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Research Article

Some thoughts regarding MIS3 marmots (*Marmota marmota*) of northwestern Italy with particular reference to those from Caverna Generosa (Centro Valle Intelvi, Como)

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Abstract

This work focuses on fossil bones of the alpine marmot *Marmota marmota* (Rodentia, Sciuridae), a topic poorly studied in previous palaeontological work. In northern Italy the alpine marmot seems to be absent during the Lower Pleistocene and very poorly represented in the Middle Pleistocene. Only during the Upper Pleistocene is this rodent widespread. The fossil remains studied herein come from Upper Pleistocene deposits of the Caverna Generosa (Centro Valle Intelvi, CO; 1450 m a.s.l.), Buco del Frate (Prevalle, BS; 253 m a.s.l.) and Büs di Tri Fradei (Oltre il Colle, BG; 1200 m a.s.l.). Furthermore, the remains of the extant alpine marmot were analysed for comparison. The morphometric study revealed that the sexual dimorphism is negligible, and that fossil and extant specimens are dimensionally similar, although most of the extant marmots seem to be slightly larger than the fossil ones. The Caverna Generosa fossil specimens were divided into classes of dental eruption and wear, associated with different ontogenetic stages. This allowed us to highlight a peak of mortality among the juvenile specimens. Furthermore, the Caverna Generosa sample was compared with those from Grotte di Pradis (Friuli Venezia Giulia, Italy) and Grotte Colomb (France) where human exploitation of the marmot is attested. This comparison confirmed that the pattern of mortality at the Caverna Generosa is not related to human exploitation. Dating of two alpine marmot bones from two different levels of two different areas of the Caverna Generosa returned ages of 35,645-34,371 y cal BC and 32,540-32,032 y cal BC, respectively. These results suggest that the frequentation of the cave by *M. marmota* is more or less contemporary with that of *Ursus spelaeus* and other Upper Pleistocene species found at the site.

Introduction

The alpine marmot (*Marmota marmota*) has been little studied from a population perspective in previous paleontological works. This species is usually included in faunal complexes and most of the literature about alpine marmot remains consists of archaeozoological studies as, for example, Tomé (2005); Gurioli et al. (2011); Romandini et al. (2012) and Nannini et al. (2022). The aim of our work is to date and analyse a marmot population that lived in a glacialized habitat during the MIS (Marine isotope stage) 3, including other fossil data from Buco del Frate (Prevalle, BS) and Büs di Tri Fradéi (Zorzone, BG), and using modern ones as a dimensional comparison. Furthermore, an interesting purpose of our study is to define the mortality development of the marmot population in a natural context, compared to mortality profiles resulting from human exploitation, as the Caverna Generosa has been frequented by *Homo neanderthalensis* (Bona et al., 2007). The richness in alpine marmot bones, dated to the Upper Pleistocene of the paleontological site of the Caverna Generosa, has allowed us to evaluate this species from a population point of view. This is possible thanks to the palaeontological fieldwork carried out by the Università degli Studi di Milano for more than 30 years (Bona et al., 2007, 2009; Sessa et al., 2021).

The alpine marmot is a rodent belonging to the Sciuridae family. Marmots are strongly social animals adapted to fossorial life, usually living in alpine meadows and rocky environments where burrow systems can be found (Colturi, 2002; Mann et al., 1993).

The first appearance of the alpine marmot in Europe is recorded in the Lower Pleistocene at a handful of sites such as Sierra de Atapuerca in Spain (Estraviz-López et al., 2021), Montoussé in France (Clot, 1975; Estraviz-López et al., 2021), Deutsch in Austria (Maul, 1990; Estraviz-López et al., 2021), Podumci, Tartinja and Draga in Croatia (Malez and Rabeder, 1984; Paunović and Rabeder, 2000; Estraviz-López et al., 2021). Even if this species is more abundant in the Middle Pleistocene than before, in particular at French and Spanish sites, it remains rarer than other rodent species (Estraviz-López et al., 2021). Most of the fossil remains attributed to *Marmota marmota* date to the Upper Pleistocene, when this species attained its greatest distribution during the Last Glacial Maximum, even reaching the lowlands (Cassoli and Tagliacozzo, 1994; Estraviz-López et al., 2021). The climate fluctuations during the Pleistocene brought environmental variations with the interchange of steppic and humid climatic conditions. Climate change thus led to the reduction of vegetation and/or the succession of different types of vegetation cover, and, consequently, to changes in the faunal dispersal of small and large mammals (Masini and Sala, 2007; Sala and Masini, 2007; Petronio et al., 2011). In the most temperate phases, the marmots were confined to mountain habitats. In fact, during the Holocene, the distribution area of the species has reduced significantly, and it is currently found only in the Alps, the Carpathians, the Pyrenees and some mountain ranges in Germany (Cassoli and Tagliacozzo, 1994; Colturi, 2002; Kryštufek and Vohralík, 2013).

In Italy, the alpine marmot first appeared in the Middle Pleistocene, as seen in the fossil records from Grotta Maggiore di San Bernardino (Mossano, VI) (Bartolomei, 1960; Fabiani, 1903) and Grotta San Leonardo (Sgonico, TS) (Bartolomei, 1982b; Kotsakis et al., 2003). During the Upper Pleistocene this species had a wider distribution that

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covered all northern Italy. The marmots expanded across the Italian peninsula reaching central and southern Italy. The evidence consists of the fossil record from Grotta Paglicci (Bari, Puglia), where marmot remains can be found in the Early Epigravettian (23,612-25,185 y cal BP – 18,549-20,133 y cal BP) and the Evolved Epigravettian levels (17,988-19,112 y cal BP – 18,220-19,245 y cal BP) (Boschin, 2019; Kotsakis et al., 2003).

Fossiliferous sites

The fossil material attributed to *Marmota marmota* included in this work comes from three sites of paleontological interest: the Caverna Generosa (CO), Buco del Frate (BS) and Büs di Tri Fradéi (BG).

