This is an Accepted Manuscript of an article published in The Holocene 24 (3) :327-345 (2014), available online: http://dx.doi.org/ 10.1177/0959683613518593

Modern non-pollen palynomorphs sedimentation along an elevational gradient in the south-central Pyrenees (southwestern Europe) as a tool for Holocene paleoecological reconstruction

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Abstract

Non-pollen palynomorphs (NPP) are microfossils other than pollen and spores from plants found within samples prepared for pollen analyses. Their utility as paleoecological indicators is rapidly growing because of their potential to complement palynological reconstructions of past communities and environments. The study of modern NPP sedimentation patterns using surface samples from different substrates, vegetation types and environmental conditions is needed to characterize the main environmental and anthropogenic factors involved in establishing ecological gradients. Here, we analyze modern NPP distribution along an elevational transect from the south-central Pyrenees. We use these data to test the potential influence of elevation, vegetation type, sampling sites and human disturbance on modern NPP distribution and to obtain a NPP modern-analog model which will enhance further paleoecological interpretations. Our study used the same surface samples obtained in a previous modern-analog palynological study, along an elevational transect from 870 to 2600 m a.s.l. We identified 55 NPP, including 13 unidentified morphotypes that were described and depicted. Individual NPP analysis and multivariate statistical methods showed that altitude plays a significant role in the NPP distribution along the transect but other factors such as soil moisture, landscape openness and grazing intensity also influenced the composition of NPP assemblages. Our results also recognized some characteristic NPP assemblages linked to elevational vegetation belts and individual NPP morphotypes related with specific microhabitats, both with potential paleoecological indicator capacity. This work is a first step to improve the knowledge of the NPP's indicator value in the study area.

Keywords: elevation, grazing intensity, non-pollen palynomorphs, paleoecological indicators, sample types, Pyrenees

1. **Introduction**

Paleoecology is an effective tool to improve predictions on the possible consequences of the current climate change on the biosphere by revealing how organisms and communities respond to past environmental changes (Vegas-Vilarrúbia et al., 2011). Modern-analog studies based on present-day sedimentation patterns along ecological gradients are widely used to calibrate paleoecological proxies in terms of the main environmental factors that drive these responses (Jackson and Williams, 2004). The obtained qualitative and quantitative relationships between modern fossil assemblages and environmental drivers are used to interpret past sedimentary records (Birks and Birks, 1980, 2006). Elevational gradients are specially suited for modern-analog studies as they display significant environmental variations in a relatively small study area (Rull, 2006).

Non-pollen palynomorphs (NPP) are microfossils other than pollen and spores from vascular plants (mainly fungal spores and mycelia, algal remains and zoological remains) observed in samples prepared for pollen analyses. The utility of NPP as paleoecological indicators is rapidly growing because of their potential to improve the reconstruction of past communities and environments (Van der Linden et al., 2012; Van Geel et al., 1994; Van Geel and Aptroot, 2006). The use of NPP in paleoecological studies has been scarce as compared to other proxies such as pollen, likely due to the limited knowledge about NPP ecological indicator value. However, during the last years, the use of NPP in Quaternary paleoecology has increased and is now a promising and expanding research. It has been shown that NPP studies can enhance paleoecological interpretations based on pollen and pteridophytes spores because of their independent ecological nature (Montoya et al., 2012). This means that NPP and pollen can be conditioned by different variables, as well as they can respond in a different manner to the same factors. In this sense, NPP studies can provide complementary and straightforward information about local effective moisture (Van Geel, 2001) or the effect of livestock on landscape (Cugny et al., 2010; Ejarque et al., 2011) and, in general, significant features of the particular habitat from where samples are collected (Montoya et al., 2010). The use of NPP in paleoecology has been mainly developed in Europe (Buurman et al., 1995; Van Geel, 1978; Van Geel and Aptroot, 2006; Van Geel et al., 2003) and also in South America (e.g. Medeanic, 2006; Montoya et al., 2010, 2011, 2012; Musotto et al., 2012; Rull and Vegas-Vilarrúbia, 1997, 1999, 2001; Rull et al., 2008), Africa (e.g. Ekblom and Gillson, 2010; Gelorini et al., 2011; Van Geel et al., 2011), Asia (De Klerk et al., 2009) and Australia (Cook-Ellyn et al., 2011).

In the Iberian Peninsula, NPP studies are scarce but widespread (Figure 1A). In the Pyrenees, NPP surveys have been mostly oriented to reconstruct historical anthropogenic influences on landscape shaping using sedimentary sequences from fens (Ejarque et al., 2009, 2010; Miras et al., 2010), lakes (Ejarque, 2013; Riera et al., 2006) and peat bogs (Cugny et al., 2010). In general, heterogeneous patterns of landscape evolution during prehistoric and proto-historical times have been documented for highlands. Interactions among environmental, cultural, demographic and economic drivers seem to be crucial to understand landscape and land-use dynamics in this region (Miras et al., 2010). Of the NPP surveys carried out in the Pyrenees, only two deal with modern analogs. Ejarque et al. (2011) analyzed highland's modern assemblages of pollen and NPP and found useful relationships with vegetation and environmental patterns, as well as with grazing activities. The study included samples from cattle excrements in order to identify potential grazing indicators. Cugny et al. (2010) analyzed NPP assemblages from moss samples and obtained relevant insights on the degree of the landscape openness, current land-uses and grazing pressure. This information was successfully applied to a fossil sequence from a peat bog situated in the same area.

In this paper, we analyzed the NPP spectra from surface samples along an elevational transect from Val d'Aran, in the south-central Pyrenees (Figure 1), to test the effects of elevation and other environmental variables. We used the same set of samples of Cañellas-Boltà et al. (2009) who studied modern analogs of pollen and pteridophyte spores, and obtained significant relationships with elevation and vegetation types. Both NPP and pollen/spores were compared to highlight the additional contributions of NPP useful for paleoecological reconstruction. The specific objectives were to: 1) characterize the NPP present and their distribution along the elevational transect (from 868 to 2585 m), 2) determine the main factors involved in the NPP distribution (elevation, vegetation type, local habitat, sample type), 3) characterize indicators for specific environmental conditions, and 4) obtain information that will improve the interpretation of NPP extracted from the sediment records in the Pyrenees. Recent modern analog-studies on other mountain ranges have shown that, in general, local elevational transects from around the paleoecological targets, rather than widespread surveys, are better for reliable past reconstructions (Rull, 2006).

2. Study area

A detailed description of the study area can be found in Cañellas-Boltà et al. (2009). In this paper, the most important aspects of mainly climate and vegetation will be emphasized. Samples analyzed in this work were from the south-central Pyrenees (Val d'Aran, NW Catalonia), in the northern peripheral zone of the National Park "Aigüestortes i Estany de Sant Maurici" (Figure 1). Climate is of the Atlantic type with moderate to high precipitation and no water deficit throughout the year (López and Majoral, 1982). Average annual precipitation ranges from 900 to 1200 mm with two maxima, one in the spring (April-March) and the other in autumn (November). Average annual temperatures are generally cool, between 9.5ºC (Viella, 974 m) and 2.7ºC (Port de la Bonaigua, 2200 m), varying at rate of -0.55ºC/100 m elevation (De Bolòs, 1994). Biogeographically, the studied area is mainly within the boreoalpine and eurosiberian zones, with some Mediterranean elements at the lower parts. The vegetation of Val d'Aran shows three main altitudinal belts, namely montane, subalpine and alpine. In the studied transect (Figure 2), Cañellas-Boltà et al. (2009) described the vegetation gradient as follows:

<u>Montane belt (below 1600 m)</u>. Characterized mainly by deciduous oak forests dominated by *Quercus petraea* with birch (*Betula pendula*); riverine forests (*Alnus glutinosa, Fraxinus excelsior* and *Salix* sp.); forests with *Tilia platyphyllos, Prunus avium* and *Corylus avellana;* and mixed forests dominated by beech (*Fagus sylvatica*) with pine (*Pinus sylvestris*). This lower belt

is characterized by the presence of anthropic pressure evidenced by towns, pastures and cultivation.

Subalpine belt (between 1600 and 2250 m). Dominated by coniferous forests of two types: *Abies alba* and *Rhododendron ferrugineum* at the lowest parts and *Pinus mugo* ssp. *uncinata* with *R. ferrugineum* at the upper stages. Wetlands within this belt are characterized by *Scirpus cespitosus* communities, assemblages of *Juncus pyrenaeus, Carex rostrata* and *Caltha palustris* with *Epilobium palustre,* and *Sphagnum* peat bogs.

In the region under study, the transition zone between coniferous forests and alpine meadows is at 2000-2250 m and is characterized by scrubs of *Rhododendron* sp. with scattered pines (*Pinus mugo* ssp. *uncinata*) and patches of *Nardus* sp. In our transect the uppermost forest limit (*treeline*) is situated at 2250 m.

Alpine belt (above 2250 m). Open and sparse vegetation dominated by meadows of *Nardus stricta* and *Festuca eskia*, with several species of *Carex* in the wettest areas.

