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Taxonomic and taphonomic analysis of Late Pleistocene faunal remains from several karst fillings at Cava Muracci travertine quarry (Cisterna di Latina, central Italy): a comprehensive study

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ABSTRACT

Cava Muracci, an archaeological and paleontological site in Cisterna di Latina (Latium, central Italy), has yielded significant faunal assemblages from the Late Pleistocene, collected from eight karst fillings. We have gained valuable insights into subsistence patterns, ecosystem dynamics, site chronology and the processes underlying the preservation of mammal remains through comprehensive palaeontological and taphonomic analysis of over three thousand mammal specimens. The evidence of carnivore activity has led to the interpretation of Area 1-2-3 as a hyena den, while Areas 4 and 7 indicate more limited hyena activity. In contrast, Areas 5, 6 and 8 likely experienced water flow events that transported faunal remains and debris. Environmental reconstructions based on faunal and pollen data suggest a mixed landscape featuring steppe or grassland, interspersed with wooded areas and marshlands along the coastal belt. Species diversity in different areas provides insights into the local ecological dynamics and the chronological sequences of the site. Radiometric dating places Areas 1-2-3 and 7 within MIS 3, with the other areas likely corresponding to a later phase of this period. This multidisciplinary research enhances our understanding of paleoenvironmental dynamics in the Pontine Plain and provides a broader perspective on central Italy's Late Pleistocene landscapes.

1. Introduction

The Pontine Plain, a region situated in central Italy, located between the Tyrrhenian Sea and the Lepini and Ausoni Mountains, stands as proof of the intricate geological history that has shaped the landscape of the Peninsula over millennia. It has long been a focal point for scientific inquiry, offering a unique window into the environmental dynamics of the Middle and Late Pleistocene. The interplay of glacial advances and retreats significantly influenced terrestrial environments worldwide, leaving a lasting impact on the Pontine Plain (Marra et al., 2019). These climatic oscillations played a pivotal role in shaping the region's topography, hydrology, and ecosystems. Water has continuously influenced the area's morphology, contributing to the formation of marine fossil beaches, known as fossil dunes, and the development of marshes during the Holocene climatic optimum - processes that still impact the landscape today (Marra et al., 2019).

The Pontine Plain is a geographical area very rich in prehistoric and historical sites. The Circeo Promontory, a prominent headland along the Tyrrhenian Sea coast, adds to the region's archaeological and paleontological significance. The coastal caves and shelters scattered across the promontory are invaluable repositories of human history. These sites, documented in the past (Blanc, 1939a, 1939b, 1940; Blanc and Segre, 1953), bear witness to the presence of a regional variant of the Mousterian lithic industry: the Pontinian (Blanc, 1939b), a distinctive regional stone tool culture associated with Neanderthals. The artifacts and tools discovered in these locations and a very high number of open-air sites (Kuhn, 1995; Rolfo et al., 2022) provide insights into the technological and cultural achievements of ancient human populations. The discovery of Neanderthal remains at Grotta del Fossellone, Grotta Breuil and Grotta Guattari (Alhaique et al., 1998; Blanc, 1939a, 1939b, 1940; Blanc and Segre, 1953) underscores the deep historical roots of human settlement strategies in this area, offering a window into the past

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and contributing to our broader understanding of human prehistory.

Over the past decade, the Pontine Plain has attracted increasing attention from a wide range of multidisciplinary studies, revealing a wealth of prehistoric and paleontological sites. These investigations have uncovered a concentration of human and faunal remains in both karst environments and open-air settings, dating back to the Late Pleistocene (Gatta et al., 2016b, 2016c, 2019; Grimaldi and Spinapolice, 2010; Petronio et al., 2021; Rolfo et al., 2022; Vitagliano and Bruno, 2012). Recent research suggests that, during this period, the region featured a far more diversified landscape, with multiple ecosystems that served as *refugia* for various faunal and floral species (Gatta et al., 2016b, 2016c, 2019, 2021; Petronio et al., 2021; Salari and Kotsakis, 2017). The discovery of one of Europe's latest narrow-nosed rhinoceroses further emphasizes the diversity of environments in the region during the Late Pleistocene (Pandolfi et al., 2017).

The study of faunal remains from these archaeological contexts, particularly through taxonomic and taphonomic analyses, is essential for reconstructing past subsistence strategies and ecological conditions. Taphonomic analyses, which examine the processes that affect the preservation and transformation of organic materials, provide critical insights into how bones and artifacts were deposited and altered through decay, mineralization, or other forms of modification (Fernández-Jalvo and Andrews, 2016). By combining taxonomy and taphonomy, it's possible to reconstruct ancient environments, track subsistence practices, and gain a deeper understanding of the mobility and social behaviours of both faunal and human populations (Romandini, 2012).

This paper provides an extensive taxonomic and taphonomic evaluation of over three thousand faunal remains recovered from eight Late Pleistocene deposits at the site of Cava Muracci (Latium, central Italy). It revisits previous studies, particularly those of Area 3, which is the only sector to have been comprehensively investigated archaeologically, geologically, and paleontologically (Gatta, 2014; Gatta and Rolfo, 2015, 2017; Gatta et al., 2016a, 2016b, 2016c, 2019). Additionally, it presents new data from recent excavation campaigns. Examining the Late Pleistocene Cava Muracci site through a multidisciplinary lens, this article aims to contribute to a broader understanding of paleoenvironmental dynamics in the Pontine Plain.

2. Archaeological setting

Cava Muracci (Fig. 1A and B) is a paleontological and archaeological site located within a travertine quarry near the town of Cisterna di Latina (Latium, central Italy), in the northeastern part of the Pontine Plain. This area of the region is characterized by slight topographic elevations above sea level, never exceeding 77 m a.s.l.

Faunal remains, artifacts, and human skeletal remains dating to both the Late Pleistocene and the Holocene were discovered during quarrying activities carried out in the 1950s. Among these, a Late Neolithic human skull—radiocarbon dated to 3620–3590 ^{14}C BP—was identified (Segre and Ascenzi, 1956; Rubini, 2003). In the early 1990s, additional human and faunal remains were recovered from a conical slit in the travertine along the northern side of the quarry (Angle and Germano, 2003). However, due to the instability of the travertine walls, no formal archaeological investigations could be conducted at that time.

In July 2012, a new assemblage of mammal remains was delivered to the Laboratory of Prehistoric Archaeology at the University of Rome "Tor Vergata." The material, predominantly consisting of fragmented bones, was collected from a disused portion of the quarry. Preliminary taxonomic analysis suggested an attribution to the Late Pleistocene (Gatta, 2014). This interpretation aligns with earlier hypotheses by Segre and Ascenzi (1956), who also reported the recovery of both Upper Palaeolithic lithic artifacts and pottery from the site. The presence of ceramics, likely deriving from later phases of occupation, underscores the complex post-depositional history of the deposit.

Excavation campaigns conducted between 2012 and 2018 focused on eight karst fillings, designated Areas 1 to 8, to retrieve faunal bones and lithic artifacts exposed to natural degradation throughout the travertine quarry. These efforts aimed to provide a comprehensive and extensive understanding of the site (Gatta, 2017). The operation confirmed the presence of karst fillings in the area, referred to as the "*pockets of red earth*" (Segre and Ascenzi, 1956), within which thin layers contained archaeological material dating to the Late Pleistocene. Additionally, over a hundred coprolites belonging to *Crocuta spelaea* were discovered (Gatta et al., 2016c, 2019).

Radiocarbon dating has contributed significantly to defining the chronological framework of the site. Four ^{14}C dates from bone samples in Area 3 place the faunal-rich layer SU11 between 34 and 41 ka cal BC (Gatta et al., 2016a; Gatta and Rolfo, 2017), while a date from Area 7 falls within 37–39 ka cal BC. Furthermore, a tephra layer identified in SU13 (Area 3) provides a terminus post quem for SU11. ^{40}Ar/^{39}Ar dating, combined with geochemical analyses, correlates this tephra with the Albano 3 eruptive phase (~69 ka), offering additional chronological limit (Gatta et al., 2017).

The morphology of the collection areas ranges from small karst pockets to larger caves (Gatta and Rolfo, 2015). Area 3 is the only one that has been fully studied and published (Gatta et al., 2017, 2019), while the assessment of the other areas has been limited to excavation data and preliminary interpretations (Gatta et al., 2016c; Gatta and Rolfo, 2015, 2017). Therefore, the comprehensive study of these karst fillings is presented for the first time in this paper. Areas 1, 2 and 3, initially considered separate entities, are now interpreted as residual parts of a larger karst network and examined as a single unit. Consequently, we have chosen to designate the three karst areas as "Area 1-2-3".

2.1. Area 1-2-3

The area from which the majority of samples were collected, referred to as Area 1 (GPS: 41°59′82.64″ N 12°85′64.56″), Area 2 (GPS: 41°59′81.77″ N 12°85′66.30″) and Area 3 (GPS: 41°59′81.22″ N 12°85′67.64″), appears to be a section of the quarry along the northern face, approximately 20 square meters in size, where most of the finds were collected stratigraphically. Morphologically identifiable as the remains of a cave and its filling, this section has been almost completely destroyed by travertine quarrying. Only the part protected by the overlying travertine formation has been preserved from the original deposit. Meanwhile, a steep colluvial slope has resulted in several cubic meters of reworked material at the base. In Area 1, a Neolithic human skull was discovered in 2000 (Angle and Germano, 2003). However, only a limited number of mammal remains were recovered here, likely due to the careful collection during the previous investigation. Area 2 consists of an underground tunnel connecting Area 1 to Area 3, the main excavation area. According to information provided by the site owner regarding the disuse of the quarry, weathering had affected the deposit for at least three decades, causing displacement of the upper layers and the artifacts contained within them (Gatta et al., 2016c). Despite the extensive disruption caused by extraction activities, Area 3 yielded a well-preserved stratigraphic sequence. The context was entirely filled with continental deposits of likely alluvial origin, within which at least seven stratigraphic levels have been identified (Fig. 2): SU7 is the modern walking surface of the quarry; SU8, travertine ceiling of the cave; SU11, highly consolidated red-brown clay soil with abundant remains of large mammals, small vertebrates, coprolites and rare lithics; SU12, reddish brown layer with frequent small vertebrates and rare lithic artifacts; SU13, greyish green layer of volcanic tephra and pyroclastic products; SU14, reddish layer with extremely rare lithic and faunal remains; SU15: travertine natural floor of the cave SU12 yielded only a few micro-vertebrates remains, while the other units contained very scarce and taxonomically indeterminate fragments (Gatta et al., 2019).