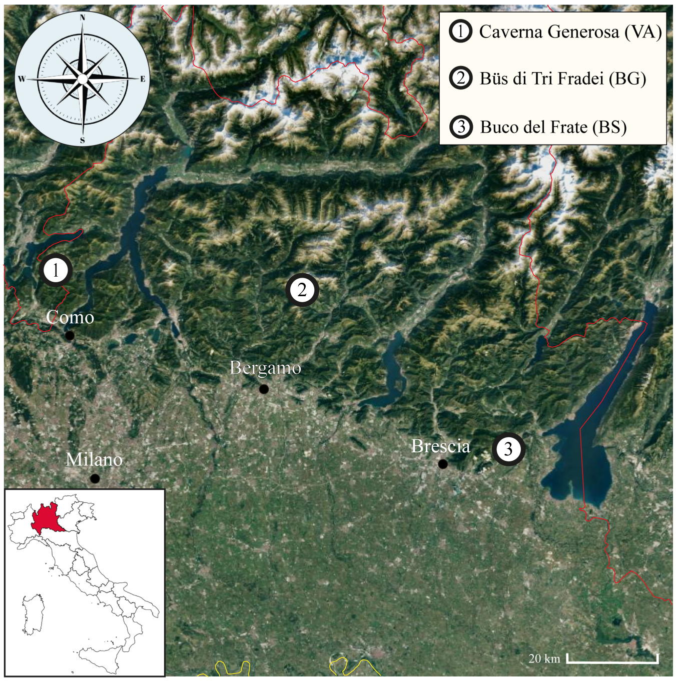

Figure 1 – Geographical position of the sites included in this work: Caverna Generosa (1), Büs di Tri Fradéi (2) and Buco del Frate (3). Modified from Google Earth.

The Caverna Generosa is a site located on the Italian side of Monte Generoso (1701 m a.s.l.) in north-western Italy (CO) at 1450 m a.s.l. (Fig. 1). The sediments in the cave testify both human and animal occupation, a rare occurrence at these altitudes during a glacial period (Bona, 2004; Bona et al., 2007). Three main areas are recognizable from the entrance: an initial narrow tunnel known as the "Cunicolo", a small room called the "Saletta", and a larger room called the "Sala Terminale". The stratigraphy of the three main parts of the Caverna Generosa has been studied and widely discussed in the following papers: Bona (2005); Bona et al. (2009); Bona and Savoldi (2016); Sessa et al. (2021). The sedimentary deposits of the Caverna Generosa have been dated through the ^{14}C analysis of various bone remains belonging to different parts of the cave. The dating of osteological elements from the first six stratigraphical units from the "Sala Terminale" (five of them are attributed to *Ursus spelaeus*), revealed an age between about 50,000 y BC and about 38.000 y BC (Tab. 2). Further cave bear bones from the stratigraphical units from the "Cunicolo" have been dated between 40,129 y BC and 34,988 y BC (Tab. 2) (Sessa et al., 2021).

The occasional human presence is indicated by some lithic artifacts: ten Mousterian flint flakes whose age is between 60,000 and 40,000 y BC (Bona et al., 2007). *Homo neanderthalensis* exploited local resources, that could be found both inside and outside the cave, to survive in an inhospitable environment. For example, bones seem to have been used to light a fire (Sessa et al., 2021).

During the Upper Pleistocene, this area was covered by glaciers that never reached the altitude of the cave (Sessa et al., 2021). The geological context is characterized by the Calcare di Moltrasio formation, with grey marly limestone and the occurrence of dark chert nodules.

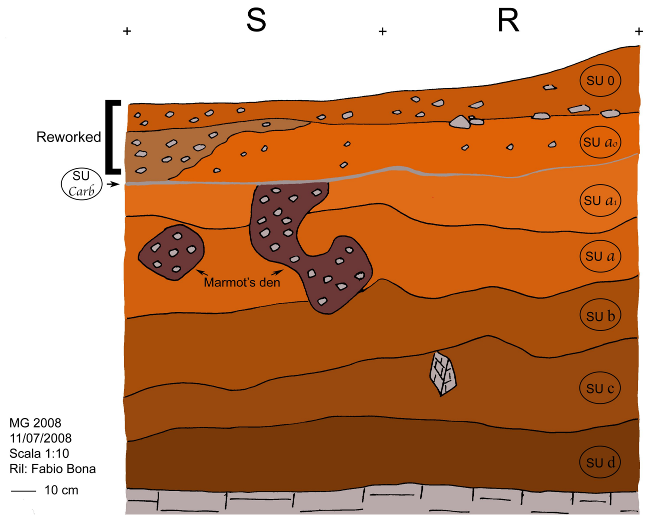

Figure 2 – S and R sector stratigraphy in the "Sala Terminale" from Caverna Generosa.

The Caverna Generosa is the result of karst processes that started during the Tertiary period (Bini and Cappa, 1975). The cavity extends for 200 metres, while the Upper Pleistocene deposits are present in the first 70 metres (Bona, 2005; Bona et al., 2009; Sessa et al., 2021). There are many factors that allowed us to evaluate the impact of the marmot population in the Caverna Generosa. Amongst these are the system of dens recorded in the stratigraphy, the high number of marmot bones recovered in levels from the different locations in the cave (the "Cunicolo", the "Saletta" and the "Sala Terminale"). Bones belonging to the same individual found almost anatomically connected and, sometimes, cave bear bones were found vertically arranged, probably due to the collapse of the marmot dens below (Bona, 2004). For instance, the S and R sectors in the "Sala Terminale" highlight bioturbation linked to the presence of a marmot's den, that was excavated in the stratigraphy (Fig. 2) described below:

- Stratigraphical Unit (SU) Carb. - thin white carbonate deposit covering the Pleistocene deposit at *Ursus*. It reaches a maximum thickness of 2-3 mm;

- SU a1 - silty-clayey matrix with light orange-red colour. Occasional remains of *Ursus* are starting to appear. There are occasional centimetre-sized carbonate clasts and some larger ones collapsed from the vault;

- SU a - clayey-silty level of yellow-orange colour, carbonate clasts up to 20 cm in diameter are present. The *Ursus* finds become more abundant and complete compared to the previous unit;

- SU b - clayey level with little silt that shows high plasticity. Light brick colour with a few yellow streaks. Clasts are almost absent and there are few bone remains;

- SU c - silty level with little clay, it is powdery when excavated. Brick red colour with orange streaks. Clasts are almost absent with the exception of large vault collapse fragments with a decarbonated surface, *Ursus* bone remains are present, including large ones, albeit not well preserved;

- SU d - there is a gradual transition from the c level with the matrix becoming darker and clayey silt but with more residual clay.

