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Neanderthal bones collected by hyena at Grotta Guattari, central Italy, 66–65 ka: U/Th chronology and paleoenvironmental setting

Mario Federico Rolfo [a], Monica Bini [b, c, d], Francesco Di Mario [e], Angelica Ferracci [a, f], Biagio Giaccio [g, *], Hu Hsun-Ming [h, i], Ilaria Isola [d], Laura Sadori [j], Chuan-Chou Shen [h, i], Cristiano Vignola [j], Giovanni Zanchetta [b, c, d, g]

[a] *Department of History, Culture and Society, University of Rome "Tor Vergata", Rome, Italy*
[b] *Department of Earth Sciences, University of Pisa, Pisa, Italy*
[c] *Centre for Climatic Change Impact, CIRSEC, University of Pisa, Pisa, Italy*
[d] *Istituto Nazionale di Geofisica e Vulcanologia (INGV), Sez. Pisa, Pisa, Italy*
[e] *Superintendence of Archeology, Fine Arts and Landscape for the Provinces of Frosinone and Latina, Rome, Italy*
[f] *Archaeological Service, S.A.B.A.P.-LAZ, Rome, Italy*
[g] *Istituto di Geologia Ambientale e Geoingegneria, Consiglio Nazionale Delle Ricerche, 00015, Monterotondo, Rome, Italy*
[h] *High-Precision MassSpectrometry and Environment Change Laboratory (HISPEC), Department of Geosciences, National Taiwan University, Taipei, 10617, Taiwan*
[i] *Research Center for Future Earth, National Taiwan University, Taipei, 10617, Taiwan*
[j] *Department of Environmental Biology, Sapienza University of Rome, Rome, Italy*

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A B S T R A C T

After eight decades since its discovery in 1939, new investigations have been undertaken at Grotta Guattari (Latium, central Italy), a coastal cave by the Tyrrhenian Sea coast and one of the iconic sites of the Italian prehistory, as it yielded an almost complete skull and other remains of Neanderthals. The new excavations of the innermost and untouched cave deposits resulted in an outstanding amount of mammal bones, 40 out of which attributable to Neanderthal, including new large portions of cranial remains. Preliminary taphonomic hints and the collected stratigraphic evidence strongly indicate that the impressive accumulation of the large mammal bones was the work of spotted hyena, in a period in which human frequentation was really sporadic or even completely absent. The new acquired U/Th chronology of Grotta Guattari speleothems provided new constraints for reconstructing the sedimentary and paleoenvironmental history of the archaeological successions and human remains. The accumulation of terrestrial sediments started at ~112 ka, immediately after the end of the Last Interglacial sea-level highstand (~116 ka). However, the hyena frequentation, and thus the bone accumulations, occurred several thousands of years after and lasted for a very short time interval, precisely between slightly before 66 ka and 65 ka. The cave became abandoned by hyena after ~65 ka and before ~59 ka, because of the cave obstruction and/or the altered environmental conditions related to the Heinrich Event 6 (~64–60 ka). The regional paleoclimatic records indicate severe conditions during the short interval of the hyena frequentation. In contrast, though providing evidence of open and arid environments, the faunal assemblage and the pollen from Grotta Guattari reveal that the local conditions were less severe, likely because of the mitigating effect of the Tyrrhenian Sea. In the framework of the Italian findings, Grotta Guattari results the richest and better chronologically constrained site of Neanderthal remains, posing it as one of the rare sites of the European prehistory that allows putting into the context an extraordinary large sample of the population of Neanderthals, and of other large mammals, in a very narrow and precisely dated temporal interval of the early Pleniglacial.

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* Corresponding author.
E-mail address: biagio.giaccio@cnr.it (B. Giaccio).

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1. Introduction

Since its first discovery in the half 19th century (King, 1864), the nature and the evolution of the Neanderthals, the human species that lived in western Eurasia during the Middle to Late Pleistocene, have aroused the interest of generations of paleoanthropologists, archaeologists and Quaternary geoscientists (e.g., French, 2021; Romagnoli et al., 2022). For many of the issues addressed in more than 150 year of studies, the chronology and the paleoenvironmental setting represented crucial needs for putting the findings into the context and understanding the timing and processes involved in the evolutionary dynamics of this human species. While great efforts and significant steps forward have been recently made about the latest evidence and the demise of the Neanderthals (e.g., Higham et al., 2014), the chronology of the earlier periods is still weak and affected by significant uncertainties. This is essentially because the Neanderthal history extends well beyond the current limit of the radiocarbon dating method (55 ka, Reimer et al., 2020), which is the most reliable and intensely applied geochronometer in the prehistory field study. As a consequence, acquiring reliable and robust chronologies for the older Neanderthals, as either anthropological (i.e., bones) or archaeological remains (i.e., lithic industry), still represents a major challenge.

In the framework of the Italian peninsula Middle Palaeolithic, the Tyrrhenian coasts preserves an important number of open-air, rocky shelter and caves containing archaeological successions with Mousterian industry, which is the typical lithic technocomplex associated with the Neanderthals (e.g., Blanc, 1939, 1954; Palma Di Cesnola A. 1968; Sarti, 1996; Boscato et al., 2009; Ronchitelli et al., 2010; Moroni et al., 2019; Spagnolo et al., 2020a,b; Fig. 1). In many coastal caves, the archaeological infilling rely on beach-shallow marine deposits correlated to a sea level high-stand, regionally known as "Tyrrhenian" (Issel, 1914; see the review by Asioli et al., 2005 and references therein). Often, the Tyrrhenian deposits contain characteristic molluscs (e.g., Taviani, 2014) indicating warm water condition and are commonly ascribed to the Last Interglacial (LIG) sea level highstand or the Marine Isotope Stage 5e (i.e., MIS 5e, e.g., Hearty et al., 1986; Paquetti et al., 2021 and reference therein), although in some instances other MIS 5 substages have been proposed (e.g., MIS 5c and/or 5a, e.g., Hearty et al., 1986; Mauz, 1999; Marra et al., 2020). Therefore, in this morpho-stratigraphic context, the LIG highstand deposits provide a *terminus post quem* for the overlying Mousterian archaeological layers of ca. 116 ka (e.g., Muhs et al., 2015).

On the other hand, the available radiometric chronology indicates that the Mousterian can spans until ~40 ka, with temporal constraints that, however, are satisfactory only for the most late MIS 3 (e.g., Higham et al., 2014; Zanchetta et al., 2018; Benazzi et al., 2011; Moroni et al., 2019; Spagnolo et al., 2020a), while they decrease in number, accuracy and precision as the chronologies pull away from the radiocarbon range, leaving large uncertainty for the remains older than 50 ka. Furthermore, despite the abundance of archaeological and faunal remains found in many of these Italian coastal caves, the associated finding of Middle Palaeolithic human remains (i.e., Neanderthal) are extremely rare (e.g., Alciati et al., 2005).

An outstanding exception is Grotta Guattari (Fig. 1), where, in the middle of the past century, a complete skull and two incomplete mandibles of Neanderthal were found (Blanc, 1939, 1961), which, according to Blanc (1961), bear evidence of cannibalism.

More than a half century after the last investigations, on October 2019 a new excavation campaign was undertaken in the inner part of the cave, in an area previously untouched by Blanc's excavation (the so called "Laghetto" area, Blanc, 1939), while later, in 2020–2023, also the external area was explored.

The new investigations of the "Laghetto" sector, which is the focus of this work, brought to light a considerable number of new Neanderthal and other large mammal remains, for which here we present the stratigraphy, a suite of U/Th dating from carbonate concretions and preliminary results of pollen analysis for the palaeoenvironmental reconstruction. Our results provide the first robust chronological framework of the earlier and the new anthropological findings, which make Grotta Guattari one of the European richest and better-dated sites of Neanderthal remains.

2. General background

2.1. Geological-geomorphological setting and historical investigations

The entrance of Grotta Guattari is located at ~7 m above sea level (a.s.l.) on the eastern slopes of Mount Morrone of the Circeo promontory (Fig. 1), made of Lias-Jurassic limestone, belonging to the Umbrian-Sabine succession (Segre, 1991).

The cave was accidently discovered on February 24, 1939, during private quarry activities. The day after, the landowner A. Guattari, with the help of some workers, identified in a lateral branch one of the best-preserved Neanderthal skulls ever found in Italy (Blanc, 1939; Sergi, 1974; Ascenzi, 1991). The systematic research at the cave began immediately after the fortuitous discovery of the first Neanderthal skull (Blanc, 1939) later known as Circeo I (Sergi, 1954, 1974; Sergi and Ascenzi, 1955). A few days later an incomplete human mandible (Circeo II) was found, just a few meters away from the skull. Finally, another human mandible (Circeo III) was found in 1954 in the section of the external deposit (Sergi, 1954; Sergi and Ascenzi, 1955; Arnaud et al., 2015). The inner sector of the Cave was then named "Antro dell'Uomo" (literally the "man's cavity").

