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The cave hyena den of Grotta Guattari (San Felice Circeo, central Italy): first faunal and environmental data from the MIS 4 deposit

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The cave hyena den of Grotta Guattari (San Felice Circeo, central Italy): first faunal and environmental data from the MIS 4 deposit

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ABSTRACT

Grotta Guattari (San Felice Circeo, central Italy) is a key site of Italian and European prehistory. The cave was a Late Pleistocene hyena den that became famous in 1939 following the discovery of one of the best-preserved Neanderthal skulls in the World. New archaeological investigations were carried out between 2019 and 2023 in a peripheral chamber previously unexcavated, known as the *Antro del Laghetto*. Thousands of bone remains, tens of coprolites and a small lithic collection were recovered from a deposit dating to 66-65 ka. This paper presents the archaeological investigations conducted and the recently uncovered large mammal assemblage. Taxonomic and taphonomic analyses allowed us to identify at least 25 different taxa, some of which had never before been recorded at this site, and which were hunted or scavenged and transported by cave hyenas. However, for the first time at Grotta Guattari, cut marks were identified on two bones, prompting further investigation into the possible human role at the site. On this topic, the discovery of several fragmented Neanderthal bones displaying evidence of gnawing is particularly noteworthy. The palaeoecology of the identified taxa provides an opportunity to propose an environmental reconstruction of the area at the end of MIS 4. This study highlights that this coastal region was characterised by different habitats, within which several faunal and floral species survived minor climate oscillations, probably due to the climate mitigation provided by the Tyrrhenian Sea.

KEY WORDS
Late Pleistocene,
large mammals,
Homo neanderthalensis,
Crocuta spelaea,
taphonomy,
paleoenvironment.

RÉSUMÉ

La tanière des hyènes de Grotta Guattari (San Felice Circeo, Italie centrale) : premières données fauniques et environnementales du dépôt du MIS 4.

La Grotte Guattari (San Felice Circeo, Italie centrale) est un site clé de la préhistoire italienne et européenne. La caverne était une tanière de hyènes du Pléistocène Supérieur qui devint célèbre en 1939 à la suite de la découverte d'un des crânes de Néandertal les mieux conservés au monde. De nouvelles fouilles archéologiques ont été menées entre 2019 et 2023 dans une chambre périphérique jusqu'alors non fouillée, connue sous le nom d'*Antro del Laghetto*. Des milliers de reste osseux, des dizaines de coprolithes et une petite collection lithique ont été récupérés dans un dépôt datant de 66-65 ka. Cet article présente les recherches archéologiques menées et l'assemblage de grands mammifères récemment mis au jour. Les analyses taxonomiques et taphonomiques nous ont permis d'identifier au moins 25 taxons différents, dont certains n'avaient jamais été observés sur ce site, qui ont été chassés ou charognés et transportés par les hyènes des cavernes. Cependant, pour la première fois à Grotta Guattari, des marques de coupure ont été identifiées sur deux ossements, ce qui a incité à poursuivre les recherches sur le rôle possible de l'homme sur le site. La découverte de plusieurs ossements fragmentés de Néandertaliens présentant des traces de rongement est particulièrement intéressante à cet égard. La paléoécologie des taxons identifiés permet de proposer une reconstruction environnementale de la région à la fin du MIS 4. L'étude a mis en évidence que cette région côtière était caractérisée par différents habitats, au sein desquels plusieurs espèces fauniques et florales ont survécu pendant de légères oscillations climatiques, probablement en raison de l'atténuation climatique apportée par la mer Tyrrhénienne.

MOTS CLÉS
Pléistocène supérieur,
grands mammifères,
Homo neanderthalensis,
Crocuta spelaea,
taphonomie,
paléoenvironnement.

INTRODUCTION

The Circeo Promontory is mainly known for the discovery of several Neanderthal remains in three cave sites (Grotta del Fossellone, Grotta Breuil and Grotta Guattari; Blanc 1939a, b, 1940, 1954; Blanc & Segre 1953; Alhaique *et al.* 1998a). However, several other highly significant Late Pleistocene fossiliferous sites have also been discovered and studied in this area (e.g. Grotta del Fossellone, Grotta delle Capre, Grotta Barbara, Grotta Breuil and Grotta Elena beyond Grotta Guattari; Blanc 1937, 1938, 1939a, c, 1954; Blanc & Segre 1953; Caloi & Palombo 1987, 1989, 1991; Alhaique *et al.* 1996, 1998a, b; Kotsakis 1991; Ruffo & Zarattini 1991; Stiner 1991a, b; Recchi 1995; Petronio *et al.* 2021) and elsewhere in the Pontine Plain (e.g. Canale Acque Alte, Campoverde, Cava Muracci and Grotta la Sassa; Blanc 1935; Farina 2016; Marra *et al.* 2018; Gatta *et al.* 2019, 2021, 2022).

The Pontine Plain, the region within which the Circeo Promontory is located, has an outstanding number of prehistoric sites. Approximately ninety open-air sites (Kuhn 1995; Rolfo *et al.* 2022) and eight cave sites have been discovered within a relatively small area of approximately 1 000 km^2 (Fig. 1). This context allowed researchers to reconstruct the dynamics of human and faunal populations over a chronological period that encompasses the entire Late Pleistocene. Unfortunately, open-air sites only yielded lithic artifacts and geochronological

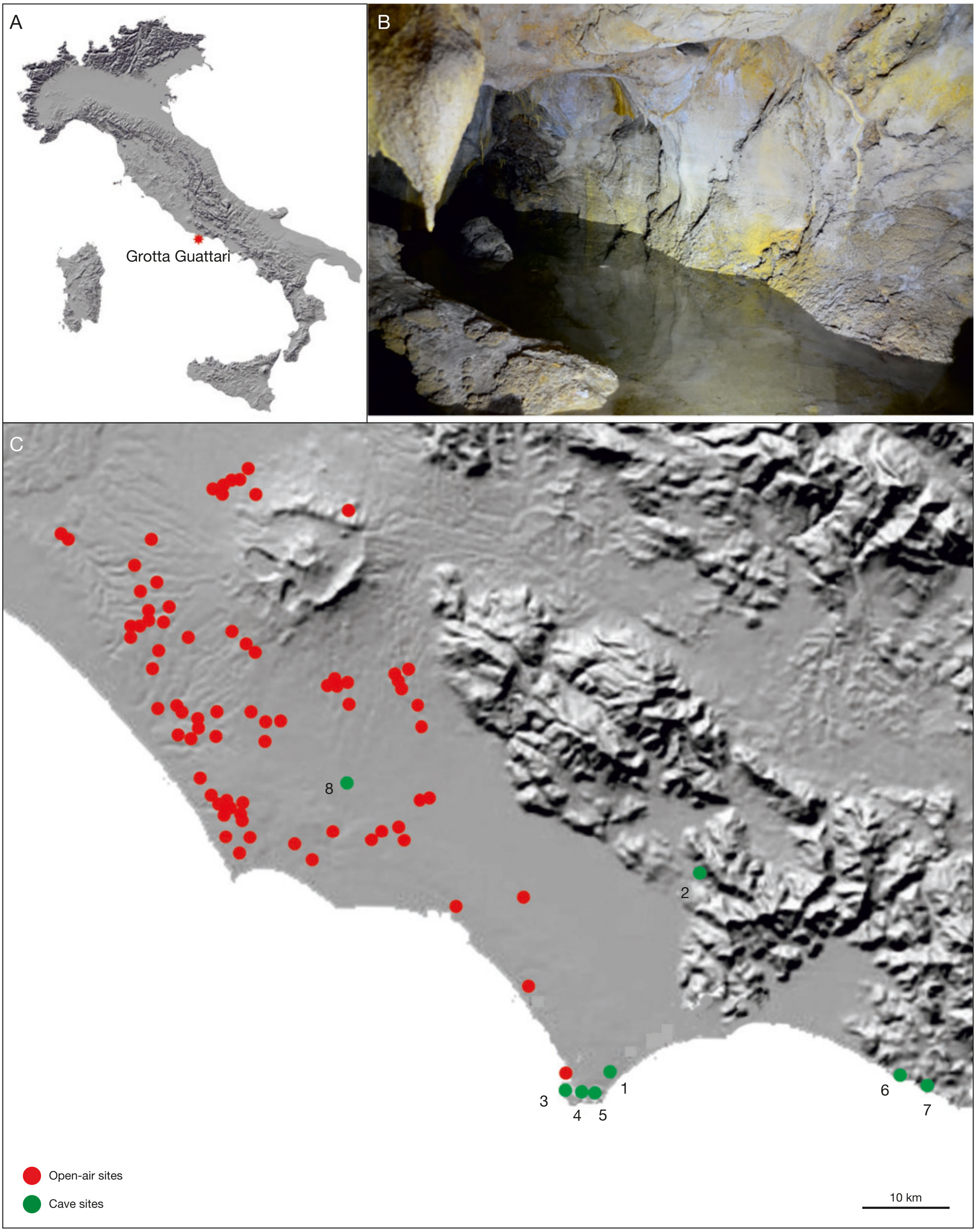


Fig. 1. — **A**, Italian map with location of Grotta Guattari (San Felice Circeo, central Italy); **B**, photo of the *Antro del Laghetto* at the beginning of the investigation in December 2018; **C**, location of Grotta Guattari and the main prehistoric open-air and cave sites of southern Latium: **1**, Grotta Guattari; **2**, Grotta La Sassa; **3**, Grotta Breuil; **4**, Grotta Barbara; **5**, Grotta del Fossellone; **6**, Grotta dei Moscerini; **7**, Grotta S. Agostino; **8**, Cava Muracci.

TABLE 1. — Number of identified specimens (NISP) from Grotta Guattari, *Antro del Laghetto*. Abbreviation: **L**, level.

	L. 2		**L. 3**		**Total**	
Taxon	**NISP**	**%**	**NISP**	**%**	**NISP**	**%**
Lepus sp.	5	0.6	1	0.2	6	0.4
Canis lupus Linnaeus, 1758	7	0.9	3	0.6	10	0.7
Vulpes vulpes (Linnaeus, 1758)	15	1.8	7	1.3	22	1.6
Ursus spelaeus Rosenmüller, 1794	–	–	3	0.6	3	0.2
Ursus arctos Linnaeus, 1758	11	1.3	19	3.7	30	2.2
Mustelidae Fischer, 1817	1	0.1	–	–	1	0.1
Felis silvestris Schreber, 1777	2	0.2	–	–	2	0.1
Panthera spelaea (Goldfuss, 1810)	1	0.1	1	0.2	2	0.1
Panthera pardus (Linnaeus, 1758)	3	0.4	–		3	0.2
Crocuta spelaea Goldfuss, 1823	163	20.0	125	24.1	288	21.6
Palaeoloxodon antiquus (Falconer & Cautley, 1847)	2	0.2	5	1.0	7	0.5
Elephantidae Gray, 1821	8	1.0	–	–	8	0.6
Stephanorhinus cf. *S. hemitoechus*	2	0.2	1	0.2	3	0.2
Rhinocerotidae Gray, 1821	5	0.6	–	–	5	0.4
Equus ferus Boddaert, 1785	55	6.7	25	4.8	80	6.0
Equus hydruntinus Regalia, 1907	–	–	8	1.5	8	0.6
Sus scrofa Linnaeus, 1758	55	6.7	39	7.5	94	7.0
Megaloceros giganteus (Blumenbach, 1799)	37	4.5	14	2.7	51	3.8
Cervus elaphus Linnaeus, 1758	230	28.2	113	21.8	343	25.7
Dama dama (Linnaeus, 1758)	40	4.9	20	3.9	60	4.5
Capreolus capreolus (Linnaeus, 1758)	2	0.2	4	0.8	6	0.4
Cervidae Gray, 1821	30	3.7	33	6.4	63	4.7
Bos primigenius Bojanus, 1827	135	16.5	98	18.9	233	17.5
Capra ibex Linnaeus, 1758	3	0.4	–	–	3	0.2
Rupicapra sp.	1	0.1	–	–	1	0.1
Caprinae Gray, 1821	3	0.4	–	–	3	0.2
Total identified specimens	816	100	519	100	1335	100
Identified specimens	816	18.8	519	10.5	1335	14.4
Indeterminate bones	3513	81.2	4443	89.5	7956	85.6
Total	4329	100	4962	100	9291	100

data, as bone remains were rarely preserved due to the soil's acidity and the region's long history of land reclamation and agricultural activity (Rolfo *et al.* 2022). Therefore, environmental and faunal reconstructions are mainly based on the multi-stratified cave sites. Six of these are on the coast (four of which are in the Circeo Promontory), while only two are inland (Fig. 1). The archaeological/paleontological deposits are linked to Neanderthal activities (e.g. the external shelter of Grotta Guattari, Grotta del Fossellone, Grotta Barbara, Grotta Breuil, Grotta dei Moscerini and Grotta S. Agostino) or/and cave hyena occupation (e.g. the inner cave of Grotta Guattari, Grotta del Fossellone, Cava Muracci and Grotta La Sassa). Unfortunately, most of these sites were investigated over thirty years ago (e.g. Grotta Barbara, Grotta del Fossellone and Grotta S. Agostino) and some remain partially unpublished (e.g. Grotta Breuil). Therefore, climate and environmental reconstructions of the Pontine Plain during Marine Isotope Stage (MIS) 4 and MIS 3 have mainly relied on recent studies at Cava Muracci (Gatta *et al.* 2019) and Grotta La Sassa (Gatta *et al.* 2022).

The general interpretation of the climate during the Last Glacial Period is that of considerable variability, marked by alternating cold and dry phases with more temperate and humid oscillations, a pattern widely observed across Mediterranean Europe (Allen *et al.* 2000; Sanchez-Goñi *et al.* 2002). The global causes of the abrupt and repeated climate shifts of this period are tipically attributed to specific phenomena, such as Heinrich events (Hemming 2004; Birner *et al.* 2016) and severe changes in precipitation (Luetscher *et al.* 2015). These environmental changes are reflected in the mammal assemblages of the last 130 ka, between MIS 5 and MIS 2. The most significant novelty among the large mammals is the first occurrence of the evolved form of fallow deer (*Dama dama dama* (Linnaeus, 1758)) which replaces *D. dama tiberina* Di Stefano & Petronio, 1997 during the MIS 5e, and the appearance of the current form of *Cervus elaphus* Linnaeus, 1758. The colder climate of MIS 4-3 is attested by the first occurrence of *Coelodonta antiquitatis* (Blumenbach, 1799) and *Mammuthus primigenius* (Blumenbach, 1799), as well as the diffusion of *Capra ibex* Linnaeus, 1758, *Rupicapra* spp. and *Marmota marmota* (Linnaeus, 1758) in hilly, plain and coastal areas (Petronio *et al.* 2007, 2011; Di Stefano *et al.* 2023). The Latium region was certainly affected by the climatic fluctuations of the Last Glacial Period, even though previous studies suggest the area was characterised by a distinct climatic regionalism (Gatta *et al.* 2016, 2019, 2022). However, a detailed environmental reconstruction at a local scale to assess its effects on the Circeo Promontory has not yet been conducted.

The investigation carried out at Grotta Guattari between 2019 and 2023 offered the opportunity to better understand the environmental and climatic conditions of the Circeo Promontory during the Late Pleistocene. The results published in this paper are part of a large archaeological and heritage development project that included the excavation of a previously unexplored chamber of Grotta Guattari, known as the *Antro del Laghetto* (Blanc 1939d; Blanc & Segre 1953; transl. Chamber of the small lake). In this chamber, a fossiliferous deposit produced by cave hyenas about 66-65 ka during the MIS 4 (Rolfo *et al.* 2023) has been brought back to light. This deposit contained few lithic artifacts, abundant mammal remains and several bones of *Homo neanderthalensis* King, 1864 displaying carnivore gnawing marks (Petronio *et al.* 2021; Rolfo *et al.* 2023; Fiore *et al.* in press; Salari *et al.* in press).