The study of the small mammals and herpetofauna has allowed us to make the following paleoclimatic and paleoenvironmental reconstructions: around 50,000 y BC the environment consisted of cold grasslands; about 45,000 y BC the fossil remains suggest a milder and wetter climate and a wooded environment; between 36,000 y BC and 30,000 y

Table 1 – ^{14}C dating from the "Cunicolo" 13 – 15 and the "Sala Terminale" sequences. Dates are calibrated with 95.4 % highest posterior density (HPD) intervals show (Sessa et al., 2021).

Sample	Square/level	Analysed fraction	δ^{13}C (%)	14C Age (BC)
UtC-10761	MG D6/2	collagene	−23,5	39876-42483 47985-46805
UtC-10762	MG AA3/4	collagene	−18,8	47546-47397
UtC-10763	MG AA3/6	collagene	−20,1	47877-47843
UtC-10764	MG AA3/6	collagene	−18,3	47931-48054
UZ 2429/ ETH 4249	MG 1/0	collagene	−23,5	38250-41543
LTL1775A	MGCUN 14A/II	collagene	−20.0 ± 0.2	34988-36717
LTL1776A	MGCUN 2 14A/II	collagene	−21.0 ± 0.3	38736-39538
LTL1777A	MGCUN 13A/II	collagene	−20.0 ± 0.2	38070-39857
LTL1778A	MGCUN 14A/III	collagene	−20.1 ± 0.2	37891-40129

BC a climatic deterioration is seen in the levels closest to the Last Glacial Maximum, with a mostly open and cold environment; the Postglacial and Holocene faunal associations suggest the spreading of wooded areas (Bona et al., 2009).

Buco del Frate is a cave located in the so-called "Carso Bresciano" at 253 m a.s.l. (Fig. 1), from which the fossil material is attributed to the second part of MIS 3 through ^{14}C analysis of a wolf (*Canis lupus*) tooth: the date is between 41,130 and 40,465 y BC. The study of the small mammal fauna permitted us to understand that the environment was very sparsely wooded and more similar to taiga (Bona et al., 2023).

Büs di Tri Fradéi is a fossil site located in the "Prealpi Bergamasche", immediately to the north of Zorzone (BG) (Fig. 1). The dating of *Ursus spelaeus* remains revealed an age between 38,582 and 34,116 y BC. The study of the small mammal fauna revealed a cold-temperate climate and an environment covered by bushy vegetation (Gurian, 1994; Carnevali, 2023).

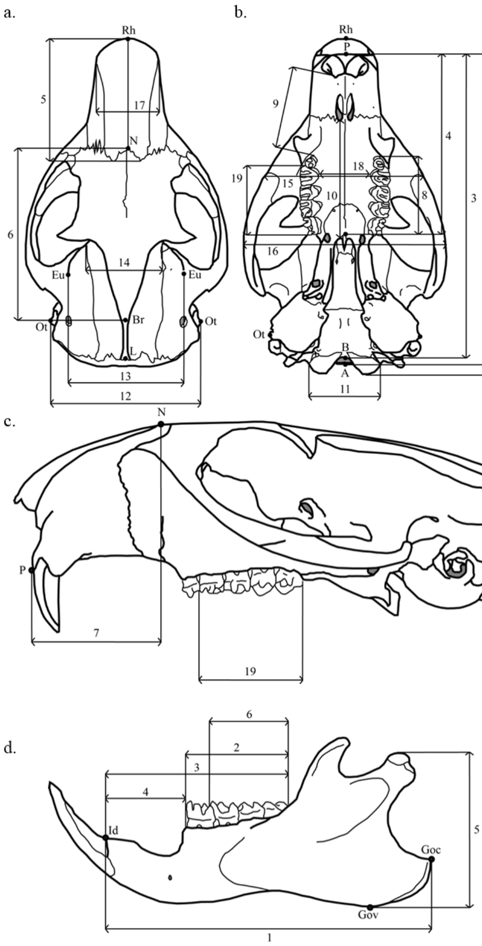

Figure 3 – Measurements for alpine marmot craniums in dorsal (a), ventral (b) and lateral (c) view and for hemimandibles in buccal view (d), drawings modified with the measurements guidelines proposed by Schmidt (1972) for Oryctolagus. These representations are based on Kryštufek & Vohralík (2013).
Cranium measurements (a, b, c).
1. Total length (Akrokranion - Prosthion);
b.Condylobasal length (aboral border of the occipital condyles - Prosthion); 3. Basal length (Basion - Prosthion); 4. Dental length (Postdentale - Prosthion); 5. Greatest length of the nasals (the median point of the intestection of the line joining the aboral borders of the nasals - Rhinion)); 6. Frontal length (Bregma - Nasion); 7. Viscerocranium length (Nasion - Prosthion); 8. Length of the cheektooth row (measured along the alveoli on the buccal side); 9. Length of the diastema (the oral border of the alveolus of P3 - aboral border of the alveolus of I2 of one side); 10. Palatal length (the length of the palatal bridge); 11. Greatest breadth of the occipital condyles; 12. Greatest breadth across the openings of the external acoustic meatus; 13. Greatest neurocranium breadth (Euryon Euryon); 14. Breadth of the skull (the points of the slide gauge are placed in the temporal fossae dorsal of the zygomatic processes of the temporal); 15. Oral zygomatic breadth; 16. Aboral zygomatic breadth; 17. Greatest breadth of the nasals; 18. Palatal breadth (breadth between the inner borders of the alveoli of the second cheekteeth); 19. Length of the jugal teeth.
Hemimandible measurements (d).
1. Length from angle (Gonion caudale - Infradentale); 2. Length of the cheektooth row (measured along the alveoli); 3. Length (aboral border of the alveolus of M3 - Infradentale); 4. Length of the diastema (oral border of the alveolus of P4 - Infradentale); 5. Height of the vertical ramus (Gonion ventral - highest point of the condyle process); 6. Length of the molars .

