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Tracing the Epigravettian in southern Italy. Faunal exploitation in layer M of Grotta della Cala (Cilento, Italy)

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ABSTRACT

Grotta della Cala (Camerota, Campania) is a key site in southern Italy from the Middle Palaeolithic to the Metal Age. Regarding the Upper Palaeolithic, a thick sequence has been preserved in the cave, including Epigravettian layers traditionally attributed to the evolved and the final phases. In this paper, we present the zooarchaeological analysis of the faunal assemblage from layer M (dated between 20,203 and 15,784 cal BP), to shed light on the subsistence strategies of the human groups inhabiting the area during the Greenland Stadial 2. The faunal assemblage included in this study consists of the materials retrieved during the 1967-68 and the 1974 excavation campaigns. The ungulate remains from the 1967-68 assemblage are here reassessed, while new data on carnivores and small mammals are presented. The 1974 assemblage, the larger of the two, is published here for the first time. The taphonomic analysis revealed an intensive exploitation of the carcasses. A correlation was observed between the representation of body parts in red deer (*Cervus elaphus*), the most abundant taxon, and their alimentary utility. Available data on mortality and biometry indicate that hunters primarily targeted young red deer individuals and prime adult males. Hunting was a seasonal activity, as evidenced by the predominance of red deer and wild boar individuals killed during the winter months. This study forms part of a wider project involving the revision of the lithic and faunal assemblages from key sites of southern Italy and contributes to the systematic re-evaluation of Epigravettian evidence in this area.

1. Introduction

The term 'Epigravettian' refers to the post-Gravettian technocomplex that developed in a vast south-eastern part of Europe within the boundaries of the Marine Isotopic Stage 2 (MIS 2; Wolff et al., 2010). In terms of absolute chronology, the Epigravettian encompasses the end of the Last Glacial Maximum and the Late Glacial (henceforth LGM and LG, respectively; Lambeck et al., 2014) and has been commonly related to the dramatic climatic and environmental changes that occurred during this period, characterised by rapid warming (GI-1 Bølling-Allerød) and cooling (GS-1 Younger Dryas), especially in its terminal phase (Naudinot et al., 2017). These transformations affected migratory phenomena, population size, adaptive behaviours, and technical knowledge of modern humans, in parallel with the decline of the pan-European Gravettian technocomplex (Bocquet-Appel et al., 2005; Fu et al., 2016; Gamble et al., 2004; Klein et al., 2020; Naudinot et al., 2017; Peresani et al., 2020; Rasmussen et al., 2006, 2014; Wolff et al., 2010; Tallavaara et al., 2015).

On a European scale, the origin of the Epigravettian has been regarded by some authors as deeply rooted in previous local cultural

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traditions (Palma di Cesnola, 1993; Djindjian et al., 1999). However, this hypothesis still requires support from multidisciplinary research at a regional level, since a close behavioural relationship between the Gravettian and the Epigravettian has not yet been demonstrated across the entire Epigravettian province (Demidenko et al., 2019).

Although difficulties in accurately dating the first appearance of the Epigravettian in Italy persist (Martini and Lo Vetro, 2005) – partly due to significant coastline modifications that occurred during the last millennia of the LGM – it is commonly accepted that the earliest Epigravettian dispersal moved southwards from the northern regions (Cancellieri, 2018; Higgins et al., 2024). In the Italian stratigraphic sequences, the Epigravettian is found in stratigraphic succession to the Gravettian occupations, and sometimes exhibits features that are likely derived from this latter technocomplex. This appears to be particularly evident in the Upper Tyrrhenian area (Palma di Cesnola, 1993).

In southern Italy, on the contrary, Palma di Cesnola identified an abrupt techno-typological transition from the final Gravettian to the early Epigravettian (i.e., the ancient phase according to Palma di Cesnola) in the lithic assemblages along the Apulian Adriatic coast (Palma di Cesnola, 1993). Recent isotopic and genetic studies from this region seem to strengthen this scenario: according to Lugli et al. (2019), isotopic analyses on human remains from Grotta Paglicci (Rignano Garganico, in the Gargano) show significant differences in mobility patterns between the final Gravettian and the early Epigravettian, while genetic data from the Epigravettian infant of Grotta delle Mura (Monopoli, near Bari) suggest the absence of Gravettian-related ancestry in the local Epigravettian populations (Higgins et al., 2024). On the southern Tyrrhenian side of the peninsula, the situation might have been different based on new evidence from Romito 9, a female burial from Grotta del Romito (Papasidero, Calabria) attributed to the Evolved Epigravettian (based on the typological study of the lithic industries at the site), who seems to share biological and cultural affinities with the Gravettian instead (Martini et al., 2026).

Historically, the Italian Epigravettian has been divided into three main phases (ancient, evolved, and final), according to the scheme proposed by G. Laplace (1964, 1997) and adopted by Palma di Cesnola (1993) and Martini (1978, 1981; Martini and Lo Vetro, 2005), mainly relaying on the typological layout of the lithic industries (Laplace, 1964, 1997). However, several scholars have challenged Laplace's model (e.g., Broglio, 1997; Montoya, 2004; Tomasso, 2017), resulting in substantial disagreement about the Epigravettian chrono-cultural partition between northern and southern Italy. In northern Italy, only two main phases (early and late) have been recognised, while in southern Italy the tripartition has been maintained, and the term 'Evolved Epigravettian' is still used to describe a stage chronologically placed between 16,000 and 14,500 uncal. BP and culturally described as a transitional phase between the Ancient and the Final Epigravettian, since it would present features that "partly recall the first and partly already introduce the second" (Palma di Cesnola, 1993, p. 248).

At Grotta della Cala (Camerota, Campania), the lowermost Epigravettian layers, including layer M, have traditionally been attributed to the evolved phase, and an early Epigravettian presence at this site has always been ruled out (Palma di Cesnola, 1993; Martini, 1978). A revision of the Gravettian and the Epigravettian lithic industries from this cave is currently underway (Rossini, 2024; Rossini et al., 2025) using the integrated techno-economic approach proposed by Tomasso (2017, 2021), which focuses on the production systems of the lithic industries and the supply systems of raw materials. It is according to this approach that an early and a late phase have been recognised in the Epigravettian of central and northern Italy, based on the identification of a significant techno-economic change in the lithic assemblages around 16,000 cal. BP (Tomasso, 2017). The first results of the revision of the materials from Grotta della Cala were published in 2025 (Rossini et al., 2025) and made it possible to identify a techno-economic behaviour typical of the early Epigravettian sensu Tomasso (structuring role of personal gears in the organization of lithic production systems and autonomous production of blades and bladelets) in the lithic industry of layer O, previously ascribed to the Evolved Epigravettian (Martini, 1978; Palma di Cesnola, 1993). This allowed the re-attribution of this layer to the early phase (Rossini, 2024; Rossini et al., 2025), confirming the existence of a major shift in the Epigravettian technical systems between the end of the LGM and the core of the LG.

These results emphasise the importance of expanding our knowledge on the Epigravettian hunter-gatherers in southern Italy, focusing on their techno-economic responses to the environment in its broadest sense. This latter aspect is especially pertinent in areas where the severe climatic conditions of the LGM and LG have been mitigated by Mediterranean latitudes, as the Cilento coast, where Grotta della Cala is located, favouring the development of specific and often confined habitats/ecological niches, and ensuring the continuity of human, animal, and plant palaeocommunities and terrestrial ecosystems (Di Pasquale et al., 2020). Achieving this goal requires an integrated multidisciplinary approach to the study of lithic industries, as well as the inclusion of precise faunal and palaeobotanical evidence in the field of investigation.

Given the need to clarify these issues, a wide-ranging project on the Gravettian and the Epigravettian has been promoted by the University of Siena in collaboration with the CEPAM (CNRS, Université Côte d'Azur), with the aim of extending and updating our understanding of subsistence strategies implemented by hunter-gatherer populations living in southern Italy during the LGM and the LG. In addition to Grotta della Cala, the project involves other two key Upper Palaeolithic sites located in Apulia: Grotta Paglicci in the Gargano (Palma di Cesnola, 1993; Dominici et al. 2022, 2023; Dominici, 2024; Rossini et al., 2022, 2023; Rossini, 2024) and Riparo delle Cipolliane in Salento (Gambassini, 1970) (Fig. 1a). The project's main long-term aims are: *i)* to identify whether cultural relationships exist between the final Gravettian and the early Epigravettian; and *ii)* to define the possible existence and, if applicable, the chrono-cultural position of an intermediate stage within the Epigravettian. The zooarchaeological study of animal resources could prove crucial in answering both questions, for its central role in the investigation of the techno-economic behaviours of Palaeolithic societies, including their interactions with the environment, the exploitation of natural resources, and the reconstruction of site function.

The present paper focuses on the taxonomic and taphonomic analysis of the faunal assemblage recovered from the Epigravettian layer M of Grotta della Cala, dated to 20,203 – 15,784 (95,4%) cal BP (n. lab. F-112, Azzi and Gulisano, 1979). The results of the analyses carried out on the faunal assemblage from layer M enabled us to achieve the following for the first time in Campania: *i)* a multidisciplinary view of the faunal association during a phase of the Epigravettian that falls within the boundaries of the Italian early Epigravettian (68.3% 18,978–16,863 cal BP and 95,4% 20,203–15,784 cal BP); *ii)* important data on the unidentified component of the macrofaunal sample; and *iii)* a zooarchaeological evaluation of the faunal assemblage that directly investigates human palaeoeconomic activities.

The results obtained were then compared with those available from other Epigravettian faunal assemblages from southern Italy, in order to identify possible changes in the exploitation of animal resources during this complex period.

1.1. Site presentation and research history

Grotta della Cala is located on the Cilento coast, close to the village of Marina di Camerota (Fig. 1a). Presently, the cave opens a few meters from the coastline, at the base of a rocky complex consisting of reliefs at altitudes between 250 and 500 m above sea level (asl), whereas during the Upper Palaeolithic the lower sea level (about −115,6 m than today in the LGM; Waelbroeck et al., 2002) implied the presence of a plain in front of the cave (Esposito et al., 2003; Sala, 2007; Benjamin et al., 2017). The cavity, which develops in a northerly direction with respect to its entrance (Fig. 1b–d), is composed of two main rooms

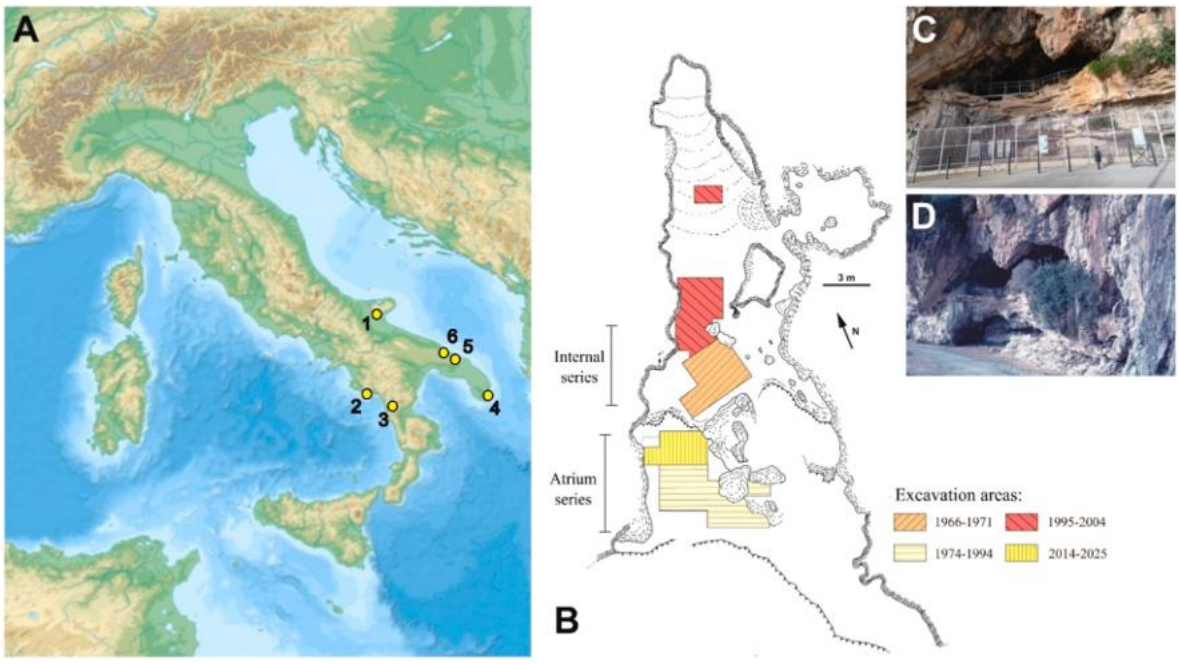


Fig. 1. Grotta della Cala (Camerota, Campania): Location, planimetry, and entrance of the cave. **A**. Geographic location of Grotta della Cala and other archaeological sites mentioned in the text: 1) Grotta Paglicci, 2) Grotta della Cala and Grotta della Serratura, 3) Grotta del Romito, 4) Riparo delle Cipolliane e Grotta Romanelli, 5) Grotta di Santa Maria di Agnano, 6) Grotta delle Mura. **B**. Planimetry of the cave with excavation areas. Modified after Martini et al. (2018). **C**–**D**. Close-up view of the entrance of Grotta della Cala today (**C**) and in the 1960s–70s (**D**).

separated by a bottleneck. Most of the excavation activities were carried out in the first chamber (Fig. 1b).

