Pollen from Late Pleistocene hyena (*Crocuta crocuta spelaea*) coprolites: an interdisciplinary approach from two Italian sites

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**Abstract**

Palynology of fossil faeces is still extremely rare and its contribution to the interpretation of the environment undervalued. In this paper we present the results of pollen analysis performed on cave hyena coprolites (*Crocuta crocuta spelaea*,Goldfuss 1832) from Marine Isotope Stage 3 (MIS 3) sites of Cava Muracci (Cisterna di Latina, central Italy) and Tana delle Iene (Ceglie Messapica, southern Italy). This study provides new insights into the vegetation of the Late Pleistocene of peninsular Italy, until now known only through long pollen records. It also shows how the content of coprolites, combined with faunal dataand geochronological investigations, can represent a potential integrative source of palaeoclimatic proxy data. Our results indicate that the surroundings of both of the hyena dens were characterised by a patchy landscape with open lowlands dominated by steppe and grassland vegetation, while a few mesophilous and thermophilous trees were present in more humid areas, probably along the marine coast and inland. The harsh glacial climate appears to have been milder at Cava Muracci than at Tana delle Iene. This could be due either to the different environmental features of the two sites or to the high climatic variability that occurred during MIS3.

*Keywords:* Central Mediterranean; Hyena coprolites; Environmental changes; Marine Isotope Stage 3; Palaeoecology; Palynology;

**1. Introduction**

The Last Glacial period (~112 ka to 11.8 ka) in Mediterranean Europe is featured by a marked climatic variability (Sanchez-Goñi et al., 2002), with extremes approaching, on one side, the dry and cold conditions of the Last Glacial Maximum and, on the other, the warm and humid conditions of a typical interglacial period (Allen et al., 2000). In particular, the period corresponding to Marine Isotope Stage 3 (MIS 3), spanning between ~58 ka and 28 ka (Railsback et al., 2015), can be seen as a paradigm of this variability, being the most unstable temporal interval of the Last Glacial period, punctuated by abrupt and short climate changes at sub-millennial to decennial-scales, i.e., not directly related to millennial-scale orbital changes considered to be the main drivers of the longer term glacial-interglacial variability (Moreno et al., 2014). Throughout the high- to mid-latitude regions of the northern hemisphere, ice, marine and terrestrial multi-proxy palaeoclimatic and palaeoenvironmental archives record the extreme climatic instability of MIS 3. They show (*i*) marked atmospheric temperature oscillations, e.g., the so-called Dansgaard-Oeschger (D-O) events in Greenland ice cores (Dansgaard et al., 1993), (*ii*) marine sea surface temperature changes and ice rafting events, i.e., Heinrich events (Birner et al., 2016; Broecker, 1994; Hemming, 2004), (*iii*) abrupt changes in rainfall regime, as revealed by speleothem (Luetscher et al., 2015) and pollen (Follieri et al., 1998; Allen et al., 2000; Margari et al., 2010) records, and other environmental changes (Moreno et al., 2014). Although a teleconnection between the climatic variability of the polar and mid-latitude regions of the boreal hemisphere has been recognised (Kandiano et al., 2014; Regattieri et al., 2015), a close and precise comparison of MIS 3 temporal series of different regions (e.g. North Atlantic and central Mediterranean) is sometimes limited by the inherent uncertainty in comparing records based on different dating methods and age models, the resolution of which is often lower than the frequency of the MIS 3 climatic variability itself. Interpretation is further complicated by possible, often undeterminable, lags in the responses of different environmental systems and proxies to the climatic changes.

The Last glacial climate has been reconstructed in central and southern Italy using long lacustrine pollen records from the volcanic lakes of Basilicata and Latium. The records are, from North to South: Lagaccione (Magri, 1999); Lago di Vico (Magri & Sadori, 1999); Stracciacappa (Giardini, 2007); Valle di Castiglione (Follieri et al., 1988; Follieri et al., 1989) and Lago Grande di Monticchio (Allen et al., 2000; Watts et al., 2000). A pollen record of the Last Glacial age is also available from an intermontane valley of Abruzzi (Chiarini et al., 2007).

In all of these records montane, mesophilous and Mediterranean tree pollen oscillations characterise that part of the glacial period corresponding to MIS 3. Follieri et al. (1995; 1998), comparing four lacustrine records of Latium, found seven main arboreal fluctuations, probably strictly related to North Atlantic events of MIS 3. An attempt to compare these slight tree expansions and contractions, mainly due to variations in humidity, to changes found in ice and marine cores of high boreal hemisphere latitudes, was carried out for the pollen record of Lago Grande di Monticchio (southern Italy) (Allen et al., 2000; Watts et al., 2000). It is worth highlighting that even between the relatively close sites of Latium it is possible to denote a discrepancy in the records, possibly due to different, local environmental conditions.

The central and southern Italian long lacustrine records offer a good general framework for palaeoenvironmental reconstruction carried out in specific sites. However, we have to consider that sites far from the above mentioned lakes could have quite different geographic and climatic features and could provide improved insights into regional variability. Analysis of local sources such as coprolites can be decisive in regions in which there are no available lacustrine archives for the period under investigation.

In this paper we present the results of pollen analysis of hyena coprolites from the karst caves of the Latium coast, central Italy, and the Apulia hinterland, southern Italy (Fig. 1) with the aim of exploring the temporally and regionally highly variable MIS 3 climate, and adding new information on the palaeoenvironmental mosaic,. The present study also has the methodological purpose of testing the potential of pollen from hyena coprolites to provide local environmental reconstructions – i.e., within a radius of 50 km from the hyena dens, in contrast to the more typical use of pollen data in interpretations of larger regional areas (Scott 1987; Yll et al., 2006) – and thus as an additional source of palaeoenvironmental data to complement the longer and more continuous pollen records from lacustrine successions.

The potential contribution of fossil faeces to palaeoecological information has been known for a long time (Bryant Jr. & Holloway, 1983; Leroi-Gourhan, 1966; Martin et al., 1961; Moe, 1983), but is nevertheless rarely exploited or treated as of marginal usefulness.

