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LATE PLEISTOCENE BAT ASSEMBLAGE WITH *EPTESICUS NILSSONII* FROM GROTTA DEL FOSSELLONE (SOUTHERN LATIUM, CENTRAL ITALY)

Leonardo Salari [1], Tassos Kotsakis [2]

[1] c/o Dipartimento Scienze della Terra, "Sapienza" Università di Roma, Italy
[2] Dipartimento di Scienze, Università "Roma Tre", Roma, Italy

Corresponding author: L. Salari <leonardosalari@virgilio.it>

ABSTRACT: The study of the Late Pleistocene fossil assemblage of bats from the Grotta del Fossellone (Circeo promontory, Central Italy) has revealed the presence of six species, *Rhinolophus ferrumequinum, Rhinolophus euryale, Myotis (Myotis) blythii, Myotis (Leuconoë) capaccinii, Eptesicus nilssonii* and *Miniopterus schreibersii*. In the late Mousterian and Aurignacian levels of the cave (MIS 3), only *M. blythii* is observed, indicating open spaces around the cave. In the Gravettian levels (MIS 2) all the species mentioned are present, which indicates a mosaic environment with forested areas alternating with open spaces (grassland or steppe) and wetlands. Particularly interesting is the presence of *E. nilssonii*, the only species of the assemblage currently distributed in Central and Northern Europe. The Italian Peninsula, and particularly its central and southern parts, have evidently acted as a *glacial refugium* during the Last Glacial Maximum for the boreal species that later, in the Lateglacial and Holocene, expanded its distribution to the northern regions recolonizing the lands liberated from the glacial coverage.

Keyword: Chiroptera, Circeo promontory (Central Italy), *Glacial refugia*, Palaeoecology, Palaeobiogeography

1. INTRODUCTION

Grotta del Fossellone (San Felice Circeo, Latium, Italy) opens in the limestone of the Middle Lias (SGI, 1960) front in the Circeo promontory, within the Circeo National Park. The stratigraphic successions present at Fossellone and in 38 further caves form an integrated group of evidences on the prehistory in this area. Today, several of these caves faces the sea, a few meters above sea level, but in the colder periods of Late Pleistocene the coast line was distant, due to the lowering of the sea level up to -120 m (Alessio et al., 1994; Benjamin et al., 2017), and the caves dominated a coastal plain (Blanc & Segre, 1953). Many of the caves have yielded notable sedimentary deposits with Pleistocene fauna, lithic industries and/or human fossils (e.g., Grotta Barbara, Grotta Breuil, Grotta delle Capre, Grotta del Fossellone, Grotta Guattari, Riparo Blanc; Fig. 1) (Vitagliano & Bruno, 2012).

Archaeological and palaeontological remains from Grotta del Fossellone were discovered in 1936 by Alberto Carlo Blanc (1906-1960), during his first excavation campaign in the Grotta delle Capre, located 200 m away (Blanc, 1937). Subsequently, there were two main phases of explorations in the cave. During the first phase, from 1937 to 1940, a few test excavations were carried out in a small group of minor caves that open in the internal main hall. In particular, some prehistoric layers in the main slope were identified, where several explorative trenches were opened. During the second phase, from 1947 to 1953, systematic excavations of the deposit in the central slope were carried out, where the most complete stratigraphic sequence was present, forming 51 layers through to the "Tyrrhenian beach", with a thickness of about 14 m (Blanc & Segre, 1953; Alhaique et al., 1996). In 1953-54 some human bone fragments, including a mandible of a baby, ascribed to *Homo neanderthalensis* were discovered (Mallegni, 1992). In 1989, systematic studies of the archaeological and palaeontological collections started (Vitagliano & Piperno, 1991; Alhaique et al., 1996, 1998; Alhaique & Tagliacozzo, 2000).

The bat fossils were given to us for the study by the late professor Amilcare Bietti (1937-2006), who was part of the archaeological team who made the last excavations in the cave. A preliminary list of the bat species was presented at the AIQUA Meeting in memory of Alberto Malatesta (1915-2007) in Rome, 4-5 February 2010 (Salari & Kotsakis, 2011).

In this paper the bat fossils collected in the Grotta del Fossellone are described and discussed.

2. STRATIGRAPHIC NOTES

Grotta del Fossellone (Fig. 1) conserves Pleistocene marine sediments ("Tyrrhenian beach") at the bottom of the sequence (Blanc & Segre, 1953; Vitagliano & Piperno, 1991; Alhaique et al., 1996). The overlying continental sequence is composed of 51 layers in the central slope. The 10 layers at the bottom did not contain lithic industry. The other layers can be grouped into three units (Blanc & Segre, 1953; Alhaique et al., 1996; Vitagliano & Bruno, 2012):

