Rivista Italiana di Paleontologia e Stratigrafia
(*Research in Paleontology and Stratigraphy*)
vol. 129(1): 79-90. **March 2023**
DOI: https://doi.org/10.54103/2039-4942/18113

PALEOCLIMATE AND PALEOENVIRONMENT IN NORTH-WESTERN ITALY (SOUTHERN ALPS) DURING THE LAST GLACIAL STAGE: THE SMALL-MAMMAL RECORD FROM THE BUCO DEL FRATE CAVE (PREVALLE – BRESCIA)

FABIO BONA[1,2,*], MARCO BAIONI[2] & ELISABETTA CILLI[3]

[1]Dipartimento di Scienze della Terra "A. Desio" – Università degli Studi di Milano, Italy. E-mail: fabgeo@libero.it
[2]MAVS, Museo Archeologico della Valle Sabbia – Gavardo, Brescia, Italy.
[3]Dipartimento di Beni Culturali, Università di Bologna, Campus di Ravenna - Ravenna, Italy.
[*]Corresponding author.

Associate Editor: Lorenzo Rook.

To cite this article: Bona F., Baioni M. & Cilli E. (2023) - Paleoclimate and paleoenvironment in north-western Italy (Southern Alps) during the Last Glacial Stage: the small-mammal record from the Buco del Frate cave (Prevalle – Brescia.). *Riv. It. Paleontol. Strat.*, 129(1): 79-90.

Keywords: Steppe environment; western Po Plain; small-mammals.

Abstract. The palaeoclimatic and palaeoenvironmental data obtained by the study of the Buco del Frate cave small-mammals indicate that, around 40,000 years ago (MIS3), the eastern part of the province of Brescia, immediately to the west of Lake Garda, was characterised by the presence of open taiga environment and watercourses crossing the plain facing the cave.

Specifically, the palaeoclimatic conditions of this part of north-western Italy around 40,000 years ago – compared to climate data for the years 1960-90 measured at Ghedi, 20 km southwest of the Buco del Frate cave – involved average temperatures some 4°C cooler and rainfall some 30% lower.

Based on the collected data we show that the western part of the Po Valley, west of Lake Garda, was characterized by a steppe-like environment, not too different from the almost contemporaneous site of Settepolesini di Bondeno (Ferrara), defined as "mammoth steppe".

We also note that the western Po Valley, if compared with deposits from high- and medium-mountain contexts in the same area, was characterized by a more steppe-like environment. Indeed, the mountain settings, in perhaps more sheltered areas, indicate the presence of environments with more trees (or, at least, bushes).

Introduction

That part of the Lombard Prealps between the western shore of Lake Garda and the city of Brescia is known as the "Carso Bresciano" ("Brescian Karst") due to the types of outcropping rocks, mostly Mesozoic limestones, which over the course of millions of years have developed karst phenomena so intense as to recall the Carso area in Friuli Venezia Giulia (Vailati 2003).

Received: September 6, 2022; accepted: December 12, 2022

The intense karst activity has acted at different levels, both superficial and deep underground: the deep phenomena have given rise to a complex system of caves and sinkholes still not fully explored today.

The caves and sinkholes of this area function (and, indeed, have so functioned for hundreds of thousands of years) as sedimentary traps (Cremaschi 2000), trapping huge quantities of sediments and fossils from at least the Middle Pleistocene onwards. Although there are conservative geological conditions for potential fossil deposits, systematic works of both paleontological and prehistoric/archaeological investigation are scarce. Mostly these works consist of episodic excavations or of emergency recovery projects in quarries that exploit the carbonate rocks as building material (Vailati 2003).

The few published papers mostly concern single finds or give only partial information about the deposits (Agosti 1970; Bona & Sardella 2014).

Since the early 2000s, some studies have been published that take into account old materials stored in local museums (Museo Civico di Storia Naturale di Brescia and Museo Archeologico della Valle Sabbia, Gavardo, Brescia), publishing important fossil findings, such as *Macaca* and all the Middle Pleistocene small-mammal fauna, previously unknown to specialists or the public (Bona & Sardella 2014; Bona et al. 2016).

These works highlight the importance of the finds only at a general level by broadly framing their chronological and environmental contexts: hence, a few important sites are today at least partially published.

Regarding the area near the site that is the focus of this paper, the first work providing an overall description of the stratigraphic succession with microfauna and macrofauna of the Middle Pleistocene dates back to 2016, when small-mammal remains and meso-mammal fossils of the genus *Macaca* were described (Bona et al. 2016).

The scientific potential of the area is enormous: in this work Late Pleistocene palaeoclimatic and palaeoenvironmental data from the important deposit of the Buco del Frate cave (Prevalle, Brescia) are presented.

The site

The Buco del Frate cave is the most famous and important in the so called "Carso Bresciano" (Vailati 2003). The importance of the Buco del Frate cave is illustrated by the fact that, given the fame achieved, it is the first cave in the Lombardy speleological catalogue (Lo BS 1).

The Buco del Frate cave lies in the municipality of Prevalle (Brescia province, east Lombardy) (Fig. 1A) and is characterized by the presence of two large entrances with downward passages that meet approximately in the middle of the main segment – it opens at 253 m a.s.l. Overall, the known extent of the cavity is about 230 metres (Bini 1975) (Fig. 1B).

The cave must have been known to man since ancient times as it is characterized by two huge entrances that made it very easy to access. Despite this, traces of ancient human presence are doubtful. The first modern written note – by Giuseppe Ragazzoni – concerning the cave dates back to 1872 (Vailati 2003).

The first publications regarding the presence of palaeontological remains date back to 1926 when members of the Gruppo Grotte Brescia and Gruppo Grotte Cremona, two local speleological associations, reported the presence of some remains of *Ursus spelaeus* Rosenmüller & Heinroth, 1794 (Agosti 1970). In the same year, Ardito Desio, the renowned explorer and geologist, recovered fossil bones which he brought to the Museo Civico di Storia Naturale di Milano where they were studied by Airaghi (1927).

The material found during these early activities was described by Airaghi (1927) as coming from a wedge-shaped rock fracture filled with uncemented red earth. Unfortunately, Desio's materials were completely destroyed during the bombing of Milan in 1943 and so there is no possibility of conducting an accurate modern taphonomic analysis.

