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# Plant foods in the Late Palaeolithic of southern Italy and Sicily: Integrating carpological and dental calculus evidence

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## Abstract

Several caves from southern Italy and Sicily provided invaluable evidence, including several human burials, for reconstructing human adaptations and subsistence in the area during the Upper Palaeolithic. A wealth of information is available concerning the exploitation of animal resources as food. However, little is still known about the role of plants in the diet of the ancient hunter-gatherers of the region. By combining the carpological data with vegetal micro-debris entrapped in human dental calculus, we provide new clues about the dietary role of plant foods in the analysed area during the Late Glacial. Our study focused on five key sites from southern Italy and Sicily: Grotta della Serratura in Campania, Grotta del Romito in Calabria, Grotta del Cavallo in Apulia, Grotta di San Teodoro and Grotta d'Oriente in Sicily. Our results demonstrate that several plant resources were exploited at these sites, including seeds, grasses, and forest fruits. Amongst the carpological remains recovered, several plant taxa are known for their medical properties. Overall, our study explores how critical climatic and environmental changes characterising the timeframe between the end of the Last Glacial Maximum and the beginning of the Holocene affected Late Upper Palaeolithic dietary habits. Moreover, it shows the methodological relevance of combining different strands of archaeological evidence for reconstructing the Palaeolithic diet.

*Keywords*: Upper Palaeolithic; Plant foods; Dental Calculus; Carpological analysis; Late Glacial; southern Italy and Sicily

## 1. Introduction

In southern Italy and Sicily, numerous caves and rock-shelters yielded a wealth of prehistoric evidence, including several human burials, and offer a unique opportunity to explore how the critical climatic and environmental changes of the Late Glacial affected human/environment interaction, eventually impacting human dietary strategies (Martini et al., 2009b; 2009a; Mannino et al., 2011a; 2016; Colonese et al., 2018). A series of climate events mark this period in Mediterranean Europe, leading to the oscillations of temperate/humid and cold/arid climatic phases (Watts et al., 1996; Seguinot et al., 2018). In particular, at the beginning of the Bølling-Allerød interstadial (around 14700 cal BP), we assist in a rapid rise in temperatures and rainfall. Conversely, during the Older and the Younger Dryas cold stadials, a decrease in the forest cover is documented along with an increase in open areas. At the end of Pleistocene, rainfall intensification together whit a strong temperature growth (ca. 7° C) marked the Younger Dryas-Preboreal transition, dated approximately 11650 cal BP, (Orombelli and Ravazzi, 1996). On a palaeoenvironmental ground, phases dominated by a rich vegetation cover alternate with conditions of a more open environment. The latter corresponds to a lower variety in Mediterranean arboreal and shrub species, which show a decrease in the presence of forest species in the arid climatic phases (Martini et al., 2009b).

The diet of Palaeolithic hunter-gatherer communities in southern Italy and Sicily during the Late Glacial has been the subject of intense research in the last decade through the application of two main methodologies: archaeozoological analysis and bone chemistry (namely carbon and nitrogen isotopic composition of bulk collagen) (Drucker and Bocherens, 2004; Naito et al., 2013). These methods primarily rely on the study of bones and teeth, which generally preserve better than plant remains in ancient sediments due to their high mineral/inorganic content. Based on the standard dietary reconstructions carried out for cave sites such as Grotta del Romito and Grotta Paglicci in southern Italy, as well as Grotta di San Teodoro and Grotta d'Oriente in Sicily, we know that late Upper Palaeolithic hunter-gatherers primarily exploited the hinterland for the specialized hunting of large herbivores, such as red deer, aurochs and hydruntine ass (Craig et al., 2010; Martini et al., 2012b; Vacca, 2012; Lugli et al., 2019). Based on the isotopic data, marine or coastal lagoon resources, such as fish, limpets, and cockle shells, seem to have contributed seldomly to the diet of Palaeolithic human groups of the Tyrrhenian regions of southern Italy and Sicily (Francalacci, 1988; Vigne, 2004; Martini et al., 2007; Mannino and Thomas, 2009; Paine et al., 2009; Craig et al., 2010; Lightfoot et al., 2011; Mannino et al., 2011b; 2011a; 2012; Goude et al., 2017; Colonese et al., 2018). Supposedly low productivity of the central Mediterranean Sea in respect to other contexts and the absence of specific technological equipment (e.g., fish hooks) were suggested for explaining such a behaviour (Mannino et al., 2011b; Colonese et al., 2014). However, this scenario changed with the beginning of the Early Holocene, when marine resources were made more available to Mesolithic groups due to the rise of the sea level (Colonese et al., 2018). Whether human dietary habits also involved plant foods during the final stages of the Late-Glacial is still unknown, primarily due to the limits in assessing plant isotopic composition (Drucker and Bocherens, 2004; Craig et al., 2010; Mannino et al., 2011a; 2016; Gazzoni et al., 2013). Nevertheless, micro-wear patterns observed on the teeth and trace element chemistry on bones have provided indirect evidence of the possible consumption of plants foods in the region during the Late Upper Palaeolithic (Carnieri and Mallegni, 2006).

Recently, new methods of analysis applied to human remains and material culture revealed that grasses and plant underground storage organs might have supplemented Upper Palaeolithic diet in Italy from the Late Glacial Maximum onwards. At the site of Bilacino II in Tuscany (central Italy), use-wear and residues have been identified on both non-flaked and flaked tools coming from the Gravettian levels dated to ca. 33,000 cal BP and suggested the processing of starchy rhizomes by local hunter-gatherer communities (Revedin et al., 2010). Plant microremains were preserved on grinding tools from Grotta Paglicci, revealing the consumption of oat and acorns in the same period in northern Apulia (southern Italy) (Revedin et al., 2010; 2015; Lippi et al., 2015). Starch granules were also identified in the dental calculus of Late Upper Palaeolithic individuals from Grotta Continenza, Riparo Tagliente, and Riparo Villabruna, together with microwear patterns supporting the consumption of plant resources (Oxilia et al., 2020; Nava et al., 2021). These works have provided the first direct evidence of a diffuse broadening in the subsistence base of Upper Palaeolithic groups from the Last Glacial and throughout the phases that preceeded the onset of the Holocene (Revedin et al., 2010; 2015; Lippi et al., 2015; Oxilia et al., 2020; Nava et al., 2021).
Remarkably, one of the most accredited methods for recovering plant food remains in ancient deposits (i.e., flotation) has only sporadically been applied to Italian Palaeolithic excavations (Carra and Marinval, 2011; Carra and Cristiani, 2020), being time-consuming and characterized by a low recovery rate. However, systematic flotation applied to Palaeolithic deposits has demonstrated that carpological macroremains can preserve quite well even without particular depositional conditions (Piperno et al., 2004; Weiss et al., 2004; 2008; Carra and Marinval, 2011; Pryor et al., 2013; Carra and Cristiani, 2020).

In this paper, we contribute to the debate on the role of plant foods in the diet of Upper Palaeolithic hunter-gatherers from southern Italy and Sicily by exploring complementary evidence from five renowned archaeological contexts, which yielded long-lasting evidence of Late Glacial occupation: Grotta della Serratura in Campania, Grotta del Romito in Calabria, Grotta del Cavallo in Apulia, Grotta di San Teodoro and Grotta

d'Oriente in Sicily. Over the years, the evidence from these sites has been the object of interdisciplinary investigations, including palaeoenvironmental and archaeozoological studies, human anthropology and genomics, lithic technology and ornamental traditions, and meat-based dietary strategies (Martini et al., 2009b). However, direct evidence regarding dietary plant use still lacks for this region. We aim to fill this gap by integrating two different strands of evidence for plant consumption: (a) carpological data in the form of charred plant remains and (b) plant micro-debris entrapped in human dental calculus.
Based on our complimentary data for southern Italy and Sicily, we suggest that a broader range of dietary resources characterized the Late Upper Palaeolithic diet and included a wide selection of plant taxa.

## 2. Archaeological contexts and materials

In this paper, we consider five key Palaeolithic caves located along the Tyrrhenian coast of southern Italy (Grotta della Serratura, Grotta del Romito), in Sicily (Grotta di San Teodoro and Grotta d'Oriente), and by the Ionian coast (Grotta del Cavallo) (fig. 1). These sites were all discovered during the middle of the last century, except for Grotta di San Teodoro which was found in 1859. These contexts have a long history of excavations and numerous multidisciplinary analyses have been conducted on their Palaeolithic record, including a good assessment of their stratigraphy and environmental reconstructions detailing the various moments of their occupation. During the Late Pleistocene, variations of the sea levels caused by changes in the climate conditions affected their distance from the shore. The stratigraphy of the sites spans the Middle Palaeolithic up to the Holocene. Their Late Upper Palaeolithic occupations represent the focus of this work (Table 1).

**FIG.1 HERE**

### *2.1 Grotta della Serratura*

Grotta della Seratura is part of a complex of caves that opens along the coast, from Capo Palinuro to Torre Mozza, and is located ca. 2m a.s.l at the foot of Monte Bulgheria, the village of Marina di Camerota. The site was discovered during the of the last century, however systematic excavation began in 1984 and yielded a wealth of evidence related to the occupation of the cave during the Upper Palaeolithic, the Mesolithic and the Neolithic (Martini, 1993).
Excavations took place at two areas of the site: the atrium and the of the cave. The atrium is located 12 m from the current entrance of the cave. Here occupational layers to the Middle Palaeolithic and the Upper Palaeolithic have been identified, while the effects of the marine erosion led to the disappearance of deposit associated with the latest phases of the Pleistocene and the early Holocene. Layers C and D in the atrium trench are attributed to the Epigravettian while layer E relates to the Gravettian and layer F the Early Upper Palaeolithic. Some radiocarbon dates of some of these levels are unpublished, the chronological attribution of other ones is based on the comparison with the stratigraphy of the innermost area. (Martini et al., 2005).
In this internal area, located 40 m from the current entrance, a sequence of 10 layers related to Late Pleistocene and Early Holocene was discovered (Martini, 1993). Specifically, layers 8 to 10 refer to the Late Epigravettian, layers 7 to 4 correspond to the Early Mesolithic, while layers 3 to 1 are associated with the Neolithic occupation of the site (Martini, 1993; Colonese et al., 2010; Vadillo Conesa et al., 2021). Several 14C dates are available for this sequence (Table 1).

A total of 56 samples were collected from Grotta della Serratura in both the Gravettian and the Epigravettian levels (Table 2). The botanical samples come from both the atrium, where layers are identified with the letters of the alphabet and the back of the cave where levels are distinguished with progressive numbers.