Material and methods

The fossil remains found during the paleontological fieldwork at the Caverna Generosa (Fig. 1), mainly consist of *Ursus spelaeus,* which used the cave for hibernation (Bona, 2004; Sessa et al., 2021). *Marmota marmota* has been found in various Stratigraphical Units (SU) in the parts of the cave known as the "Cunicolo", the "Saletta" and the "Sala Terminale". The fossil material, 593 bones in total (Tab. 2), that we have attributed to the alpine marmot (*Marmota marmota*) is stored at the Earth Science Department "A. Desio" (UniMI). The identification of the osteological remains was carried out using the reference collection from the Earth Science Department "A. Desio" (UniMI) and following Schmidt (1972) and Hillson (1996). After evaluating the Number of specimens (=N), we calculated the Percentage of the number of specimens (=N%) (Tab. 2), the Minimum Number of Individuals (MNI) (Tab. 3) of the marmot bone sample have been calculated, evaluating the most frequent skeletal element and its siding, which in our case was the right femur. We estimated the age at death of the specimens using epiphyseal fusion and teeth eruption and wear following the standards proposed by Tomé (2005). Since some remains were found in burrow levels and cannot be correlated with any particular level from the stratigraphic sequence of the cave, we have assorted them in a single level called "Den" for each of the three parts of the cave (Tab. 3). Then we have collected data related to predation marks and rodents gnawing marks (Tab. 2).

Table 2 – Marmots skeletal element, predation traces and gnawings identified. NISP = number of identified skeletal parts. NR = number of remains.

Skeletal element	NISP		Predation traces		Gnawings	
	NR	%	NR	%	NR	%
Skull	9	1,5				
Hemimandible	48	8,1	4	19,05	2	9,1
Maxillae	12	2,0			1	4,5
Humerus	55	9,3	1	4,8	1	4,5
Radius	50	8,4	1	4,76	1	4,5
Ulna	44	7,4	4	19,05	3	13,6
Coxal	30	5,1			4	18,2
Femur	74	12,5	6	28,6	4	18,2
Tibia	67	11,3	5	23,8	6	27,3
Fibula	12	2,0				
Metapodial	25	4,2				
Astragalus	3	0,5				
Calcaneus	6	1				
Rib	22	3,7				
Proximal phalanx	7	1,2				
Mesial phalanx	1	0,2				
Vertebrae	40	7				
Sacrum	4	0,7				
Isolated jugal tooth	10	1,7				
Scapula	18	3,0				
Incisor	36	6,1				
Indeterminate	20	3,4				
Tot.	593	100	21	100	22	100

The marmot bones (Tab. 2) were measured using the standard measurements proposed by Driesch Von Den (1976) for *Lepus* and *Oryctolagus*. Further, we measured the molar series for the crania and the hemimandibles (Fig. 3), and the length and the width of every single tooth, except for the incisors (see the table S1 in the supplementary material). As a comparison, we took the same measures on some marmot remains from two other sites in north-western Italy dating to the Upper Pleistocene: Buco del Frate (Prevalle, BS) (Bona et al., 2023) and Büs di Tri Fradéi (Zorzone, BG) (Gurian, 1994; Carnevali, 2023) (see the table S2 and S3 in the supplementary material).

Also, we took into account a skull (with mandible) of a modern marmot stored in the comparison collection of the Earth Science Department "A. Desio" (UniMI), measures of modern marmot taken on six skulls and seven hemimandibles from the Sondrio and Bergamo provinces stored in the "Museo Civico di Storia Naturale di Morbegno" (Morbegno, SO) (see the tables S4 and S5 in the supplementary material). Lastly, we had the opportunity to gather measurements on sixteen skulls and sixteen hemimandibles of modern specimens belonging to the "Museo di Storia Naturale di Milano", that were collected from Cuneo province in Piedmont, the Aosta province in Valle d'Aosta and one sample from Monte Bego in France (see the table S6 in the supplementary material).

Two marmot bone samples from the Caverna Generosa, in particular two right tibiae, have been ^{14}C dated through high-resolution mass spectrometry at the "Centro di Datazione e Diagnostica" (CEDAD) of Salento University. The dating calibration has been done using OxCal (v. 4.4.4, IntCal20).

Table 3 – Minimum Number of Individuals (MNI) of the marmots from the three sectors of the Caverna Generosa: Cunicolo, Saletta and Sala Terminale.

Skeletal element	Cunicolo levels							
	0	I	II	III	IV	V	VI	VII
Skull								
Hemimandible		4	4					
Maxillae		2						
Scapula			1					1
Humerus		3	1					
Radius	2	1						
Ulna	1	1	2					
Femur		4	1					
Tibia		2		1				
Isolated jugal tooth	4	1	1					
Upper incisor	1	1	1					
Lower incisor	3	3	1					
Indeterminate	1	3	1					
MNI	4	6	6					1

Table 3 – Continued.

Skeletal element	Saletta levels															
	0	1	1a	2	3	3a	3b	4	4b	5	5a	6	6b	7	8	Den
Skull				1	1			1						1		1
Hemimandible				1	4						4	4	1	2		
Maxillae							1	1								
Scapula	3				3											
Humerus	2	1			7		1	2			2	4		6		
Radius	2			2	4			2	1	1	4	1		1		1
Ulna	1		2		5			1	1	2	2	3		2		
Coxal	2			1				2	1		1					3
Femur	1	2		3	11	2	1			1	4	5	1	4		1
Tibia				2	6		1	2			6			8	1	1
Fibula				1				1			1					2
Metapodial	1			1	2											1
MNI	2	1	2	3	15	1	1	3	1	3	6	9	1	11	1	4

Table 3 – Continued.

Skeletal element	Sala Terminale levels																	
	0	1	2	a	b	3	3a	c	d	4	5	6	7	8	9	10	11	Den
Skull				1						2					1			
Hemimandible				2	1													
Maxillae	6			1														
Scapula	2			3				1				1						
Humerus											1	2	1	1			1	
Radius				2	2			1	1	1		2	1		1	2		
Ulna	1			1						1					1	1		
Coxal	1		1	2	1				1		1	1					1	
Femur	3		1	3			2	1	1				2					1
Tibia	4		1	1				1		1	1	1	1			1		1
Fibula			1												3			
Metapodial	3		2	3					1						2		1	1
Rib	1			1						1	1		1		4			
Vertebrae	1			2	1					1		2	1		10			
Sacrum	1		1															
Isolated jugal tooth	1																	
Upper incisor	3			2								1						
Lower incisor	1			1	1				1	1								
Indeterminate	1				1			2	1									
MNI	4		1	2	2		1	1	1	3	1	3	3	1	3	2	1	2