It was only in 1954, coinciding with the start of the activities of the newly-founded Gruppo Grotte Gavardo (GGG), that the most important deposit – from which the great majority of the known fossils come – was discovered (Simoni 1971).

The deposit was described for the first time by Pasa (1958: 3) as follows: "…consiste in un potente sedimento clastico, argilloso, omogeneo, di terre rosse, deposto tra enormi blocchi di distacco crollati dalla volta di una caverna anche, in origine, doveva apparire meno alta a formare una sala in diretta comunicazione con la superficie montuosa mediante una o due ripide gallerie ascendenti funzionanti da inghiottitoi" ("... it consists of a thick clastic, clayey homogeneous red sediment, deposited among enormous blocks collapsed from the vault of the cavern which, originally, must have seemed less tall, forming a room in direct communication with the surface by one or two steeply ascending galleries that function as sinkholes").

The stratigraphy of the palaeontological deposit can only be hypothesized based on the notes left by the excavators from the GGG (Simoni 1971), as follows: from the top, first, a huge stalag-

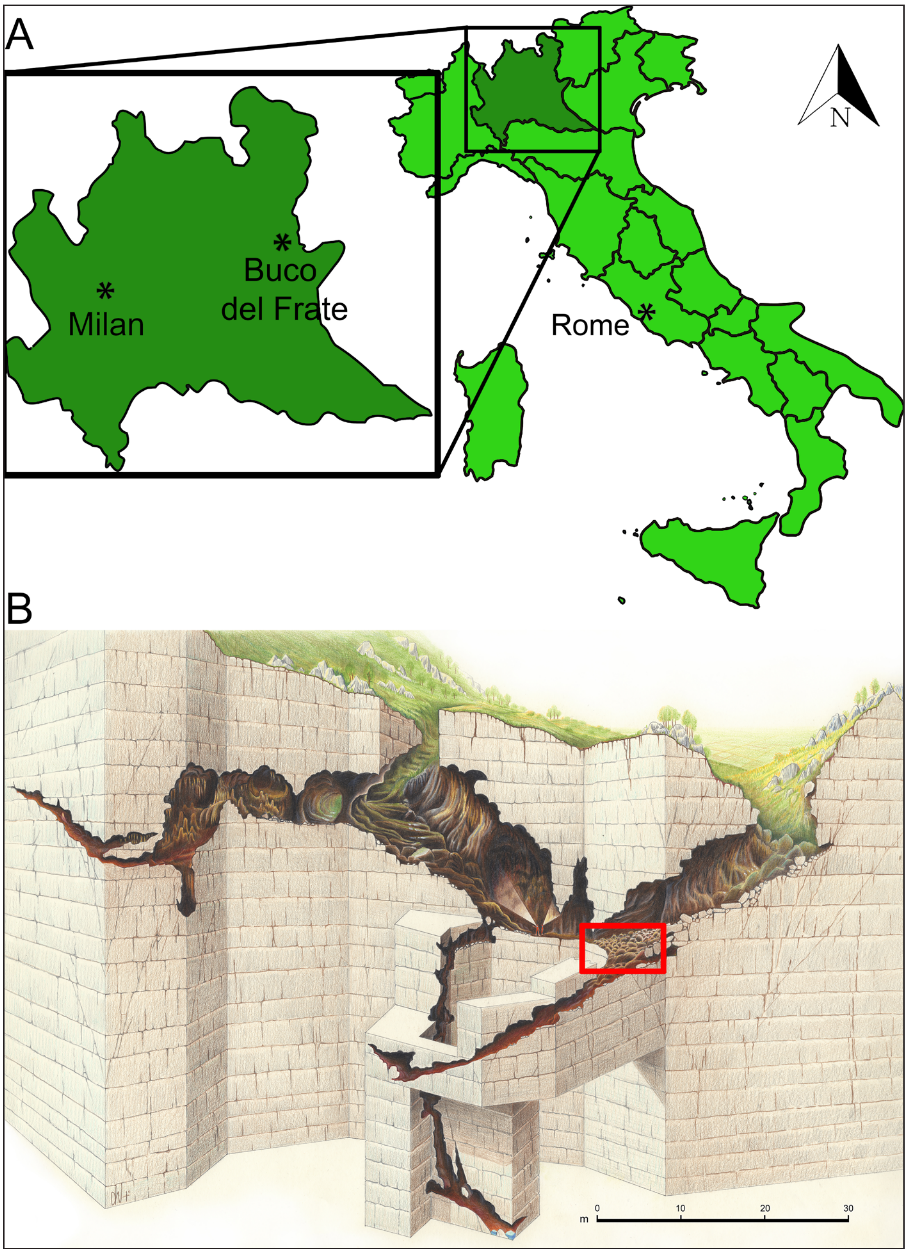

Fig. 1 – A, location of the Buco del Frate cave (Lo BS 1); B, Planimetric sketch of the cave with the place where the fossils were collected indicated by the red rectangle (Drawing by Dante Vailati).

mite crust from 20 to 30 cm thick; the fossiliferous level must have exceeded one metre where complete, considering that in the last excavation made by the GGG in 1970 this deposit still reached a thickness of 20-25 cm in a marginal portion; the third and last known level is made up of finely laminated, sterile silty clay; the thickness of this level is not known as it has never been excavated down to the substrate (Fig. 2).

The list of large mammal remains, partially compiled by Pasa (1958) and Simoni (1971), includes species like cave bear (*Ursus spelaeus*), cave hyena (*Crocuta Crocuta spelaea* Goldfuss, 1823), wolverine (*Gulo gulo* Linnaeus, 1758), alpine marmot (*Marmota marmota* Linnaeus, 1758), wolf (*Canis lupus* Linnaeus, 1758), red deer (*Cervus elaphus* Linnaeus, 1758), beaver (*Castor fiber* Linnaeus. 1758) and others (Tab. 1).

Studies of the fossil material collected in the Buco del Frate cave are very scarce and mostly of a preliminary nature, like the short note by Airaghi (1927) where the focus was making a list of fossils from Lombard caves. The first attempt to give preliminary information on the fauna specifically coming from the cave was made by Pasa (1958).

The most recent, although not very recent, work published on the fossils from the Buco del Frate cave examined the remains of cave hyenas focusing on their cranial characteristics (Agosti 1970).

