Non-pollen palynomorphs as an aid to the identification of ancient farming activities: an experimental and archaeological approach

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Declaration of original authorship

I confirm that this is my own work and the use of all material from other sources has been properly and fully acknowledged.

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Abstract

This research aims to assess the potential of non-pollen microfossils in archaeological research, as this evidence provides an important and previously overlooked contribution to the investigation Neolithic farming activities and their environmental impact. The Ligurian Neolithic provides an excellent cultural and environmental framework to test this approach, given the presence of upland mires suggesting human-driven vegetation change. In particular, the study aims to assess whether the introduction of a pastoral economy is detectable in the palaeoecological record.

The analysis of a Middle Holocene sequence from an upland mire (Prato Spilla 'A', 1550m asl) allowed new inferences, partially questioning previous studies. The sequence was rich in NPPs, showing the occurrence of several types indicating, amongst others, hydrological changes, grazing herbivores on the site and a relatively dense tree canopy. The presence of Neolithic communities settled in the region makes it difficult to distinguish between natural and human-driven changes. However, due to the probable absence of long-distance transhumance in the period, it is likely that the outlined picture mostly results from natural events.

Deep cores dated to the Early and Middle Neolithic (6th-5th Millennium BC) from a coastal alluvial plain (Genoa, Piazza della Vittoria) were analysed. The results show the unequivocal presence of herbivores around a site where possible remains of pile-dwellings were found, as well as periods of desiccation and flooding of the area. This is a significance contribution to the archaeology of the region, given the paucity of evidence for human occupation of coastal areas during this period.

The issue of prehistoric field manuring was also addressed, studying samples from a Bronze Age terraced site (Castellaro di Uscio). Palynological analysis point to a relatively open landscape during the Final Bronze Age, complementing previous studies on charcoal macro-remains and suggesting that the collection of wood was highly selective.

Archaeological layers from a Neolithic cave (Cave of Arene Candide) were analysed, showing the validity of dung fungal spores to identify stabling layers in pastoral sites. In addition, a short chapter on stable nitrogen isotopes from bulk sediment samples was added, in order to test this method as a further tool for the investigation of dung deposits.

The potential of coprophilous spores as localised indicators to identify archaeological animal enclosures was assessed through the analysis of a range of modern samples from dung heaps, stable floors and outdoor corrals from sites characterised by different animal densities and frequency of use. A reference dataset of spore concentration per unit of volume and weight is provided as an aid to the interpretation of ancient contexts. The results show the importance of surface disturbance due to animal trampling as a likely driving factor for spore abundance, as well as the variability of coprophilous assemblages and dominant taxa. Light was shed on the informative potential of newly identified microfossils strongly associated with herbivore dung and of spores of hay-inhabiting thermophilic fungi. The method was tested on a stratified deposit from an abandoned rock shelter used as a stable for several decades, and the results compared to the abundance of faecal spherulites and total phosphorus. A clear match between these proxies was shown, as well as the relevance of the study to detect in the archaeological record short-term episodes of abandonment, leading to fungal growth and sporulation.

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1. INTRODUCTION

1.1 Research context and rationale

Since the 1970s, palaeoecological studies have started to include counting and identification of non-pollen palynomorphs (NPPs - also referred to as non-pollen microfossils, NPMs) as a means of refining the interpretation. For the sake of clarity, by "NPPs" is meant a range of microscopic fossils (c. 6 - 180μm), consisting mainly of fungal spores, algal spores, plant remains, animal remains and microscopic eggs. These elements are dispersed in the environment chiefly by atmospheric agents and can be still perfectly preserved even over a period of hundreds of thousands of years (Kalgutkar and Jansonius 2000). The resilience of fungal spores is due to their relative thickness and chemical composition. Their walls are made of chitin, a highly resistant long-chain polymer which also constitutes the exoskeleton of several terrestrial and marine arthropods (Webster and Weber 2007).

The research on NPPs has developed considerably in the last forty years, mainly due to the pioneering works by Baas van Geel (1972; 1978), that first shed light on the indicator value of the most commonly recurring microfossil "types". Despite the potential of the method, the number of studies related to the subject remained relatively few until very recently (Baker et al. 2013). Over the last ten years, an increasing interest in NPPs has resulted in the publication of two issues of *Review of Palaeobotany and Palynology* (v. 141, 2006; v. 186, 2012) and *Vegetation History and Archaeobotany* (v. 19, 2010) entirely dedicated to this topic. Although many types still remain to be identified, the relationships with pollen assemblages and modern analogues are now much better understood (Blackford and Innes 2006; Cugny et al. 2010).

However, in spite of a more frequent use of NPP analysis of lakes and bogs in palaeoecology, the scarcity of NPP-based studies focusing on archaeological soils and sediments appears remarkable, as already stressed more than ten years ago by van Geel et al. (2003). Only a limited number of works - most of which are listed in **table 1.1** - have focused on terrestrial and archaeological deposits, showing the informative potential of non-pollen microfossils in this field of research.

Table 1.1. Studies of non-pollen microfossils from archaeological deposits and dryland sequences.

Reference	Site/sample type
Aptroot and van Geel 2006	Mammoth coprolites
Bos et al. 2006	Mesolithic site
Bos et al. 2013	Palaeolithic occupation
Brozio et al. 2013	Neolithic site
Buurman et al. 1995	Bronze Age site
Carrión et al. 2005	Palaeolithic cave
Chichinadze and Kvavadze 2013	Bronze hoard
Davis et al. 1984	Pleistocene cave
Ivanova and Marfenina 2015	Profiles from medieval site
Kaal et al. 2013	Bronze Age rock art site
Kvavadze et. al. 2008	Medieval grave
Kvavadze et al. 2010	Bronze Age burials
Kvavadze and Kakhiani 2010	Bronze Age barrow
López-Sáez and López-Merino 2007	Neolithic sites
Mudie and Leliévre 2013	Shell midden
Pittau et al. 2012	Neolithic settlement
Pirozynski et al. 1988	Mastodon coprolites
Revelles et al. 2016	Profiles from Early Neolithic site
Uzquiano et al. 2012	Bronze-Iron Age settlement
van Geel et al. 2003	Roman settlement
van Smeerdijk et al. 1995	Medieval plaggen soil

1.2 Hypotheses and scope of the research

The study aims to test the following hypotheses:

1. During the Middle Holocene of Liguria (north west Italy), environmental change at upland and coastal sites were driven by episodes of animal, and possibly also human, disturbance.
2. Variations in the concentrations of dung-specific NPPs from modern pastoral contexts reflect the conditions recorded on the sites, providing

information that can be used to investigate archaeological animal enclosures.

3. Non-pollen microfossil analysis from dryland archaeological stabling deposits is an overlooked approach, and can add useful information on animal management, which differs from the contribution of phytolith analysis and micromorphology.
4. NPP analysis can be employed to investigate agricultural terraces and anthropogenic soils detecting or ruling out possible manuring practices.

The main features of the study sites under investigation are summarised below, and will be treated in more detail in the respective chapters. In order to carry out NPP analysis with specific reference to issues of environmental archaeology, four sites located in northwest Italy and a number of modern analogues have been selected:

- A natural wetland site with possible evidence for Middle Holocene anthropogenic impact (Prato Spilla A, Emilia Romagna, NW Italy). According to Lowe (1991; 1992; 1994a; 1994b) it is likely that the pollen record of the area points to anthropogenic disturbance, probably including the use of fire. A recent refinement of the vegetation history of the site has provided further clues to possible human-driven environmental change, tentatively identifying a few large grass grains as cereal pollen, and recording the presence of taxa commonly regarded as indicators of human disturbance (Bedford 2013). Given this evidence for possible human activity in the uplands during late prehistory, the site has been selected as a promising context to carry out the analysis.
- A deep core taken from the alluvial plain of the river Bisagno in Genoa, next to a recently discovered Neolithic settlement (Arobba and Caramiello 2014), arguably the very first inlet used as a harbour in the history of the city (Melli et al. 2011). The site was selected given the opportunity to analyse samples that may have recorded a strong signal for human impact, and because of the scarcity of palaeoenvironmental studies from Ligurian coastal areas, as opposed to a number of studies focusing on upland wetlands.
- An archaeological site characterized by stabling episodes and phases of domestic occupation (Cave of Arene Candide, Finale Ligure, NW Italy). The site has been selected to assess the potential of NPP analysis of archaeological deposits for the following reasons: 1) the availability of results from multiple

geoarchaeological techniques, which have led to the identification of a wide range of activities carried out in the cave during late prehistory - chiefly a series of stabling episodes, which are likely to have left a signal in the NPP record (Macphail et al. 1997); 2) the availability of several radiocarbon dates for the previously investigated sequences and the succession of highly distinct ceramic styles permitting accurate chronological control; 3) the location of the site in a region where a number of palaeoenvironmental analyses have been carried out, thus providing a useful framework of data to contextualize the research.

- A man-made terrace from the hillfort of Castellaro di Uscio (Genoa), where the occurrence of on-site cultivation has been hypothesized (Macphail 1990; Nisbet 1990). The site will be used as a case study to test the potential of dung-spores to assess the application of manure in antiquity.
- Among the modern samples are included a 19th-20th century pastoral rock shelter (Arma delle Manie, Finale Ligure), and a variety of samples from floors of roofed and unroofed stables taken in southern England and northern Italy. The modern dataset aims to reach a less subjective level of interpretation regarding the abundance of NPPs found in natural or anthropic sediments.

Although the focus of this study is on the application and future developments of NPP analysis, the site selection shows that the project is geographically consistent, as most of the study sites are located in Liguria or at the border of this region. Moreover, the methods employed appear suitable to address a series of research questions that are particularly relevant for this study area in the Middle Holocene. This approach will lead to a more reliable understanding of the palaeoenvironment of the region and of the role played by the first settled communities as early as c. 7800 BP.

In spite of the number of studies in the field of environmental archaeology carried out in the last three decades in this particular area, the records are largely dominated by pollen-based studies, and the application of other proxies appears to have been sporadic (Menozzi et al. 2010; Branch and Morandi 2015). This research will provide a complementary body of data that will integrate previous palaeoenvironmental investigations with the new findings. Further, the methods applied in this work will allow the presence of wild and domestic animals in the landscape to be assessed; an

essential research focus, when it comes to discussing the influence of Neolithic shepherds on the environment.

1.3 The research subject: microfossil indicators for animal presence

Among the wide diversity of NPPs, fimicolous spores are especially relevant for the new research presented here, being acknowledged as reliable indicators of on-site herbivore presence, given their requirement for herbivore dung as a substrate for a successful growth (Baker et al. 2013). Although these microfossils have been widely employed for assessing the timing of Pleistocene and Holocene megafaunal extinctions (Burney et al. 2003; Johnson 2009; McGlone 2012), they show great promise in investigating issues regarding the adoption of agro-pastoral economies by late prehistoric communities. In particular, coprophilous spores may be reliable indicators of extra-site locations where livestock was habitually grazed and faunal remains are absent, and also indicate the on-site presence of herbivores in settlements when other dung indicators and animal bones are missing (van Geel et al. 2003; Baker et al. 2013).

Some methodological aspects concerning the abundance of NPPs in sediments appear to have been overlooked by previous studies, and will be addressed by this research. For example, when interpreting the values of coprophilous spores, the need for an interpretative framework and a coherent way of presenting the data is required. Analysts have reported a diverse range of values for ancient samples, yet, often concluding with the same interpretation involving human-caused grazing pressure. Moreover, the method for expressing the values is inconsistent, ranging from Total (Land) Pollen%, to T(L)P%+TNPP%, TNPP% and concentration values per cm^3 or grams. For example, Cugny et al. (2010), have shown that in modern samples from grazed areas the values of the dominant coprophilous type can reach percentages as high as 15-40% (TNPP%), and other types be attested on 5-10% (TNPP%). Riera et al. (2006) and Blackford et al. (2006) consider values around 2-3% (T(L)P%) as indicative of grazing, and even values of 1-2% (T(L)P%) have been interpreted as human-induced grazing when paralleled by a high charcoal incidence (Menozzi et al. 2010). Moreover, it is not always clear what the role played by humans was, i.e. whether herbivores are thought to naturally occupy (deliberately?) cleared areas, or

to be taken by shepherds or herders; a difficult issue to solve in post-Neolithic contexts.

This similarity of interpretations based on highly different values reflects the lack of a scientific approach and of uniformity in expressing the results, leading to a high degree of subjectivity. Only Davis and Schafer (2006), Blackford and Innes (2006) and lately Baker et al. (2016) have tried to coherently relate the values from fossil samples (T(L)P% or accumulation rates)) to the percentages occurring in contexts where information about grazing practices was available and recorded.

Further, a deeper understanding of NPPs from archaeological sites seems necessary, as these assemblages may differ significantly from natural archives and indicate human-related practices (e.g. fungi growing on decomposing food, human parasites, non-biological NPPs (Kvavadze and Kakhiani 2010; Kvavadze et al. 2009; 2010; Chichinadze and Kvavadze 2013; Ivanova and Marfenina 2015)).

Ova and cysts recovered from archaeological samples belong to a diverse group of intestinal parasites, that can be divided into organisms visible at naked eye, helminths, and microscopic taxa, protozoa. Cestoda and Trematoda (phylum Platyhelmintes, flatworms) are worth mentioning among the former, along with several species in the classes Secernentea and Enoplea, belonging to the phylum Nematoda (roundworms); protozoa are unicellular eukaryotic organisms, comprising amoeboid forms and other, often ciliate or flagellate species.

The interaction between humans and their parasites is a complex story that harks back to the dawn of our species, when we shared the same microbiota with the ancestors of the other great apes (Moeller et al. 2016). The current ecology of intestinal parasites is particularly complex, as it results from an evolutionary history of a million years involving adaptation to several hosts in different environments (Combes 2001). Unlike common opinion, the host/parasite relationship can also be a mutual one (McKenney et al. 2015). Parasites may have lived with humans much longer than previously thought, and species infecting both man and other mammals may have developed before the cohabitation with animals following domestication. This is indicated by phylogenetic studies supporting the presence of *Taenia saginata* (cattle tapeworm) in humans before cattle domestication, and is suggested by Mesolithic finds of possible eggs of *Trichuris trichiura* (although they might belong to *T. suis,* the boar/pig-specific parasite).

Each species follows specific life-cycles, which cannot be taken to completion without the appropriate host. Typically, a period of embryonation in a suitable environment is followed by ingestion by one or more hosts, growth within their bodies and discharge of the eggs with the stools. In the case of *T. trichiura* (human-specific whipworm), in order to survive eggs need a permanence in a warm and humid environment for a period of about three weeks. However, after this period they become extremely resilient to environmental conditions. Hosts are infected through the accidental ingestion of contaminated soil particles. *Ascaris lumbricoides* (roundworm), the largest nematode in man, follows a similar cycle but makes use of bloodstream to carry the larvae to the lungs and eventually to the pharynx, where they are swallowed, prior to growth in the small intestine. The *Dicrocoelium* cycle (lancet liver fluke) involves two intermediate hosts (a land snail and an ant) to spread, and it is transmitted through the ingestion of an infected ant at the larval stage. Dicrocoeliosis often affects cattle, sheep and goats, and human infection is referred to as a case of pseudo-parasitosis, resulting from the consumption of infected animal liver. *Taenia* spp. (tapeworms) exploit humans as well as cattle or pig in order to complete their cycle, and infection occurs through the ingestion of raw or undercooked meat (Cuomo et al. 2009).

The symptoms associated with helminth infection in humans are, in most cases, not very severe. Whipworms and roundworms may cause disturbs such as bloody diarrhea, vomiting and iron-deficiency anemia. Diphyllobothriasis is associated with several symptoms, and because of the loss in vitamin B12 the infected individual may develop anemia. The symptoms associated with dicrocoeliasis in mammals are weight loss, anemia and cirrhosis (Cuomo et al. 2009).

Parasites eggs and cysts can be recovered from excavated layers, lake deposits, coprolites, and even directly from exceptionally preserved bodies, such as mummies (Bouchet et al. 2003). The eggs are normally identified in pollen slides by means of high-power optical microscopy. Specific procedures for the extraction of eggs have been developed, involving sieving through 160 and 20µm meshes (Anastasiou and Mitchell 2013). More rarely, parasite eggs are recognized in thin sections (Pichler et al. 2014), although in this case a precise identification is arduous and bulk samples should also be prepared to allow accurate observation of the eggs' shape and surface.

Eggshells of the genera *Trichuris* and *Ascaris* (nematodes) are by far the most commonly observed by paleoparasitologists, both because of the existence of human-

specific species and the resilience of the thick-walled eggs. Eggs of *Trichuris* vary between c. 45 and c. 80μm of length according to the species, and are characterized by an elongated barrel shape with slightly convex polar plugs at both ends. The wall is smooth and formed by a superimposition of three layers (a lipid, a chitinous and a vitelline layer), with the core of the plugs being of unknown composition (Appleton and White 1989). Due to overlapping size, it is difficult to separate *T. trichiura* from *T. suis* (infecting suids) (Beer 1976). The genus *Capillaria* produces similar eggs that can be easily mistaken for *Trichuris*, but display a typical reticulate surface ornamentation and a slightly asymmetrical position of the polar plugs (Traversa et al. 2011). Fertile eggs of *Ascaris* range from c. 45 to c. 70μm in length, the most apparent feature being a knobbed coat (albuminoid uterine layer) creating an anastomosed pattern. To an untrained eye, this coat, in addition to the ovoid shape of the egg, may easily resemble fern spores of *Polypodium* spp. The outer coat of *Ascaris* eggs is often partially lost, so that the smooth surface of the underlying vitelline layer is exposed. *D. latum* produces large elliptic eggs (c. 60-75μm in length) showing a wide aperture on one side; similar but smaller and slenderer eggs (c. 34-45μm) with an aperture (after the loss of the operculum) belong to the genus *Dicrocoelium.*

It is often difficult to identify parasites to a species level, and many of the eggs recovered in archaeological deposits also derive from feces of wild and domestic animals (Dufour et al. 2013). Their value is not limited to the information they are able to provide on diseases that would not leave any trace on skeletal remains. The study of these microfossils also allows inferences on early population movements, as well as enhancing the knowledge of living conditions in ancient settlements, providing data on dietary practices, use of the space and social status.

One line of research investigates the origin and spread of human parasitic infections, using paleoparasitological evidence to shed light on large-scale movements of early human groups and the occupation of previously inhabited continents. The arrival of hunter-gatherers to North America only through Beringia has been questioned, as eggs of *Trichuris* and *Ancylostoma*, requiring warm and moist soils, would not have survived in soil in the arid and cold permafrost. It is then difficult to explain the presence of these human-specific species in the stools of pre-Columbian populations, and alternative colonization routes have been proposed (Araújo et al. 2008).

On archaeological sites, the informative potential of parasite eggs is manifold (Mitchell 2015). They are useful indicators of dietary habits (e.g. consumption of raw

fish: Yeh et al. 2014) and poor hygiene during food preparation (e.g. soil contamination: Mitchell and Tepper 2007). Changes in subsistence strategies may be inferred by increases in certain parasitic species, and accordingly a greater impact of fishing activities in Late Inca societies was hypothesized (Santoro, Vinton, and Reinhard 2003). In settlements, the knowledge of use and organization of the space can be highly enhanced, as areas such as latrines and stables would be particularly rich in eggshells (Langgut et al. 2016). Differences in social status, reflecting habits of different parts of the population, can also be detected. In late medieval France, the abundance of *Taenia* eggs in cesspits adjacent to high-rank mansions, relative to their absence in poor contexts, showed the consumption of raw meat as a specific practice diffused in aristocratic families (Bouchet 1995). In graveyards, inhumations can be specifically sampled for paleoparasitological analysis in key areas, such as around the pelvis (Fugassa et al. 2006).

In paleoecological studies, parasite eggs of herbivores are useful indicators of local grazing pressure, as, unlike pollen and spores, they are not transported over long distances by atmospheric agents, but deposited within dung pats and droppings.

1.4 Beyond environmental archives: the potential of local proxies to unveil evanescent extra-settlement areas

Since the start of large-scale field survey projects in the 1970s and 1980s (Macready and Thompson 1985), archaeologists have struggle with the interpretation of extra-settlement (off-site) areas. In spite of their apparent marginality, they have often been of primary importance for ancient societies (de Haas 2012). The relevance of such places is not restricted to their use for resource exploitation, but embraces wider cultural aspects. A paradigmatic case is that of classical antiquity, as it shows that even urbanized societies characterized by large metropoleis and complex production systems still felt the necessity to express their links to wilderness and rural environments, as largely indicated by several literary sources and pagan feasts (Dumézil 1996; Bradley 2000). A number of anthropological studies equally show the unsuspected relevance of various extra-settlement areas, most of which would result in a total lack of archaeological visibility (see e.g. Turner 1967). However, the whole

debate on off-site distributions in archaeology deals with the interpretation of material culture (chiefly potsherds) scattered on the landscape surface.

It is suggested here that it may be possible to go beyond the use of suitable natural archives as the main means of reconstructing environmental conditions associated with human occupation. Arguably, a further approach to identifying potential extra-settlement areas may be attempted through the use of local proxies for periodic human presence. Several survey projects have faced the difficulty of interpreting areas of apparent low activity beyond the settlement sites (Bintliff and Snodgrass 1988). Then, at a later stage of the research, the excavations tend to focus solely on more promising areas characterized by stronger evidence, and there is little work to interpret the meaning of off-site distributions (de Haas 2012). Moreover, because these areas are defined by a very low number of artefacts, it seems highly likely that a large number of them are not detectable at all due to a total absence of remains. Local anthropogenic proxies may be applied to address this problem, and a project following such an approach should involve mapping and sampling of each geological archive proximal to the sites, rather than focusing only on the deepest and best preserved sequence for environmental reconstruction.

It appears essential that, to identify extra-settlement areas, the best proxies have to be strictly local indicators, as is the case of NPPs and waste-derived biomarkers (human and animal stanols/sterols and bile acids). To demonstrate the potential of this approach, we point out that most of the structures and finds associated with off-site areas in field survey projects relate to pastoral activities (de Haas 2012). It is worth stressing that sampling locations do not have to be restricted to wetlands, as biogeochemical analyses can be successfully performed also in dry areas to detect manuring practices in ancient fields (Evershed et al. 1997; Bull et al. 2001). Similarly, soil profiles are valuable sources of palynomorphs (Dimbleby 1985), as well as of resilient fungal spores and parasite eggs. Furthermore, the most commonly advocated explanation for interpreting off-site areas consists of the so-called “manuring hypothesis” (Bintliff and Snodgrass 1988). The specific use of local proxies for animal- and human-derived wastes seems therefore particularly suitable to test this hypothesis, and if successful it would result in a more detailed knowledge of land-use strategies nearby the site. The identification of extra-settlement areas is crucial to locate settlement sites in their broader landscape context, allowing insights into environmental exploitation and economic systems. In favourable circumstances,

sedimentary sequences from natural archives can provide additional meaningful information on extra-site distributions and their exploitation, helping to establish links between them and periodic human presence. These circumstances are listed below:

- Chronological correlation between evidence for local anthropogenic activities from geological archives and archaeological evidence in the study area.
- Spatial relationship between potential extra-settlement areas and settlements (e.g. distance between grazing lands and permanent sites).
- Match between the palaeoecological indicators recovered and the subsistence strategy (if known) of contemporary communities settled in the study area.

Given the present state of research and knowledge, for the reasons given above, this approach is best applicable to the socio-economic context of pastoral societies, regardless of their location in space and time. It is worth saying that, in the last forty years, a similar approach has been tentatively applied by means of phosphorus analysis. However, this method presents several technical and interpretative issues (Holliday and Gartner 2007), and is less directly linkable to a specific type of human activity, e.g. areas of food waste would appear as very phosphate-rich and indistinguishable from heavily grazed areas.

1.5 Previous work on selected study contexts in the field of environmental archaeology

1.5.1 Natural sequences: lakes and bogs

Lakes and marshy areas are the most commonly investigated sedimentary environments in palaeoecology for microfossil analysis (Birks and Birks 1980). This is due to the fact that water-saturated layers allow excellent preservation, and sedimentation tends to be very homogeneous without remixing or translocation between horizons (Branch et al. 2005). In larger basins, however, internal processes caused by thermal differences at different depths may lead to water mixing and uneven rates of deposition, which account for site-specific differences in pollen

accumulation rates (Giesecke and Fontana 2008; Matthias and Giesecke 2014). In the last thirty years, a number of works have elucidated the complex relationship between vegetation, sedimentary basins and their pollen content (Prentice 1985; Sugita 2007; Hellman et al. 2008). This latter variable appears to be mainly a function of basin size, with regional vegetation being represented only in lakes measuring at least c. 700m in diameter (Sugita 1993). However, in order to be used successfully, landscape modelling based on pollen data requires a very accurate knowledge of the surrounding environment, and cannot cope easily with complex geomorphology or basins of irregular shape (Sugita 2007).

Dispersal and deposition of fungal spores and other microfossils have been much less investigated. In general, a very limited dispersal based on the proximity of fungi to the ground has been taken for granted by several authors (van Geel et al. 2003). Only a handful of targeted studies exist, and almost entirely focus on *Sporormiella* spores. Raper and Bush (2009) have recorded the abundance of *Sporormiella* at different distances from the shore along regular transects in fifteen North American lakes. They have argued for a sharp decrease of spores in a range of c. 50-80m, although this claim does not seem to be strongly supported by the data they provided. Very recently, the relationship between dung spore abundances (expressed as rate of accumulation: number cm^{-2} $year^{-1}$) and herbivore biomass density (kg ha^{-1}) has been accurately established by Baker et al. (2016), stressing the importance of surface run-off as a factor of spore dispersal and of the area immediately adjacent to the basin (<10m).

To date, a sound knowledge on the dispersal of other microfossil types is lacking. For example, the shape and weight of *Sporormiella* ascospores is likely to affect their release and dispersal, and different species may be much more efficient in releasing spores than others, having developed specific strategies and morphologies (Yafetto et al. 2008). Regarding this point, a good amount of data, almost always neglected by palaeoecologists, is offered by aerobiological studies, showing that frequently fungal spores are transported over long distances (Pady and Kelly 1954). In light of this, it seems sensible that a single spore cannot be taken as evidence of *in situ* growth of its taxon, while the consistent presence of the same types in one sample is likely to derive from fungi growing directly on the site or in its immediate vicinity.

1.5.2 Natural sequences: alluvial deposits

The factors controlling the deposition of microfossils along fluvial systems differ from those active in closed lakes and still water bodies. The pollen records of lakes and mires tend to be dominated by wind-pollinated taxa, cutting off the contribution of other pollen producers unless living in the surroundings of the basin (Jackson and Lyford 1999; Feurdean et al. 2011). On the other hand, a number of low-lying herbaceous species and spore producers (e.g. ferns) are able to disperse their grains on a greater distance by means of water transportation. This leads to a better representation of these taxa in pollen spectra from alluvial sequences. The deposition of microfossils in alluvial sediments occurs through three main stages (Chmura et al. 1999): 1) dispersal of pollen/spores from the surrounding vegetation to the channel; 2) transport along the channel by water flow; 3) final deposition in the receiving basin.

However, alluvial pollen spectra do not seem to be severely biased by river transport, as works on buried deposits and modern analogues have shown that the assemblages match quite closely the vegetation of the catchment area (Heusser 1978; Chmura and Liu 1990). Clearly, large river systems with very wide drainage basins will be potentially more prone to pollen redeposition, whilst small rivers and streams with limited basins will provide a relatively good representation of the local vegetation.

As previous studies focussed on pollen deposition, it is not known to what extent water transport may bias the NPP record. On one hand, as fungal spores are dispersed very near the ground, they can perhaps be transported over long distances more easily by water than by wind. On the other hand, they are unlikely to reach the river channel, unless their producers live directly on its edges. Moreover, the presence in the sampled sequence of algal microfossils indicative of still or slowly moving water and fine-grained clayey levels point to a low-energy environment, where water transport might have been negligible (Selley 2000; Arobba et al. 2016).

1.5.3 Caves and rock shelters

Pollen analyses of cave deposits have always been challenging to palynologists. Often, it is only possible to have no more than a patchy glimpse of the original pollen record,

due to the unfavourable chemistry of the deposit. These conditions result from the usual location of caves, in limestone or chalk aerobic deposits leading to pollen deterioration over time through oxidation and microbial activity (Branch 1997). The current knowledge of coastal palaeoenvironments is strongly limited though, so that even a 'mutilated' record may provide useful data.

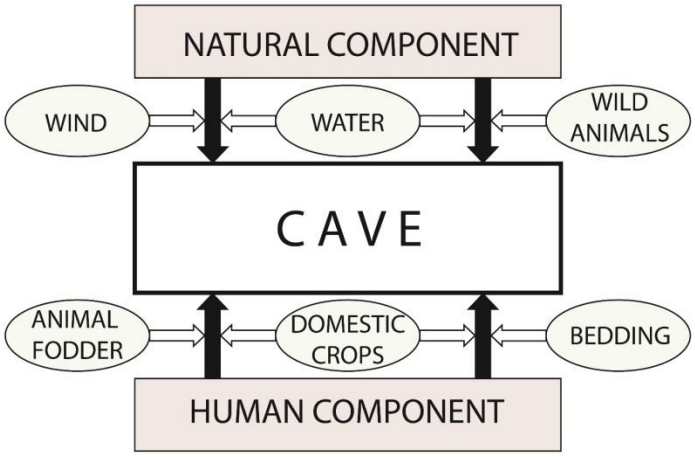

Figure 1.1. Scheme indicating the relationships between the driving factors for pollen deposition in caves.

It is undeniable that cave palynology presents aseries of issues, so that this field of research is frequently surrounded by criticism and scepticism (Bottema 1975; Turner and Hannon 1988; Coles et al. 1989; Sánchez-Goñi 1994). This is mainly due to processes such as selective preservation, preferential transport and sedimentary discontinuities. In particular, dry-wet cycles tend to destroy pollen grains, causing typically low pollen concentrations from cave deposits. All these factors affect pollen taphonomy, and there are no models of cave pollen deposition providing easy answers, as opposed to a well-established tradition of studies on the representativeness of pollen spectra from lake sediments (Branch 1997; **fig. 1.1**). A number of works have shown that pollen deposition in caves seems to be influenced by too many, and above all site-specific variables (Branch et al. 2005). However, it has also often been stressed how, bearing in mind the caveats, cave pollen records can succeed in providing a reliable picture of both, local and regional vegetation (Burney and Pigott Burney 1993; Carrión et al. 1999; Navarro Camacho et al. 2000; Navarro et al. 2001; 2002). The best and more common approach to an evaluation of cave palynology involves the sampling of surface locations from external areas (e.g. moss pollsters) and comparison with samples from inside the cave (e.g. topsoil, speleothems' surface, spider webs). Several studies have demonstrated that, rather unexpected, cave pollen spectra have proven as accurate as external surface samples, and occasionally even better (Navarro et al. 2002). It has been noticed that cave palynology plays an important role in pollen deposition (Navarro et al. 2001), and

that the highest concentrations are found in samples from the entrances. Yet, the rear of the cave better represents zoophilous taxa, whereas higher percentages of anemophilous plants are found near the entrance (Navarro et al. 2001). In general, a better representation of entomophilous taxa is gained from the analysis of cave sediments, supplementing the prevalence of anemophilous taxa from lacustrine sequences (Navarro Camacho et al. 2000). Moreover, isodiametric caves with large entrances provide more homogeneous records, whilst percentages of undeterminable grains tend to be higher in long and narrow chambers, and the total pollen concentration lower. A strong lateral variation in the pollen content of cave sediments has also been highlighted, suggesting that a multiple-profile approach should be adopted, and a good sampling strategy should avoid areas next to the cave walls and moist zones (Navarro Camacho et al. 2000). This is probably because large entrances enable stronger air circulation, determining higher accumulation rates. Branch (1997), suggested that post-depositional leaching is likely to occur in cave deposits, causing pollen translocation to take place. On the other hand, the data provided by Dimbleby (1985), seem to prove the reliability of pollen records from terrestrial profiles and the relatively low occurrence of pollen transmigration through the horizons.

Carrión et al. (1999) suggested that, in order to obtain reliable results, a series of conditions have to be met. At least 15-30 taxa should be recorded and counts should reach a minimum of 200 grains excluding Asteraceae, concentrations should be higher than 4000 grains g^{-1} and the percentages of undeterminable pollen no higher than 20%. Unfortunately, also for practical reasons (e.g. very high counts needed to excluded Asteraceae from the pollen sum), it has not been possible to meet all these requirements. However, some authors disagree with this view, arguing that high percentages of Asteraceae from archaeological deposits do not only result from selective preservation, but may reflect a real condition and the influence of human activities (Lebreton et al. 2010; Mercuri et al. 2010; Florenzano et al. 2015). Navarro et al. (2001) supported this notion, stating that high resilience cannot be the only explanation for very high values of Cichorioideae from cave sediments.

The work by Expósito and Burjachs (2016) focused on pollen grains and differential preservation in the cave of El Mirador (northern Spain), used as a stable in the Bronze Age. The high amount of crumpled and deteriorated grains found during the analysis

was linked to burning activities by the ancient shepherds. Due to this bias, most of samples were not considered to represent any actual ecosystem.

In the case of the Arene Candide, human activities on and around the site and the complex morphology of the cave make the interpretation even more difficult. For example, we do not only lack a precise knowledge of daily activities, but we also ignore the presence at times of structures that may have strongly affected pollen deposition and wind circulation, such as perishable walls or other barriers. Not to mention that air currents can follow very complex paths in irregularly shaped caves, and the sea-facing location may have exposed the site to frequent turbulences.

However, in the context of the regional archaeological and palaeoenvironmental scheme the data seem to be of some relevance, and a number of inferences can be drawn.

Relatively recently, cave palynology has been carried out in Liguria, in order to enhance the knowledge of Pleistocene vegetation, given the absence to this end of sufficiently old lake deposits. Kaniewski et al. (2004), sampled the Middle Palaeolithic occupation layers of Madonna dell'Arma (Sanremo), recording a high number of taxa. Statistical analysis (Principal Component Analysis) were applied to limit interpretational bias, and the data allowed correlations between vegetation changes and the beginning of the Pleniglacial, identifying two main climatic phases on a palynological basis. A similar study (Kaniewski et al. 2005a) aimed to investigate the sand dunes covering the cave have and highlighted the occurrence of semi-arid conditions on the western coast of Liguria from the Oxygen Isotope Stage 5a to the Oxygen Isotope Stage 4 (c. 80,000-70,000 BP). Pollen analysis and statistical elaborations proved successful also in the case of the Lower Pleniglacial (75 – 57 Kyr BP) of the cave of Santa Lucia Superiore (Toirano), in spite of preservation issues affecting the palynomorphs (Kaniewski et al. 2005b; 2005c). Despite low concentrations, in view of the high diversity of taxa and their ecological consistency, the pollen records from Mousterian layers and stalagmites from the cave of Fate (Finale Ligure), were used to directly make palaeoclimatic inferences and reconstruct Middle Palaeolithic vegetation by Karatsori et al. (2005).

With reference to the Holocene, the only studies published to date concern the Arma dell'Aquila, the Arene Candide and the Pian del Ciliegio rock shelter, all located in the territory of Finale Ligure (unpublished preliminary data from the Alpicella rock shelter near Varazze are mentioned by Arobba and Caramiello 2006).

A Late Epigravettian hearth from the Arma dell'Aquila (Arobba et al. 1987; Arobba 1990) pointed to high tree canopy dominated by *Pinus* (the presence of *Castanea*, not uncommon in the Mediterranean Late glacial, is noteworthy). The second sample from the site was taken from a fragment of plaster dated to the VBQ phase (square-mouthed pottery, Middle Neolithic). However, the pollen spectrum is contrasting and highly heterogeneous, and it has been suggested that it results from the mixing of sediments of different ages for the preparation of the plaster, thus preventing any palaeoclimatic considerations. It is relevant to stress that in both cases the amount of sample analysed was remarkable, between 30-50 g, given the low concentrations of palynomorphs typically encountered in cave deposits (Arobba 1990).

Palynological studies at the Arene Candide were carried out by Branch (1997), who reported the results from Early and Middle Neolithic sections from the eastern part of the cave. Only two sample locations turned out to be suitable for the analysis, given very low or null pollen concentrations. Both areas appeared to be dominated by Poaceae, Ericaceae, Cichorieae, with high percentages of deteriorated/broken grains and in one location low values of Cerealia. The final interpretation of the Middle Neolithic phase supported the micromorphological analysis by Macphail et al. (1997), pointing to herbivore stabling for facies 3 deposits. Steady low levels of cereal-type pollen from section 15, however, have enabled to infer a contemporaneous domestic use of the site. Overall, a remarkable spatial variation in pollen spectra was noticed, suggesting that different activities and taphonomic processes can be identified on a palynological basis. On the other hand, the main drawback lies in the limited validity of cave pollen records to reconstruct past regional vegetation history. Only partial data on the surrounding environment could be gathered, as suggested by declining values of *Quercus* possibly indicating human disturbance and the presence of termophilous taxa suggesting the prevalence of a warm and dry climate (Branch 1997).

More recently, a 4m thick sequence was sampled at the Pian del Ciliegio rock shelter, a VBQ site dated to the 5th Millennium BC, which shares similarities with the better known site of the Arene Candide. The pollen analysis has shown low concentrations (on average 631 grains g^{-1}), although the results enabled few remarks on vegetation change and human impact (Arobba and Caramiello 2009). The record embraces three pollen phases, the first two showing the presence of *Quercus*-*Corylus*-Ericales mesophilous woods, and the last one showing a decrease in arboreal pollen and an

increase in pastureland and sinanthropic markers. There is pollen evidence for agriculture, as highlighted by low percentages of *Hordeum*- and *Triticum*-type pollen. The authors also stressed the occurrence of NPPs such as algal cysts of *Pseudoschizaea*, which are also numerous from the Arene Candide, although a sound explanation for this fact appears arduous.

As regards non-pollen microfossils, no specific data on their preservation in caves are available, although personal experience have shown that they do not seem to be affected by the severe deterioration characterizing cave pollen. As to fungal spores, it is likely that this is in virtue of their composition, as chitin is made from N-acetylglucosamine units that may be more resilient in calcareous deposits (Doucet and Retnakaran 2012). Although the specific composition of other NPPs of different origins is not known as yet, such as in the case of *Pseudoschizeae*, they seem to be constantly relatively well preserved. However, high temperatures can destroy palynomorphs, and Expósito and Burjachs (2016) argued that burning activities may severely affect the preservation of fungal spores.

As regards dispersal and deposition, the natural location of fungi on the ground allows spores to be deposited fairly soon, so that long transport is unlikely (see above). In the case of cave, though, it is possible that water circulation also plays an important role in transporting both, pollen and non-pollen microfossils (Gutierrez 2012).

To date, there are no NPP-targeted studies, unless a few works on aerial microbiology of caves (Docampo et al. 2011; Ogórek et al. 2014), that therefore did not focus on sediments. This is rather surprising, considering the potential in the field of biology for mycologists interested in the long-term adaptation of fungi to cave environments (Romero Díaz 2009). Non-pollen microfossils have been occasionally counted during palynological analyses of cave deposits, but only a very limited range of types considered to be relevant by the analysts, mostly coprophilous spores or algal cysts (Buosi et al. 2014; Arobba and Caramiello 2009; González-Ramón et al. 2012), whereas elsewhere fungal spores are only mentioned but not quantified (Navarro et al. 2001). The most relevant cases are perhaps the investigation of the dung blanket in the Bechan Cave (Davis et al. 1984), that pioneered the potential of *Sporormiella* spores in palaeoecology, the analysis of early hominid beds from Sterkfontein caves including aquatic types along with other spores (Carrión and Scott 1999), and the

recent study of a guano-clay cave sequence that has quantified not only fimicolous spores but also *Kretzschmaria deusta* and *Trichuris* spp. (Onac et al. 2015).

Very recently, Expósito and Burjachs (2016) recorded dung spores and algal remains from a *fumier* sequence consisting of burnt dung, a deposit formed by repeated stabling episodes comparable to the one sampled in the Arene Candide. The values of microfossils vary from sample to sample, in spite of being almost contemporaneous. Significantly, coprophilous spores appeared to be more numerous only in certain levels. These variations were interpreted by the authors in terms of differential preservation due to burning and high temperatures.

A rather different case is represented by analyses of coprolites found in caves, or cave rocks and perennial ice cave deposits, where certain types NPPs have been extracted and counted (Carrión et al. 2001; 2005; Yll et al. 2006; Feurdean et al. 2011; Pusz et al. 2014).

1.5.4 'Fumier' deposits

A peculiar kind of deposit, mostly found in caves and rock shelters and associated with human practices is known as *fumier* (or "layer-cake" levels) (Brochier 2002; Angelucci et al. 2009). The main characteristic of *fumiers* lies in the occurrence of burnt (and often also unburnt) layers chiefly composed of dung, vegetation remains and ashes. Their thickness can vary substantially according to the site, from alternations of thick layers to multiples very thin units. Nevertheless, *fumiers* appear strikingly uniform as concerns their main traits on an extremely wide area comprising the west fringes of the Mediterranean basin up to the Near East, ranging from alpine to warm Mediterranean climates (Angelucci et al. 2009). *Fumiers* are thought to be primarily the results of reiterated pastoral activities, whose differences are reflected in the variety of layer-cake deposits. These are also remarkably homogenous from a chronological perspective, being attested only from the very onset of Neolithisation to the Copper/Bronze Age (modern *fumier*-like deposits have been also described from Sicilian and Greek caves: Brochier et al. 1992; Acovitsioti-Hameau et al. 2000).

A suit of analytical methods has been applied to the study of *fumiers* in the last few decades, in order to provide answers to formative and interpretative issues.

Undoubtedly, micromorphology has been the technique most frequently used, and has allowed the dung component to be identified in various sites (Boschian and Miracle 2007; Angelucci et al. 2009). It has also shown the striking similarity of *fumiers* from distant locations on a microscale, the occasional presence of horizontally layered phytolith chains and frequent signs of compaction probably caused by animal trampling (Macphail et al. 1997).

Phytolith analyses have often been carried out along with micromorphology. The results provide indications of the vegetation ingested by the flock, the type of material used for foddering, and possibly crop processing practices prior to the creation of animal bedding (Albert et al. 2008).

Chemical and isotopic characterizations of pastoral deposits have been attempted, but they appear to be linked more to the field of research aiming at the species identification of archaeological dung rather than to the specific investigation of *fumiérs* (Shahack-Gross et al. 2003; Shahack-Gross et al. 2008; Macharia et al. 2012).

A relevant study illustrating the chemical variation of modern *fumier* profiles according to different compositional units (e.g. burnt, unburnt, ashes, etc.) was performed by Brochier et al. (1992), in a pioneering paper on the significance and formation processes of such sequences. It is worth noting that only a few authors have paid attention to the investigation of freshwater indicators in pastoral contexts. Despite a poorer preservation compared to wetland deposits, remains of siliceous algae have been identified and interpreted as derived from the water supplied to the herd (Brochier et al. 1992). Furthermore, diatom-rich layers have been used to distinguish separate pastoral episodes and oligotrophic/eutrophic species employed as indicators of high/low pastoral pressure (Brochier 2002). The problem of water supply has indeed been largely overlooked in most studies on pastoral sites, and requires further investigation (a recent example of the potential of diatom and sponge spicule analysis of animal dung deposits is given by Golyeva 2012).

A notable enhancement of the understanding of site formation processes in pastoral contexts was provided by ethnographic works focusing on recent and sub-recent deposits. Layered sequences resembling late prehistoric *fumiers* have been analyzed providing a model of *fumiers* formation, with the aid of available oral information on pastoral practices in the last two centuries (Brochier et al. 1992; Acovitsioti-Hameau et al. 2000; Martín-Rodríguez and Vergès 2016; Vergès et al. 2016).

Palynological analyses of *fumiers* have been rarely carried out (Branch 1997), presumably due to taphonomic problems related to terrestrial samples and preservation issues. However, the analysis of terrestrial profiles can prove highly profitable (see e.g. Donaldson et al. 2009 on anthropogenic soils), and when applied to pastoral sequences new data on the environment surrounding the site can be collected (Branch 1997).

1.5.5 Agricultural settings: man-made soils and terraced slopes

Deep anthropogenic soils can provide valuable information on past farming activities. In northwest Europe, these horizons are termed "plaggen", and have resulted from the repeated addition of different manures to the fields for several centuries, with the aim of improving harvest productivity (Blume and Leinweber 1988; 2004; Pape 1970). Such practice formed part of an operational cycle consisting of different phases, which varied according to the region and the historical period. Among the most common deliberate additions to the fields were heath and grass sods, although also peat and turf ashes, seaweeds and animal carcasses are documented, and sand and till were occasionally added (van de Westeringh 1988; McKenzie 2007).

The sods were initially cut in square patches to be used as litter for cattle and sheep in stables. After a period, they became dung- and urine-impregnated and were spread on the fields as manure. It should be noted that such a system had to be thoroughly adopted, as the balance between available grazing surface and source area for sod cutting was precarious. For these reasons, in historical times plaggen-type manuring systems were commonly regulated by local authorities (Mckenzie 2007).

The repetition of this practice determined the formation of characteristic dark horizons, typically thicker than 50cm. Such soils are known in the Netherlands, northwest Germany, Belgium and Scotland, most of them being created during the last millennium (van de Westeringh 1988). Plaggic anthrosols are therefore of the greatest interest for historical archaeology, but plaggen-like soils have been identified and hypothesized also with reference to prehistoric farming. The most notable examples are found on the Islands of Sylt and Fohr (northern Germany) and several Dutch sites (Conry 1974; Blume and Leinweber 1988; Dockrill and Simpson 1994).

Plaggen soils have been investigated mainly by means of chemical, sedimentological and micromorphological analysis (Mücher et al. 1990; Dercon et al. 2005; Davidson et al. 2007). C, N and Pb isotopes have also been employed, in order to identify the source of pollution in the arable land (Meharg et al. 2006). In some favourable cases, these methods are coupled with historical and ethnographical sources providing a better understanding of past agricultural practices (Donaldson et al. 2009).

A few pollen-based investigations of plaggen horizons have been attempted (Bakels 1988; Groenman-van Waateringe 1988; 1992; Mücher et al. 1990; Donaldson et al. 2009). It is worth noting that despite the issues of grain taphonomy in terrestrial deposits and related difficulties in interpretation, these studies have proved successful. It seems possible to link the variations in the assemblages to the agricultural history of the sites, and even provide a chronological link based on regional vegetation history, given the unreliability of radiocarbon dates from anthrosols. To these ends, when possible it is recommended to collect and analyze a "control" sample from a nearby natural wetland archive, to facilitate a distinction between regional and site-specific signals and to elaborate a pollen chronology for the area (Mücher et al. 1990). However, the dating of plaggen-soils is highly problematic. Radiocarbon and pollen-based chronology fails to provide an accurate age estimate, therefore optically stimulated luminescence (OSL) has been tentatively applied (van Mourik et al. 2011).

Distinct man-made soils can be found also in the Americas, where patches of highly fertile Amazonian dark earths (*terra preta de Ìndio*) are scattered on the backdrop of naturally occurring poorly nutrient weathered soils (Glaser and Birk 2012). The origin of such anthropogenic soils is still being debated, and unlike plaggen soils it is not clear whether they were produced intentionally or unintentionally in a large period comprised between c. 2500 and 400 BP. The data point to an unintentionally prolonged formation due to the accumulation of charred organic matter (biochar), faeces, food residues and various domestic waste including several potsherds, resulting in a high P content and high productivity of these deposits (Lima et al. 2002). Elemental and soil organic matter analyses clearly separate the dark earths from the surrounding local soils (Ferrasols and Acrisols), and faecal biomarkers such as stanols and bile acids seem to indicate a massive addition of human waste (Birk et al. 2011). The formation and composition of Amazonian dark earths, and particularly their relationship with archaeological sites, farming practices and pre-Columbian

demography requires further investigation. The palaeoecologial approach applied to their European counterparts might reveal fruitful results, as suggested by the studies focusing on plaggic deposits.

Despite the extension of the phenomenon, very little is known on the origin of agricultural terraced systems characterizing the landscape of several Mediterranean regions. A few chronological attributions have been advanced on the basis of the associated archaeology such as terrace wall masonry or radiocarbon dates, the earliest cases being tentatively dated to the Copper Age and the Late Mycenaean (Grove and Rackham 2001; Bal et al. 2010). The current knowledge of farming practices taking place on the terraces is equally poor. Indeed, when ancient terraces have been buried, the commonly adopted approach was normally limited to a pedological assessment, allowing the ancient soil surface to be identified. However, in a few cases a more refined analysis has been carried out with the aid of charcoal and phytolith analysis and micromorphology (Nisbet 1983). The most detailed investigation was performed by Bal et al. (2010), by means of charcoal analysis. In spite of the reworking of the deposit, radiocarbon dated charcoal enabled distinction between different phases of construction and local vegetation dynamics.

On the contrary, the widespread diffusion of terracing in pre-Columbian America has been investigated in far greater detail, given the combination of archaeological (Healy et al. 1983), pedological (Smith and Price 1994; Kemp et al. 2006), palaeoecological (Trombold and Israde-Alcantara 2005; Branch et al. 2007) and even isotopic investigations (Webb et al. 2004). Through these methods it has been possible not only to identify buried terraces, but also gain information on the cultivated plants and the local palaeoenvironment. It is worth noting that Trombold and Israde-Alcantara (2005) have also considered the problem of water management involved in terraced agriculture, assuming that water was purposely collected in the valley and brought up to the fields on the basis of diatoms frustules recovered on the terraces.

1.5.6 The use of modern parallels in palaeoecology and archaeology

When outlining the roots of approaches targeted at the present in order to get a better understanding of the past, it is appropriate to look back at the pioneering era of modern geology and evolutionary biology. It was not until then, that a full

awareness of the principle of uniformitarianism of was first gained and maintained as a sound guideline in the following decades (although the concept had already been touched on before by a few great thinkers of the Muslim and Christian Middle Ages: Saliba 2007; Rosenberg 2009).

The use of modern analogues in ecology became common from the late 1960s. An analogue was defined as a form of inference assuming that two similar entities share similarities in more than one respect (e.g. fossil pollen assemblage/modern pollen assemblage and past vegetation community/modern vegetation community) (Jackson and Williams 2004). Back in the 1960s, Hesse (1966) formulated three key criteria for the validity of analogues: 1) the similarities between the compared entities have to be clear and definable; 2) a hierarchy can be established so that relevant positive analogies are more important than negative and irrelevant ones; 3) it is possible to demonstrate a causal relationship between entities. Besides, it is necessary to watch out for pitfalls, such as: 1) erroneous inference of a positive match (false positive); or erroneous inference of a mismatch (false negative) (Wahl 2004).

In its early days, the analogue approach was developed mainly in Europe and North America, as a means of identifying modern vegetation communities matching fossil pollen assemblages. The method formed the basis for elaborating pollen-based models allowing for accurate correlations between pollen rain and the actual vegetation structure (Sugita 2007; Hellman et al. 2008). The approach has also been adopted to elucidate the ecological value of non-pollen palynomorphs and their relationship with vegetation communities and animal husbandry, looking at a range of modern samples from surface lake muds and moss pollsters (Blackford and Innes 2006; Mazier et al. 2009; Raper and Bush 2009; Cugny et al. 2010; Dietre et al. 2012; Baker et al. 2016).

Roughly fifty years ago, alternative approaches looking at long- and short-term contemporary processes also made their way in archaeology. It was realized that issues in post-depositional processes could be better understood, both by observing living communities and their contribution to the creation of new archaeological records (ethnoarchaeological approach), and deliberately creating stratigraphies and looking at them through time (experimental archaeology) (David and Kramer 2001). The experiments show that a relatively short time of burial is sufficient to create steady chemical and pedological conditions comparable to the cases unearthed in prehistoric excavations (Bell et al. 1996). The effect of burial and biological activity in

relation to pollen grains was also evaluated by scattering *Lycopodium* spores on the land surface, showing that upward and downward movement does occur, although only to an extent of a few centimetres (Dimbleby 1965; 1996; Ashbee and Jewell 1998).

The value of contemporary or sub-recent deposits for interpreting pastoral shelters in caves and open-air sites was illustrated in an exemplary way by Brochier et al. (1992). The formation and properties of sharply banded stratifications were examined by means of several biological and geochemical proxies, providing relevant implications for understanding various Mediterranean sites spanning from the Neolithic to the Bronze Age. In recent years, further experiments were conducted to assess the degree of compaction undergone by cave stabling layers and the effect of burning (Albert et al. 2008; Vergès 2008; Martín-Rodríguez and Vergès 2016; Vergès et al. 2016).

Figure 1.2. Physical map of Italy showing the location of the northern Apennines range and the study sites. 1. Cave of Arene Candide. 2. Prato Spilla 'A'. 3. Genoa Piazza Vittoria. 4. Castellaro di Uscio.

1.6 Geographical setting and vegetation history of the study region

The northern Apennines are defined as a subdivision of the Apennine chain lying between Mt. Cadibona and the mountain pass of Bocca Trabaria (**fig. 1.2**). The area

comprises, from south to north, the modern regions of Tuscany, Emilia-Romagna and Liguria. The orogenesis of the range is highly complex and originates in the Jurassic and Cretaceous periods (c. 200-65 Ma), when oceanic ophiolites were deposited in the area.

The Apennine landscape is mostly hilly, with only a few peaks extending above 2000m asl (average height 800m, versus 1300m of the Alps), and limited stripes of plain along the coasts. Unlike the Central Apennines, no major rivers are located in the northern area, the main ones being the Vara (58km) and the Magra (70km), flowing between Tuscany and Liguria.

1.6.1 Current floral assemblages in Liguria and northern Apennines

At present, the vegetation types of Liguria (Gentile 1984; Terzuolo et al. 2006; Vagge and Mariotti 2010) are as follows:

Oak woodlands (*Quercus ilex* and *Q. suber*)

Forests composed of sclerophyll oaks (for the greatest part only *Q. ilex*, being *Q. suber* much less diffused) were very common on all the hills facing the sea prior to the massive deforestation to gain agricultural soils. *Q. ilex* forests are now diffused especially between Chiavari and the Cinque Terre, and in the territory around Imperia. In these latter areas, the species can be found up to 1000m asl if sunny and rocky slopes are available. These two zones show the most typical Mediterranean climate, whereas the humidity of the areas around Genova and Savona tend to favour mountain species, enabling their presence even near sea level.

Mesophilous broadleaved woodlands

Forests of this type are typical of valley floors, low slopes, and abandoned mountain pastures or hazel orchards following invasions. Two mesophilous species normally co-dominate these woodlands, locally prevailing on other trees generally more diffused on a regional scale. There is no continuity in the distribution of this vegetation type, it often being the result of local processes in areas of relatively high humidity.

Manna ash-hop hornbeam woodlands (*Fraxinus ornus* and *Ostrya carpinifolia*)

This type includes a coenosis mainly populated by *F. ornus* and *O. carpinifolia*, occasionally coupled with *Q. pubescens*, *Q. ilex*, *Fagus sylvatica* and *Castanea sativa.* Its diffusion is prevalently concentrated in the backcountry of Genoa and in the area of Finale Ligure, where carbonatic soils prevail. *O. carpinifolia* is particularly diffused on mountain reliefs, where it survives up to 1000m asl. *F. ornus* has a more xerophile and heliophilous predilection and can thrive on any substrate, so that it is often a colonizing species.

Chestnut woodlands (*Castanea sati*va)

On a regional scale *Castanea sativa* is nowadays the most diffused species, and chestnut woods constitute up to 30% of the total Ligurian forest composition. They appear to be evenly distributed across the territory, and particularly frequent in the provinces of Genoa, Savona and La Spezia, whilst the calcareous subsoils around Imperia are less suitable for their growth. The species has a wide altitudinal range, spanning from 100m asl to the beech woods in the mountain areas (c. 1000m asl).

Coastal pine woodlands (*Pinus alepensis* and *P. pinaster*)

The type is less relevant to our purposes as most of the coastal pine forests have been artificially created over the last 100-40 years. The main populations of *P. alepensis* are located in the areas of La Spezia and Imperia, given its resistance to drought allowing it to grow directly on rock slopes facing the sea. *P. pinaster* has higher water requirements, so that it is localized in the hinterland between Savona and Genoa and on the shores of eastern Liguria.

Mountain pine woodlands (*Pinus sylvestris* and *mugo*)

Natural populations of Scots pines are strongly localized, although very much diffused in reforestations along with *Pinus nigra* and *pinaster*. The main groups are localized in the backcountry of Imperia and Savona, while elsewhere they have been artificially introduced. Scots pines is also present as isolated specimens among beech forests, *Q. petraea* woodlands, chestnut groves and rocky woods. Altitudinal limits vary between 700 and 1700m asl. Dwarf mountain pine can be regarded as a relict, presently occurring solely in the upper Negrone valley, and only with single specimens on the

southern slopes of the Mt. Maggiorasca. The optimal altitude ranges from 1300 to 1700m asl.

Beech woodland (*Fagus sylvatica*)

Beech is currently highly prevalent in the upland areas, as well as being the most common arboreal species in the region along with chestnut. It is distributed all over the territory, but more intensively in the provinces of Imperia, Savona and Genoa. The reasons for this success lie in the cool and oceanic climate of Liguria, which is particularly favourable to the ecology of *Fagus sylvatica*. Although the optimal altitudinal range spans between 500 and 1700m asl, it can be found also around 200m asl in the Geonoa's hinterland, where some mountain species are able to colonize even cool hillslopes of near-sea-level areas (e.g. *Geranium nodosum*).

Silver fir woodlands (*Abies alba*)

Natural forests of *Abies alba* are presently extremely rare in the whole region. Small clusters have survived only in relatively remote areas due to difficult access. The main groups are situated on the Mt. Aveto and Mt. Alfeo (Genoa), and in the upper valleys of Tanarello, Negrone and Argentina. Elsewhere, silver fir is present due to artificial reforestation. The optimal altitude is between 1300 and 1700m asl.

Larch woodlands (*Larix decidua*)

Larix forests are rare and very localized in the region, being confined to the western part between the valleys of Argentina and Tanarello. The reason for their scarcity is to be sought in the climate of the region, which does not suit the ecological requirements of the species. Larch's natural habitat is typically alpine, and where it coexists with beech this is due to human intervention. The altitudinal range varies from 100 to 1800m asl.

Riparian formations

This coenosis is formed by mesophilous, mesoigrophilous and mesoxerophilous species, typical of riversides. Along the principal rivers, the most frequent forest types are formed by rows of *Populus* and *Salix* spp. on sandy and gravel soils. The dominant species slightly vary in mountain locations, where along with *Populus* we find *Salix*

alba, *Alnus glutinosa* and *incana*, these latter also common on middle and- low-altitude cool hillslopes.

Pioneer and invading woodlands

This is a highly heterogeneous category, distributed all over the regional territory. The main invasion-prone habitats are abandoned cultivated fields and rocky areas, from the sea level to the mountainous areas, characterized by strong erosion, shallow soils and fire events favouring recolonization. Normally two or more co-dominant mesoxerophile or xerophile species coexist, the most frequent being *Corylus avellana* and *Robinia pseudoacacia*.

Shrublands and Mediterranean maquis

This vegetation type is present all over the region, particularly on sunny slopes or in fire-prone zones. Six main associations can be identified, all composed by evergreen Mediterranean species able to reproduce on hot, arid and windy environments. The simplest type is the *Erica arboria*/*scoparia-Arbutus unedo* maquis, distributed between 200 and 1000m. Directly facing the sea shore we find instead the thermomediterranean maquis (*Pistacia lentiscus*, *Myrtus communis*, *Euphorbia dendroides*). Typically, *Pinus pinaster*, *P. alepensis* and *Olea europaea* also occur, testifying to the origin of the maquis as derived from a previous pine wood or from abandoned cultivated fields.

1.6.2 Past vegetation changes in Liguria and the northern Apennines: anthropogenic influence and natural environmental change

Due to the historical development of Italian prehistoric archaeological research ("palaeoethnology"), attention has always been paid in our study region to human/environment interactions (Maggi 1997). In the late 19th century, the scholars working in the field and directing excavations had a close relationship with natural sciences. This fact strongly influenced their methods, while southward an art-history oriented approach followed by classical archaeologists took over (Guidi 1988; De Pascale et al. 2008). Thanks to this tradition, already in the 1940s during the first large-scale investigations of Arene Candide conducted by Bernabò Brea botanical and

malacological samples were collected (Bernabò Brea 1946; 1956). Subsequently, the field of environmental archaeology flourished in the region, and palaeoecological studies in more recent years have been often integrated in the archaeological scheme, continuing and consolidating this tradition of study (Maggi 1997).

Increasing attention has been devoted to the northern Apennines since the early 1980s, allowing specific local vegetation changes to be defined and contextualized in the Mediterranean milieu. Initially, the efforts focused on a few upland peatbogs located in northeast Liguria and southwest Emilia: Lago Padule, Lago Pratignano, Pavullo, Ospitale (Watson 1994; 1996). In spite of a rather poor chronology these attempts, along with previous works (Baffico et al. 1987), employed palynology and micromorphology to stress the importance of the onset of peat accumulation, which was interpreted as a result of late prehistoric anthropogenic activities in the highlands leading to charcoal and fine material deposition and subsequent soil impermeabilization (Baffico et al. 1987; Courty et al. 1989; Maggi 2004b). According to these authors, this evidence is sufficient to prove the use of controlled fires as a means of clearing the mountain slopes since the Copper Age, for hunting and mountain pasture. Moreover, the main regional events in the vegetation succession were detected, such as the shifting from *Abies*-dominated to *Fagus*-dominated forest communities, the *Ulmus* decline, the rise of herbaceous taxa and later the appearance of ruderal species (Branch and Marini 2014). The picture was widened and the number of study sites increased by the works of Lowe and Branch (Lowe 1991; 1992; Lowe et al. 1994a; 1994b; Branch 1997; 1999), that proceeded to carry out pollen studies in the region. A first pollen-based chronological scheme was developed and still holds true in its main lines (Lowe et al 1994a). The sequences were better investigated and dated in the following years, and the scheme refined accordingly (Branch 2013; Branch and Marini 2014; Branch et al. 2014; Branch and Morandi 2015). Occasionally, new proxies were applied to integrate Holocene fire history and vegetation history (see e.g. Branch 2013), this latter being very likely affected by burning, be that natural or human-induced. As of today, a reliable chrono-palynological scheme for the Ligurian-Emilian Apennines is shown in **table 1.2**.

Table 1.2. Main phases of Holocene vegetation change in the northern Apennines.

Regional Pollen Assemblage zones (PAZs)	Composition	Time scale (Cal yr BP)
PAZ-8	Woodland reduction and anthropogenic landscape: scattered *Fagus* and *Quercus* woods	2000 to present
PAZ-7	*Fagus-Abies-Quercus (-Alnus)*	4000 to 2000
PAZ-6	*Abies-Quercus*	7500 to 4000
PAZ-5	*Abies-Quercus-Ulmus*	10,300 to 7500
PAZ-4	*Quercus-Betula-Fraxinus-Corylus*	10,600 to 10,300
PAZ-3	*Pinus-Abies*-herb associations	11,600 to 10,600
PAZ-2	*Abies-Pinus-Quercus-Corylus*	>12,360 to 11,600
PAZ-1	*Pinus-Quercus*-Compositae	Not dated

A variety of past ecosystems have been detected, not necessarily having perfectly matching equivalents in the present (**fig. 1.3**). The oldest vegetation community known for the region has been identified in the rare deposits dating back to the Late Würm Late Glacial (Rovegno, Lagdei, Prato Spilla C, Prato Spilla D). At lower altitudes it consisted of a steppe-like environment dominated by *Artemisia*, mixed with pine populations and evolving toward a *Juniperus*

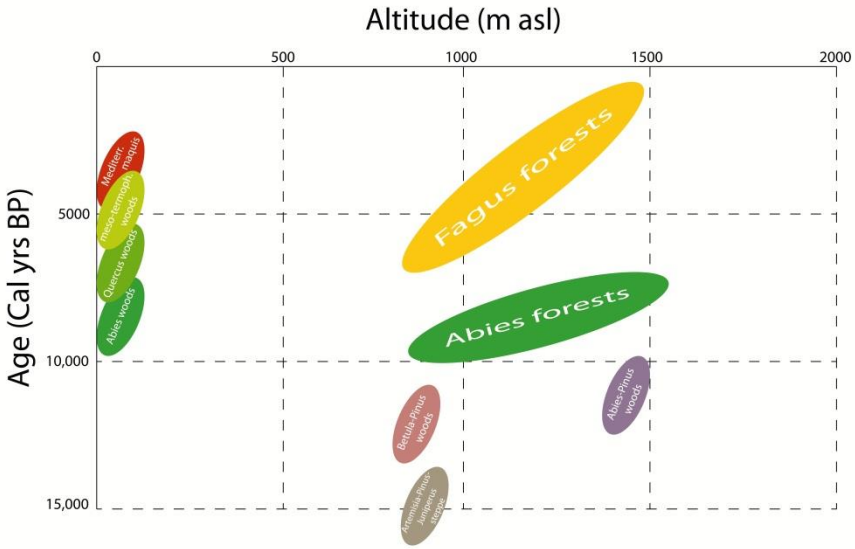

Figure 1.3. Paleo-ecosystems identified in the northern Apennines by means of pollen analysis: chronology and altitudinal gradient.

shrubland. This phase is followed by *Pinus-Betula* woodlands and then termophilous taxa indicating the Late Glacial interstadial, whereas in the uplands *Abies* is already diffused at this time, along with *Pinus*. Forests of *Abies alba* become dominating during the Early Holocene in all the mountain locations, and remain the principal ecosystem for more than 3000 years. The species is today very rare in the region (Menozzi et al. 2010; Arobba et al. 2016), although good analogues can be found elsewhere in southern Europe, for examples in eastern France and Bulgaria (Becker et al. 1992; Roussakova and Dimitrov 2005). Since about 7000 BP Fagus woodlands start rising and then take over in most sites, *Quercus, Corylus* and *Fraxinus* being often cohabiting species. Towards lower altitudes the picture seems to be more varied and perhaps locally differentiated. No old lake deposits are known from along the shore, so that deep cores from very thick alluvial plains are the main sources for reconstructing lowland environments. Meso-termophilous woods and Mediterranean maquis dominated by *Erica* along the coasts of eastern Liguria and northern Tuscany during the Middle Holocene were identified by Bellini et al (2009). Conversely, a near-sea area in the Bisagno valley seems to have been occupied by a coastal silver fir forest (Montanari et al. 1998), a habitat that lacks a contemporary analogue at such a low altitude. The authors specifically stress the negligibility of the other arboreal species, usually more common at lower altitudes. A further different and contrasting picture is provided by very recent investigations in the centre of Genoa, next to the Bisagno river delta. Here, a number of arboreal taxa were recorded (riparian, pyrophilous and heliophilous trees), *Quercus* being highly dominant in some levels, in particular around 7200 BP and 6500 BP (Arobba et al. 2016). It is worth stressing that records from alluvial deposits are more likely to be affected by taphonomic issues that are often very challenging to interpret, such as the transport down valleys of pollen grains produced by upland species.