This work aims to describe the mammal assemblage from the *Antro del Laghetto* and discuss its archaeological, environmental and climatic implications.

ARCHAEOLOGICAL BACKGROUND

The obstructed entrance of Grotta Guattari was accidentally discovered on 24th February 1939 during quarrying activities on private land at the base of the slope of Monte Morrone (San Felice Circeo, central Italy). While the entire Circeo Promontory is well known for the presence of caves and natural shelters, the first exploration of the cave by the landowner (i.e., Alessandro Guattari) and his workers immediately revealed the cave's exceptional character. Thousands of bones were lying on the palaeosurface but the attention was caught by a human skull (i.e., Circeo I), found in a room later called *Antro dell'Uomo* (Blanc 1939a; Blanc & Segre 1953; transl. Chamber of Man). Archaeological investigations began immediately and led only a few days later to the discovery of a fragmented human mandible (i.e., Circeo II). After a hiatus caused by World War II, excavations resumed intermittently until 1951 (Blanc & Segre 1953). Thousands of faunal remains were recovered, along with hundreds of coprolites and lithic artifacts. A second human mandible (Circeo III) was later found by chance outside the cave in 1950 (Sergi & Ascenzi 1955).

The skull, recognised as one of the best-preserved Neanderthal's in the World, was found within a supposed circle of stones. A first study noted an unnaturally enlarged foramen magnum, prompting several scholars to hypothesize a cannibalistic ritual (Blanc 1939b; Sergi 1974; Ascenzi 1991). However, gnawing traces on most of the faunal remains and the abundance of coprolites from a large carnivore were instead interpreted as evidence of an alternating frequentation of the cave by humans and hyenas. Fifty years after the discovery, new in-depth studies on the skull demonstrated that the bone modifications had also been performed by hyenas and the cave was finally interpreted as a den (Stiner 1991a, b; Piperno & Giacobini 1991; Toth & White 1991).

MATERIAL AND METHODS

Archaeological investigation

The *Antro del Laghetto* is a 22 m^2 chamber investigated between 2019 and 2023. The seasonal rise of the groundwater, a water pump was required to preserve the deposit from flooding during the archaeological campaigns. Due to the geomorphology of the room prevented to physically grid the palaeosurface, which was instead divided into seven areas spatially georeferenced by a network of fixed points (Fig. 2). The excavation tools were chosen layer by layer based on the sediment's characteristics. These ranged from hammer and chisel – used to carefully remove the superficial calcium carbonate crust – to plastic and metal probes and scalpels, used to investigate the bone deposit without compromising subsequent taphonomic analyses. All finds were spatially recorded using a Leica FlexLine TS09 and by hand drawing, also recording their azimuth and elevation angles. A GIS map was subsequently developed during the post-excavation laboratory.

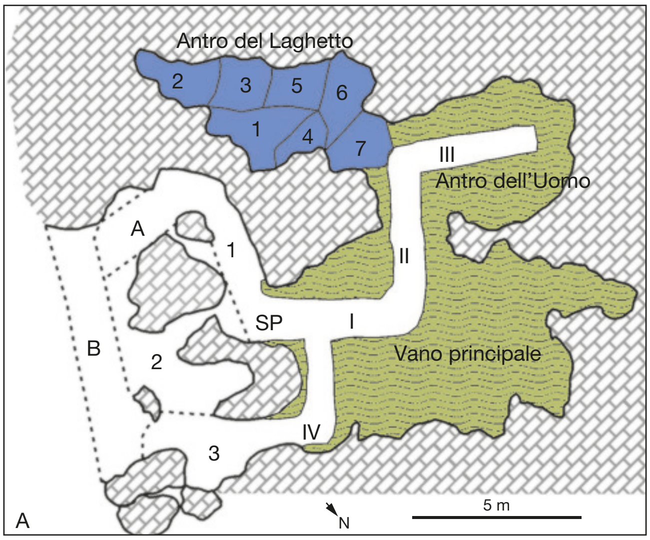


Fig. 2. — **A**, Map of Grotta Guattari with names of every trench and excavation area since 1939. Areas investigated within the *Antro del Laghetto* between 2019-2023 in **blue**. The **green colour** indicates the area where the bone paleosurface is preserved.

The sediment was first sieved using a 5 mm mesh to recover centimetre-sized finds and then floated with a 2 mm mesh to collect tiny fragments and microfauna. No selection occurred during either excavation or sieving, and all types of finds were recovered (e.g. lithic, bones, shells, charcoal, coprolites etc.).

The findings were individually labelled, stored in drilled zip-bags and transported to the University of Rome "Tor Vergata" where they were studied in the Laboratory of Prehistoric Archaeology.

Paleontological study

The mammal assemblage discussed in this paper concerns the finds recovered between 2019 and 2022. The faunal remains were studied and identified with the support of the osteological material hosted at the Laboratory of Prehistoric Archaeology at the University of Rome "Tor Vergata" and the atlas by Pales & Lambert (1971). A large portion of the assemblage is very fragmented, often in a state of preservation that does not allow the recognition of the anatomical element or the species. The majority of remains consist of long bone splinters less than 5 cm in length. Furthermore, a high percentage of the fossils are covered by calcium carbonate concretions. These are particularly evident on the finds from the higher layers, closer to the palaeosurface, but are also common within lower layers. Nonetheless, this did not hinder taxonomic or anatomical identification, albeit careful measurements were sometimes impossible. Fragments of ribs, vertebrae and long bones that were not possible to identify taxonomically were counted among indeterminate remains. Age at death was estimated by observing the fusion of long bone epiphyses and the stages of tooth eruption, replacement and use-wear. Age at death of *Bos primigenius* Bojanus, 1827 and *Equus ferus* Boddaert, 1785 were estimated according to observations by Barone (1974, 1981) and Grant (1982) on present-day domestic cattle and horse, *Sus scrofa* Linnaeus, 1758 according to Bull & Payne (1982), *Cervus elaphus* Linnaeus, 1758 according to Mariezkurrena (1983) and *Crocuta spelaea* Goldfuss, 1823 according to Brugal *et al.* (1997).

The number of identified specimens (NISP) and minimum mumber of individuals (MNI) were calculated following Grayson (1984) and Bökönyi (1970). Fallen and fragmented cervid antlers were not considered for the MNI. Measurements were taken with a standard calliper following Driesch (1976) and Eisenmann (1986). Wither heights were estimated using the parameters by Kiesewalter (1888) for horse, Teichert (1969) for wild boar, Matolcsi (1969) for aurochs and Wilkens (1989) for red deer. Body masses of horse and aurochs were based on the studies of Eisenmann & Sondaar (1998) and De Gusta & Vrba (2005).

Environmental and climatic considerations were based on the ecology and biogeographic distribution of the identified species (Dorst & Dandelot 1988; Boitani *et al.* 2003; Amori *et al.* 2008; Conti *et al.* 2010; Pandolfi *et al.* 2011; Petronio *et al.* 2014; Callaway 2016; Salari & Masseti 2016 and references therein) in addition to the recently published pollen analysis (Rolfo *et al.* 2023).

TAPHONOMIC ANALYSIS

Macroscopic evidence of gnawing activity by a large carnivore (i.e., cave hyenas) were clearly visible on the bone remains from all areas and both levels of the *Antro del Laghetto*. However, taphonomic analysis was performed on a sample of 1 136 mammal remains recovered from Area 1 of the *Antro del Laghetto*. This area was selected due to the discovery of a third of the entire fossil assemblage. Therefore, the careful analysis of bone modifications was carried out to verify whether the origin of the mammal assemblages was solely the result of carnivore activity or involved additional depositional agents.

Taphonomic observations were carried out with the aid of a 10× optical lens and a Dino-Lite Edge microscope, albeit bones were often covered by hard concretions, which in some cases prevented the analysis of the original surface (Fiore 2021; Fiore *et al.* in press). Some particularly significant specimens were analyzed by SEM at the microscopy laboratory of the *Museo delle Civiltà* of Rome and with the Hirox 3D Digital Microscope at LTFAPA within the Department of *Scienze dell'Antichità*, "Sapienza" University of Rome. The analysis of the bone surfaces of mammal remains from Grotta Guattari had already been conducted in previous studies of other areas of the cave (Piperno & Giacobini 1991; Stiner 1991a, b). The degree of surface alteration due to pre- and post-depositional phenomena (Behrensmeyer 1978; Shipman 1981; Lyman 1984; Fisher 1995), as well as fracture typology and the state of the margins (Johnson 1985; Villa & Mahieu 1991; Outram 2002, 2004; Outram *et al.* 2005), were recorded. Particular attention was paid to the missing portions of the bones (e.g. complete, missing one or both epiphyses, only diaphyses; Fig. 3). The typologies of modifications recorded included: pits and puncture (Binford 1981; Delaney-Rivera *et al.* 2009), scores (Marguire *et al.* 1980), furrows (Binford 1981; Haynes 1983), ragged edged chewing and crenulated fractures (Marguire *et al.* 1980; Binford 1981), scooping out (Sutcliffe 1970; Haynes 1980, 1983; Marguire *et al.* 1980; Binford 1981) licking traces (Haynes 1980, 1983; Binford 1981; Pokines & Kerbis-Peterhans 2007). The intensity and position of tooth marks were analysed on anatomical elements missing one or both epiphyses (Marguire *et al.* 1980; Binford 1981; Haynes 1983; Fernández-Jalvo & Andrews 2016).

Gnawing types were analysed by referencing extensive bibliography (Sala *et al.* 2012; Saladié *et al.* 2019; Stewart *et al.* 2021; Katsagoni *et al.* 2023) and through comparison with a reference collection of bones gnawed by large canids (Fig. 4). Although canids and hyenas differ in some of their hunting and carcass exploitation behaviours, they often leave similar gnawing patterns (e.g. pits, scoring, scooping out, crenatidens, overlapping pits and scoring).

COPROLITES

Over one hundred coprolites were collected from both the inner and outer soundings of Grotta Guattari between 2019 and 2022. All specimens were studied at the Laboratory of Prehistoric Archeology at the University of Rome "Tor Vergata", where they were cleaned and dried in a temperature-controlled environment. The fossil faeces from the internal chambers are generally better preserved, therefore it is not surprising that most of the specimens were recovered from inside the cave, while those from the outer shelter were highly fragmented and sometimes were reduced to powder within the layers.

A comparison, following the parameters by Diedrich (2012a), was made with the coprolite collection housed at the University of Rome "Tor Vergata".

RESULTS

STRATIGRAPHIC SETTING

The *Antro del Laghetto* is one of the inner and smaller rooms of Grotta Guattari, placed in front of the abovementioned *Antro dell'Uomo* (Fig. 2). It has an irregular shape, elongated and narrow, with a maximum length of 9.93 m and a width of 3.6 m. The maximum height before excavations was 2.6 m in Area 5 and the minimum was 1.27 m in Area 2.

The name of this chamber, first mentioned by Blanc (1939d) since the very first discovery of the cave, derives from the seasonal (October to May) presence of a modest water basin

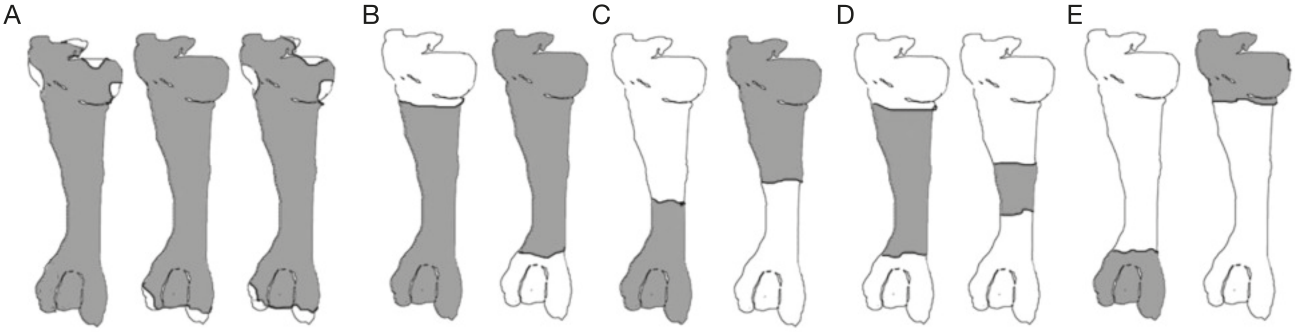


FIG. 3. — Bone damage stages from Grotta Guattari, *Antro del Laghetto*: **A**, stage 0, whole bones with traces of gnawing on one or both ends; **B**, stage 1, bones with complete diaphysis missing one or both epiphyses; **C**, stage 2, bones missing one or both epiphyses and a large portion of diaphysis; **D**, stage 3, long and short central portion of diaphysis are preserved; **E**, stage 4, only epiphyses are preserved (data in Table 12).

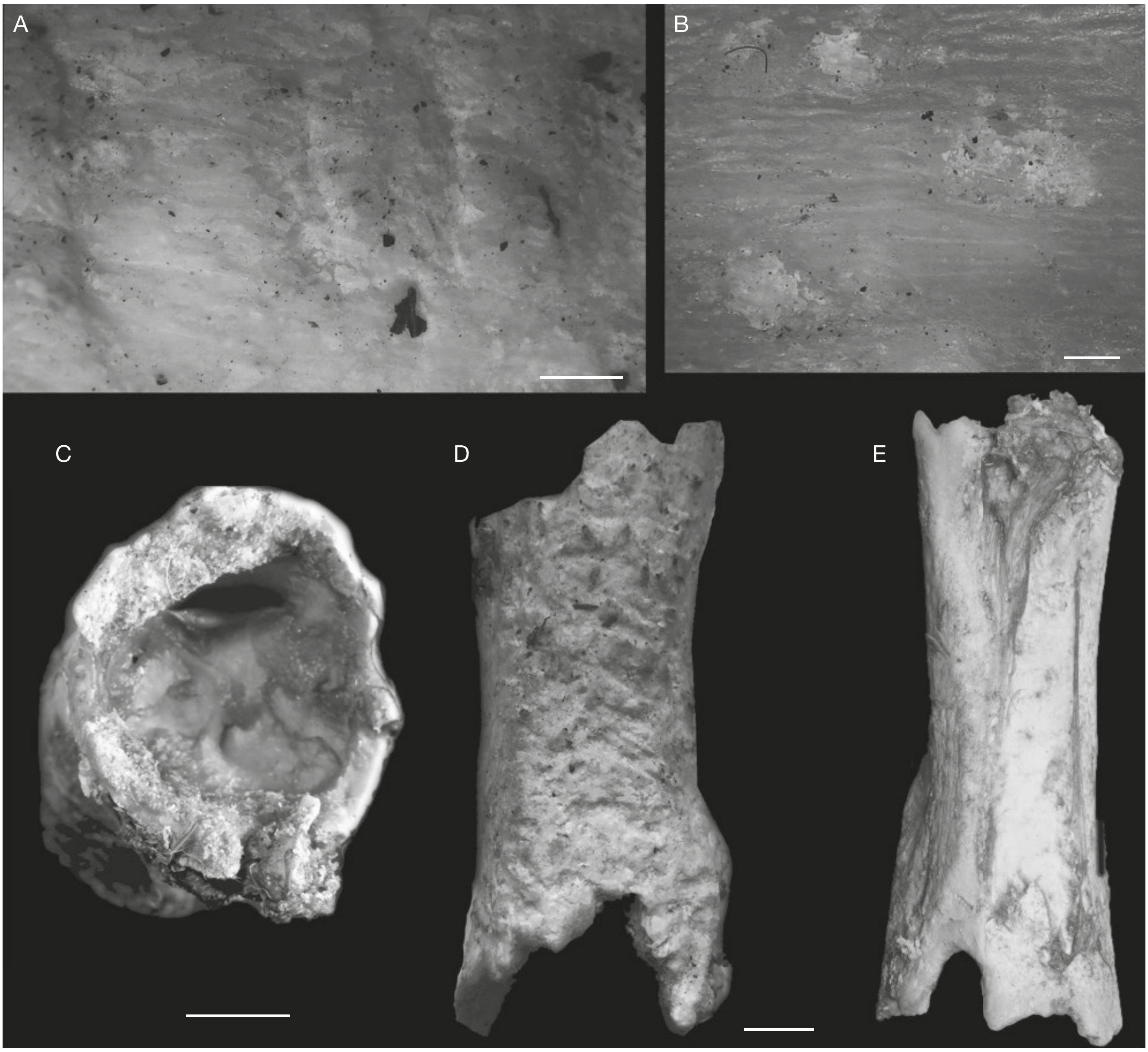


FIG. 4. — Tooth marks used as a comparison from Grotta Guattari, *Antro del Laghetto*: **A**, furrows; **B**, pits; **C**, edges are rounded and polished by scooping out and licking; **D**, the bone surface appears rough and with diffuse gaps due to heavy gnawing; **E**, edges rounded and polished by severe licking. Scale bars: A, B, 1 mm; C-E, 1 mm.