### *2.2 Grotta del Romito*

Grotta del Romito is located at 275 m a.s.l, in the Lao Valley, a mountainous region with peaks reaching 2000 m, situated ca. 25 km away from the Tyrrhenian coast. The cave is sited in proximity of a narrow tributary of the Lao river. Excavations at the site exposed a thick deposit of more than 8 meters consisting in a long sequence of archaeological layers ranging from the Late Pleistocene to the Early Holocene; more than 40 radiocarbon dates are available for the whole sequence (Blockley et al., 2018; Martini and Lo Vetro, 2018). Due to intense episodes of water runoff, an intermittent occupation of the site is documented during the Last Glacial, from Evolved Gravettian to Evolved Epigravettian (ca. 23000 to 16000 uncal BP) (Ghinassi et al., 2009), while an intense human activity characterises the Late Glacial (Late Epigravettian) and the Early Holocene (Early Mesolithic - Sauveterrian) (Martini, 2002; Martini et al., 2004; 2006; Martini and Lo Vetro, 2005; 2018; Craig et al., 2010) (Table 1). Nine well preserved individuals have been found at the site and chronologically associated with the Epigravettian occupation of the cave (Graziosi, 1962; 1966; Fabbri et al., 1989; Mallegni and Fabbri, 1995; Martini, 2006; Craig et al., 2010; Martini and Lo Vetro, 2011). Eight of these inhumations refer to Late Epigravettian: Romito 1-2 and Romito 5-6, double burials, and Romito 3,4,7,8 single burials; the ninth individual, Romito 9, dating back to the Evolved Epigravettian (De Silva et al., 2015; Martini and Lo Vetro, 2018) (Table 3).

At Grotta del Romito a total of 59 samples were collected inside the cave from Late Epigravettian levels dated between 12170 ± 60 and 11660 ± 70 BP (Martini and Lo Vetro, 2018) and underwent flotation. Within the analysed samples, only one comes from the visual screening of the sediments from the 2016 field season (Table 2).

A total of 76 samples originally destined for the study of pollen were used to recover macroremains. They come from 3 different locations: the excavation trench (40), the Romito 8 burial pit (22) and the southern section within the excavation trench (14). The chronology of the samples is mainly referable to the Late Epigravettian (D), the deeper layers (F-L) instead refer to the Ancient Epigravettian (17500-18500 BP) and the evolved Gravettian (20000-24000 BP) (Table 2) (Martini and Lo Vetro, 2018).

Dental calculus samples were collected from 5 individuals of Grotta del Romito (Romito 4,5,6,7,8) (Table 4).

### *2.3 Grotta del Cavallo*

Located at 15 m a.s.l., Grotta del Cavallo is part of a karstic systems of the Uluzzo Bay in southern Apulia. The site was first discovered in 1961 and excavations exposed a long stratigraphic sequence including Mousterian (layers M-F), and Uluzzian (layers D and E) occupations separated by a thin ash layer dated to 45500±1,0 ky (Romagnoli, 2015; Martini and Sarti, 2017; 2021). The Uluzzian is separated from the Upper Palaeolithic by a sterile tephra lens (layer C) while the uppermost layer of the site (layer B) is associated with the final phases of the Epigravettian (Romanellian facies) and lies below a disturbed Neolithic level (layer A).

A total of 53 samples were analyzed from Grotta del Cavallo. The samples come from layers that are attributed the Neolithic (layer A1), the Mesolithic (layer A2) and the Late Upper Palaeolithic/Epiromanellian (layer B1) and Romanellian (layer B2) (Table 2), including a small pit with material of uncertain dating.

### *2.4 Grotta di San Teodoro*

Located in NE Sicily between the cities of Palermo and Messina, Grotta di San Teodoro stands at an altitude of 135 m a.s.l on the northern slope of the Nebrodi mountains, about 2km from the sea. Excavations at the site began at the end of the XIX century and lasted until the first decade the current century. Two main archaeological units were identified: the upper unit (layers A-D) attributed to late Upper Palaeolithic (Late Epigravettian) and characterized by intense occupation, abundant lithic artefacts, mammal bones and mollusc remains (Vigliardi, 1968; Bonfiglio et al., 2008; Catalano et al., 2020; Garilli et al., 2020); and a lower unit (layers E-G), which yielded remains from Upper Pleistocene endemic mammals. During the excavations carried out between 1937 and 1942, seven human burials (ST1-7) were unearthed, all belonging to adult individuals, two males (ST 3 and, probably, 7), four females (ST 1, 4, 5, 6) and one indeterminable (Fabbri and Lo Vetro, 2021). Based on the association with faunal and lithic remains six individuals (ST1-4,6,7) were chronologically attributed to the Late Epigravettian (ca. 15000- 11000 years BP) (Lo Vetro 2012, D'Amore et al 2009). Recently this attribution has been confirmed by tree almost contemporary AMS dates, all falling around 12600-12500 uncal BP, obtained on bones from individuals ST1 (Lo Vetro and Martini, 2006; Craig et al., 2010; Colonese et al., 2011; Martini et al., 2012a; Colonese et al., 2014; 2018) and ST4 and ST5 (Fabbri and Lo Vetro, 2021) (Table 3). Dental calculus samples were collected from 3 individuals buried at Grotta di San Teodoro (ST 3,5,6) (Table 4).

### *2.5 Grotta d'Oriente*

Grotta d'Oriente is located 40 m a.s.l. On the island of Favignana, part of the Egadi archipelago 5km from the NW coast of Sicily. The cave is made of two main areas, a small chamber at the entrance and a large gallery. The first excavation at the site dates back to 1972, while more recent and systematic excavations were carried out in 2005 (Lo Vetro and Martini, 2006; Craig et al., 2010; Colonese et al., 2011; 2014; 2018; Martini et al., 2012a). The latest excavations exposed a 2-m sequence which is divided in 8 archaeological layers. Layers 7 to 3 are associated with the prehistoric human occupation of the cave and relate to the Late Upper Palaeolithic (layer 7), Early Mesolithic (layer 6), Late Mesolithic or Early Neolithic (layer 5) and the Bronze Age (layers 4-3) (Martini et al., 2012a; Catalano et al., 2020). Three human burials have been found at the site, namely Oriente A, Oriente B and Oriente C. Oriente A and B were discovered in 1972 by G. Mannino (2002). Oriente A is a Mesolithic or Late Palaeolithic adult male burial, while Oriente B is a Mesolithic adult female burial recently AMS dated to the $10^{th}$ millennium uncal BP (Mannino et al., 2012). Oriente C, found in layer 7, has not been directly dated, however two AMS dates on charcoal fragments from the layers in which the individual stands (sublayers 7D, 12149 ± 65 BP, and 7E, 12132 ± 80) are consistent whit the cultural attribution to the Late Epigravettian based on stone tools assemblages (Table 1). Dental calculus from the individual Oriente C were collected for this study (Table 4).

## 3. Materials and Methods

### *3.1 Carpological analysis*

A total of 245 archaeobotanical samples were analysed: 136 from the Grotta del Romito, 56 from Grotta della Serratura, and 53 from Grotta del Cavallo. Samples for carpological study were selected from: (a) sieving carried out during the excavations (47); (b) systematic flotation of the archaeological sediments performed during the excavations between 2018 and 2019 (112); and (c) samples previously collected for pollen analysis, yet no longer suitable for such investigation (86) (see Table 2).

Samples collected during the 2018 and 2019 field seasons at Grotta del Romito and Grotta del Cavallo are the most abundant (Table 2). Each of these samples has a volume between 4 and 10 litres of sediment and their sampling followed the rules of capillarity and homogeneity. The samples were subjected to both manual and mechanic flotation at Grotta del Romito while only manual flotation was applied to Grotta del Cavallo (500µm and 300µm mesh sieves). Subsequently the residue was sieved and screened to recover archaeological materials. Only the light fraction was sifted under the stereomicroscope. The concentration of the finds and the number of carpological remains was greater at Grotta del Cavallo; at Grotta del Romito, the carpological remains were mostly diluted in the sediments. No specific structures linked to the accumulation of plants were found in the two sites; vegetal remains represent usual waste scattered in sediments.

Old pollen samples, each about 500 ml in volume, come from Grotta del Romito and Grotta della Serratura. It is known that pollen samples tend to deteriorate the micro-remains over time, especially if not properly stored.

Conversely, plant remains can be recovered even from samples that have been stored for a long time in warehouses. For this reason, we analysed samples collected between 1984 and 1990 at Grotta della Serratura and at Grotta del Romito during the 2000-2004 field seasons (Table 2).
The samples were subjected to manual flotation, using 500µm and 300µm mesh sieves, and residue sieving. Residues were sifted under a stereomicroscope and both light and heavy fractions were collected.

Last, 47 samples are represented by carpological findings recovered during the visual screening of residues coming from sieving activity carried out using a 1 mm mesh at Grotta della Serratura and Grotta del Romito (Table 2). These samples were selected during the excavation and only the work of determination was carried out on them. It was not possible to calculate the concentration of remains per litre in these samples.

For the determination of the finds, we used a collection of seeds and fruits of the flora of Italy and the Balkans is present at Sapienza University (DANTE – Diet and ANcient TEchnology laboratory) (Fig.3) as well as botanical atlases (Cappers and Neef, 2012; Cappers et al., 2012). The botanical nomenclature refers to Pignatti 2017 (Pignatti, 2017). A multifocal stereo microscope (Zeiss Axio Zoom V16) was used for determination of remains with magnifications ranging from 10X to 100X. Photographs of the specimens were taken using a high-definition Zeiss AxioCam 506 colour.