Until mid-1900s, the human activities in the region were cattle raising –mainly cows, sheeps, goats and, to a lesser extent, horses- and forest exploitation and management. Hydroelectricity generation was also a common activity and dam building proliferated. The second half of the past century was characterized by a spectacular increase in tourism activities and an intense emigration of local population to large cities. At present, transhumance seems to experience a revival, and livestock from other Pyrenean areas use to pasture in the Vall d'Aran meadows. However, focus has clearly shifted towards tourism, which has resulted in an increase in urbanization (roads, buildings, etc.), mainly in the montane zone but also in the subalpine and alpine belts by a significant growth of ski stations, with the corresponding increase in deforestation practices. It is noteworthy that an important part of the sampling area belongs to the northern peripheral zone of the National Park "Aigüestortes i Estany de Sant Maurici". This Area is under protection but some human activities, as for example mushroom gatherings, hunting, fishing, hiking, skiing, pasturing and forest exploitation, are allowed under the corresponding administration control.

3. Materials and methods

This work used 33 moss samples collected and processed by Cañellas-Boltà et al. (2009). These samples were distributed along an altitudinal transect ranging from 868 m (A-32), to 2585 m (A-22) (Figures 1 and 2). Moss polsters were chosen as sampling material because they are the only palynomorph traps regularly present along the whole altitudinal transect (lakes and peat bogs are located mainly on the alpine zone). In addition, mosses effectively capture the pollen rain and other microfossils like the NPP, and include both local and extra-local representatives thus becoming suitable palynomorph traps for this type of studies (Birks and Birks, 1980; Wilmshurst and McGlone, 2005). Mosses have been often and successfully used in modern-analog studies on pollen (Court-Picon et al., 2006; Mazier et al., 2006) and on NPP (Ejarque et al., 2011; Montoya et al., 2010). In each sampling site, 2-4 moss fragments of different species were collected and mixed to obtain one single sample. The local and regional flora and vegetation of each location was carefully described using Braun-Blanquet phytosociological methods (Cañellas-Boltà et al., 2009). Tablets of *Lycopodium* spores were added to each sample, to control the efficiency of chemical processing and to estimate palynomorph concentrations (Stockmarr, 1971).

Samples were processed according to standard palynological procedures (Chambers et al., 2011; Faegri and Iversen, 1989), including KOH digestion, sieving, HCl and HF digestions, and acetylation. HF digestion was used to follow the same methodology as in fossil samples. After sequential dehydration with ethanol and tert-butanol, samples were mounted and stored in silicone oil. NPP identification was carried out using the available keys (Ellis, 1971, 1976) and atlases (Cugny et al., 2010; Gelorini et al., 2011; Hooghiemstra and Van Geel, 1998; Montoya et al., 2010, 2011; Payne et al., 2012; Van Geel, 2001; Van Geel and Aptroot, 2006; Van Geel et al., 2011). Unknown morphotypes were named using the code IBB (for Institut Botànic de Barcelona) and a sequential number, and included in our institutional data base with their corresponding descriptions and illustrations. Ecological preferences of the NPP encountered in this study are in Appendix II. Unidentifiable fungal spores were grouped into a general category and were not considered for statistical analyses. Sample A-12 was also rejected for statistics as it did not contain any identified morphotype. Counting was performed according to the diversity saturation criterion (Rull, 1987). NPP abundances were expressed as a percentage based on the pollen sum, which included all pollen taxa except that from aquatic and semi-aquatic plants (Cañellas-Boltà et al., 2009). *Psimpoll 4.27* was used for diagram plotting. Clustering (Euclidean distance and minimum variance agglomerative method) and correspondence analysis (CA) were carried out with *MVSP 3.1* (Kovach, 1989) after root-square transformation of percentages. Rare taxa were not downweighted.

4. Results

A total of 55 NPP morphotypes were encountered, corresponding to fungal remains, zoological remains and algal remains (Table 1). Two of these morphotypes, IBB-255, described here, and IBB-42 previously described by Montoya et al. (2011) have an unknown origin. 42 of the recorded NPP morphotypes were identified to some level (Appendix II) while other 12 fungal taxa and one, possibly plant origin (IBB-255), have not been identified so far. These 13 morphotypes were codified using the IBB system, depicted and described (Appendix II). The altitudinal distribution of fungal, zoological and algal groups as a whole is shown in Figure 3. In general, the most abundant NPP were fungal spores, showing little altitudinal differentiation in terms of total abundance. However, the diversity showed more variability, with the highest values in the montane belt (Table 1). Zoological remains were very scarce and almost restricted to the lower parts of montane and subalpine belts, whereas algae only appeared at the lower part of the alpine zone. Below we analyze the altitudinal distribution of these groups in detail.

4.1. Zoological remains, algal remains and others

Seven zoological morphotypes were recognized corresponding to thecamoebas (3), rotifers (1), turbellarians (1), chironomids (1) and cladocerans (1). Generally, zoological morpholotypes were concentrated below 1978 m and were virtually absent above this altitude (Figure 4). Higher abundances as a group occurred at the bottom of the subalpine belt, where it reached its maximal values (sample A-26, 1711 m), as well as in the upper montane zone. The main element was the tecamoeba *Assulina* sp., occurring at two discontinuous zones: the basal montane belt (868 to 994 m), and the transition between montane and subalpine belts (1362 to 1910 m), being the responsible for the maximum values of sample A-26 (1711 m). Above this elevation, *Assulina* sp. occurred only at the base of the alpine belt (2276 m) and disappeared above this point. Most components of this group (*Neorhabdocoela* sp., cladocera, *Callidina* sp. and *Amphitrema flavum*) showed a similar pattern, being only present between 1825 and 1978 m, within the lower subalpine belt. Chironomid remains appeared only in the uppermost sample (2585 m) while the tecamoeba *Centropyxis aculeatea* was present only in the lowermost sample (868 m), both with very low values.

Pediastrum (Chlorophyta) was the only algal morphotype present in the studied transect, appearing with very low abundances in two samples of the lower alpine zone, below 2280 m (Figure 4). The unknown IBB-255, likely of plant origin, appeared exclusively in the subalpine belt, between 1644 and 2075 m with low to moderate values, with a maximum at 1980 m (Figure 4).

4.2. Fungal remains

A total of 45 fungal morphotypes were recorded, showing a much greater diversity and more continuous distribution than the other two groups (Table 1 and Figure 3). Higher values, as a group, occurred in the montane belt, with an absolute maximum at ca. 1300 m, as well as in the alpine belt. Lowermost values occurred at the transition between montane and subalpine belts and also in the whole subalpine zone. The montane belt holds the highest fungal diversity with 31 taxa (Table 1). The most abundant morphotype was the unknown IBB-261 (likely belonging to the order Xylariales), although it appeared in a single sample of the mid-montane belt (Figure

5). Also in the montane zone, morphotypes showing significant values were *Sordaria*-type, IBB-3, *Glomus* sp. and *Clasterosporium* sp., whereas *Brachysporium bloxamii, Sporormiella* sp.*,* cf. *Trichocladium* sp., *Cercophora*-type, and cf. *Paratomenticola lanceolatus* showed lower values (Figure 5). In the subalpine zone, *Sordaria*-type, IBB-3 and *Glomus* sp. showed a decrease in their values and *Clasterosporium* sp. disappeared. Contrarily, *Sporormiella* sp., *Cercophora*-type, *Podospora* sp., and *Apiosordaria verruculosa,* were among the more abundant, together with the unknown IBB-264 and IBB-266, which only occurred in single samples of this zone. The alpine belt showed the lowest fungal diversity of the whole transect (Table 1) but it contained a characteristic group of fungal remains that did not occur at lower elevations (IBB-265, HdV-495, *Byssothecium* spp., and *Arthirinium luzulae*). The upper alpine belt was dominated again by *Sporormiella* sp. and *Sordaria*-type while UG-1106 increased their values and *Glomus* sp. disappeared.

4.3. Statistical analysis

Cluster analysis classified the NPP morphotypes into three main groups and four subgroups (Figure 6A), whose altitudinal distribution is also shown (Figure 6B). Group 1 was formed by two coprophilous morphotypes such as *Sporormiella* sp. and *Sordaria*-type and was distributed quite continuously throughout the transect, although their maximum values occurred in montane and alpine belts. Group 2 included 4 fungal types with diverse ecological requirements such as coprophilous-like (*Cercophora*-type) and mycorrhizic (*Glomus* sp.). Two additional unknown morphotypes (IBB-261 and IBB-3) were also within this group, which was present in all three vegetation belts but in a more discontinuous manner. Maximum abundances of group 2 were in the mid-montane belt. Group 3 was the most diverse assemblage and contained 49 taxa distributed into four subgroups. Subgroup 3A included two morphotypes (cf. UG-1106 and *Byssothecium* spp.), distributed almost exclusively in the alpine zone and the uppermost subalpine belt. Subgroup 3B was entirely formed by fungal spores and was especially important in the montane zone where its maximum abundances were recorded. Subgroup 3C was highly heterogeneous including a wide range of morphotypes of different origin. Indeed it contained all zoological morphotypes except *Assulina* sp., the alga *Pediastrum* sp., and a large array of fungal spore types. This subgroup was more or less homogeneously distributed along the transect. Subgroup 3D was formed exclusively by *Assulina* sp., whose altitudinal distribution has been already described (Section *4.1*).

