

Large mammal faunas and ecosystem dynamics during the late Middle to early Late Pleistocene at Grotta Romanelli (southern Italy)

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ABSTRACT

Since the beginning of the XIX century, Grotta Romanelli gained recognition in European stratigraphy as an important site for the Late Pleistocene, due to the attribution of its basal sediments to the Last Interglacial (MIS 5e). Its abundant archaeological and paleontological findings made the cave a key reference point for the study of human evolution and faunal dynamics in the larger Mediterranean area over approximately the last 130,000 years. After a century, a new chronostratigraphic reassessment of Grotta Romanelli revised the timeframe of its lower levels, predating them to the late Middle Pleistocene.

In this study, we re-evaluate selected historical museum collections from the so-called "lower complex" of Grotta Romanelli and examine the new fossils excavated between 2015 and 2022. We identify three main mammal assemblages associated with three different interglacial periods spanning the last 350,000 years. Our findings offer new insights into terrestrial ecosystems in Mediterranean Europe from the late Middle Pleistocene to early Late Pleistocene. Additionally, they provide valuable information to the biochronological framework of the European large mammal faunas.

1. Introduction

The Apulia region, situated in the southern portion of the Italian Peninsula, features numerous archaeological and paleontological sites, making it a key area in Mediterranean Europe for studying the correlation between climatic shifts and the evolution of terrestrial ecosystems over the last 350 ka. Its unique longitudinal layout resembles a peninsula within the peninsula, covering a broad latitudinal range in the Italian context.

Apulia is home to a significant number of Quaternary sites and associated deposits containing mammal remains, often linked to Middle Palaeolithic lithic industries (Mousterian) and Neanderthal fossils. Examples include Fondo Cattie (Corridi, 1989), Grotta delle Tre Porte (Blanc, 1958), Grotta Uluzzo C (Borzatti von Löwenstern, 1964, 1965, 1966; Borzatti von Löwenstern and Magaldi, 1969; Spinapolice et al.,

2022), Grotta Santa Croce (Crezzini et al., 2023), and Grotta del Cavallo (Sarti et al., 1998, 2002; Sarti and Martini, 2020). Over 40 site localities have been documented in this region, several of which were discovered from the late 19th to the early 20th century (e.g., Botti, 1874a,b, 1890; Blanc, 1920). The abundance of sites and the pioneering research conducted here immediately made the region a crucial area for investigating the interplay between mammal fauna evolution and climatic changes during the Middle-Late Pleistocene in the Mediterranean.

Grotta Romanelli stands out as one of the most significant sites in this region for stratigraphic and faunal correlations. Blanc's pioneering works in 1920 and 1928 attributed the marine pebbly basal level of the cave's sedimentary succession to the Last Interglacial (Tyrrhenian or MIS 5e). Subsequently, much of the literature associated the marine deposits at the base of sedimentary successions in several coastal caves with the Last Interglacial, constraining their record to the Late

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Pleistocene. Examples include Grotta del Cavallo (Sarti et al., 1998, 2002; Sarti and Martini, 2020; Zanchetta et al., 2018), Grotta del Sarcofago (Di Stefano et al., 1992), Grotta delle Tre Porte (Cardini, 1958), and Grotta delle Striare (Di Stefano et al., 1992).

Although the vertebrate record from the lowermost levels of Grotta Romanelli has not been extensively studied, the cave's context has been frequently used for paleontological and archaeological correlations, primarily based on the faunal list published by Blanc (1920, 1928). Despite the general lack of detailed taxonomical descriptions, the mammal record of Grotta Romanelli has been widely used as biochronological marker. For instance, the mammals recovered from the cave quickly became a reference for fossils found in reddish sediments in the region, consequently referred to the Late Pleistocene (Mecozzi et al., 2021a and reference therein). After nearly a century, several studies focusing on a limited number of remains recovered at Grotta Romanelli marked the initial step towards a comprehensive revision of the entire fossil record of the cave (see 2.4 section).

In 2015, a new research project concerning Grotta Romanelli was launched, aiming to resume fieldwork activities and conduct a comprehensive review of all historical archaeological and paleontological findings within the cave. One significant outcome of this project is the reassessment of Grotta Romanelli's chronostratigraphic context (Pieruccini et al., 2022) which led to the attribution of the lowermost coarse-grained levels of the succession (ISU1 and ISU2) to the late Middle Pleistocene (MIS 9–7), and the reddish fine-grained sediments (ISU3) to MIS 5. Considering the importance of the site over the years, reevaluating the age of Grotta Romanelli holds profound implications for understanding the evolution of terrestrial ecosystems and human occupation in the Mediterranean.

Throughout the historical excavations at Grotta Romanelli, thousands of recovered mammal remains have been distributed among various museums and institutions (Fig. 1). This study provides an overview and revision of selected historical museum collections from the lower complex of Grotta Romanelli (ISU1, ISU2 and ISU3) alongside newly discovered fossil mammals retrieved during the 2015–2022 excavations. Our results promise to contribute fresh perspectives to the biochronological framework of European large mammal faunas.

2. Grotta Romanelli

Situated within the administrative boundaries of the Castro municipality, the site is a coastal cave located at the southeastern tip of Apulia (Lecce, southern Italy), overlooking the Adriatic Sea (Fig. 1).

2.1. The history of research

Discovered in 1874 by Ulderico Botti, Grotta Romanelli was described as a cave nearly entirely filled by a mostly unconsolidated deposit, that closed almost completely the cavity whose entrance was dammed by cemented breccias where the presence of several vertebrate fossils was reported (Botti, 1874a, Table 1).

In 1900, Paolo Emilio Stasi led the first excavation activity in the cave, collecting thousands of palaeontological and archaeological remains (Stasi and Regàlia, 1904, Table 1).

By 1914, Gian Alberto Blanc coordinated new fieldwork activities, which persisted for more than 40 years, albeit discontinuously (Table 1). Through the application of a multidisciplinary approach and more rigorous methods, Grotta Romanelli became a reference site for the archaeological and paleontological research on European Quaternary (Sardella et al., 2018, 2019 and reference therein). These excavation campaigns led to the initial assessment of the first stratigraphic setting (Blanc, 1920, 1928). In 1940, Luigi Cardini, the assistant of G.A. Blanc, coordinated the fieldwork activities (Table 1) which were interrupted during World War II.

In 1949, Angelo Pasa, a member of the *Museo di Storia Naturale di Verona*, visited the cave during a geological survey and collected several



Fig. 1. Geographical location of the Italian Institutions where archaeological and/or paleontological material from Grotta Romanelli are stored. Abbreviations: MSNV - Natural History Museum of Verona; IGF - Museum of Natural History of the University of Florence, section of Geology and Paleontology; MUCIV - Museum of Civilization; PF - PaleoFactory Laboratory, Department of Earth Sciences, Sapienza University of Rome; IsIPU - Istituto Italiano di Paleontologia Umana; MAN - Museo di Antropologia dell'Università degli Studi di Napoli Federico II; MAC - Museo Archeologico di Castro; ALCA - Museo Civico di Paleontologia e Paleoetnologia Decio de Lorentiis di Maglie; MARTa - Museo Nazionale Archeologico di Taranto. Legend: Blue - fossil collections considered in our work. Orange: collections not included in our work. MAC also indicates the geographical position of Grotta Romanelli. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

vertebrate fossils and lithic tools (Pasa, 1953).

The work of G.A. Blanc was carried on by his son, Alberto Carlo Blanc, who reopened the site in the 1954, and carried out another excavation campaign in 1958 (Table 1). Unfortunately, A.C. Blanc passed away prematurely in 1960.

During the 1960s new fieldwork activities were backed by the *Istituto Italiano di Paleontologia Umana* (IsIPU) and directed by Cardini (Blanc et al., 1962; Cardini, 1963; Cardini and Biddittu, 1967, Table 1). The last excavation campaign occurred in 1970, led by Pier Francesco Cassoli and Marcello Piperno (Table 1). The results of the excavations conducted between the 1950s and 1970s were synthesized in Piperno (1974).

The new project concerning Grotta Romanelli started in 2015, led by Sapienza University of Rome under the auspice of the *Soprintendenza ai Beni Archeologici della Puglia* (now *Soprintendenza Archeologia Belle Arti e Paesaggio di Brindisi e Lecce*).

The results of the multidisciplinary research have been published in numerous papers (Conti et al., 2017; Giustini et al., 2018; Sardella et al., 2018, 2019; Sigari, 2018; Calcagnile et al., 2019; Mecozzi et al., 2021b, 2022; Sigari et al., 2021, 2024; Pieruccini et al., 2022; Russo Ermolli et al., 2022) (Table 1).

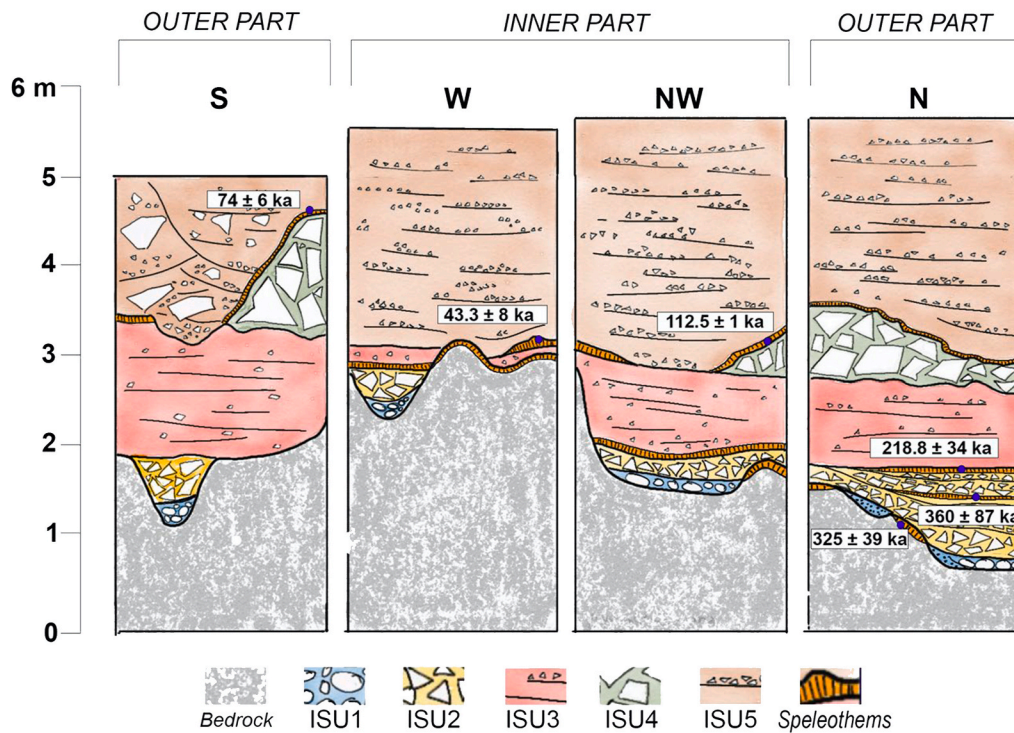
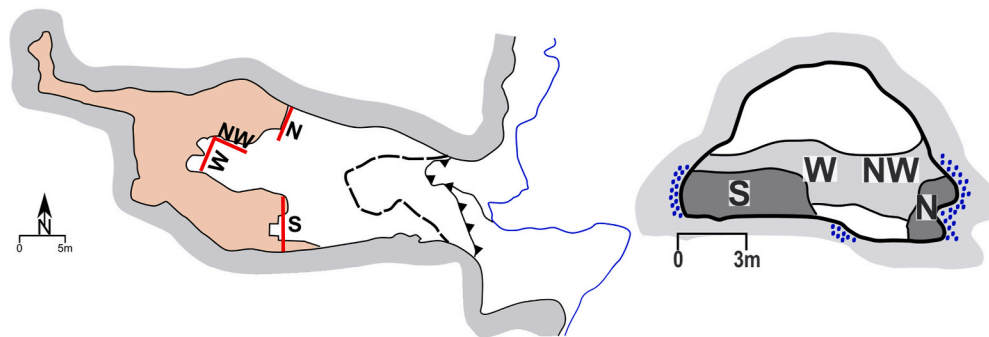


Fig. 2. – The entrance of Grotta Romanelli taken by the sea, its planimetry and stratigraphic succession (modified by Pieruccini et al., 2022). The arrow indicates the entrance of the cave. Abbreviations: ISU - stratigraphic unit recognized inside the cave. Violet point indicate the exact position of the sample dated with U/Th method. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

artifacts are later identified by Piperno, 1974), and burnt and charred vertebrate bones. During the recent fieldwork activities, ISU1 was excavated in both the South and the North sectors, revealing new fossils situated either on top of the pebbles or directly on the bedrock. Therefore, the upper surface of ISU1 hosts the earliest evidence of human frequentation in the cave, corresponding to a sea-level fall prior to the onset of the ISU2 terrestrial sedimentation.

