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The palaeoenvironmental context of MIS 3 and the use of plants by Neanderthal groups in southern Italy: results from the Riparo l'Oscurusciuto site[☆]

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ABSTRACT

Neanderthal populations occupied caves and rockshelters across the Mediterranean, leaving behind evidence of their daily activities, including plant remains. By studying these remains, we can gain a better understanding of how these populations used plant resources and adapted to their environment. A critical period for studying Neanderthal behaviour is Marine Isotope Stage 3 (MIS 3) which was characterized in Europe by millennial-scale climatic instability involving fluctuations between warming and cooling events. These changes may have impacted the dispersal and dynamics of Neanderthal populations, prompting new behavioural, subsistence and settlement adaptations.

A key site for studying Neanderthal groups in southern Italy during MIS 3 is Riparo l'Oscurusciuto in the Ginosa Ravine. The site's long stratigraphic sequence and well-preserved faunal and material culture remains, including hearths, span the period from ~55 ka to ~42.8 ka BP. This makes the site central to our understanding of Neanderthal life and how they adapted to the environment until their disappearance from the region. Here, we present the results of a high-resolution study of plant microremains (phytoliths and pollen) and aquatic siliceous microremains (diatoms and chrysophyte cysts), alongside the mineralogical characterisation of their sedimentary contexts using Fourier Transform Infrared (FTIR) spectroscopy. The ~12,200-year long reconstruction of the palaeoenvironment reveals a changing landscape starting with semi-open woodlands and forests at ~55 ka and changing to more open woodland steppe environments starting sometime before ~52 ka. The woody vegetation was composed of evergreen and deciduous oak woodlands with a continued presence of other mesophytes and Mediterranean woody taxa, including gymnosperms. The grasses (mostly C_3 Pooid), are associated with a wide range of herbaceous species, probably reflecting the opening up of the landscape. Neanderthals responded to these changes by adapting their activities to the surrounding vegetation, by for example using grasses for the hearths, the ashes of which were later spread around the site.

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1. Introduction

During the late Pleistocene, groups of Neanderthals lived in caves and rockshelters all over the Mediterranean, leaving behind remains of their daily activities, including, where preserved, the presence of macro and micro plant remains. The recovery and study of these remains from a multidisciplinary perspective is a valuable source of information, not only to increase our knowledge of their lifestyles and technological abilities to exploit plant resources, but also to learn about the interaction between environmental conditions and their economic strategies and use of available resources over time. This, in turn, help us learn how Neanderthals adapted to climatic and environmental changes and how these changes affected their daily activities and internal dynamics.

A critical period for studying the impact of environmental and climatic pressures on Neanderthal populations was during the Marine Isotope Stage 3 (MIS 3) (from ~59.4 to 27.8 ka BP) (Svensson et al., 2006; Sánchez-Goñi and Harrison, 2010). During this period, Europe experienced a cooling trend, with rapid climatic oscillations involving abrupt warming episodes followed by cooling periods, which sometimes occurred on a millennial to centennial scale (Dansgaard-Oeschger and Heinrich events) (Hemming, 2004; Long and Stoy, 2013). This period also marked the arrival of *Homo sapiens* and the decline of Neanderthal populations. Several authors have suggested that these extreme climatic conditions led to a decrease in population demographics, eventually resulting in the disappearance of the Neanderthals (Hublin, 2009; Albouy et al., 2023, 2024; d'Errico and Sánchez Goñi, 2003; van Andel and Davies, 2003; Banks et al., 2008; Melchionna et al., 2018). However, this hypothesis does not seem to be consistent with the archaeological

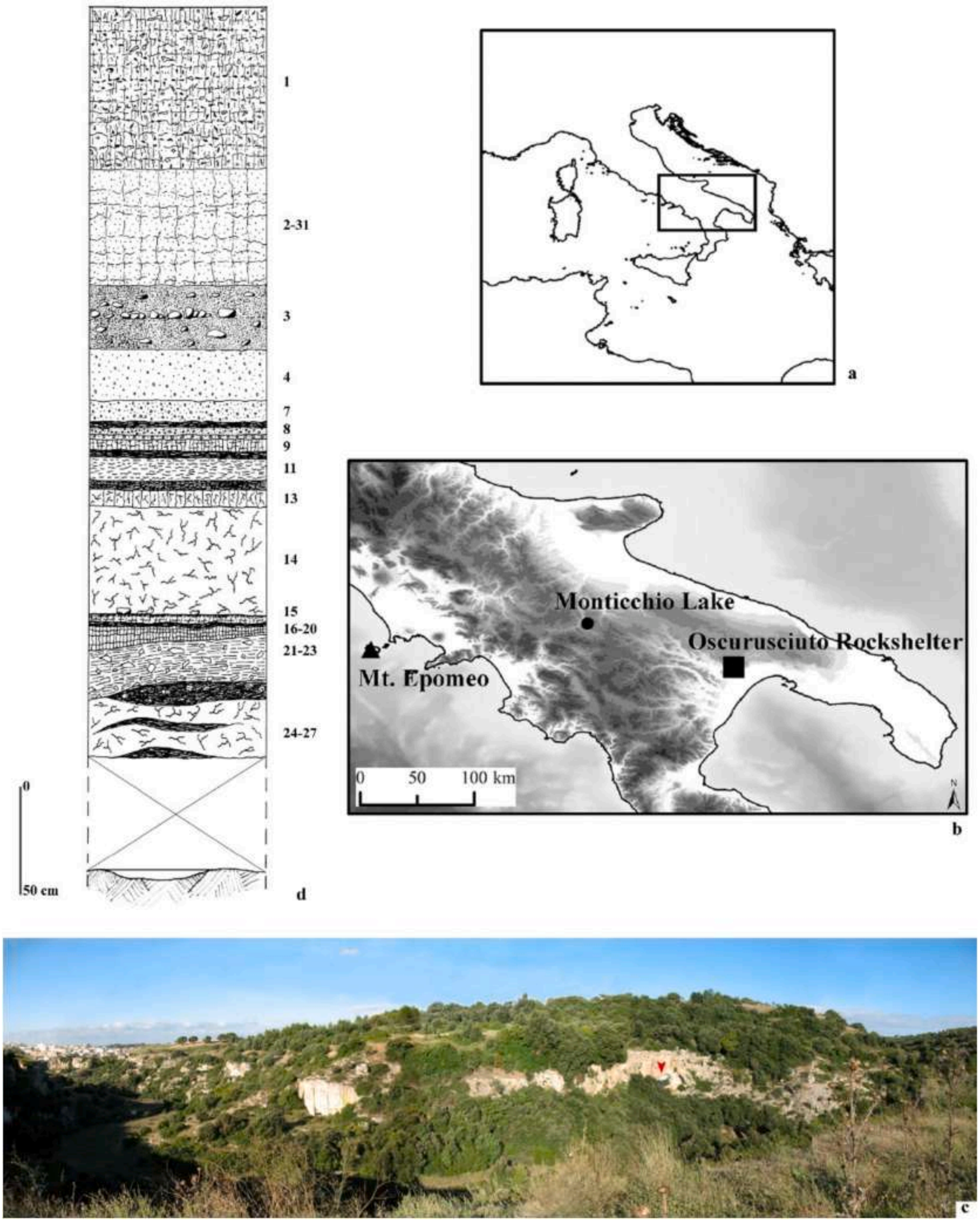

Fig. 1. Map of southern Italy indicating the location of Oscuruscciuto in relation to Lake Monticchio and Mt. Epomeo. Stratigraphic section of the rockshelter and panoramic view of the Ginosa Gorge showing the location of Oscuruscciuto (red arrow).

evidence, particularly in certain European regions where the results suggest that Neanderthals exhibited a diverse range of behaviours in terms of technology, economics, and settlement strategies (e.g. Gabucio et al. (2018a, 2018b), Rosell et al. (2019), Spagnolo et al. (2019, 2020), Moclán et al. (2023), Moncel et al. (2024), Sossa Ríos et al. (2024, 2025), and Lubrano et al. (2025). Moreover, during harsh climatic periods, particularly the coldest phases, Neanderthals adapted by migrating to more temperate regions (Hublin and Roebroeks, 2009), including the Mediterranean coast of Europe. These regions may have served as refuges when thermophilous and temperate species migrated southwards (Boschin et al., 2022; Sommer and Zachos, 2009), thereby ensuring the persistence, conservation and survival of biodiversity, including plant species, animal species and human populations (Ordóñez and Svenning, 2017; Morales-Barbero et al., 2018).

Apulia, in the Italian peninsula, is a key region for studying Neanderthal lifestyles and adaptations to climate and environment. The abundance of archaeological sites with stratified Mousterian levels indicates a continuous Neanderthal presence in the region during the Late Pleistocene (MIS 5, 4 and early MIS 3), until their demise just before or during the arrival of modern humans (Boschin et al., 2022; Higham et al., 2024). This demonstrates the region's suitability as a refuge for human populations.

Riparo l'Oscurusciuto (hereafter Oscurusciuto) is a rockshelter located in the Ginosa Ravine (Taranto) in Apulia, south-eastern Italy (Fig. 1), 20 km from the present Ionian coastline. Because of its geographical position between the eastern and western regions of southern Italy, the long stratigraphic sequence, and the good preservation of the identified combustion structures and other archaeological remains, the site is considered crucial for understanding the life of the Palaeolithic groups of Apulia and Lucania (Boschin et al., 2022). Due to rainfall regimes and to the permeability of carbonate bedrocks, Apulia was often a dry territory during the Upper Pleistocene, in contrast to the Tyrrhenian side of the Italian peninsula. Mousterian people often hunted horses and aurochs, both adapted to steppe and forest-steppe environments (Crezzini et al., 2023). More humid environments were also locally spread, as testified by some faunal records in the peninsular part of Apulia and in the area around Oscurusciuto, where streams flowed in ravines.

This study presents the results of the paleoenvironmental research of Oscurusciuto during the late Neanderthal occupation of the rockshelter, spanning ~12,200 years (from ~55 ka to ~42,8 ka BP) (Higham et al., 2024; Marciani et al., 2020; Spagnolo et al., 2016). Within MIS 3, this work addresses the time period during which Dansgaard-Oeschger events 15–10 and Heinrich events 5 and 5a occurred. The latter is interpreted as an additional Heinrich event, which is correlated with a Dansgaard-Oeschger event (Long and Stoy, 2013, Rashid and Hesse, 2003). Oscurusciuto represents one of the latest Middle Palaeolithic occupations known in southern Italy so far and possibly partially overlap with the arrival of the first Sapiens in the peninsula (Higham et al., 2024). Therefore, collecting multi-proxy paleoenvironmental data from the site is essential to better understand the influence of short-term climatic fluctuations and the general climatic cooling that took place during this period, with subsequent landscape changes, on different aspects of the daily lives of late Neanderthals. This includes seasonal mobility, the management of available resources, and their changing strategies over time. Overall, it may help to better understand the reasons of the biological and cultural turnover that marked the demise of Neanderthals.

The research is based on a high-resolution multi-proxy study of plant microremains (phytoliths and pollen) and other aqueous siliceous microremains (diatoms and chrysophyte cysts), and the mineralogical study of sediments using Fourier Transform Infrared (FTIR) spectroscopy. These later analyses allow us to better understand the mineral and plant content of the deposits, as well as the site formation processes that may have affected the preservation of the microremains, including the effects of fire and/or water, which are critical to reliable interpretation of the data. All this information was used to interpret the palaeoenvironmental conditions over time and their possible impact on Neanderthal activities during the occupation of the rockshelter (e.g., a presence/absence of correlation between climatic conditions intensity in the use of hearths, changes in hearths fuels relatable to environmental evolution, changes of the settlement organization).

1.1. *Regional setting*

Research at Oscurusciuto has been carried out since 1998 by the Unità di Ricerca di Preistoria e Antropologia (Dipartimento di Scienze Fisiche, della Terra e dell'Ambiente) of the University of Siena (Italy). The rockshelter opens on the right bank of the Ginosa Ravine (Taranto), in a particularly friable Pleistocene calcarenite (Fig. 1), ~15 m from the present bottom of the ravine and at ~235 m above sea level. Repeated collapses caused the progressive reduction of the shelter and the consequent erosion of part of the deposit. At present, the entire stratigraphic series extends downwards at a depth of ~6 m, reaching a maximum area of about 60 m^2 at the base of the deposit and includes several Stratigraphic Units (SU 1-SU 27). A detailed study of the sedimentary processes recognizes four main sedimentary facies, two of which are characteristic of cave-rockshelter environments (fine-grained infiltrated deposits and rockfall deposits); one facies is due to aeolian activity, while the other is related to stream deposits (see Martini et al., 2021).The extensively excavated series and focus of this study (SU 14 to SU 1) is included in the first 3 m of the stratigraphy and corresponds chronologically to the final phase of the Middle Palaeolithic during MIS 3 (see section 1.2 for a detailed description of the SU analysed). SU 15, a living floor, and SU 16 to SU 27, which correspond to a sequence of sandy matrix units interspersed with local vault shelter collapses and tephra layers are currently tested with a small trench) (Fig. 2) and do not form part of this study. The date of the lower part of SU 1 is 38.5 ± 0.9 ka BP e AMS, Beta 181165; 44.074–41.621 ka cal BP (95.4 % probability, unmodelled) (for calibration see OxCal v4. 44, Bronk Ramsey, 2021; Reimer et al., 2020). A second indirect date is derived from the identification of tephra layer (SU 14) as the Mt. Epomeo Green Tuff of Ischia (Spagnolo et al., 2016; Marciani et al., 2020). The eruption took place at ~55 ka BP. A recent revision of the site's chronology reinforced this picture with new OSL data (Higham et al., 2024), confirming that the span between SU 1 and SU 26 can be attributed to the very late MIS 4 and the MIS 3.

The archaeological succession is characterised by the presence of living-floors, both short-term and long-term palimpsests, the study of which has made it possible to reconstruct some aspects of the settling strategies of Middle Palaeolithic populations (Boscato et al., 2011; Boscato and Ronchitelli, 2017; Marciani et al., 2020; Spagnolo et al., 2016, 2019, 2020). The spatial organization of Neanderthal camps has been reconstructed for Stratigraphic Units (SUs) 13 and 11 using an interdisciplinary approach (Spagnolo et al., 2016, 2019, 2020). Currently, no analytical data are available for the other layers of the sequence. The upper units (SUs 1-to-3) are unsuitable for spatial analysis due to the limited preserved area caused by erosion, while SU 8 has been affected by stream processes. For the remaining units, only macroscopic information on general organization is available, inferred from the presence and distribution of specific features, as hearths, charcoal/ashy areas, stones (Figs. 2-3; see section 1.2 for the description of the spatial patterns recognized in these Units).

From a cultural perspective, lithic technology is well framed in the late Mousterian context (Marciani et al., 2016, 2018; Marciani, 2024), even if the uppermost layers revealed interesting aspects that deserved to be better understood (Carmignani et al., 2024).