TABLE 2. — Minimum number of individuals (**MNI**) from Grotta Guattari, *Antro del Laghetto*. Abbreviations: **a**, adult; **o**, old; **vy**, very young; **y**, young; **ya**, young-adult.

	Layer 2							**Layer 3**						
Taxon	**MNI**	**%**	**vy**	**y**	**ya**	**a**	**o**	**MNI**	**%**	**vy**	**y**	**ya**	**a**	**o**
Lepus sp.	2	2.4	–	–	–	2	–	1	1.7	–	–	–	1	–
Canis lupus Linnaeus, 1758	1	1.2	–	–	–	1	–	1	1.7	–	–	–	1	–
Vulpes vulpes (Linnaeus, 1758)	3	3.6	–	–	–	3	–	1	1.7	–	–	–	1	–
Ursus spelaeus Rosenmüller, 1794	–	–	–	–	–	–	–	1	1.7	–	–	–	1	–
Ursus arctos Linnaeus, 1758	3	3.6	–	1	–	2	–	2	3.4	–	–	–	2	–
Mustelidae Fischer, 1817	1	1.2	–	–	–	1	–	–	–	–	–	–	–	–
Felis silvestris Schreber, 1777	1	1.2	–	–	–	1	–	–	–	–	–	–	–	–
Panthera spelaea (Goldfuss, 1810)	1	1.2	–	–	–	1	–	1	1.7	–	–	–	1	–
Panthera pardus (Linnaeus, 1758)	1	1.2	–	–	–	1	–	–	–	–	–	–	–	–
Crocuta spelaea Goldfuss, 1823	14	16.9	1	–	1	7	5	12	20.7	1	1	–	7	3
Palaeoloxodon antiquus (Falconer & Cautley, 1847)	1	1.2	1	–	–	–	–	2	3.4	2	–	–	–	–
Elephantidae Gray, 1821	1	1.2	–	–	–	1	–	–	–	–	–	–	–	–
Stephanorhinus cf. *S. hemitoechus*	2	2.4	–	1	–	1	–	1	1.7	–	–	–	1	–
Rhinocerotidae Gray, 1821	1	1.2	–	–	–	1	–	–	–	—	–	–	–	–
Equus ferus Boddaert, 1785	6	7.2	–	1	–	5	–	3	5.2	–	1	1	1	–
Equus hydruntinus Regalia, 1907	–	–	–	–	–	–	–	2	3.4	–	–	–	2	–
Sus scrofa Linnaeus, 1758	7	8.4	–	2	–	4	1	5	8.6	1	1	–	3	–
Megaloceros giganteus (Blumenbach, 1799)	4	4.8	–	–	–	4	–	1	1.7	–	–	–	1	–
Cervus elaphus Linnaeus, 1758	15	18.1	–	3	1	9	2	13	22.4	–	2	–	10	1
Dama dama (Linnaeus, 1758)	4	4.8	–	–	–	4	–	2	3.4	–	–	–	2	–
Capreolus capreolus (Linnaeus, 1758)	1	1.2	–	–	–	1	–	2	3.4	–	–	–	2	–
Bos primigenius Bojanus, 1827	11	13.3	1	2	–	7	1	8	13.8	–	1	1	5	1
Capra ibex Linnaeus, 1758	1	1.2	–	–	–	1	–	–	–	–	–	–	–	–
Rupicapra sp.	1	1.2	–	–	–	1	–	–	–	–	–	–	–	–
Caprinae Gray, 1821	1	1.2	1	–	–	–	–	–	–	–	–	–	–	–
Total	83	100	4	10	2	58	9	58	100	4	6	2	41	5

TABLE 3. — Distribution of anatomical elements of *Crocuta spelaea* and the main ungulates from Grotta Guattari, *Antro del Laghetto*. Abbreviation: **L.**, Level.

	Crocuta spelaea		***Equus ferus***		***Sus scrofa***		***Cervus elaphus***		***Bos primigenius***	
Skeletal elements	**L. 2**	**L. 3**	**L. 2**	**L. 3**	**L. 2**	**L. 3**	**L. 2**	**L. 3**	**L. 2**	**L. 3**
Horn/Antler	–	–	–	–	–	–	47	23	2	3
Skull	12	6	2	–	–	–	5	3	1	–
Maxillary	5	6	2	–	4	1	–	2	–	–
Upper teeth	39	37	8	5	9	7	11	10	9	12
Mandible	17	9	–	–	4	3	–	–	5	3
Lower teeth	52	51	9	8	10	16	16	4	5	7
Indeterminate teeth	3	2	–	–	–	–	–	–	–	–
Atlas	4	–	–	–	–	–	–	–	–	–
Axis	1	2	–	–	–	–	–	–	2	–
Vertebrae	8	3	–	–	–	–	7	6	10	2
Scapula	–	–	–	–	1	–	2	3	7	4
Humerus	1	–	–	–	13	7	12	1	12	7
Radius	–	–	1	–	3	–	17	7	15	5
Ulna	9	1	2	–	–	1	2	1	3	2
Carpal bones	–	–	1	3	–	1	4	2	5	6
Metacarpus	–	3	6	2	2	1	16	9	10	11
Pelvis	–	1	–	–	1	–	2	–	1	3
Femur	3	–	1	–	–	1	2	1	5	4
Patella	–	2	–	–	–	–	–	–	–	1
Tibia	2	–	1	–	1	–	14	7	6	1
Fibula	–	–	–	–	–	–	–	–	–	–
Malleolar bone	–	–	–	–	–	–	1	–	–	2
Talus	–	–	2	1	–	1	8	3	6	6
Calcaneus	–	–	3	1	–	–	10	5	6	4
Tarsal bones	1	–	2	–	–	–	5	6	6	4
Metatarsus	2	1	6	1	–	–	28	12	9	7
Metapodial bones	–	–	5	2	1	–	18	5	–	2
Sesamoids	–	–	–	–	–	–	1	–	–	–
Phalanx I	1	–	3	1	3	–	1	2	6	1
Phalanx II	3	1	–	1	2	–	1	1	4	1
Phalanx III	–	–	1	–	1	–	–	–	–	–
Total	163	124	55	25	55	39	230	113	132	97

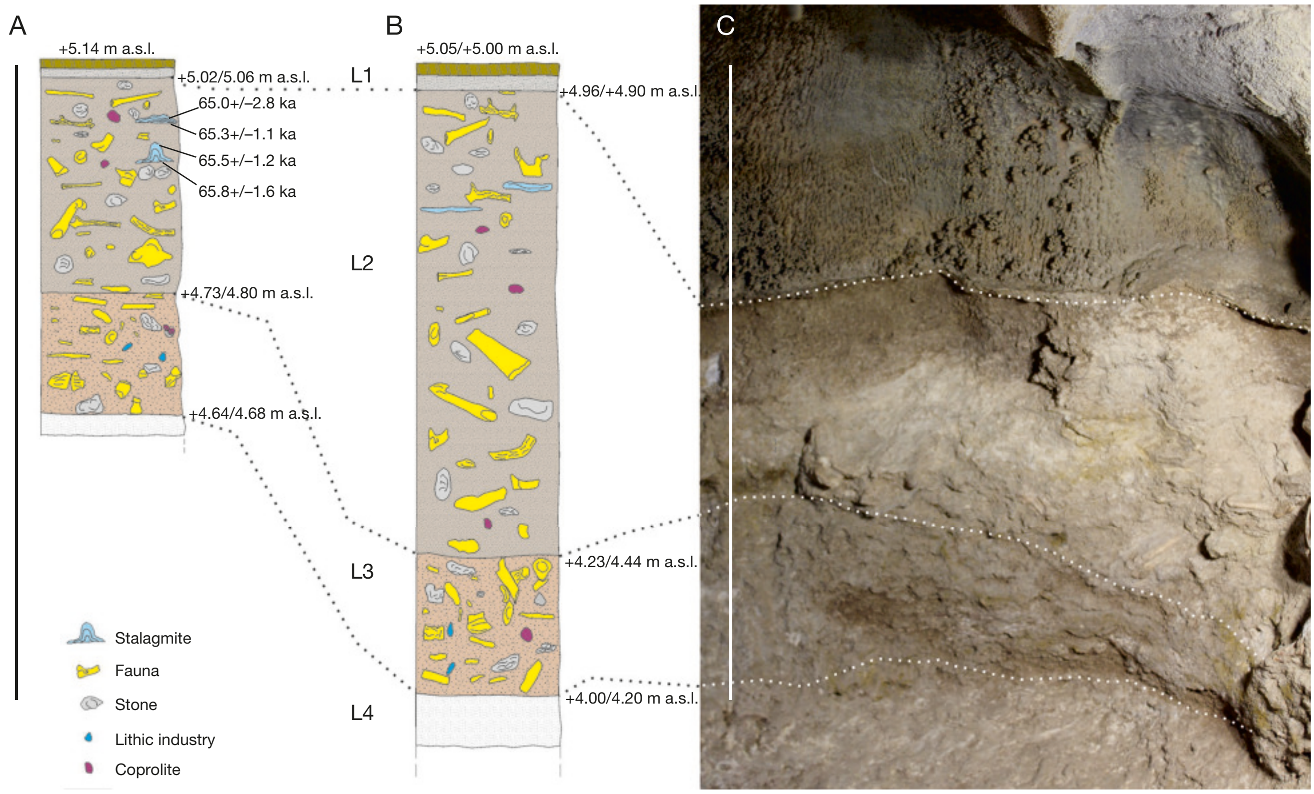


FIG. 5. — Stratigraphy of the *Antro del Laghetto*: **A**, stratigraphy of areas 1-4; **B**, stratigraphy of areas 2-3; **C**, photo of the stratigraphic deposit from the *Antro del Laghetto*. Scale bars: 90 cm.

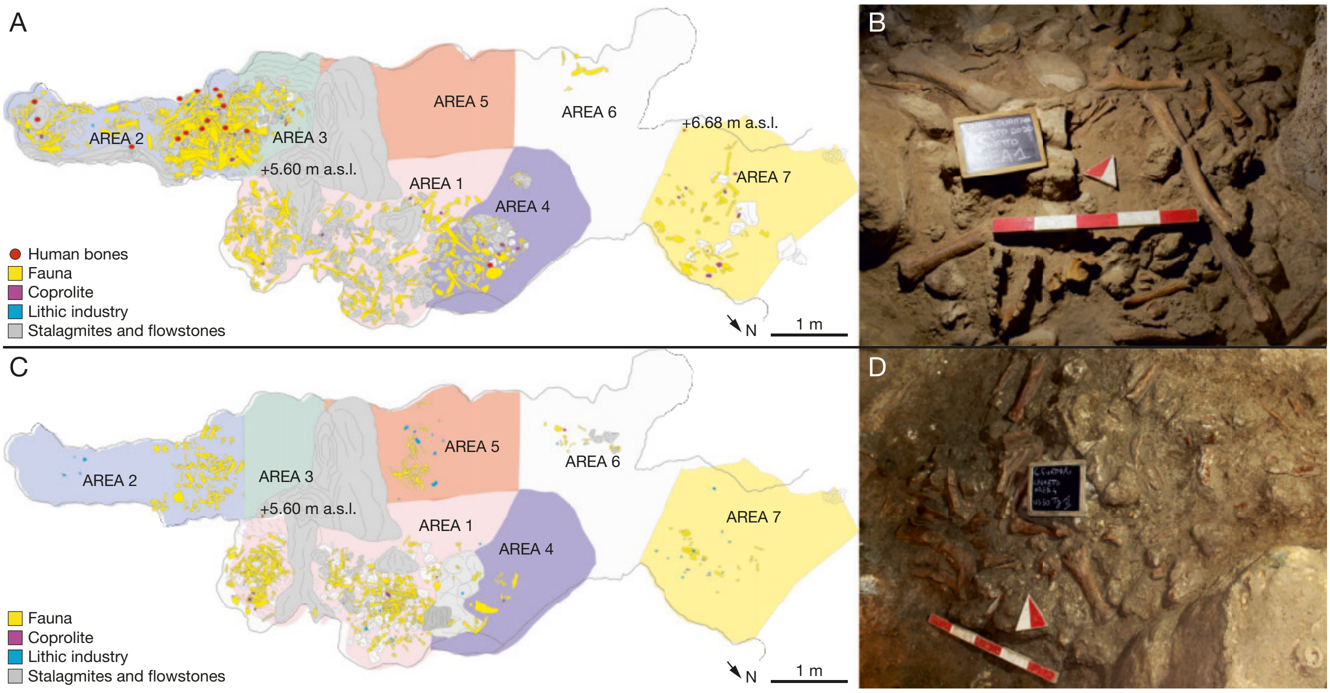


FIG. 6. — Spatial distribution of the finds within the *Antro del Laghetto*: **A**, **B**, map (**A**) and panoramic view (**B**) of Level 2; **C**, **D**, map (**C**) and panoramic view (**D**) of Level 3. Scale bars: B, D, 0.5 m.

Table 4. — Wither height of the main ungulates from Grotta Guattari, *Antro del Laghetto*.

Species/element	Wither heights (cm)
Equus ferus Boddaert, 1785	
Metatarsus III	140.2
Metacarpus III	141.7
Metacarpus III	141.7
Metacarpus III	142.3
Metacarpus III	144.2
Metacarpus III	148.7
Metacarpus III	150.6
Metatarsus III	151.4
mean	145.1
Sus scrofa Linnaeus, 1758	
Metacarpus IV	102.7
Cervus elaphus Linnaeus, 1758	
Metatarsus	112.6
Metatarsus	115.5
Calcaneus	117.6
Calcaneus	117.6
Metacarpus	120.1
Metacarpus	121.9
Calcaneus	122.1
Calcaneus	122.6
Calcaneus	124.2
mean	119.4
Bos primigenius Bojanus, 1827	
Metatarsus	143.9
Metatarsus	146.6
Metacarpus	151.4
Metacarpus	152.6
Metacarpus	154.5
Metatarsus	156.4
Metatarsus	156.4
Metacarpus	157.6
Metatarsus	161.9
Metacarpus	166.9
Metatarsus	167.4
Radius	172.9
Radius	179.3
mean	159.1

powered by rising groundwater. The water flows through a natural siphon from the lowest area of the room (i.e., Area 2) and rises to a maximum of about 2 m above the ground surface (*c.* 7 m a.s.l.) according to the local rainfall pattern.