Well preserved coprolites, due to their hardness and durability (Bearder, 1977; Larkin et al., 2000), can insulate organic matter, including pollen, preventing oxidation of the granules (Scott et al., 2003). Therefore, pollen contained in coprolites is often well preserved and closely identifiable with the associated sediments (Carrion et al., 2001; Scott, 1987; Scott et al., 2003). All these reasons make the coprolites a valuable resource, especially for those contexts in which typical pollen traps such as lakes and swamps do not occur (González-Sampériz et al., 2003; Scott, 2000).

Pollen analysis has been carried out elsewhere on coprolites of extinct giant birds (Wood et al., 2008) and herbivores (Carrion et al., 1999; Carrion et al. 2000; Yll Aguirre et al., 2001). The amount of pollen in coprolites is extremely variable and may be affected by a number of factors, such as the age of the samples, seasonality of deposition, sediment conditions, gastric action, diet and behaviour of carnivores and their prey and other differential preservation processes. However, although pollen concentration in herbivore coprolites is usually higher (González-Sampériz et al., 2003), palaeoecological analyses of carnivore coprolites, such as hyena, have been successfully achieved on samples with low pollen concentration (Argant & Dimitrijevic, 2007; Carrion et al., 2001; Scott et al., 2003; Yll et al., 2006). The reliability of the pollen data from hyena coprolites and vegetation reconstructions based on them is also confirmed by comparisons with pollen spectra from other archives (Argant & Dimitrijevic, 2007; Carrion et al., 2001; González-Sampériz et al., 2003; Scott et al., 2003; Yll et al., 2006).

**2. Study sites**

2.1 Present day setting

The two selected sites are Cisterna di Latina (Latium, central Italy) and to Ceglie Messapica (Apulia, southern Italy) (Fig. 1).

The current climate of central and southern Italy consists of warm summers and wet conditions in autumn and winter. The climate is typically Mediterranean along the coast while temperature and rainfall vary greatly in the hills and mountains of the Apennines, where the sub-Alpine climate provides cold and snowy winters and cool summers. Cisterna di Latina is situated in the mesomediterranean thermotype class, with a high average annual temperature and long warm, dry summers. Winters are never harsh and temperatures rarely reach 0 °C. The position of the small plain between the sea and the mountains makes the botanical framework extremely varied and complex, causing sensitive changes of vegetation within a few kilometres. The rich vegetation of the plain is typically characterised by oak plain forest where mesophilous species (*Quercus cerris, Q. frainetto, Carpinus betulus*) and thermophilic (*Fraxinus ornus, Quercus ilex*) coexist (Barbieri et al., 1999; Blasi et al., 1994).

Cava Muracci (Cisterna di Latina) is located close to the foot of the Lepini Mountains, which is a very interesting area from both a floristic and a vegetation point of view (Guarrera, 1996; Rosati et al., 2006). The arboreal vegetation of the Lepini Mountains is mainly constituted, at lower altitude, by evergreen elements, among which holm oak (*Quercus ilex*) is the most representative. At higher elevations evergreen elements are replaced by deciduous trees, mainly the semideciduous Turkey oak (*Quercus cerris*), and other mesophilous elements, like the European hop hornbeam (*Ostrya carpinifolia*) and the Bosnian maple (*Acer obtusatum*). Beech (*Fagus sylvatica*), yew (*Taxus baccata*) and holly (*Ilex aquifolium*) form the forest above 1200 m. On the slopes facing the sea, the garrigue, replacing abandoned olive orchards, is often colonized by steppe elements like the common thatching grass (*Hyparrhenia hirta*) and, in particular, by the large Mauritanian grass, *Ampelodesmos mauritanicus* (Pignatti et al., 1961; Di Pietro & Blasi, 2002). At lower altitude the natural vegetation is often replaced by groves of olive (*Olea europaea*), and at higher altitudes by chestnut (*Castanea sativa*). Remnants of natural forest vegetation are very rare in the plain area and are restricted to S. Biagio wood located near Cisterna di Latina. This very small wood is therefore an important legacy of the past lowland vegetation in this area.

The climatic zone around Tana delle Iene (Ceglie Messapica) is characterised by isotherms of January and February between 14 and 16 °C. The forest vegetation is characterised by Macedonian oak (*Quercus trojana*), often constituting mixed formations together with downy oak (*Quercus pubescens*). Macedonian oak is widespread in the Balkans. In Italy it is exclusively present in the South-eastern Murge territories between the regions of Apulia and Basilicata, in which it has the western limit of its distribution. This kind of vegetation grows on limestone substrates in the lower mesomediterranean bioclimatic belt (Biondi et al., 2004; Biondi et al., 2010). Macedonian and downy oaks are generally accompanied by Mediterranean sclerophyllous elements like *Phillyrea latifolia, Pistacia lentiscus, Rhamnus alaternus*, *Arbutus unedo*, *Cistus salvifolius*, but also by mesophylous deciduous elements such as *Fraxinus ornus*, *Prunus spinosa*, *Vitex agnus-castus*, *Pyrus amygdaliformis*, *Paliurus spina-christi* (Macchia et al., 2000). Macedonian oak woods are subjected to heavy grazing causing the spread of common species as *Asphodelus microcarpus*, *Asphodeline lutea* and *Charybdis pancration*. In these woods, however, it is possible to find some interesting species, such as apulian arum (*Arum apulum*), an endemic species of the Murge territory in central Apulia (Conti et al., 1997; Wagensommer et al., 2013). Holm oak woods (*Quercus ilex*) are also frequent.

2.2 Archaeological and stratigraphic setting

2.2.1. Cava Muracci – Cisterna di Latina

An extensive bench of Quaternary travertine is present in the North-East corner of the Pontine Plain, between the Colli Albani and Monti Lepini. At the centre of this area, in the territory of Cisterna di Latina (Latina, Latium), is the travertine quarry “Cava Muracci” (hereinafter CM) (41°35'54"N 12°51'25"E) where important palaeontological and archaeological discoveries have been documented since the middle of the last century (Segre & Ascenzi, 1956; Angle & Germano, 2003).