The Circeo I skull, which presented an evident enlargement of the foramen magnum, was found, inside a stone circle, resting on the surface of the cave infilling, along with a large number of mammal bones and stones. Subsequent excavations of the underlying deposits, coordinated by A.C. Blanc, with the collaboration of L. Cardini, were discontinuously carried out until 1951. The excavation evidenced the occupation by hyena in the layers below Circeo I skull. Based on this stratigraphic and taphonomic evidence, Blanc concluded that the human skull was subjected to cannibalistic practices, likely by individuals belonging to the same group of Neanderthals, which ritually placed the skull of their similar into the cave, where hyenas had previously occupied the cave as a den (Blanc, 1961). During subsequent excavations, which also involved the rock shelter area at the cave entrance, the Blanc's team found abundant lithic industry, concluding that human occupation of the cave could have alternated with that of the hyena.

In the following decades, the contributions of various scholars helped to better interpret the findings and the deposit, suggesting that the inner part of the cave was exclusively occupied by hyena (e.g., White and Toth, 1991; Stiner, 1991). Specifically, according to these authors, the modifications of the skull, which brought Blanc to speak of cannibalism, were actually due to the simple gnawing activity of hyenas (White and Toth, 1991; Stiner, 1991).

The Circeo 1 skull and the other surficial remains were featured by a "coralloid" calcite concretion, dated by Schwarcz et al. (1991), with the U/Th isochron method to 50 ± 3 ka. Additional dating using the Electron Spin Resonance (ESR) method on tooth enamel of faunal remains found at the surface of the infilling and covered by the concretions, yielded, consistently, a cumulative age of 57 ± 6 ka (Schwarcz et al., 1991). From the 1990s, the cave and the surrounding access areas have remained closed pending acquisition by the state. In October 2019 a new excavation campaigns was undertaken in the inner part of the cave previously untouched by

Fig. 1. Reference maps. **a)** Location of the Italian sites with Neanderthal remains (updated from Alciati et al., 2005; see Table 3 for details). **b)** Location of Grotta Guattari and of other sites with Neanderthal remains in the Monte Circeo area.

Blanc's excavation, in the area of the "Laghetto" (Fig. 2). The new excavation brought to light a considerable number of new Neanderthal remains mixed with hyena prey and in this work we describe in details the stratigraphy of the "Laghetto" and a new suite of U/Th dating from carbonate concretions.

2.2. Stratigraphy

The excavated areas by Blanc between 1939 and 1951, with indications of the different trenches, are reported in Fig. 2a. The general cave stratigraphy was summarized several decadal after by Segre (1991). Segre (1991) divided the inner and external cave deposits into 13 units (Figs. 2 and 3). The units attributed to the Late Pleistocene are six (Units 8-9-10-11-12-13), with lowermost one consisting in fossil beach deposit (Unit 8) containing remains of *Persististrombus latus* (formerly *Strombus bubonius*, e.g., Taviani, 2014), a gastropod species distinctive of the MIS 5e highstand (e.g., Taviani, 2014; Antonioli et al., 2018). The attribution of this beach deposit to the MIS 5e sea level high-stand has been recently confirmed by the $^{40}Ar/^{39}Ar$ dating of the detrital sanidine extracted from the beach sand yielding the age of 121.5 ± 5.8 ka (Marra et al., 2023). Segre (1991) described in the adjacent "Antro dell'Uomo" a

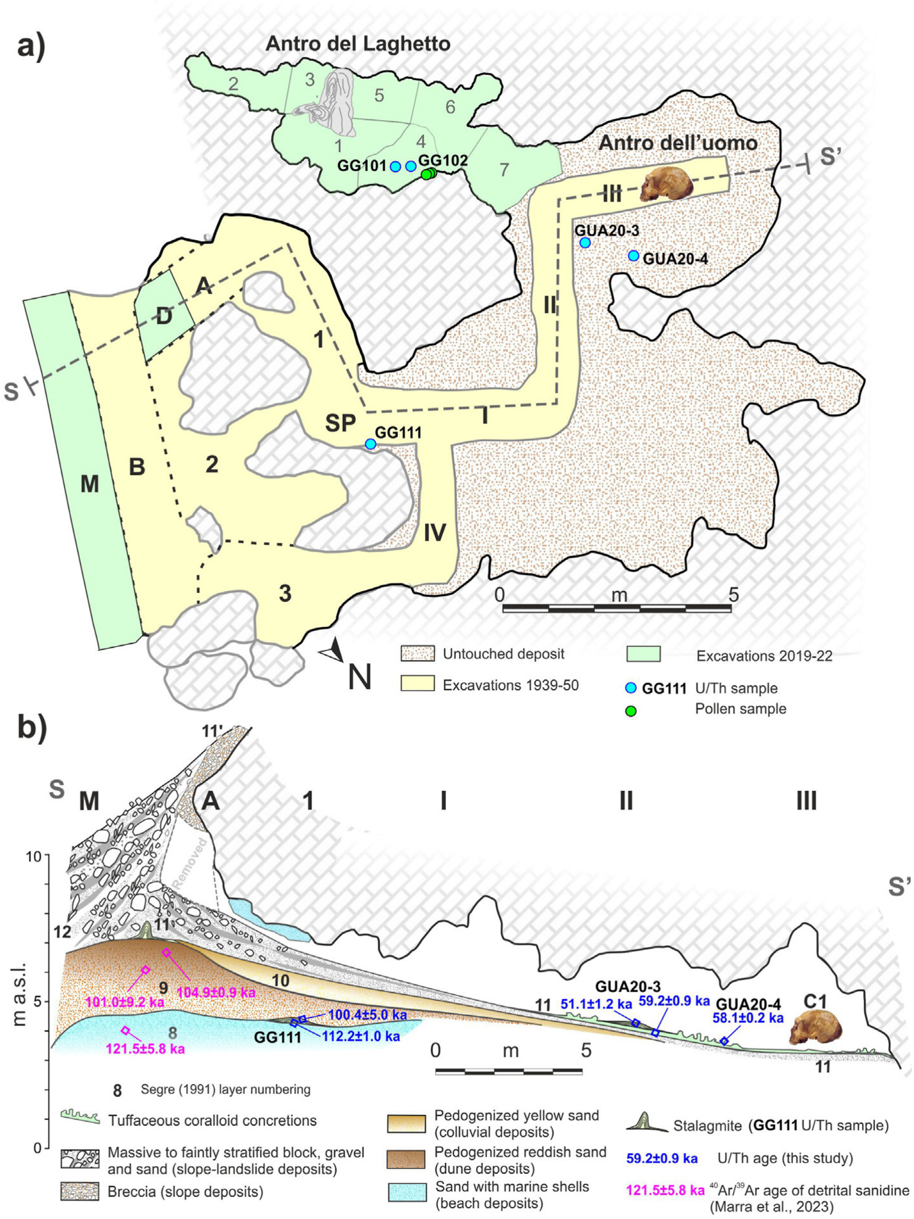

Fig. 2. Planimetry **(a)** and simplified geological section **(b)** of Grotta Guattari, with the location of the historical and recently investigated sectors and of the U/Th and pollen samples (modified after Segre, 1991).

level of breccia with faunal remains (level 8 of the inner sector, equivalent to the uppermost interval of the Unit 10 of the general stratigraphy, Fig. 2b and 3) that corresponds to the uppermost unit-palaeosurface well-documented and recognizable in all of the cave's recesses, with the exception of the area of the pond, where such surface was masked by younger shallow deposits.

Above this level, Segre (1991) described the presence of a series of irregular concretions: level 9 is a flowstone microlayer; level 10 is composed of discontinuous flowstone (tuffaceous) concretion; 11 and 11′ are "coralloid" concretions that cover all the clasts and finds of the palaeosurface, equivalent to the Unit 11 of the general stratigraphy (Fig. 2b and 3). Below level 7′-7″, Segre (1991) describes the presence of a crumbly calcite deposits followed by a sequence of sterile sandy levels.

2.3. Geomorphological and hydrological setting of the newly investigate "laghetto"

The "Laghetto" (which is Italian for "little pond"), is the cave sector so named by Blanc in various contributions since 1939 (Blanc, 1939, 1954, 1961) due to the periodic presence of an ephemeral stagnation of water. The "Laghetto" is the innermost area of Grotta Guattari and is set in front of the "Antro dell'Uomo" (Fig. 2a), where the Neanderthal skull and jawbone were found in the February of 1939. The "Laghetto" sector has a maximum length of 9.93 m along the NE-SW axis and is narrow in width, ranging from 3.6 m to 0.75 m along duct 2 (Fig. 2a). The maximum height calculated before excavations was 2.6 m in the centre of the cave sector, corresponding to Area 5 in Fig. 2a, whereas the minimum