Systematic research at Grotta della Cala started in the 1960s and was conducted by A. Palma di Cesnola of the University of Siena for the years 1966-1971 in the rear part of the first room (the 'internal series', Fig. 1b). A test trench (trench S, 1.00 × 1.10 m wide × 0.60 m deep) was initially opened in 1966. From 1967, the excavation area was extended up to a total of 12 m^2 (3.80 × 3.20 m wide × 3.00 m deep), by first adding a second trench measuring 1.90 × 1.00 m (trench 1) to the 1966 trench, and then adding a further area that was divided into 4 sectors (*a*, *b*, *c*, and *d*, Fig. 2b; the latter only included the excavation of the Holocene superficial layer A and was left as a reference profile – Martini, 1978; Palma di Cesnola's fieldwork notes 1966-67, unpublished material).

In 1972-1973, the cave was visited by looters, who caused the collapse of the eastern section of Palma di Cesnola's trench. In 1974, P. Gambassini (University of Siena) took on the direction of the excavations. Firstly, he reclaimed the trench from the soil left by the illegal activities extending Palma di Cesnola's trench over an area of 300 × 40 cm, going through the whole series again. This area was horizontally subdivided into three sectors (I, II, III from the outside to the inside; Fig. 2b) and the deposit was excavated in cuts following lithological characteristics (cuts 13-29 for the Epigravettian series, of which 17-21 belong to layer M). Later, Gambassini opened another excavation area located closer to the entrance of the cave (the 'atrium series'), where he excavated the early Gravettian, the Aurignacian, the Uluzzian and the Mousterian occupations. Presently, excavations are ongoing under the direction of one of the authors (A.M.).

The deposit of Grotta della Cala encompasses a time interval that spans from the Mousterian to the Bronze Age. Nonetheless, this cave is particularly notable for its high-resolution Upper Palaeolithic (UP) succession over the last 40,000 years (Higham et al., 2024). A stalagmite crust, called α, sealed the UP deposit, separating it from the overlying Holocene deposit and preserving it from any possible reworking ab antiquo.

To date, the Epigravettian has been exclusively excavated in the internal series, in the years between 1963 and 1974, and includes layers P, O, N, M and layers L-I, H, G, which were formally referred to the evolved and final phases, respectively (Fig. 2a; Martini, 1978, 1981; Palma di Cesnola, 1993). Since then, layer O was reattributed to the Early Epigravettian based on a techno-economic study of the lithic assemblage (Rossini et al., 2025). Layer F was first ascribed by Palma di Cesnola and Martini (1978;1981) to the final Epigravettian. However, in the 2000s, this attribution was challenged by Gambassini, who noted that layer F was in the same stratigraphic position as the Mesolithic layer 7 he had excavated in the area adjacent to the internal trench (Moroni et al., 2016). Therefore, the attribution of layer F remains pending until a complete revision of the materials has been carried out.

Charcoal samples were collected from layers N, M and H for dating (Azzi et al., 1973; Azzi and Gulisano, 1979). These radiometric results are consistent with the stratigraphic sequence and the Italian Epigravettian chronological framework (Table 1).

The 1967-1974 excavations at Grotta della Cala were carried out strictly following the stratigraphic succession and any sedimentological change within the main layers was further detailed by sub-layers/cuts. According to Palma di Cesnola's and Gambassini's descriptions, layer M (20-50 cm thick) was lithologically composed of cemented fine, brown-reddish, sandy-silty sediments, and was separated from the overlying Final Epigravettian deposit by a stratigraphic discontinuity (Palma di Cesnola, 1993, p. 303). The contact with the sandy layer L-I was wavy (Fig. 2c). Layer M was divided into cuts approximately 10-15 cm thick depending on sedimentological features: MI – rich in lithic artefacts, strongly cemented and present all over the excavation area; MII – looser and darker, richer in (often burnt) bones and limited to sector *b*; MIII and MIV – found only in sector *c*, where the layer was thicker than in *a* and *b*; and MV – consisting of a small 'pocket' that penetrated the upper part of N (Martini, 1978; Palma di Cesnola's fieldwork notes 1967, unpublished material; Palma di Cesnola, 1993, p. 256). A lens rich in bones was found in sector II at the top of M, while a 'pavement' of bones was discovered in MIV (Fig. 2a).

Recently, the stratigraphic sequence exposed at Grotta della Cala was investigated from a sedimentological and allostratigraphic point of view

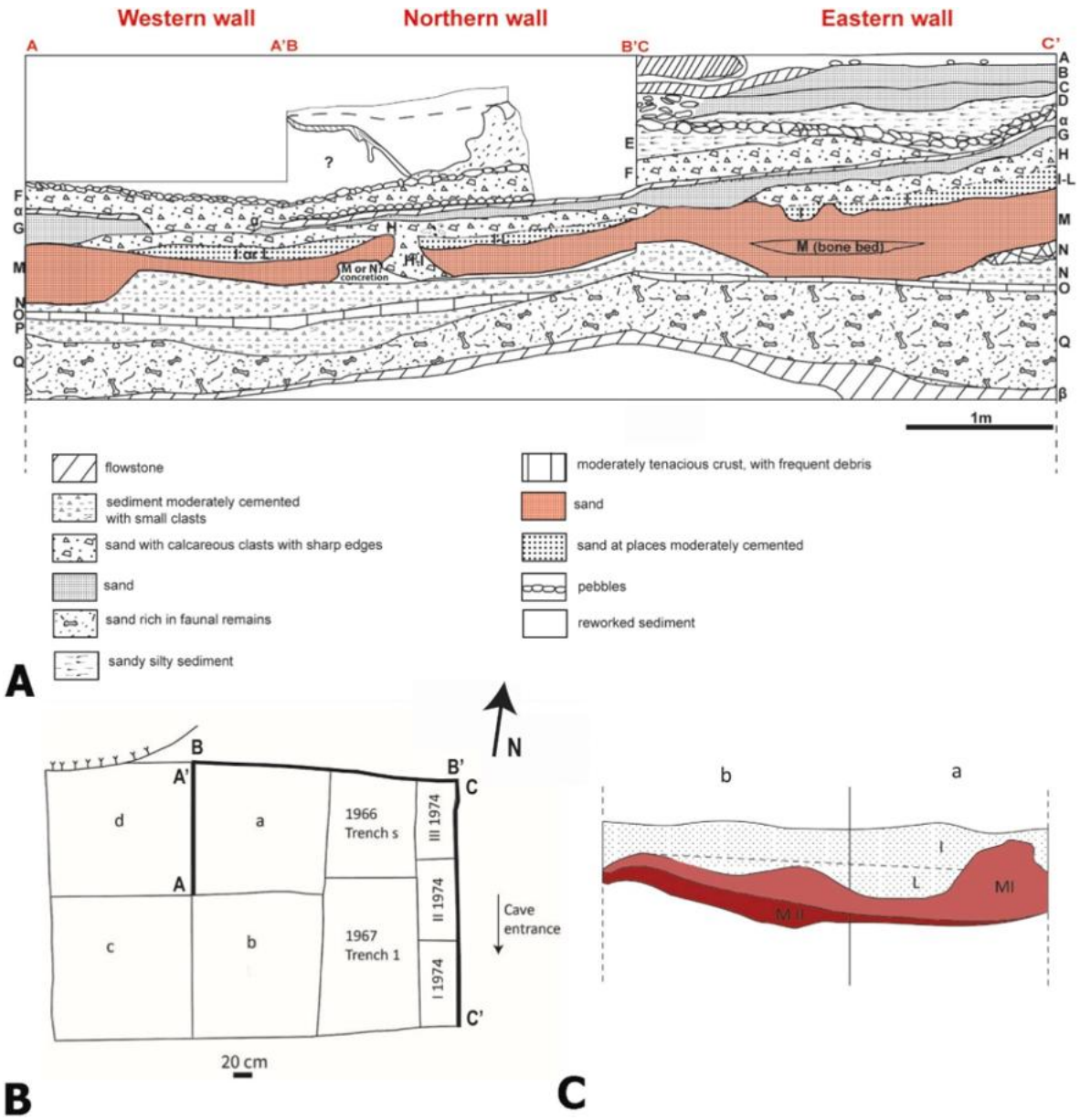


Fig. 2. Profiles and planimetry of the internal series. **A**. Profiles of the Holocene and Upper Palaeolithic layers as seen on the Western, Northern and Eastern walls of the internal series. The symbols used are the same as those used by Gambassini in the original drawings. **B**. Planimetry of the internal trench showing the years in which the different excavation areas were opened. In 1966, a test trench (trench s = 'sondaggio') was opened. During the first systematic excavation season, in March 1967, trench 1 was opened alongside the 1966 test trench. During the second excavation season, in September 1967, the investigated area was widened and divided into four sectors (*a*, *b*, *c*, and *d*). In sector *d*, only the Holocene layer A was excavated, while the Palaeolithic deposit was left in situ (Palma di Cesnola's field notes, 1967; Martini, 1978). In 1974, an area 300 × 40 cm divided into three sectors (I, II and III; 100 × 40 cm each) was added to the previous one (Martini, 1978). Drafted from the original field notes sketch. A-A′ location of the western profile; B-B′ location of the northern profile; C-C′ location of the eastern profile. **C**. N-S profile of layer M as it appeared in sectors *a* and *b* during the 1967 excavation season (modified from Palma di Cesnola's field notes – September 1967).

Table 1
Available radiometric results for the Epigravettian layers of Grotta della Cala in stratigraphic order. Calibration: OxCal v4.4.4 (Bronk Ramsey, 2021). Atmospheric data from Reimer et al. (2020).

Layer	^{14}C age BP	Cal. age BP 95,4%	Lab code	Material	References
N (different cuts)	16,320 ± 850	22,240–18,150	F-113	charcoal	Azzi and Gulisano (1979)
M	14,740 ± 850	20,203–15,784	F-112	charcoal	Azzi and Gulisano (1979)
H	12,030 ± 220	14,845–13,471	F-21	charcoal	Azzi et al. (1973)
H (lower cuts)	12,020 ± 210	14,838–13,463	F-111	charcoal	Azzi and Gulisano (1979)
H (upper cuts)	12,350 ± 250	15,313–13,767	F-110	charcoal	Azzi and Gulisano (1979)

(Martini et al., 2018). The deposit pertaining to layer M, together with the rest of the Epigravettian series, was attributed to the allostratigraphic unit CC2, which shows a variable thickness ranging from 1.20 m (internal series) to 1.60 m (atrium series).

The faunal remains of the Epigravettian layers from Palma di Cesnola's excavations (1967-68) were analysed from a palaeontological standpoint by Bartolomei et al. (1975) and Sala (1983) and then re-examined by Boscato (2000), but were never approached from a zooarchaeological perspective, with the exception of layer O (Rossini et al., 2025). The data presented by Sala (1983) for the entire Epigravettian series show a consistent trend from layers Q (late Gravettian) to M, with a high percentage of deer remains (82–90%), indicating an open forest environment. In layers I to G, a progressive decrease in deer (from 70% in layer I to 44% in layer G) is observed, in favour of taxa indicative of forest environments, such as roe deer and wild boar (Table 2).

The Epigravettian lithic assemblages of Grotta della Cala were published by Martini in 1978 and 1981 according to the typology of Laplace (1964) and were attributed to the evolved (layers P–M) and final (layers L–G) phases of this technocomplex (Martini, 1978, 1981). Specifically, the lithic assemblage of layer M is described as consisting mainly of substratum (side scrapers, points and denticulates), backed pieces (blades, points and backed items with truncation) and end scrapers. Some geometrics were also noticed. Burins, foliates and splintered pieces were scarce. According to the classical tripartition used for the Epigravettian in southern Italy (Palma di Cesnola, 1993), the industry of layer M has been considered a transitional subphase from the evolved to the final Epigravettian due to the decrease in backed pieces with truncation and the increase in geometrics and long end scrapers.