Figure 7A shows the results of correspondence analysis (CA), displaying the analyzed samples in a biplot of the first two axes accounting for 24.9% of the total variance. The first axis (14.7% of the total variance) roughly separated samples collected in forests of several types, situated on the positive side, from samples taken in peat bogs, marshes, wetlands and meadows, on the negative side. However, five forest samples were situated in the negative side thus disrupting the pattern. These samples were from (1) abandoned crops secondarily colonized by deciduous woody vegetation very rich in *Brachypodium sylvaticum* (Poaceae) (A-29), (2) open conifer forests of *Pinus mugo* ssp. *uncinata* with *Rhododendron ferrugineum* (A-9), (3) light hazel (*Corylus avellana*) forests with marginal vegetation and close to a town (A-3), (4) riverine forests on flooded soils surrounded by open vegetation (A-2), and (5) ash (*Fraxinus excelsior*) forests rich in *B. sylvaticum* in the surroundings of a small towm (A-1) (See Appendix I). In general, samples from alpine and subalpine belts were placed at the negative side of axis 1, while samples from montane belt were mostly at the positive part. All samples belonging to the transition zone (A-13, A-14, A-15 and A-25) lie within the subalpine samples, situated at the negative side of axis 1. The Pearson product-moment correlation coefficient between sample elevation and the scores of axis 1 is $r= -0.442$, which is significant at $p<0.02$. Axis 2 explained 10.2% of the total variance and did not show a clear pattern in the distribution of the samples. However, spring vegetation, wetlands and some peat bogs and marshes were consistently situated at the positive half, whereas samples taken at more rocky and less humid environments (Appendix I) were situated at the negative side.

Figure 7B shows the distribution of the NPP morphotypes along the first two CA axes. Axis 1 separated *Assulina* sp., situated at the positive side, from the other zoological remains, which are around the center of the plot. *Assulina* sp. coincides with most samples from densely forested sites (Figure 7A). Fungi are arranged along axis 1 as well, with coprophilous forms grouped at the negative side and most saprobic morphotypes placed at the positive part. NPP arrangement along axis 2 does not show any conspicuous pattern.

5. Discussion

5.1. NPP and elevation

In mountain areas, elevation is intimately linked to keystone climatic parameters as for example annual average temperatures and total precipitation. Therefore, paleoaltitude estimations from palynomorph assemblages based on modern-analog comparisons may provide relevant paleoclimatic information (Rull, 2006). In our transect, previous studies showed a highly significant correlation ($r=0.988$, $p<0.001$) between pollen trends and elevation (Cañellas-Boltà et al., 2009). According to the results of this study, NPP-elevation correlation using the same methodology are remarkably lower, although statistically significant ($r=-0.442$, $p<0.02$). Therefore, elevation may explain in part the altitudinal NPP distribution but other independent factors should be invoked to fully account for the observed trends. As previously shown, the arrangement of samples along CA axis 1 follows an altitudinal-like trend with some exceptions, notably the presence of samples from montane and subalpine zones within the alpine group (Figure 7A), indicating that this axis may represent not only elevation but also other factors. For example, samples located at the negative side are mostly from meadows and marshes –excepting 5 samples from relatively open forests- while samples at the positive side were taken in forested areas, suggesting a gradient of landscape openness from right to left. In concordance to this, coprophilous fungi, which are dominant in open grazed sites, are mostly placed at the negative side of the CA axis 1, whereas saprobic fungi and *Assulina* sp., mostly from forested sites, are situated at the positive part (Figure 7B). In addition, all samples with high values of *Sporormiella* sp. and *Sordaria*-type (Group 1) (samples A-3, A-13, A-18, A-22, A-24 and A-29, Figure 7A), including some forested sites (A-29 and A-3), are in the negative side of this axis. On the other hand, all samples placed at the positive side, especially those with the highest positive scores of axis 1 (A-4, A-26, A-27 and A-28), show low values for coprophilous fungi. Therefore, Axis 1 also could suggest a graxing gradient linked to landscape openness (See section 5.4). Axis 2 provided additional information such as samples from moist or flooded habitats were at the positive side, whereas samples at the negative values come from less humid rocky soils (Appendix I), thus suggesting a likely moisture gradient. Therefore, in addition to elevation, landscape openness and soil moisture gradients are also relevant to account for the features of the NPP spectra analyzed. Other works developed on the Pyrenees also showed a variety of factors influencing NPP assemblages. For example, Court-Picon et al. (2006) found that elevation was the more important environmental driver, whereas Cugny et al. (2010) emphasize the role of grazing pressure, regardless the altitude and the local habitat conditions. Ejarque et al. (2011) suggested that elevation did not play a significant role in the composition of NPP assemblages, which features were more related to sample type, landscape openness and grazing pressure. Taken individually, some of the NPP groups obtained in the cluster analysis show elevational trends while others do not. For example, subgroups 3B and 3D are indicators of lower elevations while subgroup 3A is typical of the uppermost levels of the transect (Figure 6B). Therefore, these subgroups could be useful for paleoecological and paleoclimatic reconstructions.

5.2. NPP and vegetation

Some associations between specific groups of NPP and vegetation belts are evident. For example, IBB-256, IBB-261, *Clasterosporium* sp. and cf. *Brachysporium bloxamii* characterize the montane zone, whereas IBB-264, HdV-65, IBB-255 and IBB-263 only occur in the subalpine zone. *Byssothecium* spp. is exclusive of the alpine zone only. These relationships could be used as indicators in further paleoecological studies. Another important issue, from a paleoecological point of view, is the position of the upper limit of the forest (treeline). Variations in the elevation of the treeline may be climatically controlled and can provide insights on paleotemperatures and paleoprecipitation. In our transect, the transition zone between pine forests and alpine meadows (2000-2250 m) was previously characterized palynologically by a significant increase in Cyperaceae and Poaceae (Cañellas-Boltà et al., 2009). In the case of NPP, this zone is less well defined, although some peculiarities have been observed. This transition zone is characterized by the disappearance of IBB-255 and almost all the zoological remains, especially *Assulina* sp., and by an increase of fungal spores, specifically *Sporormiella* sp. and *Sordaria*-type (Figures 3, 4 and 5). Immediately above the uppermost forest boundary (2250 m), *Byssothecium* spp. appears and increases their abundances progressively with elevation. In summary, NPP can contribute to locate the position of the treeline and its variations through time in the studied zone, which is encouraging for paleoecological reconstructions. It should be noted, however, that the treeline location may be influenced not only by climatic changes but also by human activities, which complicates past inferences. However, it is expected that human activities associated to treeline variations would be manifested in other indicators (charcoal from fires, pollen from cultivated plants, NPP as indicators of grazing, etc.), thus allowing separation of natural from anthropic drivers.

Some relationships exist among individual NPP and some forest communities that would be relevant for paleoecological interpretation. For example, *Assulina* sp., a tecamoeba typical of non-saturated moss polsters (Charman et al. 2000), occurs at two elevational bands, namely the lowermost montane belt and the montane/subalpine transition (Figure 4), always in forest samples (Appendix I). In the montane zone, *Assulina* sp. occurs in deciduous and mixed forests (A-31, A-32 and A-33), whereas in the montane/subalpine transition (from 1362 to 1749 m), this tecamoeba is only present in mixed (A-4, A-27 and A-28) and coniferous forest samples (A-5, A-6 and A-26). It is also noteworthy that in the montane belt, *Assulina* sp. is absent from moist riverine forests surrounded by open vegetation (A-1 and A-2), from small stream between old hayfields and forested patches (A-11) and also from three highly anthropic and relatively open sites (A-3, A-29 and A-30). These three samples also have high values of dung-related fungi (*Sporormiella* sp., *Sordaria*-type and *Cercophora*-type). Therefore, this tecamoeba would be associated to the presence of deciduous, mixed and coniferous forests growing on non-flooded soils, avoiding low forested and/or heavily grazed sites. Similar results were obtained by Ejarque et al. (2011), who related this morphotype to poorly grazed pine forests with abundant mosses in the understory. Another coincidence to be considered involves the unknown IBB-255, only present in coniferous forests of *Pinus mugo* and *Abies alba*. Cluster analysis grouped IBB-255 with *Trichocladium* sp., cf. *Brachysporium bloxamii* and cf. *Paratomenticola lanceolatus*, which use to grow on wood and bark from a variety of forest trees (Ellis, 1971; Shirouzu and Harada, 2008). Other relationships are less clear but they are worth mentioning to be confirmed in future studies. For example, IBB-3 and IBB-261 are particularly abundant in samples from *Corylus avellana* and *Fagus sylvatica* forests of the montane belt, both with a thick litter layer on the soil (Appendix I). These morphotypes might correspond to plant remain decomposers but further studies are needed for a definite assessment.