Widespread evidence for pastoralism (and on a smaller scale for agriculture) from a number of sites (Lowe et al. 1994a), has led many authors to assume a relationship between certain changes in vegetation structure and composition and the human communities settled in the area (Branch 2013; Branch et al. 2014). (**table 1.3**). Namely, the replacement of *Abies* by *Fagus* as a dominant forest species after 6000 BP, a slight increase in grasses and locally *Corylus*, and the occurrence in some deposits of microcharcoal particles. A relationship between these events and human

Table 1.3 Indicators of human disturbance identified in previous palaeoecological studies on the Holocene of the northern Apennines.

REFERENCE	ANTHROPOGENIC INDICATORS MENTIONED						SITE
	Palynology	**Fungal spores**	**LOI**	**Litholog.**	**Chemistry**	**Micromorph.**	
Baffico et al. 1987	*Juglans*, *Castanea*, *Olea*, *Plantago lanceolata*, Cruciferae, Poaceae + microcharcoal					microcharcoal	Prato Mollo (1500 m asl)
Cruise 1990	*Juglans*, *Castanea*, *Plantago lanceolata*						Agoraie (1330 m asl), Casanova (1055 m asl)
Lowe et al. 1994a	*Ulmus* and *Fraxinus* (fluctuations) + *Olea*, *Plantago*, *Artemisia*, Compositae, *Rumex*, Umbelliferae			mineroge nic horizons			Prato Spilla 'A' (1550 m asl)
Lowe et al. 1994b	*Fagus, Quercus*, *Corylus*, *Fraxinus*, Ericaceae, Poaceae (fluctuations), *Plantago*, Compositae, Umbelliferae			mineroge nic horizons			Prato Spilla 'A' (1550 m asl), Lago Padule (1260 m asl)
Watson 1996	*Juglans, Castanea*						Lago Padule (1260 m asl), Lago Pratignano (1305m asl)
Cruise et al. 2009	*Juglans*, *Castanea*, *Ole*a, *Artemisia*, Chenopodiaceae, Cerealia		miner ogenic inputs		rise in phosphate s	herbivore dung?, microcharcoal	Lago di Bargone (830 m asl)
Menozzi et al. 2010	*Juglans*, *Castanea*, Chenopodiaceae, *Rumex*, *Artemisia*, *Plantago lanceolata*, *Pteridium aquilinum*, Cichorioideae, Urticaceae, Poaceae, Cerealia + microcharcoal	*Delitschia*, *Chaetomium*, *Apiosordaria verruculosa*, *Sordaria*-type, *Sporormiella*, *Cercophora*, *Glomus*					Mogge di Ertola (1115 m asl)

Vescovi et al. 2010a	*Juglans*, *Castanea*, *Olea*, *Plantago lanceolata, Rumex acetosella*, Cerealia, monolete spores + microcharcoal	*Diporotheca* recorded but not taken as an A.I.					peat-bog of San Pellegrino (670 m asl)
Vescovi et al. 2010b	*Abies* and *Fagus* (fluctuations), *Juglans*, *Castanea*, *Olea* + microcharcoal						Lago del Greppo (1440 m asl)
Branch 2013	*Fagus*, *Abies*, *Fraxinus*, *Ulmus*, *Tilia*, *Ostrya*, *Corylus* (fluctuations), *Castanea*, *Juglans*, *Olea*, Cyperaceae, *Plantago lanceolata*, *Artemisia*, *Rumex* + microcharcoal		miner ogenic inputs				Lago Riane (1280 m asl)
Guido et al. 2013	*Juglans*, *Castanea*, *Olea*, Cerealia, *Artemisia*, Chenopodiaceae, *Centaurea cyanus*, R*umex*, *Plantago lanceolata*, *Plantago media/major*, Urticaceae, Apiaceae, *Ranunculus acri*, *Humulus/Cannabis*, *Melampyrum*-type, Fabaceae, Campanulaceae, Brassicaceae, *Solanum dulcamara*, *Linum*, *Papaver*, *Knautia*, *Apshodelus*, *Polygonum aviculare* + microcharcoal						Mogge di Ertola (1115 m asl)

activities, such as fodder gathering and landscape clearings, has been repeatedly suggested (Branch and Marini 2014).

There is strong evidence for early animal domestication and husbandry in south-western Emilia and Liguria. In this latter region, the onset of the process can be dated to the Early Neolithic, although the data increase notably in the Middle and Late Neolithic. The event occurs against the backdrop of cultural changes, involving the diffusion of the VBQ culture (squared-mouth pottery) during the VII Millennium BP, replacing the Early Neolithic impressed ware (Biagi 1996).

Most of the evidence comes from a number of rock shelter and cave deposits located in the cave-rich area of western coastal Liguria, while there is scant evidence for open-air sites, this probably being an effect of their lesser archaeological visibility. Considerable bone assemblages have being recovered, showing a prevalence of domestic species such as sheep, goats and cows. A seasonal or continuous occupation has been suggested for these sites (Barker et al. 1990; Maggi and Nisbet 1991). Aside from the zoological remains, a few sequences have been investigated by a suit of techniques, among which micromorphology, botanical and charcoal analyses (Del Lucchese 2009; Nisbet 1997; Macphail et al. 1997).

The picture resulting from the best known deposit in the cave of the Arene Candide indicates the presence of the herd within the cave, probably used as a permanent or temporary stable, with occasional episodes of human occupation (Maggi 1997). It has been suggested that the animals were kept in a fenced area, periodically swept and cleared by burning to dispose of large masses of dung and perhaps prevent the spread of parasites (Macphail et al. 1997). The cyclic repetition of this practice is thought to be the origin of distinctive banded deposits characterizing several cave sites in the Mediterranean basin from the Early Neolithic to the Early Bronze Age (Angelucci et al. 2009). Although pigs are also included in the bone assemblages, Neolithic specimens were still in the wild state. The introduction of domestic pig is commonly dated to the Early Copper Age with the spread of the Chassey culture from south-eastern France to north-western Italy (Maggi 2004c; Maggi and Campana 2008). Aside from clear changes in the material culture, new species of sheep of bigger size are also introduced by the Chasséen shepherds (Maggi 2004a). These latter are probable responsible for significant landscape modifications involving the use of fire to create open pastures, as suggested by multiple natural archives (Maggi 2004b). However, a clear relationship with anthropogenic disturbance remains

dubious (Branch 2013; Branch and Morandi 2015), as the contemporaneous archaeological evidence is mainly found on the western coast. A few findings from Castellaro di Uscio and Tana delle Fate, though, seem to suggest the presence of Chassey groups also in the eastern part (Branch et al. 2014).

It appears clearly that the record is very much pollen-depending (**table 1.3**), and alternative methods have been applied only sporadically and not always systematically - e.g. mesh sizes used in palynology make it difficult to reliably reconstruct fire history, and are likely to provide only a regional picture resulting from airborne particles (Clark 1988). Future studies should then aim to integrate complementary proxies to help distinguish human-driven from climate-driven changes, otherwise the whole debate would keep resting on assumptions which are hard to demonstrate (Branch and Morandi 2015).

2. LABORATORY METHODS AND MATERIALS

Different preparation protocols initially developed for pollen analysis may have various effect on the preservation of fungal spores (Ciara 1994; van Asperen et al. 2016). The use of Hydrofluoric acid is a particularly aggressive treatment, and it was never applied to any of the sites under investigation. Acetylation was also avoided when possible, and used only if it was necessary to improve visibility removing protoplasm.
Non-pollen palynomorphs are normally counted alongside pollen grains, following slight modification to the pollen extraction procedure and mounting in an appropriate medium (Chambers et al. 2011).

Details of the sample preparation are given below:
A volumetric sampler was used to receive the required amount of sample for example 1cm^3, and then the sample extruded into a 100ml graduated glass beaker.
10ml of distilled water were poured into the beaker before step, one or two *Lycopodium* tablets added (noting batch number and total amount of pollen per tablet).
The beaker was covered with aluminium foil, and following addition of 25ml of 1% sodium pyrophosphate was placed onto a hotplate and simmered for 40 minutes at 80 degrees centigrade, stirring frequently. This deflocculates the sample. If after 40 minutes the sample was still intact and sticky, the treatment was continued adding more sodium pyrophosphate.
For each sample place a coarse sieve (125 μm or 200 μm) was placed on top of a fine mesh (5 μm). The lower sieve was flooded with distilled water and the sample poured into the upper sieve, washing out the beaker with distilled water. The coarser fraction was washed until all fine particulate matter was suspended in the lower sieve. The coarse sieve was then removed and the fine sieve washed to remove gne silts and clays.
After reducing the amount of water in the lower sieve, the sample retained was transferred from the sieve to a labelled round bottom centrifuge tube (15ml capacity with screw cap).
Ensuring that the water level in each tube is the same, tubes were centrifuged for 5 minutes at 2500rpm and the supernatant poured off and. The washing procedure was repeated with 10ml of distilled water until the supernatant was clear.

When dissolution of calcium carbonate was required:

A small amount of hydrochloric acid (10%) was added to the centrifuge tube (and the pellet stirred with a wooden stick if necessary). After the reaction had stopped, distilled water was added to the 15ml mark, and the tube centrifuged for 5 minutes at 2500rpm with brake on. The supernatant was then poured off and the washing procedure repeated with distilled water.

For heavy liquid separation, 6ml of sodium polytungstate (specific gravity of 2.0g/cm^3) were added to the centrifuge tubes, that were agitate using a vortex mixer (Labdancer) (30 seconds per sample). With the centrifuge brake to 0, tubes were centrifuged for 20 minutes at 2500rpm.

An appropriate number of conical base centrifuge tubes (15ml capacity, screw cap) were selected and labelled. The organic suspension was poured off from the round bottom tube into the conical tube, and 10ml of distilled water added. The cap was replaced and the tube shaken for 30 seconds to mix/dilute the sodium polytungstate.

After resetting the centrifuge brake on, the tubes were centrifuged for 5 minutes at 2500rpm. The supernatant was poured off and the procedure two more times.

When acetylation was applied, each centrifuge tube was filled with approximately 10ml of glacial acetic acid, then agitated and centrifuged for 5 minutes at 2500rpm (this step dehydrates the sample prior to acetylation). The supernatant was poured off in the fume cupboard (safety clothing and eye protection were worn).

The acetylation mixture was made up in a ratio of 9:1 acetic anhydride and sulphuric acid. 5ml of acetolysis mixture were poured off into the tubes, and the tubes agitated and placed in boiling water bath for 3-4 minutes. The samples were then centrifuged for 5 minutes at 2500rpm and the supernatant poured off into running water in fume cupboard. 10ml of distilled water were added, and the tubes were agitated and centrifuged gain for 5 minutes at 2500rpm. 1.5ml of distilled water were to each conical centrifuge tube, and the residue agitated and transferred using a pipette to 1.5ml or 2ml micro-centrifuge tubes. These latter were centrifuged for 5 minutes at 2500rpm and supernatant poured off.

A small amount of glycerol was added to the pellet and stirred with a clean wooden stick. The residue was then smeared onto a slide, and a cover slip placed over the glycerol allowing it to spread.

For this research, a fluid mountant (liquid glycerol) was preferred to a hard mountants. The choice arises from the following considerations:

- Personal experience has repeatedly shown that fungal spores of primary importance for a sound analysis (e.g. *Sporormiella*-type spores) cannot be correctly recognized unless their distinctive features (e.g. germ slits) are observed. To so do, it is often necessary to turn the objects by gently tapping the slide.
- Many fungal spores are dark-coloured and thick-walled. For this reason, the microfossils are not easily penetrated by light as in the case of pollen grains, and their rotation is required to observe the shape of the objects.
- Unlike pollen grains, most of fungal spores are psilate (having non-ornamented smooth surfaces), therefore it is not possible to use surface patterns as a parameter of identification, and a clear view of the object's shape must be obtained by moving it within the mountant.
- If necessary, unsealed slides prepared with fluid mountants allow rotation of large microfossils (>100 μm), by gently moving the coverslip. This should be done at the end of the counting as all the other smaller microfossils will tend to move across the slide.

Given the difficulty of creating a comprehensive NPP reference collection (an almost impossible task), several articles were used as reference material for the identification of microfossils: Bakker and van Smeerdijk 1982; van der Wiel 1982, van Geel 1972; 1978, van Geel et al. 1981; 1983; 1986; 1989; 2003; 2011; Gelorini et al. 2011; Prager et al. 2012; Ellis and Ellis 1985. The nomenclature of the NPPs follows the common practice indicating a type number and the code of the laboratory where the reference specimens are kept: HdV-type no. = Hugo de Vries Laboratory, University of Amsterdam - The Netherlands, EMA-type no. = Ernst-Moritz-Arndt-University of Greifswald - Germany, TM-type no. = University of Toulouse – le Mirail, Toulouse - France. Newly unidentified microfossil were labelled UR + type no., where UR = Allen Laboratory, University of Reading - United Kingdom.
More detailed explanations of the methodology applied to each site are provided below.

2.1 Prato Spilla 'A' (Chapter 3)

On July 2012, a 730cm long core was taken using a Russian peat corer. The sampling spot was located c. 15m from the northern edge of the basin, next to a minor pool.
At the base of the core, the deposition of fine sand and detrital lake sediment points to the presence of a freshwater lake on the site. The inclusion of fine and corse sand across the core testifies to the deposition of material, probably originating from the erosion of the slopes around the mire. From about 5.60m upwards the formation of woody peat indicates a transition to a terrestrial environment favourable for plant colonisation, following the gradual filling of the lake (**fig. 2.1**).

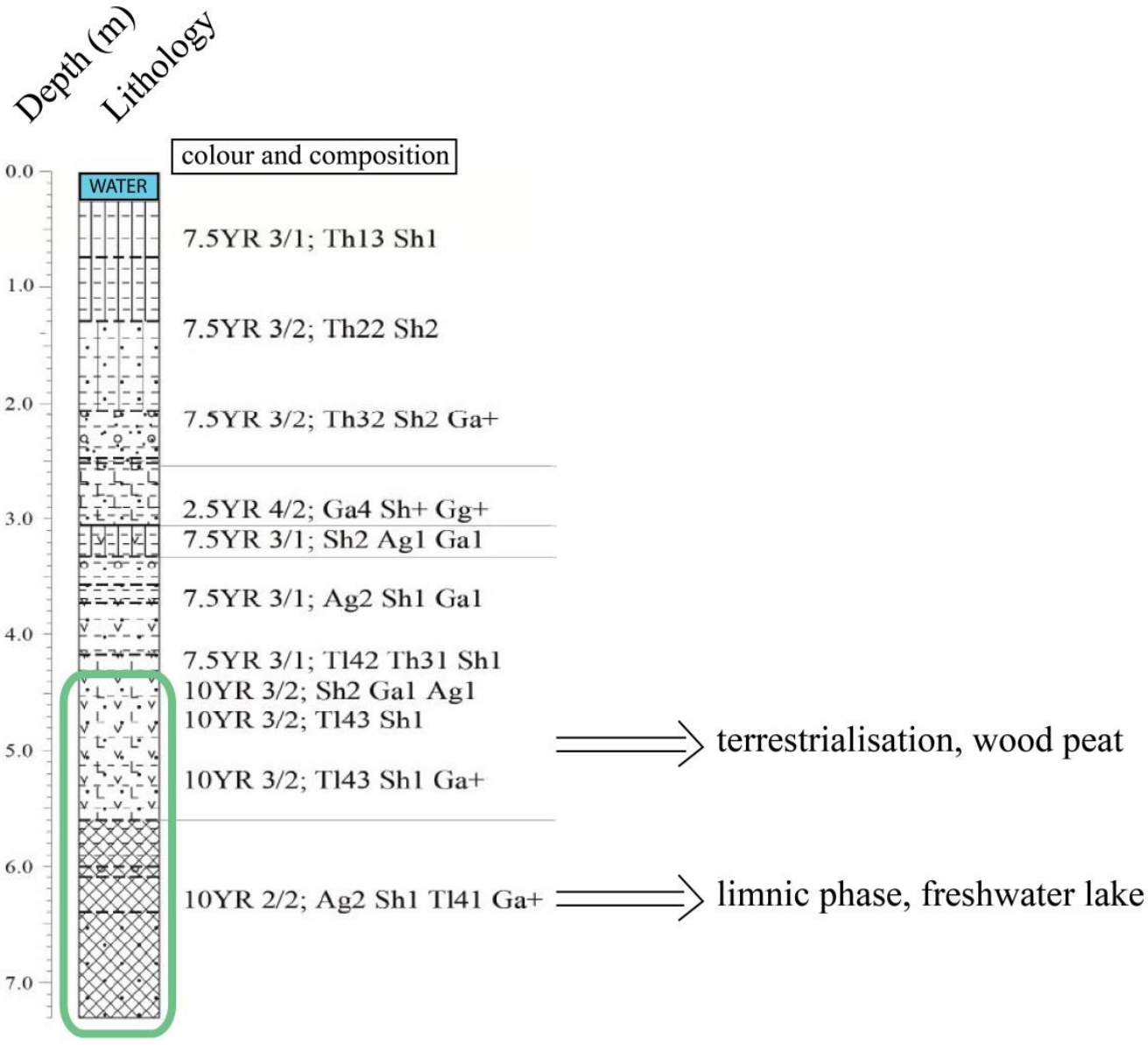

Figure 2.1. Prato Spilla 'A': lithology and main depositional events. The green rectangle marks the part of the sequence investigated.

Subsamples of 1cm^3 were taken from the core every 8cm from the part of the sequence comprised between 730 to 602cm, and every 16cm between 602 and 442cm. Five superficial samples have also been collected using a clean spatula, in the hope of using the relationship between the current vegetation and the current fungal/algal assemblages to help interpret the Middle Holocene deposit.

Bulk sediment samples from four horizons were used for radiocarbon determinations. The results were calibrated with OxCal 4.2.4 (Bronk Ramsey 2013) using the Intcal13 atmospheric curve (Reimer et al. 2013) (**table 2.1**).

Lab code	Depth	d13C	^{14}C years	Cal BP years range at 95.4% probability
OxA-34439	723-722cm	-27.76	7595 ± 40 BP	8457-8341 BP
OxA-34440	667-666cm	-27.48	6636 ± 39 BP	7579-7441 BP
OxA-34441	540-539cm	-27.28	4960 ± 36 BP	5844-5601 BP
OxA-34674	490-489cm	-27.63	4242 ± 30 BP	4861-4655 BP

Table 2.1. Prato Spilla 'A': radiocarbon dated horizons and calibrated ages.

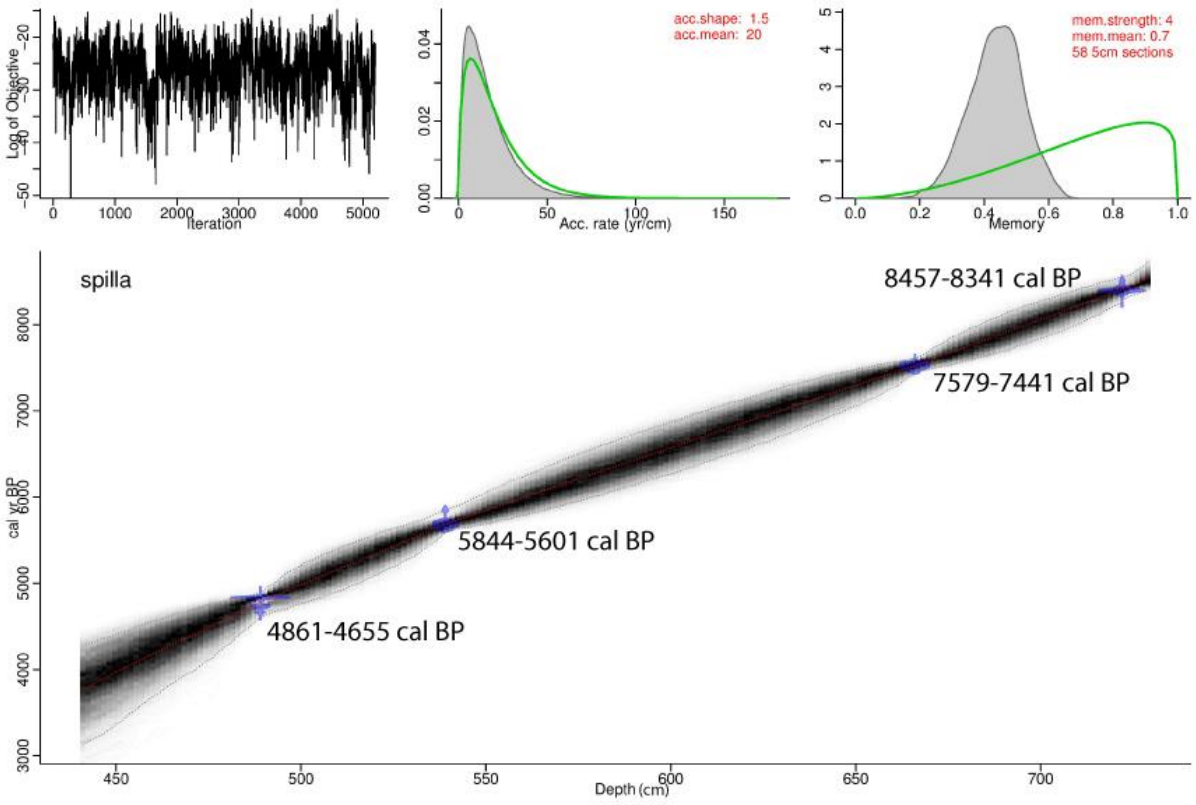

Figure 2.2. Prato Spilla 'A': age-depth model showing the dated horizons (cal. years BP, 95.4 % probability) and the confidence ranges (black/grey curve).

The sequence was then elaborated with Bacon, subdividing the core into 5cm thick sections that were used to create and Age-depth model (**fig. 2.2**). From the uppermost and lowermost dates, the model was stretched to the top and bottom of the sequence by means of interpolation.

Microscope slides were prepared at the University of Reading sieving through 125 and 10μm meshes and applying acetolysis treatment prior to mounting in glycerol. A Leica DME light microscope (400x and x1000x magnification) was used for the analysis. A high number of small or particularly significant microfossils have been identified in oil immersion at x1000 magnification.

In total, 27 samples were analyzed, with counts averaging 460 NPPs, ranging from 361 to 630 total microfossils per sample, and including a minimum sum of 200 fungal spores/fungal hyphopodia/algal remains (numbers ranging from 209 to 306). High values of indeterminable microfossils (see e.g. Menozzi et al. 2010, fig. 3; Latałowa et al. 2013, fig. 4) arise from the incidence of multiseptate types, rarely distinguishable and often incompletely preserved, and other broken or poorly preserved microfossils.

As NPPs were counted separately from the pollen, values are expressed as percentages of Total Non-Pollen (spores + hyphopodia + algae) Palynomorphs Sum (TNPP) (Mazier et al. 2009; Cugny et al. 2010). Chironomid remains, other microfossils of animal origin, other microfossils of vegetal origin and fungal fruit bodies are reported as TNPP %.

2.2 Genoa, Piazza della Vittoria (Chapter 4)

The part of the core comprised between 15.10 and 24.74m from the surface is characterized by an abundance of organic material, and was therefore selected for the study. Provisional data are available from sedimentological and palynological analyses (Melli et al. 2011; Arobba and Caramiello 2014; Arobba et al. 2016). The sequence is characterized by the deposition of silty/silty clayey levels, intercalated with sporadic thin organic-rich and peaty horizons (**fig. 2.3**). Below 25m lies a series of minerogenic silty clayey levels intercalated with sand and gravel, until the Pliocenic deep geology localized at 45.30m below the surface and consisting of the Clays of Ortovero. Further deep (-111m) is the top of the Cretaceous formation known as Limestone of Monte Antola (Arobba et al. 2016). It is likely that the upper 25m of the deposit have formed

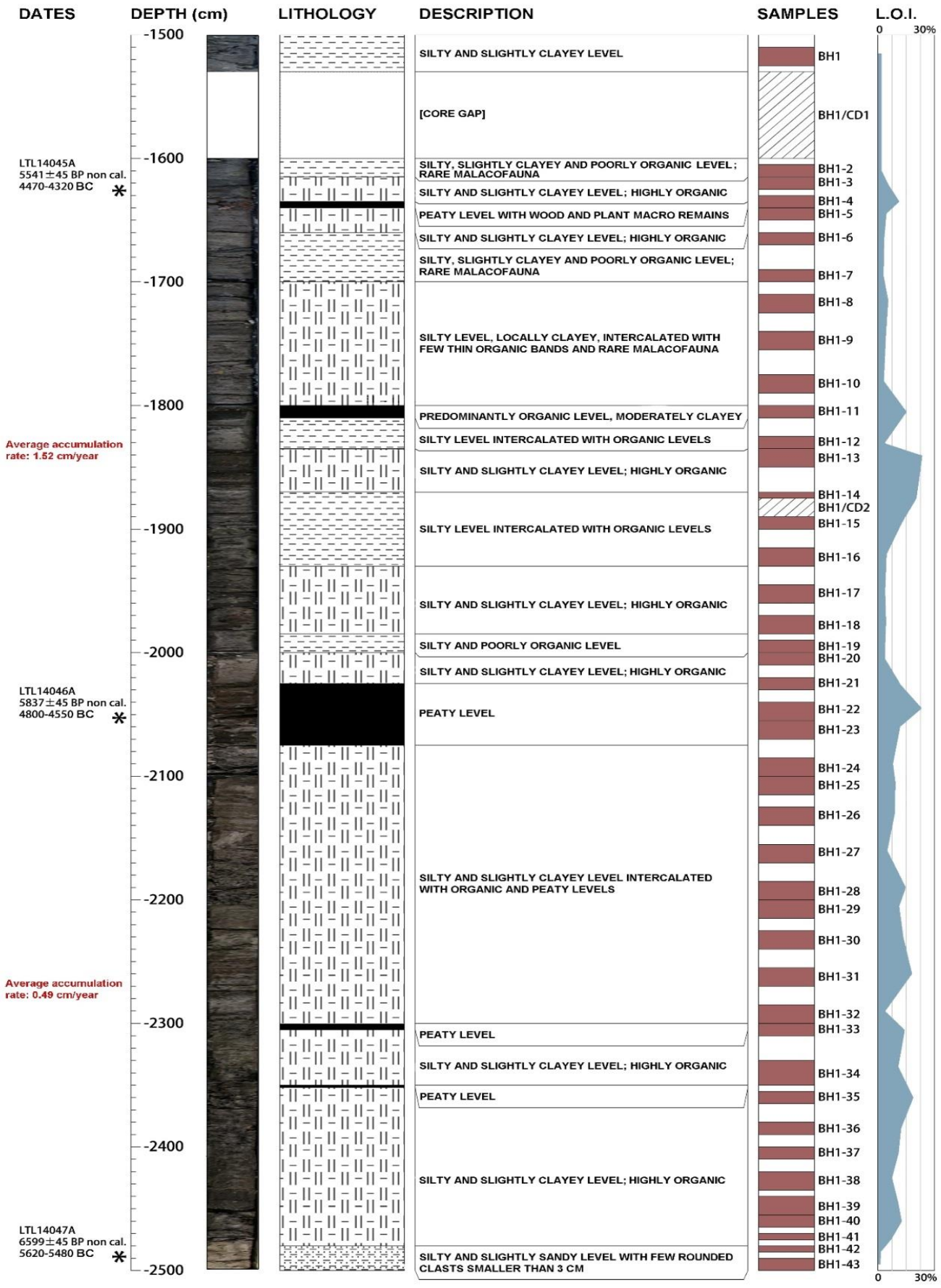

Figure 2.3. Genoa, Piazza della Vittoria. Diagram showing the sequence from the borehole BH1 and its main depositional units.

due to an alternation of several complex high- and low-energy episodes involving alluvial deposition, as typical of river deltas. The data seem to point to an inlet formed by a palaeomeander of the Bisagno, localized up to 1km inland of the current shoreline, which constituted the very first harbour of Genoa since late prehistory, than silted up by the river and replaced (Melli et al. 2011).

Forty-three samples were taken at distances varying between 10 and 15cm. The sediment was deflocculated in KOH and then sieved through 5 and 180μm meshes. Microfossils were isolated by means of heavy liquid separation (Thoulet liquid, specific gravity 2.1), avoiding the use of acetylation in order to preserve pollen and spores as best as possible. The residue was then mounted in liquid glycerol under 24 x 40mm microscope cover slips and sealed with histolaque LMR®. As pollen and NPP analysis were carried out independently, a count of a minimum of 200 fungal/algal spores and hyphopodia per sample was reached (averaging 244, ranging from 205 to 659), except for seven samples less rich in microfossils, whose counts range from 110 to 183 NPPs (mean 141). A Leica DME compound microscope was used for the analysis (400x and 1000x magnification). A high number of small or particularly significant microfossils have been identified in oil immersion at x1000 magnification. NPP values are expressed as percentages of total fungal/algal spores + hyphopodia (TNPP sum) (following Mazier et al. 2009 and Cugny et al. 2010). Chironomid remains, testate amoebae, parasite eggs, flatworm eggs, stomata, sporangia, other microfossils of animal origin and fungal fruit bodies are reported as TNPP%.

Newly identified microfossils were labelled with the code UR (University of Reading, Allen Laboratory), followed by a sequential number. In order to avoid unnecessary multiplication of types, when the identification was certain the codes used in the previous literature have been used (Miola 2012). All new types, their possible biological identification and equivalence with previously described types are listed in the final Appendix. Three radiocarbon dates were obtained (Ce.Da.D. Laboratory, Universitá del Salento) from wood macro remains near the top of the sequence (16.20m = LTL14045A, 6345 ± 68 cal BP), from the middle (20.47m = LTL14046A, 6625 ± 120 cal BP), and near the base (24.82m = LTL14047A, 7500 ± 67 cal BP), pointing to a steady and rapid deposition.

2.3 Samples from modern animal pens and dung pats (Chapter 5)

As much oral information as possible was gathered on the sites from the owners, and details about animal density, species, diet and other farming practices were recorded. Dung pats and droppings and mixed soil/dung samples were collected from a variety of sites (**figs. 2.4, 2.5, 2.6, 2.7, 2.8**), listed in **table 2.2**. The information collected on the site, including the degree of continuity of surface disturbance (CSD) is reported in **table 2.3**.

Table 2.2

Sites of sample collection form modern dung heaps, stable floors and outdoor corrals.

Location	Altitude	Sample nos.
Arborfield (Berkshire, UK)	50m asl	2, 4, 11, 15, 16, 27a-b
Besnate (Lombardy, Italy)	280m asl	1, 22
Semogo (Valdidentro, Lombardy, Italy)	1810m asl	28
Somma Lombardo (Lombardy, Italy)	250m asl	7, 12, 23, 24, 26
Tarquinia (Lazio, Italy)	160m asl	3, 8, 9, 10
Vaccarezza (Bobbio, Emilia-Romagna, Italy)	727m asl	5, 17, 18, 19, 21
West Overton (Wiltshire, UK)	150m asl	6, 13, 14, 20, 25

Table 2.3

Conditions recorded on the sampling locations. CSD = continuity of surface disturbance.

Sample no.	Structure/context	Animal species	Approximate quantity of specimens (if known)	Diet	Other	CSD
1	Roofed stable; floor made of cement	Cows (*Bos taurus*): Holstein Friesians		Hay collected in the surroundings of the farm		high
2	Roofed stable; floor made of cement	Cows (*Bos taurus*): Holstein Friesians		Grass/maize silage		high
3	Roofed stable; earthen floor	Sheep (*Ovis aries*): Apennine	The stable hosts a maximum of c. 100 sheep	Grass	Sheep freely graze on grassland during the day, and are kept here overnight, especially younger specimens	moderate
4	Roofed stable; floor made of cement	Cows (*Bos taurus*): Holstein Friesians		Grass/maize silage		high

5	Roofed stable; floor made of cement	Cows (*Bos taurus*): Piedmontese		Mixture of maize, barley and bran and also with Lucerne (*Medicago sativa*)		high
6	Roofed stable; earthen floor	Sheep (*Ovis aries*): Suffolk + North Country Mule		When kept, sheep are fed with hay and grass	Sheep are kept in in the stable from January to the end of April and graze on the surroundings of the farm for the rest of the year	low
7	Small outdoor corral	Horse (*Equus ferus caballus*): cross between Haflinger and Quarter Horse	1	Hay and oat		moderate
8	Medium sized corral	Sheep (*Ovis aries*): Apennine variety	A few hundred	Grass	Sheep freely graze on grassland during the day, and are kept here overnight all year round	moderate
9	Medium sized corral	Sheep (*Ovis aries*): Apennine		Grass	Sheep freely graze on grassland during the day	moderate
10	Medium sized outdoor corral	Sheep (*Ovis aries*):		Grass	Lambs with their mothers are kept here from January to April	low

		Apennine				
11	Medium sized outdoor corral	Sheep (*Ovies aries*): unknown breed	c. 10 specimens	Grass	Occasionally, sheep are kept here for some weeks, where they are free to graze	low
12	Medium sized outdoor corral	Goats (*Capra hircus*): 2 Tibetan + 1 Chamois coloured	3	Grass and herbs	Goats are free to get out of the fenced area for a few hours a day, freely grazing on the understory; when kept, they spend most of the time resting in a small wooden shelter inside the enclosure	moderate
13	Large grazing area covered in grassland	Sheep (*Ovis aries*): Suffolk + North Country Mule		Grass		moderate
14	Large grazing area covered in grassland	Sheep (*Ovis aries*): Suffolk + North Country Mule		Grass		moderate
15	Cow dung heap	Cows (*Bos taurus*): Holstein Friesians		Grass/maize silage		low

16	Cow dung heap	Cows (*Bos taurus*): Holstein Friesians	Grass/maize silage	low
17	Cow dung heap	Cows (*Bos taurus*): Piedmontese	Mixture of maize, barley and bran and also with Lucerne (*Medicago sativa*)	low
18	Cow dung heap	Cows (*Bos taurus*): Piedmontese	Mixture of maize, barley and bran and also with Lucerne (*Medicago sativa*)	low
19	Cow dung heap	Cows (*Bos taurus*): Piedmontese	mixture of maize, barley and bran and also with Lucerne (*Medicago sativa*)	low
21	Cow dung heap	Cows (*Bos taurus*): Piedmontese	Mixture of maize, barley and bran and also with Lucerne (*Medicago sativa*)	low
20	Sheep dung heap	Sheep (*Ovis aries*):	Hay and grass	low

		unknown breed		
22	Cow dung heap	Cows (*Bos Taurus*): Holstein Friesians	Hay collected in the surroundings of the farm	low
23	Horse dung heap	Horses (*Equus ferus caballus*): unknown breed	Hay and oat	low
24	Horse dung heap	Horses (*Equus ferus caballus*): unknown breed	Hay and oat	low
25	Droppings	Sheep (*Ovis aries*): unknown breed	Hay and grass	low
26	Droppings	Goat (*Capra hircus*): unknown breed. Either Tibetan or Chamois coloured	Grass and herbs	low
27a-b	Droppings	Sheep (*Ovis aries*):	Grass	low

		unknown breed		
28	Droppings	Red deer (*Cervus elaphus*)	Diet may vary; in winter it is most likely made of wild fruits, dried grass and tree bark	low

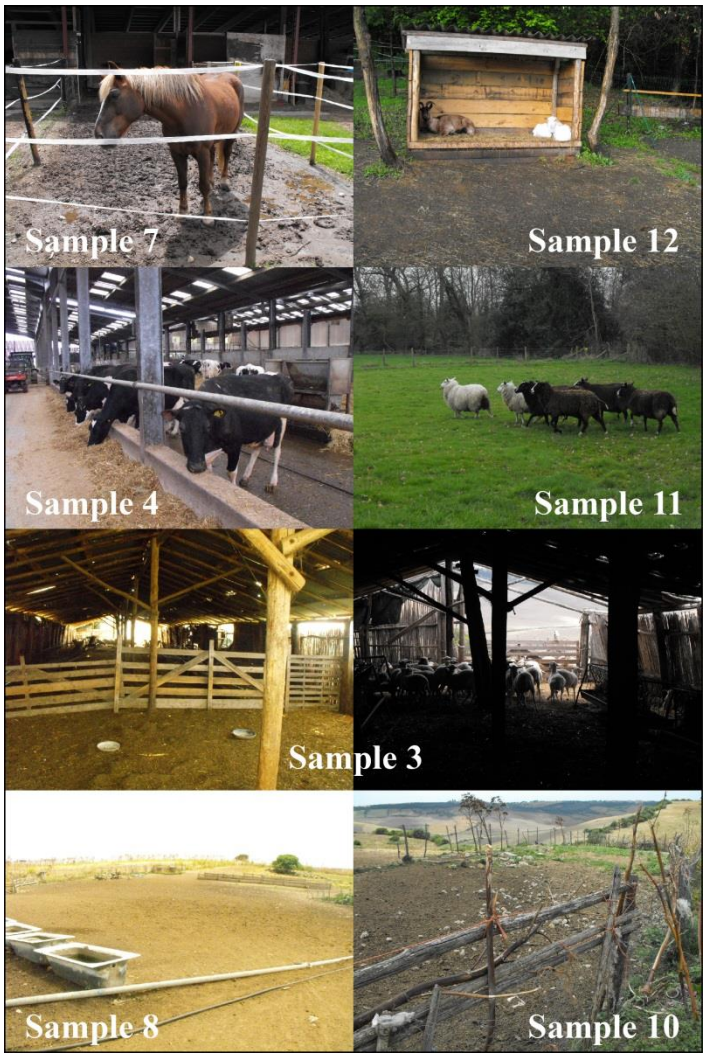

Figure 2.4. Modern samples: selection of sample locations.

The herding site of Arma delle Manie was also selected for investigation, following the pioneering work by Brochier et al. (1992), which studied pastoral deposits through the excavation of recent Mediterranean rock shelters. The site is located c. 2km inland from the coast of Finale Ligure and Varigotti (Liguria, Italy), at an altitude of 270m asl (**fig. 2.9**). Oral accounts indicate that it was used to corral livestock, at least in the last two centuries. This was still the case in the 1980s when sheep were kept; previously, the site was used for keeping cows. The animals were taken to graze elsewhere on a daily basis and then brought back to the shelter. Moreover, the presence of a circular millstone platform also suggests the use of a mule. Possible evidence for wool polish generated by animals (Vergès and Morales 2016; Vergès et al. 2016) was noted along some of the walls.

Figure 2.5. Site of Vaccarezza. Accumulation of cow dung resulting from the stabulation of cattle.

Figure 2.6. Site of Tarquinia. View of the pastureland used for sheep farming.

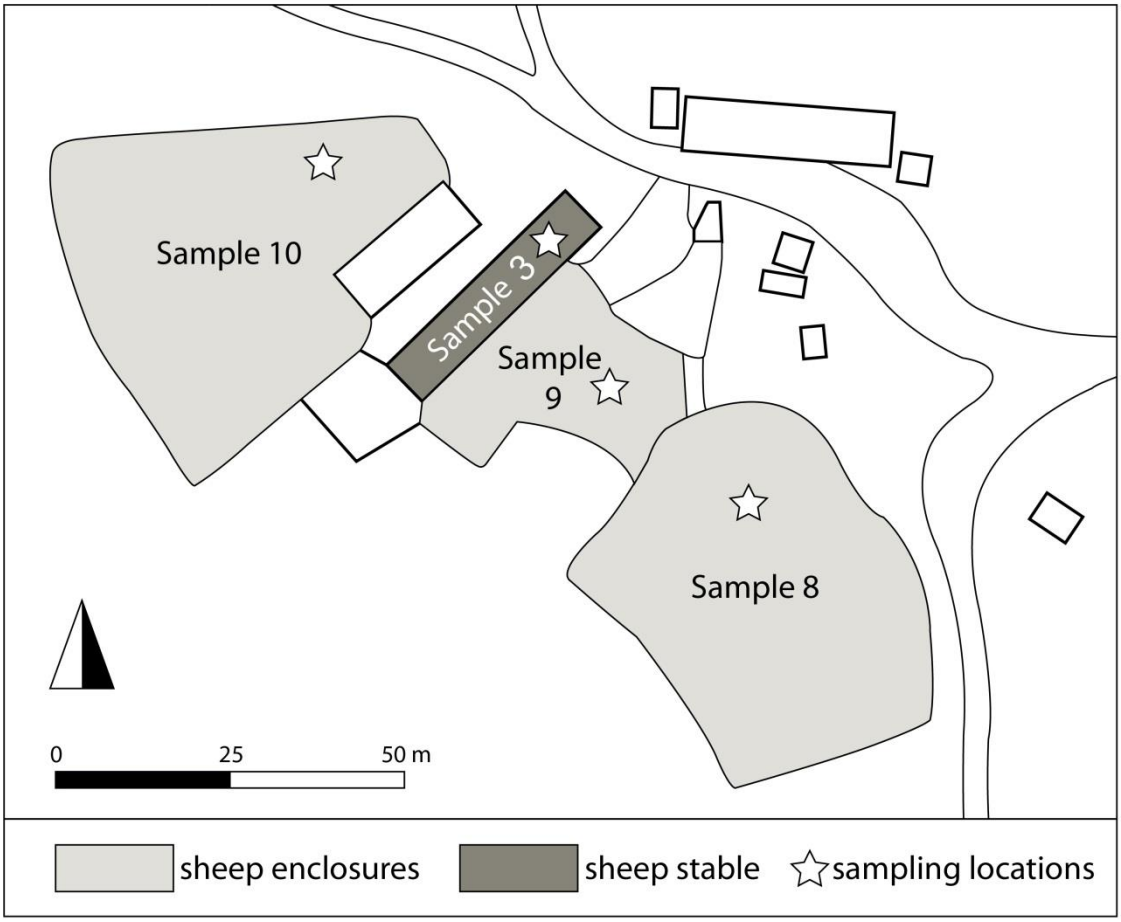

Figure 2.7. Civita di Tarquinia (Lazio, Central Italy): map of a local sheep farm showing the area occupied by the enclosures and the sampling locations (samples 3, 8, 9, 10).

Figure 2.8. Vaccarezza (Emilia-Romagna, NW Italy): cattle stabled in a local (sample 5).

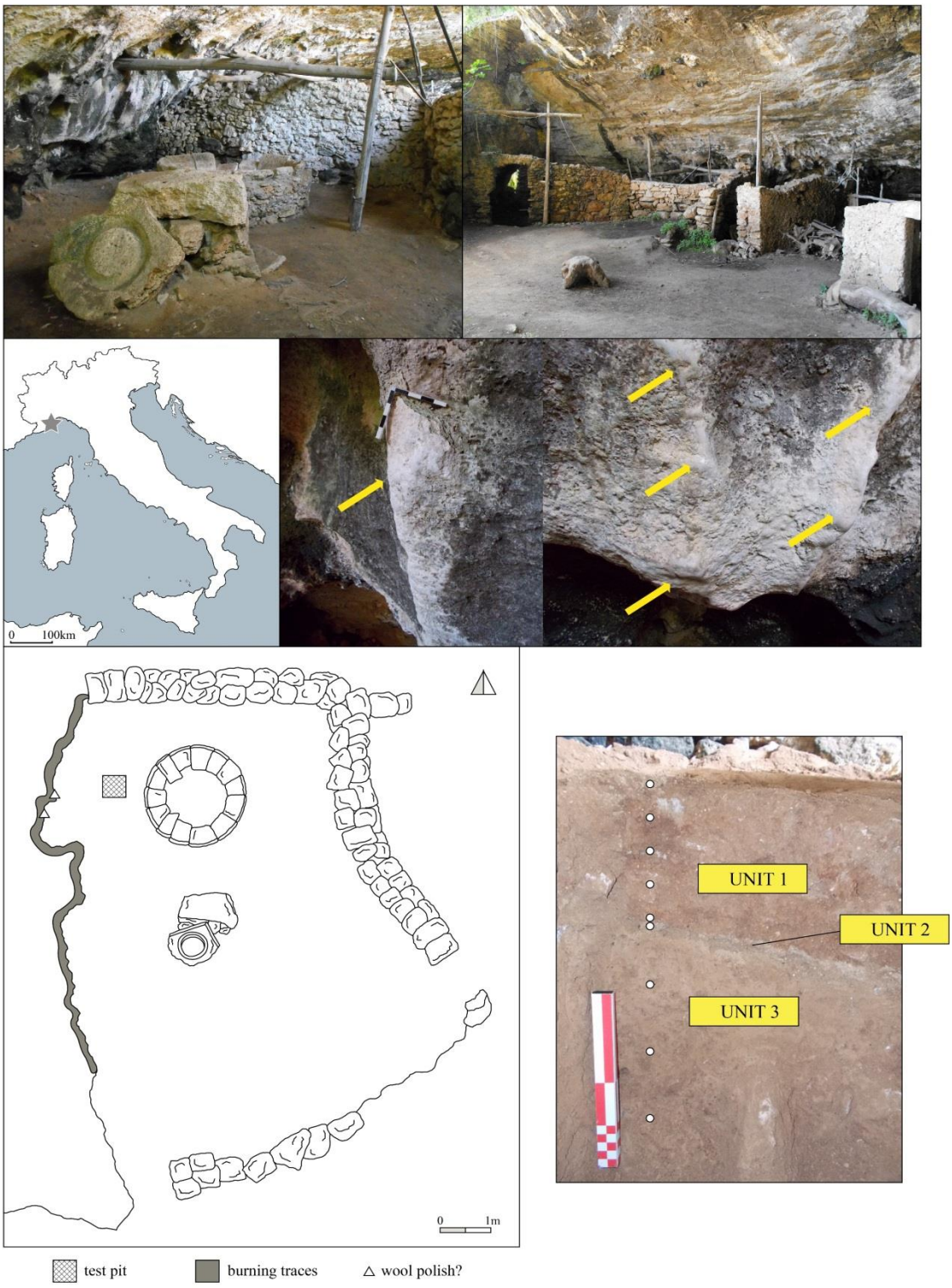

Figure 2.9. Finale Ligure (Liguria, NW Italy): pastoral rock shelter of Arma delle Manie. The site was used in the last centuries for keeping livestock, primarily sheep and cows. The yellow arrows indicate possible traces of wool polish along the western wall of the shelter.

For livestock enclosures, subsamples were collected from different locations within the fenced area and then homogenised together in order to obtain a sample as representative as possible. In archaeological deposits it is not always possible to distinguish between different dung loads and related interfaces due to the following compaction and homogenization of colour and texture. Consequently, care was taken when sampling dung heaps, in order to mix material collected from the surface with that taken from c. 2-3cm below the surface. In one case, material from the surface of sheep droppings (Sample 27a) was collected and prepared separately from that collected from the core of the faeces (Sample 27b). At Arma delle Manie, a 1 m^2 test pit was dug and the exposed section sampled at regular intervals (every 4 and every 8cm, in addition to a stratigraphic unit located between 17 and 18cm of depth).

Subsamples of 1cm^3, 2g or 5g were taken and processed with acetylation and heavy liquid separation (Sodium polytungstate, specific gravity 2.0g/cm^3) following deflocculation in Sodium pyrophosphate (1%), sieving through 5 and 200μm meshes and mounting in liquid glycerol (Branch et al., 2005). The samples from the rock shelter of Arma delle Manie were treated with HCl to dissolve carbonates, but acetylation was not applied to avoid degradation of fragile microfossils. A known quantity of *Lycopodium* spores was added, and in order to calculate NPP concentration a minimum sum of 200 (exotic markers + dung spores) was counted to obtain statistically reliable and representative results (Finsinger and Tinner 2005), although in several cases much higher counts were reached (up to 1748 dung spores). Identifications were made at 400x and 1000x (oil immersion) magnifications, and for Arma delle Manie a standard depth/concentration diagram was created using TILIA 1.7.16 (Grimm 2011).

All volumetric samples were weighted, in order to enable calculation as microfossil number per gram, and 1cm^3 of material from all of the other samples was weighted in order to also enable conversion of the results into microfossil number per cm^3. This is essential to provide both values to permit comparisons between sites, as some authors report values as concentrations per unit of weight of dry sediment (g) whilst others as concentrations per unit of volume (cm^3) (Bosi et al. 2011; Dietre et al. 2012; Expósito and Burjachs 2016; Vaccaro et al. 2013). When possible, microfossils were labelled according to the existing literature (Miola, 2012). For new types and when identification with previously described NPPs was uncertain, the prefix UR- (University of Reading) was adopted.

For the examination and quantification of faecal spherulites, the material from the pit profile at Arma delle Manie was subsampled using a precision scale, in order to collect 1 mg of dried and untreated sediment from each of the levels selected for NPP extraction. This was ground and smeared on a microscope slide with a drop of liquid glycerol. The entire slide was then examined under cross-polarised light at 400x magnification, counting all of the spherulites. Abundance was then expressed as spherulite number per mg of sediment. Reference slides from fresh sheep droppings collected at Arborfield (Berkshire, UK) were also prepared in order to observe a high number of elements and train the eye to confidently distinguish faecal spherulites from similar features (Canti, 1998).

Previous studies on spherulites have employed different methods for counting and reporting values, ranging from the number of elements per 30-50μg (Canti, 1999), to the number per gram (Portillo and Albert 2011; Portillo et al. 2009, 2010, 2011), to relative abundance (Brochier 1991; Brochier et al. 1992; Elliott et al. 2014; Goren 1999). The procedure followed here resembles the method used by Portillo et al. (2009), although the whole slide was scanned instead of a number of randomly chosen fields, hopefully improving the accuracy of the results. It seems appropriate that future studies adopt a similar approach expressing the results as spherulite number per unit of weight, in order to enable comparison between sites.

On the stratigraphic units from Arma delle Manie, phosphorus analysis was also performed, in order to quantify the presence of total phosphorus (Ptot) from the pit profile in the rock shelter. The samples were dried, ground to a powder in order to obtain a flat surface and tested using a Niton XL3t GOLDD+ portable XRF analyser fixed to a shielded stand. Values were expressed as part per million (ppm).

2.4 Cave of Arene Candide (Chapter 6)

Sixteen samples were obtained from a newly exposed Neolithic section characterized by the alternation between charred and uncharred layers (**fig. 2.10**). The sequence, facing south, is located in the eastern part of the cave, near the 1972-1977 excavation (Maggi et al. 1997). This is due to the fact that extensive stabling layers were excavated in this area in the previous campaigns, leaving only the section on the northern limit intact for sampling. Irrespective of the sediment colour, ranging from black to light brown and grey, all layers presented a sandy-silty texture.

Figure 2.10. Cave of Arene Candide: the profile sampled for the analysis. Note the alternation between burnt and unburnt horizons, as typical of Mediterranean *fumiers*.

Radiocarbon dates for the deposit are not available as yet, although based on correlation with the other excavated layers the sequence is expected to span from the Middle Neolithic to the Early Copper Age.

It was decided to collect a large amount of sample (20 grams) given the probable low number of preserved microfossils (cf. Arobba 1990). A known amount of exotic markers was added to the samples, which were then treated in Sodium pyrophosphate (1%) for deflocculation and sieved through 5 and 200µm meshes. Pollen and spores were isolated by means of heavy liquid separation (Sodium polytungstate, 2.0g/cm^3), avoiding the use of acetolysis not to damage the microfossils, especially the more delicate pollen grains. The pellets were stored in liquid glycerol, and mounted under 22 x 40mm cover slips sealing the edges with clear nail polish.

Pollen grains and NNPs were counted at the same time. A minimum pollen sum of 300 grains was chosen (total pollen sum), and NPPs were calculated as percentages of this sum. Only samples with a sufficient amount of material preserved could be included in

the analysis. Pollen of the tribe Cichoriaeae have been divided into three size classes following Florenzano et al. (2012), in order to increase the level of taxonomic accuracy.
A specific extraction method was applied in an attempt to recover parasite eggs from the archaeological layers, following Anastasiou and Mitchell (2013; slightly modified), involving deflocculation in Sodium pyrophosphate (1%) of 10g of sediment, addition of exotic markers, sieving through 38 and 150µm meshes and heavy liquid separation (Sodium polytungstate, 2.0g/cm^3). The residue was then mounted in tap water to obtain temporary microscope slides.

2.5 Castellaro di Uscio (Chapter 7)

A soil profile was exposed on the eastern limit of the upper terrace excavated in 1982-1985, in order to sample the dark Final Bronze Age horizon (Layer 3U). Samples were also taken from the topsoil (Layer 1U) and the underlying horizon (Layer 2U), and from the subsoil beneath the occupation layer (Layer 4U) (**fig. 2.11**). The same sequence was identified and sampled at the western limit of the excavated lower area (Layers 1L, 2L, 3L, 4L). 10g of material were subsampled from each layer and dissolved in Sodium pyrophosphate (1%) following the addition of a known number of *Lycopodium* spores to enable calculation of pollen concentration. The samples were sieved through 5 and

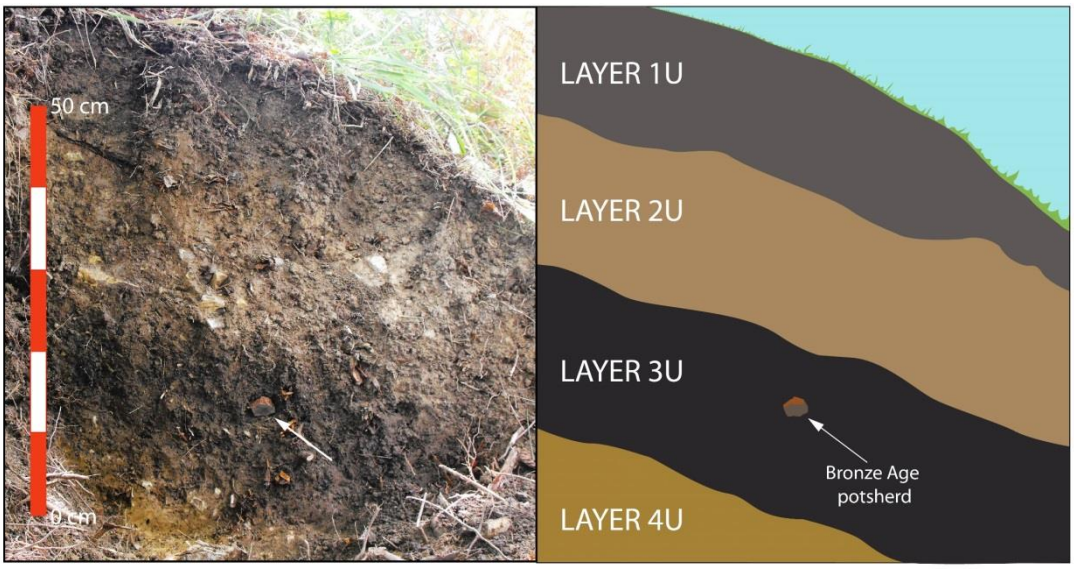

Figure 2.11. Castellaro di Uscio: soil profile exposed at the upper terrace. The dark horizon (layer 3U) results from the Bronze Age occupation of the site.

200µm meshes, and the organic content was separated from mineral matter by means of heavy liquid separation (Sodium polytungstate, specific gravity 2.0 g/cm^3). Because the grains appeared to be still obscured by cellulose after this stage, acetylation was successfully applied in order to clean the grain surface and facilitate identification. Microscope slides were then prepared using liquid glycerol as a mounting medium. Modern reference collections and manuals (Reille 1992; Beug 2004) were used as an aid to the identification.

For total phosphorus analysis, the samples were dried, ground to powder in order to obtain a flat surface and tested using a Niton XL3t GOLDD+ portable XRF analyser fixed to a shielded stand. Values are expressed as part per million (ppm).

3. PRATO SPILLA 'A': A MIDDLE HOLOCENE UPLAND MIRE

3.1 Geographical setting and previous studies

The site of Prato Spilla 'A' (44°21'16'' N 10°05'51'' E) - here indicated by a letter in order to distinguish the bog from three other sites, Prato Spilla 'B', 'C' and 'D' - is located in the Liguro-Emilian Apennines, about 40km north of the town of La Spezia and 65km south of Parma, at 1560m asl (**fig. 3.1**). The modern vegetation of the area consists of a dense beech forest. The basin measures c. 40m along its major axis, and the wetland is currently dominated by sedges and grasses (**fig. 3.2**).

Previous work on the site has shown that 9m of sediments have accumulated since the Early Holocene, the whole sequence spanning c. 10,000 years. The vegetation history of the area shows that irregular variations in the percentages of tree taxa occurred, resembling the trends recorded at Ligurian sites associated with Middle Holocene archaeological remains (Lowe 1991). Strong evidence for the *Ulmus* decline commencing around 5500 BP is attested, slightly preceded by the rise of *Fagus* and paralleled by peat initiation (Lowe 1991; Lowe et al. 1994b) (**fig. 3.3**).

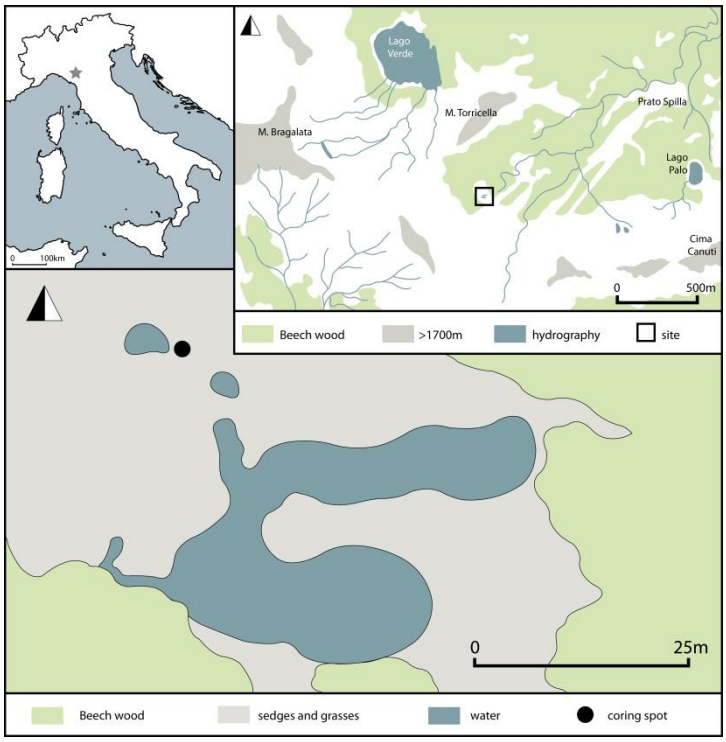

Figure 3.1. Prato Spilla 'A': map showing the location of the site 'A'.

Figure 3.2. View of the site from the south.

What is more important for the human/environment interaction throughout the Holocene, the pollen record has highlighted the occurrence of factors suggesting possible anthropogenic disturbance in the area at least since c. 5000 cal BP (Lowe et al. 1994a; 1994b). According to Lowe (1991) it is likely that the vegetation history of the area points to anthropogenic disturbance. A recent refinement of the vegetation history of the site has provided further clues to possible human-driven environmental changes. A few large grass grains were tentatively identified as cereal pollen, but no clear microcharcoal peaks were identified (Bedford 2013).

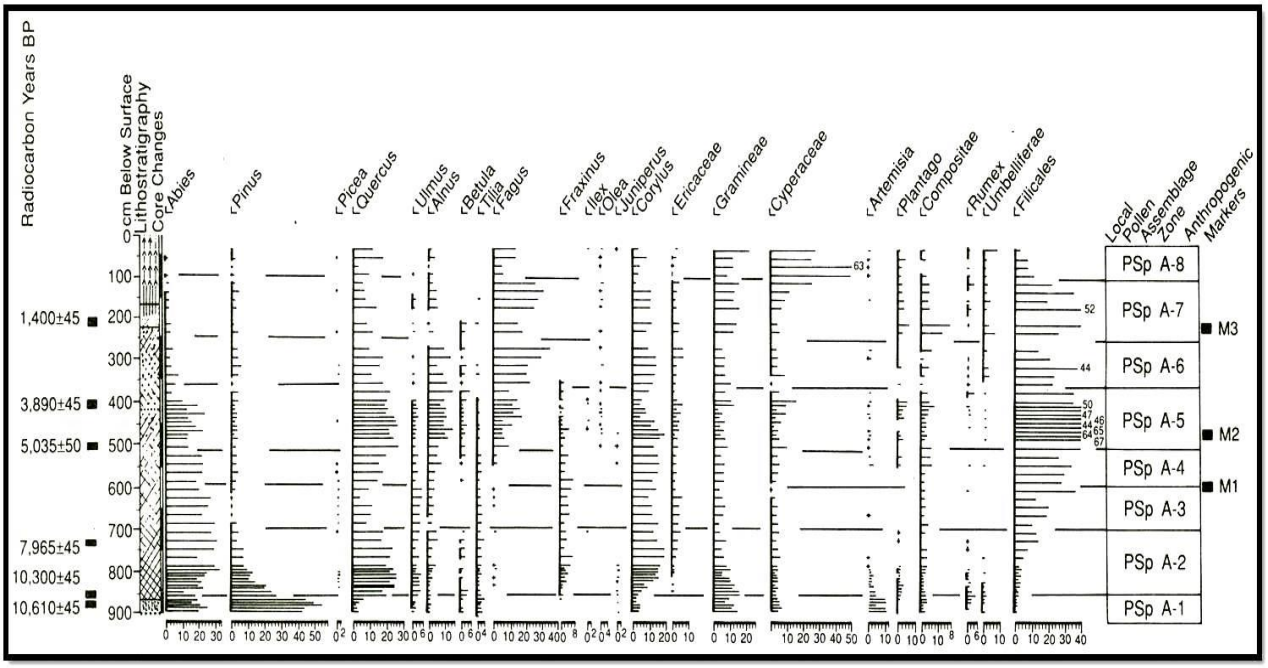

Figure 3.3. Prato Spilla 'A': pollen diagram from Lowe 1991.

Therefore, given the evidence for possible human activity during late prehistory, the site has been selected as a promising context to carry out a NPP analysis. This technique may indeed help assess the degree of anthropogenic influence, and provide additional data on the past ecology of the wetland. Moreover, the identification of coprophilous fungal spores is currently one of the few existing methods for assessing the local presence of herbivores in off-site contexts (Linseele et al. 2013), and it proves particularly suitable when investigating a region long inhabited by Late Neolithic and Copper Age pastoral societies.

The area north of Prato Spilla is characterized by a large fertile plain, densely inhabited during the Neolithic. Before the emergence of the VBQ culture, in the Early Neolithic the Fiorano culture emerges as a distinct facies (Bagolini and Biagi 1977). Many open-air settlements were identified, some of them reaching a noticeable extent (Degasperi et al. 1998). Although they are less known than the contemporary north-eastern sites in Friuli, there is evidence for plant domestication since the Early Neolithic (second half of the 8th millennium BP) (Rottoli and Castiglioni 2009). However, faunal assemblages show a high proportion of wild species, and subsistence strategies are not clearly known as yet (Bagolini and Pedrotti 1998; Rowley-Conwy et al. 2013).

The origin and characteristics of the first transhumance in southern Europe have been long discussed (Maggi et al. 1991; Arnold and Greenfield 2006; Jourdan-Annequin and Duclos 2006). In broad terms, this form of livestock management involves the seasonal movement of flocks to upland pastures during the summer months, under the care of one or more shepherds (Braudel 1949). The method aims to make the best possible use of resources exploiting the richness of the mountain pastures in the warm season and avoiding drought in the valleys (Sullivan and Homewood 2003). In the cold season, the herds are kept in the permanent lowland settlements. This practice may leave a trace in livestock diet, as it has been demonstrated for Swiss lake shore settlements (Akeret and Jacomet 1997; Akeret et al. 1999).