2. Materials and methods

2.1. Materials

The faunal assemblage from layer M is composed of two samples, which were analysed separately. One sample was collected during fieldwork conducted by Palma di Cesnola from 1967 to 1968. At that time, all the fragments that were taxonomically indeterminable were handed over to the local Archaeological Office. The other sample was yielded by the excavation led by Gambassini in 1974 along the eastern wall of the trench to restore the cut profile. The collection procedure from both excavations involved wet and dry sieving by using 1.00 mm meshes, allowing the recovery of meso- and micro-faunal remains from both excavations. Part of the sample excavated by Palma di Cesnola in 1967-68 was curated and studied by Bartolomei et al. (1975) and later published by Sala (1983). The sample currently stored at the University of Siena consists of identifiable remains. This material, already curated as part of the previous study, was recently re-evaluated in relation to biometric analysis (see also Dominici and Boschin, 2025) and age classes, and will be referred to as the 1967-68 sample from now on. The sample excavated by Gambassini in 1974 was studied for the first time between 2019 and 2020 (Dominici, 2020). It consists of both identifiable and unidentifiable materials, coming from an overall area of 1.2 m^2. Given its integrity, the full set of zooarchaeological analyses were carried out on this sample, hereafter referred to as 1974 sample.

Table 2
Faunal composition of the Upper Palaeolithic and Holocene layers of the internal series of Grotta della Cala. Percentage values of ungulate remains from layers Q ÷ F of the internal series of Grotta della Cala and total Number of Remains (NR) per layer, as presented by Sala (1983). Data from layer M are highlighted. *Eh* = *Equus hydruntinus*; *Ss* = *Sus scrofa*; *Bp* = *Bos primigenius*; *Ci* = *Capra ibex*; *Rr* = *Rupicapra rupicapra*; Cap. = Caprinae undet.; *Ce* = *Cervus elaphus*; *Cc* = *Capreolus capreolus*.

Layer	*Eh*	*Ss*	*Bp*	*Ci*	*Rr*	Cap.	*Ce*	*Cc*	Total NR
F	-	39.3	1.8	-	-	10.7	33.9	14.3	**56**
G	-	22.7	-	5.3	5.3	-	44.0	22.7	**75**
H	-	19.0	1.9	0.7	0.7	0.7	60.1	16.8	**268**
I	-	15.4	1.5	-	9.2	1.5	70.8	1.5	**65**
M_{1+2}	-	7.6	0.3	0.8	1.6	-	88.0	1.8	**620**
M_{3+4}	-	8.2	-	1.8	1.4	-	87.5	1.1	**281**
N	-	5.0	1.4	1.4	3.6	-	87.1	1.4	**140**
$N_{I\ e\ II}$	-	6.4	-	1.3	1.6	-	90.4	0.3	**314**
O	-	8.1	2.9	0.6	1.7	-	86.0	0.6	**172**
P	0.2	5.8	1.5	0.6	2.4	0.4	84.4	2.6	**530**
Q_1	-	4.0	1.3	0.5	0.6	-	90.0	3.5	**1105**
Q_2	-	3.9	2.6	0.1	2.1	-	87.0	4.2	**848**
Q_3	0.1	3.6	3.4	0.5	2.2	-	83.8	6.4	**1251**
Q_4	0.1	2.4	2.6	0.7	2.4	-	82.0	10.0	**1012**
Q_5	0.05	2.4	2.0	-	1.4	-	87.5	6.7	**1906**
$Q_{6\text{-}7}$	-	3.1	3.7	0.3	2.3	-	85.5	5.1	**353**

2.2. Methods

2.2.1. Anatomical and taxonomic determination

All the identifiable remains were classified at the anatomical and – when possible – taxonomic level using the osteological reference collection of the Department of Physical Science, Earth and Environment of the University of Siena, in the Research Unit of Prehistory and Anthropology. Two exceptions were represented by the only *Equus* tooth retrieved from the faunal assemblage of the whole layer, whose attribution to *E. hydruntinus* was based on Davis (1980), and a premolar of *Lepus* sp. that was attributed to *L. corsicanus* based on the observation of its cross-section under a portable digital microscope (DinoLite 5 MP Edge Digital Microscope AM-7915MZT) following the method proposed by Vismara (2012) and reported by Boschin (2019).

All chamois remains were formally attributed to the genus *Rupicapra* sp. since no diagnostic bones for species identification were retrieved in the assemblage. Specimens for which it was not possible to discern between *Capra ibex* and *Rupicapra* sp. were attributed to the subfamily Caprinae (Gray, 1821), while all uncertain remains of either *Cervus elaphus*, *Dama dama*, or *Capreolus capreolus* were labelled under the family name Cervidae (Goldfuss, 1820). For all the ungulate remains that could not be identified more specifically, the generic categories 'large ungulate' (LU), 'medium ungulate' (MU), and 'small ungulate' (SU) were used, referring to ungulate remains dimensionally compatible with: *i)* aurochs and wild horse; *ii)* red deer, hydruntine and the juvenile stages of aurochs and wild horse; and *iii)* ibex, chamois, roe deer, wild boar and the juvenile stages of the taxa classified in the MU and SU categories, respectively. The term 'ungulate' (U) was used whenever a dimensional range could not be certainly assigned. The category 'small carnivore' (SC) was used with reference to all the remains dimensionally compatible with *Felix silvestris*, *Vulpes vulpes* and mustelids. The classification of the undetermined remains was made following Boscato and Crezzini (2012).

The localization of the identifiable fragmentary remains of the appendicular skeleton was recorded by dividing each element into numbered areas, based on our own reworking of the tables by Fiore et al. (2003) following Münzel's (1988) proposal.

2.2.2. Quantification of the remains

In addition to the Number of Remains (NR; Lyman, 2008), three zooarchaeological indices were used to quantify the faunal remains: the Number of Identified Specimens (NISP; Lyman, 1994a), the Minimum Number of Elements (MNE; Lyman, 1994b), and the Minimum Animal Units (MAU; Binford, 1984). The NISP is reported for all identified taxa. The MNE was calculated for *C. elaphus* in both samples. The MAU of *C. elaphus* was calculated only for the 1974 sample.

2.2.3. Bone density and food utility of anatomical parts

The relationship between the representation rates of *C. elaphus* anatomical elements in the 1974 sample and bone density was calculated following Lam et al. (1999), using *Rangifer tarandus* density values given the consistency of bone density models among ungulates (Lam et al., 1999). For the same sample, the nutritional value of red deer anatomical parts was calculated using the Food Utility Index (FUI; Metcalfe and Jones, 1988), the Unsaturated Marrow Index (UMI; Morin, 2007), the marrow cavity size of long bones and intact phalanges

(Morin, 2007), and the relationship between the survival rate of long bone epiphyses and their fat yield (following Binford, from Lyman, 1994a). In the FUI, only intact bones were considered (Metcalfe and Jones, 1988). The survival rate of long bone epiphyses was calculated based on their MNE values as: [(*MNE of the single epiphysis/total MNE of the whole element)* × *100*]. The values of the undetermined distal metapodials were equally distributed between metacarpus and metatarsus. Statistical analyses were carried out using PAST (Hammer et al., 2001) and Origin (© OriginLab Corporation).

2.2.4. Taphonomic analysis

Bone integrity was assessed through the categories 'fragmentary', 'almost complete' and 'intact'. Four dimensional classes (1–3 cm, 3–6 cm, 6–10 cm, and >10 cm) were considered in the evaluation of the fragmentation rates of the assemblage and recorded for each specimen. Regarding bone fragmentation patterns, the Fracture Freshness Index (FFI) was applied to identified and undetermined long bones to assess bone freshness at the time of breakage, as proposed by Outram (2002).

Bone modifications were recorded for the 1967-68 sample as well as the 1974 sample, but their percentage incidence was only calculated for the integer sample. Bone surfaces were analysed with a magnifying glass and oblique lighting to detect both natural and anthropogenic modifications. When necessary, bone surface analysis was implemented with a HIROX KH-7700 3D digital microscope and a ZEISS Axio Imager.M2m (magnifications ranging from 2.5× to 10×) following the technical protocols by Boschin and Crezzini (2012) and Duches et al. (2019). Among the natural modifications, exfoliation, concretion, split line cracking, water dripping, and rootlet etching were recorded, as was the presence of rodent or carnivore marks in the form of scoop marks, perforation holes, scratches, chewed edges, or digestion signs (Johnson, 1985). Single or multiple cut marks, bone cones, bone flakes, single or multiple impact points, impact points with recoil, incipient ring cracks, and cone negative scars were recorded among the anthropogenic marks (Johnson, 1985). Thermic exposure was evaluated through the following categories: 0 – absence of combustion marks; 1 – partially burnt remain, 2 – charred remain, 3 – calcined remain.

2.2.5. Biometric analysis

All *C. elaphus* measurements were taken with a Vernier calliper and a measuring box, following von den Driesch (1976) for postcranial bones and Klein et al. (1981) for tooth height. The log ratio method (Simpson, 1941; Simpson et al., 1960) was implemented for biometric comparisons, involving the application of the log formula [log*(measure/standard)*] and the use of reference standards. In this study, the reference standard consisted of average measurements compiled by Bosold (1968) from contemporary central European populations of male red deer. To limit the analysis to fully grown individuals, only the breadth measurements of ossified epiphyses characterised by late fusion were considered, including the distal epiphyses of the metapodials, the proximal epiphyses of the first and second phalanges, the proximal femur, and the distal tibia. A complete list of all measurements can be found in the SI of Dominici and Boschin (2025).

2.2.6. Age determination and death seasonality

Dental use wear stages in *C. elaphus* were recorded following Lowe (1967) for third lower molars (M_3) and Mariezkurrena (1983) for all other mandibular teeth. Teeth wear stages in *S. scrofa* were attributed following Grant (1982). For *C. elaphus*, age determination was based on M_3 wear stages (Lowe, 1967) and crown height of fourth deciduous teeth (dP_4) due to their abundance in the faunal assemblage. The distribution of age classes was then plotted per year, restricting the age range of the dP_4 to the interval between 8 and 24 months based on the crown height (Klein et al., 1981) and considering an equal probability (p) for each observation to fall in the months included in this interval (calculated as: [$p = \text{NISP}_{dP4}/(24 - 8)$]). The number of observations in either the '0–1 years' or the '1–2 years' classes were then calculated as $p \times 4$ (months from 8th to 12th) for the former and $p \times 12$ (months from 13th to 24th) for the latter.

Death seasonality was calculated on lower teeth (both isolated teeth and hemimandibles) following Carter (2002) for *C. elaphus* and Magnell (2002) for *S. scrofa*.

3. Results

The faunal assemblage from layer M consists of 15,544 bone and tooth remains, out of which 14,383 from the 1974 sample and 1161 from the 1967-1968 sample (Table 3). In the 1974 sample, 647 remains were identified anatomically and taxonomically (including genus, subfamily, and family names). The entire 1967-1968 sample was identified at the anatomical and taxonomic level.

3.1. Faunal composition of layer M

Twelve species and one genus were identified in the faunal assemblage, for a total of 13 taxa (Table 3). The most abundant taxon registered was the red deer (*C. elaphus*), representing 85.0% of the NISP (85.9% in the 1967-1968 sample and 83.5% in the 1974 sample). The second most abundant taxon, although considerably less represented, was the wild boar (*S. scrofa*), with 4.7% of the NISP for the entire layer (4.9% in the 1967-1968 sample and 4.2% in the 1974 sample). All other ungulate taxa were represented in minimal numbers (Table 3). Among these, noteworthy is the recovery of a single remain belonging to the genus *Equus*, a first or second lower molar ($M_{1\text{-}2}$) that was attributed to the hydruntine (*E. hydruntinus*) based on the morphological analysis of the lingual groove between the metastylid and the metaconid (Davis, 1980) (n. 290; Fig. 3). Among non-ungulate taxa, lagomorphs represent a special case in the faunal assemblage from layer M, as they were the third most abundant taxon with 3.5% NISP (3.9% in the 1967-68 sample and 2.7% in the 1974 sample). Notably, the presence of the diagnostic criteria for the recognition of the Italic or Apennine hare (*L. corsicanus*) in a lower third premolar (P_3) of *Lepus* sp. (n. 521; Fig. 4)

Table 3
Faunal composition of layer M. The Number of Identified Specimens (NISP) per taxon and the Number of Remains (NR) per category are shown separately for the 1974 sample, the 1967-1968 sample, and layer M as a whole. Percent NISP values (%NISP) were calculated for all identified remains.

