aurescens* has not been confirmed (Agnelli et al. 2006, Lanza 2012).

The taxa identified are mainly species of Mediterranean affinities (*sensu lato* and *sensu stricto*, Horáček et al. 2000), both in terms of the number of identified remains and invididuals and the number of sites where they were found. The presence of nemoral and especially boreal species is not significant (Table 6), which is similar to the trend on the peninsula for the extant bat fauna (Lanza & Agnelli 2002, Salari & Di Canzio 2009).

Comparing the taxa identified only with those present today in the caves examined or their surroundings might be misleading, although in some cases this could provide data about the stability of the roost choices of those species. By widening the comparisons to species that live in Umbria, Latium and Abruzzi today (Agnelli et al. 2006, Russo et al. 2010, Biscardi et al. 2012), integrating the data discussed so far with the literature of the bat remains from Grotta del Lago, Grotta Sant'Angelo and Grotta dei Cocci (Taliana et al. 1996, Wilkens 1996, Salari & Di Canzio 2009, Salari 2011), it can be noted instead that the bat fauna of these regions in the early and middle Holocene was already very similar to the present (Table 6). Regional peculiarities can be also noted, such as the presence of *Myotis capaccinii* and *Rhinolophus euryale* in Abruzzi, a region where they are not recorded after 1980 (Agnelli et al. 2006). The key presence to be considered in this framework, however, is that of *Rhinolophus mehelyi*, a species that now does not live in the area, at Grotta Continenza and Grotta dei Cocci in the early and middle Holocene.

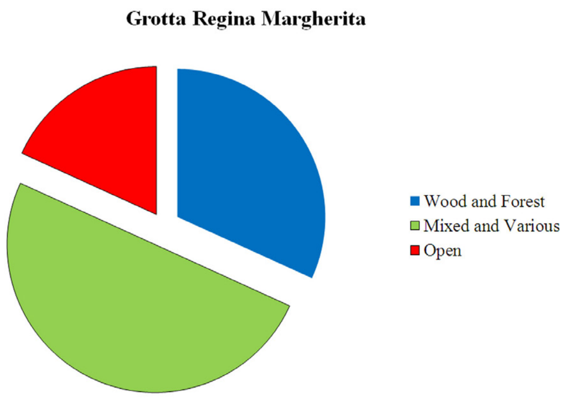

Fig. 2 - Grotta Regina Margherita, Bronze Age, Chiroptera: percent ratio (number of individuals) according to foraging environment (see Tab. 6).