ISU2 consists of a matrix supported, roughly bedded, coarse-grained breccia with a dark brown to yellowish brown sandy-silty matrix. The autochthonous debris of ISU2 derives from the weathering of the limestone hosting the cave, with minimal reworking over very short-distance within the cave boundaries (Pieruccini et al., 2022). Thin flowstones and impregnative carbonate crusts locally cap the lower beds, as well as the uppermost part of this unit (correlated to the level H of Blanc, 1920). According to the recent excavations, paleontological remains within ISU2 are seldom found within the beds, and typically consist of isolated large mammal teeth and fragmentary postcranial vertebrate remains (birds and small-sized mammals). The most substantial accumulation of large mammal bones was discovered over the topmost bed of ISU2 in the North-West sector of the cave. During the 2015–2022 excavations, this area yielded long bones from medium- and large-sized mammals, a fragmented hippopotamus cranium, elephant teeth, and a fallow deer antler.

ISU3 consists of thinly bedded reddish clays and silts, with rare angular to subangular and strongly weathered limestone clasts. ISU3 was not excavated during recent fieldwork, but only investigated through the straightening and cleaning of existing sections in the outer part (South sector) and the inner part (North-West sector) of the cave (Fig. 2). As a result, the majority of ISU3 fossils were unearthed during historical excavations and summarized by Piperno (1974).

2.4. Overview of previous paleontological research

Despite over a century of research, the interpretation of the vertebrate fauna from the lower levels (see section 3) relied solely on the faunal list provided by Blanc (1920, 1928). However, over the past thirty years there has been a revision of selected mammal remains from ISU1, ISU2 and ISU3, as summarized below:

- Hippopotamuses remains from the top of ISU1 and ISU2, stored at the *Istituto Italiano di Paleontologia Umana*, were re-examined by Mazza (1995): the author referred this sample to *Hippopotamus tiberinus* (= *Hippopotamus antiquus*);
- Canid specimens from ISU3, housed in Rome at the *Museo delle Civiltà* (ex. *Museo di Preistoria e Etnografico di Roma "Luigi Pigorini"*), were described for the first time by Sardella et al. (2014) and ascribed to *Canis lupus*;
- A third metacarpal of rhinoceros collected in ISU2 during 1950–1960s excavations and stored at *Museo delle Civiltà*, was identified as *Coelodonta antiquitatis* by Pandolfi and Tagliacozzo (2013);
- Rhinoceros specimens from ISU3, housed in the *Museo delle Civiltà*, were assigned to *Stephanorhinus hemitoechus* by Pandolfi et al. (2017);
- Rhinoceros remains from the top of ISU1 and ISU2, stored at *Museo delle Civiltà*, were attributed to *Stephanorhinus hundsheimensis* by Pandolfi et al. (2018);
- An isolated hemimandible of *Lutra lutra* from ISU3, housed in the *Museo delle Civiltà*, was described for the first time by Mecozzi et al. (2021b).

The record of Grotta Romanelli has stimulated debates concerning taxonomic classifications and the evolutionary trajectories of several taxa during the late Middle to Late Pleistocene in southern Europe.

The specific attribution of the canid sample from ISU3 has been a subject of dispute for decades, resulting in various taxonomical

interpretations (Blanc, 1920, 1928; Masini et al., 1990; Sala et al., 1992). One interpretation suggested the presence of *Canis mosbachensis*, implying either the survival of this species in southern Italy during the Late Pleistocene or an older age for these levels (Masini et al., 1990; Sala et al., 1992). The resolution of this debate came with the first comprehensive description of material by Sardella et al. (2014), definitely attributing the sample to *Canis lupus*.

The record from ISU3, particularly following the publication of pioneering radiometric dating studies in the 1960s (Fornaca-Rinaldi, 1968a, 1968b; Fornaca-Rinaldi and Radmilli, 1968), established the timeframe for the extinction of *Palaeoloxodon antiquus* and *Hippopotamus amphibius* in the Italian Peninsula. This extinction event was generally considered to have occurred during the MIS 4–3 (Minieri et al., 1995; Mecozzi et al., 2021a, 2023a; Martino and Pandolfi, 2022; Martino et al., 2022).

Pandolfi et al. (2018) assigned the rhinoceros remains found in the lower levels of the sequence (top of ISU1 and ISU2) to *Stephanorhinus hundsheimensis*. Considering that this species disappeared from Europe approximately 600 ka ago, the authors referred these levels to early Middle Pleistocene.

Finally, the presence of *Dama dama* documented in the lower levels represents one of the earliest occurrences of modern fallow deer in the Italian Peninsula (Bologna et al., 1994; Di Stefano, 1994).

3. Material & methods

For this study, we conducted osteological analyses on the large mammal fauna found in both historical collections and recent excavations from the top of ISU1 and in ISU2 (referred to late Middle Pleistocene), and in ISU3 (attributed to early Late Pleistocene).

3.1. Historical collections

The historical collections recovered from the lower levels are currently housed at.

- *Museo di Storia Naturale dell'Università di Firenze*, section of Geology and Paleontology (IGF): 146 remains gathered during the initial fieldwork directed by Paolo Emilio Stasi. The vertebrate collection at IGF represents the fossil material studied by Ettore Regàlia, who carried out the first paleontological examination of the Grotta Romanelli material. However, this collection does not include all the materials collected during this early phase of exploration. Thousands of archaeological and paleontological remains from the Stasi collection were bought by the *Università degli Studi di Napoli Federico II* in the early 1900s. These items are not considered in this review.
- *Istituto Italiano di Paleontologia Umana* (IsIPU): 365 remains collected during fieldwork directed by Gian Alberto Blanc, Alberto Carlo Blanc, Luigi Cardini, Pier Francesco Cassoli and Marcello Piperno. Unfortunately, there is a lack of information regarding the specific year of excavation, except for the fossils recovered from the fireplace discovered in ISU2, as noted by Blanc (1920, 1928). These fossil specimens are stored in a box containing 322 vertebrate remains (Table 2).
- *Museo delle Civiltà* (MUCIV): 2907 specimens collected during the excavations directed by Gian Alberto Blanc, Alberto Carlo Blanc, Luigi Cardini, Pier Francesco Cassoli and Marcello Piperno. Some of these specimens are associated with a specific year of excavation: 1954, 1958, 1963, 1964, 1970. Generally, the stratigraphic information is directly recorded on the fossils themselves, and many specimens show abbreviations such as IXi, IXm, and IXs, indicating their position within the lower, middle or upper part of level IX (ISU3). Piperno (1974) formally subdivided ISU3 into three main units (G1 = IXs; G2 = IXm; G3 = IXi) during the 1963 excavation, a subdivision retained in subsequent activities in 1964 and 1970. Consequently, these abbreviations (IXi, IXm, and IXs) are found only

Table 2

– Mammal fossil remains (NISP) from the lower levels of Grotta Romanelli. Abbreviations: IGF – Museo di Storia Naturale dell'Università di Firenze, section of Geology and Paleontology; ISIPU – Istituto Italiano di Paleontologia Umana; MUCIV – Museo delle Civiltà; NHMV – Museo di Storia Naturale di Verona; PF – Laboratorio PaleoFactory, Dipartimento di Scienze della Terra, Sapienza University of Rome.

Excavations	Stasi		Blanc - Cardini				MUCIV			Natural History Museum of Verona		Sapienza University of Rome		
Acronym museum	IGF		ISIPU				MUCIV			NHMV		PF		
Original levels	"breccia"	"terre rosse"	K (=XII)	I (=XI) - hearts	I (X-XI)	G (IX)	K (=XII)	I (X-XI)	G (IX)	ISU2	ISU3	tISU1	ISU2	ISU3
Levels according to Pieruccini et al. (2022)	ISU2	ISU3	tISU1	ISU2 - hearts	ISU2	ISU3	tISU1	ISU2	ISU3	ISU2	ISU3	tISU1	ISU2	ISU3
Species														
<i>Palaeoloxodon antiquus</i>	8				1		5		6	1	1		3	
<i>Stephanorhinus hemitoechus</i>									19					1
<i>Stephanorhinus hundsheimensis</i>	3												19	
<i>Stephanorhinus</i> sp.									2					
<i>Equus ferus</i>									9					
<i>Sus scrofa</i>		2					34		5			1		
<i>Hippopotamus cf. amphibius</i>		1				1			23					1
<i>Hippopotamus</i> sp.	2		26		3		2	2	89	3	3		4	2
<i>Bos primigenius</i>	2	7			1		17	2	2			10	2	2
<i>Capra ibex</i>							2	3	2				3	
Cervidae					1			4	7				5	
<i>Cervus elaphus</i>		27						1	41	2	4			5
<i>Dama dama</i>		77							2524		9			76
<i>Dama</i> sp.	10			7			35	18				4	39	
<i>Capreolus capreolus</i>		1							4					
<i>Meles meles</i>									3					
<i>Lutra lutra</i>									1					
<i>Canis lupus</i>		3							28			13	4	4
<i>Vulpes vulpes</i>							1	1	6			1	2	4
<i>Crocuta crocuta</i>	3								3				1	
<i>Lynx</i> sp.							1		1					
<i>Felis silvestris</i>									3					
<i>Monachus monachus</i>														1
Total	28	118	26	7	6	1	103	31	2774	6	17	29	83	93

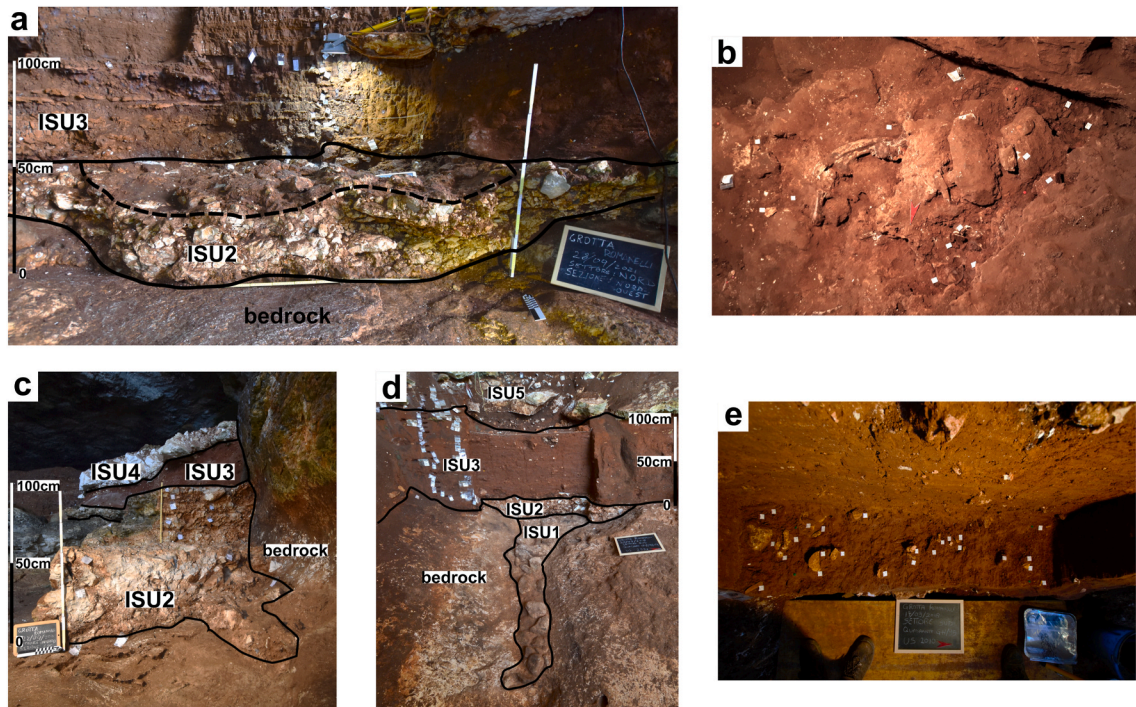


Fig. 3. – The main excavation areas of the lower levels of Grotta Romanelli during the new fieldwork activities coordinated by Sapienza University of Rome. A – North-West sector in the inner part; B – surface of the top of the ISU2 in North-West sector in the inner part; C – North sector in the outer part; D – South sector in the outer part; E – 2010 stratigraphic unit from ISU3 in South sector in the outer part.

on a limited number of remains from ISU3. On the other hand, the presence of fossils lacking any of such direct marks on the bone surface suggests that a portion of the specimens preserved at MUCIV was collected prior to 1954. One such example is the hemimandible of *Lutra lutra*, the only fossil of this species in the MUCIV collection, with its occurrence at Grotta Romanelli reported by Blanc (1920, 1928).