Taxon	NISP/NR (1974 sample)	NISP/NR (1967-68 sample)	NISP/NR Layer M	% NISP
Equus hydruntinus	1	0	1	0.05
Bos primigenius	7	5	12	0.66
Capra ibex	9	14	23	1.26
Rupicapra sp.	20	11	31	1.70
Caprinae	2	0	2	0.11
Cervus elaphus	553	997	1550	84.98
Capreolus capreolus	6	16	22	1.21
Cervidae	0	4	4	0.22
Bovidae/Cervidae	15	0	15	0.82
Sus scrofa	28	57	85	4.66
Lynx lynx	1	3	4	0.22
Felis silvestris	1	2	3	0.16
Canis lupus	0	2	2	0.11
Vulpes vulpes	1	4	5	0.27
Meles meles	0	1	1	0.05
Lepus sp.	18	45	63	3.51
Undet.	12,157	0	12,157	
Large ungulate	11	0	11	
Medium ungulate	462	0	462	
Small ungulate	398	0	398	
Ungulate	687	0	687	
Small carnivore	2	0	2	
Carnivora/ Lagomorpha	4	0	4	
Total NR	**14,383**	**1161**	**15,544**	

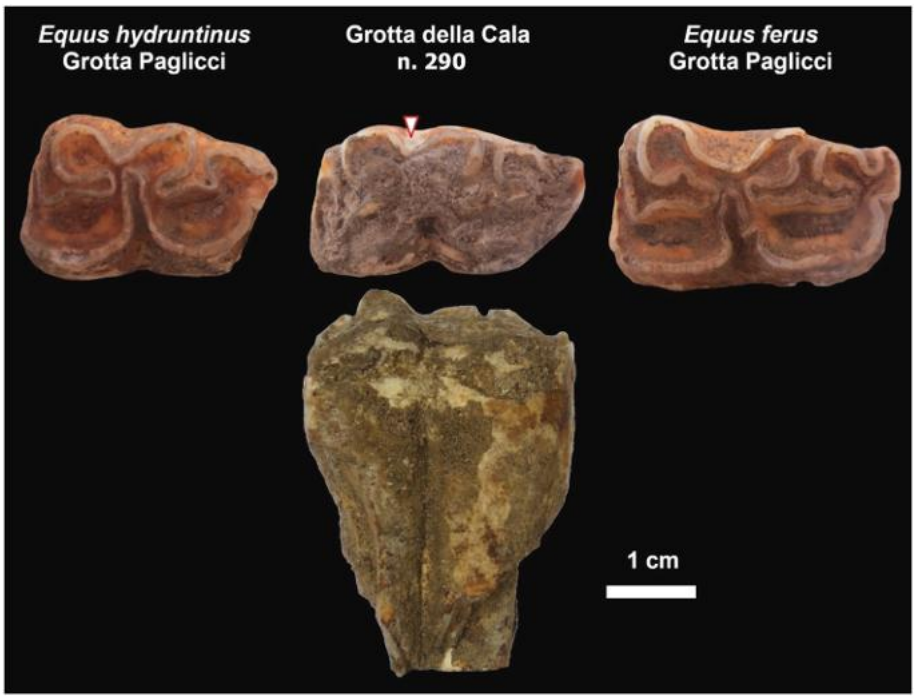


Fig. 3. Determination of the first or second lower molar (M_{1-2}) of *Equus* (n. 290). The comparison of the sole *Equus* specimen recovered in layer M with 2 M of *E. hydruntinus* (left) and *E. ferus* (right) from the Epigravettian layers of Grotta Paglicci (Rignano Garganico, Apulia) illustrates how the shape of the lingual groove between the metastylid and metaconid (red and white arrow in the picture) varies between the two species, allowing the attribution of the specimen to *E. hydruntinus* (Davis, 1980). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

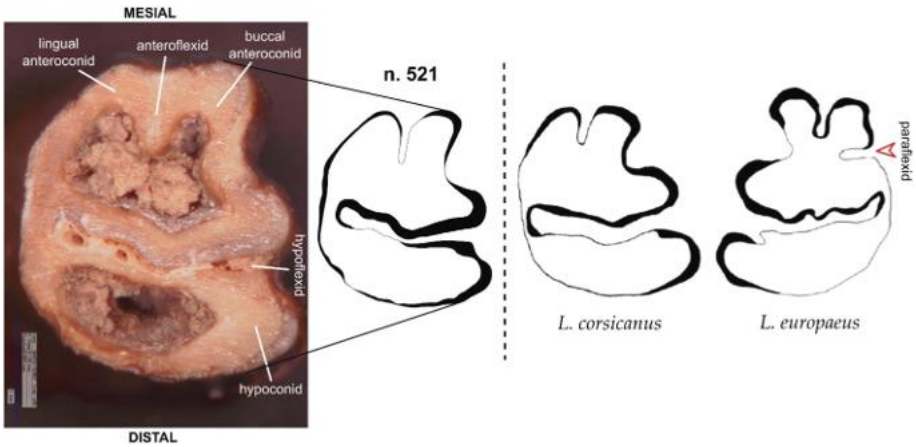


Fig. 4. Determination of the third lower premolar (P_3) of *Lepus* sp. (n. 521). The sole diagnostic specimen of *Lepus* sp. identified in the faunal assemblage, a left P_3, was attributed to *L. corsicanus* following the dichotomous keys proposed by Vismara (2012). The cross-section of the tooth photographed using a Hirox KH-7700 (left) and the outline of its enamel folds (middle) are compared to the outline of two P_3 of *L. corsicanus* and *L. europaeus* (right) (taken from Vismara, 2012). The symmetrical termination of the hypoflexid, no crenulation of the hypoconid, and the absence of a paraflexid on the antero-lingual border of the tooth can all be observed in the specimen from layer M, supporting its attribution to *L. corsicanus* (Palacios, 1996; Vismara, 2012).

allowed for the identification of this species at the site (Vismara, 2012). Among carnivores, the presence of the lynx (*Lynx lynx*), the wildcat (*F. silvestris*), and the fox (*V. vulpes*) was recorded in both samples, while the wolf (*Canis lupus*) and the badger (*Meles meles*) were identified only in the 1967-1968 sample (Table 3).

3.2. Distribution of anatomical parts

The distribution of anatomical parts per taxon for the 1967-68 sample and the 1974 sample are shown in Tables 4 and 5, respectively. The distribution of anatomical parts for the undetermined taxa from the 1974 sample is shown in Table 6 (NR 939). Regarding the anatomically undetermined remains from the 1974 sample (NR 12,797), 35.2% were classified as undetermined fragments, 21.4% as compact bone fragments, 17.5% as flat bone fragments, 15.6% as spongy bone fragments, 10.3% as diaphysis fragments, and 0.1% as epiphysis fragments.

By visually comparing the MNE of the appendicular skeleton of the predominant taxon in the assemblage, *C. elaphus*, in the 1967-1968 and 1974 samples (Fig. 5a and b, respectively), the artificial composition of the former stands out for the sole presence of highly diagnostic elements that were identified on the field. The MAU for the red deer was therefore calculated only for the 1974 sample, as visualized in Fig. 6a (SI Tab. 1). Here, the abundance of mandibular and maxillary remains is related to

Table 4
Anatomical parts of the determined taxa (1967–68 sample). Number of Identified Specimens (NISP) per anatomical element per taxon: *Bp* = *Bos primigenius*; *Ci* = *Capra ibex*; *R* sp. = *Rupicapra* sp.; *Ce* = *Cervus elaphus*; *Cc* = *Capreolus capreolus*; Cer. = undetermined cervid; *Ss* = *Sus scrofa*; *Ll* = *Lynx lynx*; *Fs* = *Felis silvestris*; *Cl* = *Canis lupus*; *Vv* = *Vulpes vulpes*; *Mm* = *Meles meles; Lc* = *Lepus corsicanus*.

Anatomical element	*Bp*	*Ci*	*R* sp.	*Ce*	*Cc*	Cer	*Ss*	*Ll*	*Fs*	*Cl*	*Vv*	*Mm*	*Lc*
antler	-	-	-	5	-	4	-	-	-	-	-	-	-
cranium	-	3	-	36	1	-	-	-	-	-	-	-	1
mandible	1	2	-	68	1	-	8	-	1	-	-	-	3
isolated teeth	1	6	7	416	3	-	26	1	-	-	-	-	22
epistropheus	-	1	-	-	-	-	-	-	-	-	-	-	-
cervical vertebrae	-	-	-	-	-	-	1	-	-	-	-	-	-
thoracic vertebrae	-	-	-	1	-	-	-	-	-	-	-	-	-
lumbar vertebrae	-	-	-	-	-	-	-	-	-	-	-	-	1
sacrum	-	-	-	1	-	-	-	-	-	-	-	-	-
ribs	-	-	-	3	-	-	-	-	-	-	-	-	-
scapula	-	-	-	1	-	-	1	-	-	-	-	-	1
humerus	-	-	-	4	1	-	-	-	-	-	1	-	3
radius	-	-	1	8	1	-	-	-	-	-	-	-	1
radius-ulna	-	-	-	1	-	-	-	-	-	-	-	-	-
ulna	-	-	-	4	1	-	-	-	-	-	-	1	-
carpals	-	1	-	58	-	-	1	-	-	-	-	-	-
metacarpal	-	-	-	20	-	-	1	1	-	-	-	-	2
pelvis	-	-	-	4	-	-	-	-	-	-	-	-	1
femur	-	-	-	5	-	-	-	-	-	-	-	-	-
patella	-	-	-	1	-	-	1	-	-	-	-	-	-
tibia	-	-	1	13	-	-	-	-	-	-	1	-	2
malleolar bone	-	-	-	10	-	-	-	-	-	-	-	-	-
tarsals	-	-	-	39	1	-	3	-	1	-	2	-	4
metatarsal	-	1	-	36	1	-	2	-	-	-	-	-	1
metapodial	2	-	1	31	1	-	1	-	-	-	-	-	-
1st phalanx	1	-	1	91	3	-	2	1	-	2	-	-	2
2nd phalanx	-	-	-	94	2	-	4	-	-	-	-	-	1
3rd phalanx	-	-	-	32	-	-	1	-	-	-	-	-	-
vestigial 1st phalanx	-	-	-	-	-	-	1	-	-	-	-	-	-
vestigial 2nd phalanx	-	-	-	1	-	-	3	-	-	-	-	-	-
vestigial 3rd phalanx	-	-	-	-	-	-	1	-	-	-	-	-	-
sesamoid bones	-	-	-	14	-	-	-	-	-	-	-	-	-
Total	**5**	**14**	**11**	**997**	**16**	**4**	**57**	**3**	**2**	**2**	**4**	**1**	**45**

their quantification based on the association of isolated teeth according to laterality and wear status. Vertebrae, ribs, and scapular and pelvic girdle, on the contrary, are probably underrepresented due to their higher fragility, which likely resulted in their inclusion in the undetermined portion of the sample under the MU or flat bone categories.

The correlation between the representation rates of red deer anatomical parts in the complete sample and their bone density calculated following Lam et al. (1999) (SI Tab. 2) was evaluated to test whether this distribution could reflect natural bone preservation patterns. This correlation was found to be non-significant (Spearman's rank correlation, $p = 0.58$), as evidenced by the plotted values presented in Fig. 6b.

3.3. Taphonomy

In the 1974 sample, 98.7% of the remains were fragmentary, 0.4% were almost complete, and 0.9% were intact. The intact specimens were primarily teeth and small bones, such as carpals, tarsals, sesamoids, malleolar bones, non-fused epiphyses, atrophic phalanges of wild boar and red deer, or first and second phalanges of fox, wolf, wildcat, lynx, and hare. Remains falling in the 1–3 cm dimensional class were the most abundant, accounting for 74.9% of the total, followed by those comprised between 3 and 6 cm at 21.7%. Fragments larger than 6 cm represented 3.4% of the total, with only 0.2% of the remains exceeding 10 cm.

Concretion and exfoliation were mainly identified among natural surface alterations, followed by split line cracking. Plaques of strongly cemented sediment were observed in 93.4% of the faunal remains of the 1974 sample. Exfoliated remains accounted for 25.2% of the total, while cracking affected 15.6% of the remains. Traces of roots-related alterations were observed on two findings. Extremely sporadic rounding phenomena, perhaps due to water dripping, represented the 0.32% of the total remains of the 1974 sample. In the 1967-1968 sample, natural alterations were mainly represented by very hard concretions.

FFI values (Outram, 2002) were assessed for a total of 437 determined and undetermined diaphyses from the 1974 sample, as well as 56 determined diaphyses from the 1967-1968 sample. In the former, 58.4% of the total scored 0, 14.0% scored 1, and 13.0% scored 2 (Table 7). Medium fresh fractures (score 3) accounted for 9.8%, while dry-bone fractures (score 4) and highly dry-bone fractures (score 5) represented 3.7% and 1.1% of the total, respectively. Extremely dry-bone fractures (score 6) were not observed. The general freshness of the fractures observed in the 1974 sample was confirmed by the 1967-1968 sample, in which all the diaphyses considered were assigned FFI values between scores 0 and 2. Notably, this observation extends to the mesofaunal remains: two fox diaphyses (a left humerus and a left tibia) and an undetermined diaphysis of carnivore/lagomorph scored 0, while a right humerus of hare was assigned score 1. A fox tibia exhibiting a fresh fracture, which was caused by twisting processes that have been reported in the literature as being used to disarticulate small game (Boschin, 2019), was also recorded.