There is a certain degree of confusion around the definition of transhumance, especially in terms of horizontal transhumance as this often merges with the concept of nomadism (Cribb 1991). It would be incautious, however, to label prehistoric forms of herding with any of the modalities known in the better documented post-Roman centuries. It is possible that in prehistory the practice had a character of

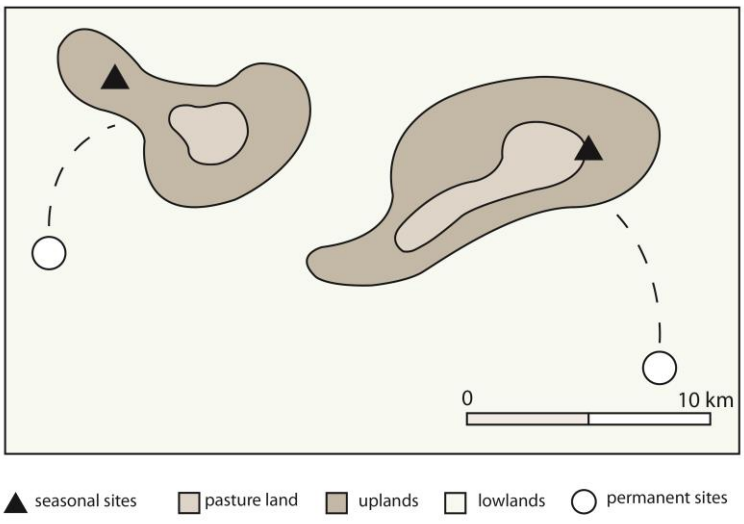

Figure 3.4. Schematic model of short-range vertical transhumance.

short-range nomadism involving the movement of a single family group along the route (Maggi 2004a) (**fig. 3.4**). According to Maggi and Nisbet (1991), this may be indicated by the skeletons found in the high-altitude cave of Grotta del Pertuso (1330m asl), used as a burial site for individuals of both genders and various ages.

The data from our study region, based upon evidence from archaeological sites and palaeoenvironmental records suggest a gradually more frequent use of mountain pastures as early as the Late Neolithic (Branch and Marini 2014). The signal seems to become increasingly stronger during the Copper and Bronze Age, when important landscape modifications associated with burning episodes and woodland clearance occur. The evidence includes pastures located at very high altitudes. The shelter of Tana del Barletta (950m asl) was used as a stable between the Late Neolithic and the Bronze Age, suggesting a seasonal exploitation of the pastures of Mt. Galero at 1700m asl (Del Lucchese et al. 1987; Barker et al. 1990). Indirect evidence for high-altitude herding is also indicated by a number of rock engravings found on Mt. Bego (above 2000m asl) and dated to the Copper and Bronze Age (De Lumley 1984; Maggi and Nisbet 1991; Maggi 1998a; 2004b). It has been suggested that only small groups of individuals were involved in these first pastoral activities (Maggi and Nisbet 1991). This point should be taken into consideration when interpreting palaeoecological records from lakes and mires because small populations may have had restricted spatial impact on the environment and therefore produced only a weak anthropogenic signal (Branch and Morandi 2015).

It has been suggested that Tana del Barletta and Arene Candide should be viewed as part of a pastoral system linking these sites to possible villages located in the plain of Albenga, some 20km away on the coast (Maggi and Nisbet 1991). However, on the basis of the cull of domestic species, Rowley-Conwy (1997) has argued that Arene

Candide was occupied all year long and should thus be seen as a permanent outlying settlement. Moreover, the site is not located in the highlands, therefore it cannot be part of a vertical farming system. With very few exceptions (Spindler 1994; 2003), long-range transhumance (>100km) is considered implausible in prehistory, because it is dependent on extensive social and economic networks only found later in the Roman and especially medieval periods (Barker 1985; Marzatico 2007; Robb 2007).

3.2 Results

More than 260 NPP types have been recorded during the analysis. Following Mazier et al. (2009), in order to highlight the main changes in the fungal community the sequence has been divided into five Non-Pollen Palynomorph Assemblage Zones (NPPAZs) (**fig. 3.6**), which differ from the Local Pollen Assemblage Zones (LPAZs) distinguished during the pollen analyses (Lowe 1991; Lowe et al. 1994b; Bedford 2013). This choice is due to the biological difference between plants and the fungal community, which reflects a diverse ecology and different succession mechanisms (Neville and Webster 1985). Moreover, symbiotic relationships between fungi and host plants may vary through time, without apparent changes in the vegetation community (Gange et al. 2011).

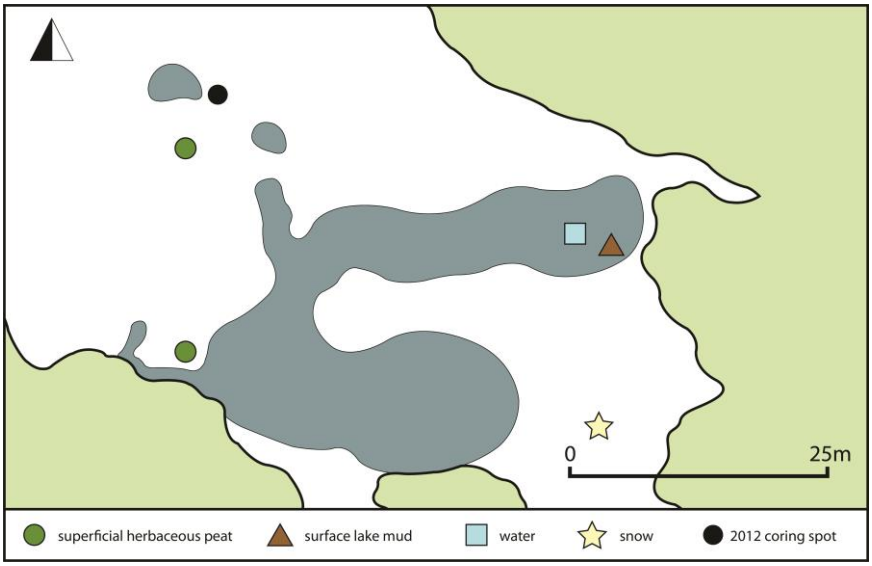

Figure 3.5. Prato Spilla 'A': location of modern surface samples.

The modern surface sediment and water samples (**fig. 3.5**) have not yielded useful results, as they were virtually devoid of fungal and algal spores. It is therefore likely that local conditions on the site have changed notably since c. 4000 BP, which is the latest date represented by the top part of the core.

NPPAZ PSA-1 · Depth: 729cm - 689cm · ~7500-6700 yr cal BP

The zone is dominated by remarkable values of 128B, reaching 28% in the lowermost sample, and then sharply decreasing to 7%. Aquatic taxa are perhaps represented also by HdV-181, rising up to 9%. Wood saprophytes are recorded in low percentages, whereas coprophilous and potentially coprophilous taxa are well represented, although in low percentages (especially *Delitschia* and Melanosporaceae). *Clasterosporium caricinum* rises to 5%, and disturbance indicators such as *Kretzschmaria deusta* and *Diporotheca rhizophila* occur. Possible spores of Sclerodermataceae/Ustilaginaceae (UR-3) are near 5% and Scleroderma is recorded in low percentages. *Glomus* clamydospores rise to 7% towards the top of the zone. Eggs of flatworms (Rhabdocoela) are present.

NPPAZ PSA-2 · Depth: 689cm – 602cm · ~6700-5550 yr cal BP

HdV-128B keeps dropping down until it disappears, while HdV-181 increases to 10% in the middle part of the zone. *Zygnema*-type occurs among the other aquatics. Spores of *Cirrenalia donnae* are recorded in high values throughout the whole zone, and reach a maximum value of 15%, then decrease at the end of the zone. The same trend is followed by HdV-572, although in lower percentages (7%). At the boundary with the upper zone there is a peak in *Pediastrum* (12%). Low values of *Sordaria*-type and *Delitschia* are recorded, while *Cercophora*-type increases to 3%. *Clasterosporium caricinum* rises again in the middle part of the zone (5%), and *Kretzschmaria deusta* occurs in several samples. *Scleroderma* is present in low percentages. The unidentified type UR-1 increases up to 6%, resembling the saprobic trend. The thecamoeba *Arcella* is present and locally growing ferns are indicated by spore cases.

NPPAZ PSA-3 · Depth: 602cm - 521cm · ~5550-4950 cal yr BP

The dominant aquatic organism is now *Pediastrum*, and the potential aquatic type HdV-181 remains steady around 4%. *Cirrenalia donnae* and HdV-572 are both attested in low values in the lower and upper part of the zone, and increase (namely 15% and 11%) in the middle of it. Among the largely coprophilous taxa *Arnium*-type is now recorded, and the potentially coprophilous taxa Melanosporaceae and *Cercophora*-type slightly increase (3-4%). *Clasterosporium caricinum* and *Scleroderma* drop to null values, while *Kretzschmaria deusta* and *Diporotheca rhizophila* are present. *Glomus* is steady around 3%, and UR-1 increases to 6% in the middle of the

zone, broadly following the trend of the major saprobic taxa. The thecamoeba *Arcella* is present.

NPPAZ PSA-4 · Depth: 521cm - 473cm · ~4950-4550 cal yr BP

Between the top of the sequence and NPPAZ-4 *Pediastrum* rises to 16%. The main event in the zone is the sharp rise in *Scleroderma*, reaching 10%. A slight peak in *Cirrenalia donnae* and HdV-572 (c. 10%) seems detectable in the middle part of the zone. *Sporormiella*-type (2%) is the main largely coprophilous taxon and Melanosporaceae slightly increase again (2%). A new and slight increase in *Clasterosporium caricinum* occurs between this zone and NPPAZ-5, and UR-1 decreases steadily. *Arcella* is recorded, as well as fern spore cases.

NPPAZ PSA-5 · Depth: 473cm - 441cm · ~4550-4300 cal yr BP

The zone is defined by a sharp decrease in *Pediastrum* among the aquatic taxa and by a sharp increase in *Cirrenalia donnae* (16%) among the wood saprophytes. Several coprophilous taxa occur in low values, and Melanosporaceae and *Cercophora*-type slightly increase towards the top of the zone. *Diporotheca rhizophila* occurs again.

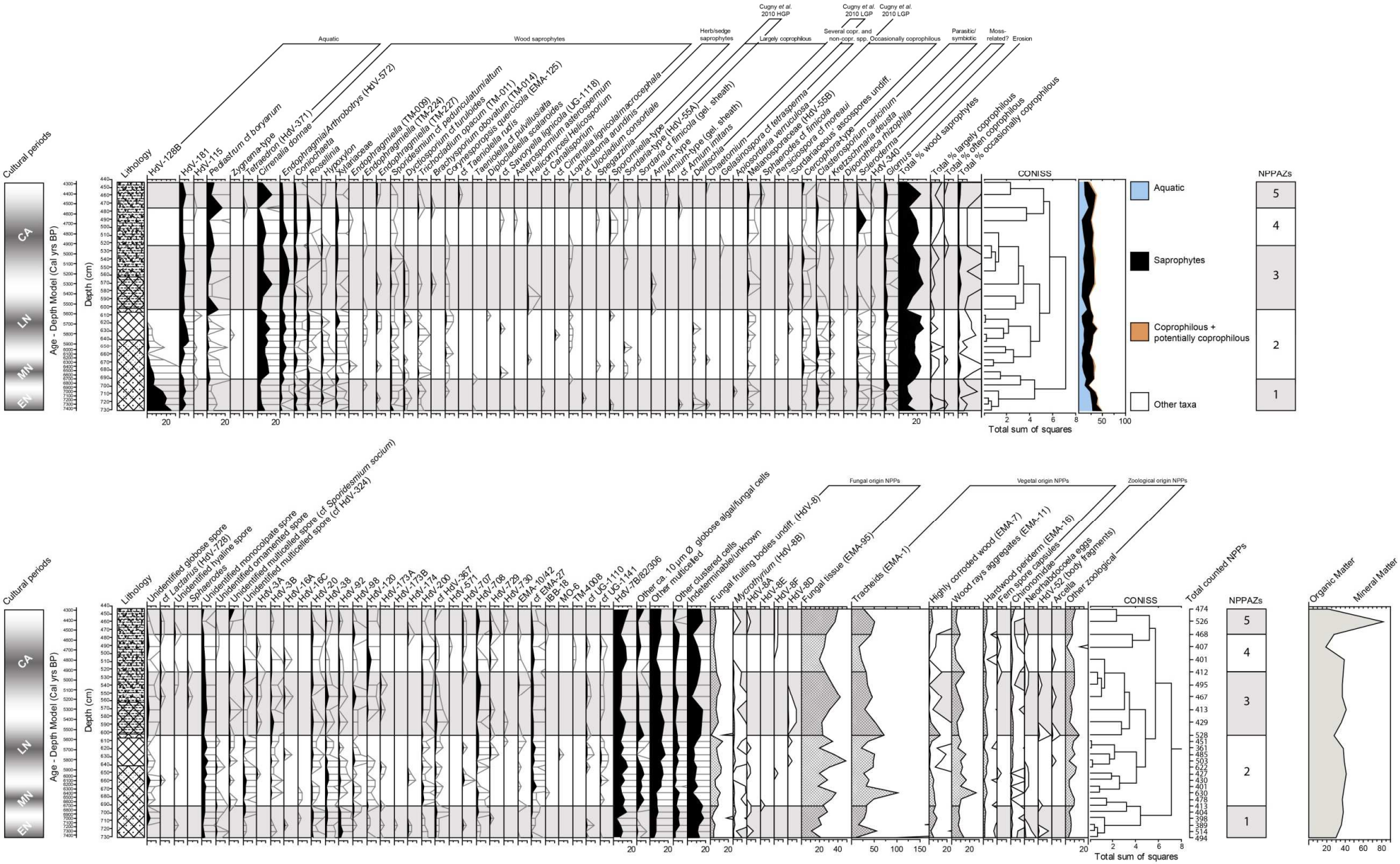

Figure 3.6. Prato Spilla 'A': selected taxa NPP diagram. Values expressed as percentages of total NPPs. Empty curves represent 10x exaggeration. HGP: high grazing pressure; LGP: low grazing pressure; EN: Early Neolithic; MN: Middle Neolithic; LN: Late Neolithic; CA: Copper Age. Ecological grouping of coprophilous species follows Krug et al. 2004.

3.3 Interpretation and discussion

3.3.1 Fimicolous spores at Prato Spilla 'A': an ambivalent signal

A wide range of coprophilous and potentially coprophilous spores have been recorded, confirming the presence of grazing animals on the site. For a clearer exposition, following Krug et al. (2004) the taxa have been grouped into "largely coprophilous" (LC), "mixed ecology" (ME, i.e. genera comprising several coprophilous and non-coprophilous spp.) and "occasionally coprophilous" (**fig. 3.6**). The LC taxa represent the most reliable proxies for the local presence of herbivores. Among these, *Sporormiella*-type and *Sordaria*-type have been shown to be statistically correlated with high grazing pressure in modern analogue studies (Cugny et al. 2010). It appears evident that the LC are distributed throughout the whole sequence, without any evident peaks or gaps. It is only possible to spot three apparent major concentrations, namely localized at 721-722cm from the top (*Sporormiella*-type and *Delitschia*), in the whole of NPPAZ-2 (*Sporormiella*-type, *Sordaria*-type, *Delitschia*) and between NPPAZs 4 and 5 (*Sporormiella*-type, *Sordaria*-type, *Arnium* spp.).

A wide range of other potentially coprophilous spores was also recorded, including rare taxa infrequently represented in NPP diagrams. *Chaetomium* and *Gelasinospora* include a number a coprophilous and non-coprophilous species, but as in the case of the LC they are distributed across the entire sequence. Among these, the presence of *Gelasinospora* is worthy of note as it also favours burnt soils (Ellis and Ellis 1988). Whether natural or induced burning, the genus may be taken as indicative of local fires.

The large group of ME taxa appears dominated by Melanosporaceae and *Cercophora*-type. Although the latter is often directly regarded as a dung indicator, high values of *Cercophora* may simply derive from the saprobic habit of many species growing on rotten wood and leaves (Lundqvist 1972). Indeed, as its percentage curve broadly reflects the cumulative curve of the wood saprophytes, this is likely to be the case at Prato Spilla 'A'. Further research is necessary to clarify the ecological value of HdV-55B. The spores found on the site, showing two protruding apical pores, correspond to the first described type 55B in the NPP literature by van Geel (1978). However, other studies have included under the same type biporate spores lacking protruding

pores (Cugny et al. 2010). As these latter are likely to represent *Arnium* spp. or other unidentified taxa, we argue that the protrusion of the pores is an important taxonomic features and only spores showing this character should be recorded as HdV-55B. The type strongly resembles spores of *Melanospora brevirostris*, though the protruding pores may point to identification as *Sphaerodes* spp. While fimicolous *Sphaerodes* spp. exhibit a reticulate surface pattern (in the diagram as *Sphaerodes* cf. *fimicola*), *M. brevirostris* produces psilate spores and has occasionally been isolated from dung (Doveri 2007). More commonly, the species is found parasitizing on Pezizales (Doveri 2007), whose spores are often not sufficiently distinctive to enable recognition and infer a relationship with HdV-55B. As in the other cases, spores of Melanosporaceae are diffused throughout the whole sequence. Although no clear peaks are detectable, they seem to increase slightly in the upper part (NPPAZs-3-4-5, transition from Late Neolithic to Copper Age and the whole Copper Age).

Given the absence of any distinguishable rise, it is likely that the abundance of coprophilous and potentially coprophilous taxa, spanning from the Early Neolithic to the Late Copper Age, only reflects a natural "background noise". The signal is probably a result of wild herbivores periodically grazing around the mire. It is worth saying, however, that the dispersal of dung spores does not automatically occur in every high-altitude mire, as occasionally NPP analyses of southern European sites have provided no evidence for such indicators (Argant et al. 2006). In an entirely natural condition, this situation may simply reflect a lack of herbivores nearby the site; on the other hand, when humans are likely to have played a role, zero counts of dung-specific microfossils are explicable by the absence of animal husbandry (e.g. in pre-Neolithic contexts).

The finding of coprophilous spores at Prato Spilla 'A' is thus significant, as it allows apparently problematic phases of forest disturbance to be accounted for (Lowe et al. 1994a; 1994b), given the physiological stress imposed on the vegetation by wild animals (bark stripping, soil trampling, etc.). This scenario is further supported by the occurrence of *Kretzschmaria deusta*, as the spread of this fungus is favoured by disturbances such as bark removing and root exposure due to intense animal trampling. Different ungulates are likely to have been the major factor responsible for the presence of dung near the site. Red deer, roe deer, ibex and chamois are at present diffused on the Apennines and their presence in northwest Italy during the Holocene is certain and documented also by the zooarchaeological assemblages

(Rowley-Conwy 1997; Lorenzini et al. 2002). Moreover, several coprophilous species successfully grow on lagomorph dung, which is likely to have been deposited by mountain hares (Lunqvist 1972; Doveri 2007).

In light of this, it is suggested that patterns of increasing/decreasing herbivore activity may have been one of the driving factors behind irregular fluctuations in *Abies* pollen recorded throughout the Holocene in the study region, as shown by a number of pollen diagrams (Lowe et al. 1994a; 1994b; Branch 2013; Vescovi et al. 2010a; 2010b). This might be particularly true in case of local presence of *Abies*. Although on a large scale these data probably reflect a response to climate change, several works have focused on the impact on the vegetation by herbivore ungulates (Bradshaw et al. 2003; Danell et al. 2003; Senn and Suter 2003). Their predation pressure during the sapling stage of *Abies alba*, thus preventing regeneration, has been highlighted, with particular reference to high-altitude areas (Senn and Suter 2003). Among the other tree species, *Abies* is largely preferred by ungulates, especially by roe deer, whose browse may consist of up to 50% of silver fir. While their role as seeds and seedlings predators is negligible, there is a consistent body of evidence indicating a strong effect on young *Abies* specimens which may eventually lead to their total disappearance, often regardless of the size of the herbivore population. The strongest impact occurs when trees are less than 1.3-2m high, enabling animals to easily remove twigs, shoots, needles and flowers (Danell et al. 2003; Senn and Suter 2003). Over one thousand enclosures aimed at excluding ungulate herbivores have experimentally proven that, without browsing pressure, *Abies alba* successfully regenerates, unlike the areas where ungulates are free to browse (Senn and Suter 2003). Moreover, there is also a consistent match between patterns of *Abies* regeneration and density of ungulate populations (Senn and Suter 2003). It is therefore arguable that, at least in the area of Prato Spilla, wild ungulates may have played a role in determining minor fluctuations in the *Abies* population.

Alternatively, a more anthropogenic scenario may be pictured; in this situation the curves of type 55B and *Cercophora*-type would entirely represent coprophilous species. If so, it may be suggested that their slight increase from NPPAZ-3 onwards derives from a more continuous presence of small domestic flocks around the mire. However, further points against this argument exist. While coastal or upland grazing lands suitable as pastures are located at a relatively short (0-10km) distance from the cave sites of western Liguria, Prato Spilla 'A' appears rather isolated.

As mentioned above, Maggi and Nisbet (1991) have found a plausible seasonal movement of shepherds along distances of maximum 20km. Although there are no sharp boundaries to define transhumance modalities, a greater distance should be termed as medium/long range transhumance, and there is general agreement on the unlikelihood of long-distance pastoral systems in prehistory (Barker 1985; Marzatico 2007). It seems also necessary to stress that in previous studies the site of Prato Spilla 'A' has been considered in the context of a well-developed tradition of environmental archaeology focusing solely on Liguria (e.g. Lowe *et al.* 1994b). However, its position on the northern side of the Liguro-Emilian watershed suggests taking into account also the archaeological evidence in the area north of Valditacca. Here, as the last northern Apennine slopes decline, a wide plain extends around the territory of Parma. The area was densely populated during the Neolithic, and culturally dissimilar from the Ligurian milieu (particularly in the Early Neolithic) (Pessina and Tiné 2008). If we turn our attention to the plain of Parma, we note that its southern fringes lie about 20km from Prato Spilla. The important settlement of Sant'Ilario d'Enza (Maffi and Tirabassi 2013) is located some 30km from the site (like Pianaccia di Suvero in Liguria), and sporadic Neolithic artefacts are documented also in the near site of San Polo d'Enza (Tirabassi 1987). Further south-east, a Late Eneolithic lithic assemblage was found at Bagioletto, a site located at 1700m asl *c*. 20km from Prato Spilla, previously already occupied during the Mesolithic (Cremaschi et al. 1981; Cremaschi 1990). These distances are more compatible with short-range pastoral systems, which are more likely to have occurred in later prehistory (**fig. 3.7**). In this respect, it is useful to stress that the Early Neolithic rhomboid point found in eastern Liguria at Mt. Aiona-Prato Mollo (Province of Genova) is near to the Fiorano types (Baffico et al. 1987), suggesting that also the Apennine watershed was exploited by groups culturally linked to the plain of Parma. Moreover, a number of studies have stressed multiple relationships between Emilia and Liguria in the Neolithic (Biagi 1973; Bagolini and Biagi 1973; 1974).

However, even if we accept the existence of any form of transhumance, including long-range systems, the absence of known seasonal sites in the vicinity of the mire (presumably in a range of 0-5km) remains difficult to explain. Potential summer pastures should indeed be associated with sites interpreted as possible seasonal camps (or at least with archaeological artefacts), as is the case of Mt. Galero and Tana del Barletta in western Liguria (Barker et al. 1990; Maggi and Nisbet 1991). In our

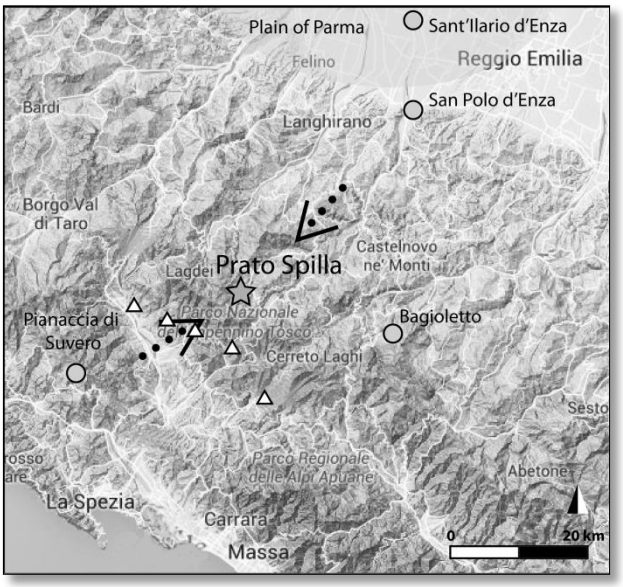

Figure 3.7. Prato Spilla 'A' (star), the nearest finds of Eneolithic statue-stelae (triangles), and the nearest Neolithic and Eneolithic sites south and north of the Apennine threshold (dots).

case, it is relevant to stress that the north-eastern most finds of statue-stelae lie 7 to 12km from Prato Spilla and belong to the Filetto-Malgrate-type, which is dated to the Copper Age on the basis of the weapons and ornaments represented (de Marinis 1994). These monuments are characteristic of the Eneolithic of Lunigiana and Garfagnana (between eastern Liguria and north-west Tuscany), and are interpreted as ritual images placed along pastoral routes linking settlements and pastures (Maggi 1998b).

Two high-altitude mires in eastern Liguria have provided direct evidence for *in situ* human presence, albeit scant and sporadic. An ornament dated probably to the Copper Age has been collected at Lago di Bargone (830m als) (Campana et al. 1998), where contemporary low anthropogenic disturbance has been suggested by pedological and palynological analyses (Cruise et al. 2009). At Mt. Aiona-Prato Mollo (1700-1500m als), there is instead evidence for periodic human presence since the Early Neolithic (Baffico et al. 1987). A further point supporting the existence of this extra-settlement area being used as an upland pasture is the presence of a number of arrowheads from the Copper Age - Early Bronze Age (Baffico et al. 1987; Maggi 1998c; Maggi and Campana 2008). Although commonly interpreted as related to hunting, and occasionally as ritual offers (Leonardi and Arnaboldi 1998), the finds may be consistent with the interpretations from similar sites, that stress the necessity to guard the livestock against robbers or rival groups (Marzatico 2007; on the rise of violence during later prehistory see Meyer et al. 2015). The importance of controlling and defending upland resources seems confirmed by the case of Talheim (southern Germany), where a large Early Neolithic mass grave containing the bones of 34 individuals of both genders and various ages was found. Isotopic evidence has suggested that some of the deceased, considered as a family group killed by a rival

community, may possibly have been involved in forms of vertical transhumance between high pastures and *Linearbandkeramik* valley settlements (Price et al. 2006).

3.3.2 Other ecological changes: a NPP-based reconstruction

NPPAZ-1 is defined by remarkably high percentages of HdV-128B. Although this microfossil is known to the analysts since the 1980s, its identity and ecology, and therefore its indicative value, are still a matter of debate. Usually, it is mostly taken as an algal organism favouring meso-eutrophic environments (van der Wiel 1982; van Geel et al. 1983; 1989; Miola et al. 2006). Only in a few cases genus/species identifications have been attempted. The need for a greater taxonomic accuracy appears clearly when it is considered that type 128B has been variously identified with organisms of different families, and even of different classes. Moreover, these attempts have not been supported by critical evidence, but in most cases simply proposed as a matter of fact, nor questioned by other authors.

In view of the spiny ornamentation, Mudie et al. (2010) have suggested an identification with *Sigmopollis psilatum*. There is scant information on these organisms included in the class Prasinophyceae, often recorded in pre-Quaternary contexts (Batten 1996). However, other authors favour identification with Chlamydomonadales (syn. Volvocales) (Miola et al. 2010). Magny et al. (2012) and Kramer et al. (2010) have gone further, proposing a family-level identification (Volvocaceae).

Chlamydomonaceae consist of biflagellate unicellular algae, which have been considered to represent also the smooth globose microfossil HdV- 303. These algae have several different ecological requirements at a species level (Harris 2008), but neither of them seem to be compatible with the morphological features characterizing HdV-128. *Chlamydomonas* spp. show a relatively smooth or irregularly hairy surface, an often slightly elliptic shape and are characterized by flagella (Harris 2008). Besides, a largely spaced (type 128A) or closely spaced (type 128B) spiny pattern should be visible on the surface of the potential candidate for identification.

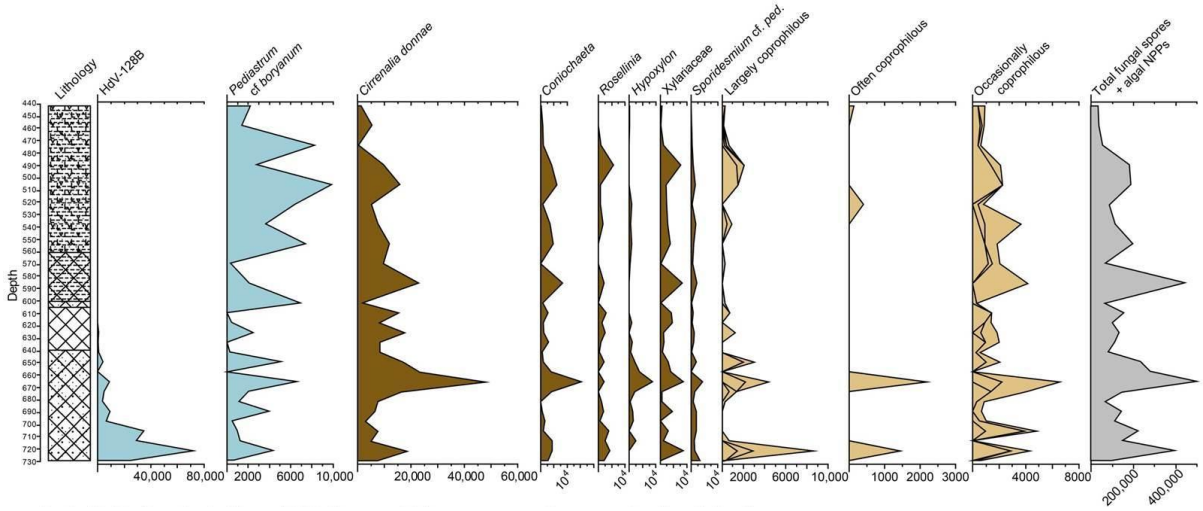

Figure 3.8. Prato Spilla 'A': selected taxa concentration diagram. Values expressed as microfossils no./cm^3.

The same problem affects an identification with Volvocaceae (genus *Volvox*), as these organisms are constituted by a multitude of *Chlamydomonas*-like cells. Moreover, if identification with *Volvox* is proposed, this should be taken into account in terms of interpreting abundance, as a single specimen may be constituted by up to 500,000 algal cells (Kirk 2005). These algae would thus appear highly overrepresented when compared to the percentages of the other microfossils.

This confusing situation has therefore encouraged an attempt to capture SEM images of HdV-128B in the Centre for Advanced Microscopy of the University of Reading, hoping to shed light on its identity. To this end, a bulk sample has been collected between 722 and 721cm, as the highest concentration per cm^3 of HdV-128B was recorded at this level (**fig. 3.8**). Although the spiny ornamentation should stand out clearly in electron microscopy, parameters such as colour and wall thickness, distinctive in light microscopy, could not be observed. Five promising microfossils were photographed (**fig. 3.9**). Only a smaller microfossil (**fig. 3.9E**) showing a closely spaced ornamentation really resembles the surface pattern of HdV-128B. Moreover, none of the elements photographed shows the typical sigmoid slit running through the surface, therefore the images captured may represent other

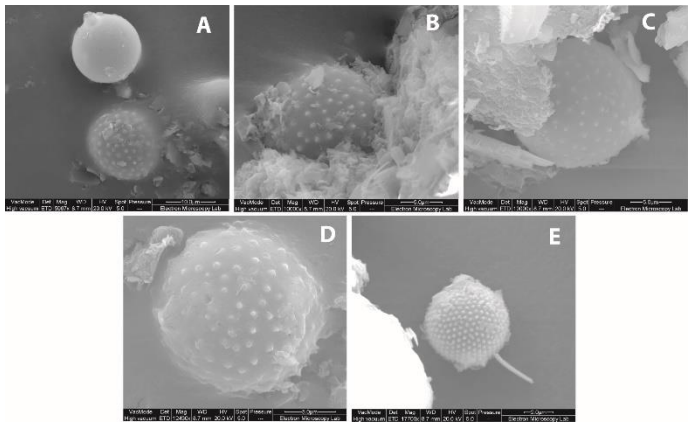

Figure 3.9. SEM images of microfossils of unknown origin resembling HdV-128B.

spores, given the extreme variability of fungal assemblages (Hawksworth and Wiltshire 2011) and the difficulties arising from the colourless tridimensional view of SEM images.

The largest group of spores sharing a similar ecology can be grouped as wood saprophytes. The assemblage is highly dominated by *Cirrenalia donnae* and HdV-572. Fossil *Cirennalia* spores have been rarely recorded (Pirozynski et al. 1988; López-Vila et al. 2014), and recently found in modern analogue studies. Cugny et al. (2010) recorded low values of *Cirrenalia* analyzing modern samples from oak and beech-dominated forests, a mire and a peatland. Very low percentages of *Cirrenalia* have been recorded also by Gelorini et al. (2011) from eastern African lake surface sediments. Dietre et al. (2012) have carried out multivariate analysis on modern samples from the Jura Mountains (eastern France), suggesting that *Cirrenalia* spores are positively correlated with forested sites and should thus be regarded as indicators of tree cover. The morphology of the conidia allows species identification with *C. donnae* (López-Vila et al. 2014). Scanty mycological literature is available on this hyphomycetes (Ellis 1976; Goos 1985; Zhao and Liu 2005). However, the data seem to indicate a strong preference for *Abies* wood as a host tree (Ellis 1976; Kew Herbarium online database: http://www.herbimi.info/herbimi/results.htm?name=Cirrenalia%20donnae) (accessed September 2016). This mutualism is highly likely for the Middle Holocene at Prato Spilla, characterized by constantly elevated percentages of pollen of *Abies alba*. It is worth noting that *Cirrenalia* species produce conidia, which being non-motile spores have a particularly narrow range of dispersal. Although no conifer stomata were recorded and macrofossil analysis was not carried out, it is suggested that high values of *C. donnae* may point to the on-site presence of *A. alba.* This view would be consistent with the above hypothesized predatory pressure exerted by roe deer on *Abies* saplings.

The trend followed by *Cirrenalia* strongly resembles the values of HdV-572. This microfossil has been first recorded and described only relatively recently (Speranza et al. 2000) in a central European peat bog. The analysts recorded extraordinarily high values of HdV-572 (91% of the pollen sum) from their study site located in an elevated area highly influenced by ancient anthropogenic activities. The associated lithology shows a *Sphagnum*-dominated oligotrophic environment, but no apparent correlation between the remarkable peak in this NPP type and other taxa emerge.

Later works on modern samples from southwest France have shown a relationship between HdV-572 and beech forests (Cugny et al. 2010). The authors report a value around 10% calculated as TNPP%, which allows a more accurate comparison with our data to be made. Multivariate analysis by Dietre et al. (2012), have suggested a strong relationship between tree cover and HdV-572. In our region of study, type 572 has been recorded in a Ligurian highland peat bog (Menozzi et al. 2010) and in a coastal alluvial plain (Arobba et al. 2016). Given the similarities with many other uniseptate conidia, it is not possible to suggest any precise link between HdV-572 and suitable hosts. The type strongly resembles conidia of *Endophragmia* (e.g. *pinicola*) and *Arthrobotrys* (e.g. *conoides*) spp. Both genera include wood and herbaceous saprophytes with different ecological requirements. Yet, the percentage curve of HdV-572 closely resembles the fluctuations of *C. donnae*, suggesting its inclusion among the wood saprophytes. If so, it is likely that type 572 indicates the presence of dead wood on the bog surface, hence possibly periods of higher tree cover.

Similarly, *Sporidesmium* and *Dyctiosporium* spp. do not allow specific plant-fungal relationships to be inferred, although they can be considered further indicators of decaying wood. It is possible that also the unidentified monocolpate type UR-1 is produced by a wood decomposer, as its curve broadly reflects the trend of the main saprobic taxa.

The range of saprophytes on herbaceous plants is much more limited. However, a refined picture of the local ecology of the area can be traced due to the presence of *Lophiostoma arundinis*. The species is almost invariably associated with *Phragmites*, thus indicating the on-site presence of this genus and an aquatic origin for part of the Poaceae grains identified in the pollen analysis.

The parasitic fungus *Kretzschmaria deusta* sparsely occurs throughout the sequence. The species is known for affecting broadleaved taxa such as *Fagus*, *Tilia*, *Quercus*, *Ulmus*, *Fraxinus* and *Corylus*, colonizing the roots and taking advantage of periods of physiological stress. As noted above, it is appropriate to point out that browsing and bark-stripping animals are considered facilitating factors for the spread of the parasite (Latałowa et al. 2013). However, despite being deadly for the host tree, *K. deusta* does not necessarily lead to a decrease in the hosting population (as shown by the *Tilia* rise recorded by Latałowa et al. (2013)).

A better knowledge of the ecosystem of the site is achieved through the finding of *Diporotheca rhizophila* spores in the middle and upper part of the sequence (NPPAZs-

1, 3 and 5). Although a possible mutualism in the past with *Thelypteris palustris* has been proposed (van Geel et al. 1986), the species is currently known as a parasite of the host plant *Solanum nigrum* (van Geel et al. 2003; Hillbrand et al. 2012). This latter requires wet meso-eutrophic habitats matching the conditions documented at Prato Spilla during the investigated period. Be that as it may, the occurrence of *D. rhizophila* allows the presence of *S. nigrum* or of a different suitable host to be proved, in spite of its absence in the pollen record. Moreover, *S. nigrum* is also associated with episodes of soil disturbance as derived by forest clearings, agricultural activities and animal trampling, a fact that lately led to consider *D. rhizophila* as an indicator of such events (Hillbrand et al. 2012).

It is likely that at Prato Spilla *D. rhizophila* naturally occurs, given the presence of a habitat appropriate for the growth of its host. Nevertheless, it is worth noting that *D. rhizophila* was found on a site where ecological changes possibly partly due to human intervention have been identified. In this respect, an evaluation of the presence of cereal pollen would be essential, as it would be further supported by the occurrence of *D. rhizophila* as an indicator of anthropogenic impact. In this view, the increase in *Corylus* recorded in the pollen record may not be fortuitous, as its growth may be facilitated within disturbed forest ecosystems.

Given their dispersal by soil erosion, *D. rhizophila* spores are often associated with *Glomus* chlamydospores. However, at Prato Spilla neither *D. rhizophila* nor *Glomus* peak in correspondence of an increased mineral inwash. It follows that, as lately argued by Kołaczek et al. (2013), *Glomus* chlamydospores were probably associated with plants growing in the peaty layers, whose roots can penetrate and sporulate within the underlying sediments.

As expected, the peak in fungal hyphopodia (*Clasterosporium caricinum*?) between NPPAZ-1 and 2 correlates with the increase in Cyperaceae recorded in the pollen analysis. This data indicates the local occurrence of the genus *Carex*, as *Clasterosporium* hyphopodia adhere to the surface of the epidermis of *Carex* species.

Although it deserves further research, the peak in spiny spores released by *Scleroderma* spp. during NPPAZ-4 points to a damp environment with frequent mosses, these latter being a suitable substrate for this basidiomycetes (Guzmán 1970; Kuo 2011).

Detrended Correspondence Analysis (DCA) was also performed on all microfossils occurring in percentages higher than 1%, in an attempt to detect similarities between

taxa and identify types with similar requirements (PAST software, Hammer et al. 2001) (**fig. 3.10**). The NPPs occurring at the extremities of the axes (e.g. HdV.-128B) are less likely to have affinities with the other taxa. The main freshwater microfossils of the sequence, HdV-128B and *Pediastrum* sp., show clearly opposite behaviours.

The plot also suggests that spores of *Cercophora*-type spores are likely to represent saprophitic species affecting rotten vegetal matter rather than coprophilous species, given their association with HdV-572 (probably conidia of *Endophgramia* or *Arthrobotrys* spp.) and *Cirrenalia donnae*.

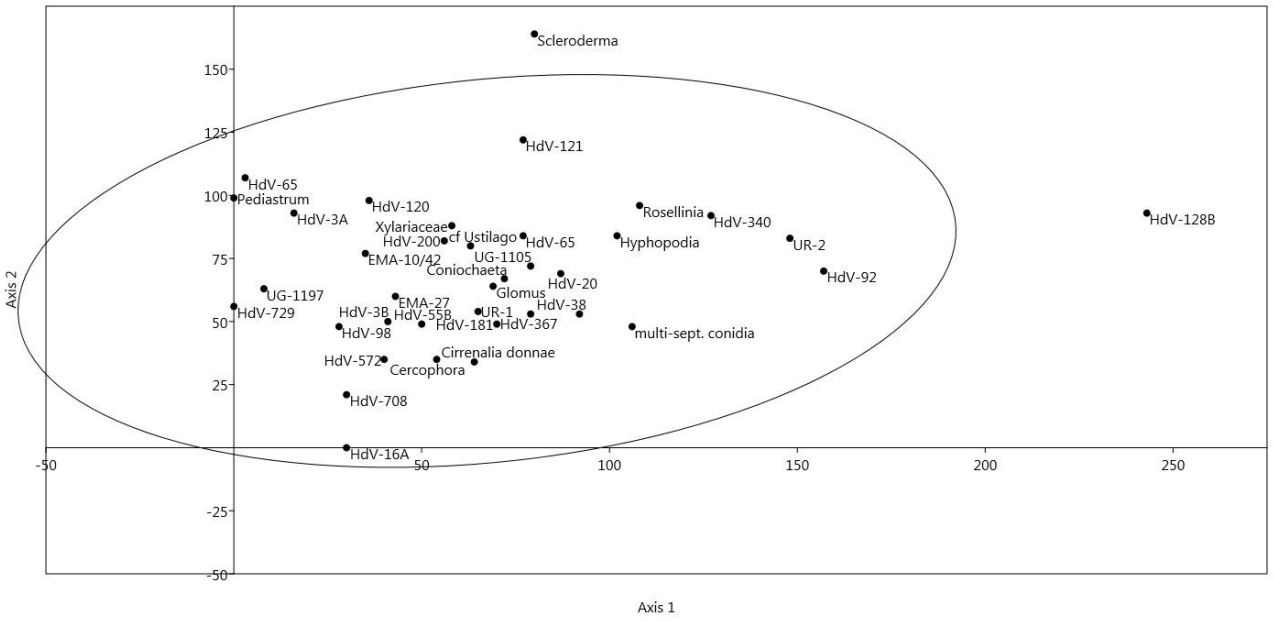

Figure 3.10. Prato Spilla 'A'. DCA plot showing 95% confidence ellipse. Eigenvalue for axis 1 is 0.292, eigenvalue for axis 2 is 0.007.

4. THE MIDDLE HOLOCENE ALLUVIAL SEQUENCE FROM GENOA PIAZZA DELLA VITTORIA

4.1 Geographical setting and archaeology

Geognostic coring was performed in 2006 at Piazza della Vittoria in Genoa. The coring location is presently located 600m north of the shore, in a small alluvial plain formed by the river Bisagno, about 2km^2 wide, enclosed by low hills on the northern edge (**fig. 4.1**). The main channel of the Bisagno measures 25km, its catchment area totals 95km^2 and it extends from the coast to about 15km inland (Provincia di Genova 2009). The average altitude of the drainage basin is relatively low (around 300m asl), although on its fringes there are peaks reaching 900-1000m asl (Mt. Candelozzo, Mt. Croce di Fo, Mt. Bado). The pollen analysis has pointed to a coastal marshy/swampy area, possibly brackish (*Ruppia*, *Nuphar*, *Nymphaea*, *Potamogeton*, *Typha*), dominated by deciduous *Quercus* and hosting riparian species such as *Alnus*, *Salix* and *Populus*, but relatively opened as suggested by the percentages of wild grasses (Arobba and Caramiello 2014; Arobba et al. 2016).

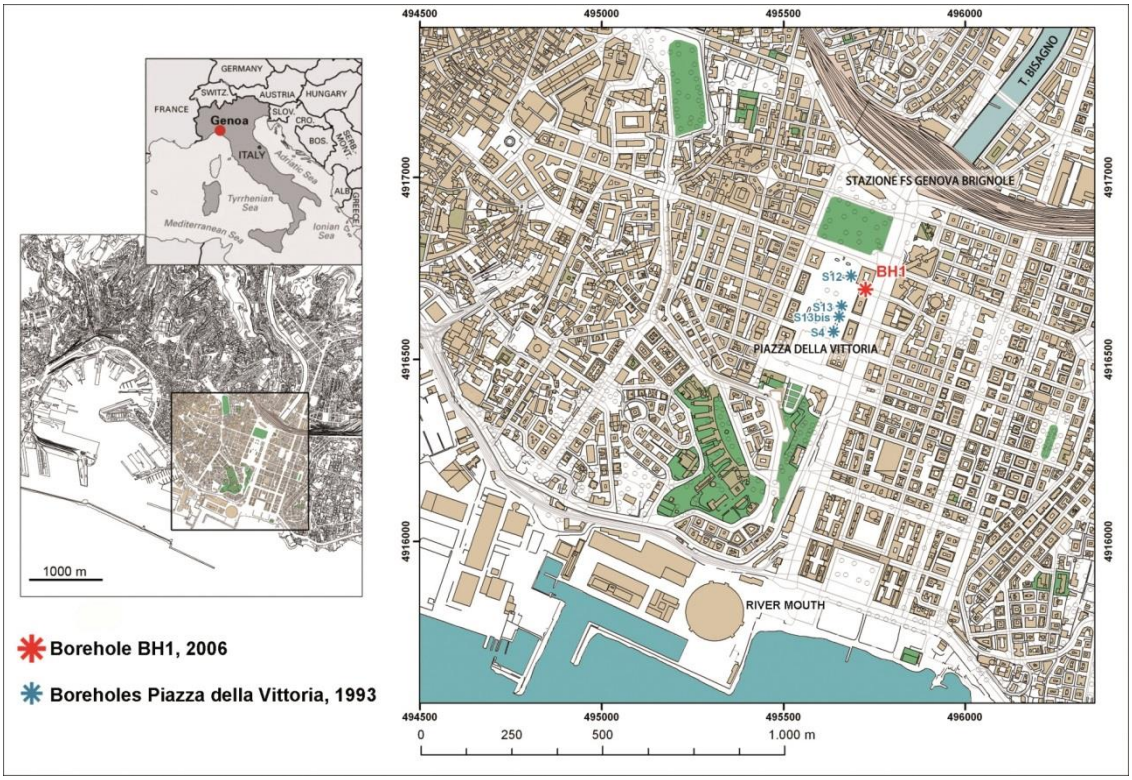

Figure 4.1. Map showing the location of the coring site in relation to the modern topography.

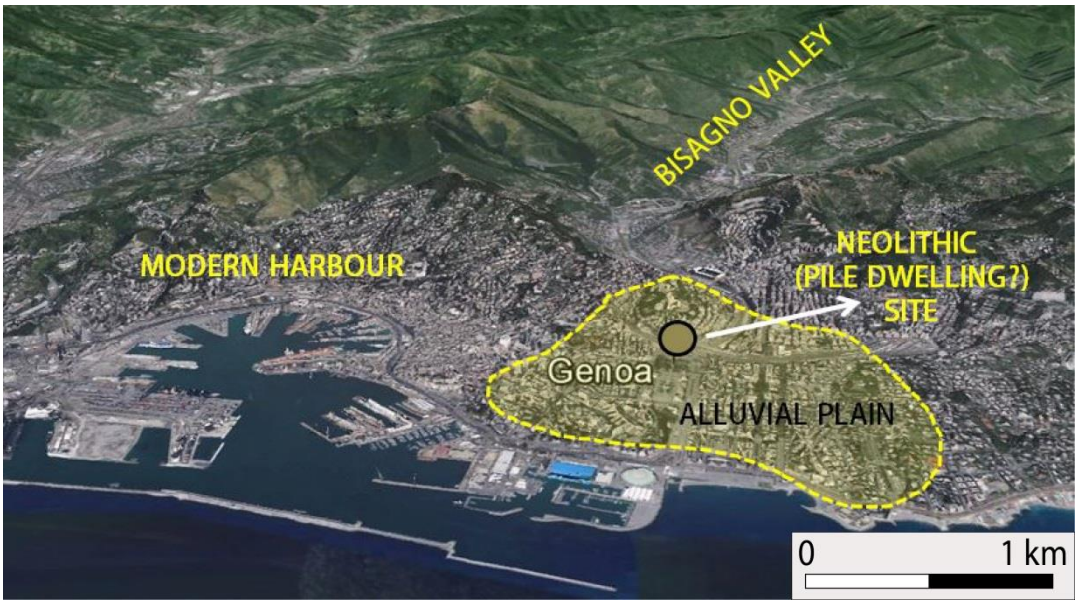

Figure 4.2. Map showing the morphology of the site and the position of the Neolithic finds.

It is worth stressing that other deep cores from the same area, in a range of a few tens of metres, have revealed the presence of several potsherds and a wooden artefact dated 5770 ± 70 cal yr BP, testifying to human occupation (**fig. 4.2**). On the basis of the wooden remains, the existence of a Neolithic pile-dwelling site possibly related to a prehistoric harbour was postulated (Maggi 1996). Indeed, during the excavation for the underground at Brignole, about 150m north of Piazza della Vittoria, a Late Neolithic site was found (late 5th Millennium BP), as revealed by fires places, pottery and animal bones (Del Lucchese 2010; 2014). Although the size of the site and its structure is not clear, it is likely that it took advantage of the location on the right side of the river Bisagno and of the proximity to the see. The sea level at that time was probably slightly lower than at present. Unlike previous estimates based on caraibic coral reefs (Fairbanks 1989; Bard et al. 1996; Chappel et al. 1996), recent works on the archaeological structures of the ancient harbour of Marseille and the Upper Palaeolithic paintings of the Cosquer Cave have allowed precise estimates for Holocene sea-level fluctuations (Lambeck and Bard 2000; Morhange et al. 2001), that can be considered reliable for the whole Mediterranean area. On the basis of biostratigraphy, artefacts and a number of radiocarbon dates it is possible to demonstrate that during the Neolithic the water level was about 2-1.5m lower.

Importantly, the site of Brignole has also provided the first evidence of deliberate pollarding of *Fraxinus* in the region, after it was hypothesised on the basis of the botanic remains from the Arene Candide (Arobba and Caramiello 2010; 2014). This

practice involves cutting of branches in late spring and summer in order to increase the amount of fodder prior to the winter season, and leaves clear marks in the wood pores. Its use is documented until very recently in the Ligurian-Emilian Apennines (*scalvatura*) to provide fodder to ovi-caprines and cattle over summer (Salvi 1982).

4.2 Results

A separate zonation was adopted to represent the main NPP assemblages and related ecological changes (Non-Pollen Palynomorph Assemblage Zones - NPPAZs) (Carrión and Navarro 2002; Mazier et al. 2009; Cugny et al. 2010; Miras et al. 2010) (**fig. 4.3**). Therefore, the phases identified do not necessarily overlap with the pollen zonation, as fungal, algal and plant communities respond to different driving factors (Baker et al. 2013). On the other hand, they better represent the main naturally and human-driven changes on a very local scale (van Geel et al. 2003; Mazier et al. 2009).

NPPAZ GPV-1 · Depth: 24.72m – 24.05m · ~7480-7345 cal yr BP
This zone is characterized by the dominance of UR-15 (25%) and a rise in UR-20 (14%), coupled with a slight increase in *Glomus* (7%). Among the aquatics, *Zygnema*-type spores are recorded.

NPPAZ GPV-2 · Depth: 24.05m – 23.05m · ~7345-7145 cal yr BP
Pseudoschizaea increases (3%), along with *Spirogyra* (3%). *Coniochaeta* decreases (7%), whilst UR-11 and *Cirrenalia basiminuta* reaches high values (15% and 17%).

NPPAZ GPV-3 · Depth: 23.05m – 22.62m · ~7145-7055 cal yr BP
Coniochaeta rises up to 26%, coupled with a peak in fungal hyphopodia (7%), but the dominant taxon is UR-17, reaching 25%.

NPPAZ GPV-4 · Depth: 22.62m – 21.07m · ~7055-6745 cal yr BP
Coniochaeta occurs in lower percentages (c. 10%), whereas *C. basiminuta* (25%) and UR-12 (15%) become dominant. A rise in fern sporangia occurs (5%).

NPPAZ GPV-5 · Depth: 21.07m – 20.05m · ~6745-6595 cal yr BP

The zone is characterized by a sharp increase in *Spirogyra* (20%), along with a new rise in *Coniochaeta* (41%), a peak in *Kretzschmaria deusta* (14%) and the first considerable rise in *Sporoschisma* (7%).

NPPAZ GPV-6 · Depth: 20.05m – 18.95m · ~6595-6525 cal yr BP
A new rise in *Pseudoschizaea* occurs (11%), along with the first notable increase in *Glomus* (12%). *Sporoschisma* reaches its highest value (9%), coupled with *Cercophora*-type (7%).

NPPAZ GPV-7 · Depth: 18.95m – 18.55m · ~6525-6505 cal yr BP
Glomus decreases (less than 3%), while *C. basiminuta* becomes dominant (25%), along with UR-11 (20%).

NPPAZ GPV-8 · Depth: 18.55m – 18.25m · ~6505-6485 cal yr BP
The zone is defined by a new peak in Spirogyra (7%), paralleled by a sharp rise in *Sordaria*-type (9%) and *Coniochaeta* (42%).

NPPAZ GPV-9 · Depth: 18.25 m – 16.95m · ~6485-6395 cal yr BP
A second notable rise in *Glomus* occurs (32%), along with an increase in *Cercophora*–type (8%) and a decrease in *Coniochaeta* (17%). Among the aquatics, *Pseudoschizaea* rises again (3%). UR-18 reaches remarkable values (38%). A rise in conifer stomata occurs (5%).

NPPAZ GPV-10 · Depth: 16.95m – 16.45m · ~6395-6360 cal yr BP
The zone is absolutely dominated by HdV-119, which reaches extremely high percentages (70%).

NPPAZ GPV-11 · Depth: 16.45m – 16.20m · ~6360-6345 cal yr BP
A very sharp rise in fungal hyphopodia occurs (48%), along with a rise in *Coniochaeta* (43%), UR-46 (15%) and *Pseudoschizaea* (3%). HdV-200 reaches high values (19%).

NPPAZ GPV-12 · Depth: 16.20m – 15.10m · ~6345-? cal yr BP
The zone is dominated by *Glomus* (near 60%), which rises coupled with UR-15 (13%). The main aquatic taxon is represented by *Pseudoschizaea* (5%).

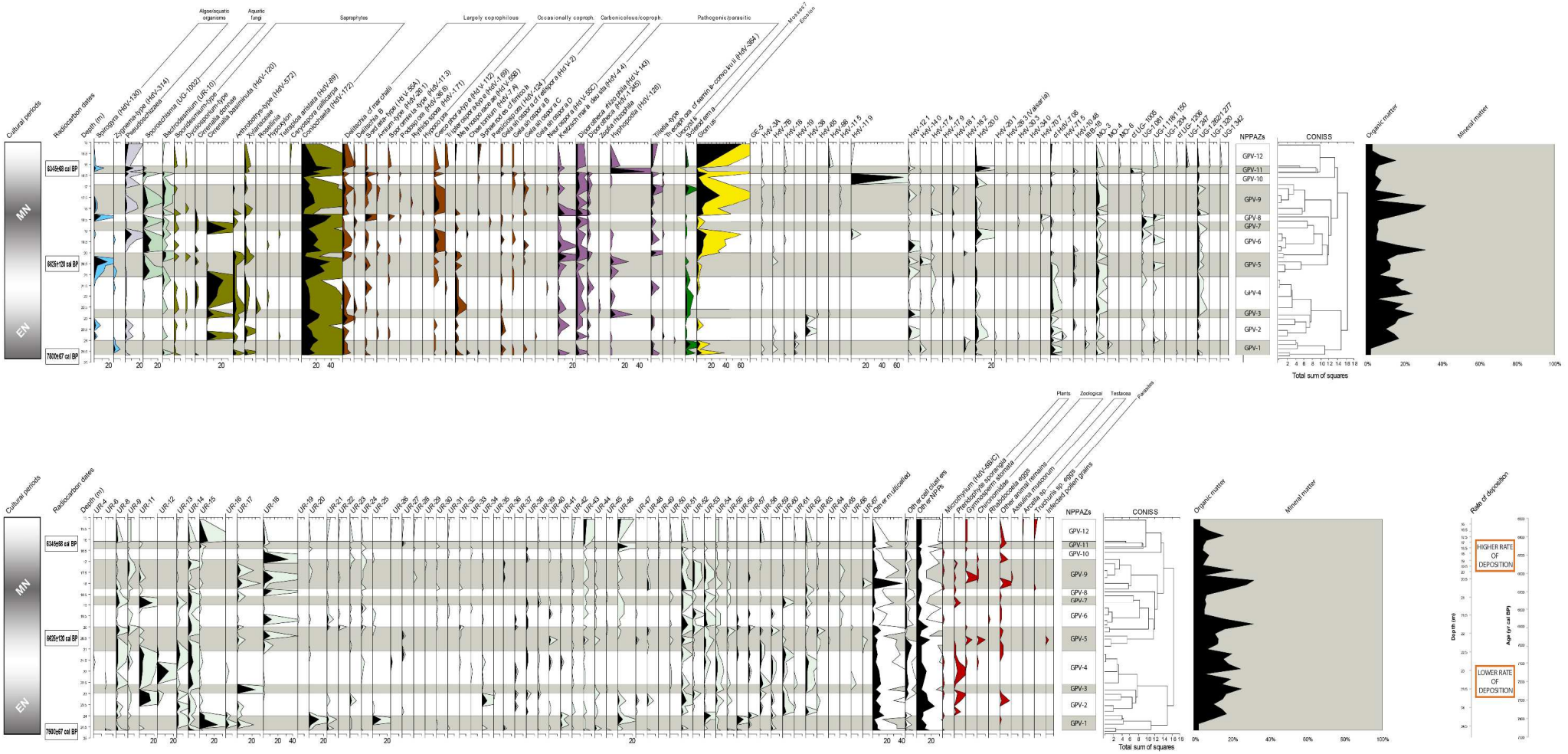

Figure 4.3. Genoa, Piazza della Vittoria, borehole 1: NPP diagram. Values expressed as percentages of NPPs + fungal hyphopodia. Exaggeration factor = 5x. EN = Early Neolithic; MN = Middle Neolithic.

4.3 Interpretation and discussion

4.3.1 Diachronic changes in the NPP assemblage

The sequence has proved very rich in both well-known and unidentified microfossils, and several insights into natural and possibly anthropogenic changes can be developed.

First, a rough subdivision into erosional events, although of undeterminable intensity, seems possible. The percentage curve of *Glomus* points to GPV-1, GPV-6, GPV-9 and GPV-12 as episodes of more intense transport and deposition compared to the other phases. However, there is no clear match between *Glomus* spores and increased amounts of mineral matter. Indeed, it is complicated to interpret the peaks in mineral matter from an alluvial sequence, as inorganic inputs are likely to result mainly from water transport, whilst in lacustrine environment they are well-established erosion indicators (van Geel 2001). Although it has been suggested that *Glomus* spores may prove unreliable to infer erosion, this holds true especially in very peaty sequences (Kołaczek et al 2013). *D. rhizophila* spores are only indirect indicators, as they represent parasitic species, but are usually dispersed by erosional processes, given their preference for disturbed and bare soils (Hillbrand et al. 2012).

During GPV-1, a small peak in *Kretzschmaria deusta* occurs. This is in agreement with the suggested picture, as this parasitic sordariomycetes prevails in disturbed conditions, such as root exposure, attacking the trunk of a range of broadleaved trees (Latałowa et al. 2013). Arguably, *Quercus* wood has been the most likely host for the parasite in this phase. The presence of rotten wood on the site at this time is confirmed by *Coniochaeta*, *Xylariaceae* and HdV-572.

Various largely and potentially fimicolous taxa (*Delitschia*, Melanosporaceae, *Gelasinospora*, *Coniochaeta*) are also documented at the very bottom of the sequence, suggesting herbivore involvement in the spread of *K. deusta* and Glomeromycota (van Geel and Aptroot 2006).

It is possible that GPV-1 is characterized by a relatively wet environment, given the resemblance of UR-15 with NPPs of supposed aquatic origin (e.g. HdV-983, Carrión and van Geel 1999; Carrión and Navarro 2002). Damp conditions may also be suggested by spores of *Scleroderma*, often colonizing mossy substrates. The genus is

somewhat a further indicator for erosional events, as all *Scleroderma* species are ectomycorrhizal (Guzmán 1970; Kuo 2011).

GPV-2-3-4 and 5 are characterized by higher percentages of wood saprophytes. The fact might point to a denser tree canopy on the site, and correlates well with one of the major peaks in *Quercus* revealed by the pollen analysis (localized around 7150 cal yr BP). Grazing pressure seems to increase between GPV-2 and GPV-3 (*Delitschia*), whereas the peak in UR-11 requires further research to unveil its indicator value. A range of newly identified and unidentified microfossils (HdV-120, UR-12, UR-14) also increases during GPV-4. HdV-120 was first recorded in a brackish lake by Pals et al. (1980). It seems possible to associate this conidium and its main peaks during GPV-4 and GPV-7 with the occurrence of relatively salty pools, as its morphology points to identification with *Cirrenalia basiminuta* (Raghu-Kumar et al. 1988; http://www.niobioinformatics.in/fungi/Micro-cd/htm/47.htm), a rare and cosmopolitan hyphomycetes consistently collected in environments characterized by some degree of salinity (Leong et al. 1991; El-Sharouny et al. 2009).

A rise in *Sordaria*-type in the NPP zone GPV-5, along with a peak in *Coniochaeta*, testifies to grazing pressure, and the corresponding decrease in *Delitschia* may be accounted for by mechanisms of fungal competition or changes in the main dung substrates (Wicklow 1992).

The abundance of HdV-55B between GPV-3 and GPV-4 is of difficult interpretation, as the spore morphology points to identification with Melanosporaceae (*Melanospora brevirostris*? *Sphaerodes* spp.? Doveri 2007; García et al. 2004; Vujanovic and Goh 2009), which are only partly fimicolous, and mostly parasitic on other fungi (Zhang and Blackwell 2002; Doveri 2007).

A first sharp rise in Spirogyra in the NPP zone GPV-5 points to shallow and stagnant water, as supported by a rise in fungi predominantly known from submerged habitats (*Sporoschisma* and *Bactrodesmium* spp.; Hu et al. 2010). It is difficult to argue whether the corresponding peak in *Coniochaeta* derives from animals attracted to the water body. In the same phase, the parasitic attack by *K. deusta* may have affected not only *Quercus*, but also *Ulmus* or *Fagus*, that are represented in the pollen diagram. Elm is particularly sensitive to *K. deusta* attacks (Latałowa et al. 2013), and its slight decrease before 6600 cal BP may have been facilitated by the spread of the disease.

Later, the main event during GPV-6 lies in erosional episodes and indications of soils disturbance, as suggested by *Glomus* and *D. rhizophila*, whose spread was presumably

facilitated by herbivore activity. A less dense tree cover is indicated by the gradual decrease of wood saprobic species. Higher values of *Pseudoschizaea* cannot be straightforwardly interpreted, as its biological identity is a matter of debate as yet (Scott 1992; Milanesi et al. 2006).

The data from GPV-8, showing a new increase in *Spirogyra* spores, point to a shallow and eutrophic water body, about or less than 0.5m deep (van Geel 2001). This environment is likely to have attracted herbivores as a watering place, as shown by a sharp increase in *Sordaria*-type, coupled with *Sporormiella* and *Podospora,* although *Spirogyra* can also inhabit brackish waters (Aleem 1961). Presumably, also part of the *Coniochaeta* spores recovered from this level represents fimicolous species. The fall in *Delitschia* may be determined by Sordariales fungi, here grouped in the *Sordaria*-type, able to out-compete rival species on the same substrates (Wicklow 1992).

The area was at this time probably too wet to allow arboreal taxa to grow within the pool, as significantly shown by relatively high and steady percentages of aquatic fungi between GPV-5 and GPV-10. Unlike what could be expected, erosion seems now reduced (GPV-7-8), as are root- and soil-inhabiting taxa. *Glomus* newly become abundant during GPV-9, and grazing pressure seems to remain constant, as indicated by several obligate fimicolous genera coupled with *Cercophora*-type spores. The trend followed by *Cercophora* spp., however, may mostly reflect the presence of rotten wood, as it seems to be broadly consistent with *Sporoschisma*, which occasionally colonizes also dry substrates (Shearer et al. 2007). A different hydrology is suggested by the disappearance of *Spirogyra*, suggesting a different regime (e.g. drier conditions or running water).