- Museo di Storia Naturale di Verona (NHMV): 23 remains represent a small collection of vertebrate fossils collected by Angelo Pasa in September 1949. This is somewhat unexpected since there are no records about fieldwork activities coordinated by NHMV at Grotta Romanelli. In 1953, Pasa authored a publication focusing on the paleogeographic context of Apulia, a result of his research conducted in the region between the late 1940s and early 1950s. In this work, Pasa acknowledges Mr. Agostino Lazzari and the municipality of Castro for their logistical support, and provides a detailed sketch of the Romanelli bay and the cave infilling deposits (Fig. 8, pag. 200; Pasa, 1953), further evidence of his visit to Grotta Romanelli.

3.2. Materials from new fieldwork

Laboratorio PaleoFactory, Dipartimento di Scienze della Terra, Sapienza University of Rome (PF): 205 specimens recovered during recent fieldwork activities (2015–2022; Fig. 3). This collection includes every paleontological specimen taxonomically identified with a length ≥ 2.5 cm, or smaller if diagnostically significant, found within a reference grid consisting of one-square meter units (1 m \times 1 m).

3.3. Methods

Each specimen from the recent excavations is recorded into a Geographic Information System (GIS) framework, which integrates total station data, digital photogrammetry, and a comprehensive database. Every specimen is assigned a code (indicated by the initials RR followed by a progressive number) and linked to a database containing pertinent information, such as sector, square, stratigraphic unit, discovery date, material, preliminary identification, coordinates (x, y, z), axis direction, tilt, and additional notes. Fossil remains recovered during the washing and picking of the sediments removed from the cave are catalogued using the acronym GR, followed by the excavation year and a progressive number (example: GR2015-1).

Taxonomic and skeletal element identifications conducted in this study rely on the reference collection housed at the PF (Table S1).

Surface analysis of the bones was performed to identify indications such as bite marks, rodent gnaw marks or traces of human butchering and exploitation, thereby yielding preliminary archeozoological insights. The methodology reported by Stiner et al. (1995) was used to assess the degree of combustion.

Age classes were established by assessing the fusion degree of the proximal and distal epiphyses, cranial epiphyses, tooth type (milk or permanent) and their dental wear patterns (Laws, 1953; Ferrara, 1965; Lowe, 1967; Morris, 1972).

The count of the number of individual remains (NISP) followed Grayson (1984), while the estimate of the minimum number of individuals (MNI) was based on Bökönyi (1970).

Measurements of cranial, dental, and postcranial fossils were taken following von den Driesch (1976), with a digital caliper to the nearest 0.1 mm.

We carried out biometric comparisons for a selection of taxa relevant for their biochronological and paleoenvironmental significance: medium-sized deer (*Dama* spp. and *Dama*-like), rhinoceroses and canids. For medium-sized deer, we measured the maximum meso-distal length above the root-crown junction of the lower third molar (M_3L) following von den Driesch (1976). For rhinoceroses, measurements of the III metacarpal and III metatarsal were taken following Lacombat (2005). For canids, we measured the maximum meso-distal length above the

root-crown junction of the lower first molar (M_1L) following von den Driesch (1976).

Comparative dataset considered here are reported in Supplementary Material (Table S2-S4).

4. Taxonomical identifications

The data regarding the number of mammal remains examined in this study and their stratigraphic distribution are presented in Tables 2 and 3 and Fig. 4.

4.1. Elephantidae

Among the megaherbivores, elephants are the least represented group but are found across all levels. The sample includes fragmentary tusks, teeth, and vertebrae. Dental remains exhibit several features typically associated with *Palaeoloxodon antiquus*, including hypsodonty, a high number of laminae, high lamellar frequency, reduced enamel thickness and less developed cementum (Palombo, 1986, 1995; Palombo and Villa, 2003).

4.2. Rhinocerotidae

Rhinoceroses remains are found in all levels, representing one of the most well-represented mammal groups. In addition to the material presented here, Pandolfi et al. (2018) described 45 remains found at the top of ISU1 and seven remains in ISU2 attributed to *Stephanorhinus* sp. and *Stephanorhinus hundsheimensis*. Pandolfi et al. (2017) reported several teeth and postcranial bones of *Stephanorhinus hemitoechus* in ISU3. The recent excavations in ISU2 recovered material mostly consisting of postcranial bones, confirming the presence of *S. hundsheimensis*. Additionally, other fossils from ISU3 housed at MUCIV also suggest the presence of *S. hemitoechus* (Tables 2 and 3). Moreover, Pandolfi and Tagliacozzo (2013) ascribed a fragment of the third metacarpal recovered in ISU2 to *Coelodonta antiquitatis*. We conducted a morphological comparison between this fossil and two third metacarpals of *S. hundsheimensis*: one published by Pandolfi et al. (2018) recovered from the top of ISU1, and another collected during the recent

Table 3

– Minimum number of individuals of mammals (MNI) from the lower levels of Grotta Romanelli.

Species	Levels					
	tISU1		ISU2		ISU3	
	NISP	NMI	NISP	NMI	NISP	NMI
<i>Palaeoloxodon antiquus</i>	5	1	13	2	7	1
<i>Stephanorhinus hemitoechus</i>					20	2
<i>Stephanorhinus hundsheimensis</i>			22	1		
<i>Stephanorhinus</i> sp.	2	1				
<i>Equus ferus</i>					9	1
<i>Sus scrofa</i>	35	2			7	2
<i>Hippopotamus cf. amphibius</i>					25	2
<i>Hippopotamus</i> sp.	28	1	11	2		
<i>Bos primigenius</i>	17	2	10	2	101	3
<i>Capra ibex</i>	12	1	6	1	2	1
<i>Cervus elaphus</i>	2	1	3	1	72	3
<i>Dama dama</i>					2677	50
<i>Dama</i> sp.	46	2	65	5		
<i>Capreolus capreolus</i>					5	1
<i>Meles meles</i>					3	1
<i>Lutra lutra</i>					1	1
<i>Canis lupus</i>	15	1	3	1	35	2
<i>Vulpes vulpes</i>	2	1	3	1	8	1
<i>Crocota crocuta</i>			4	1	3	1
<i>Lynx</i> sp.	1	1			1	1
<i>Felis silvestris</i>					3	1
<i>Monachus monachus</i>			1	1		
Total	165	14	141	19	2954	75

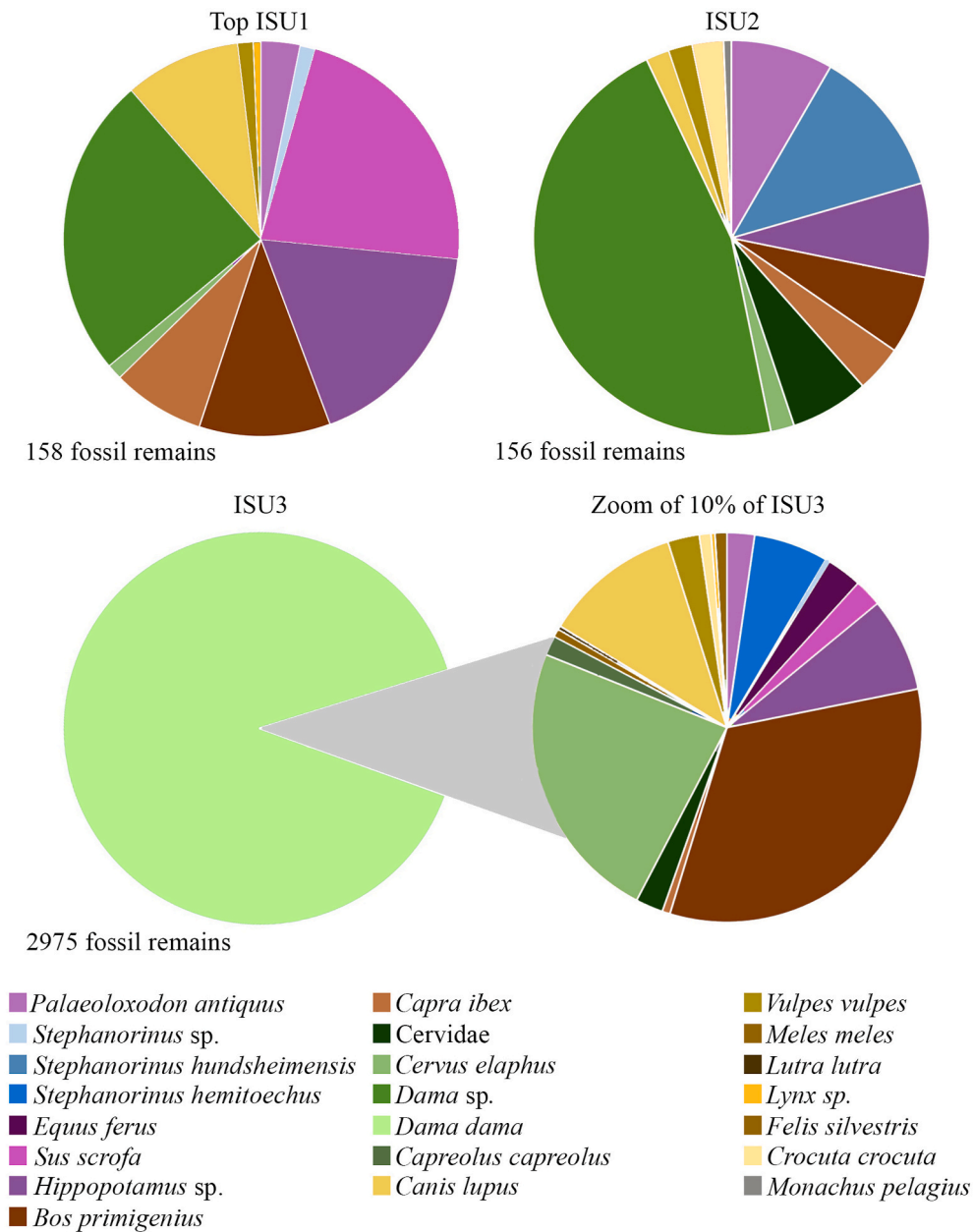


Fig. 4. – Percentage of the number of mammal remains from the lower levels of Grotta Romanelli identified in our work. Both fossils from old and new activities are separated by stratigraphic unit (ISU) following Pieruccini et al. (2022).

activities, recovered from ISU2 (Fig. S1). These fossils exhibit distinct features: a marked salience separates the articular surface for the magnum, trapezoidal in shape, from that of the uncinate in proximal view; in proximal epiphysis, the dorsal border displays a quite straight profile; in lateral view, the two articular surfaces for the MUCIV are in contact or fused, the anterior articular surface is oval in shape, palmar-dorsally elongated, and the posterior articular surface is quite triangular in shape. Postcranial bones of Plio-Pleistocene rhinoceroses possess a wide variability with several polymorphic characters and a strong morphological affinity among taxa (see Stefanelli et al., 2024 for discussion). Therefore, the morphologies of the anterior and posterior articular surfaces for the IV metacarpal of these specimens could be interpreted as intraspecific variability. Attributing the fossil described by Pandolfi and Tagliacozzo (2013) to *S. hundsheimensis* seems the most parsimonious interpretation rather than considering this specimen as the only evidence of *C. antiquitatis* in the Middle Pleistocene of southern Italy.