Butchering traces were reported in the 1974 sample for a total of 173 observations, out of which more than 50% were bone cones (50.3%) (Fig. 7d). Bone cone (or cone flake) formation can be associated with anthropogenic (i.e., percussion) or carnivore activity (Johnson, 1985). In the present case, the absence of any other evidence of predatory activity (e.g., chewing, gnawing, or bone digestion marks) supported their association with anthropogenic activities. The second most common butchering trace were cut marks (21.4%). The occurrence of single or multiple cut or percussion marks, bone flakes, and impact points with recoil was also reported. Five remains showed impact marks on the same side, among which a red deer metatarsal (Fig. 7a) and a chamois

Table 5
Anatomical parts of the determined taxa (1974 sample). Number of Identified Specimens (NISP) per anatomical element per taxon: *Eh* = *Equus hydruntinus*; *Bp* = *Bos primigenius*; *Ci* = *Capra ibex*; *R* sp. = *Rupicapra* sp.; Cap = Caprinae undet.; *Ce* = *Cervus elaphus*; *Cc* = *Capreolus capreolus*; *Ss* = *Sus scrofa*; *Ll* = *Lynx lynx*; *Fs* = *Felis silvestris*; *Vv* = *Vulpes vulpes*; *Lc* = *Lepus corsicanus*.

Anatomical element	*Eh*	*Bp*	*Ci*	*R* sp	Cap	*Ce*	*Cc*	*Ss*	*Ll*	*Fs*	*Vv*	*Lc*
antler	-	-	-	-	-	1	1	-	-	-	-	-
cranium	-	-	1	-	-	12	-	1	-	-	-	-
mandible	-	-	-	1	-	10	-	2	-	-	-	-
isolated teeth	1	1	6	6	-	147	-	6	-	-	-	4
hyoid	-	-	-	-	-	1	-	-	-	-	-	-
thoracic vertebrae	-	-	-	-	-	-	-	-	-	-	-	2
lumbar vertebrae	-	-	-	-	-	-	-	1	-	-	-	-
sacrum	-	-	-	-	-	1	-	-	-	-	-	-
ribs	-	-	-	-	-	8	-	-	-	-	-	-
scapula	-	-	-	-	-	2	1	-	-	-	-	-
humerus	-	-	-	1	-	12	-	2	-	-	-	1
radius	-	-	-	-	-	10	-	1	-	-	-	2
ulna	-	-	-	-	-	11	-	-	-	-	-	-
carpals	-	-	-	-	-	14	1	1	-	1	-	-
metacarpals	-	-	-	2	-	55	1	6	-	-	-	2
pelvis	-	-	-	-	-	2	-	-	-	-	-	1
femur	-	-	-	2	-	23	1	-	-	-	1	-
patella	-	-	-	-	-	1	-	-	-	-	-	-
tibia	-	-	-	-	-	21	-	-	-	-	-	1
fibula	-	-	-	-	-	-	-	-	1	-	-	-
malleolar bone	-	-	-	-	-	3	-	-	-	-	-	-
tarsals	-	-	1	-	-	10	-	-	-	-	-	1
metatarsal	-	-	-	2	1	78	-	1	-	-	-	2
metapodial	-	1	-	-	-	20	-	4	-	-	-	-
1st phalanx	-	2	-	-	-	7	-	-	-	-	-	-
2nd phalanx	-	-	-	-	-	6	-	-	-	-	-	-
3rd phalanx	-	-	-	-	-	2	-	-	-	-	-	-
phalanx	-	2	1	6	1	85	1	1	-	-	-	2
vestigial 1st phalanx	-	-	-	-	-	-	-	1	-	-	-	-
vestigial 2nd phalanx	-	-	-	-	-	1	-	1	-	-	-	-
vestigial 3rd phalanx	-	-	-	-	-	1	-	-	-	-	-	-
sesamoid bones	-	1	-	-	-	9	-	-	-	-	-	-
Total	**1**	**7**	**9**	**20**	**2**	**553**	**6**	**28**	**1**	**1**	**1**	**18**

Table 6
Anatomical parts of the undetermined taxa (1974 sample). Number of Identified Specimens (NISP) per anatomical element per taxon: B/C = bovid/cervid; LU = large ungulate; MU = medium ungulate; SU = small ungulate; U = ungulate; SC = small carnivore; C/L = carnivore/lagomorph; ND = undetermined.

Anatomical element	B/C	LU	MU	SU	U	SC	C/L	ND
cranium	-	-	-	-	-	-	-	380
mandible	-	-	-	2	8	-	-	21
isolated teeth	15	-	-	-	80	-	-	47
cervical vertebrae	-	-	4	6	-	-	-	-
thoracic vertebrae	-	-	8	4	12	-	-	-
lumbar vertebrae	-	-	14	1	2	-	1	1
caudal vertebrae	-	-	-	-	-	-	-	2
vertebrae	-	-	1	1	11	-	-	1
ribs	-	1	45	139	45	1	1	67
scapula	-	-	-	-	1	-	-	-
humerus	-	-	-	-	1	-	-	-
pelvis	-	-	-	-	1	-	-	-
femur	-	-	-	-	2	-	1	-
tibia	-	-	-	-	2	-	-	-
metatarsal	-	-	-	-	2	-	-	-
metapodial	-	-	1	2	1	-	-	-
1st phalanx	-	-	-	-	1	-	-	-
phalanx	-	-	-	1	2	-	-	-
Total	**15**	**1**	**73**	**156**	**171**	**1**	**3**	**519**

humerus (Fig. 7b). A bone cone in place was also observed on an undetermined diaphysis fragment (Fig. 7c). Multiple well-defined cut marks were recorded on the lingual side of the horizontal branch of a red deer hemimandible from the 1967-1968 sample (n. 1759), possibly relating to the removal of the tongue (Fig. 7e). Except for this case, cut marks on red deer remains from both samples were mainly found on the joints, while impact marks were mainly concentrated along the shafts. In addition to the red deer, butchering traces were recorded also on two chamois (Fig. 7b) and two roe deer remains.

The occurrence of repeated cut marks was recorded also on carnivore remains, specifically a lynx metapodial (n. 1376) and a fractured fox humerus (n. 991): the former shows a single cluster of deep, oblique cuts along the diaphysis (Fig. 8a), while the latter presents very abundant cut marks clustered in several groups along both the diaphysis and the distal joint (Fig. 8b).

Regarding thermic alterations, 95.0% of the remains from the 1974 sample exhibited no evidence of burning (grade 0), while 2.5% were classified in grade 1 (mild thermic activity), 1.4% in grade 2 (strong thermic activity), and 1.1% in grade 3 (extremely intense thermic activity).

3.4. Food utility indices

Given the non-significant correlation between red deer anatomical part distribution and density values in the complete sample, combined with extensive evidence of anthropogenic modification in the faunal assemblage, the correlation between red deer MAU and zooarchaeological indices of food utility for each anatomical part was tested.

Due to its value as a general measure of food utility, the FUI (Metcalfe and Jones, 1988) was tested first (Fig. 9a; SI Tab. 3). Here, a non-significant correlation (Spearman's rank correlation, $p = 0.10$) emerged when considering all anatomical parts together. However, a partial correlation was observed when considering specific anatomical districts singularly (i.e., forelimb, hindlimb, metacarpal, metatarsal, phalanges; Fig. 9a).

In contrast to what observed for the FUI, the correlation of anatomical parts with the UMI (Morin, 2007, Fig. 9b), on the one hand,

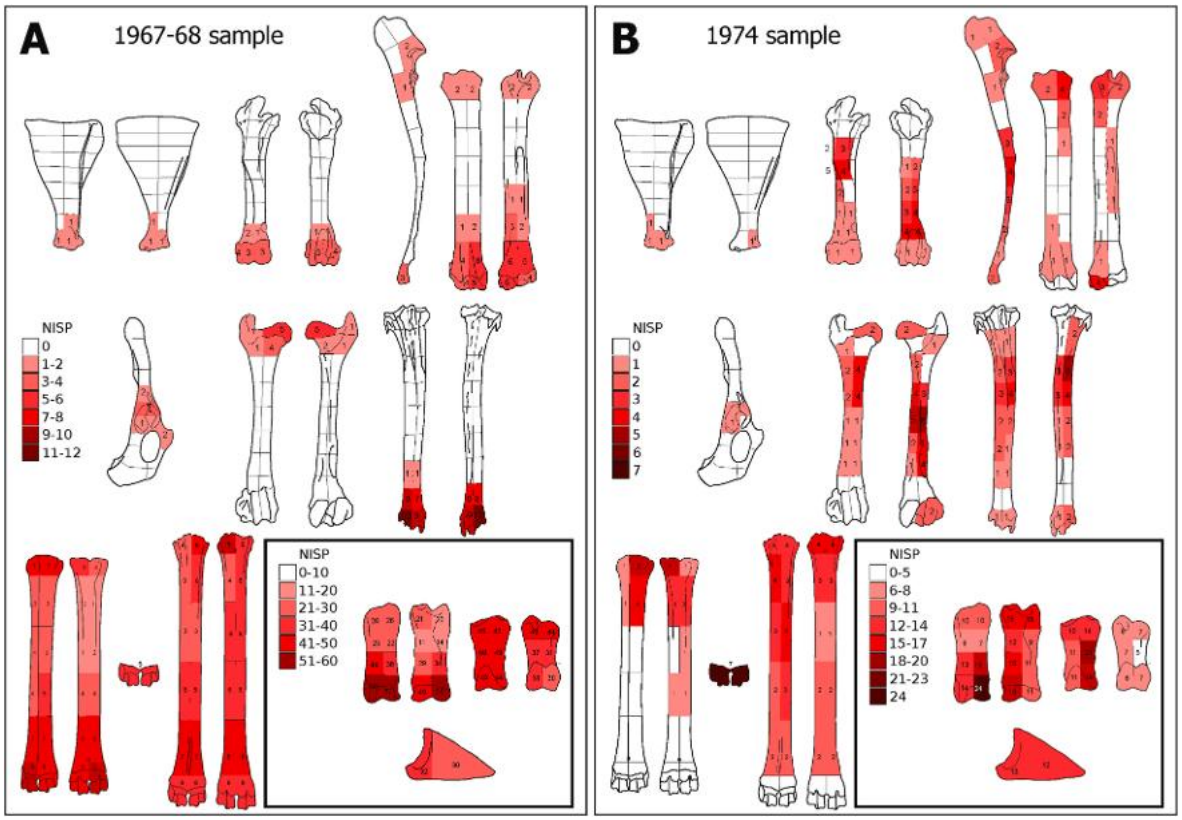


Fig. 5. MNE of the appendicular skeleton of *C. elaphus* (layer M). The comparison between the MNE of the appendicular skeleton of *C. elaphus* in the 1967-68 sample (**A**) and the 1974 sample (**B**) clearly illustrates a different pattern, with the former sample mainly consisting of highly diagnostic epiphyses or fragments of metapodials. Conversely, the 1974 sample is mainly represented by the diaphyses of long bones that were determined in the laboratory.

and the marrow cavity size of long bones and intact phalanges (Morin, 2007, Fig. 9c), on the other hand, was positive and significant in both cases (Spearman's correlation: $p = 0.03$ and $p = 0.02$, respectively; SI Tab. 4).

Lastly, the correlation between the survival rate of long bone epiphyses and their yield in terms of non-marrow fat (Lyman, 1994a) was negative, although non-significant (Spearman's rank correlation, $p = 0.09$) (Fig. 9d; SI Tab. 5). Based on these results, the preferential destruction of the more nutritious epiphyses could have played a side role, given the particularly low p-value recorded in this case.

3.5. Prey selection

Concerning prey selection, a distribution of red deer age classes comprised between 0 and 12 years old was observed, with the occurrence of two main peaks corresponding to '1–2 years' and '4–5 years' classes (Fig. 10). Data on the wild boar showed a broad age range, devoid of any distribution (Table 8).

Data on death seasonality of the red deer indicated that no animals were killed during the summer months, but during the autumn-winter ($n = 6$), winter ($n = 2$), autumn-to-spring ($n = 2$), winter-spring ($n = 1$), or autumn ($n = 1$) months instead (Table 9).

These results were confirmed by the two wild boar specimens that yielded significant data in this regard, namely two dP_4-M_1 associations corresponding to the periods November–May and September–May based on their wear stage (Magnell, 2002).

Lastly, biometric data of certainly adult red deer individuals from both samples were standardised according to Bosold (1968) (SI Tab. 6) and plotted in Fig. 11. Here, the curve trend highlights a significant asymmetry in favour of the largest individuals of the range, indicating their preponderance in the faunal assemblage from layer M.

4. Discussion

The study of the faunal assemblage of layer M of Grotta della Cala yielded a well-defined faunal association for both samples. The most abundant taxon was the red deer, in accordance with what was expected based on the paleontological data already published on part of the materials (Bartolomei et al., 1975; Sala, 1983). The poor representation of all other ungulates – which, with the only exception of the wild boar, display percentages lower than 2% – makes the determined sample extremely homogeneous. Among the non-ungulate taxa, lynx, wildcat, and fox remains were attested in both samples, while the wolf and the badger were only retrieved among the unstudied materials of the 1967-68 sample.