**FIG.2 HERE**

*3.2 Dental calculus – sampling, extraction, decontamination and examination procedures*
Dental calculus samples were removed from a total of 10 individuals dated to the Late Upper Palaeolithic (Late Epigravettian) and buried at Grotta del Romito (Romito 4,5,6,7,8), Grotta di San Teodoro (ST 3,5,6) and Grotta d'Oriente (Oriente C) (Table 4).
The sampling was conducted following the protocol systematized by (Sabin and Fellow Yates, 2020) with some variation (e.g., disposable blades were changed after each sample extraction).
Extraction and decontamination procedures followed standard published protocols (Cristiani et al., 2016; Radini et al., 2017; Sabin and Fellow Yates, 2020) and were conducted in dedicated clean spaces not connected to modern botanical work and under strict environmental monitoring of the DANTE laboratory of Sapienza University of Rome.
Cleaning was carried out daily in order to prevent any type of modern contamination. Bench space surfaces were cleaned prior to the analysis of each sample, using soap and ethanol, followed by covering of the surfaces by aluminium foil, and using of clean starch-free nitrile gloves at all times. Calculus cleaning was carried out under the stereomicroscope, on a Petri dish previously washed, with magnifications up to 100X. The removal of the mineralized soil adhering on the surface of the calculus was meticulously carried out using sterile tweezers to hold the sample and a fine acupuncture needle to gently scrape off the soil attached to the external layer of the mineralized plaque. The procedure was performed using drops of 0.5 M HCl acid to dissolve the mineralized flecks of soil and ultrapure water to block the demineralization, as well as to wash and remove the contaminants. The mineralized soil removed was stored in plastic tubes for monitoring analysis. Then, the clean calculus was washed in ultrapure water up to three times to remove any trace of loose sediment, dissolved in a solution of 0.5 M HCl and subsequently mounted on slides using a solution of 50:50 glycerol and ultrapure water.
Furthermore, control samples from the clean working tables and dust-traps were collected and analysed for comparative purposes in order to prevent any type of modern contamination– this is a practice routinely done in our laboratories, even at times where no archaeological analysis occur, to allow a better understanding of the flow of contaminations through seasons. We did not retrieve any debris morphologically similar to any of the remains in the environmental control samples. Starch granules amounted to a very minor fraction of the laboratory 'dust'.

The examination of micro-debris embedded in the calculus matrix was performed using a Zeiss Imager2 cross with magnifications ranging from 100X to 630X. For the identification of archaeological starch granules, a modern reference collection of 300 plants native to the Mediterranean region, and Europe was used along with published literature.

**FIG.3 HERE**

## *4.* Results

### *4.1 Carpological remains*

A total of 587 plant macroremains were retrieved from our study. Specifically, 106 carpological remains were recovered at Grotta della Serratura; 55 remains at Grotta del Romito; and 426 at Grotta del Cavallo (Table 2, Figs.4,5).

**FIG.4 HERE**

### *4.1.1 Grotta della Serratura*

The analysis and determination of the samples was carried out separately, depending on the origin of the sample origins: 46 from the visual screening operations (Supplementary Information 1), and 10 from the flotation and microscope screening (Supplementary Information 2). The first group contains the largest and most intact finds, while in the other samples the carpological remains are more fragmentary. Observations after the determination were made jointly.

Overall, 106 carpological remains were found, all belonging to herbaceous plants. Finds related to fruits of woody plants are instead completely missing. The majority of the findings come from the Final Epigravettian (layers 8F-G), while only indeterminable fragments were retrieved from the Gravettian deposit (layer 9 and E3, Fig. 4). Overall, our results reveal an exploitation of vegetable resources deriving from herbaceous plants most likely available in the palaeoenvironment neighbouring the site and, in some cases, still present and used today (Guarino et al., 2008; Salerno and Guarrera, 2008).

Vetch seeds (*Vicia* spp., Fig. 4) are the most common remains, their statistically significant presence indicates a possible food use and not just a chance. In fact, vetch is a pulse found in other contemporary Mediterranean sites and linked to food (Asouti et al., 2018; Martínez Varea and Badal García, 2018; Martínez-Varea, 2020). The state of preservation of the seeds affected the visibility of the hilum, the key feature for species determination. Other less preserved finds have morphologies that can be confused with grass pea (*Lathyrus* sp.) or the pea (*Pisum* sp.) (www.actaplantarm.org). Pulses are well represented in the Epigravettian trench at the bottom of the cave while they are missing in the samples coming from the atrium).

Undeterminable fragments of *Poaceae* grains have also been identified and ascribed to food species. Unfortunately, the lack of a specific determination does not allow other considerations and comparisons. Several genera are included among the *Poaceae* food species; however, caution is needed, due to the great diffusion in the environment of this botanical family (Pignatti 2017).

Amongst the findings, of note is the finding of *Galium* sp., *Arctium* sp., *Echium* sp. and *Lithospermum officinale* (Guarino et al., 2008). Given the low occurrence of these remains, their use is only suggested here. Besides their medical properties, these plants are very common in nature and provide data on the vegetation in the area adjacent the site (Fig. 4).

**FIG.5 HERE**

#### *4.1.2 Grotta del Romito*

Grotta del Romito has provided the lowest number of finds considering the sample size, probably because of the incoherent sediment, which limited the preservation of plant remains (Fig.6). Analogously, many of the samples examined for pollen turned out to be sterile (Ricciardi 2004).

The sample referable to layer D3 (Square F8 II) returned 6 fragments of bloodtwig dogwood (*Cornus sanguinea* L.), almost certainly parts of a single stone. The interest of this find concerns the possible food and/or medical use of the fruits, as well as the extraction of oil and colouring pigments (Lanzara 1997).

Carpological fragments that could not be determined due to the poor state of conservation come from the 59 samples that undergone flotation during the 2018 field season (supplementary information3). Most of the finds identified are related to fruits of tree and shrub species: hazel (*Corylus avellana* L.), blackthorn (*Prunus* sp. L.), bramble (cf. *Rubus* gr. *ulmifolius*), elder (*Sambucus nigra* L., *Sambucus* sp. L.) and probably a pine seed (cf. *Pinus* sp. L.) (Fig.4). Many of these fruits are edible, even if they have not been found inside specific structures. Carpological findings related to herbaceous species such as dock (*Rumex* sp. L.) and a fragment of the same botanical family (*Polygonaceae*) were also identified. All the plants identified are present in the environment, and may have a dietary and/or medicinal use (Lanzara 1997).

The study of the 76 pollen samples is much more complex (Supplementary Information 4). The samples come from 2 different locations of the cave: the interior of the cave and a southern section (always in the internal trench) in which the samples are identified by their metric location (from -58 to -350).

The poorest samples of plant remain are those of the southern section. Only 2 out of 14 samples tested returned seeds or fruits. The chronology of the layers with plant remains (-80 and -137) refers to the Late Epigravettian; only three carpological remains were found: a seed and a fragment of cardoon (*Galium* sp. L.) and an indeterminable fragment.

Cardoon is a weed that grows in meadows and undergrowth (Pignatti 2017) and some species have medical properties (www.actaplantarum.org). The presence of the cardoon may be due to intentionality but also to chance; in fact, the rough hairs that cover the seed make it adhere to humans and animals, favouring its unintentional transport to the anthropic areas.

62 samples come from the trench inside the cave and their study has allowed the discovery of 30 carpological fragments. Originally, these samples were taken for pollen analysis but, given the scarcity of results, after a preliminary search for pollen (Ricciardi, 2005), the samples were used for the recovery of macroremains.

A fair amount of plant finds (16 carpo-remains in 22 sediment samples) comes from the filling of the burial pit of the individual called "Romito 8". Discovered in 2002, this grave consists of a narrow and deep pit, filled with numerous stones placed over the body of the deceased. The study of the burial did not reveal any grave goods. The anthropological analysis revealed an impairment of the individual, or a paralysis that must have affected the left upper limb. The great dental wear proves that the individual must have compensated for the lack of use of the arm with the mouth, used as a real tool (Martini and Lo Vetro, 2018).

The plant macroremains found include 3 botanical families: *Polygonaceae*, *Poaceae* and *Fabaceae* (among which two clover seeds - *Trifolium* sp. are identifiable), to which we must add a fragment of the indeterminable fruit epidermis and 9 indeterminate carpological fragments (Fig. 4). The botanical families identified enclose numerous edible and medical genera, including clover (Pieroni et al., 2002). We cannot exclude that the presence of stones filling the pit burial might have favoured the preservation of plant materials. The Romito 7 and Romito 8 burials were subjected to pollen analysis (Ricciardi 2004), but no sporopollinic content was identified.

**FIG.6 HERE**

In addition to the finds found in the burial, other carpological remains were identified in unit D; it consists in over 35 levels (layers) dated to the Late Epigravettian (ca. 11000-13000 uncal BP, Martini 2012). A vetch

fragment (*Vicia* sp.) was found in layer D6, along with some indeterminable carpological fragments from layers D3, D4, D5 and D13.
A pit (pit 1) found in Layer D19 (dated around 12400 uncal BP), deserves a particular mention. It is an ovoid-shaped pit at the top of which there are some limestone blocks intentionally placed and emerging from the pit filling. A fragment of a webbed deer stag (*Cervus elaphus palmilodactyloceros*), other red deer remains, a skullcap, a cervical vertebra, a perforated atrophic canine, were found inside the pit, along with some perforated shells and a few other faunal fragments. All of this seems to outline an intentional deposition for ritual purposes (Martini et al., 2012b), but it does not contain important evidence of plant remains.
At Romito, the stratigraphy includes more ancient levels, in which other carpological remains have been found, such as the layer F1 (AMS date: 17376±90 uncal BP) related to the Early Epigravettian, and the layer H4 (AMS date: 20210±245 uncal BP) which refers to the Evolved Gravettian. The presence of a mineralized fig stone (*Ficus carica* L.) in the layer F needs further discussion. The presence of the fig tree in this chronological horizon contrasts with the palaeoclimatic reconstructions of southern Italy starting from the Last Glacial Maximum (Incarbona et al., 2010) marked by a much lower temperature than today, which would not favour the presence of a thermophilic plant such as the fig tree. The pollen analysis of layer F identified specimens altered by erosive phenomena or collapses (Ricciardi 2004). The latter ones might have caused vertical movements within the stratigraphy, which would explain the presence of a single mineralized find (the fig) in a context of charred fragments. Alternatively, anthropogenic activity preceding the glacial peak, i.e. pits excavated in more ancient layers (e.g. H), could also be considered to explain the presence of the fig in layer F.

### *4.1.3 Grotta del Cavallo*

At Grotta del Cavallo, the archaeological materials are well placed within the relative stratigraphic structure, in some cases the lithic remains are well arranged horizontally, to testify the original position of the deposit (Martini, Pers. Comm. 2021). However, remains of cultivated plants (mainly cereals) have been identified throughout the deposit, even in the layers attributed to the Late Upper Palaeolithic (Fig. 4). The presence of homogeneous plant material throughout the stratigraphic column has been explained considering some peculiarities of the depositional sequence, which is characterised by small burrows of ground wasps. The lairs of these insects can reach a depth of 20 cm. Since plant material is very light, the activity of the insects let to the displacement of remains of cultivated species into the deeper layers.
The data obtained from the carpological study of Grotta del Cavallo provides a picture of the Apulian Neolithic, with fragments of grains and glume bases of barley (*Hordeum vulgare*) and wheat, emmer in particular (*Triticum turgidum* ssp. *dicoccon*) (Castelletti et al., 1987; Fiorentino et al., 2013) (Fig. 5,7).