1.2. *Stratigraphic setting*

In chronological sequence, the oldest SU from which samples were collected is SU 14, which is a thick aeolian deposit of tephra. Volcanic

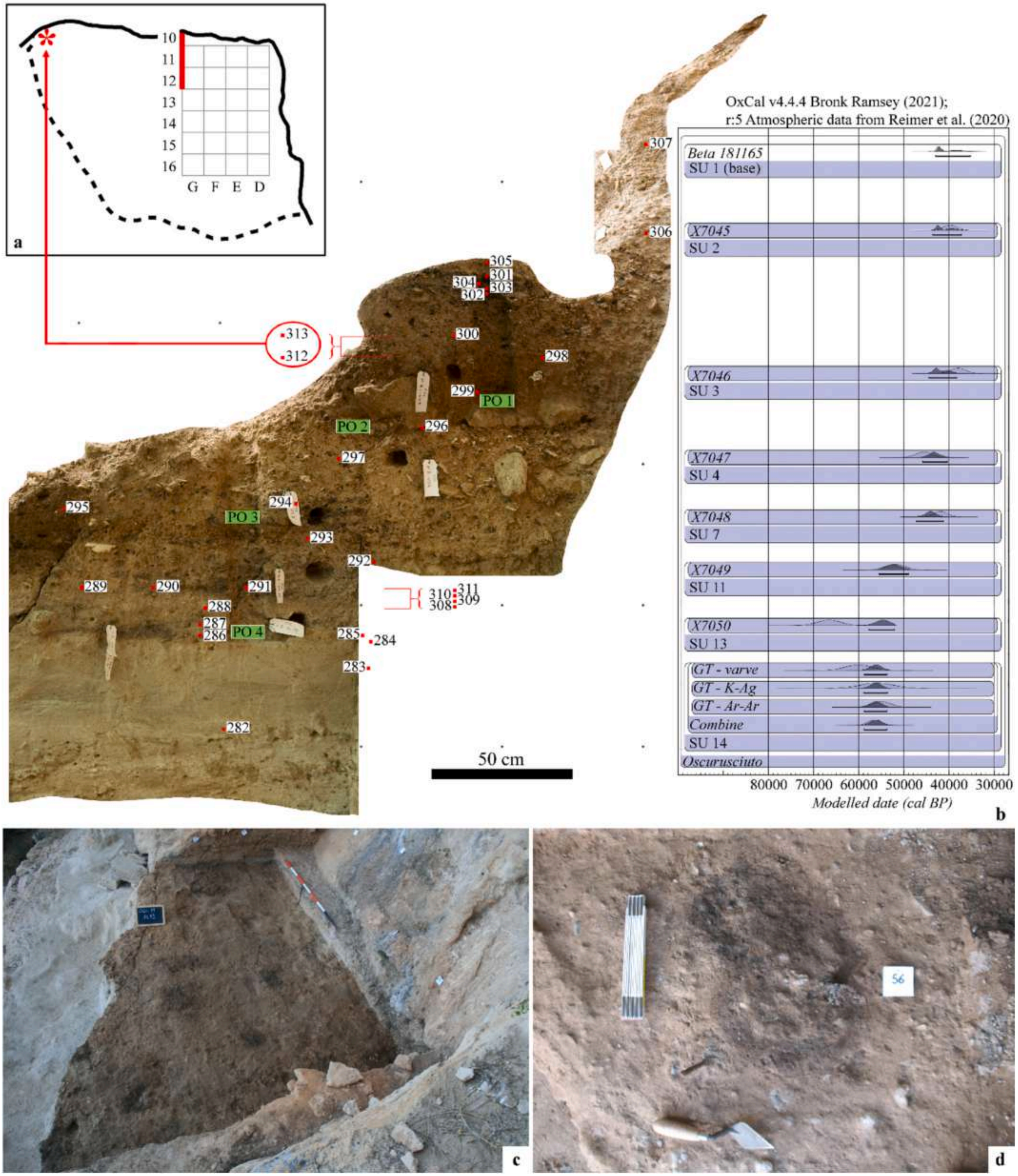

Fig. 2. Excavation grid of Oscurusciuto indicating the location of the section from which the samples were taken (in red) (a). The location of the analysed samples is plotted on the image of the section (Red dot for phytoliths and FTIR and PO for pollen). Chronometrically modelled data are shown next to it (b). The relationship of the different samples to their corresponding SU is listed in Tables 1 and 2. Panoramic picture of the SU 13 showing the relation between hearths and shelter wall (c). Exemplificative photo of a hearth of Oscurusciuto: SU 56 is a small-sized hearth related to the Unit 11b (d).

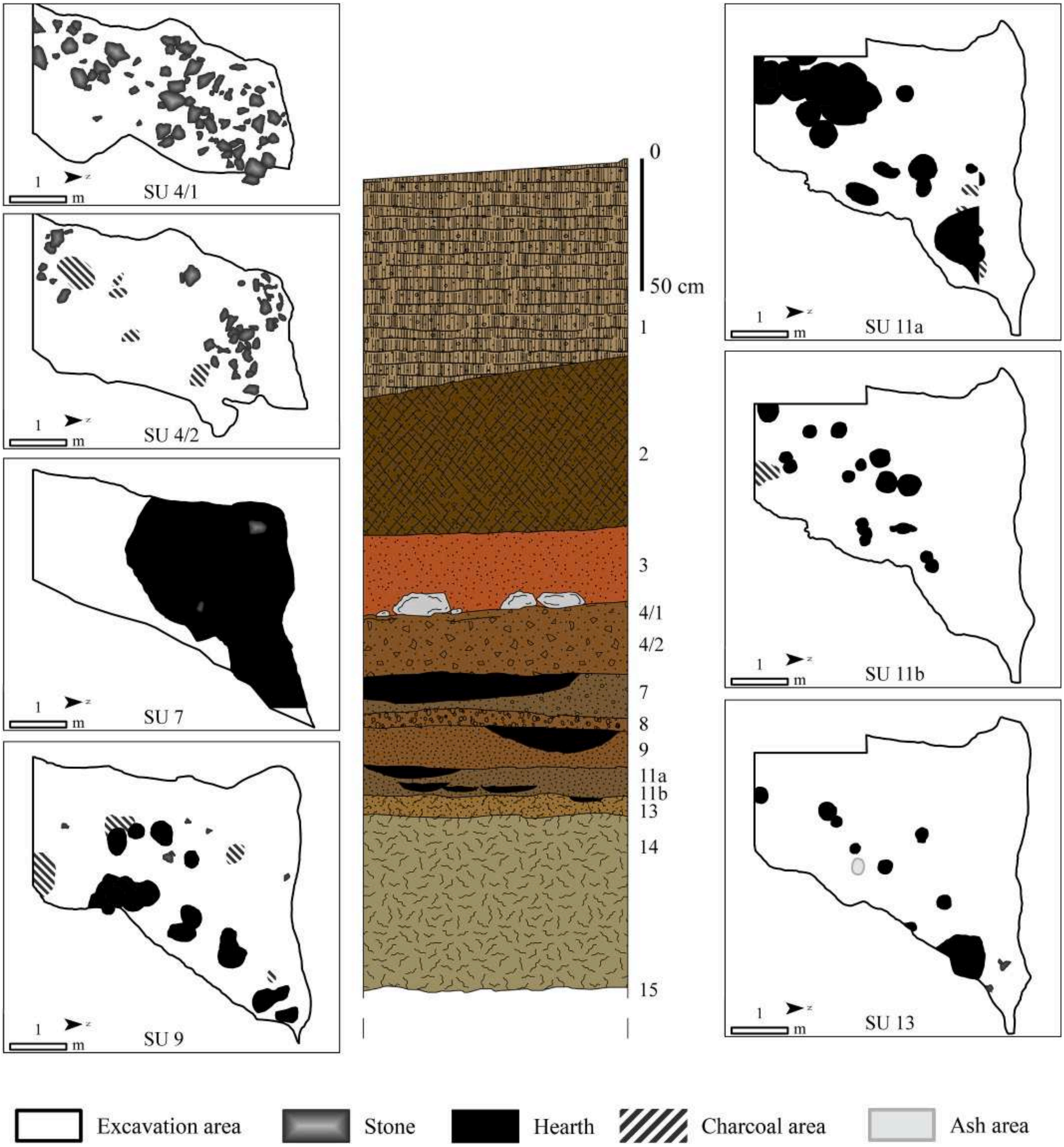

Fig. 3. Excavated sequence of Oscurusciuto with schematic maps of the main Units.

ash was transported by the wind from nearby areas into the shelter, where it accumulated covering the living floor (SU 15) and sealing the site, thereby preserving the original depositional context of a Neanderthal campsite. Therefore, the formation of SU 14 occurred under particular environmental conditions and over a short sedimentological time period, during which there was a single human occupation. The presence of this occupation is documented only in the upper decimetre of this Unit, the rest of which is completely sterile. Articulated activity areas are suggested by spatial patterns of faunal remains and lithics as a whole (Marciani et al., 2020; Martini et al., 2021). SU 13 to SU 3 are coarse and silt matrix units, compact and often hardened. SU 13 is a short-term palimpsest, consisting of sandy, partly concreted sediments with a volcanic fraction, which indicate the persistence of erodible tephra deposits. An alignment of small hearths in pits was found (Figs. 2-3). SU 11 is a long-term palimpsest of greyish sandy, partly concreted sediments, characterised by the presence of several hearths about 25–50 cm in diameter (Figs. 2-3). SU 9 consists of greyish sandy, partly concreted sediments associated with an array of hearths in sub-circular, shallow pits. In general terms, SUs 13 to 9 are characterized by the presence of multiple hearths arranged sub-parallel to the shelter wall, while the north-western corner of the shelter was left unoccupied (Fig. 3). Evidence of hearth-related activity areas, including knapping and butchering, has been detected in SUs 13 and 11 (the latter is archaeo-stratigraphically dissected into two sub-units) (Spagnolo et al., 2019, 2020). In contrast, SU 8 shows no clear structures and was affected by erosion phenomena associated with low-energy stream water (Martini et al., 2021). SU 7 represents a substantial change in space management and yielded abundant archaeological material. It exhibits a single and large hearth located precisely in the north-western corner of the shelter, which had previously been left free from fire activity (Fig. 3). This change is consistent with the stratigraphic and chronological hiatus recognised in the SU 8 (Boscato et al., 2011; Boscato and Ronchitelli, 2017; Martini et al., 2021; Higham et al., 2024). SU 4 is a thick palimpsest rich in faunal and lithic remains, although small mammal, bird, mollusc, and plant remains are sporadic. Several medium-sized and relatively well-sorted stones – some of them allochthonous (limestone) in origin – found in the upper part of the layer suggest they were brought into the shelter by humans, possibly indicating remnants of constructed spaces (Boscato and Ronchitelli, 2017; Martini et al., 2021; Spagnolo et al., 2019). Charcoal traces are also present in this layer, indicating fire use (Fig. 3). SU 3 is composed of reddish sand and contained lithic artefacts and faunal remains, mostly concentrated in its lower part. In some squares, the uppermost part of this layer was almost sterile. SU 2 and SU 1 are strongly cemented by calcium carbonate deposits that were caused by the percolation of meteoric water along the rock surface (Boscato et al., 2011; Boscato and Ronchitelli, 2017; Martini et al., 2021). Both units were reduced by erosion to a narrow strip (60–100 cm wide) of deposits running along the wall and containing lithic artefacts and faunal remains.

2. Material and Methods

2.1. Phytoliths and siliceous aqueous microremains

Thirty samples collected during the 2023 field season from archaeological layers spanning from SU 14 at the bottom to SU 1 at the top were analysed for phytoliths and aqueous siliceous microremains and measured by FTIR spectroscopy (Fig. 2). Of these, six samples corresponded to combustion structures from different units. These combustion structures were named with a different SU that was later integrated into the SU from which they were identified (see Table 1). In addition, two non-anthropogenic samples from the southern side of the rock-shelter, equivalent to SU 2 and SU 3 (OSC_313 and OSC_312), and two modern soil samples collected in the vicinity of the site (OSC_RC09 and OSC_RC11) were analysed for comparison as reference material (Fig. 2). All samples were processed at the Department of Prehistory of the Autonomous University of Barcelona (UAB). Table 1 lists the description of the samples and the main results of the study.

During the phytolith analysis, we also identified siliceous aqueous microremains, mainly diatoms and chrysophyte cysts. These are also shown in Table 1, as are the results of the mineralogical study by FTIR spectroscopy. Chrysophyte cysts are siliceous structures produced by golden-brown freshwater algae within the Heterokontophyta, mainly Chrysophyceae and Synurophyceae, and are found in a wide range of environmental conditions (Kristiansen, 2000). They produce a siliceous stage in their life cycle, known as stomatocysts or cysts, which serve as a dormant stage in their life cycle in response to sudden changes in environmental conditions (e.g. under dry conditions), population density or predation pressure (Silver, 2020). When the conditions become favourable, they germinate to initiate a new population. Morphologically, they are hollow structures, more or less spherical in shape, about 10 μm in size and with a germination pore. Diatoms are microalgae characterized by possessing outer siliceous valves that also preserve extremely well in sediments and water bodies (Rivera-Rondón and Catalan, 2017). Diatoms are widely used as indicators of environmental conditions, water quality, acidification, eutrophication or salinisation.

We followed the protocol of Katz et al. (2010) for the extraction and quantification of phytoliths and aqueous siliceous microremains. This protocol mainly involves the removal of carbonates and the density separation of sediments to isolate the phytoliths. Quantitative analysis was performed by calculating the number of phytoliths within 20 different fields at 200× magnification and then relating this number to the initial weighed sample. Morphological identification was carried out at 400× -600× on a petrographic microscope (Olympus BX43) and was based on our modern reference collection (https://www.phytcore.org), together with other more specific literature consulted where necessary (see Results section). Phytolith nomenclature followed the International Code for Phytolith Nomenclature (ICPN 2.0 – Neumann et al., 2019) whenever possible. We counted at least 200 recognisable phytoliths where possible, the minimum required for reliable interpretation (Albert and Weiner, 2001). When this was not possible, we included samples with more than 50 recognisable morphotypes, following the findings of Rodríguez-Cintas et al. (2020), who showed that samples with lower numbers of phytoliths (between 50 and 200) exhibited a similar distribution of dominant morphotypes to those with higher numbers from the same context.

In addition, several tests were carried out. Firstly, to improve our understanding of phytolith preservation and identify potential biases affecting interpretation, we compared phytolith concentration with: (i) the percentage of weathered morphotypes; (ii) the percentage of fragile or delicate morphotypes that disappear first during certain post-depositional processes, such as hair cells, stomata, papillae, articulated phytoliths, and parenchyma strands from dicotyledonous plants; and (iii) the number of morphotypes identified in each sample unit (SU). We also analysed the relationship between phytolith concentration and the number of chrysophytes and diatoms identified in each SU (Esteban et al., 2018). Secondly, to correlate the different phytolith morphotypes and improve plant identification, we used Spearman's correlation coefficient. Thirdly, to assess changes in vegetation over time using phytolith assemblages, we performed a non-metric multidimensional scaling (NMDS) analysis to validate proximity relationships. This is a particularly useful technique when a small number of samples are available, as was the case here. We performed an abundance (Bray–Curtis) NMDS analysis to obtain clustering patterns of the data and assess the relative abundance of each morphotype, giving more weight to the most abundant ones. All analyses were computed using RStudio 2024.12.0 software.

2.2. Pollen

Samples for pollen were collected during the 2022 fieldwork campaign (sample IDs OSC_Po1 to OSC_Po4) from SU 3, 4, 7 and 13 (squares *H*10/II, *H*11/I, *H*11/II of the excavation grid; Fig. 2; Table 2). See description of SUs above. Samples were processed at the Department of Environmental Biology (Sapienza University of Rome) and at the Department of Plant Biology (University of Murcia). For pollen extraction in the laboratory, after weighing the sediment samples (Table 2), the "Classic Chemical Method" for the extraction of palynomorphs was followed (Erdtman, 1969; Dimbleby, 1985). To calculate pollen concentration, we added three tablets of *Lycopodium* spores (BATCH No. 177745.500) to each sediment sample (Ochando et al., 2024, 2025). The palynological identification was made by conventional microscopy (400× and 1000×) using an optical microscope. We used the palynomorph reference collection of the Department of Environmental Biology (Sapienza University of Rome). We excluded the counts of Asteroideae and *Centaurea* from the total pollen sum, assuming that they might be overrepresented due to their local occurrence. The pollen count data was treated with the Tilia Graph 1.7.16 program in order to plot the pollen diagrams.

Pinus halepensis – *pinea* type included pine pollen grains with corpus >60 μm (Desprat et al., 2015) and *Pinus nigra* – *sylvestris type* included pine pollen grains with corpus <60 μm.