The presence of *Lepus* sp. was significant, being the third most represented taxon in the assemblage. Notably, the Italic hare was attested at the site during the occupation of layer M, thanks to the retrieval of a lower third premolar with preserved diagnostic features (Vismara, 2012). While in agreement with previous findings from late Upper Pleistocene sites in Apulia (Grotta delle Mura and Grotta Romanelli, (Vismara, 2012); Grotta Paglicci, (Boschin, 2019); Grotta di Santa Maria di Agnano – Esterno, (Mecozzi et al., 2025)), this marks the earliest certain attestation of the Italic hare on the Tyrrhenian side of the peninsula. The attribution to the Italic or European hare (*L. europaeus*) has special relevance in Pleistocene contexts since the former has been formally recognised as a distinct species based on both morphometric and molecular evidence only quite recently (Palacios, 1996; Pierpaoli et al., 1999). This implies that, in older taxonomic lists, the attribution to the European hare is not conclusive and hare remains should be considered as *Lepus* sp. until the material is revised (Vismara, 2012; Angelone et al., 2020). The Pleistocene distribution of the Italic hare is also currently not known, as its sole attestations from precise stratigraphic contexts come from Grotta Mora Cavorso (Jenne, Latium)

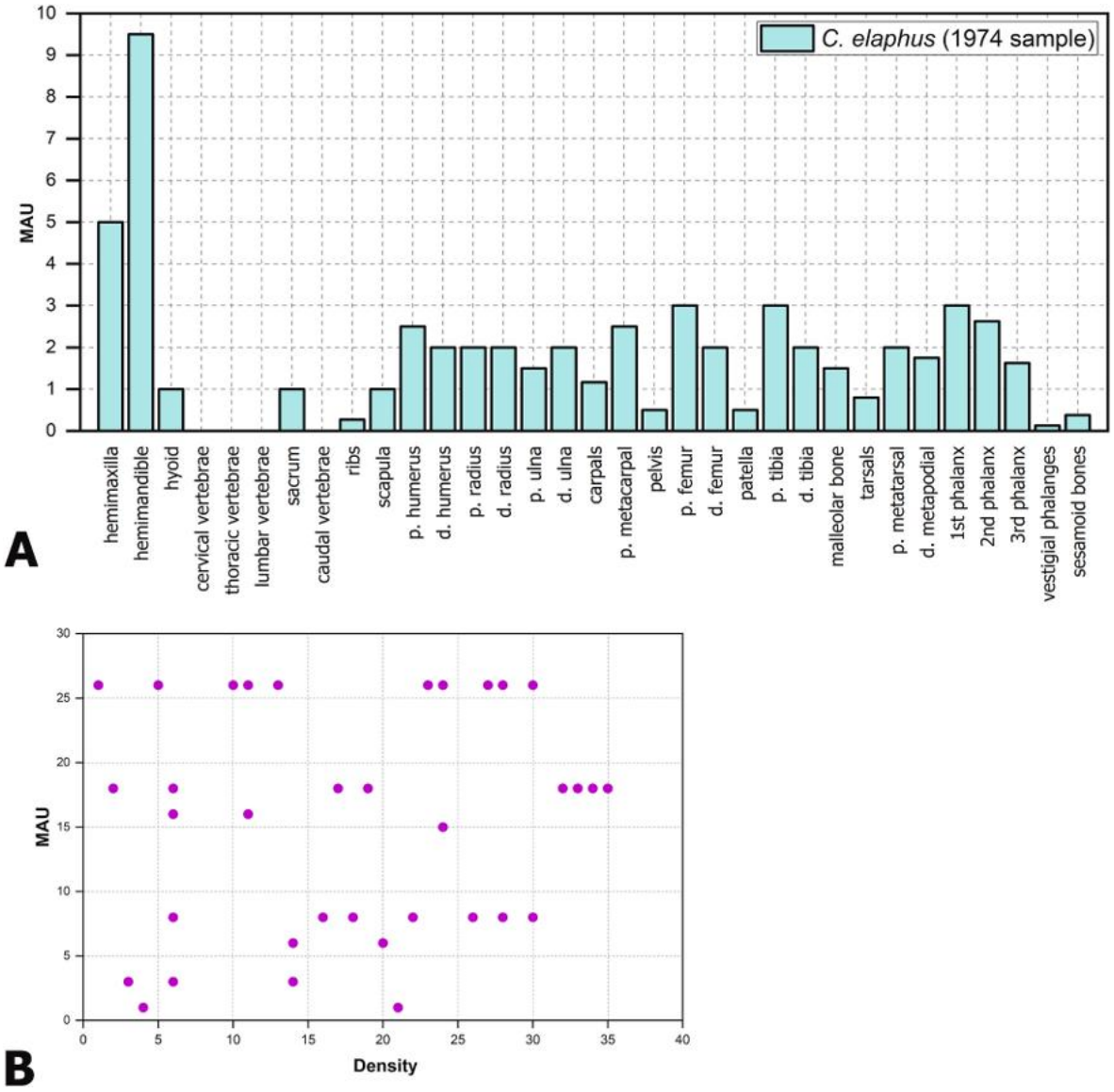


Fig. 6. Minimal Animal Unit (MAU) and bone density of *C. elaphus* (1974 sample). **A** MAU values of *C. elaphus* in the 1974 sample show a relevant number of hemimandibles and hemimaxillae. This is not strange considering that these were quantified based on the association of isolated teeth (according to laterality and wear status). On the other hand, elements of the axial skeleton are likely underrepresented due to their high fragmentation rate. MAU values were calculated following Binford (1984) based on the MNE of all anatomical elements (SI Tab. 1). **B** The relationship between MAU and bone density values of *R. tarandus* (Lam et al., 1999) was non-significant (Spearman's rank correlation, $p = 0.58$), implying that a pattern of natural destruction does not explain the distribution of anatomical parts observed for *C. elaphus* in this sample. MAU and density values were treated with the RANGO.UG function of Microsoft Excel®. Data displayed in this plot are consultable in the Supplementary Information (SI Tab. 2).

Table 7
Freshness of long bone diaphyses at the moment of breakage (1974 sample). The Fracture Freshness Index (FFI) (Outram, 2002) was calculated for a total of 437 diaphyses in the 1974 sample. The results indicate that more than 50% of the remains exhibited signs of extremely fresh fractures (category *0*), while a minimal number exhibited medium fresh to extremely dry-bone fractures (categories *3* to *6*, accounting for less than 15% of the total remains).

FFI	NR (1974 sample)	%NR
0	255	58.35
1	61	13.96
2	57	13.04
3	43	9.84
4	16	3.66
5	5	1.14
6	0	0.00
Total	**437**	-

(Fiorillo et al., 2025)starting from L7 (older than 43,500 BP; Salari et al., 2017), Grotta Paglicci (Boschin, 2019) from layer 17a (20,789–19,952 cal. BP; Boschin et al., 2018), and Grotta di Santa Maria di Agnano (Mecozzi et al., 2025) layer 8 (28,463–27,787 cal. BP), to which add the results of the present study.

The state of preservation of the remains attested to very high levels of tenacious concretion in both sub-samples, in addition to exfoliation and cracking. A limited number of instances of surface rounding and polishing were also documented, unrelated to carnivore activity. These phenomena are likely associated with the percolation of water within the cave system.

No signs of carnivore or rodent activity was detected in the assemblage. In contrast, evidence of intensive human activity was found in remains showing signs of thermal activity and well-preserved butchering traces. The presence of a significant number of cone flakes was particularly noteworthy, suggesting that bone breakage occurred

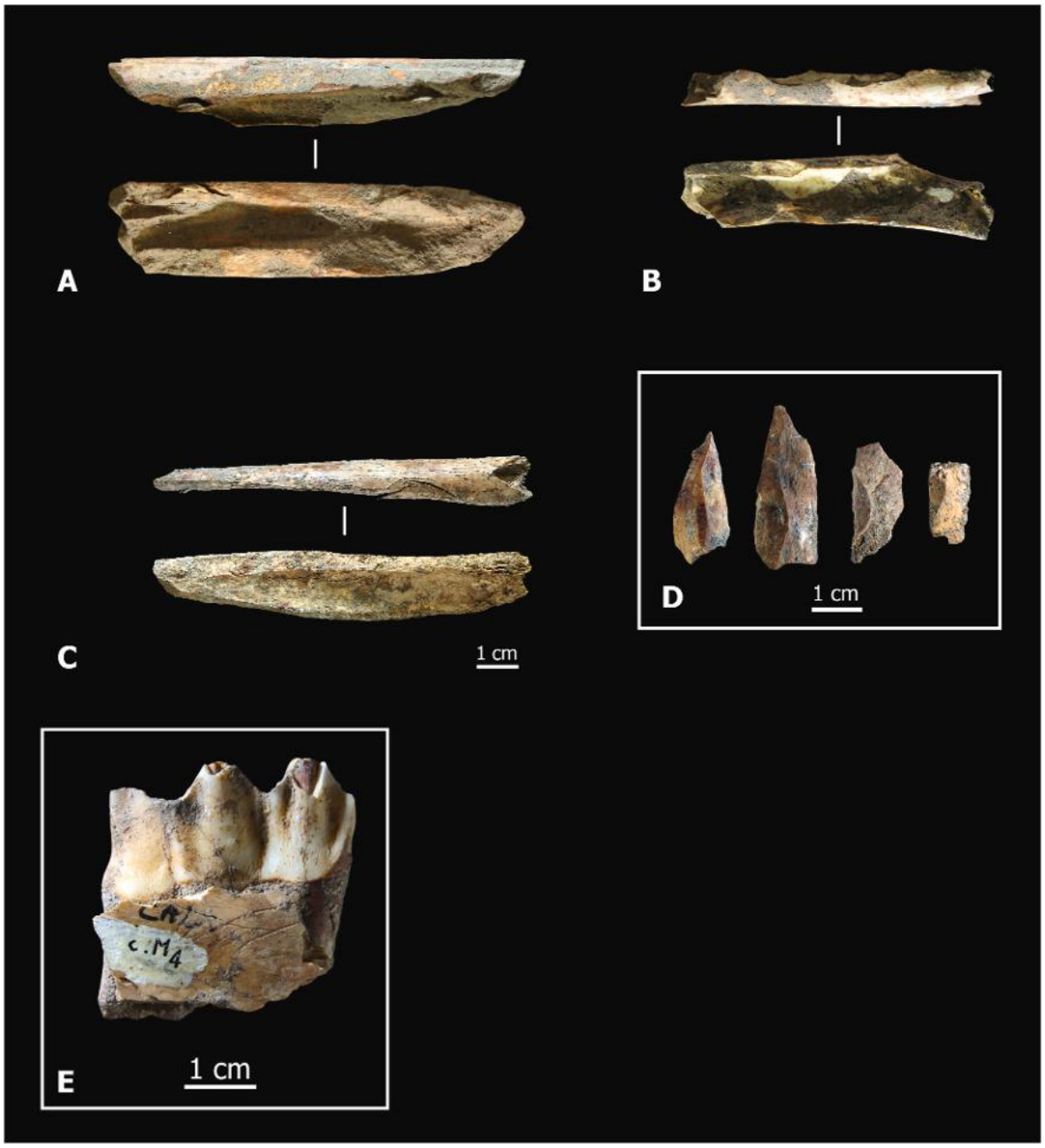


Fig. 7. Anthropogenic modifications on ungulate remains. Among the ungulate remains with butchering traces were recorded: (**A**) a red deer metatarsal with two percussion marks on the same side and recoil on the other side (n. 25); despite the tenacious concretion covering the bone, two cone flakes in place can be observed in correspondence of the blows; (**B**) a chamois humerus with two percussion marks on the same side and rebound on the other side (n. 533); (**C**) an undetermined diaphysis affected by weathering cracks with a cone flake in place showing a fresh bone fracture; (**D**) four examples of bone cones, the most abundant anthropogenic modification registered in the occupation of layer M; (**E**) cut marks on the lingual side of an hemimandible fragment attached to a third lower molar (M_3) from the 1967-68 sample (n. 1759). Photographs courtesy of Stefano Ricci (Università degli Studi di Siena).

regularly in situ. The FFI analysis also provided clear evidence that the bones were fresh at the time of their breakage. The elevated fragmentation rate documented for the assemblage further reinforces this finding.

The presence of a fox humerus and a lynx metapodial bearing clear butchering traces suggests that carnivores were exploited at the site during the occupation of layer M. A fox tibia, which was presumably fractured during the process of disarticulation, was also found. Direct butchering traces were not identified on lagomorph remains, but the presence of a distal humerus exhibiting signs of fresh fracture, as well as a metatarsus with evidence of thermic alteration, were both observed.

When it comes to the exploitation of ungulates, the main considerations apply to red deer and wild boar, as they are the two most abundant taxa registered in the assemblage. In the case of red deer, cut marks were observed close to joints and on the distal portions of the limbs, which often indicates tendon removal. Percussion traces identified on the diaphyses indicate an attempt to break the bone for marrow extraction. Two percussions with recoil – on a femur and a tibia – were likely caused by the use of an anvil (Johnson, 1985).