**FIG.7 HERE**

The spontaneous vegetation identified in various layers deserves further comments. While the fig (*Ficus carica*) is present only in the most superficial layers and the grapevine (mainly fragments of grape stones of *Vitis vinifera*) predominates in the intermediate ones (B1B-B1B/4), different herbaceous plants, including fat-hen (*Chenopodium* spp.), sedge (*Carex* spp.), common porcelain (*Portulaca oleracea*) and many fragments of *Poaceae* grains have been identified in the oldest layers yielded (Fig.4). These findings attest to a series of possible plant foods that could have been used during the late Upper Palaeolithic phases.

## *4.2 Dental calculus analysis*

Archaeological dental calculus preserved various vegetal and animal micro-debris (Table 5). Few and very small charcoal fragments and vegetal tissues were retrieved in the matrix. However, their dimensions, frequency and typology did not allow to formulate any identification or hypothesis about their presence in the matrix (Fig.2). Starch granules were recovered in the dental calculus of 5 individuals only (Romito 5, 7; San

Teodoro 3, 6; Oriente C). Overall, 4 morpho-types have been retrieved in this study (Fig. 8). In order to avoid misinterpretation granules smaller than 5 μm (transitory starches) were not considered (Haslam, 2004).

**Type I.** Type I granules were retrieved in 2 individuals (Romito 5 and Oriente C) (Table 4) in small quantities and some of them were found still partly embedded within the calculus remains (Fig. 8a,b,g,m,o,q,r). Size, shape, morphology and bimodal distribution that characterize granules of this type are encountered in the members of the plant tribe *Triticeae* (*Poaceae* family) and considered diagnostic features for taxonomic identification (Stoddard, 1999; Henry and Piperno, 2008; Yang and Perry, 2013). Starch distribution involves the presence of large granules (A-Type), round to sub-oval in 2D shape, ranging between 21.1 and 45,1 μm in maximum dimensions (mean size of 33,1 μm), lenticular 3D shape, a central hilum, a visible equatorial groove and deep lamellae concentrated in the mesial part; and small (< 10 μm) granules (B-Type) with round/sub-oval shapes and a central hilum (Stoddard, 1999; Geera et al., 2006; Yang and Perry, 2013). A-Type granules possess diagnostic features while smaller B-Type granules are rarely diagnostic to taxa (Yang and Perry, 2013). However, in our archaeological population, variability in the proportion and dimension of small B-type granules has been noticed. Based on literature (Henry et al., 2011; Yang and Perry, 2013) and our modern reference collection, this characteristic is common in the species of the genus *Aegilops* of *Triticeae* tribe (Fig. 8s) and can be attributed to both environment (Blumenthal et al., 1994; 1995) and genetics (Stoddard and Sarker, 2000; Howard et al., 2011).

**Type II.** Starch granules attributed to this type are characterized by a polyhedral to sub-polyhedral 3D morphology, a central hilum, and fine cracks. They were recovered in 2 individuals (Romito 5 and San Teodoro 6) (Fig. 8e,f,h). These features are consistent with starch granules of the tribe *Paniceae* of the grass family *Poaceae*, which is well known in ancient starch research (Madella et al., 2016). Dimensions of starch granules assigned to type II in our samples reach 21μm of maximum width, a size range found in several species of *Setaria* spp., *Panicum* spp., and *Echinochloa* spp. (Lucarini et al., 2016; Nava et al., 2020).

**Type III.** Starch granules attributed to this type were recovered in one individual (Romito 5) (Fig. 8c,d). They are characterized by round to sub-polyhedral 3D morphology, a central open hilum and a maximum width of 20,8 μm. These features may be consistent with *Andropogoneae* tribe (Madella et al., 2016).

**Type IV.** Granules belonging to this morpho-type have been identified in the individual 3 of Grotta di San Teodoro. They are characterized by a sub-polyhedral 2D morphology, a central depression and marked cracks (Fig. 8i,j). The maximum recorded width is 16,8 μm. These features are consistent with starch granules of the family *Adoxaceae* and has tentatively been attributed to the genus *Sambucus* through comparison with our modern reference (Fig. 8k,l).

Together with vegetal material also two barbules were recovered in the dental calculus of individual 5 from Grotta del Romito and individual 6 of San Teodoro. Unfortunately, microscopic characters which generally aid in the identification of groups of birds from their barbs were not visible in our remains.

**Figure 2.** *Micro-debris in dental calculus:* a,b) Starch granules attributed to type I from individual 5 of Grotta del Romito; c, d) Starch granule attributed to type III from individual 5 of Grotta del Romito ; e) Starch granule attributed to type II from individual 5 of Grotta del Romito; f) Starch granule attributed to type II from individual 5 of Grotta del Romito; g) Starch granule attributed to type I; h) Starch granule attributed to type II from individual 6 of Grotta di San Teodoro; i, j) Starch granule attributed to type IV from individual 3 of Grotta di San Teodoro; k, l) modern experimental starch granule of *Sambucus nigra*; m) Starch granule attributed to type I; n) Starch granule attributed to type I from individual 7 of Grotta di San Teodoro; o) Starch granule attributed to type I from individual 3 of Grotta di San Teodoro; p) Starch granule attributed to type I trapped in dental calculus from individual 3 of Grotta di San Teodoro; q) Starch granule attributed to type I

from Oriente C; r) Starch granule attributed to type I from Oriente C; s) modern experimental starch granules of *Aegilops crassa*.

## 5. Discussion and conclusions

By integrating macro-botanical remains from the sites of Grotta della Serratura, Grotta del Romito, and, to a less extent, Grotta del Cavallo, and micro-botanical evidence preserved in the dental calculus of the individuals buried at Grotta di San Teodoro, Grotta d'Oriente, and Grotta del Romito, we show that hunter-gatherer communities that occupied these sites during the Late Glacial collected different plant resources, including seeds, grasses and forest fruits, and used them for nutritional or medical purposes.

Grotta della Serratura yielded most of the plant remains analysed in this study. The abundance of vetch seeds (*Vicia* spp.) at this site, like in other coastal sites of Greece (Franchti cave) and Spain (Cueva de les Cendres) occupied in the same period, reveals a specific interest in this protein-rich plant foods by hunter-gatherer communities of the Mediterranean area (Asouti et al., 2018; Martínez Varea and Badal García, 2018; Martínez-Varea, 2020). Fragments of *Poaceae* plants are also documented at this site although an attribution to a species level was not possible. Along with the food species, some plants recovered at Grotta della Serratura are also renowned for their healing properties, such as *Galium* sp., *Arctium* sp., *Echium* sp. and *Lithospermum officinale*. All these plants are common in the Mediterranean environment and their presence in the stratigraphy of the cave can testify to their possible use as medicinal remedies at the end of the Palaeolithic.
Our results are congruent with the palaeoenvironmental data available for Grotta della Serratura. In particular, the anthracological study emphasises the presence of oak forest surrounding the cave (Abbate Edlmann et al., 1997) characterised by the presence of oaks, pines and various broad-leaved trees (*Acer*, *Carpinus*, *Fraxinus*, *Sorbus*), and more specifically Mediterranean species (*Ilex*, *Laurus*). However, no remains of fruits from tree plants were recovered at this site.
In the Late Epigravettian layer 8C and 8G, pollen sequence supports the carpological examination and indicate a predominantly herbaceous environment with few forest *taxa*, possibly influenced by the proximity of the cave to a series of coastal dunes. The botanical family *Asteraceae,* also represented in the carpological remains, stands out amongst the herbaceous plants (Cattani, 1993).

Our data from Grotta del Romito testify to the deep interaction between Upper Palaeolithic communities and the surrounding environment, which reflects in the exploitation of various available plant taxa.
The greater distance of the site from the coast is reflected in the larger exploitation of fruits that are typical of the forest environment surrounding the cave: bloodtwig dogwood (*Cornus sanguinea* L.), hazel (*Corylus avellana* L.), blackthorn (*Prunus* sp. L.), bramble (cf. *Rubus* gr. *ulmifolius*), elder (*Sambucus nigra* L., *Sambucus* sp. L.) and probably a pine seed (cf. *Pinus* sp. L.). Analogous macro-remains were recovered in the Late Upper Palaeolithic sediments of Grotta di Pozzo in the Fucino region of Abruzzo (central Italy), where forest fruits were the only plants identified (Lubell et al., 1999). Amongst the macro-botanical remains recovered at Grotta del Romito fragments of herbaceous edible plants, such as dock (*Rumex* sp. L.) and fragments belonging to the same botanical family (*Polygonaceae*) are documented, together with the vetch (*Vicia* sp. L.) and fragments of *Poaceae* grains. Plants with medicinal properties, such as the cardoon (*Galium* sp. L.) were also recovered.

The palaeoclimatic record documented at Grotta del Romito for the Late Glacial highlights a predominantly pine tree-like environment, with a lower presence of herbaceous plants of the *Rosaceae*, *Boraginaceae*, *Plantaginaceae*, *Ranunculaceae*, *Fabaceae*, and *Poaceae* botanical families (Ricciardi 2004). Our analysis of the corresponding levels shows a similar distribution of these botanical families, while the presence of edible fruits in the upper stratigraphy indicates the spread of broad-leaved trees at the end of the Late Glacial.

Similarly, woodland mammals appear in the microfauna while the malacofauna suggests a more open environment (Martini et al., 2009b).

*Poaceae* remains were also identified in the burial filling of Romito 8, together with *Polygonaceae* and *Fabaceae* remains (including clover seeds) and a fragment of the epidermis of an indeterminable fruit. The recovery of *Poaceae* grasses at both Grotta del Romito and Grotta della Serratura suggest that Upper Palaeolithic communities of southern Italy knew and possibly consumed plants of this botanical family. Unfortunately, the numerous genera of *Poaceae* family widespread in Southern Italy and Sicily (Huntley et al., 1999; Sadori and Narcisi, 2001; Ermolli and di Pasquale, 2002; Pignatti, 2017) and the absence of specific diagnostic parts in the macro-remains recovered at the investigated sites prevented from a precise determination of the remains at the species level. Nonetheless, starch grains belonging to *Poaceae* family were recovered in dental calculus of two individuals buried at Grotta del Romito (Romito 5 and Romito 7) and attributed to *Triticeae* tribe, based on their morpho-dimensional features. Complementary evidence for a diet rich in starchy foods comes also from the anthropological analysis of dental remains, which identifies the presence of one interproximal caries at the neck of the first molar of the individual Romito 1 (Fabbri and Mallegni, 1988).
In the most recent phases (D3-D5), the carpological remains are more closely related to fruit of tree species, while in the earlier layers (D6-D7) herbaceous plants seem to predominate. Starch granules retrieved from dental calculus complement this picture by suggesting the consumption of grasses of *Triticeae* tribe during the Late Glacial period. This highlights an expansion in the plants used, under the pressure of an environment that is changing in a thermophilic way, with the increase in deciduous forest cover and the exploitation of edible fruits.