Also relevant is the occurrence of IBB-266 in one single sample from the alpine belt. This morphotype likely belongs to *Cortinarius* (Agaricales), some of which species have mycorrhizal relationships with the dwarf willow *Salix herbacea* in the alpine zone (Mühlmann and Peintner, 2008). *S. herbacea* is a boreoalpine species common in the uppermost levels of the Pyrenean alpine belt, where it grows around snow smelt banks (Vigo, 2005), and was found by Cañellas-Boltà et al. (2009) at the same altitudinal level than the sample in which IBB-266 occurs. Therefore, IBB-266 would be indicator not only of the uppermost alpine belt but also of the presence of *S. herbacea*.

5.3. NPP and sample type

In general, the diversity and abundance of zoological and algal remains recorded in this survey are comparatively low. *Pediastrum* sp. is the only algal representative found and is only present in two alpine samples along the whole transect. The presence of springs and water bodies around these sampling sites could explain the appearance of *Pediastrum* sp. at this altitude (Appendix I). *Pediastrum* is a genus of colonial green algae that lives in different freshwater habitats (Komárek and Jankovská, 2001). Depending on the species, *Pediastrum* can be common in the plankton from eutrophic lakes, as well as in the littoral zone from oligotrophic water bodies (Weckström et al., 2009). As a NPP, maximum *Pediastrum* abundances occur in peat bogs and lake sediments (Montoya et al., 2010). Therefore, the scarcity of this morphotype in the Pyrenean transect studied here could be due to the use of mosses as sampling material. The same would be true for zoological remains, as most of the usually found in pollen slides are from aquatic or semi-aquatic habitats (Charman et al., 2000; Haas, 1996; Korhola and Rautio, 2001; Walker, 2001). Further studies should analyze a wider range of sample types, in order to complement our results on modern NPP sedimentation. The combined study of samples from mosses, wet soils, and lake and bog sediments is needed to properly evaluate the local factors influencing NPP assemblages (Montoya et al., 2010), in order to obtain more useful paleoecological indicators. However, as stated in the methods section, the handicap is that bogs and lakes are usually restricted to higher elevations and their altitudinal distribution is not as continuous as moss polsters.

5.4. NPP and human pressure

Sporormiella sp. and *Sordaria*-type are typical of cattle dung (Ejarque et al., 2011; Gauthier et al., 2010; Van Geel and Aptroot, 2006), and are commonly used as indicators of grazing pressure in the Pyrenees (Cugny et al., 2010; Ejarque et al., 2011) and elsewhere. In our transect, although these taxa appear along the whole elevational gradient, their maximum values occur in alpine meadows dominated by herbaceous vegetation and close to water bodies (Appendix I), which are sites prone to be visited by cattle. In addition, *Sordaria*-type shows high values in the montane belt in three forested sites, either covered by a hazel forest (A-3) or close to abandoned crops colonized by *Tilia platyphyllos*, *Prunus avium* and *Corylus avellana* (A-29 and A-30). These sites include relatively open forests rich in fruits and herbivory is also favored. In addition to *Sordaria*-type, theses samples hold relatively high values of other two coprophilous fungi (*Sporormiella* sp. and *Cercophora*-type), strongly suggesting the presence of herbivore grazing in these three sites. Cañellas-Boltà et al. (2009) did not find palynological evidence of cultivation or grazing activities and concluded that there was no clear evidence of human disturbance. However, the relatively high abundances of coprophilous NPP (*Sordaria*-type and *Sporormiella* sp.) in several parts of the studied transect, suggest local grazing. On the other hand, *Sordaria*-type and *Sporormiella* sp. form a distinct group on cluster analysis (Figure 6A) showing their maximum abundances at open and grazed sites. This coincides with observations by Ejarque et al. (2011) and Cugny et al. (2010), who suggested that the mentioned fungi are good grazing indicators. On the contrary, *Coniochaeta* cf. *ligniaria,* growing on decomposed wood and dung (Appendix II) is placed at the positive side of CA axis 1 (Figure 7B) together with most saprobic fungi, suggesting that this morphotype may be a suitable indicator for litter accumulation. On the other hand, *Glomus* sp. spores have their maximal values in several forested sites from the montane belt, in contrast with the greater abundance of this taxon in subalpine meadows from other Pyrenean areas (Ejarque et al., 2011). In our transect, the highest values of *Glomus* occur in samples from forested sites close to pathways and forest tracks built mainly for touristic and recreation purposes. This agrees with studies from elsewhere showing that high abundances of this endomycorrhizal fungus in surface samples have been related to increased erosive phenomena and other mechanical soil disturbances (Van Geel et al., 1989). Therefore, the occurrence and abundance of spores from coprophilous fungi and *Glomus* sp. suggest that the studied region, despite the official protection as the peripheral zone of a national Park, is under certain degree of human pressure, mainly related to grazing and tourism which are manifest throughout the whole transect. As a consequence, human pressure should be added to elevation, vegetation type, landscape openness and local moisture conditions, as one more environmental driver controlling the NPP distribution along the studied transect.

6. Conclusions

The study of NPP assemblages along an elevational transect from south-central Pyrenees using moss samples revealed that fungal spores were, by far, more diverse and abundant than algal and zoological remains. A total of 55 morphotypes were found, of which 13 were described and depicted for the first time. Our results suggest that elevation have a significant influence on the NPP distribution in the studied region but other factors such as soil moisture, vegetation type, landscape openness and grazing pressure are also influencing. These factors, however, are not totally independent from elevation thus determining a complex altitudinal pattern. Useful relationships between NPP assemblages and specific vegetation belts have been recognized. Also, the transition zone between subalpine to alpine belts (*treeline*) has been characterized on the basis of NPP assemblages. The low diversity and abundance of zoological and algal remains was likely due to the lack of lake and bog samples in the transect. This NPP study has been able to find signs of anthropogenic disturbance (notably soil erosion and grazing), previously unnoticed by palynological analyses, emphasizing the utility of NPP to obtain more thorough paleoecological reconstructions. This work should be considered the starting point to improve the knowledge of the NPP indicator capacity in the study area, aimed to improve further paleoecological interpretations. Further studies should increase the number of transects, considering several differential conditions (geology, slope exposure, degree and type of human disturbance), as well as enhance sampling types including surface sediments from peat bogs, marshes and lakes. Next step should be to test the paleoecological utility of the modern analogs obtained in this study, in sedimentary sequences obtained in the same transect.

Acknowledgements

This work is included in a project funded by the Institute for Catalan Studies (IEC) (Principal Investigator, V. Rull). We thank Josep Vigo and Arnau Mercadé for their help in sampling and floristic work, and Jaume Llistosella and the participants of the 5th Workshop on Non-Pollen Palynomorphs (University of Amsterdam, 2-4th July 2012) in the identification of several fungal spores. Finally we are also grateful to the constructive comments and the revision by Will Gosling and by the anonymous referee, who contributed to improve the manuscript.

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Table 1. Number of morphotypes, percentage of the total NPP, and NPP diversity expressed in number of identified morphotypes per vegetation zone, based on their origin. “Other” includes IBB-255 and IBB-42, with an unknown origin.

	Zoological remains	**Algal remains**	**Others**	**Fungal remains**
Nº of Morphotypes	7	1	2	45
% of total NPP	12,73	1,82	3,63	81,82
Alpine	2	1	0	18
Subalpine	5	0	2	27
Montane	2	0	0	31

Figure 1. A) Location of studies that included NPP in the Iberian Peninsula. The present study is marked by a box. White circles are Holocene reconstructions and black circles are modern analogs studies. Those articles based on both types of studies include a white circle outside the black one. 1) Asturias (López-Merino et al., 2010, 2011); 2) Gredo’s range, Central Mountain System (Currás et al., 2012; López-Merino et al., 2009); 3) Northern-central littoral Portugal (Danielsen, 2008); 4) Cádiz (López-Sáez et al., 2002); 5) South East of Iberian Peninsula (Carrión and Navarro, 2002); 6) Eastern Pyrenees (Miras et al., 2010; Ejarque, 2013; Ejarque et al., 2010, 2011); 7) Eastern pre-Pyrenees (Ejarque et al., 2009, 2011); 8) Western pre-Pyrenees (Riera et al., 2006); 9) Western Pyrenees (Cugny et al., 2010); 10) North East coast of the Iberian Peninsula (López-Sáez et al., 2009); 11) Western Catalan plain of Catalonia and Northern Guadalajara (Currás, 2012). Map source: XTEC (Enrique Alonso). B) Schematic map of the sampling sites location (black dots). Open dots correspond to towns and the highest mountains are represented by triangles. Grey dots indicate the location of two Holocene cores, currently under study. (Redrawn from Cañellas-Boltà et al. (2009)).