The ratio between maximum length and minimum transversal

diameter of the diaphysis is plotted for the III metacarpal and the III metatarsal shows that the specimens from Grotta Romanelli occupy the left and lower part of the graphs (Fig. 5). Their dimensions are closer to small fossils of *Stephanorhinus etruscus* and *S. hundsheimensis*.

4.3. Equidae

Only 9 remains documenting large-sized equids have been found in ISU3. Dental remains display the following features: the protocone is elongated and asymmetric, its distal part is more developed, and the parastyle and the mesostyle are grooved and equally developed on the P⁴; the space of postflexid reaches the postflexid, long vestibular groove, and straight labial border of the protoconid on lower premolars. These observed features correspond to those of *Equus ferus* (Boulbes, 2009; van Asperen et al., 2012; Boulbes and Gardeisen, 2018). The morphologies of three fragmentary postcranial bones, two distal portions of tibia and a proximal epiphysis of humerus, are also indicative of *Equus ferus*.

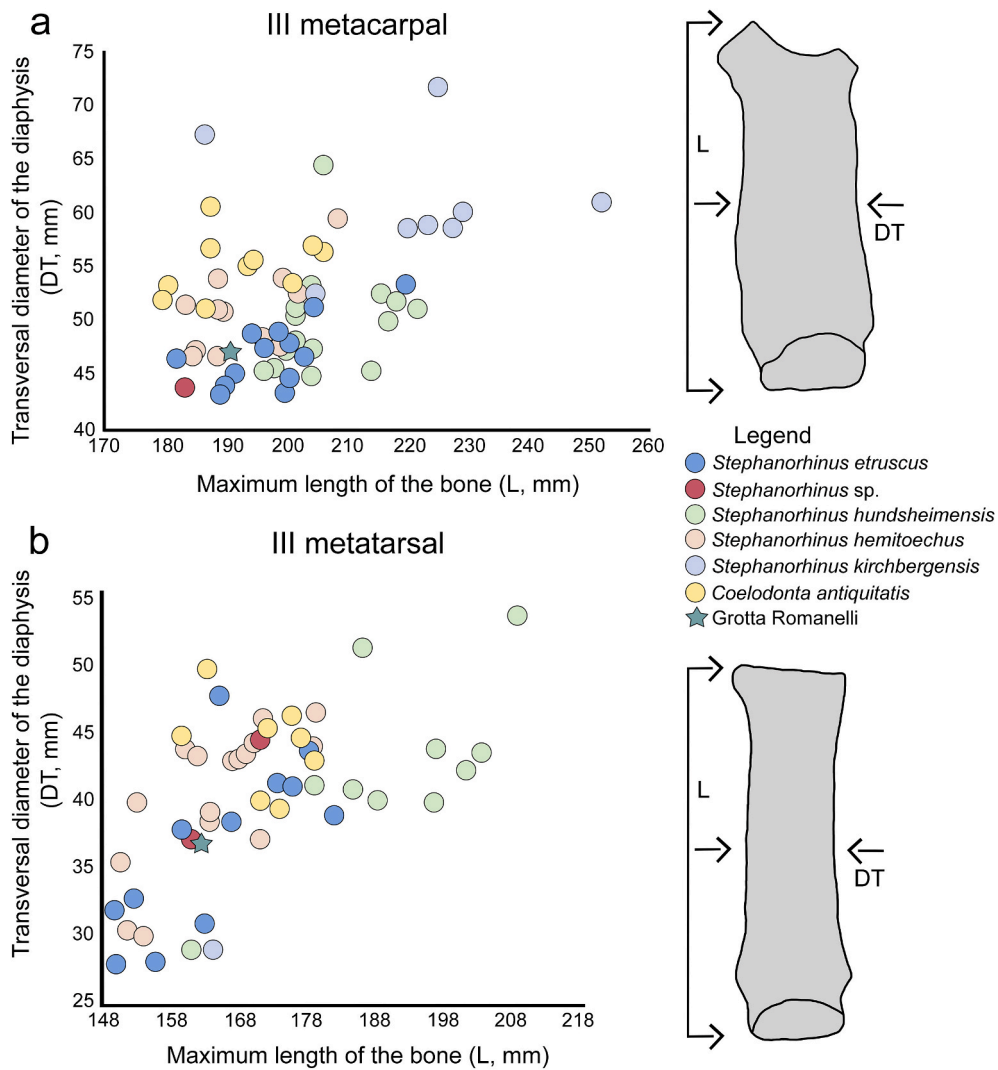


Fig. 5. – Scatter diagram of the maximum length (L) and minimum transverse diameter of the diaphysis (DT) of the third metacarpal (a) and of the third metatarsal (b) of rhinoceros species. All measurements and their relative reference are reported in Supplementary Material (Table S2).

4.4. *Suidae*

The presence of wild boar was limited to the layers at the top of ISU1 and within ISU3 (Tables 2 and 3). With 35 remains, consisting of 5 teeth and 30 postcranial bones, this taxon is one of the most represented

species of the top of ISU1. 7 remains were found in ISU3, including a fragment of maxillary, a lower deciduous tooth, a fragment of lower canine and four postcranial bones. The morphological characteristics of these specimens point to *Sus scrofa* (Iannucci et al., 2020).

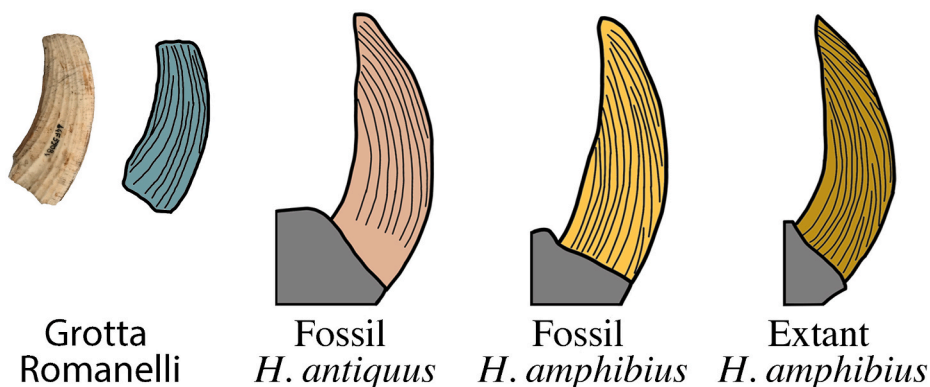


Fig. 6. – Morphology of hippopotamus lower canines. IGF5508V of *Hippopotamus* cf. *amphibius* from ISU3 of Grotta Romanelli (dark green) preserved at the Museo di Storia Naturale dell'Università di Firenze, section of Geology and Paleontology. Fossil *H. antiquus* (light pink), fossil *H. amphibius* (light orange), and extant *H. amphibius* (dark orange) modified (and mirrored) from Mecozzi et al. (2024). Images not in scale. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4.5. Hippopotamidae

During the Quaternary, Europe hosted two hippopotamus species, with their primary distinguishing features found in the cranial features (Caloi et al., 1980; Mecozzi, 2023). Initial efforts to differentiate between these species using postcranial bones were made by Mazza (1995), which were further developed by subsequent studies (e.g., Fidalgo et al., 2023; Mecozzi, 2023), though definitive conclusions have yet to be reached.

Hippopotamus remains were found at the top of ISU1, ISU2 and ISU3. Mazza (1995) re-examined historical specimens housed at ISIPU, attributing those collected at the top of ISU1 and in ISU2 to *Hippopotamus antiquus*. These findings primarily consist of postcranial bones, belonging to juvenile individuals (the sutures of proximal and/or distal epiphyses are not completely fused). Only two teeth, an upper fragmentary molar and a lower premolar can be assigned to adult individuals. Additional remains from ISU2 were identified in the Stasi collection and uncovered during recent activities, although these lack sufficient taxonomical identification.

The fossils recovered from ISU3 are fragmentary postcranial bones and isolated teeth. Among them, the only specimen enabling specific identification is the right lower canine IGF5508V, found during the Stasi excavations and not previously examined by Mazza (1995); its description is provided here for the first time. This fossil exhibits distinct features on its external surface, notably prominent and convergent enamel ridges and grooves, which are characteristic of *H. amphibius* (Fig. 6). In contrast, *H. antiquus* typically displays enamel ridges and grooves with parallel development (Blandamura and Azzaroli, 1977; Caloi et al., 1980; Mecozzi et al., 2023a, 2024).

Given the absence of definitive characteristics for distinguishing hippopotamus skeletons, the specimens recovered from the top of ISU1 and from ISU2 are classified as *Hippopotamus* sp., whereas those from ISU3 are provisionally identified as *Hippopotamus* cf. *amphibius*.

4.6. Bovidae

Bovinae material was collected from all levels. The sample mainly consists of fragmentary postcranial bones and few isolated teeth, alongside an isolated fragmentary horn core from ISU2. The latter, despite its incomplete state, has an oval cross-section in the preserved proximal part, elongated antero-posteriorly (Fig. 7). Though incomplete, its profile extends anteriorly and upwards. Dental remains reveal distinctive features: a well-developed entostyle and a columnar, hypodont appearance (swelling absent) of both upper and lower molars in lingual and labial view; V-shaped enamel around the central cavity of both the upper molars in labial view and lower molars in buccal view; the two main lobes mesiodistally developed in lower molars in occlusal view. Diagnostic characteristics in postcranial bones are relatively fewer; however, several are evident in the studied sample. For instance,



Fig. 7. – ISIPU-GR6, isolated fragmentary horn core of *Bos primigenius* from ISU2 of Grotta Romanelli preserved at the Istituto Italiano di Paleontologia Umana (ISIPU).

the calcaneal articular surface has consistent breadth across its antero-posterior depth in proximal view in the naviculocuboid while the medial and lateral intercondylar crests diverge distally in metapodials. The overall morphology of the Grotta Romanelli sample strongly suggests *Bos primigenius* (Sala, 1986; Balkwill and Cumbaa, 1992).

The presence of *Capra ibex*, though sporadic, is confirmed across all levels. Within the MUCIV collection, this taxon is represented by a few postcranial bones, whereas additional finds from recent excavations include two horn cores, three teeth and eight postcranial remains. The following features can be detected: in the upper molar, the protocone and the hypocone display a triangular shape and the mesial border of the hypocone is strongly oriented posteriorly in occlusal view; in the humerus, the proximal and caudal border of the lateral tuberosity form an acute angle, and the major tubercle is proximally elongated and the depression on the proximal surface of the major tubercle is absent; in the metacarpal, the proximal articular surface is medio-laterally elongated, and the profile of the lateral portion of the anterior border of the proximal articular surface is straight in proximal view. These morphological traits align with those typically observed in *Capra ibex* (Fernandez, 2001; Halstead et al., 2002).

4.7. Cervidae

The cervid sample includes four taxa: *Cervus elaphus*, *Dama dama*, *Dama* sp. and *Capreolus capreolus*.

Red deer specimens primarily consist of fragmentary postcranial bones, and by isolated dental remains found in all levels. Dental features indicative of *Cervus elaphus* include a prominent bifurcate entostyle and a marked buccal cingulum in the upper molars, V-shaped enamel around the central cavity of the upper molars in labial view and the lower molars in buccal view; the metaconid and entoconid form a closed lingual wall (molarization) in P₄ in buccal view; protoconid connects to entoconid in lower molars in occlusal view; the step between the lingual walls of second and third lobes is absent in M₃ in buccal view. These features are commonly observed in *Cervus elaphus* (Di Stefano, 1996; Lister, 1996).

Fallow deer was found across all levels. The material from the top of ISU1 included fragmentary postcranial bones, of poor taxonomic value, and thus, attributed to *Dama* sp.

Dental and postcranial bones, in addition to a juvenile basal part of antler, were collected from ISU2. Dental remains show the following features: in the P₃, the entoconid is weakly angled with the long axis of the tooth in two remains, whereas is perpendicular in one specimen; in the P₄, the molarization is absent (3 specimens), and the anterior hypoconid wing is present and connected to the entoconid (2 specimens), whereas the hypoconid and entoconid are separated in one case; in the lower molars, the ectostylid of the M₁ is generally more developed than M₂ one; in the M₃, the additional stylid between hypoconid and talonid is absent, the ectostylid between 1st and 2nd lobe is present, and the step between the lingual walls of 2nd and 3rd lobes is present in one specimen and absent in the second specimen. These morphologies were observed in both *Dama clactoniana* and *Dama dama* (Lister, 1996; Mecozzi et al., 2023b), hence the classification as *Dama* sp.