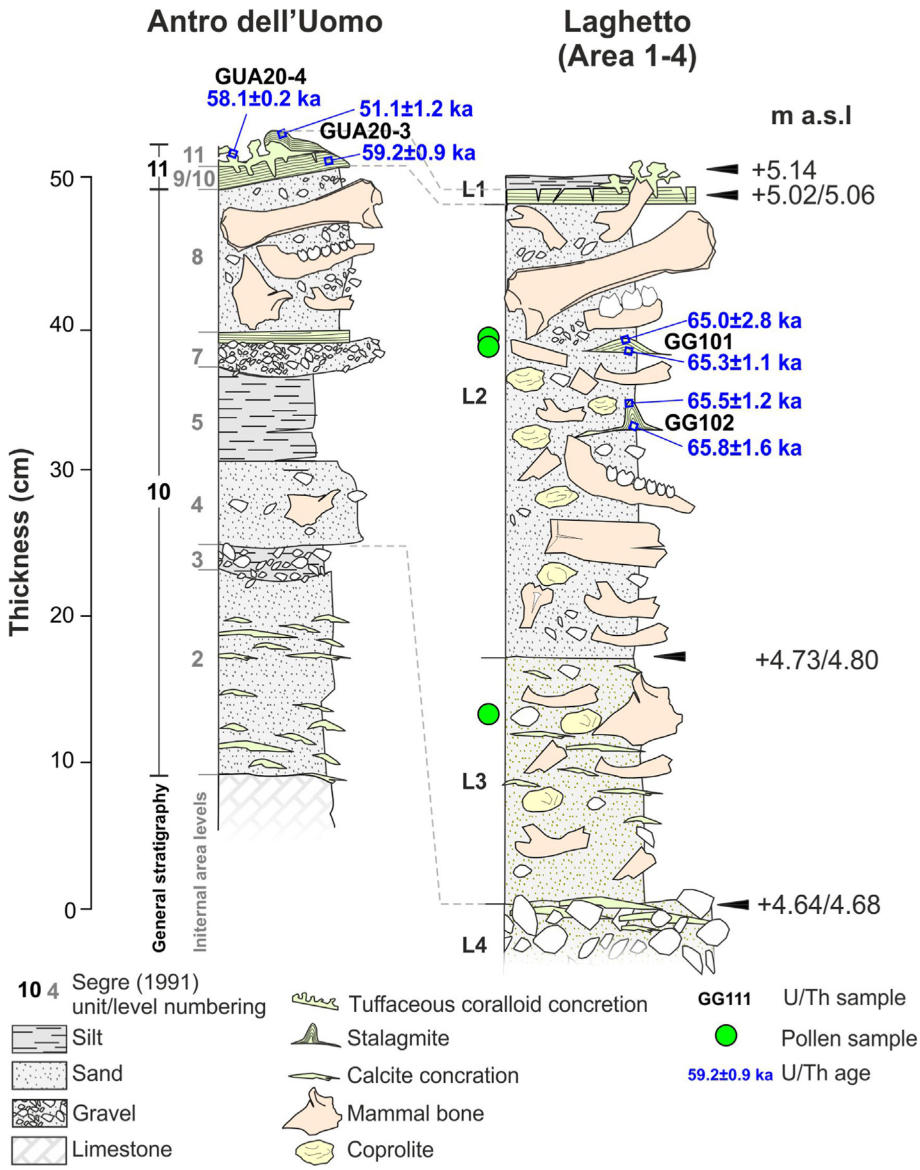

Fig. 3. Stratigraphic log of the "Laghetto" sector (Fig. 1a) and its tentative correlation with the Antro dell'Uomo sector (modified from Segre, 1991) (Fig. 1a).

was of 1.27 m, along Area 2. The latter is also the area with the lowest elevation in the cave measured prior to the excavation, ranging between +5.52 m asl and +4.98 m a.s.l., which is lower than the elevation of the pristine surface of the neighbouring "Antro dell'Uomo" (+5.91; +5.97 m asl).

Unfortunately, the excavation of Trenches II and III between 1939 and 1951 (Fig. 2a) removed the portion of the deposit that joined the "Laghetto" to the "Antro dell'uomo" and to the rest of the cave's deposit, so interrupting the physical continuity of the sedimentary succession and making it more difficult to correlate the stratigraphy of the two areas. The sector of the "Laghetto", as suggested by its name, differs from the other areas of the cave being affected, especially from October to May, by the rise of groundwater through a natural siphon placed in the lowest point at the end of the room. Over a period of three years, it was possible to monitor the water inflow, which is linked to the local rainfall regime, and to observe a maximum flooding of approximately +2 m above the ground surface (~7 m asl) in the lowest part of the area, reaching the same height as the threshold of the cave's entrance. The areas that are most affected by the rising waters are those at lower elevations along the northern and eastern sectors of the cavity, whereas flooding is reduced in the western sector near Trenches II and III (Fig. 2) and near the above-mentioned leap in elevation.

3. Materials and methods

3.1. The 2019-ongoing excavations

3.1.1. The internal "laghetto" sector

The "Laghetto" room was investigated extensively, covering the entire surface (Fig. 2a). The excavation went on from October 2019 to August 2021, with a forced break between March and May 2020 due to the Covid-19 health emergency. The recurring above-mentioned raising of the groundwater prevented a continuous and extensive investigation of the entire paleosurface, therefore it was decided to divide the whole area into seven distinct areas (Fig. 2a) that were individually investigated.

The deposit was investigated using stratigraphic units (SUs), which allow to identify distinct sedimentary bodies here conceived/labelled like levels. The characteristic of the deposit (friable carbonate concretions and loose sediments) allowed the use of special plastic and wooden probes for the excavation, so as not to ruin the surface of the finds and compromise taphonomic analyses. The excavated sediment was processed using flotation with sieves of 5 mm mesh size for the heavy fraction and of 2 mm for the light fraction. Due to the conformation of the cavity, rather than dividing the area with a grid, it was preferred to construct a network of fixed points. After being uncovered and defined on the ground, the finds were documented through a topographical survey using a Leica FlexLine TS09 Total Station. In addition, for a more detailed graphical documentation, all the finds were recorded through plan drawing by hand on graph paper at a 1:10 scale, after which a digital map and relative GIS project were elaborated. To study the taphonomy and the processes of the bone accumulation, the azimuth and the elevation angles of major axis of the finding were measured using an inclinometer (ZZAMG). The findings were individually bagged and univocally numbered at the site to then be cleaned and labelled at the Laboratory of Prehistoric Archaeology of the University of Rome “Tor Vergata”.

3.1.2. Preliminary information on the excavation of the external sector

The excavation of the external sector started in 2020 and is currently ongoing. The preliminary results indicate that the overall stratigraphic and chronological setting and the nature of the archaeological remains substantially differ from that of “Laghetto” sector. Therefore, the results of the investigation of this sector will be the subject of future papers, while here we only provide basic information.

The excavation was carried in two distinct areas: the ‘stratigraphic baulk’ of the Blanc's Trench B, identified as area M; and the portion of the Blanc's Trench A, which in previous excavations (1939–1951, yellow areas in Fig. 2a) had not reached the level of the Tyrrhenian fossil beach, identified as area D (Fig. 2b). The investigation of area M uncovered the remaining portion of Trench B: towards E, up to the current boundary wall that divides the cave's archaeological area from the private property opposite it; and towards N, in line with the jump in elevation created in 1939 as northern limit of Trench B. The 6-m-long and approximately 1-m-wide trench has been investigated, to date, to a depth of approximately 1.25 m. The ongoing excavation of the Unit 9, according to the Segre's (1991) stratigraphy, has revealed a structured paleosurface of human occupation. It is characterized by abundant faunal remains, many of which burnt, areas with high concentration of charcoals (hearth) and conspicuous lithic industry, which, basing on the preliminary geochronological data, span between ~121 ka and ~105 ka (Marra et al., 2023) (Fig. 2b).

3.2. U/th geochronology

3.2.1. Sampling

During the excavation of the “Laghetto” room, several stalagmites and thin flowstone crusts were found interlayered with the sediment, indicating local phases of dripping and calcite deposition. Two well-preserved stalagmites, occurring within the Level 2 (SUs 20–21; samples GG101 and GG102), were selected (Fig. 2a and 3; Supplementary Fig. S1). Additionally, two samples of the coralloid concretion covering the top surface at the “Antro dell'Uomo”, were taken (GUA20-3 and GUA20-4; Figs. 2 and 3), the same that was previously dated by Schwarcz et al. (1991). The sample GAU20-3 was also featured by a thin layer of laminated flowston growth above the tuffaceous concrections (Fig. S1). In order to constrain the basal age of the internal continental infilling of the cave, a sample of a thin flowstone covering the basal marine deposit was collected (sample GC111; Fig. 2a–b; Fig. S1). The samples were transported to the Laboratory of the Paleoclimatology and Geoarchaeology of the Earth Science Department of the University of Pisa. They were halved and a cm-thick slice was polished and used for the U/Th dating. The other sections where used for thin section. Thin sections were used to selected the position of U/Th dating to avoid layer with evident post-depositional alteration.

3.2.2. Dating

The 230Th/U dating were performed at the High-Precision Mass Spectrometry and Environment Change Laboratory (HISPEC), Department of Geosciences, National Taiwan University. All U–Th isotopic measurements were conducted on a Thermo-Finnigan Neptune multi-collector inductively coupled plasma mass spectrometer (Shen et al., 2012; Cheng et al., 2013). A gravimetrically calibrated triple-spike, ^{229}Th–^{233}U–^{236}U, and the isotope dilution method were employed to correct for mass bias and to determine U–Th isotopic compositions and contents (Cheng et al., 2013). Half-lives of U–Th nuclides used for ^{230}Th age calculation are given in Cheng et al. (2013). Uncertainties in isotopic data and ^{230}Th dates are given at the two-sigma (2σ) level or two standard deviations of the mean ($2\sigma_m$) unless otherwise noted. Table 1 shows all U–Th contents, isotopic compositions and ^{230}Th ages. An initial ^{230}Th/^{232}Th atomic ratio of $(4 \pm 2) \times 10^{-6}$ was applied for age correction. Results are shown in Table 1.