Figure 2. Sketch of the altitudinal arrangement of vegetation and the three main belts defined in the studied transect. Numbers at the right side are the sampling codes. (Reproduced from Cañellas-Boltà et al. (2009)).

Figure 3. Percentage diagram of NPP’s main groups. Vegetation zones, sample code and sample elevations are shown at the left side. Within the Subalpine belt we highlighted the transition zone (TZ).

Figure 4. Percentage diagram of zoological and algal remains and others, following the same graphical display as in Figure 3.

Figure 5. Percentage diagram of fungal remains, following the same graphical display as in Figure 3. Fungal morphotypes have been ordered sequentially according to elevation.

Figure 6. NPP assemblages. A) Results of cluster analysis; B) Percentage diagram of the groups obtained in the cluster analysis, following the same graphical display as in Figure 3, and ordered sequentially according to elevation.

Figure 7. Correspondence analysis (CA). A) Results of CA showing the arrangement of the 32 sample sites, in the space defined by the two first axes. Locations have been differentiated according to the habitat and the altitude (See legend). “Other” includes different vegetation types: meadows (A-13 and A-23), wetlands (A-8), streams between rocks (A-11) and snow banks (A-21). Samples with the highest values of *Sporormiella* sp. and *Sordaria*-type (cluster group 1) are marked with an asterisk. Samples from the transition zone are underlined. B) Results of CA showing the arrangement of the 55 NPP morphotypes using the first two axes. NPP have been differentiated according to their origin and their ecologic preferences (Appendix II). “Other fungi” includes those morphotypes with no defined autoecological preferences, and “Other” include NPP of unknown origin (IBB-255 and IBB-42). Numbers correspond to *Coniochaeta* cf. *ligniaria* (1) and *Assulina* sp. (2).

Figure 1

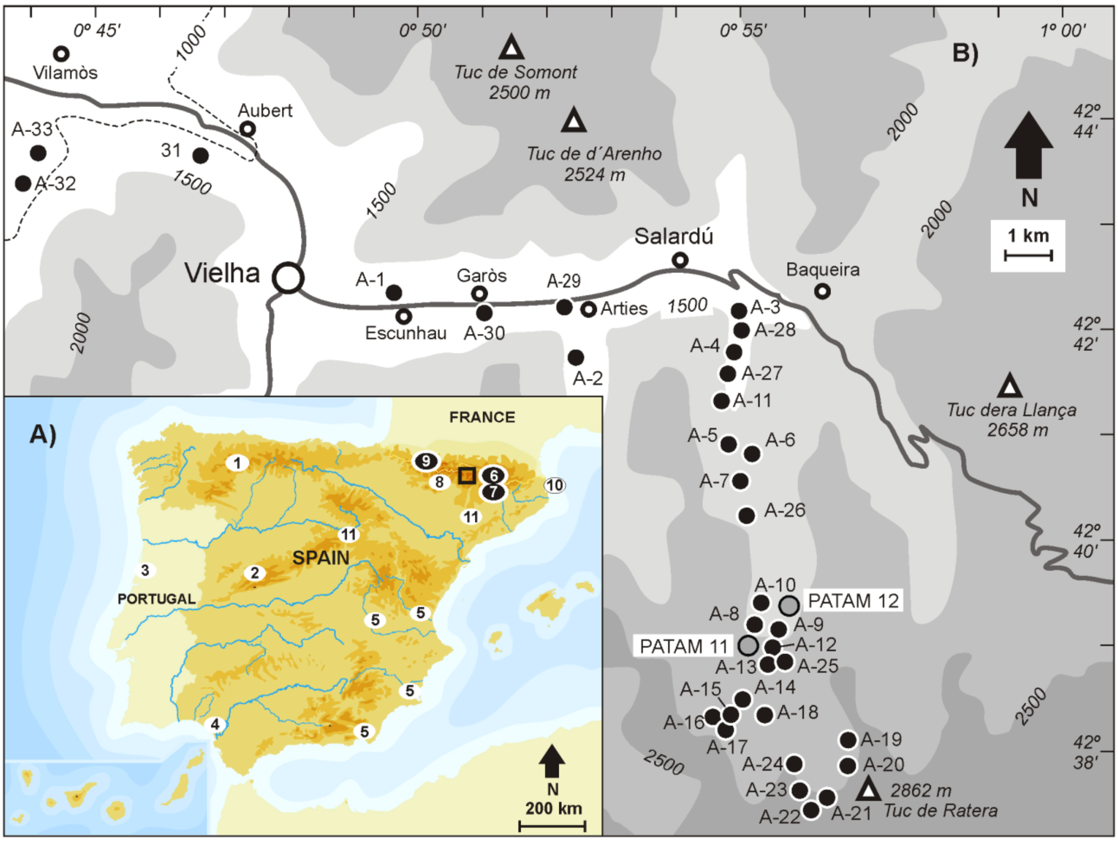
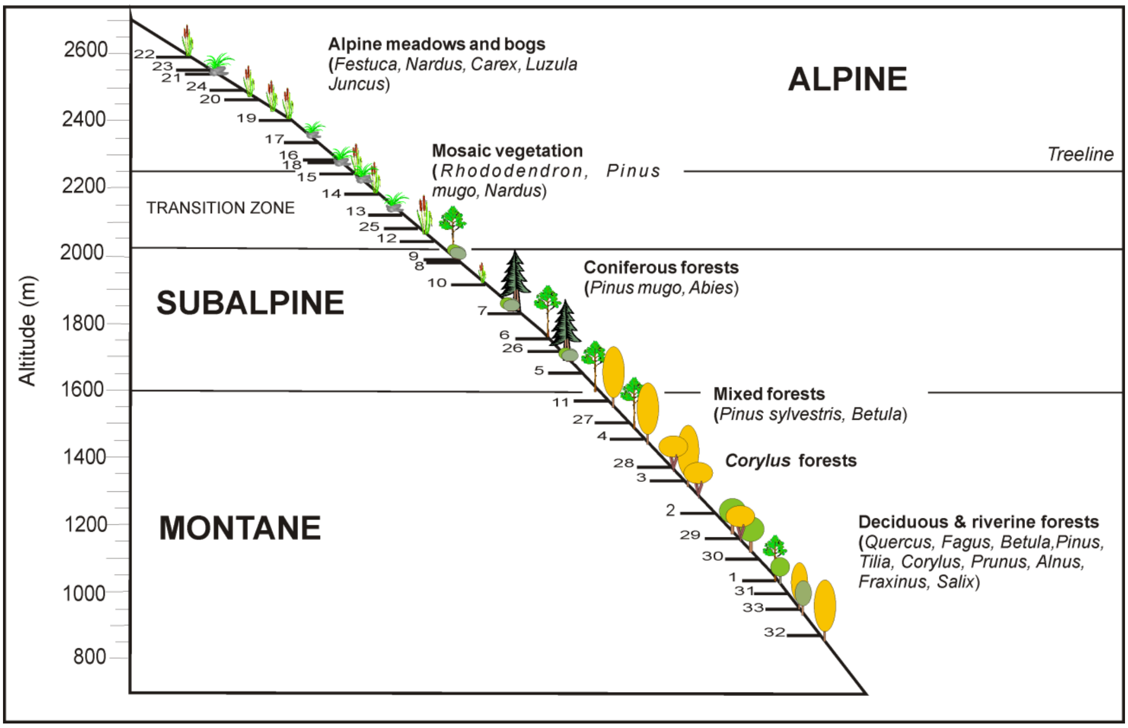


Figure 2


Altitude (m)
2600
2400
2200
2000
1800
1600
1400
1200
1000
800
ALPINE
Treeline
TRANSITION ZONE
SUBALPINE
MONTANE
Alpine meadows and bogs
(*Festuca, Nardus, Carex, Luzula Juncus*)
Mosaic vegetation
(*Rhododendron, Pinus mugo, Nardus*)
Coniferous forests
(*Pinus mugo, Abies*)
Mixed forests
(*Pinus sylvestris, Betula*)
Corylus forests
Deciduous & riverine forests
(*Quercus, Fagus, Betula,Pinus, Tilia, Corylus, Prunus, Alnus, Fraxinus, Salix*)
22
23
21
24
20
19
17
16
18
15
14
13
25
12
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8
10
7
6
26
5
11
27
4
28
3
2
29
30
1
31
33
32