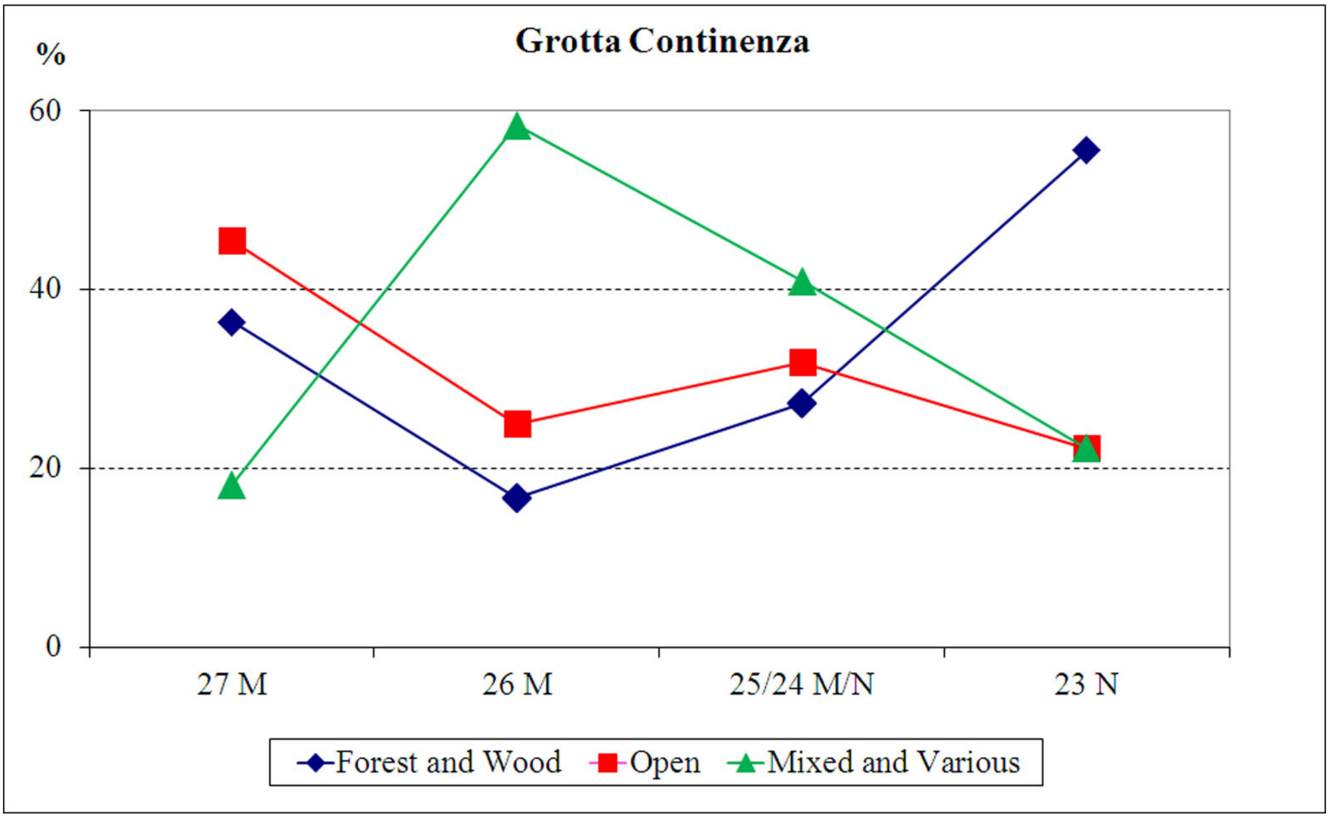

Fig. 3 - Grotta Continenza, Mesolithic and Neolithic, Chiroptera: percent ratio (number of individuals) between layer 27 and layer 23 according to foraging environment (see Tab. 6). M: Mesolithic; N: Neolithic.

R. mehelyi is a cave-dwelling bat particularly sensitive to human disturbance, and in Italy presently limited in its distribution to Sardinia and Sicily, and probably Apulia (Agnelli et al. 2006, Mucedda et al. 2009, Lanza 2012, Dondini et al. 2014). Before 1980, the only ascertained occurrences in the peninsula were restricted to Apulia (Grotta della Cava, Grotte di Castellana and Grotta Zinzulusa, these latter open to tourism), whereas the past and the recent records in Calabria and Campania have been subsequently not confirmed (Mucedda et al. 2009, Lanza 2012). In the entire range of its distribution, *R. mehelyi* is today considered vulnerable and endangered: it has declined in numbers in the Iberian peninsula, where it is relatively more abundant, close to extinction in France and perhaps already extinct in Corsica, Croatia and Israel (Agnelli et al. 2006, Mucedda et al. 2009, Lanza 2012), but after about 45 years it has reappeared in Apulia, at Grotta Zinzulusa (Dondini et al. 2014). In the Lateglacial, Mehely's horseshoe bat is reported in few sites of Mediterranean Europe and Caucasus; in Italy it occurs both in the Northern (Caverna delle Arene Candide, Isola di Palmaria, Grotta del Broion) and in the Central-Southern part of the Peninsula (Grotta Continenza, Grotta Paglicci) (Salari & Di Canzio 2009, Salari 2010, 2011, 2012) and in the less recent Holocene in Grotta Continenza and Grotta dei Cocci. Given that this species is linked to a certain extent to forested areas, these records might indicate a reduction of an initially wider range caused by the reduction of woodland (for natural or human causes) in a large portion of the Italian territory during the Holocene.

Human activity

With regards to the human-bats interaction, it is known that chiropterans generally avoid caves that are intensively frequented by humans (Guillem Calatayud 1997, Rossina 2006, Rossina et al. 2006, Salari & Kotsakis 2011, López-García & Sevilla 2012). In addition, there is no evidence that they were preyed on by prehistoric hunters for food or other purposes in Europe, whereas exceptions in other parts of the world have been recorded (e. g., Hand & Grant-Mackie 2012). Bats can be occasional targets by birds of prey (see "Taphonomic observations"), which do not usually frequent caves that are regularly occupied by humans. Therefore, the bones examined are likely to testify to periods of abandonment or sporadic frequentation by humans. It has been well documented that the number of bat remains is generally inversely proportional, if not specular, to the quantity of lithic finds and/or anthropogenic traces found on animal bones (Jullien 1972, Salari 2010, 2012, Salari & Kotsakis 2011). A considerable presence of bats, in addition, can provide indirect data also on the seasonality of human frequentation, along with other indicators such as the presence or absence of juveniles among the most commonly hunted species in prehistory.