Also in Sicily, starch granules recovered in the dental calculus of the individuals 3and 6 of Grotta di San Teodoro and Oriente C suggest grasses of *Poaceae* family, and more likely grasses of *Paniceae* and *Triticeae* tribes, were consumed since the end of the Oldest Dryas. *Poaceae* botanical family is very widespread and also includes many genera suitable for living in colder climatic conditions (e.g. *Avena*) and therefore their use can be suggested even for cold phases (Lippi et al., 2015). *Setaria* is one of the possible genera to which starch granules retrieved from San Teodoro individuals were assigned, and some species (e.g. *Setaria verticillata*) grow in Sicily at altitudes up to 1000 m above sea level (Pignatti, 2017). Based on regional palaeoenvironmental record (Sadori and Narcisi, 2001; Ermolli and di Pasquale, 2002), the presence of the herbaceous taxa is confirmed in southern Italy during the Late Glacial and at the onset of the warm Bølling-Allerød interstadial phase and linked to an increase of the moisture and temperatures. Grasses of *Paniceae* tribes prefer mild climates and became more widespread in proximity of water courses and in coastal zones during the Late Glacial. At San Teodoro, the high rate of precipitations would have guaranteed water to numerous streams and rivers, hence providing ideal environment for such species. The faunal assemblage at Grotta d'Oriente suggests the presence of both forest and open environments where species of the *Triticeae* tribe could have grown.
A Late Upper Palaeolithic familiarity with *Poaceae* taxa seems to emerge as a part of a well-documented dietary pattern also in other regional case studies that document the use of many genera of this botanical family as edible plants from the first part of the Late Glacial until the early phases of the Holocene.

In Italy, the consumption of plants of this botanical family was suggested based on the starch remains identified in the dental calculus of one individual buried at Riparo Tagliente (Oxilia et al 2020), the oldest known archaeological site on the southern slope of the Alps to be re-occupied by human groups after the Late Glacial Maximum. Similar evidence was also retrieved in Late Upper Palaeoloithic individuals of Grotta Continenza, in central Italy (Nava et al., 2021). A diet, including meat as well as plant foods was also hypothesised on the basis of the dental microwear and trace element analysis for the individuals of San Teodoro (Carnieri and Mallegni, 2006). A caries identified during the dental calculus sampling on the neck of the upper left second molar of the individual 6 from the same site would suggest the consumption of carbohydrates (Fig. 3d). In the same period, evidence from Grotte des Pigeons in Morocco show the high occurrence of caries in individuals dated between 15,000 and 13,700 cal BP and yielded evidence of systematic harvesting and processing of edible wild plants, including acorns and pine nuts (Humphrey et al., 2014).

The dental calculus of the individual 3 of San Teodoro also preserved evidence for the consumption of forest fruits. Based on the comparison with fruits, drupes and berries from our modern reference collection, ancient starch granules attributed in ST3 were possibly attributed to elderflower (*Sambucus* sp.). This forest fruit is rich in carbohydrate and proteins and renowned for peculiar bioactive properties (Sidor and Gramza-Michałowska, 2015). Interestingly, a broadening in the local resources exploited at San Teodoro was already suggested based on the isotopic study for the individual 7, which purportedly consumed a wide range of foods, including terrestrial and marine resources. The specific topography and hydrology of the area and the proximity of the site to the Nebrodi mountain chain, characterised by high precipitation rate, might have made plenty of plant resources available. Forest diffused in this area would have certainly provided a perfect habitat for elderflowers and herbaceous species, as documented also today (Martini et al., 2005; Colonese et al., 2018).

Complimentary evidence for assessing the role of plant foods in Late Glacial human diet comes from Grotta della Serratura and Grotta d'Oriente. Here, the presence of non-food shell debris suggests that aquatic plants growing in the coastal lagoons and estuaries close to the sites were collected and likely used as dietary supplement (Martini et al., 2005; Colonese et al., 2018). One of the most common species of seagrass meadows growing in the Tyrrhenian littoral and in Sicily, the *Zostera* spp., is rhizomatous herb which produces seeds known for being a good source of carbohydrate and proteins.

More complex to interpret are the remains from Grotta del Cavallo, due to their stratigraphic position. However, the oldest remains might indicate the exploitation of a series of herbaceous edible plants such as fat-hen (*Chenopodium*), common porcelain (*Portulaca oleracea*) and many fragments of *Poaceae* grains, which are typical in the Mediterranean environment.

Based on the rich data discussed in this paper, we infer a broadening in the dietary base since the earliest phases of the deglaciation in the Southern region of Italy and Sicily. Herbaceous species were used since the earliest phases of the Late Glacial together with drupes and fruits from tree plants. While it is possible that the spread of the deciduous forest cover prompted humans to explore new plant resources in the deglaciation period, our results underline the interpretative limits of dietary reconstructions based on the application of single methodologies, e.g. stable isotope study or archaeozoological analysis, when attempting the reconstruction of dietary habits in Palaeolithic contexts.

## Author contributions

EC., M.C. conceived the study and designed the experiments. M.C., performed the carpological analysis, A.Z., E.F. and E.C. performed the laboratory work on dental calculus and modern reference; F.M., L.S. and D.L.V. provided the samples; E.C., F.M., L.S. and D.L.V. supervised the work; E.C., provided funding for the analyses. All authors contributed to writing the manuscript.

## Data Availability

Not applicable

## Declaration of competing interest

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

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**Captions**

**Figure 1**. The location of the five analysed contexts from southern Italy and Sicily

**Figure 2.** Sample of experimental carpological remains from modern reference collection. a) *Hordeum vulgare*, glume base; b) *Triticum turgidum* ssp. d*icoccon*, glume base; c) *Vicia sylvatica*, seed; d) *Trifolium campestre*, seed,; e)*Prunus spinosa*, stone; f) *Sambucus nigra*, stone; g) *Quercus pubescens*, cicatrix; h)*Corylus avellana*, stone fragment; i) *Rumex crispus*, fruit; j) *Chenopodium album*, seed; k) *Echium vulgare*, seed; l) *Ficus carica*, stones

**Figure 3**. Some of the teeth sampled in this study. a) San Teodoro 5; b, c) Romito 3; d) Sant Teodoro 6

**Figure 4.** Carpological remains found at Grotta del Cavallo (a-h), Grotta del Romito (i-p) and Grotta della Serratura (q-x). a) *Ficus carica;* b) *Triticum* sp., glume bases; c) *Vitis vinifera* fragments; d) *Triticum turgidum* ssp. *dicoccon;* e) *Carex* sp.; f) *Quercus* sp.; g) *Chenopodium gr. album;* h) *Hordeum vulgare,* glume bases; i) *Sambucus nigra* sp.; j) *Galium sp.* ; k) *Corylus avellana* fragment; l) *Rumex* sp.; m) *Rubus* gr. *ulmifolius;* n) *Prunus* sp; o) *Sambucus sp.*; p) *Trifolium sp.* ; q) *Lithospermum officinale* (side a)*; r) Lithospermum officinale* (side b)*;* s) *Echium* sp. (ventral view); t) *Arctium* sp.; u) *Vicia/Lathyrus; v) Vicia* sp.; w) *Vicia* sp., seed fragments*;* x) *Vicia* sp., seeds

**Figure 5.** Occurrence of carpological findings in each of the analysed sites.

**Figure 6.** Distribution of tree/shrub, weeds, and indeterminable findings within the analysed layers at Grotta del Romito.

**Figure 7**. Distribution of domestic species, wild species, and indeterminable findings within the analysed layers of Grotta del Cavallo.

**Figure 8.** *Micro-debris in dental calculus:* a,b) Starch granules attributed to type I from individual 5 of Grotta del Romito; c, d) Starch granule attributed to type III from individual 5 of Grotta del Romito ; e) Starch granule attributed to type II from individual 5 of Grotta del Romito; f) Starch granule attributed to type II from individual 5 of Grotta del Romito; g) Starch granule attributed to type I; h) Starch granule attributed to type II from individual 6 of Grotta di San Teodoro; i, j) Starch granule attributed to type IV from individual 3 of Grotta di San Teodoro; k, l) modern experimental starch granule of *Sambucus nigra*; m) Starch granule attributed to type I; n) Starch granule attributed to type I from individual 7 of Grotta di San Teodoro; o) Starch granule attributed to type I from individual 3 of Grotta di San Teodoro; p) Starch granule attributed to type I trapped in dental calculus from individual 3 of Grotta di San Teodoro; q) Starch granule attributed to type I from Oriente C; r) Starch granule attributed to type I from Oriente C; s) modern experimental starch granules of *Aegilops crassa*.

**Table 1.** Radiocarbon dates available from the Late Palaeolithic sites analyzed in this paper.

**Table 2.** Finding numbers, stratigraphic provenance, chronology, and relative frequencies.

**Table 3.** Radiocarbon dates available from the Late Palaeolithic burials analysed in this paper. The dates were calibrated with Oxcal 4.4 using the IntCal20 calibration curve in the burial (Catalano et al 2020; Lo Vetro and Martini 2012).