The dominance of an unidentified NPP with a characteristic rupture pattern resembling HdV-119 in the NPP zone GPV-10 requires an explanation. Similar microfossils have been recorded in Mediterranean and northern European contexts, where they seem to be associated with aquatic environments, possibly characterized by stagnant or slow moving waters (Pals et al. 1980; Carrión and Navarro 2002; Demey et al. 2013). Although these conditions may well match our situation, these indications seem too general to be of any help, and cannot account for such a sharp rise in the abundance (70%). On the other hand, HdV-119 shows an exagonal rupture that is found on dynoflagellate cysts, (for example *Brigantedinium* spp., which also has a smooth surface), although their morphology slightly differs, these latter being usually spherical. Dinocysts have been employed in freshwater palaeolimnology to

infer previous marine/brackish conditions of lake basins (Leroy and Alban 2010). Therefore, it seems plausible to assume a short-lived episode of marine transgression, resulting in a brackish pool, as also suggested by the palynological results.

An important episode of parasitism occurs at the top of the sequence (GPV-11). Previous research has highlighted the match between polylobate fungal hyphopodia and *Carex* species (e.g. van Geel et al. 1983). It is not possible to observe any correlation in our case, but it should be pointed out that very similar hyphopodia may be produced by different genera (Pirozynski et al. 1988). It is thus possible that the sharp rise here recorded results from a different host-pathogen association. To this end, it is worth stressing that closely resembling hyphopodia of *Buergenerula spartinae* are typical of brackish environments along the coasts of north and south-western Europe (Kohlmeyer and Gessner 1976), and that such conditions may be indicated by the above mentioned peak in HdV-119. Infection of pollen grains by fungal hyphae filling the apertures has also been observed in one case (**fig. 4.4**). The process has unknown causes and has been first reported only very recently (Shumilovskikh et al. 2015). Apparently, fungal material is able to colonize the areas of angiosperm grains occupied by pori and colpi, thus avoiding the protective outer layer made of sporopollenin. However, a relationship with dry phases, as suggested by Shumilovskikh et al., cannot apply to our case, given the concurrent presence of *Spirogyra*.

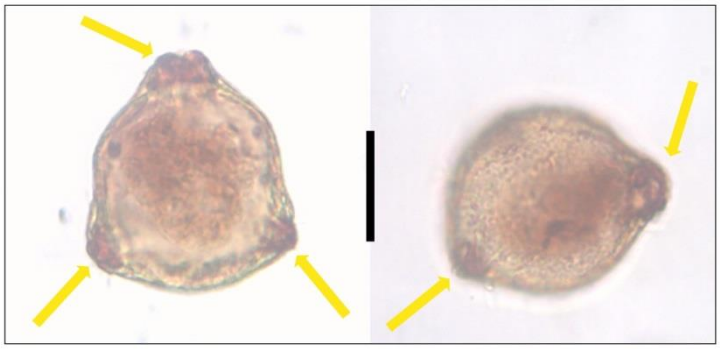

Figure 4.4. Pollen grain of *Corylus* showing darker fungal material inside the pores. Scale bar = 20µm.

In order to identify affinities among microfossils of unknown ecology, Detrended Correspondence Analysis (DCA) was also performed (PAST Software, Hammer et al. 2001). The technique clearly separates HdV-119 from the other taxa (**figs. 4.5, 4,6**). It is also noteworthy that *Gelasinospora* spores showing small pores (in the diagram as *Gelasinospora* B, different from *G.* cf *retispora*) (are closely correlated with *Sporormiella*, indicating their probable association with herbivore dung rather than burnt soils. The same can be argued for *Gelasinospora* spores with one apical pore (*Gelasinopora* C), showing affinity with *Sordaria*-type and *Cercophora*-type (**fig. 4.7**).

Given the ecology of *Cirrenalia basiminuta*, it is also tempting to suggest a correlation between the unknown NPPs UR-12 and UR-60 and saline environments.

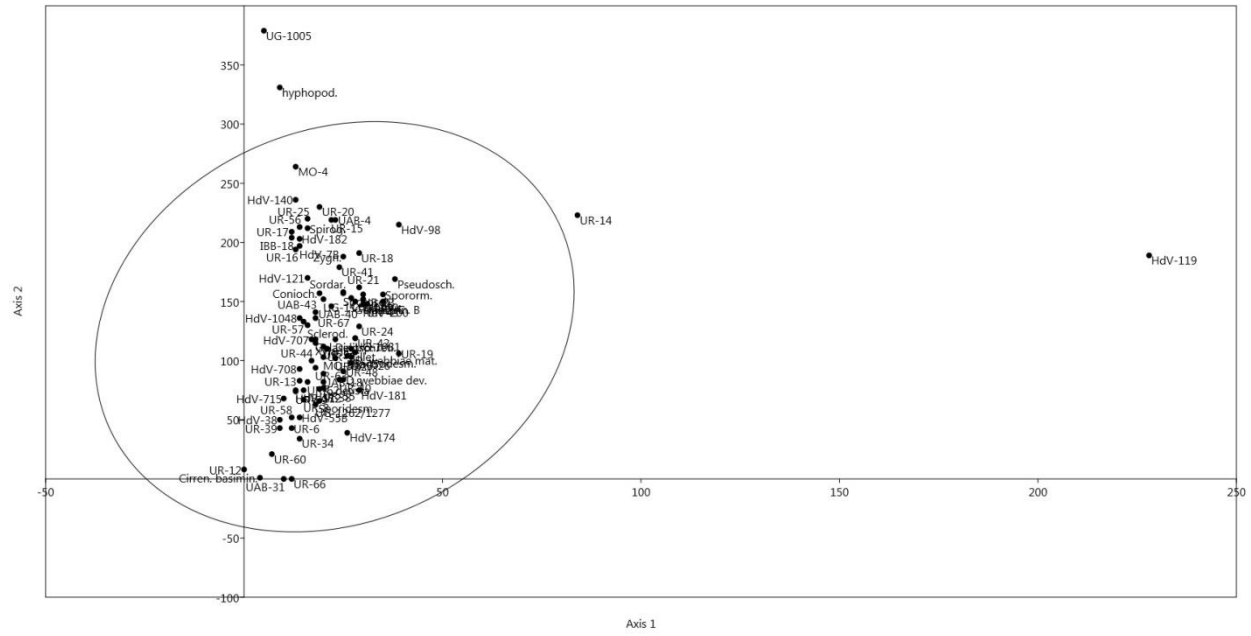

Figure 4.5. Genoa Piazza Vittoria. DCA plot showing 95% confidence ellipse. Eigenvalue for axis 1 is 0.705, eigenvalue for axis 2 is 0.446.

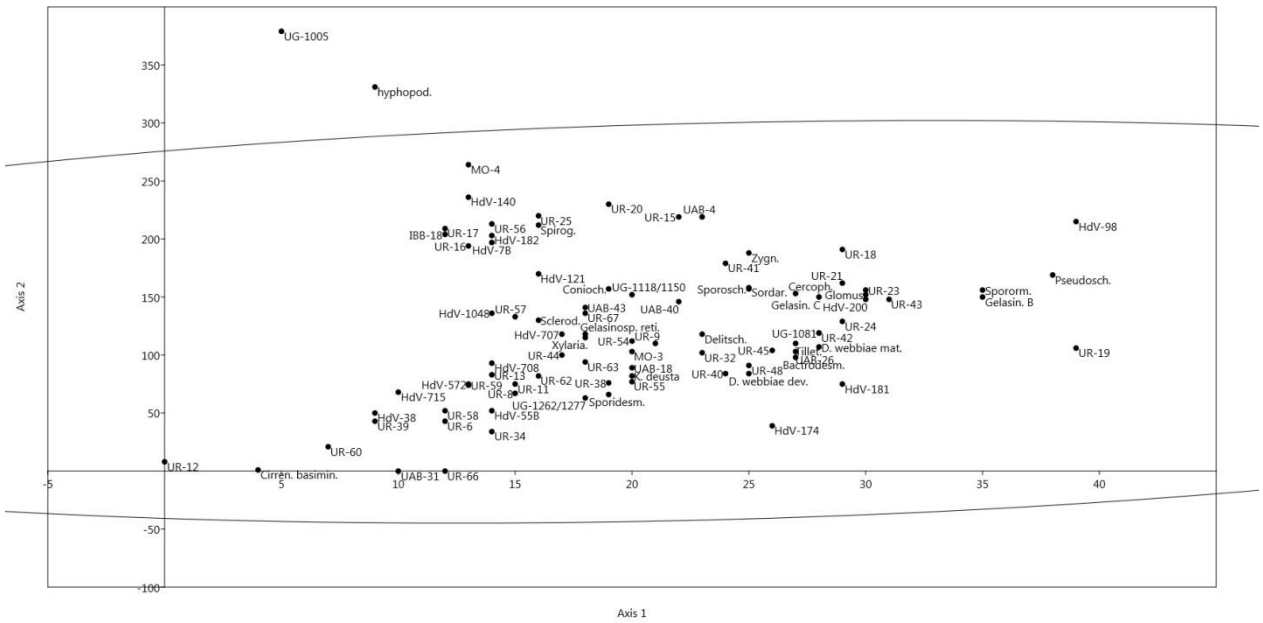

Figure 4.6. Genoa Piazza Vittoria. DCA plot excluding HdV-119, in order to improve the legibility of the main cluster of taxa.

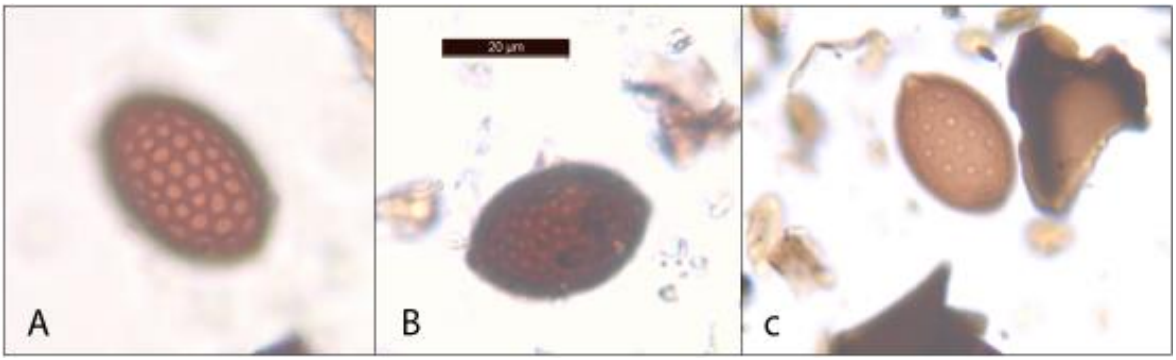

Figure 4.7. Genoa Piazza Vittoria. A: *Gelasinospora* cf *retispora*; B: *Gelasinospora* B; C: *Gelasinospora* C. Scale bar = 20μm (applies to all photos).

4.3.2 Hydrology

Summarising, the abundance of aquatic taxa allows some remarks on the hydrology of the site. Four episodes of shallow and eutrophic stagnant/slowly moving water (*Spirogyra*: GPV-2-5-8-11) might be inferred. These changes can be accounted for by the presence of temporary oxbow basins formed from meanders of the Bisagno (Arobba et al. 2016). On the other hand, ecologists do not have a univocal view on the value of *Pseudoschizaea*, mostly thought to be originated from an unknown aquatic organism (Grenfell 1995; Scott 1992, favouring the hypothesis of a plant or animal origin; unexpected results pointing to a relationship with angiosperms based on DNA extraction were reported by Milanesi et al. 2006). The microfossil seems to be an indicator of summer drought and periodical drying out of wet areas in warm climates, coupled with increased mineral inwashes (Carrión and Navarro 2002). For this reason, in view of its characteristic morphology it is normally considered to represent a freshwater algal cyst. Encystment is a well-known strategy used by phytoplankton species in order to survive in periods of extreme environmental conditions, involving the formation of a resistant outer shell protecting the living cell until favourable conditions (Bold and Wynne 1985; Blackburn and Parker 2005). Because the annual range of variability of planktonic habitats is often wider than the degree of tolerance of the algal cells, their blooms and reproduction cycles often follow a seasonal pattern (Sandgren 1983). It is thus likely that periodic desiccation and flooding of the area triggered algal encystment, in order to enable survival during dry periods. All these conditions match very closely our reconstruction of the middle Holocene

environment in the Bisagno river delta, most likely characterized by frequent changes in wetness and erosion rates, as typical of alluvial regimes. This view also gains support in the agreement between the rises in *Pseudoschizaea* and the main erosional events as indicated by *Glomus* spores from GPV-6 onwards. It is also worth stressing how *Spirogyra* and *Pseudoschizaea* mainly tend to exclude each other, presumably responding differently to variations in hydrologic parameters such as pH, temperature and nutrient supply.

4.3.3 Omnivores and herbivores

Data on omnivore species are provided by the eggs of intestinal parasites recovered (Arobba et al. 2016), that measure between 31.6 and 48.6μm in length (mean 39.1μm), falling within the size range of whipworms infecting humans (*Trichuris trichiura*) and pigs (*T. suis*). The specimens found around 6300 and 6480 cal BP appear particularly small (31.6μm - 40.8μm), although a few similar cases are known in the literature. The smallest *Trichuris* eggs found in Mesolithic levels at Goldcliff measured 41μm in length (Dark 2004), the eggs of *T. trichiura* and *T. suis* studied by Sondak (1948) ranged respectively between 34-41μm and 34-45μm, and the eggs of *T. suis* examined by Beer (1976) ranged from 35 to 62μm. Further, Hall et al. (1983), showed that *T. trichiura* eggs treated with standard procedure for pollen preparation measure from 34.7 to 47μm. Although the eggs of *T. suis* are thought to be slightly longer than the eggs of *T. trichiura* (Beer 1976; Florenzano et al. 2012), the size range considerably overlaps so that a distinction on morphometric basis is not possible. Moreover, although domestic pigs were introduced in Liguria only during the late Neolithic by Chassey groups (Rowley-Conwy 1997), *T. suis* can also infect wild suids as well as humans (Beer 1976), and bones of wild boar/pig were found very near the coring spot in late Neolithic levels at Brignole (Fontana et al. 2010). Both suid and human infections are thus plausible in our context. It is worth noting that, in this latter case, to our knowledge this would be the earliest evidence for human trichuriasis in the Italian Peninsula, whereas the only earlier record for *Trichuris* spp. (probably from wild animals) was found in southern Italy (Torri et al. 2012).

A high amount of dung spores was also recorded (Arobba et al. 2016). In the absence of specific data to address herbivore composition (lipid/bile analysis, DNA metabarcoding (D'Anjou et al. 2012; Giguet-Covex et al. 2014)), geographical and

ecological remarks allow us to advance some conclusions. Several data from mycological collections point to a very wide variety of animal families (chiefly Bovidae, Equidae, Caprinae, Cervidae, Leporidae, Mustelidae) for the main coprophilous families identifiable in the fossil record. Although due to a lack of sound experimental data fungal spore analyses can give, if any, only a very general indication in terms of animal identification (Richardson 1972; 2001; Angel and Wicklow 1975; Parker 1979; Doveri 2011), the coastal location of our site may help restrict the number of candidates.

Mycologists have carried out statistical analyses on a large number of samples of different dung types collected from different biozones. Their results are of some value for palaeoecologists, although some warnings are worth stressing. First, the most widely diffused fungal species colonizing dung unfortunately produce rather undistinctive hyaline spores, which are unlikely to be correctly identified during the analysis, and strongly resemble a number of other non-coprophilous spores (e.g. *Ascobolus* spp.). Secondly, these taxa may be more deeply affected by degradation compared to thick-walled brown spores, but to our knowledge there are no experimental data aimed at assessing this issue thus far. Richardson (1972) stresses the prevalence of the genera *Ascobolus*, *Lasiobolus*, *Coprobia*, *Cheylimenia*, *Ascoplanus* and *Podospora* (*curvula*) on the dung of ruminants. Among these, only *Podospora curvula* and *Ascobolus* spores would be recognizable in the subfossil records, the former being probably classified as *Sordaria*-type 55A, and the latter perhaps as *Neurospora* (the name *Neurospora*-type should thus be adopted in the future as routinely done for *Sporormiella* and *Sordaria*; on the relationship between NNP type terminology and actual biological attributions see Baker et al. 2013). The group of taxa favouring lagomorph substrate that would survive in the record is larger, including *Coniochaeta*, *Podospora appendiculata* and *setosa* (*Podospora*-type), and *Sporormia* (*Sporormiella*-type). However, *Sporormia* is well attested also on ruminant an horse dung (Parker 1979), and *Coniochaeta* has also commonly a saprobic behaviour (Krug et al. 2004). Richardson again (2001), highlights a statistical significant abundance of *Coniochaeta* spp. on dung of deer, and of *Schizothecium* (*decipiens* and *conicum*) and *Podospora* (*decipiens*) on sheep and cattle dung (these latter taxa recordable as *Sordaria*-type 55A in terms of NPP classification). It seems therefore highly problematic to convincingly use these studies for interpreting past animal presence, so that an examination of zooarchaeological assemblages and

animal population distributions in the Middle Holocene seems a more promising direction to follow.

The most common cervids documented in the Ligurian Holocene (*Capreolus capreolus*, *Cervus elaphus*, *Rupicapra rupicapra*, *Capra ibex*) all have relatively marked preferences for elevated habitats (up to 2000m asl), and only sporadically graze at lower altitudes. No hills exceeding 500m asl occur in a range of 5km from the site, suggesting that a more than negligible contribution to the coprophilous assemblage from cervid populations is unlikely. Moreover, it is not certain that fallow deer, typically Mediterranean, was diffused in the region in prehistory (Minelli 2002). Leporidae (notably *Lepus* spp.) and Mustelidae (e.g. *Meles meles*) are likely to be represented in our fimicolous record, but presumably only on a limited scale.

Omnivores such as wild boar should be ruled out, given the rarity of fungi isolated from non-herbivore dung (Lundqvist 1972).

As finally regards equid populations, although very scanty groups may have survived the last glaciation, horses are almost non-existent in the Italian zooarchaeological record prior to their reintroduction as domesticated species from eastern Europe during the Eneolithic (Pessina and Tiné 2008; Wilkens 2012).

In light of this, it is most likely that the only significant contribution to the coprophilous signal results from bovine and ovi-caprine dung, which are also the highly predominant dung types affected by fungal growth (percentages in Richardson 2001 and Doveri 2011). It should be borne in mind that ovicaprines were introduced in the peninsula already in a domesticated form, as their wild predecessors were not originally present on the Italian territory (Pessina and Tiné 2008). Although aurochs were diffused in the region prior to domestication, as shown by the bone assemblages from the Arene Candide (Rowley-Conwy 1997), bovine remains largely belong to domesticated species in middle-late Neolithic contexts. Therefore, given the complementary evidence for cattle and ovi-caprines bones at Brignole (Fontana et al. 2010) and the relevance for animal husbandry in the region (Barker et al. 1990; Maggi and Nisbet 1991), our data point to intense grazing pressure on the site. An overall schematic reconstruction of the main phases of landscape development at the mouth of river Bisagno during the Middle Holocene, integrating the results from pollen analysis (Arobba et al. 2016) and the current NPP analysis, is given in **fig. 4.8**.

The limited knowledge of the Neolithic phase of Genoa does not allow more refined inferences, as the nature of the occupation is not clear as yet (Maggi 1996; Del

Lucchese 2010). The alluvial plain may have been particularly suitable for domestic flocks, given the presence of handy watering places with still water and salt availability, a precious element for bovine and ovi-caprine diet (Tasić 2000; Di Fraia 2006).

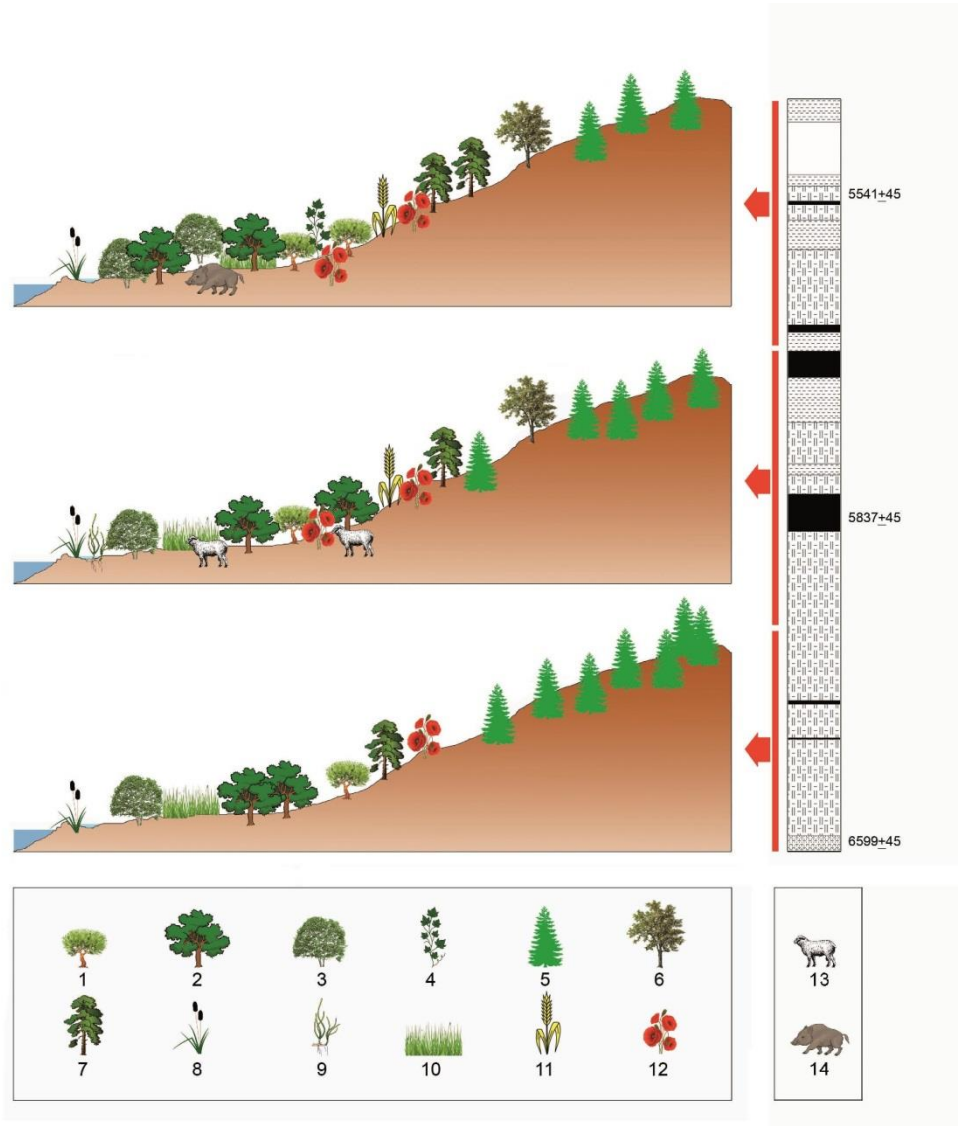

Figure 4.8. Vegetation and land use change in the valley of Bisagno during the Middle Holocene: 1. Mediterranean plant communities; 2. Mesophile oak wood; 3. Arboreal riparian vegetation; 4. Wild vine; 5. Silver fir; 6. Beech; 7. Pine; 8. Hygrophilous herbaceous plants; 9. Widgeon grass; 10. Sedges; 11. Cereals; 12. Synanthropic plants; 13. (Domestic?) herbivores; 14. Wild boar.

5. THE EXPERIMENTAL APPROACH: COPROPHILOUS FUNGAL SPORES FROM RECENT PASTORAL SEDIMENTS

5.1 Introduction

A considerable amount of research has been directed at the development of methods for identifying cattle pens in archaeological sites. Among the more commonly used techniques are micromorphology and phytolith analysis (Brochier et al. 1992; Canti 1997, 1998, 1999; Lancelotti and Madella 2012; Macphail et al. 1997; Shahack-Gross 2011; Shahack-Gross et al. 2003). Biomarker analysis and a method based on stable nitrogen isotopes have also been experimented, following the investigation of both archaeological layers and modern analogues (Bull et al. 2005; Shahack-Gross and Finkelstein 2008; Shahack-Gross et al. 2008). Although each of these methods has been successfully applied, they can also prove ineffective, as their validity may change according to site-specific factors such as taphonomic conditions and soil chemistry (Bull et al. 2005; Canti 1999).

This chapter aims to assess the reliability of dung spore analysis as an additional method for the existing 'toolbox' for the identification of ancient animal pens (Lancelotti and Madella 2012; Macharia et al. 2012; Shahack-Gross 2011). The study highlights the potential of these microfossils as localised and reliable indicators of archaeological animal enclosures. To this end, data have been collected from a number of sample locations such as dung heaps, floors of roofed stables and outdoor corrals, each characterised by different animal densities and frequency of use (**fig. 5.1**; **Chapter 2, table 2.3**). The article also aims to explore the value of other dung-related palynomorphs, as well as assessing the visibility of water indicators in pastoral sediments and the taphonomy of dung spores in stratified deposits. In order to show the applicability of the method, a recent pastoral site (rock shelter of Arma della Manie, Liguria, Italy) was excavated and the abundance of spores compared to other indicators (faecal spherulites and total phosphorus).

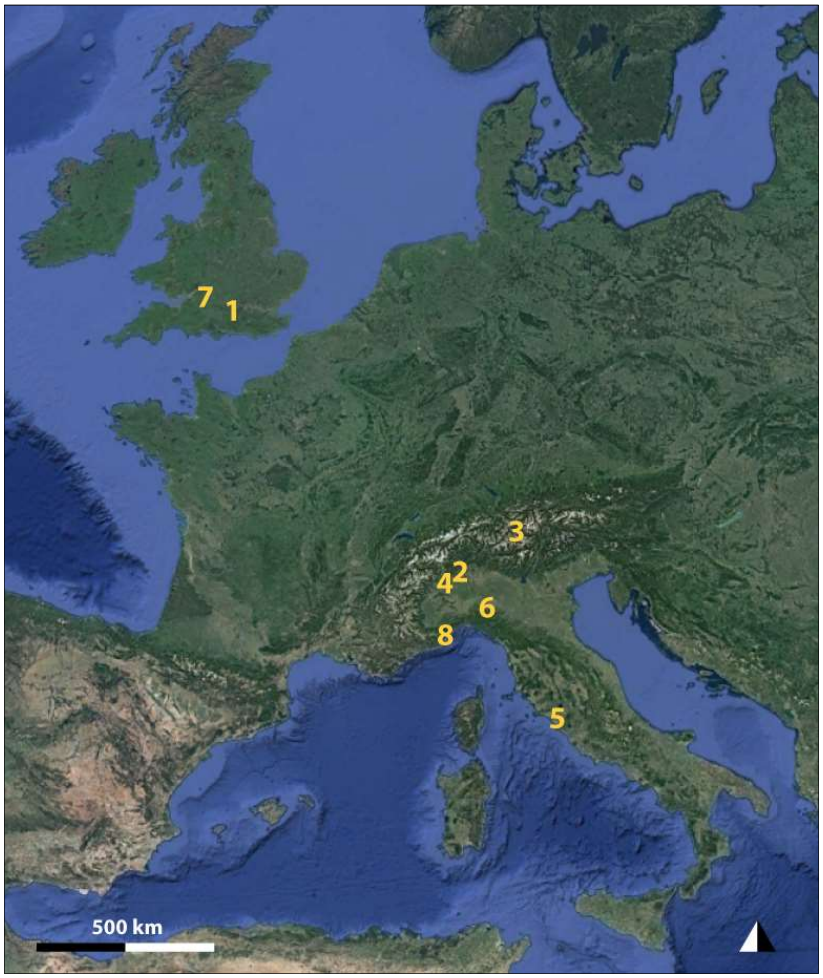

Figure 5.1. Map showing the location of the sites from which samples have been collected. 1. Arborfield, UK. 2. Besnate, Italy. 3. Semogo, Italy. 4. Somma Lombardo, Italy. 5. Tarquinia, Italy. 6. Vaccarezza, Italy. 7. West Overton, UK.

Coprophilous fungal spores are a suitable analytical tool, as they are often recorded in dung samples (Dietre et al. 2012; Gauthier et al. 2010) and have a relatively limited spatial dispersal (Baker et al. 2016; van Geel et al. 2003) - especially in protected conditions such as when found within caves or other sheltered environments. Previous research on fimicolous fungi has focused mainly on wild grazed environments (e.g. Baker et al. 2016; Blackford and Innes 2006; Cugny et al. 2010; Davis and Schafer 2006), and while natural sequences adjacent to archaeological sites are frequently investigated (e.g. lakes and mires), only a limited number of non-pollen palynomorph studies from terrestrial archaeological deposits have been conducted (e.g. Expósito and Burjachs 2016; Ivanova and Marfenina 2015; Kvavadze and Kakhiani 2010; Revelles et al. 2016; van Geel et al. 2003). Research on analogues for archaeological structures and the issue of differential abundance and distribution of dung spores is missing from these deposits. Moreover, while the use of percentages of the total pollen or the more independent parameter of accumulation rates appear suitable for natural archives (Baker et al. 2013, 2016; Wood and Wilmshurst 2013), they may not be adequate for anthropogenic layers, where the formation of thick sequences is often the result of single events occurring on a much shorter time scale (e.g. material being dumped, or

dung deposited on a small area by stabled animals) (Angelucci et al. 2009; Shahack-Gross et al. 2005; Schiffer 1987: 266). For this reason, spore concentration per unit of volume and weight has been chosen as most appropriate parameter in this work.

5.2 Results

5.2.1 Dung spore analysis

Most of the samples proved to be rich in a wide range of spores of fungi characterised by different degrees of coprophily (Krug et al. 2004); accordingly they were grouped in the tables to summarise the results (**tables 5.1 and 5.2**). Eggs of intestinal parasites were also quantified (**table 5.3**). In addition, when recovered in high amounts, the abundance of unidentified microfossils of unknown ecological preference was recorded (**table 5.1**). The results were also plotted according to the site type (**fig. 5.2**).

In the profile from the rock shelter, 17 obligate and occasionally coprophilous fungal taxa were identified in the upper two units, and the values are similar to the results obtained from modern stables and corrals (**table 5.4**). At the depths of 4 and 12cm two decreases in dung spores were recorded. Conversely, no spores were found in the lower part of the sequence (**fig. 5.3**). Parasite eggs and cysts of *Pseudoschizaea* were also recovered (**tables 5.3 and 5.5**).

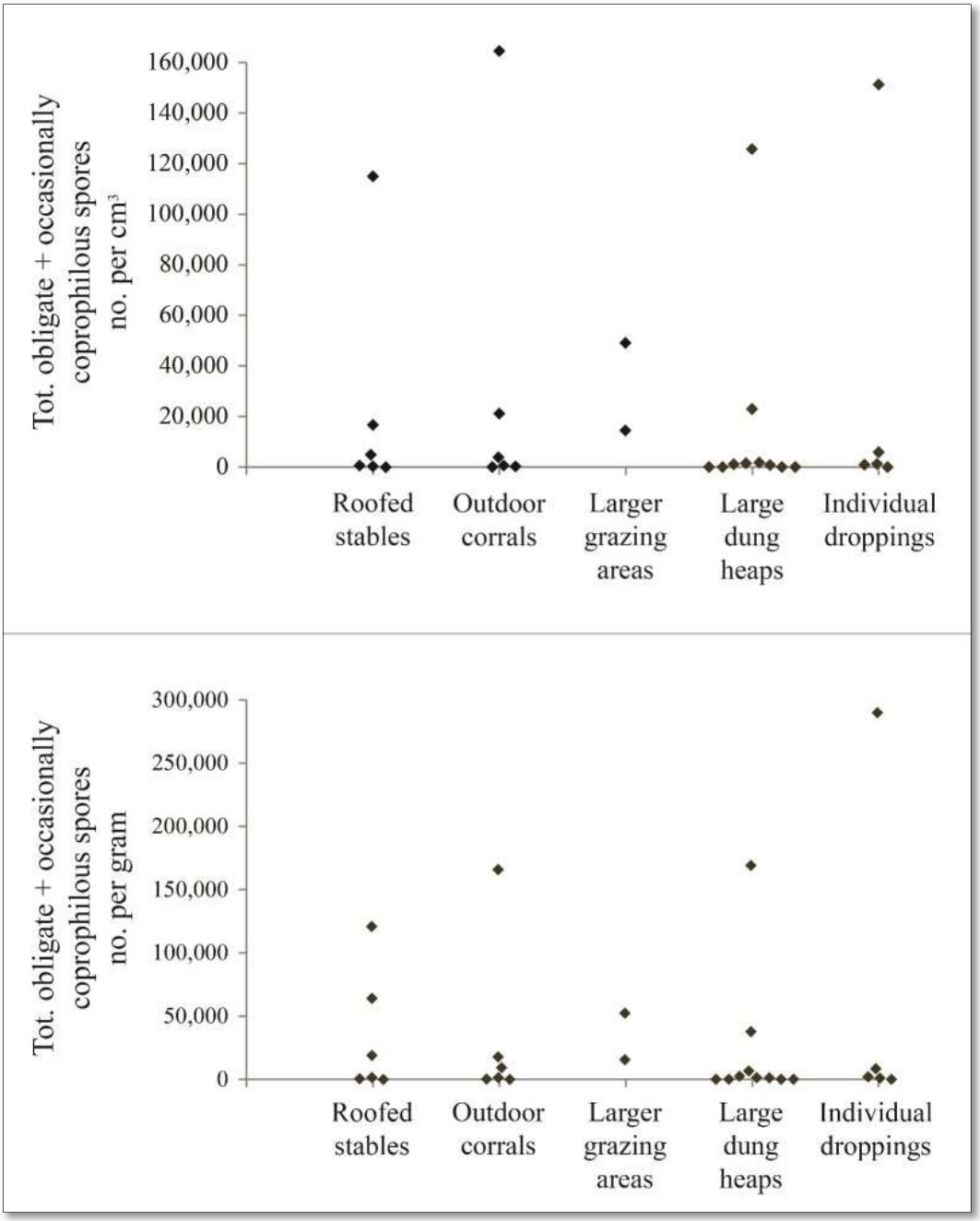

Figure 5.2. Scatterplots showing the abundance of dung spores (no./cm^3 and no./g) according to the site type (data points jittered for visibility).

Table 5.1. Number of obligate and occasionally coprophilous taxa and microfossils of unknown ecology per unit of volume (cm^3) and unit of weight (g).

Sample 1	**NPPs of unknown ecology:** UR-2 = 1985 spores/cm^3 (= 9452 spores/g)	
Sample 2	**Largely coprophilous fungi:** *Sordaria*-type = 116 spores/cm^3 (= 464 spores/g) **NPPs of unknown ecology:** UR-2 = 1,347,554 spores/cm^3 (= 5,390,216 spores/g)	**Dominant copr. taxon:** *Sordaria*-type
Sample 3	**Largely coprophilous fungi:** *Arnium*-type + *Sordaria fimicola*-type + *Sordaria*-type = 188 spores/cm^3 (= 382 spores/g) **Occasionally[1] coprophilous fungi:** *Coniochaeta* + *Thermomyces stellatus* = 326 spores/cm^3 (= 666 spores/g)	**Dominant copr. taxon:** *Thermomyces stellatus*
Sample 4	**Occasionally coprophilous fungi:** *Thermomyces stellatus* = 4833 spores/cm^3 (= 19,332 spores/g) **NPPs of unknown ecology:** UR-2 = 3,305,772 spores/cm^3 (= 13,223,088 spores/g)	**Dominant copr. taxon:** *Thermomyces stellatus*
Sample 5	**Occasionally coprophilous fungi:** *Chaetomium* + *Coniochaeta* + *Thermomyces stellatus* = 16,620 spores/cm^3 (= 63,923 spores/g)	**Dominant copr. taxon:** *Thermomyces stellatus*
Sample 6	**Largely coprophilous fungi:** *Arnium*-type + *Sordaria*-type + *Sporormiella*-type = 89,004 spores/cm^3 (= 93,689 spores/g) **Occasionally coprophilous spores:** *Chaetomium* + *Coniochaeta* + *Gelasinospora* + Melanosporaceae (HdV-55B) = 25,659 spores/cm^3 (= 27,009 spores/g) **NPPs of unknown ecology:** UR-1 = 15,235 spores/cm^3 (=16,037 spores/g); UR-2 =	**Dominant copr. taxon:** *Sordaria*-type

	10,424 spores/cm^3 (= 10,973 spores/g)	
Sample 7	Ø	
Sample 8	**Largely coprophilous fungi:** *Sporormiella*-type = 47 spores/cm^3 (= 82 spores/g) **Occasionally coprophilous fungi:** *Coniochaeta* = 24 spores/cm^3 (= 41 spores/g)	**Dominant copr. taxon:** *Sporormiella*-type
Sample 9	**Largely coprophilous fungi:** *Podospora*-type + *Sordaria*-type + *Sporormiella*-type = 594 spores/cm^3 (= 1266 spores/g) **Occasionally coprophilous fungi:** *Chaetomium* = 54 spores/cm^3 (= 116 spores/g) **NPPs of unknown ecology:** UR-2 = 216 spores/cm^3 (= 460 spores/g)	**Dominant copr. Taxon:** *Sordaria*-type
Sample 10	**Largely coprophilous fungi:** *Arnium*-type + *Sordaria fimicola*-type + *Sordaria*-type + *Sporormiella*-type = 2770 spores/cm^3 (= 6440 spores/g) **Occasionally coprophilous fungi:** *Chaetomium* + *Cercophora*-type + *Coniochaeta* + *Gelasinospora* + *Sphaerodes* = 1133 spores/cm^3 (= 2634 spores/g)	**Dominant copr. Taxon:** *Sordaria*-type
Sample 11	**Largely coprophilous fungi:** *Sordaria*-type + *Sporormiella*-type = 6444 spores/cm^3 (= 5461 spores/g) **Occasionally coprophilous fungi:** *Apiosordaria verruculosa*[2] + *Ascodesmis* + *Chaetomium* + *Cercophora*-type + *Neurospora* + *Thermomyces stellatus* = 14,499 spores/cm^3 (= 12,287 spores/g)	**Dominant copr. Taxon:** *Cercophora*-type and *Sporormiella*-type
Sample 12	**Largely coprophilous fungi:** *Arnium*-type + *Sordaria*-type + *Sporormiella*-type = 71,478 spores/cm^3 (= 72,200 spores/g) **Occasionally coprophilous fungi:** *Chaetomium* + Melanosporaceae (HdV-55B)+	**Dominant copr. taxon:**

	Thermomyces stellatus = 92,327 spores/cm^3 (= 93,260 spores/g)	*Thermomyces stellatus*
	NPPs of unknown ecology**:** HdV-708 = 5956 spores/cm^3 (= 6016 spores/g)	
Sample 13	**Largely coprophilous fungi:** *Arnium*-type + *Sordaria*-type + *Sporormiella*-type = 9078 spores/cm^3 (= 9657 spores/g)	**Dominant copr. taxon:** *Apiosordaria*-type
	Occasionally coprophilous fungi: *Apiosordaria*-type + *Chaetomium* + *Gelasinospora* = 5380 spores/cm^3 (= 5723 spores/g)	
	NPPs of unknown ecology: UR-2 = 1345 spores/cm^3 (= 1431 spores/g)	
Sample 14	**Largely coprophilous fungi:** *Arnium*-type + *Delitschia* + *Sordaria*-type + *Sporormiella*-type + = 48,040 spores/cm^3 (= 51,106 spores/g)	**Dominant copr. taxon:** *Sporormiella*-type.
	Occasionally coprophilous fungi: *Apiosordaria*-type = 906 spores/cm^3 (= 964 spores/g)	
	NPPs of unknown ecology: UR-2 = 13,596 spores/cm^3 (= 14,464 spores/g)	
Sample 15	**NPPs of unknown ecology:** UR-2 = 2,062,080 spores/cm^3 (= 4,482,782 spores/g)	
Sample 16	**NPPs of unknown ecology:** UR-2 = 908,604 spores/cm^3 (= 663,214 spores/g); UR-68 = 1,051,661 spores/cm^3 (= 767,636 spores/g)	
Sample 17	**NPPs of unknown ecology:** UR-2 = 1208 spores/cm^3 (= 3265 spores/g); UR-69 = 2819 spores/cm^3 (= 7619 spores/g); UR-71 = 151,031 spores/cm^3 (= 408,192 spores/g)	
Sample 18	**NPPs of unknown ecology:** UR-69 = 71,242 spores/cm^3 (= 229,813 spores/g)	

Sample 19	**Largely coprophilous fungi:** *Sordaria fimicola*-type = 239 spores/cm^3 (= 412 spores/g) **Occasionally coprophilous fungi:** *Thermomyces stellatus* = 477 spores/cm^3 (= 822 spores/g) **NPPs of unknown ecology:** UR-69 = 32,220 spores/cm^3 (= 55,552 spores/g); UR-71 = 9785 spores/cm^3 (= 16,871 spores/g)	**Dominant copr. taxon:** *Thermomyces stellatus*
Sample 20	**Largely coprophilous fungi:** *Sporormiella*-type = 1158 spores/cm^3 (= 2068 spores/g) **NPPs of unknown ecology:** HdV-708 = 235,119 spores/cm^3 (= 419,855 spores/g); UR-2 = 16,215 spores/cm^3 (= 28,955 spores/g)	**Dominant copr. taxon:** *Sporormiella*-type
Sample 21	**Largely coprophilous fungi:** *Sordaria*-type = 1017 spores/cm^3 (= 3390 spores/g) **Occasionally coprophilous fungi:** *Thermomyces stellatus* = 1017 spores/cm^3 (= 3390 spores/g) **NPPs of unknown ecology:** HdV-708 = 113,957 spores/cm^3 (= 379,858 spores/g); UR-69 = 5087 spores/cm^3 (= 19,956 spores/g); UR-71 = 294,049 spores/cm^3 (= 980,163 spores/g)	**Dominant copr. taxon:** *Sordaria*-type and *Thermomyces stellatus*
Sample 22	**Largely coprophilous fungi:** *Sporormiella*-type = 2156 spores/cm^3 (= 1373 spores/g) **NPPs of unknown ecology:** HdV-708 = 143,779 spores/cm^3 (= 91,578 spores/g); UR-2 = 2865 spores/cm^3 (= 1825 spores/g); UR-70 = 46,000 spores/cm^3 (= 29,299 spores/g); UR-71 = 22,285 spores/cm^3 (= 14,194 spores/g)	**Dominant copr. taxon:** *Sporormiella*-type.
	Largely coprophilous fungi: *Sordaria*-type + *Sporormiella*-type = 18,762 spores/cm^3 (= 30,757 spores/g)	

Sample 23		**Occasionally coprophilous fungi:** *Apiosordaria*-type + *Chaetomium* = 4170 spores/cm^3 (= 6836 spores/g) **NPPs of unknown ecology:** HdV-708 = 164,699 spores/cm^3 (= 269,998 spores/g); UR-2 = 14,593 spores/cm^3 (= 23,923 spores/g); UR-71 = 179,292 spores/cm^3 (= 293,922 spores/g)	**Dominant copr. taxon:** *Sporormiella*-type.
Sample 24		**Largely coprophilous fungi:** *Sporormiella*-type = 111,189 spores/cm^3 (= 150,255 spores/g) **Occasionally coprophilous fungi:** *Apiosordaria*-type = 13,899 spores/cm^3 (= 18,782 spores/g) **NPPs of unknown ecology:** HdV-708 = 48,645 spores/cm^3 (= 65,736 spores/g); UR-2 =17,373 spores/cm^3 (= 23,477 spores/g); UR-70 = 97,290 spores/cm^3 (= 131,473 spores/g); UR-71 = 535,098 spores/cm^3 (= 723,105 spores/g)	**Dominant copr. taxon:** *Sporormiella*-type
Sample 25		**NPPs of unknown ecology:** UR-2 = 8736 spores/cm^3 (= 15,600 spores/g)	
Sample 26		**Largely coprophilous fungi:** *Sordaria*-type + *Sporormiella*-type = 1303 spores/cm^3 (= 1760 spores/g) **NPPs of unknown ecology:** UR-2 = 29,969 spores/cm^3 (40,499 spores/g)	**Dominant copr. taxon:** *Sordaria*-type
Sample 27	a (outer surface)	**Largely coprophilous fungi:** *Sordaria fimicola*-type + *Sordaria*-type = 602 spores/cm^3 (= 463 spores/g) **Occasionally coprophilous fungi:** *Apiosordaria*-type + *Chaetomium* = 602 spores/cm^3 (= 463 spores/g)	**Dominant copr. taxon:** *Sordaria*-type
	b (inner	**Largely coprophilous fungi:** *Sordaria*-type = 3912 spores/cm^3 (= 5588	**Dominant**

	part)	spores/g)	**copr. taxon:**
		Occasionally coprophilous fungi: *Cercophora*-type = 1956 spores/cm^3 (= 2794 spores/g)	*Sordaria*-type
Sample 28		**Largely coprophilous fungi:** *Delitschia* + *Podospora*-type + *Sordaria*-type + *Sporormiella*-type = 150,676 spores/cm^3 (= 289,761 spores/g)	**Dominant copr. taxon:** *Sporormiella*-type

[1]Given the sampling contexts, it is highly likely that most of the occasionally coprophilous taxa recovered in the analysis actually represent coprophilous species.

[2]*Apiosordaria verruculosa* (HdV-169, verrucate gelatinous sheath, *sensu* Aptroot and van Geel, 2006) was maintained distinct from *Apiosordaria*-type (UG-1171, smooth gelatinous sheath, *sensu* Gelorini et al., 2011).

Table 5.2. Total sums of spores of obligate and occasionally coprophilous fungi per unit of volume (cm^3) and unit of weight (g), divided by site types.

Site type	Sample no.	Tot. obligate + occasionally coprophilous spores no. per cm^3	Tot. obligate + occasionally coprophilous spores no. per gram
Roofed stables	1	0	0
	2	116	464
	3	514	1048
	4	4833	19,332
	5	16,620	63,923
	6	114,663	120,698
Outdoor corrals	7	0	0
	8	71	123
	9	649	1382
	10	3903	9074
	11	20,943	17,748
	12	163,805	165,460
Larger grazing areas	13	14,458	15,380
	14	48,946	52,070
Large dung heaps	15	0	0
	16	0	0
	17	0	0
	18	0	0
	19	716	1234
	20	1158	2068
	21	2034	6780
	22	2156	1373
	23	22,932	37,593
	24	125,088	169,037
Individual droppings	25	0	0
	26	1303	1760
	27a[1]	1204	926
	27b	5868	8382
	28	150,676	289,761

[1]The inverse proportion between number of spores per cm^3 and per gram in the two subsamples is due to the slightly heavier weight of the coprolite surface (27a, $1cm^3 = 1.3g$) relative to its inner part (27b, $1cm^3 = 0.7g$).

Table 5.3. Eggs of intestinal parasites per unit of volume (cm^3) and unit of weight (g).

Sample no.	Parasite eggs					
	Trichuris sp.		*Ascaris sp.*		*Dicrocoelium* sp.	
	no. per cm^3	no. per g	no. per cm^3	no. per g	no. per cm^3	no. per g
3	77	158	0	0	0	0
10	0	0	0	0	169	292
A. Manie						
(depth in cm)						
0-1	153	82	77	41	39	21
4-5	0	0	90	55	0	0
8-9	124	69	101	56	25	14
12-13	49	36	16	12	0	0
16-17	0	0	0	0	0	0
17-18	64	36	0	0	0	0

N.B.: Although in modern industrial farms the use of pesticides would highly affect the data, this is probably not the case of Samples 3 and 10, taken from a traditional private farming context, as well as the samples from the rock shelter of Arma delle Manie.

Table 5.4. Arma delle Manie: total sums of spores of obligate and occasionally coprophilous fungi per unit of volume (cm^3) and unit of weight (g).

Unit	Depth (cm)	Tot. obligate + occasionally coprophilous spores no. per cm^3	Tot. obligate + occasionally coprophilous spores no. per gram
1	0-1	67,189	35,930
	4-5	5072	3093
	8-9	4810	2672
	12-13	3193	2365
	16-17	128	72
2	17-18	3537	1987
3	24-25	0	0
	32-33	0	0
	40-41	0	0

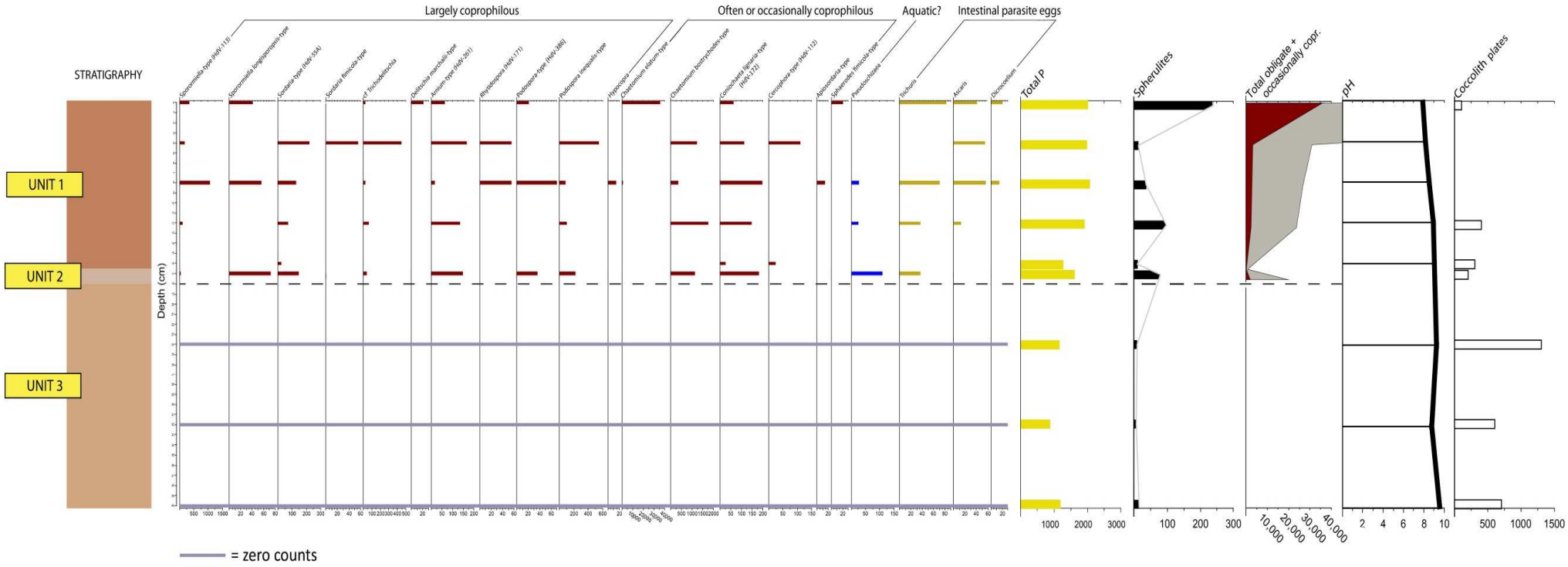

Figure 5.3. Arma della Manie: diagram showing the abundance of dung spores (10x exaggeration factor applied to the total coprophilous sum), probable aquatic microfossils and eggs of intestinal parasites (values expressed as microfossil no./g), the amount of total phosphorus (ppm), the concentration of faecal spherulites and coccolith plates (no./mg), as well as the alkalinity of the sediments. Ecological grouping according to Krug et al. 2004.

5.2.2 Analysis of faecal spherulites

Spherulite abundance per mg ranged from zero counts to a maximum of 240 particles (uppermost unit). Although Canti (1998) identified several types of spherulites, the elements observed here seem to broadly fall into two categories, as noted by Korstanje (2004): larger (c. 10-15μm) and slightly yellowish particles showing bands of interference colours (type A; **fig. 5.4A**), and smaller (c. 5μm) whiter particles, occasionally showing a basketball-like/dumbbell-like appearance upon rotation (type B; **figs. 5.4B and 5.4C**). During the analysis, the presence of calcareous nannoplankton was also noted (**fig. 5.4D**), and the number of coccolith plates (often closely resembling faecal spherulites: Canti 1998) quantified. Spherulites and coccolith plates are clearly concentrated in different parts of the deposits, the former being numerous mostly in the upper levels and the latter in the lower levels. This suggests that they were correctly separated during identification and are the products of different formation processes.

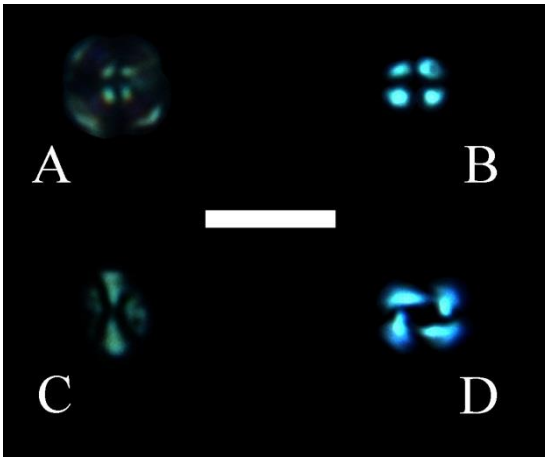

Figure 5.4. Types of faecal spherulites (A-B-C). Figure D shows a coccolith plate (calcareous nannoplankton). Scale bar = 10μm.

5.2.3 Total phosphorus analysis

A higher content of Ptot was measured from Units 1 and 2 (c. 2000-1600 ppm), whilst values sharply decrease in Unit 3 (c. 1200-900 ppm) (**fig. 5.3**).

5.3 Discussion

5.3.1 Differential taphonomy, differential abundance of dung spores

As shown, coprophilous spores are not always necessarily recovered within dung samples (Samples 15, 16, 17, 18, 25). Their presence therefore strictly depends upon successful sporulation and dispersal, and the absence of spores cannot be taken as a certain evidence for the absence of herbivores.

There seems to be a relationship between periods of limited soil disturbance and higher values of dung spores. The structures used only for some months a year (Samples 6 and 10), show higher concentrations compared to the places where animals are corralled continuously. This is particularly evident in the case of Samples 1 and 7, taken from a stable floor and an outdoor corral. Similarly, the sheep enclosures regularly used to keep all of the specimens overnight have yielded low values (Sample 8), and almost equally negligible is the concentration in Sample 2 from another stable floor. Presumably, as dung fungal spores need a certain amount of time and the appropriate degree of aeration to colonise fresh substrates (Wicklow 1992), continuous soil disturbance may impede successful fungal colonisation and prevent fungi from growing and releasing high numbers of spores, and repeated remixing and compaction of dung are likely to be factors responsible for their absence.

In stabling sequences from caves, the occurrence of sporadic peaks in dung spores only in certain samples (Expósito and Burjachs 2016) may reflect such conditions and not only burning-caused destruction, with spore-rich layers being an indication of episodes during which the herd was taken away leaving the surface undisturbed, at least for a period long enough to allow fungal growth and spore dispersal. According to mycological studies, this period can be quantified from 3 to 30 days, depending on the coprophilous species (Harper and Webster 1964; Richardson 2002). This information would be precious to shed light on the farming practices adopted by early farmers.

Rapid burial of pellets under fresh dung before sporulation takes place may be a further cause of zero counts from dung heaps and stabling layers. As spores would be dispersed mainly on the surface of dung pats and droppings, the rapid accumulation of thick layers may cause anaerobic conditions across the deposit and impede

sporulation, resulting in spore-free horizons. However, to assess this effect the surface and the inner part of sheep droppings were subsampled and processed separately, with the core of the droppings being richer in coprophilous spores (Samples 27a and 27b).

It is possible that Samples 10 and 11 represent an intermediate condition, where soil disturbance occurs only to some extent, preventing a peak in dung spores but allowing the recovery of between c. 4000-20,000 spores per cm^3. High values from Sample 12 may instead be due to the goats' preference for resting mainly in the sheltered area, resulting in a relatively low disturbance of the remaining part of the enclosure.

The analysis has also provided somehow unexpected data. First, a remarkable diversity in spore concentration and dominant coprophilous taxa has emerged, even on a small (a few tens of metres) and very small scale (less than 3m). This is shown by Samples 18-19-21 and 23-24, all located within the same area but characterised by highly different values and different dominant taxa. The data indicate the importance of locally growing and sporulating fungi, in spite of the fact that the same cows and horses, fed with the same feed, provided the substrates.

A few unidentified as well as already known microfossils have been found to be strongly associated with herbivore dung (HdV-708, UR-2, UR-68, UR-69, UR-70, UR-71) (**fig. 5.7**). The newly identified NPP types may be further reliable indicators of grazing pressure, as they occurred in exceptionally high concentrations in samples from dung heaps and stable floors. Therefore, further research on non-coprophilous but potentially pasture-related NPPs seems promising, as is suggested by other studies (Revelles et al. 2016; van den Bos et al. 2014).

It is worth noting that there is some degree of consistency between the values recovered from the 28 samples analysed, with the total coprophilous concentration comprising between a minimum of 0 and a maximum of c. 160,000 spores per cm^3. Occasionally, similar contexts from different sites have also produced comparable results (e.g. Sample 11-13, 21-22). Extremely high values, such as those recorded in the case of UR-2, UR-68 and UR-71 in Samples 2, 4, 15, 16 and 24, never occur in the coprophilous record.

Canonical Correspondence Analysis (CCA) was used to plot the data, assessing the occurrence of groups of samples or NPP assemblages sharing affinities. Furthermore, this method is suitable to check the influence of abiotic variables on biotic variables.

In this case, three environmental variables, corresponding to different degrees of surface disturbance, were inserted in the dataset: low, moderate and high continuity of surface disturbance (CSD).

Following CCA, a discrete group of samples appears to be correlated with high CSD and characterised by the abundance of the microfossil type UR-2 (**fig. 5.5**). On the other hand, although some of the other taxa form small clusters, they are distributed over a large portion of the graph. It is possible that this is an effect of differential resiliency of fungal species to animal trampling or other environmental variables (e.g., moisture, temperature), as well as an effect of differences in the length of the period necessary for spore production and dispersal (Richardson 2002). Clustering of rare taxa (e.g. *Neurospora* and *Sphaerodes*) result from their presence only in a few samples, and therefore no reliable inferences can be drawn about them.

Although low concentrations of coprophilous taxa can occasionally occur in samples correlated with moderate and low CSD, it seems significant that none of the samples with high dung spore concentrations (black, green and violet dots, **fig. 5.6**) show correlations with high CSD. This supports the empirical observation that animal trampling constitutes a factor in determining the ability of coprophilous taxa to produce and disperse spores.

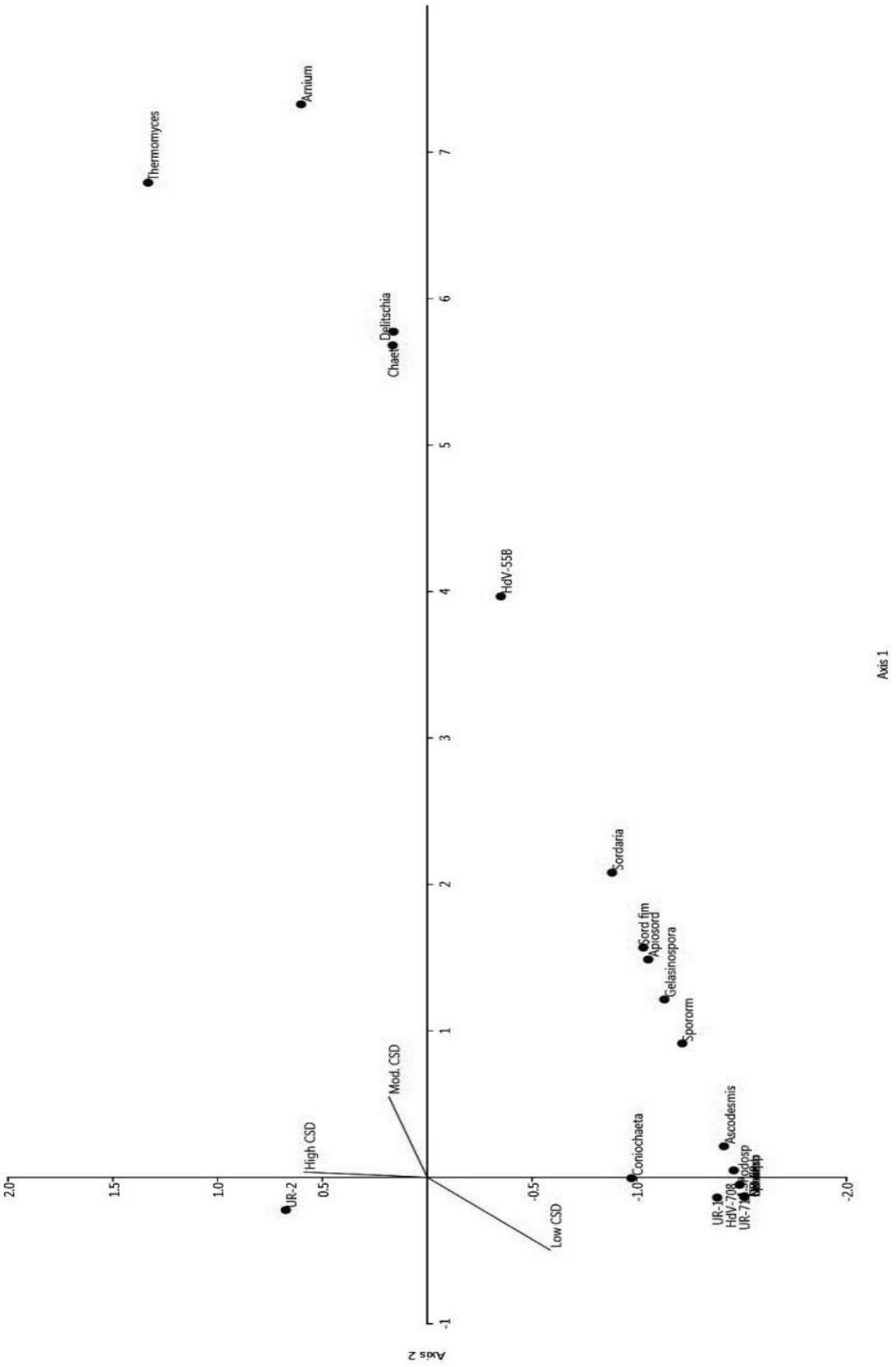

Figure 5.5. NPP types from modern samples: CCA plot. Eigenvalue for axis 1 is 0.48, eigenvalue for axis 2 is 0.31. The cluster of taxa around Y -1.50 is formed by *Cercophora*, *Sphaerodes*, *Neurospora*, UR-68, UR-69, UR-70 and UR-71.

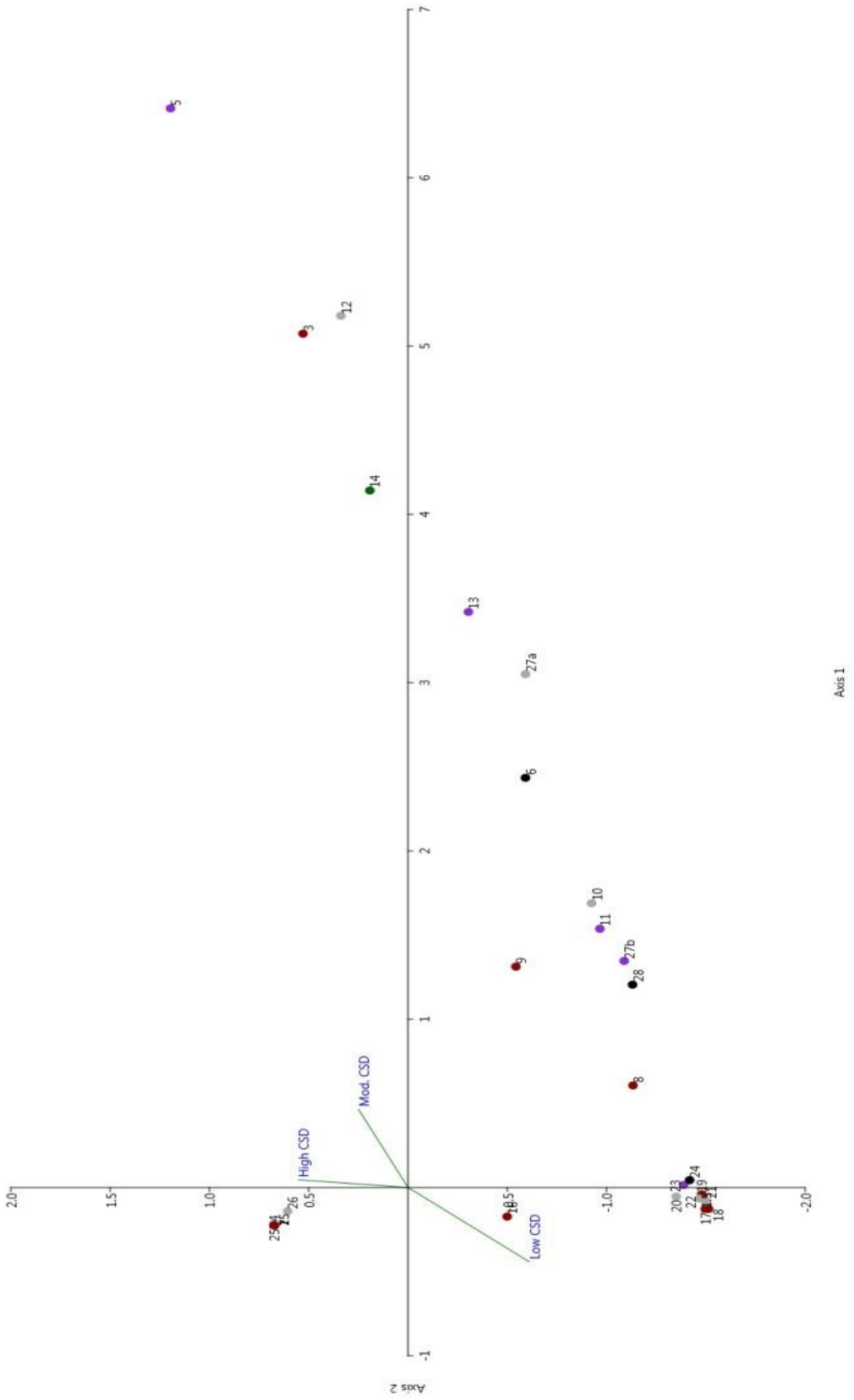

Figure 5.6. Modern samples: CCA plot. Eigenvalue for axis 1 is 0.48, eigenvalue for axis 2 is 0.31. Dark red dots = 0-1000 spores/cm^3; grey dots = 1000-5000 spores/cm^3; violet dots = 5000-25,000 spores/cm^3; green dots = 25,000-1000,000 spores/cm^3; black dots = 100,000-150,000 spores/cm^3.