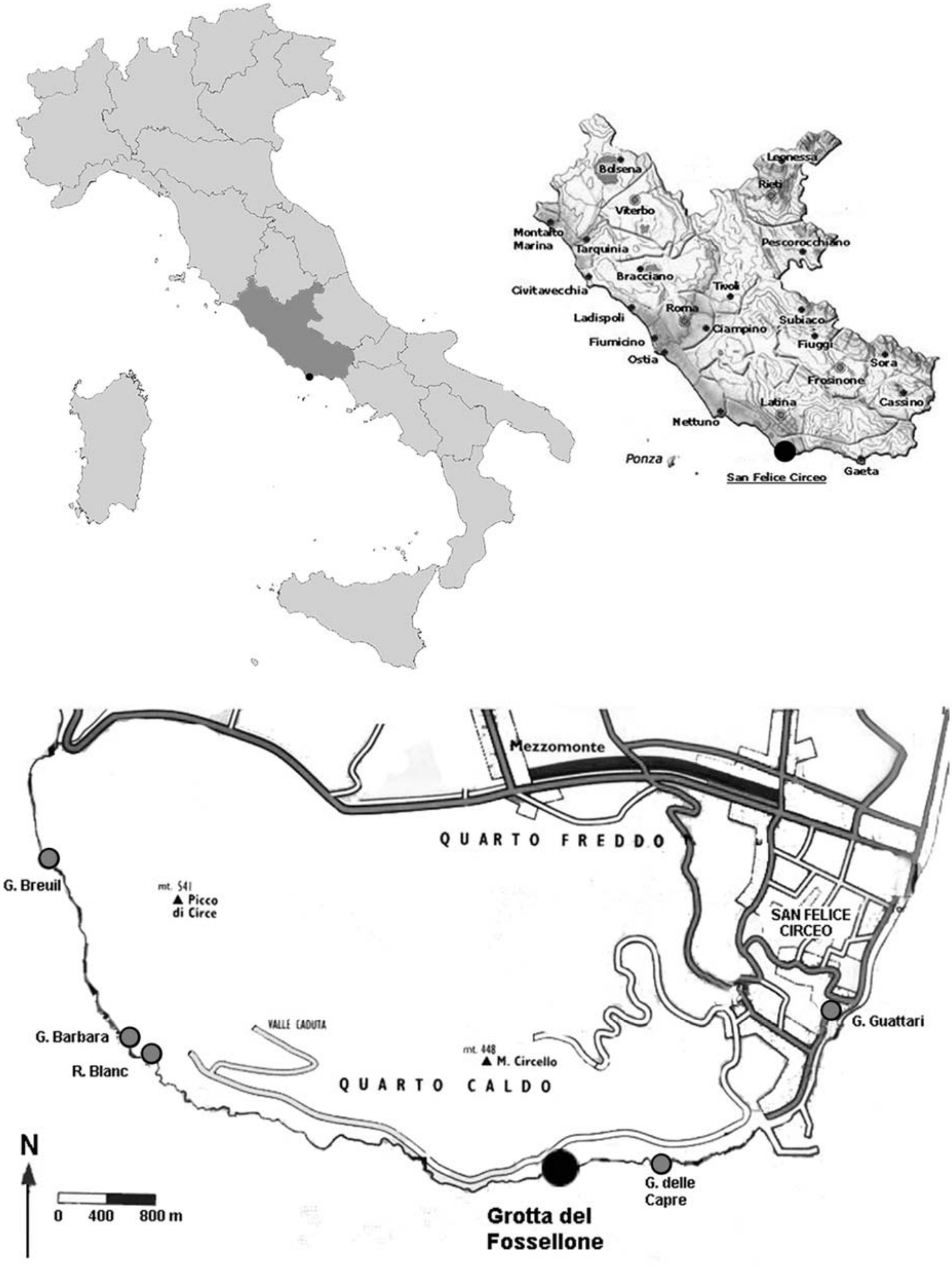

Fig. 1 - Grotta del Fossellone (Latium, Italy): location of the site.

- Levels 41-23 with lithic industries referred to the Middle Palaeolithic (Mousterian);
- Levels 21-17, separated from the Mousterian levels by a layer of sterile red clay (Level 22), with Aurignacian industry;
- Levels 16-1 with bone and lithic artefacts referred to Gravettian.

In the Levels 27-23 a peculiar industry referred to the late and final Mousterian was found (Vitagliano & Bruno, 2012). In these layers, the large mammal remains are scarce; the most frequent species is *Bos primigenius* followed by *Cervus elaphus* and less frequent wild horse, whereas wild boar, ibex and *Equus hydruntinus* are rarer (Alhaique et al., 1998; Alhaique & Tagliacozzo, 2000). The mammal assemblage in Level 21, is considerably more abundant and it is dominated by *E. hydruntinus* followed by *C. elaphus*, whereas *B. primigenius*, wild horse, ibex, wild boar and roe deer are less frequent (Alhaique et al., 1998; Alhaique & Tagliacozzo, 2000). Bird bones, which are rare in Levels 27-23, are abundant in Level 21, Aurignacian, and mainly consist of *Perdix perdix*, *Columba livia* and *Pyrrhocorax graculus*; from a climatic and environmental point of view, the occurrence of *Nyctea scandiaca* and *Anser albifrons*, cold and boreal birds, is particularly interesting (Alhaique et al., 1998; Alhaique & Tagliacozzo, 2000). Such as for bone and lithic artefacts, also the Vertebrate remains are very scarce in Levels 16-1, Gravettian (Alhaique et al., 1996; Vitagliano & Bruno, 2012).