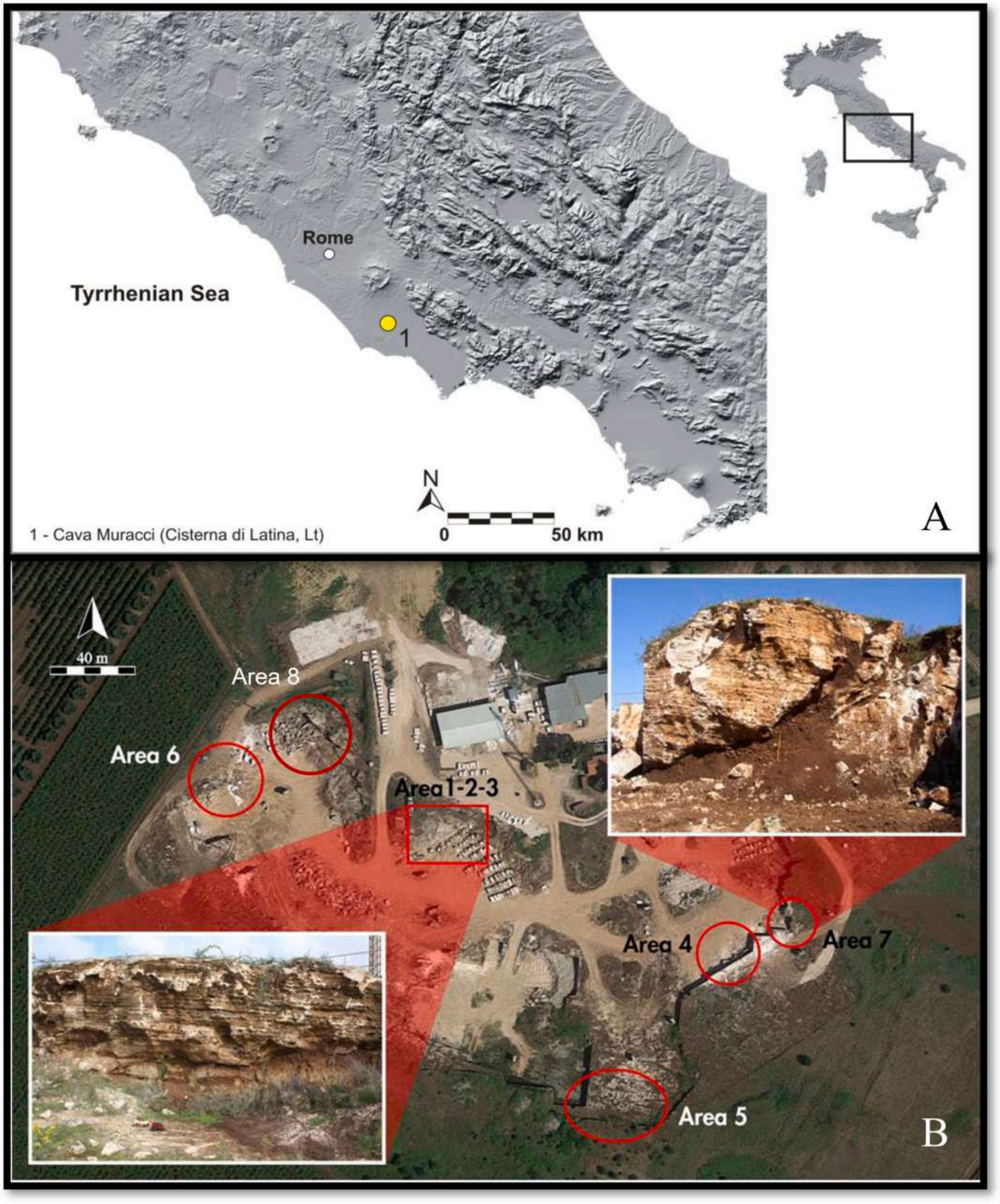


Fig. 1. A) Geolocalization of Cava Muracci site (Gatta and Rolfo, 2017); B) Satellite image and photos showing the investigated areas in Cava Muracci (Gatta and Rolfo, 2017).

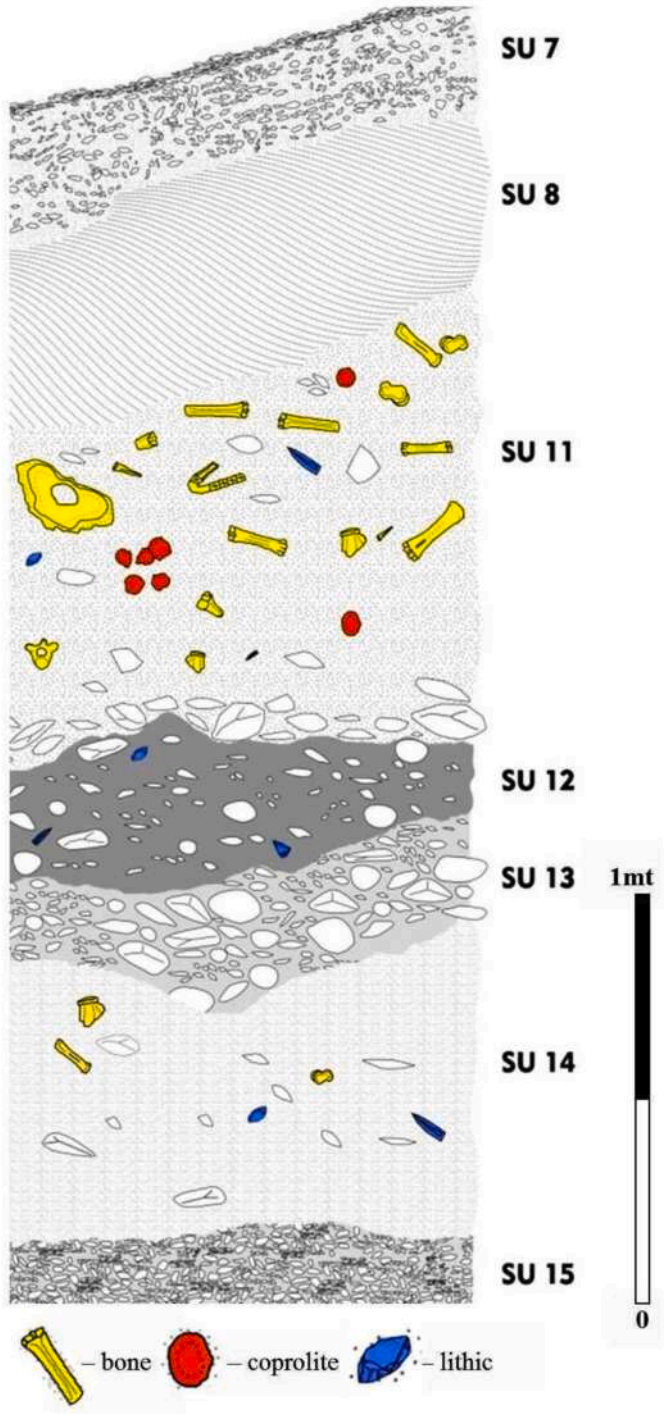


Fig. 2. Stratigraphy of area 3 from Cava Muracci (Gatta et al., 2019).

2.2. Area 4

Area 4 (GPS: 41°59′77.47″ N 12°85′80.37″), located along the eastern wall of the quarry, appeared to be a narrow and deep karst ravine within the travertine. A significant portion of the deposit, which contained a substantial quantity of animal remains, had been eroded by natural weathering processes. In total, hundreds of bones were collected from the surface, consistent with the species identified in Area 3.

2.3. Area 5

Area 5 (GPS: 41°59′69.66″ N 12°85′74.66″), located on the southern edge of the quarry, represents another expansive cave within the travertine. Most of the soil filling had shifted, exposing numerous faunal remains.

2.4. Area 6

Area 6 (GPS: 41°59′85.64″ N 12°85′51.53″), located along the western face of the quarry, yielded few findings. However, it was included in the excavations to complete the series of surveys around the perimeter of the quarry.

2.5. Area 7

The excavation of Area 7 was conducted following a recent phase of travertine extraction along the eastern face of the quarry. A partially preserved soil layer was found along the edge of a travertine wall, extending about 7 m, and identified as the inner edge of a cave. Within this soil layer, an extensive accumulation of faunal remains was visible, including cave hyena remains and dozens of coprolites.

2.6. Area 8

Particularly noteworthy is Area 8, located along the north-west face of the quarry, where hundreds of faunal bones were collected from several pockets of brown earth.

3. Materials and methods

3.1. Excavation and chronology

The excavation of the eight karst fillings at Cava Muracci took place between 2012 and 2018, posing significant challenges due to the morphology of the collection areas - narrow sinkholes, disrupted sediment layers caused by quarrying and safety concerns. These factors made comprehensive excavations impossible in certain areas. As a result, accurate stratigraphic data were only available for Area 3.

Each of the 3011 bones recovered at Cava Muracci was assigned a unique find number. However, detailed coordinates and depth data within a 1x1m excavation grid system were recorded only for the remains from Area 3. Sieving was used to recover faunal remains, coprolites, and lithic artifacts larger than 2 mm in mesh size.

Four radiocarbon (^{14}C) dates (Table 1) obtained from bones found in Area 3 helped to establish the chronological framework of layer SU11, the richest in faunal remains, placing it within the range of 34–41 ka cal BC (Gatta et al., 2016a; Gatta and Rolfo, 2017). Additionally, two radiocarbon analyses performed on cave hyena coprolites from Area 3 yielded anomalously young ages of approximately 17–20 ka cal BC (Gatta et al., 2016a; Gatta and Rolfo, 2017). This outcome highlights the well-documented susceptibility to contamination associated with such materials (Bon et al., 2012; Diedrich, 2012a). Moreover, the organic carbon content of the coprolites is extremely low, approximately 1 %, making them particularly vulnerable to contamination even with a small amount of contaminants (Gatta et al., 2016c). The discovery of *Stephanorhinus hemitoechus* remains in Area 3 (Pandolfi et al., 2017), along with *Panthera pardus* and *Dama dama,* species that were undoubtedly already extinct during the timeframe suggested by the coprolite datings, raises further questions regarding the accuracy of the lattest. *Crocuta spelaea* did not survive beyond 40 ka in Central Europe and Russia (Diedrich, 2024; Stuart and Lister, 2014), and not beyond 31 ka ago in Southern Europe (Stuart and Lister, 2014). However, it might have persisted until 25 ka in France (Brugal et al., 2020) and until the Last Glacial Maximum, around 20 ka, in Italy, similar to the survival timeline of other Ice Age large mammals such as the leopard and cave bear (Petronio et al., 2007). Therefore, the dating of cave hyena coprolites should be considered inaccurate.

The identification of tephra in SU13 of Area 3 provides a reliable

Table 1
Dates from the specimens were obtained at CEDAD in Lecce (LTL), ETH in Zurich (ETH), and ORAU (OxA). Dating OxA-X-2756-42 was conducted using the single amino acid protocol at ORAU (Devièse et al., 2017, 2018) and subsequently corrected (uncorrected age 44,400 ± 3700 BP). OxA-X-2772-28 and OxA-X-2772-33 were produced using the laboratory's routine "AG" protocol (Brock et al., 2010) and are provided with warnings due to slightly elevated CN ratios (both 3.6) but are (or are calibrated to) background ages. The dates were calibrated using the IntCal20 calibration curve (Reimer et al., 2020) in OxCal v. 4.4.4 (Bronk Ramsey, 2009, Bronk Ramsey, 2017).