The archaeological investigation of the *Antro del Laghetto* allowed us to study a deposit thick between 0.47 m and 1.02 m. Twenty-five stratigraphic units, belonging to four main levels, have been identified and documented. The peculiar geomorphology of the room and its deposit, which corresponds to the lowest area of the cave, severely influenced by the periodic presence of water, made every stratigraphic comparison with the other areas of the cave extremely challenging. This challenge was further increased by the excavation of trenches II and III (Fig. 2), over eighty years ago, which stratigraphically isolated the room from the rest of the cave (Rolfo *et al.* 2023).

Here, the four levels identified during the recent investigation of the *Antro del Laghetto* are described (Fig. 5):

– Level 1 (the uppermost level) is a thin deposit found throughout the chamber characterised by two layers: a 1 cm thick unit of mud, recently deposited by rising groundwater; 2-3 cm of calcium carbonate crust, which is friable and not particularly difficult to investigate. The shape of findings within the lower layer was sometimes guessable below the thin crust, which covered them like a veil. A coralloid concretion similar to that visible on the paleosurface of other rooms at Grotta Guattari was sometimes preserved on the bone remains from the *Antro del Laghetto*. This stratigraphic horizon is already dated in the *Antro dell'Uomo* to 59-51 ka (Schwarcz *et al.* 1991; Rolfo *et al.* 2023).

– Level 2 is a sandy deposit including small limestone pebbles and sporadic clasts and crust areas. It extends across the entire room with a variable thickness of about 27 cm in areas 1, 4, 5, 6 and 7 while it reaches a thickness of up to 82 cm in Area 2. This level returned an assemblage of 4329 mammal remains, few lithic artifacts and coprolites (Fig. 6A, B). Finally, the human remains recovered from the chamber belong to this level. The number of human remains could increase through ongoing zooarchaeology by mass spectrometry (ZooMS) analysis.

– Level 3 is a harder deposit characterised by a grey-encrusted matrix with clasts often incorporating bone remains. The investigation of this layer, on average 20 cm thick, returned 4962 mammal remains in addition to lithic artifacts and coprolites (Fig. 6C, D). Unfortunately, severe post-depositional processes acted on the biological findings of this deposit, deteriorating the bone surface, in some cases, completely destroying it.

– Level 4 is at the bottom of the stratigraphy within the *Antro del Laghetto*. It is a consistent flowstone concretion producing an irregular surface with natural pools later filled by the sandy matrix of the upper Level 3, it covers large clasts that probably collapsed from the vault of the room. The base of this level has not been reached anywhere in the chamber.

The thirty-nine lithic artifacts recovered within the *Antro del Laghetto*, were mainly discovered within Level 3 (= 31) and Level 2 (= 8). However, direct evidence of human activities carried out in this room is completely missing. Moreover, this data strongly diverges from the outer rock shelter, where the archaeological investigation of the deposit brings back to light many lithic artifacts in several paleosoils with hearths, butchered faunal remains and rare human remains dating back to MIS 5. It is possible that the artifacts reached the *Antro del Laghetto* through the ancient access to the cave (Rolfo *et al.* 2023), now sealed, placed at the bottom of Area 2. The erosion of the older external deposit, following the trampling of the hyenas, could have induced these industries to slide into the chamber. Further analyses and studies of the outer area are ongoing to support this hypothesis.

The mammal assemblage

The total amount of bone remains analysed is about 9300, of which 1335 (14.4%) were taxonomically determined (Table 1). The number of indeterminate remains, above all splinters of long bones measuring less than 5 cm, is relatively high, and it is consistent with previous studies (Stiner 2004 and references therein). This is mainly due to the high fragmentation produced by the cave hyena's gnawing, but also due to trampling, typical of restricted spaces such as caves, and to water action due to the aforementioned rising groundwater.

Fig. 7. — Faunal remains from Grotta Guattari, *Antro del Laghetto*: **A**, **D**, **E**, *Cervus elaphus* Linnaeus, 1758: **A**, fragmented skull with basal portions of the antlers; **D**, left metatarsus (distal end lack) in dorsal view; **E**, left radius in dorsal view; **B**, *Dama dama* (Linnaeus, 1758), skull fragment with basal portion of antler; **C**, *Megaloceros giganteus* (Blumenbach, 1799), basal portion of fallen antler; **F**, **G**, *Bos primigenius* Bojanus, 1827: **F**, Left metacarpus in dorsal view; **G**, left metatarsus in dorsal view; **H**, **I**, *Equus ferus* Boddaert, 1785: **H**, right metacarpus in dorsal view; **I**, right metatarsus in dorsal view; **J**, *Capra ibex* Linnaeus, 1758, proximal right metacarpus in dorsal view; **K**, *Palaeoloxodon antiquus* (Falconer & Cautley, 1847), upper premolar of a cub in occlusal view; **L**, *Rupicapra* sp., first posterior phalanx in lateral view; **M**, *Sus scrofa* Linnaeus, 1758 maxillary fragment in occlusal view. Scale bars: 5 cm.

TABLE 5. — Measurements (mm) of carnassial teeth of *Crocuta spelaea* Goldfuss, 1823 from Grotta Guattari, *Antro del Laghetto*, Cava Muracci and Grotta La Sassa (southern Latium, Italy). Abbreviations: **L**, length; **max**, maximum; **min**, minimum; **n**, number of measurements; **s.d.**, standard deviation; **W**, width.

	Grotta Guattari					Cava Muracci					Grotta La Sassa				
	n.	**min**	**max**	**mean**	**s.d.**	**n.**	**min**	**max**	**mean**	**s.d.**	**n.**	**min**	**max**	**mean**	**s.d.**
L P4	21	37.6	44.0	40.65	1.678	2	36.7	37.2	36.95	0.354	5	38.2	39.8	38.92	0.729
W P4	18	20.3	23.8	22.45	1.035	2	20.4	20.4	20.40	0	5	18.2	20.4	19.32	0.965
L m1	23	29.2	34.2	31.07	1.314	4	29.8	31.3	30.53	0.695	4	29.4	30.2	29.80	0.365
W m1	21	12.4	14.8	13.47	0.610	4	13.2	13.8	13.38	0.287	4	13.6	14.2	13.85	0.252

TABLE 6. — Remains analysed divided by species with the ratio of gnawed to non-gnawed remains from Grotta Guattari, *Antro del Laghetto*. The number of identified specimens (**NISP**) are 222 excluded 87 isolated teeth and tooth fragments and 37 with unobservable surfaces, total 346.

Taxa	NISP Analysed	NISP with gnaw.	NISP with gnaw.%
Crocuta spelaea Goldfuss, 1823	48	14	29.2
Equus ferus Boddaert, 1785	12	5	41.2
Sus scrofa Linnaeus, 1758	5	4	80.0
Megaloceros giganteus (Blumenbach, 1799)	9	8	88.8
Cervus elaphus Linnaeus, 1758	71	58	81.7
Dama dama (Linnaeus, 1758)	2	1	50.0
Cervidae Gray, 1821	24	19	79.2
Bos primigenius Bojanus, 1827	51	47	92.1
Total NISP	222	156	70.2
Mammal large size	100	54	54.2
Mammal medium size	90	46	51.0
Indeterminate	724	260	35.9
Total Indeterminate	914	360	49.4
Total remains	1136	516	43

TABLE 7. — Bone surface modifications from Grotta Guattari, *Antro del Laghetto*. Stages of abrasion and weathering.

	Low	Medium	High	Total
Abrasion				
NISP	6	45	85	136
NISP %	4.6	34.4	61.0	100
Weathering				
NISP	70	36	19	125
NISP %	56.0	28.8	15.2	100

The most frequent species among the 1 335 taxonomically determined remains in both levels, considering NISP and MNI values (Tables 1-3), is *Cervus elaphus* (Fig. 7A, D, E), following *Crocuta spelaea* (Fig. 8) and *Bos primigenius* (Fig. 7F, G). *Equus ferus* (Fig. 7H, I) and *Sus scrofa* (Fig. 7O) are also abundant, while other taxa are less common and a few are rare (i.e., less than five remains, Table 1). Several taxa not previously recorded at Grotta Guattari were identified, i.e., *Panthera spelaea* (Goldfuss, 1810) in both the levels, *Rupicapra* sp. (Fig. 7N) and *Felis silvestris* Schreber, 1777 in Level 2, and *Equus hydruntinus* Regalia, 1907 in Level 3 (Tables 1; 2). Over 60 remains, most of which fragmented antlers, were assigned to Cervidae Gray, 1821 since it was impossible to establish the species. According to the same principle, some remains of a very young ibex or chamois were attributed to Caprinae Gray, 1821 and postcranial fragments of elephant and rhinoceros to Elephantidae Gray, 1821 and Rhinocerotidae Gray, 1821.

The faunal list from the *Antro del Laghetto* is composed of common species in the Italian Late Pleistocene record. Most of the species have been present in Italy since the Middle Pleistocene, except for the modern forms of red deer and fallow deer, which are only attested from the Late Pleistocene (Petronio *et al.* 2007, 2011, 2019). The extinction of *Palaeoloxodon antiquus* (Falconer & Cautley, 1847) and *Stephanorhinus hemitoechus* (Falconer, 1868) is currently dated to MIS 3 (Palombo & Ferretti 2005; Pandolfi *et al.* 2017; Di Stefano *et al.* 2023). *Ursus spelaeus* Rosenmüller, 1794, *Panthera pardus* (Linnaeus, 1758), *C. spelaea* and *Dama dama* (Linnaeus, 1758) (Fig. 7B) disappeared shortly before or during the Last Glacial Maximum, while the latest occurrences of *P. spelaea*, *E. ferus*, *E. hydruntinus* and *Megaloceros giganteus* (Blumenbach, 1799) (Fig. 7C) date to the Late Glacial or early Holocene (Petronio *et al.* 2007, 2011; Di Stefano *et al.* 2023). *Bos primigenius* died out in historical times, while the other species are still living (Boitani *et al.* 2003; Petronio *et al.* 2007), although *Capra ibex* (Fig. 7L) and *Rupicapra* spp. have changed the altitudinal distribution (Di Stefano *et al.* 2023). Therefore, the biochronological framework of the species discovered ranges between the beginning of the Late Pleistocene and the MIS 3 and agrees with the radiometric dating between 66 and 65 ka returned from Level 2 of the *Antro del Laghetto* (Rolfo *et al.* 2023).

A high percentage of the remains belong to adult individuals (82% within Level 2 and 80% within Level 3), while young specimens are very scarce. However, *C. spelaea*

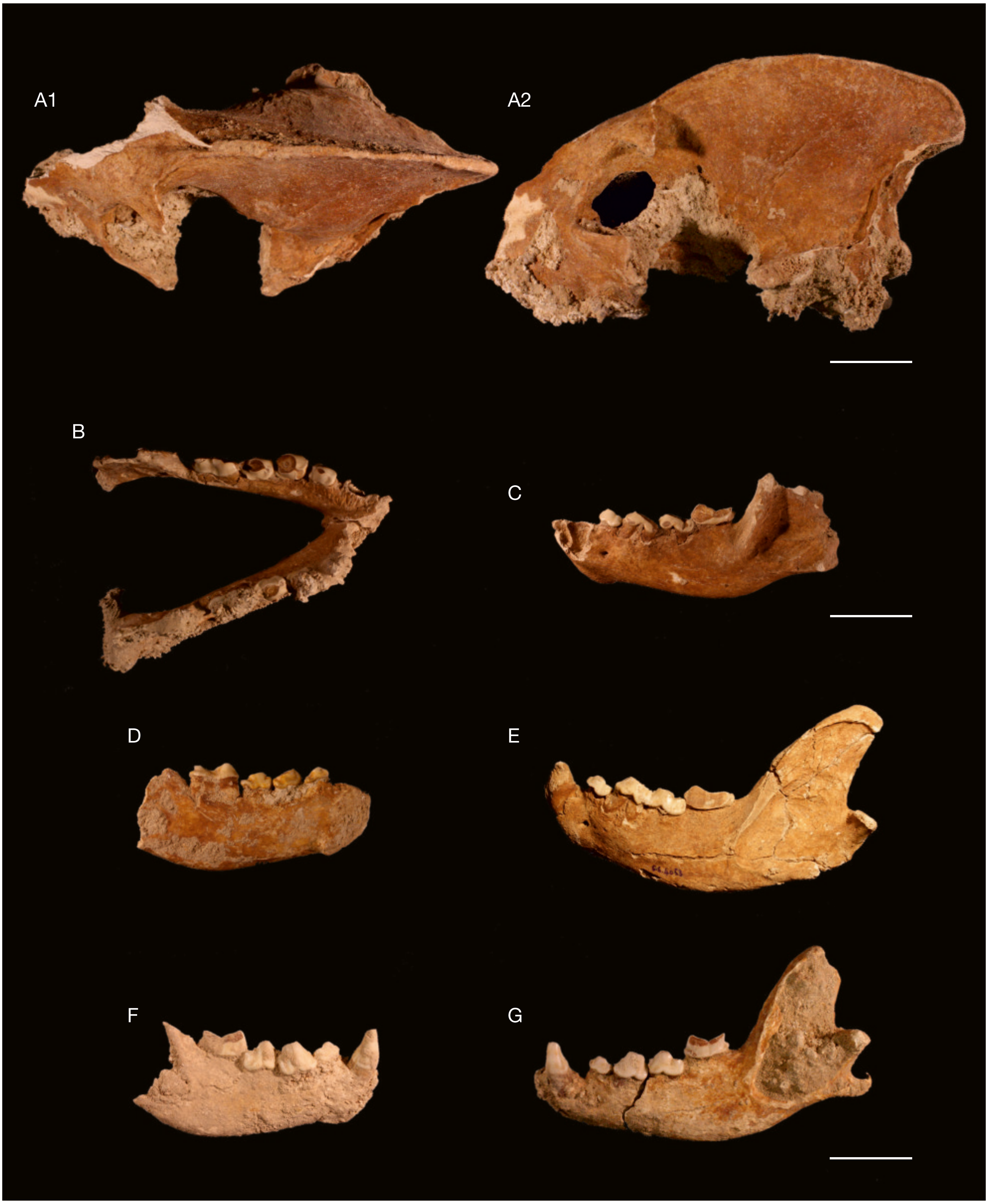


FIG. 8. — *Crocuta spelaea* Goldfuss, 1823 from Grotta Guattari, *Antro del Laghetto*: **A**, fragmented skull in frontal view (**A1**) and in lateral view (**A2**); **B**, mandible in occlusal view; **C**, left mandible in labial view; **D**, left mandible fragment in lingual view; **E**, left mandible in labial view; **F**, right mandible fragment in labial view; **G**, left mandible in labial view. Scale bar: 5 cm.

TABLE 8. — Summary of the presence of different gnawing types on skeletal portions. Abbreviation: **NISP**, number of identified specimens.