In 2012, new mining activities accidentally brought to light faunal remains, launching a series of interdisciplinary investigations which are still underway (Gatta & Rolfo, 2015). These surveys revealed seven accumulation areas along the entire perimeter of the quarry (Fig. 2) with >2000 remains of mammals, >100 coprolites belonging to cave hyena (*Crocuta crocuta spelaea*) and rare lithic artefacts. The morphology of the collection areas varies from small karst pockets to wider caves (Gatta & Rolfo, 2015). The widespread presence of gnaw marks and coprolites allowed three of the areas analysed to be interpreted as hyena dens (Area 3, 4 and 7), in which the selection operated by the carnivore determined the remains found (Gatta & Rolfo, 2015). The remaining deposits are interpreted as pockets filled with debris and fossils accumulated by water flow events, probably during the frequent flooding of the nearby river Treppia (Gatta & Rolfo, 2015). The highest concentration of finds was detected at the base of the travertine cave called “Area 3”, where a careful stratigraphic investigation has been carried out and one major archaeological layer (SU 11) revealed (Fig. 2).

A process of fossilisation by mineralisation has been triggered by the closed context of the cave and the calcium carbonate-rich travertine characterises coprolites and fossils, which are in a very good state of preservation (Gatta & Rolfo, 2015). Taxonomic and taphonomic analysis is still ongoing, but preliminary data from this area has identified at least eleven taxa including *Equus ferus* (wild horse)*, Stephanorhinus hemitoechus* (narrow-nosed rhinoceros)*, Bos primigenius* (auroch)*, Capreolus capreolus* (roe deer)*, Cervus elaphus* (red deer)*, Dama dama* (fallow deer)*, Sus scrofa* (wild boar)*, Crocuta crocuta spelaea* (cave hyena)*, Canis lupus* (wolf)*, Meles meles* (badger)*, Lepus sp.* (hare) (Gatta & Rolfo, 2015).

2.2.2. Tana delle Iene – Ceglie Messapica

Tana delle Iene (hereinafter TI) (40°38'25"N 17°30'58"E) is a karst cave in the limestone formation of Altamura in Apulia (Ciaranfi et al., 1988) discovered accidentally during building works. The cave consists of two chambers with a total area of about 110 m2, appearing to be largely damaged by human intervention.

The stratigraphic excavation of 48 m2 revealed eleven stratigraphic units and two main archaeological/palaeontological layers (US 5 and US 8) buried by pyroclastic deposits (unit US1, Giaccio and Coppola, 2000; Conti et al., 2012), which permitted the preservation of the finds, including bones, lithic industries and a large number of coprolites (Fig. 3). The unit US8, from which the coprolites analysed in this paper were recovered, is a dm-thick horizon of hyena occupation that yielded more than 4300 bones accumulated by the carnivores (Giaccio and Coppola, 2000). The taxonomic analysis led to the identification of a large number of mammals, including *Microtus arvalis* (common vole)*, Terricola savii* (Savi’s pine vole), *Apodemus sylvaticus* (wood mouse), *Lepus* sp. (hare), *Vulpes vulpes* (fox), *Canis lupus* (wolf)*, Crocuta crocuta spelaea* (cave hyena), *Felis silvestris* (wildcat), *Equus ferus* (wild horse)*, Equus hydruntinus* (European ass), *Sus scrofa* (boar), *Capreolus capreolus* (roe deer), *Cervus elaphus* (red deer), *Dama dama* (fallow deer) and *Bos primigenius* (auroch)(Conti et al., 2012). The taphonomic study showed a lack of cut marks but most of the remains have traces of carnivore gnawing (Conti et al., 2012). The overlying US5 revealed rare traces of human activity, including a fireplace with burnt remains that yielded an age of 19,880±160 14C yr BP (Conti et al., 2012). Giaccio et al. (2008) correlated the uppermost pyroclastic unit US1 to the Codola eruption from Vesuvius, dated to ~33 ka (Fig. 3), based on tephrochronological analyses, which is consistent with the attribution of the underlining US8 to the early-mid MIS 3 (60–40 ka; Giaccio and Coppola, 2000).

**3. Materials and methods**

3.1. Chronology

In order to define the chronological framework, we performed radiocarbon dating of bones and coprolites from layer SU11 and tephrochronological analyses of the volcanic layer SU13 of CM (Fig. 2).

Radiocarbon dating of two types of material was undertaken. Three bone fragments from CM were submitted to the Centro di Datazione e Diagnostica (CEDAD) of the Università del Salento (Italy) and successfully analysed. Another set of 3 bones were sent to Beta Analytic (USA) but resulted in no collagen. A set of 2 bones and 2 coprolites was sent to the ETH Zürich laboratory (Switzerland) for radiocarbon dating by means of accelerator mass spectrometry (AMS). Poor preservation of bones prevented use of Ultra Filtration as a preparation method. An alternative method of treatment with base prior to gelatinization (Hajdas et al., 2009) resulted in gelatine for the hyena bone that was then combusted and graphitized for 14C AMS analysis. This sample showed an acceptable C/N ratio of 3.15 but a very low C content of 2%. Coprolite samples were treated with acid (Hajdas, 2008) and organic carbon was analysed for 14C content.

No new radiocarbon dating has been performed for the hyena occupation layer (SU 8) at TI.

Due to the strong weathering of the juvenile clasts, major-element composition was determined on melt inclusions in clinopyroxene crystals from the tephra SU13, occurring below the palaeontological horizon SU13 (Fig. 2). Elemental analyses were carried out at the Institute of Environmental Geology and Geoengineering of the Italian National Research Council (IGAG-CNR) (Rome, Italy) using a Cameca SX50 electron microprobe analyser equipped with a five-wavelength dispersive spectrometer, with operating conditions as described in Giaccio et al. (2013). Full analytical data for the individual measurements are given in Table 1.