Table 1
List and description of samples analysed for siliceous microremains and FTIR at Oscurusciuto and main results of the study: Number of phytoliths morphologically identified; % of weathered morphotypes (phytoliths that could not be identified morphologically); estimated number of phytoliths per 1 g of material; number of siliceous aqueous microremains abbreviations: CC: Chrysophyte cysts; D: Diatoms. FTIR abbreviations: Ca: Calcite; Cl: Clay; Q: Quartz; K: Kaolinite: Sm: Smectite; CHA; carbonate hydroxyapatite; Observations.

Sample	SU	Description	N of phyt morphotypes	% WM	N of phyt per 1 gr of material	N Siliceous aqueous microremains	FTIR	Observations
OSC_307	1	Light-brown cemented	140	16,2	600,000	2 CC; 2 D	Ca, CHA, Q, fresh Cl (K + Sm)	
OSC_306	1	Light-brown cemented	99	34	500,000	23 CC;4 D	Pyrogenic Ca, CHA, Q, fresh Cl (K + Sm)	
OSC_305	2	Brown with gravels	411	15,9	2,000,000	132 CC; 4D	Ca, CHA, Q, fresh Cl (K + Sm)	
OSC_313 C	2	Light-brown	6	–	50,000	–	Geogenic Ca, fresh Cl (K + Sm), Q	**NOT INTERPRETED** Southern side with no anthropic activity. Equivalent to SU 2
OSC_301 H	29 (2)	**Hearth**	393	28	3,000,000	302 CC;5 D	Pyrogenic Ca, CHA, Q	
OSC_304	30 (2)	Brown cemented with gravels	286	14,1	3,000,000	76 CC	Ca, CHA, Q, fresh Cl (K + Sm)	In between OSC_301 and OSC_303 H
OSC_303 H	30 (2)	**Hearth**	426	20,7	3,000,000	214 CC; 10 D	Pyrogenic Ca, CHA, Q	
OSC_302	30 (2)	Brown	372	12,9	2.300.000	185 CC; 1 D	Ca, CHA, Q, fresh Cl (K + Sm)	below lower OSC_303
OSC_300	30–31 (2)	Light-brown cemented with gravels	23	–	200,000	37 CC	Pyrogenic Ca, fresh Cl (K + Sm), Q	**NOT INTERPRETED**
OSC_298	3	Brown-reddish	19	–	80,000	21 CC	Fresh Cl (K + Sm), Q, Ca	**NOT INTERPRETED**Uppermost SU3 in contact with SU2.
OSC_299	3	Brown-reddish	10	–	60,000	5 CC	Fresh Cl (K + Sm), Q, Ca	**NOT INTERPRETED**
OSC_312 C	3	Brown-reddish	3	–	30,000	–	Ca, Fresh Cl (K + Sm), Q.	**NOT INTERPRETED**. Southern side with no anthropic activity. Equivalent to SU 3.
OSC_297	4	Light brown-orange	172	27,4	1,400,000	21 CC	Fresh Cl (K + Sm), Ca, Q	Middle of SU4
OSC_296	4	Brown-orange loose surface	12	–	55.000	1 CC	Fresh Cl (K + Sm), Ca, Q	**NOT INTERPRETED.** Beneath a rock
OSC_294	7	Brown-grey	401	21.4	2,300,000	138 CC	Ca, Fresh Cl (K + Sm), Q	
OSC_295	7	Brown-orange	192	21.6	1,500,000	111 CC	Fresh Cl (K + Sm), Ca, Q	
OSC_293	8	Light brown with gravels	132	24,1	1,400,000	100 CC; 1 D	Fresh Cl (K + Sm), Ca, Q	
OSC_292	9	Brown	128	42,6	1,500,000	82 CC; 2 D	Ca, CHA, Q, fresh Cl (K + Sm)	
OSC_291 H	50 (11)	**Hearth**	267	19,6	1,800,000	430 CC; 14 D	Ca, CHA, Fresh Cl (K + Sm), Q	
OSC_308	11	Light-brown cemented	386	14,4	3,000,000	118 CC; 12 D	Mix Ca, fresh Cl (K + Sm), CHA, Q	
OSC_290	11	Grey	289	32,9	2,500,000	116 CC; 10 D	Ca, Fresh Cl (K + Sm), CHA, Q	
OSC_289	11	Light-brown	340	22,9	4,000,000	144 CC; 46 D	Fresh Cl (K + Sm), Ca, Q. CHA	Lowermost SU 11
OSC_311 H	53 (11)	**Hearth**	49	−2	300,000	3 CC; 1 D	Geogenic Ca, Cl traces	**NOT INTERPRETED.** Upper SU 53
OSC_310	53 (11)	Brown-grey	203	21,6	700,000	35 CC; 2 D	Mix Ca, fresh Cl (K + Sm), CHA, Q	In between OSC_311 and OSC_309
OSC_309 H	53 (11)	**Hearth**	300	15	1,100,000	51 CC; 1 D	Mix Ca, fresh Cl (K + Sm), CHA, Q	Lower SU 53
OSC_288	13	Brown-grey	264	26,3	2,000,000	91 CC; 13 D	Ca, Fresh Cl (K + Sm), Q	Uppermost SU 13
OSC_287	82 (13)	Grey	175	43,2	1,000,000	28 CC; 10 D	Ca, Fresh Cl (K + Sm), Q, CHA	
OSC_286 H	82 (13)	**Hearth**	350	26,8	3,000,000	122 CC; 26 D	Fresh Cl (K + Sm), Ca, Q	
OSC_285	13	Brown-orange	55	60,4	600,000	0	Clay	Surface on lowermost SU 13

(*continued on next page*)

Table 1 (*continued*)

Sample	SU	Description	N of phyt morphotypes	% WM	N of phyt per 1 gr of material	N Siliceous aqueous microremains	FTIR	Observations
OSC_284	14	Tephra	20	–	500,000	2 D	Pozzolana	**NOT INTERPRETED**. Contact with SU13
OSC_283	14	Tephra	18	–	700,000	0	Pozzolana	**NOT INTERPRETED**
OSC_282	14	Tephra	35	–	500,000	0	Ca, volcanic glass(?)	**NOT INTERPRETED** Bottom of section
OSC_RC09		Modern soil	40	–	120,000	2 D	Cl (K + Sm),Q, Ca	**NOT INTERPRETED** Lower elevation of the rockshelter, grassy vegetation
OSC_RC11		Modern soil	17	–	110,000	1 CC	Cl (K + Sm),Q, Ca	**NOT INTERPRETED** Lower elevation of rockshelter, grassy vegetation
OSC_Calcarenite		Calcarenite					Geogenic Ca, Cl traces	
Average % phytolith WM				**25.6**				

Table 2

List of samples analysed for pollen and summary of palynological features at the Oscurusciuto sequence.

Sample	Stratigraphic Units	Square	Gross Weight (g)	Net Weight (g)	Concentration (grains/g)	Indeterminable (%)	Pollen sum	[a]Pollen sum	Number of taxa (Pollen)
Osc-Po1	3	*H*10/II	25.4	19.9	983.3	2.35	212	212	28
Osc-Po2	4	*H*11/I	25.7	18.8	379.7	4.39	215	205	34
							TOTAL 427	417	
Sterile samples									
Osc-Po3	7	*H*11/II	26.0	17.9	–	–	Sterile	–	–
Osc-Po4	13	*H*11/II	25.0	17.0	–	–	Sterile	–	–

[a] Asteroideae and *Centaurea* excluded.

2.3. FTIR spectroscopy

FTIR spectroscopy provides a qualitative assessment of the mineral composition of sediments and the diagenetic processes that have affected the archaeological remains. The approach used follows Weiner (2010). Tens of micrograms of archaeological sediment were suspended in KBr pellets. Spectra were collected in transmission mode between 4000 and 400 cm^{-1} spectral range, using a Nicolet iS5 spectrometer with 4 cm^{-1} resolution and 32 scans. The origin of calcite, when present, was assessed according to Regev et al. (2010) and Xu and Poduska (2014), using the ratio between the carbonate $\nu 2$ and $\nu 4$ band intensities (874 and 713 cm^{-1}, respectively). We distinguished geogenic calcite ($\nu_2/\nu_4 \geq 2.5 \leq 3.2$), authigenic calcite ($\nu_2/\nu_4 \geq 3.2$; ≤ 4.0) and pyrogenic calcite ($\nu_2/\nu_4 \geq 4.0$). Band shifts of clay minerals exposed to elevated temperatures, as described by Berna et al. (2007), were used to determine the possible thermal alteration of clay minerals in the sediments. In addition, the FTIR reference collection of standard materials provided by the Kimmel Center of Archaeological Science, Weizmann Institute of Science was consulted (https://www.weizmann.ac.il/kimmel-arch/infrared-spectra-library).

3. Results

3.1. Phytoliths

Phytoliths were abundant in most of the archaeological deposits, with concentrations of around 3–4 million per gram of material in some samples (e.g., OSC_289 from lowermost SU 11). Eight samples had low numbers of phytoliths (≤50) and were not morphologically analysed (see Table 1) (Albert and Weiner, 2001; Rodriguez-Cintas et al., 2020). These were the three tephra samples from SU 14, the upper-surface black layer from hearth SU 53 (within SU 11), one sample from beneath the rock from SU 4, three samples from SU 3, and one sample from SU 30–31 (within SU 2). Furthermore, none of the non-anthropogenic samples yielded enough phytoliths for morphological interpretation (Table 1). This high accumulation of phytoliths is consistent with the interpretation that the phytoliths identified in the archaeological units represent an accumulation of plants deliberately introduced by the Neanderthal populations that inhabited the site.

A salient feature of the study was the chemical weathering exhibited by many phytoliths, mainly in the form of etching and pitting on their surfaces. However, this weathering did not prevent the morphological identification of the phytoliths. The average percentage of weathered morphotypes (phytoliths that could not be identified morphologically) (hereafter WM) was 25.6 %, with one sample showing >60 % (OSC_285) (Table 1 and Fig. 4 a, b). The results of Spearman's rank correlation analyses did not show significant p-values that could relate phytolith concentration to % WM or to the presence of more fragile morphotypes. In other words, we cannot conclude that the correlation is different from 0 and this could be due to the small sample size (SM 1: table). Alternatively, it could be that the phytolith weathering was continuous over time or that phytoliths were exposed for long periods due to slow sedimentation. On the other hand, the results showed a strong positive correlation between phytolith concentration and the presence of chrysophyte cysts, meaning that as concentration increases, chrysophyte cyst values tend to increase significantly (SM 1: graph).

Based on the morphological results of the phytoliths, three main groups of plants were identified: monocotyledons, dicotyledons and conifers. SM 2 lists all identified morphotypes, their taxonomic/anatomical assignment and their distribution in all analysed samples (number and % presence).

The monocotyledonous group included mainly grasses, although a small number of phytoliths characteristic of sedges were detected. Within grasses, the grass silica short cells (GSSCP), namely Rondel (Fig. 4

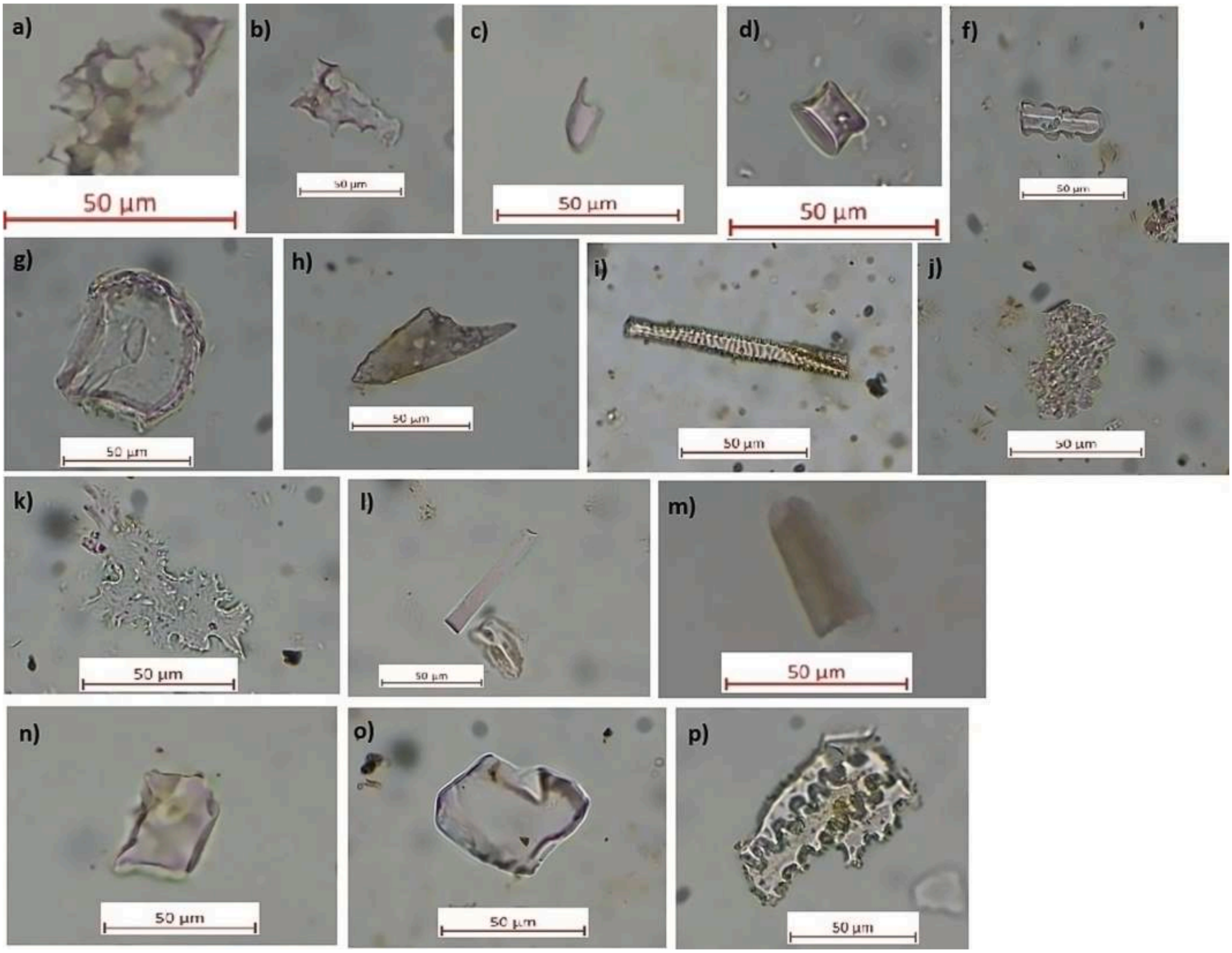

Fig. 4. Photomicrographs of phytoliths identified on Oscurusciuto samples. Images taken at 400x. a) and b) chemically altered phytoliths; c) mechanically broken Trapezoid; d) Rondel; f) Crenate; g) Bulliform flabelate; h) Acute bulbosus; i) Tracheary pitted; j) and k) Tabular sinutate/echinate; l) Elongate entire; m) Elongate thick entire; n) and o) Blocky; p) Elongate dendrític multicell.

d) were the most identified morphotypes. The occurrence of this morphotype, together with Trapezoid, also abundant, and Crenate to a lesser extent, indicates the major presence of the C_3 pooid subfamily of grasses (Fig. 4 c, d, e). The results of the Spearman's rank correlation test for the association of different morphotypes (Fig. 5) show a positive correlation between these morphotypes. Bilobate and Polylobate, common in C_4 panicoids, reeds and the *Stypa* C_3 grass, and Saddle (C_4 chloridoids) were also identified, although in smaller numbers (SM 2). Other common grass morphotypes identified were Bulliform flabellate and Acute bulbosus characteristic of the leaves (Fig. 4 g, h). Interestingly, Elongate sinuate, which is commonly associated with grasses, is strongly distant from Rondel and Trapezoid, while showing a positive correlation with Blocky according to the correlation test (Fig. 5).

Phytoliths characteristic of the leaves of dicotyledons and conifers included Sclereid, Tracheid annulate or Hair. Furthermore, Tabular sinuate/echinate, similar to those identified by Gao et al. (2017 and 2018) in Picea, were also identified in the samples (Fig. 4 j, k).