3. MATERIALS AND METHODS

The material analysed is housed in the Department of Geological Sciences of the "Roma Tre" University and it is numbered from LPVRT 00411 to LPVRT 00431. A few fossil remains come from Level 23, Mousterian, and Level 21, Aurignacian, and 46 specimens from Levels 12, 9, 5, 4 and 1, Gravettian (Tab. 1).

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" and in the Department of Geological Sciences of the "Roma Tre" University. Moreover, we use morphological and morphometric data and dichotomous keys given by Felten et al. (1973), Sevilla García (1988), Niethammer & Krapp (2001), Salari (2004) and Lanza (2012). The analyses were performed with a stereoscopic microscope Nikon SMZ-U in the Department of Sciences of the "Roma Tre" University; the pictures and the measurements were taken with a Leika DFC290 system using the Leica Application Suite software.

For taxonomic determinations the analyzed material was chosen on the basis of its systematic importance (cranium, mandible and humerus). 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.

In this work we follow Simmons (2005), with the following exceptions.

- Miniopteridae are considered as family, distinct from Vespertilionidae, in agreement with Mein & Tupinier (1977), Agnelli et al. (2006), Miller-Butterworth et al. (2007) and Lanza (2012).
- We use the taxon *Myotis blythii* instead of *Myotis oxygnathus*, according to Agnelli et al. (2006), Furman et al. (2014) and Juste & Paunović (2016). This is also in agreement with most palaeontological works identifying remains of European large-sized *Myotis*, distinct from *M. myotis*, as *M. blythii* (not as *M. oxygnathus* or *M. blythii oxygnathus*).

Environmental reconstructions are based on studies on the ecology and biogeographical distribution of modern taxa (Horáček et al., 2000; Niethammer & Krapp, 2001; Agnelli et al., 2006; Lanza, 2012).

Quaternary chronostratigraphy and geochronology according to Gibbard et al. (2010). For Italian continental biochronology we follow Kotsakis et al. (2003).

4. TAXONOMY

Order Chiroptera Blumenbach, 1779
Family Rhinolophidae Gray, 1825
Genus *Rhinolophus* Lacépède, 1799
Rhinolophus ferrumequinum (Schreber, 1774)

A mandible (LPVRT 00412), three humeri and two distal portions of humerus (LPVRT 00411, 00413-14) (Figs. 2A-B; Tab. 1) have the typical morphology of the genus Rhinolophus. In the mandible, p4 is subquadrangular with pyramidal cusp; the molars are of nyctalodontic type, m1 and m2 have trigonid slightly longer than the talonid and the cingulum, very thin, more evident on the trigonid; m3 is relatively small and the cingulum is thin, especially on the talonid. In the distal epiphysis of humerus, epicondyle, trochlea, inner ridge

Species	L. 23	L. 21	L. 12	L. 9	L. 5	L. 4	L. 1
	NISP/MNI	NISP/MNI	NISP/MNI	NISP/MNI	NISP/MNI	NISP/MNI	NISP/MNI
Rhinolophus ferrumequinum			1 / 1				5 / 3
Rhinolophus euryale			1 / 1		1 / 1	2 /2	24 / 14
Myotis blythii	5 / 5	1 / 1	1 / 1	2 / 2	4 / 3		
Myotis capaccinii							1 / 1
Eptesicus nilssonii							1 / 1
Miniopterus schreibersii				1 / 1			2 / 1

Tab. 1 - Grotta del Fossellone, Late Pleistocene: number of identified specimens (NISP) and minimum number of individuals (MNI) of species identified. L.: Level.