3.2. Description of the coprolites

The identification of coprolites and their attribution to cave hyena was made according to their morphology and size. Although showing various degrees of preservation, the coprolites from both sites appear similar. The coprolites of CM and TI can be classified into seven shapes according to the morphological types proposed by Diedrich (2012). The colour varies from pale yellow to light brown on the external surface with yellow-white shades internally. The diameter of the pellets varies between 15–85 mm, with a weight between a few grams and over two hundred grams. Macroscopic analysis showed the presence of medium to small fragments of partially digested bones typical of cave hyena coprolites (Horwitz & Goldbergb, 1989).

Surfaces of almost all the samples were quite solid and compact with no cracks and with an internal structure which is porous and granular-like because of the shrinking caused by dehydration which started immediately after the deposition of faeces. The preservation of coprolites seems to be significantly related to their components and to the depositional environment. The phosphatic faeces of hyena, in particular, are more likely to be preserved due to the high number of ingested bones, which makes them hard and compact allowing easier fossilisation (Larkin et al., 2000). This model has also been verified by comparisons with modern species of dogs (Diedrich 2012, p. 372). Furthermore, the high calcium carbonate values of both karst caves have triggered a strong mineralisation of organic material, allowing a solid fossilisation.

During the excavations, the majority of coprolites were found as isolated elements, albeit close to each other. However, longer segments composed of several pellets have been found, confirming that fossilisation must have occurred fairly quickly with minimal or no post-depositional disturbances.

3.3. Pollen extraction from coprolites

For CM a “pilot study” was carried out to assess the potential of coprolites for plant analysis in the pollen-sterile laboratory of University of York. Ten coprolites, selected among those recovered in the hyena level (layer 11) of Area 3 at CM, were processed. We estimated that about 10% was a representative percentage of the entire collection. The choice of the samples was determined according to their size, with a preference for those with weights between 33–196 g, in order to ensure that some material is left over for future analysis. We avoided specimens with eroded surface or cracks, so as to reduce the risk of penetration of modern contaminants. The subsampling procedure followed a generic protocol for multi-proxy analysis (Wood & Wilmshurst, 2016).

Following a control of the external surface of each sample to ensure the total absence of modern contamination, we proceeded to the extraction of the matrix. This was carried out in four phases: (i) washing and removal of the external surface (2 mm) of the samples; (ii) cutting the samples into two halves; (iii) sampling and crumbling of 5 g of coprolites from the centre of each coprolite, where no trace of penetration of external soil or contamination was visible (Fig. 4); (iv) dissolving samples with HCl at 20% for 48 h and mounting on slides. The slides were fully scanned revealing the presence of a wide range of biological remains (e.g. pollen, fibres, fungal spores, phytoliths). Among these the most frequent were pollen grains, confirming the validity for further analysis. A more aggressive processing was then implemented in the subsequent pollen analysis, in order to retrieve and concentrate such plant remains.

A total of 3 coprolites from TI and 16 from CM have been chemically processed in the pollen-sterile laboratory of Sapienza University. The same cleaning and subsampling method described above has been applied for the pre-processing of the samples. A known amount of dry sediment (4-5 g) was taken from the inside of each coprolite. The treatment was carried out following a standard procedure: chemical removal of calcium carbonate (cold HCI fuming 37%), silica (cold HF 40% for 12 h) and humic acids (boiling in NaOH 10%), and mounting in glycerine. A known amount of *Lycopodium* spores was added to each sample to calculate the pollen concentration (Stockmarr, 1971).

**4. Results**

4.1. Radiocarbon dating and tephrochronology

Four calibrated 14C dating from bones in layer SU11 of the “Area 3” of CM, yielded ages ranging between 34810 cal BP (Hyena bone R. 632; ETH-66210) and 44054 cal BP (LTL15758A) (Table 2).

Two coprolites yielded 16,141±42 14C BP (19640-19292 cal BP) and 18,313±51 14C BP (22378-21952 cal BP), which are substantially younger than the ages obtained from the bone fragments. Diedrich (2012, p. 372) has shown a similar discrepancy between coprolites and bone. Indeed, the organic carbon content of the coprolites is very low, i.e., approximately 1%, making this material potentially vulnerable to contamination even with a small quantity of contaminants. In view of the faunal taxa listed above and the broad disagreement with the radiocarbon dates from bones (Table 2), we are inclined to consider the dates from coprolites as abnormally young, and do not consider them further.

Chemical fingerprinting of the tephra SU13 from CM has also been achieved. The layer SU13 is a dm-thick, partially reworked layer of coarse leucite-bearing greyish scoria with abundant, up to mm-sized clinopyroxene, leucite and phlogopite crystals. Melt inclusions in clinopyroxene crystals from the layer SU13 are foiditic in composition (Fig. 5; Tab. 1), which is the typical composition of the glass from the Colli Albani pyroclasts (Giaccio et al., 2013).

Based on the available chronological constraints, layer SU13 can be correlated to the most recent activity of the Colli Albani caldera documented at the Albano maar by seven explosive events (Freda et al., 2006; Giaccio et al., 2007, 2009; De Benedetti et al., 2008; Sottili et al., 2009; Gaeta et al., 2011; Cross et al., 2014) clustered in two groups of eruptions dated between ~70–69 ka or ~73–71 ka (Albano 1 to 3) and ~40–36 ka (Albano 4 to 7) (Freda et al., 2006; Giaccio et al., 2009). Unfortunately, the recognition of the individual unit or cluster of units dated to 70 ka and 40-36 ka is currently limited by the poor and incomplete chemical dataset available for the composition of the melt inclusions in clinopyroxene from Albano units. Therefore, at present, an age estimation better than 36–70 ka for layer SU13 cannot be supported.

4.2. Pollen from coprolites

All 19 coprolite pollen residues have been microscopically analysed.

Six out of sixteen coprolites from CM turned out too poor in pollen; therefore only 10 coprolites were reliable for palaeoecological considerations. Pollen concentration values of the analysed samples from CM vary between 650 and 2200 pollen grains/g and the number of pollen taxa is 27, with 15 herbaceous taxa and two aquatic ones (Fig. 6a). The state of preservation is rather poor, with very high percentages (from 11 to 24%) of indeterminable pollen grains.