3.3. Pollen analysis

The pollen analysis was carried out on three sediment samples recovered from the top and bottom of SU 20 in Level 2 and from SU 53 in Level 3 (Fig. 2a and 3). Fossil pollen grains and Non-Pollen Palynomorphs (NPPs) were extracted from a known amount of dry sediment (3 g) with standard chemical treatment (HCl 37%, HF 40%, NaOH 10%; Fægri and Iversen, 1989, modified) and ultrasonic sieving (10 μm). In order to estimate pollen concentration, tablets with known content of *Lycopodium* spores were added to the sediment (Stockmarr, 1971). The identification of pollen grains was based on atlases (Reille, 1992, 1995, 1998) and reference collections. According to pollen morphology, oaks were grouped in three pollen types following Smit (1973). Pollen grains of *Ostrya carpinifolia* and *Carpinus orientalis* cannot be morphologically distinguished, as *Fraxinus excelsior* and *F. angustifolia*. As Cichorieae is the only European tribe of Asteraceae Cichorioideae (Florenzano et al., 2015) we used this term.

4. Results

4.1. Stratigraphy

In the “Laghetto”, the excavation removed the deposit for a depth ranging between 47 cm and 102 cm. 25 stratigraphic units (SUs) were identified (SU18 to SU63), allowing the recognition of four distinct levels, with different geological and archaeological characteristics (Fig. 3). From the top to the bottom they are:

Level 1 – SUs 18–19. It extends throughout the whole surface of the area and it is characterized by a very porous and friable layer of 2–3 cm of thick tuffaceous whitish flowstone (SU18), above which there is a thin level – of around 1 cm of thickness – of ancient and recent mud that was deposited by groundwater (SU19). In certain points, the bone remains of the level below (Level 2) were partly visible despite the cover of Level 1. Protruding bones are covered by friable and dirty porous tuffaceous coralloid concretion (Fig. 3) which resemble those developed on most of the specimens present on the paleosurface throughout the cave and on the cranium found

Table 1
Analytical data of the U/Th dating.

Sample	Weight	^{238}U		^{232}Th		$\delta^{234}U$		$[^{230}Th/^{238}U]$		$^{230}Th/^{232}Th$		Age (kyr before 2021)				$\delta^{234}U_{initial}$	
ID	g	10–9 g/g [a]		10–12 g/g		measured[a]		activity[c]		atomic ($\times 10^{-6}$)		uncorrected		corrected [c,d]		corrected[b]	
GG111–1	0.0526	347.80	±0.39	7143	±20	155.4	±1.5	0.7587	±0.0035	609.1	±3.2	112.63	±0.93	**112.18**	**± 0.96**	213.3	±2.1
GG111–2	0.0502	206.57	±0.21	76,553	±589	162.9	±1.5	0.748	±0.011	33.29	±0.55	108.7	±2.7	**100.4**	**± 5.0**	216.2	±3.6
GG101–1	0.0536	334.65	±0.36	56,030	±397	87.0	±1.3	0.514	±0.010	50.6	±1.1	69.10	±1.9	**65.0**	**± 2.8**	104.5	±1.8
GG101–2	0.0615	234.17	±0.24	19,750	±150	118.3	±1.8	0.5199	±0.0018	101.65	±0.84	67.30	±0.35	**65.3**	**± 1.1**	142.3	±2.2
GG102–1	0.0701	309.04	±0.94	26,212	±222	78.0	±5.1	0.5012	±0.0019	97.42	±0.86	67.57	±0.59	**65.5**	**± 1.2**	93.8	±6.2
GG102–2	0.0723	234.22	±0.26	29,374	±239	99.1	±1.7	0.5185	±0.0014	68.17	±0.58	68.79	±0.30	**65.8**	**± 1.6**	119.3	±2.1
GUA20-3-1	0.0540	174.33	±0.34	12.571	±0.062	130.2	±2.7	0.43712	±0.0059	100.0	±1.4	52.76	±0.93	**51.1**	**± 1.2**	150.4	±3.2
GUA20-3-2	0.0785	223.08	±0.47	7.210	±0.025	116.3	±3.0	0.47590	±0.0044	242.8	±2.3	59.92	±0.76	**59.17**	**± 0.85**	137.4	±3.5
GUA20–4	0.0490	448.58	±0.58	74.2	±9.5	270.8	±1.7	0.5337	±0.0013	53,231	±6811	58.10	±0.21	**58.10**	**± 0.21**	319.0	±2.0

[a] $[^{238}U] = [^{235}U] \times 137.818$ (±0.65‰) (Hiess et al., 2012); $\delta^{234}U = ([^{234}U/^{238}U]_{activity} - 1) \times 1000$.
[b] $\delta^{234}U_{initial}$ corrected was calculated based on ^{230}Th age (T), i.e., $\delta^{234}U_{initial} = \delta^{234}U_{measured} \times e^{\lambda 234 \times T}$, and T is corrected age.
[c] $[^{230}Th/^{238}U]_{activity} = 1 - e^{-\lambda 230 T} + (\delta^{234}U_{measured}/1000)[\lambda_{230}/(\lambda_{230} - \lambda_{234})](1 - e^{-(\lambda 230 - \lambda 234)\, T})$, where T is the age.
[d] Age corrections, relative to chemistry date in 2021, were calculated using an estimated atomic $^{230}Th/^{232}Th$ ratio of 4 (±2) x 10^{-6}. Decay constants are 9.1705×10^{-6} yr^{-1} for ^{230}Th, 2.8221 x 10^{-6} yr^{-1} for ^{234}U (Cheng et al., 2013), and 1.55125 x 10^{-10} yr^{-1} for ^{238}U (Jaffey et al., 1971).

in 1939. The tuffaceous concretion of Level I can be thus reasonably correlated to the Layer 11 of the Antro dell'Uomo area (Fig. 3).

Level 2 – SUs 20–21. It was identified and investigated across the whole extension of the area of the "Laghetto", the sediment is sandy with a distinct yellow colour, admixed with small, rounded pebbles of limestone and some stalagmites concretions. Within it, sparse clasts and thin cemented spots were also found. The average thickness is of 27 cm in areas 1-4-5-6-7, whereas it is thicker in areas 2 and 3. In area 2, by the natural siphon, in the direction of an ancient entrance, the thickness varies between 63 and 82 cm at the bottom. The level yielded a total of 4434 findings, specifically: 4378 mammal bone remains, 28 of which humans, 44 coprolites and 7 lithic elements (Fig. 4). The lithic elements comprise 3 small pebbles (18–26 mm in diameter) and a III flake (from production) identified as a Levallois flake. This level is characterised by a strong concentration of finding (557 identified) in areas 2 and 3. At the centre and at the end of the small pond (areas 1-2-3-4) the sediment is loose, sandy, with small, rounded limestone pebbles, incorporating sparse lens of flowstone. On the other hand, in the inner areas, the sediment is less homogenous and there is an increased presence of wide concretions, often containing bone fragments. Towards the trenches dug by Blanc, the sediment was partly compromised by last century's excavations. To be noted, in area 3, a concentration of faunal remains was found in a depression in the concretion (SU 38). The finds laid mainly perpendicular to the centre of the depression and this suggests that the depression already existed and that it was filled by the faunal remains as they piled up in time. Based on the lithostratigraphic features and the large amount of bone found, Level 2 can be tentatively correlated to the sub-layer 8 of the Antro dell'Uomo area (Uppermost sub layer of the Layer 11 of the general stratigraphy showed in Fig. 2b).

Level 3 – SUs 41-42-44-45-50-51-53. It covers the whole investigated area and is up to 20 cm thick (Fig. 3), however in areas 1 and 4 it was not fully investigated. The level differs from the above Level 2 for an increase of compact tuffaceous flowstone patches and an accentuated superficial alteration of the bone remains, whose superficial portion is in some cases nearly completely deteriorated. The level was investigated to a depth of 10 cm in area 4, and to a depth of 14 cm in area 1, whereas in areas 2 and 3, it was not reached. Level 3 yielded a total of 5006 finds: 4976 mammal bone remains, including 5 humans, and 28 lithic artefacts, plus 7 hyena coprolites. The highest concentration of finds was found in areas 1 and 4, with 681 findings identified. The lithic artefacts are more numerous in this level: 30 in addition to 23 small pebbles, there are 3 cores on pebbles, a III Levallois flake and 5 retouched flakes (scrapers and denticulates). Level L3 is tentatively correlated to the middle part of the Layer 10 of the general stratigraphy (Fig. 2a and 3).