Additional morphotypes, which do not align directly with any specific plant grouping or taxa classification, were also abundantly identified in the samples. These include the Elongate entire and Blocky morphotypes. Elongate entire is common of the leaves and stems of grasses, although it is also found in other monocots such as sedges and palms, and to a lesser extent in dicots and conifers, and is therefore considered to be of low taxonomic value (Fig. 4 l) (Albert and Weiner, 2001; An, 2016; Neumann et al., 2019 (ICPN 2.0)). The results of the Spearman's rank correlation test show a positive correlation between this morphotype and Spheroid psilate and a strong negative correlation with Rondel, Trapezoid and Crenate, and other characteristic grass morphotypes (i.e., Bilobate or Saddle), indicating that for these samples this morphotype may be more closely related to dicotyledons and/or conifers than to the Poaceae family (Fig. 5). Two subgroups of this morphotype were identified in the samples, albeit in smaller numbers: Elongate entire thick and Elongate entire tabular (see SM 2). Despite some Elongate entire thick show similarities to those reported by other authors (Fig. 4 m), it is generally difficult to confidently assign them to monocots, dicots or conifers (An, 2016). Furthermore, the alteration of many of these morphotypes complicates this interpretation. In any case, both morphotypes also show a negative correlation with Rondel and Trapezoid, suggesting also a closer relationship with dicotyledons and/or conifers (Fig. 5).

Blocky can be found in grasses and sedges (representing parallelepipedal bulliform cells), but also in the bark of woody dicotyledons and conifers (Albert and Weiner, 2001; An, 2016; Carnelli et al., 2004; Collura and Neumann, 2017; Gao et al., 2017; Klein and Geiss, 1978; ICPN 2.0 – Neumann et al., 2019 and references therein). This morphotype was identified in most of the samples, but in smaller numbers

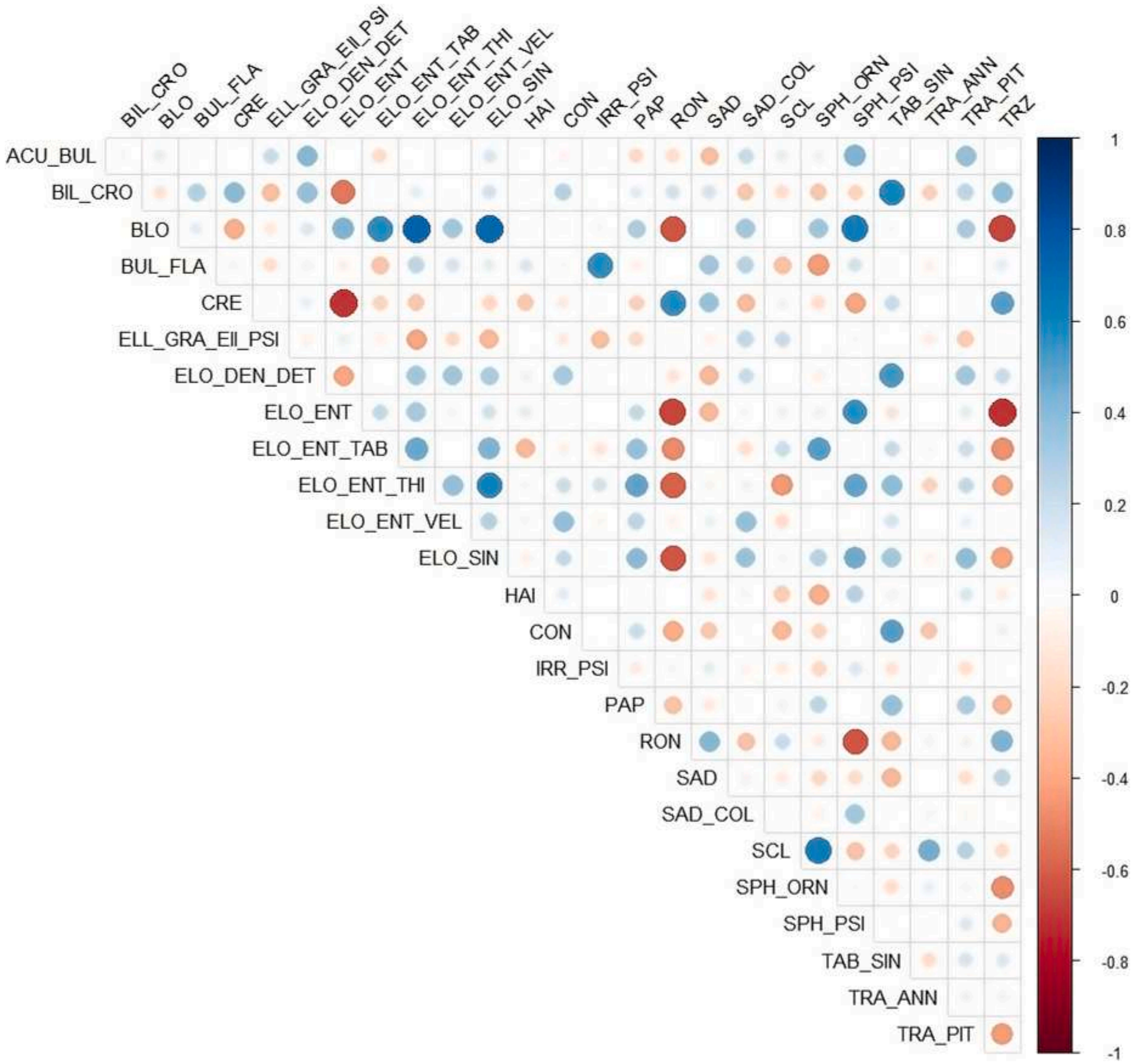

Fig. 5. Plot of Spearman's correlation test between phytolith morphotypes. Positive correlation: blue dots. Negative correlation: red dots.

than Elongate entire (SM 2). The results of the Spearman's rank correlation test show a strong positive correlation between this morphotype and Elongate entire thick, Elongate entire tabular, Elongate sinuate and Spheroid psilate, and a strong negative correlation with Rondel, Trapezoid and Crenate (Fig. 5). This suggests that, as in the case of Elongate entire, the Blocky morphotype is more closely related to dicotyledons and/or conifers than with C_3 Pooid grasses.

Fig. 6 shows the ratio between the two most abundant groups of phytolith morphotypes identified in the samples that showed a negative relationship in Spearman's rank correlation test (Elongate entire group and the C_3 Pooid group) in stratigraphic position. The results show three distinct groups. In the lower part of the sequence (SU 13 and SU 11), the samples show a high presence of the Elongate entire group and a low presence of C_3 phytoliths (ratio >2). Remarkably, the only samples from SU 11 that do not show this tendency, but the opposite, a significant presence of grass phytoliths in relation to the Elongate entire group (ratio <1), are the two hearths analysed from SU 11: SU 50 and SU 53 (a hearth structure in the western part of the rockshelter), which also included a brown-grey layer between the hearth and the sample immediately below (Table 1). In addition, samples from SU 9, SU 7 and SU 2 (including SU 30 and SU 29) also show a predominant presence of characteristic C_3 grass phytoliths (ratio <1). Finally, the one sample from SU 8 and SU 4 and the two samples from SU 1 show a more balanced presence between the two groups (ratio between 1 and 2) (Fig. 6).

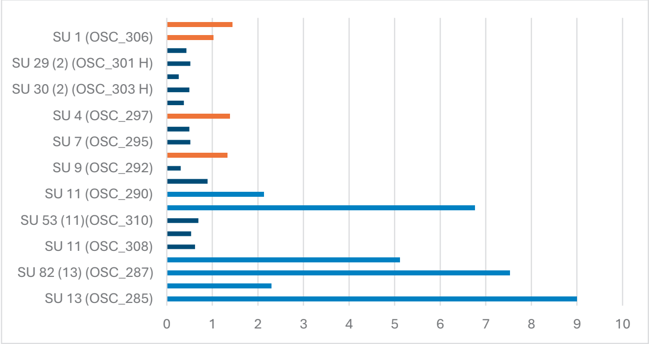

Fig. 6. Ratio between the two most abundant groups of phytolith morphotypes identified with a negative relationship in Spearman's rank correlation test (Elongate entire group and the C_3 Pooid group) in stratigraphic position.

The results of the NMDS analysis, which grouped the samples according to the distribution of phytolith morphotypes, are shown in Fig. 7. The Bray-Curtis stress indicator = 0.07924003 falls within the

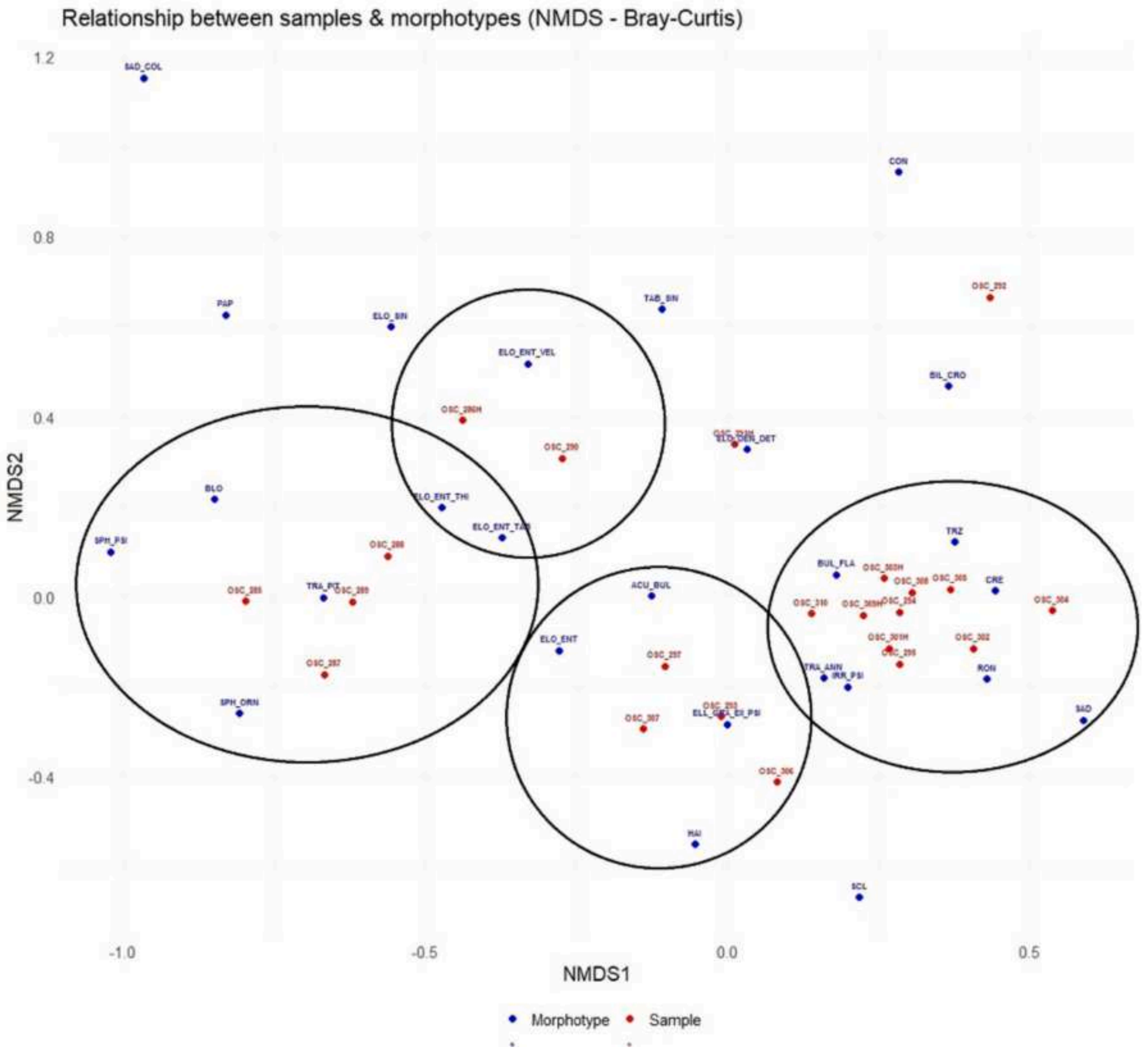

Fig. 7. Graph showing the results of the NMDS analysis, grouping the samples according to the distribution of phytolith morphotypes.

reliable parameters (0.05—–0.10), confirming the reliability of the test. The samples are clustered into four distinct groups, plus two outliers, which roughly matches the stratigraphic distribution of the samples in Fig. 6. In addition to the inverse relationship between the Elongate entire group and the C_3 grass characteristic phytoliths, samples from the lower part of the sequence (SU 11 and SU 13) could be further subdivided into two distinct groups (A and B). Samples from group A are mostly associated with Spheroid ornate, S. Psilate, Blocky, Tracheary pitted and Elongate entire thick and E. tabular from woody plants whereas samples from Group B are associated with Elongate entire thick and E. entire tabular as well as Elongate velloate (Fig. 7). Consistent with Fig. 6 and the grouping of samples with a more balanced presence between grasses and the Elongate entire group, group C includes the one sample from SU 8 and SU 4 and the two samples from SU 1 and is related to Ellipsoid granulate and E. psilate and Elongate entire, possibly from dicots, but also to Hair and Acute bulbosus, the latter more characteristic of grass leaves. Group D includes most of the samples with a large presence of grass characteristic phytoliths (Fig. 6) and is mostly represented by characteristic grass morphotypes (i.e. Trapezoid, Crenate, Rondel, Bulliform flabellate and Saddle), but also with some possible morphotypes from dicots such as Irregular psilate and Tracheary annulate. The exceptions to this later group are the two outliers: OSC_291 H (SU 50 within SU 11), characterised by a significant presence of Elongate dentate/dendritic from the inflorescence of grasses, and OSC_292 (SU 9), defined by a large number of characteristic C_4 grass phytoliths (Bilobate and Cross).

3.2. *Siliceous aqueous microremains*

Stomatocysts of chrysophyte algae and diatoms were also identified in the samples (Fig. 8 and Table 1). All chrysophyte cysts identified were apparently unornamented. However, at least 3 morphospecies appeared to be present based on the germination pore and overall shape (Fig. 8 a-d). Diatoms were not present in large numbers and sample OSC_289 had the highest number (Table 1). Most of the diatoms belong to the genera *Nitzschia* sp., *Cyclotella* sp., *Pinnularia* sp. and *Hantzschia* sp. Other genera may have been present, but their poor preservation prevented their identification. In contrast to the relationship observed between phytoliths and chrysophyte cysts, there is no apparent relationship between phytoliths and diatoms.

In addition to phytoliths and siliceous aqueous microremains, small fragments of microcharcoal were also recorded in most samples, including hearth and hearth-associated samples.