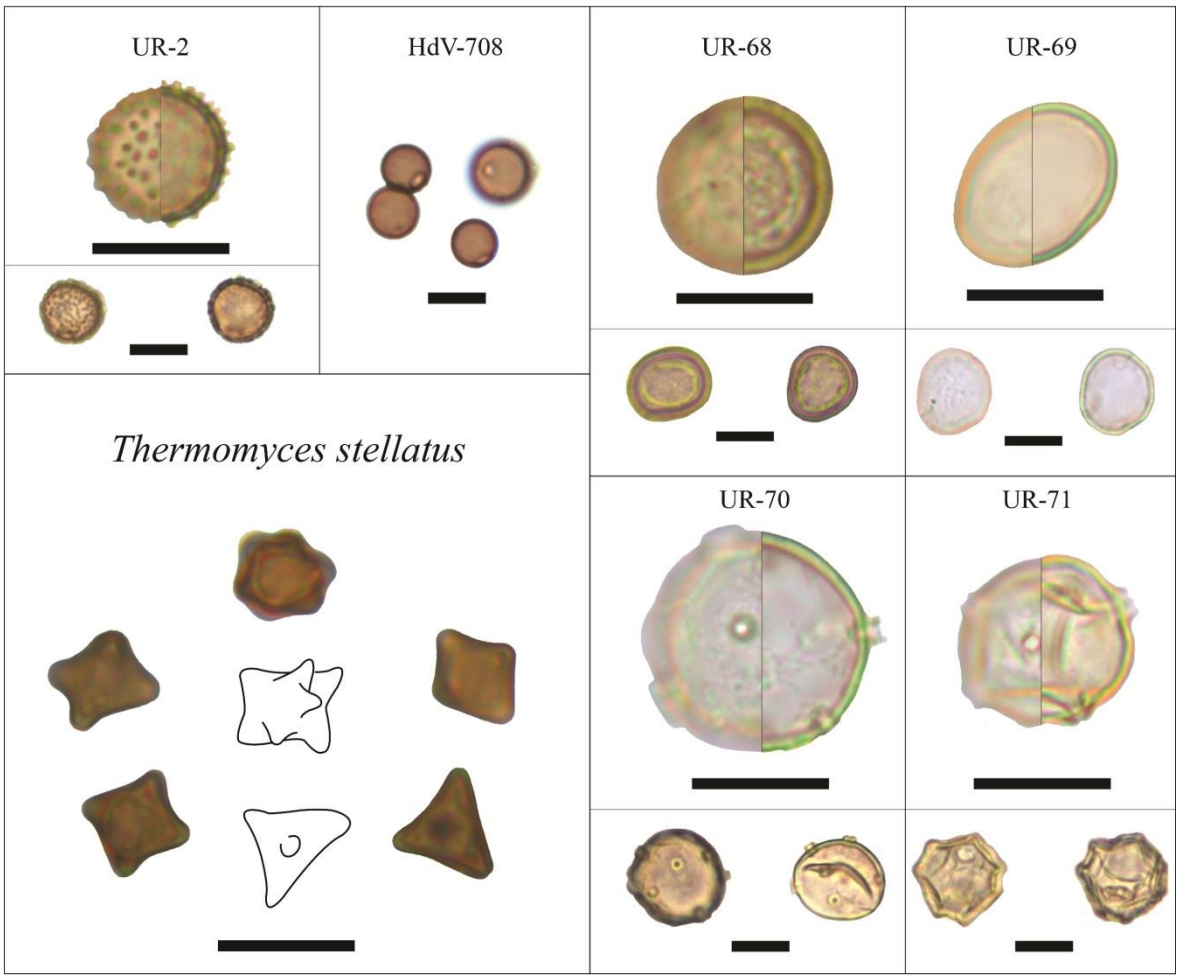

Figure 5.7. Microfossils of unknown origin and ecology (composite images showing high and low focus) and conidiospores of *Thermomyces stellatus* (micrographs and graphic representation to better show the features of its irregularly shaped spores). HdV-708: globose, 1-2 pores, psilate, reddish-brown, often in a series or two or more cells. Newly described types: UR-2: globose, with short protuberances densely distributed across the surface, yellowish-brown; UR-68: globose, thick-walled, psilate, yellowish-brown; UR-69: globose to ovoid, psilate, hyaline; UR-70: globose, 8-10 protruding pores, psilate, hyaline; UR-71: more irregular than UR-70, wrinkled, double-walled, with internal membrane forming 8-10 pores by piercing the external wall, psilate, hyaline. *T. stellatus*: very irregularly shaped, 4-8 rounded projections, no proper pores but thinner walls at the end of the projections, psilate, reddish-brown. Scale bars = 10µm.

5.3.2 Thermophilic fungi: ecology and future research potential

The study represents a rare recorded case of thermophilic fungi. This small assemblage of Eukaryota is virtually absent in the extant literature on non-pollen palynomorphs, where so far they have only been briefly mentioned twice (Hawksworth et al. 2016; Ivanova and Marfenina 2015). The ecology of these organisms is very specific, as they necessitate elevated temperatures in order to thrive, normally between 20°C and 40°C, with optimal growth around 50°C-60°C in a humid and aerobic environment (Mouchacca 1999; Salar and Aneja 2007). This is the first record of the thermophilic fungus *Thermomyces stellatus* (Bunce) Apinis (Ascomycota: Eurotiomycetes: Eurotiales) from a sedimentary context. This species was unknown to biologists until 1961, when it was first described by Bunce (1961) as a member of the genus *Humicola*, and subsequently assigned to the genus *Thermomyces* by Apinis (1963).

T. stellatus finds its most suitable habitat on hay, although it has also been isolated from dung (Sreelatha et al. 2013). Its strong association with hay and capability of growing on dung leave little doubt about the correctness of the identification. Its presence within sedimentary sequences testifies to a warm microclimate on or within the colonised substrate, as well as providing a substantial contribution to the issue of the archaeological visibility of hay (Hodgson et al. 1999), given its strong preference for this host. Arguably, *T. stellatus* may even enable distinction between spontaneous bacteria-driven combustion of hay and manure (Browne 1929; Firth and Stuckey 1947; Woodward 2004) and deliberate dung burning in archaeological pastoral deposits (Brochier et al. 1992; Vergès et al. 2016), as in the latter case temperatures would rise more abruptly, without allowing thermophilic taxa to grow and release spores. Temperatures suitable for thermophilic fungi would occur for sufficient time afterwards during the slow cooling process (Vergès et al. 2016), but at this point fungal organisms would have been destroyed by previous high temperatures. On the contrary, in self-combustion temperatures rise progressively over a prolonged period, providing an optimal microclimate for heat-loving species, as even two months may pass before the deposit catches fire (Musselman 1935; Rothbaum 1963). Chitin-composed fungal spores (Ruiz-Herrera 1991) are effectively resilient, and can be successfully recovered also from layers of burnt dung (Expósito and Burjachs 2016; Morandi 2016).

T. stellatus is named after the morphology of its small (ø 7-10µm) conidia, presenting from four to eight rounded projections (**fig. 5.7**). These conidiospores should not be mistaken for the triangular spores of *Chaetomium trigonosporum* (Doveri 2008; Torri, 2010: pl. 7, fig. 1) or the more rounded conidia of *Arhtrinium puccinioides* (Ellis 1971: 573). Also the microfossil type HdV-365 reported by van Geel et al. (1981), in spite of its similar morphology, is by far too large to be *T. stellatus*, and cannot even represent *Humicola stellata* var. *gigantea* (Khanna 1963). This latter name is misleading and clearly derives from a misidentification of hyphopodia of *Gaeumannomyces graminis* (Walker 1972), rather than of aleuriospores of *Arthrinium pterospermum* (Mouchacca 2000). However, the microfossil identified as type 365 by Shumilovskikh et al. (2015: fig. 5J) may actually represents spores of *T. stellatus*, in view of its low number of projections relative to spores of *Inocybe* sp., although its size seems slightly larger.
Thermophilic fungi have also been reported from lakes (Tubaki et al. 1974), suggesting that palaeoecological research could greatly benefit from their identification. In particular, some genera (e.g. *Humicola*, *Rhizopus*, *Thermomyces*) include species producing morphologically distinct spores, that would reliably indicate the occurrence of elevated temperatures near the site, at least for a period long enough to enable fungal growth and sporulation (Ellis D.H. 1981; Ellis M.B. 1971: 59; Hawksworth et al. 2016).

5.3.3 Dung spores from a stratified deposit: application of the method to a recent pastoral site

The rock shelter of Arma delle Manie has proven very rich in dung spores in its top 18cm (**fig. 5.8**), the spore concentration being remarkably consistent with the modern dataset (**table 5.4**). The profile was macroscopically divided into three different units, each characterised by a different texture and colour (**fig. 5.3,** see also **Chapter 2**, **fig. 2.9**). A sharp stratification, although commonly formed by black and pale layers, is typical of Mediterranean pastoral cave deposits since Neolithic times (Angelucci et al. 2009; Brochier et al. 1992). All of the coprophilous-rich levels are located in the thick uppermost layer (Unit 1) and in the thin underlying layer (Unit 2). The difference in abundance between Units 1-2 and Unit 3 is striking, the latter being totally devoid of dung spores (**fig. 5.3**). It is highly likely that the two upper units

represent decomposed and partially mineralised compacted dung layers, directly accumulated above the natural calcareous topsoil. Such a sharp difference in microfossil composition clearly shows the validity of dung spore analysis as a further method to identify ancient animal enclosures, along with other well-established indicators (Shahack-Gross 2011; Shahack-Gross et al. 2003, 2008).

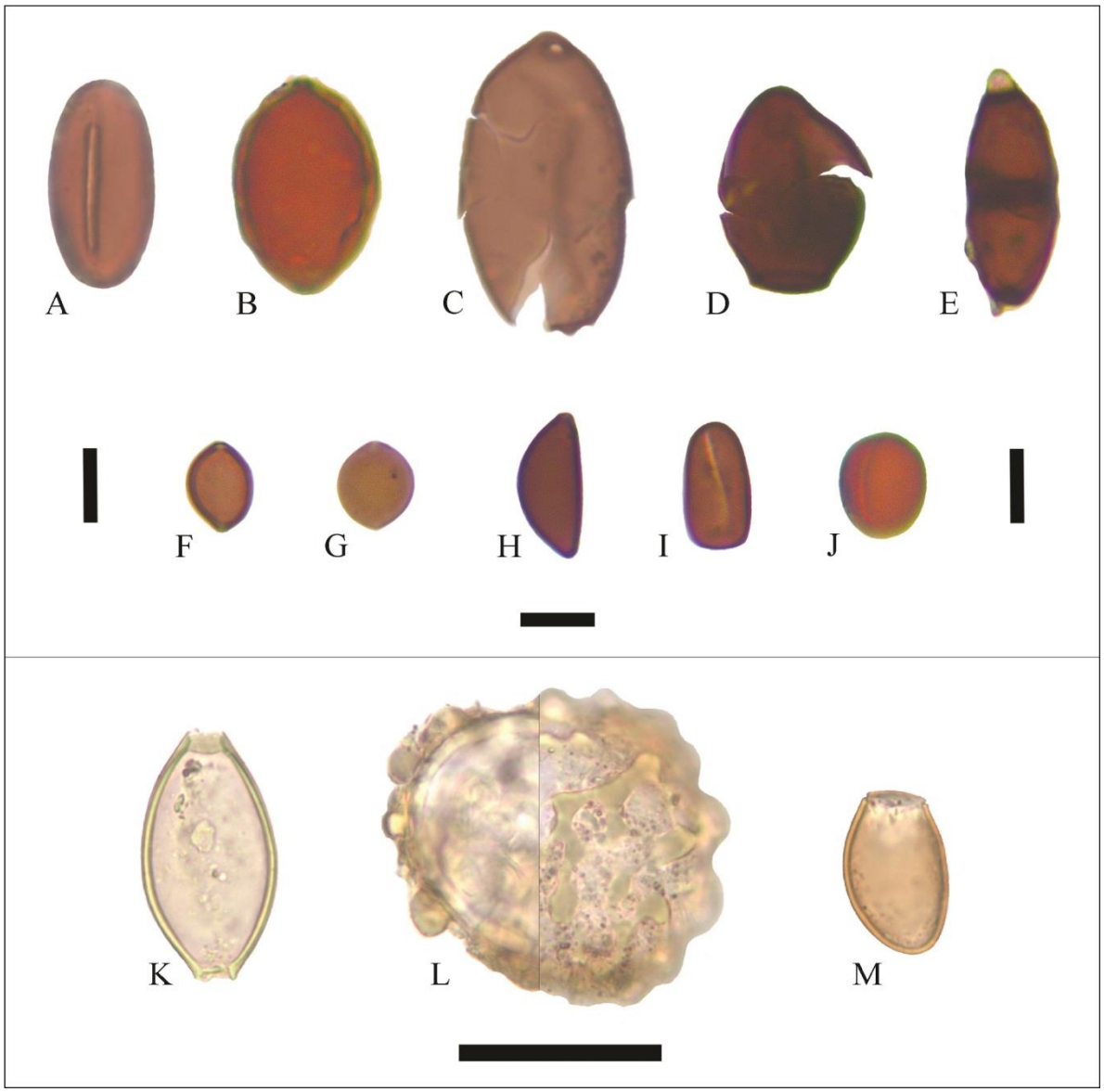

Figure 5.8. Arma delle Manie: selection of non-pollen microfossils. Spores of fungal taxa obligately or occasionally coprophilous: A. *Hypocopra*; B. *Rhytidospora*; C. *Podospora*-type; D. *Apiosordaria*-type; E. Probable spore of *Trichodelitschia*; F. *Chaetomium elatum*-type (thick-walled); G. *Chaetomium bostrychodes*-type (thin-walled); H. *Podospora inequalis*-type; I. *Sporormiella*-type; J. *Coniochaeta lignaria*-type. Scale bars = 10µm. Eggs of intestinal parasites: K. *Trichuris* sp.; L. *Ascaris* sp. (high and low focus); M. *Dicrocoelium* sp. Scale bar = 40µm.

In the absence of micromorphological data, it is difficult to better specify the formation processes for the sequence, as it slightly differs from the typical *fumier* deposits showing several burnt layers and ash lenses (Angelucci et al. 2009; Brochier et al. 1992). However, Unit 2 has a very ashy texture and colour, and burnt units are located in other areas of the shelter which were not excavated.

Among the aspects touched on by Brochier et al. (1992), the finding of aquatic indicators in pastoral sequences is one of particular interest. The authors stress the presence of diatoms in *fumiers* and grazed areas, suggesting a relationship between the places used to water the herd and aquatic microfossils. Micromorphology has also provided some examples of diatoms within coprolites, which probably derived from the water drunk (Banerjea et al. 2015; Macphail and Goldberg 2010). With a few exceptions (*Arcella* tests mentioned in van Geel et al. 2003) the subject has been either mostly neglected, or when evidence was found no links have been mentioned between algal remains and the water ingested by animals (Expósito and Burjachs 2016).

In fact, the topic appears to be relevant as there are often no clues as to the off-site locations where the flocks were grazed or water brought from. Future developments seem possible, as aquatic indicators of animal and possibly algal origin were present in modern samples (**fig. 5.9**), as shown in **table 5.5** (on the debated biological identity of *Pseudoschizaea* see Grenfell (1995), Scott (1992) and Milanesi et al. (2006)). Although these components were recorded in limited amounts, they may contribute to widening the knowledge of animal management.

Faecal spherulites have so far mostly been considered only in soil thin section studies, and little attention has been paid to their use as proxies for herbivore presence in other contexts. With the exception of a pioneering article by Canti (1999), only a

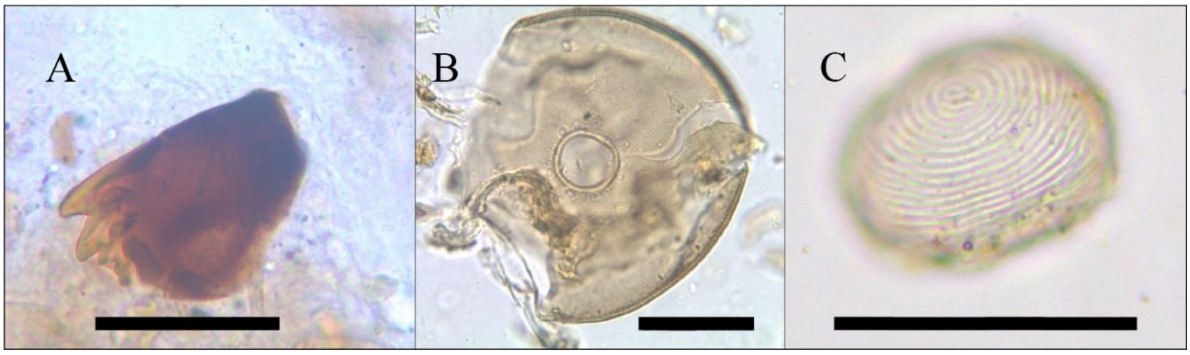

Figure 5.9. A. Chironomidae; B. *Arcella* sp. (Testacea); C. Cyst of *Pseudoschizaea*.
Scale bars = 40µm.

Table 5.5. Elements of certain and probable aquatic origin recovered in the samples.

Sample no.	**Aquatic organisms**		
	Chironomidae	*Arcella* sp.	*Pseudoschizaea*
6	x		
13	x		
14	x		
17		x	
20		x	
27b (inner part)		x	
A. Manie			
(depth in cm)			
4-5	x		
8-9			x
12-13			x
16-17			x

handful of works have tried to quantify in terms of absolute frequency the amount of spherulites in dung layers, counting them along with phytoliths (Portillo and Albert 2011; Portillo et al. 2009, 2010, 2011). Their results are summarised in **Table 5.6**.

Table 5.6. Spherulite counts obtained in previous studies (samples with zero counts have been excluded) and results obtained from the abandoned rock shelter of Arma delle Manie (this study).

Reference	**Number of spherulites per mg of sediment**		
	Min.	Max.	Average
Canti, 1999	unknown	c. 107,500	c. 7960
Portillo and Albert, 2011	13	846	182
Portillo et al., 2009	16	175	52
Portillo et al., 2010	8	1638	125
Portillo et al., 2011	515	1065	790
Arma delle Manie	7	240	56

N.B.: Values were converted into number per mg from the original units used in the papers: µg (Canti, 1999), and g (Portillo and Albert, 2011; Portillo et al., 2009, 2010, 2011). For Canti, 1999 (studying fresh dung) only the samples from herbivore species were considered.

Quantitatively, the data presented here display a remarkable similarity with the values reported by Portillo et al. (2009). The results show a very clear match between dung spores and spherulites, indicating an obvious difference in composition for Units 1 and 2, most likely consisting of herbivore dung. Both proxies are correlated with the values of total phosphorus measured throughout the profile, supporting an organic origin for Units 1 and 2. It is worth noting that spherulites also closely reflect the two declines in dung spores occurring between 0 and -4cm and between -12 and -16cm, as well as the small rise at -17cm (**table 5.4**; **fig. 5.3**). It is more challenging to explain for which reason, unlike coprophilous spores, they follow an increasing trend from -4 to -12cm.

The complexity of factors governing spherulite abundance and preservation has long been highlighted (Canti 1999). First, a possible explanation for variations deals with the animals responsible for dung deposition, as sheep are known to be large spherulite producers, whilst bovine tend to be slightly less productive (Canti 1997, 1999). This could match the statements gathered from informants on the site, according to which sheep were the last animals kept in the shelter, which was previously used for cows. Secondly, it has been pointed out that seasonal variations in spherulite production may occur (Canti 1999), and this may account for fluctuations in the abundances from deposits spanning several decades, where the sampled levels correspond to different and unknown periods of the year. Thirdly, albeit minimally, spherulites might be subject to some degree of translocation through the profile, which seems suggested by very low values of presumably intrusive elements recovered from Unit 3. Bioturbation may also have played a role, as spherulites are likely to be destroyed following digestion by soil-eating organisms (Canti 1999).

The pH of the whole profile (**fig. 5.3**) is ideal for the preservation of spherulites, which are attacked and dissolved only when values are lower than 7.7 (Canti 1999). Therefore, the higher counts recorded in the two upper units must reflect a real difference in herbivore presence, as also indicated by the abundance of dung spores.

6. THE CAVE OF ARENE CANDIDE: THE NEOLITHIC SEQUENCE

6.1 Geographical setting and archaeology

The cave of Arene Candide is located in western Liguria (Italy), in the territory of Finale Ligure, and is regarded as a key site for the prehistory of the central Mediterranean, given the richness of its Palaeolithic and Neolithic deposits. The cave, extending from the west to the east and measuring c. 70m in length and 10-20m in width, lies on Miocene limestone, and at the present day opens on a steep rocky slope facing south toward the coast, at 89m asl (**figs. 6.1, 6.2, 6.3**). It is likely that originally high aeolic sand dunes, now removed for modern quarrying, connected the entrance of the cave directly to the coast, as shown by an early 20th century photograph (Maggi et al. 1997). Following the very first investigations back in the 19th century,

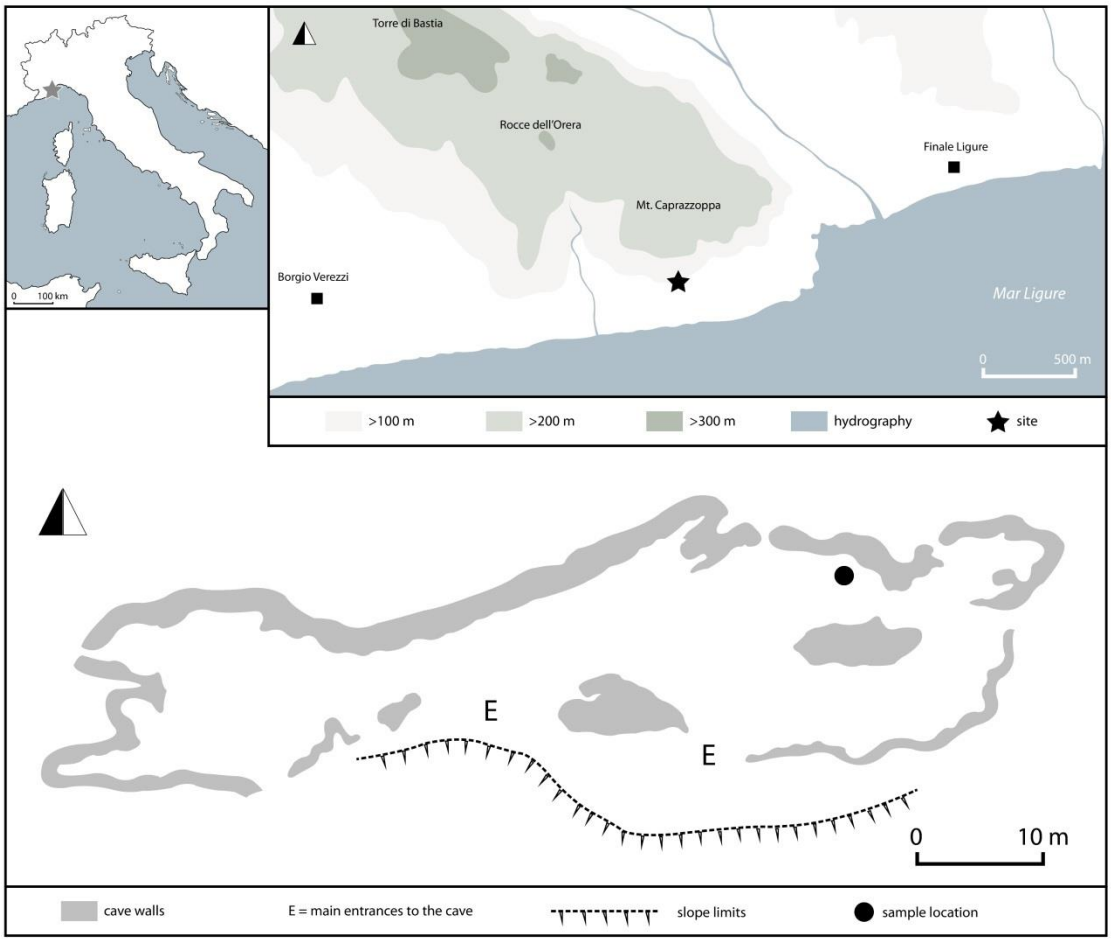

Figure 6.1. Cave of Arene Candide: map showing the location of the site.

the cave was systematically excavated since the 1940s. The site was periodically occupied from the Upper Palaeolithic to the Neolithic (both for domestic and funerary purposes), with a few traces of later occupations (Maggi et al. 1997). The finely stratified Holocene sequence has allowed multiple cross-cultural connections to be traced, enabling the creation of a reliable chrono-cultural scheme for the region (Bernabò Brea 1956; Maggi 1997; Pessina and Tiné 2008). The Neolithic assemblages show the presence of impressed ware (Early Neolithic, 7800-7000 BP), VBQ 1-2 pottery (squared-mouth culture, Middle Neolithic, 7000-6200 BP), and Chassey pottery (Late Neolithic, 6200-5600 BP).

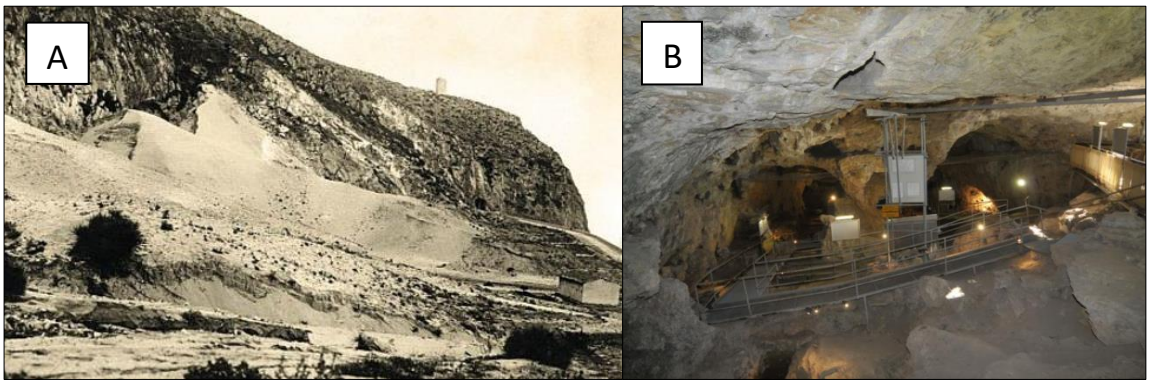

Figure 6.2. Cave of Arene Candide. A. Early 20th century photo showing the sand dune at the entrance of the cave. B. View of the eastern part of the cave (May 2013).

Figure 6.3. Cave of Arene Candide: the profile sampled for the analysis. Note the alternation between burnt and unburnt horizons, as typical of Mediterranean *fumiers*.

6.2 Results of the pollen analysis

The samples are too distant to allow a reliable pollen zonation. However, the lower part of the sequence (-220cm/-150cm) is clearly dominated by pollen of Cichorieae (syn. Lactuceae), whose percentages decrease quite sharply at the depth of 150cm, where a peak in Ericaceae and Gramineae occurs (**fig.**

6.4). A major rise in Gramineae takes place at -80cm, along with a new peak in Cichorieae. The sample at -55cm sees again a rise in Ericaceae and Gramineae, this time coupled with Apiaceae. The upper part of the sequence is dominated by Cichorieae, with *Quercus* reaching the highest value. A wide variety of arboreal taxa occurs between -150 and -180cm, and the highest percentages of *Abies* occur in the lower part of the deposit.

6.3 Interpretation and discussion of the pollen analysis

In our case, the pollen record is very much biased by the following factors: 1) most importantly, differential pollen preservation in calcareous soils. It is well known how fern spores and certain pollen types (e.g. *Polypodium* spp. and Cichorieae spp.) are highly resilient and can be still identified even when badly corroded or folded (Florenzano et al. 2012). On the other hand, a wide range of arboreal and herbaceous taxa are strongly underrepresented, and their percentages are not a direct reflection of low values in past environments; 2) human activities involving plant collection from unknown distances around the site for various purposes, such as human and animal food and fodder; 3) dietary preferences of ovi-caprines and cattle when (if ever) freely grazing outside, presumably not very far from the cave.

It is nonetheless possible to make the most of the data, assessing whether a relationship with the current knowledge of coastal palaeoenvironment and vegetation changes through time is detectable. It should be taken into account, however, that at the moment the chronology of the sampled sequence (study in progress) is poor and only a rough periodization can be established on the basis of potsherds.

As stated above, given the issues of pollen taphonomy in caves, it is difficult to establish to what extent the record includes airborne pollen grains from distant locations. It seems therefore likely that the sporadic presence of *Abies* pollen throughout the whole deposit results from wind transport from higher altitudes. Indeed, areas above 1000m asl are found only 10km inland of the site at Piano Corso. However, it is tempting to suggest a relationship between the slightly higher percentages of *Abies* pollen at the base of the sequence and the results obtained by

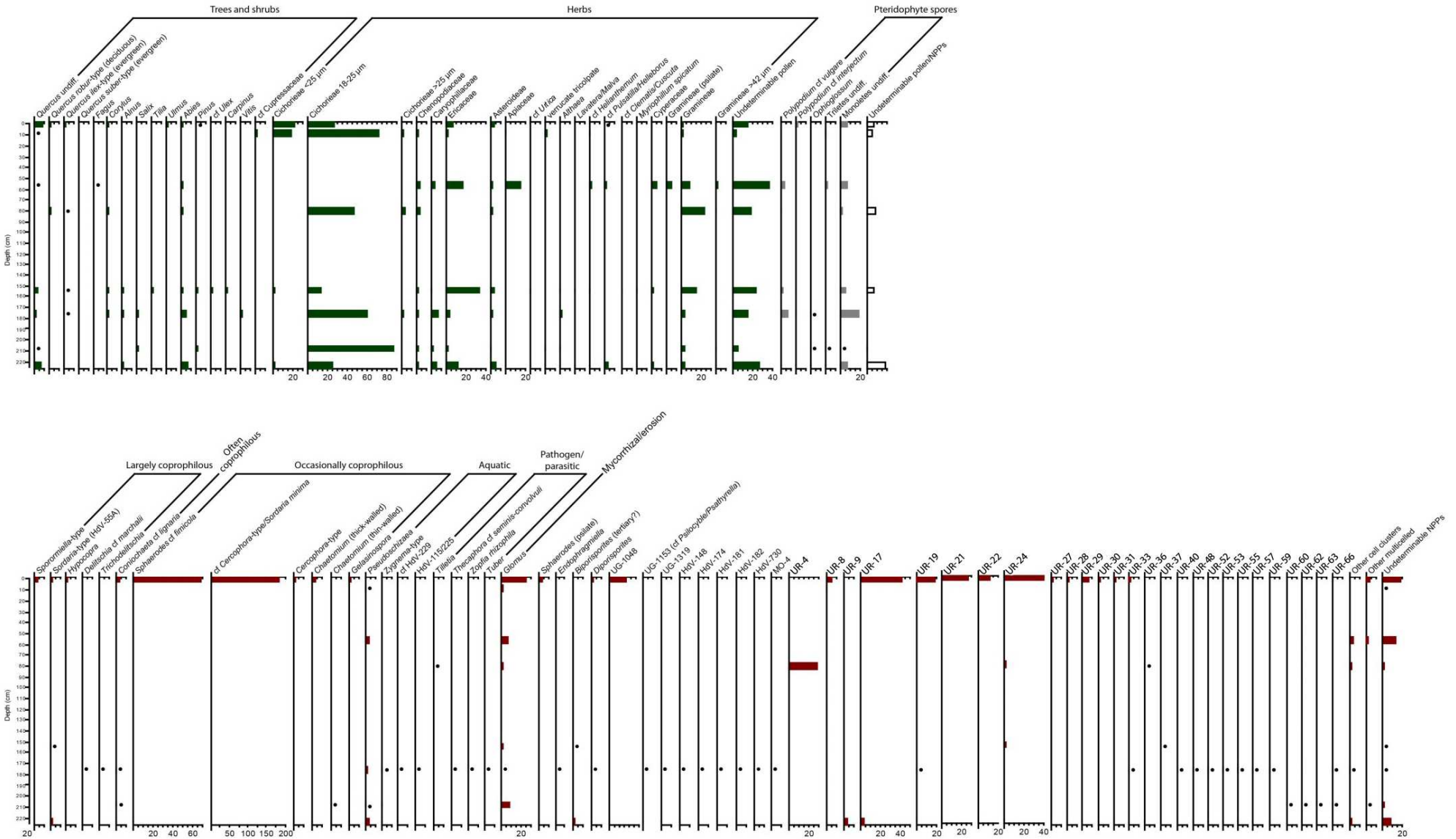

Figure 6.4. Cave of Arene Candide: pollen and NPP diagram. Values expressed as percentages of the total pollen. ● = presence.

Montanari et al. (1998) from a coastal site. These authors have assumed a different ecology for *A. alba* in the Middle Holocene, suggesting that silver fir woods occurred even at lower altitudes. If this view is valid, our data may similarly point to a more intense silver fir population in the coastal lowlands, although the timing of this event still needs to be determined through radiocarbon dates.

What is more evident from the pollen diagram are the high values of Cichorieae (subfamily: Cichorioideae) recorded in almost every level. Pollen grains of Cichorioideae are known to be highly resistant to corrosion, and their morphology allows indentification even in bad conditions (Florenzano et al. 2012). For this reason, Cichorioideae often reach high values in archaeological sites and other poorly preserving deposits. A further explanation for high percentages of Cichorioideae lies in the presence of pasturelands, so that the pollen type is also considered as a reliable grazing marker (Mazier et al. 2009; Kouli et al. 2009). In fact, several authors (Florenzano et al. 2015; Lebreton et al. 2010; Mercuri et al. 2010) argue that an overrepresentation of Cichorioideae is likely to result from the actual incidence of grazing activities rather than from selective deterioration. This view may be partly supported by our record, as it appears that there is no relationship between higher percentages of Cichorieae and increases in indeterminable (corroded and broken) pollen grains. Consistently with the use as a grazing marker, a strong relationship between Cichorioideae and open environments has also been proved by previous studies (Florenzano and Mercuri 2013; Mercuri et al. 2010; Florenzano et al. 2015). Besides, a thorough evaluation of Cichorioideae pollen from modern vegetation communities has shown how high values naturally occur in Mediterranean riparian environments (Florenzano et al. 2015).

In light of this, it seems likely that the dominance of Cichorieae at the base and at the top of the sequence reflects the actual use of the cave and the abundant presence of animal fodder. Cichorieae may thus indictae the presence of pasturelands in the adjacent small coastal plains formed by the streams Aquila and Bottassano, or may have been collected from riparian habitats along these streams and the flow of the Pora and brought to the site as animal feed. An indication of hygrophilous environments, albeit scanty, is indeed present in the record in four levels, where low percentages of *Alnus*, *Salix* and *Myriophyllum* were found.

The second more common taxon in the diagram is represented by pollen of Ericaceae, that become dominant at -60 and -160cm. It is again challenging to provide a satisfactorily explanation, discriminating between vegetation change in the surrounding area and human-collected plants on the site. The use of *Erica* for animal bedding is well known from medieval analogues (Bakels 1988; Webb 1998), and it is highly palatable to sheep and cattle (Jáuregui et al. 2009; Osoro et al. 2012). Hence, fodder may have been collected from a heather-dominated area for a period of time, leading to a predominance upon Cichorieae. Alternatively, the change may reflect the use of a different pastureland to which the herd was taken to graze. However, it is expedient to remind here that Bellini et al. (2009), have shown the rise of the *Erica*-dominated Mediterranean maquis along northwest Italian coasts during the Middle Holocene. This ecosystem would find a suitable environment on the sea-facing rocky slope of the cave, and future refinement of the chronology of our sequence will allow assessing a relationship between high values of Ericacae and Mediterranean maquis. It is worth stressing that there seems to be no relationship between Cichorieae/*Erica* and higher percentages of herbaceous taxa potentially suggesting landscape openings, which instead seem to be higher in the middle part of the sequence. On the other hand, the only evidence for large grains of possible domestic grass has been recorded at -50cm, along with high values of Ericaceae and a peak in Apiaceae. Relatively high proportions of *Quercus* are instead in agreement with the results from the deep cores in the alluvial plain of Genoa, where oak woods are likely to have been predominant (Arobba and Caramiello 2010; 2014; Arobba et al. 2016).

The development of the Mediterranen maquis is also supported by the presence of *Vitis* and the sporadic finding of *Lavatera*, which is a typical salt-tolerant coastal and perennial herb (Okusanya 1980). It may be of some interest to mention that its seeds are edible, and its use as antirheumatic and antineuralgic is known in the traditional medicine of Mediterranean coasts (El Beyrouthy et al. 2008).

In regard to the fern community, two species of *Polypodium* (*vulgare* and *interjectum*) seem to be identifiable on the basis of the spore morphology, both favouring shady and humid habitats, probably characterizing the margins of the cave (Bernardello and Girani 2007). The finding of *Ophioglossum* is consistent with this environment, as it tends to grow on calcareous substrates with shallow soils, among vegetation communities that include typical Mediterranean species such as *Erica* and *Euphorbia* (Giovannini and

Pierini 2006). As the samples come from an archaeological site, it is interesting to stress that these fern taxa also have well-known healing properties for various illnesses (Bernardello and Girani 2007).

6.4 Results of the NPP analysis

The base of the sequence shows relatively high values of *Pseudoschizaea*, and the presence of obligate coprophilous fungi (*Sordaria*-type) was recorded (**fig. 6.4**). A peak in *Glomus* occurs at the depth of 210cm, and the sample localised at -180cm is characterized by a wide variety of NPP types occurring in very low values. The central part of the deposit is poor in microfossils, whereas a notable rise in the unidentified type UR-4 occurs at -80cm. The sample at -60cm shows a new rise in *Pseudoschizaea* and *Glomus*, but the main interest of the sequence lies in the remarkable peaks in *Sphaerodes* cf. *fimicola* and *Cercophora* spp. occurring in the uppermost sample, along with other potentially coprophilous taxa and a further increase in *Glomus* and other types of unknown ecology.

6.5 Interpretation and discussion of the NPP analysis

Being the pollen record of the site highly biased, NPP analysis was attempted in order to gain additional information. More than 60 microfossil types were identified. As expected, among them coprophilous spores were recorded, consistently with the use of this part of the site as a stable as suggested by the banded *fumier*-like stratigraphy. The assemblage is rather rich, and both obligate and occasionally coprophilous taxa are present. Consistently with the bone assemblages (Rowley-Conwy 1997), all these species are known to grow on sheep, goat and cow dung (Richardson 1972; 2001; Doveri 2007). Possible human coprolites (Macphail et al. 1997) cannot have biased the species composition, as omnivore dung is almost totally unsuitable to fimicolous genera. Low values are likely to be a result of the flock being kept in the cave all year round (Rowley-Conwy 1997), consequently leading to continuous trampling and soil disturbance inhibiting or severely limiting fungal growth and sporulation. This view

seems to gain support also by the analysis of modern surface samples (see below, Chapter 6).

There is a remarkable exception though, allowing more elaborate inferences based on the fungal record, as shown by the extremely high percentages reached by two taxa at the top of the sequence. Here, *Cercophora*-type rises up to more than 160% of the pollen sum, along with *Sphaerodes* cf *fimicola* (more than 70%) (**fig. 6.5**). The latter belongs to a genus including a few species showing a reticulate surface pattern (García et al. 2004). One of these, *S*. *fimicola*, is often coprophilous, and known from samples of sheep and rabbit dung (Richardson 2006; Watling and Richardson 2010). *Cercophora* spp. colonise not only animal dung but also similar substrates such as rotten leaves and grasses.

This sudden and remarkable peak in dung spores is rather challenging to interpret, but a possible explanation may lie in the topsoil conditions at the time the spores were deposited and be related to the activities taking place in the area. Mycological data allow for a rather precise quantification of the time period required by these species to produce and release spores. Spore dispersal and fungal growth do not occur earlier than three days, and typically require a period between three and thirty days according to the species (Harper and Webster 1964; Richardson 2002). It should then be assumed that fungi were allowed to grow in a favourable condition for a minimum of a few days, until the reproductive cycle began. This implies that ascocarps were able to reach maturity producing a high number of spores prior to dispersal, or before being squashed by hooves. Such a condition points to the absence of soil disturbance, suggesting that animal and possibly human trampling was strongly reduced or absent for a period of at least three-four days or more. This would be compatible with the – periodical? – absence of the flock from the cave for a short period, for reasons unknown (e.g. exploitation of nearby resources).

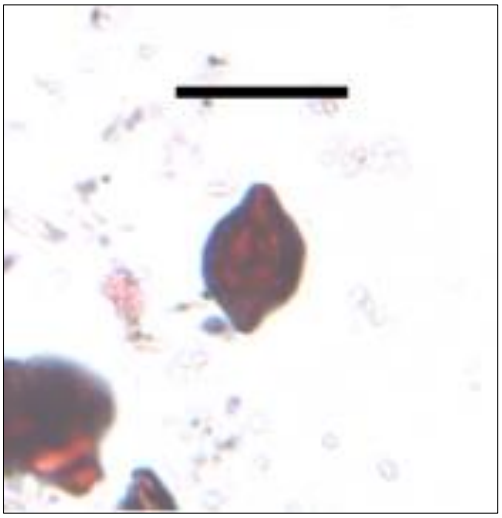

Fig. 6.5. Cave of Arene Candide: spore of *Sphaerodes* cf *fimicola*.

If the suggested interpretation holds true, we may integrate this picture with the commonly accepted formation model for *fumier* deposits in Mediterranean caves (**fig.**

6.6). Following stabling episodes (a), the dung layers are deliberately burnt by the shepherds (b), resulting in the typical banded stratigraphy (c). The cycle is repeated, and a thick cake-layer sequence builds up (d-e-f). In the proposed view, the flock is then carried away (g), leaving the dung undisturbed and causing fungal growth and sporulation on the surface (h), which is subsequently buried again by new stabling episodes (g), only preserving microscopic evidence of the event. It is noteworthy that such event in theory may be extremely short-lived compared to the usual millennial life-span of *fumiérs* (Angelucci et al. 2009), but still detectable in the microfossil record. It is noteworthy that also Expósito and Burjachs (2016) recorded one level characterised by higher values of dung spores from cave deposit in the *fumier* of El Mirador. This may not be a coincidence, and these variations in dung spores may well by a product of ancient farming practices, rather than only a result of burning activities.

As anticipated, although this reconstruction should be better assessed by the ongoing geoarchaeological analysis (G. Boschian, in preparation), there is some supporting evidence from the modern samples collected from stable floors. On the one hand, these data show the viability of coprophilous spores as an evidence of *in situ* stabling deposits, and on the other hand they seem to suggest a relationship between spore abundance and reduced trampling (see below, Chapter 6).

To better illustrate the events leading to the creation of a spore-rich layer, it would be helpful to list here the stages following which a dung spore gets incorporated into a deposit. In spite of its relevance for the interpretation, this point has never been clearly developed in the specific literature. These stages are best represented in the form of sketches (**fig. 6.7**). There are multiple explanations accounting for dung spore dispersal, and the one that best suits the context under examination should be selected as the most likely. In this particular case, to our current knowledge the occurrence and variability of coprophilous spores from a stabling deposit may reflect the following situations:

- continuous/sporadic presence of animals;
- natural fungal succession on the same dung type;
- disappearance of a suitable substrate (dung type) for certain species, probably caused by a change in the composition of the herbivore population, now producing a substrate more suitable to different species;

- the use of a different grazing area where the main species of fimicolus fungi differ from the former grazed area.

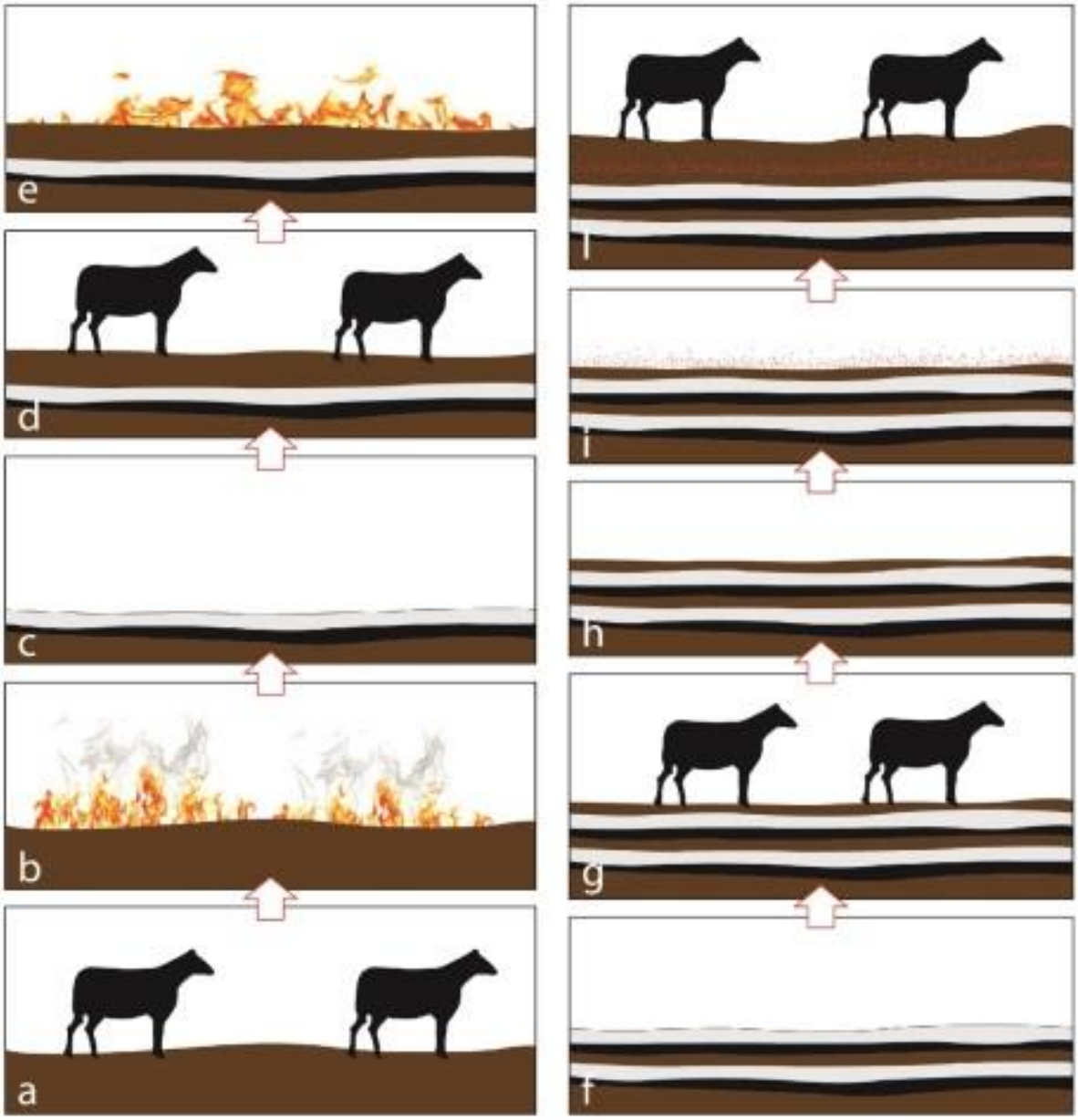

Figure 6.6. Model of spore dispersal on stable sediments integrating the accepted model of formation of *fumier* deposits.

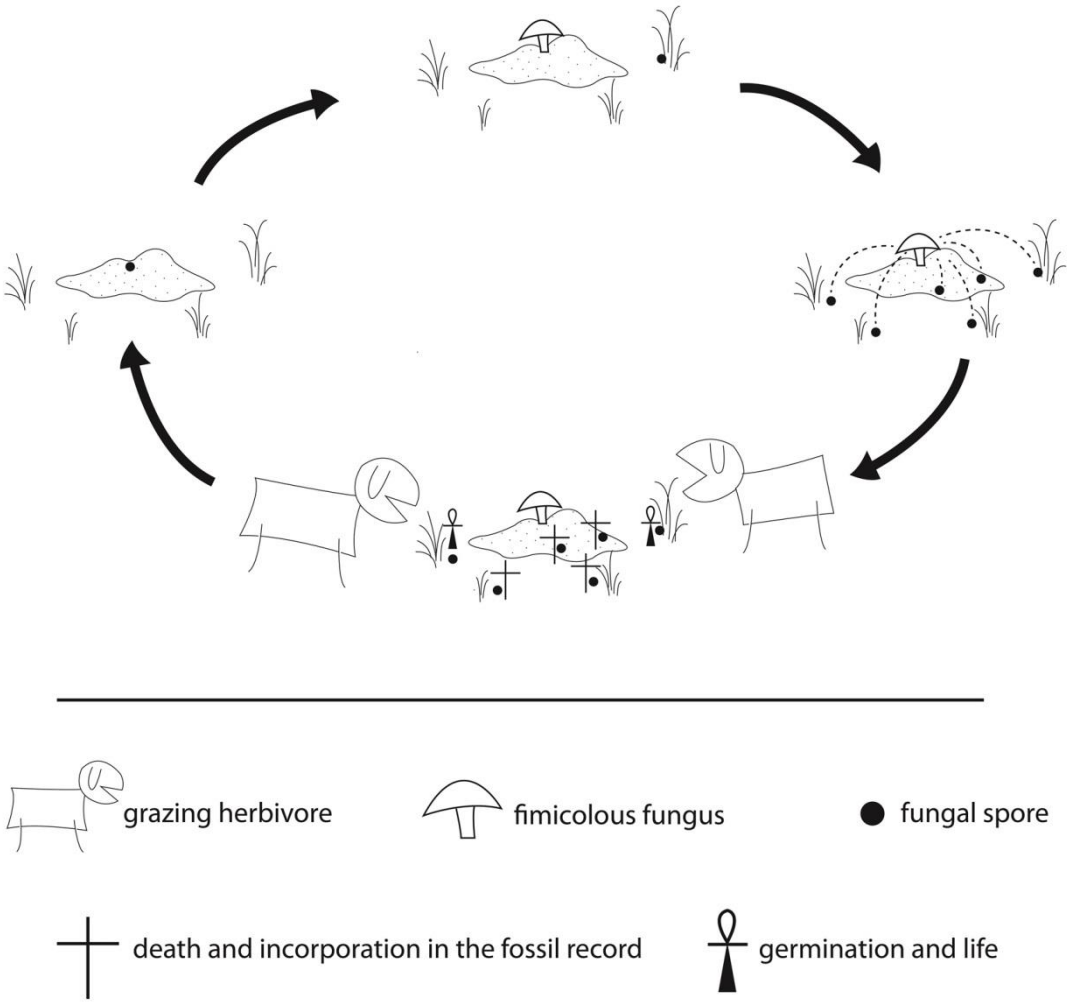

Figure 6.7. The life cycle of a dung fungal spore. The ingestion by a herbivore is a necessary stage to trigger germination.

If the micromorphological analysis will fail to identify evidence for stabling deposits in the lower part of the sequence, alternative explanations are possible, such as the prevalence of a domestic occupation followed by the use as a stable in the level marked by higher concentrations of dung spores. It is well known, however, that faecal spherulites do not always preserve successfully (Canti 1997; 1998; 1999), and a comprehensive interpretation cannot rely on micromorphology alone (the reports presented in Maggi 1997 seem to be very much micromorphology-dependent).

A variety of other microfossils helps to complement the data from the pollen analysis. Unfortunately, many types still lack biological identifications, although their occurrence in pollen-rich natural sequences encourages their use as ecological indicators in the near future when their value will be hopefully unveiled (see e.g. HdV-179, found across

many sites in northern and southern Europe: Carrión et al. 2000). A few types are instead identifiable at least to the genus level, and some of them were never reported before in the palaeoecological literature.

A large uniseptate and constricted spore represents *Zopfia rhizophila*. It is of some interest that the species, as well as being parasitic on other taxa, is associated with edible plants such as *Asparagus* (Ellis and Ellis 1985; Shumilovskikh et al. 2015). These taxa do not occur in the pollen record or may have not been preserved, but are still detectable through their specific and more resilient fungal parasite. Similarly, a few types (UR-21, UR-22) may have been produced by Tuberales (truffle species). Deliberate gathering of truffles as a source of food in prehistory has been hypothesized in other cultural contexts (Horrocks et al. 2002; 2008; Horrocks 2004; Horrocks and Rechtman 2009), and should be taken into account in our case too. *Thecaphora seminis-convolvuli* is commonly associated with *Calystegia* and *Convolvulus* (Ellis and Ellis 1985), whereas a range of generic wood saprobes have also been recorded (*Endophragmiella* spp.).

Aside from fungal spores, it is worth focusing on the finding of microfossils of aquatic origin. *Pseudoschizaea* was recorded at various levels and a few *Zygnema*-type spores also appear in the sequence. The biological identity of *Pseudoschizaea* is still a matter of debate, although ecological associations and a number of studies point to a relationship with shallow and eutrophic basins with still or slowly moving water (Scott 1992; Carrión and Navarro 2002). *Zygnema*-type can instead be confidently ascribed to *Zygnema* spp., a genus of Zygnemataceae inhabiting wet environments such as shallow ponds and bogs.

Three possible scenarios can be advocated to explain the presence of aquatic taxa in a dryland archaeological context. First, their occurrence may be an indirect result of pastoral activities involving the movement of the flock to a water source nearby, be it occasionally or on a regular basis. This would cause the microfossils to be ingested along with water and then dispersed on the stable floor following animal urination. On the other hand, in this case the presence of aquatic pollen would be expected, although this absence can be an artefact of differential pollen preservation (see above). A second and similar explanation assumes that water was brought to the cave for the animals by the cave inhabitants, avoiding moving the herd, and here possibly stored (perhaps also

for human use). After being drunk by sheep and cattle, aquatic microfossils would enter the archaeological record in the same way through organic wastes.

An alternative scenario contemplates a local origin for the enigmatic NPP known by most authors as *Pseudoschizaea*. The origin of this organism is not entirely clear as yet, and a few palynological studies have stressed their occurrence in other cave deposits (Arobba and Caramiello 2009). Moreover, this autochthony hypothesis is in agreement with the microfossil record from a 19-20th century stable floor from a rock shelter (see below, Chapter 6), where *Pseudoschizaea* was identified even in the uppermost levels (unfortunately, a detailed knowledge of water provision on the site is missing, in spite of the oral accounts gathered). It seems therefore plausible that small temporary pools formed in caves (e.g. due to rock dripping) may provide a favourable habitat for algal forms, that then undergo encystment as a surving strategy following desiccation (on the process of cyst formation and its causes see Sandgren 1983; Blackburn and Parker 2005). The scanty values for Zygnemataceae may follow the same explanation. This view would also account for the absence of aquatic pollen. Although this latter condition might indeed be a result of poor preservation, spores of aquatic ferns (e.g. *Thelypteris palustris*), normally more resilient, are missing too, supporting the autochthony of the algal organisms in our sequence. As an analogue, one might cite the case of blue-green algae (Cyanobacteria), some of whom are known to be living on damp soils of Mediterranean caves, such as *Chroococcidiopsis* spp. (Friedman 1961; 1962).

Finally, the absence of eggs of intestinal parasites, elsewhere found in prehistoric archaeological contexts and natural deposits (see also above, III.1.2), appears worth noting and it is somehow unexpected. The data deserves a comment, and a possible explanation may lie in the formation of the layer-cake stratigraphy, involving burning at high temperatures (Shahack-Gross et al. 2003). Brochier et al. (1992), have collected ethnographical information about the practice of burning dung for hygienical purposes before the advent of modern veterinary care, thus preventing the spread of animal diseases. It is not known to what extent prehistoric shepherds may have been aware of this advantage, but they may have accidentally obtained the same result by burning manure for other purposes, such as simply to get rid of a large mass of refuse. It may have been handier to burn the dung in situ than removing it manually from the cave. It has been shown that fire is a very effective means to this end, allowing the dung deposit to be reduced by 97% of its volume (Shahack-Gross et al. 2005). However, this also

implies that the dung cannot be used for other purposes, such as field manuring and wattle and daub construction.

A further speculation can be made in light of no parasite eggs. The life cycle of *Trichuris* spp., the most common genus recovered in archaeological samples, involves the ingestion of contaminated plants by the potential hosts, prior to egg hatching in the intestine (Dark 2004; Morandi, in press). Therefore, when the flock is freely grazing outside, the chance of contamination due to the faeces deposited on the soil surface is very high. On the contrary, if new feed is brought to the animals a little at a time (e.g. in troughs or piled in bales), the risk of contamination may be reduced.

A relationship between degradation processes and the absence of eggs should also be considered. It is known that parasite eggs are made of three or four layers depending on the species, namely a lipid layer, a chitinous layer, a vitelline and a uterine layer (Appleton and White 1989; Mahmoud 2002). However, the specific composition of the chitin layer slightly differs from that of fungal spores (Ruiz-Herrera 1991), and it is has been noted that a low proportion of proteins in the polar plugs triggers enzymic attack and dissolvence (Perry and Clarke 1982). There is thus still a possibility that chitinous eggs may have undergone degradation due to the alkaline nature of the soil (Gray and Baxby 1968; Nawani and Kapadnis 2003).

7. THE BRONZE AGE HILLFORT OF CASTELLARO DI USCIO

7.1 Introduction

7.1.1 Historical, geographical and environmental setting

More than forty years ago, the first excavation conducted on Mt. Borgo led to the finding of a hilltop settlement spanning from the Copper Age to the Iron Age. The research resulted in a comprehensive monograph (Maggi and Campana 1990) enabling a better understanding of the diffusion and function of pre-Roman hilltop settlements (*Castellari*), numerous in Liguria and Piedmont. Sites of this type become more frequent during the Middle/Final Bronze Age (1300-900 BC), seem to be abandoned in the early Iron Age and tend to be reoccupied in the later Iron Age. In

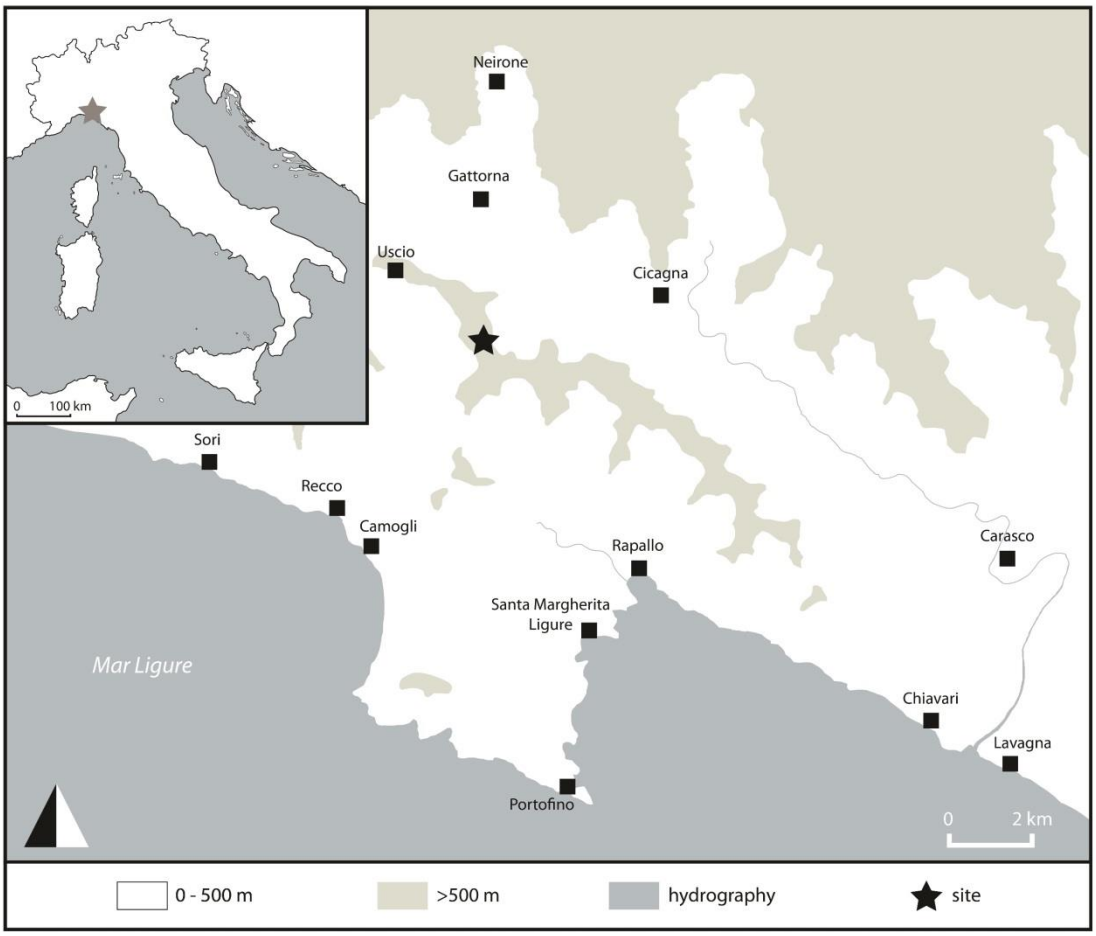

Figure 7.1. Castellaro di Uscio: map showing the location of the site.

spite of their location perched on top of hillocks, these settlements do not normally show any signs of fortification. It is possible that the diffusion of *Castellari* relates to the rise of a new territorial organisation and economy during the latest prehistory (Tizzoni 1975).

Figure 7.2. Castellaro di Uscio: the yellow arrow indicates the position of the site in relation to the coast and the geomorphology of the surrounding territory.

The site of Uscio lies on a limestone formation in eastern Liguria, at the junction between the ridge heading inland from the promontory of Portofino and the crests running alongside the coast toward Chiavari. Here is Mt. Borgo (732m asl), overlooking the valley of the Lavagna, and visually controlling the Gulf of Tigullio and the Gulf of Paradise (**figs. 7.1, 7.2, 7.3**). The natural soil on the site consists of an argillic brown earth formed, from top to bottom, by an A, A2 (Eb), and Btg horizons (Macphail 1990).

Along with the excavation, an extensive vegetation survey of the area was carried out in the 1980s to better evaluate patterns of landscape modification throughout the centuries. At that time the hilltop appeared to be kept clear by local farmers, and except for *Corylus avellana* and *Lonicera caprifolium* the assemblage was dominated by herbaceous taxa and ferns (*Brachypodium pinnatum*, *Bromus erectus*, *Arrhenatherum elatius*, *Scabiosa columbaria*, *Helianthemum mummularium*, *Pteridium aquilinum*). The northern, southern and northwestern slopes were forested, the most common trees being *Corylus avellana* and *Ostrya carpinifolia*, and other diffused taxa consisting of *Acer* spp., *Castanea sativa*, *Fraxinus ornus*, *Laburnum*

Figure 7.3. View of the Gulf of Tigullio from the site, facing south-east.

anagyroides, *Quercus* spp. and *Sorbus aria*. *Alnus glutinosa* was recorded only on the southern slope near the course of small creeks. Nowadays, due to the end of local animal farming, also the excavated area on the hilltop is densely covered in woodland.

7.1.2 Previous archaeobotanical and geoarchaeological investigations

Several aspects of the site were examined, including palaeoecology and palaeopedology. Charcoal macro-remains have allowed identification of a number of tree/shrub taxa (Nisbet 1990). Although up to eleven species in total were recorded, during the Final Bronze Age the assemblage was dominated by *Quercus pubescens*, followed by *Laburnum anagyroides* and *Acer* sp. (**table 7.1**). Since only a few species reach high percentages, the collection of wood was probably highly selective for specific purposes (Nisbet 1990). However, the occurrence of a patchy landscape with relatively open and dry areas was suggested on the ground of light-demanding taxa such as *Juniperus*, *Pinus* and *Prunus*. The macrofossil record shows instead the importance of cereals (*Triticum* and *Hordeum* spp.), recovered on the upper terrace and in the lower area, and the relevance of legumes and acorn gathering, as shown by the amount found in the eastern part of the excavation. It was suggested that the concentration of wheat caryopses on the upper terrace may point to the existence of a structure for storing cereals, while acorns may have been collected either for human consumption or pig farming (although soil acidity has prevented bone preservation) (Nisbet 1990).