Figure 3

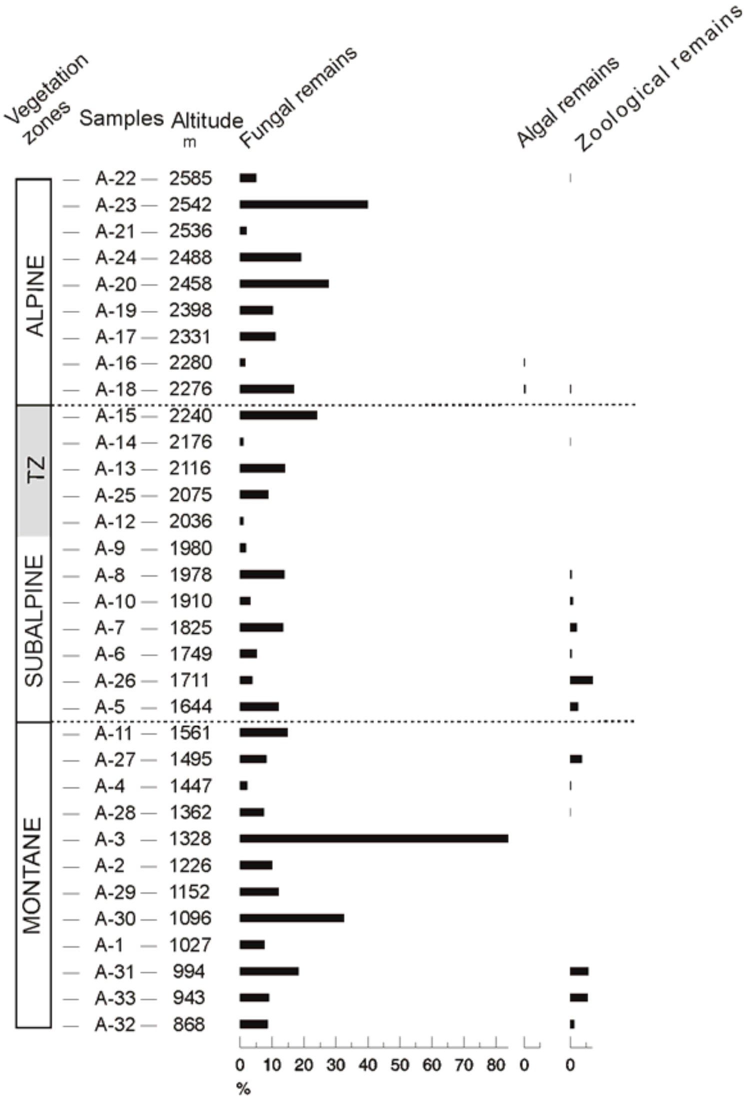

Vegetation zones
Samples
Altitude m
Fungal remains
Algal remains
Zoological remains
ALPINE
TZ
SUBALPINE
MONTANE
A-22 2585
A-23 2542
A-21 2536
A-24 2488
A-20 2458
A-19 2398
A-17 2331
A-16 2280
A-18 2276
A-15 2240
A-14 2176
A-13 2116
A-25 2075
A-12 2036
A-9 1980
A-8 1978
A-10 1910
A-7 1825
A-6 1749
A-26 1711
A-5 1644
A-11 1561
A-27 1495
A-4 1447
A-28 1362
A-3 1328
A-2 1226
A-29 1152
A-30 1096
A-1 1027
A-31 994
A-33 943
A-32 868
0 10 20 30 40 50 60 70 80
%
0
0