A biometric analysis has been performed through statistical methods. The measures dataset of skulls, hemimandibles and teeth have greater data completeness than other skeletal elements across the different measurements. This is the main reason why analysis focused on the crania, hemimandibles and teeth (in particular the upper and the lower third molars). As the Caverna Generosa dataset has been augmented with the data on other fossil marmots from Buco del Frate and Büs di Tri Fradéi and modern marmots from Lombardy, Piedmont, Valle d'Aosta and France. So, we had the opportunity to use a substantial amount of modern material, composed of skulls, hemimandible and teeth, in order to conduct a dimensional comparison for the above-mentioned skeletal elements. A paleontological sample like ours is often characterized by a high frequency of fragmentary bones, therefore, unlike modern skeletons, it is more complicated to acquire all the necessary standard measurements. So, our choice is based on the most commonly detected measurements between the standard ones illustrated in (Fig. 3. The focus of our analysis are the following dimensions (Fig. 3): length of the cheektooth row, measured along the alveoli; length, that is the aboral border of the alveolus of M_3 (third lower molar) - Infradentale; length of the diastema, measured from the oral border of the alveolus of P_4 (fourth lower premolar) – Infradentale, M^3 (third upper molar) length and width, M_3 length and width. Firstly, we investigated the possible evidence of sexual size dimorphism and dimensional differences between fossil and current marmots using scatterplots (Fig. 4). Then, we would have used a t-test to inspect the size difference between current and fossil marmots, but that would be possible only after verifying the assumptions. Our hypothesis was that the modern alpine marmot samples average measurements are a little larger than the fossil ones from the Caverna Generosa, Buco del Frate and Büs di Tri Fradéi along the dimensions that have been chosen. We set a significance threshold of 0.05, in order to define when the results of the statistical analysis presented below, represent a statistically significant outcome (p-value < 0.05) or not (p-value > 0.05). We checked the normality assumption of the means of the measures of the samples through the Shapiro-Wilk test, then we used the Levene test (car package in R) to verify the homoscedasticity assumption. So, we performed a t-test and a nonparametric Wilcoxon-Mann-Whitney test, the latter in the case of samples that are not normally distributed. Analyses using the R software (v. 4.3.1).

Table 4 – Alpine marmot radiocarbon dates from Caverna Generosa, with 95.4 % highest posterior density (HPD) intervals show.

Sample	**Square/level**	**Osteological element**	δ^{13}**C** (‰)	**Calibrate dating (confidence interval 2 σ)**
MG-NO-863	S6/c	Tibia	-20.5 ± 0.2	35645 y BC (95.4 ‰) 34371 y BC
MG-NO-868	AA28/7	Tibia	-24.8 ± 0.4	32540 y BC (95.4 ‰) 32032 y BC

Results

Dating

Two remains attributed to *Marmota marmota* from the Caverna Generosa have been ^{14}C dated. One of them is a right tibia fragment from the sector S6 and level c (tana) (tana= from sediment that filled a den dug by marmots into the level c) (Fig. 2) from the "Sala Terminale". The calibrated date of the marmot bone is between 35,645 and 34,371 y BC (Tab. 4). The second sample is a right tibia from the "Saletta", whose location was in sector AA28 level 7, which contained a large burrow. The calibrated age of this right bone is between 32,540 and 32,032 y BC (Tab. 4). So, we can state that the marmots from the Caverna Generosa and their frequentation of the cave can be attributed to the Marine Isotope Stage 3 (MIS 3).