3.3. *Palynological results*

Two of the four pollen samples analysed contained pollen, corresponding to SU 3 and SU 4 (samples ID Osc-Po1 to Osc-Po2), while the other two, from SU 7 and SU 13, were barren (Table 2). A total of 427 pollen grains were identified. The percentage of indeterminable grains is < 5 %. The number of pollen types varies between 28 and 34, with a total of 46 identified taxa. The pollen concentration ranges between

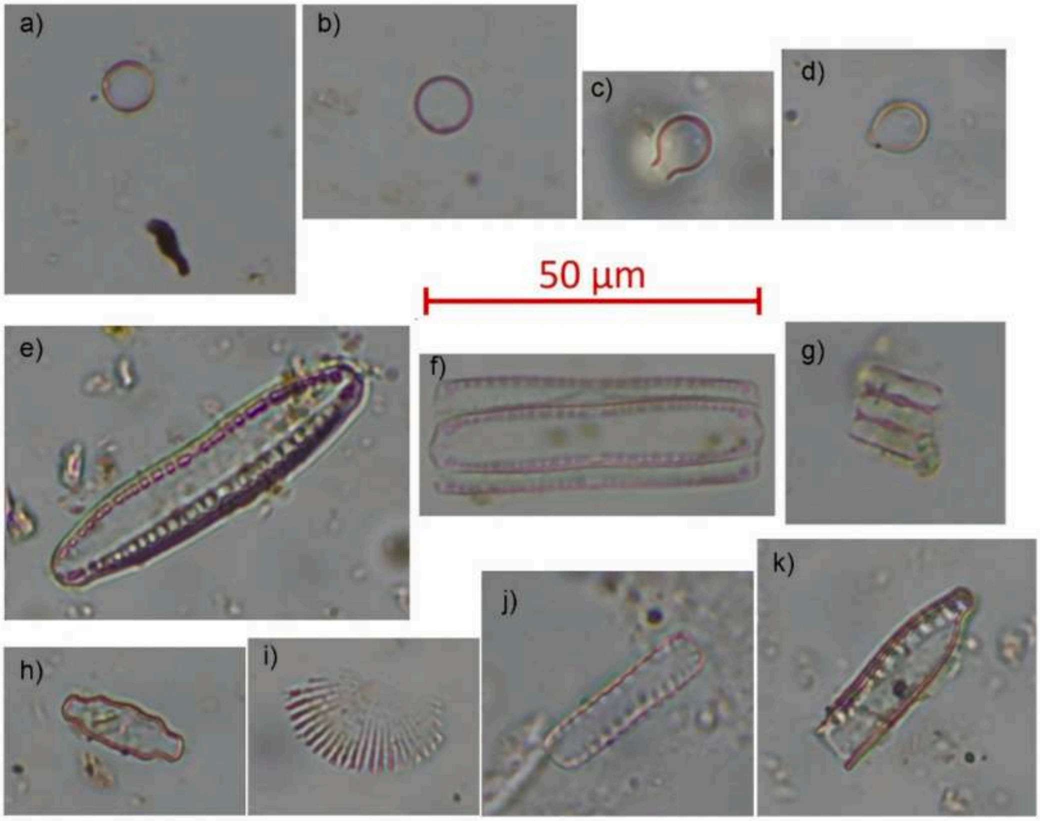

Fig. 8. Photomicrographs of chrysophyte cysts and diatoms. Images taken at 400x. a-d) chrysophyte cysts. The differences noted particularly between a-b, c and d seem to indicate different morphospecies; e-k) diatoms e-f) *Nitzschia* sp.; g) unknown; h) cf. *Luticula*; i) *Cyclotella* sp.; j) *Pinnularia* sp.; k) *Hantzschia* sp.

379.7 and 983.3 grains/g (Table 2). A pollen diagram representing Trees, Shrubs, Herbs, and Spores was prepared (Fig. 9), together with a summary of Arboreal Pollen (AP) and Non-Arboreal Pollen (NAP).

SU 4.

This unit only includes sample Osc-Po2 (Fig. 9). The AP is >62 %, with dominance of evergreen *Quercus* (24 %), *Fraxinus* (7 %), and deciduous *Quercus* (7 %). Occurrences of *Olea*, *Pinus halepensis/pinea*, Genisteae, *Pistacia*, and *Castanea* is also ecologically meaningful. Among NAP (Fig. 9), Poaceae (7 %), *Artemisia* (5 %), and Lamiaceae (4 %) are remarkable. Additionally, Asteroideae, *Centaurea*, Fabaceae, and *Verbascum* are frequent. The presence of *Pluricellaesporites*, *Diporisporites*, *Hypoxylonites*, and other fungal spores is significant (Fig. 9).

SU 3.

This unit includes sample Osc-Po1 (Fig. 9). AP is predominant, reaching values >89 %. The most noteworthy characteristic is the abundance of evergreen *Quercus* (40 %), deciduous *Quercus* (17 %), and *Pinus halepensis/pinea* (6 %). Other AP includes *Olea*, *Fraxinus*, *Pistacia*, *Daphne* t., and *Erica*. In NAP (Fig. 9), Poaceae (5 %) dominate. Other NAP includes *Artemisia*, *Plantago*, Apiaceae, Cannabinaceae, Fabaceae, *Helianthemum/Halimium* t., *Asphodelus*, and Cyperaceae. Spores are represented by *Pluricellaesporites*, *Monoporisporites*, *Diporisporites*, *Microsporonites*, and other fungal spores.

3.4. FTIR results

FTIR results indicate that the samples analysed are mainly composed of calcite, a clay mineral mixture of kaolinite and smectites, quartz and carbonate hydroxyapatite (from dispersed bone fragments) (Table 1 and Fig. 10). The local bedrock calcarenite is mainly composed of geogenic calcite with traces of clay minerals. The calcite of the sediments shows characteristics of being derived from reworked wood ash, with FTIR absorptions characteristic of both pyrogenic and authigenic calcite. Pyrogenic calcite is observed associated with combustion structures although in some of these (OSC_309H) it appears to be altered to authigenic calcite. These mixed phases spectra patterns have been described in many other archaeological sites and likely interpreted (see Goldberg et al., 2017 for a review).

4. Discussion

4.1. Dissolution and taphonomy

A significant finding of this study is the high level of weathering observed on the phytoliths throughout the sequence. While this weathering was evident in the form of pitting and etching on the surfaces of most morphotypes, it also impeded the morphological identification of some morphotypes (see Table 1 and Fig. 4a and 4b). In order to understand the implications of this phytolith alteration for interpreting the samples in terms of vegetation and palaeoenvironment, we first need to understand the causes of the phytolith alteration and dissolution and secondly establish whether these affect the entire assemblage or only specific morphotypes (i.e. differential preservation).

Phytoliths are incorporated into sediments following the decay of organic plant matter. They may then undergo diagenetic or post-depositional processes involving physical, chemical and/or biological changes. Several studies suggest that phytolith dissolution primarily occurs at the surface, with solubility decreasing with depth. This underlines the importance of rapid burial for the effective preservation of phytoliths (Goldberg and Macphail, 2006; Karkanas et al., 2002). A key chemical factor affecting phytolith preservation is exposure to highly alkaline conditions (pH >8.5) (Fraysse et al., 2009; Stromberg et al., 2018).

At Oscurusciuto, the pitting and etching observed in the phytoliths is more pronounced in the blocky and bulliform types than in the GSSCPs.

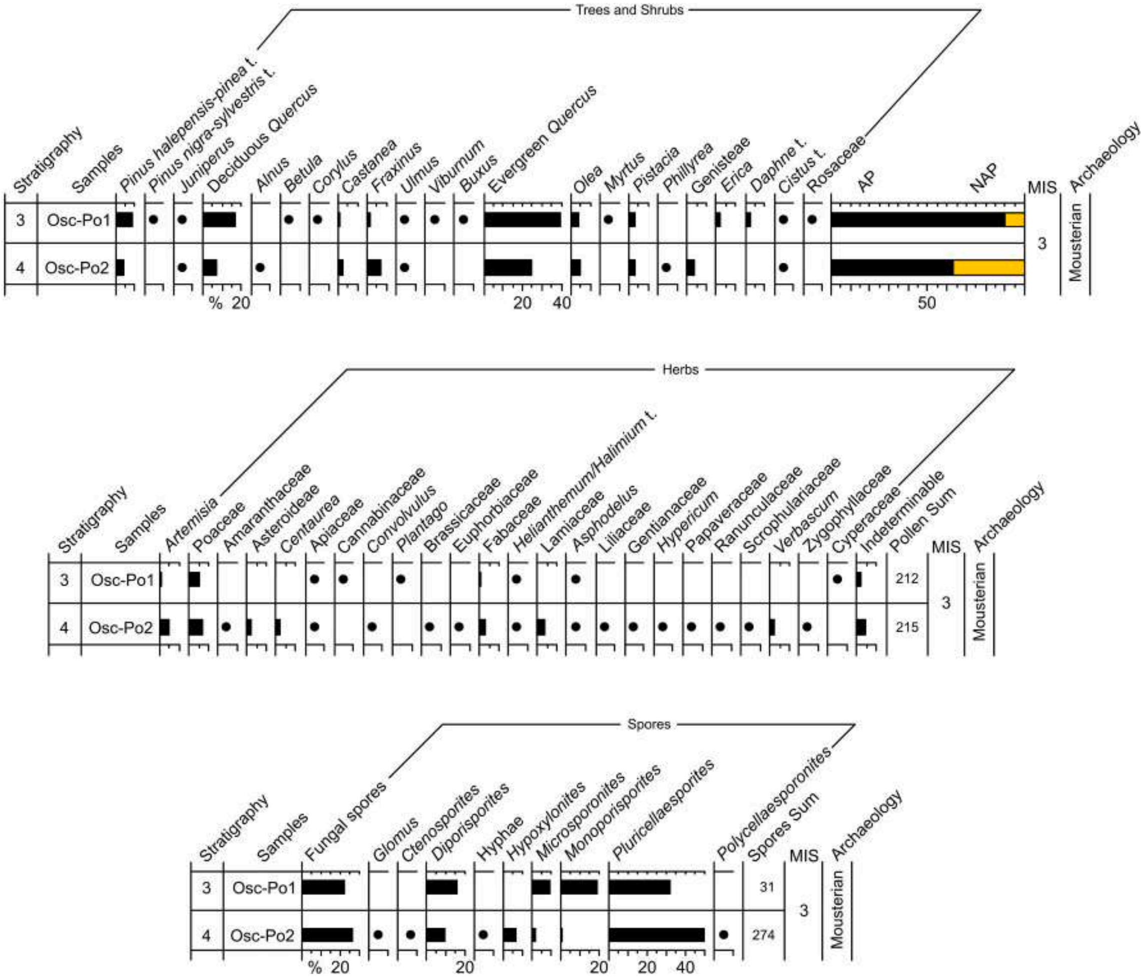

Fig. 9. Percentage pollen diagram of the sediment samples of Oscurusciuto including Trees, Shrubs, Herbs, summatory of arboreal pollen (AP) and non-arboreal pollen (NAP), together with the diagram of spore and non-pollen palynomorphs. Black dots for percentages below 3 %.

This is consistent with alkaline processes and the experimental results of Liu et al. (2023). This chemical alteration is probably due to the combined effects of calcium carbonate-rich sediments derived from the weathering of calcarenite bedrock, a large input of wood ash (pyrogenic calcite) and exposure to meteoric water. Given the limited protection offered by the rockshelter, this alteration is consistent with it having taken place at or near the surface, in line with previous studies (Goldberg and Macphail, 2006; Karkanas et al., 2002). These taphonomic conditions may also imply that the sedimentation rate at Oscurusciuto was slow.

Several authors have addressed the issue of differential preservation of phytolith morphotypes (e.g. Albert et al., 2006; Bartoli and Wilding, 1980; Bartoli, 1985; Cabanes et al., 2011; Cabanes and Shahack-Gross, 2015; Liu et al., 2023; Stromberg et al., 2018; Wilding and Dress, 1974). Their results demonstrate that GSSCPs are more resilient to dissolution than non-grass phytoliths, even under highly alkaline conditions. In contrast, other morphotypes known as 'delicate or fragile morphotypes', such as sedge hat cones, are more susceptible to dissolution and are therefore rarely found in soil and/or sedimentary records (Albert et al., 2006; Bartoli and Wilding, 1980; Bartoli, 1985; Cabanes and Shahack-Gross, 2015; Liu et al., 2023).

The most prevalent morphotypes in our samples were Elongate entire, Rondel and Trapezoid, all of which are more resistant to high alkaline conditions. In contrast, more fragile morphotypes such as sedge hat-cone and dicotyledonous leaf phytoliths were recovered in low numbers. Thus, the results imply that alkaline conditions may have affected the preservation and identification of sedges and dicotyledonous leaf plants in the samples. In the latter case, the possible dissolution of the more fragile dicotyledonous leaf phytoliths alongside the lower overall production of phytoliths in this group of plants (Albert and Weiner, 2001) suggests that these plants were more abundant than the phytoliths indicate, as shown by the pollen results.

Spearman's rank correlation test showed no significant p-values relating phytolith concentration to %WM or the preservation of more fragile morphotypes. This indicates that high alkaline conditions were probably continuous over time, likely due to the periodic dripping of water along the rock surface, which would have affected the phytoliths similarly throughout the sequence.

The absence of phytoliths in samples with no evidence of human activity (SU 3 upper region, SU 4 beneath a rock, and the three tephra samples) is probably due to a lack of accumulated plant material rather than dissolution. The same applies to the two control samples from the south side of the shelter that did not present evidence of anthropic activity.

Being siliceous, diatoms and chrysophyte cists would also have been affected by dissolution. Furthermore, previous studies have shown that the dissolution rates of diatoms are higher than those of phytoliths (Fraysse et al., 2009; Van Cappellen and Qiu, 1997). This has been attributed to the presence of Al and other trace elements in phytoliths compared to diatoms, which would contribute to their better preservation. This higher dissolution of diatoms may explain the low number recovered and why many could not be identified. A higher presence of diatoms would indicate higher humidity, but we can't say yet to what extent. The same may apply for stomatocysts.

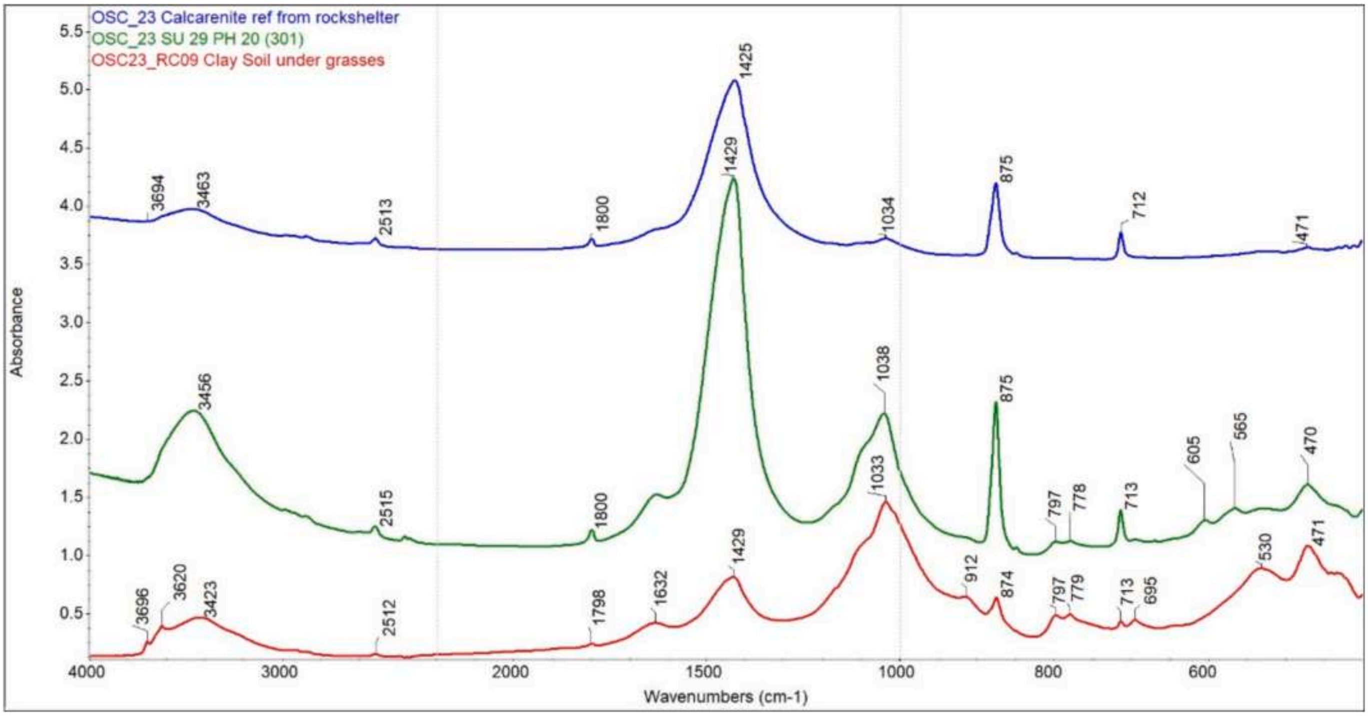

Fig. 10. Representative FTIR spectra from local soil (red), archaeological sediment (green), and calacarenitic bed rock (purple) showing the absorptions of calcite (712, 875, 1425, 2512 cm-1), quartz (695, 778, 798 cm-1), carbonate hydroxyapatite (565, 605, 1038 cm-1), which is the mineral component of bone, and clay minerals kaolinite (912, 1033, 3620, 3696 cm-1) and smectite (1033 and 3620 cm-1). The three samples have different v2/v4 (875/712 cm-1) ratios. The calcite v2/v4 ratios are 3.7 for the local soil (authigenic values), 2.7 for the calcarenite (geogenic value), and 4.3 for archaeological deposit SU 29 (pyrogenic value).