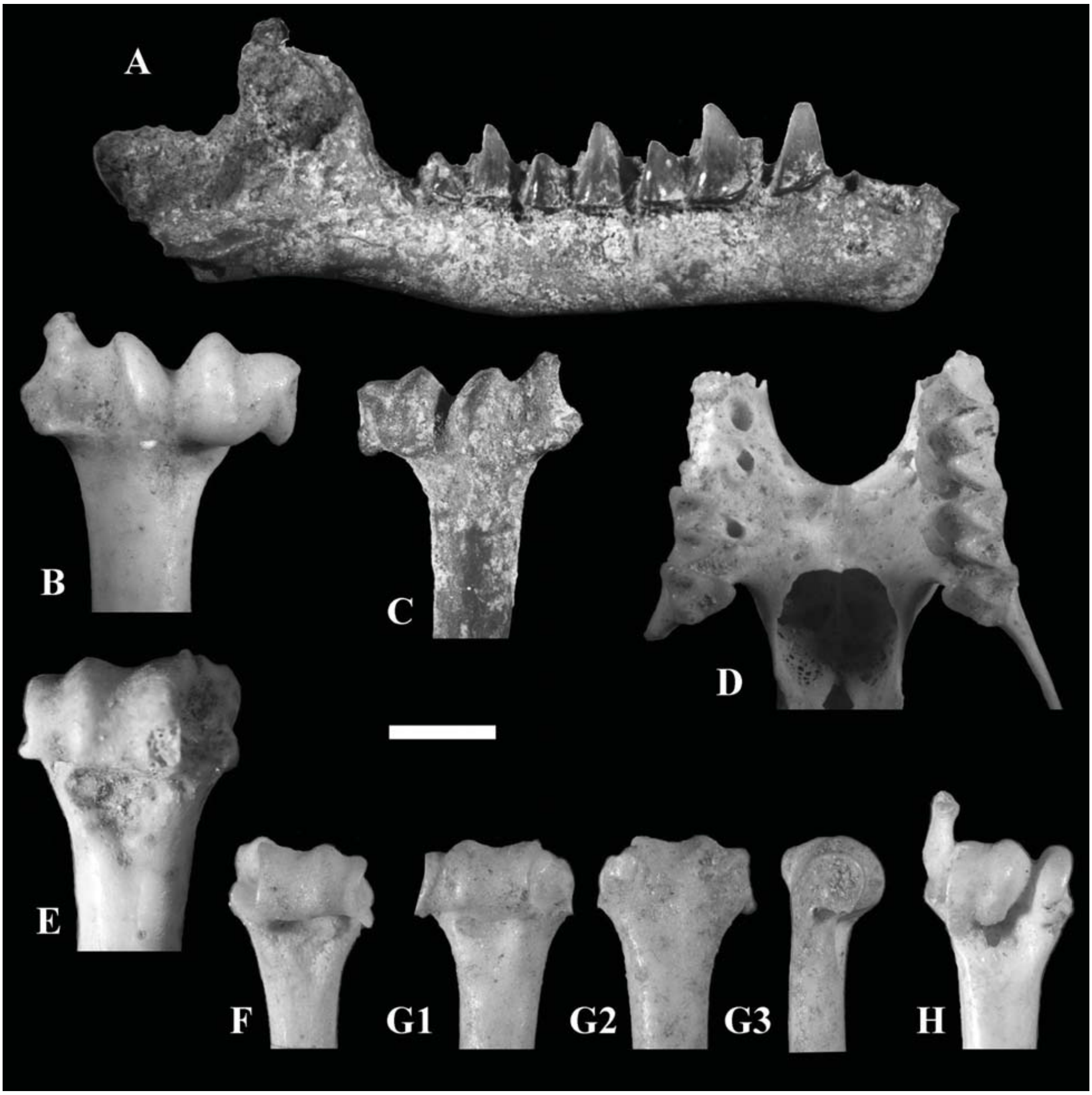

Fig. 2 - Grotta del Fossellone, Late Pleistocene: *Rhinolopus ferrumequinum*: A) right mandible (LPVRT 00413), labial view, B) distal epiphysis of right humerus (LPVRT 00412); *Rhinolophus euryale*: C) portion of cranium (LPVRT 00418), occlusal view, D) distal epiphysis of left humerus (LPVRT 00419); E) *Myotis blythii*, distal epiphysis of left humerus (LPVRT 00421); F) *Myotis capaccinii*, distal epiphysis of right humerus (LPVRT 00427); G) *Eptesicus nilssonii*, distal epiphysis of left humerus (LPVRT 00428) (1 external, 2 internal, 3 dorsal views); H) *Miniopterus schreibersii*, distal epiphysis of right humerus (LPVRT 00430).

and lateral ridge are separated by grooves, less deep that dividing inner and lateral ridges; the styloid process is relatively long and thin, slightly dorsally inclined in lateral view (Felten et al., 1973). These morphological features and the large size (Tab. 2), enables a definite attribution to the big horseshoe bat.

R. ferrumequinum is a species of Mediterranean affinities and today's range of distribution includes Central Europe, extending from Southern England, and the Mediterranean basin through Asia to Japan; in Italy this species occurs in all regions (Horáček et al., 2000; Gaisler, 2001a; Agnelli et al., 2006; Lanza, 2012).

The earliest fossil records of R. ferrumequinum come from some Italian and Spanish localities referred to the late Early Pleistocene (middle Early Biharian, Late Villafranchian; Salari et al., 2013; Galan et al., 2016a). Indeed, many specimens of Pliocene or early Early Pleistocene, assigned in the past to R. ferrumequinum or R. cf. ferrumequinum have been ascribed to other species of the group (Topal, 1979; Wołoszyn, 1987). Some Pliocene or early Early Pleistocene remains recently assigned to the same taxa are reported in preliminary lists and their attribution must be confirmed. Fossil remains of this species have been collected in several sites of Middle Pleistocene in Central and Southern Europe and in North Africa, and in many sites of Late Pleistocene from Portugal and England to Japan and South to Maghreb and Near East (Capasso Barbato & Kotsakis, 1986; Kotsakis, 1987, 1991; Esu et al., 1990; Lindenau, 2005; Tata & Kotsakis, 2005; Argenti et al., 2008; Tang & Kotsakis, 2008; Salari, 2009, 2010; Salari & Di Canzio, 2009; Salari et al., 2013, and references therein; Horáček et al., 2013; Galan et al., 2016b; Sevilla, 2016; Spena et al., 2017).

Rhinolophus euryale Blasius, 1853

Two incomplete crania (LPVRT 00418), five humeri and several distal portions of humerus (LPVRT 00415-17, 00419-20) (Figs. 2C-D; Tab. 1) belonging to the middle-sized species of genus *Rhinolophus*. The preorbital bridge is strong (Lanza, 2012), first and second upper molars have a distal concave edge and the labial cingulum is very prominent (Sevilla García 1988), and the styloid process of distal humerus is long and thin, slightly dorsally inclined in lateral view (Felten et al., 1973). These morphological features and the measurements (Tab. 2) enables a sure attribution to Mediterranean horseshoe bat.