Tooth marks	Scores	Pits	Punctures	Notch	Furrows	Scooping out	Licking/Chipped back edges	Crenatidens
Skull	5	5	–	1	–	–	6	–
Skull-Antler	22	23	1	11	–	–	–	22
Skull-Maxillary	1	2	–	1	–	–	2	–
Skull- Mandible	2	2	–	–	–	–	1	–
Skull-Teeth	–	–	–	–	–	–	–	–
Vertebrae	7	9	3	1	1	–	–	7
Scapula-Pelvis	8	8	1	2	–	–	–	6
Long bones	47	51	6	13	23	21	35	4
Short bones	13	13	6	1	2	1	3	3
Total NISP	105	113	17	30	26	22	47	42

TABLE 9. — Detail of the presence of different gnawing types on the different skeletal elements according to the size of the animals. Abrreviations: **Ant**, antler; **Fe**, femur; **Hum**, humerus; **Long b.**, long bones; **LSM**, mammal large size; **Mand**, mandible; **Max**, maximum; **Mp**, metapodial; **MSM**, mammal medium size; **NISP**, number of identified specimens; **Pel**, pelvis; **Phal**, phalanx; **Ra**, radius; **Sc**, scapula; **Short b.**, short bones; **Sk**, skull; **Tb**, tibia; **Ul**, ulna; **Vt**, vertebrae.

Tooth marks	Sk	Ant	Max	Mand	Vt	Sc	Hum	Ra	Ul	Pel	Fe	Tb	Short b.	Mp	Phal	Long b.	NISP
LSM	–	–	1	2	3	4	5	3	–	1	3	3	10	11	–	1	47
MSM	5	22	–	–	4	1	1	3	1	2		4	2	8	1	4	58
Scores	5	22	1	2	7	5	6	6	1	3	3	7	12	19	1	5	105
LSM	–	–	2	2	4	4	5	3	–	1	3	3	10	11	–	1	49
MSM	5	23	–	–	5	1	2	6	1	2	–	4	2	8	1	4	64
Pits	5	23	2	2	9	5	7	9	1	3	3	7	12	19	1	5	113
LSM	–	–	–	–	2	1	2	1	–	–	–	–	5	2	–	–	13
MSM	–	1	–	–	1	–	–	–	–	–	–	–	–	–	1	1	4
Punctures	–	1	–	–	3	1	2	1	–	–	–	–	5	2	1	1	17
LSM	–	–	1	–	–	–	1	1	–	1	–	1	–	1	–	1	7
MSM	1	11	–	–	1	–	2	3	–	1	–	1	–	2	1	–	23
Notch	1	11	1	–	1	–	3	4	–	2	–	2	–	3	1	1	30
LSM	–	–	1	–	–	–	–	2	–	–	–	1	2	7	–	–	13
MSM	–	–	–	–	–	–	2	2	1	–	–	2	–	4	–	1	12
Furrows	–	–	1	–	–	–	2	4	1	–	–	3	2	11	–	1	25
LSM	–	–	–	–	–	–	3	2	–	–	–	1	–	4	–	–	10
MSM	–	–	–	–	–	–	2	4	–	–	–	2	–	2	1	1	12
Scooping out	–	–	–	–	–	–	5	6	–	–	–	3	–	6	1	1	22
LSM	–	–	2	1	–	–	3	3	–	–	1	2	–	7	–	–	19
MSM	6	–	–	–	–	–	3	4	1	–	–	4	2	5	1	2	28
Licking	6	–	2	1	–	–	6	7	1	–	1	6	2	12	1	2	47
LSM	–	–	–	–	1	3	–	–	–	1	–	1	2	2	–	–	10
MSM	–	22	–	–	6	–	–	–	–	2	–	–	1	–	–	1	32
Crenatidens	–	22	–	–	7	3	–	–	–	3	–	1	3	2	–	1	42

is represented by abundant senile but some young and very young specimens are also present (Table 2). *Palaeoloxodon antiquus* (Fig. 7M) is only attested by a few puppies and very young individuals (Table 2).

Wither heights have also been calculated for several species (Table 4): one measurement for *S. scrofa* (102.7 cm), comparable to those from Avetrana (Salari *et al.* 2019); nine measurements for *C. elaphus* (between 112.6 and 124.2 cm; 119.4 cm average), eight for *E. ferus* (between 140.2 and 151.4 cm; 145.1 cm average) and thirteen for *Bos primigenius* (between 143.9 and 179.3 cm; 159.1 cm average). The size of red deer from Grotta Guattari is relatively large, greater than those of the current Italian populations and the Late Pleistocene ones from the nearby Grotta del Fossellone and quite similar to those from Grotta Parignana (Di Stefano *et al.* 2015). Moreover, the body mass of the aurochs was estimated based on four first phalanges. It is comprised between 945 and 2 740 kg (average of 1 520 kg) which is slightly higher than those from Avetrana (411-2 330 kg; an average of 1 043 kg) (Pandolfi *et al.* 2013; Salari *et al.* 2019) and modern adult bovids of Chianina breed (over 1 600 kg for males; over 1 000 kg for females) (anabic.it). The body mass of *E. ferus* was also estimated, based on the size of five metacarpi and two metatarsi, between 332 and 486 kg (average of 434 kg).

Fig. 9. — Typologies of concretions: **A**, red deer antler with: **1**, coralloid concretions; **2**, stalagmitic incrustations; **3**, encrusted soil; **B**, cave hyena skull: **1**, coralloid concretions. Scale bars: 5 cm.

The wither heights and body mass values of our horses are slightly higher than those from Cardamone, Tana delle Iene and Melpignano (Conti *et al.* 2010) but significantly lower than those of the "gigantic horses" (Eisenmann 2003) from San Sidero 3, San Sidero 6 and Torre in Pietra (Conti *et al.* 2010). *Crocuta spelaea* from Grotta Guattari is also relatively large. The length of the upper carnassial (P4) is included between 37.6 and 44.0 mm (average of 40.7 mm) and the lower carnassial (m1) between 29.2 and 34.2 mm (average of 31.1 mm). These measures are significantly larger than

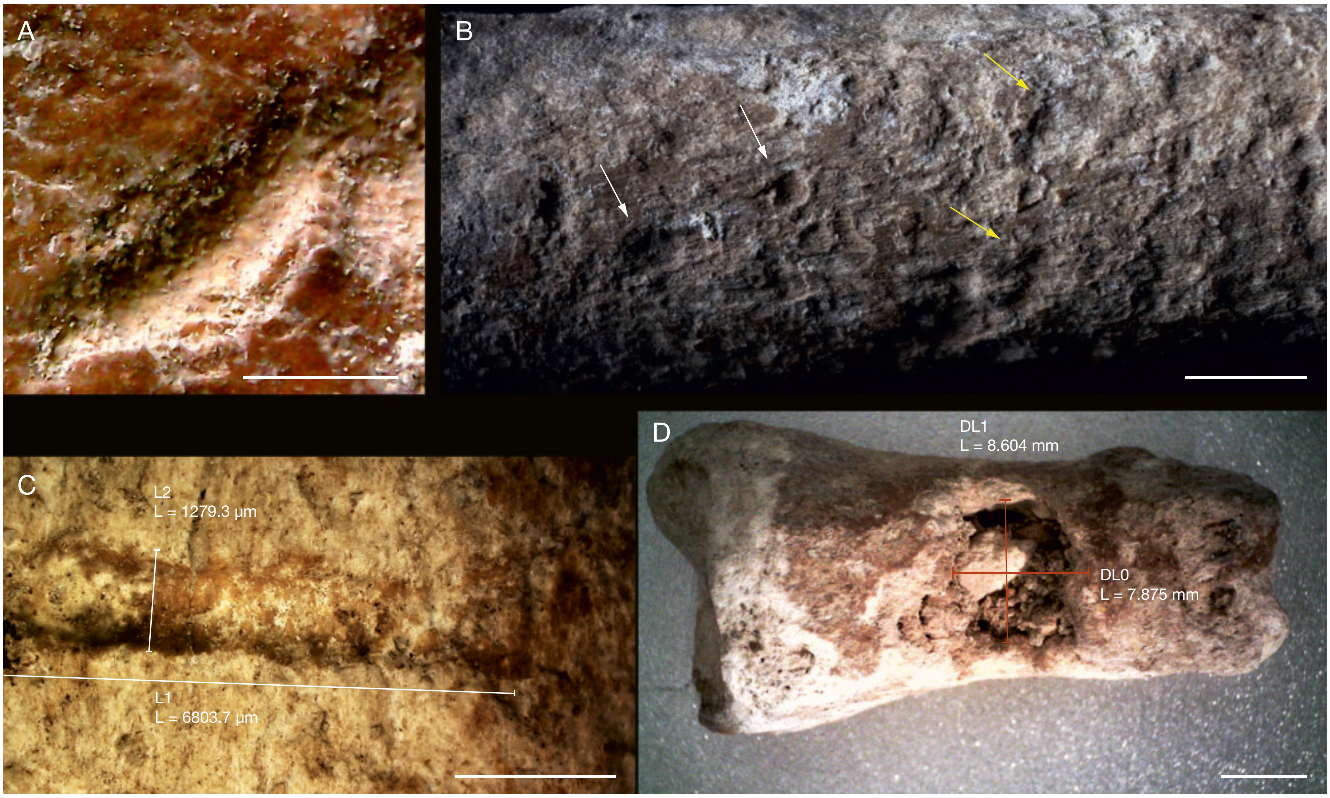


FIG. 10. — Types of modifications found on bone remains from Grotta Guattari, *Antro del Laghetto*: **A**, **C**, tibia of *Bos primigenius* Bojanus, 1827 and tibia of *Cervus elaphus* Linnaeus, 1758 with furrow caused by sliding the tooth (photo with Microscopy Hirox); **B**, *Equus ferus* Boddaert, 1785, metapodial with high degree gnawing the surface with pits (**white arrows**) and furrows (**yellow arrows**) overlapping; **D**, *Sus scrofa* Linnaeus, 1758, phalanx I with punctures, the holes caused by tooth pressure. Abbreviations: **L**, lenght. Scale bars: A, B, 1 cm; C, 2 mm; D, 5 mm.

Late Pleistocene cave hyenas of closer sites such as Cava Muracci and La Sassa (Table 5) but also the modern spotted hyena and suggest that several specimens from Grotta Guattari were among the biggest of western Europe (see Testu 2006; Iannucci *et al.* 2021; Lewis & Werdelin 2022).

HUMAN REMAINS

A few dozen possible neanderthal bones were found and delivered to the *Soprintendenza Archeologia, Belle Arti e Paesaggio per le Province di Frosinone e Latina* between 2019 and 2023. At present, 16 of them have been confirmed as human by the anthropologists. The Neanderthal remains have only been found within Level 2 (Fig. 6A) within a limited area of the *Antro del Laghetto* (i.e., Area 2-3-4) and consist of skull fragments, teeth and few post-cranial bones. The new remains, which represent an exceptional addition to the Italian Middle Palaeolithic record and to the broader European paleoanthropological dataset, will allow us to better understand the already high presence of Neanderthals in the Circeo Promontory and in general in the Pontine Plain.

TAPHONOMIC OBSERVATIONS

A study of the bone surface modifications on the mammal assemblage from the *Antro del Laghetto* was also carried out. The taphonomic analysis presented in this study focused on the finds from Area 1. The bone assemblage from Area 1 consists of over 3 500 bone remains, of which 346 were taxonomically determined. Taphonomic analysis was performed on remains which were identified taxonomically and on 914 unidentified specimens. The NISP excluded 87 isolated teeth and tooth fragments, and 37 bone remains are too fragmentary to allow for accurate analysis.

The analysis mostly involved large and medium-sized ungulates and several remains of cave hyenas (Table 6). However, a human femur and portions of a skull clearly show traces of gnawing. The remains are often covered by a hard concretion that hindered the study of the bone surfaces (Fig. 9). These are characterized by a high degree of abrasion, probably due to deposition within the sandy layer and the action of water that flooded part of the cave until recent times. Various degrees of cracking have also been observed. Finds with slightly cracked surfaces predominate but specimens with macroscopic fissures due to weathering are also present (Table 7). This data suggest that cave hyenas introduced both fresh prey and bones already affected by weathering into the cave.

Preliminary data indicate that over 50% of the remains display traces of gnawing by a large carnivore (i.e., the cave hyena). These data agree with previous results by Piperno & Giacobini (1991) and Stiner (1994). However, our study provides greater detail on how the Grotta Guattari hyenas processed ungulate bones – examining the types of traces, their anatomical distribution, and bone fracturing.

Fig. 11. — Red deer humerus with gnawing from Grotta Guattari, *Antro del Laghetto*: **A**, lateral view; **B**, medial view; **C**, detail of the posterior face damaged by gnawing. Scale bars: A, B, 3 cm; C, 2 cm.

Tooth marks

Gnawing traces are particularly evident and well represented on ungulate bones, particularly on the remains of *Bos primigenius* and *Cervus elaphus* (Table 6; Figs 10; 11), which are the most common species in the cave , with large and well-preserved bones. However, traces of gnawing were also found on cave hyena remains (Fig. 12) and at least two Neanderthal remains (Fiore 2021; Fiore *et al.* in press).

Almost all long bone fragments analyzed displayed typical damage due to the action of carnivore teeth. Marks on bones are mainly produced by molars and premolars (e.g. scores, pits, etc.), more rarely by incisors and canines (e.g. punctures).

The following types of modifications were identified (Tables 8-10):

Pits. Small subcircular or triangular non-punching depressions often repeated and insistent.

Scores. Insisted and repeated furrows caused by sliding the tooth across the surface with removal of bone surface.

Pits and scores are the most frequent traces and affect all anatomical elements of prey species. However, they are particularly abundant on antlers of Cervidae and on the epiphyses and metaphyses of long bones across all taxa (Tables 8-10; Fig. 10A-C). Observations of modern hyenas suggest that this carnivore is usually more interested in the epiphyseal ends than the diaphysis (Piperno & Giacobini 1991; Marean *et al.* 1992; Stiner 1994, 2004; Tyler Faith 2007; Pokines & Kerbis-Peterhans 2007; Schick *et al.* 2007; Fourvel *et al.* 2015; Arriaza *et al.* 2019; Stewart *et al.* 2021).

However, the presence of pups at Grotta Guattari has probably altered the distribution of gnawing marks on some anatomical elements.

Punctures. Punctures are the holes caused by tooth pressure and are found mainly on vertebrae, short bones, and epiphyseal ends, where trabecular bone is abundant, and canines can penetrate the surface and leave a mark. Punctures are not related to recovering meat parts but are probably related to the transport of body they were made by a large carnivore, such as a hyena (Fig. 10D).

TABLE 10. — Summary of the presence of different gnawing types according to NISP animal size. The percentages are derived from the NR with trace type compared to the total NISP of gnawed fragments for size (e.g. scores 47/51). Abbreviation: **NISP**, number of identified specimens.

Tooth mark - Ungulata	Large size	Medium size	Large size %	Medium size %
Scores	47	58	92.2	64.4
Pits	49	64	96.5	71.1
Punctures	13	4	25.5	4.4
Notch	7	23	13.7	25.8
Furrows	13	12	23.5	13.3
Scooping out	10	12	19.6	13.3
Licking/Chipped back edges	19	28	37.3	31.1
Crenatidens	10	32	19.6	35.6
Total NISP with gnaw	51	90	100	100

TABLE 11. — Breakage analysis of major long bones from Grotta Guattari, *Antro del Laghetto*. Abbreviation: **NISP**, number of identified specimens.

Fracture outline	Transversal	Oblique	Longitudinal
Large Size			
Humerus	2	4	–
Radius	–	2	2
Tibia	–	5	1
Metapodials	–	2	8
NISP	2	13	11
Medium Size			
Humerus	–	1	2
Radius	1	–	1
Femur	–	1	–
Tibia	–	1	–
Metapodials	3	–	1
NISP	4	3	4
Total NISP	6	16	15

Notch. Tooth profile recess at the fracture margin (Fig. 11A).