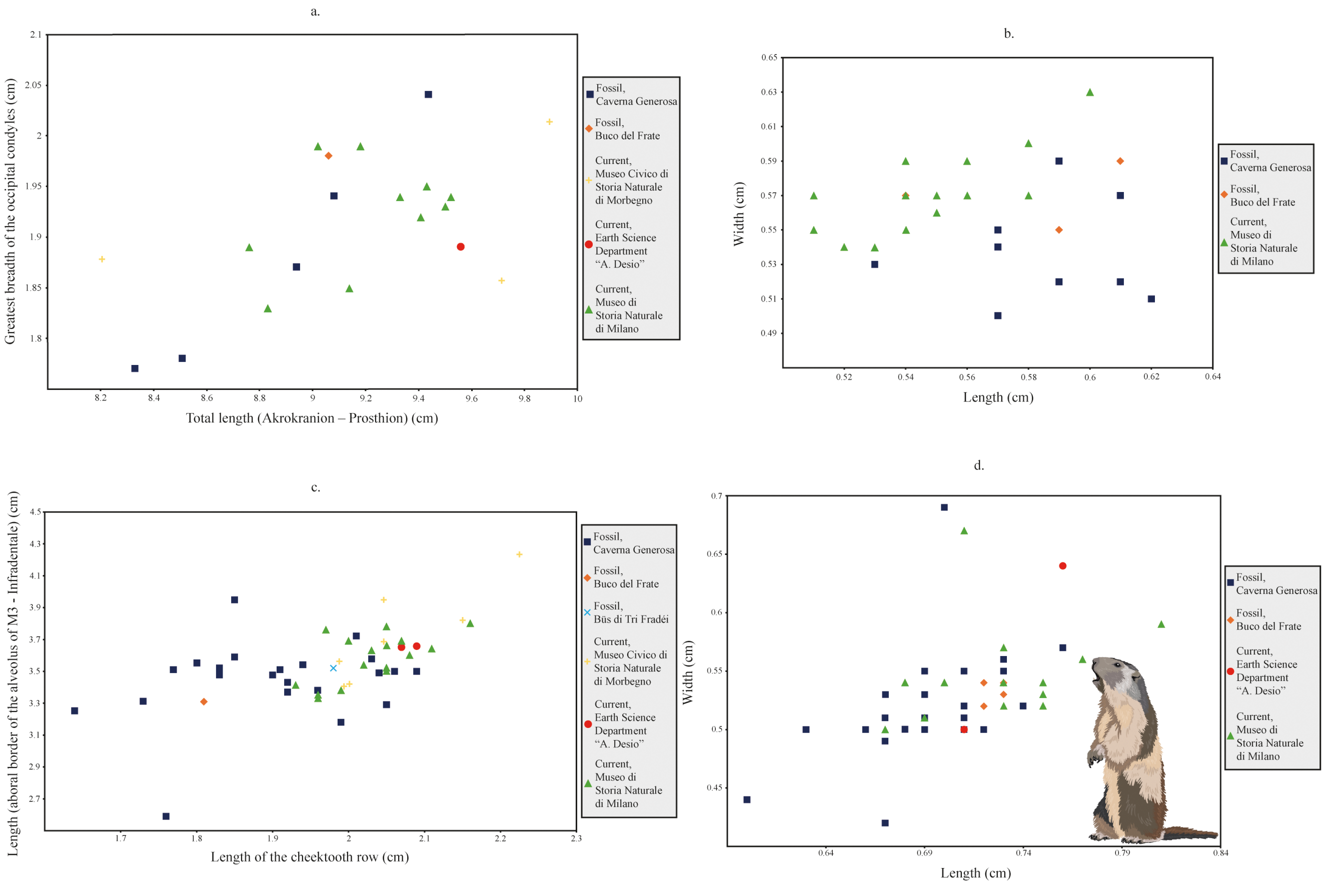

Figure 4 – Graphic dimensional representation of crania (a), upper third molar (b), hemimandible (c), lower third molar (d), artwork by Valeria Carnevali -@natur_val.

Figure 5 – Marmot hemimandibles from the Caverna Generosa mortality class: a. stage 1 (early juvenile), b. stage 2 (juvenile), c. stage 3 (adult), d. stage 4 (senescent).

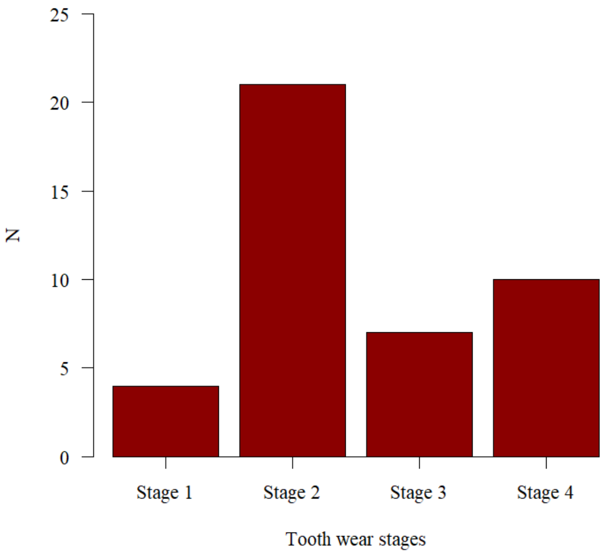

Figure 6 – Mortality stages of the marmots from Caverna Generosa.

Biometric analysis

The measures available on marmot fossils and current bones allowed us to evaluate some hypotheses about their population. First, the scatterplot in (Fig. 4, allowed us to notice the absence of any partition in the data distribution that would suggest some kind of sexual body size dimorphism. The observed situation shows that modern marmots seem to be slightly larger in size than fossil marmots, although the differences observed are almost negligible (Fig. 4). This aspect has been evaluated statistically for the hemimandibles, the M^3 and the M$_3$, because they have a higher amount of data. Defined our hypothesis for the t-test and a threshold of α=0.05, we present below the results. It turned out that in the sample of the length of the cheektooth row (Fig. 3), data aren't normally distributed, as the Shapiro-Wilk test p-value is higher than the threshold (Tab. 5); for the sample of the length (aboral border of the alveolus of M3 - Infradentale) (Fig. 3) data distribution is normal as the p-value is lower than the threshold (Tab. 5); for the length of the diastema (Fig. 3) sample, the p-value is higher than the threshold, so the distribution is normal (Tab. 5). In the case of the M$_3$, the Shapiro-Wilk test shows that the length sample p-value is higher than the threshold

(Tab. 5) so its distribution could be considered normal; at the opposite the width sample p-value is lower than the threshold (Tab. 5) so it doesn't follow the normality assumption. The sample of the M^3 length p-value and the width sample one are higher than the threshold (Tab. 5), so we could state that they have a normal distribution. Then we checked the assumption of homoscedasticity through the Levene test. The outcome for the sample of the cheektooth row length (Fig. 3) is that it doesn't respect the assumption of homoscedasticity between the two groups, as the p-value is lower than the threshold (Tab. 5). Conversely, the p-values returned for the samples of the length measured as the aboral border of the alveolus of M3 - Infradentale and of the length of the diastema (Fig. 3) are higher than the threshold so they respect the above mentioned assumption (Tab. 5). The length and width of both the M_3 and the M^3 samples highlight a p-value that exceeds the threshold, so there are homoscedastic between the two groups (Tab. 5). The length of the cheektooth row (Fig. 3) sample for the modern and fossil groups doesn't respect the t-test assumptions. The result of the nonparametric Wilcox-Mann-Whitney test was a p-value much higher than the threshold (Tab. 5), thus we aren't able to reject the null hypothesis of equality of means between the fossil and modern samples in favour of the alternative hypothesis that the modern samples are larger on average. We used the same statistical test and we got the same result (Tab. 5) as before for the length between the aboral border of the alveolus of M_3 and the Infradentale (Fig. 3). The length of the diastema (Fig. 3) dataset followed the t-test assumptions. The t-test had a p-value higher than the threshold, so we couldn't reject the null hypothesis that the fossil and modern populations have equal means (Tab. 5). The M_3 length sample follows the t-test assumptions, it shows that we couldn't reject the null hypothesis of equal means between the fossil and the current marmots groups (Tab. 5). Instead, the width sample doesn't follow the normality assumption, so the Wilcox-Mann-Whitney test shows that neither in this case we were able to reject the null hypothesis (Tab. 5). The M^3 length and width sample aren't homoscedastic. We have applied the nonparametric Wilcoxon-Mann-Whitney test, whose outcome allowed us to reject the null hypothesis of equal means and in favour of the alternative hypotesis of a higher mean (Tab. 5) of the current group for the length sample for the length sample; while the width sample p-value is higher than the threshold, so we couldn't reject the null hypothesis (Tab. 5).