ISU3 yielded over 2500 *Dama dama* specimens, making it the most represented species. The sample includes mainly isolated postcranial bones, often complete, vertebrae and rarely cranial and dental remains. This sample offers insights into the variability of *D. dama* dental features. Notable features include the fusion between the anterior hypoconid wing and the entoconid in the P₄ (13 of 20 specimens), the entoconid weakly angled to the long axis of the tooth in the P₄ (16 of 19 specimens), the absence of molarization in the P₄ (12 of 19 specimens), the presence of the step between the lingual walls of 2nd and 3rd lobes in the M₃ (11 of 18 specimens), the presence of the ectostylid between 1st and 2nd lobes in the M₃ (10 of 17 specimens), the absence of the additional stylid between 2nd and 3rd lobes in the M₃ (17 of 17 specimens). More variable are: the morphology of the entoconid in the P₃ (16 weakly

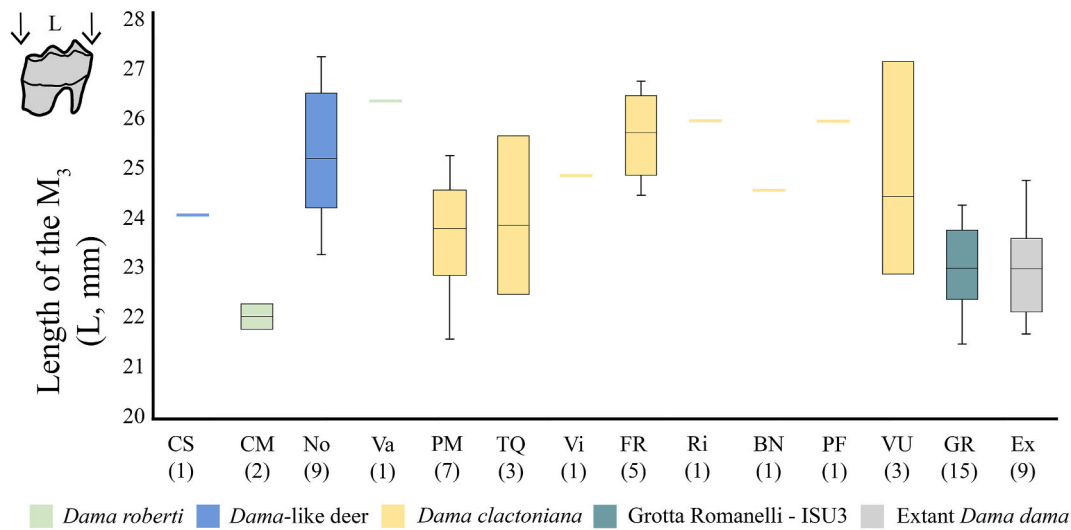


Fig. 8. – Boxplot of the length of the lower third molar (M_3) of *Dama* species of the Italian Peninsula, chronologically arranged from the Middle to Late Pleistocene, compared with extant *Dama dama*. *Dama*-like deer from Cava di Breccia - Casal Selce 2 (CS); Notarchirico (No); *Dama roberti* from Contrada Monticelli (CM), Valdemino (Va); *Dama clactoniana* from Ponte Molle (PM), Tor di Quinto (TQ), Visogliano (Vi), Fontana Ranuccio (FR), Riano (Ri), Batteria Nomentana (BN), Prati Fiscali (PF), Vitinia – upper level (VU); *Dama dama* from ISU3 of Grotta Romanelli (GR); extant *Dama dama* (Ex). The number of specimens are reported in brackets. All measurements and their relative reference are reported in [Supplementary Material \(S2\)](#).

angled, 10 perpendicular to the long axis of the tooth), the development of the ectostylids in the lower molars (absent in 1 specimen, less developed in 26 specimens, developed in 18 specimens, and well developed in 6 specimens), and the development of the mesial cingulum of the lower molars (absent in 1 specimen, less developed in 17 specimens, developed in 25 specimens, and well developed in 3 specimens). While some features overlap with *Dama clactoniana* (Mecozzi et al., 2023b), they are generally indicative of *Dama dama* (Lister, 1996).

The biometric analysis on M_3L revealed that the teeth of Grotta Romanelli are quite similar to the extant sample of *Dama dama*, being

among the smallest specimens of Quaternary Italian *Dama* (Fig. 8).

Small cervids are documented by 5 specimens from ISU3, including a lower first molar, a distal fragment of humerus, a distal fragment of tibia, and two carpals. Their size and morphologies are indistinguishable from the extant specimens of *Capreolus capreolus*.

4.8. Mustelidae

The European badger is represented by an upper fourth premolar, a second phalange and a lumbar vertebra found in ISU3 (Tables 2 and 3).

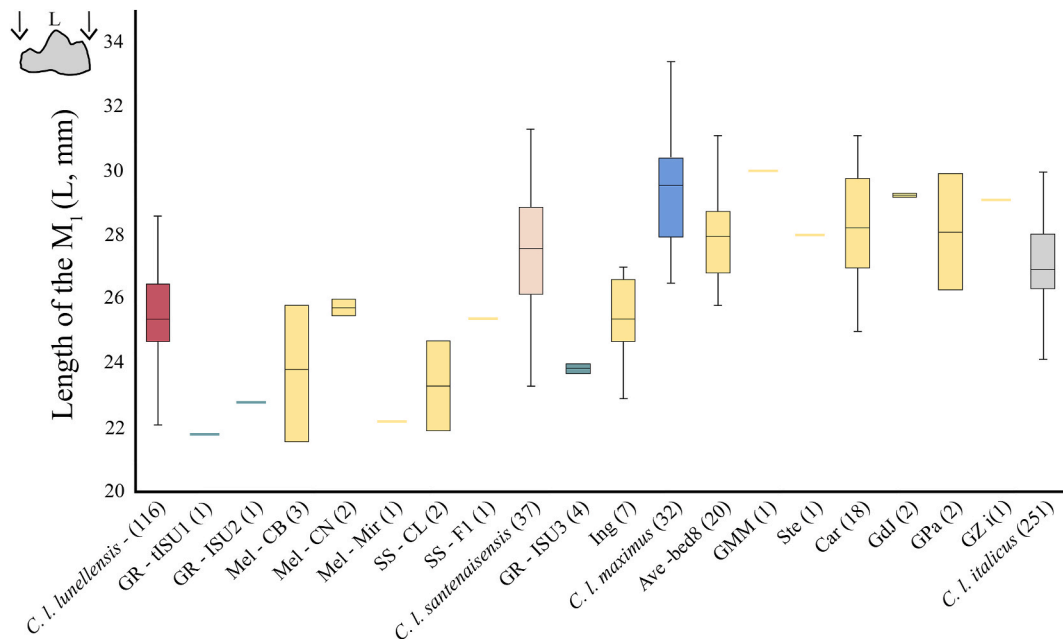


Fig. 9. – Boxplot of the length of the lower third molar (M_1) of Middle and Late Pleistocene grey wolves and extant *Canis lupus italicus*. *Canis lupus lunellensis* (*C. l. lunellensis*), Grotta Romanelli – top of ISU1 (GR-aISU1); Grotta Romanelli ISU2 (GR-ISU2), Melpignano – Cava Bianco (Mel-CB), Melpignano – Cava Nuzzo (Mel-CN), Melpignano – Mirigliano Collection (Mel-Mir), San Sidero – Cava L (SS-CL), San Sidero – Fissure 1 (SS-F1), *Canis lupus santenaisensis* (*C. l. santenaisensis*), Grotta Romanelli – ISU3 (GR-ISU3), Ingarano (Ing), *Canis lupus maximus* (*C. l. maximus*), Avetrana – bed8 (Ave-bed8), Grotta della Masseria del Monte (GMM), Sternatia (Ste), Cardamone (Car), Grotta della Jena (GdJ), Grotta Paglicci (GPa), Grotta Zinzulusa (GZi), extant *Canis lupus italicus* (*C. l. italicus*). The number of specimens are reported in brackets. All measurements and their relative reference are reported in [Supplementary Material \(S3\)](#).

The morphologies of these specimens distinctly indicate *Meles meles* (Mecozzi et al., 2019; Mecozzi, 2021).

Additionally, ISU3 yielded a complete hemimandible of the European otter, originally excavated by Blanc (Blanc, 1920, 1928). Recent reassessment by Mecozzi et al. (2021b), confirmed its classification as *Lutra lutra*.

4.9. Canidae

Wolf remains are distributed across all lower levels (Tables 2 and 3).

Historical material from the top of ISU1 is scarce and lacks taxonomic significance, while no fossils were referred to ISU2. Recent excavations recovered two hemimandibles from the top of ISU1 and in ISU2. The following features can be observed in the M_1 : the paraconid is large and its mesial margin is inclined distally, the protoconid is high and stout, the metaconid is reduced and closely attached to the lingual side of the protoconid, and the hypoconid is the largest cups of the talonid. These features are typically found in *Canis lupus* (e.g., Sardella et al., 2014; Mecozzi and Bartolini Lucenti, 2018). Apart from the specimens listed in Table 2, an additional 25 specimens recovered from ISU3, including a complete cranium, housed at the MUCIV have been assigned to *Canis lupus* by Sardella et al. (2014). Further remains recovered in ISU3 during both previous and recent activities exhibit morphologies consistent with *Canis lupus*.

Biometric comparison of the lower first molar (M_1L) shows that the specimens from Grotta Romanelli (top of ISU1, ISU2 and ISU3) are of small size, similar to earliest forms of the wolf lineage (*Canis lupus lunellensis sensu* Brugal and Boudadi-Maligne, 2011, Fig. 9).

The red fox is poorly documented in the levels under consideration. The upper teeth display these features: the protocone is near the paracone in the P^4 , the protocone is well developed, and the metaconule is few marked in the M^1 . These morphologies fall in the variability of *Vulpes vulpes* (Madurell-Malapeira et al., 2021).

4.10. Felidae

The lynx sample includes two fragments of postcranial bones recovered from the top of ISU1 (a fragmentary II metatarsal) and in ISU3 (a distal fragment of humerus). Recent revisions in the evolutionary history of European fossil lynxes have identified *Lynx pardinus* (= *Lynx spelaeus/Lynx pardinus spelaeus*) as the only lynx species recognized during the Middle Pleistocene (Boscaini et al., 2015, 2016; Mecozzi et al., 2021c). Consequently, the remains of Grotta Romanelli, hold limited taxonomic value. Thus, these specimens are classified as *Lynx* sp., avoiding taxonomical attribution based on chronological considerations.

The second felid species identified is *Felis silvestris*, documented by only three remains found during historical excavations in ISU3, a lower canine, a distal fragment of humerus and a distal fragment of metapodial. Morphologically, they cannot be distinguished by the extant wildcat specimens.

4.11. Hyaenidae

This group is represented by fossils, and coprolites found in ISU2 and ISU3. Coprolites are of extreme importance in the reconstruction of the cave frequentation during the late Middle and early Late Pleistocene. These findings indicate that, although transiently, the cave was frequented by hyaenas, and therefore not stably occupied by humans.

The evolutionary lineage of *Crocota* during Middle-Late Pleistocene has been subject of debate, particularly regarding the validity of the cave hyaena *Crocota spelaea* (as a species or subspecies), which possess differences in limb proportions compared to extant spotted hyaenas (Kurtén, 1956). Consequently, the Middle and Late Pleistocene records were referred to *Crocota spelaea* (e.g., Baryshnikov, 1999; Bocherens et al., 2011), *Crocota crocota spelaea* (e.g., Kurtén, 1956; 1968; Turner,

1984; Diedrich and Zak, 2006; Diedrich, 2008) and *Crocota crocota* (Werdelin and Solounias, 1991; Sardella and Petrucci, 2012; Iannucci et al., 2021a and reference therein). However, genetic investigations have indicated no clear separation between cave hyaena and extant spotted hyaena (Rohland et al., 2005). Dental remains display the labial margin quite straight and the distal accessory cusp connected to the paracone with a weak crest in the P^3 , the anterior face of protocone approximately at the level of the anterior face of parastyle in the P^4 , the talonid extremely reduced with two cusps in the M_1 . These features are characteristic of *Crocota crocota* (Werdelin and Solounias, 1991).