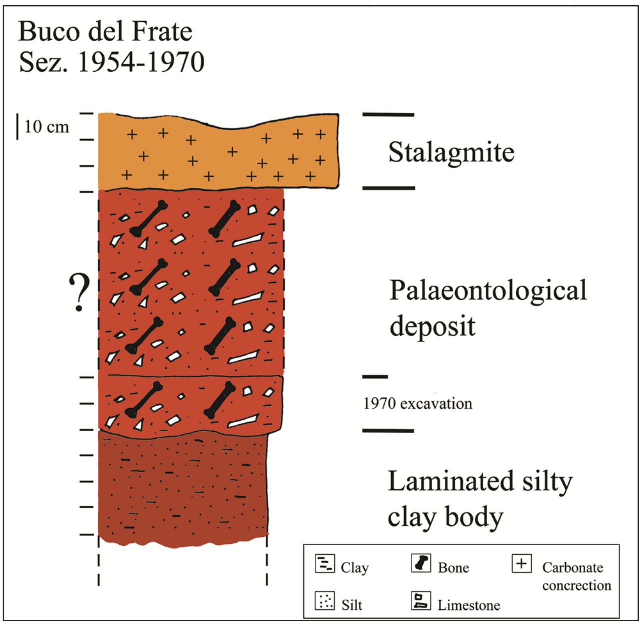

Fig. 2 – Reconstruction of the stratigraphical section of the deposit based on the information reported by Pasa (1958) and Simoni (1971). The "?" on the left of the stratigraphical scale means that we do not have information about the actual thickness of the deposit before the last excavation, carried out in 1970.

Species	Pasa 1958	Simoni 1971
Carnivora		
Canis lupus	x	x
Crocuta crocuta spelaea	x	x
Gulo gulo	x	x
Martes martes	x	
Meles meles		x
Mustela putorius	x	
Ursus arctos	x	
Ursus spelaeus	x	x
Vulpes vulpes	x	x
Artiodactyla		
Bison priscus	x	x
Cervus elaphus	x	x
Bos primigenius ?	x	
Rodentia		
Castor fiber	x	x
Marmota marmota	x	x
Small-mammals	x	x
Aves		x

Tab. 1 – List of fossil fauna from Buco del Frate.

Materials and methods

The small-mammal collection here presented was generated during the final, 1970, field excavation season when all the excavated sediments have been systematically sieved with a 1 mm mesh sieve.

The collection of small mammals from the Buco del Frate cave is stored in the Museo Archeologico della Valle Sabbia MAVS (Gavardo, Brescia).

The complete list of small mammals comprises 453 fossils identified at the genus or species level, corresponding to a Minimum Number of Individuals (MNI) of 157 (Tab. 1 and Fig. 3).

To establish the MNI and the relative frequencies of the species, the most represented skeleton portion was used. The most frequently-recovered element of the voles is typically the first lower molar. The counts have been estimated considering these factors: 1) the siding of the same bones (for example: 3 left humerus and 2 right humerus mean the presence of at least 3 individuals); 2) the ontogenetic stages (for example the development of rooted teeth of *Clethrionomys glareolus* (Schreber, 1780) or the dental wear of *Apodemus* spp. in which teeth are different in juveniles, sub-adults and adults).

The remains of microvertebrates have been identified based on their skeletal elements using a binocular microscope – the 'Leica MZ 6' model – with a magnification from 6.3 x to 40 x.

Then, the best diagnostic small-mammal elements were identified following Chaline et al. (1974) and Niethammer and Krapp (1978; 1982; 1990). The taxonomic identification of the chiropters was based on the diagnostic characteristics identified in Dodelin (2001) and Menu & Popelard (1987).

Data on the distribution and habitat of the species were taken from Amori et al. (2008), Boitani et al. (2003), and Mitchell-Jones et al. (1999).

For the reconstruction of the palaeoenvironment, we use the Habitat Weighting method described in Berto et al. (2018; and bibliography therein), attributing each small mammal taxon to habitat(s) where it can be found today in Europe; dividing the habitats into six types: OD and OH respectively open dry and open wet meadows; woodland environments, OW open and W forested; Wa presence of water of different types, ponds, lakes or along rivers; R where the habitat is dominated by the emergence of the bedrock (Tab. 2).

Tab. 2 – List of small mammal remains from the Buco del Frate cave (n= number of remains; MNI= minimum number of individuals; MNI % R+E= MNI percentages of only Rodents and Eulipotyphla; MNI% Tot= MNI percentages of all small mammals identified).

Species	n	n%	MNI	MNI% R+E	MNI% Tot
Rodentia					
Arvicola amphibius	139	30,68	28	19,58	17,83
Microtus (Microtus) arvalis	75	16,56	41	28,67	26,11
Microtus (Microtus)agrestis	36	7,95	23	16,08	14,65
Microtus (M.) arvalis/agrestis	6	1,32	4	2,80	2,55
Microtus (Terricola) cf. *savii*	6	1,32	5	3,50	3,18
Microtus (Alexandromys) oeconomus	3	0,66	2	1,40	1,27
Clethrionomys glareolus	7	1,55	4	2,80	2,55
Chionomys nivalis	21	4,64	10	6,99	6,37
Microtus sp.	61	13,47			0,00
Apodemus (Silvaemus) gr. *silv.-flavic.*	18	3,97	8	5,59	5,10
Eulipotyphla					
Talpa europaea	39	8,61	12	8,39	7,64
Crocidura leucodon	1	0,22	1	0,70	0,64
Neomys sp.	1	0,22	1	0,70	0,64
Sorex araneus	4	0,88	3	2,10	1,91
Suncus etruscus	1	0,22	1	0,70	0,64
Rodentia+Eulipotyphla	**418**		**143**	**100**	
Chiroptera					
Myotis blythii	21	4,64	9		5,73
Mytois myotis	1	0,22	1		0,64
Myotis nattereri	2	0,44	2		1,27
Myotis blythii/myotis	8	1,77			
Chiroptera indet	3	0,66	2		1,27
Tot	**453**	**100**	**157**		**100**

To calculate the Bioclimatic Component (BC) we use the formula: $BC_i = (\Sigma\ CRI_i) \times 100/S$, where CRI is the Climatic Restriction Index ($CRI_i = 1/n$, "n" is the number of climatic zones inhabited by the species and "i" indexes the climatic zones where species are present) and S in the total number of species (Tab. 2).

$$BC_i = \frac{100(\sum_i CRI_i)}{S}$$

To obtain palaeoclimatic information we used the bioclimatic models proposed by Royer et al. (2020). The parameters used in this paper are: Mean Temperature of the Warmest month (MTW), Mean Temperature of the Coldest month (MTC), Mean Annual Temperature (MAT) and annual total Precipitation (P). The parameter values obtained were compared to recent data (recorded between 1960 and 1990) regarding conditions at the Ghedi meteorological station (Brescia, 45°24'07.2"N, 10°16'49.08"E, 85 m a.s.l data from www.meteoAM.it – Aeronautica militare italiana, Ministero della Difesa) 20 km south of the Buco del Frate cave (Tab. 3).