Age profile

The marmot hemimandibles from the Caverna Generosa have been divided into four classes of dental eruption and wear associated with different phases of the animal's life, following the standard proposed by Tomé (2005) (Fig. 5). We have been able to assess mortality trends studying 42 hemimandibles out of a total sample of 48 (87.5 %). Below we will illustrate the results that we can observe in (Fig. 6. Stage 1, represented by the youngest individuals, includes 4 hemimandibles. Stage 2 includes the juveniles and contains 21 specimens whose teeth have totally emerged and are not especially worn, with erosion noticeable on the second and the third molars. Stage 3, the adult individuals, is represented by 7 specimens showing more widespread wear, the molars revealing the dentin on their surface and a hint of erosion on the fourth premolar. Stage 4 is represented by 10 hemimandibles of senescent individuals showing abrasion and dentin in all the teeth. We observed that the first stage has low mortality while, in contrast, the second stage reveals a peak of mortality. The third and the fourth stages show an intermediate mortality between the first two stages. The senescent stage shows a slightly higher mortality than the third one. To better understand the situation, we have analysed the marmots' causes of death. The alpine marmot osteological elements from the population of the Caverna Generosa reveals the presence of peri-mortem and post-mortem traces originating in biological activities (Tab. 2). We can distinguish between traces of predation, like linear marks or punctures and gnawing resulting from rodent activity (Fig. 7). Punctures were mainly concentrated on the proximal end of the long bones such as the ulnar olecranon and femora and could have resulted in bone breakage (Fig. 7).

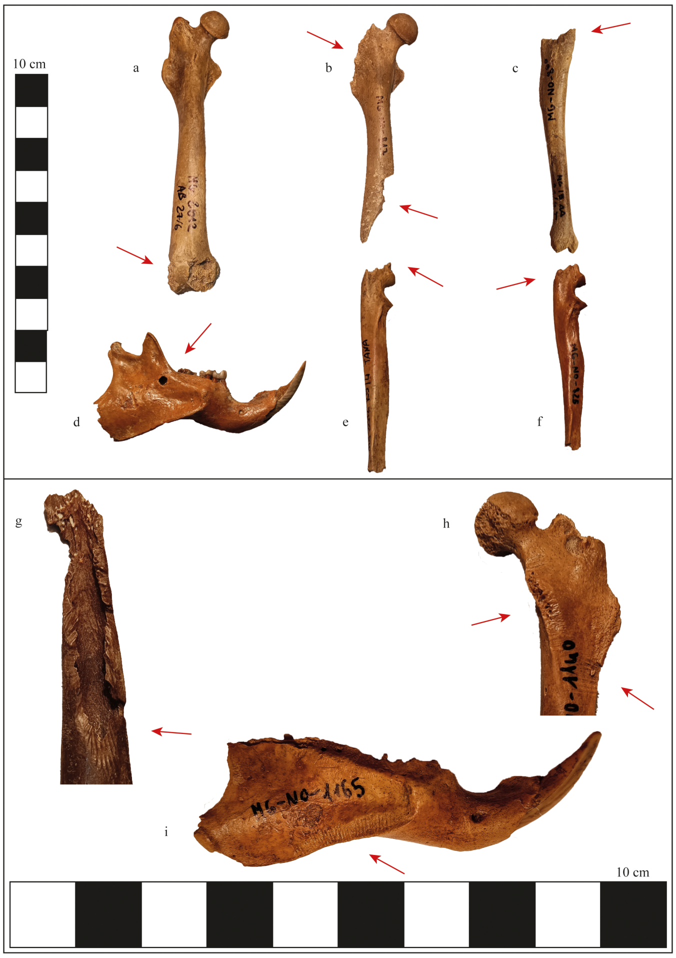

Figure 7 – Location of predation traces. a and b: right femora in frontal view. c: left tibia in medial view. d: right hemimandible in labial view. e and f: left ulnae in medial view. Location of gnawing marks.
g : femur diaphysis. h : femur diaphysis right femur in caudal view. i: right hemimandible in labial view.

Table 5 – Statistical analysis outcomes ($\alpha = 0.05$).

	Tested variable	**Levene test**		**Shapiro-Wilk test**		**T-test for equality of means**			**Wilcox-Mann-Whitney test**	
		F	**P-value**	**W**	**P-value**	**T**	**df**	**P-value**	**W**	**P -value**
Hemimandible	Length of the cheektooth row	6,0131	0,0178	0,9667	0,16				554	1
	Length (aboral border of the alveolus of M3 - Infradentale)	0,0163	0,8991	0,9135	0,0016				449,5	0,9987
	Length of the diastema	0,0184	0,8926	0,9750	0,3899	0,4378	45,576	0,6682		
M_3		0,3624	0,5502	0,9772	0,4825	2,5965	30,395	0,9928		
	Width	0,0348	0,8528	0,8667	0,0001			354,5	0,9872	
M^3	Lenght	0,0093	0,9241	0,9571	0,2971	$-3,6268$	24,958	0,0006		
	Width	1,1875	0,2858	0,9700	0,5805	2,5585	23,31	0,9913		

Discussion

Given the marmot bones dating results we can draw some considerations. The level c of the S sector (Fig. 2) can be correlated with levels 4 and 5 from "Sala Terminale", dated between 44,000 and 43,000 y BC (Tab. 1). So, these were expected to be the date of the right tibia, which location was sector S6 and level c (tana), while the calibrated date (35,645 – 34,371 y BC) is more or less 10,000 years younger than the ones we have foreseen (Tab. 4). Our prediction on the right tibia date, located in sector AA28 and level 7, where a large burrow developed, was approximatively 40,000 and 35,000 y BC (Tab. 1). However, even the calibrated age of this bone (32,540 and 32,032 y BC) is younger than expected (Tab. 4). The dating of the marmot samples agrees with the exploitation of the Caverna Generosa by marmots during the Upper Pleistocene. In fact, rodents, including the marmots, are widely recognized as a component of post-depositional disturbance (Bocek, 1986). Accordingly, we can assert that this marmot population dug its dens into sediments already in place in the cave altering the stratigraphy (Fig. 2). Its frequentation of the Caverna Generosa is more or less contemporary with that of *Ursus spelaeus* and the other Upper Pleistocene (MIS3) species found in this deposit, but the younger dating may suggest that the marmot frequentation of the cave continued a little longer, when the environmental conditions were too extreme for other species.