R. euryale is a species of strict Mediterranean affinities, typically troglophilous; today's range of distribution includes Southern Europe, South-Western Asia and North-Western Africa; in Italy this species occurs throughout the territory with the probable exception of some northern regions (Horáček et al., 2000; Gaisler, 2001b; Agnelli et al., 2006; Lanza, 2012).

Bat *fossils* referred to *Rhinolophus* ex gr. *R. euryale* are known in Eastern Europe since the Early Pliocene (Late Ruscinian), and in Italy from late Early Pleistocene (middle Early Biharian, Late Villafranchian; Salari et al., 2013). Fossil remains of the Mediterranean horseshoe bat come from several Middle and Late Pleistocene localities of the Mediterranean basin, Poland and Near East (Kotsakis & Petronio, 1980; Kotsakis, 1991; Lindenau, 2005; Tata & Kotsakis, 2005; Salari & Di Canzio, 2009; Salari, 2010; Salari et al., 2013, and references therein; Horáček et al., 2013; Sevilla, 2016;

Species	Grotta del Fossellone					Grotta Breuil		Caverna delle Arene Candide		Extant	
	n.	min	max	med	s.d.	n.	min-max	n.	min-max	n.	min-max
Rhinolophus ferrumequinum											
L. mandible	1			16.0		1	15.8	7	15,0-15,2	27	14,9 - 15,9
c-m3	1			9.6		1	9.4	16	8,8-9,3	27	9,0 - 9,3
m1-m3	1			6.2		1	6.3	19	5,8-6,5		
L. humerus	3	33.0	34.0	33.3	0.58	2	32,2-33,1	6	32,8-34,0		
Bd humerus	5	5.1	5.2	5.1	0.06	5	5,0-5,3	29	4,9-5,4		5.1
Rhinolophus euryale											
L. cranium						1	17.4			80	17.4-18.9
C-M3						4	6,0-6,5	1	6.4	80	6,1-6,7
M1-M3	1			4.1		8	3,9-4,2	2	3,7-4,0	80	3,7-4,1
M3-M3	1			6.8		2	6,7-6,9			80	6,3-7,1
L. humerus	5	26.0	27.0	26.4	0.55	28	25,0-27,7	2	27.4		
Bd humerus	24	4.2	4.4	4.3	0.04	84	4,2-4,4	15	4,2-4,4		4.3
Myotis blythii											
L. humerus						2	32,1-33,8	32	31,4-34,2		
Bd humerus	13	4.0	4.2	4.2	0.06	14	4,0-4,3	536	3,8-4,3		4,0-4,6*
Myotis capaccinii											
L. humerus						8	21,5-22,4	3	22,8-23,2		
Bd humerus	1			2.8		12	2,8-2,9	10	2,6-2,9		2.7
Eptesicus nilssonii											
Bd humerus	1			2.8							2.7
Miniopterus schreibersii											
L. humerus	1			26.0		20	25,0-26,6	2	26,3-26,8		
Bd humerus	3			2.8		42	2,6-2,9	265	2,6-2,8		2.7

Tab. 2 - Grotta del Fossellone, Late Pleistocene: osteometric measurements (mm) and comparison with other sites. Abbreviations: L. = maximum length; C-M3 = length of upper tooth-row between C and M3 (incl.); M1-M3 = length of upper molars; M3-M3 = rostral width between third upper molars (incl.); c-m3 = length of lower tooth-row between c and m3 (incl.); m1-m3 = length of lower molars; Bd = distal breadth; n. = number of measurements; min = minimum; max = maximum; mea = mean; s.d. = standard deviation. *: *M. myotis* and *M. blythii*. Grotta Breuil unpublished data; Caverna delle Arene Candide by Salari (2010); mandible of extant *R. ferrumequinum* by Gaisler (2001a); cranium of extant *R. euryale* by Popov & Ivanova (2002); distal breadth of humerus of all extant species by Felten et al. (1973).

Spena et al., 2017).

Family Vespertilionidae Gray, 1821

Genus *Myotis* Kaup, 1829

Subgenus *Myotis* Kaup, 1829

Myotis (Myotis) blythii (Tomes, 1857)

Several distal portions of humerus (LPVRT 00421-26) (Fig. 2E; Tab. 1) belonging to the great-sized species of genus *Myotis*: the epicondyle is reduced, with trochlea, inner and outer ridges separated by grooves; the styloid process is strongly reduced but still present.

With respect to the distinction between the large-bodied *Myotis* (excluding *M. punicus* for palaeobiogeographic reasons), the only certain morphological difference between the teeth of *M. myotis* and *M. blythii* occurs on the talonid of third lower molar, which is more reduced in *M. myotis* (see Topál & Tusnadi, 1963; Sevilla García, 1988). 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 our sample there are no particularly robust specimens and also the measurements (Tab. 2) support the attribution to *M. blythii*.