Pollen grains were identified in SU 3 and SU 4 with a percentage of indeterminate grains <5 % (Table 2), indicating generally good preservation. However, from a palaeoecological perspective, the Oscurusciuto pollen record should be interpreted with caution given its limited size (two samples: OSC-Po1 and OSC-Po2). The low pollen preservation in SUs 7 and 13 may indicate oxidation, which occurs in dry climates where depositional layers are exposed to prolonged erosion. The absence of pollen in SU 13 may also be related to the presence of volcanic sediments, which indicates the persistence of erodible tephra deposits near Oscurusciuto. Thus, the preservation of pollen grains, may have been influenced by the previous tephra event stratigraphy (SU 14).

4.2. Palaeoenvironments of Oscurusciuto

The results show that over the approximately 12,200 years of the sequence analysed at Oscurusciuto, there were significant changes in the composition of the vegetation, which varied considerably over time. These changes encompassed a transition from forested settings in the lower strata (~55 ka) to more open environments in the upper levels (~42.8 ka). The woody nature of the vegetation is evident in the lower units and continues throughout the sequence in the upper levels, although in lower proportions than the herbaceous vegetation (Fig. 6). These changes in vegetation are chronologically correlated with the cooling Heinrich events 5a and 5 (~55 ka to ~48 ka), and the onset of the Greenland Stadial 12 (culminating at ~44 ka), which probably impacted the changing landscape and the opening up of the environment. Despite the palimpsest nature of some of the SUs at Oscurusciuto not allowing for more precise chronological correlations, it is possible to assess the impact of this cooling periods on the vegetation and environmental conditions by examining the changes in the different SUs. From SU 11 onwards, there is a notable increase in Poaceae from the C_3 Pooid subfamily in the samples, with alternating periods of mixed vegetation. This pattern featured semi-open woodlands and woodlands (SU 8, SU 4, SU 3 and SU 1), interspersed with more open forest steppe environments in SU 9, SU 7 and SU 2. The arboreal vegetation would comprise evergreen and deciduous oak forests, with the continued presence of other mesophytes and Mediterranean woody taxa. The woody vegetation included abundant *Pinus halepensis/pinea*, *Juniperus*, *Castanea*, *Fraxinus*, *Olea* and *Pistacia*, which were continuously accompanied by broad-leaved *Alnus*, *Betula*, *Corylus*, *Ulmus* and Rosaceae, as well as by Mediterranean taxa, such as *Buxus*, *Viburnum*, *Myrtus*, *Phillyrea*, *Erica*, *Daphne* and *Cistus*. The xerophytic component is mainly represented by Poaceae, *Artemisia* and Lamiaceae (Fig. 9). The open woodland consisted of abundant evergreen *Quercus*, deciduous *Quercus*, *Fraxinus*, Poaceae, *Pinus halepensis/pinea*, *Olea*, *Pistacia*, *Castanea*, Genisteae, *Artemisia*, Fabaceae and Lamiaceae (Fig. 9), with the occurrence of *Pinus nigra/sylvestris*, *Juniperus*, *Alnus*, *Betula*, *Corylus*, *Ulmus*, *Viburnum*, *Buxus*, *Myrtus*, *Phillyrea*, *Erica*, *Daphne*, *Cistus*, Rosaceae, Apiaceae, *Helianthemum/Halimium*, *Asphodelus* and *Verbascum*, among others (Fig. 9).

The Lago Grande di Monticchio sequence in southern Italy is one of the most complete records of Italian Quaternary vegetation (Allen et al., 2000; Watts et al., 1996), covering the last 130 thousand years (ka) (Allen et al., 2000; Allen and Huntley, 2009). This provides a valuable framework for the current study. Our results from Oscurusciuto (SU 14–1) fit well within the regional context and are consistent with the vegetation documented in the Monticchio pollen record during GI-14, GI-13 and GI-12, which are dated to around 52–42 ka BP (Allen et al. 2000; Fletcher et al., 2010). These periods are characterised by relatively high percentages of woody taxa, including *Pinus*, *Quercus*, *Betula*, *Juniperus*, *Ulmus*, *Fraxinus* and *Corylus*, among others, and by relatively warm conditions followed by a period of cooling and increased moisture. Nevertheless, the pollen record of Oscurusciuto also indicates a more wooded habitat than Monticchio. The transition from pollen assemblage zone 11 to zone 10 at Monticchio is marked by a decrease in wooded vegetation and an increase in cool, dry conditions becoming colder. This transition starts at ~44 ka BP and fits well with the chronology of SUs 4–2.

Together with the changes in vegetation and climate, the fauna identified during the study of the site provide a more complete picture of the environment during this period (SM3). Forest ungulates (red deer, fallow deer, and roe deer) have been recovered from SU 14 to SU 4 (Boscato et al., 2011; Boschin et al., 2022; Marciani et al., 2018, 2020; Spagnolo et al., 2016, 2020), along with those adapted to more open vegetation (aurochs, horse, rhino and caprines). The ravines in this area of Apulia represent significant ecotones, denoting an abrupt transition from the comparatively flat (and presumably drier) uplands to the deeper and more humid valleys that characterise the region. Furthermore, a transition in vegetation from SU 4, characterised by an open environment and forest steppe, to SU 3, characterised by a moister and more temperate phase with a *Quercus*-dominated forest environment, can be seen when integrating the results with those of the fauna. Specifically, the higher frequency of aurochs herds (*Bos primigenius*) at SU 4, along with *Cervus elaphus, Dama dama*, and, in minor quantity, *Equus ferus*, *Capreolus capreolus, Capra ibex,* and *Rupicapra* sp. (Boscato et al., 2011) confirms the existence of open woodlands and forest steppes in the vicinity of the rockshelter. The subsequent SU 3 includes *Equus ferus*, *Cervus elaphus* and *Bos primigenius*, accompanied by a smaller percentage of *Stephanorhinus* sp., *Capreolus capreolus, Dama dama* and *Capra ibex* (Boscato et al., 2011). Although phytolith data are not available for SU 3, the results for SU 2 indicate a transition back to a more open environment. This is consistent with the increase in horse remains in this phase. It is interesting to note that caprines became present at the site, although not in great numbers, in the uppermost part of the sequence, at least from SU 4. In Apulia, ibex is often associated with horse during more arid phases when steppe environments spread and rocky slopes became more barren (e.g., Boschin et al., 2018). Thus, the presence of these taxa is likely indicative of a long-term trend of vegetation opening in the ravine, with an increased presence of grasses and less forest vegetation. This picture is further supported by magnetic susceptibility data of the sediments, which indicates a shift towards more arid and colder conditions from the bottom to the top of the excavated part of the sequence (Boschin et al., 2022).

4.2.1. Siliceous aqueous microremains

The presence of stomatocysts and diatoms in the rockshelter indicates that humid conditions, or at least the presence of water, prevailed throughout the sequence (see Table 1). Stomatocysts are of particular interest because, although they are primarily found in shallow and deep lake sediments, as well as in peatlands, marshes and bogs (Kristiansen, 2000), they have also been identified in other sediments and on various substrates, including the leaves and branches of bryophytes. These microhabitats and food sources favour the growth of these microalgae (Bai et al., 2021; Van de Vijver & Beyens, 1997; Wilkinson et al., 2001). Unfortunately, to our knowledge, there are no records addressing the presence of stomatocysts in prehistoric soils, which limits other possible explanations. Until further studies address this issue, one possible hypothesis is that they developed on bryophytes and/or mosses growing in the rockshelter during wet periods, such as spring runoff (Adam and Mahood, 1981). Despite the poor preservation of diatoms, this explanation is consistent with the few species that have been identified, such as Pinnularia, Luticola and Nitzschia, which typically thrive in moist soils (Rivera-Rondón and Catalan, 2017). Alternatively, the bryophytes and/or mosses may have been introduced to the site deliberately, or they may be associated with other plants, as suggested by the strong correlation observed in the Spearman correlation test (SM1).

4.3. Hearths

Hearths are a central element of the anthropic visible structures at Oscurusciuto. In this study, we examined six hearths to determine the fuels used to ignite and/or maintain fires, and the possible relationship between fuel selection and hearth functionality and/or habitat type. Phytoliths were abundant in most of the hearth samples analysed, with the exception of the uppermost sample from SU 53 (OSC_311 H). The exposure of this sample and subsequent erosion and mixing with the natural sediment probably explains the low number of phytoliths recovered from this sample. The presence of geogenic calcite, confirmed by FTIR analysis, further supports this hypothesis (Table 1).

Overall, the study of the hearths reveals two main features: the abundance of grass phytoliths and the morphological similarity of the phytolith assemblage between the hearth samples and their associated samples with few exceptions (Fig. 7). As shown in Fig. 6, grasses are abundant in most hearth samples, the exception being OSC_286 H in SU 82 (SU 13). In this later sample, as in the associated samples, grasses are scarce compared to the non-grass phytoliths, which would support the hypothesis that during this more wooded period, the inhabitants used the available resources for fires. Unlike SU 13 and the non-hearth samples from SU 11, the two hearth structures (SU 53 and SU 50, also from SU 11) show a dominance of grass phytoliths. However, the palimpsest nature of SU 11 limits our ability to refine the chronology of these samples, and thus the relationship between the hearth and non-hearth samples. In any case, the pattern of grass predominance in the hearths continues throughout the sequence.

Previous studies of modern reference collections from the Mediterranean region have shown that grass phytoliths can attach to tree bark (~30 %) (Albert and Weiner, 2001; Tsartsidou et al., 2007). Hence, the identification of grasses in hearths could be partially explained by their association with the bark of woody plants. This situation was observed in various Middle Palaeolithic sites from the Levant, such as Kebara, Tabun and Hayonim caves (Albert et al., 1999, 2000, 2003).

Additionally, the presence of grasses in hearth structures may serve different purposes. For instance, they are known to have been, and still be, used by hunter-gatherer communities as tinder to start fires. This is the case among the Hadza (RMA personal observation) or the!Kung of Nyae Nyae (Marshall, 1976). Given the limited number of studies that have focused on identifying phytoliths from Palaeolithic hearths, it is worth noting that few of these studies have revealed a higher concentration of grasses in the hearths. One such site is the Abrigo de Quebrada in Valencia, Spain (Esteban et al., 2017). The significant number of grass phytoliths found in the hearths and hearth-related samples at this site was interpreted as indicating their potential use in setting fires, achieving specific combustion properties or other purposes beyond firemaking. At Grotte XVI in France, the high abundance of grasses during the Upper Palaeolithic was interpreted as possibly representing bedding that was subsequently burned to clean the site (Karkanas et al., 2002). At Amud Cave (Madella et al., 2002), the grass phytoliths identified in association with the hearths mainly came from the husk, the outer covering of seeds. In such instances, the presence of grasses was interpreted as indicating a process involving the removal of the husk from the seeds, followed by drying and subsequent consumption.

The results from Oscurusciuto show a higher concentration of grass phytoliths in the hearths than in the hearth-related samples. This pattern is consistent throughout the sequence, starting from SU 11 (SM 2). Although we identified phytoliths characteristic of grass husks in some hearth samples, unlike at Amud Cave, these were never abundant. Therefore, while we cannot rule out the possibility that grass seeds were consumed at Oscurusciuto, the low quantity of phytoliths from husks, together with the presence of phytoliths from other plant parts (e.g., leaves and stems) in the hearths, provides insufficient evidence to consider them a potential source of consumption.

Therefore, based on the current data and until a more detailed study of the fires is carried out to determine temperature and integrate it with other fire-related analyses, we interpret the higher abundance of grass phytoliths in these hearths to Neanderthal decisions regarding the type of fuel selected to start and/or maintain fires or to their specific thermal properties (i.e. to produce smoke for specific purposes such as smoking meat (Valensi et al., 2013)).

The similarity in phytolith composition between hearths and hearth-related samples in most samples is probably due to the dispersion of ash in the living floors. This is supported by the identification of wood ash calcite in the hearths and hearth-related sediments, as well as the presence of microcharcoal. Ash scattering has been identified at other Middle Palaeolithic sites such as Kebara Cave, Abrigo de Quebrada or Grotte XVI (Albert et al., 2000; Esteban et al., 2017; Karkanas et al., 2002) and at Middle Stone Age sites such as Border Cave in South Africa (Wadley et al., 2020). In the latter study, the authors hypothesised that the ash scattering identified in this site 200 thousand years ago may have been the result of cleaning and maintenance. This is based on several ethnographic studies and the experimental results of Hakbijl (2002), which showed that ash repels crawling insects and blocks their breathing and biting apparatus. Despite further studies focusing on this aspect would be needed, at this stage, this might well be a plausible explanation for the presence of scattered ashes observed both at Oscurusciuto and other Middle Palaeolithic sites from the Mediterranean. On the other hand, we were unable to detect plant bedding in the analysed samples based on phytolith or FTIR analyses. This absence could be due to the samples analysed not perfectly corresponding to the bedding area used by Neanderthals. It could also be due to bedding being prepared with materials other than plants (e.g., skins). Another explanation, which might be related to a brief occupation of the shelter by Neanderthals, preventing them from preparing efficient plant bedding, is contradicted by the archaeological clues. Indeed, evidence of an articulated spatial organization (including multipurpose activity areas, signs of preventive maintenance of workspaces, and a segregated refuse disposal sector) is more commonly associated with planned, long-term camps than with brief stopping place or short-term occupations. An extension to the study area, in conjunction with the currently ongoing micromorphological analyses, will contribute to clarifying this aspect.

In summary, our results at Oscurusciuto indicate that the late Neanderthal populations in southern Italy adapted their daily activities in response to the changing environment of MIS 3 by selecting and making use of the variable vegetation resources available in the surrounding landscape. It also appears that, alongside other woody plants, grasses were preferentially used in fires, either as starting materials or because of their specific thermal properties. The presence of wood ash as a major component of the deposits, including non-hearth samples, suggests that it was deliberately spread, possibly for maintenance and cleaning purposes, as has been observed at other prehistoric sites.

5. Conclusions

Oscurusciuto was occupied by late Neanderthals during 12,200 ka (~55 ka to ~42.8 ka BP). Our results show significant changes in vegetation composition during this period, with considerable temporal variation. These changes included a transition from forested environments in the lower levels (~55 ka) to more open environments in the upper levels (~42.8 ka). From SU 11 onwards, an increase in presence of Poaceae plants from the C_3 Pooid subfamily was observed, with alternating periods of mixed vegetation. This pattern included semi-open woodlands and woodlands (SU 8, SU 4, SU 3 and SU 1) interspersed with more open forest steppe environments during SU 9, SU 7 and SU 2. The arboreal vegetation consisted of evergreen and deciduous oak forests, with a continued presence of other mesophytes and Mediterranean woody taxa. Furthermore, a transition in vegetation from SU 4, featuring an open environment and forest steppe, to SU 3, marked by a wetter and more temperate phase with a *Quercus*-dominated forest environment, can be seen when integrating the results with those of the fauna. SU 2 marks a transition back to a more open environment. This is consistent with the increase in the number of horse and goat remains in this phase.

The chemical alteration observed in most of the phytoliths is probably due to the presence of calcium carbonate-rich sediments resulting from the weathering of the calcarenite bedrock, combined with wood ash (pyrogenic calcite) and exposure to meteoric water. Stomatocysts would develop on various substrates, such as the leaves and branches of bryophytes, which would provide microhabitats and sustenance for these microalgae. The potential presence of mosses and/or bryophytes could be due to high humidity throughout the sequence, but also to their deliberate introduction to the site, either alone or with other plants, as shown by the strong positive link between phytoliths and chrysophytes.