Poaceae (4–34%), Amaranthaceae (1–52%) and *Artemisia* (4–39%) and Asteroideae (0–21%) are the main taxa. Other taxa reach high percentages in particular samples, e.g. the freshwater plant *Typha*, 70%, in sample 4, and Cichorioideae, 38%, in sample 2. The first is a clear indication of the presence of water pools/low energy streams, and the second is an indication of grazing. Cichorioideae belong to Asteraceae (sunflower) family and their growth is favoured by nitrophilous elements (Florenzano et al., 2015).

Deciduous elements like *Quercus* deciduous, *Q. cerris*/*suber*, *Acer*, *Ulmus*, *Fraxinus* cf. *excelsior* and *F.* cf. *ornus* are sporadically present in the samples, while evergreen ones like *Q. ilex* type and *Juniperus* are more abundant. *Plantago lanceolata* pollen type includes, in addition to the anthropogenic indicator *P. lanceolata*, also *P. argentea*, *P. bellardii* and *P. lagopus*.

Mesophilous trees are always present and show significant values in sample 8 (>13 %).

The three coprolites from TI show pollen concentration values between 600 and 2300 pollen grains/g. The total number of pollen taxa is 30, with 19 herbaceous taxa (Fig. 6b). The state of preservation is rather poor, with indeterminate pollen grains around 5%.

Cichorioideae are the most abundant taxon (24–49%), accompanied by Poaceae (9–23%) and Amaranthaceae (3–12%). The high percentage of Cichorioideae detected in coprolite 2 (49%), similar to that found at CM, could be linked to the more resistant pollen exine of this taxon (Bottema, 1992) but also to grazing activity (Florenzano et al., 2015). Arboreal plant pollen is rather scarce and mainly constituted by *Pinus*. Many mesophilous and thermophilous trees are present, but with very low percentages (always less than 5%).

**5. Discussion**

5.1. Source(s) of pollen

In interpreting pollen from coprolites we have to bear in mind that the results are notably unique, since, rather than representing only the pollen rain, they constitute an indication of pollen contained in the food and drink of both prey and predator.

Quantity and variety of pollen grains is indeed influenced by several factors. It is believed that pollen can be mainly incorporated in hyena coprolites in three different ways:

* the ingestion of a prey and the related content of its digestive system plus the airborne pollen deposited on the victim itself;
* the direct ingestion of pollen by the hyena with food and water;
* the post-depositional contamination of the samples in contact with external agents such as soil and/or water flow.

The coprolite pollen record is usually a combination of all these (Scott et al., 2003).

External cleaning of coprolites with removal of the outer, possibly contaminated portion, rules out the possibility of recording post depositional events. Post-depositional air contamination of samples occurs quasi-simultaneously with the deposition of faeces, and thus could reflect vegetation contemporaneous with the hyena life-span. But circulation of water containing pollen could take place at a later stage and therefore offer a distorted picture of the vegetation.

In the first two factors, we have a combination of air-diffused/water-diffused pollen (pollen in drink water) and of grazed vegetation pollen.

Direct ingestion of pollen occurs through the consumption of food and water (Argant & Dimitrijevic, 2007; Carrion et al., 2001; Scott et al., 2003). The hyena in particular has an omnivorous diet including vegetable matter (Argant & Dimitrijevic, 2007; Mills, 1989; Skinner, 1976). However in this type of intake, the consumption of large herbivores, the stomach of which contains large amounts of pollen, plays a decisive role (Carrion et al., 2000). The pollen spectra therefore do not faithfully reflect the actual vegetation of an area, but the diet preferences of herbivores (Scott, 1987). Previous studies have revealed, however, that although grass and herb taxa largely prevail in the food diet of herbivore prey, coprolite and sediment records do not show differences in the general composition of vegetation (Argant, 2004; Argant & Dimitrijevic, 2007; Carrion et al., 2001; Scott et al., 2003).

Modern studies provide us with a basis for understanding the behaviour of Pleistocene hyena, and have revealed that spotted hyenas can hunt up to 50 km from their den (Mills, 1989), although they usually remain within 15 km (Scott, 1987) or less (Argant, 2004; Argant & Dimitrijevic, 2007). Pollen from coprolites provides invaluable data therefore on the near vicinity of the investigated sites and depicts a local vegetation picture in comparison with regional reconstructions provided by conventional pollen trap records such as lakes (Argant & Dimitrijevic, 2007; Djamali et al., 2011).

5.2 Reconstruction of past vegetation

*5.2.1 Cisterna di Latina – Cava Muracci*

The site of Cisterna di Latina is chronologically attributed to a period of the Late Pleistocene between 35 and 44 ka approximately (Table 2). Although it was not possible to achieve direct dating of coprolites, they can be considered as broadly contemporaneous with the dated bones, indicating hyena activity in the cave over the 35–44 ka time interval. This interval is characterised by extreme variability. It comprises parts of the last two long-term-cooling cyclesor Bond cycles (Bond et al., 1992; Bond & Lotti, 1995) of MIS 3 period, which occurred between ~48 ka and 30 ka, and include eight D-O cycles (NGRIP Members, 2004). All the pollen spectra indicate open environments. Poaceae, Amaranthaceae and *Artemisia* are typical of the steppe/grassland formations which occurred during glacial periods. *Artemisia*, the typical steppe plant indicating strong aridity, is in fact accompanied by Amaranthaceae, steppe plants demanding more water, and Poaceae, typical plants of grasslands. Steppe formations are also indicated by *Plantago* pollen (Reille, 1992). The pollen assemblage of CM also suggests that there was a certain degree of humidity. This is also clear from mesophilous/thermophilous tree curves, which present values up to 10%, and *Typha,* which suggests the presence of inland water pools and swamps.