4.12. Phocidae

The seal is represented by a single specimen, discovered during the recent excavations in ISU2. RR350 is a proximal phalanx of the hind limb characterized by a long, slender diaphysis and a wider proximal epiphysis. Its proximal surface is oval in shape in proximal view. The distal epiphysis, on the other hand, is narrow medio-laterally and flattened antero-posteriorly. The proximal epiphysis is unfused, while the distal one is fused. This indicates that the specimen falls within age group 3 (young adult; Storå, 2000). Its morphological features and dimensions are indicative of the Mediterranean monk seal *Monachus monachus*.

5. Discussion

The results are here analysed within the chronostratigraphic context of Grotta Romanelli. The information available in the existing literature will be supplemented by fieldwork observations gathered during the 2015–2022 excavations (Fig. 4; Tables 2 and 3).

5.1. Fossil from the top of the ISU1

The earliest presence of lithic tools and terrestrial mammals was traditionally attributed to ISU1, interpreted by Blanc as a fossil beach. However, recent excavations have confirmed their presence both at the

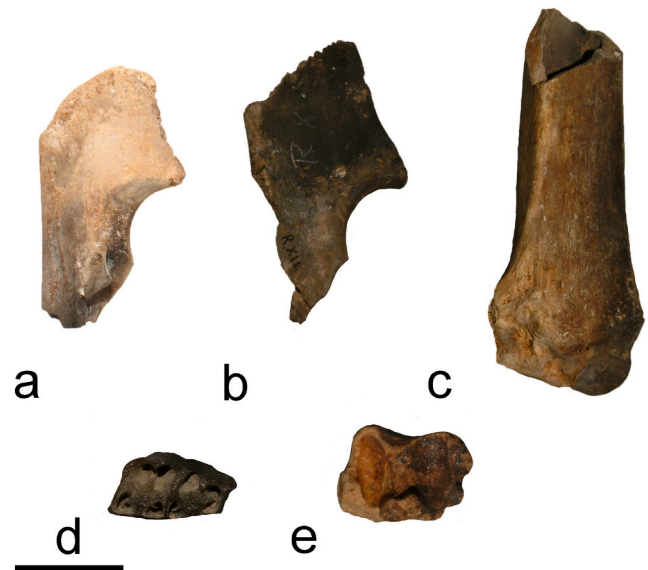


Fig. 10. – Charred bones from the lower levels (top of ISU1 and ISU2) of Grotta Romanelli preserved at the Museo delle Civiltà. Top of ISU1: MUCIV-GR2, right proximal epiphysis of ulna of *Dama* sp. in lateral view (a); MUCIV-GR37, right proximal epiphysis of ulna of *Dama* sp. in medial view (b); MUCIV-GR107, fragment of left diaphysis and distal epiphysis of radius of *Sus scrofa* in posterior view (c). ISU2: MUCIV-GR216, fragment of left maxillary of *Dama* sp. in occlusal view (d); left distal epiphysis of tibia of *Capra ibex* in distal view (e). Scale bar 3 cm.

top of the marine pebbles and buried beneath the ISU2 breccias, as already noted by Blanc (1920, 1928). Additionally, Blanc described the discovery of a fireplace resting over the marine pebbles of ISU1, containing charcoals, flint tools, burnt and charred bones and blackened pebbles, suggesting minimal reworking of the fire-related materials. The fireplace yielded bones from *Rhinoceros merckii*, *Hippopotamus amphibius*, *Dama dama* and *Oryctolagus cuniculus*. Rhinoceros remains from Blanc' excavation, housed at MUCIV, were revised by Pandolfi et al. (2018) and identified as *S. hundsheimensis*. Taphonomic analyses performed by the Authors revealed evidence of combustion on six bones, although no evidence of human exploitation was detected. Additional charred bones belonging to *Dama* sp., *Sus scrofa* and other indetermined mammals were identified in the MUCIV collection (Fig. 10). Given the limited information available from the previous descriptions, it is possible that some or all of the specimens described by Pandolfi et al. (2018) and analysed here, were recovered from the fireplace. Nonetheless, the fireplace resting on the top of ISU1 represents the earliest known record from the Italian Peninsula, and one of the oldest in the European context (Pieruccini et al., 2022).

Through a comprehensive analysis and reinterpretation of the stratigraphic position of the archaeological and paleontological samples, it is evident that the material historically attributed to ISU1 (or level K) cannot be contemporaneous with the subaqueous deposition of pebbles, which occurred during a full marine highstand (MIS 9). Instead, these materials might be associated to the earliest human occupation of Grotta Romanelli.

Paleontological analyses indicated that fossils from the top of ISU1 belong to *Palaeoloxodon antiquus*, *Stephanorhinus* sp., *Sus scrofa*, *Hippopotamus* sp., *Bos primigenius*, *Capra ibex*, *Cervus elaphus*, *Dama* sp., *Canis lupus*, *Vulpes vulpes* and *Lynx* sp., in addition to *Stephanorhinus hundsheimensis* as described by Pandolfi et al. (2018).

Palaeoloxodon antiquus exhibited mixed feeding dietary traits and occupied different habitats, with a preference for forested areas where it consumed leaves, branches and soft grass (Palombo et al., 2005; Pushkina, 2007; Rivals et al., 2012). Representatives of the fallow deer (genus *Dama*) were considered browsers, typically inhabiting forested landscapes (Rivals et al., 2008; Saarinen et al., 2016; Rivals and Ziegler, 2018; Strani et al., 2022). *Cervus elaphus* can thrive in various habitats, but it is commonly found in deciduous, mixed, and coniferous woodlands, and Mediterranean maquis scrub (Koubek and Zima, 1999; Gebert and Verheyden-Tixier, 2001; Benvenuti et al., 2017). *Bos primigenius* also displayed stable mixed feeding dietary preferences, but was frequently found in open environments (Saarinen et al., 2016; Rivals and Ziegler, 2018; Pushkina et al., 2020). The presence of *Capra ibex* is strongly linked to rocky landscapes, favouring open rocky habitats or open and sunny woodlands interspersed with rocky surfaces (Villaret et al., 1997; Grignolio et al., 2003). *Stephanorhinus hundsheimensis* had a generalist feeding behavior, adaptable to both browse- and graze-dominated diets (Kahlke and Kaiser, 2011). Modern *Sus scrofa* populations in Europe generally inhabit forests, especially evergreen oak forests, but can also be found in more open habitats such as steppe and Mediterranean shrubland, with a highly plastic diet (Spitz, 1986, 1999). Hippopotamus fossils serve as good paleoenvironmental indicators, suggesting humid conditions, mild winters, and the presence of water bodies as lakes, ponds, or rivers during the Quaternary (Mecozzi et al., 2023a). The mammal assemblage suggests the presence of wooded environments, with sparse steppe, and the existence of lakes or ponds, indicating a deterioration of the fully interglacial conditions marked by the marine highstand (MIS 9) after the onset of marine regression, or the initial stadial stages of the subsequent glacial period.

5.2. ISU2

ISU2 stands out as the least rich in fossil remains within Grotta Romanelli. The ISIPU collection houses 13 remains identified at taxonomical level, 31 in the MUCIV collection and 6 in the NHMV



Fig. 11. – Fossil remains collected from ISU2 during the excavations coordinated by Paolo Emilio Stasi with their original label. Material preserved at the Museo di Storia Naturale dell'Università di Firenze, section of Geology and Paleontology.

collection. Although the first excavations reported only two levels (Stasi and Regalia, 1904) without mentioning coarse-grained deposits, the revision of the IGF collection revealed that several fossils' original labels indicated material recovered from breccia, thereby confirming their association with ISU2 (Fig. 11). Consequently, 28 remains of the Stasi's collection can be referred to ISU2.

The limited abundance of fossils from ISU2 (78 remains) could be attributed to the challenges posed by the strongly cemented breccia and the poor preservation conditions of the remains. It is plausible that the excavation methods used in previous activities were not optimal for recovering all the paleontological remains. This hypothesis is supported



Fig. 12. – Part of the fossil remains collected in the a fireplace found in ISU2 and described by Blanc (1920) with the original labels. Material stored at the Istituto Italiano di Paleontologia Umana.

by the fact that ISU2 yielded a rich and significant mammal sample during the 2015–2022 excavation activities (Table 2).

ISU2 was excavated in the North and South sectors (outer part) and North-West sector (inner part) (Fig. 2). Fossils in ISU2 are sporadically found within beds and generally consist of isolated teeth of mammals and fragmentary postcranial remains of vertebrate, including birds and small-sized mammals. However, towards the top of ISU2 in the North-West sector, long bones of medium- and large-sized mammals, a fragmentary hippopotamus cranium, elephant teeth, and a fallow deer antler were collected during the 2015–2022 excavations.

Blanc (1928) documented the discovery of several fireplaces within the various layers of ISU2, providing evidence of human frequentation of the cave during that period. However, detailed descriptions of associated lithic tools or vertebrate remains were not provided, hindering their revision. One of these fireplaces was remarkably preserved intact and stored in a single box at ISIPU, including 322 vertebrate remains (Table 2; Fig. 6). Nevertheless, most of these remains consists of small bone fragments measuring between 1 and 3 cm in size (Fig. 12). Among these materials, only the presence of *Dama* sp. and lagomorphs can be confidently identified. Similarly to the discussion regarding the top of ISU1, additional charred bones of *Dama* sp. and *Capra ibex*, along with other unidentified mammals were recovered from ISU2 in the sample housed at MUCIV (Fig. 10).

ISU2 is an autochthonous deposit formed from limestone weathering material reworked within the cave over short distances. Due to the irregular topography of the cave floor, this unit thickens notably in the North sector of the outer part, where the floor is at its lowest elevation. Its chronology spans between ca 300 ka and ca. 220 ka, a period during which the cave was almost empty with only a few allochthonous sediments reaching its interior (Pieruccini et al., 2022). Apart from fossils found near the top of ISU2 in the North sector, the vertebrate remains collected during the recent excavations do not provide clear indications of specific paleoenvironmental or biochronological contexts. This is partly due to the isolated nature of these finds.

Moving back to the fossils found near the uppermost layers of ISU2 in the North sector (Fig. 13), these specimens were collected from a distinct paleosurface, characterized by a concentrated accumulation of remains. In this limited area, articulated postcranial bones of mammals are occasionally found. The mammal remains are referred to *Palaeoloxodon*

antiquus, *Stephanorhinus hundsheimensis*, *Hippopotamus* sp., *Bos primigenius*, *Cervus elaphus*, *Dama* sp., *Canis lupus*, *Vulpes vulpes* and *Crocota crocuta*. The presence of *P. antiquus*, *C. elaphus* and *Dama* sp. suggests wooded environments, *B. primigenius* indicates relatively open spaces, and *Hippopotamus* sp. hints at the presence of water bodies. This faunal assemblage also implies warm and humid climatic conditions, indicative of an interglacial environment. Situated near at the top of this unit, this paleosurface can be considered as the last paleontological evidence of ISU2. Examining the chronostratigraphic framework proposed by Pieruccini et al. (2022), the paleosurface found near the top of ISU2 could be referred MIS 7 (late Middle Pleistocene).

5.3. ISU3

ISU3 has gained considerable attention in literature due to its rich paleontological and archeological record described by several authors over the decades (e.g., Blanc, 1920, 1928; Piperno, 1974; Sardella et al., 2014; Spinapolice, 2018). This unit is particularly renowned as the richest in mammal fossils in its lower part, with a total of 3002 taxonomically identified mammal remains, and 1131 lithic tools (as reported in Piperno, 1974).

During the recent excavations, since this unit was only subject to minimal cleaning of existing sections, the collection of fossils and artifacts is limited in number, predominantly from the lowermost layers. This is consistent with the observations made by Piperno (1974), who noted that the bulk of the sample was collected from the lower part of ISU3.

The data collected during the recent excavations, albeit limited, appear to confirm this distribution pattern. As illustrated in Fig. 14, 81 out of 125 remains from the new excavations were found in SU 1019 in the North-West sector, while 66 out of 123 were collected from SU 2010 in the South sector (the number of remains here reported include taxonomically identified mammals, indeterminate remains and bird).