**Table 4.** Details of dental calculus sampled for the study (n=9).

Figure 1

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Figure 2

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Figure 3

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Figure 4



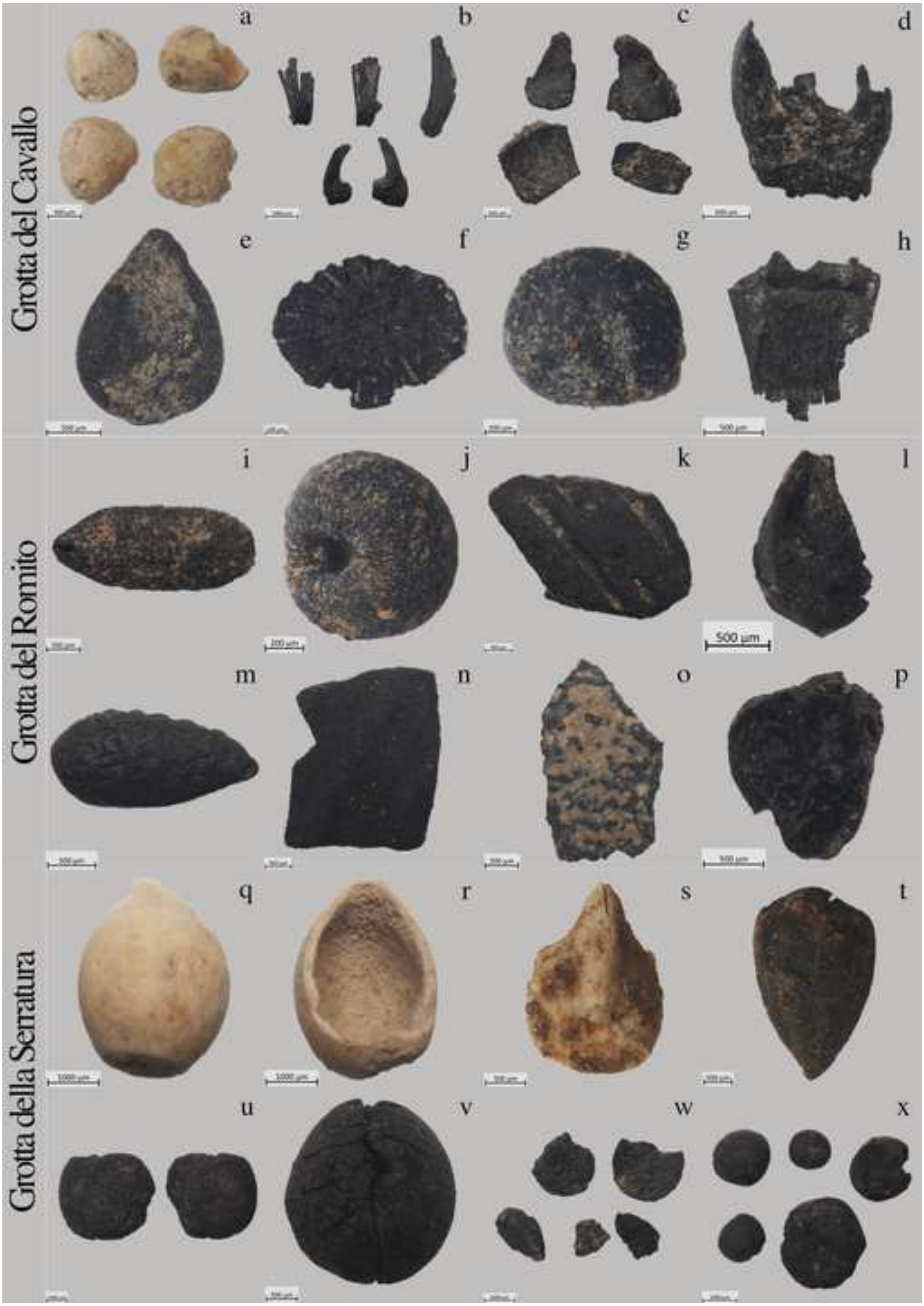
Grotta del Cavallo
a
b
c
d
e
f
g
h
500 µm
Grotta del Romito
i
j
200 µm
k
l
500 µm
m
n
o
p
Grotta della Serratura
q
1000 µm
r
1000 µm
s
t
u
v
w
x

Figure 5

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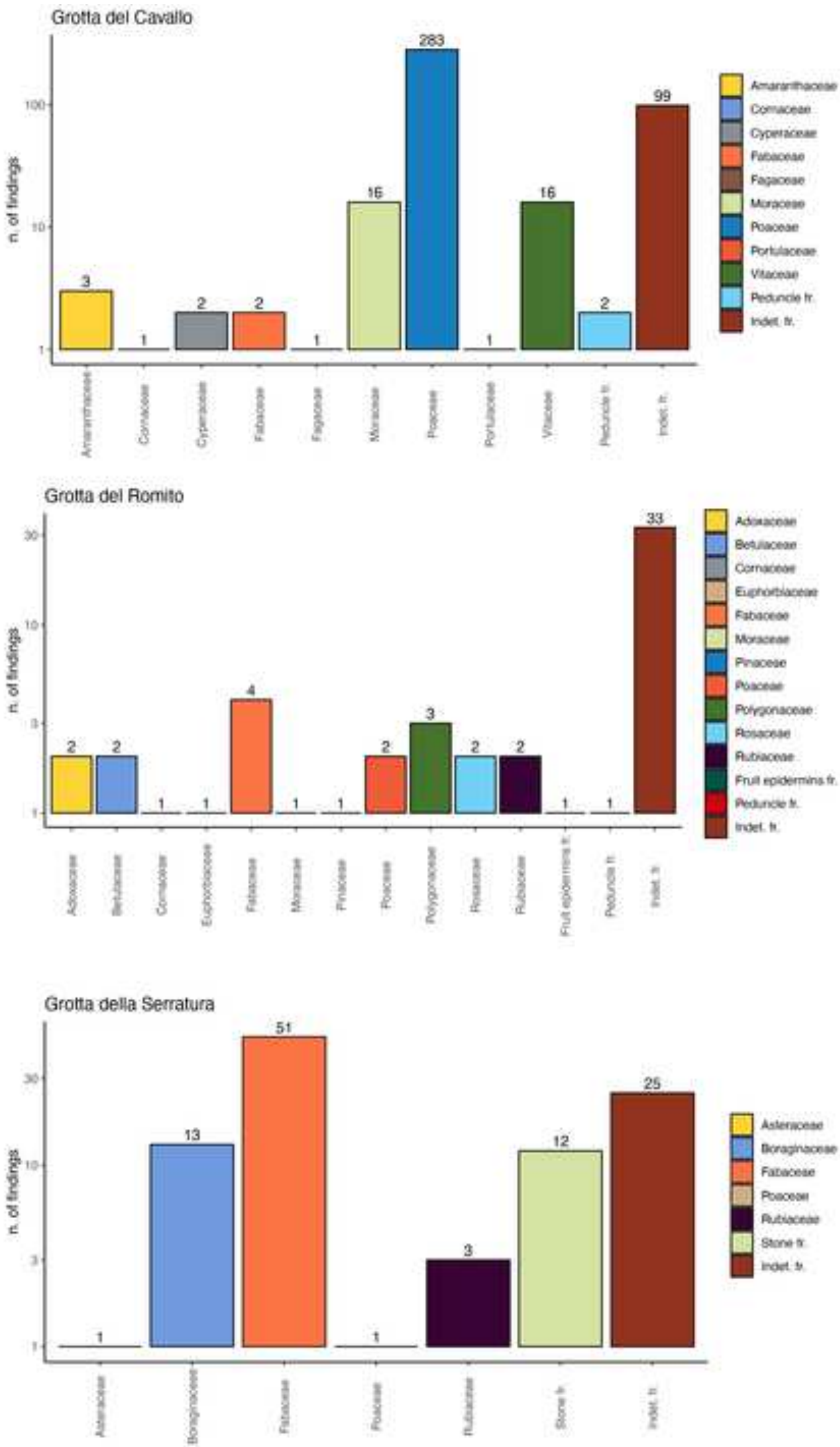

Figure 6

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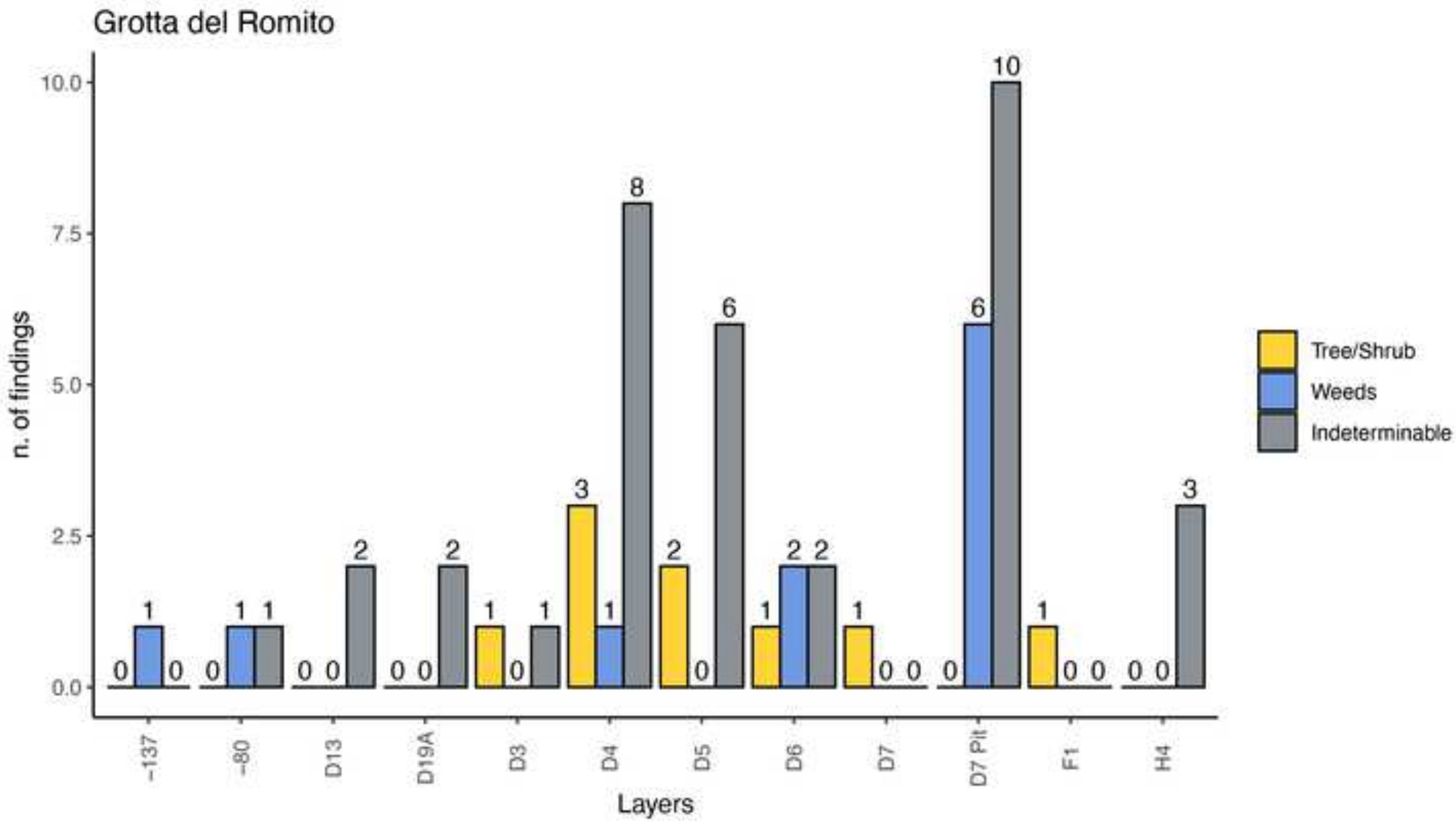