Figure 4

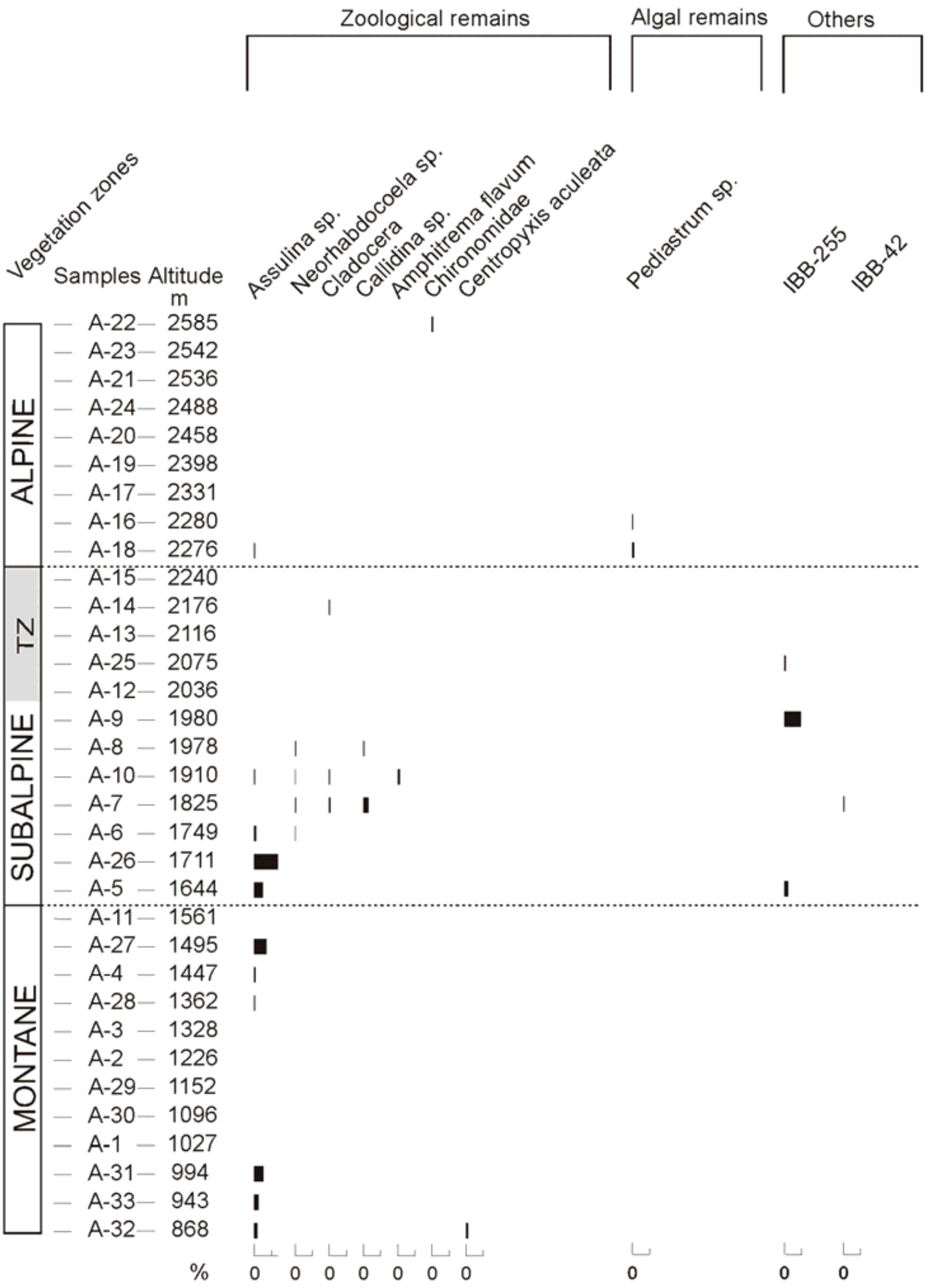


Figure 5

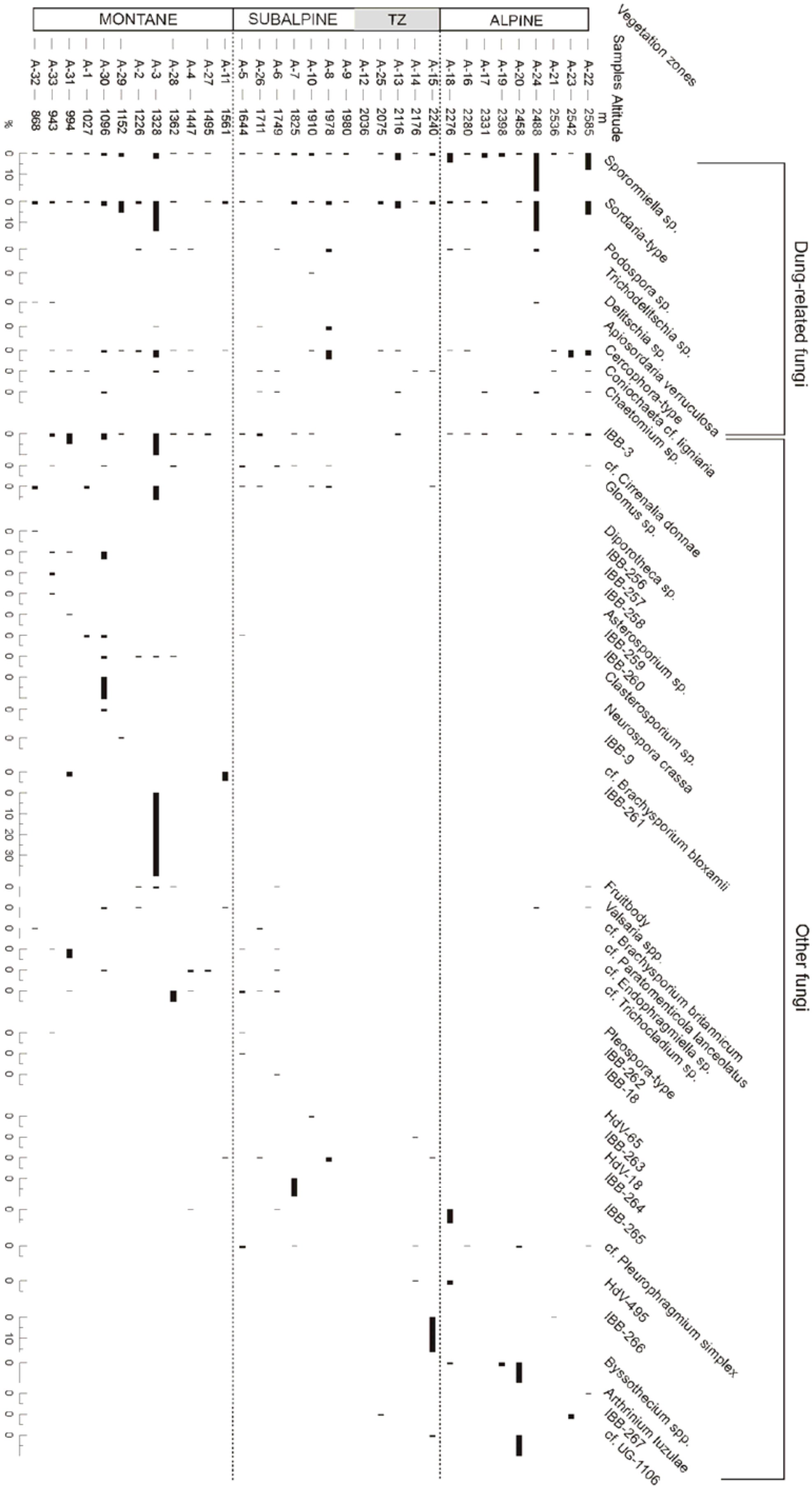

Vegetation zones
MONTANE
SUBALPINE
TZ
ALPINE
Samples
Altitude m
A-32 868
A-33 943
A-31 994
A-1 1027
A-30 1096
A-29 1152
A-2 1226
A-3 1328
A-28 1362
A-4 1447
A-27 1495
A-11 1561
A-5 1644
A-26 1711
A-6 1749
A-7 1825
A-10 1910
A-8 1978
A-9 1980
A-12 2036
A-25 2075
A-13 2116
A-14 2176
A-15 2240
A-18 2276
A-16 2280
A-17 2331
A-19 2398
A-20 2458
A-24 2488
A-21 2536
A-23 2542
A-22 2585
%
0
10
20
30
Dung-related fungi
Sporormiella sp.
Sordaria-type
Podospora sp.
Trichodelitschia sp.
Delitschia sp.
Apiosordaria verruculosa
Cercophora-type
Coniochaeta cf. ligniaria
Chaetomium sp.
Other fungi
IBB-3
cf. Cirrenalia donnae
Glomus sp.
Diporotheca sp.
IBB-256
IBB-257
IBB-258
Asterosporium sp.
IBB-259
IBB-260
Clasterosporium sp.
Neurospora crassa
IBB-9
cf. Brachysporium bloxamii
IBB-261
Fruitbody
Valsaria spp.
cf. Brachysporium britannicum
cf. Paratomenticola lanceolatus
cf. Endophragmiella sp.
cf. Trichocladium sp.
Pleospora-type
IBB-262
IBB-18
HdV-65
IBB-263
HdV-18
IBB-264
IBB-265
cf. Pleurophragmium simplex
HdV-495
IBB-266
Byssothecium spp.
Arthrinium luzulae
IBB-267
cf. UG-1106

Figure 6

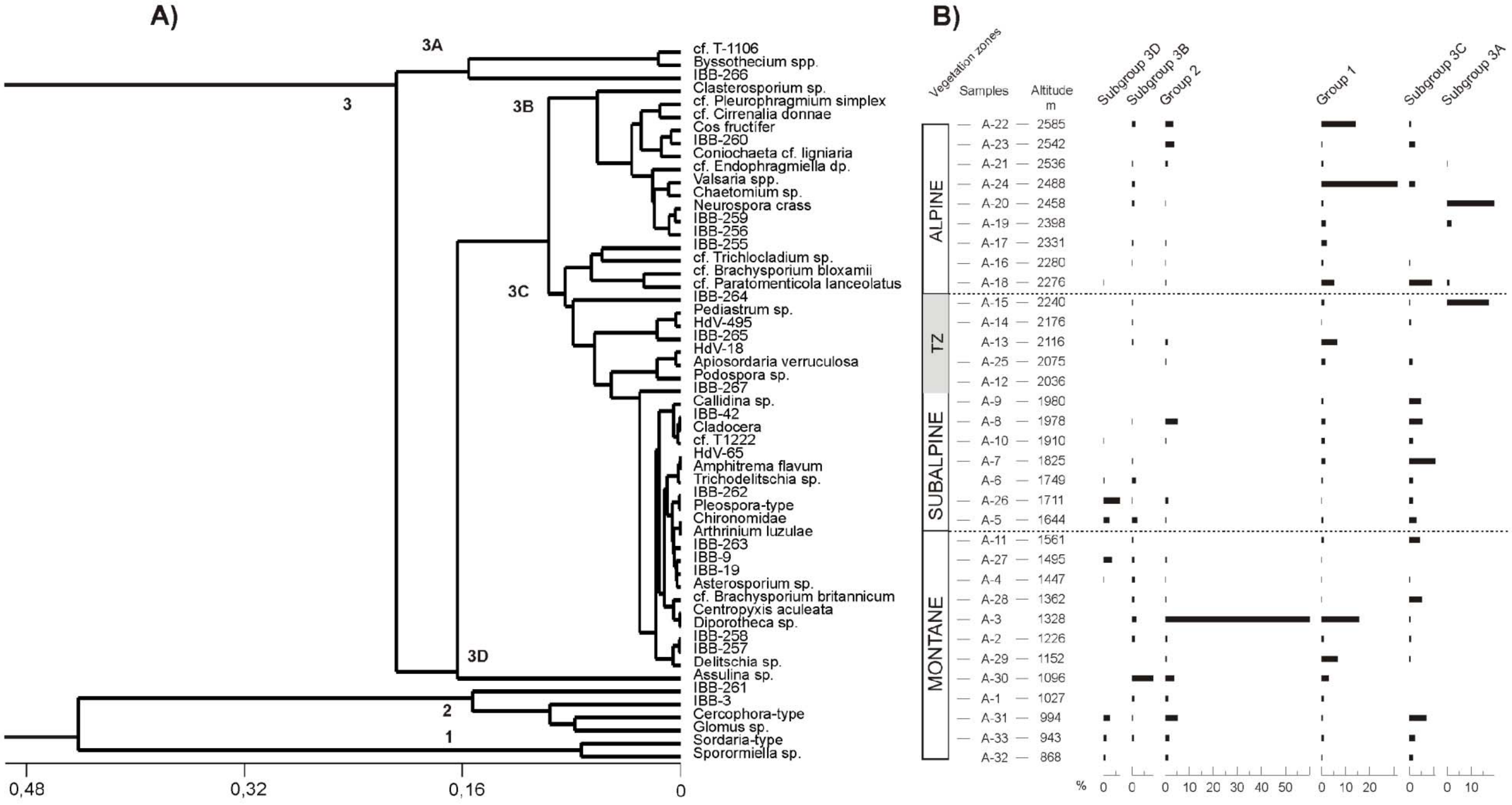
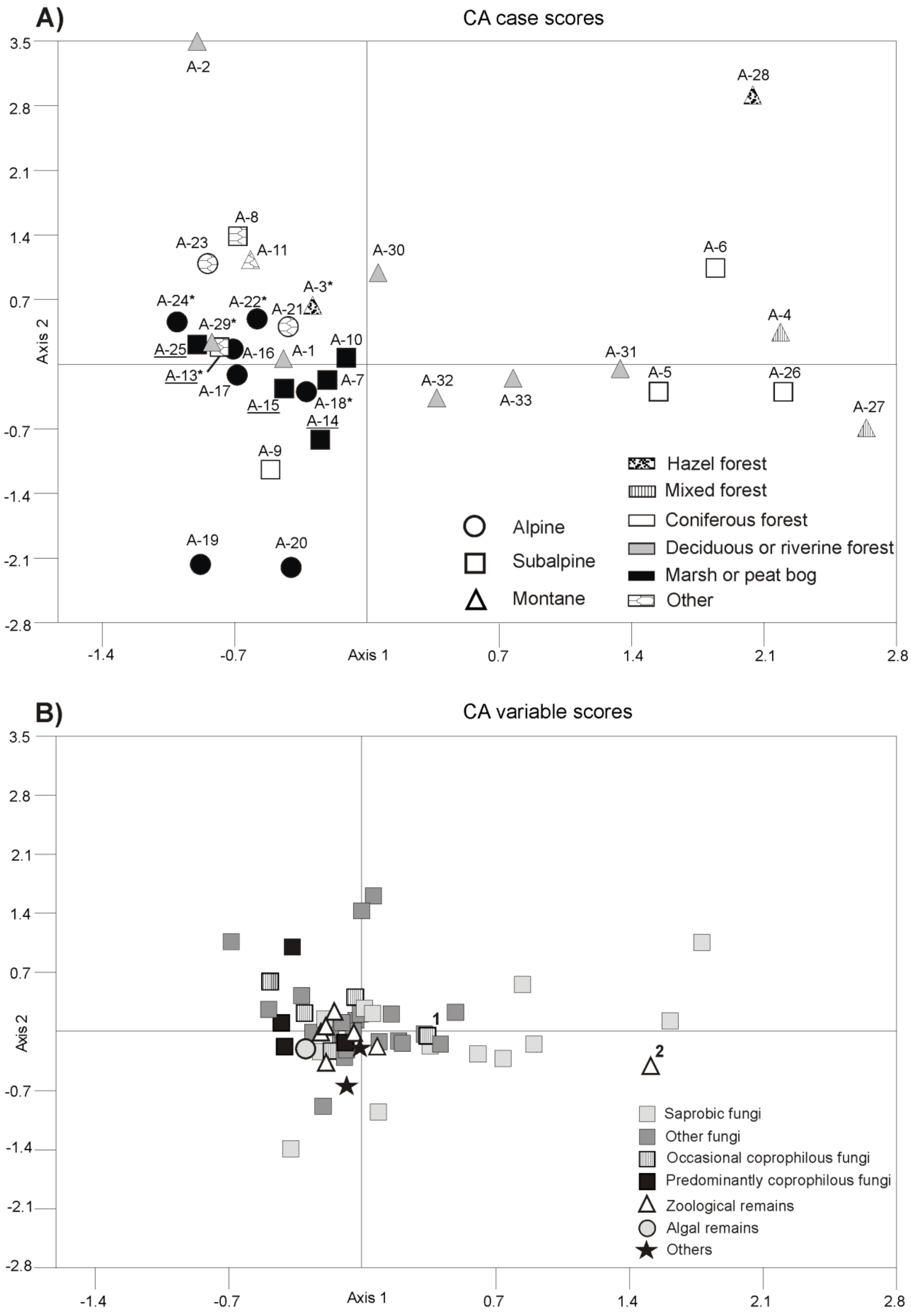