To evaluate the Biodiversity rate, the Simpson Diversity index was calculated (1-D) (Odum 1988).

Sample BdF 69, a fragment of *Canis lupus* premolar, was sent for radiocarbon dating using high resolution accelerator mass spectrometry (AMS) technology, at the Dating and Diagnostic Centre (CEDAD) of the University of Salento.

Results

The complete list of small-mammal fossil remains identified consists of 21 taxa: 10 Rodentia, 5 Eulipotyphla and 6 Chiroptera.

The small mammal fauna of the Buco del Frate cave shows, despite possible stratigraphic problems, a good degree of homogeneity from the taphonomic and systematic point of view, with only a few finds that may be out of context (not here discussed), allowing us to make a focused analysis of the environmental conditions at the site during the second half of MIS 3.

The assemblage is dominated by the presence of *Microtus* (*Microtus*) *arvalis* (Pallas, 1778) and

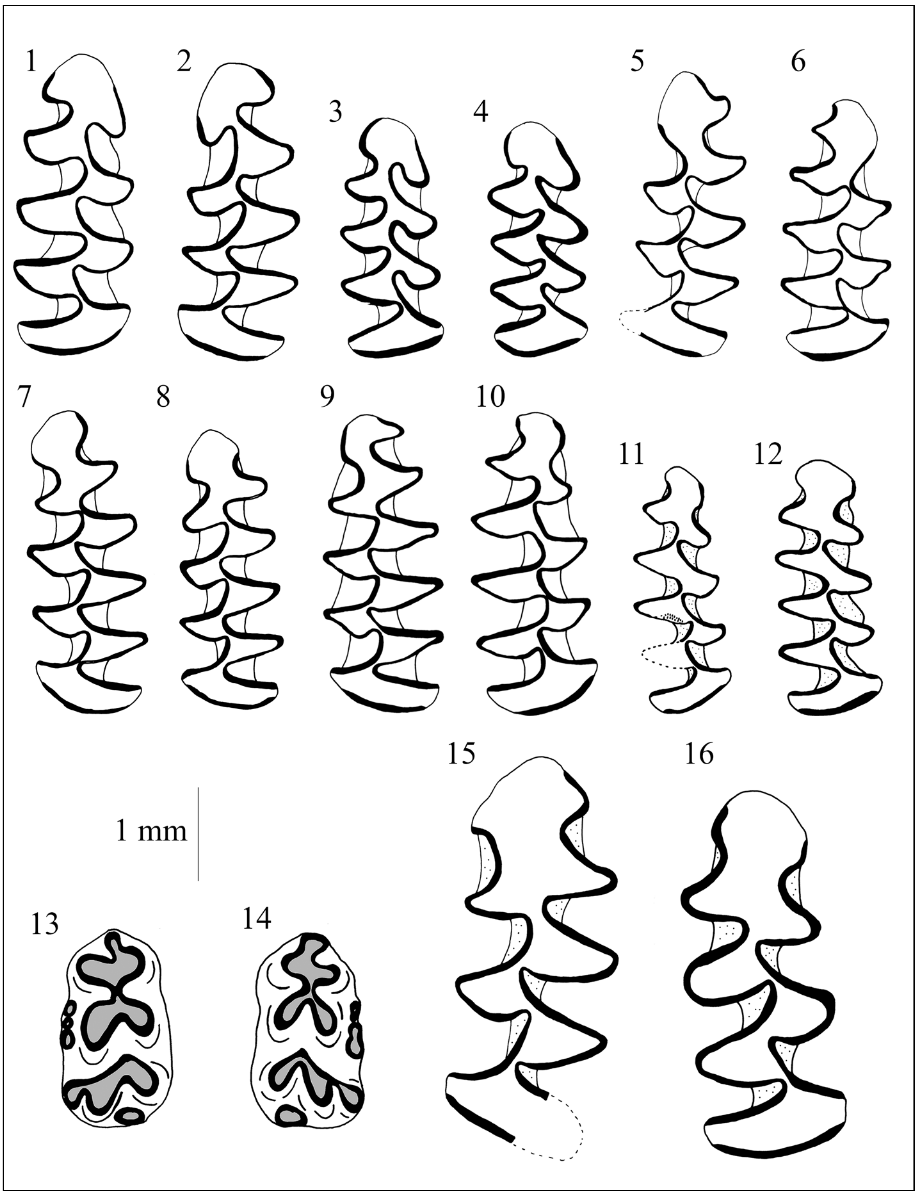

Fig. 3 – Some selected rodent samples from the Buco del Frate cave. All teeth are lower first molars. 1-2: *Chionomys nivalis*; 3-4: *Clethrionomys glareolus*; 5-6: *Microtus* (*Alexandromys*) *oeconomus*; 7-8: *Microtus* (*Microtus*) *arvalis*; 9-10: *Microtus* (*Microtus*) *agrestis*; 11-12: *Microtus* (*Terricola*) cf. *savii*; 13-14: *Apodemus* (*Silvaemus*) gr. *silvaticus*/*flavicollis*; 15-16: *Arvicola amphibius*.