Level 4 – SUs 43-46-47. Below Level 3, was identified as a level of clasts collapsed from the cave bedrock walls and ceiling, partially cemented by calcite concretion. The top of Level 4 appears to be a series of natural pools that were filled by the sandy deposit of Level 3 together with faunal finds brought in by the hyenas. Level 4 was reached in areas 5-6-7 and, partially, in areas 1 and 4. The base of this level was not reached. Level L4 could be correlated to the sub-layer 2–3 of the Antro dell'Uomo stratigraphy (Fig. 3).

4.2. *Chronology*

The sample GG111, laying on the beach deposits underlying the continental cave infilling (Fig. 2), is characterized, in thin section, by an open columnar fabric with some clastic layers. (Fig. S2, Frisia et al., 2000). Two dating (top-bottom) of this thin flowstone yielded the age of 112.6 ± 0.9 ka and 100.4 ± 5.9 ka (Table 1). The sample yielding the oldest age shows little detrital contamination (lower ^{232}Th) and small age correction, while the contamination and correction are more conspicuous for the younger one (Table 1).

Following the scheme of Frisia et al. (2000), the stalagmites from Level 2 (Figs. 2 and 3), GG101 and GG102, display, in thin section, columnar calcite fabric at the bottom followed by a dendritic fabric and toward the top, columnar fabric with frequent alternations of tufa layers. (Fig. S2). Top and basal ages of both stalagmites show that they grew in a very short period between ~66 ka and 65 ka (Table 1), which can be considered reasonably the period of deposition of the Level 2, which is the richest in human bone remains of the entire succession. These ages were characterized by a relatively variable $^{230}Th/^{232}Th$ ratio which accounts for relatively modest age corrections.

The tuffaceous concretion (GUA20-3) from layer 11 (Fig. 3) shows, in thin section, an elongated columnar microcrystalline fabric at the bottom, transitioning to a mosaic fabric with tufa layers (Fig. S2). The upper portion is characterized by a new columnar level, followed by a popcorn-like structure topping (Fig. S2). It yields a basal age of 59.17 ± 0.85 ka (GUA20-3-2, Table 1) and a top age of 51.1 ± 1.2 ka (GUA20-3-1, Table 1).

The coralloid concretions of the top of the surface in the Antro dell'Uomo resulted consistently contaminated by clastic material, obligating Schwarcz et al. (1991) to use the isochronous methods. We were able to select more cleaned samples, thanks also to the lower amount of material necessary for dating with the modern

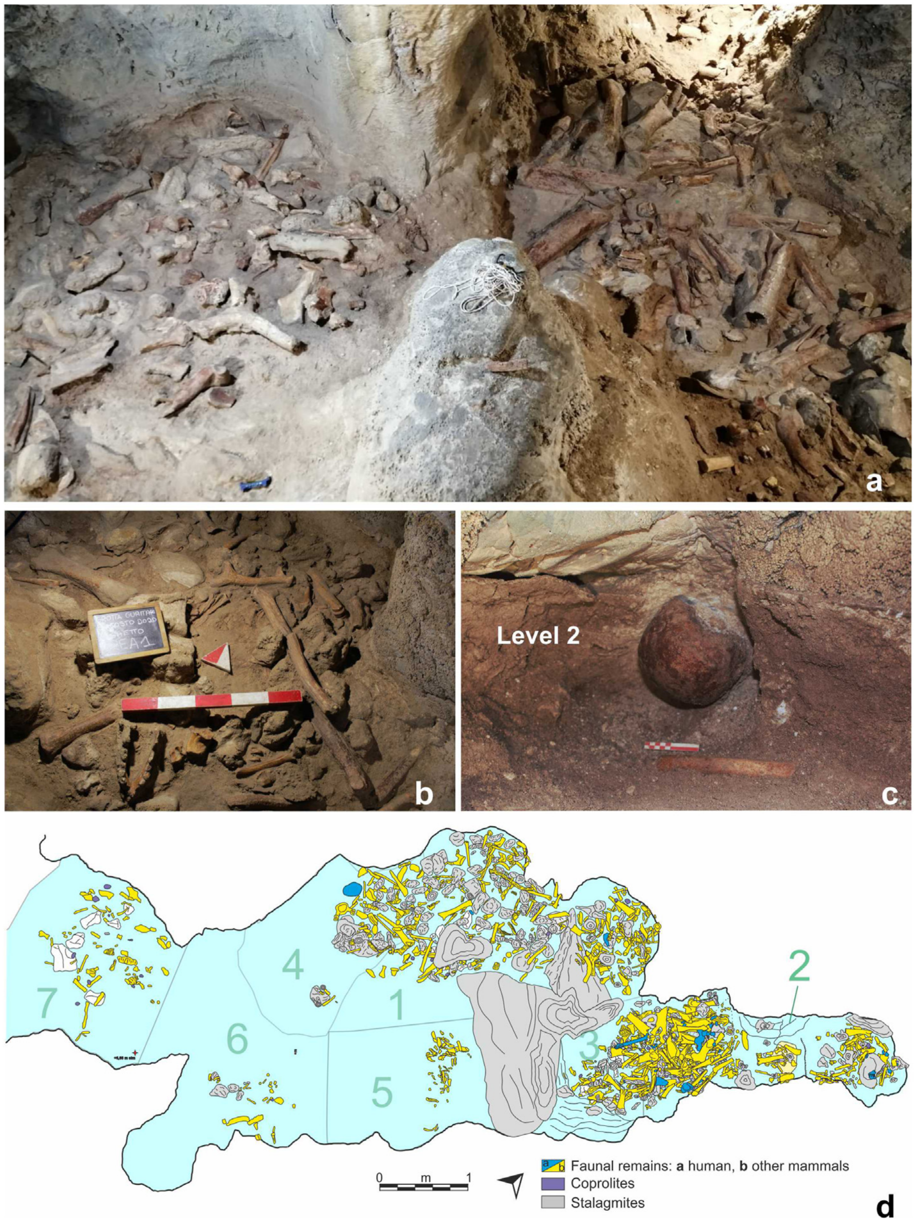

Fig. 4. Pictures and planimetry showing the bone accumulation in Level 2 of the "Laghetto". **a)** Panoramic view of the sectors 1, 2 and 3 (Fig. 2a); **b)** details of the areas 1–4; **c)** Neanderthal skullcap at margin of area 4. **d)** planimetric survey of the bone distribution.

techniques, obtaining consistent ages of 58.10 ± 0.21 ka of the basal portion of the concretion (GUA 20–4, Table 1, Fig. S1) (Figs. 2 and 3) (Table 1).

Overall, the new U/Th ages were obtained from sections of the concretions where there are no evidences of post-depositional alteration and all ages are consistent with their stratigraphic position However, some of the ages were performed on porous fabric (i.e., GUA20-3-2 and GG111), which can be prone to cryptic producing older-than-real ages diagenesis and difficult to identify without an intense dating protocol, (Bajo et al., 2016). However, the general stratigraphic consistence seems to rule out this possibility.

Those are the values for a material at secular equilibrium, with the crustal $^{232}Th/^{238}U$ value of 3.8. The errors are arbitrarily assumed to be 50%.

4.3. Pollen

Pollen counts of the investigated Level 2 (SU 20) and Level 3 (SU 53) are quite low due to the very low concentration values ranging from 20.5 grains/g in Level 3 to 101.7 grains/g in Level 2 (Table 2). Despite the low pollen content, preservation of grains is outstanding. From SU 53 eight pollen taxa have been identified although the total sum is the lowest of the study samples (11.5 grains). Mediterranean shrubs prevail (*Juniperus*, *Pistacia*) whereas trees are represented by *Quercus cerris* type (comprehending both Turkey and Cork oak) and *Fagus* (beech). *Vitis* (grape vine) is also present. Herbaceous plants are dominated by Poaceae (grasses). At the bottom of SU 20 pollen sum and taxa variability increase (46.5 grains and 11 taxa respectively). *Juniperus* (juniper) and Poaceae are

Table 2
Number of pollen grains, NPPs and microcharcoals in samples from Level 3 and 2 of the “Laghetto” deposit.

Grotta Guattari			
Central Italy)	Level 3	Level 2	
Taxa/SUs	53	20 Bottom	20 Top
Juniperus	4	16	8
Pinus	0.5	0.5	0.5
Fagus	1	0	1
Fraxinus excelsior/angustifolia	0	0	1
Ligustrum	0	1	0
Olea	0	2	0
Ostrya/Carpinus orientalis	0	0	1
Pistacia	1	0	0
Quercus robur type	0	1	2
Quercus cerris type	1	0	1
Quercus ilex type	0	1	1
Ulmus	0	1	0
Vitis	1	0	0
Amaranthaceae	0	1	1
Brassicaceae	0	2	1
Cichorieae	1	0	0
Fabaceae	0	0	1
Plantago	0	3	1
cf. *Plumbago*	0	0	1
Poaceae	2	18	10
unidentified pollen grains	1	1	3
Total pollen sum	**12.5**	**47.5**	**33.5**
Pollen taxa	**8**	**11**	**14**
Pollen concentration (grains/g)	**20.5**	**101.7**	**60.2**
Trilete spores	0	0	1
Zygnemataceae	0	0	1
Glomus	0	3	2
charcoals (>10 μm)	23	17	21

the most abundant taxa, followed by Mediterranean trees (*Olea* – olive tree, *Ligustrum* - privet, *Quercus ilex* type – evergreen oaks) and herbs like *Plantago* (plantain) and Brassicaceae (crucifers). The number of pollen taxa reaches the highest value in the top sample of SU 20 (14 taxa) from which a total of 30.5 pollen grains have been identified. Apart from *Juniperus* and Poaceae, mesophilous trees are abundant (*Quercus robur* type – deciduous oaks, *Quercus cerris* type, *Ostrya/Carpinus orientalis* - hornbeams) and *Fagus* is attested. Remains of the mycorrhizal fungus *Glomus* are present in both samples of Level 2, whereas microcharcoals are ubiquitous.