Conif.	***Pin.***	***Junip.***	***Alnus* sp**	***Cor. av.***	***Fag. syl.***	***Q. pub.***	***Frax.***	***Fr. or.***
2	1	5	/	/	23	57	3	/
***Acer* sp**	***Labur.***	***Ost. c.***	***Ost.-Car.***	***Corn.***	***Prun.***	***Pr.-Sor.***	***Cl. vit.***	***Ind.***
41	56	12	10	/	1	1	1	3

Table 7.1. Castellaro di Uscio, macro-charcoal remains. Total number of findings from the final Bronze Age horizon. Conif. = Coniferae; Pin. = *Pinus* sp.; *Junip*. = *Juniperus* sp.; *Cor. av*. = *Corylus avellana*; *Fag*. *syl*. = *Fagus sylvatica*; *Q. pub*.= *Quercus* cf *pubescens*; *Frax*. = *Fraxinus* sp.; *Fr. or*. = *Fraxinus ornus*; *Labur.* = *Laburnum* cf *anagyroides*; *Ost. c.* = *Ostrya carpinifolia*; *Ost.-Car*. = *Ostrya* vel *Carpinus*; *Corn*. = *Cornus* sp.; *Prun.* = *Prunus* sp.; *Pr.-Sor*. = *Prunus* vel *Sorbus*; *Cl. vit*. = *Clematis vitalba*; Ind. = Indeterminate. Data re-elaboration from Nisbet 1990. Charred wood of *Alnus* sp., *Corylus avellana* and *Cornus* sp. was found only in the Copper Age/early Bronze Age and in the Iron Age.

Soil thin sections were made to elucidate formation processes and detect which activities had been carried out on the site (Macphail 1990). In the lower area, the sterile subsoil beneath the Bronze Age occupation (layer 6F) is likely to be the product of colluviation following the erosion of a Bt and A2 horizon, as suggested by nodules, papulae and organic matter. On the upper terrace, a similar subsoil was found (layer 6K), although this latter appears to be in situ and was interpreted as a deforested soil. A pattern of voids resulting from bioturbation in the upper part of layer 6K was regarded as a possible evidence for Copper Age cultivation following deforestation. The dark overlying Final Bronze Age deposits in the lower area and on the upper terrace (layer 3) were taken as indicators of on-site tillage, although this explanation was thought to be appropriate especially for the upper terrace, given the evidence of a dense domestic occupation in the lower part (potsherds and high values of magnetic susceptibility: Macphail 1990).

7.1.3 Aims of the new investigation

In view of the high amount of cereal caryopses recovered on the upper terrace (Nisbet 1990) and of the possible evidence for on-site tillage suggested by the micromorphological report (Macphail et al. 1985; Macphail 1990), the deposit was sampled in an attempt to establish whether local cultivation had taken place. The study aimed to carry out a palinological analysis of the natural and cultural layers, as ancient fields have been successfully identified by means of pollen analysis (Kristiansen 1990; Bakels 2000). The slides were scanned for the presence of non-pollen microfossils in order to identify possible evidence for manuring (e.g. dung spores) and irrigation (freshwater algae).

The study was supplemented by geochemistry (pXRF) to assess the level of P in the potential cultivation layer (Oonk et al. 2009; Elliott et al. 2014). The hand-held analiser detected the amount of total phosphorus, which includes both, organic P (relatively immobile and resistant to dissolution) as well as inorganic P (more Easily taken up by plants). All these parameters have been previously used for P analysis in geoarchaeology, and both total P and organic P have been shown to be good indicators of agricultural use of soils (Leonardi et AL., Holliday and Gartner). Although the accuracy of pXRF has been questioned (Shackley 2010; Grave et al.

2012), there are studies making use of it to identify the dung components in archaeological sites (e.g. Elliot et al.). Moreover, it was originally planned to use the hand-held device for in situ analysis of the archaeological deposit. This was not possible due to flight restrictions, so that column samples were taken with metal boxes, and then analysed with the pXRF.

The investigation also aimed to use the pollen spectrum to improve the knowledge of the environment associated with the occupation of the site, supplementing and compensating the picture resulting from macro-charcoal remains (Nisbet 1990). Moreover, the late Holocene pollen record of the region largely derives from lake sediments at high elevations, whereas terrestrial records are rare (Branch 2013; Branch et al. 2014).

7.2 Results

7.2.1 Pollen and spore analysis

In both profiles, arboreal pollen prevails only in the recent topsoil (layer 1), whereas the lower layers show a wide range of herbaceous taxa (in particular, *Scabiosa* in the upper terrace), the only exceptions being *Carpinus* (upper terrace) and *Alnus* (lower area). Layer 3 in the lower area is also dominated by trilete spores of *Pteridium aquilinum.*

Coprophilous spores, eggs of intestinal parasites and aquatic indicators were recorded only in layer 1, both in the upper terrace and in the lower area (**table 7.2**).

Layer	Dung spores /g	Parasite eggs	Aquatics	Coproph. taxa	Parasitic taxa	Aquatic taxa
1U	1611	161	161	*Arnium* *Chaetomium* *Gelasinospora* *Sordaria* *Sporormiella*	*Dicrocoelium*	*Pseudoschizaea*
1L	2900	0	966	*Coniochaeta* *Sporormiella*	/	*Arcella*

Table 7.2. Castellaro di Uscio: abundance of coprophilous spores (no./g).

7.2.2 Analysis of total phosphorus

The amount of total phosphorus (comprised between 244 and 380ppm) does not vary significantly in different layers, the highest values not always being recorded in layer 3 (Bronze Age occupation) (**table 7.3**).

Upper Terrace	Ptot	Error (1σ)	Lower area	Ptot	Error (1σ)
Layer 1U	299.78	52.37	**Layer 1L**	295.43	48.2
Layer 2U	253.68	52.13	**Layer 2L**	295.43	58.99
Layer 3U	327.52	53.34	**Layer 3L**	380.6	54.98
Layer 4U	337.81	56.6	**Layer 4L**	244.68	57.29

Table 7.3. Castellaro di Uscio: amount of total P from the sampled layers. Values expressed as ppm (parts per million).

7.3 Interpretation and discussion

Although most pollen studies are conducted on lake sediments, a number of works show that terrestrial archives have their own potential for vegetation reconstruction. There is now a well-established tradition focusing on samples from cultural layers in dryland archaeological sites (Dimbleby 1985; Navarro Camacho et al. 2000; Branch et al. 2005; Mercuri et al. 2010; 2014). The results obtained from these contexts cannot be straightforwardly employed as a means of palaeoenvironmental reconstruction, especially in cases of poor pollen preservation and selective degradation (see above, Chapter 4), and when bioturbation is significant (e.g. in brown soils) (Davidson et al. 1999). According to Dimbleby (1985) pollen grains appear to be mostly locked up in humic aggregates, so that only a small fraction is left free to move downwards through the profile; moreover, unlike the case of lake sediments, animal-pollinated taxa tend to be better represented than wind-pollinated plants (Navarro et al. 2001). Davidson et al. (1999) found no evidence for such humic complexes, and using soil

micromorphology were able to demonstrate that pollen movements depends on the type of soil and the invertebrate population ingesting and transporting grains. However, downwashing of pollen was found to be limited (Davidson et al. 1999).

Bearing these warnings in mind and taking into account that a minority of pollen grains may be intrusive, it is possible to fruitfully employ soil pollen analysis to dryland cultural layers.

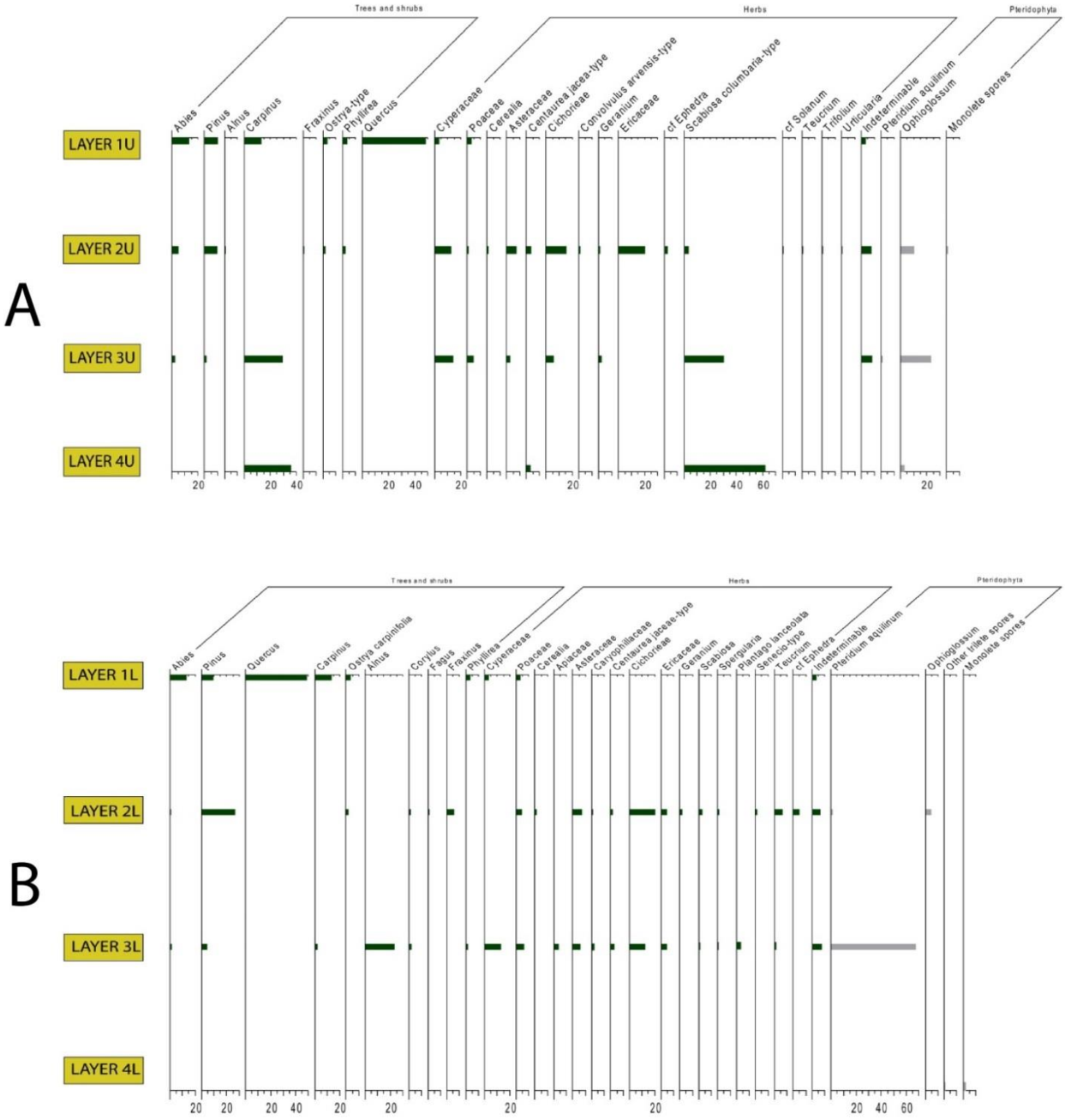

Figure 7.4. Castellaro di Uscio. A: Pollen diagram from the upper terrace. B: Pollen diagram from the lower area. Values expressed as percentages of the total pollen.

Although the possibility of a mosaic landscape with open areas was mentioned in the report on macro-remains, the area of the site was considered to be relatively forested throughout all occupation phases (Nisbet 1990). The new pollen spectrum appears to bear relevant implications for the reconstruction of the palaeoenvironment of the settlement, suggesting an anthropisation stronger than previously thought (**fig. 7.4A-B**).

The pollen content of layer 4U seems to broadly agree with the micropedological work, that indicated a deforested soil resulting from pre-Bronze Age clearance. A mixed open/wooded condition is suggested by the high values of *Scabiosa* and *Carpinus*. It is difficult to interpret layer 4L, in which no pollen grains were found. The horizon has probably formed through colluviation, and may include eroded materials from different horizons (Macphail 1990).

In light of the previous works, the composition of the dark occupation layers (3U, 3L) is particularly significant for the following reasons: 1) the noticeable dominance of herbaceous taxa, except for *Alnus* and *Carpinus*; 2) the total absence of domestic Gramineae, only found in very low percentages in the overlying horizon (2L and 2U); 3) the total absence or very low values of the most common arboreal taxa recorded in the charcoal record; 4) the high percentages of *Alnus* and *Pteridium* in layer 4L.

The value reached by herbs (ca. 60%) is close to what was found elsewhere in cleared sites (Mercuri et al. 2013), and speaks for a largely open environment. The abundance of *Scabiosa* (**fig. 7.5**) is noteworthy, especially when considering that its characteristic pollen grains have not been frequently recorded on other sites (Bottema and Woldring 1994; Woldring and Bottema 2003). It is likely that it results from the local presence of the herb on the upper terrace, as insect-pollinated species do not disperse their grains over large

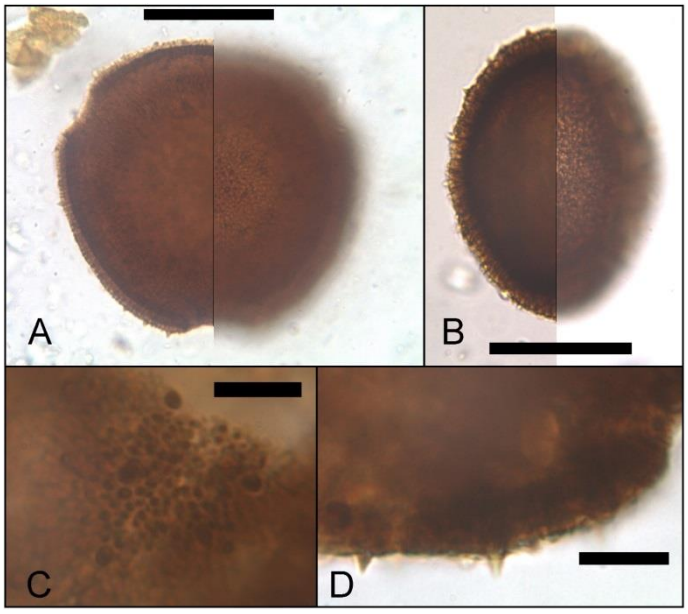

Figure 7.5. Pollen grain of *Scabiosa* sp. A: polar view (scale bar = 20μm). B: equatorial view (scale bar = 20μm). C-D: details of the surface sculpturing (scale bars = 10μm).

distances (Navarro et al. 2001). The species is perennial and favours open meadows, pastures, and slopes on dry calcareous soils (Grime et al. 1988). Its presence (*Scabiosa columbaria*) was also noted on the site during the vegetation survey before the excavation, when the area was kept clear by local farmers (Colella et al. 1990). Conversely, the amount of *Scabiosa* pollen found in the modern surface samples (layers 1U-1L) is significantly lower, showing the imcompatibily of the species with a close canopy.

The data also help to clarify the function of the stone terraces built on the site since the final Bronze Age. Grass pollen occurs, but no domestic species were recorded from this horizon (layer 3U). The scarcity of cereal grains, even from contexts bearing unequivocal signs of on-site cultivation (e.g. ard marks) has been stressed before (Bakels 2000), and seems explicable in light of the position of the grains which are held between the glumes, so that they are only released during threshing (Behre 1981; Bakels 2000). However, at least a limited amount of grains should be recovered (Edwards et al. 2005). Furthermore, in agricultural environments, above-average values of weeds and ruderals such as *Rumex*, Chenopodiaceae, Caryophyllaceae and *Plantago* should be expected (Behre 1981; Dimbleby 1985; Edwards et al. 2005). In agreement with the absence of chaff and glume remains in the macrofossil record, it can thus be inferred that cereals where cropped and processed at some distance from the settlement (e.g. in the valleys), and then brought to the site for consumption and storing. This would account for the absence of cereal pollen, as storing of unprocessed spikes with pollen trapped in the husks would have probably resulted in a large amount of grains incorporated in the deposit (Mercuri et al. 2006). Moreover, experiments show that at least a hectare of terrain should be seeded to obtain ca. 1000/2500 kg of caryopses (Carra et al. 2012). Narrow strips of ground do not seem ideal for cereal cultivation, as a relatively large cropped area is necessary in order to feed a settlement, albeit small. Once local cultivation is ruled out, the existence on the upper terrace of structures for storing seeds suggested by Nisbet (1990) gains plausibility. The terraces may then have been built in order to stop soil erosion and facilitate the organisation of the domestic space, creating flat surfaces for structures and daily activities.

The pollen diagram also shows the unexpected rarity of the arboreal taxa that dominate the charcoal record, these being trees such as *Quercus, Laburnum, Acer and Fagus* (**table 7.1**). The probable existence of a largely cleared environment has been

stressed in relation to the high values of herbaceous taxa from the ancient cultural layers, contrasting with the larger amount of arboreal pollen recovered from the modern surface samples. With the exception of *Carpinus* and *Alnus*, the absence or high rarity of tree pollen in the Final Bronze Age raises questions over the extent of landscape openness, suggesting that it was not limited to the settled area but extended at least to the slopes of the hill. It is indeed singular that not a single pollen grain of *Quercus*, *Laburnum* and *Acer* were deposited (nor translocated from the upper horizons), although they provided almost the whole of the wood used on the site. It seems plausible that wood collection occurred presumably far from the settlement and was targeted at specific taxa non present *in situ*, confirming the high selectiveness of the charcoal record (Nisbet 1990). Low soil pH and the excellent preservation of the other grains seem to rule out any selective destruction of oak pollen.

A further point should be made in relation to the abundance of *Alnus* pollen and spores of *Pteridium aquilinum* in the lower area. *Alnus glutinosa* grows nowdays only sporadically on Mt. Borgo, where it is limited to the wet areas along rills on the southern slope (Colella et al. 1990). *Alnus* notoriously requires humid habitats, and the condition of the site in the past does not seem to have met this requirements. It is difficult to find a convincing explanation; clearance practices may have spared *Alnus* trees thriving along streams, leading to high values in the pollen diagram due to wind pollen dispersal.

Modern dense plots of grey alder on the hills of the Aveto and Trebbia valleys, far from the usual riparian environments, are thought to have originated through a traditional arboricultural practice diffused in eastern Liguria between the 19th and 20th century (*alnocoltura*). This land use system consisted of a cycle (lasting 5-10 years) involving coppicing of *Alnus incana*, collection of new branches and leaves as fuel and manure, turf stripping and burning, crops sowing and cattle grazing (Moreno et al. 1998; Cevasco 2009). Grey alder was selected in view of its fast growth on mineral soils and property to fix atmospheric nitrogen, fertilising the soil. Sampling terrestrial profiles from former *alnocultura* sites, Molinari and Montanari (2016) have identified the palynological signal for this practice, characterised by low percentages of *Alnus* pollen, coupled with anthropogenic indicators, a rise in Ericaceae and high values of charred particles. Once the system is abandoned, the

percentages of *Alnus* pollen rise remarkably (from c. 20% to 50%), as the growth of inflorescences is prevented for four years after coppicing.

It is too early to hypothesise the existence of a specific land use system leading to high percentages of *Alnus* (more than 20%) in layer 3L. However, it is tempting to see a connection between historical land use systems and prehistoric wood management. In fact, large-scale clearance for the creation of pastureland, still characterising the landscape of Uscio only thirty years ago, was initiated in the northern Apennines between Copper Age and Bronze Age (Moreno et al. 1992).

The dominance of *Pteridium aquilinum* in layer 4L is notable if compared with layer 4U. Bracken spores are highly invasive and can grow up to a eight of 2 m, so that higher values would not be expected in the denser phase of occupation of the site, when the lower area was occupied for domestic activities, as shown by hearths, querns, pottery and possible huts (Maggi and Melli 1990). Deliberate collection of bracken leaves may be suggested, given their utility for thatching hut roofs (Dimbleby 1985). Arguably, the collapse of a thatched roof would lead to a very abundant incorporation of spores in the ground, as they are attached in high numbers to the inferior surface of the foliage.

In an effort to detect evidence for local cultivation on the terraces, the amount of total phosphorus (Ptot) in the sampled sections was calculated. P is a good marker for human activity, as it is relatively immobile in the soil and it is not washed away by leaching. Besides, most forms of soil P are insoluble (Chapin III et al. 2011). Ptot is considered to be a better parameter in archaeology than available P, as this latter only represents the P available for plants and is more appropriate for agrarian studies (Hollyday and Gartner 2007). If the soil was deliberately enriched through the addition of organic fertilisers, above-average values of Ptot should be recorded. Soils normally have a natural amount of Ptot around 400 ppm, although the range of variation is quite broad and also depends on the local geology. In her classical study, Eidt (1977) has considered values between 300 and 2000 or more ppm as indicative of intense occupation, dump disposal and farming activities, and according to Kim et al. (2001) organic farm fields have Ptot value of 2973 ppm. If layer 3U was subjected to intensive manuring, much higher contents of Ptot would be expected. In the case of terra pretas, the amount Ptot is found to be forty times higher than in the surrounding natural Ferrisols (Glaser and Birk 2012). Elliott et al. (2014), have provided a number of pXRF measurements for ovi-caprine and cattle dung, which are

shown to include around 10,000 ppm of Ptot. The value recorded at Uscio appears to be fairly low and very close to the amount of Ptot recorded from the natural subsoil and the modern surface (**table 7.3**), suggesting that no further organic matter was added to the soil. The results from the lower area (layer 3L) do not differ significantly from the upper terrace, although a higher occupation density was proved by previous works in light of enhanced magnetic susceptibility (Macphail 1990).

The total absence of coprophilous spores in layers 2, 3 and 4 from both profiles points to absence of herbivores (and dung) on the site in antiquity. This is a further element to rule out manuring practices on the terraces. On the other hand, the frequency of dung spores in layer 1 in both sample locations (**table 7.2**), along with eggs of intestinal parasites and aquatic elements probably derived from the water drunk by the animals, is consistent with the recent presence of shepherds with their herds, still observed on the site in the 1980s (Maggi, personal communication 2015).

8. CONCLUSIONS

8.1 Natural sequences (Chapters 3 and 4)

The first aim of this work was to test the assumption of human influence and grazing pressure in the environment around the upland bog of Prato Spilla 'A' and the alluvial deposit located on the coast of Genoa.

As regards the first site, the data do not allow to reach a univocal view, although, as discussed above, there is scant evidence to support prehistoric anthropogenic impact in the area. An involvement of prehistoric shepherds in the uplands cannot be totally ruled out, but it is likely that the continuous presence of coprophilous fungal spores in the middle Holocene sediments originates from wild mountain herbivores, most likely ungulates, and perhaps also lagomorphs. The main difficulties for assuming pastoralism lie in the distance from known archaeological sites (c. 30km), and the unlikelihood of long range transhumance in prehistory, that has often been questioned in the literature (Marzatico 2007). Nevertheless, small family-sized groups may have produced a low signal compatible with the one detected, and contemporary human presence on isolated uplands is witnessed by the case of Pratomollo.

A much stronger evidence for anthropogenic disturbance and farming activities on the site (also supported by archaeological and palaeobotanical data) is available for the sequence from Genoa Piazza Vittoria. Abundant dung spores largely support animal farming around the site, especially in view of its coastal location, that enables to rule out mountain herbivores. Occasionally, a correspondence between water pools and herbivore presence can be observed. In addition, eggs of intestinal parasites specific of wild boar/pig or human hosts have been recovered. In case of Suidae this is in agreement with the zooarchaeological analysis, while if the eggs belong to humans this would represent the first case of trichuriasis known for the Italian Neolithic.

A range of microfossils identified for the first time through a survey of the extant mycological literature point to brackish conditions on the site, as it was also suggested by previous pollen analysis (Arobba and Caramiello 2010). Moreover, episodes of repeated flooding leading to the creation of temporary pools of still water

have been detected through the identification of algal taxa (Zygnemataceae). Algal cysts also point to periodic desiccation of the site.

8.2 Samples from modern animal enclosures and dung pats (Chapter 5)

Research into variations in dung spore concentrations from modern animal enclosures can be successfully linked to animal management practices on herding sites. This information can then be employed to better interpret both open air archaeological animal enclosures and cave stabling deposits.

The results demonstrate the validity of coprophilous spore analysis from terrestrial samples for identifying ancient animal enclosures, and show that higher concentrations seem to be associated with periodically undisturbed sediments and locally growing fungi. As stressed for faecal spherulites by Canti (1999), there are no univocal relationships between the abundance of coprophilous spores and the presence of animal faeces, so that zero counts do not necessarily imply absence of dung. Arguably, a wider dataset may enable a future use of spore concentration as a parameter to infer the frequency of stabling episodes, so that very high concentrations (>100,000 dung spores per cm^3) are likely to indicate discontinuous animal presence, allowing fungal sporulation to take place. In addition, the concentration of parasite eggs and faecal spherulites may provide a useful key to distinguishing low values of coprophilous spores resulting from scarce presence of animals, from low values due to high animal density and related fungi-destroying soil disturbance, as in this latter case the eggs would still be present.

The pit profile from the rock shelter of Arma delle Manie has shown the potential of dung spores as proxies for the identification of stabling cave deposits, a recurrent type of site in the later prehistory of the Mediterranean region (Angelucci et al., 2009). It has been demonstrated that coprophilous spores are able to reflect very closely the trend followed by faecal spherulites (Units 1-2), and can therefore be used in a similar way to identify localised stabling deposits where spherulites are not preserved. Moreover, the total absence of dung spores and the extremely low amount of spherulites from Unit 3 suggest that they are left relatively unaffected by percolation of liquids such as urine or water through the profile. A different origin for Unit 3 is also indicated by higher concentrations of coccolith plates.

8.3 Cave of Arene Candide (Chapter 6)

The study of the deposits in the cave of Arene Candide has shown the potential of NPP analysis from dryland archaeological stabling deposits to address important research questions.

Assuming a constant presence of the herd on the site based on the previous studies (Rowley-Conwy 1997), patterns of abundance and absence of dung spores throughout the profile are likely to originate from changes in animal management. The explanation which was advanced here makes use of the observations and analyses made on contemporary stabling contexts, and deals with a short absence of the animals from the site, yet prolonged enough to allow fungal sporulation. If this view holds true, the microfossil record would be able to shed some light on subtle and short-lived events, although an accurate chronology for the deposit and knowledge of accumulation rates would be needed (Angelucci et al. 2009). Possible indicators of fresh water were identified along with fungal spores. They might point to the environments grazed by the flock, although an origin from temporary pools formed in the cave through water dripping is also possible. Zero counts of parasite eggs were somewhat unexpected, and it was suggested that this may be accounted for by degradation in alkaline soils or specific feeding practices.

In spite of the limitations exposed above, pollen analysis of the deposit has also provided useful data. The assemblage is apparently dominated by resilient pollen taxa, although their validity as pasture indicators also suits a pastoral context. Clear shifts from Cichoriaeae to Ericaceae may be significant events and represent changes in the grazed environments, in the feed brought to the cave or even the spread of coastal Mediterranean maquis along the north-western Italian coasts in the Middle Holocene (Bellini et al. 2009).

Given issues in differential preservation related to calcareous soils, future approaches may take into account speleothem palynology to complement the record from cave layers (McGarry and Caseldine 2004). Palynology of coprolites is already being applied to the site and is proving successful (Arobba, in preparation). Further attempts, with specific reference to animal dietary habits and grazed environments, may be made by sampling residues of dental calculus (Armitage 1975; Dimbleby 1985; Middleton 1990).

At the Cave of Arene Candide, the use of bulk sediment samples to assess the $^{15}N/^{14}N$ ratio has proved promising, and values higher than 9‰ ($\delta^{15}N$) have been detected. This is consistent with the interpretation of the sequence as a *fumier* deposit resulting from the continuous accumulation of animal dung.

8.4 Castellaro di Uscio (Chapter 7)

An attempt has been made in order to elucidate the occurrence of on-site manuring on agricultural terraces by means of NPP and phosphorus analysis.

The hilltop site of Uscio was sampled in order to assess whether Bronze Age on-site cultivation had occurred and gather further data on the palaeoenvironment (Macphail 1990). The analysis of the crucial dark soil horizons showed the absence of dung spores possibly indicating manuring, but with the absence of domestic grasses. In spite of the finding of caryopses, these data, coupled with average values of total phosphorus, do not suggest local cultivation, which is in agreement with the view expressed by Nisbet (1990). However, good pollen preservation has enabled a new picture of the environment around the site, showing a highly open landscape dominated by *Scabiosa*, which seems to contrast with the number of arboreal taxa revealed by charcoal macro-remains (Nisbet 1990). It was concluded that cereals were cropped and processed elsewhere (presumably in the lowlands) and then brought to the site, and that also most of the wood was probably gathered at some distance from the site.

Palynological analysis (bearing in mind the *caveats* from dryland layers stressed in the relevant chapter) has allowed further insights into the palaeoenvironmental reconstruction of the site. The only relatively high values of tree pollen in the diagram appear to derive form *Carpinus* and *Alnus*, this latter probably pointing the presence of rills on the hill slopes providing moist soils. It is also tempting to see a correlation between high values of *Alnus* and prehistoric antecedents of traditional land-use systems still used in the region in the early 20th century (Molinari and Montanari 2016).

8.5 Final considerations and recommendations for future work

The main flaw with the method applied appears to be the low potential of dung spores to differentiate between domestic and wild herbivores. This is a crucial point to an evaluation of human impact, and when not properly addressed it tends to lead to very general and cautious – ultimately, of scarce value – interpretations. A successful way to overcome this problem and formulate more confident remarks has been pointed by organic geochemistry and DNA metabarcoding, this latter appeared only very recently (D'Anjou et al. 2012; Giguet-Covex et al. 2014; Guillemot et al. 2015).

A high number of palynomorphs still cannot be successfully employed, in spite of their repeated occurrence in the deposits. This is a widespread problem in the field of NPP research, where the quantity of obscure microfossils designated merely by a code number is constantly increasing (Miola 2012). Although this classificatory effort may be of some utility to sort out a diverse assemblage, it is certainly not an end in itself. Not many authors seem to be concerned with this point, and long lists of types are often given without trying to account for their presence in term of implications for past ecology. As far as this research is concerned, a considerable amount of time has been spent examining the cryptogamic literature in an attempt to assign a probable indicator value to some recurrent palynomorphs and improve previous identification. This approach has finally proven fruitful in both sites, as it is illustrated by the case of Melanosporaceae, *Cirrenalia donnae* and *basiminut*a, fungal hyphopodia and other minor taxa. A detailed NPPs analysis also creates room for relevant results in the field of palaeomycology (e.g. tracing changes and continuity in ecological preferences through time; Tiffney and Barghoorn 1974). Although a closer collaboration with mycologists has been advocated (Baker et al. 2013), the analysts should have a competence in mycology, at least with regard to their knowledge of the main taxa, and their habitats and ecological requirements.

In spite of an established tradition of study investigating patterns of pollen dispersal, the factors governing spore deposition in lakes and mires have been less investigated. Robust studies focusing on coprophilous spores – almost exclusively *Sporormiella* – are available (Raper and Bush 2009; Parker and Williams 2012; Etienne et al. 2013), although it is not entirely clear which role is played by wind transport in upland wetlands and how far spores are carried over long distances in complex hydrological

systems with inlets and outlets (see above, **Chapter 1**). On the one hand spores are released very close to the ground, making it easier for them to enter streams and rivers when dispersed in their vicinity, while on the other hand this is also likely to limit the effect of wind as a carrying agent above the canopy.

In order to escape the realm of subjective opinion, both a shared way of expressing findings and a more robust knowledge of mechanisms controlling dung spore abundance in modern contexts are needed. However, the amount of data available for grazed areas surrounding modern lakes and the relationship with spore abundance is of little help, mainly because NPP values may vary significantly from site to site if expressed as total pollen percentages, and because information on animal presence (quantity, species, frequency with which they graze around the shore) has rarely been recorded in detail. Baker et al. (2013), and Wood and Wilmshurst (2013) have argued for the use of accumulation rates as the best independent variable to express abundances and enable comparisons between sites. The method has been very sporadically applied (Yeloff and van Geel 2006), and recent papers still maintain the use of percentages of total pollen (e.g. Szal et al. 2015).

This approach does not seem very promising for comparisons between sites, although accumulation rates would also have complications, such as derived from lake internal processes, making them very much site-dependent and poorly understood (Giesecke and Fontana 2008; Matthias and Giesecke 2014). The method might work well in the Boreal region, thanks to the numerous work conducted on the small lakes of the area, but would not be usable for comparison elsewhere (T. Giesecke, pers. comm.). For this reason, for the sites investigated in this work the use of total NPP percentages has been favoured. This is listed by Baker et al. (2013) among the possible alternatives to pollen percentages, and points to a more independent future for NPP analysis in the field of palaeoecology (see Wang et al. 2014, with total NPP percentages).

An extensive survey of the mycological literature suggests that the picture of grazing pressure resulting from subfossil archives may be highly biased. This is due to the scarce visibility of a number of morphologically indistinctive hyaline and coloured dung spores that seem to have been neglected in palaeoecological research. The main 'invisible' coprophilous taxa - *Pilobolus*, *Lasiobolus, Thelebolus*, *Iodophanus*, *Coprobia*, *Cheylimenia, Petriella, Coprotus*, *Ascobolus*, *Saccobolus*, *Mucor*, *Coprinus.*– ironically, are often among the best known species to mycologists (Richardson 1972; 2001;

Doveri 2007). This casts doubts on the reliability/unreliability of using only one or two well-established dung spores to infer past herbivore abundance (e.g. *Sporormiella*-type; Gill et al. 2013), which has been often done in studies investigating Pleistocene megafaunal extinctions (Davis 1987; Burney et al. 2003; Davis and Shafer 2006). **Chapters 3** and **4**, as several terrestrial samples analysed in **Chapter 5**, have shown how the dominant coprophilous taxa can be site-specific and driven by numerous factors (fungal competition, humidity, dung types), that remain largely poorly understood. The awareness of this issue leads to stress once again the importance of applying different proxies for herbivore presence, in order to understand if and how complementary they are (e.g. do they respond differently to different parameters?). Furthermore, it should be borne in mind that not all coprophilous fungi are likely to be represented in the NPP record, due to the production of scarcely diagnostic or poorly resistant spores (Haberle et al., 2004). It follows that, when a dung substrate had been colonised primarily by species such as *Peziza vesiculosa or Pilobolus* spp. (Doveri, 2007), this will not have resulted in a clearly detectable signal in the fossil record.

One of the biggest difficulties in discerning human impact in mid-Holocene off-site locations lies with the problem of population estimates. Up to which level the population density of a group of early farmers must grow in order for it to leave a distinct signal in the limnological record of mires lying tens of kilometres outside permanent settlements?

Several methods have been attempted in order to achieve reliable estimates of past populations. Unless complete graveyards associated with settlements are known (Cerasuolo 2011 - issues in funerary representation may still occur though), other approaches do not seem able to avoid the obligate used of analogies drawn from other contexts thought to be more or less comparable with their ancient counterparts. The subject has been developed primarily in Mesoamerican contexts, through the relationship between total floor area and number of inhabitants (Naroll 1962; Casselberry 1974). A similar approach makes use of the number of households found in a settlement, coupled with a mean value for family size obtained from written sources or inferred from ethnographic parallels (Lahiri 1998). When a detailed knowledge of the site cannot be achieved, the estimate is obtained by multiplying a sensible figure for the number of inhabitants per unit area for the whole settled area (e.g. Di Gennaro and Guidi 2010). In order to get reliable estimates, all

these approaches need very high data requirements. Even in the most favourable cases, it is often difficult to know if all the structures were in use at the same time, and to be certain about the total extent of the settlement, especially when patchy areas occur among dwellings.

Although standard modules representing dwelling units are largely known in the European Neolithic (e.g. Lepenski Vir or LBK sites: Srejović 1969; Bakels 1982), the situation is much more complex for the Neolithic and Copper Age periods in Liguria, where permanent settlements (if any) are thought to be buried somewhere in lowland coastal plains, and most of the evidence for domestic activities comes from caves and rock shelters. Maggi and Nisbet (1991) have argued for small family-sized groups acting in the upland on the grounds of the skeletal remains found in burial caves at higher elevations. However, the picture might have been quite different in coastal areas if our knowledge is severely biased by issues of site visibility (**Chapter 4**), as is suggested by the probable presence of a pile-dwelling site at Genoa and by the anthropic indicators revealed from the cores taken on the site (Maggi 1996; Arobba et al. 2016).

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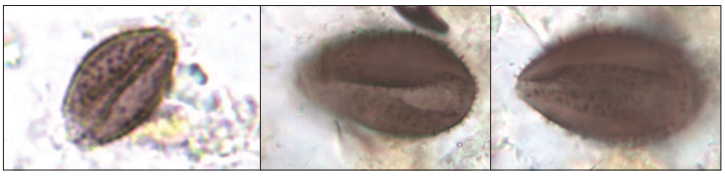

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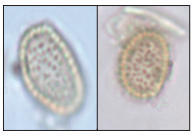

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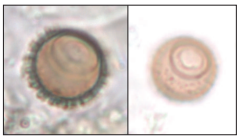

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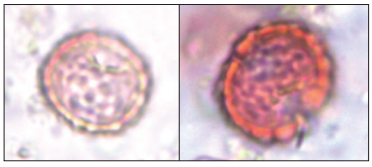

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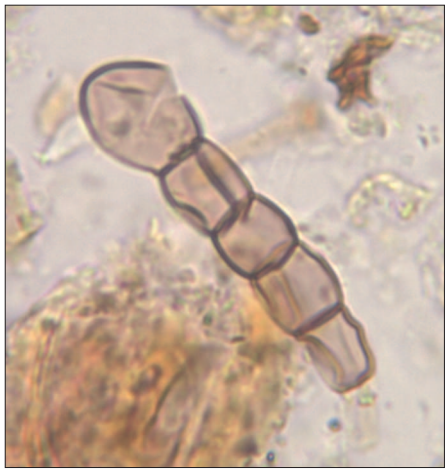

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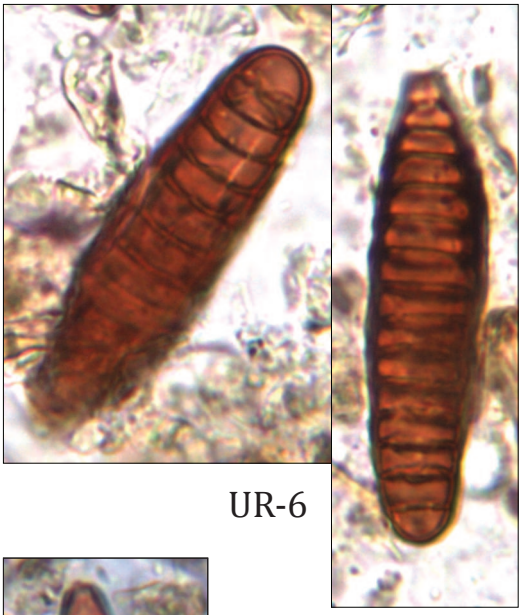

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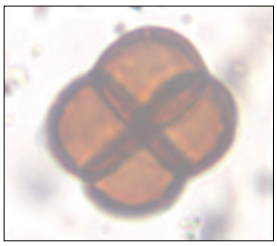

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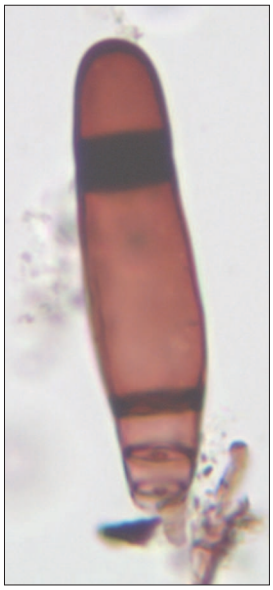

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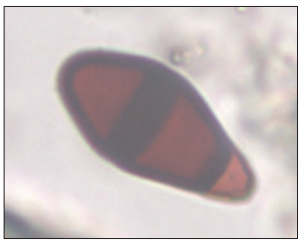
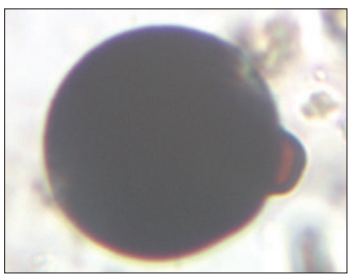
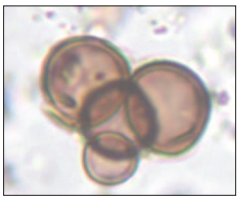


UR-9

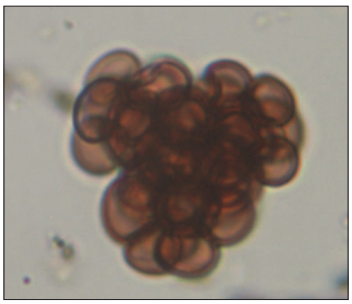


UR-11

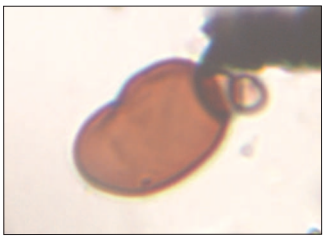
0 10 20µm



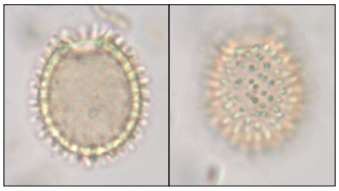
UR-12



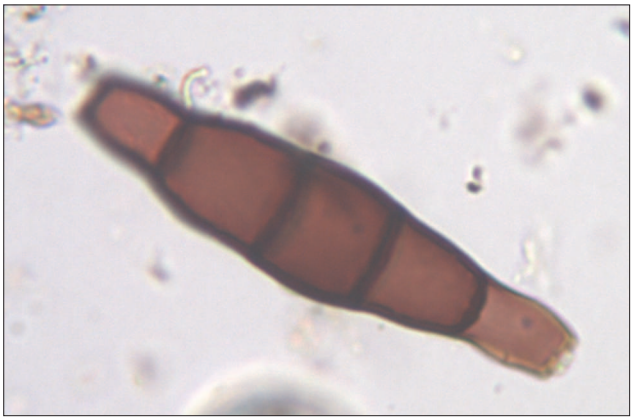
UR-13



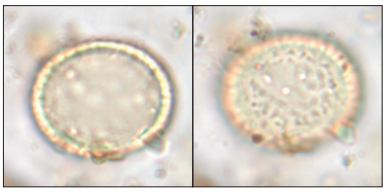
UR-14



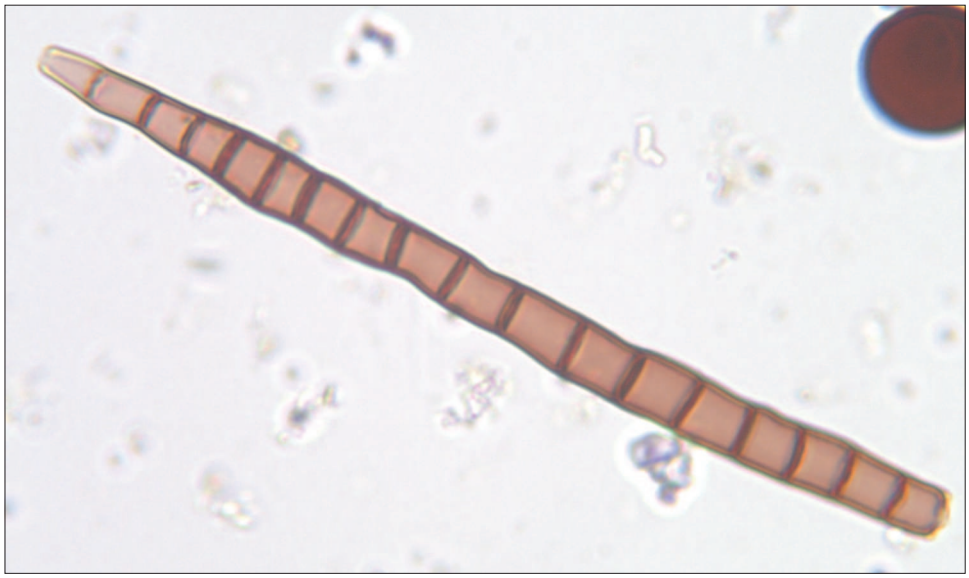
UR-15



UR-17

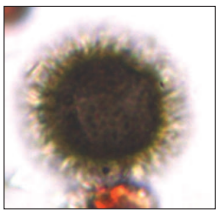


UR-16

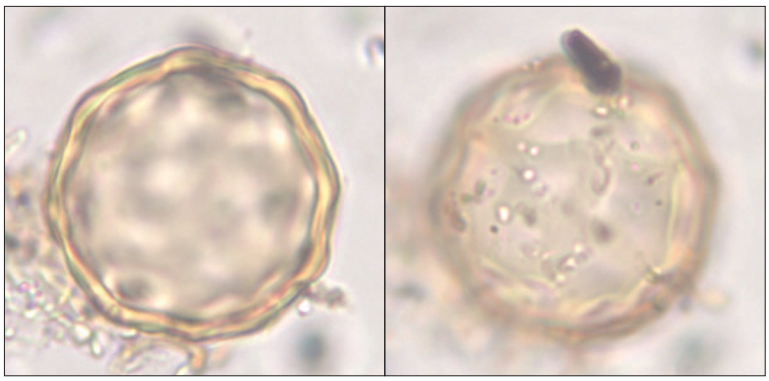


UR-18

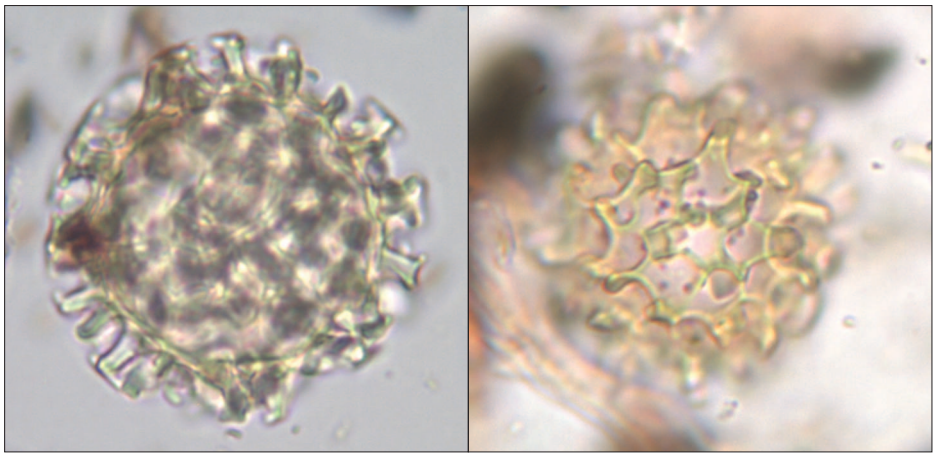
0 10 20µm



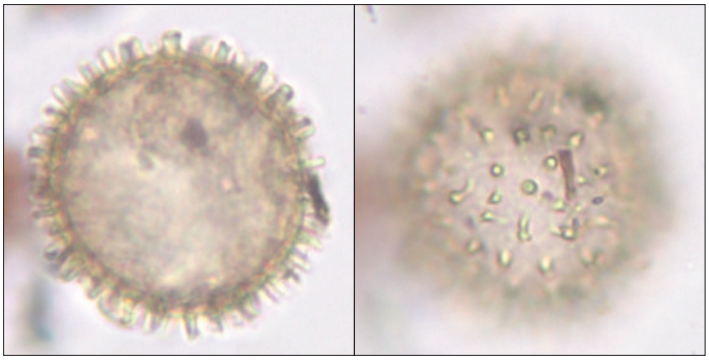
UR-19



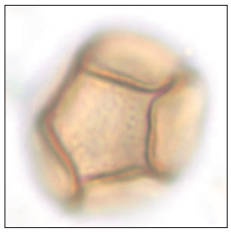
UR-20



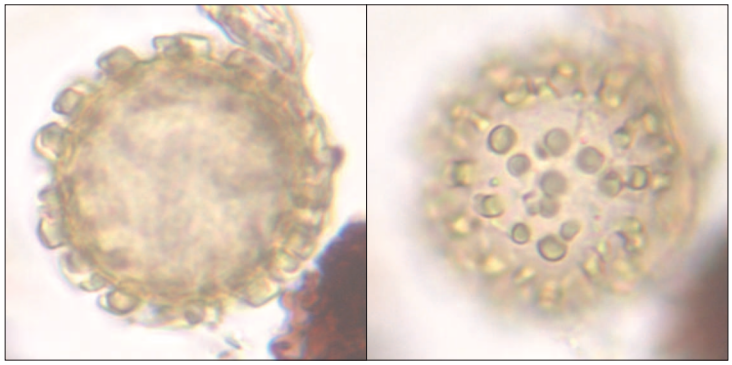
UR-21



UR-22

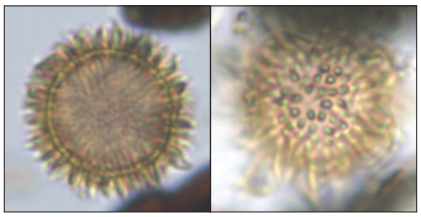


UR-23

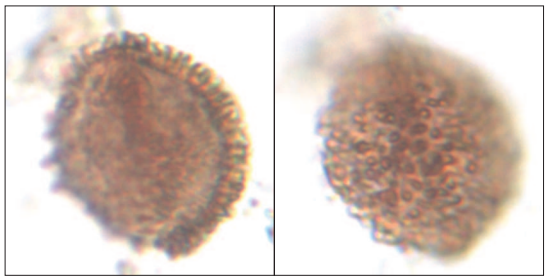


UR-24

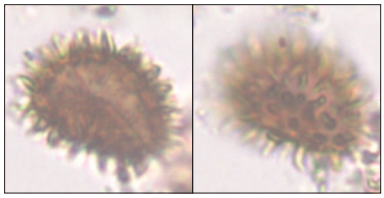
0 10 20µm



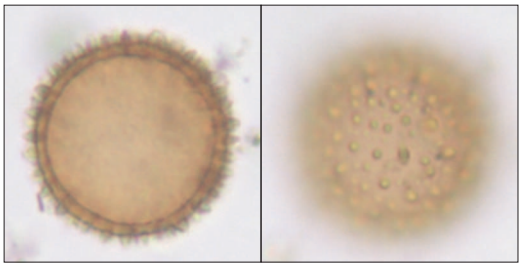
UR-25



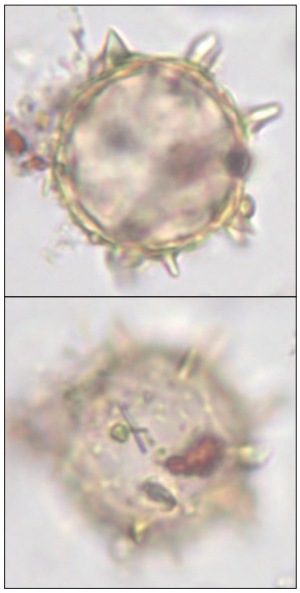
UR-27



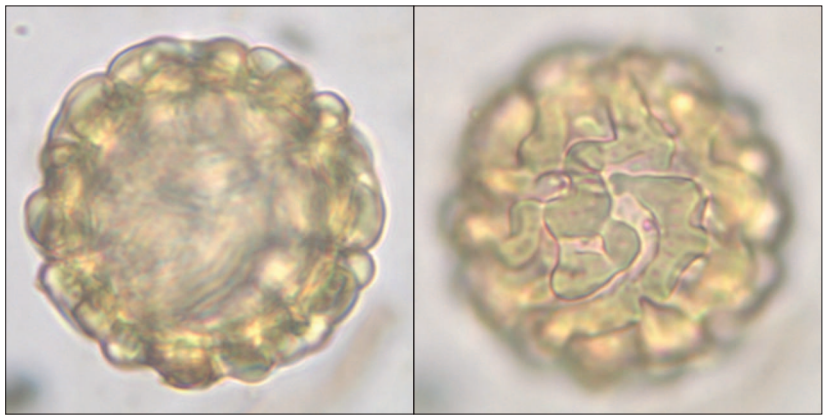
UR-26



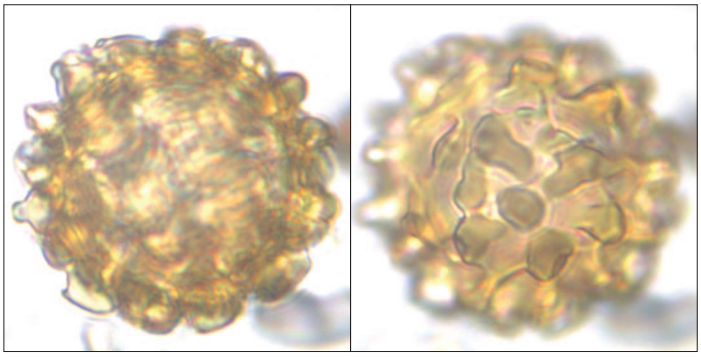
UR-28



UR-29

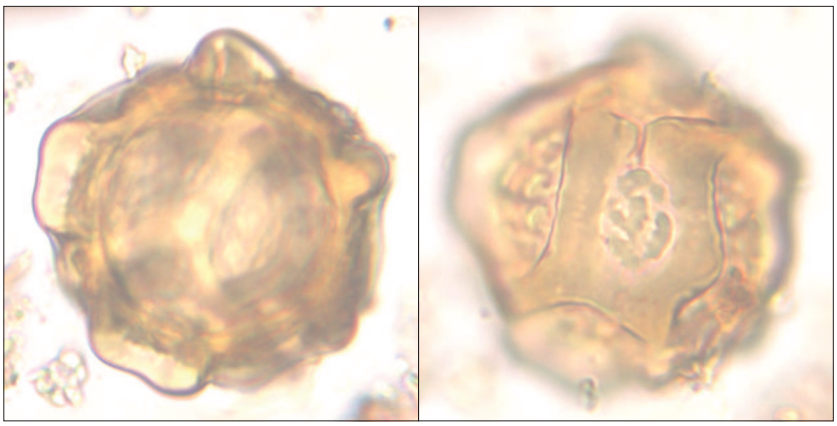


UR-30

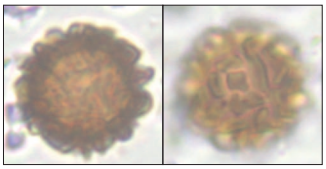


UR-31

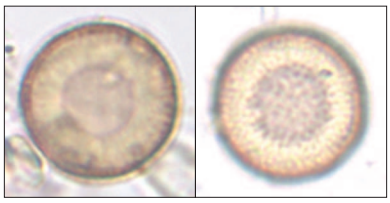
0 10 20µm



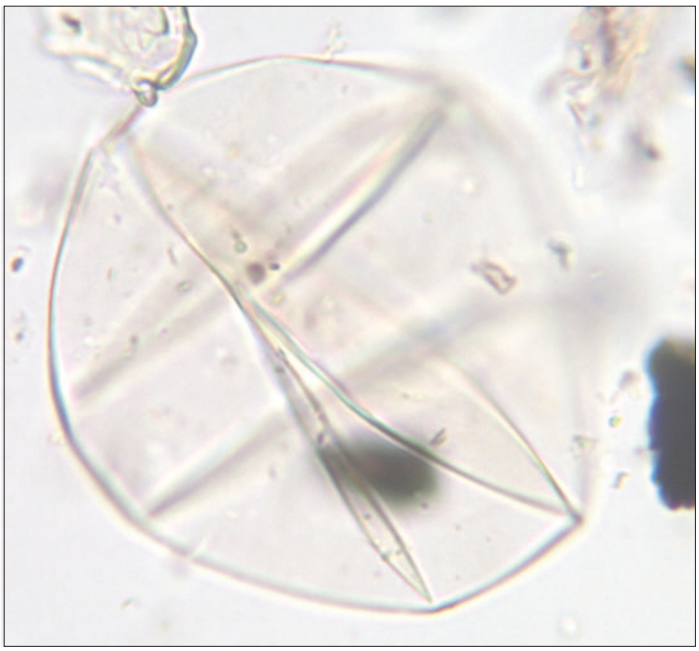
UR-32



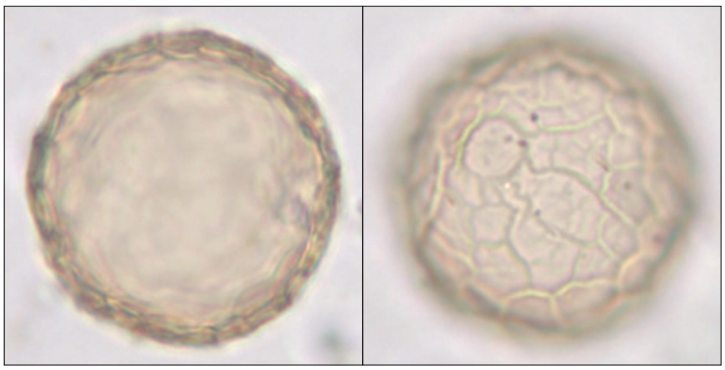
UR-33



UR-34

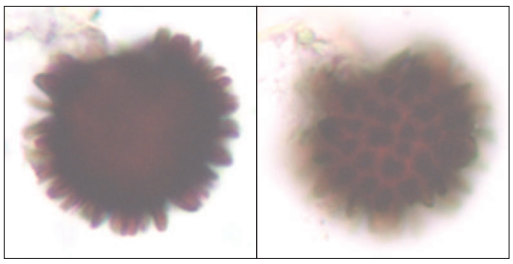


UR-35

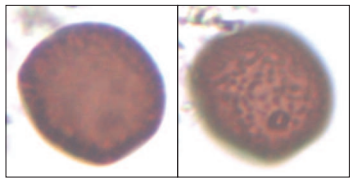


UR-36

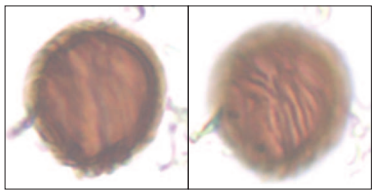
0 10 20µm



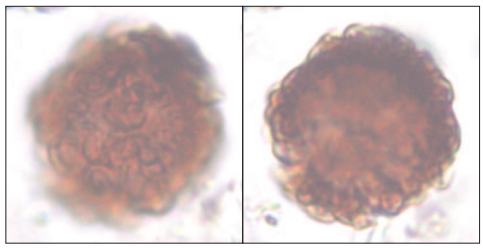
UR-37



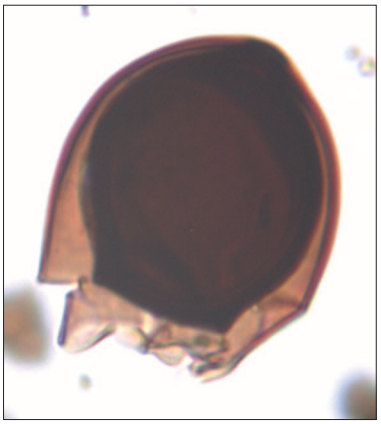
UR-38



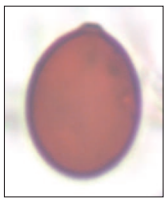
UR-39



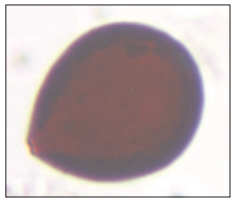
UR-40



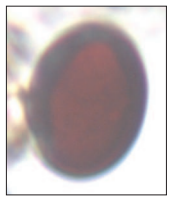
UR-41



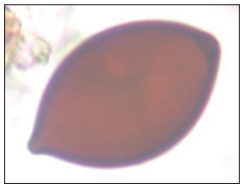
UR-42



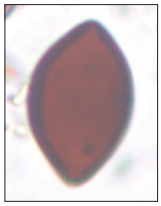
UR-43



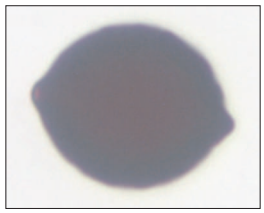
UR-44



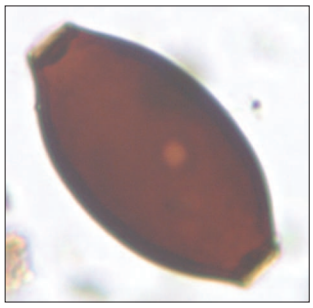
UR-45



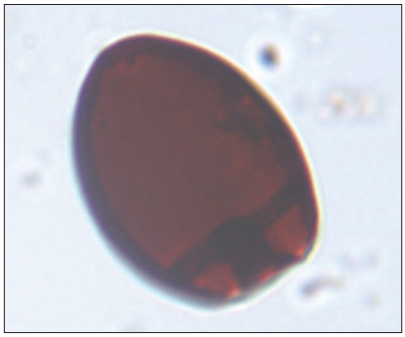
UR-46



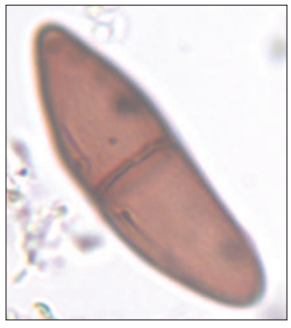
UR-47



UR-48

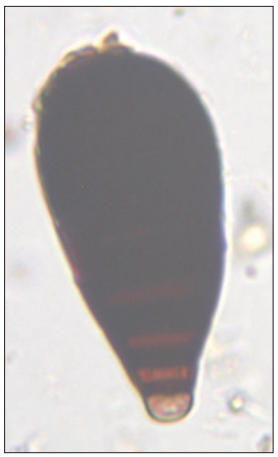


UR-49

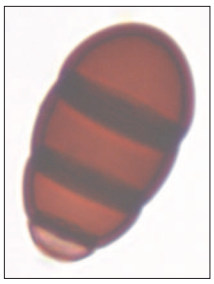


UR-50

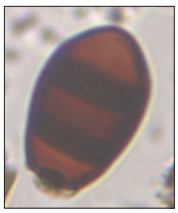
0 10 20µm



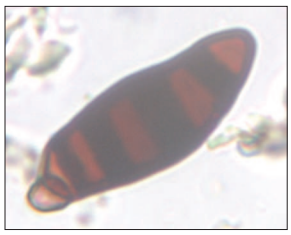
UR-51



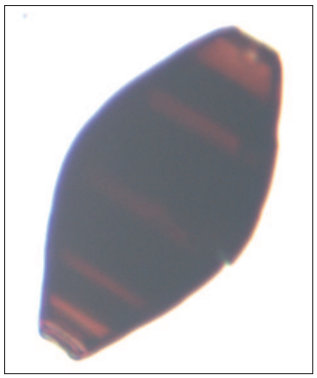
UR-52



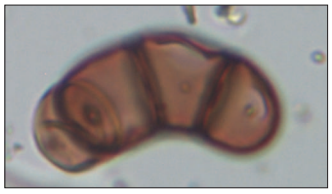
UR-53



UR-54



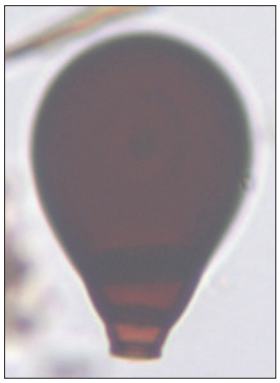
UR-55



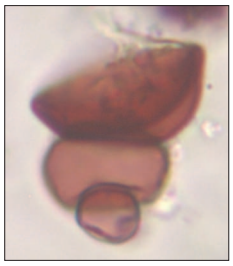
UR-56

UR-57

UR-58

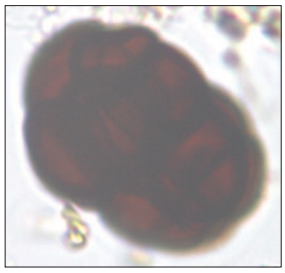


UR-59

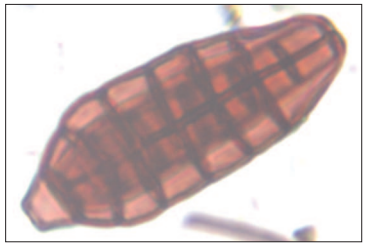


UR-60

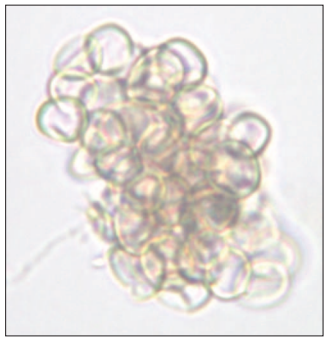
UR-61



UR-62

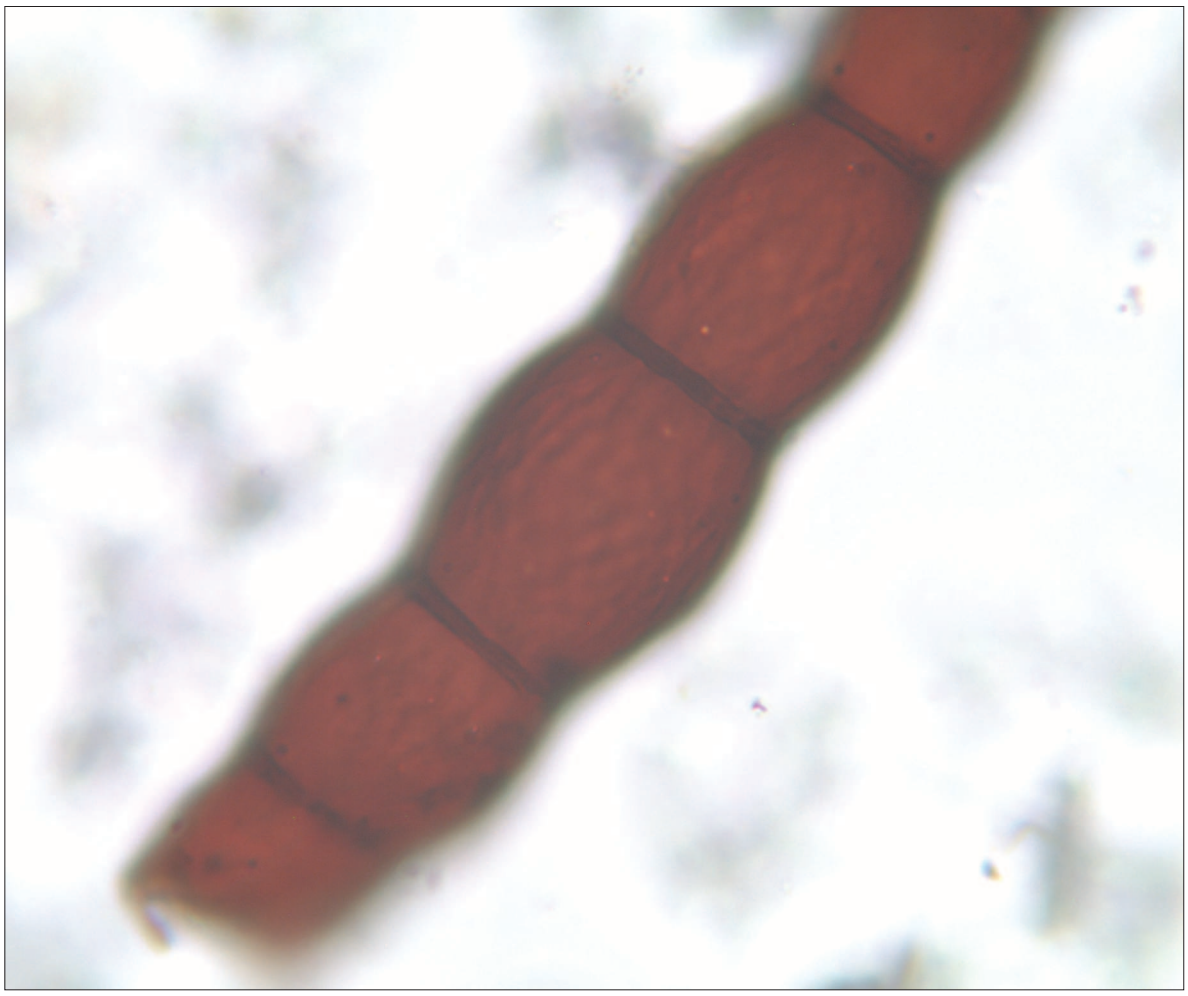


UR-63

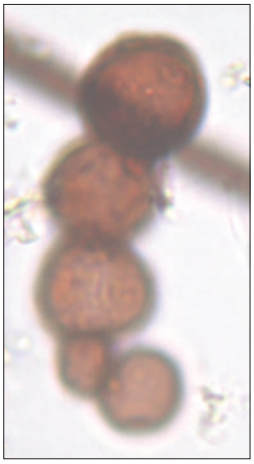


UR-64

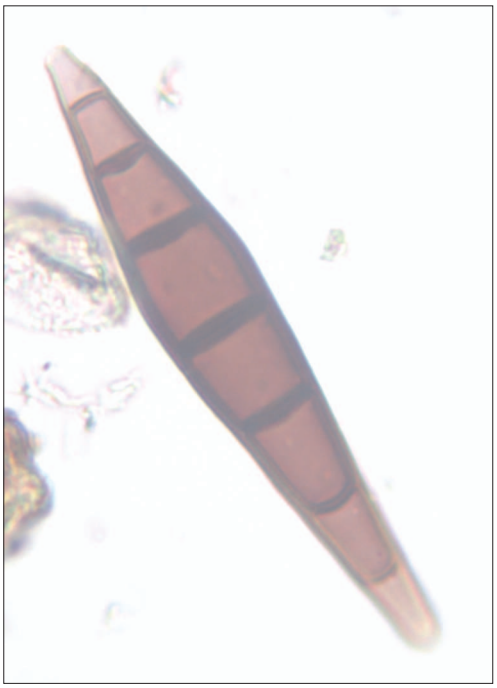
0 10 20µm



UR-65

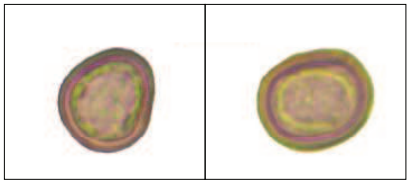


UR-66

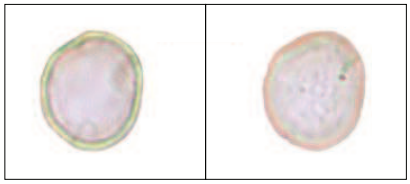


UR-67

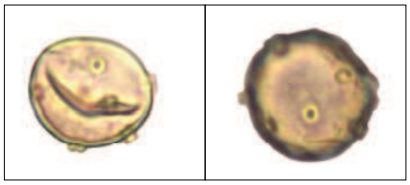
0 10 20µm



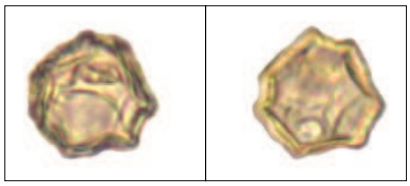
UR-68



UR-69



UR-70



UR-71

0 10 20µm

BM-2

UG-1285

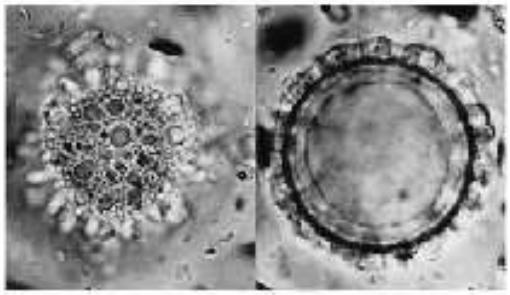
UG-1310

UG-1312

HdV-983

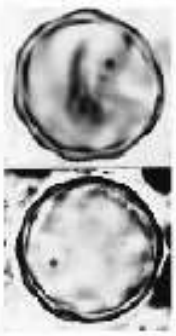
HdV-111

HdV-733

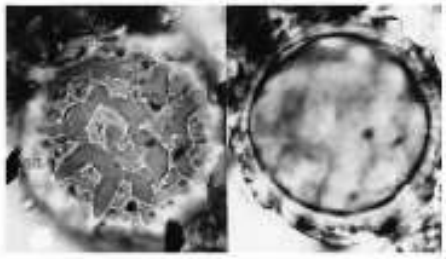


HdV-984

HdV-985

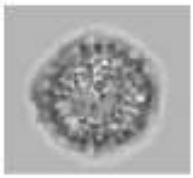


HdV-988

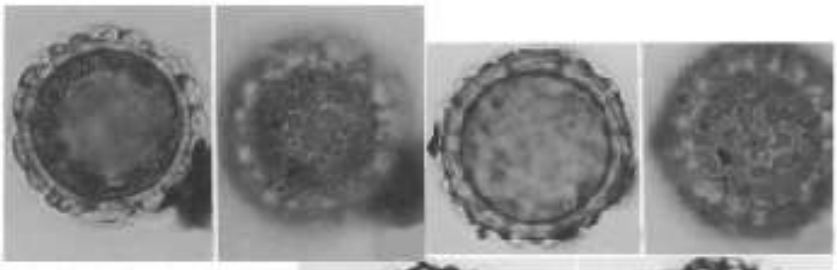


HdV-989

HdV-1036



EMA-118



Form A

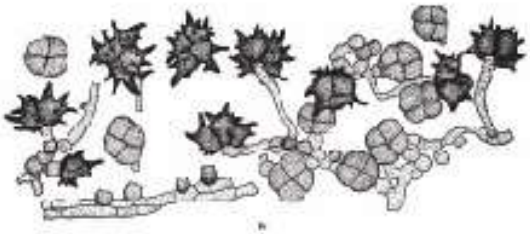
TM-011

Chalaropsis sp.