Figure 7



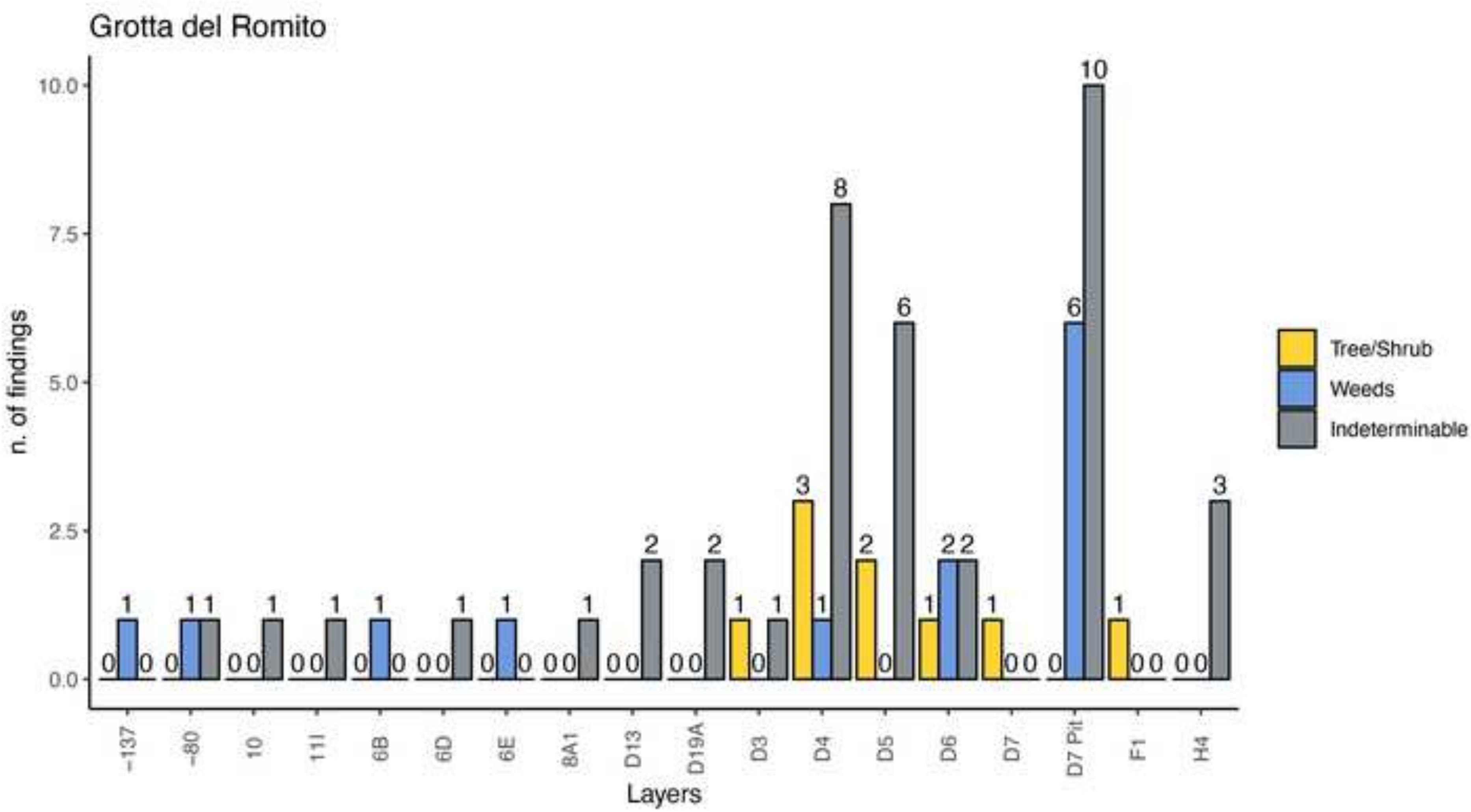
Grotta del Romito
n. of findings
0.0
2.5
5.0
7.5
10.0
Layers
−137
−80
10
11I
6B
6D
6E
8A1
D13
D19A
D3
D4
D5
D6
D7
D7 Pit
F1
H4
Tree/Shrub
Weeds
Indeterminable