Microtus (*M.*) *agrestis* (Linnaeus, 1761) with a good representation of *Chionomys nivalis* (Martins, 1842). *Arvicola amphibius* (Linnaeus, 1758) is also abundant, while *Microtus* (*Terricola*) cf. *savii* and *Apodemus* (*Silvaemus*) gr. *silvaticus*/*flavicollis* are poorly represented. It is important to underline the presence of *Microtus* (*Alexandromys*) *oeconomus* (Pallas, 1776), a rare but significant species that is quite common in north-eastern Italy but it has, to date, been found only in the Buco del Frate cave in areas west of Lake Garda. In north-eastern Italy we can find the rare *Microtus* (*A.*) *oeconomus* in the small mammal faunal lists of the Fumane cave (Verona) (López-García et al. 2014), Broion cave (Vicenza) (Zanalda 1994) and Caverna degli Orsi (Trieste) (Berto & Rubinato 2013). In north-western Italy the complete absence of this species is implied by the small mammal lists of the Ciota Ciara cave (Piedmont) (Berto et al. 2016), Fontana Marella cave (Bona 2007; Bona et al. 2008) and the Salnova quarry in Saltrio (Varese) (Bona 2011), Caverna Generosa (Como) (Bona et al. 2009; Bona & Savoldi 2016) (Fig. 4). Eulipotyphla and Chiroptera are present, but they are not as common as Rodentia. The best represented Eulipotyphla is *Talpa europaea* Linnaeus 1758, while for Chiroptera the best represented taxon is the large bat *Myotis blythii* (Tomes, 1857) (Tab. 2).

The application of the bioclimatic models proposed by Royer et al. (2020) to the small mammal fauna from the Buco del Frate cave provides important information about the palaeo-meteorological conditions, apparently very different from those of today, with significantly lower temperatures and less precipitation.

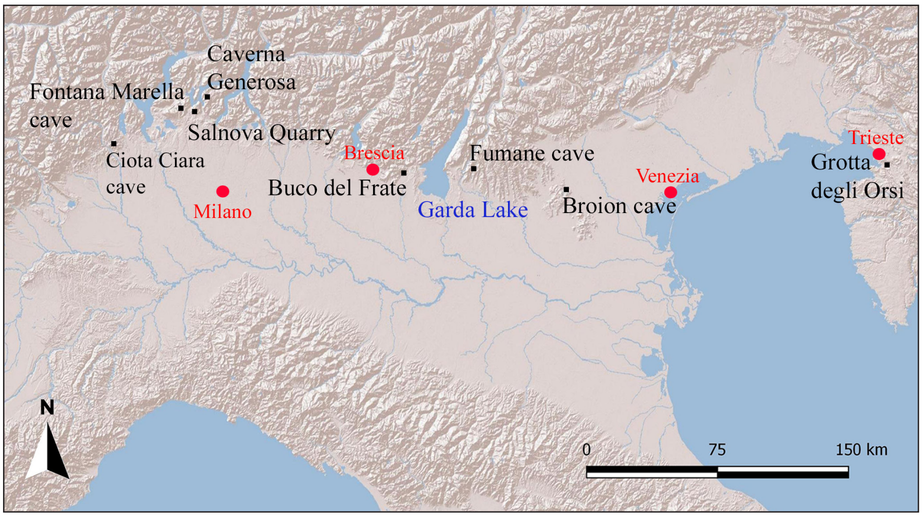

Fig. 4 – Geographical position of the sites discussed in the text.

The biodiversity of the Buco del Frate small mammal fauna, 21 taxa determined, is high, testified by a high Simpson index (= 0.864).

Discussion

Hypothesis regarding the origin of the deposit

Taking account of the relatively limited data available (Airaghi 1927; Simoni 1971; Pasa 1958; Agosti 1970), we can propose a possible origin for the deposit. It is possible that, at a particular point during MIS3, the karst system was functioning as a sinkhole, and a part, specifically the left branch to the entrance, became clogged. This allowed the stagnation of water which led to the formation of the clayey silt laminate deposit. Probably towards the end of the last glaciation stage, a room above the sinkhole may have collapsed, which would explain the presence of the large collapsed blocks along the so called "lower entrance". This could have moved and resettled the palaeontological deposit, formed in the previously existing space, in a chaotic way, also incorporating a few older remains, these last few faunal elements representing evidence of much older karstic activity, but most of the faunal association appears to be consistent with the MIS3. So, the fossiliferous level was probably formed during a mass-movement of sediments from a now-disappeared chamber, or from some other now unknown original location shortly after its formation.

The water present at that time in the area of the cave covered a large part of the fossiliferous deposit, allowing the formation of a stalagmite blanket, probably during the hottest phases of the Holocene.

Age of the fossiliferous deposit

As mentioned above, the processes leading to the formation of the deposit are not clear. The only certain fact is the presence of a fossiliferous deposit with faunal elements typical of a particular glacial stage, such as the wolverine, the marmot and the bison, in association with animals that could also have lived in more temperate phases, like the red deer or the hyena.

This faunal association could lead us to hypothesise that the original deposit, before mass deposition (sensu Pasa 1958) took place, could have been composed of two continuous levels representing the transition from a colder to a slightly more temperate interval or vice versa. This last is only a hypothesis, but a fixed point in terms of when this deposit may have been formed, at least a moment within that process, can be established based on the new C14 date on a wolf (*Canis lupus*) tooth.

The date is 41,130 - 40,465 cal BC (LTL22178 – CEDAD Lecce), which falls in the second part of MIS 3, suggesting that the fossiliferous layer can be attributed to the final part of MIS 3 (Fig. 5).

Palaeoclimatic interpretation

Palaeoclimatic interpretation indicate that the environment in the eastern part of Brescia province, immediately west of Lake Garda, was characterized by scarce arboreal cover in an overall context of open taiga. There were streams of water in the

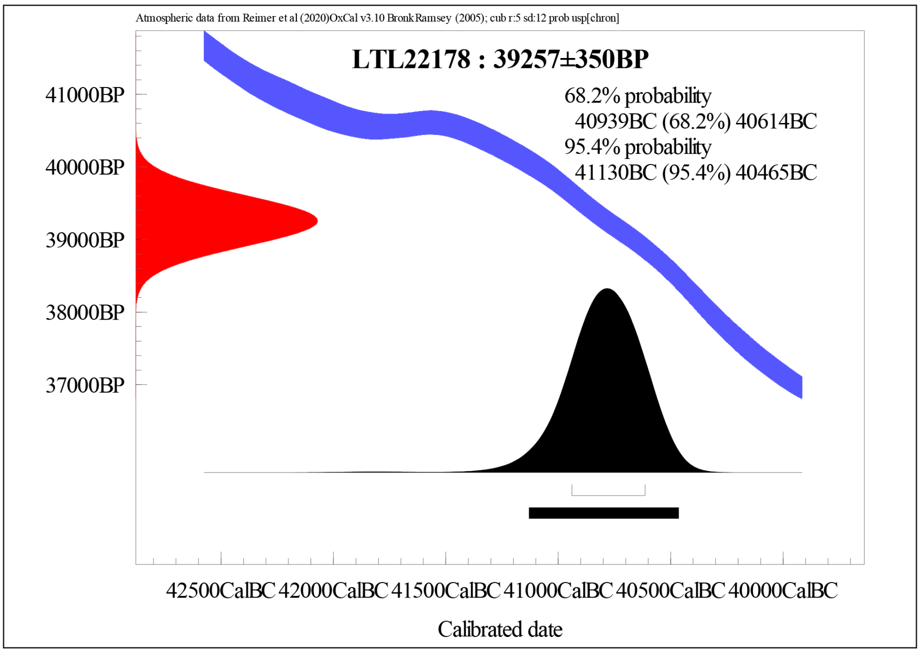

Fig. 5 – Radiocarbon dating of the BdF 69 *Canis lupus* premolar fragment. This represent the first dating ever of Buco del Frate deposit.