5. Discussion

5.1. Nature of the bone accumulation in the “laghetto” area

Petronio et al. (2021) discussed preliminarily the faunal assemblage and the taphonomic features of the remains collected in the “Laghetto” succession. No significant differences appear between the two investigated levels L2 and L3. In addition to the rare, but significant, presence of remains of *Homo neanderthalensis* (Fig. 4c–d), the faunal assemblage from the “Laghetto” consists of abundant *Cervus elaphus*, followed by *Crocuta*, *Bos primigenius*, *Sus scrofa* and *Equus ferus* (Petronio et al., 2021). Although sporadic, the occurrence of chamois, ibex and Irish elk, together with the prevalence of the red deer compared to the rare fallow deer, suggests that the fossil deposit accumulated in colder times than present. The preliminary taphonomic study of bone remains shows modifications typical of large carnivores’ activity (Fiore et al., in press). This is further supported by the widespread presence of abundant spotted hyena (*Crocuta*) bone remains as well as numerous coprolites.

These results conflict with Blanc's interpretations, according to which the hominid and the other animal remains lying on the preserved cave floor provide evidence of Neanderthal ritual behaviour (Blanc, 1961). On the other hand, they are fully consistent with previous, but more recent taphonomic analyses, which revealed that the bone accumulation and modification from the surface deposit, including the Neanderthal skull (Circeo I), are largely if not wholly related to the work of denning spotted hyenas (White and Toth, 1991; Stiner, 1991).

It is worth noting that in the “Laghetto” succession were found only 35 lithic artefacts, which are mainly concentrated in Level 3, with 28 artefacts, whereas only 7 artefacts were found in Level 2. The low overall number of lithic artefacts suggests that a strong human presence inside the cave concomitantly with the hyena's occupation can be ruled out. This is further confirmed by the absence of other indications of human occupation in Levels 2 and 3, such as stratigraphic-taphonomic evidence of fire use (e.g., lens of ash, burnt bones, charcoal concentrations) or of other significant human activity. Clear evidence of human occupation is instead well-documented in the outer and older deposits (of the Unit 9, area M in Fig. 2a), where ongoing excavations, as already mentioned in section 3.1.2., are revealing series of structured palaeosurfaces of human occupationwhich are dated at ~120–105 ka, i.e., 50–60 kyr before than hyena occupation. Overall, both previous investigations and the observations and data collected in this study consistently indicate that the hyena was the main agent responsible for the transport, modification and accumulation of the faunal remains, including those of the Neanderthal, found in Level 3 and 2 and on the surface of Level 2.

5.2. Chronology and paleoenvironmental evolution

The whole inner continental clastic succession of the cave infilling developed between the age of the flowstone overlying the beach deposits, dated at 112.2 ± 1.0 ka-100.4 ± 5.0 ka (Fig. 2b; Table 1), and before 59.9 ± 0.8 ka, the age of oldest coralloid concretions (Fig. 3), which represents a *terminus ante quem* for the end

Table 3
Summary of the Neanderthal bone finding in Italy dated MIS5-4-and 3. Most of the sites are quoted in the review from Alciati et al., (2005).

Number	Site	Chronology (S: stratigraphy; R: radiometric or similar)	References
1	Archi°	S: MIS4 or MIS3 (?)[a]	Ascenzi and Segre (1971) Mallegni F. and Trinkaus E. 1997
2	Bisceglie (Grotta Santa Croce)	S: MIS4 or MIS3 (?)	Mallegni et al. (1987)
3	Grotta Breuil	S/R: post-marine transgression MIS5e- older than 36.6 ± 2.7 ka	Bietti et al. (1991); Manzi and Passarello 1995; Schwarcz et al. (1991).
4	Riparo Broion	R: MIS3	Peresani et al. (2019); Romagnoli et al., 2022
5	Buca del Tasso	S: MIS4-MIS3?	Cotrozzi et al. (1985)
6	Ca' Verde	S: MIS5? – MIS4?	Leonardi and Broglio (1962)
7	Grottoni di Calascio	S: MIS5? Or MIS4?	Giustizia (1979), Tozzi, 2003
8	Grotta del Cavallo	R: 45,600–42,900 cal yr BP and older than 45.5 ± 1.0 ka.	Fabbri et al. (2016); Zanchetta et al. (2018); Sarti (2020)
9	Ciota Ciara	Out of a stratigraphic context**	Mottura A. 1980 Villa and Giacobini (1996); Arzarello et al. (2012)
10	Ciutarun	Out of a stratigraphic context	Villa and Giacobini (1996)
11	Caverna della Fate	R: Late MIS5-MIS4	Falgueres et al. (1990) Echassoux et al., (1989) Giacobini et al. (1984)
12	Grotta del Fossellone	S: MIS3	Blanc, A.C. (1954) Vitagliano and Bruno, 2012
13	Ripapro-grotta di Fumane	S/R: MIS3	Peresani et al. (2008); Benazzi et al., 2011
14	Grotta Guattari	R:MIS4-Early MIS3(?)	This work, Schwarcz et al. (1991)
15	Leuca (Grotta delle tre porte)	S: post MIS5e (?)[b]	Blanc (1961)
16	Maglie° Fondo Cattie	S: stratigraphy unclear	Borgognini Tarli S. 1983
17	Melpigliano (Nuzzo Quarry)°	S: stratigraphy unclear (MIS5-3?)	Bologna et al. (1994)
18	Il Molare	S: MIS5 (post MIS5e)[b]	Mallegni and Ronchitelli (1989); Spagnolo et al., 2020a
19	Contrada Ianni°	S: MIS5 (post MIS5e)	Bonfiglio et al., (1986)
20	Quinzano°	S: stratigraphy unclear (post MIS5?)	Battaglia (1943)
21	Grotta di San Bernardino	R: MIS3	Falguéres et al. (1966); Vacca and Alciati (2000)
22	Grotta di Taddeo	S: MIS5 (post MIS5e)**	Vigliardi (1968); Messeri (1975)
23	Tagliente	S: MIS4-MIS3	Bartolomei et al., (1982), Arnaud et al. (2016)
24	Torre dell'Alto	S: MIS5-MIS3 (?)	Borzatti von Löwenstern, 1969

°Open air site.
[a] This attribution is unlikely, considering the brackish layer (P) above the layer C-3 where fossils were found and the modern knowledge of the Marine succession and tectonic evolution of the area. It would be MIS5 or also older. **Arzarello et al., 2012 report a possible age for the human frequentation of the cave during MIS5.
[b] This attribution is related to the presence of coastal marine deposits at the base of the succession correlated with the so called "Tyrrhenian", usually related to MIS 5e highstand.

of the accumulation of the clastic sediment in the cave (Fig. 5). Overall, the new chronological results are in good agreement with the recent $^{40}Ar/^{39}Ar$ dating of detrital sanidines extracted from the units 8 and 9 (Marra et al., 2023), which yielded the age of 122 ± 6 ka and 101 ± 9 ka/105 ± 1 ka, respectively, and represents *terminus post quem* for the depositions of these units (Fig. 2a). They are in relatively good agreement also with the ESR date from auroch tooth found above the beach deposit close to the entrance (Taschini, 1979), which gave an average age of 78 ± 9 ka, and with previous dating of the surficial coralloid-flowstone concretions at ~57–50 ka (Schwarcz et al., 1991).

The age of the flowstone GG111, which marks the start of the continental sedimentation in Grotta Guattari, confirms the attribution of the basal beach deposit to the MIS 5e (Segre, 1991; Marra et al., 2023). Specifically, flowstones indicate that the marine deposition terminated before 112 ka, which thus represents a terrestrial limiting point for the MIS 5e sea level high-stand (Rovere et al., 2015).