Specimen	Laboratory No.	14C age yr BP	Calibrated age yr BC (OneSigma)
Area 3, SU11 – *Bos primigenius*	LTL15758A	39417 ± 450	41505-40436 (91.7 %)
Area 3, SU11 – *Stephanorhinus hemitoechus*	LTL15760A	36885 ± 350	40201-39290 (95.4 %)
Area 3, SU11 – *Crocuta spelaea*	ETH-66210	31339 ± 168	34171-33395 (95.4 %)
Area 3, SU11 – *Crocuta spelaea*	OxA-X-2772-28	≥41700	Background
Area 3, SU11 – *Crocuta spelaea*	OxA-X-2756-42	49300 ± 10200	Background
Area 5 – *Stephanorhinus hemitoechus*	OxA-X-2772-33	46500 ± 3900	Background
Area 7 – *Cervus elaphus*	LTL15759A	35231 ± 350	39121-37723 (95.4 %)
Area 3 – Coprolite	ETH-66212	16141 ± 42	17640-17423 (95.4 %)
Area 3 – Coprolite	ETH-66213	18313 ± 51	20446-20180 (95.4 %)

terminus post quem for SU11 and allows a precise chronological-stratigraphic interpretation of this deposit and the finds contained within it. Previously, this layer had been dated using the $^{40}Ar/^{39}Ar$ method, yielding an age of 70 ± 2 ka, and was tentatively assigned to an unspecified Albano unit. A new $^{40}Ar/^{39}Ar$ data, combined with trace element analysis and complemented by the previously determined major element composition, collectively suggest a correlation between tephra CIS-1 and Albano 3, with an approximate age of ~69 ka (Gatta et al., 2017).

For Area 7, a radiocarbon dating of a *Cervus elaphus* find places the faunal assemblage within the range of 37–39 (ka cal BC).

3.2. Taxonomy

The taxonomic study of faunal remains from Cava Muracci was conducted on middle and large mammal specimens from Area 1-2-3 (=2055), Area 4 (=305), Area 5 (=30), Area 6 (=1), Area 7 (=236) and Area 8 (=387). A total of 3014 finds were analysed, with approximately 49,6 % (=1494) taxonomically identified, highlighting the presence of at least 15 *taxa* (Table 2). A significant number of remains were highly fragmented, making species identification challenging for a portion of the assemblage (42.4 % of specimens were indeterminate; = 1278). Lastly, bones identified as fragments of vertebrae (=148) and ribs (=93), which could not be taxonomically attributed (overall 8 %), were categorized by size (small, medium, large) (Table 2).

The taxonomic analysis was performed at the Laboratory of Prehistory, University of Rome "Tor Vergata". A detailed palaeontological study of the faunal assemblage from Area 3 (micro-vertebrates and middle-large mammals) has already been published (Gatta et al., 2019), including species determinations, comparative criteria, and figures of the most representative specimens. In the present study, the taxonomic attribution of assemblages from the other areas was based on direct comparison with the material previously identified in Area 3, together with osteological collection and relevant reference literature (Pales et al., 1971; Schmid, 1972). The number of identified specimens (NISP) and minimum number of individuals (MNI) were determined using established methods (Bökönyi, 1970; Grayson, 2014). Age at death estimates were compared with those from studies on various species, including North American wolves (Gipson et al., 2000), Balkan and North American brown bears (Guskov, 2014), Pleistocene hyenas (Brugal et al., 1997), *Sus scrofa* from Turkey (Bull and Payne, 1982), *Cervus elaphus* from Spain (Mariezkurrena, 1983), *Capreolus capreolus* from northern France (Tomé and Vigne, 2003), and present-day domestic cattle and horse as proxies for equids and *B. primigenius* (Barone, 1980; Grant, 1982). The ecological and biogeographical distribution of both modern (Amori et al., 2008; Boitani et al., 2003) and extinct *taxa* (Conti et al., 2010, 2012; Pandolfi et al., 2013; Petronio et al., 2008) provided the basis for environmental reconstructions.

Fragmentation indices and survival coefficients of anatomical elements were calculated to assess skeletal preservation and evaluate the survival rates of different species (Binford, 1981; Lyman, 1994). The distribution of body parts was examined for *Cervus elaphus, Dama dama* and *Bos primigenius,* the most abundant ungulates. The skeleton was divided into seven anatomical regions (RA), following standard methodology (Fosse, 1994; Fourvel and Fosse, 2017), which included cranial elements (RAI), vertebrae (RAII), ribs (RAIII), pelvis (RAIV), long bones (RAV), metapodial bones (RAVI), and short bones (RAVII).

3.3. Taphonomy

The preservation of mammal remains at Cava Muracci was exceptional, likely due to fossilization facilitated by the mineral-rich travertine and calcium carbonate deposits, which contributed to the preservation of both coprolites and fossilized bones and teeth. There is notable variability in the degree of fragmentation of the fossil specimens, with bones found in both intact and fragmented conditions, ranging in size from 1 cm to several decimetres.

The study was carried out on all the identified and unidentified remains over 2 cm long using a Leica S9I Stereomicroscope and a 10x magnifier. Bone surface modifications were analysed to identify both biostratinomic and diagenetic alterations (Fernández-Jalvo and Andrews, 2016). Anthropogenic traces on bones, such as cut marks and the degree of thermoalterations, were recorded (Binford, 1981; Galán and Domínguez-Rodrigo, 2013; Nilssen, 2000; Stiner et al., 1995). Carnivore traces were identified as deep punctures on the cortical bone surface, primarily concentrated at the articular ends of the bones. Additional marks included pits - small, subcircular or triangular, non-puncturing depressions often repeated and insistent - and scores and furrows created by teeth sliding across the surface, leaving U-shaped striations on the bone (Binford, 1981). Additionally, traces of digestion, gnawing by rodents and small carnivores, and dermestid pupal chambers were also examined (Andrews and Jalvo, 1997; Bocheński et al., 1998; Fiorillo et al., 2023; Gatta et al., 2021; Huchet et al., 2013; Lloveras et al., 2009; Pirrone et al., 2014; Thompson et al., 2018). Biological and physicochemical alterations, such as root etching, carbonate deposits (Fisher, 1995; R. L. Lyman, 1994; Shipman, 1981), and the formation of mineral coatings (mainly manganese) were also recorded (Behrensmeyer, 1978; Fisher, 1995; Shipman, 1981).

Taphonomic observations were complemented by ternary diagrams made to investigate the mortality profile of the most abundant ungulates, ultimately supporting the hypothesis of a hyena-den accumulation (Gatta et al., 2019, 2022; Pandolfi et al., 2013; Stiner, 1990). For the ternary diagrams, the MNI was estimated considering the stage of teeth eruption, replacement, and wear (Stiner, 1990).

4. Results

Approximately 53 % (=1925) of the total finds (=3014), exhibit

Table 2
Number of identified specimens (NISP) and Minimum number of individuals (MNI) by age at death at Cava Muracci.

	Area 1-2-3				Area 4				Area 5				Area 7				Area 8				Total remains			
	NISP	%	MNI	%	NISP	%	MNI	%	NISP	%	MNI	%	NISP	%	MNI	%	NISP	%	MNI	%	NISP	%	MNI	%
Lepus sp.	17	1,8	2	2,5	7	3,3	2	7,7	0	0,0	0	0,0	16	7,7	3	17,6	5	3,4	2	11,8	45	3,0	9	6,3
Canis lupus	2	0,2	1	1,2	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	2	0,1	1	0,7
Vulpes vulpes	4	0,4	2	2,5	2	0,9	1	3,8	0	0,0	0	0,0	1	0,5	1	5,9	41	28,1	2	11,8	48	3,2	6	4,2
Ursus sp.	1	0,1	1	1,2	0	0,0	0	0,0	0	0,0	0	0,0	1	0,5	1	5,9	0	0,0	0	0,0	2	0,1	2	1,4
Meles meles	1	0,1	1	1,2	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	1	0,1	1	0,7
Panthera pardus	1	0,1	1	1,2	0	0,0	0	0,0	0	0,0	0	0,0	1	0,5	1	5,9	0	0,0	0	0,0	2	0,1	2	1,4
Crocuta spelaea	41	4,5	9	11,1	2	0,9	2	7,7	0	0,0	0	0,0	4	1,9	1	5,9	21	14,4	4	23,5	68	4,6	16	11,2
Carnivora	1	0,1	–	–	0	0,0	–	–	0	0,0	–	–	3	1,4	–	–	2	1,4	–	–	6	0,4	–	–
Stephanorhinus hemitoechus	1	0,1	1	1,2	2	0,9	1	3,8	2	28,6	1	50,0	0	0,0	0	0,0	0	0,0	0	0,0	5	0,3	3	2,1
Equus ferus	213	23,1	12	14,8	12	5,6	3	11,5	0	0,0	0	0,0	2	1,0	1	5,9	6	4,1	1	5,9	233	15,6	17	11,9
Equus sp.	4	0,4	2	2,5	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	2	1,4	1	5,9	6	0,4	3	2,1
Sus scrofa	3	0,3	3	3,7	1	0,5	1	3,8	0	0,0	0	0,0	2	1,0	1	5,9	18	12,3	2	11,8	24	1,6	7	4,9
Cervidae	26	2,8	–	–	20	9,4	–	–	1	14,3	–	–	20	9,7	–	–	9	6,2	–	–	76	5,1	–	–
Capreolus capreolus	9	1,0	3	3,7	2	0,9	1	3,8	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	0	0,0	11	0,7	4	2,8
Cervus elaphus	168	18,2	15	18,5	41	19,2	6	23,1	0	0,0	0	0,0	33	15,9	3	17,6	17	11,6	2	11,8	259	17,3	26	18,2
Dama dama	79	8,6	12	14,8	96	45,1	6	23,1	4	57,1	1	50,0	124	59,9	5	29,4	21	14,4	2	11,8	324	21,7	26	18,2
Bos primigenius	350	38,0	16	19,8	28	13,1	3	11,5	0	0,0	0	0,0	0	0,0	0	0,0	4	2,7	1	5,9	382	25,6	20	14,0
Total identified specimens	**921**	**100**	**81**	**100**	**213**	**100**	**26**	**100**	**7**	**100**	**2**	**100**	**207**	**100**	**17**	**100**	**146**	**100**	**17**	**100**	**1494**	**100**	**143**	**100**
Indeterminate bones	1080	52,6			59	19,3			7	23,3			17	7,2			115	29,7			1278	42,4		
Vertebrae S	5	0,2			0	0,0			11	36,7			0	0,0			7	1,8			23	0,8		
Vertebrae M	21	1,0			18	5,9			0	0,0			6	2,5			73	18,9			118	3,9		
Vertebrae L	7	0,3			0	0,0			0	0,0			0	0,0			0	0,0			7	0,2		
Ribs S	0	0,0			0	0,0			2	6,7			0	0,0			6	1,6			8	0,3		
Ribs M	15	0,7			14	4,6			3	10,0			5	2,1			33	8,5			70	2,3		
Ribs L	6	0,03			1	0,3			0	0,0			1	0,4			7	1,8			15	0,5		
Total remains	**2055**	**100**			**305**	**100**			**30**	**100**			**236**	**100**			**387**	**100**			**3013**	**100**		

surface alterations on bones. Human activity is entirely excluded in all areas, as no anthropogenic evidence - such as cutting, defleshing, butchering, skinning, cooking or processing marks - has been identified. In contrast, the evidence of animal involvement is quite evident.