plain in front of the cave and the karst portion of the massif favoured the presence of exposed rock (Tab. 3).

The open taiga conditions are confirmed by the dominant presence of species such as *Microtus* (*M.*) *arvalis*, *Microtus* (*M.*) *agrestis*, species that live in open meadows with scarce or absent tree cover, as well as the presence of the large *Myotis myotis* Borkhausen, 1797 and *Myotis blythii*, hunters typically found in an open forest environment. The presence of *Microtus* (*A.*) *oeconomus* could be interpreted with the presence of meadows and marshes even if in the past England it was found in both open woodland and damp environments (interstadial types), as well a cold, dry grassland environments (Cuenca-Bescós et al. 2009). The presence of water is shown by the occurrence of species that today live near water streams, such as *Arvicola amphibius* and *Castor fiber* Linnaeus, 1758. *Chionomys nivalis* found its habitat among the exposed karst rocks. A poor vegetation cover is testified by the scarce presence of species typical of an arboreal or bushy environment such as *Apodemus* gr. *silvaticus*/*flavicollis* and *Clethrionomys glareolus* (Tab. 2, 3).

The data proxies from the small-mammals analysis, compared to recent data (recorded between 1960 and 1990) from the town of Ghedi (30 km south-west of Buco del Frate cave), confirm that, during the deposition of the sediments linked to the faunal remains studied, the climatic conditions were very different from today, with significantly lower temperatures and less precipitation (Tab. 4). The palaeoclimatic conditions of the area around the Buco del Frate cave, inferred from the small mammal record, suggest an average of 4°C lower temperature and precipitation more than 30% lower than in Ghedi in recent times (years 1960-1990). We can thus hypothesise that these climatic conditions supported the development of an environment characterized by scarce tree cover and large open areas.

The likely age of the small-mammal fauna from the Buco del Frate cave – at least 41-40,000 years cal BC – corresponds with the so called "Mammoth steppe" interval at Settepolesini (Ferrara, northern Italy), characterised by a fauna dominated by the presence of *Mammuthus primigenius* Blumenbach, 1799 (Gallini & Sala 2001), where the environment was not so very different from that of Prevalle and its surroundings.

Furthermore, if we compare the paleoenvironmental conditions around the Buco del Frate cave about 40,000 years ago with those of high-altitude caves in western Lombardy such as Caverna Generosa (1450 m a.s.l.) (Bona et al. 2009; Bona & Savoldi 2016), Grotta sopra Fontana Marella (1050 m a.s.l.) (Bona 2007) or the breccia of the Salnova quarry in Saltrio (800 m a.s.l.) (Bona 2011), it is possible to understand how the environmental conditions on the plain during the second half of MIS 3 were quite different from those suggested by high-altitude cave deposits. In fact, in certain mountain

Species	**Habitat**						**Climatic zone**						
	OD	**OH**	**OW**	**W**	**R**	**Wa**		**IV**	**V**	**VI**	**VII**	**VIII**	**IX**
Rodentia													
Arvicola amphibius						1		0,25	0	0,25	0,25	0,25	0
Microtus (Microtus) arvalis	0,75		0,25					0	0	0,5	0	0,5	0
Microtus (Microtus) agrestis		1						0	0	0,5	0	0,5	0
Microtus (Terricola) cf. *savii*		0,5	0,5					0	0	0,333	0	0,333	0,333
Microtus (Alexandromys) oeconomus			0,5			0,5		0	0	0,333	0	0,333	0,333
Clethrionomys glareolus			0,25	0,75				0	0	0,333	0	0,333	0,333
Chionomys nivalis					1			0,25	0	0,25	0	0,25	0,25
Apodemus (Silvaemus) gr. *silvaticus-flavicollis*				1				0,25	0	0,25	0,25	0,25	0
Eulipotyphla													
Talpa europaea		0,5	0,5										
Crocidura leocodon		0,5	0,5										
Neomys sp.		0,75				0,25							
Sorex araneus		0,75	0,25										
Suncus etruscus													
% Habitat Weighting	**21,5**	**24,5**	**15,4**	**7,69**	**6,99**	**20,5**	**BC**	**10,71**	**0**	**39,27**	**7,143**	**39,27**	**17,84**

Tab. 3 – Small mammal species distribution by Habitat (OD= Open Dry; OH= Open Humid; OW= Open Woodland; R= Rocky; Wa= Water) and by Climatic zone (IV= winter rain and summer drought; V= warm-temperate; VI= typical temperate; VII= arid-temperate; VIII= cold-temperate -boreal-; IX= arctic).

slope areas, residual shrub vegetation was preserved, probably in more sheltered valleys, while in the Po plain near the Buco del Frate cave the landscape must have been open with trees or shrubs near the water in the form, probably, of ponds, as the presence of beavers, *Arvicola amphibius* and *Microtus* (*A.*) *oeconomus* seems to indicate.

It seems, then, that the environment of the Po plain around 40,000 years ago must have been an open forest similar to an open taiga.

	Buco del Frate	**Ghedi (1960-1990)**
MAT	7,8°	12,3°
MTW	19,5°	23,2°
MTC	-3,6°	0,75°
P	628 mm	849 mm

Tab. 4 – Comparison between paleoclimatic information obtained using the Buco del Frate cave small mammal data according to the method of Royer et al. (2020) and data on recent conditions registered at Ghedi meteorological station (Brescia, 45°24'07.2"N, 10°16'49.08"E, 85 m a.s.l data from www.meteoAM.it – Aeronautica militare italiana, Ministero della Difesa). MAT= Mean Annual Temperature; MTW= mean temperature of the warmest month; MTC= mean temperature of the coldest month, P= annual total Precipitation.