*Crocuta crocuta spelaea* and *Canis lupus* are widely distributed species, surviving in a wide range of climates and landscapes, and therefore contribute little towards environmental reconstruction (Churchill, 2014; Conti et al., 2012). Nevertheless, the herbivorous prey can provide a narrower frame. *Bos primigenius* inhabited wooded hill areas rich with glades in a temperate climate (Pandolfi et al., 2011; Van Vuure, 2002). The presence of *Equus ferus* indicates large areas of grassland steppe-plain and continental climate. *Stephanorhinus hemitoechus* preferred instead a mixture of the previously described environments, with temperate open habitats such as prairie or open wooded areas (Fortelius, 1982; Guérin, 1980). The presence of cervids attests open forests, and the simultaneous presence of *Cervus elaphus* and *Dama dama* indicates a temperate climate. Finally, *Sus scrofa* indicates the presence of lacustrine and swampy areas (Rustioni et al., 2003).

The resulting environmental reconstruction seems to reflect either the marked climatic variability of the 35–44 ka interval or the morphology of the area surrounding the site which, as at present, varies considerably within a few miles. Pollen and fauna associations are in fact consistent with either diachronic or synchronic variability of the environment, related, respectively either to the rapid MIS 3 climatic oscillations, or both to the coexistence of a mixed environment with large areas of steppe or prairie alternating with woodland areas characterised by Mediterranean and mesophilous plant thickets, especially in the hilly area. Swampy areas were present along either the sea coast or water courses. The climate would appear to have been cool and arid, and fauna could have found suitable habitats in the steppe/grasslands and open forests typical of the minor warm and humid oscillations of the Last Glacial. The presence of arboreal angiosperms during the last Pleniglacial has already been reported in the past in lacustrine sequences in central (Follieri et al., 1998; Chiarini et al., 2007) and southern (Watts et al., 1996) Italy and is related to climatic changes evidenced by Dansgaard-Oeschger events in Greenland ice records (Dansgaard et al., 1993) and Heinrich events of marine sea surface temperature changes (Birner et al., 2016; Broecker, 1994; Hemming, 2004). However, as discontinuous records that are not stratigraphically ordered, neither the coprolite pollen nor the faunal assemblages are suitable for assembling a high-resolution temporal series, thus making it impossible to discriminate between diachronic climatic-driven variability versus synchronic geomorphological-controlled variability.

*5.2.2 Tana delle Iene*

The hyena occupation layer (SU 8) and coprolites of TI can be dated between 60 and 40 ka (Giaccio & Coppola, 2000).

For the first time pollen from coprolites has yielded palynological information of the Apulia region for this time-span (Petrucci et al., 2005). Poaceae, Amaranthaceae and *Artemisia* indicate the presence of steppe/grassland formations, Cichorioideae and low percentages of many mesophilous trees suggest a temperate-dry environment. These seem to indicate an open lowland environment with sporadic mesophilous and thermophilous trees, typical of the glacial periods. The presence of *Fagus* pollen is noteworthy because beech is a low pollen producer. Nowadays its presence is limited to the *Foresta Umbra* of the Gargano Peninsula in Apulia.

The faunal assemblage from TI bears witness to various environments, again probably related to either the morphology of the surrounding area or the climatic variability over the time of hyena occupation, which, although poorly constrained, conceivably spans several millennia.

*Bos primigenius*, cervids and wild cats indicate the presence of open forested areas and extensive high wooded hills (Conti et al., 2012). Equines, hare, bustard and arvicolinae suggest instead lowland steppe-grassland areas. Remains of *Sus scrofa* suggest the presence of marshy areas, likely near the Adriatic coast, at present 10 km from TI (Conti et al., 2012). Amaranthaceae pollen could in fact either come from steppe plants or from salty plants typical of salty lagoons. The carnivores from TI are also widely distributed over different types of environment and therefore of little help.

Summarising, the fossil fauna and the pollen from coprolites suggests a steppe-grassland environment most likely with swampy and saltwater areas. The climate was probably cold and arid, but with a certain degree of humidity as indicated by the coexistence of species such as *Microtus arvalis* and *Dama dama* (Conti et al., 2012) and of plant taxa typical of steppe/grasslands and forests. In view of this evidence and the available date, this deposit can be referred to one or more very slight temperate-cool oscillation of MIS 3.

**6. Conclusion**

Pollen and fauna from the two investigated sites yield similar evidence for variable environments compatible with previous regional reconstructions of MIS 3. Pollen shows that steppe/grassland vegetation was widespread in central and southern Italy during this unstable temporal interval of the Last Glacial period. This environmental information is generally supported by faunal data. The mammal species are relatively common in fossil deposits of the Italian Late Pleistocene. The presence of *Stephanorhinus hemitoechus* at Cisterna di Latina, is one of the most recently dated examples from the Italian Peninsula (Pandolfi et al., 2016), and suggests that this area was a refuge for this species. The large quantity of *Typha* pollen found in one coprolite indicates the presence of freshwater ponds.

Pollen inside coprolites was directly ingested by the carnivores and therefore we have to consider it coeval with the deposition of faeces. This implies three important statements about pollen preserved in coprolites:

(i) given that the outer, possibly “polluted” part of the coprolite is removed, the pollen has to be considered an indication of the vegetation present in the area immediately surrounding the den, within the daily range of hyena activity;

(ii) the pollen represents a single event, or a palimpsest of events, representing the feeding activity of the hyena on a given day or over a few days at most and reflects the environments visited on a daily basis. Every coprolite corresponds therefore to a very short period of time, enough to indicate the season when it was produced (Argant, 1990; Argant, 2004; Tomescu, 2006), while seasons in pollen from lake sediments cannot be detected unless the sediments are annually laminated;

(iii) since the pollen reflects landscapes frequented by the hyena and its prey, each pollen spectrum reflects the existence of “local environments” in the vicinity of the den. With pollen rain represented in lake sediments, it is not possible to disentangle local and regional vegetation.