4.1. Area 1-2-3

Although Area 3 has been extensively studied and documented in previous works (Gatta, 2014, 2017; Gatta et al., 2016a, 2016a, 2019, 2021, 2016a; Gatta and Rolfo, 2015, 2017; Pandolfi et al., 2017), this paper aims to provide an updated, comprehensive analysis of faunal bones coming from SU11 of this karst filling, together with the finds from Area 1 and 2. This update is prompted by recent excavation campaigns, which have yielded new insights and data. A total of 2055 mammal remains were recovered from Area 1-2-3 (Table 2), representing the highest concentration of finds across the site.

Taxonomic identification of the mammal remains (about 44 %, = 921) revealed a dominance of large ungulates, including *B. primigenius* (Fig. 3G), *Equus ferus* (Fig. 3C) and *Cervus elaphus* (Fig. 3F), followed by *Dama dama* (Fig. 3D), *Sus scrofa* and a single deciduous tooth fragment (d3) of a juvenile specimen of *Stephanorhinus hemitoechus* (Fig. 3B). A total of forty-one remains, primarily consisting of cranial elements (teeth – including deciduous ones -, mandibular and maxillary fragments) attributable to *Crocuta spelaea* (Fig. 3A), were recovered. Additional carnivore remains include two metapodials of *Canis lupus*, teeth and long bones of *Vulpes vulpes*, an incisor of a juvenile specimen of *Ursus* sp., a tibia of *Meles meles*, and a canine of *Panthera pardus*, indicating a substantial carnivore component within the stratified deposit. Additionally, hares (*Lepus* sp.) are present (Fig. 3E), though in relatively small percentages. The MNI (Table 3) was estimated at 81 individuals, with a preponderance of adults (33), followed by young (20), senile (16) and very young (12). The study of body part composition (Fig. 4) for the main ungulate species from Area 1-2-3 led to several observations. For *C. elaphus*, cranial elements (RAI) and metapodial bones and phalanges (RAVI) are prevalent. The same pattern is observed for *D. dama*, while for *B. primigenius*, cranial elements (RAI) are the most common, followed by long bones (RAV). The analysis of body part fragmentation in the main ungulate species from Area 1-2-3 (Table 4) compared to indeterminate bones, shows a preponderance of diaphysis fragments, followed by skull fragments and teeth, though nearly all anatomical parts have been found.

Bone surface observations revealed that approximately 72 % of the assemblage exhibited evidence of carnivore activity. Hyena gnawing is observed on about 85 % of the bone remains with altered surfaces (=1496; Fig. 5; Fig. 6A–B). This included fragmented diaphyses with cracks and puncture marks typical of carnivore bites (pits and punctures), widespread scores, underrepresented epiphyses with furrows, and an abundant presence of chewed Cervidae antlers, along with chewed long bones (Table 5). Several bones display digestive traces (Fig. 6C–D), and some long fragments, referred to as "nibbling sticks", were identified, indicating they had been gnawed to create chewed sticks (Fig. 6E). Rodent activity (Fig. 5) has also been identified on 4 remains, a lower percentage compared to carnivore activity, along with 11 bone fragments showing pupal chambers by dermestid beetles (Fig. 5; Fig. 6F). Additionally, vegetation (Fig. 5) left traces on 5 finds, which clearly displayed signs of root action. The remaining 13,3 % of traces are attributed to different patinas (Fig. 5), likely resulting from the chemical composition of the ground.

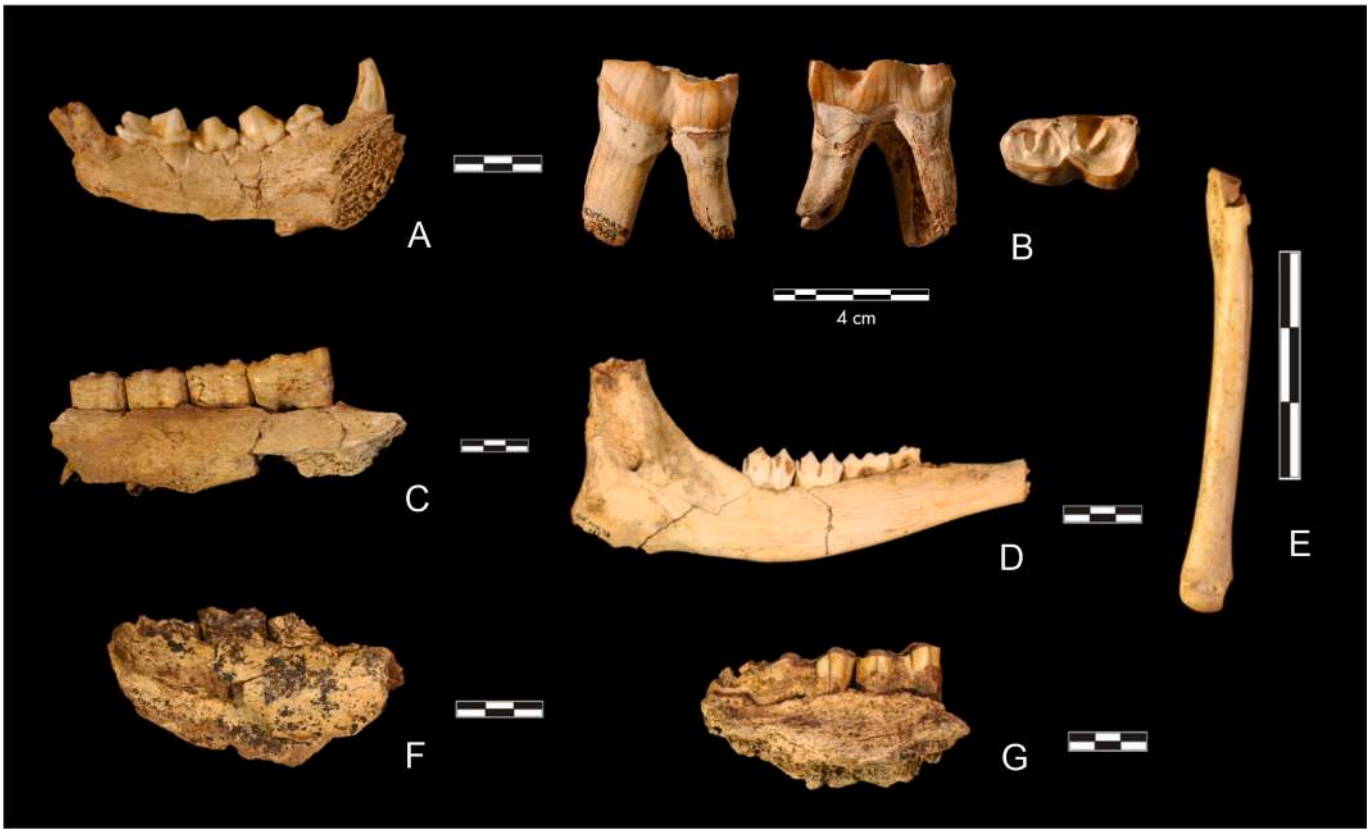


Fig. 3. Selected specimens of middle and large mammals from Cava Muracci: A) Left hemimandible with dentition (c, p2-m1) of *Crocuta crocuta* from Area 1-2-3 in lingual view; B) Left lower third deciduous molar (d3) of *Stephanorhinus hemitoechus* from Area 5 in labial, lingual and occlusal views; C) Left hemimandible with p2-m1 of *Equus ferus* from Area 1-2-3; D) Left hemimandible with d3,d4,m1,m2 of *Dama dama* from Area 1-2-3 in lingual view; E) Left metatarsal II of *Lepus* sp. from Area 1-2-3; F) Right fragmentary mandible of *Cervus elaphus* with m2,m3 from Area 1-2-3 in labial view; G) Right fragmentary mandible of *Bos primigenius* with m2,m3 with ectostylids from Area 1-2-3 in labial view (Data from Gatta et al., 2019; Pandolfi et al., 2017).

Table 3
Minimum number of individuals (MNI) by age of death of macromammals remains from all Areas of Cava Muracci. YY: very young; Y: young; A: adult; S: senile.

	Area 1-2-3				Area 4				Area 5				Area 7				Area 8			
	YY	Y	A	S	YY	Y	A	S	YY	Y	A	S	YY	Y	A	S	YY	Y	A	S
Lepus sp.	0	1	1	0	0	0	1	1	0	0	0	0	0	1	2	0	0	1	1	0
Canis lupus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Vulpes vulpes	1	1	0	0	0	0	1	0	0	0	0	0	0	0	1	0	0	2	0	0
Ursus sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Meles meles	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Panthera pardus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Crocuta spelaea	2	3	2	2	1	0	1	0	0	0	0	0	0	1	0	0	1	2	1	0
Stephanorhinus hemitoechus	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Equus ferus	1	2	4	5	0	1	1	1	0	0	0	0	0	0	1	0	0	0	1	0
Equus sp.	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Sus scrofa	1	1	1	0	0	0	1	0	0	0	0	0	0	1	0	0	0	1	1	0
Capreolus capreolus	0	0	2	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Cervus elaphus	2	3	6	4	2	2	2	0	0	0	0	0	1	1	1	0	2	0	0	0
Dama dama	2	2	7	1	1	3	2	0	1	0	0	0	1	2	2	0	0	1	0	1
Bos primigenius	2	4	7	3	1	1	1	0	0	0	0	0	0	0	0	0	0	0	1	0
Total MNI	**12**	**20**	**33**	**16**	**5**	**8**	**11**	**2**	**1**	**0**	**1**	**0**	**2**	**6**	**9**	**0**	**3**	**7**	**6**	**1**