Evidence of human use of plants has been found in both the living floors and the hearths. The analyses of samples corresponding to some of the hearths revealed two main features: the abundance of grass phytoliths in hearths from SU 11 onwards, and a high degree of morphological similarity between phytolith assemblages in hearth samples and their associated samples, with few exceptions. These results suggest that grasses were deliberately used in the fires, probably to help start and/or maintain them, or for their specific thermal properties. The similarity observed in the phytolith composition of hearths and associated samples is probably due to the dispersal of ash in the living floors probably for maintenance and cleaning purposes. At present, it is not possible to consider the use of grasses as a potential food source.Bedding cannot be proven at this stage and requires further analysis.

CRediT authorship contribution statement

Rosa M. Albert: Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Conceptualization. **Juan Ochando:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Formal analysis. **Ivan Martini:** Writing – review & editing, Resources. **Carlos Alberto Rivera-Rondón:** Writing – review & editing, Investigation, Formal analysis. **Jacopo Crezzini:** Writing – review & editing. **Clarissa Dominici:** Writing – review & editing. **Vincenzo Spagnolo:** Writing – review & editing, Resources. **Paolo Boscato:** Writing – review & editing. **Annamaria Ronchitelli:** Writing – review & editing. **Francesco Boschin:** Writing – review & editing, Funding acquisition, Resources. **Francesco Berna:** Writing – review & editing, Resources, Methodology, Investigation, Funding acquisition, Conceptualization.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jasrep.2025.105399.

Data availability

Data will be made available on request.

References

Adam, D.P., Mahood, A.D., 1981. Chrysophyte Cysts as potential Environmental Indicators. Geol. Soc. Am. Bull. 92, 839–844.

Albert, R.M., Tsatskin, A., Ronen, A., Lavi, O., Estroff, L., Lev-Yadun, S., Weiner, S., 1999. Mode of occupation of Tabun Cave, Mt Carmel Israel during the Mousterian period: a study of the sediments and the phytoliths. J. Archaeol. Sci. 26 (10), 1249–1260. https://doi.org/10.1006/jasc.1999.0355.

Albert, R.M., Weiner, S., Bar-Yosef, O., Meignen, L., 2000. Phytoliths in the Middle Palaeolithic deposits of Kebara Cave, Mt Carmel, Israel: study of the plant materials used for fuel and other purposes. J. Archaeol. Sci. 27 (10), 931–947. https://doi.org/10.1006/jasc.2000.0507.

Albert, R.M., Weiner, S., 2001. Study of phytoliths in prehistoric ash layers from Kebara and Tabun caves using a quantitative approach. In: Meunier, J.D., Colin, F., Faure-Denard, L. (Eds.), Phytoliths, Applications in Earth Science and Human History. Balkema, Lisse, pp. 251–266.

Albert, R.M., Bar-Yosef, O., Meignen, L., Weiner, S., 2003. Phytolith and mineralogical study of hearths from the Middle Palaeolithic levels of Hayonim Cave (Galilee, Israel). J. Archaeol. Sci. 30 (3), 461–480. https://doi.org/10.1006/jasc.2002.0854.

Albert, R.M., Bamford, M.K., Cabanes, D., 2006. Taphonomy of phytoliths and macroplants in different soils from Olduvai Gorge (Tanzania) and the application to Plio-Pleistocene palaeoanthropological samples. Quat. Int. 148, 78–94. https://doi.org/10.1016/j.quaint.2005.11.026.

Albouy, B., Paquin, S., Hinz, M., Wren, C.D., Burke, A., 2023. The last of them. investigating the paleogeography of the last neanderthals in Europe (marine isotopic stage 3). In: Seuru, S., Albouy, B. (Eds.), Modelling Human-Environment Interactions in and beyond Prehistoric Europe, Themes in Contemporary Archaeology, 2. Springer, Cham.

Albouy, B., Paquin, S., Riel-Salvatore, J., Kageyama, M., Vrac, M., Burke, A., 2024. Evaluating the impact of climate change and millennial variability on the last Neanderthal populations in Europe (Marine Isotope Stage 3). Quat. Sci. Rev. 338 (108812). https://doi.org/10.1016/j.quascirev.2024.108812.

Allen, J.R., Watts, W.A., Huntley, B., 2000. Weichselian palynostratigraphy, palaeovegetation and palaeoenvironment; the record from Lago Grande di Monticchio, southern Italy. Quat. Int. 73–74, 91–110. https://doi.org/10.1016/S1040-6182(00)00067-7.

Allen, J.R.M., Huntley, B., 2009. Last Interglacial palaeovegetation, palaeoenvironments and chronology: a new record from Lago Grande di Monticchio, southern Italy. Quat. Sci. Rev. 28, 1521–1538. https://doi.org/10.1016/j.quascirev.2009.02.013.

An, X.-H., 2016. Morphological characteristics of phytoliths from representative conifers in China. Palaeoworld 116–127. https://doi.org/10.1016/j.palwor.2016.01.002.

Bai, X., Piatek, J., Wolowski, K., Bu, Z.-J., Chen, X., 2021. Chrysophyte stomatocysts and their associatons with environmental variables in three peatlands in the subtropical monsson climate zone of China. Ecol. Ind. 121, 107–125. https://doi.org/10.1016/j.ecolind.2020.107125.

Banks, W.E., d'Errico, F., Peterson, A.T., Kageyama, M., Sima, A., Śanchez-Goñi, M.-F., 2008. Neanderthal extinction by competitive exclusion. PLoS One 3, e3972.

Bartoli, F., 1985. Crystallochemistry and surface properties of biogenic opal. J. Soil Sci. 36, 335–350.

Bartoli, F., Wilding, L.P., 1980. Dissolution of biogenic opal as a function of its physical and chemical properties. Soil Sci. Soc. Amer. J. 44, 873–878.

Berna, F., Behar, A., Shahack-Gross, R., Berg, J., Boaretto, E., Gilboa, A., Sharon, I., Shalev, S., Shilstein, S., Yahalom-Mack, N., Zorn, J.R., Weiner, S., 2007. Sediments exposed to high temperatures: reconstructing pyrotechnological processes in late Bronze and Iron Age Strata at Tel Dor (Israel). J. Archaeol. Sci. 34 (3), 358–373. https://doi.org/10.1016/j.jas.2006.05.011.

Boscato, P., Gambassini, P., Ranaldo, F., Ronchitelli, A., 2011. Management of Paleoenvironmental resources and exploitation of raw materials at the Middle Paleolithic Site of Oscurusciuto (Ginosa, Southern Italy): units 1 and 4. In: Conard, N.J., Richter, J. (Eds.), Neanderthal Lifeways, Subsistence and Technology. One Hundred Fifty Years of Neanderthal Study. Springer, New York, pp. 87-96. Dordrecht: Springer Netherlands. https://doi.org/10.1007/978-94-007-0415-2_9.

Boscato, P., Ronchitelli A. 2017. Le strutture di combustione al Riparo l'Oscurusciuto (Ginosa e TA). In Radina F., (ed.) Atti XLVII Riunione Scientifica I.I.P.P., pp. 175–180.

Boschin, F., Boscato, P., Berto, C., Crezzini, J., Ronchitelli, A., 2018. The palaeoecological meaning of macromammal remains from archaeological sites exemplified by the case study of Grotta Paglicci (Upper Palaeolithic, southern Italy). Quat. Res. 90, pp. 470-482. https://doi.org/ 10.1017/qua.2018.59.

Boschin, F., Columbu, A., Spagnolo, V., Crezzini, J., Bahain, J.-J., Falguères, C., Benazzi, S., Boscato, P., Ronchitelli, A., Moroni, A., Martini, I., 2022. Human occupation continuity in southern Italy towards the end of the Middle Palaeolithic: a palaeoenvironmental perspective from Apulia. J. Quat. Sci. 37, 204–216. https://doi.org/10.1002/jqs.3319.

Bronk Ramsey, C., 2021. Oxcal 4.4.4 calibration program. arch. ox. ac. uk/oxcal/OxCal. Website https://c14.

Cabanes, D., Weiner, S., Shahack-Gross, R., 2011. Stability of phytoliths in the archaeological record: a dissolution study of modern and fossil phytoliths. J. Archaeol. Sci. 38, 2480–2490. https://doi.org/10.1016/j.jas.2011.05.020.

Cabanes, D., Shahack-Gross, R., 2015. Understanding Fossil Phytolith Preservation: the Role of Partial Dissolution in Paleoecology and Archaeology. PLoS One 10 (5), e0125532. https://doi.org/10.1371/journal.pone.0125532.

Carmignani, L., Soressi, M., Ronchitelli, A., Boschin, F., 2024. IUP Technological Signatures or Mousterian Variability? the Case of Riparo l'Oscurusciuto (Southern Italy. J. Paleolit. Archaeol. 7, 31. https://doi.org/10.1007/s41982-024-00196-w.

Carnelli, A.L., Theurillat, J.P., Madella, M., 2004. Phytolith types and type-frequencies in subalpine–alpine plant species of the European Alps. Rev. Palaeobot. Palynol. 129, 39–65. https://doi.org/10.1016/j.revpalbo.2003.11.002.

Collura, L.V., Neumann, K., 2017. Wood and bark phytoliths of West african woody plants. Quat. Int. 434, 142–159. https://doi.org/10.1016/j.quaint.2015.12.070.

Crezzini, J., Boscato, P., Ronchitelli, A., Boschin, F., 2023. A peculiar exploitation of ungulates at Grotta di Santa Croce: bone grease rendering and nutritional patterns among neanderthals in southern Italy. Hist. Biol. 1–13. https://doi.org/10.1080/08912963.2023.2242630.

d'Errico, F., Sánchez Goñi, M.F., 2003. Neandertal extinction and the millennial scale climatic variability of OIS 3. Quat. Sci. Rev. 22, 769–788. https://doi.org/10.1016/S0277-3791(03)00009-X.

Desprat, S., Díaz-Fernández, P.M., Coulon, T., Ezzat, L., Pessarossi-Langlois, J., Gil, L., Morales-Molino, C., Sánchez Goñi, M.F., 2015. *Pinus nigra* (European black pine) as the dominant species of the last glacial pinewoods in south-western to central Iberia: a morphological study of modern and fossil pollen. J. Biogeogr. 42, 1998–2009. https://doi.org/10.1111/jbi.12566.

Dimbleby, G.W., 1985. The palynology of archaeological sites. Academic Press, London.

Erdtman, G., 1969. Handbook of Palynology. Hafner Publishing Company, Nueva York.

Esteban, I., Albert, R.M., Eixea, A., Zilhao, J., Villaverde, V., 2017. Neanderthal use of plants and past vegetation reconstruction at the Middle Paleolithic site of Abrigo de la Quebrada (Chelva, Valencia, Spain). Archaeol. Anthropol. Sci. 8, 265–278. https://doi.org/10.1007/s12520-015-0279-7.

Esteban, I., Marean, C.W., Fisher, E.C., Karkanas, P., Cabanes, D., Albert, R.M., 2018. Phytoliths as indicator of early modern humans plant gathering strategies, fire fuel and site occupation intensity during the Middle Stone Age at Pinnacle Point 5-6 (south coast, South Africa). PLoS One 13 (6), e0198558. https://doi.org/10.1371/journal.pone.0198558.

Fletcher, W.J., Sánchez Goñi, M.F., Allen, J.R., Cheddadi, R., Combourieu-Nebout, N., Huntley, B., Lawson, I., Londeix, L., Magri, D., Margari, V., Müller, U.C., Naughton, F., Novenko, E., Roucoux, K., Tzedakis, P.C., 2010. Millennial-scale variability during the last glacial in vegetation records from Europe. Quat. Sci. Rev. 29, 2839–2864. https://doi.org/10.1016/j.quascirev.2009.11.015.

Fraysse, F., Pokrovsky, O.S., Schott, J., Meunier, J.-D., 2009. Surface chemistry and reactivity of plant phytoliths in aqueous solutions. Chem. Geol. 258, 197–206. https://doi.org/10.1016/j.chemgeo.2008.10.003.

Gabucio, M.J., Cáceres, I., Rivals, F., Bargalló, A., Rosell, J., Saladié, P., Vallverdú, J., Vaquero, M., Carbonell, E., 2018a. Unraveling a Neanderthal palimpsest from a zooarcheological and taphonomic perspective. Archaeol. Anthropol. Sci. 2018 (10), 197–222. https://doi.org/10.1007/s12520-016-0343-y.

Gabucio, M.J., Fernández-Laso, C., Rosell, J., 2018b. Turning a rock shelter into a home. Neanderthal Use of Space in Abric Romanílevels M and o, Historical Biology 30 (6), 743–766. https://doi.org/10.1080/08912963.2017.1340470.

Gao, G., Jie, D., Wang, Y., Liu, L., Liu, H., Li, D., Li, N., Shi, J., Leng, C., 2017. Phytolith reference study for identifying vegetation changes in the forest grassland region of northeast China. Boreas. https://doi.org/10.1111/bor.12280. ISSN 0300-9483.

Gao, G., Jie, D., Liu, L., Liu, H., Gao, Z., Li, D., Li, N., 2018. Phytolith characteristics and preservation in trees from coniferous and broad-leaved mixed forest in an eastern mountainous area of Northeast China. Rev. Palaeobot. Palynol. 255, 43–56. https://doi.org/10.1016/j.revpalbo.2018.05.001.

Goldberg, P., Macphail, R.J., 2006. Practical and Theoretical Geoarchaeology. Wiley-Blackwell, 468 pp. ISBN: 978-0-632-06044-3.

Goldberg, P., Miller, C.E., Mentzer, S., 2017. Recognizing Fire in the Paleolithic Archaeological Record. Curr. Anthropol. 58 (16), 175–190. https://www.journals.uchicago.edu/doi/epdf/10.1086/692729.

Hakbijl, T., 2002. The Traditional, Historical and Prehistoric use of Ashes as an Insecticide, with an Experimental Study on the Insecticidal Efficacy of Washed Ash. Environ. Archaeol. 7 (1), 13–22. https://doi.org/10.1179/env.2002.7.1.13.

Hemming, S.R., 2004. Heinrich events: Massive late Pleistocene detritus layers of the North Atlantic and their global climate imprint. Review of Geophysics 42 (1).

Higham, T., Frouin, M., Douka, K., Ronchitelli, A., Boscato, P., Benazzi, S., Crezzini, J., Spagnolo, V., McCarty, M., Marciani, G., Falcucci, A., Rossini, M., Arrighi, S., Dominici, C., Devièse, T., Schwenninger, J.-L., Martini, I., Moroni, A., Boschin, F., 2024. Chronometric dating and stratigraphic data support discontinuity between neanderthals and early *Homo sapiens* in the Italian Peninsula. Nat. Commun. 15, 8016. https://doi.org/10.1038/s41467-024-51546-9.

Karkanas, P., Rigaud, J.P., Simek, J.F., Albert, R.M., Weiner, S., 2002. Ash, bones and guano: a study of the minerals in the sediments of Grotte XVI (Dordogne, France). J. Archaeol. Sci. 29 (7), 721–732. https://doi.org/10.1006/jasc.2001.0742.

Katz, O., Cabanes, D., Weiner, S., Maeir, A.M., Boaretto, E., Shahack-Gross, R., 2010. Rapid phytolith extraction for analysis of phytolith concentrations and assemblages during an excavation: an application at tell es-Safi/Gath. Israel. J. Archaeol. Sci. 37, 1557–1563. https://doi.org/10.1016/j.jas.2010.01.016.

Kimmel Center of Archaeological Science, Weizmann Institute of Science FTIR reference collection of standard materials (http://www.weizmann.ac.il/kimmel-arch/infrared-spectra-library).

Klein, R.L., Geis, J.W., 1978. Biogenetic opal in the Pinaceae. Soil Sci. 126, 145–156.