The results obtained here clearly indicate the (co?)existence of different environments, and the reconstruction of a patchy landscape. This study shows how pollen analyses from hyena faeces, combined with faunal and chronological investigations, represents a powerful method for obtaining well-defined local environmental reconstructions that would otherwise be unavailable. We, nevertheless, have to recognise also a limit inherent in the pollen record from coprolites, i.e., its unsuitability for generating temporally well-ordered and high-resolved proxy series, which remains a prerogative of long sedimentary successions. In spite of this limit, the results of this study shows that the balance among strengths and weaknesses of this approach is positive, highlighting the value of this hitherto poorly exploited resource for understanding in more detail the extraordinarily variable MIS 3 landscapes of the central Mediterranean.

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**Figure and Table captions**

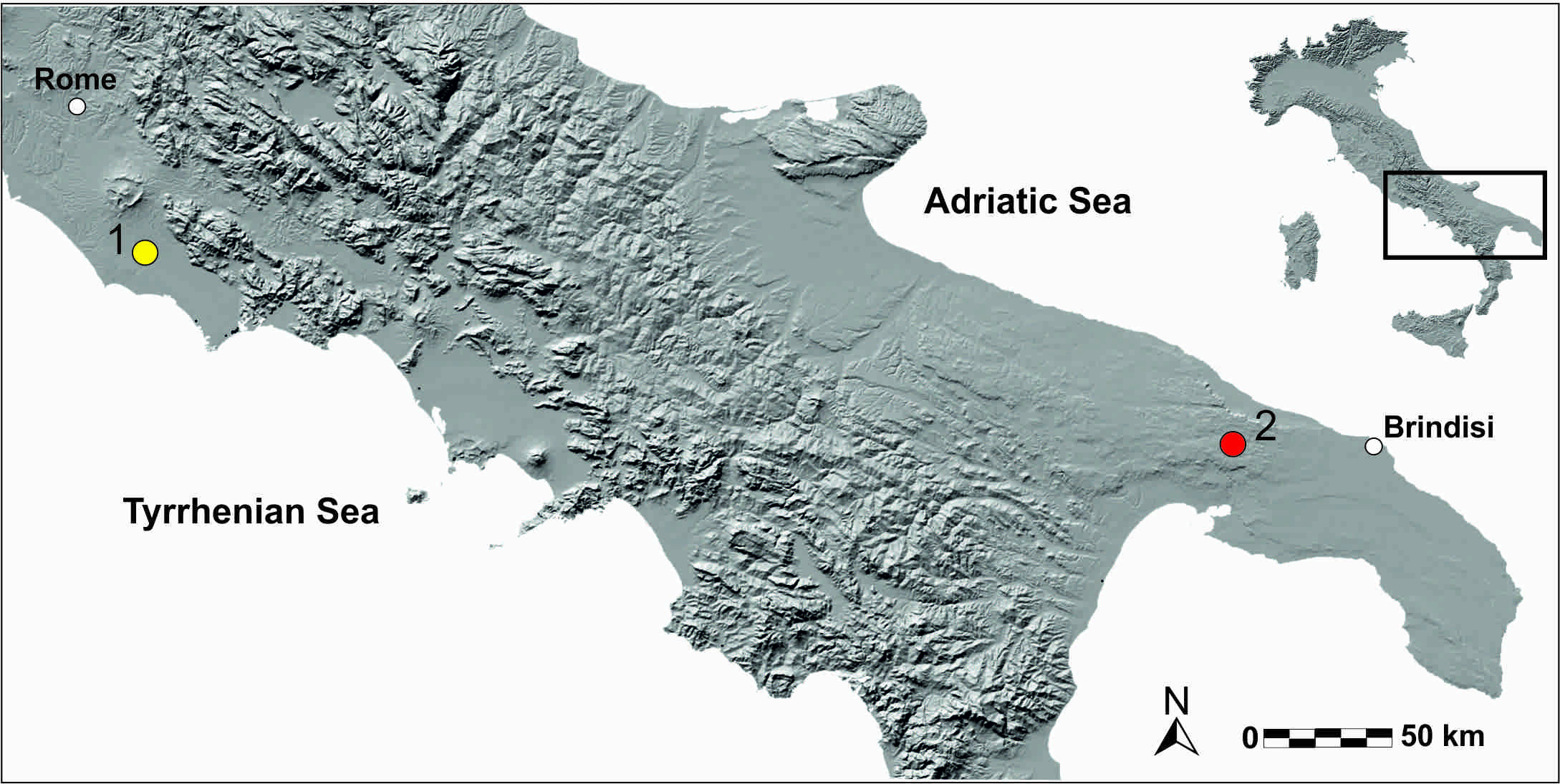


Fig. 1. Location of the investigated successions. 1- Cava Muracci Cave, Cisterna di Latina; 2 - Tana delle Iene site, Ceglie Messapica.



Fig. 2. Location of collection areas within the quarry.   
Stratigraphy of Area 3 from Cava Muracci (from Gatta and Rolfo, 2015). SU 7 – Modern surface composed of soil and gravel; SU 8 – Upper edge of the cave in travertine; SU 11 – Brown occupation layer with archaeological remains; SU 12 – Reddish brown layer with volcanic products and occasional finds of stone artefacts; SU 13 – Sterile layer composed of volcanic tephra; SU 14 –Reddish layer with sporadic lithic and faunal remains.

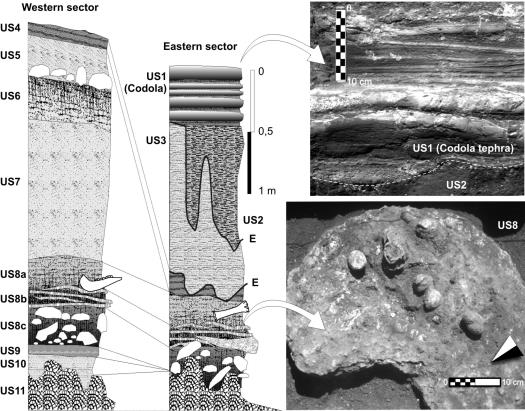


Fig. 3. Stratigraphy of Tana delle Iene (from Giaccio and Coppola, 2000). US1 – Grey reworked tephra layer correlated to Codola eruption (~33 ka; Giaccio et al., 2008); US2 – Reddish silty-clay; US3 – Reddish-yellowish sandy-silt containg volcanic materials; US4 – Yellowish-greenish tephra layer; US5 – Reddish silty-clay and gravels; US6-US7 – Reddish silty-clay; US8 – Horizon of hyena occupation; US9 – Weathered tephra layer; US10 – Reddish silty-clay; US11 – Stalagmite; E – erosion.