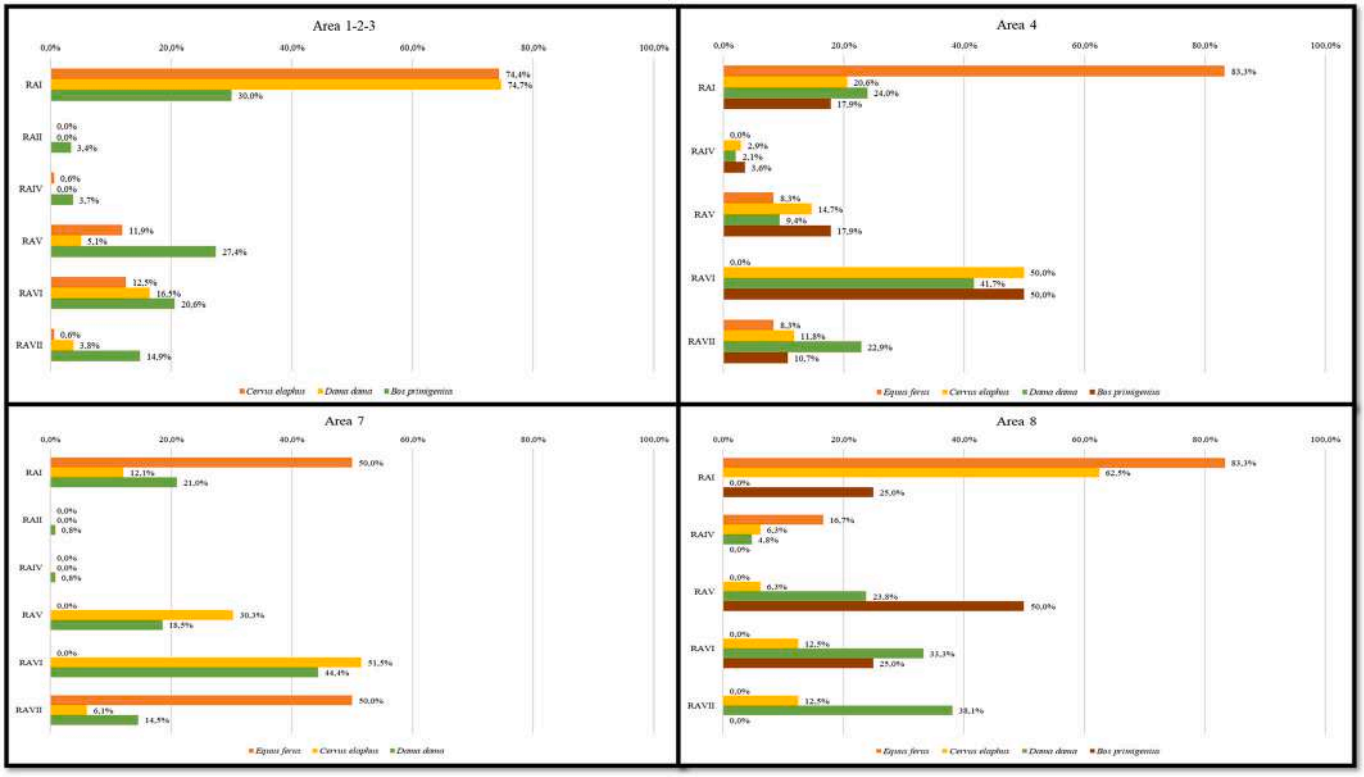


Fig. 4. Analysis of body part composition for the main species of ungulates of Cava Muracci. The skeleton is divided, following Fosse (1994), into: cranial elements (RAI), vertebrae (RAII), ribs (RAIII), pelvis (RAIV), long bones (RAV), metapodials and phalanges (RAVI) and short bones (RAVII).

4.2. Area 4

Area 4 yielded 305 mammal remains (Table 2), of which 69 % (=213) were taxonomically recognized. A predominance of *D. dama* finds was observed, followed by *C. elaphus* and *B. primigenius,* with only a few remains of *E. ferus*, mainly teeth*, C. capreolus, S. hemitoechus* (a tibia and a femur from a juvenile specimen) and *S. scrofa*. Carnivores are represented by a canine and an ulna fragment of *Crocuta spelaea*, as well as by a mandible and a calcaneus of *Vulpes vulpes*. Additionally, some finds of *Lepus* sp. was also identified. Adult individuals (11) were the most prevalent (Table 3), followed by young (8) very young (5) and senile individuals (2). The body part composition (Fig. 4) differs slightly from that of Area 1-2-3. For *E. ferus*, cranial elements (RAI) were the most common, while for the other ungulates, the most frequently found anatomical regions were metapodial bones and phalanges (RAVI), followed by cranial elements (RAI) with a lower percentage of other anatomical regions. The fragmentation analysis of body part composition in the main ungulate species from Area 4 (Table 4) shows that diaphysis fragments were found in numbers comparable to taxonomically identified intact bones, a slight variation from the other areas.

Bone surface analysis (Fig. 5) revealed a lower proportion of traces, with 28 % (=87) showing alterations. Hyena gnawing is present on approximately 84 % of the bone remains with altered surfaces (=73; Fig. 5). The remaining 16 % of traces are attributed to different patinas (Fig. 5).

Table 4
Analysis of fragmentation of body part composition of the main ungulates' species from all Areas of Cava Muracci compared to indeterminate bone.

AREA 1-2-3																		
Taxa	Intact bones		Vertebrae		Ribs		Antlers/Horn		Skull + Teeth		Diaphysis		Proximal Epiphysis		Distal Epiphysis		Tot.	
	N.	%	N.	%	N.	%	N.	%	N.	%	N.	%	N.	%	N.	%	N.	%
E. ferus	26	35,6	0	0,0	0	0,0	0	0,0	134	37,0	19	12,8	13	20,6	16	18,4	208	25,8
C. elaphus	5	6,8	0	0,0	0	0,0	52	85,2	73	20,2	16	10,8	12	19,0	10	11,5	168	20,8
D. dama	5	6,8	0	0,0	0	0,0	6	9,8	54	14,9	12	8,1	2	3,2	1	1,1	80	9,9
B. primigenius	37	50,7	12	100	0	0,0	3	4,9	101	27,9	101	68,2	36	57,1	60	69,0	350	43,4
Tot.	**73**	**100**	**12**	**100**	**0**	**0,0**	**61**	**100**	**362**	**100**	**148**	**100**	**63**	**100**	**87**	**100**	**806**	**100**
Indet.	15	17,0	33	73,3	21	100	0	0,0	6	1,6	1056	87,7	3	4,5	0	**0,0**	1134	58,5
Tot.	**88**	**100**	**45**	**100**	**21**	**100**	**61**	**100**	**368**	**100**	**1204**	**100**	**66**	**100**	**87**	**100**	**1940**	**100**
AREA 4																		
Taxa	**Intact bones**		**Vertebrae**		**Ribs**		**Antlers/Horn**		**Skull + Teeth**		**Diaphysis**		**Proximal Epiphysis**		**Distal Epiphysis**		**Tot.**	
	N.	**%**	**N.**	**%**	**N.**	**%**	**N.**	**%**	**N.**	**%**	**N.**	**%**	**N.**	**%**	**N.**	**%**	**N.**	**%**
C. elaphus	12	17,4	0	0,0	0	0,0	1	100	6	17,6	4	25,0	4	26,7	14	46,7	41	24,8
D. dama	46	66,7	0	0,0	0	0,0	0	0,0	23	67,6	8	50,0	8	53,3	11	36,7	96	58,2
B. primigenius	11	15,9	0	0,0	0	0,0	0	0,0	5	14,7	4	25,0	3	20,0	5	16,7	28	17,0
Tot.	**69**	**100**	**0**	**100**	**0**	**0,0**	**1**	**100**	**34**	**100**	**16**	**100**	**15**	**100**	**30**	**100**	**165**	**100**
Indet.	0	0,0	18	100	15	100	0	0,0	1	2,9	58	78,4	0	0,0	0	**0,0**	92	35,8
Tot.	**69**	**100**	**18**	**100**	**15**	**100**	**1**	**100**	**35**	**100**	**74**	**100**	**15**	**100**	**30**	**100**	**257**	**100**
AREA 7																		
Taxa	**Intact bones**		**Vertebrae**		**Ribs**		**Antlers/Horn**		**Skull + Teeth**		**Diaphysis**		**Proximal Epiphysis**		**Distal Epiphysis**		**Tot.**	
	N.	**%**	**N.**	**%**	**N.**	**%**	**N.**	**%**	**N.**	**%**	**N.**	**%**	**N.**	**%**	**N.**	**%**	**N.**	**%**
C. elaphus	10	19,2	0	0,0	0	0,0	0	0,0	4	13,8	3	13,6	6	42,9	10	26,3	33	21,0
D. dama	42	80,8	1	0,0	0	0,0	1	100	25	86,2	19	86,4	8	57,1	28	73,7	124	79,0
Tot.	**52**	**100**	**1**	**100**	**0**	**0,0**	**1**	**100**	**29**	**100**	**22**	**100**	**14**	**100**	**38**	**100**	**157**	**100**
Indet.	2	3,7	6	85,7	6	100	0	0,0	0	0,0	14	38,9	0	0,0	1	**0,0**	29	15,6
Tot.	**54**	**100**	**7**	**100**	**6**	**100**	**1**	**100**	**29**	**100**	**36**	**100**	**14**	**100**	**39**	**100**	**186**	**100**
AREA 8																		
Taxa	**Intact bones**		**Vertebrae**		**Ribs**		**Antlers/Horn**		**Skull + Teeth**		**Diaphysis**		**Proximal Epiphysis**		**Distal Epiphysis**		**Tot.**	
	N.	**%**	**N.**	**%**	**N.**	**%**	**N.**	**%**	**N.**	**%**	**N.**	**%**	**N.**	**%**	**N.**	**%**	**N.**	**%**
S. scrofa	12	37,5	0	0,0	0	0,0	0	0,0	1	9,1	1	25,0	2	40,0	2	50,0	18	32,1
C. elaphus	5	15,6	0	0,0	0	0,0	0	0,0	10	90,9	0	0,0	1	20,0	1	25,0	17	30,4
D. dama	15	46,9	0	0,0	0	0,0	0	0,0	0	0,0	3	75,0	2	40,0	1	25,0	21	37,5
Tot.	**32**	**100**	**0**	**100**	**0**	**0,0**	**0**	**100**	**11**	**100**	**4**	**100**	**5**	**100**	**4**	**100**	**56**	**100**
Indet.	0	0,0	80	100	46	100	0	0,0	4	26,7	111	96,5	0	0,0	0	**0,0**	241	81,1
Tot.	**32**	**100**	**80**	**100**	**46**	**100**	**0**	**100**	**15**	**100**	**115**	**100**	**5**	**100**	**4**	**100**	**297**	**100**

4.3. Area 5

Area 5 yielded a relatively small assemblage, consisting of only 30 specimens (Table 2), with just 7 taxonomically identified. This area, along with Area 6, represents the context with the lowest number of findings, contrasting notably with the richer assemblages observed in other areas (1-2-3, 4, 7 and 8). Four remains of *D. dama* and two molar teeth from *S. hemitoechus* were found. The number of individuals is very low, with only an adult and a very young one recorded (Table 3). This scarcity of discoveries prompts further investigations into the factors influencing the faunal composition in this specific karst filling.

The low percentage of bones in this deposit is also reflected by the absence of significant taphonomic traces. Only a single Cervidae antler fragment showed gnawing traces by cave hyenas. No other taphonomic traces were found.

4.4. Area 6

Area 6 returned only a single faunal specimen - a cervid antler fragment - with no taphonomic alterations.