Scooping out. Insistent furrows with the removal of major portions of trabecular bone to access the marrow. These traces are visible on the epiphysis end (Fig. 11C).

Crenulated edges. Traces of crenatidens are observed on the fracture edges of flat bones such as vertebrae, scapulae and coxals.

Chipped back edges. Denticulated fracture margins of long bones, often with a notch (Fig. 11A, B).

Licking. Traces of licking and chipped back edges are visible as rounded and polished fracture margins in bone remains with internal nutrients, such as long bones with medullary cavities but also some portions of the skull.

Tooth marks were observed on most of the remains analysed although different specimens show varying degrees of intensity from heavy to high. The observed traces are consistent with those left by a large carnivore, while some thinner traces can be referred to hyena pups rather than to a small carnivore.

The presence of nibbling sticks (Fig. 13A), which are fragments of bone or antler chewed intensively by cubs during the teething, provides direct evidence of gnawing by young hyenas on the findings from Grotta Guattari. The teething of cubs can produce long, deep and narrow striae and triangular or oval marks (Diedrich 2006: fig. 14), which are common on nibbling sticks. Similar traces were also found on some fragments of diaphysis at Grotta Guattari, which is why it is hypothesised that they may be produced by hyena cubs rather than a small carnivore. Moreover, these traces had already been identified at Grotta Guattari (Stiner 1994: 124). Sometimes it is possible to recognize clusters of grooves and pits but in some cases these are repeated and overlapping. The bone surface appears rough and with diffuse gaps when high-degree gnawing is present, making it impossible to distinguish specific types of marks. These types of traces have also been observed on Neanderthal skull fragments from Grotta Guattari. The statistical analysis of the anatomical distribution of the traces reveals a higher frequency on large-sized prey compared to medium-sized ones (Table 10). This is probably due to the greater density and thickness of the large bones, which are more resistant to damage and require greater effort by hyenas.

Breakage analysis

The breakage analysis of major long bones shows that oblique fractures with complete diaphysis circumference and longitudinal fractures with incomplete diaphysis are equally represented, while transverse fractures are less represented (Table 11). These fractures are usually visible on dry bone

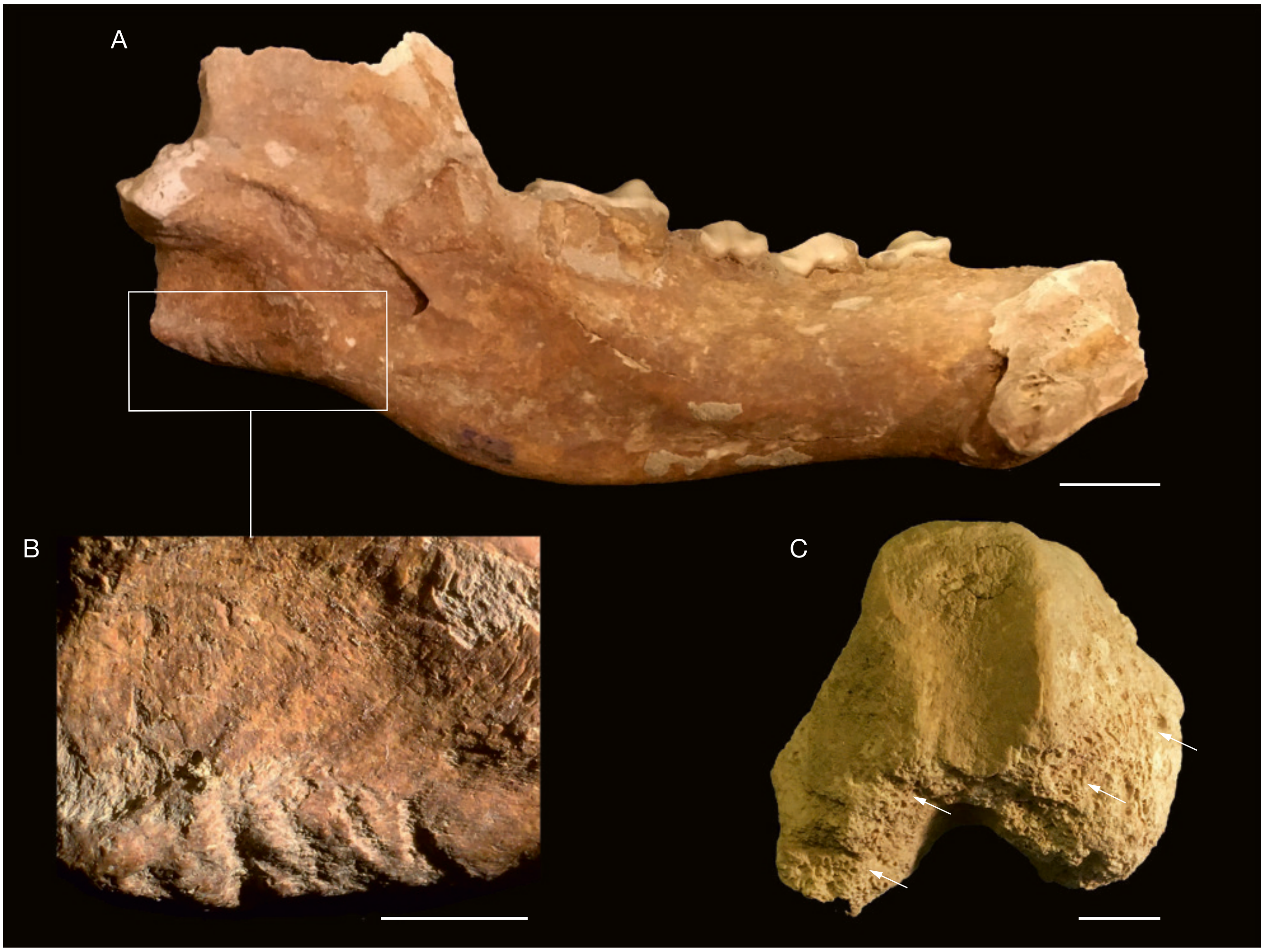


Fig. 12. — Hyena bone remains with traces of gnawing from Grotta Guattari, *Antro del Laghetto*: **A**, left mandible with: **B**, detail of gnawing; **C**, distal femur in posterior view. Scale bars: A, 2 cm; B, 5 mm; C, 1 cm.

with irregular margins, lacking the grooves and lines typical of fractures on fresh bone such as hackle marks and ribs along the fracture margins (Johnson 1985). However, these traces are often obscured by gnawing, making direct observation of fracture margins difficult.

A detailed study was conducted on long bone fragments with evidence of gnawing, focusing on missing portions. Ungulate long bones were divided into four categories (from Stage 0 to Stage 4), based on the progressive reduction of the epiphysis and diaphysis (Table 12; Fig. 3).

Stage 0. Whole elements with traces of gnawing on one or both ends without significant removal of the epiphyseal portion. Includes nearly complete elements (Table 12; Fig. 3) with traces involving the proximal epiphysis of radius and metapodials, with minimal removal of epiphysis surface.

Stage 1. Elements with complete diaphysis but missing one or both epiphyses. It mainly consists of metapodials missing the distal epiphysis, while the diaphysis remains preserved for almost their entire length (Table 12; Fig. 3).

Stage 2. Elements missing one or both epiphyses and a large portion of diaphysis. It is the most numerous group, consisting of fragments missing the mid-proximal part of metapodials, humerus and tibia. Those missing the mid-distal part are less represented.

Stage 3. Only a small central portion of the diaphysis (a few cm) is preserved.

Stage 4. Only epiphyses are preserved. It is the least represented group, mostly consisting of femurs and tibiae fragments.

The forty-two findings analysed were predominantly metapodials (NISP 44), less represented are femurs and the other elements have similar values (Table 12). The data obtained allow us to reconstruct the sequence and mode of long bone destruction by the cave hyena at Grotta Guattari. The gnawing begins from the epiphyseal parts with the removal of the trabecular bone and then proceed to the reduction of the diaphysis to reach the marrow. Sometimes the circumference of the diaphysis is intact, in other cases shattered. A large proportion of the

Table 12. — Bone damage stages. The drawing scheme in Figure 3. Abbreviations: **a**, long; **b**, short; **d**, distal; **dia**, diaphysis; **ep**, epiphysis; **NISP**, number of identified specimens; **p**, proximal.

	0 p	0 d	0 p d	1 p	1 d	2 p	2 d	3 dia a	3 dia b	4 ep d	4 ep p	Total
Bone damage stages												
Humerus	–	–	–	–	–	5	–	1	1	–	–	7
Radius	1	–	3	–	–	–	2	1	1	–	–	8
Femur	–	–	–	–	–	–	–	–	1	2	1	4
Tibia	1	–	–	1	–	3	–	1	–	1	–	7
Metapodials	2	–	5	–	3	5	2	1	–	–	–	18
Total NISP	4	–	8	1	3	13	4	4	3	3	1	44
Large size (*Bos/Equus*)												
Humerus	–	–	–	–	–	3	–	1	1	–	–	5
Radius	–	–	1	–	–	–	–	1	1	–	–	3
Femur	–	–	–	–	–	–	–		1	2	1	4
Tibia	–	–	–	–	–	1	–	1	–	1	–	3
Metapodials	2	–	5	–	1	1	1	1	–	–	–	11
Total NISP	2	–	6	–	1	5	1	4	3	3	1	26
Medium size (Cervidae)												
Humerus	–	–	–	–	–	2	–	–	–	–	–	2
Radius	1	–	2	–	–	–	2	–	–	–	–	5
Femur	–	–	–	–	–	–	–	–	–	–	–	–
Tibia	1	–	–	1	–	2	–	–	–	–	–	4
Metapodials	–	–	–	–	2	4	1	–	–	–	–	7
Total NISP	2	–	2	1	2	8	3	–	–	–	–	18

specimens observed appear to represent early or slightly advanced stages of gnawing, prior to the crushing and destruction of the bone.

Gnawing on the different taxa

Cave hyenas are mainly represented by isolated teeth, attributable to at least four adult individuals, displaying traces of cannibalism (Table 6). The body part with the greatest number of traces is the skull but gnawing on the post cranium was also documented (Figs 9B; 12).

A neurocranial fragment, thus lacking the anterior part of the face due to gnawing, shows an open occipital portion with zig-zag and rounded margins (Fig. 9B). There are minor and medium cracks on the mandible fragments. The most obvious traces of gnawing are located on the ramus on the lower/ventral edges of the mandibles, the traces consist of overlapping grooves and pits. Two teeth display circular traces indicative of tooth pressure, while furrows are visible on the partially preserved enamel of another specimen. An almost completely intact atlas shows gnawing along the lateral edges of the wings. A small portion of the coxal bone with part of the acetabulum appears heavily chewed. The humerus has a moderate degree of gnawing, with the proximal epiphysis missing and rounded fracture margins suggestive of scooping-out activity. The diaphysis and distal epiphysis bear scattered punctures and score marks. The ulnae have varying degrees of gnawing. One lacks the olecranon and shows light gnawing on the mid-distal shaft; another is heavily chewed, preserving only the medial portion, with intense traces of scoring. A tibia with a moderate degree of gnawing is missing the proximal epiphysis, which shows jagged and rounded fracture edges. The middle to distal portion is preserved with sparse pits and scoring.

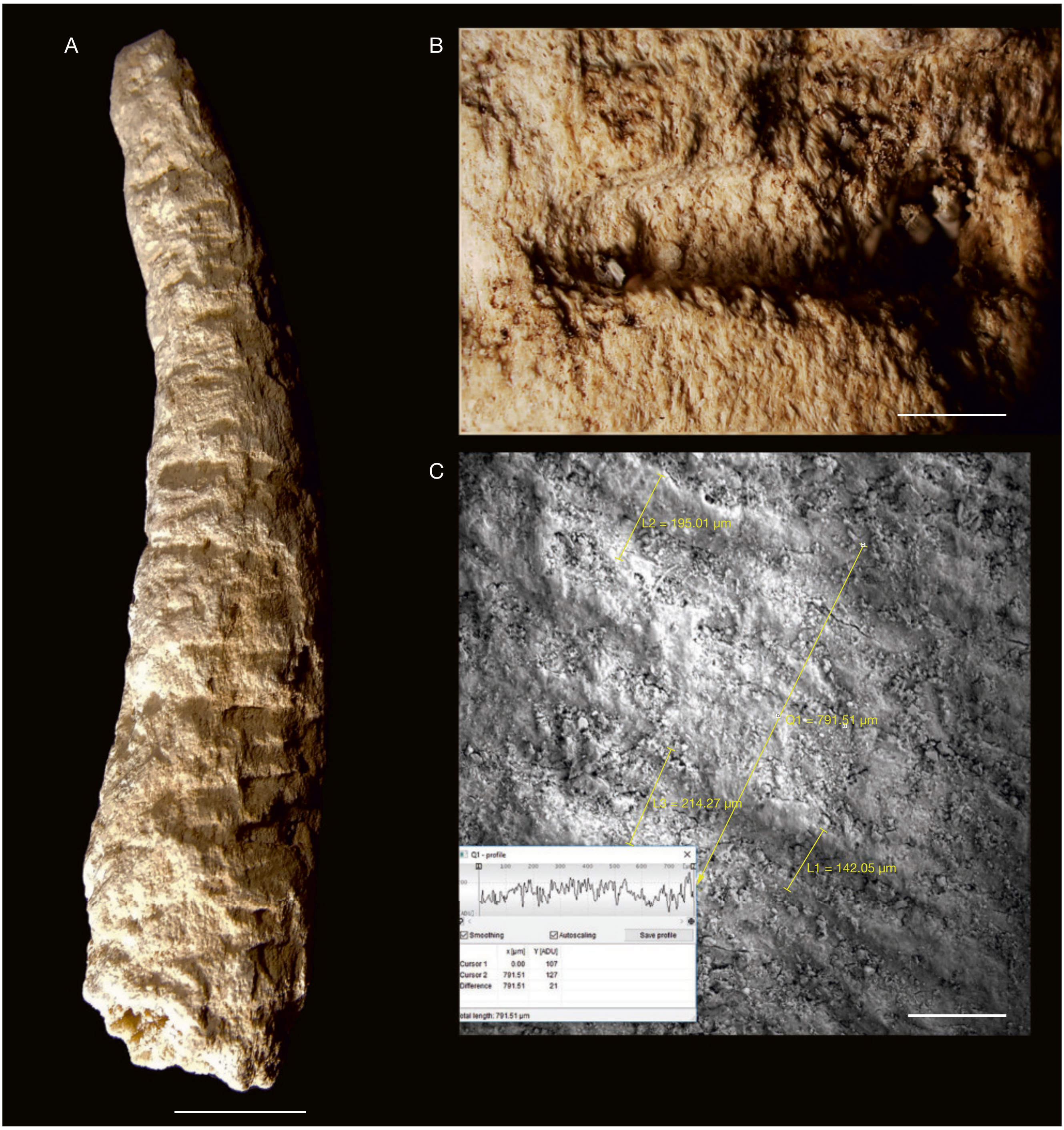
Cannibalism among hyenas is a frequent behaviour (Cruz-Uribe 1991; Diedrich 2012b, 2014). Their carnivore dentition consists of strong and stubby teeth with sharp edges specialised in bone-crushing. Some hyena teeth show oblique intrusive wear and deep longitudinal and oblique grooves, probably due to bone-crushing activity.

Equus ferus is represented by a few remains belonging to adult and young-adult individuals. Traces of gnawing documented from the denticulated edge and punctures were found on maxillary bones. Two complete metapodials show gnawing on proximal and distal epiphyses (Table 6).