Taking into account that the time intervals studied might have been unequal and that environmental factors might also have been influential, the decrease in remains from the Mesolithic to the Neolithic at Grotta Continenza (Tables 1 and 2) suggests progressive intensification of human frequentation of the cave. The alternating frequentation of the cave by bats and humans might be pluriannual or even seasonal (late spring - early autumn for humans, late autumn - early spring for bats). With regards to the Neolithic, the second scenario would be supported by the funerary and/or ritual use of the cave in this period (Barra et al. 1990).

With regards to the caves of Latium, archaeological and zooarchaeological studies are still ongoing, but it might not be the case that, at Grotta di Pastena, the only bat remains found were located in the niche "E10", next to the lowest quantity of faunal remains presumably brought into the cave by humans (a fragment of juvenile radius of *Ovis* vel *Capra*) (Angle et al. 2010a). At Grotta Regina Margherita, the majority (68.6%) of the bat remains are from Dig C (1 sq m); the other finds are equally divided between Dig A (8 sq m) and Dig D (9 sq m), whereas Dig B (3 sq m) and Dig E (1 sq m) did not hold any (Angle et al. 2010b). Therefore, a small portion of the sediment deposited in a roughly equal time period produced a higher number of finds. Still keeping in mind that such an unequal distribution of bat osteological remains might be connected to microclimatic factors and preferences in the selection of roosts, it is plausible that human disturbance (smoke from hearths, light and noise) of the bats was lower in the area of Dig C compared to elsewhere in the cave.

Conclusions

This study documents the presence of bats in five caves of Central Italy (Umbria, Lazio, Abruzzi) in the early and middle Holocene (between the Mesolithic and the Bronze Age, i.e. between the Preboreal and the Subboreal chronozones). Sixteen taxa have been identified, subdivided into three families (Rhinolophidae, Vespertilionidae and Miniopteridae) and seven genera (*Rhinolophus*, *Myotis*, *Nyctalus*, *Plecotus*, *Barbastella*, *Miniopterus* and *Hypsugo* vel *Pipistrellus*). The remains examined are morphologically and morphometrically indistinguishable from the extant species.

The taphonomical observations suggest that the bat assemblages examined are autochthonous thanatocoenoses, except for that from Grotta di Pastena, which may have been accumulated by a predator. It has been briefly shown how the relative abundance of bat remains in the sediments can reveal periods of absence or occasional frequentation of the caves by prehistoric humans. Analysis of their ecological attributes has allowed formulation of some hypotheses on the winter microclimate of the caves, as well as on the environments surrounding the various sites. The estimated microclimate for the inner chambers of Grotta Mora Cavorso has been supported by study of the speleothems and monitoring of the current physical parameters (temperature, relative humidity) of the karst cave. The environmental indications provided by bats are generally compliant with those derived from the study of other microvertebrates, rodents and soricomorphs in particular.

The comparison between the taxa identified in the caves examined, integrated with published data, and those taxa still found in Umbria, Latium and Abruzzi, sheds new light on the dynamics of bat populations between the end of the Pleistocene and the present-day in these regions. In the latest phases of the Pleistocene (Last Glacial Maximum and Lateglacial), some boreal species were present in Central Italy, such as *Myotis dasycneme* and *Eptesicus nilssonii*, alongside various taxa of Mediterranean affinities (Salari & Di Canzio 2009, Salari & Kotsakis 2011). In the initial phases of the Holocene, the global warming that pushed the "cold" species North to their original distribution range has clearly favoured a similar trend of the bat fauna population as today, also in the innermost areas of the Apennines.

Finally, the occurrence of *Rhinolophus mehelyi* in the Central Apennines during the early and middle Holocene provides new information on the past geographical distribution of this species, which today occurs only in Sicily and Sardinia and which has been recently re-discovered in Apulia.

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