The middle-upper part of the Laghetto successions, and thus of the bulk of bone accumulation by hyena, is chronologically precisely constrained by four very concordant U/Th dating in the narrow temporal window of ~66-65 ka, during the Greenland Stadial (GS) 19.1 (Rasmussen et al., 2014, Fig. 5), while the start of the hyena frequentation in Level 3 has to be slightly older than 66 ka (Table 1; Fig. 5). Comparison with regional and extra-regional proxy records indicates this time-interval as one of the harsher of the MIS 4 glacial period (Fig. 5). In the Apulian stalagmite record from Pozzo Cucù Cave, this short interval coincides with driest conditions, marked by the maximum increase in $\delta^{18}O$ of the whole record (Fig. 5; Columbu et al., 2020). In the Abruzzo region, the Fucino paleolake records the maximum clastic input from the lake catchment, as documented by the high values of Ti concentration in lake sediments (Fig. 5; Mannella et al., 2019). Consistently, the Monticchio pollen record, in southern Italy, indicates open and arid condition in this interval (Fig. 5; Brauer et al., 2007). At Valle di Castiglione, near Rome, the maar lake was completely dried as witnessed by a paleosol in the drilled successions (Follieri and Magri Sadori, 1989). Speleothem growth rates in the Apuan Alps, central Italy, suggest glacial prone condition (i.e., temperature below zero °C) at least at elevation above 800 m a.s.l. (Isola et al., 2019).

The harsh conditions during the GS 19.1 suggested by the regional paleoclimatic evidence are in relatively contrast with local paleoenvironmental indications from pollen and fauna. Though the pollen evidence from the "Laghetto" deposit indicates a cold open environment dominated by grasslands in the surrounding of the cave, the presence of sparse evergreen vegetation trees and shrubs and of elements of the humid plain forest, as *Fraxinus excelsior/F. angustifolia* – common ash/narrow-leaved ash, *Ulmus* – elm and *Vitis*, denote less severe conditions with respect to the regional pattern, likely due to the mildening influence of the Tyrrhenian Sea. Peculiar is the presence of *Fagus*, a mountain tree that at present grows at altitudes over 1000 m. The well-preserved pollen grains of *Fagus* suggest the presence of nearby glacial refuge areas for this tree. Significant is also the absence of two pollen taxa: *Abies* (fir) and *Artemisia*. *Abies* was in fact widespread in Latium during St.

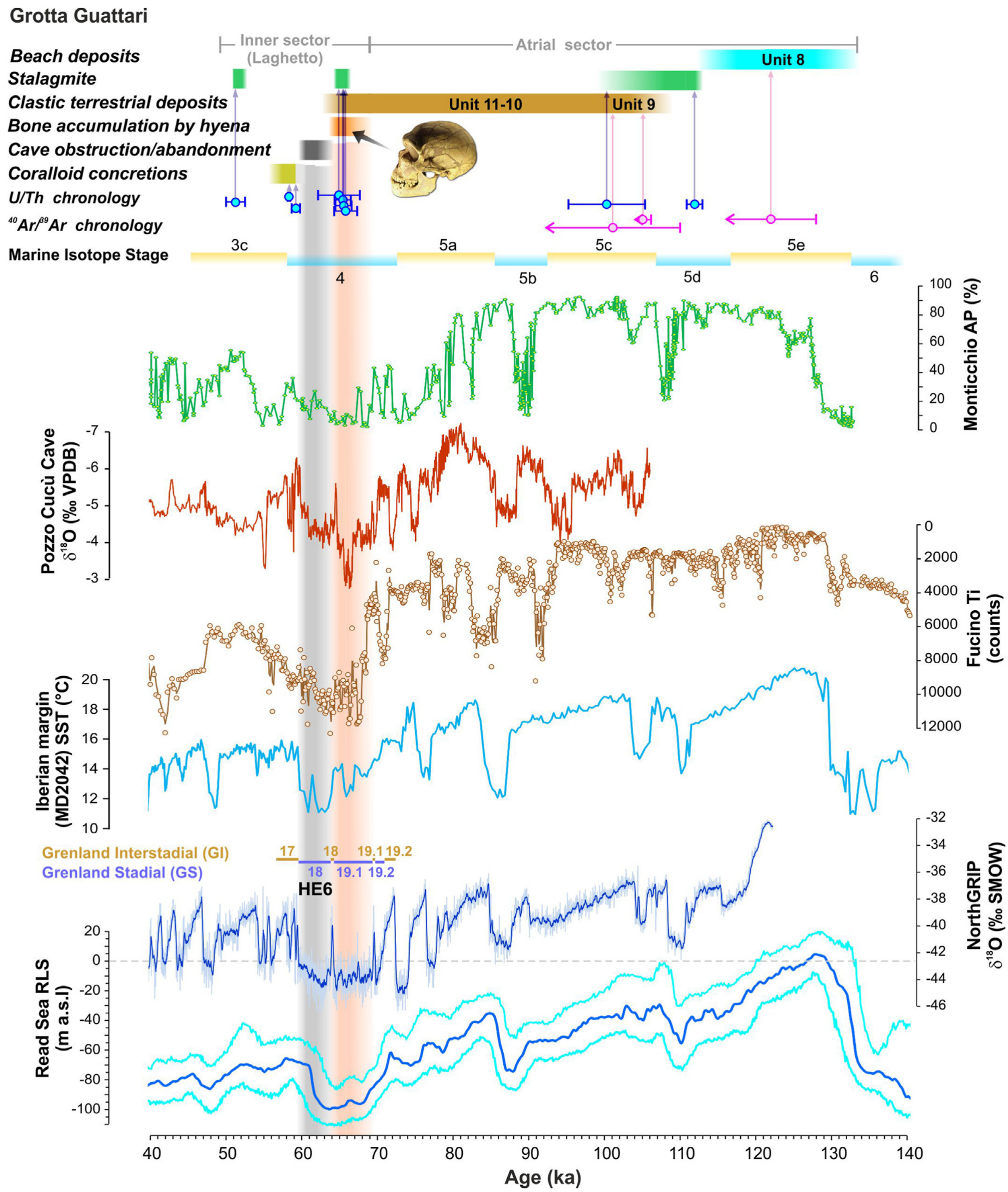

Fig. 5. Synopsys of the sedimentary, paleoenvironmental, and paleoecological history of Grotta Guattari compared to regional (Monticchio, southern Italy, pollen record, Brauer et al., 2007; Apulian stalagmite δ^{18}O record, Columbu et al., 2020; Fucino, central Italy Ti record, Mannella et al., 2019) and extra-regional (Iberian Margin sea surface temperature, Martrat et al., 2007; Red Sea relative seal level, Grant et al., 2014; Greenland NorthGRIP δ^{18}O record, Rasmussen et al., 2014) paleoclimatic and paleoenvironmental records. The ^{40}Ar/^{39}Ar ages of the marine Unit 8 and the terrestrial Unit 9, according to Segre's (1991) stratigraphy, are from Marra et al. (2023). They were obtained from detrital sanidine extracted from deposits and have thus be considered as *terminus post quem* for the units' deposition.

Germain II (MIS 5a) and almost disappeared at the beginning of MIS 4 (Follieri et al., 1998). In the sediment core of Piana Pontina (Barbieri et al., 1999), ~30 km away from Grotta Guattari, *Abies* and *Fagus* show a continuous record during MIS7/MIS9 and have a sporadic presence after the interglacial Eemian. *Artemisia* is a herb genus featuring the arid steppes of the glacial all over Europe. Its absence can be taken as an indication of not harsh glacial conditions, and as confirmation of a relatively humid environment, as suggested by elements of the wet plain forest. In agreement with pollen, the ecological features of the Guattari mammal taxa also indicate a forested environment on the Circeo promontory, with large open spaces and steep rocky areas. Therefore, the Guattari palaeoecological indicators suggest that during the GS 19.1 in the coastal area of the Circeo the general plaeoclimatic and paleoenvironmental conditions could have been less severe than commonly observed at a regional scale.

In this brief period (~66–65 ka), hyena used the cave as a shelter accumulating an impressive amount of mammal bones, including the 40 remains of Neanderthals, found within the Level 2 e 3 and on the surface of Level 2 (Fig. 4). The presence of hyena is well-documented in Pontina Plain, but the findings refer to the second half of the MIS 3 period (~45–30 ka; Gatta et al., 2016, Gatta et al., 2019, 2022), thus 20–35 kyr younger than Guattari site. Aridity was more severe during that period, as attested by the prevalence of pollen of steppe plants (*Artemisia*, Amaranthaceae) preserved in hyena coprolites, although a certain degree of humidity seems to have always characterized the Pontina Plain environments (Gatta et al., 2016).

After ~65 ka and before 59 ka, the hyena interrupted the frequentation of the cave, possibly because the obliteration of the entrance(s) by sediment accumulation from the external slope, as testified by the slowdown of the clastic sedimentation in the "Laghetto" and by the growth of the coralloid concretions on the surface of the Level 2 and on the last bone left by the hyena on the cave floor. This time interval matches the Heinrich Event 6 (HE6) which corresponds to marked aridity events in Mediterranean area (e.g., Roucoux et al., 2005). Such a chronological coincidence would suggest that the HE6 could have played a possible role of contributing factor of the abandonment by hyena, as a possible consequence of the environmental modifications linked to this event (e.g., more arid conditions and rapid rise of the sea level with consequent alteration of the coastal ecosystems), which would have pushed prey and predators away. The dating of the thin flowstone, growth on the tuffaceous coralloid concretion sealing the mammal bone at 51.2 ± 1.1 ka (Fig. 3, Fig. S1), provide a further, though later, *terminus ante quem* for the cave closure. The cave left sealed and untouched until its discovery on the first half of the twentieth century.