Kristiansen, J., 2000. Cosmopolitan chrysophytes. Systematics and Geography of Plants. Vol. 70, No. 2, Fresh Water Algae: Taxonomy, Biogeography and Conservation, pp. 291-300.

Hublin, J.-J., 2009. The origin of Neandertals. PNAS 106, 16022–16027. https://doi.org/10.1073/pnas.0904119106.

Hublin, J.-J., Roebroeks, W., 2009. Ebb and flow or regional extinctions? on the character of Neandertal occupation of northern environments. C.R. Palevol 8, 503–509. https://doi.org/10.1016/j.crpv.2009.04.001.

Liu, H., Meunier, J.D., Grauby, O., Labille, J., Alexandre, A., Barboni, D., 2023. Dissolution does not affect grass phytolith assemblages. Palaeogeogr. Palaeoclimatol. Palaeoecol. 610, 111345. https://doi.org/10.1016/j.palaeo.2022.111345.

Long, J.A., Stoy, P.C., 2013. Quantifying the periodicity of Heinrich and Dansgaard–Oeschger events during marine oxygen isotope stage 3. Quat. Res. 79 (3), 413–423. https://doi.org/10.1016/j.yqres.2013.02.003.

Lubrano, V., Rufà, A., Blasco, R., Rivals, F., Rosell, J., 2025. Solving the puzzle of neanderthal occupations: a reassessment of temporal indicators of occupation duration. Archaeol. Anthropol. Sci. 17, 61. https://doi.org/10.1007/s12520-025-02163-0.

Madella, M., Jones, M.K., Goldberg, P., Goren, Y., Hovers, E., 2002. The exploitation of plant resources in Amud Cave (Israel): the evidence from phytolith studies. J. Archaeol. Sci. 29, 703–719. https://doi.org/10.1006/jasc.2001.0743.

Marciani, G., Spagnolo, V., Aureli, D., Ranaldo, F., Boscato, P., Ronchitelli, A., 2016. Middle Palaeolithic technical behaviour: material import-export and Levallois production at the SU 13 of Oscurusciuto rockshelter. Southern Italy. J. of Lithic Studies 3. https://doi.org/10.2218/jls.v3i2.1414.

Marciani, G., Arrighi, S., Aureli, D., Spagnolo, V., Boscato, P., Ronchitelli, A., 2018. Middle Palaeolithic lithic tools. Techno-functional and usewear analysis of target objects from SU 13 at the Oscurusciuto rockshelter. Southern Italy. J. of Lithic Studies 5, 1–30.

Marciani, G., Spagnolo, V., Martini, I., Casagli, A., Sulpizio, R., Aureli, D., Boscato, P., Ronchitelli, A., Boschin, F., 2020. Neanderthal occupation during the tephra fall-out: Technical and hunting behaviours, sedimentology and settlement patterns in SU 14 of Oscurusciuto rockshelter (Ginosa, southern Italy). Archaeol. Anthropol. Sci. 12, 152. https://link.springer.com/article/10.1007/s12520-020-01116-z.

Marciani G., 2024. Flexibility of the Levallois Concept in the Italian Late Middle Palaeolithic. A view from the Oscurusciuto rockshelter. BAR International Series 3183, BAR Publishing, Oxford.

Martini, I., Baucon, A., Boschin, F., 2021. Depositional processes and environmental settings in rockshelters: the case of the prehistoric Oscurusciuto site (Southern Italy). Geol. Mag. 158, 891–904. https://doi.org/10.1017/S0016756820001041.

Marshall, L., 1976. The !Kung of Nyae Nyae. Harvard University Press, Cambridge (MA).

Melchionna, M., Di Febbraro, M., Carotenuto, F., Rook, L., Mondanaro, A., Castiglione, S., Serio, C., Vero, V.A., Tesone, G., Piccolo, M., Diniz-Filho, J.A.F., Raia, P., 2018. Fragmentation of neanderthals' pre-extinction distribution by climate change. Palaeogeogr. Palaeoclimatol. Palaeoecol. 496, 146–154. https://doi.org/10.1016/j.palaeo.2018.01.031.

Moclán, A., Huguet, R., Márquez, B., Álvarez-Fernández, A., Laplana, C., Arsuaga, J.L., Pérez-González, A., Baquedano, E., 2023. Identifying activity areas in a neanderthal hunting camp (the Navalmaíllo Rock Shelter, Spain) via spatial analysis. Archaeol. Anthropol. Sci. 15, 44. https://doi.org/10.1007/s12520-023-01746-z.

Moncel, M.H., Guillemot, P., Chacón, M.G., Abrunhosa, A., Richard, M., Fernandes, P., Hardy, B., Allué, E., Pois, V., 2024. Site Settlement patterns during MIS 3 in the Southeast of France: the Lithic Assemblages of two Phases of Occupation (Levels 4.1 and 4.2) at the Abri du Maras. J. Paleol Archaeol. 7, 23. https://doi.org/10.1007/s41982-024-00190-2.

Morales-Barbero, J., Martinez, P.A., Ferrer-Castán, D., Olalla-Tárraga, M.Á., 2018. Quaternary refugia are associated with higher speciation rates in mammalian faunas of the Western Palaearctic. Ecography 41 (4), 607–621.

Neumann, K., Strömberg, C., Ball, T., Albert, R.M., Vrydaghs, L., Scott Cummings, L., 2019. International Code for Phytolith Nomenclature (ICPN) 2.0. Ann. Bot. 124 (2), 189–199. https://doi.org/10.1093/aob/mci172.

Ochando, J., Carrión, J.S., Magri, D., Marín-Arroyo, A.B., Di Rita, F., Munuera, M., Michelangeli, F., Amorós, G., Milošević, S., Bogićević, K., Dimitrijević, V., Nenadić, D., Roksandic, M., Mihailović, D., 2024. Balkan neanderthals: the Late Pleistocene palaeoecological sequence of Pešturina Cave (Niš, Serbia). Quat. Sci. Rev. 330, 108600.

Ochando, J., Di Rita, F., Magri, D., Crezzini, J., Burgassi, A., Marciani, G., Berna, F., Boschin, F., Moroni, A., Spagnolo, V., 2025. Environment and hunting territories for Late Neanderthals in central Italy: new palaeoecological data from Grotta dei Santi (Monte Argentario Tuscany, Italy). In: Val-Peón, C., Ochando, J., Fernández-García, M. (Eds.), Neanderthal landscapes in southern Europe. J. Archaeol. Sci. Rep. 66, 105319.

Ordonez, A., Svenning, J.C., 2017. Consistent role of Quaternary climate change in shaping current plant functional diversity patterns across European plant orders. Sci. Rep. 7 (1), 42988.

Rashid, H., Hesse, R., 2003. Evidence for an additional Heinrich event between H5 and H6 in the Labrador Sea. Paleoceanography 18 (4), 1077.

Regev, L., Poduska, K.M., Addadi, L., Weiner, S., Boaretto, E., 2010. Distinguishing between calcites formed by different mechanisms using infrared spectrometry: archaeological applications. J. Archaeol. Sci. 37, 3022–3029. https://doi.org/10.1016/j.jas.2010.06.027.

Reimer, P.J., Austin, W.E.N., Bard, E., Bayliss, A., Blackwell, P.G., Bronk Ramsey, C., Butzin, M., Cheng, H., Edwards, R.L., Friedrich, M., Grootes, P.M., Guilderson, T.P., Hajdas, I., Heaton, T.J., Hogg, A.G., Hughen, K.A., Kromer, B., Manning, S.W., Muscheler, R., Palmer, J.G., Pearson, C., van der Plicht, J., Reimer, R.W., Richards, D.A., Scott, E.M., Southon, J.R., Turney, C.S.M., Wacker, L., Adolphi, F., Büntgen, U., Capano, M., Fahrni, S.M., Fogtmann-Schulz, A., Friedrich, R., Köhler, P., Kudsk, S., Miyake, F., Olsen, J., Reinig, F., Sakamoto, M., Sookdeo, A., Talamo, S., 2020. The IntCal20 Northern Hemisphere radiocarbon age calibration curve (0–55 cal kBP). Radiocarbon 62 (4), 725–757. https://doi.org/10.1017/RDC.2020.41.

Rivera-Rondón, C.A., Catalan, J., 2017. The ratio between chrysophycean cysts and diatoms in temperate, mountain lakes: some recommendations for its use in paleolimnology. J. Paleolimnol. https://doi.org/10.1007/s10933-017-9946-2.

Rodríguez-Cintas, A., Albert, R., Bamford, M.K., Stanistreet, I.G., Stollhofen, H., Stone, J., Rivera-Rondon, C., Pronzato, R., Njau, J.K., Schick, K., Toth, N., 2020. Paleovegetation changes recorded in Palaeolake Olduvai OGCP core 2A (2.09-2.12 Ma) Naibor Soit Formation Olduvaig Gorge, Tanzania. Palaeogeogr. Palaeoclimatol. Palaeoecol. 557. https://doi.org/10.1016/j.palaeo.2020.109928.

Rosell, J., Modesto-Mata, M., Fernández-Laso, M.C., Modolo, M., Blasco, R., 2019. Refitting bones to reconstruct the diversity in Middle Palaeolithic human occupations: the case of the Abric Romaní site (Capellades, Barcelona, Spain). Archaeol. Anthropol. Sci. 11, 4601–4619. https://doi.org/10.1007/s12520-019-00887-4.

PhytCore DB. 2016. Phytolith online database. https://phytcore.org/phytolith/.

Sánchez Goñi, M.F., Harrison, S.P., 2010. Millennial-scale climate variability and vegetation changes during the last Glacial: concepts and terminology. Quat. Sci. Rev. Vegetation Response to Millennial-Scale Variability during the Last Glacial 29, 2823–2827. https://doi.org/10.1016/j.quascirev.2009.11.014.

Silver, P.A., 2020. Remarkably preserved cysts of the extinct synurophyte, Mallomonas ampla, uncovered from a 48 Ma freshwater Eocene Lake. Nat. Sci. Rep. 10, 5204. https://doi.org/10.1038/s41598-020-61993-1.

Sommer, R.S., Zachos, F.E., 2009. Fossil evidence and phylogeography of temperate species:‘glacial refugia’and post-glacial recolonization. J. Biogeogr. 36 (11), 2013–2020.

Sossa-Ríos, S., Mayor, A., Sánchez-Romero, L., Mallol, C., Vaquero, M., Hernández, C.M., 2024. The time of the stones: a call for palimpsest dissection to explore lithic record formation processes. J. Archaeol. Method Theory. https://doi.org/10.1007/s10816-024-09666-5.

Sossa-Ríos, S., Mayor, A., Tomé, L., Davara, J., Kleinhapl, S., Mallol, C., Sánchez-Romero, L., Vaquero, M., Hernández, C.M., 2025. Knapping… Sleeping and Consuming? Spatial Variability in the High-Resolution Neanderthal Context of Abric del Pastor (Alcoi, Eastern Iberia). J. Paleol. Archaeol. 8, 23. https://doi.org/10.1007/s41982-025-00222-5.

Spagnolo, V., Marciani, G., Aureli, D., Berna, F., Boscato, P., Ranaldo, F., Ronchitelli, A., 2016. Between hearths and volcanic ash: the SU 13 palimpsest of the Oscurusciuto rockshelter (Ginosa – southern Italy): analytical and interpretative questions. Quat. Int. 417, 105–121. https://doi.org/10.1016/j.quaint.2015.11.046.

Spagnolo, V., Marciani, G., Aureli, D., Berna, F., Toniello, G., Astudillo, F., Boschin, F., Boscato, P., Ronchitelli, A., 2019. Neanderthal activity and resting areas from stratigraphic unit 13 at the Middle Palaeolithic site of Oscurusciuto (Ginosa-Taranto, Southern Italy). Quat. Sci. Rev. 217, 169–193. https://doi.org/10.1016/j.quascirev.2018.06.024.

Spagnolo, V., Marciani, G., Aureli, D., Martini, I., Boscato, P., Boschin, F., Ronchitelli, A., Martini, I., 2020. Climbing the time to see Neanderthal behaviour's continuity and discontinuity: SU 11 of the Oscurusciuto rockshelter (Ginosa, Southern Italy). Archaeol. Anthropol. Sci. 9. https://doi.org/10.1007/s12520-019-00971-9.

Stromberg, C.A., Dunn, R.E., Crifo, C., Harris, E.B., 2018. Phytoliths in Paleoecology: Analytical considerations, current use and Future directions. In Methods in Paleoecology: reconstructing Cenozoic Terrestrial Environments and Ecological Communities (Ed. D. A. Croft, D. F.Su, S.W., Simpson). Vertebrate Paleobiology and Paleoantrholpology Series. Springer Nature Switzerland AG 2018, 235–288.

Svensson, A., Andersen, K.K., Bigler, M., Clausen, H.B., Dahl-Jensen, D., Davies, S.M., Johnsen, S.J., Muscheler, R., Rasmussen, S.O., Röthlisberger, R., Peder Steffensen, J., Vinther, BoM., 2006. The Greenland Ice Core Chronology 2005, 15–42ka. Part 2: comparison to other records. Quat. Sci. Rev. Critical Quaternary Stratigraphy 25, 3258–3267. https://doi.org/10.1016/j.quascirev.2006.08.003.

Tsartsidou, G., Lev-Yadun, S., Albert, R.M., Miller-Rosen, A., Efstratiou, N., Weiner, S., 2007. The phytolith archaeological record: strengths and weaknesses evaluated based on a quantitative modern reference collection from Greece. J. Archaeol. Sci. 34 (8), 1262–1275. https://doi.org/10.1016/j.jas.2006.10.017.

Valensi, P., Michel, V., El Guennouni, K., Liouville, M., New data on human behaviour from a 160,000 year old Acheulean occupation level at Lazaret cave, south-east France: An archaeozoological approach. Quat. Int. 316, 123-139. Doi: 10.1016/j.quaint.2013.10.034.

van Andel, T.H., Davies, W. (Eds.), 2003. Neanderthals and Modern Humans in the European Landscape during the Last Glaciation: Archaeological Results of the Stage 3 Project. McDonald Institute monographs. McDonald Institute for Archaeological Research ; Distributed by Oxbow Books, Cambridge : Oxford.

Van Cappellen, Ph., Qiu, L., 1997. Biogenic silica dissolution in sediments of the Southern Ocean. II. Kinetics. Deep-Sea Res II. 44, 1129–1149.

Van de Vijver, B., Beyens, L., 1997. The chrysophyte stomatocyst flora of the moss vegetation from Strømness Bay area, South Georgia. Arch. Protistenk. 148, 505–520.

Wadley, L., Esteban, I., de la Peña, P., Wojcieszak, M., Stratford, D., Lennox, S., d'Errico, F., Rosso, D.E., Orange, F., Backwel, L., Sievers, C., 2020. Fire and Grass-bedding construction 200 thousand years ago at Border Cave, South Africa. Science 369, 863–866. https://doi.org/10.1126/science.abc7239.

Watts, W.A., Allen, J.R., Huntley, B., 1996. Vegetation history and palaeoclimate of the last glacial period at Lago Grande di Monticchio, southern Italy. Quat. Sci. Rev. 15 (2–3), 133–153. https://doi.org/10.1016/0277-3791(95)00093-3.

Weiner, S., 2010. Microarchaeology. Beyond the Visible Archaeological Record. Cambridge University Press, New York.

Wilding, L.P., Drees, L.R., 1974. Contributions of forest opal and associated crystalline phases to fine silt and clay fractions of soils. Clays Clay Miner. 1974 (22), 295–306.

Wilkinson, A.N., Zeeb, B.A., Smol, J.P., 2001. Atlas of Chrysophycean Cysts vol. II, 169.

Xu, B., Poduska, K.M., 2014. Linking crystal structure with temperature sensitive vibrational modes in calcium carbonate minerals. Phys. Chem. Chem. Phys. 2014 (16), 17634. https://doi.org/10.1039/c4cp01772b.