The ISU3 mammal record has been regarded as indicative of human hunting activity. Blanc (1920, 1928) documented evidence of bone exploitation, and the concurrent presence of lithic tools attributed to the Middle Paleolithic appeared to support his hypothesis.

Another plausible explanation for the presence of vertebrate fossils in a cave is carnivoran hunting activity. It is reasonable to assume that

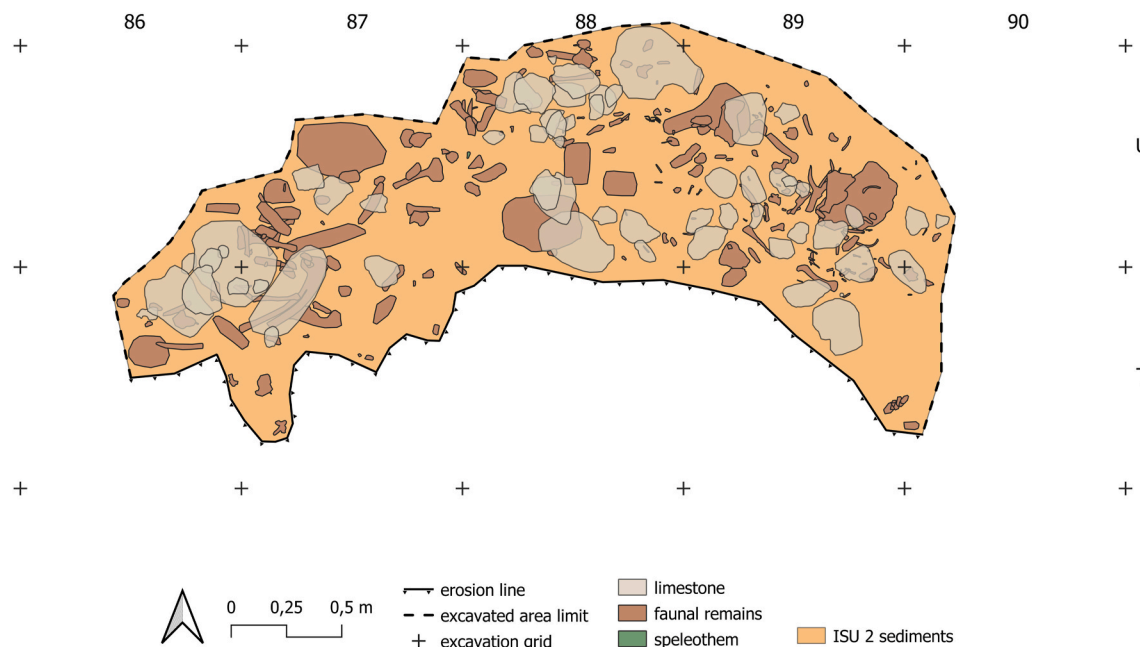


Fig. 13. – Reconstruction of the spatial distribution of faunal remains and lithic artifacts collected in stratigraphic unit (SU) 1023, exposed almost at the top of ISU2 in the North sector during the 2015–2022 excavations coordinated by Sapienza University of Rome.

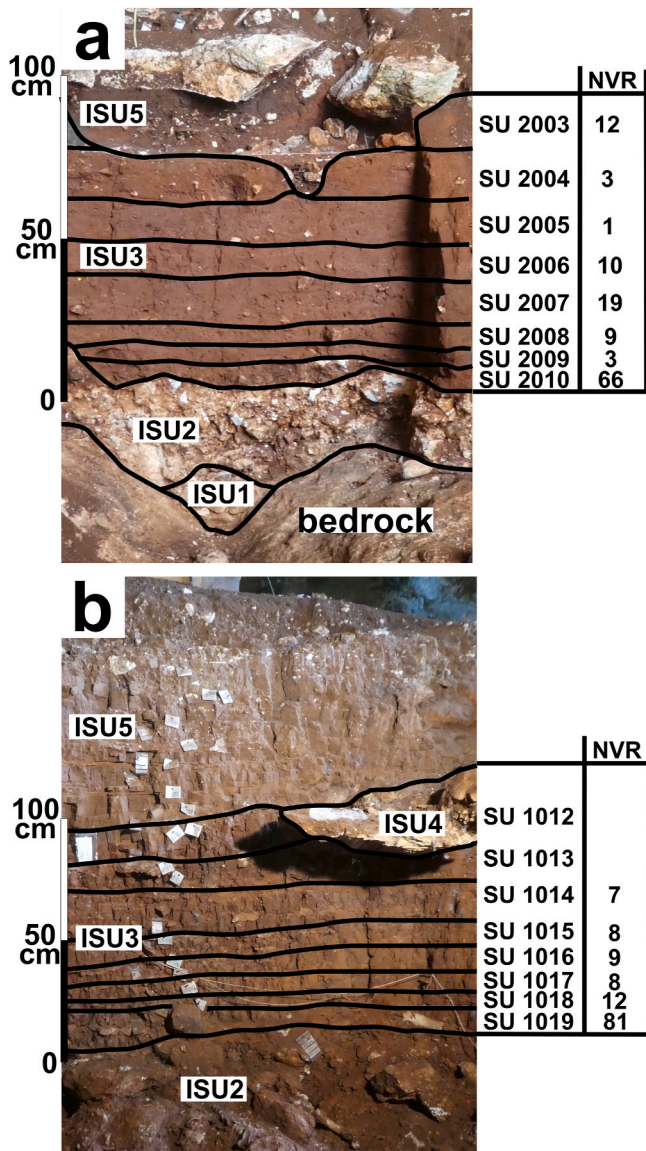


Fig. 14. – ISU3 deposits investigated at Grotta Romanelli with their stratigraphic logs. In the right columns are reported the stratigraphic unit (SU) and the number of vertebrate remains (NVR) identified during fieldwork activities. A – South sector in outer part; B – North-West sector in the inner part.

carnivorans might have utilized the cave as a shelter or den (similar to hyaenas). Blanc (1928) also documented the sporadic presence of coprolites attributed to hyenas in ISU3, indicating that this species occasionally frequented the site. During straightening and cleaning operations on the section in the South sector (outer part), an interesting paleosurface was uncovered (SU, 2010) at the base of the unit. Although limited in size (1,50 m x 0,50 m), SU 2010 yielded 63 vertebrate remains, 24 Middle Paleolithic calcareous tools and 3 hyena coprolites (Fig. 15). This complicates the situation, emphasizing that only an archeozoological study could clarify the methods and timing of human exploitation of carcasses, as well as the role of carnivorans in cave frequentation, whether occasional or not. If the cave was indeed used as a den by carnivorans during the deposition of ISU3, one would expect to find cubs, which often perish inside the cave due to various factors such as stillbirths, abandonment, disease, hunger, accidents, infanticide and siblicide (Jimenez et al., 2022 and reference therein). Other carnivorans may also perish inside the den during nighttime rest or hibernation (e.g., Germonpré and Sablin, 2001; Grandal-d’Anglade and Mosquera, 2008). However, carnivoran fossils are quite rare in ISU3, consisting mainly of

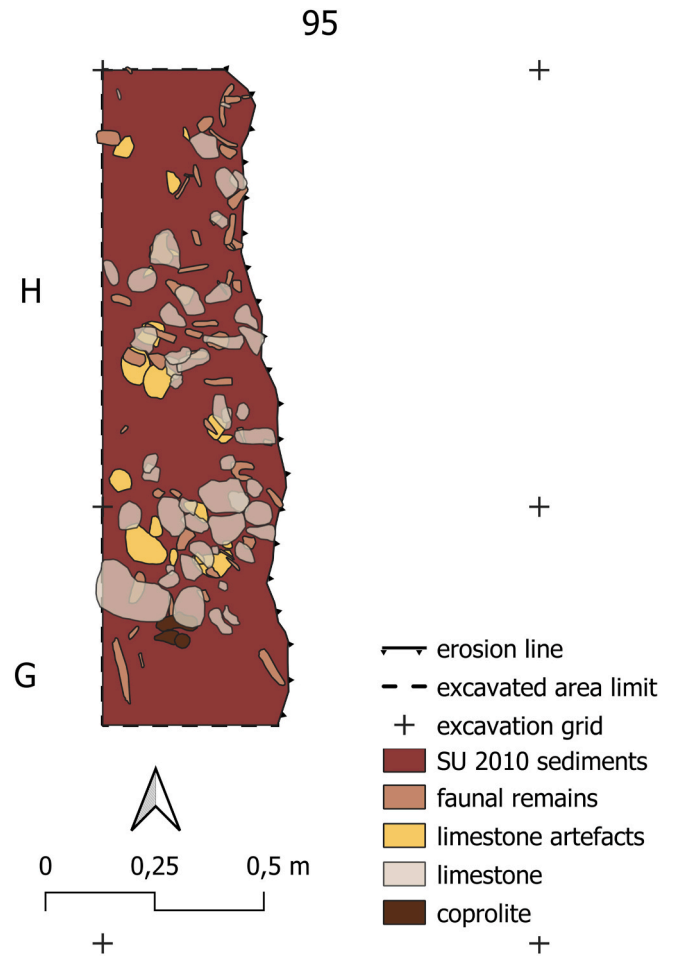


Fig. 15. – Reconstruction of the spatial distribution of faunal remains and lithic artifacts collected in SU 2010, exposed at the base of ISU3 in the South sector during the 2015–2022 excavations coordinated by Sapienza University of Rome.

few isolated and fragmentary remains, with juvenile or cub individuals virtually absent and no articulated remains found. The overall paleontological evidence discourages the hypothesis of the cave being used as a carnivoran den during the deposition of ISU3.

The mammal record of ISU3 is largely dominated by the presence of fallow deer (*Dama dama*), representing over 90% of the sample (Tables 2 and 3). Although modern fallow deer populations inhabit various habitats with diverse food preferences (Esattore et al., 2022 and reference therein), a browsing feeding behavior is commonly accepted for Quaternary *Dama* (Rivals and Ziegler, 2018; Strani et al., 2022). Blanc (1928) noted that the fallow deer was the preferred animal hunted by humans. However, the apparent human selection of this species appears to correlate with its abundance in the region. This suggests that wooded environments were predominant in the area during the deposition of ISU3, as also testified by fossils of other species in ISU3 (e.g., *Capreolus capreolus*, *Cervus elaphus* and *Sus scrofa*). Two species clearly indicative of open spaces are quite scarce, comprising less than 1% (Tables 2 and 3). *Stephanorhinus hemitoechus* primarily occupied open grasslands (van Asperen and Kahlke, 2015; Rivals and Ziegler, 2018; Pushkina et al., 2020) while *Equus ferus* indicates the extensive presence of open spaces such as steppe or grasslands (Strani et al., 2022). One of the most significant paleoenvironmental indicators in ISU3 is *Lutra lutra*, whose presence is strongly associated with large freshwater bodies (rivers or lakes). Along with the presence of hippopotamuses, these species document landscapes that are no longer present in the southern part of Apulia.

Overall, the mammal assemblage collected in ISU3 includes taxa adapted to different environments, indicating the significant presence of woodlands (e.g., cervids and wild boar), limited open spaces (e.g., rhinoceroses and equids), and large freshwater bodies such as rivers, lakes or coastal lagoons (e.g., hippopotamuses and European otter).

5.4. Biochronological implications

During the Middle Pleistocene, significant environmental and climatic shifts occurred, leading to substantial changes in European terrestrial ecosystems. These transformations resulted in major faunal turnovers, with the emergence of new species and the disappearance of previous ones from the Villafranchian period (e.g., Gligozzi et al., 1997). This period witnessed the early dispersal of several taxa closely related to extant lineages or species, such as red deer, wild boar and hyenas (e.g., Gligozzi et al., 1997; van der Made et al., 2017; Iannucci et al., 2021a). Recent research over the last decade has led to the redefinition of many of these early dispersals, highlighting the period between 550 ka and 400 ka as a crucial phase in Quaternary faunal renewal. During this period, significant arrivals of species like *Canis lupus*, *Hippopotamus amphibius* and *Bos primigenius* occurred (Iannucci et al., 2021b; Mecozzi et al., 2021d, 2023a; Iurino et al., 2022).