The lack of correlation between the representation of red deer anatomical parts and their bone density confirms the primary role of anthropogenic activity in the formation of the faunal assemblage. This was furtherly tested through the application of indices to evaluate the food utility of the anatomical parts found at the site. Among these, the

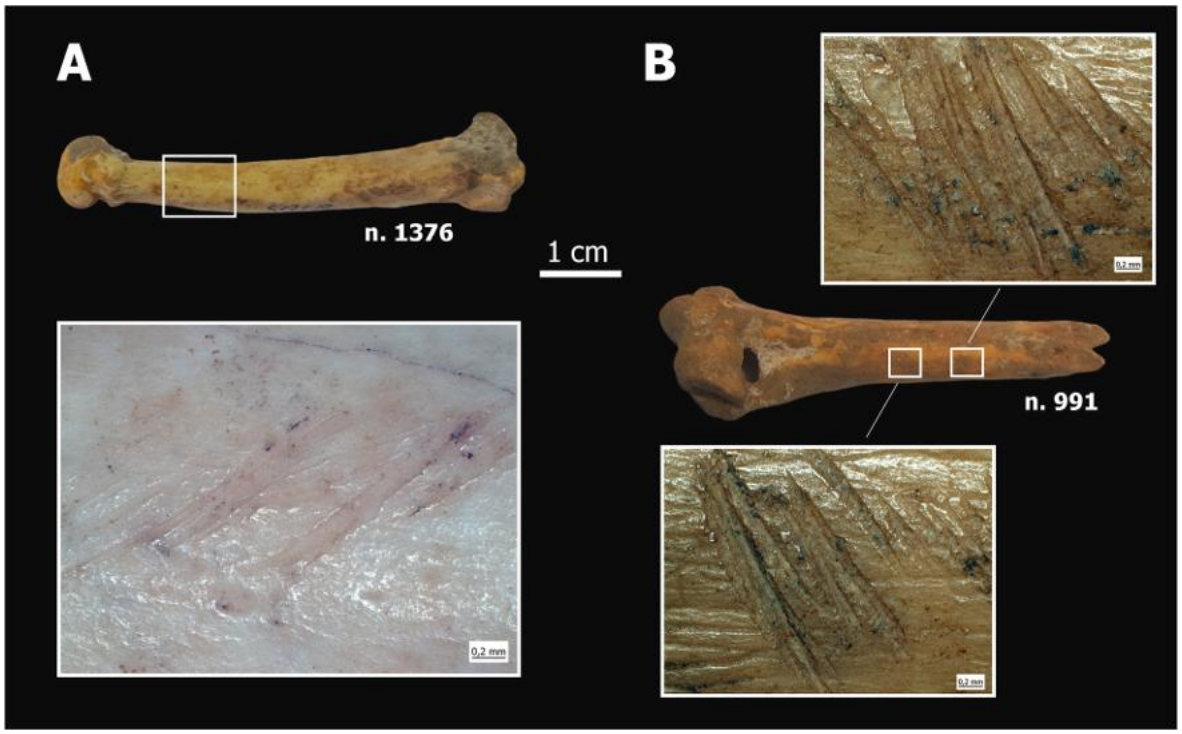


Fig. 8. Butchering traces on carnivore remains. Two carnivore remains with butchering traces were found in the faunal assemblage of layer M: a *L. lynx* metapodial (**A**) and a *V. vulpes* mesio-distal humerus (**B**). Deep, oblique cut marks were found clustered on the shaft of the *L. lynx* metapodial (n. 1376), while several groups of cut marks were observed both on the shaft and different areas of the distal joint of the *V. vulpes* humerus (n. 991). Micrographs were taken with a ZEISS Axio Imager.

correlation between the MAU of red deer and the FUI was not statistically significant. However, it is noteworthy that the hindlimb bones, which have the highest food utility values based on this method, were well represented in the sample. A positive, albeit not statistically significant, correlation was also observed between the MAU and the FUI for the forelimb bones, metapodials, and phalanges. No correlation was observed for the scapula, pelvis, ribs, or head. The correlation of the MAU with the UMI of all anatomical districts, as well as the marrow cavity size of metapodials and phalanges, were both significant and positive. The latter case may suggest that, although metapodials and phalanges are not significant sources of meat, they were transported to the campsite for the quality of their marrow, which is particularly nutritious and rich in fats (Morin, 2007). Overall, it is likely that the entire carcass was usually transported to the site, and the most nutritious anatomical parts were prioritized when multiple prey were killed in the same hunt. This scenario is consistent with the presence of all anatomical parts in the assemblage, with those that are more useful in terms of food utility being more abundant than the others. The correlation between the representation of the epiphyses and their fat yield was not statistically significant. However, the existence of a negative trend suggests the potential for preferential destruction of the ones with the highest nutrient value.

Regarding age classes of red deer, the peak at 4-5 years is consistent with the possible selection of young, solitary adults, which are predominantly male. This finding is supported by the biometric analysis, which revealed a predominance of large-sized individuals. These considerations, together with the fact that red deer males reach their largest size at around five years of age in favourable environments (Mustoni et al., 2002), allow us to hypothesise the selection of *i)* young individuals (aged between 1 and 2 years) in herds led by females, and *ii)* solitary males who recently moved away from their herd, more likely to be inexperienced and easier to catch (Sala, 2000).

Notably, data on red deer seasonality of death indicated that layer M human occupation took place in all seasons except for summer. This is furtherly confirmed by the absence of new-borns hunted during their first summer of life based on the crown heights of the dP_4 (Klein et al., 1981). Therefore, from a taxonomic perspective, it can be concluded that the Epigravettian people who inhabited the site during the occupation of layer M practiced opportunistic hunting, while targeting specific age classes of red deer.

Regarding the wild boar, the only two findings that were suitable for analysis confirmed the seasonality data observed for the red deer, corresponding to the period between September/November and May, once again excluding summer. A lower average age was also observed compared to red deer, although the number of observations is too low to make any assumption. As this pattern may also result from dietary variations (Magnell, 2002), it will not be discussed further.

From a palaeoenvironmental perspective, the prevalence of red deer, in conjunction with the presence of wild boar and roe deer, indicates a humid, forested environment with abundant, albeit open, plant cover. The other identified taxa complement this picture, with the presence of chamois and ibex being linked to the location of the site at the base of a hilly-mountainous area (Boscato, 2000). The presence of the lynx and the wildcat among the carnivores indicates the existence of a forest environment with shrub areas along the coast, as suggested by the presence of the hare, confirming the role of refugium of this area along the Tyrrhenian coast (Di Pasquale et al., 2020). The few remains of aurochs and hydruntine, which are characteristic of open prairies with sparse arboreal coverage and more arid climatic conditions, may be attributable to sporadic hunting activities in the open areas adjacent to the site.

In the Upper Palaeolithic sequence of Grotta della Cala, the interval (layers P, O and N) between the Evolved Gravettian (layer Q) and the Epigravettian occupation corresponding to layer M exhibits notable similarities in its faunal associations, with a high prevalence of red deer (Bartolomei et al., 1975; Sala, 1983; Rossini et al., 2025), which is considered a proxy for colder climate phases in this area (Boscato, 2000). However, beginning with layer L-I (so far considered as Final

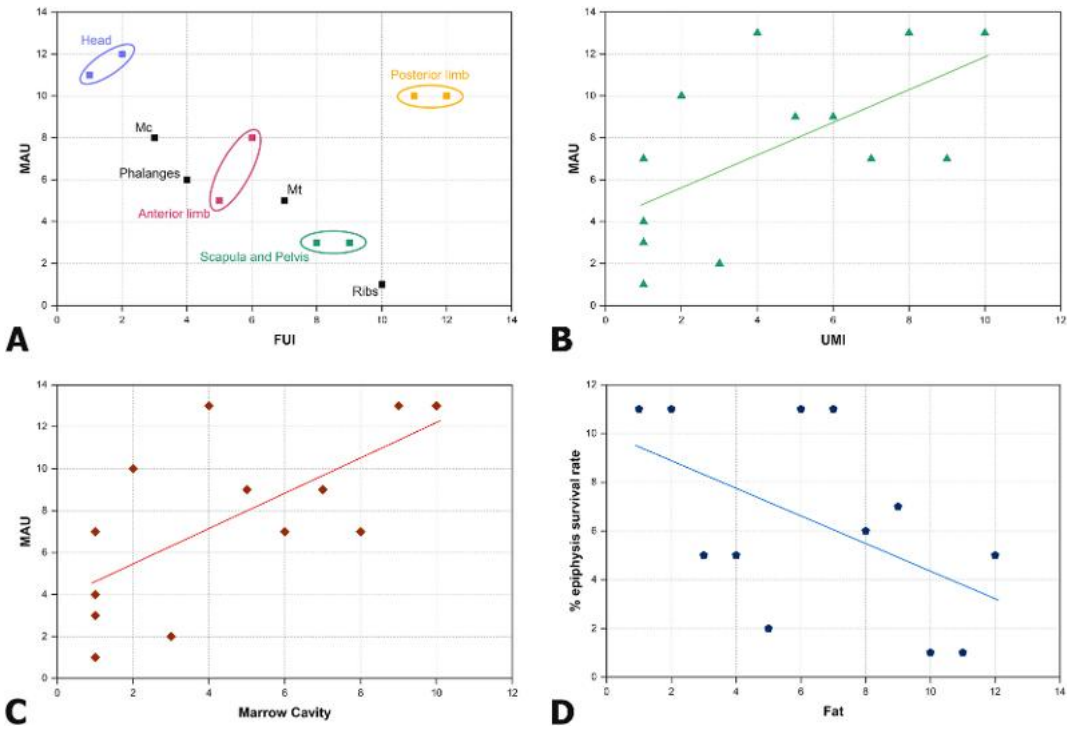


Fig. 9. Food utility of anatomical parts of *C. elaphus* (1974 sample). Based on the non-significant results obtained for bone density (Fig. 7a), four indices were calculated to measure the utility of anatomical parts and were then related to the MAU of *C. elaphus* in the integer sample. The Food Utility Index (FUI) (Metcalfe and Jones, 1988) (**A**) was calculated for all intact bones and gave a non-significant correlation (Spearman's rank correlation, p = 0.10), although a positive correlation was appreciated for some anatomical districts, like the anterior and posterior limbs, the phalanges and the metapodials (*Mc* = metacarpal; *Mt* = metatarsal). The results obtained for the Unsaturated Marrow Index (UMI) (**B**) and the marrow cavity size of long bones and intact phalanges (**C**), both calculated according to Morin (2007) were quite similar one to another: a significant, positive correlation was observed in both cases (Spearman's rank correlation: p = 0.03 and p = 0.02, respectively), indicating a higher representation of those elements whose yield in high-quality marrow is higher. Finally, the relationship between the survival rate of long bone epiphyses and the fat yielded (Lyman, 1994b) (**D**) gave a negative but non-significant correlation (Spearman's rank correlation, p = 0.09). All data here displayed were ranked using the RANGO.UG function of Microsoft Excel® and are included in the SI (SI Tables 3–5).

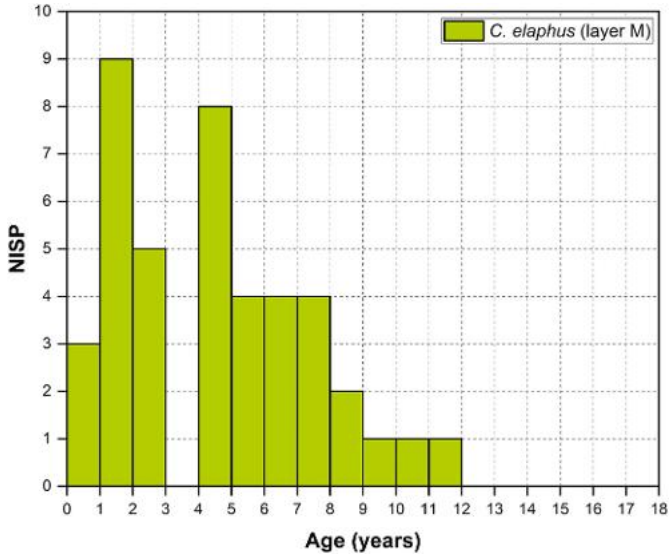


Fig. 10. Age classes of *C. elaphus* (layer M). *C. elaphus* age classes were determined based on the wear stages of lower third molars (M_3) (Lowe, 1967) and the crown heights of lower fourth deciduous teeth (dP_4) (Klein et al., 1981). An age distribution ranging from 0 to 12 years old was observed, with two main peaks corresponding to the 1-2 and 4-5 age groups.

Epigravettian), after a sedimentological discontinuity, a different trend emerged, characterised by a gradual decline in red deer and a substantial increase in roe deer and wild boar (Sala, 1983). These changes suggest a transition to a warmer phase, in which the environment shifted from open to closed more temperate forest (Boscato, 2000). The faunal evidence is corroborated by calibrated ^{14}C ages, which place layer M in correspondence with Greenland Stadial 2 subphases a and b, and layer H in correspondence with Greenland Interstadial 1 subphases e–c (Rasmussen et al., 2014). Therefore, the latter layer developed during the Bølling-Allerød interstadial. According to the faunal association, the most recent Epigravettian layer (G) may also have formed within the Bølling-Allerød interstadial.