Another interesting point to note is the presence in the faunal list of *Microtus* (*A.*) *oeconomus*. This was present (and sometimes common) in north-eastern Italy, as far as Lake Garda, during the last stadial (Bartolomei 1960, 1964; Bartolomei and Broglio 1975; Bartolomei et al. 1982; Berto et al. 2018; Bon et al. 1991; Bona et al. 2007; Pasa 1947). However, according to researches in north-western Italy (Bona 2007; Bona 2011; Bona et al. 2009; Berto et al. 2016), they are much less common to the west of Lake Garda. This might suggest the presence of a sort of ecological barrier that was difficult to cross for these small-mammals.

Conclusions

North-eastern Italy is, and has long been, an ecotonal area, where species of the Po basin are associated with species of the Pannonian one. More or less the same happened in the north-west, but with some differences. The data on small-mammal fauna distribution in north-west Italy, which have been notably augmented in the last twenty years (Bona 2007, 2011; Bona et al. 2008, 2009; Berto et al. 2016), seem to indicate that, from the Middle Pleistocene onwards, at least for small mammals, the circulation of species was much more limited.

Fig. 6 – Paleoenvironment reconstruction of the Buco del Frate area around 40,000 years ago (drawing by Valeria Carnevali -@natur_val-).

Some species never reached beyond the karstic massif that lies between Lake Garda to the east and the city of Brescia to the west, while others only managed to cross it at times that saw particular combinations of environmental and climatic conditions.

According to current knowledge, relatively common specie in the deposits of north-eastern Italy such as *Microtus (A.) oeconomus*, common in caves with deposits from the last glacial period in the Berici Hills and Lessini mountains, has only been found in Lombardy in the Buco del Frate cave.

Cricetus cricetus, not present in the faunal list of Buco del Frate and in others cave in the western part of Lombardy during the MIS3 (Bona 2007, 2011; Bona et al. 2008, 2009), also seems to have failed to cross the boundary of Lake Garda during the last glacial maximum, while it is present during MIS 5a at Ciota Ciara (Berto et al. 2016).

The Buco del Frate cave thus represents a cavity that, being located immediately to the west of Lake Garda and just a few tens of metres above sea level, bears witness to which species were able to pass, during the second half of MIS 3, through this area, which must have functioned as a natural barrier at least for small-mammals. Area that, during the second half of the MIS3, was to resemble the open taiga of the today north Europe (Fig. 6).

Acknowledgements: The authors thank G. Cuenca Bescós, T. Mörs and an anonymous referee for the critical reading of the manuscript and fruitful suggestions. We thank all the people who have worked over the years to make possible the study of the material from the Buco del Frate cave, from the volunteers of the Gruppo Grotte Gavardo to the first discoverers of the 1920s. However, we would particularly like to thank one of the participants in the last GGG excavation, Angelo Lando, for his amazing memory regarding the details of the project. We thank Marco Zanon for IT support for R programme, Dante Vailati for the cave section drawing and Valeria Carnevali for the drawing of the palaeoenvironmental reconstruction. We also thank Craig Alexander for a thorough review of the English text – all remaining infelicities are our own!

References

Agosti F. (1970) - La *Hyaena Crocuta spelaea* Goldf. del Buco del Frate 1 lo (Prevalle - Brescia) porzioni craniche - mandibole - denti. *«Natura bresciana» Annali del Museo Civico di Scienze Naturali di Brescia*, 7: 83-102.

Airaghi C. (1927) - Elenco dei mammiferi fossili delle grotte lombarde. *Atti della Società Italiana di Scienze Naturali (Milano)*, 66 (l-2): 142-154.

Amori G., Contoli L., Nappi A. (Eds.) (2008) - Fauna D'Italia: Mammalia II. Erinaceomorpha, Soricomorpha, Lagomorpha, Rodentia. Calderini, Bologna, 736 pp.

Bartolomei G. (1960) - Nota preliminare sulla fauna della grotta maggiore di S. Bernardino nei Colli Berici (Vicenza). *Annali dell'Università di Ferrara, sez. IX*, 3(7): 119-123.

Bartolomei G. (1964) - Mammiferi di brecce Pleistoceniche dei Colli Berici (Vicenza). *Memorie del Museo Civico di Storia Naturale di Verona*, 12: 221-289.

Bartolomei G. & Broglio A. (1975) - Risultati preliminari delle nuove ricerche nei depositi Quaternari della grotta A di Veia. Bollettino del Museo Civico di Storia Naturale di Verona, 2: 217-238.

Bartolomei G., Broglio A., Cattani L., Cremaschi M., Guerreschi A., Mantovani E., Peretto C. & Sala B. (1982) - I depositi Wurmiani del riparo Tagliente. *Annali dell'Università di Ferrara, sez. XV*, 3: 61-105.

Berto C., Bertè D., Luzi E., Lòpez-García J. M., Pereswiet-Soltan A. & Arzarello M. (2016) - Small and large mammals from the Ciota Ciara cave (Borgosesia, Vercelli, Italy): An Isotope Stage 5 assemblage. *Comptes Rendus Palevol,* 15: 669-680.

Berto C., Luzi E., Montanari Canini G., Guerreschi A. & Fontana F. (2018) - Climate and landscape in Italy during Late Epigravettian. The Late Glacial small mammal sequence of Riparo Tagliente (Stallavena di Grezzana, Verona, Italy). *Quaternary Science Reviews,* 184: 132-142.

Berto C. & Rubinato G. (2013) - The upper Pleistocene mammal record from Caverna degli Orsi (San Dorligo della Valle e Dolina, Trieste, Italy): A faunal complex between eastern and western Europe. *Quaternary International*, 284: 7-14.

Bini A. (1975) - "Natura in Lombardia", 3 "Le Grotte". Regione Lombardia. Stabilimento Grafico Scotti, Milano. 220 pp.

Boitani L., Lovari S. & Vigna Taglianti A. (2003) - Fauna D'Italia. Mammalia III. Carnivora, Artiodactyla, 38. Edagricole, Milano, 434 pp.

Bon M., Piccoli G. & Sala B. (1991) - I giacimenti quaternari di vertebrati fossili nell'Italia nord-orientale. *Memorie di Scienze Geologiche,* 43: 185-231.