The late Middle to Late Pleistocene mammal assemblages from the Italian Peninsula exhibit a relatively consistent taxonomic composition, with occasional occurrences of taxa associated with cold environments typical of glacial stages. However, representatives of these cold-adapted, open environment species are quite rare (e.g., *Mammuthus primigenius*, *Coelodonta antiquitatis*), and their presence is mostly confined to the northern regions of the Italian Peninsula. The combination of pronounced climatic fluctuations and the overall homogeneous taxonomic composition make it challenging to identify bioevents that could contribute to the European biochronological scheme of large mammals. Moreover, different species responded differently to environmental

changes, adding complexity to the recognition of such events.

Nevertheless, the study of the mammal sample from Grotta Romanelli, coupled with the revised chronostratigraphic framework outlined by Pieruccini et al. (2022), provides insights for the evolution of Mediterranean European large mammal faunas (Fig. 16).

Pandolfi et al. (2018) studied the historical rhinoceros collection preserved at MUCIV, identifying the presence of *Stephanorhinus hundsheimensis* (Toula, 1902) from the top of ISU1 and in ISU2. Subsequent discoveries were made during recent excavations. The Hundsheim rhinoceros is a characteristic species of the latest Early and Middle Pleistocene of Europe, with its latest occurrence reported by several authors around 0.6 Ma (MIS 15; Pandolfi and Tagliacozzo, 2013). Based on this, Pandolfi et al. (2018) proposed that these levels should be attributed to the early Middle Pleistocene. However, more recent findings have extended the presence of *Stephanorhinus hundsheimensis* to the early Late Pleistocene levels (MIS 5) of Cova del Rinoceront (García-Fernández et al., 2023), challenging the idea of its extinction during the Middle Pleistocene. This indicates that the Hundsheim rhinoceroses persisted in southern Europe until MIS 5, highlighting the need to revise the *Stephanorhinus* record of the mid and late Middle Pleistocene to a better understanding of its evolution history. In this updated context, fossils from Grotta Romanelli confirm the late persistence of *Stephanorhinus hundsheimensis* in southern Europe, representing its last occurrence in the Italian Peninsula (MIS 7).

Fossil remains of *Dama* from ISU3 are attributed to *Dama dama*. As discussed by Mecozzi et al. (2023b), the transition between *Dama clactoniana* and *Dama dama* remains vaguely defined. However, confirming the presence of *Dama dama* in ISU3 reinforces the prevailing consensus that this species was widespread in Europe during the early Late Pleistocene (MIS 5). During the late Middle Pleistocene, *Dama clactoniana* was still present in Europe, with its latest occurrence likely documented in the upper levels of Vitinia (MIS 7, Mecozzi et al., 2023b). Nevertheless, a comprehensive review of fossil samples from several key

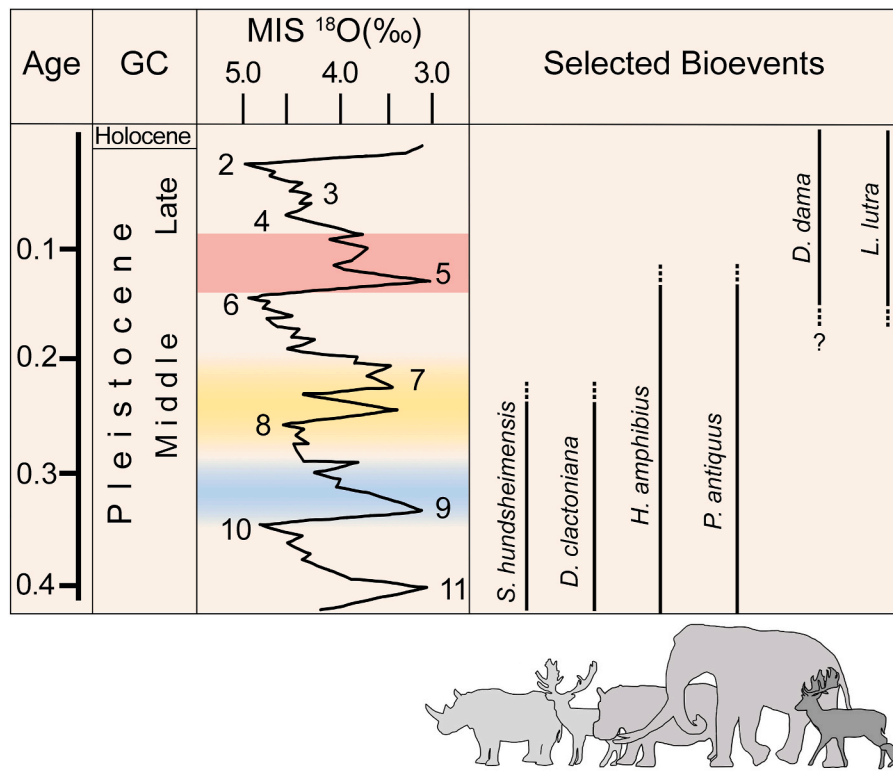


Fig. 16. – Biochronological scheme and selected European mammal bioevents. Abbreviations: GC - geochronology; MIS – Marine Isotope Stage. Levels of Grotta Romanelli: blue: top of ISU1; orange: ISU2; red: ISU3. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

European sites (e.g., Bolomor Cave, Grotte du Lazaret) could provide additional data on the timing and mode of transition between these two taxa.

The identification of wolves from Grotta Romanelli, and more broadly from southern Italy, has been the subject of long-standing debate among specialists (Sardella et al., 2014, 2018, 2019). One of the hypotheses in the literature relies on the geographical position of Apulia, situated in the heel of Italian Peninsula and relatively isolated from the European continent. This region might have served as a refugium for European mammals, allowing them to survive drastic climatic changes affecting in the rest of the continent. The small size of the remains from Grotta Romanelli and other Apulian deposits (e.g., Melpignano and San Sidero) was initially interpreted as evidence of the persistence of the Middle Pleistocene species *Canis mosbachensis* in southern Italy, despite a lack of direct examination of the specimens (Masini et al., 1990; Sala et al., 1992). Sardella et al. (2014) first described the craniodental remains collected in ISU3, who, in addition to traditional techniques, performed a CT analysis of the exceptionally preserved cranium. The authors noted a relatively small body size of the specimens, but their features fell within the variability of *Canis lupus*. Additional craniodental and postcranial material of *Canis lupus* was discovered at the top of ISU1 and in ISU2 during the new excavations. These remains also displayed reduced dimensions, further supporting the presence of small-sized *Canis lupus* in Apulia during the late Middle Pleistocene (Fig. 9). A similar conclusion was reached by Mecozzi et al. (2021a), who demonstrated that the findings of *Canis lupus* from the karst cavities of Melpignano and Sidero (not so far from Grotta Romanelli) attributed to the late Middle Pleistocene are characterized by reduced dimensions. Studies of the last two decades have widely documented an evolutionary size trend in *Canis lupus*, shifting from the smaller representatives of the late Middle Pleistocene (referred to as *Canis lupus lunellensis*) to the larger form of the Late Pleistocene (*Canis lupus maximus*) (Brugal and Boudadi-Maligne, 2011; Boudadi-Maligne, 2012; van der Made et al., 2017; Mecozzi and Bartolini Lucenti, 2018; Iurino et al., 2023). Furthermore, in addition to the time factor, the geographic variability of this species needs to be discussed. In fact, the extant *Canis lupus* is one of the most widely distributed species globally, with huge ecological tolerance, occupying environments ranging from Arctic tundra to Arabian desert (Mech, 1970; Boitani et al., 2003). The extant grey wolf follows the ecogeographic Bergmann's Rule, which implies that populations from higher latitudes have larger body sizes compared to those from lower latitudes (Meiri et al., 2004). This size pattern suggests that populations (or subspecies) in southern peripheral areas of the species' areal tend to be smaller. In this framework, the small size of the remains from Grotta Romanelli and other Apulian localities appears consistent with these earlier and smaller forms of *Canis lupus* (also named as *Canis lupus lunellensis*) that occupied the southern and peripheral territory within a vast European paleoarea.

The mammal remains from ISU3 have played a pivotal role in shedding light on the extinction of *Palaeoloxodon antiquus* and *Hippopotamus amphibius*. Previously, it was thought that these taxa persisted until MIS 4-3 based on the old chronological framework of the cave (e.g., Martino and Pandolfi, 2022; Martino et al., 2022). However, the uncertainty surrounding the stratigraphic contexts of the recovered fossils and the absence of reliable chronological constraints have complicated the issue of their extinction. This ambiguity is exemplified by findings from sites like Ingarano (Petronio and Sardella, 1998), Canale Mussolini (Caloi and Palombo, 1995; Farina, 2011) or Grotta dei Moscerini (Alhaique and Tagliacozzo, 2000). Presently, attributing the mammal assemblage from ISU3 of Grotta Romanelli to early Late Pleistocene is consistent with the distribution of these species across the entire Italian Peninsula during this period. Moreover, it supports the notion that their extinction likely occurred towards the end of the MIS 5.

Mecozzi et al. (2021b) presented the first description of the hemimandible of *Lutra lutra* collected in ISU3 during the initial stage of excavations coordinated by G.A. Blanc, marking one of its earliest findings

in Europe. However, it is clear that its appearance in the European record does not fully reflect its real distribution.

6. Conclusion

Our study presents the first systematic study and reassessment of all the mammal fossils recovered from Grotta Romanelli, encompassing both the findings from the historical excavations and the recent fieldwork carried out between 2015 and 2022. Moreover, this review is based on a novel stratigraphic framework, which is a significant departure from the previously established understanding of the site and the broader context of the Italian peninsula. This new framework carries profound implications not only for Grotta Romanelli but also for a larger European and Mediterranean context. In fact, the reassignment of sedimentary units formerly assumed as Late Pleistocene to the late Middle Pleistocene shifts the previous paradigm and substantially alters the perceived antiquity of both the mammal assemblages and the human frequentation at the site.

Considering the revised chronostratigraphic framework, Grotta Romanelli emerges as a rare European site where mammal fossils were discovered in three distinct levels corresponding to consecutive interglacial stages.

- The earliest and most substantial collection of remains was found at the top of ISU1, marking the first human occupation of the cave. This layer also contains evidence of human-related fire activities, estimated to have occurred around 350 ka (after the marine highstand of MIS 9).
- ISU2 yielded a less abundant fossil record, with notable concentrations near its uppermost layers, dated to approximately ca. 220 ka (MIS 7);
- An impressive number of fossils come from ISU3, attributed to the early Late Pleistocene (MIS 5).

Our study indicates that the faunal assemblages from these three levels share a relatively consistent composition with species predominantly adapted to wooded environments and fewer indicators of open spaces. Additionally, the occurrence of several mammals suggests the presence of nearby water bodies.

Our results offer new insights into the biochronological evolution of large mammals in southern Mediterranean Europe and their interactions with early human populations.

- The presence of *Stephanorhinus hundsheimensis* in ISU2 marks the youngest presence of this species on the Italian Peninsula (MIS 7);
- Fossils of *Palaeoloxodon antiquus* and *Hippopotamus cf. amphibius* are dated to the early Late Pleistocene (MIS 5), making them among the latest records of these species in the Italian Peninsula;
- ISU3 yielded an isolated remain of *Lutra lutra*, considered one of the oldest fossils of this carnivore in Europe;
- A rich sample is attributed to *Dama dama* in ISU3 and represents one of the earliest documented occurrences of fallow deer in Europe.

Finally, this study represents the first step toward a comprehensive review of the vertebrate record from Grotta Romanelli recovered during historical excavations. In addition to enhancing our understanding of mammal paleocommunities, these results enabled the reassessment of historical museum collections often neglected for decades.

CRedit authorship contribution statement

B. Mecozzi: Writing – review & editing, Writing – original draft, Visualization, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **F. Bona:** Writing – review & editing, Conceptualization. **J. Conti:** Writing – review & editing. **G. Lembo:** Writing – review & editing, Visualization. **G.S. Mariani:** Writing –

review & editing. **I. Mazzini:** Writing – review & editing, Supervision. **B. Mutillo:** Writing – review & editing. **P. Pieruccini:** Writing – review & editing, Writing – original draft, Visualization, Supervision. **R. Sardella:** Writing – review & editing, Supervision, Project administration, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data that has been used is confidential.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.qsa.2024.100237>.

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