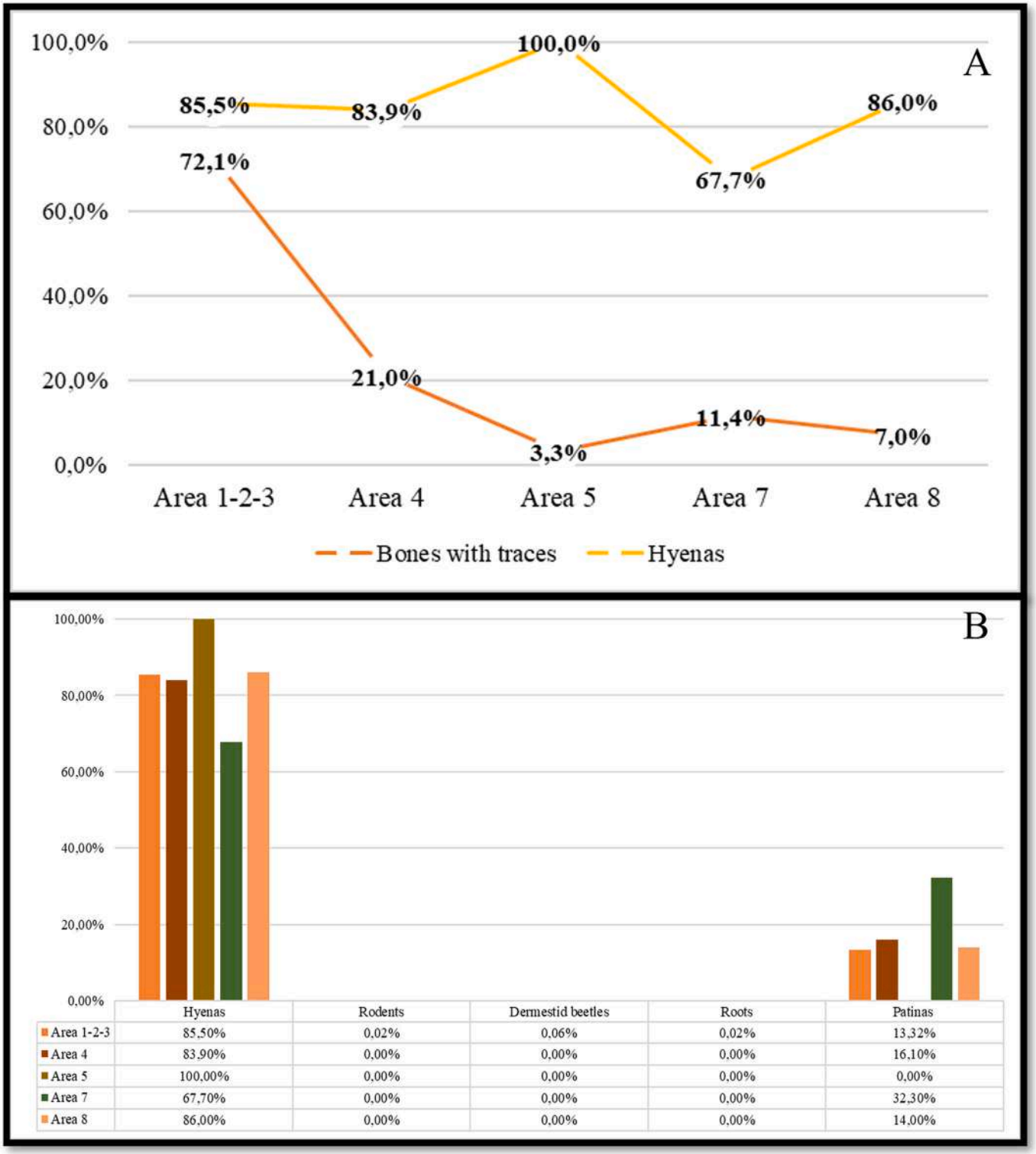
4.5. Area 7

Area 7 yielded a total of 236 mammal remains (Table 2), 88 % of which were taxonomically recognized (=207). *D. dama* was the most common species, followed by *C. elaphus* and, surprisingly, *Lepus* sp., with only a few remains of *E. ferus* and *S. scrofa*. A particularly noteworthy aspect of the analysis is the complete absence of *B. primigenius,* a species that is often predominant in other examined areas. *Crocuta spelaea* is the most represented carnivore, documented by two teeth, a mandible, and a metatarsus. Other carnivore remains include a mandible of *Vulpes vulpes*, a canine of *Ursus* sp., and a canine of *Panthera pardus.* According to the MNI, the age-at-death classes show a similar trend to Area 4, with 9 adults, 6 young and 2 very young (Table 3). The body part composition (Fig. 4) shows an equal percentage of cranial elements (RAI) and short bones (RAVII) for *E. ferus,* while for the other ungulates, the most common anatomical regions are metapodial bones and phalanges (RAVI), followed by long bones (RAV), and a lower percentage of the other anatomical regions. The analysis of fragmentation of body part composition from the main ungulate species of Area 7 (Table 4), compared to indeterminate bones, differs from the other areas, with a preponderance of intact bones on diaphysis fragments.

The analysis of bone surface (Fig. 5) shows that approximately 37 % (=87) of the bones are altered. Hyena gnawing is present on 83,9 % of the bone remains with altered surfaces (=73; Fig. 5). The remaining 16,2 % of traces are attributed to different patinas (Fig. 5), likely due to the chemical composition of the ground, which differs slightly from the other karst caves, featuring pockets of brown soil.

4.6. Area 8

Area 8, the last to be investigated and previously unpublished, stands out as the second richest in faunal remains after Area 1-2-3, with a total of 387 specimens, of which only 37 % have been taxonomically identified (=146). *D. dama* was the most common ungulate, as in Area 7, followed by *C. elaphus, S. scrofa, E. ferus* and a few *B. primigenius* finds. The MNI reveals that *V. vulpes* was the predominant carnivore, represented by a total of 44 skeletal elements, followed by *C. spelaea*, with 21 finds. *Lepus* sp. is present in low percentages. In terms of age at death, Area 8 differs from the other areas (Table 3), showing 7 young specimens, followed by 6 adults, 3 very young and 1 senile individual. The analysis of fragmentation of body part composition for the main



	Hyenas	Rodents	Dermestid beetles	Roots	Patinas
Area 1-2-3	85,50%	0,02%	0,06%	0,02%	13,32%
Area 4	83,90%	0,00%	0,00%	0,00%	16,10%
Area 5	100,00%	0,00%	0,00%	0,00%	0,00%
Area 7	67,70%	0,00%	0,00%	0,00%	32,30%
Area 8	86,00%	0,00%	0,00%	0,00%	14,00%

Fig. 5. Faunal bones with traces from all areas of Cava Muracci. A) Percentage of faunal bones with traces and traces of hyena activity; B) Number of remains divided for all the traces found on the bone surfaces.

ungulate species in Area 8 (Table 4), compared to indeterminate bones, shows a preponderance of diaphysis fragments, followed by a large number of vertebrae and ribs, with nearly all anatomical parts represented.

Surface observations revealed that only 7 % of bone remains had altered surfaces. Evidence of carnivore gnawing is present on approximately 86 % of the bones with altered surfaces (=49; Fig. 5). Patinas are found on 14 % of the altered bones, likely due to the pH of the ground, similar to Area 7.

5. Discussion

The taxonomic and taphonomic analysis conducted across various areas of Cava Muracci has revealed both differences and similarities

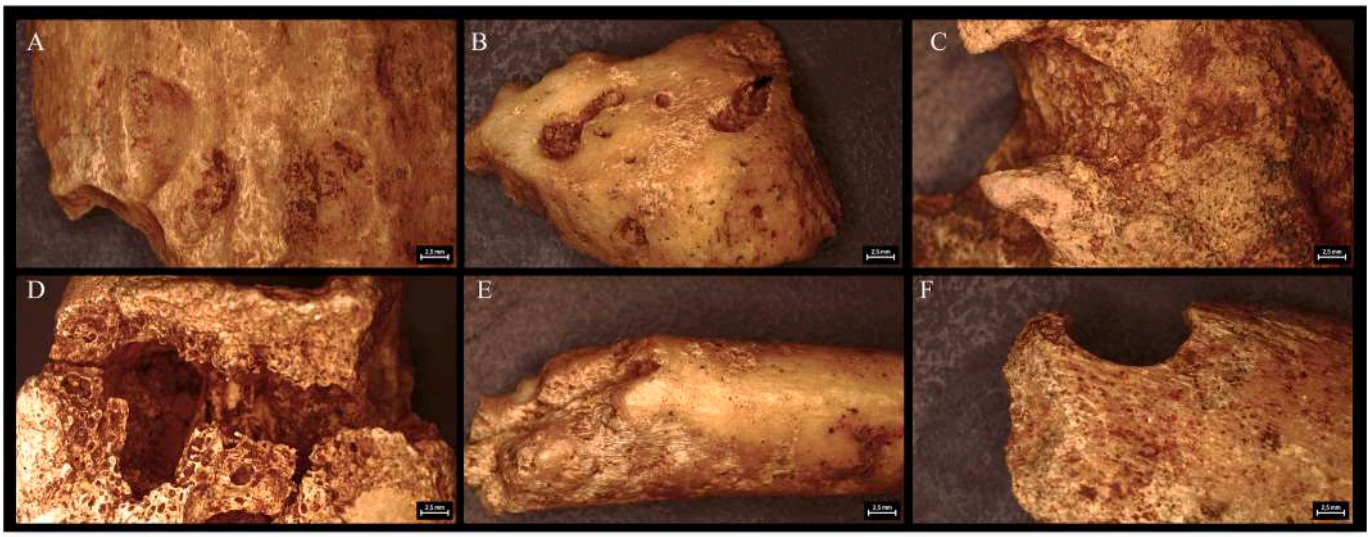


Fig. 6. Faunal bones with traces from Area 3 of Cava Muracci. A-B) Digested; C-D) Gnawed; E) "Nibbling stick"; F) Ichnotraces.

among the karst fillings. Area 1–2–3 shows extensive evidence of hyena activity, including gnawing and digestion traces (Fig. 5; Table 5), as well as the presence of hyena coprolites. These findings, alongside the high concentration of carnivore-altered bones, suggest that this area functioned as a den for cave hyenas. This interpretation was initially suggested during excavation and in earlier studies of Area 3 (Gatta et al., 2016c, 2019, 2021). Cave hyena remains are relatively abundant, ranking as the most prevalent carnivore in the majority of karst fillings, according to the NISP and MNI counts (Tables 2 and 3), with widespread gnaw marks already observed. Several studies have noted strong similarities between these marks and those found in both modern and Pleistocene cave hyena dens, reflecting similar damage patterns and systematic exploitation of specific anatomical parts (Diedrich, 2012a, 2012b; Fosse et al., 2010; Gatta et al., 2019; Stiner, 1991). For instance, severely chewed fallen cervid antlers, a hallmark of Late Pleistocene hyenas (Diedrich, 2014; Lam, 1992) were discovered. Furthermore, over one hundred coprolites, all attributable to cave hyenas (Gatta et al., 2016c), have been recovered form Areas 1-2-3, 4, and 7, with ongoing analysis of three coprolites from SU11 of Area 3 aimed to extract ancient DNA.