5.3. The guattari findings in the framework of the Italian Neanderthal remains

Table 3 and Fig. 6 show the synthesis of the chronological constraints available for the main Upper Pleistocene Neanderthal bone remains discovered in Italy (from Alciati et al., 2005; with updating and revised stratigraphies). What emerges from the synopsis of Fig. 6 is the relatively poor constrained chronology, mainly due to the lack of radioisotopic dating, for many Neanderthal findings, which are mostly based on the general stratigraphic information. Very few specimens can securely be correlated to the last interglacial (MIS 5e; Fig. 6).

This circumstance likely reflects the fact that many of the investigated sites are coastal caves, which were submerged during the Last Interglacial sea level high-sand, and thus became accessible by humans only starting from the end of MIS 5e, ~116 ka (Marra et al., 2020; Zanchetta et al., 2018), though a recent study indicates that the fall of the Last Interglacial highstand may have occurred as early as before ~120 ka (Bini et al., 2020). Several Neanderthal remains are related to the post-MIS 5e, with a significant number of Neanderthal remains ascribed to the early-middle Pleniglacial, i.e., MIS 4 and MIS 3 (Fig. 6). This is the case of the abundant human remains of Grotta Guattari and other sites in the Mt. Circeo area (i.e. Breuil Cave, Fossellone Cave, Fig. 6).

The uneven and uncertain chronological distribution of the Italian Neanderthal remains may depend on different causes, but it mostly relays on the intrinsic difficulty to get reliable radioisotopic constraints for the early MIS 3-MIS 5, which, to great extent, is beyond the current radiocarbon limit (~55 ka; Reimer et al., 2020), representing the most common and effective geochronometer in late Palaeolithic (e.g., Higham et al., 2014). To this regard, in the Italian framework of the Neanderthal remains, Grotta Guattari, and

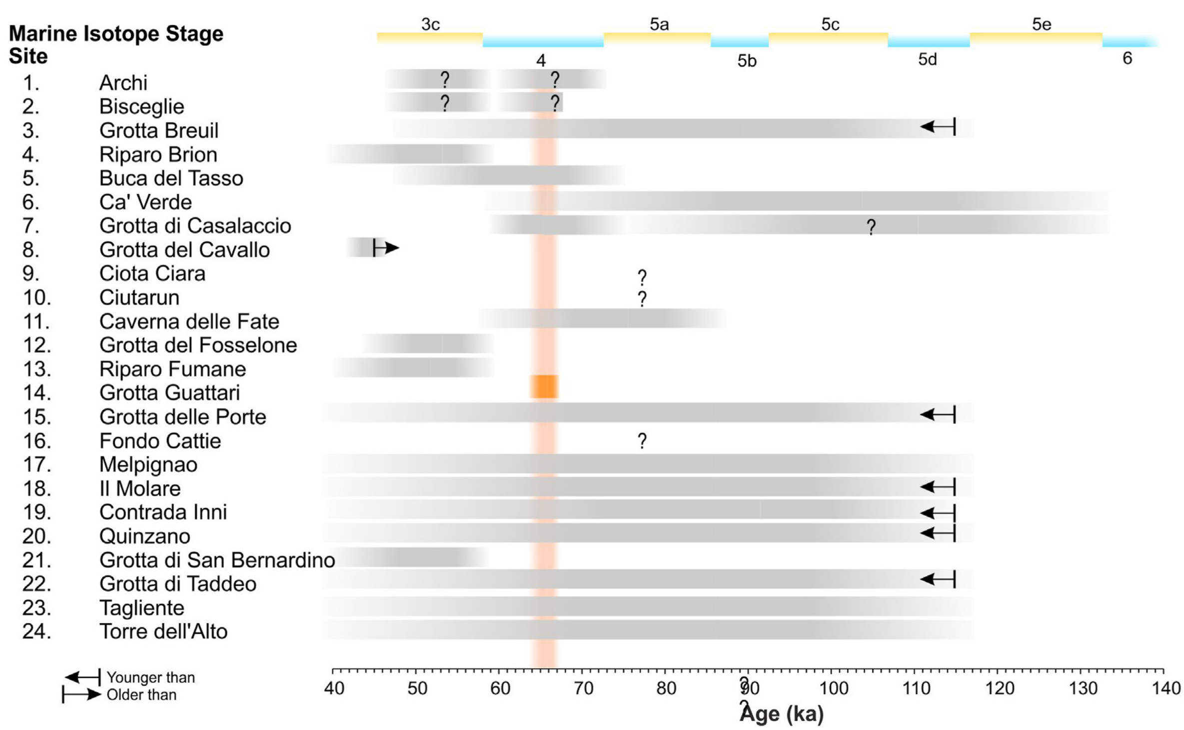

Fig. 6. Synthesis of the chronological constraints available for the Italian Upper Pleistocene Neanderthal remains. Number refer to the site showed in Fig. 1 (see Table 3 for further details).

in particular the “Laghetto” succession, is a notable exception, standing out for the outstanding number of remains and its really well-constrained chronology.

6. Concluding remarks

Stratigraphic and taphonomic evidence, provided in this and previous studies, consistently indicate that the main agent of the transport, modification and accumulation of Neanderthal bones, and of other large mammals, in the innermost sector of Grotta Guattari (“Laghetto” and Antro dell’Uomo areas), was the hyena. In agreement with recent $^{40}Ar/^{39}Ar$ dating of the beach and the lowermost continental deposits, our U/Th dating of a thin stalagmitic crust above the basal beach layer indicates that the whole continental sedimentary and archaeological succession within the cave is younger than ~112 ka, i.e., postdating the MIS 5e sea level highstand.

Our U/Th chronology places the occupation of hyena, and thus the Neanderthal remains, found in Level 2 and 3 of the “Laghetto”, within an extremely narrow interval of ~1 or, at most, ~2 kyr of MIS 4, between ~66/65 ka and ~65 ka, within the GS 19.1. Regional paleoenvironmental and paleoclimatic proxy records indicate this interval as one of the drier and colder of the MIS 4 glacial period. However, the local pollen and faunal evidences from the “Laghetto” sediments, though confirming a cold open environment typical of glacial conditions, which also favoured the spread of beech at pretty lower altitudes than at present, suggest that the proximity of the sea likely mitigated the climate, allowing the subsistence of elements of the Mediterranean arboreal vegetation.

The new U/Th ages on coralloid concretions, which represent a *terminus ante quem* for the end of the bone accumulation by hyena, suggest that the cave become abandoned, and possibly obstructed, after 65 ka and before 59 ka, i.e., during the HE6. This suggests that this event could have played a possible role in determining climatic-environmental conditions no longer suitable for the subsistence of large populations of herbivorous in the Circeo areas and thus of the large predators, like the hyena. This also brings to consider the Circeo I Neanderthal skull, found by Blanc on 1939 on the fossilized surface, as likely attributable to the same phase of hyena frequentation and thus to the same temporal interval of accumulation of sediments and bones in “Larghetto”, that is 66–65 ka.

An overall paucity of radiometric dating and large chronological uncertainties, often accompanied by poorly constrained stratigraphic-paleoeavironmental information, arise from a review of Upper Pleistocene Neanderthal findings in Italy. Though posing Grotta Guattari as an outstanding case in the Italian framework, this hampers regional and extra-regional scale comparisons and makes, at the moment, any evaluation on the timing and dynamics of the MIS 5-MIS 3 Italian Neanderthal population hardly addressable. A general reappraisal of the chronology of most of the previous Neanderthal remains is thus in order.

Author contributions

M. F. Rolfo: Conceptualization, Investigation (excavation), Validation, Formal analysis, Data curation, Writing - Original Draft preparation, Writing - Review and Editing, Visualization, Project administration, Funding acquisition. **M. Bini**: Investigation (field observations, sampling), Validation, Formal analysis, Writing - Review and Editing. **F. Di Mario**: Supervision, Project administration, Funding acquisition. **A. Ferracci**: Investigation (excavation), Writing - Review and Editing. **B. Giaccio**: Conceptualization, Investigation (field observations, sampling), Validation, Formal analysis, Data curation, Writing - Original Draft preparation, Writing - Review and Editing. **H. Hsun-Ming**: Investigation (U/Th chronology), Validation, Formal analysis, Data curation, Writing - Review and Editing. **I. Isola**: Investigation (field observation, sampling, sample preparations), Validation, Formal analysis, Data curation, Writing - Original Draft preparation, Writing - Review and Editing. **L. Sadori**: Investigation (sampling, pollen analysis), Validation, Formal analysis, Data curation, Writing - Original Draft preparation, Writing - Review and Editing. **C–C. Shen**: Investigation (U/Th chronology), Validation, Formal analysis, Data curation, Writing - Review and Editing. **C. Vignola**: Investigation (sampling, pollen analysis), Validation, Formal analysis, Data curation, Writing - Original Draft preparation, Writing - Review and Editing. **G. Zanchetta**: Conceptualization, Investigation (field observations, sampling), Validation, Formal analysis, Data curation, Writing - Original Draft preparation, Writing - Review and Editing, Project administration, Funding acquisition.

Declaration of competing interest

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

Data availability

Data will be made available on request.

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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.2023.108132.

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