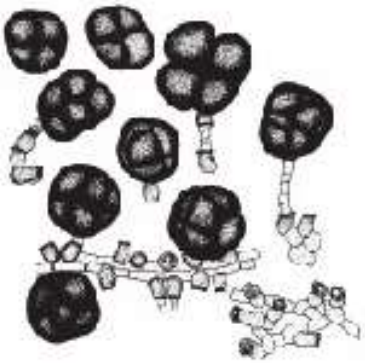
Craspedodymum elatum

Endophragmia glanduliformis

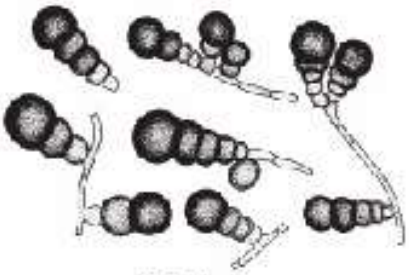
Gilmaniella humicola



Spegazzinia sp.



Spegazzinia parkeri



Culcitalna achraspora

Dydimosphaeria

Diporisporites

Biporisporites

Appendix I. Microfossil types from this work (Plates 1-9): codes, morphology, possible determinations and equivalencies with previously published articles (Plates 10-11).

Code	Site	Morphology	Biological determination	Probable equivalence	Reference
UR-1	PSA	1-colpate, spiny	Bryophyta?		
UR-2	PSA	Inaperturate, scabrate	*Scutellinia barlae?*		
UR-3	PSA	1-porate, scabrate	Sclerodermataceae? Ustilaginaceae?		
UR-4	PSA-AC	Inaperturate, verrucate	*Scutellinia* cf *hyperborea*?	EMA-118	Prager et al. 2012
UR-5	PSA	3-4 septate, psilate			
UR-6	PSA	Multiseptate, psilate	*Sporidesmium socium*?		
UR-7	PSA	8-septate, psilate	*Lophiostoma* sp.?		
UR-8	GPV-AC	Clustered, psilate	*Uleothyrium* sp.? *Spegazzinia* sp.? *Sarcinella* sp.?		Ellis 1971
UR-9	GPV-AC	2-septate, psilate	*Triadelphia* sp.?	UG-1049 · BM-2	Gelorini et al. 2011; Shumilovskikh et al. 2015; Ellis 1976
UR-10	GPV	6-septate, psilate	*Bactrodesmium* sp.	[Although considered as Bactrodesmium sp., UG-1091 shows a different morphology]	Gelorini et al. 2011
UR-11	GPV	1-2-septate, psilate	*Brachysporium* sp.?	HdV-1036	van Geel et al. 2011
UR-12	GPV	Clustered, psilate			
UR-13	GPV	Clustered, psilate			
UR-14	GPV	Inaperturate, concave, psilate			
UR-15	GPV	1-2-porate, spiny	Achritarcha? Algae? Gasteromycetes?	HdV-983	Carrión and van Geel 1999; Carrión and Navarro 2002
UR-16	GPV	1-porate, scabrate (flagellate?)		HdV-983	Carrión and van Geel 1999; Carrión and Navarro 2002
UR-17	GPV-AC	4-septate, psilate	*Clasterosporium* sp.?		

UR-18	GPV	Multiseptate, psilate			
UR-19	GPV-AC	Inaperturate, spiny			
UR-20	GPV	Inaperturate, reticulate		HdV-988	Carrión and van Geel 1999
UR-21	GPV-AC	Inaperturate, reticulate and spiny			
UR-22	GPV-AC	Inaperturate, spiny			
UR-23	GPV	Inaperturate, furrowed and scabrate			
UR-24	GPV-AC	Inaperturate, spiny	*Calostoma* sp.?	HdV-984 · Form-A	Carrión and van Geel 1999; Carrión and Navarro 2002; Jarzen and Elsik 1986
UR-25	GPV	Inaperturate, spiny			
UR-26	GPV	Inaperturate, spiny			
UR-27	GPV-AC	Inaperturate, spiny	Bryophyta?	HdV-340 · UG-1310	van Geel et al. 1989; Gelorini et al. 2011
UR-28	GPV-AC	Inaperturate, spiny			
UR-29	GPV-AC	Inaperturate, spiny		HdV-985	Carrión and van Geel 1999; Carrión and Navarro 2002
UR-30	GPV-AC	Inaperturate, vermiculate		Form-A	Jarzen and Elsik 1986
UR-31	GPV-AC	Inaperturate, vermiculate		UG-1285 · Form-A	Gelorini et al. 2011; Jarzen and Elsik 1986
UR-32	GPV	Inaperturate, reticulate		HdV-989 · MO-5	Carrión and van Geel 1999; Torri 2010
UR-33	GPV-AC	Inaperturate, vermiculate	*Ascodesmis* sp.?	UG-1285	Gelorini et al. 2011
UR-34	GPV	1-pored, scabrate	Bryophyta?	UG-1312?	Gelorini et al. 2011
UR-35	GPV	Furrowed? psilate			
UR-36	GPV-AC	1-pored, reticulate		HdV-111	van Geel et al. 1978
UR-37	GPV-AC	Inaperturate, spiny			
UR-38	GPV	1-porate, scabrate		HdV-733	Bakker and van Smeerdjik 1982
UR-39	GPV	Inaperturate, gelatin-coated, striated			

UR-40	GPV-AC	Inaperturate, gelatin-coated			
UR-41	GPV	1-porate, gelatin-coated			
UR-42	GPV	1-porate, psilate			
UR-43	GPV	1-porate, psilate	*Chalaropsis* sp.?		Ellis 1976
UR-44	GPV	Inaperturate, psilate	*Craspedodymum elatum*?		Ellis 1976
UR-45	GPV	2-porate, psilate			
UR-46	GPV	2-porate, psilate	*Arnium* sp.? *Chaetomium* sp.?		
UR-47	GPV	2-porate, psilate			
UR-48	GPV-AC	2-septate, psilate	*Brachydesmiella biseptata*? *Diporisporites*sp.?		Ellis 1971; Jarzen and Elsik 1986
UR-49	GPV	2-pored, 1-septate psilate	*Biporisporites* sp.		Kalgutkar and Jansonius 2000
UR-50	GPV	1-septate, striated	*Dydimosphaeria* sp.?		Nitiu et al. 2010
UR-51	GPV	Multiseptate, psilate	*Trichocladium* sp.?		
UR-52	GPV-AC	4-5 septate, psilate	*Trichocladium* sp.?		
UR-53	GPV-AC	3-septate, psilate	*Trichocladium* sp.?		
UR-54	GPV	3-5-septate, psilate	*Trichocladium opacum*	HdV-359 · TM-011	van Geel et al. 1981; Cugny et al. 2010
UR-55	GPV-AC	Multiseptate, psilate			
UR-56	GPV	4-5-septate, psilate			
UR-57	GPV-AC	4-5-septate, psilate			
UR-58	GPV	5-septate, psilate			
UR-59	GPV-AC	3-septate, psilate	*Brachysporiella* sp.? *Endophragmia glanduliformis*?		Ellis 1971; Ellis and Ellis 1985
UR-60	GPV-AC	3-4-septate, psilate	*Culcitalna achraspora*		Ellis 1976
UR-61	GPV	1-septate, psilate			
UR-62	GPV-AC	Clustered, psilate	*Uleothyrium* sp.? *Monodyctis* sp.? *Spegazzinia parkeri*?		Ellis 1971; 1976
UR-63	GPV-AC	Muriform, psilate			

UR-64	GPV	Clustered, psilate			
UR-65	GPV	Multiseptate, striated			
UR-66	GPV-AC	4-5-septate, scabrate	*Gilmaniella humicola*?		Ellis 1971
UR-67	GPV	Multiseptate, psilate			
UR-68	Modern	Inaperturate, psilate			
UR-69	Modern	Inaperturate, psilate			
UR-70	Modern	3-4-porate, wrinkled			
UR-71	Modern	3-4-porate, wrinkled, thin-walled			

Appendix II. Raw data

Prato Spilla 'A'	**DEPTHS (cm)**										
TAXA	441	457	473	489	505	521	537	553	569	585	601
HdV-128B	0	0	0	0	0	0	0	0	0	0	0
HdV-181	8	17	7	8	7	11	11	15	11	9	11
HdV-115	0	0	1	0	0	0	0	0	0	0	0
Pediastrum cf boryanum	17	10	39	4	13	16	8	8	1	1	25
Zygnema-type	0	0	0	0	0	0	0	0	0	0	0
Tetraedron (HdV-371)	0	0	1	0	0	0	0	0	0	0	0
Cirrenalia donnae	10	39	2	14	21	13	17	13	33	11	7
cf Cirrenalia lignicola/macrocephala	0	0	0	0	0	0	0	0	0	0	0
Endophragmia/Arthrobotris (HdV-572)	3	8	6	8	17	4	18	21	16	7	4
Coniochaeta	2	6	5	6	8	2	8	5	0	4	3
Rosellinia	0	0	4	8	1	2	4	0	0	1	0
Hypoxylon	1	1	0	0	0	2	1	1	1	0	0
Xylariaceae	5	2	6	11	3	6	6	4	1	4	1
Endophragmiella (TM-009)	0	0	0	1	0	0	0	0	0	0	0
Endophragmiella (TM-224)	0	0	0	0	1	1	0	0	0	0	1
Endophragmiella (TM-227)	1	1	0	0	0	0	0	0	1	0	0
Sporidesmium cf pedunculatum/altum	0	2	2	1	2	1	4	1	2	1	1
Dyctiosporium cf turuloides	0	0	0	0	0	0	0	1	1	1	0
Trichocladium opacum (TM-011)	0	1	2	0	0	0	0	0	1	0	0
Brachysporium obovatum (TM-014)	0	0	1	0	0	0	0	0	1	0	0
Corynesporopsis quercicola (EMA-125)	0	0	0	0	0	1	1	0	1	1	1
cf Taeniolella rudis	0	1	0	0	0	0	0	0	0	0	0
Taeniolella cf pulvillus/alta	0	0	0	0	0	0	0	0	0	0	0
Diplocladiella scalaroides	0	0	0	0	0	0	0	0	0	0	0
cf Savoryella lignicola (UG-1118)	0	0	0	1	0	0	0	0	0	0	0
Asterosporium asterospermum	0	0	0	1	0	0	0	0	0	0	0
Helicomyces/Helicosporium spp.	0	0	0	0	1	0	0	0	0	3	1
cf Canalisporium	0	0	0	0	0	0	0	0	0	0	0

Lophiostoma arundinis	1	0	0	0	0	1	1	0	0	1	0
cf Ulocladium consortiale	0	0	0	0	0	0	0	0	0	0	0
Spegazzinia	0	0	0	1	0	0	0	0	0	0	0
Sporormiella-type	2	0	0	2	2	0	0	0	0	0	0
Sordaria-type (HdV-55A)	0	0	1	1	0	0	1	0	0	0	0
Sordaria cf fimicola (gel. sheath)	0	0	1	0	0	0	0	0	0	0	0
Arnium-type	0	0	0	0	0	0	0	0	1	0	1
Arnium-type (gel. sheath)	0	1	0	0	0	0	0	0	0	0	0
cf Arnium imitans	0	0	1	0	0	0	0	0	0	0	0
Delitschia	0	0	0	0	0	0	1	0	0	0	0
Chaetomium	1	0	0	0	0	0	0	0	0	0	0
Gelasinospora cf tetrasperma	0	0	0	0	0	1	0	0	0	0	0
Apiosordaria verruculosa	0	0	0	0	0	0	0	0	0	0	0
Melanosporaceae (HdV-55B)	3	4	2	2	3	0	1	1	4	0	0
Sphaerodes cf fimicola	0	1	0	0	0	0	0	0	0	0	0
Persiciospora cf moreaui	0	0	0	0	0	0	0	0	0	0	0
Sordariaceous' ascospores undiff.	0	0	0	0	0	1	1	0	1	0	1
Cercophora-type	4	1	1	1	0	1	6	1	2	2	0
Clasterosporium caricinum	1	0	7	5	0	1	1	0	0	2	3
Kretzschmaria deusta	0	0	0	1	0	0	1	0	0	0	0
Diporotheca rhizophila	0	1	0	0	0	0	0	0	0	1	1
Glomus	3	6	4	1	2	7	2	5	1	6	5
Scleroderma	0	2	4	24	2	2	0	0	0	1	3
HdV-340	1	0	1	0	0	0	0	0	0	1	0
cf Ustilago enneapogonis/bullata	0	1	2	5	1	3	2	2	6	3	2
cf Lactarius (HdV-728)	0	1	1	0	0	1	0	1	0	0	0
cf Scutellinia hyperborea/minor	0	0	2	0	0	1	1	0	0	0	0
Sphaerodes	0	0	0	0	0	1	0	1	0	0	0
UR-1	4	1	6	5	7	8	11	9	13	8	4
UR-2	0	0	1	1	0	0	0	0	0	0	0

HdV-3A	0	0	0	1	0	2	1	1	0	1	0
HdV-3B	0	1	0	0	3	4	2	3	1	7	2
HdV-16A	0	0	0	0	2	0	0	2	0	0	0
HdV-16C	0	0	0	0	0	0	0	0	0	0	0
HdV-20	0	1	4	3	2	2	4	0	1	3	2
HdV-38	1	2	1	0	1	1	2	6	1	2	0
HdV-92	0	1	0	0	1	1	1	2	0	2	0
HdV-98	0	1	6	0	1	1	0	8	1	1	1
HdV-120	3	3	4	5	11	5	3	2	3	0	0
HdV-173A	0	0	0	0	0	0	2	0	1	0	0
HdV-173B	0	0	0	0	0	0	0	0	0	0	0
HdV-174	0	0	2	0	0	0	0	0	0	0	0
HdV-200	2	1	2	5	2	3	3	2	2	1	4
cf HdV-367	2	0	0	1	1	0	1	1	2	3	1
HdV-571	0	0	0	1	0	0	0	0	0	0	0
HdV-707	0	1	1	1	0	1	0	0	0	0	0
HdV-708	4	8	2	0	3	3	11	7	5	1	5
HdV-729	0	1	3	0	2	0	0	0	1	0	1
HdV-730	0	1	0	0	0	0	0	0	0	1	0
EMA-10/42	0	0	1	0	1	2	4	0	0	0	1
cf EMA-27	1	2	6	2	7	2	5	4	3	4	4
IBB-18	0	0	1	0	0	0	0	0	0	0	0
MO-6	0	0	0	0	0	0	0	0	0	0	0
TM-4008	0	0	0	1	1	0	0	0	0	0	0
cf UG-1110	0	0	0	1	0	0	1	1	0	0	1
cf UG-1141	0	0	0	2	1	1	1	1	1	0	0
Unknown multicelled (cf Sporidesmium socium)	14	1	0	0	0	1	0	0	3	0	1
Unknown multicelled (cf HdV-324)	1	0	1	1	4	5	0	2	1	1	1
Elliptic spores cf HdV-7B/82/306	39	29	17	33	34	18	22	18	13	27	22
Other ca. 10 µm Ø globose algal/fungal cells	18	3	5	11	4	1	3	4	6	4	17

Other multicelled	28	27	28	23	16	22	27	28	22	31	28
Other clustered cells	8	0	15	13	7	5	6	11	7	5	9
Indeterminable/unknown	35	42	14	31	37	28	27	11	38	33	32
Geoglossum-type	0	0	1	0	0	0	0	0	0	0	0
cf UG-1081	1	0	0	0	0	0	0	0	0	0	0
EMA-28	1	0	1	0	0	0	0	0	0	0	0
EMA-56	1	0	0	0	0	0	0	1	0	0	0
cf UG-1147	1	0	0	0	0	0	0	0	0	0	0
(other multi near to HdV-324)	4	0	0	1	0	1	1	0	0	1	0
HdV-65	1	0	0	0	0	3	1	0	0	0	0
HdV-121	1	0	2	2	1	0	0	0	0	1	1
multi-septate conidia	2	1	0	1	1	1	1	1	0	1	0
cf UG-1185	1	0	0	0	0	0	0	0	0	0	0
EMA-20	0	1	1	0	2	2	0	0	0	0	0
cf HdV-87	0	1	0	0	0	0	0	0	0	0	0
cf HdV-701	0	1	0	0	0	0	0	0	0	0	0
UG 1036 Brach	0	1	2	0	0	0	0	0	1	0	0
cf UG-1197	0	1	0	1	0	0	0	0	1	2	2
HdV-64	0	1	0	0	0	0	1	0	1	0	0
cf UG-1199	0	1	0	0	0	0	0	0	0	0	0
Spirogyra	0	2	1	0	0	0	0	1	0	1	0
cf Thielavia	0	1	0	0	0	0	0	0	0	0	0
EMA-2	0	0	1	0	0	0	0	0	0	0	0
HdV-359	0	0	1	2	0	0	1	0	0	0	0
EMA-33	0	0	1	0	0	0	0	0	0	0	0
EMA-99	0	0	1	0	0	0	0	0	0	0	0
HdV-22	0	0	1	0	0	0	0	0	0	1	0
cf UG-1153	0	0	1	0	0	0	0	0	0	0	0
HdV-65	0	0	4	1	0	0	0	2	0	1	0
cf HdV-1055	0	0	0	1	0	0	0	0	0	0	0

cf UG 1138/1148	0	0	0	1	0	0	0	0	0	0	1
cf UG-1098	0	0	0	1	0	0	0	0	0	0	0
HdV-179	0	0	0	1	0	0	0	0	1	0	0
cf UG-1105	0	0	0	1	1	1	0	0	0	2	1
cf UG-1080	0	0	0	0	1	0	0	0	0	0	0
cf UG-1147	0	0	0	0	1	1	0	0	0	0	0
cf UG-1005 Brach	0	0	0	0	1	0	0	0	0	0	0
HdV-308	0	0	0	0	2	0	0	0	0	0	0
HdV-17	0	0	0	0	1	0	1	0	0	1	1
pitted Helicosporium	0	0	0	0	1	0	0	0	0	0	0
HdV-25	0	0	0	0	0	1	0	0	0	0	0
HdV-715	0	0	0	0	0	1	0	0	0	0	0
Rivularia?	0	0	0	0	0	1	1	0	0	0	0
HdV-151	0	0	0	0	0	1	1	0	0	1	0
Allungato 553-537-521	0	0	0	0	0	1	1	1	0	0	0
Allungato 537	0	0	0	0	0	0	1	0	0	0	0
EMA-2	0	0	0	0	0	0	2	0	0	0	0
EMA-44	0	0	0	0	0	0	1	0	0	0	0
HdV-51	0	0	0	0	0	0	0	1	0	0	0
TM-015	0	0	0	0	0	0	0	0	1	0	0
HdV-10	0	0	0	0	0	0	0	0	1	0	0
HdV-334	0	0	0	0	0	0	0	0	0	1	0
HdV-90	0	0	0	0	0	0	0	0	0	1	0
cf HdV-140	0	0	0	0	0	0	0	0	0	1	1
cf HdV-381	0	0	0	0	0	0	0	0	0	0	1
HdV-365	0	0	0	0	0	0	0	0	0	0	1
HdV-83	0	0	0	0	0	0	0	0	0	0	0
cf EMA-30	0	0	0	0	0	0	0	0	0	0	0
HdV-714	0	0	0	0	0	0	0	0	0	0	0
cf UG-1311	0	0	0	0	0	0	0	0	0	0	0

HdV-18	0	0	0	0	0	0	0	0	0	0	0
cf UG-1307	0	0	0	0	0	0	0	0	0	0	0
HdV-23	0	0	0	0	0	0	0	0	0	0	0
cf UG-1111	0	0	0	0	0	0	0	0	0	0	0
HdV-119	0	0	0	0	0	0	0	0	0	0	0
HdV-152	0	0	0	0	0	0	0	0	0	0	0
HdV-360	0	0	0	0	0	0	0	0	0	0	0
cf Ellis 1139	0	0	0	0	0	0	0	0	0	0	0
HdV-99	0	0	0	0	0	0	0	0	0	0	0
cf UG-1053	0	0	0	0	0	0	0	0	0	0	0
cf HdV-361	0	0	0	0	0	0	0	0	0	0	0
cf UG-1203	0	0	0	0	0	0	0	0	0	0	0
EMA-86	0	0	0	0	0	0	0	0	0	0	0
EMA-134	0	0	0	0	0	0	0	0	0	0	0
HdV-33B	0	0	0	0	0	0	0	0	0	0	0
HdV-5	0	0	0	0	0	0	0	0	0	0	0
cf UG-1125	0	0	0	0	0	0	0	0	0	0	0
cf UG-1285	0	0	0	0	0	0	0	0	0	0	0
Miola III,24	0	0	0	0	0	0	0	0	0	0	0
cf UG-1221	0	0	0	0	0	0	0	0	0	0	0
LCE-27	0	0	0	0	0	0	0	0	0	0	0
HdV-23	0	0	0	0	0	0	0	0	0	0	0
cf Ellis 771	0	0	0	0	0	0	0	0	0	0	0
cf UG-1319	0	0	0	0	0	0	0	0	0	0	0
HdV-10	0	0	0	0	0	0	0	0	0	0	0
HdV-11	0	0	0	0	0	0	0	0	0	0	0
cf UG-1110 non septate	0	0	0	0	0	0	0	0	0	0	0
cf UG-1032 smooth	0	0	0	0	0	0	0	0	0	0	0
cf UG-1155	0	0	0	0	0	0	0	0	0	0	0
cf UG-1075	0	0	0	0	0	0	0	0	0	0	0

cf UG-1091	0	0	0	0	0	0	0	0	0	0	0
HdV-502	0	0	0	0	0	0	0	0	0	0	0
cf T.1162	0	0	0	0	0	0	0	0	0	0	0
HdV-53	0	0	0	0	0	0	0	0	0	0	0
HdV-85	0	0	0	0	0	0	0	0	0	0	0
cf UG-1194	0	0	0	0	0	0	0	0	0	0	0
cf UG-1124	0	0	0	0	0	0	0	0	0	0	0
cf UG-1061	0	0	0	0	0	0	0	0	0	0	0
cf UG-1182	0	0	0	0	0	0	0	0	0	0	0
cf UG-1106	0	0	0	0	0	0	0	0	0	0	0
cf Ellis 1046	0	0	0	0	0	0	0	0	0	0	0
Ellis 589	0	0	0	0	0	0	0	0	0	0	0
cf EMA-21	0	0	0	0	0	0	0	0	0	0	0
cf UG-1059	0	0	0	0	0	0	1	0	0	0	1
HdV-95	0	0	0	0	0	0	0	0	0	0	0
cf UG-1122	0	0	0	0	0	0	0	0	0	0	0
cf UG-1352	0	0	0	0	0	0	0	0	0	0	0
Ellis 355	0	0	0	0	0	0	0	0	0	0	0
Dydimella D	0	0	0	0	0	0	0	0	0	0	0
HdV-47	0	0	0	0	0	0	0	0	0	0	0
cf UG-1274	0	0	0	0	0	0	0	0	0	0	0
Leptospaeria K-N(but 4 cells) or UG-1112	0	0	0	0	0	0	0	0	0	0	0
cf UG 1084	0	0	0	0	0	0	0	0	0	0	0
cf UG-1042 Montagnula	0	0	0	0	0	0	0	0	0	0	0
cf Ellis 1335	0	0	0	0	0	0	0	0	0	0	0
Thielavia?	0	0	0	0	0	0	0	0	0	0	0
HdV-64	0	0	0	0	0	0	0	0	0	0	0
cf UG-1061	0	0	0	0	0	0	0	0	0	0	0
cf EMA-59	0	0	0	0	0	0	0	0	0	0	0
cf UG-1311	0	0	0	0	0	0	0	0	0	0	0

cf HdV-702	0	0	0	0	0	0	0	0	0	0	0
EMA-8	0	0	0	0	0	0	0	0	0	0	0
cf Ellis 988	0	0	0	0	0	0	0	0	0	0	0
cf 698	0	0	0	0	0	0	0	0	0	0	0
cf HdV-718	0	0	0	0	0	0	0	0	0	0	0
cf UG-1085	0	0	0	0	0	0	0	0	0	0	0
cf Ellis 1344-1796	0	0	0	0	0	0	0	0	0	0	0
Ellis 1512	0	0	0	0	0	0	0	0	0	0	0
cf HdV-1223	0	0	0	0	0	0	0	0	0	0	0
cf HdV-9	0	0	0	0	0	0	0	0	0	0	0
cf UG-1127	0	0	0	0	0	0	0	0	0	0	0
HdV-15	0	0	0	0	0	0	0	0	0	0	0
cf Ellis 326	0	0	0	0	0	0	0	0	0	0	0
cf UG-1274	0	0	0	0	0	0	0	0	0	0	0
HdV-332	0	0	0	0	0	0	0	0	0	0	0
168 (dung?)	0	0	0	0	0	0	0	0	0	0	0
cf USNP MS 3163	0	0	0	0	0	0	0	0	0	0	0
Ellis 306	0	0	0	0	0	0	0	0	0	0	0
cf UG-1138	0	0	0	0	0	0	0	0	0	0	0
HdV-306	0	0	0	0	0	0	0	0	0	0	0
HdV-242	0	0	0	0	0	0	0	0	0	0	0
HdV-124	0	0	0	0	0	0	0	0	0	0	0
cf UG-1176	0	0	0	0	0	0	0	0	0	0	0
cf Ellis 365	0	0	0	0	0	0	0	0	0	0	0
TM-036	0	0	0	0	0	0	0	0	0	0	0
cf UG-1072	0	0	0	0	0	0	0	0	0	0	0
Ellis 1096/1156/306	0	0	0	0	0	0	0	0	0	0	0
cf HdV-733	0	0	0	0	0	0	0	0	0	0	0
cf UG-1114	0	0	0	0	0	0	0	0	0	0	0
cf HdV-223	0	0	0	0	0	0	0	0	0	0	0

cf HdV-305	0	0	0	0	0	0	0	0	0	0	0
cf UG-1185	0	0	0	0	0	0	0	0	0	0	0
cf Ellis 1208	0	0	0	0	0	0	0	0	0	0	0
cf Ellis 1168	0	0	0	0	0	0	0	0	0	0	0
HdV-221	0	0	0	0	0	0	0	0	0	0	0
cf 1125	0	0	0	0	0	0	0	0	0	0	0
cf HdV-339	0	0	0	0	0	0	0	0	0	0	0
cf Ellis 793	0	0	0	0	0	0	0	0	0	0	0
cf UG-1276	0	0	0	0	0	0	0	0	0	0	0
cf Ellis 1271	0	0	0	0	0	0	0	0	0	0	0
Total	236	243	241	260	244	209	247	210	216	210	217
Fungal fruiting bodies undiff. (HdV-8)	12	15	11	10	15	15	29	16	14	19	3
Microthyrium (HdV-8B)	0	2	0	0	0	2	2	4	1	3	4
HdV-8A	0	1	0	0	0	0	0	0	0	0	0
HdV-8E	0	0	0	0	0	0	0	0	0	0	0
HdV-8F	1	1	1	1	0	0	0	0	0	0	0
HdV-8D	0	0	0	0	0	0	0	1	2	2	0
Bryophyte capsules	0	0	0	1	0	1	0	0	0	0	0
Other zoological	26	17	18	4	21	21	24	11	15	10	33
Chironomidae	10	1	1	2	5	2	1	6	2	5	5
Neorhabdocoela eggs	0	0	1	0	0	1	1	0	0	0	0
HdV-52 (body fragments)	0	0	0	0	0	0	1	0	0	0	3
Arcella	0	0	0	0	1	0	0	1	0	0	2
Tracheids (EMA-1)	64	124	102	45	54	67	88	96	63	109	156
Highly corroded wood (EMA-7)	7	11	2	2	0	3	0	3	1	5	27

Wood rays aggregates (EMA-11)	15	12	23	9	11	29	11	19	28	12	17
Hardwood periderm (EMA-16)	8	9	2	8	1	6	6	10	3	7	10
Fungal tissue (EMA-95)	95	90	66	65	49	56	85	90	68	47	51
Lycopodium	320	297	197	60	55	105	92	45	141	20	151

TAXA	609	617	625	633	641	649	657	665	673
HdV-128B	0	0	1	1	2	4	0	4	7
HdV-181	8	11	17	19	27	7	11	8	3
HdV-115	2	0	0	0	0	1	0	1	0
Pediastrum cf boryanum	0	1	4	0	1	5	0	3	3
Zygnema-type	0	0	0	1	0	0	0	0	0
Tetraedron (HdV-371)	0	0	0	0	0	0	0	0	0
Cirrenalia donnae	22	18	29	17	31	17	18	22	24
cf Cirrenalia lignicola/macrocephala	0	0	0	1	0	0	0	0	0
Endophragmia/Arthrobotris (HdV-572)	10	9	14	6	7	14	8	7	12
Coniochaeta	4	2	2	6	2	1	3	7	6
Rosellinia	4	3	4	2	1	2	0	1	0
Hypoxylon	0	2	0	2	2	2	3	4	3
Xylariaceae	6	10	2	3	3	3	3	4	1
Endophragmiella (TM-009)	0	0	0	0	0	0	0	0	2
Endophragmiella (TM-224)	1	0	1	1	1	0	0	0	0
Endophragmiella (TM-227)	1	1	1	0	0	0	0	0	1
Sporidesmium cf pedunculatum/altum	1	1	2	2	1	2	0	2	2
Dyctiosporium cf turuloides	1	2	0	0	0	0	0	1	0
Trichocladium opacum (TM-011)	1	0	2	3	2	0	1	0	1

Brachysporium obovatum (TM-014)	0	0	0	0	0	0	0	0	0
Corynesporopsis quercicola (EMA-125)	2	2	1	0	0	1	2	0	1
cf Taeniolella rudis	0	0	0	0	0	0	0	0	0
Taeniolella cf pulvillus/alta	0	0	0	0	0	0	0	0	0
Diplocladiella scalaroides	1	0	0	0	0	0	0	0	0
cf Savoryella lignicola (UG-1118)	0	0	1	0	0	0	0	0	0
Asterosporium asterospermum	0	0	0	0	0	0	0	0	0
Helicomyces/Helicosporium spp.	0	0	0	0	0	0	0	1	0
cf Canalisporium	0	0	0	0	0	0	0	0	0
Lophiostoma arundinis	1	0	1	1	1	1	0	0	0
cf Ulocladium consortiale	0	0	0	0	0	0	0	0	0
Spegazzinia	0	0	0	0	0	0	0	0	1
Sporormiella-type	1	0	0	0	0	0	0	0	1
Sordaria-type (HdV-55A)	0	0	0	0	0	2	0	0	1
Sordaria cf fimicola (gel. sheath)	0	0	0	0	0	0	0	1	0
Arnium-type	0	0	0	0	0	0	0	0	0
Arnium-type (gel. sheath)	0	0	0	0	0	0	0	0	0
cf Arnium imitans	0	0	0	0	0	0	0	0	0
Delitschia	0	0	2	0	0	1	0	1	0
Chaetomium	0	0	0	0	0	0	0	1	0
Gelasinospora cf tetrasperma	0	0	0	0	0	0	0	0	0
Apiosordaria verruculosa	0	0	0	0	0	0	0	0	0
Melanosporaceae (HdV-55B)	2	2	0	2	1	1	0	0	2
Sphaerodes cf fimicola	0	0	0	0	0	0	0	0	0
Persiciospora cf moreaui	0	0	0	0	0	0	0	1	0
Sordariaceous' ascospores undiff.	0	0	1	0	0	0	0	0	0
Cercophora-type	0	1	2	2	1	1	0	2	4
Clasterosporium caricinum	6	3	2	1	4	5	8	2	5
Kretzschmaria deusta	0	1	0	1	0	0	1	0	0
Diporotheca rhizophila	0	0	0	0	0	0	0	0	0

Glomus	8	3	1	4	3	3	1	1	3
Scleroderma	0	1	0	3	0	3	5	0	1
HdV-340	1	1	0	0	0	0	1	1	0
cf Ustilago enneapogonis/bullata	1	0	1	2	2	0	7	2	1
cf Lactarius (HdV-728)	0	0	0	0	0	0	1	0	0
cf Scutellinia hyperborea/minor	0	0	0	0	0	1	0	0	0
Sphaerodes	0	0	0	0	0	0	0	0	0
UR-1	9	11	4	14	8	12	4	9	7
UR-2	1	0	0	1	3	0	0	0	1
HdV-3A	0	0	0	0	0	1	0	0	0
HdV-3B	2	1	1	2	1	1	3	1	3
HdV-16A	0	0	2	0	0	0	0	0	0
HdV-16C	0	0	0	0	0	0	0	0	1
HdV-20	1	1	3	2	3	0	0	2	2
HdV-38	2	2	1	4	4	7	8	2	4
HdV-92	0	1	0	2	2	2	3	1	2
HdV-98	0	1	2	5	0	1	0	2	2
HdV-120	0	0	0	2	2	0	2	2	1
HdV-173A	0	0	0	0	2	1	0	0	0
HdV-173B	0	0	0	0	0	0	0	0	0
HdV-174	0	0	0	0	0	1	2	0	0
HdV-200	1	2	0	1	3	1	1	5	2
cf HdV-367	1	2	0	0	2	1	0	2	1
HdV-571	0	0	0	0	0	0	0	0	0
HdV-707	0	1	0	0	0	1	3	0	0
HdV-708	6	6	6	0	4	0	0	1	4
HdV-729	0	1	2	0	0	0	0	0	0
HdV-730	1	0	0	0	0	0	0	0	0
EMA-10/42	2	1	0	0	1	0	0	1	0
cf EMA-27	3	9	4	7	2	5	4	12	1

IBB-18	0	0	0	0	0	0	0	0	1
MO-6	0	0	1	0	0	0	0	0	0
TM-4008	0	0	0	0	0	0	0	0	0
cf UG-1110	0	1	2	0	1	0	0	0	0
cf UG-1141	1	1	2	2	2	0	2	0	0
Unknown multicelled (cf Sporidesmium socium)	1	1	0	2	0	0	1	0	0
Unknown multicelled (cf HdV-324)	5	3	0	1	4	4	9	6	5
Elliptic spores cf HdV-7B/82/306	16	23	15	29	41	20	25	16	19
Other ca. 10 µm Ø globose algal/fungal cells	3	2	0	5	15	18	10	12	7
Other multicelled	26	30	33	22	36	31	24	27	13
Other clustered cells	9	14	8	12	9	4	7	2	15
Indeterminable/unknown	23	16	18	15	30	21	17	26	12
Geoglossum-type	0	0	1	0	0	0	0	0	1
cf UG-1081	0	0	0	0	0	0	0	0	0
EMA-28	0	0	0	0	0	0	0	2	0
EMA-56	1	1	2	0	0	0	0	0	0
cf UG-1147	0	0	0	0	0	0	0	0	0
(other multi near to HdV-324)	1	1	0	1	0	0	0	1	0
HdV-65	0	0	0	0	0	0	0	0	1
HdV-121	0	0	0	0	2	0	0	0	0
multi-septate conidia	0	0	2	2	3	1	2	2	2
cf UG-1185	0	0	0	0	0	0	0	0	0
EMA-20	0	0	0	0	0	0	0	0	0
cf HdV-87	0	0	0	0	0	0	0	0	0
cf HdV-701	0	0	0	0	0	0	0	0	0
UG 1036 Brach	1	0	0	0	1	2	1	0	2
cf UG-1197	1	0	0	0	0	0	0	0	0
HdV-64	0	0	1	1	0	0	0	0	0
cf UG-1199	0	0	0	0	0	0	0	0	0
Spirogyra	1	0	0	0	0	0	0	0	0

cf Thielavia	0	0	0	0	0	0	0	0	0
EMA-2	1	0	0	0	0	0	0	0	1
HdV-359	1	0	0	0	0	0	0	0	0
EMA-33	0	0	0	0	0	0	0	0	0
EMA-99	0	0	0	0	0	0	0	0	0
HdV-22	0	0	0	0	1	0	1	0	0
cf UG-1153	0	0	0	0	1	0	0	0	0
HdV-65	1	0	0	0	0	0	0	0	0
cf HdV-1055	0	0	0	0	0	0	0	0	0
cf UG 1138/1148	0	0	0	0	0	0	0	0	0
cf UG-1098	0	0	0	0	0	0	0	0	0
HdV-179	0	0	0	0	0	1	0	0	0
cf UG-1105	1	0	0	0	0	4	0	4	1
cf UG-1080	0	0	0	0	0	0	0	0	0
cf UG-1147	1	0	0	1	0	1	0	0	1
cf UG-1005 Brach	0	0	0	0	0	0	0	0	0
HdV-308	0	0	0	0	0	0	0	0	0
HdV-17	0	1	0	0	0	0	0	0	0
pitted Helicosporium	0	0	0	0	0	0	0	0	0
HdV-25	0	0	0	0	0	0	0	0	0
HdV-715	0	0	0	0	0	0	0	0	0
Rivularia?	0	0	0	0	0	0	0	0	0
HdV-151	0	0	0	0	0	0	0	0	0
Allungato 553-537-521	0	0	0	0	0	0	0	0	0
Allungato 537	0	0	0	0	0	0	0	0	0
EMA-2	0	0	0	0	0	1	0	0	0
EMA-44	0	0	0	0	0	0	0	0	0
HdV-51	0	0	0	0	0	0	0	0	0
TM-015	0	0	0	0	0	0	0	0	0
HdV-10	0	0	0	0	0	0	0	0	0

HdV-334	0	0	0	0	0	0	0	0	0
HdV-90	0	0	2	0	0	0	0	0	0
cf HdV-140	0	0	0	0	0	1	0	0	0
cf HdV-381	0	0	0	0	0	0	0	0	0
HdV-365	0	0	1	0	0	1	0	0	0
HdV-83	1	0	0	0	0	2	0	0	1
cf EMA-30	1	0	0	0	0	0	0	0	0
HdV-714	1	0	0	0	0	0	0	1	0
cf UG-1311	1	0	0	0	0	0	0	0	0
HdV-18	1	1	0	0	0	0	0	0	0
cf UG-1307	1	0	0	0	0	0	0	0	0
HdV-23	0	1	0	0	0	0	0	0	0
cf UG-1111	0	1	0	0	0	0	0	0	0
HdV-119	0	1	0	0	0	0	0	0	0
HdV-152	0	1	0	0	0	0	0	0	0
HdV-360	0	1	0	0	0	0	0	0	0
cf Ellis 1139	0	1	0	0	0	0	0	0	0
HdV-99	0	1	0	0	0	0	0	0	0
cf UG-1053	0	1	0	0	0	0	0	0	1
cf HdV-361	0	0	1	0	0	0	0	0	0
cf UG-1203	0	0	1	0	0	0	0	0	0
EMA-86	0	0	1	1	0	0	2	0	2
EMA-134	0	0	1	0	0	0	0	0	0
HdV-33B	0	0	1	0	0	0	0	0	0
HdV-5	0	0	1	0	0	0	0	0	0
cf UG-1125	0	0	1	0	0	0	0	0	0
cf UG-1285	0	0	0	1	0	0	0	0	0
Miola III,24	0	0	0	1	0	0	0	0	0
cf UG-1221	0	0	0	0	1	0	0	0	0
LCE-27	0	0	0	0	1	0	0	0	0

HdV-23	0	0	0	0	1	0	0	0	0
cf Ellis 771	0	0	0	0	1	0	0	0	0
cf UG-1319	0	0	0	0	1	0	0	0	2
HdV-10	0	0	0	0	0	1	0	0	0
HdV-11	0	0	0	0	0	1	0	0	0
cf UG-1110 non septate	0	0	0	0	0	1	0	0	0
cf UG-1032 smooth	0	0	0	0	0	1	0	0	0
cf UG-1155	0	0	0	0	0	1	0	0	0
cf UG-1075	0	0	0	0	0	0	1	0	0
cf UG-1091	0	0	0	0	0	0	1	0	0
HdV-502	0	0	0	0	0	0	1	0	0
cf T.1162	0	0	0	0	0	0	1	0	0
HdV-53	0	0	0	0	0	0	2	0	0
HdV-85	0	0	0	0	0	0	1	0	0
cf UG-1194	0	0	0	0	0	0	1	0	0
cf UG-1124	0	0	0	0	0	0	0	1	0
cf UG-1061	0	0	0	0	0	0	0	2	0
cf UG-1182	0	0	0	0	0	0	0	1	0
cf UG-1106	0	0	0	0	0	0	0	1	0
cf Ellis 1046	0	0	0	0	0	0	0	1	0
Ellis 589	0	0	0	0	0	0	0	1	0
cf EMA-21	0	0	0	0	0	0	0	1	0
cf UG-1059	0	0	0	0	1	0	1	0	1
HdV-95	0	0	0	0	0	0	0	0	1
cf UG-1122	0	0	0	0	0	0	0	0	1
cf UG-1352	0	0	0	0	0	0	0	0	1
Ellis 355	0	0	0	0	0	0	0	0	1
Dydimella D	0	0	0	0	0	0	0	0	1
HdV-47	0	0	0	0	0	0	0	0	1
cf UG-1274	0	0	0	0	0	0	0	0	1

Leptospaeria K-N(but 4 cells) or UG-1112	0	0	0	0	0	0	0	0	1
cf UG 1084	0	0	0	0	0	0	0	0	0
cf UG-1042 Montagnula	0	0	0	0	0	0	0	0	0
cf Ellis 1335	0	0	0	0	0	0	0	0	0
Thielavia?	0	0	0	0	0	0	0	0	0
HdV-64	0	0	0	0	0	0	0	0	0
cf UG-1061	0	0	0	0	0	0	0	0	0
cf EMA-59	0	0	0	0	0	0	0	0	0
cf UG-1311	0	0	0	0	0	0	0	0	0
cf HdV-702	0	0	0	0	0	0	0	0	0
EMA-8	0	0	0	0	0	0	0	0	0
cf Ellis 988	0	0	0	0	0	0	0	0	0
cf 698	0	0	0	0	0	0	0	0	0
cf HdV-718	0	0	0	0	0	0	0	0	0
cf UG-1085	0	0	0	0	0	0	0	0	0
cf Ellis 1344-1796	0	0	0	0	0	0	0	0	0
Ellis 1512	0	0	0	0	0	0	0	0	0
cf HdV-1223	0	0	0	0	0	0	0	0	0
cf HdV-9	0	0	0	0	0	0	0	0	0
cf UG-1127	0	0	0	0	0	0	0	0	0
HdV-15	0	0	0	0	0	0	0	0	0
cf Ellis 326	0	0	0	0	0	0	0	0	0
cf UG-1274	0	0	0	0	0	0	0	0	0
HdV-332	0	0	0	0	0	0	0	0	0
168 (dung?)	0	0	0	0	0	0	0	0	0
cf USNP MS 3163	0	0	0	0	0	0	0	0	0
Ellis 306	0	0	0	0	0	0	0	0	0
cf UG-1138	0	0	0	0	0	0	0	0	0
HdV-306	0	0	0	0	0	0	0	0	0
HdV-242	0	0	0	0	0	0	0	0	0

HdV-124	0	0	0	0	0	0	0	0	0
cf UG-1176	0	0	0	0	0	0	0	0	0
cf Ellis 365	0	0	0	0	0	0	0	0	0
TM-036	0	0	0	0	0	0	0	0	0
cf UG-1072	0	0	0	0	0	0	0	0	0
Ellis 1096/1156/306	0	0	0	0	0	0	0	0	0
cf HdV-733	0	0	0	0	0	0	0	0	0
cf UG-1114	0	0	0	0	0	0	0	0	0
cf HdV-223	0	0	0	0	0	0	0	0	0
cf HdV-305	0	0	0	0	0	0	0	0	0
cf UG-1185	0	0	0	0	0	0	0	0	0
cf Ellis 1208	0	0	0	0	0	0	0	0	0
cf Ellis 1168	0	0	0	0	0	0	0	0	0
HdV-221	0	0	0	0	0	0	0	0	0
cf 1125	0	0	0	0	0	0	0	0	0
cf HdV-339	0	0	0	0	0	0	0	0	0
cf Ellis 793	0	0	0	0	0	0	0	0	0
cf UG-1276	0	0	0	0	0	0	0	0	0
cf Ellis 1271	0	0	0	0	0	0	0	0	0
Total	213	216	211	216	281	228	213	224	212
Fungal fruiting bodies undiff. (HdV-8)	29	15	17	21	34	27	12	13	23
Microthyrium (HdV-8B)	2	1	3	6	1	0	0	3	3
HdV-8A	0	1	0	0	1	1	0	0	0
HdV-8E	0	0	0	0	0	0	0	0	0
HdV-8F	0	0	0	0	0	1	0	0	0
HdV-8D	1	0	0	1	0	0	0	0	0
Bryophyte capsules	0	0	0	0	0	1	0	0	0
Other zoological	19	15	22	9	33	24	9	9	14
Chironomidae	5	3	5	4	5	0	4	0	3

Neorhabdocoela eggs	0	0	0	0	1	1	1	1	0
HdV-52 (body fragments)	0	0	0	0	0	0	0	0	0
Arcella	0	0	0	1	0	0	0	0	0
Tracheids (EMA-1)	77	48	107	104	135	61	83	73	216
Highly corroded wood (EMA-7)	7	2	4	3	2	7	11	10	13
Wood rays aggregates (EMA-11)	22	15	33	21	34	23	34	22	57
Hardwood periderm (EMA-16)	3	2	8	11	8	8	2	5	8
Fungal tissue (EMA-95)	73	43	75	106	87	45	61	41	81
Lycopodium	59	92	68	84	154	41	32	19	61

TAXA	681	689	697	705	713	721	729
HdV-128B	13	14	13	36	47	50	79
HdV-181	3	10	9	16	8	19	7
HdV-115	0	1	1	0	0	0	0
Pediastrum cf boryanum	4	6	1	1	2	3	2
Zygnema-type	0	0	0	0	0	0	0
Tetraedron (HdV-371)	0	0	0	0	0	0	0
Cirrenalia donnae	27	10	6	8	8	13	24
cf Cirrenalia lignicola/macrocephala	0	0	0	0	0	0	0
Endophragmia/Arthrobotris (HdV-572)	4	8	2	2	4	0	5
Coniochaeta	0	1	3	1	7	3	9

Rosellinia	4	3	1	4	4	3	7
Hypoxylon	1	2	3	0	4	0	0
Xylariaceae	2	7	0	3	2	6	1
Endophragmiella (TM-009)	0	0	0	0	0	0	0
Endophragmiella (TM-224)	0	0	1	0	0	0	0
Endophragmiella (TM-227)	0	0	0	0	1	0	1
Sporidesmium cf pedunculatum/altum	3	3	4	2	2	1	11
Dyctiosporium cf turuloides	1	1	0	1	2	1	1
Trichocladium opacum (TM-011)	4	0	1	2	1	1	2
Brachysporium obovatum (TM-014)	0	0	0	0	0	0	0
Corynesporopsis quercicola (EMA-125)	1	1	0	1	0	0	0
cf Taeniolella rudis	0	0	0	0	0	0	0
Taeniolella cf pulvillus/alta	0	1	0	0	0	0	1
Diplocladiella scalaroides	0	0	0	0	0	0	0
cf Savoryella lignicola (UG-1118)	2	0	0	0	0	0	0
Asterosporium asterospermum	0	0	0	0	0	0	1
Helicomyces/Helicosporium spp.	0	0	0	0	0	0	0
cf Canalisporium	0	0	0	1	0	0	0
Lophiostoma arundinis	0	1	0	0	0	0	0
cf Ulocladium consortiale	0	0	0	0	1	0	0
Spegazzinia	0	0	0	0	0	0	0
Sporormiella-type	0	0	0	0	0	1	1
Sordaria-type (HdV-55A)	1	0	0	0	0	0	0
Sordaria cf fimicola (gel. sheath)	0	0	0	0	0	0	0
Arnium-type	0	0	0	0	0	0	0
Arnium-type (gel. sheath)	0	0	0	0	0	0	0
cf Arnium imitans	0	0	0	0	0	1	0
Delitschia	0	0	0	0	1	4	0
Chaetomium	0	0	0	0	0	1	0
Gelasinospora cf tetrasperma	0	0	0	0	0	0	0

Apiosordaria verruculosa	0	0	0	1	0	0	0
Melanosporaceae (HdV-55B)	1	0	1	3	0	2	0
Sphaerodes cf fimicola	0	0	0	0	0	0	0
Persiciospora cf moreaui	0	0	0	0	0	0	0
Sordariaceous' ascospores undiff.	0	0	0	0	0	0	1
Cercophora-type	2	1	1	1	0	1	1
Clasterosporium caricinum	2	1	3	8	3	8	3
Kretzschmaria deusta	1	0	0	0	1	0	0
Diporotheca rhizophila	0	0	0	1	0	0	0
Glomus	4	4	10	2	4	2	5
Scleroderma	3	2	5	1	3	3	1
HdV-340	0	0	0	4	1	1	0
cf Ustilago enneapogonis/bullata	2	0	3	7	0	0	0
cf Lactarius (HdV-728)	0	0	0	0	0	0	0
cf Scutellinia hyperborea/minor	0	0	0	0	1	0	0
Sphaerodes	0	0	0	0	0	0	0
UR-1	7	6	7	5	3	5	11
UR-2	2	3	2	1	0	4	2
HdV-3A	0	0	0	0	0	0	0
HdV-3B	0	0	0	0	1	2	0
HdV-16A	0	0	0	0	1	0	0
HdV-16C	1	0	0	1	0	0	0
HdV-20	1	0	4	3	1	2	7
HdV-38	3	2	5	4	2	3	3
HdV-92	0	0	3	3	5	9	5
HdV-98	0	2	2	0	1	0	0
HdV-120	2	3	0	1	1	0	3
HdV-173A	0	1	0	0	1	0	1
HdV-173B	0	0	0	0	1	0	0
HdV-174	0	0	0	0	1	1	0

HdV-200	5	0	0	1	1	2	2
cf HdV-367	0	1	5	1	1	1	1
HdV-571	0	0	0	0	0	0	0
HdV-707	0	0	0	0	1	0	0
HdV-708	2	2	6	0	1	1	1
HdV-729	0	0	0	1	0	0	0
HdV-730	0	0	0	0	0	0	0
EMA-10/42	0	2	0	0	0	0	1
cf EMA-27	1	2	2	1	1	0	4
IBB-18	0	0	0	0	0	0	0
MO-6	0	0	0	0	0	0	0
TM-4008	0	0	0	0	0	0	0
cf UG-1110	0	0	0	0	2	0	1
cf UG-1141	1	0	0	0	0	0	1
Unknown multicelled (cf Sporidesmium socium)	2	1	0	0	0	0	0
Unknown multicelled (cf HdV-324)	1	5	5	0	1	1	0
Elliptic spores cf HdV-7B/82/306	25	20	30	8	16	26	23
Other ca. 10 µm Ø globose algal/fungal cells	17	8	0	0	1	3	1
Other multicelled	16	16	17	14	13	18	12
Other clustered cells	9	8	15	12	15	7	6
Indeterminable/unknown	28	35	31	42	29	32	43
Geoglossum-type	0	0	0	0	0	0	1
cf UG-1081	0	0	0	0	0	0	0
EMA-28	0	0	0	0	0	0	0
EMA-56	0	0	0	2	0	0	0
cf UG-1147	0	0	0	0	0	0	0
(other multi near to HdV-324)	0	1	0	0	0	1	0
HdV-65	0	0	3	0	1	0	0
HdV-121	0	0	0	3	1	0	0
multi-septate conidia	0	0	1	1	2	4	2

cf UG-1185	0	0	0	0	0	0	0
EMA-20	0	0	0	0	0	0	0
cf HdV-87	0	0	0	0	0	0	0
cf HdV-701	0	0	0	0	0	0	0
UG 1036 Brach	1	0	0	1	0	1	1
cf UG-1197	0	0	0	0	0	0	0
HdV-64	0	0	0	1	0	0	0
cf UG-1199	1	0	0	0	0	0	0
Spirogyra	0	0	0	0	0	0	0
cf Thielavia	0	0	0	0	0	0	0
EMA-2	0	0	0	0	0	1	1
HdV-359	0	0	0	0	0	0	0
EMA-33	0	0	0	0	0	0	0
EMA-99	0	0	0	0	0	0	0
HdV-22	0	0	0	0	1	0	0
cf UG-1153	0	0	0	0	1	0	0
HdV-65	0	1	0	0	0	0	0
cf HdV-1055	0	0	0	0	0	0	0
cf UG 1138/1148	0	0	1	1	0	0	0
cf UG-1098	0	0	0	0	0	0	0
HdV-179	0	0	0	0	0	0	1
cf UG-1105	1	0	0	0	2	0	0
cf UG-1080	0	0	0	0	0	0	0
cf UG-1147	0	0	0	0	0	0	1
cf UG-1005 Brach	0	0	0	0	0	0	0
HdV-308	0	0	0	0	0	0	0
HdV-17	0	0	0	0	0	0	0
pitted Helicosporium	0	0	1	0	0	0	0
HdV-25	0	0	0	0	0	2	0
HdV-715	0	0	0	0	0	0	0

Rivularia?	0	0	0	0	0	0	0
HdV-151	0	0	0	0	0	0	0
Allungato 553-537-521	0	0	0	0	0	0	0
Allungato 537	0	0	0	0	0	0	0
EMA-2	0	0	0	0	0	0	0
EMA-44	0	0	0	0	0	0	0
HdV-51	0	0	0	0	0	0	0
TM-015	0	0	0	0	0	0	0
HdV-10	0	0	0	0	0	1	0
HdV-334	0	0	0	0	0	0	0
HdV-90	0	0	0	0	0	0	0
cf HdV-140	0	0	0	0	0	0	0
cf HdV-381	0	0	0	0	0	0	0
HdV-365	0	0	0	0	0	0	0
HdV-83	1	0	0	0	0	0	0
cf EMA-30	0	0	0	0	0	0	0
HdV-714	0	0	0	0	0	0	0
cf UG-1311	0	0	0	0	0	0	0
HdV-18	0	0	0	1	0	0	0
cf UG-1307	0	0	0	0	0	0	0
HdV-23	0	0	0	0	0	0	0
cf UG-1111	0	0	0	0	0	0	0
HdV-119	0	0	0	0	0	0	0
HdV-152	0	0	0	1	0	0	0
HdV-360	0	0	0	0	0	0	0
cf Ellis 1139	0	0	0	0	0	0	0
HdV-99	0	0	0	0	0	0	0
cf UG-1053	1	0	0	0	0	0	0
cf HdV-361	0	0	0	0	0	0	0
cf UG-1203	0	0	0	0	0	0	0

EMA-86	0	0	0	0	0	0	0
EMA-134	0	0	0	0	0	1	0
HdV-33B	0	0	0	0	0	0	0
HdV-5	0	0	0	0	0	0	0
cf UG-1125	0	0	0	0	0	0	0
cf UG-1285	0	0	0	0	0	0	0
Miola III,24	0	0	0	0	0	0	0
cf UG-1221	0	0	0	0	0	0	0
LCE-27	0	0	0	0	0	0	0
HdV-23	0	0	0	0	0	0	0
cf Ellis 771	0	0	0	0	0	0	0
cf UG-1319	0	0	0	0	0	0	0
HdV-10	0	0	0	0	0	0	0
HdV-11	0	0	0	1	1	0	0
cf UG-1110 non septate	0	0	0	0	0	0	0
cf UG-1032 smooth	0	0	0	0	0	0	0
cf UG-1155	0	1	0	0	0	0	0
cf UG-1075	0	0	0	0	0	0	0
cf UG-1091	0	0	0	0	0	0	0
HdV-502	1	0	0	0	0	0	0
cf T.1162	0	0	0	0	0	0	0
HdV-53	0	0	0	0	0	0	0
HdV-85	0	0	0	1	0	0	0
cf UG-1194	0	0	0	0	1	0	0
cf UG-1124	0	0	0	0	0	0	0
cf UG-1061	0	0	0	0	0	0	0
cf UG-1182	0	0	0	0	0	0	0
cf UG-1106	0	0	0	0	0	0	0
cf Ellis 1046	0	0	0	0	0	0	0
Ellis 589	0	0	0	0	0	0	0

cf EMA-21	0	0	0	0	0	0	0
cf UG-1059	0	2	0	0	0	0	1
HdV-95	0	0	0	0	0	0	0
cf UG-1122	0	0	0	0	0	0	0
cf UG-1352	0	0	0	0	0	0	0
Ellis 355	0	0	0	0	0	0	0
Dydimella D	0	0	0	0	0	0	0
HdV-47	0	0	0	0	0	0	0
cf UG-1274	0	0	0	0	0	0	0
Leptospaeria K-N(but 4 cells) or UG-1112	0	0	0	0	0	0	0
cf UG 1084	1	0	0	0	0	0	0
cf UG-1042 Montagnula	1	0	0	2	1	0	0
cf Ellis 1335	2	0	0	0	0	0	0
Thielavia?	1	0	0	0	0	0	0
HdV-64	0	1	0	1	0	0	0
cf UG-1061	0	1	0	0	0	0	0
cf EMA-59	0	1	0	0	0	0	0
cf UG-1311	0	2	0	0	0	0	0
cf HdV-702	0	1	0	0	0	0	0
EMA-8	0	2	0	0	0	0	0
cf Ellis 988	0	1	0	0	0	0	0
cf 698	0	1	0	0	0	0	0
cf HdV-718	0	1	0	0	0	0	0
cf UG-1085	0	0	1	0	0	0	0
cf Ellis 1344-1796	0	0	1	0	0	0	0
Ellis 1512	0	0	1	0	0	0	0
cf HdV-1223	0	0	1	0	0	0	0
cf HdV-9	0	0	1	0	0	0	0
cf UG-1127	0	0	0	1	0	0	0
HdV-15	0	0	0	1	0	0	0

cf Ellis 326	0	0	0	1	0	0	0
cf UG-1274	0	0	0	1	0	0	0
HdV-332	0	0	0	2	0	0	0
168 (dung?)	0	0	0	0	1	0	0
cf USNP MS 3163	0	0	0	0	1	2	0
Ellis 306	0	0	0	0	1	0	0
cf UG-1138	0	0	0	0	1	0	0
HdV-306	0	0	0	0	1	0	0
HdV-242	0	0	0	0	1	0	0
HdV-124	0	0	0	0	1	0	0
cf UG-1176	0	0	0	0	4	0	0
cf Ellis 365	0	0	0	0	1	1	0
TM-036	0	0	0	0	0	1	0
cf UG-1072	0	0	0	0	0	1	1
Ellis 1096/1156/306	0	0	0	0	0	1	0
cf HdV-733	0	0	0	0	0	1	0
cf UG-1114	0	0	0	0	0	1	0
cf HdV-223	0	0	0	0	0	1	0
cf HdV-305	0	0	0	0	0	1	0
cf UG-1185	0	0	0	0	0	1	0
cf Ellis 1208	0	0	0	0	0	1	0
cf Ellis 1168	0	0	0	0	0	1	2
HdV-221	0	0	0	0	0	1	1
cf 1125	0	0	0	0	0	1	0
cf HdV-339	0	0	0	0	0	1	0
cf Ellis 793	0	0	0	0	0	0	1
cf UG-1276	0	0	0	0	0	0	1
cf Ellis 1271	0	0	0	0	0	0	1
Total	219	210	213	226	230	268	306