Figure 8 Click here to access/download;Figure;Figure 8.tif

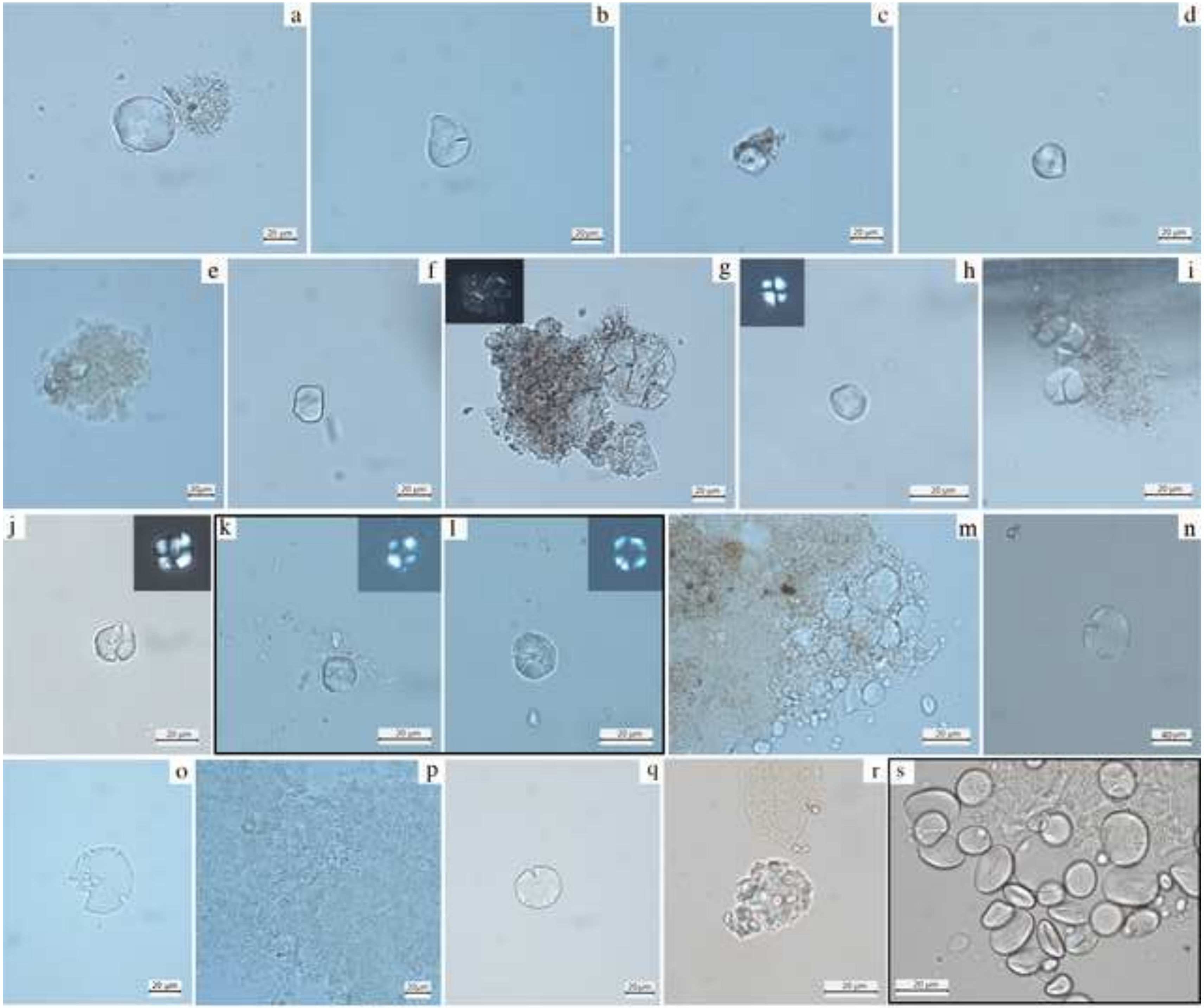

Table 1 

| Site | Lab label | Cultural attribution | AMS dating (IntCal 20) | | | *Material* | |
|---|---|---|---|---|---|---|---|
| | | | *Lab Code* | *$^{14}$C age (BP)* | *95.4% confidence, cal BP* | | |
| Oriente C | 7E | Late Palaeolithic | LTL873A | 12132 ± 80 | 14235-13796 | Charcoal | Lo Vetro and Martini, 2006 |
| | Sublayer 7D | | LTL14260A | 12149 ± 65 | 14217-13803 | Charcoal | Lo Vetro and Martini, 2006 |
| Serratura | Unit 4 | Undif. Epipaleolithic | UtC - 750 | 10000±200 | 12469-10875 | Charcoal | Martini et al. 2005 |
| | Unit 5 | | UtC - 751 | 9790±170 | 11814-10693 | Charcoal | Martini et al. 2005 |
| | Unit 5 | | Bln - 3568 | 9720±60 | 11248-10800 | Charcoal | Martini et al. 2005 |
| | Unit 6 | Sauveterrian | Bln - 3569 | 9620±60 | 11185-10760 | Charcoal | Martini et al. 2005 |
| | Unit 6 | | UtC - 752 | 9770±140 | 11690-10715 | Charcoal | Martini et al., 2005 |
| | Unit 7 | | Bln - 3570 | 9870±70 | 11612-11177 | Charcoal | Martini et al., 1993 |
| | Unit 7 | | UtC - 753 | 10230±130 | 12578 -11398 | Charcoal | Martini et al., 2005 |
| | Unit 8A | Evolved Epigravettian | UtC - 754 | 10000±130 | 11941 -11198 | Charcoal | Martini et al., 2005 |
| | Unit 8B | | UtC - 755 | 10270±140 | 12610-11403 | Charcoal | Martini et al., 2005 |
| | | | Bln - 3571 | 10220±60 | 12441-11642 | Charcoal | Martini et al., 2005 |
| | Unit 8C | | UtC - 1418 | 11290±90 | 13405-13067 | Charcoal | Martini et al., 2005 |
| | Unit 8E | | UtC - 1420 | 11490±160 | 13743 -13095 | Charcoal | Martini et al., 2005 |
| | Unit 8F | | UtC - 1463 | 11460±80 | 13476-13175 | Charcoal | Martini et al., 2005 |
| | Unit 8FI | | Beta - 63289 | 11240±90 | 13314-12929 | Charcoal | Martini et al., 2005 |
| | Unit 8FII | | Beta - 63290 | 12100±100 | 14311-13762 | Charcoal | Martini et al., 2005 |
| | Unit 8FIII | | Beta - 63291 | 11880±120 | 14037-13503 | Charcoal | Martini et al., 2005 |
| | Unit 8G | | Beta - 63292 | 12060±90 | 14165-13756 | Charcoal | Martini et al., 2005 |
| | Unit 9 | | Beta - 63293 | 13100±120 | 16055-15315 | Charcoal | Martini et al., 2005 |
| | Unit 10A | | Beta - 63294 | 15350±200 | 18997-18240 | Charcoal | Martini et al., 2005 |
| | Unit 10C | | UtC - 1421 | 15700±110 | 19228-18776 | Charcoal | Martini et al., 2005 |
| | Unit 11 | Gravettian | Beta - 88907 | 24380±1530 | 32889-25927 | Charcoal | Martini et al., 2005 |
| | Unit 12 | | Beta - 88908 | 29020±2650 | 44010-28708 | Charcoal | Martini et al., 2005 |
| Romito | D1 | Late Epigravettian | Beta-160,300 | 11660 ± 70 | 13742-13345 | Charcoal | Blockley et al., 2018 |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | D1 | Late Epigravettian | ROM 5-1 | 11765±50 | 13760-13502 | Charcoal | Blockley et al., 2018 |
| | D1 | Late Epigravettian | ROM 5-2b | 12415±50 | 14907-14246 | Charcoal | Blockley et al., 2018 |
| | D5a | Late Epigravettian | Beta-160,302 | 12060±90 | 14165-13756 | Charcoal | Blockley et al., 2018 |
| | D5b | Late Epigravettian | Beta-160,303 | 12160±50 | 14297-13813 | Charcoal | Blockley et al., 2018 |
| | D8 | Late Epigravettian | LTL234A | 12170 ± 60 | 14308-13813 | Charcoal | Blockley et al., 2018 |
| | D11 | Late Epigravettian | LTL238A | 12334±75 | 14844-14080 | Charcoal | Blockley et al., 2018 |
| | D13 | Late Epigravettian | LTL607A | 12258±75 | 14821-14026 | Charcoal | Blockley et al., 2018 |
| | D14 | Late Epigravettian | LTL603A | 12377±95 | 14933-14103 | Charcoal | Blockley et al., 2018 |
| | D15 | Late Epigravettian | LTL608A | 12331±55 | 14829-14091 | Charcoal | Blockley et al., 2018 |
| | D16 | Late Epigravettian | LTL601A | 12369±100 | 14935-14091 | Charcoal | Blockley et al., 2018 |
| | D20 | Late Epigravettian | LTL602A | 12438±85 | 14996-14188 | Charcoal | Blockley et al., 2018 |
| | F1 | Early Epigravettian | LTL1593A | 17376±90 | 21345-20760 | Charcoal | Blockley et al., 2018 |
| | F2 | Early Epigravettian | LTL239A | 18978±130 | 23152-22511 | Charcoal | Blockley et al., 2018 |
| | F3I | Early Epigravettian | LTL606A | 18483±95 | 22618-22185 | Charcoal | Blockley et al., 2018 |
| | G1 | Late Gravettian | LTL236A | 19351±180 | 23761-22987 | Charcoal | Blockley et al., 2018 |
| | G2 | Late Gravettian | LTL237A | 19373±90 | 23742-23043 | Charcoal | Blockley et al., 2018 |
| | H4 | Late Gravettian | LTL604A | 20210±245 | 24974-23800 | Charcoal | Blockley et al., 2018 |
| | I | Evolved Gravettian | LTL1048A | 23475±190 | 27925-27295 | Charcoal | Blockley et al., 2018 |

Table 2 [Click here to access/download;Table;Table 2.docx](#)

| | Sample Origin | Site and sampling area | Layer | Chronology | N. sample | N. remains | Frequencies (remains per litre) |
|---|---|---|---|---|---|---|---|
| *Grotta della Serratura* | Old Pollen Samples | Back of the Cave trench | 4 | Undifferentiated. Epipaleolithic | 1 | 0 | |
| | | | 8 | Final Epigravettian | 3 | 24 | |
| | | | 9 | Late Epigravettian | 1 | 17 | |
| | | | 11 | Gravettian | 2 | 3 | |
| | | | 13 | Gravettian | 1 | 0 | |
| | | Atrium trench | E | Gravettian | 1 | 1 | |
| | | | F | Gravettian | 1 | 0 | |
| | | | | | **Total 10** | **Total 45** | **9** |
| | Sifting operation | Back of the Cave trench | 8 | Final Epigravettian | 33 | 51 | |
| | | | 9 | Late Epigravettian | 1 | 1 | |
| | | | 10 | Late Epigravettian | 3 | 7 | |
| | | Atrium trench | C | Final Epigravettian | 1 | 1 | |
| | | | D | Gravettian | 2 | 1 | |
| | | | E | Gravettian | 6 | 0 | |
| | | | | | **Total 46** | **Total 61** | **0** |
| *Grotta del Romito* | Manual flotation | 2018 excavations | D (D4-D7) | Late Epigravettian | 59 | 21 | |
| | | | | | **Total 59** | **Total 21** | **0,07** |
| | Old Pollen Samples | 2000-2004 excavation | D (2-22) | Late Epigravettian | 24 | 10 | |
| | | | F | Early Gravettian | 3 | 1 | |
| | | | G | Late Gravettian | 2 | 0 | |
| | | | H | Late Gravettian | 8 | 3 | |
| | | | I | Evolved Gravettian | 2 | 0 | |
| | | | L | Gravettian | 1 | 0 | |
| | | Southern section | -58/60 | Late Epigravettian | 1 | 0 | |
| | | | -75 | | 1 | 0 | |
| | | | -80 | | 1 | 2 | |
| | | | -95 | | 1 | 0 | |
| | | | -110 | | 1 | 0 | |
| | | | -133 | | 1 | 1 | |
| | | | -137 | | 1 | 0 | |
| | | | -190 | | 1 | 0 | |
| | | | -255 | | 1 | 0 | |
| | | | -290 | | 1 | 0 | |
| | | | -330 | | 1 | 0 | |
| | | | -345 | | 1 | 0 | |
| | | | -350 | | 1 | 0 | |
| | | Burial – Romito 8 | D7 pit | Late Epigravettian | 22 | 16 | |
| | | | | | **Total 76** | **Total 33** | **0.87** |
| *Grotta del Cavallo* | Sifting operation | 2016 excavation | D (D3) | Epigravettian | 1 | 6 | |
| | | | | | **Total 1** | **Total 6** | **0** |

| | | | | | | | |
|---|---|---|---|---|---|---|---|
| | | | | | | | |
| | Manual flotation | Excavation 2018/2019 | A1 | Neolithic | 2 | 35 | |
| | | | A2 | Mesolithic | 2 | 13 | |
| | | | B1 | Epiromanellian | 25 | 196 | |
| | | | B2 | Romanellian | 15 | 115 | |
| | | | B2 Pit | Upper Paleolithic (?) | 5 | 67 | |
| | | | | | **Total 53** | **Total 426** | **1,08** |
| | **TOTAL** | | | | **245** | **592** | |

| **Site** | **Lab label** | **Cultural attribution** | **AMS dating (IntCal 20)** | | | *Material* | *References* |
|---|---|---|---|---|---|---|---|
| | | | *Lab Code* | *$^{14}$C age (BP)* | *95.4% confidence, cal BP* | | |
| Oriente C | 7E | Late Epigravettian | LTL873A | 12132 ± 80 | 14235-13796 | Charcoal | Lo Vetro and Martini, 2006 |
| Oriente C | Sublayer 7D | Late Epigravettian | LTL14260 A | 12149 ± 65 | 14217-13803 | Charcoal | Mannino et al., 2011 |
| San Teodoro | 1 | Late Epigravettian | ETH-34451 | 12580 ± 130 | 15315-14255 | Human bone | Mannino et al., 2011 |
| San Teodoro | 4 | Late Epigravettian | LTL14278 A | 12531 ± 80 | 15130-14229 | Human bone | Mannino et al., 2011 |
| San Teodoro | 5 | Late Epigravettian | LTL14277 A | 12637 ± 100 | 15322-14432 | Human bone | Martini et al., 2013 |
| Romito | 4 | Late Epigravettian | LTL3032A | 11340±90 | 13366-13095 | Human bone | Martini and Lo Vetro, 2018 |
| Romito | 5 | Late Epigravettian | LTL3033A | 10862±70 | 12930-12716 | Human bone | Martini and Lo Vetro, 2018 |

Table 4 

| | **Site** | **Individual** | **Cultural attribution** | **Calculus location** | | |
|---|---|---|---|---|---|---|
| | | | | *Tooth* | *Surface* | *Weight (mg)* |
| 1 | Romito | Romito 4 | Late Epigravettian | 43 | buccal | 3.4 |
| 2 | | Romito 5 | Late Epigravettian | 43 | buccal | 10.6 |
| 3 | | Romito 6 | Late Epigravettian | 46, 14, 42 | lingual | 3.1,2.9,1.5 |
| 4 | | Romito 7 | Late Epigravettian | | buccal | 0.5 |
| 5 | | Romito 8 | Late Epigravettian | | lingual | 2.2 |
| 6 | San Teodoro | ST 3 | Late Epigravettian | 38,42, 47 | lingual | 4.1, 2.4, 2.2 |
| 7 | | ST 5 | Late Epigravettian | 32, 44 | lingual | 0.5, 0.3 |
| 8 | | ST 6 | Late Epigravettian | 12;14 | lingual | 4, 3.1 |
| 10 | Oriente C | Oriente | Late Epigravettian | 34 | buccal | 2.1 |

| | Site | Burial label | Chrono-cultural attribution | Type I *Triticeae* | Type II *Paniceae* | Type IV *Andropogoneae* | Type IV *Adoxaceae* |
|---|---|---|---|---|---|---|---|
| 2 | Grotta del Romito | **ROMITO 5** | Late Upper Palaeolithic | 3 | 3 | 4 | |
| 4 | Grotta del Romito | **ROMITO 7** | Late Upper Palaeolithic | >50 | | | |
| 6 | Grotta di San Teodoro | **ST3** | Late Upper Palaeolithic | >15 | 11 | | 4 |
| 7 | Grotta di San Teodoro | **ST5** | Late Upper Palaeolithic | 2 | | | |
| 8 | Grotta di San Teodoro | **ST6** | Late Upper Palaeolithic | | | | |
| 9 | Grotta di Oriente | **ORIENTE C** | Late Upper Palaeolithic | 10 | | | |
| | **Total** | | | >80 | 14 | 4 | 4 |