Bona F. (2007) - Last glacial (OIS 4, OIS 3 and OIS 2) paleoenvironmental analysis for Western Lombardy (North Italy) cave bear sites. *Scientific Annali,* special volume 98: 153-159.

Bona F., Zorzin R., Accordini M., Gatto R., Accorsi C.A. & Mazzi R. (2007) - First paleo-environmental considerations on the Pleistocene deposits of the Lower Cave of Covoli di Velo (VR - Italy). *Scientific Annali,* special volume 98: 229-239.

Bona F., Sala B. & Tintori A. (2008) - Early Toringian small mammals fauna from Fontana Marella cave (Varese, Lombardy, north Italy). *Rivista Italiana di Paleontologia e Stratigrafia,* 114 (1): 133-144.

Bona F., Laurenti B. & Delfino M. (2009) - Climatic fluctuations during the Last Glacial in the north-western Lombardian Prealps: the Upper Pleistocene faunal assemblages of the Caverna Generosa (Como, Italy). *Rivista Italiana di Paleontologia e Stratigrafia,* 115(2): 253-267.

Bona F. (2011) - Upper Pleistocene small mammal fauna from Salnova quarry (Saltrio – Varese – Northwestern Lombardy): paleoenvironmental reconstruction and *Chionomys nivalis* population study. *Rivista Italiana di Paleontologia e Stratigrafia,* 117(2): 323-330.

Bona F. & Sardella R. (2014) - Co-occurrence of a sabertoothed cat (*Homotherium* sp.) with a large lion-like cat (*Panthera* sp.) in the Middle Pleistocene karst infill from nuova «Cava Zanola» (Paitone, Brescia, Lombardy, Northern Italy). *Bollettino della Società Paleontologica Italiana,* 53: 81-88.

Bona F., Bellucci L., Casali D., Sardella R. & Schirolli P. (2016) - *Macaca sylvanus* Linnaeus, 1758 from the Middle Pleistocene of Quecchia Quarry (Brescia, Northern Italy). *Hystrix*, 27(2): 158-162.

Bona F. & Savoldi M. (2016) - The first record of the birch mouse *Sicista* in the Upper Pleistocene sediments of Caverna Generosa (Como, NW Italy), with morphometrical, morphological and ecological considerations. *Rivista Italiana di Paleontologia e Stratigrafia*, 122(2): 1-12.

Chaline J., Baudvin H., Jammot D. & Saint Girons M.-C. (1974) - Les proies des rapaces: petits mammifères et leur environnement. Doin éditeurs, Paris, 141 pp.

Cremaschi M. (2000) - Manuale di geoarcheologia. Editori Laterza, Roma-Bari, 386 pp.

Cuenca-Bescós G., Lawrence G., Straus González Morales M.R. & García Pimienta JC. (2009) - The reconstruction of past environments through small mammals: from the Mousterian to the Bronze Age in El Mirón Cave (Cantabria Spain). *Journal of Archaeological Science,* 36: 947-955.

Dodelin B. (2001) - Identification des Chiroptères de France à partir de restes osseux. Fédération Française de Spéléologie, La Ravoire: Gap édition, 48 pp.

Gallini V. & Sala B. (2001) - Settepolesini di Bondeno (Ferrara – Eastern Po Valley): the first example of mammoth steppe in Italy. In: Cavarretta G., Gioia P., Mussi M & Palombo M.R. (Eds) – Proceedings of the 1st international Congress "The world of Elephants": 272-275. Consiglio Nazionale delle Ricerche, Roma.

López-García J.M., dalla Valle C., Cremaschi M. & Peresani M. (2015) - Reconstruction of the Neanderthal and Modern Human landscape and climate from the Fumane cave sequence (Verona, Italy) using small-mammal assemblages. *Quaternary Science Reviews*, 128: 1-13.

Menu H. & Popelard J.-B. (1987) - Utilisation des caractères dentaires pour la détermination des Vespertilionines de l'Ouest Européen. *Le Rhinolophe,* 4: 1-88.

Mitchell-Jones A.J., Amori G., Bogdanowicz W., Krystufek B., Reijinders P.J.H., Spitzenberger F., Stubbe M., Thissen J.B.M., Vohralik V. & Zima J. (1999) - The Atlas of European Mammals. Academic Press, London.

Niethammer J. & Krapp F. (1978) - Handbuch der Säugetiere Europas. Band 1, Rodentia I (Sciuridae, Castoridae, Gliridae, Muridae). Akademische Verlagsgesell, Wiesbaden, 476 pp.

Niethammer J. & Krapp F. (1982) - Handbuch der Säugetiere Europas. Band 2/1. Rodentia II (Cricetidae, Arvicolidae, Zapodidae, Spalacidae, Hystricidae, Capromidae). Akademische Verlagsgesell, Wiesbaden, 649 pp.

Niethammer J. & Krapp F. (1990) - Handbuch der Säugetiere Europas. Band 3/1. Insektenfresser, Insectivora - Herrentiere, Primates. Akademische Verlagsgesell, Wiesbaden, 484 pp.

Odum E. (1988) - Basi di ecologia. Piccin, Padova, 544 pp.

Pasa A. (1947) - I mammiferi di alcune antiche brecce veronesi. *Memorie del Museo Civico di Storia Naturale di Verona*, 1: 1-111.

Pasa A. (1958) - La fauna del Buco del Frate (Brescia). Nota preliminare. *Commentari Ateneo Brescia*: 231-235.

Royer A., García Yelo B.A., Laffont R. & Fernandez M.H. (2020) - New bioclimatic models for the quaternary palaearctic based on insectivore and rodent communities. *Palaeogeography, Palaeoclimatology, Palaeoecology,* 560: 110040.

Simoni P. (1971) - Ricerche paleontologiche nella grotta Buco del Frate (n. 1 LO - Prevalle, Brescia). *Annali del Museo Notiziario di preistoria e archeologia edito dalla Associazione Civico Museo Gruppo Grotte Gavardo,* 9: 43-86.

Vailati D. (2003) - Il “carso bresciano” e il Buco del Frate. Puntografico, Brescia, 60 pp.

Zanalda E. (1994) - Variazioni delle associazioni a micromammiferi indicatrici dei cambiamenti climatico-ambientali dell’ultimo glaciale. Ph.D. Dissertation, Milano University, 229 pp.