The lesser mouse-eared bat is a species of Mediterranean affinities, thermophilous, the recent range of the species includes Southern Europe, the southern part of the Central Europe, East to China and Mongolia; in Italy it occurs in all regions with the possible exception of Sardinia (Horáček et al., 2000; Topál & Ruedi, 2001; Agnelli et al., 2006; Lanza, 2012).

The earliest records of fossils referred to *Myotis* cf. *M. blythii* come from some Eastern Europe sites referred to Late Pliocene (Late Ruscinian), and in Italy from early Early Pleistocene (Late Villanyan, Middle Villafranchian; Salari et al., 2013). Fossil remains of this specie occur in several Middle Pleistocene localities and in many Late Pleistocene sites of Southern and Eastern Europe and Near East (Capasso Barbato & Kotsakis, 1986; Lindenau, 2005; Tata & Kotsakis, 2005; Tang & Kotsakis, 2008; Salari, 2009, 2010; Salari & Di Canzio, 2009; Salari et al., 2013, and references therein; Horáček et al., 2013; Sevilla, 2016; Spena et al., 2017).

Subgenus *Leuconoë* Boie,1830

Myotis (Leuconoë) capaccinii (Bonaparte, 1837)

A distal portion of a right humerus (LPVRT 00427) from Level 1 (Fig. 2F; Tab. 1) is very similar in morphology (Felten et al., 1973) and dimensions (Tab. 2) to the humerus of living *M. capaccinii*: epicondyle with reduced trochlea, inner and outer ridges separated by grooves, and the styloid process is moderately developed.

The long-fingered bat is a species of strict Mediterranean affinities, typically troglophilous; the current range includes the Mediterranean basin, Southern Europe, North-Western Africa, South-Western Asia to Iran and Uzbekistan; in Italy this species occurs in all regions (Horáček et al., 2000; Spitzenberger & Helversen, 2001; Agnelli et al., 2006; Lanza, 2012).

The oldest fossils of the long-fingered bat are known in some Mediterranean localities, including Italy, since the late Early Pleistocene (middle Early Biharian, Late Villafranchian; Salari et al. 2013). It is found in some Middle and Late Pleistocene sites from Central and Southern Italy and other circum-Mediterranean localities, invariably represented by few remains, whereas in Northern Italy and in the remaining Western Palaearctic it is rarely reported (Kotsakis & Petronio, 1980; Kotsakis, 1987; Lindenau, 2005; Tata & Kotsakis, 2005; Tang & Kotsakis, 2008; Salari, 2009; 2010; Salari & Di Canzio, 2009; Salari et al., 2013, and references therein; Spena et al., 2017).

Genus *Eptesicus* Rafinesque, 1820

Eptesicus nilssonii (Keyserling and Blasius, 1839)

A distal portion of a left humerus (LPVRT 00428) from Level 1 (Figs. 2G1, 2G2, 2G3; Tab. 1) is very similar in morphology (Felten et al., 1973) and dimensions (Tab. 2) to the humerus of living *E. nilssonii*: the epicondyle is reduced, inner and outer ridges separated by grooves, and the passage from the trochlea to the condyle is almost straight; the styloid process (a little broken) is moderately developed and the articular fossette is clear and wide.

The Northern bat is a species of boreal affinities 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; Agnelli et al., 2006). Its current range of distribution includes Central and Northern Europe, extending from the Northern Balkans through the Palearctic Asia to Sakhalin, Korea and Japan (Gerel & Rydell. 2001; Agnelli et al.. 2006; Lanza. 2012). 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 & Horàček, 1986; Gerel & Rydell, 2001; Lanza, 2012). The scarce records available for Italy show that its presence is limited to some mountain resorts of the Alpine arch (Agnelli et al., 2006; Lanza, 2012; Patriarca & Debernardi, 2014).

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 former Soviet Union, such as Crimea, Altai, Siberia and Far East (Rydell, 1993; Rossina, 2006; Rosina, 2012; Tiunov, 2016), Central Europe (Horáček, 1995; Popov, 2000; Piksa & Wołoszyn, 2001; Ochman, 2003; Ochman & Wołoszyn, 2003; Noël et al., 2008; Pazonyi et al., 2014), and only at Grotta del Broion (Veneto) in Italy (Pasa, 1953).

Family Miniopteridae Dobson, 1875

Genus *Minioperus* Bonaparte, 1837

Miniopterus schreibersii (Kuhl, 1819)

A humerus *and* two distal portions of humerus (LPVRT 00429-31) (Fig. 2H; Tab. 1) belong to the genus *Miniopterus*: the medial epicondyle is relatively narrow, the trochlea is separated from the inner ridge by a not deep groove, while inner and lateral ridges are separated one from each other by a deep groove; the styloid process is long and narrow and is parallel to the axis of the humerus. These morphological features (Felten et al., 1973) and the measurements (Tab. 2) enables a definite attribution to *M. schreibersii*.

Schreiber's bat is a species sub-cosmopolitan, but of strict Mediterranean affinities, typically troglophilous;

the current range comprises all populations living from Southern Europe and Morocco to sub-Saharan Africa, Madagascar and through Southern Asia to Oceania; in Italy this species occurs throughout to the whole country (Horáček et al., 2000; Agnelli et al., 2006; Lanza, 2012).