Fungal fruiting bodies undiff. (HdV-8)	17	19	9	4	12	10	12
Microthyrium (HdV-8B)	2	3	7	3	5	1	3
HdV-8A	0	1	1	0	0	2	0
HdV-8E	0	1	0	0	0	0	0
HdV-8F	0	0	0	0	0	0	0
HdV-8D	0	0	0	0	0	0	0
Bryophyte capsules	0	0	0	0	0	0	0
Other zoological	21	19	9	13	14	15	10
Chironomidae	0	2	4	2	5	2	2
Neorhabdocoela eggs	0	0	0	0	1	2	4
HdV-52 (body fragments)	0	1	0	0	0	3	0
Arcella	0	0	0	0	0	0	0
Tracheids (EMA-1)	106	70	68	63	37	147	30
Highly corroded wood (EMA-7)	14	16	10	20	14	6	16
Wood rays aggregates (EMA-11)	23	19	17	20	17	25	42
Hardwood periderm (EMA-16)	4	2	5	4	3	3	4
Fungal tissue (EMA-95)	72	50	61	43	51	30	65
Lycopodium	147	63	83	43	67	29	135

Genoa Piazza Vittoria	**DEPTHS (cm)**									
TAXA	441	457	473	489	505	521	537	553	569	585
HdV-128B	0	0	0	0	0	0	0	0	0	0
HdV-181	8	17	7	8	7	11	11	15	11	9
HdV-115	0	0	1	0	0	0	0	0	0	0
Pediastrum cf boryanum	17	10	39	4	13	16	8	8	1	1
Zygnema-type	0	0	0	0	0	0	0	0	0	0
Tetraedron (HdV-371)	0	0	1	0	0	0	0	0	0	0
Cirrenalia donnae	10	39	2	14	21	13	17	13	33	11
cf Cirrenalia lignicola/macrocephala	0	0	0	0	0	0	0	0	0	0
Endophragmia/Arthrobotris (HdV-572)	3	8	6	8	17	4	18	21	16	7
Coniochaeta	2	6	5	6	8	2	8	5	0	4
Rosellinia	0	0	4	8	1	2	4	0	0	1
Hypoxylon	1	1	0	0	0	2	1	1	1	0
Xylariaceae	5	2	6	11	3	6	6	4	1	4
Endophragmiella (TM-009)	0	0	0	1	0	0	0	0	0	0
Endophragmiella (TM-224)	0	0	0	0	1	1	0	0	0	0
Endophragmiella (TM-227)	1	1	0	0	0	0	0	0	1	0
Sporidesmium cf pedunculatum/altum	0	2	2	1	2	1	4	1	2	1
Dyctiosporium cf turuloides	0	0	0	0	0	0	0	1	1	1
Trichocladium opacum (TM-011)	0	1	2	0	0	0	0	0	1	0
Brachysporium obovatum (TM-014)	0	0	1	0	0	0	0	0	1	0
Corynesporopsis quercicola (EMA-125)	0	0	0	0	0	1	1	0	1	1
cf Taeniolella rudis	0	1	0	0	0	0	0	0	0	0
Taeniolella cf pulvillus/alta	0	0	0	0	0	0	0	0	0	0
Diplocladiella scalaroides	0	0	0	0	0	0	0	0	0	0
cf Savoryella lignicola (UG-1118)	0	0	0	1	0	0	0	0	0	0
Asterosporium asterospermum	0	0	0	1	0	0	0	0	0	0
Helicomyces/Helicosporium spp.	0	0	0	0	1	0	0	0	0	3
cf Canalisporium	0	0	0	0	0	0	0	0	0	0

Lophiostoma arundinis	1	0	0	0	0	1	1	0	0	1
cf Ulocladium consortiale	0	0	0	0	0	0	0	0	0	0
Spegazzinia	0	0	0	1	0	0	0	0	0	0
Sporormiella-type	2	0	0	2	2	0	0	0	0	0
Sordaria-type (HdV-55A)	0	0	1	1	0	0	1	0	0	0
Sordaria cf fimicola (gel. sheath)	0	0	1	0	0	0	0	0	0	0
Arnium-type	0	0	0	0	0	0	0	0	1	0
Arnium-type (gel. sheath)	0	1	0	0	0	0	0	0	0	0
cf Arnium imitans	0	0	1	0	0	0	0	0	0	0
Delitschia	0	0	0	0	0	0	1	0	0	0
Chaetomium	1	0	0	0	0	0	0	0	0	0
Gelasinospora cf tetrasperma	0	0	0	0	0	1	0	0	0	0
Apiosordaria verruculosa	0	0	0	0	0	0	0	0	0	0
Melanosporaceae (HdV-55B)	3	4	2	2	3	0	1	1	4	0
Sphaerodes cf fimicola	0	1	0	0	0	0	0	0	0	0
Persiciospora cf moreaui	0	0	0	0	0	0	0	0	0	0
Sordariaceous' ascospores undiff.	0	0	0	0	0	1	1	0	1	0
Cercophora-type	4	1	1	1	0	1	6	1	2	2
Clasterosporium caricinum	1	0	7	5	0	1	1	0	0	2
Kretzschmaria deusta	0	0	0	1	0	0	1	0	0	0
Diporotheca rhizophila	0	1	0	0	0	0	0	0	0	1
Glomus	3	6	4	1	2	7	2	5	1	6
Scleroderma	0	2	4	24	2	2	0	0	0	1
HdV-340	1	0	1	0	0	0	0	0	0	1
cf Ustilago enneapogonis/bullata	0	1	2	5	1	3	2	2	6	3
cf Lactarius (HdV-728)	0	1	1	0	0	1	0	1	0	0
cf Scutellinia hyperborea/minor	0	0	2	0	0	1	1	0	0	0
Sphaerodes	0	0	0	0	0	1	0	1	0	0
UR-1	4	1	6	5	7	8	11	9	13	8
UR-2	0	0	1	1	0	0	0	0	0	0

HdV-3A	0	0	0	1	0	2	1	1	0	1
HdV-3B	0	1	0	0	3	4	2	3	1	7
HdV-16A	0	0	0	0	2	0	0	2	0	0
HdV-16C	0	0	0	0	0	0	0	0	0	0
HdV-20	0	1	4	3	2	2	4	0	1	3
HdV-38	1	2	1	0	1	1	2	6	1	2
HdV-92	0	1	0	0	1	1	1	2	0	2
HdV-98	0	1	6	0	1	1	0	8	1	1
HdV-120	3	3	4	5	11	5	3	2	3	0
HdV-173A	0	0	0	0	0	0	2	0	1	0
HdV-173B	0	0	0	0	0	0	0	0	0	0
HdV-174	0	0	2	0	0	0	0	0	0	0
HdV-200	2	1	2	5	2	3	3	2	2	1
cf HdV-367	2	0	0	1	1	0	1	1	2	3
HdV-571	0	0	0	1	0	0	0	0	0	0
HdV-707	0	1	1	1	0	1	0	0	0	0
HdV-708	4	8	2	0	3	3	11	7	5	1
HdV-729	0	1	3	0	2	0	0	0	1	0
HdV-730	0	1	0	0	0	0	0	0	0	1
EMA-10/42	0	0	1	0	1	2	4	0	0	0
cf EMA-27	1	2	6	2	7	2	5	4	3	4
IBB-18	0	0	1	0	0	0	0	0	0	0
MO-6	0	0	0	0	0	0	0	0	0	0
TM-4008	0	0	0	1	1	0	0	0	0	0
cf UG-1110	0	0	0	1	0	0	1	1	0	0
cf UG-1141	0	0	0	2	1	1	1	1	1	0
Unknown multicelled (cf Sporidesmium socium)	14	1	0	0	0	1	0	0	3	0
Unknown multicelled (cf HdV-324)	1	0	1	1	4	5	0	2	1	1
Elliptic spores cf HdV-7B/82/306	39	29	17	33	34	18	22	18	13	27

Other ca. 10 µm Ø globose algal/fungal cells	18	3	5	11	4	1	3	4	6	4
Other multicelled	28	27	28	23	16	22	27	28	22	31
Other clustered cells	8	0	15	13	7	5	6	11	7	5
Indeterminable/unknown	35	42	14	31	37	28	27	11	38	33
Geoglossum-type	0	0	1	0	0	0	0	0	0	0
cf UG-1081	1	0	0	0	0	0	0	0	0	0
EMA-28	1	0	1	0	0	0	0	0	0	0
EMA-56	1	0	0	0	0	0	0	1	0	0
cf UG-1147	1	0	0	0	0	0	0	0	0	0
(other multi near to HdV-324)	4	0	0	1	0	1	1	0	0	1
HdV-65	1	0	0	0	0	3	1	0	0	0
HdV-121	1	0	2	2	1	0	0	0	0	1
multi-septate conidia	2	1	0	1	1	1	1	1	0	1
cf UG-1185	1	0	0	0	0	0	0	0	0	0
EMA-20	0	1	1	0	2	2	0	0	0	0
cf HdV-87	0	1	0	0	0	0	0	0	0	0
cf HdV-701	0	1	0	0	0	0	0	0	0	0
UG 1036 Brach	0	1	2	0	0	0	0	0	1	0
cf UG-1197	0	1	0	1	0	0	0	0	1	2
HdV-64	0	1	0	0	0	0	1	0	1	0
cf UG-1199	0	1	0	0	0	0	0	0	0	0
Spirogyra	0	2	1	0	0	0	0	1	0	1
cf Thielavia	0	1	0	0	0	0	0	0	0	0
EMA-2	0	0	1	0	0	0	0	0	0	0
HdV-359	0	0	1	2	0	0	1	0	0	0
EMA-33	0	0	1	0	0	0	0	0	0	0
EMA-99	0	0	1	0	0	0	0	0	0	0
HdV-22	0	0	1	0	0	0	0	0	0	1
cf UG-1153	0	0	1	0	0	0	0	0	0	0
HdV-65	0	0	4	1	0	0	0	2	0	1

cf HdV-1055	0	0	0	1	0	0	0	0	0	0
cf UG 1138/1148	0	0	0	1	0	0	0	0	0	0
cf UG-1098	0	0	0	1	0	0	0	0	0	0
HdV-179	0	0	0	1	0	0	0	0	1	0
cf UG-1105	0	0	0	1	1	1	0	0	0	2
cf UG-1080	0	0	0	0	1	0	0	0	0	0
cf UG-1147	0	0	0	0	1	1	0	0	0	0
cf UG-1005 Brach	0	0	0	0	1	0	0	0	0	0
HdV-308	0	0	0	0	2	0	0	0	0	0
HdV-17	0	0	0	0	1	0	1	0	0	1
pitted Helicosporium	0	0	0	0	1	0	0	0	0	0
HdV-25	0	0	0	0	0	1	0	0	0	0
HdV-715	0	0	0	0	0	1	0	0	0	0
Rivularia?	0	0	0	0	0	1	1	0	0	0
HdV-151	0	0	0	0	0	1	1	0	0	1
Allungato 553-537-521	0	0	0	0	0	1	1	1	0	0
Allungato 537	0	0	0	0	0	0	1	0	0	0
EMA-2	0	0	0	0	0	0	2	0	0	0
EMA-44	0	0	0	0	0	0	1	0	0	0
HdV-51	0	0	0	0	0	0	0	1	0	0
TM-015	0	0	0	0	0	0	0	0	1	0
HdV-10	0	0	0	0	0	0	0	0	1	0
HdV-334	0	0	0	0	0	0	0	0	0	1
HdV-90	0	0	0	0	0	0	0	0	0	1
cf HdV-140	0	0	0	0	0	0	0	0	0	1
cf HdV-381	0	0	0	0	0	0	0	0	0	0
HdV-365	0	0	0	0	0	0	0	0	0	0
HdV-83	0	0	0	0	0	0	0	0	0	0
cf EMA-30	0	0	0	0	0	0	0	0	0	0
HdV-714	0	0	0	0	0	0	0	0	0	0

cf UG-1311	0	0	0	0	0	0	0	0	0	0
HdV-18	0	0	0	0	0	0	0	0	0	0
cf UG-1307	0	0	0	0	0	0	0	0	0	0
HdV-23	0	0	0	0	0	0	0	0	0	0
cf UG-1111	0	0	0	0	0	0	0	0	0	0
HdV-119	0	0	0	0	0	0	0	0	0	0
HdV-152	0	0	0	0	0	0	0	0	0	0
HdV-360	0	0	0	0	0	0	0	0	0	0
cf Ellis 1139	0	0	0	0	0	0	0	0	0	0
HdV-99	0	0	0	0	0	0	0	0	0	0
cf UG-1053	0	0	0	0	0	0	0	0	0	0
cf HdV-361	0	0	0	0	0	0	0	0	0	0
cf UG-1203	0	0	0	0	0	0	0	0	0	0
EMA-86	0	0	0	0	0	0	0	0	0	0
EMA-134	0	0	0	0	0	0	0	0	0	0
HdV-33B	0	0	0	0	0	0	0	0	0	0
HdV-5	0	0	0	0	0	0	0	0	0	0
cf UG-1125	0	0	0	0	0	0	0	0	0	0
cf UG-1285	0	0	0	0	0	0	0	0	0	0
Miola III,24	0	0	0	0	0	0	0	0	0	0
cf UG-1221	0	0	0	0	0	0	0	0	0	0
LCE-27	0	0	0	0	0	0	0	0	0	0
HdV-23	0	0	0	0	0	0	0	0	0	0
cf Ellis 771	0	0	0	0	0	0	0	0	0	0
cf UG-1319	0	0	0	0	0	0	0	0	0	0
HdV-10	0	0	0	0	0	0	0	0	0	0
HdV-11	0	0	0	0	0	0	0	0	0	0
cf UG-1110 non septate	0	0	0	0	0	0	0	0	0	0
cf UG-1032 smooth	0	0	0	0	0	0	0	0	0	0
cf UG-1155	0	0	0	0	0	0	0	0	0	0

cf UG-1075	0	0	0	0	0	0	0	0	0	0
cf UG-1091	0	0	0	0	0	0	0	0	0	0
HdV-502	0	0	0	0	0	0	0	0	0	0
cf T.1162	0	0	0	0	0	0	0	0	0	0
HdV-53	0	0	0	0	0	0	0	0	0	0
HdV-85	0	0	0	0	0	0	0	0	0	0
cf UG-1194	0	0	0	0	0	0	0	0	0	0
cf UG-1124	0	0	0	0	0	0	0	0	0	0
cf UG-1061	0	0	0	0	0	0	0	0	0	0
cf UG-1182	0	0	0	0	0	0	0	0	0	0
cf UG-1106	0	0	0	0	0	0	0	0	0	0
cf Ellis 1046	0	0	0	0	0	0	0	0	0	0
Ellis 589	0	0	0	0	0	0	0	0	0	0
cf EMA-21	0	0	0	0	0	0	0	0	0	0
cf UG-1059	0	0	0	0	0	0	1	0	0	0
HdV-95	0	0	0	0	0	0	0	0	0	0
cf UG-1122	0	0	0	0	0	0	0	0	0	0
cf UG-1352	0	0	0	0	0	0	0	0	0	0
Ellis 355	0	0	0	0	0	0	0	0	0	0
Dydimella D	0	0	0	0	0	0	0	0	0	0
HdV-47	0	0	0	0	0	0	0	0	0	0
cf UG-1274	0	0	0	0	0	0	0	0	0	0
Leptospaeria K-N(but 4 cells) or UG-1112	0	0	0	0	0	0	0	0	0	0
cf UG 1084	0	0	0	0	0	0	0	0	0	0
cf UG-1042 Montagnula	0	0	0	0	0	0	0	0	0	0
cf Ellis 1335	0	0	0	0	0	0	0	0	0	0
Thielavia?	0	0	0	0	0	0	0	0	0	0
HdV-64	0	0	0	0	0	0	0	0	0	0
cf UG-1061	0	0	0	0	0	0	0	0	0	0
cf EMA-59	0	0	0	0	0	0	0	0	0	0

cf UG-1311	0	0	0	0	0	0	0	0	0	0
cf HdV-702	0	0	0	0	0	0	0	0	0	0
EMA-8	0	0	0	0	0	0	0	0	0	0
cf Ellis 988	0	0	0	0	0	0	0	0	0	0
cf 698	0	0	0	0	0	0	0	0	0	0
cf HdV-718	0	0	0	0	0	0	0	0	0	0
cf UG-1085	0	0	0	0	0	0	0	0	0	0
cf Ellis 1344-1796	0	0	0	0	0	0	0	0	0	0
Ellis 1512	0	0	0	0	0	0	0	0	0	0
cf HdV-1223	0	0	0	0	0	0	0	0	0	0
cf HdV-9	0	0	0	0	0	0	0	0	0	0
cf UG-1127	0	0	0	0	0	0	0	0	0	0
HdV-15	0	0	0	0	0	0	0	0	0	0
cf Ellis 326	0	0	0	0	0	0	0	0	0	0
cf UG-1274	0	0	0	0	0	0	0	0	0	0
HdV-332	0	0	0	0	0	0	0	0	0	0
168 (dung?)	0	0	0	0	0	0	0	0	0	0
cf USNP MS 3163	0	0	0	0	0	0	0	0	0	0
Ellis 306	0	0	0	0	0	0	0	0	0	0
cf UG-1138	0	0	0	0	0	0	0	0	0	0
HdV-306	0	0	0	0	0	0	0	0	0	0
HdV-242	0	0	0	0	0	0	0	0	0	0
HdV-124	0	0	0	0	0	0	0	0	0	0
cf UG-1176	0	0	0	0	0	0	0	0	0	0
cf Ellis 365	0	0	0	0	0	0	0	0	0	0
TM-036	0	0	0	0	0	0	0	0	0	0
cf UG-1072	0	0	0	0	0	0	0	0	0	0
Ellis 1096/1156/306	0	0	0	0	0	0	0	0	0	0
cf HdV-733	0	0	0	0	0	0	0	0	0	0
cf UG-1114	0	0	0	0	0	0	0	0	0	0

cf HdV-223	0	0	0	0	0	0	0	0	0	0
cf HdV-305	0	0	0	0	0	0	0	0	0	0
cf UG-1185	0	0	0	0	0	0	0	0	0	0
cf Ellis 1208	0	0	0	0	0	0	0	0	0	0
cf Ellis 1168	0	0	0	0	0	0	0	0	0	0
HdV-221	0	0	0	0	0	0	0	0	0	0
cf 1125	0	0	0	0	0	0	0	0	0	0
cf HdV-339	0	0	0	0	0	0	0	0	0	0
cf Ellis 793	0	0	0	0	0	0	0	0	0	0
cf UG-1276	0	0	0	0	0	0	0	0	0	0
cf Ellis 1271	0	0	0	0	0	0	0	0	0	0
Total	236	243	241	260	244	209	247	210	216	210
Fungal fruiting bodies undiff. (HdV-8)	12	15	11	10	15	15	29	16	14	19
Microthyrium (HdV-8B)	0	2	0	0	0	2	2	4	1	3
HdV-8A	0	1	0	0	0	0	0	0	0	0
HdV-8E	0	0	0	0	0	0	0	0	0	0
HdV-8F	1	1	1	1	0	0	0	0	0	0
HdV-8D	0	0	0	0	0	0	0	1	2	2
Bryophyte capsules	0	0	0	1	0	1	0	0	0	0
Other zoological	26	17	18	4	21	21	24	11	15	10
Chironomidae	10	1	1	2	5	2	1	6	2	5
Neorhabdocoela eggs	0	0	1	0	0	1	1	0	0	0
HdV-52 (body fragments)	0	0	0	0	0	0	1	0	0	0
Arcella	0	0	0	0	1	0	0	1	0	0
Tracheids (EMA-1)	64	124	102	45	54	67	88	96	63	109

Highly corroded wood (EMA-7)	7	11	2	2	0	3	0	3	1	5
Wood rays aggregates (EMA-11)	15	12	23	9	11	29	11	19	28	12
Hardwood periderm (EMA-16)	8	9	2	8	1	6	6	10	3	7
Fungal tissue (EMA-95)	95	90	66	65	49	56	85	90	68	47
Lycopodium	320	297	197	60	55	105	92	45	141	20
TAXA	601	609	617	625	633	641	649	657	665	673
HdV-128B	0	0	0	1	1	2	4	0	4	7
HdV-181	11	8	11	17	19	27	7	11	8	3
HdV-115	0	2	0	0	0	0	1	0	1	0
Pediastrum cf boryanum	25	0	1	4	0	1	5	0	3	3
Zygnema-type	0	0	0	0	1	0	0	0	0	0
Tetraedron (HdV-371)	0	0	0	0	0	0	0	0	0	0
Cirrenalia donnae	7	22	18	29	17	31	17	18	22	24
cf Cirrenalia lignicola/macrocephala	0	0	0	0	1	0	0	0	0	0
Endophragmia/Arthrobotris (HdV-572)	4	10	9	14	6	7	14	8	7	12
Coniochaeta	3	4	2	2	6	2	1	3	7	6
Rosellinia	0	4	3	4	2	1	2	0	1	0
Hypoxylon	0	0	2	0	2	2	2	3	4	3
Xylariaceae	1	6	10	2	3	3	3	3	4	1
Endophragmiella (TM-009)	0	0	0	0	0	0	0	0	0	2
Endophragmiella (TM-224)	1	1	0	1	1	1	0	0	0	0
Endophragmiella (TM-227)	0	1	1	1	0	0	0	0	0	1
Sporidesmium cf pedunculatum/altum	1	1	1	2	2	1	2	0	2	2
Dyctiosporium cf turuloides	0	1	2	0	0	0	0	0	1	0
Trichocladium opacum (TM-011)	0	1	0	2	3	2	0	1	0	1
Brachysporium obovatum (TM-014)	0	0	0	0	0	0	0	0	0	0

Corynesporopsis quercicola (EMA-125)	1	2	2	1	0	0	1	2	0	1
cf Taeniolella rudis	0	0	0	0	0	0	0	0	0	0
Taeniolella cf pulvillus/alta	0	0	0	0	0	0	0	0	0	0
Diplocladiella scalaroides	0	1	0	0	0	0	0	0	0	0
cf Savoryella lignicola (UG-1118)	0	0	0	1	0	0	0	0	0	0
Asterosporium asterospermum	0	0	0	0	0	0	0	0	0	0
Helicomyces/Helicosporium spp.	1	0	0	0	0	0	0	0	1	0
cf Canalisporium	0	0	0	0	0	0	0	0	0	0
Lophiostoma arundinis	0	1	0	1	1	1	1	0	0	0
cf Ulocladium consortiale	0	0	0	0	0	0	0	0	0	0
Spegazzinia	0	0	0	0	0	0	0	0	0	1
Sporormiella-type	0	1	0	0	0	0	0	0	0	1
Sordaria-type (HdV-55A)	0	0	0	0	0	0	2	0	0	1
Sordaria cf fimicola (gel. sheath)	0	0	0	0	0	0	0	0	1	0
Arnium-type	1	0	0	0	0	0	0	0	0	0
Arnium-type (gel. sheath)	0	0	0	0	0	0	0	0	0	0
cf Arnium imitans	0	0	0	0	0	0	0	0	0	0
Delitschia	0	0	0	2	0	0	1	0	1	0
Chaetomium	0	0	0	0	0	0	0	0	1	0
Gelasinospora cf tetrasperma	0	0	0	0	0	0	0	0	0	0
Apiosordaria verruculosa	0	0	0	0	0	0	0	0	0	0
Melanosporaceae (HdV-55B)	0	2	2	0	2	1	1	0	0	2
Sphaerodes cf fimicola	0	0	0	0	0	0	0	0	0	0
Persiciospora cf moreaui	0	0	0	0	0	0	0	0	1	0
Sordariaceous' ascospores undiff.	1	0	0	1	0	0	0	0	0	0
Cercophora-type	0	0	1	2	2	1	1	0	2	4
Clasterosporium caricinum	3	6	3	2	1	4	5	8	2	5
Kretzschmaria deusta	0	0	1	0	1	0	0	1	0	0
Diporotheca rhizophila	1	0	0	0	0	0	0	0	0	0
Glomus	5	8	3	1	4	3	3	1	1	3

Scleroderma	3	0	1	0	3	0	3	5	0	1
HdV-340	0	1	1	0	0	0	0	1	1	0
cf Ustilago enneapogonis/bullata	2	1	0	1	2	2	0	7	2	1
cf Lactarius (HdV-728)	0	0	0	0	0	0	0	1	0	0
cf Scutellinia hyperborea/minor	0	0	0	0	0	0	1	0	0	0
Sphaerodes	0	0	0	0	0	0	0	0	0	0
UR-1	4	9	11	4	14	8	12	4	9	7
UR-2	0	1	0	0	1	3	0	0	0	1
HdV-3A	0	0	0	0	0	0	1	0	0	0
HdV-3B	2	2	1	1	2	1	1	3	1	3
HdV-16A	0	0	0	2	0	0	0	0	0	0
HdV-16C	0	0	0	0	0	0	0	0	0	1
HdV-20	2	1	1	3	2	3	0	0	2	2
HdV-38	0	2	2	1	4	4	7	8	2	4
HdV-92	0	0	1	0	2	2	2	3	1	2
HdV-98	1	0	1	2	5	0	1	0	2	2
HdV-120	0	0	0	0	2	2	0	2	2	1
HdV-173A	0	0	0	0	0	2	1	0	0	0
HdV-173B	0	0	0	0	0	0	0	0	0	0
HdV-174	0	0	0	0	0	0	1	2	0	0
HdV-200	4	1	2	0	1	3	1	1	5	2
cf HdV-367	1	1	2	0	0	2	1	0	2	1
HdV-571	0	0	0	0	0	0	0	0	0	0
HdV-707	0	0	1	0	0	0	1	3	0	0
HdV-708	5	6	6	6	0	4	0	0	1	4
HdV-729	1	0	1	2	0	0	0	0	0	0
HdV-730	0	1	0	0	0	0	0	0	0	0
EMA-10/42	1	2	1	0	0	1	0	0	1	0
cf EMA-27	4	3	9	4	7	2	5	4	12	1
IBB-18	0	0	0	0	0	0	0	0	0	1

MO-6	0	0	0	1	0	0	0	0	0	0
TM-4008	0	0	0	0	0	0	0	0	0	0
cf UG-1110	1	0	1	2	0	1	0	0	0	0
cf UG-1141	0	1	1	2	2	2	0	2	0	0
Unknown multicelled (cf Sporidesmium socium)	1	1	1	0	2	0	0	1	0	0
Unknown multicelled (cf HdV-324)	1	5	3	0	1	4	4	9	6	5
Elliptic spores cf HdV-7B/82/306	22	16	23	15	29	41	20	25	16	19
Other ca. 10 µm Ø globose algal/fungal cells	17	3	2	0	5	15	18	10	12	7
Other multicelled	28	26	30	33	22	36	31	24	27	13
Other clustered cells	9	9	14	8	12	9	4	7	2	15
Indeterminable/unknown	32	23	16	18	15	30	21	17	26	12
Geoglossum-type	0	0	0	1	0	0	0	0	0	1
cf UG-1081	0	0	0	0	0	0	0	0	0	0
EMA-28	0	0	0	0	0	0	0	0	2	0
EMA-56	0	1	1	2	0	0	0	0	0	0
cf UG-1147	0	0	0	0	0	0	0	0	0	0
(other multi near to HdV-324)	0	1	1	0	1	0	0	0	1	0
HdV-65	0	0	0	0	0	0	0	0	0	1
HdV-121	1	0	0	0	0	2	0	0	0	0
multi-septate conidia	0	0	0	2	2	3	1	2	2	2
cf UG-1185	0	0	0	0	0	0	0	0	0	0
EMA-20	0	0	0	0	0	0	0	0	0	0
cf HdV-87	0	0	0	0	0	0	0	0	0	0
cf HdV-701	0	0	0	0	0	0	0	0	0	0
UG 1036 Brach	0	1	0	0	0	1	2	1	0	2
cf UG-1197	2	1	0	0	0	0	0	0	0	0
HdV-64	0	0	0	1	1	0	0	0	0	0
cf UG-1199	0	0	0	0	0	0	0	0	0	0
Spirogyra	0	1	0	0	0	0	0	0	0	0

cf Thielavia	0	0	0	0	0	0	0	0	0	0
EMA-2	0	1	0	0	0	0	0	0	0	1
HdV-359	0	1	0	0	0	0	0	0	0	0
EMA-33	0	0	0	0	0	0	0	0	0	0
EMA-99	0	0	0	0	0	0	0	0	0	0
HdV-22	0	0	0	0	0	1	0	1	0	0
cf UG-1153	0	0	0	0	0	1	0	0	0	0
HdV-65	0	1	0	0	0	0	0	0	0	0
cf HdV-1055	0	0	0	0	0	0	0	0	0	0
cf UG 1138/1148	1	0	0	0	0	0	0	0	0	0
cf UG-1098	0	0	0	0	0	0	0	0	0	0
HdV-179	0	0	0	0	0	0	1	0	0	0
cf UG-1105	1	1	0	0	0	0	4	0	4	1
cf UG-1080	0	0	0	0	0	0	0	0	0	0
cf UG-1147	0	1	0	0	1	0	1	0	0	1
cf UG-1005 Brach	0	0	0	0	0	0	0	0	0	0
HdV-308	0	0	0	0	0	0	0	0	0	0
HdV-17	1	0	1	0	0	0	0	0	0	0
pitted Helicosporium	0	0	0	0	0	0	0	0	0	0
HdV-25	0	0	0	0	0	0	0	0	0	0
HdV-715	0	0	0	0	0	0	0	0	0	0
Rivularia?	0	0	0	0	0	0	0	0	0	0
HdV-151	0	0	0	0	0	0	0	0	0	0
Allungato 553-537-521	0	0	0	0	0	0	0	0	0	0
Allungato 537	0	0	0	0	0	0	0	0	0	0
EMA-2	0	0	0	0	0	0	1	0	0	0
EMA-44	0	0	0	0	0	0	0	0	0	0
HdV-51	0	0	0	0	0	0	0	0	0	0
TM-015	0	0	0	0	0	0	0	0	0	0
HdV-10	0	0	0	0	0	0	0	0	0	0

HdV-334	0	0	0	0	0	0	0	0	0	0
HdV-90	0	0	0	2	0	0	0	0	0	0
cf HdV-140	1	0	0	0	0	0	1	0	0	0
cf HdV-381	1	0	0	0	0	0	0	0	0	0
HdV-365	1	0	0	1	0	0	1	0	0	0
HdV-83	0	1	0	0	0	0	2	0	0	1
cf EMA-30	0	1	0	0	0	0	0	0	0	0
HdV-714	0	1	0	0	0	0	0	0	1	0
cf UG-1311	0	1	0	0	0	0	0	0	0	0
HdV-18	0	1	1	0	0	0	0	0	0	0
cf UG-1307	0	1	0	0	0	0	0	0	0	0
HdV-23	0	0	1	0	0	0	0	0	0	0
cf UG-1111	0	0	1	0	0	0	0	0	0	0
HdV-119	0	0	1	0	0	0	0	0	0	0
HdV-152	0	0	1	0	0	0	0	0	0	0
HdV-360	0	0	1	0	0	0	0	0	0	0
cf Ellis 1139	0	0	1	0	0	0	0	0	0	0
HdV-99	0	0	1	0	0	0	0	0	0	0
cf UG-1053	0	0	1	0	0	0	0	0	0	1
cf HdV-361	0	0	0	1	0	0	0	0	0	0
cf UG-1203	0	0	0	1	0	0	0	0	0	0
EMA-86	0	0	0	1	1	0	0	2	0	2
EMA-134	0	0	0	1	0	0	0	0	0	0
HdV-33B	0	0	0	1	0	0	0	0	0	0
HdV-5	0	0	0	1	0	0	0	0	0	0
cf UG-1125	0	0	0	1	0	0	0	0	0	0
cf UG-1285	0	0	0	0	1	0	0	0	0	0
Miola III,24	0	0	0	0	1	0	0	0	0	0
cf UG-1221	0	0	0	0	0	1	0	0	0	0
LCE-27	0	0	0	0	0	1	0	0	0	0

HdV-23	0	0	0	0	0	1	0	0	0	0
cf Ellis 771	0	0	0	0	0	1	0	0	0	0
cf UG-1319	0	0	0	0	0	1	0	0	0	2
HdV-10	0	0	0	0	0	0	1	0	0	0
HdV-11	0	0	0	0	0	0	1	0	0	0
cf UG-1110 non septate	0	0	0	0	0	0	1	0	0	0
cf UG-1032 smooth	0	0	0	0	0	0	1	0	0	0
cf UG-1155	0	0	0	0	0	0	1	0	0	0
cf UG-1075	0	0	0	0	0	0	0	1	0	0
cf UG-1091	0	0	0	0	0	0	0	1	0	0
HdV-502	0	0	0	0	0	0	0	1	0	0
cf T.1162	0	0	0	0	0	0	0	1	0	0
HdV-53	0	0	0	0	0	0	0	2	0	0
HdV-85	0	0	0	0	0	0	0	1	0	0
cf UG-1194	0	0	0	0	0	0	0	1	0	0
cf UG-1124	0	0	0	0	0	0	0	0	1	0
cf UG-1061	0	0	0	0	0	0	0	0	2	0
cf UG-1182	0	0	0	0	0	0	0	0	1	0
cf UG-1106	0	0	0	0	0	0	0	0	1	0
cf Ellis 1046	0	0	0	0	0	0	0	0	1	0
Ellis 589	0	0	0	0	0	0	0	0	1	0
cf EMA-21	0	0	0	0	0	0	0	0	1	0
cf UG-1059	1	0	0	0	0	1	0	1	0	1
HdV-95	0	0	0	0	0	0	0	0	0	1
cf UG-1122	0	0	0	0	0	0	0	0	0	1
cf UG-1352	0	0	0	0	0	0	0	0	0	1
Ellis 355	0	0	0	0	0	0	0	0	0	1
Dydimella D	0	0	0	0	0	0	0	0	0	1
HdV-47	0	0	0	0	0	0	0	0	0	1
cf UG-1274	0	0	0	0	0	0	0	0	0	1

Leptospaeria K-N(but 4 cells) or UG-1112	0	0	0	0	0	0	0	0	0	1
cf UG 1084	0	0	0	0	0	0	0	0	0	0
cf UG-1042 Montagnula	0	0	0	0	0	0	0	0	0	0
cf Ellis 1335	0	0	0	0	0	0	0	0	0	0
Thielavia?	0	0	0	0	0	0	0	0	0	0
HdV-64	0	0	0	0	0	0	0	0	0	0
cf UG-1061	0	0	0	0	0	0	0	0	0	0
cf EMA-59	0	0	0	0	0	0	0	0	0	0
cf UG-1311	0	0	0	0	0	0	0	0	0	0
cf HdV-702	0	0	0	0	0	0	0	0	0	0
EMA-8	0	0	0	0	0	0	0	0	0	0
cf Ellis 988	0	0	0	0	0	0	0	0	0	0
cf 698	0	0	0	0	0	0	0	0	0	0
cf HdV-718	0	0	0	0	0	0	0	0	0	0
cf UG-1085	0	0	0	0	0	0	0	0	0	0
cf Ellis 1344-1796	0	0	0	0	0	0	0	0	0	0
Ellis 1512	0	0	0	0	0	0	0	0	0	0
cf HdV-1223	0	0	0	0	0	0	0	0	0	0
cf HdV-9	0	0	0	0	0	0	0	0	0	0
cf UG-1127	0	0	0	0	0	0	0	0	0	0
HdV-15	0	0	0	0	0	0	0	0	0	0
cf Ellis 326	0	0	0	0	0	0	0	0	0	0
cf UG-1274	0	0	0	0	0	0	0	0	0	0
HdV-332	0	0	0	0	0	0	0	0	0	0
168 (dung?)	0	0	0	0	0	0	0	0	0	0
cf USNP MS 3163	0	0	0	0	0	0	0	0	0	0
Ellis 306	0	0	0	0	0	0	0	0	0	0
cf UG-1138	0	0	0	0	0	0	0	0	0	0
HdV-306	0	0	0	0	0	0	0	0	0	0
HdV-242	0	0	0	0	0	0	0	0	0	0

HdV-124	0	0	0	0	0	0	0	0	0	0
cf UG-1176	0	0	0	0	0	0	0	0	0	0
cf Ellis 365	0	0	0	0	0	0	0	0	0	0
TM-036	0	0	0	0	0	0	0	0	0	0
cf UG-1072	0	0	0	0	0	0	0	0	0	0
Ellis 1096/1156/306	0	0	0	0	0	0	0	0	0	0
cf HdV-733	0	0	0	0	0	0	0	0	0	0
cf UG-1114	0	0	0	0	0	0	0	0	0	0
cf HdV-223	0	0	0	0	0	0	0	0	0	0
cf HdV-305	0	0	0	0	0	0	0	0	0	0
cf UG-1185	0	0	0	0	0	0	0	0	0	0
cf Ellis 1208	0	0	0	0	0	0	0	0	0	0
cf Ellis 1168	0	0	0	0	0	0	0	0	0	0
HdV-221	0	0	0	0	0	0	0	0	0	0
cf 1125	0	0	0	0	0	0	0	0	0	0
cf HdV-339	0	0	0	0	0	0	0	0	0	0
cf Ellis 793	0	0	0	0	0	0	0	0	0	0
cf UG-1276	0	0	0	0	0	0	0	0	0	0
cf Ellis 1271	0	0	0	0	0	0	0	0	0	0
Total	217	213	216	211	216	281	228	213	224	212
Fungal fruiting bodies undiff. (HdV-8)	3	29	15	17	21	34	27	12	13	23
Microthyrium (HdV-8B)	4	2	1	3	6	1	0	0	3	3
HdV-8A	0	0	1	0	0	1	1	0	0	0
HdV-8E	0	0	0	0	0	0	0	0	0	0
HdV-8F	0	0	0	0	0	0	1	0	0	0
HdV-8D	0	1	0	0	1	0	0	0	0	0
Bryophyte capsules	0	0	0	0	0	0	1	0	0	0
Other zoological	33	19	15	22	9	33	24	9	9	14
Chironomidae	5	5	3	5	4	5	0	4	0	3

Neorhabdocoela eggs	0	0	0	0	0	1	1	1	1	0
HdV-52 (body fragments)	3	0	0	0	0	0	0	0	0	0
Arcella	2	0	0	0	1	0	0	0	0	0
Tracheids (EMA-1)	156	77	48	107	104	135	61	83	73	216
Highly corroded wood (EMA-7)	27	7	2	4	3	2	7	11	10	13
Wood rays aggregates (EMA-11)	17	22	15	33	21	34	23	34	22	57
Hardwood periderm (EMA-16)	10	3	2	8	11	8	8	2	5	8
Fungal tissue (EMA-95)	51	73	43	75	106	87	45	61	41	81
Lycopodium	151	59	92	68	84	154	41	32	19	61

TAXA	681	689	697	705	713	721	729
HdV-128B	13	14	13	36	47	50	79
HdV-181	3	10	9	16	8	19	7
HdV-115	0	1	1	0	0	0	0
Pediastrum cf boryanum	4	6	1	1	2	3	2
Zygnema-type	0	0	0	0	0	0	0
Tetraedron (HdV-371)	0	0	0	0	0	0	0
Cirrenalia donnae	27	10	6	8	8	13	24
cf Cirrenalia lignicola/macrocephala	0	0	0	0	0	0	0
Endophragmia/Arthrobotris (HdV-572)	4	8	2	2	4	0	5
Coniochaeta	0	1	3	1	7	3	9
Rosellinia	4	3	1	4	4	3	7

Hypoxylon	1	2	3	0	4	0	0
Xylariaceae	2	7	0	3	2	6	1
Endophragmiella (TM-009)	0	0	0	0	0	0	0
Endophragmiella (TM-224)	0	0	1	0	0	0	0
Endophragmiella (TM-227)	0	0	0	0	1	0	1
Sporidesmium cf pedunculatum/altum	3	3	4	2	2	1	11
Dyctiosporium cf turuloides	1	1	0	1	2	1	1
Trichocladium opacum (TM-011)	4	0	1	2	1	1	2
Brachysporium obovatum (TM-014)	0	0	0	0	0	0	0
Corynesporopsis quercicola (EMA-125)	1	1	0	1	0	0	0
cf Taeniolella rudis	0	0	0	0	0	0	0
Taeniolella cf pulvillus/alta	0	1	0	0	0	0	1
Diplocladiella scalaroides	0	0	0	0	0	0	0
cf Savoryella lignicola (UG-1118)	2	0	0	0	0	0	0
Asterosporium asterospermum	0	0	0	0	0	0	1
Helicomyces/Helicosporium spp.	0	0	0	0	0	0	0
cf Canalisporium	0	0	0	1	0	0	0
Lophiostoma arundinis	0	1	0	0	0	0	0
cf Ulocladium consortiale	0	0	0	0	1	0	0
Spegazzinia	0	0	0	0	0	0	0
Sporormiella-type	0	0	0	0	0	1	1
Sordaria-type (HdV-55A)	1	0	0	0	0	0	0
Sordaria cf fimicola (gel. sheath)	0	0	0	0	0	0	0
Arnium-type	0	0	0	0	0	0	0
Arnium-type (gel. sheath)	0	0	0	0	0	0	0
cf Arnium imitans	0	0	0	0	0	1	0
Delitschia	0	0	0	0	1	4	0
Chaetomium	0	0	0	0	0	1	0
Gelasinospora cf tetrasperma	0	0	0	0	0	0	0
Apiosordaria verruculosa	0	0	0	1	0	0	0

Melanosporaceae (HdV-55B)	1	0	1	3	0	2	0
Sphaerodes cf fimicola	0	0	0	0	0	0	0
Persiciospora cf moreaui	0	0	0	0	0	0	0
Sordariaceous' ascospores undiff.	0	0	0	0	0	0	1
Cercophora-type	2	1	1	1	0	1	1
Clasterosporium caricinum	2	1	3	8	3	8	3
Kretzschmaria deusta	1	0	0	0	1	0	0
Diporotheca rhizophila	0	0	0	1	0	0	0
Glomus	4	4	10	2	4	2	5
Scleroderma	3	2	5	1	3	3	1
HdV-340	0	0	0	4	1	1	0
cf Ustilago enneapogonis/bullata	2	0	3	7	0	0	0
cf Lactarius (HdV-728)	0	0	0	0	0	0	0
cf Scutellinia hyperborea/minor	0	0	0	0	1	0	0
Sphaerodes	0	0	0	0	0	0	0
UR-1	7	6	7	5	3	5	11
UR-2	2	3	2	1	0	4	2
HdV-3A	0	0	0	0	0	0	0
HdV-3B	0	0	0	0	1	2	0
HdV-16A	0	0	0	0	1	0	0
HdV-16C	1	0	0	1	0	0	0
HdV-20	1	0	4	3	1	2	7
HdV-38	3	2	5	4	2	3	3
HdV-92	0	0	3	3	5	9	5
HdV-98	0	2	2	0	1	0	0
HdV-120	2	3	0	1	1	0	3
HdV-173A	0	1	0	0	1	0	1
HdV-173B	0	0	0	0	1	0	0
HdV-174	0	0	0	0	1	1	0
HdV-200	5	0	0	1	1	2	2

cf HdV-367	0	1	5	1	1	1	1
HdV-571	0	0	0	0	0	0	0
HdV-707	0	0	0	0	1	0	0
HdV-708	2	2	6	0	1	1	1
HdV-729	0	0	0	1	0	0	0
HdV-730	0	0	0	0	0	0	0
EMA-10/42	0	2	0	0	0	0	1
cf EMA-27	1	2	2	1	1	0	4
IBB-18	0	0	0	0	0	0	0
MO-6	0	0	0	0	0	0	0
TM-4008	0	0	0	0	0	0	0
cf UG-1110	0	0	0	0	2	0	1
cf UG-1141	1	0	0	0	0	0	1
Unknown multicelled (cf Sporidesmium socium)	2	1	0	0	0	0	0
Unknown multicelled (cf HdV-324)	1	5	5	0	1	1	0
Elliptic spores cf HdV-7B/82/306	25	20	30	8	16	26	23
Other ca. 10 µm Ø globose algal/fungal cells	17	8	0	0	1	3	1
Other multicelled	16	16	17	14	13	18	12
Other clustered cells	9	8	15	12	15	7	6
Indeterminable/unknown	28	35	31	42	29	32	43
Geoglossum-type	0	0	0	0	0	0	1
cf UG-1081	0	0	0	0	0	0	0
EMA-28	0	0	0	0	0	0	0
EMA-56	0	0	0	2	0	0	0
cf UG-1147	0	0	0	0	0	0	0
(other multi near to HdV-324)	0	1	0	0	0	1	0
HdV-65	0	0	3	0	1	0	0
HdV-121	0	0	0	3	1	0	0
multi-septate conidia	0	0	1	1	2	4	2
cf UG-1185	0	0	0	0	0	0	0

EMA-20	0	0	0	0	0	0	0
cf HdV-87	0	0	0	0	0	0	0
cf HdV-701	0	0	0	0	0	0	0
UG 1036 Brach	1	0	0	1	0	1	1
cf UG-1197	0	0	0	0	0	0	0
HdV-64	0	0	0	1	0	0	0
cf UG-1199	1	0	0	0	0	0	0
Spirogyra	0	0	0	0	0	0	0
cf Thielavia	0	0	0	0	0	0	0
EMA-2	0	0	0	0	0	1	1
HdV-359	0	0	0	0	0	0	0
EMA-33	0	0	0	0	0	0	0
EMA-99	0	0	0	0	0	0	0
HdV-22	0	0	0	0	1	0	0
cf UG-1153	0	0	0	0	1	0	0
HdV-65	0	1	0	0	0	0	0
cf HdV-1055	0	0	0	0	0	0	0
cf UG 1138/1148	0	0	1	1	0	0	0
cf UG-1098	0	0	0	0	0	0	0
HdV-179	0	0	0	0	0	0	1
cf UG-1105	1	0	0	0	2	0	0
cf UG-1080	0	0	0	0	0	0	0
cf UG-1147	0	0	0	0	0	0	1
cf UG-1005 Brach	0	0	0	0	0	0	0
HdV-308	0	0	0	0	0	0	0
HdV-17	0	0	0	0	0	0	0
pitted Helicosporium	0	0	1	0	0	0	0
HdV-25	0	0	0	0	0	2	0
HdV-715	0	0	0	0	0	0	0
Rivularia?	0	0	0	0	0	0	0

HdV-151	0	0	0	0	0	0	0
Allungato 553-537-521	0	0	0	0	0	0	0
Allungato 537	0	0	0	0	0	0	0
EMA-2	0	0	0	0	0	0	0
EMA-44	0	0	0	0	0	0	0
HdV-51	0	0	0	0	0	0	0
TM-015	0	0	0	0	0	0	0
HdV-10	0	0	0	0	0	1	0
HdV-334	0	0	0	0	0	0	0
HdV-90	0	0	0	0	0	0	0
cf HdV-140	0	0	0	0	0	0	0
cf HdV-381	0	0	0	0	0	0	0
HdV-365	0	0	0	0	0	0	0
HdV-83	1	0	0	0	0	0	0
cf EMA-30	0	0	0	0	0	0	0
HdV-714	0	0	0	0	0	0	0
cf UG-1311	0	0	0	0	0	0	0
HdV-18	0	0	0	1	0	0	0
cf UG-1307	0	0	0	0	0	0	0
HdV-23	0	0	0	0	0	0	0
cf UG-1111	0	0	0	0	0	0	0
HdV-119	0	0	0	0	0	0	0
HdV-152	0	0	0	1	0	0	0
HdV-360	0	0	0	0	0	0	0
cf Ellis 1139	0	0	0	0	0	0	0
HdV-99	0	0	0	0	0	0	0
cf UG-1053	1	0	0	0	0	0	0
cf HdV-361	0	0	0	0	0	0	0
cf UG-1203	0	0	0	0	0	0	0
EMA-86	0	0	0	0	0	0	0

EMA-134	0	0	0	0	0	1	0
HdV-33B	0	0	0	0	0	0	0
HdV-5	0	0	0	0	0	0	0
cf UG-1125	0	0	0	0	0	0	0
cf UG-1285	0	0	0	0	0	0	0
Miola III,24	0	0	0	0	0	0	0
cf UG-1221	0	0	0	0	0	0	0
LCE-27	0	0	0	0	0	0	0
HdV-23	0	0	0	0	0	0	0
cf Ellis 771	0	0	0	0	0	0	0
cf UG-1319	0	0	0	0	0	0	0
HdV-10	0	0	0	0	0	0	0
HdV-11	0	0	0	1	1	0	0
cf UG-1110 non septate	0	0	0	0	0	0	0
cf UG-1032 smooth	0	0	0	0	0	0	0
cf UG-1155	0	1	0	0	0	0	0
cf UG-1075	0	0	0	0	0	0	0
cf UG-1091	0	0	0	0	0	0	0
HdV-502	1	0	0	0	0	0	0
cf T.1162	0	0	0	0	0	0	0
HdV-53	0	0	0	0	0	0	0
HdV-85	0	0	0	1	0	0	0
cf UG-1194	0	0	0	0	1	0	0
cf UG-1124	0	0	0	0	0	0	0
cf UG-1061	0	0	0	0	0	0	0
cf UG-1182	0	0	0	0	0	0	0
cf UG-1106	0	0	0	0	0	0	0
cf Ellis 1046	0	0	0	0	0	0	0
Ellis 589	0	0	0	0	0	0	0
cf EMA-21	0	0	0	0	0	0	0

cf UG-1059	0	2	0	0	0	0	1
HdV-95	0	0	0	0	0	0	0
cf UG-1122	0	0	0	0	0	0	0
cf UG-1352	0	0	0	0	0	0	0
Ellis 355	0	0	0	0	0	0	0
Dydimella D	0	0	0	0	0	0	0
HdV-47	0	0	0	0	0	0	0
cf UG-1274	0	0	0	0	0	0	0
Leptospaeria K-N(but 4 cells) or UG-1112	0	0	0	0	0	0	0
cf UG 1084	1	0	0	0	0	0	0
cf UG-1042 Montagnula	1	0	0	2	1	0	0
cf Ellis 1335	2	0	0	0	0	0	0
Thielavia?	1	0	0	0	0	0	0
HdV-64	0	1	0	1	0	0	0
cf UG-1061	0	1	0	0	0	0	0
cf EMA-59	0	1	0	0	0	0	0
cf UG-1311	0	2	0	0	0	0	0
cf HdV-702	0	1	0	0	0	0	0
EMA-8	0	2	0	0	0	0	0
cf Ellis 988	0	1	0	0	0	0	0
cf 698	0	1	0	0	0	0	0
cf HdV-718	0	1	0	0	0	0	0
cf UG-1085	0	0	1	0	0	0	0
cf Ellis 1344-1796	0	0	1	0	0	0	0
Ellis 1512	0	0	1	0	0	0	0
cf HdV-1223	0	0	1	0	0	0	0
cf HdV-9	0	0	1	0	0	0	0
cf UG-1127	0	0	0	1	0	0	0
HdV-15	0	0	0	1	0	0	0
cf Ellis 326	0	0	0	1	0	0	0

cf UG-1274	0	0	0	1	0	0	0
HdV-332	0	0	0	2	0	0	0
168 (dung?)	0	0	0	0	1	0	0
cf USNP MS 3163	0	0	0	0	1	2	0
Ellis 306	0	0	0	0	1	0	0
cf UG-1138	0	0	0	0	1	0	0
HdV-306	0	0	0	0	1	0	0
HdV-242	0	0	0	0	1	0	0
HdV-124	0	0	0	0	1	0	0
cf UG-1176	0	0	0	0	4	0	0
cf Ellis 365	0	0	0	0	1	1	0
TM-036	0	0	0	0	0	1	0
cf UG-1072	0	0	0	0	0	1	1
Ellis 1096/1156/306	0	0	0	0	0	1	0
cf HdV-733	0	0	0	0	0	1	0
cf UG-1114	0	0	0	0	0	1	0
cf HdV-223	0	0	0	0	0	1	0
cf HdV-305	0	0	0	0	0	1	0
cf UG-1185	0	0	0	0	0	1	0
cf Ellis 1208	0	0	0	0	0	1	0
cf Ellis 1168	0	0	0	0	0	1	2
HdV-221	0	0	0	0	0	1	1
cf 1125	0	0	0	0	0	1	0
cf HdV-339	0	0	0	0	0	1	0
cf Ellis 793	0	0	0	0	0	0	1
cf UG-1276	0	0	0	0	0	0	1
cf Ellis 1271	0	0	0	0	0	0	1
Total	219	210	213	226	230	268	306
Fungal fruiting bodies undiff. (HdV-8)	17	19	9	4	12	10	12

Microthyrium (HdV-8B)	2	3	7	3	5	1	3
HdV-8A	0	1	1	0	0	2	0
HdV-8E	0	1	0	0	0	0	0
HdV-8F	0	0	0	0	0	0	0
HdV-8D	0	0	0	0	0	0	0
Bryophyte capsules	0	0	0	0	0	0	0
Other zoological	21	19	9	13	14	15	10
Chironomidae	0	2	4	2	5	2	2
Neorhabdocoela eggs	0	0	0	0	1	2	4
HdV-52 (body fragments)	0	1	0	0	0	3	0
Arcella	0	0	0	0	0	0	0
Tracheids (EMA-1)	106	70	68	63	37	147	30
Highly corroded wood (EMA-7)	14	16	10	20	14	6	16
Wood rays aggregates (EMA-11)	23	19	17	20	17	25	42
Hardwood periderm (EMA-16)	4	2	5	4	3	3	4
Fungal tissue (EMA-95)	72	50	61	43	51	30	65
Lycopodium	147	63	83	43	67	29	135

TAXA	Modern samples - Number per cm3										
Sample	Sordaria	Podosp.	Arnium	S. fimicola	Spororm.	Delitsc.	Conioch.	Chaetom.	Apiosord.	Gelasinosp.	Cercoph.
1	0	0	0	0	0	0	0	0	0	0	0
2	116	0	0	0	0	0	0	0	0	0	0
3	31	0	31	124	0	0	15	0	0	0	0
4	0	0	0	0	0	0	0	0	0	0	0
5	0	0	0	0	0	0	340	340	0	0	0
6	26460	0	20047	0	42497	0	1604	12028	0	4009	0
7	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	47	0	24	0	0	0	0
9	324	54	0	0	216	0	0	54	0	0	0
10	1384	0	125	125	1133	0	504	252	0	125	125
11	1611	0	0	0	4833	0	0	1611	3222	0	4833
12	17869	0	32761	0	20848	0	0	23826	0	0	0
13	2690	0	4371	0	2017	0	0	1681	3026	673	0
14	2719	0	32631	0	11784	906	0	0	906	0	0
15	0	0	0	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0	0	0	0
19	0	0	0	239	0	0	0	0	0	0	0
20	0	0	0	0	1158	0	0	0	0	0	0
21	1017	0	0	0	0	0	0	0	0	0	0
22	0	0	0	0	2156	0	0	0	0	0	0
23	6254	0	0	0	12508	0	0	2085	2085	0	0
24	0	0	0	0	111189	0	0	0	13899	0	0
25	0	0	0	0	0	0	0	0	0	0	0
26	977	0	0	0	326	0	0	0	0	0	0
27a	389	0	0	213	0	0	0	389	213	0	0

27b	3912	0	0	0	0	0	0	0	0	0	1956
28	36958	2843	0	0	110306	569	0	0	0	0	0

TAXA

Sample	Sphaerod.	Neurosp.	Ascodesm.	HdV-55B	Thermomyc.	UR-1	UR-2	HdV-708	UR-68	UR-69	UR-70	UR-71
1	0	0	0	0	0	0	1985	0	0	0	0	0
2	0	0	0	0	0	0	1347554	0	0	0	0	0
3	0	0	0	0	311	0	0	0	0	0	0	0
4	0	0	0	0	4833	0	3305772	0	0	0	0	0
5	0	0	0	0	15940		0	0	0	0	0	0
6	0	0	0	8018	0	15235	10424	0	0	0	0	0
7	0	0	0	0	0	0	0	0	0	0	0	0
8	0	0	0	0	0	0	0	0	0	0	0	0
9	0	0	0	0	0	0	216	0	0	0	0	0
10	125	0	0	0	0	0	0	0	0	0	0	0
11	0	1611	1611	0	1611	0	0	0	0	0	0	0
12	0	0		5957	62544	0	0	5956	0	0	0	0
13	0	0	0	0	0	0	1345	0	0	0	0	0
14	0	0	0	0	0	0	13596	0	0	0	0	0
15	0	0	0	0	0	0	2062080	0	0	0	0	0
16	0	0	0	0	0	0	908604	0	1051661	0	0	0
17	0	0	0	0	0	0	1208	0	0	2819	0	151031
18	0	0	0	0	0	0	0	0	0	71242	0	0
19	0	0	0	0	477	0	0	0	0	32220	0	9785
20	0	0	0	0	0	0	16251	235119	0	0	0	0
21	0	0	0	0	1017	0	0	113957	0	5087	0	294049
22	0	0	0	0	0	0	2865	143779	0	0	46000	22285

23	0	0	0	0	0	0	14593	164699	0	0	0	179292
24	0	0	0	0	0	0	17373	48645	0	0	97290	535098
25	0	0	0	0	0	0	8736	0	0	0	0	0
26	0	0	0	0	0	0	29969	0	0	0	0	0
27a	0	0	0	0	0	0	0	0	0	0	0	0
27b	0	0	0	0	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0	0	0	0	0

Arma delle Manie	**DEPTHS (cm)**					
TAXA	0	4	8	12	16	17
Chaetomium	1723	0	43	0	0	0
Chaetomium thin-walled	0	66	25	147	0	62
Sporormiella-type	16	9	77	8	0	2
Sporormiella-type 2	2	0	4	0	0	4
sordaria (type 55A)	0	12	9	6	3	8
Trichodelitschia	1	24	2	5	0	2
Coniochaeta cf lignaria	3	6	14	12	3	10
Cercophora-type	0	6	0	0	3	0
Apiosordaria	0	0	1	0	0	0
Delitschia	1	0	0	0	0	0
Arnium-type	3	9	1	11	0	8
Rhytidospora	0	3	4	0	0	0
Podospora	1	0	5	0	0	1
Sphaerodes cf fimicola	1	0	0	0	0	0
cf Podospora inequalis	0	30	6	8	0	12
Sordaria (gel sheath)	0	3	0	0	0	0
Hypocopra	0	0	1	0	0	0
Pseudochizaea	0	0	2	2	0	6
Trichuris trichiura	4	0	5	3	0	2
Ascaris lumbricoides	2	3	4	1	0	0
Dicrocoelium eggs	1	0	1	0	0	0
sample quantity	10	10	10	10	10	10
Lycopodium added	19332	19332	19332	19332	19332	19332
Lycopodium counted	94	105	139	161	243	214

Cave of Arene Candide	**DEPTHS (cm)**							
TAXA	42	34	-14	-38	-112	-134	-166	-182
Quercus undiff.	32	4	8		14	8	2	32
Quercus robur type (deciduous)	8			9				
Quercus ilex type (evergreen)	9			3	1	1		
Quercus suber type (evergreen)								4
Fagus			7					
Corylus	4			6	2	1		
Alnus					5	1		4
Salix						1	1	
Tilia					1			
Ulmus	4							
Abies	4		8	3	7	18		24
Pinus	presence				1		1	
Ulex					1			
Carpinus					1			
Vitis						2		
Cupressaceae	20	2						
Cichorieae <18	72	54			3			4
Cichorieae 18-25	88	219		180	50	216	304	100
Cichorieae >25		4		9		5		
Chenopodiaceae		7	14	12	2	2	2	4
Caryophillaceae			15		1	20	2	20
Ericaceae	20	3	77		134	11	7	48
Asteroideae	8		7	6	12	2	2	16
Apiaceae		1	69					
Urtica					1			
Centaurea nigra		2					1	
Althaea					1	6	1	
Lavatera/Malva					2			
Helianthemum		1	8		1			

Pulsatilla			7					8
Pulsatilla								8
Cuscuta					1			
Myriophillum spicatum					1			
Cyperaceae			22		10			8
Gramineae smooth			21					
Gramineae	8	4	42	90	60	10	12	12
Gramineae >42 μm			6	3			1	4
Filicales spores	24		35	9	25	66	3	28
Pteridium aquilinum								
Polypodium cf vulgare			14	3	5	28		
Polypodium cf interjectum	4		1848		3	2		
Botrychium						1	1	
other triletes		1	7				3	
Undeterminable pollen	48	10	182	69	97	55	19	104
Undeterminable pollen/NPP	20	15		36	30		2	72
Euphorbia	4							
Carya	4							
Valerianella	presence							
Total	381	301	311	321	312	304	336	296

Castellaro di Uscio									
LOWER SECTION	**Layer 1**	**Layer 2**	**Layer 3**	**UPPER SECTION**		**Layer 1**	**Layer 2**	**Layer 3**	**Layer 4**
Centaurea	0	4	4	Centaurea		0	8	0	6
Scabiosa	0	6	1	Scabiosa columbaria		0	8	52	126
Carpinus	28	0	3	Carpinus		60	0	50	72
Ophioglossum	0	10	0	Ophioglossum		0	24	40	6
Cichorieae	0	44	19	Cichorieae		0	36	10	0
Asteraceae	0	16	9	Asteraceae		0	18	4	0
Pteridium aquilinum	0	2	104	Pteridium aquilinum		0	0	2	0
Poaceae	7	10	10	Poaceae		15	2	8	0
Pinus	21	58	7	Pinus		45	22	2	0
Geranium	0	4	0	Geranium		0	2	4	0
Abies	28	2	2	Abies		60	12	4	0
Indeterminable	6	14	12	Indeterminable		15	18	14	0
Cyperaceae	7	0	20	Cyperaceae		15	30	24	0
Quercus	104	0	0	Ericaceae		0	48	0	0
Ostrya carpinifolia	6	4	0	Ostrya-type		15	4	0	0
Phyllirea	7	0	2	Cerealia		0	2	0	0
Ericaceae	0	10	7	cf Ephedra		0	6	0	0
Apiaceae	0	0	6	Trifolium		0	2	0	0
Spergularia	0	2	1	Corylus		0	2	0	0
Plantago lanceolata	0	0	5	cf Solanum		0	1	0	0
Caryophillaceae	0	2	3	Monolete spores		0	2	0	0
Corylus	0	2	3	Urticularia		0	2	0	0
Monolete spore	0	0	3	Alnus		0	2	0	0
Alnus	0	0	36	Teucrium		0	1	0	0
Teucrium	0	14	2	Convolvulus arvensis-type		0	2	0	0
Other trilete spores	0	0	1	Fraxinus		0	2	0	0
Senecio-type	0	2	0	Phyllirea		2	6	0	0

cf Ephedra	0	10	0	Quercus		15	0	0	0
Cerealia	0	2	0	Total		242	262	214	210
Fraxinus	0	12	0						
Fagus	0	2	0						
Total	214	232	260						

Appendix III. Papers resulting from work undertaken in this thesis