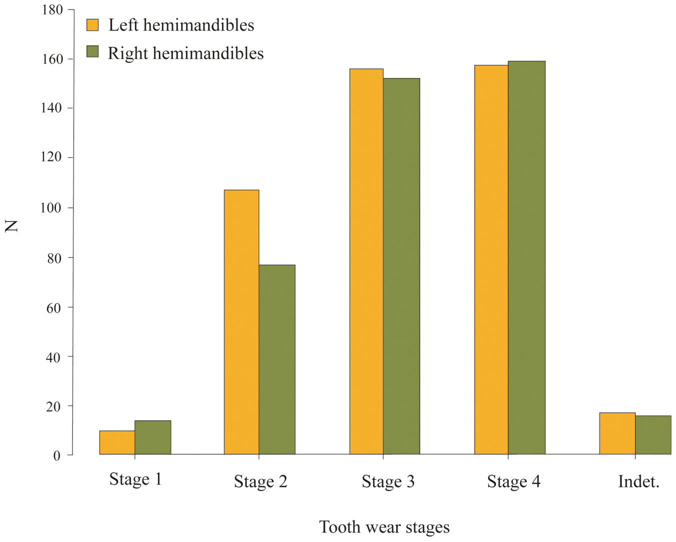

Figure 8 – Mortality stages of the marmots from Grotte Colomb, based on Tomé (2005).

The biometric analysis has showed that sexual body size dimorphism seems to be too negligible to state clearly the sex of the marmots from the Caverna Generosa, as can be observed in (Fig. 4. This result agrees with Matějů and Kratochvíl (2013) and Kryštufek and Vohralík (2013), who state that *Marmota marmota* is the marmot species with the lowest sexual size dimorphism among the Palearctic marmot species on the basis of the condilobasal length and the hind foot length. Alpine marmots have a really low dimorphism in comparison with all the other species of its genus, although the males are still larger than the females Kryštufek and Vohralík (2013). Furthermore, Cardini (2003) shows that the mandible shape shows a modest sexual dimorphism if compared to the interspecific differences. So, we aren't able to identify the sexes in our fossil marmots sample on the bases of biometric measures. Even if it's known that a little sexual size dimorphism does exist in this species, we can state that it can be considered too negligible for the marmots from the Caverna Generosa.

The body size differences between modern and fossil marmots, included in this work, were evaluated by first considering bivariate graphs (Fig. 4). Then, the observed situation was studied from a statistical perspective to seek further support for the conclusions. Among the three hemimandible measures and the four teeth measures that were analysed, only the length of the M_3 width showed significant results (Tab. 5). So, only in this case we can testify differences between fossil and current samples, in according with our hypothesis that the current group seems to be slightly larger than the fossil one. Conversely, the other measures do not give statistically significant results. We have demonstrated in a statistical perspective that, overall, there aren't significant dimensional differences between the current marmots from Lombardy, Piedmont, Valle d'Aosta and France being a bit bigger than the fossil ones from Caverna Generosa, Buco del Frate and Büs di Tri Fradéi. More data on fossil and living marmot bones measures will be needed to further investigate this topic in future studies.

The mortality profile we observed for the Caverna Generosa alpine marmot population shows a peak for the juvenile specimens, a minimum for the very young specimens and an intermediate mortality rate for the adults and the senescent (Fig. 6). As a comparison we can observe a similar situation in the cave bear population from the Caverna Generosa, where the distribution of growth classes shows a peak of mortality for the juvenile individuals, from their birth until an age of 12-16 months (Bona, 2004).

The analysis of the traces (Tab. 2 and Fig. 7) left on the marmot bones has allowed us to confirm the occurrence of predation events. Traces of predation are seen on 3.5 % of the sample. Predation, while important, was not the main cause of death for the marmots. Furthermore, according to the shape and dimensions of the traces on the bones, the predators could have been small carnivores, for example red fox (*Vulpes vulpes*) and Mustelidae (genus *Martes* or *Mustela*). These animals left linear marks on the marmot bones by chewing them, we have also observed punctures produced by canines, molars or premolars (Fig. 7).

We made a comparison between the mortality trend from the Caverna Generosa and that for two other sites where human exploitation is evident: Grotte Colomb (France) (Tomé, 2005) and Grotte di Pradis (Friuli, Italy) (Nannini et al., 2022). The Grotte Colomb mortality profile shows comparable peaks of mortality for the adult and the senescent marmots, while the very young individuals have low mortality, and the juvenile ones have an intermediate mortality (Fig. 8) (Tomé, 2005). A similar situation is seen at Grotte di Pradis (Nannini et al., 2022). Both Grotte Colomb and Grotte di Pradis show evidence of the exploitation of marmots as a source of food and fur by Epigravettian hunter-gatherers. This played a role in producing a mortality trend quite different from that of the Caverna Generosa: hunting activity was mostly focused on adult marmots and only occasionally on juveniles. Hence, the marmot assemblages from Grotte Colomb and Grotte di Pradis present a high percentage of adult remains (Tomé, 2005; Nannini et al., 2022). The death profile of the marmot population from the Caverna Generosa shows the opposite situation. It is important to point out the absence of traces of human activities on the Caverna Generosa marmot bones. We can conclude that the pattern of mortality registered at the Caverna Generosa is not related to human exploitation.

Conclusions

Marmota marmota exploited the Caverna Generosa producing burrow systems inside the cave and bioturbating the stratigraphy towards the end of MIS 3.

The study of the Upper Pleistocene alpine marmot population of the Caverna Generosa allowed us to reach many conclusions: 1- Sexual size dimorphism can be considered negligible as underlined by the biometric analysis above; 2- There aren't statistically significant dimensional differences between the fossil marmots and the modern ones, with the current marmots being slightly bigger than the fossil sample as we hypothesized; 3- Traces of predation on marmot bones are rare with just 3.5 % of the sample exhibiting them. We should note that the largest part of the remains did not come from outside the cave where predators might have dragged them but, rather, were found within the cave. So, the formation of the marmot assemblage is mainly a result of the death of individuals in the burrows and is less influenced by the predation activities of the carnivores that frequented the cave. 4- The comparison between the mortality profiles observed for the marmot population from the Caverna Generosa and those from Grotte Colomb (France) and Grotte di Pradis (Italy), where there is evidence of human exploitation, has allowed us to conclude that the marmots of the Caverna Generosa were exploited by human hunter-gatherers as a source of food and fur.

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Supplemental information

Additional Supplemental Information may be found in the online version of this article:

Table S1 Caverna Generosa.
Table S2 Buco del Frate.
Table S3 Büs di Tri Fradéi.
Table S4 Earth Science Department "A. Desio".
Table S5 Museo Civico di Storia Naturale di Morbegno.
Table S6 Museo Civico di Storia Naturale di Milano.