M. schreibersii is known since the early Early Pleistocene (Late Villanyan, Middle Villafranchian) in various localities of Central Europe, and in Italy from late Early Pleistocene (middle Early Biharian, Late Villafranchian; Salari et al., 2013). Schreiber's bat disappeared from Central Europe during the glacial phases of Middle and Late Pleistocene but was present in the Mediterranean basin and expanded its area of distribution further north during the interglacial phases (Kotsakis & Petronio, 1980; Kotsakis, 1987, 1991; Lindenau, 2005; Tata & Kotsakis, 2005; Tang & Kotsakis, 2008; Salari, 2009, 2010; Salari & Di Canzio, 2009; Salari et al., 2013, and references therein; Horáček et al., 2013; Galan et al., 2016b; Sevilla, 2016; Spena et al., 2017).

5. DISCUSSION

All *the* six species identified at Grotta del Fossellone (Tab. 1) are still part of the extant Italian bat fauna (Agnelli et al., 2006; Lanza, 2012). Among these, *Rhinolophus ferrumequinum*, *Rhinolophus euryale*, *Myotis blythii*, *Myotis capaccinii* and *Miniopterus schreibersii* today occur in Latium (Crucitti, 2011; Capizzi et al., 2012) and also within the Circeo National Park territory, except probably for *M. blythii* (see Mastrobuoni & Zerunian, 2003; Mastrobuoni, 2009a, 2009b), whereas *Eptesicus nilssonii* occurs only in a few localities of Alpine arch (Agnelli et al., 2006; Lanza, 2012; Patriarca & Debernardi, 2014).

Except for *E. nilssonii*, all the fossils belong to troglophilous species (Tab. 3), and ascertained traces of digestion on the bone surfaces were not found (except for two remains of *R. euryale* and *R. ferrumequinum*). Therefore, it is very likely that the bat remains consisted mainly of the natural accumulation of animals that lived and died in the cave (Sevilla García, 1988; Kowalski, 1995; Salari & Silvestri, 2015).

Bats have a foraging range of several kilometres from their roosts (Niethammer & Krapp, 2001; Agnelli et al., 2006; Lanza, 2012). Therefore, by analysing the present distribution areas and foraging environments of the species identified (Tab. 3), the study of the fossil assemblage provides interesting information on the surroundings of the cave 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, others form smaller colonies, from a few individuals to several hundred or have more solitary behaviours (Tab. 3). However, despite the limited numerical significance of our sample, it can still provide useful environmental information.

In the Levels 23, Mousterian, and 21, Aurignacian, only few remains of *M. blythii* were found, and one can only admit that probably in the surrounding of cave were also open spaces, as confirmed by the occurrence of equids (Alhaique et al., 1998; Alhaique & Tagliacozzo, 2000). Instead, in the Mousterian layers of the Grotta Breuil, also in the Circeo promontory, a rich fossil bat assemblage was found (Kotsakis, 1991; Salari & Di Canzio, 2009; Salari & Kotsakis, 2011). The ecological features of the species found in this cave are compatibles with the environmental reconstruction outlined by Alhaique et al. (1998) and Alhaique & Tagliacozzo (2000) for the surroundings of Grotta del Fossellone. Also in the Mousterian of nearby Grotta Barbara were found several bat fossils and even the ecological features of the species found in this cave suggest a variety

Species	Foraging environment	Roosting habits	Zoogeographical patterns
Rhinolophus ferrumequinum	habitat mosaics: pastures interspersed with hedgerow and broadleaved woodland, and wetland from 0 to 2000 m a.s.l.	caves; small nursery and hibernation colonies	Mediterranean s.l.
Rhinolophus euryale	karstic habitats with broadleaved woodland and scrubland from 0 to 1000 m a.s.l.	caves; middle nursery colonies, smaller hibernating colonies	Mediterranean s.s.
Myotis blythii	open areas, meadows with tall grass, steppes, pastures from 0 to 1000 m a.s.l.	caves; massive nursery colonies, smaller hibernating colonies	Mediterranean s.l.
Myotis capaccinii	woods with shrubs and mainly wetlands from 0 to 830 m a.s.l.	caves; middle to massive nursery colonies, smaller hibernating colonies	Mediterranean s.s.
Eptesicus nilssonii	various: open spaces, forest edges and wetland in mountain valleys up to 2300 m a.s.l.	rock crevices, tree cavities; small nursery and hibernation colonies	Boreal
Miniopterus schreibersii	various: forest and open habitats, herbaceous vegetation areas and steppes from 0 to 1230 m a.s.l.	caves; massive nursery and hibernation colonies	Mediterranean s.s.

Tab. 3 - Synthetic notes on foraging environment and roosting habits in Italy and zoogeographical pattern for the species considered. Data from Horáček et al. (2000), Agnelli et al. (2006), Salari & Di Canzio (2009), Lanza (2012); m a.s.l.: meters above sea level; s.l.: *sensu lato*; s.s.: *sensu stricto*.

of environments in the Circeo promontory during this phase of Late Pleistocene (Salari & Kotsakis, 2011).