A few elements of adult and young-adult individuals of *Sus scrofa* were analysed. Two complete phalanges I show markings and probable punctueres with moderate gnawing. The talus displays heavy gnawing on the edges and missing portions.

Nine *Megaloceros giganteus* remains attributable to adult individuals were studied. The elements show a moderate degree of weathering with medium to low-grade gnawing. Observed marks include pits, furrows and crenated margins on three skull pedicles and three shed antlers (Table 6).

Cervus elaphus is represented by remains referable to adult individuals (Table 6). The remains mostly consist of antler fragments, although all portions of the skeleton are represented. Long bone diaphyseal fragments add to the abundant category of indeterminate remains. Among the larger fragments, there is a high incidence of shed antlers with preserved roses, while skulls with antlers are less represented. The antler fragments show localised chewing on the fracture margins, which are transverse and oblique, while the circumference is usually complete. Only in one case the antler is dissected longitudinally. A pointed fragment is completely gnawed with deep transverse furrows and can be classified as a nibbling stick (Fig. 13A). The SEM analyses



	x [µm]	Y [ADU]
Cursor 1	0.00	107
Cursor 2	791.51	127
Difference	791.51	21

otal length: 791.51 µm

Fig. 13. — **A**, Nibbling stick on red deer antler from Grotta Guattari, *Antro del Laghetto*; **B**, details of a furrow; **C**, profile of the gnawing (SEM). Abbreviation: **L**, length. Scale bars: A, 1 cm; B, 1 mm; C, 200 µm.

shows that the investigated area is affected by persistent gnawing with furrows of the same depth as if the bone had been munched between molars and premolars (Fig. 13B, C) and bites were not aimed to fracture the bone, since pits or punctures are absent.

The anatomical distribution and frequency of gnawing traces are consistent with previous studies (Stiner (2004 and references therein). Several Italian Late Pleistocene sites with hyena presence show a marked preference for horns/antlers, an apparent behavioural trait unique to hyenas (Webbs 1989; Stiner 2004), and the upper levels of Grotta Guattari are a perfect case study (Stiner 1991b, 1994: 257-260).

Several finds display weathering traces with prominent and intrusive cracks confirming that these were collected and transported within the cave by carnivores. Among the tibiae, one is complete with chewing traces on the proximal portion, while the remaining fragments are all mid-distal fragments with traces.

TABLE 13. — Spatial distribution and preservation of Grotta Guattari coprolites.

	Fragmented	Semi-intact	Intact	Total
Small Lake	16	17	17	50
Morphotype 1	5	7	11	23
Morphotype 2	–	2	4	6
Not identifiable	11	8	2	21
Other soundings	20	5	23	48
Inside the cave	10	5	22	37
Outside the cave	10	–	1	11
Total	36	22	40	98

Dama dama is a relatively rare species at Grotta Guattari. A frontal bone with a basal antler shows fracture margins with visible browning.

Remains generically attributed to Cervidae mostly consist of antler and long bone fragments. Many elements have gnawed margins with abundant pits and scores on bone surfaces.

Bos primigenius is the second most common ungulate in the *Antro del Laghetto* after red deer (Table 6). The remains analysed in this preliminary study refer to at least four individuals (two young and two adults). All the elements, except some teeth, present traces of gnawing: holes, grooves, and ragged edges. The long limb bones and scapulae show the greatest damage with large portions of bone having been destroyed. The long bones of the limbs show variable degrees of gnawing: some are missing one or both epiphyses, others are missing the metaphyses, and some preserve only small diaphyseal segments. Tarsal bones are generally intact, but show holes, furrows and small lacunae on the surface. In particular, the calcaneus displays invasive gnawing on the caput. The gnawing is therefore concentrated in the areas that present the richest number of organic substances (e.g. fat, cartilage and ligaments), which are abundant on the epiphyses. This sample of gnawed but still identifiable remains probably reflects the initial stages of gnawing.

The most destructive activity is attested by the hundreds of indeterminate diaphyseal remains under 5 cm in size (many fragments are comparable in size and thickness to auroch bones). These fragments show gnawing and fracture patterns typical of large carnivore activity. Some small bone fragments exhibit modifications suggestive of digestive corrosion; however, thick concretions cover the surfaces hindering a detailed analysis.

Anthropogenic traces

Prior to this study, no evidence of human activity had ever been documented on bones from Grotta Guattari. Therefore, the identification of butchery traces on a radius of *C. elaphus* and probably on a humerus from a large mammal is an absolute novelty (Fig. 14).

A distal humeral diaphysis shows a fracture pattern and surface modifications that could be intentional, given the presence of a large notch with flaked areas on the medullary face and no evidence of gnawing. Moreover, a fragmented radius displays cut marks. A wide notch on the anterior face at mid-diaphysis could be the result of intentional fracturing. The edge displays removals consistent with percussion impact, and the margins exhibit characteristics of fresh breakage, including small grooves and surface roughness. Three distinct groups of oblique cuts are located on the anterior diaphysis, all oriented antero-laterally (Figs 14; 15): two short, oblique cuts near the epiphyses (Fig. 14B); long arcuate cuts on the metaphysis (Fig. 14C); long arcuate cuts on the mid-diaphysis (Fig. 14D). The high-magnification analysis of the second group of cuts highlighted a V-shaped cross-section at the point of lithic tool entry (Fig. 15A, B), while thin striae caused by the shoulder effect (i.e., raised edge along one side of the cut mark) are visible along the incision edge. The inner surface of the groove is covered with a thin layer of concretion (Fig. 15A, B), which probably contributed to the optimal preservation of the marks.

Based on their morphology, location, and orientation, these cut marks can be interpreted as resulting from a single fleshing activity. Particularly noteworthy are the traces found on the pointed end of the radius, which is blunted and marked by a cluster of streaks. These typologies of traces are problematic as can be related to occasional trampling, but their placement and extent suggest intentional use by humans – possibly as an expedient tool for scraping.

The coprolites

Fifty coprolites were recovered from the *Antro del Laghetto*. All seven investigated areas returned coprolites, but a notable concentration is attested in Area 4.

Fossil faeces were commonly found as single pellets during excavation. In many cases, multiple pellets were found close to each other, suggesting they originally formed part of the same dropping; however, physical connections were rarely attested. The closed environment of the cave, extremely rich in calcium carbonate from sustained water dripping, had a key role in the fossilisation of the dung. Consequently, carbonate concretions are commonly found on the surface of the fossil dung. The level of preservation of the coprolites from this chamber is evenly distributed between intact (34%), semi-intact (34%) and fragmented specimens (32%; Table 13). The coprolites are generally solid, though a few have a softer or powdery consistency. The external cortex is usually compact, due to the presence of intestinal lubricant that facilitates the dejection (Horwitz & Goldberg 1989). Traces of trampling on fresh excrements are also visible on a small number of specimens.

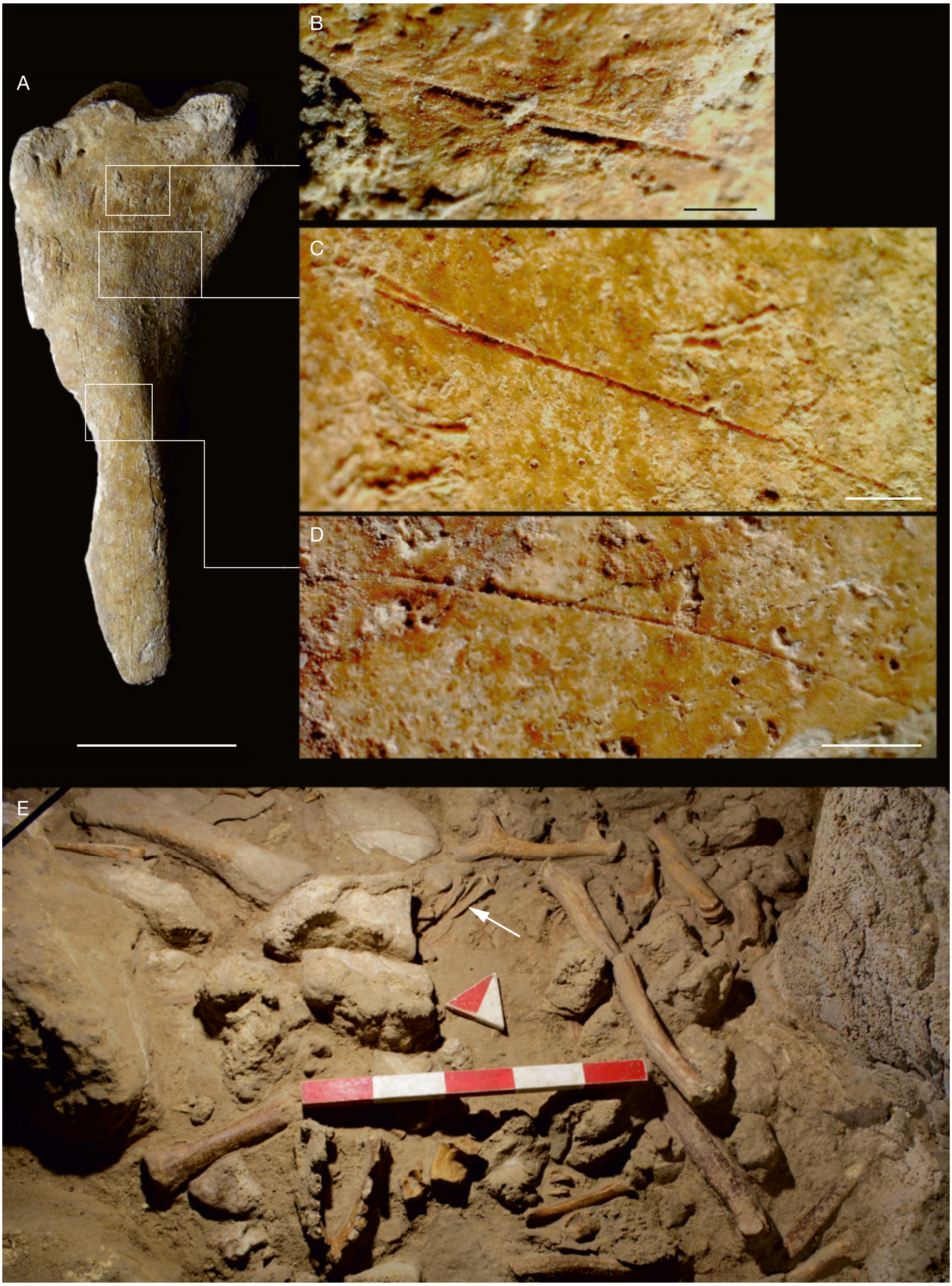


FIG. 14. — Butchery traces on remains from Grotta Guattari, *Antro del Laghetto*: **A**, mid-proximal radius of adult *Cervus elaphus* Linnaeus, 1758; **B**-**D**, zoom of the cut marks on the bone; **E**, position of the find (**white arrow**) in the paleosurface. Scale bars: A, cm; B, 1 mm; C, D, 2 mm.

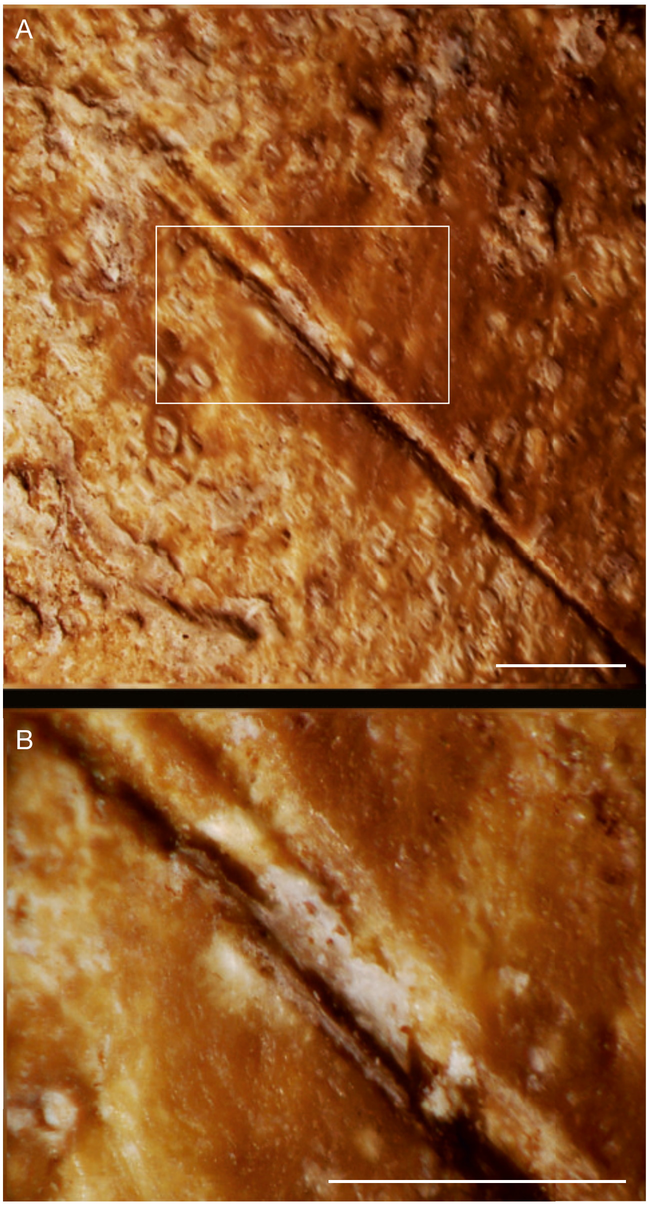


Fig. 15. — Butchery traces from Figure 14C observed with a Hirox microscope: **A**, overall view; **B**, enlargement of an area of **A**. Scale bars: 1 mm.

Internally, the coprolites are characterised by a granular texture, a result of post-depositional dehydration. A whitish colour characterises both the cortex and interior of the coprolites, although a few specimens show yellowish or light brown hues, possibly reflecting a slightly different process of mineralisation.

All coprolites underwent a general morphometric study, including weighing on a centigram-sensitive scale and measuring with a standard calliper. This study revealed the presence of at least two morphotypes (Table 13). Morphotype one specimens (Fig. 16A-E) are generally diagnostic. Their diameter ranges from 3 to 6.9 cm, and their dry weight varies between 13 and 156 grams. Macroscopic inspection frequently revealed the inclusion of small bone fragments. Morphotype two specimens (Fig. 16F) are significantly smaller, measuring between 1.1 and 2.9 cm in diameter, with an average weight of 3-4 grams per pellet. These pellets display a well-defined and recurring globular shape with a pointed/tapered end. Interestingly, this morphotype was also recovered from the same layers in another room of the cave, the nearby *Antro dell'Uomo*.

DISCUSSION

Taphonomic observations, together with the significant taxonomic diversity, and the abundance of *C. spelaea* remains and coprolites, suggest that this carnivore was the main agent responsible for the transport, modification and accumulation of the bone remains in the *Antro del Laghetto*, including both fauna and Neanderthals. This interpretation is consistent with previous analyses of the mammal remains from other rooms of the cave, including the Neanderthal skull that was first discovered (Piperno & Giacobini 1991; Stiner 1991a, b; Toth & White 1991). Although remains of other carnivores have been found at Grotta Guattari, gnawing marks attributable to species other than hyenas are absent. Therefore, these other carnivores were likely introduced in cave as prey. Nonetheless, the intensity and prevalence of hyena-related modifications may have obscured any marginal actions by other predators.