The discovery of hyena coprolites, along with neonatal and juvenile cave hyena remains and only a few wolf specimens, strengthens the hypothesis that Area 1-2-3 functioned as a cave hyena accumulation site (Gatta et al., 2016a, 2019; Gatta and Rolfo, 2017). Observations of modern hyenas suggest that this carnivore is usually more interested in the epiphyseal ends than the diaphysis (Arriaza et al., 2019; Faith, 2007; Fourvel et al., 2015; Stewart et al., 2021). The role of wolves in this context is unlikely, given the lower frequency of gnaw marks on diaphysis compared to epiphyses (Yravedra et al., 2011) and the atypical damage to compact bones associated with wolves (Haynes, 1983). Additional support for this interpretation comes from the taphonomic condition of specific anatomical elements, which exhibit damage consistent with systematic exploitation by hyenas (Fernández-Jalvo and Andrews, 2016). The collection and chewing of cervid antlers by cave hyenas during the Late Pleistocene is well-documented (Diedrich, 2014; Lam, 1992), and the gnaw marks on antlers from Cava Muracci resemble those found at other cave hyena dens (Gatta et al., 2022). Furthermore, some partially digested long bone fragments were recovered, and the regurgitation of long bone fragments is typical of medium-to-large carnivores, such as canids, cave hyenas and cave lions during the Late Pleistocene (Kolska Horwitz, 1990). The teething of cubs can produce nibbling sticks, which are fragments of bone or antler chewed intensively with long, deep and narrow striae and triangular or oval marks (Diedrich and Zák, 2006).

The anatomical composition of the main *taxa* (Fig. 4; Table 4) offers valuable insight into cave hyena behaviour in Area 1-2-3. The distribution of anatomical elements suggests that hyenas transported only portions of carcasses or certain parts of preyed or scavenged animals. The overabundance of skull bones, a common trait in carnivore accumulations, is likely due to their low nutritional value and hardness, making them less prone to chewing and thus better preserved in the fossil record. Furthermore, the higher number of diaphysis fragments compared to proximal and distal epiphyses suggests a subsistence strategy focused on gnawing the spongy parts of bones and breaking the diaphysis to access the marrow. The significant number of cervid antler fragments further supports the idea of scavenging shed antlers, a typical behaviour of cave hyenas (Diedrich, 2014; Lam, 1992).

The considerable number of small indeterminate bone fragments (≤5 cm), although not useful for taxonomic identification, revealed widespread gnawing and regurgitation marks. These aspects contribute to understanding the typology of the den to which Area 1-2-3 of Cava Muracci belongs.

Based on studies of similar deposits (Diedrich, 2014; Palomares et al., 2022), cave hyena sites can be classified into several categories:

1) "Feeding shelter" or "Communal den": Areas where carnivores bring prey to consume it safely.
2) "Prey depot" or "Storage den": Locations where prey is stored and consumed over time.
3) "Breeding den" or "Cub raising den": These include natality, breeding or maternity dens. Natality and maternity dens are where females give birth, while breeding dens encompass both natal dens and successive dens where females continue to carry and rear their cubs.

High fragmentation rates are typically associated with "feeding shelter" or "communal den" types (Diedrich, 2011, 2014), where there is an almost complete absence of cubs. However, this classification does not apply to Area 1-2-3 of Cava Muracci, where young cave hyena specimens are abundant. The "prey depot" type, as partially observed at "Antro del Laghetto" deposit in Grotta Guattari (Petronio et al., 2021; Rolfo et al., 2025), together with the "communal den" typology, can also be ruled out, given the lack of key characteristics such as articulated anatomical elements without gnaw marks and the scarcity of coprolites (Diedrich, 2014). The most appropriate classification for Area 1-2-3 of Cava Muracci, is a "cub raising den" or "breeding den", as previously

Table 5
Body parts with gnaw marks from all Areas of Cava Muracci.

	AREA 1-2-3							AREA 4								AREA 7					AREA 8				
Gnaw marks	*E. ferus*	Cervidae	*C. elaphus*	*D. dama*	*B. primigenius*	Indet.	**Total**	*S. hemitoechus*	*E. ferus*	Cervidae	*C. elaphus*	*D. dama*	*B. primigenius*	Indet.	**Total**	Cervidae	*C. elaphus*	*D. dama*	Indet.	**Total**	Carnivora	*E. ferus*	*B. primigenius*	Indet.	**Total**
Horn/Antler		15	48	5	2		**70**			1	1				**2**	4				**4**					**0**
Skull		1	4	1		1	**7**								**0**					**0**					**0**
Maxillary	1						**1**								**0**					**0**					**0**
Mandible			3		1		**4**								**0**					**0**					**0**
Epistropheus					1		**1**								**0**					**0**					**0**
Vertebrae					11	25	**36**							1	**1**				1	**1**				5	**5**
Ribs						22	**22**								**0**				2	**2**					**0**
Scapula					1		**1**					1			**1**					**0**					**0**
Humerus	3		3	1	26	1	**34**				1		1		**2**					**0**			1		**1**
Radius	2	1	5		8		**16**						1		**1**					**0**					**0**
Ulna			1	1	3		**5**				1				**1**		1			**1**					**0**
Radius + Ulna	2				9		**11**		1						**1**					**0**					**0**
Metacarpus	1	1	2	2	24		**30**								**0**					**0**					**0**
Pelvis	6		1		12	1	**20**						1		**1**					**0**		1			**1**
Femur	1		1		11		**13**	1					1		**2**		1			**1**					**0**
Tibia	4		3	1	27		**35**	1			1	1			**3**					**0**			1		**1**
Astragalus	4		1		23		**28**		1						**1**					**0**					**0**
Calcaneus	4				13		**17**								**0**					**0**					**0**
Tarsal bones					2		**2**								**0**					**0**					**0**
Metatarsus	7	1	12	3	28		**51**					2			**2**			1		**1**					**0**
Metapodial bones	3			2	3		**8**								**0**					**0**			1		**1**
Phalanx I	2				1		**3**				1	5			**6**			1		**1**	1				**1**
Indet.						1074	**1074**							37	**37**				5	**5**				39	**39**
Total	**40**	**19**	**84**	**16**	**206**	**1124**	**1489**	**2**	**2**	**1**	**5**	**9**	**4**	**38**	**61**	**4**	**2**	**2**	**8**	**16**	**1**	**1**	**3**	**44**	**49**

proposed for Area 3 (Gatta et al., 2019).

The percentage of bones with surface alterations in each area (Fig. 5; Table 5) shows that cave hyenas more intensively exploited faunal remains in Area 1-2-3 compared to Areas 4, 5, 6, 7 and 8. Areas 4 and 7, where coprolites and juvenile hyena remains have been found alongside traces of cave hyena activity, appear to represent karst systems used by hyenas, but less intensively than Area 1-2-3. In contrast, Areas 5, 6 and 8 seem to have been more affected by natural water flow events, possibly linked to flooding from the nearby Teppia River. Nonetheless, cave hyena remains, including cubs, confirm the presence of this species in the surrounding area. The same suggestion can be made even for the sporadic presence of lithic industries discovered in Area 3, representing different cultures and chronologies (Gatta and Rolfo, 2017). These tools were found on the surface of the cave hyena den, likely deposited either during or after carnivore activity, but before the cave was sealed. This reconstruction is supported by initial trace wear observations (Gatta and Rolfo, 2017), suggesting that the tools were not originally deposited at this site but were transported from nearby locations, which reinforces the hypothesis that humans attended the surrounding area.

Taphonomic observations were supplemented by ternary diagrams (Fig. 7) to assess the mortality profile of *B. primigenius*, the most abundant species from Area 1-2-3 of Cava Muracci. This analysis aimed to support the hypothesis of cave hyena den formation, following an established methodology (Stiner, 1990). Based on the tooth-wear classification (Stiner, 1990), at least sixteen individuals of the species are represented: six young (mainly indicated by left deciduous teeth, d4), 7 adults (identified by lower unworn or slightly worn M3 molars) and 3 old individuals (identified by very worn upper molars).

The ternary diagram of the aurochs' population from Area 1-2-3 of Cava Muracci falls into the living-structure field (Fig. 7). The high percentage of adults closely aligns with those reported for other carnivore accumulations, both from archaeological and palaeontological sites, as well as modern bones accumulations. This suggests an attritional accumulation of skeletal remains from animals that died of natural causes, similar to those observed in several catastrophic death assemblages from Late Pleistocene to recent times sites (Pandolfi et al., 2013; Salari et al., 2019; Stiner, 1990). However, some bone accumulations by opportunistic predators that kill prey based on availability, such as extant lions, humans and, occasionally, wolves and hyenas, are also positioned within this field (Stiner, 1990). Mass mortality can certainly be ruled out in Cava Muracci, as intact bones are rare and anatomical connections are completely absent (Pandolfi et al., 2013). Furthermore, a key role by wolves can be excluded, as the number of gnaw marks on the shafts is lower than those on the epiphyses (Yravedra et al., 2011), and the severity of damage to compact bones observed in the sample is atypical for wolves (Haynes, 1983).

This pattern closely resembles the faunal assemblage from Grotta La Sassa, where a dominance of adult-old prey individuals has been observed (Gatta et al., 2022). In contrast, different mortality profiles of the main *taxa*, such as at Buca della Iena, which show a dominance of young individuals (Stiner, 1990), may reflect a different use of the den.

Although there has been a selection by cave hyenas for certain areas, the ecological characteristics of the identified *taxa*, particularly of the ungulates, and their relative percentages provide valuable clues for a preliminary reconstruction of the environmental landscape and climate of the Pontine Plain during the time of deposition.

B. primigenius preferred open pasture environments as well as wooded areas with clearings and a temperate climate (Conti et al., 2012; Petronio et al., 2008). The presence of *E. ferus* and *S. hemitoechus*, on the other hand, points to extensive steppe and plain grassland with a continental climate (Conti et al., 2010; Pandolfi et al., 2013). Cervids, in general, suggest an open forest environment: red deer thrive in mature

forest, roe deer in dense forest and fallow deer in Mediterranean bush. Notably, red deer are typically dominant in temperate, cold climates (Boitani et al., 2003). *S. scrofa* indicates the presence of marshy areas (Boitani et al., 2003), which were historically common in the region until the mid-20th century. The absence of caprines, such as *Capra ibex* and *Rupicapra* sp., as well as marmots, suggests the lack of extreme climatic conditions (Amori et al., 2008; Boitani et al., 2003). Other *taxa*, such as hares, wolves and bears are adapted to a variety of environments, providing limited additional information for the palaeoecological reconstruction.