The six species found in the Gravettian layers of Grotta del Fossellone foraging in various environments (Tab. 3), and its ecological features allow us to outline a composite landscape with extensive woodlands interspersed with open spaces (steppe, grasslands and scrubland), rocky areas and marginal wetland. Levels 12-5 yielded few remains and the species more frequent is *M. blythii*, while Level 1 makes more numerous bat fossils, *M. blythii* disappear and the species dominant is *R. euryale* (Tab. 1). Despite the limited amount of fossils that precludes any definitive conclusion, it can be assumed that the environment surrounding the cave has evolved from more open towards greater forest cover. The occurrence of *E. nilssonii*, a non troglophilous species, cold and boreal bat, far to the south of the limit of its current distribution, suggests a colder climate than the present.

According to Alhaique et al. (1998) and Alhaique & Tagliacozzo (2000), the bird and mammal assemblages from Level 21 indicate a climate colder than that documented in the Mousterian layers. The bat assemblage seems to suggest that during the Gravettian the climate further evolved towards the cold. The Levels 27-23, Mousterian, can be referred to temperate oscillations of Marine Isotope Stage (MIS) 3, the Aurignacian layers to the final MIS 3 or the beginning of MIS 2 (Salari & Kotsakis, 2011), and the Gravettian layers can be referred to MIS 2, around to the Last Glacial Maximum (LGM). Indeed, according to some authors (e.g., Mussi, 2002; Antonioli & Vai, 2004; Sala, 2005) the Gravettian industry is well documented in Italy during this coldest period of the Late Pleistocene.

In the LGM, Iberian and Italian peninsulas and the Balkans played the role of main *glacial refugia* for many temperate or warm animal and plant species, which repopulated the rest of Europe during the Lateglacial and Holocene (Bilton et al., 1998; Stewart & Lister, 2001; Sommer & Nadachowski, 2006; Gavin et al., 2014). As for European bats, Fahlke (2009) reported that these have deserted the area north to the Alps in the LGM, and that it was only in the first stages of the Lateglacial, during the Bølling-Allerød temperate oscillations, that some species (*Eptesicus serotinus* followed by *Plecotus auritus* and *Barbastella barbastellus*) returned to the area. In effect, few other bats, including *E. nilssonii*, *Nyctalus noctula* and a few species of the genera *Myotis* and *Pipistrellus* are reported in the Lateglacial sequences of Central-Northern Europe (Horáček, 1995; Ochman, 2003; Horáček & Jahelková, 2005). Moreover, according to Fladerer (2000), in the southeastern side of the Alps in the LGM the only presence of *P. auritus* is documented, then during the Lateglacial the area would be populated by *Vespertilio murinus*, followed by *E. serotinus*, *M. myotis*, *Myotis bechsteinii*, *Myotis nattereri* and *B. barbastellus*.

In the cold periods of Late Pleistocene, Central-Southern Italy and Liguria hosted many species which are now largely distributed in Central and Northern Europe (e.g., *Rhinolophus hipposideros*, *Myotis dasycneme*, *M. myotis*, *M. bechsteinii*, *Myotis mystacinus*, *P. auritus*, *N. noctula* and *B. barbastellus*) (Argenti et al., 2008; Salari, 2010; Salari & Kotsakis, 2011; Bogdanowicz et al., 2015), and that have returned to these lands, but even in some regions South of the Alps (e.g., Canton Ticino, Switzerland), only in the Holocene (Horáček, 1995, 2007; Horáček & Jahelková, 2005; Blant et al., 2008; Ruedi et al., 2008; Fahlke, 2009; Hutterer et al., 2012). Thus, the occurrence of *E. nilssonii* in the LGM at Grotta del Fossellone show that Circeo promontory played a role of *glacial refugium* in the Late Pleistocene for this boreal species currently distributed in Central and Northern Europe.

6. CONCLUSION

Six species of bats divided into three families (Rhinolophidae, Vespertilionidae and Miniopteridae) and four genera (*Rhinolophus*, *Myotis*, *Eptesicus* and *Miniopterus*) have been discovered in the fossil assemblage from Grotta del Fossellone. All the species identified are still part of the extant Italian bat fauna and today also occur in Latium, except for *Eptesicus nilssonii* that is now distributed in Central-Northern Europe.

The fossil bat assemblage examined is probably an autochthonous thanatocoenosis. The bat remains do not show major morphological or morphometric differences from other Late Pleistocene and extant populations of the same species.

The ecological needs of the species of bats present at Grotta del Fosselone allow to outline for the Gravettian period a composite environment with wooded areas interrupted by open spaces (grassland or steppe), rocky areas and wetlands.

The occurrence in the latest Gravettian layer of *E. nilssonii*, far to the south of the limit of its current distribution, suggests a colder climate than the Mousterian and Aurignacian layers and the present. Probably the Gravettian layers were deposed in the LGM.

Grotta del Fossellone represents the southernmost limit of *E. nilssonii* in Europe, even considering its distribution in the Pleistocene. The occurrence of this species in the LGM at Grotta del Fossellone, as well as of *M. dasycneme* in the Lateglacial of Grotta di Cittareale (Argenti et al., 2008; Salari & Kotsakis, 2011), show that during the coldest stages of the Late Pleistocene the coastal regions and the Apennine of Latium must have played an important role of *glacial refugia* for these boreal species which are now distributed in Central-Northern Europe.

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