A similar pattern emerged from the Final Epigravettian evidence found in the nearby Grotta della Serratura, where the overall

Table 8
Age determination of *S. scrofa* (layer M). The wear stages of the isolated teeth and tooth associations of *S. scrofa* were assigned according to Grant (1982), and the age ranges were attributed according to Magnell (2002). Unlike the observations reported for *C. elaphus* (Fig. 9), these data did not reveal a distinctive distribution pattern. However, the limited number of observations prevents further evaluation.

Teeth wear stages				Age (months)
dP_4	M_1	M_2	M_3	
D	-	-	-	1.5-13.0
-	E	-	-	9.0-36.0
-	C	B	-	14.0-18.0
-	-	-	A	25.0-48.0
-	G	F	-	24.0-60.0
J	C	-	-	7.0-13.0
F	A	-	-	5.0-13.0

Table 9
Death seasonality of *C. elaphus* (layer M). The age range (in months) and corresponding season of death were attributed to all the isolated teeth and tooth associations of *C. elaphus* found in the assemblage (Carter, 2002). The symbol + indicates teeth that were found in association. Two age ranges are reported for two first or second lower molars ($M_{1\text{-}2}$) based on their attribution to the former or the latter case, respectively. Overall, death seasonality corresponding to the winter-autumn months was observed, with no cases corresponding to summer. *Win* = Winter, *Spr* = Spring, *Sum* = Summer, *Aut* = Autumn.

NISP	Element	Age range (months)	Corresponding Season			
			Win	Spr	Sum	Aut
2	$M_{1\text{-}2}$ *if* M_1	4	-	-	-	×
	if M_2	8-12	×	×	-	-
1	$dP_2 + dP_3 + dP_4$	5-8	×	-	-	×
1	$M_1 + M_2$	7-8	×	-	-	-
1	P_3	16-18	×	-	-	×
1	P_2	16-19	×	-	-	×
1	P_4	16-19	×	-	-	×
1	M_3	16-20	×	-	-	×
1	M_3	17-20	×	-	-	×
1	$P_3 + P_4$	18-19	×	-	-	-
4	M_3	27-35	×	×	-	×
1	$M_2 + M_3$	27-35	×	×	-	×

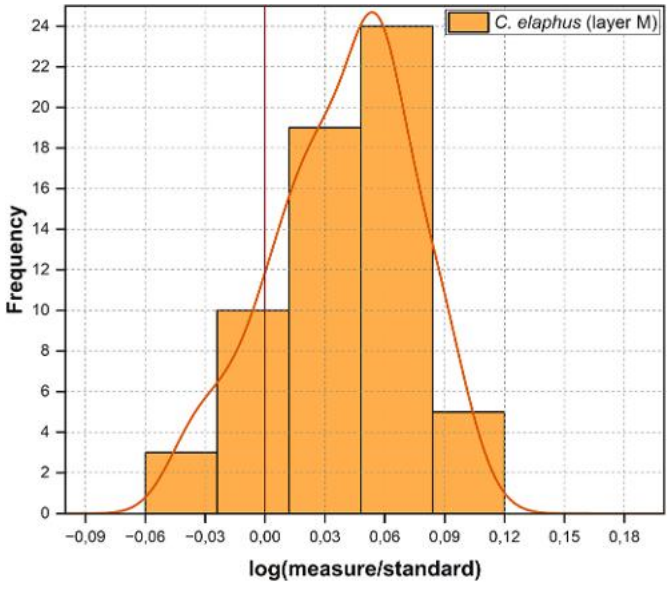


Fig. 11. Biometric data of *C. elaphus* (layer M). Breadth measurements of the distal (*Bd*) and proximal (*Bp*) epiphyses of metacarpals, metatarsals, and 1st and 2nd phalanges (von den Driesch, 1976) were standardised to their equivalent values reported by Bosold (1968) with the log ratio method (Simpson, 1941; Simpson et al., 1960; the vertical red line indicates the reference standard). The Kernel density histogram obtained by plotting the standardised values (bin number = 5) shows a higher representation of large-sized individuals, in good accordance with one of the two most represented age groups recorded in the assemblage (4-5 years, Fig. 9). Data shown in this plot are available in the SI (SI Tab. 6). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

percentages of red deer (59.1%), roe deer (19.9%), and wild boar (17.5%) in layer 8C (13,331–12,987 cal. BP 95,4%) are nearly equal to those recorded in layer H of Grotta della Cala (Hellemans et al., 1993; Ricci et al., 2019). Conversely, the attribution, at the same site, of layer 9 to the Bølling temperate phase on a faunal basis (Ricci et al., 2019) is not consistent with the chronological interval occupied by this layer (16,063–15,302 cal. BP – 95,4%).

The process of change that occurred in the faunal association from layers L-I upwards at Grotta della Cala seems to start between 16 and 15 ka ago, namely approximately during the time span proposed by Tomasso (2017) as a boundary between the Early and Late Epigravettian basing on the techno-economic characteristics of lithic assemblages. Given the current state of knowledge at the site, it is premature to make a correlation between adaptations in techno-economic behaviour, subsistence strategies and environmental changes, due to the need for a more accurate chronological and palaeoecological framework that covers all techno-economic aspects concerning the toolkit, as well as hunting activities including zooarchaeological data, across the sequence. Data emerging from the present study and previous works (Dominici, 2024; Dominici and Boschin, 2025; Rossini, 2024; Rossini et al., 2025) pave the way for a revision of the entire Epigravettian series of Grotta della Cala in this sense.

When evaluated within southern Italy, the scarcity of sites with stratigraphic sequences encompassing the Epigravettian from its early to final phases poses a significant challenge. Among these, the most significant are Grotta del Romito near Cosenza in Calabria (Bertini Vacca, 2012) and Grotta Paglicci in Apulia (Boschin, 2013, 2019; Boschin and Boscato, 2017; Boschin et al., 2018).

Grotta del Romito (Papasidero, Calabria) is situated in the Apennines of northern Calabria at an elevation of approximately 275 m asl and 25 km from the Tyrrhenian coast. The region is distinguished by the presence of mountain ranges that can exceed 2000 m in altitude. Here, an Upper Palaeolithic sequence from the Mid-Late Gravettian to the Late Epigravettian was identified, chronologically included between 27,925 and 12,764 cal. BP (95,4%) (Bertini Vacca, 2012).

The study of the faunal assemblage from the Epigravettian layers revealed the absolute predominance of the ibex (65-80% of NISP) over all other ungulate taxa in both layers F (22,846–20,235 cal. BP) and E (19,476–15,784 cal. BP), reportedly referred to the Early and Middle/Late Epigravettian, respectively (Bertini Vacca, 2012). Beginning with layers D and C, attributed to the Late Epigravettian (15,859–12,853 cal. BP), the wild boar becomes the most abundant taxon, passing from 2% to 35% of NISP and overturning the ibex (31%) (Bertini Vacca, 2012). Data on the exploitation of small mammals and large to medium-sized carnivores are unfortunately not available for this site.

Of the nine human individuals buried at Grotta del Romito, the most ancient specimen is Romito 9, who was found in a pit in layer E16, which was attributed to the Evolved Epigravettian, based on typological analysis of the lithic assemblages. This specimen was directly dated to 17,000–16,150 (Craig et al., 2010) and more recently to 17,047–16,742 cal. BP (95,4%; Martini et al., 2026). Interestingly, Romito 9 exhibits distinct funerary practices and biological traits compared to the Late Epigravettian individuals unearthed at the same site. These differences include dietary habits, as – despite the site's internal location – Romito 9 revealed evidence of the consumption of freshwater and/or marine fish (Craig et al., 2010). Taken together, these data could suggest a behavioural shift and/or different mobility patterns at the boundary between the Early and Late Epigravettian.

The Epigravettian stratigraphic sequence of Grotta Paglicci has been studied in detail for what concerns both large mammal and mesofaunal remains (Berto et al., 2017; Boschin, 2013, 2019; Boschin and Boscato, 2017; Boschin et al., 2018). Grotta Paglicci is located on the southern slope of the Gargano Promontory facing the vast Foggia Plain. This location places the site on the border between two very different environments: the plain to the south and the highlands to the north. These environments were important in determining the type and variety of game available (Boschin, 2013; Dominici et al., 2024). The Epigravettian deposit of this cave was subdivided into 15 main layers (from 17 to 3) dated between 20,000 cal BP (layer 17) and 13,500 cal BP (layer 3). Based on ungulate associations, Boschin et al. (2018) identified four different phases at the site, characterised by the strong predominance of ibex in layer 17 (ca. 20,000 cal. BP), its decrease in favour of the horse in layers 16 to 10b (ca. 20,000–18,500 cal. BP), a new increment of ibex at detriment of the horse in layers 10a to 6d (ca. 18,500–18,000 cal. BP), and an abrupt faunal turnover between layers 6d and 6c. This turning

point, dated to 17,933–16,878 years cal. BP (layer 6, Boschin et al., 2018), opens a last phase that goes from layers 6c to 3a (ca. 18, 000–13,500 cal. BP) and is characterised by a huge increase in wild boar and red deer frequencies, along with the constant presence of the roe deer, an increase of the hydruntine, and the nearly disappearance of both horse and ibex. This last phase aligns with a climatic shift towards more humid and temperate conditions (Boschin, 2013; Boschin et al., 2018). A substantial increment in the exploitation of non-ungulate taxa is also observed at the site towards the end of the Epigravettian, with 45% of total NISP being represented by these taxa in the upper part of the sequence (Boschin, 2019). This progressive increase in the exploitation of non-ungulate resources is peculiar of the Final Epigravettian and has been reported for archaeological sites across the Italian peninsula (Boschin, 2019; Cassoli and Tagliacozzo, 1994; Cassoli et al., 2003; Crezzini et al., 2014; Fiore, 2003; Fiore et al., 2004; Gala and Tagliacozzo, 2012; Mussi et al., 2008; Romandini et al., 2012; Wierer and Boscato, 2006).

The results of the present study can be contextualised to some extent in the whole Epigravettian series of Grotta della Cala based on the paleontological data published by Sala (1983) to draw comparisons to the data from the sites previously mentioned. This is only possible for ungulate taxa, since mesofaunal and carnivore remains from the rest of the series were not encompassed by Sala's work (1983). For what concerns ungulate associations, the faunal assemblage from layer M precedes the environmental turnover evidenced at Grotta del Romito between layers E and D and at Grotta Paglicci between layer 6d and 6c, as seen at Grotta della Cala starting from layer L-I (Sala, 1983). Although data on non-ungulate taxa for the rest of the Epigravettian series from Grotta della Cala are still to be studied, with the exception of those from layer O (Rossini et al., 2025), it is possible to say that the contribution of these resources during the occupation corresponding to layer M was not as substantial as seen at Grotta Paglicci and other Italian sites (Boschin, 2019) in the most recent phase of the Epigravettian. These results further bring the faunal assemblage from layer M closer to an early Epigravettian phase than a recent one.

5. Conclusions

The present study identified humans as the sole accumulation agent for the faunal assemblage from layer M of Grotta della Cala. Red deer predominated within the faunal association. All other ungulate and non-ungulate taxa were scarce. The exploitation of red deer carcasses was characterised by significant marrow extraction activity from long bones. Analysis to determine the age classes and season of death of this taxon revealed a selection for very young individuals and young adults. Seasonality data were also confirmed by the results obtained for wild boar, indicating that the site was occupied year-round, except in summer. The faunal association provided evidence of the presence of arboreal and open spaces in lowland areas that are now covered by the sea.

When the results of the present study are compared to the faunal associations of the entire Epigravettian sequence of Grotta della Cala, the first notable occurrence is the change in red deer percentages at the threshold between the Evolved (layer M) and Final (layers L–I) Epigravettian. From layers L–I onward, a trend towards a decrease in red deer and an increase in wild boar and roe deer is observed. This trend presumably began at the site around 16,000–15,000 years ago and reached its peak in the more recent Epigravettian layer G, for which a terminus post quem is represented by the absolute dating from layer H. This indicates a shift to stable temperate climatic conditions. Even considering the differences due to the variety of ecosystems present in the southern part of the peninsula, a similar pattern was recorded at other sites during the transition from earlier to later phases of the Epigravettian, with special reference to Grotta del Romito in Calabria and Grotta Paglicci in Apulia. Although it is too early to establish a correlation between pieces of evidence operating at different resolution scales – mainly due to the current scarcity of available studies – there is concrete evidence indicating that a series of human behavioural modifications occurred around 16,000–15,000 years ago, at the onset of the climate change that led to the establishment of the more temperate GI-1 (Bølling-Allerød) conditions.

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Declaration of competing interest

All authors have participated in (a) conception and design, or analysis and interpretation of the data; (b) drafting the article or revising it critically for important intellectual content; and (c) approval of the final version.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.quascirev.2026.110169.

Data availability

All data and/or code is contained within the submission.

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