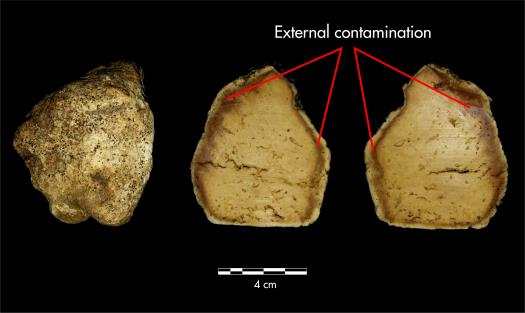


Fig. 4. A dissected coprolite. It is possible to note the penetration of external contamination in the two halves.

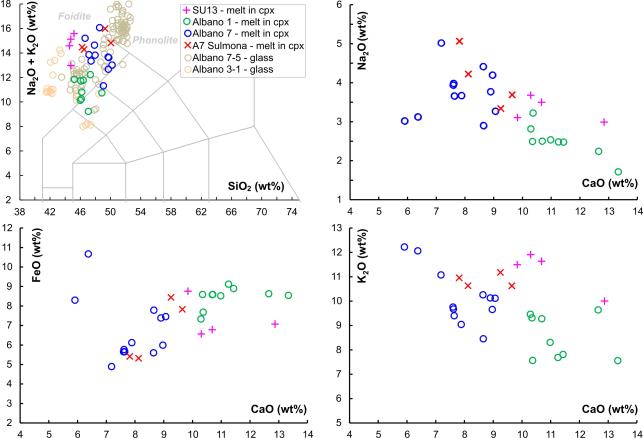


Fig. 5. Total alkali versus silica classification diagram and representative bi-plots for the melt inclusions in clinopyroxene from tephra SU13 compared with both melt inclusions in clinopyroxene (cpx) and glass in matrix from proximal or distal Albano units. Data source: proximal Albano 7 and Albano 1-3 cpx-melt inclusions, Freda et al. (2006); distal Albano 7 (Sulmona) cpx-melt inclusions, Galli et al. (2015); glass from proximal Albano 7-5: Giaccio et al. (2007); Cross et al. (2014).

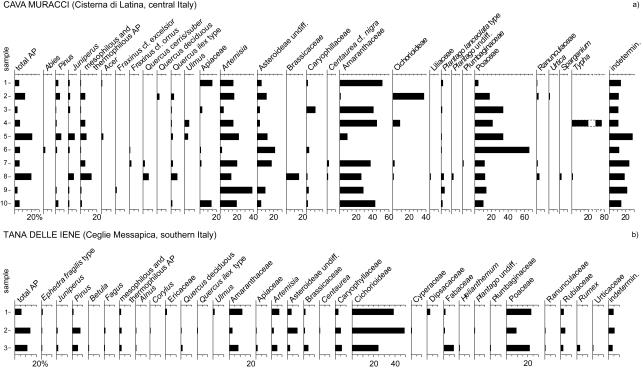


Fig. 6. Pollen diagrams. a) Cava Muracci (Cisterna di Latina, central Italy Percentage pollen diagram of coprolites.. AP=pollen of arboreal plants, mesophilous and thermophilous AP= all AP minus *Abies*, *Pinus*, *Juniperus*; b) Tana delle Iene (Ceglie Messapica, southern Italy). Percentage pollen diagram of coprolites.,. AP=pollen of arboreal plants, mesophilous and thermophilous AP= all AP minus *Ephedra* *fragilis* type, *Pinus*, *Juniperus*. *Betula*, *Fagus*.

Table 1. Major-element compositions (normalized to 100 wt%) of melt inclusion in clinopyroxene crystals from tephra SU13.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| **SiO2** | 44,59 | 44,78 | 44,77 | 45,19 |
| **TiO2** | 0,94 | 0,64 | 0,74 | 0,77 |
| **Al2O3** | 18,53 | 17,99 | 19,32 | 19,39 |
| **FeO** | 8,75 | 7,06 | 6,77 | 6,55 |
| **MnO** | 0,24 | 0,18 | 0,19 | 0,20 |
| **MgO** | 1,86 | 2,99 | 1,61 | 1,43 |
| **CaO** | 9,84 | 12,85 | 10,67 | 10,30 |
| **Na2O** | 3,09 | 2,98 | 3,49 | 3,67 |
| **K2O** | 11,49 | 10,00 | 11,63 | 11,90 |
| **P2O5** | 0,66 | 0,54 | 0,81 | 0,61 |
| **F** | 0,36 | 0,21 | 0,40 | 0,59 |
| **Cl** | 0,15 | 0,14 | 0,18 | 0,14 |
| **SO3** | 1,04 | 0,96 | 1,23 | 1,08 |
| **Analytic total** | 93,98 | 94,94 | 93,83 | 93,72 |

Table 2. Results of AMS radiocarbon dating from Cava Muracci.  
\*OxCal v4.2.4 Bronk Ramsey (2013); r:5; IntCal13 atmospheric curve (Reimer et al 2013)

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| Specimen |  | Laboratory No. |  | 14C age yr BP |  | Calibrated age yr BP\* |
| Bos Bone  Red deer Bone  Rhinoceros Bone  Hyena Bone  Coprolite  Coprolite |  | LTL15758A  LTL15759A  LTL15760A  ETH-66210  ETH-66212  ETH-66213 |  | 39417±450  35231±350  36885±350  31339±168  16141±42  18313±51 |  | 44054-42523  40658-38945  42054-40804  35638-34810  19640-19292  22378-21952 |