The limited presence of lithic industries in the *Antro del Laghetto*, in addition to the apparent absence of any other evidence of human activities such as charcoal or ash, suggests humans probably did not occupy the cave during the cave hyena frequentation (late MIS 4). The main interpretation is that the sporadic artifacts discovered reached the cave hyena living floor as a result of the carnivore's own activity, which caused the erosion and dispersal of the older external archaeological deposit through daily trampling and digging. A detailed study of wear traces on the lithic collection is currently ongoing and will hopefully shed light on the origin of the artifacts from the *Antro del Laghetto*. Therefore, the red deer radius bearing traces of butchering could represent a discarded butchering waste introduced by hyenas along with other remains, albeit a sporadic frequentation of the cave by Neanderthals who lived in the surrounding area cannot be excluded.

Modifications produced by large carnivores are the most prominent traces on bones and shed antlers. The epiphyseal ends of the long bones were removed through chewing by large carnivores (i.e., hyenas), as evidenced by irregular, rounded fracture margins in a zig-zag pattern (ragged-edged chewing); in some cases, the margins also retain tooth notches and traces of gnawing. Carnivores mainly gnaw the epiphyseal and trabecular ends and remove part of the tissue (i.e., scooping out) to reach the epiphyseal and diaphyseal bone marrow. The powerful jaws of these carnivores allow them to gnaw the long bones reducing them to small diaphyseal fragments. The presence of cave hyena remains, including some teeth, with traces of gnawing activity reflect cannibalistic behaviour (Diedrich 2020). Additional evidence supporting the use of the cave as a den includes the presence of nibbling sticks, which are bone fragments intensively chewed

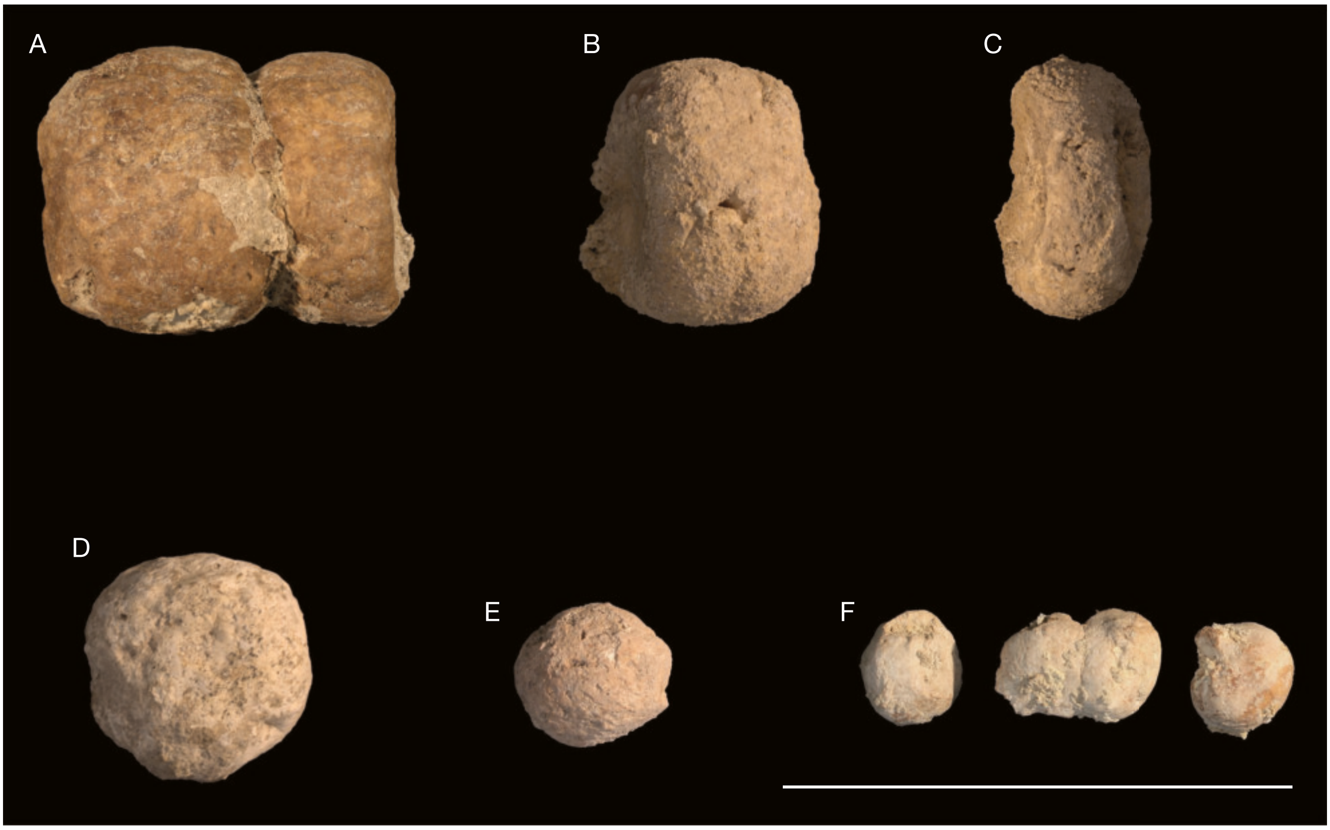


Fig. 16. — Coprolites from Grotta Guattari, *Antro del Laghetto*: **A**-**E**, cave hyena faeces: **A**, oval + disk; **B**, oval; **C**, disk; **D**, **E**, round; **F**, unknown carnivore coprolites. Scale bar: 10 cm.

by young hyenas during feeding and teething (Diedrich & Žák 2006). Moreover, skeletal representation shows that only portions of the prey (Table 3) were transported inside the den, a common behaviour among present-day hyenas (see also Pokines & Kerbis-Peterhans 2007; Egeland *et al.* 2008; Lansing *et al.* 2009; Diedrich 2010). Weathering is limited degree, indicating that bones were not exposed to weathering for extended periods.

The numerous coprolites discovered underwent macroscopic observation and morphometric analysis, allowing us to recognise several pellet types of different sizes. The structure and the presence of skeletal inclusions of small-medium size are typical features of carnivore faeces. From this perspective, the white colour of the faeces can also be explained by the presence of calcium deriving from the ingestion of bones (Bellusci *et al.* 2021). These features, in addition to comparison with the coprolite collection housed at the University of Rome “Tor Vergata” and according to the parameters by Diedrich (2012a), strongly support the identification of a large part of the assemblage as cave hyena coprolites (i.e., morphotype 1). This identification is further supported by the paleontological interpretation of the site as a cave hyena den. The interpretation is more uncertain for a smaller group of six coprolites (i.e., morphotype 2) which were recovered from the same stratigraphic units associated with cave hyena occupation. The presence of bone fragments confirms that these faeces belong to a carnivore. Preliminary morphometric studies indicate that these originated from a small-medium size species, while comparison with modern faeces suggests a possible resemblance with those produced by felids. Since bone remains of members of this family have been found in the cave, this interpretation appears plausible. These specimens suggest that Grotta Guattari was probably briefly frequented by another carnivore species , alongside the multiple and more intense occupations by cave hyenas. Further studies on the coprolites, such as pollen analysis and aDNA, are currently ongoing and will hopefully provide valuable information to enhance our understanding of this Late Pleistocene site.

Unfortunately, it was not possible to determine whether the coprolites were in primary or secondary deposition. Therefore, this accumulation could be linked to the morphology of the room, as the natural gradient of Areas 7 and 6 could have caused post-depositional movement downslope Area 4 (Figs 1-3), where the more confined and less accessible geological formations may have favoured better preservation. Alternatively, it could reflect a deliberate choice by the carnivores inhabiting the cave. Interestingly, it is well-attested that hyenas prefer to defecate near the entrance of their dens to alert and ward off possible predators (Diedrich 2014, 2015). Therefore, as proposed by Rolfo *et al.* (2023), it is possible the *Antro del Laghetto* was one of the many entrances to the cave about 65 ka BP and was later obstructed by the collapses that sealed the entire cave until 1939.

The analysis of bone remains of the main ungulates (Table 3) revealed that most of them are limb extremities (e.g. carpals, metacarpals, tarsals, metatarsals and phalanges), followed by skull bones, and mostly isolated teeth. This characteristic of the bone deposit is probably due to the compact and resistant structure of these anatomical portions. Furthermore, bones from the front limbs are more numerous than those from the hind limbs, suggesting that *C. spelaea* mostly transported selected portions of prey or specific anatomical elements (e.g. shed antlers) into the cave.

The selection operated by cave hyenas does not diminish the relevance of the prey's habitat requirements to propose an environmental reconstruction of the Circeo Promontory during the final stages of MIS 4. Wild boar prefers woods and wet areas, red deer is widespread in woods with glades, while fallow deer inhabit open woods or Mediterranean bushes (Boitani *et al.* 2003). Roe deer lives in dense broadleaf forests full of undergrowth and clearings, while *M. giganteus* and *P. antiquus* populated several habitats but generally favoured woods or forests with nearby bodies of water (Boitani *et al.* 2003; Petronio *et al.* 2014; Callaway 2016). Chamois is typical of coniferous and broadleaf woods with rich undergrowth interspersed with rocky walls and stony areas, alpine meadows, bare patches and grassy ledges, ibex prefers open and arid spaces and rocky mountain areas, while aurochs prefer open fields or meadows next to woods with large clearings (Boitani *et al.* 2003; Pandolfi *et al.* 2011). *Equus ferus*, *E. hydruntinus* and *Stephanorhinus hemitoechus* favoured open environments such as steppes and grasslands (Conti *et al.* 2010; Pandolfi *et al.* 2011, 2017; Salari & Masseti 2016). The Italian hare could live in several environments but seems to prefer dry shrub areas and grasslands alternating with broad-leaved woods with large grassy clearings; in contrast the European hare occupies open environments such as meadows and steppes (Amori *et al.* 2008). Wild cats and brown bears choose wooded areas close to water sources, while wolves and foxes are adapted to a variety of environments albeit generally placing their dens within woods with gorges and stony areas (Boitani *et al.* 2003). *Panthera spelaea* and *C. spelaea* also inhabited several habitats with a probable predilection for open spaces, exactly like present-day lions and spotted hyenas prefer the savannah, while leopard adapts to evergreen forests, savannahs, woods, rocky hills and swamps (Dorst & Dandelot 1988).

The palaeoecology of the taxa and their relative abundances allows us to reconstruct a landscape surrounding the cave largely covered by woods and forests with large clearings and Mediterranean scrub , alternating with open spaces with steppe and meadows, marginal rocky areas in the highest part of the promontory and probably coastal wetlands. Moreover, the palaeontological studies highlighted a few differences in the presence and frequency of several taxa within Levels 2 and 3 (Tables 1; 2). Equidae within Level 2 slightly decreased compared to Level 3 and *E. hydruntinus* disappeared, while rhinoceros slightly increased. The decrease of red deer and roe deer was partially balanced by the increase of *M. giganteus*. Finally, Caprines appeared. This data suggests that the environment during the deposition of Level 2 was probably less forested and with slightly more wetlands and exposed rocky areas than at the time of Level 3. Overall, the presence of chamois and ibex, together with the strong predominance of red deer over fallow deer and the presence of *M. giganteus*, which occurred in central-southern Italy only in the coldest phases of the Late Pleistocene (Petronio *et al.* 2014), suggests that the faunal deposit of Grotta Guattari accumulated in colder times than present day. This environmental picture is perfectly consistent with the radiometric dating and recent pollen analyses (Rolfo *et al.* 2023). Furthermore, given that ibex and chamois appear only in Level 2 and that *M. giganteus* occurs in this same layer with a higher percentage than in Level 3, it can be assumed that during the deposition of Level 2 the climate was a little colder than at the time of Level 3.

The environmental reconstruction outlined above is well attested in the Late Pleistocene of the Circeo Promontory and the Pontine Plain (Caloi & Palombo 1989, 1991; Gatta *et al.* 2016, 2019, 2022; Marra *et al.* 2018). This environmental mosaic has allowed the survival of many species of bats and other small vertebrates during the cold phases of the Late Pleistocene (Salari & Kotsakis 2011, 2017; Chiocchio *et al.* 2024), as well as plant species (e.g. *Fagus*) (Rolfo *et al.* 2023; Chiocchio *et al.* 2024), which then repopulated the peninsula and even central-northern Europe (Sommer & Nadachowski 2006; Salari & Kotsakis 2011, 2017).

CONCLUSIONS

This paper describes the mammal assemblage discovered within a single room (i.e., *Antro del Laghetto*) at Grotta Guattari. The study involved over 9 300 mammal remains from two stratigraphic levels, 1 335 of which have been taxonomically determined, allowing us to recognise at least 25 different taxa. Most of the fossil remains display gnawing traces from a large carnivore, namely *C. spelaea*, including some human bones and those of the cave hyena itself. Modifications produced by this carnivore are also evident on many shed antlers of cervids. These observations concern the bone remains of all the areas and the two levels of the *Antro del Laghetto*, even if the quantitative taphonomic analysis was conducted on a significant sample of 1 136 remains from Area 1.

The most abundant species identified are *C. elaphus*, *C. spelaea* and *B. primigenius*, followed by *S. scrofa*, *E. ferus* and other taxa, including some not previously identified at Grotta Guattari, such as *F. silvestris*, *P. spelaea*, *E. hydruntinus* and *Rupicapra* sp. These species were mainly hunted or scavenged by cave hyenas, which used the cave as a storage/communal den. It is notable the presence of several Neanderthal remains, killed or scavenged by the carnivore, a circumstance attested for the first time in the Italian Peninsula.

Crocuta spelaea was perfectly adapted to the environment of the Pontine Plain, as also suggested by the nearby dens of Cava Muracci (Gatta *et al.* 2019), Grotta La Sassa (Gatta *et al.* 2022) and Grotta del Fossellone (Alhaique *et al.* 1996), where the species survived at least until the end of MIS 3. Finally, the cave hyena of Grotta Guattari was larger on average than coeval Italian specimens, resembling *C. spelaea* from north-western Europe. A considerable size is also recognised among horses, red deer and aurochs.

The bioecology of this mammal assemblage suggests that the environment surrounding the cave was mostly forested with large glades but also included wetlands and steep rocky areas. The presence of chamois and ibex in lowland areas near the coast, along with the widespread occurrence of *M. giganteus* in central Italy and the higher frequency of red deer over fallow deer hint that the cave hyenas accumulated this faunal deposit in cooler times than present-day. These data align with radiometric dating and pollen analysis, which highlighted that the chronological framework around 66-65 ka corresponds to one of the coldest and driest phases of MIS 4 (Rolfo *et al.* 2023). However, pollen and fauna indicate that both woodland and forests persisted in the area, along with the co-existing of temperate and colder climate species, probably due to the climate mitigation provided by the Tyrrhenian Sea. Moreover, a comparison between the fauna of Level 2 and 3 allowed us to recognise that Level 2 was deposited during a slightly colder oscillation around the final stages of MIS 4.

The presence of human remains among the preys transported by cave hyenas into the cave around 66-65 ka BP strengthen the interpretation of a densly inhabited Pontine Plain, as suggested by the outstanding number of open-air sites discovered (Rolfo *et al.* 2022).

The results of this study significantly enhance our understanding of the Pontine Plain environment during the Late Pleistocene. New palaeoecological and paleontological data from Grotta Guattari revealed the region was inhabited by numerous animal and plant species with different habitat requirements, endorsing the hypothesis that the Pontine Plain could have served as a *glacial refugium* (see Sommer & Nadachowski 2006; Salari & Kotsakis 2011, 2017; Chiocchio *et al.* 2024) between MIS 4 and MIS 3, also for *Fagus* (Rolfo *et al.* 2023), cave hyenas and Neanderthals.

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