Pollen analyses of coprolites from Area 3, with the presence of Poaceae, Amaranthaceae, *Plantago* and *Artemisia* revealed an open environmental landscape dominated by steppes, pastures and arid meadows, with some humidity, highlighted by mesophilous/thermophilous tree curves, which present values up to 10 %, and *Typha*, provided by the presence of freshwater pools and marshes (Gatta et al., 2016c). Small mammals and reptiles from Area 3 have also been studied as part of the environmental reconstruction (Gatta et al., 2019), while ongoing investigations are still underway for the other areas. The inclusion of small vertebrate in the environmental analysis of Area 3 provides a more comprehensive approach to understanding the ecological dynamics of this location. Micro-mammals, due to their smaller size and specialized ecological niches, can offer insights into the past environmental conditions and ecological interactions within the area. Temperate conditions are supported by small vertebrates from Area 3. *Bufotes* sp. and *Microtus (Terricola) savii* indicate the presence of open environments while *Apodemus* gr. *sylvaticus-flavicollis*, *Clethrionomys glareolus* and *Glis glis* prefer forested habitats. The presence of water/humid demanding fauna (i.e. *Bufo bufo*; *Rana* (s.l.); *Anguis veronensis*; *Natrix natrix*; *Arvicola* gr. *Amphibius-italicus*) and some fish remains indicate the presence of water bodies. Finally, it is worth mentioning the presence of *M. (Microtus) arvalis* in SU12 as opposed to *M. (T) savii* in SU11, which suggests a cooler phase during SU12 (Gatta et al., 2019). The environmental reconstruction suggests either significant climatic variability or the varied morphology of the surrounding area, which, like today, changes notably within a few kilometres (Gatta et al., 2016c). Both the pollen and faunal assemblages align with a diachronic or synchronic variability in the environment, respectively linked to the rapid climatic oscillations of MIS 3 or the coexistence of a mixed environment: extensive steppe or meadow areas interspersed with wooded zones containing patches of Mediterranean and mesophilic plants, particularly in the hilly regions. Swampy areas were present along the seacoast and river courses. The climate appears to have been cool and arid, with fauna likely thriving in the steppe, swamp and open forest habitats typical of the small warm and humid fluctuations during the Last Glacial (Gatta et al., 2016c, 2019).

Compared to the higher latitudes of Europe, most of Italy maintained a relatively mild climate and high ecological diversity during the Quaternary cold stages (Riel-Salvatore and Negrino, 2009). The influence of the Tyrrhenian Sea likely had a moderating effect on local climates, adding a layer of complexity to the observed variations in fauna. The environmental conditions of Tyrrhenian Latium during the late Quaternary can be summarized as alternating between two vegetation phases driven by climatic oscillations. One period, marked by the presence of forests during temperate times, contrast with another dominated by open grasslands and steppe during colder intervals (Gatta, 2017). For most of the time, however, the extensive coastal plains resembled today's landscape, featuring wide-open spaces (Follieri and Magri, 2001).

The presence or absence of specific species, as well as their relative abundance, serves as a valuable indicator of the complex ecological dynamics and chronology of the site. Most of the species identified have been present in the Italian peninsula since the Middle Pleistocene. Exceptions include the modern forms of red deer and fallow deer, which are documented only from the Late Pleistocene onwards (Petronio et al., 2019; Di Stefano et al., 2023). *Stephanorhinus hemitoechus* became extinct during MIS 3 (Pandolfi et al., 2017), whereas *Panthera pardus, Crocuta spelaea*, and *Dama dama* disappeared shortly before or during the Last Glacial Maximum. The most recent occurrences of *Equus ferus* are dated to the early Holocene (Petronio et al., 2007; Di Stefano et al., 2023). *Bos primigenius* persisted into historical times, while the remaining taxa are still extant (Petronio et al., 2007; Boitani et al., 2003). The contemporary occurrence of animals such as the cave hyena (Areas 1-2-3, 4, 7, 8), narrow-nosed rhinoceros (Areas 1-2-3, 4, 5), and fallow deer (all areas) is undeniably indicative of a chronological window spanning between MIS 5 and MIS 3 (Di Stefano et al., 2023;

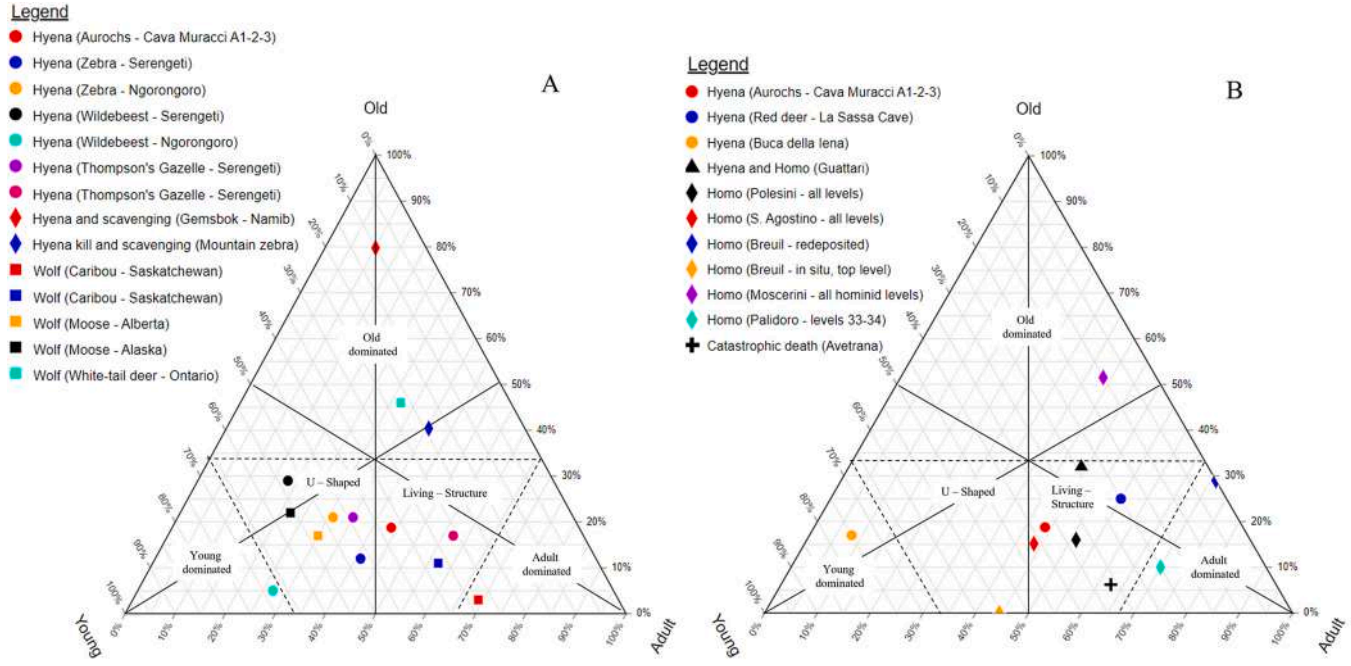


Fig. 7. Ternary diagrams showing the mortality profile of *Bos primigenius* (aurochs) from Area 1-2-3 of Cava Muracci compared with mortality profiles of main preys of extant large carnivores (A) and other Late Pleistocene sites of central and southern Italy (B) (Gatta et al., 2019, 2022; Pandolfi et al., 2013; Stiner, 1990).

Petronio et al., 2007). These species are strongly associated with the Late Pleistocene. Furthermore, faunal deposits with a dominance of red deer over fallow deer likely correspond to a cooler climatic phase, while a dominance of fallow deer may indicate a temperate climatic phase. This observation offers a potential correlation between faunal composition and climatic conditions during the time of deposit formation.

The prevalence of red deer over roe deer in Areas 1-2-3 likely reflects an environmental preference for colder, temperate climates, consistent with the species' distribution patterns in response to varying temperatures. In contrast, the dominance of fallow deer in Areas 5 and 7 points to a milder or warmer climatic context, as this species is more adapted to such environments. Areas 4 and 8, however, show no clear dominance between the two species. Moreover, the absence of *B. primigenius* in Area 7 may suggests variations in habitat or differences in the timing of material deposition. Investigating the reasons behind the absence of certain species, such as *B. primigenius*, is crucial to understanding the ecological dynamics of the context.

The paleoclimatic and paleoenvironmental similarities and differences observed across the various Areas, as mentioned before, may also reflect a chronological bias.

The stratigraphic unit 13 (SU13) has been identified at the base of the paleontological and archaeological deposit in Area 3. This layer consists of volcanic tephra and is not present in other areas of Cava Muracci. The volcanic tephra in Area 3 has been dated to ~69 ka BP (Gatta et al., 2017). Therefore, the absence of this tephra in the other areas suggests that the deposits in those locations are likely more recent than the established date of ~69 ka BP. This tephra layer serves as a definitive *terminus post quem*, marking a chronological boundary for the geological context under examination.

Both Area 1-2-3 and Area 7 fall within MIS 3 based on the radiometric dating of specimens from the corresponding deposits (Table 1). For the other areas, the discovered species align with fauna from the second half of MIS 3, corresponding with the radiometric dating results from Area 3 and Area 7. The interplay between environmental factors, climatic shifts and chronological fluctuation within MIS 3 adds complexity to the interpretation of faunal composition in this karst landscape. These distinctions likely reflect oscillations between temperate-cool and temperate-warm conditions.

6. Conclusions

The Late Pleistocene faunal assemblages from Cava Muracci, consisting of 3011 mammal remains, offer significant insights into the paleoenvironmental conditions and ecological dynamics of the Pontine Plain during MIS 3. The study revealed some differences among the various analysed areas.

Through an examination of the assemblage, spatial analyses and ternary plots, the cave hyena was identified as the primary contributor to the accumulation in Area 1-2-3. Cave hyena appears to have exploited faunal remains more extensively in this area compared to Areas 4, 7, and 8. Areas 4 and 7 can also be interpreted as caves frequented by hyenas, but with less intensity than in Area 1-2-3. Areas 5, 6, and 8 likely represent natural caves or pockets containing residual red soils, debris and faunal remains, which may have been transported by flooding from the nearby Teppia River. This interpretation is supported by the trace wear observed on lithic remains found in Area 3, suggesting that the industries were not originally deposited there but were likely transported from nearby locations.

The taxonomic and taphonomic analyses provide crucial context for interpreting the integrity of the faunal assemblages, aiding in the reconstruction of palaeoecological dynamics and contributing to the understanding of the environmental evolution of the Pontine Plain. This analysis is closely tied to previous researches conducted at other key sites such as Grotta La Sassa (Alessandri et al., 2021; Fiorillo et al., 2024; Gatta et al., 2022), Grotta Guattari (Petronio et al., 2021; Rolfo et al., 2025), Canale delle Acque Alte (Farina, 2011), and Campoverde upper level (Marra et al., 2018; Mazza et al., 1992), all of which are associated with the study of the MIS 5-4-3. These contexts provide valuable insights into the ecological changes that have shaped the Pontine Plain over time, enhancing our understanding of the region's environmental dynamics in a crucial chronological and geographical framework. They also contribute to our knowledge of faunal exploitation patterns by cave hyenas in the Latium region, while offering new perspectives on the interactions between animals during the Last Pleistocene.

Declaration of Generative AI and AI-assisted technologies in the writing process

During the preparation of this work the authors used ChatGPT-4o to improve readability and language. After using this tool, the authors reviewed and edited the content as needed and assume full responsibility for the content of the publication.

CRediT authorship contribution statement

Angelica Fiorillo: Writing – review & editing, Writing – original draft, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Maurizio Gatta:** Writing – review & editing, Validation, Supervision, Formal analysis, Data curation, Conceptualization. **Mario Federico Rolfo:** Validation, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition. **Leonardo Salari:** Writing – review & editing, Writing – original draft, Validation, Supervision, Methodology, Data curation, Conceptualization.

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.

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