A)
B)
3
3A
3B
3C
3D
1
2
0,48
0,32
0,16
0
cf. T-1106
Byssothecium spp.
IBB-266
Clasterosporium sp.
cf. Pleurophragmium simplex
cf. Cirrenalia donnae
Cos fructifer
IBB-260
Coniochaeta cf. ligniaria
cf. Endophragmiella dp.
Valsaria spp.
Chaetomium sp.
Neurospora crass
IBB-259
IBB-256
IBB-255
cf. Trichlocladium sp.
cf. Brachysporium bloxamii
cf. Paratomenticola lanceolatus
IBB-264
Pediastrum sp.
HdV-495
IBB-265
HdV-18
Apiosordaria verruculosa
Podospora sp.
IBB-267
Callidina sp.
IBB-42
Cladocera
cf. T1222
HdV-65
Amphitrema flavum
Trichodelitschia sp.
IBB-262
Pleospora-type
Chironomidae
Arthrinium luzulae
IBB-263
IBB-9
IBB-19
Asterosporium sp.
cf. Brachysporium britannicum
Centropyxis aculeata
Diporotheca sp.
IBB-258
IBB-257
Delitschia sp.
Assulina sp.
IBB-261
IBB-3
Cercophora-type
Glomus sp.
Sordaria-type
Sporormiella sp.
Vegetation zones
Samples
Altitude m
Subgroup 3D
Subgroup 3B
Group 2
Group 1
Subgroup 3C
Subgroup 3A
ALPINE
TZ
SUBALPINE
MONTANE
A-22 — 2585
A-23 — 2542
A-21 — 2536
A-24 — 2488
A-20 — 2458
A-19 — 2398
A-17 — 2331
A-16 — 2280
A-18 — 2276
A-15 — 2240
A-14 — 2176
A-13 — 2116
A-25 — 2075
A-12 — 2036
A-9 — 1980
A-8 — 1978
A-10 — 1910
A-7 — 1825
A-6 — 1749
A-26 — 1711
A-5 — 1644
A-11 — 1561
A-27 — 1495
A-4 — 1447
A-28 — 1362
A-3 — 1328
A-2 — 1226
A-29 — 1152
A-30 — 1096
A-1 — 1027
A-31 — 994
A-33 — 943
A-32 — 868
%
0
0
0 10 20 30 40 50
0 10 20
0
0 10

Figure 7



APPENDIX I

Sample	Altitude (m)	Vegetation features	Main plant composition	Coordinates UTM
A-22	2585	Herb bog near a pond, surrounded by granite boulders	*Carex pyrenaica, Nardus stricta, Saxifraga stellaris, Veronica alpina*	42º 35' 58'' N 0º 55' 58'' E
A-23	2542	*Nardus stricta* meadow	*Nardus stricta, Carex pyrenaica, Gentiana alpina, Gnaphalium supinum, Saxifraga stellaris*	42º 36' 1,'' N 0º 55' 52'' E
A-21	2536	Herb patch close to a permanent snow bank beneath large rock blocks	*Luzula alpinopilosa, Salix herbacea, Nardus stricta, Sibbaldia procumbens*	42º 36' 58'' N 0º 56' 9'' E
A-24	2488	Acidic herb bog near a small stream	*Carex nigra, Juncus filiformis, Nardus stricta, Saxifraga stellaris*	42º 36'' N 42º 37' 44'' E
A-20	2458	Acidic herb bog on rocky soil dominated by *Carex nigra*, at the shore of a pond and close to a spring	*Carex nigra, Carex echinata*	42º 36' 7'' N 0º 56' 23'' E
A-19	2398	Acidic herb bog surrounded by small streams and large rock blocks	*Carex nigra, Viola palustris, Carex echinata, Nardus stricta, Saxifraga stellaris*	42º 36' 21'' N 0º 56' 27'' E
A-17	2331	Herb bogs at both sides of a small stream	Edges of the small stream: *Scirpus cespitosus, Carex* gr. *flava, Festuca* gr. *rubra;* Meadow: *Festuca eskia, Festuca* gr. *rubra, Nardus stricta*	42º 37' 8'' N 0º 54' 28'' E
A-16	2280	Herb bog close to a small spring and stream, situated at the upper boundary of *Pinus mugo* ssp. *uncinata*	Spring and herb bog: *Carex nigra, Carex* gr. *flava, Scirpus cespitosus, Juncus alpinus*	42º 37' 14'' N 0º 54' 27'' E
A-18	2276	Acidic herb bog close to a small pond, surrounded by pastures on rocky substrate	Herb bog: *Scirpus cespitosus* Meadow: *Calluna vulgaris, Molinia coerulea, Nardus stricta, Primula integrifolia*	42º 37'' N 0º 55'' E
A-15	2240	Small springs among granitic blocks, surrounded by herb bogs and meadows	At the springs: *Saxifraga stellaris, Carex nigra, Epibolium alsinifolium* Herb bog: *Carex nigra, Scirpus cespitosus* Meadow: *, Festuca* gr. *rubra,, Nardus stricta, Carex nigra, Primula integrifolia*	42º 37' 16'' N 0º 54' 46'' E
A-14	2176	*Carex nigra* bog near a stream and some small ponds	Herb bog: *Carex nigra, Leontodon duboisii, Parnassia palustris, Viola palustris* Wet meadows: *Nardus stricta, Festuca* gr. *rubra,Trifolium repens, Poa supina, Selinum pyrenaeum* Among granitic blocks: *Rumex pseudoalpinus, Festuca eskia, Athyrium distentifolium*	42º 37' 20' N' 0º 55'' E
A-13	2116	Vegetation mosaic at both sides of a stream	*Carex sempervirens* spp. *pseudotristis, Alchemilla coriacea, Carex nigra, Deschampsia cespitosa, Festuca eskia, F. Rivularis, Luzula alpino-pilosa, Parnassia palustris*	42º 37' 31'' N 0º 55' 10'' E
A-25	2075	Slightly alkaline herb bog near a small stream of quiet waters	*Narthecium ossifragum, Scirpus cespitosus, Carex davalliana*	42º 37' 44'' N 0º 55' 27'' E

A-12	2036	Shore of a small pond	Small pond: *Carex rostrata* Edges of the small pond: *Carex nigra, Viola Palustris, Potentilla erecta, Succisa pratensis* Outside the pond: acidic wet meadow: *Festuca rubra, Nardus stricta, Potentilla erecta, Succisa pratensis, Luzula multiflora, Selinum pyrenaeum*	42º 37' 48'' N 0º 55' 33,7'' E
A-9	1980	Light woods of *Pinus mugo* ssp. *uncinata* with *Rhododendron ferrugineum* on granitic soil	*Rhododendron ferrugineum, Homogyne alpinus, Pinus mugo* ssp. *uncinata, Solidago virgaurea, Vaccinium uliginosum*	42º 38' 17'' N 0º 55' 18'' E
A-8	1978	Herb bog at both sides of a small stream, surrounded by rush	*Carex* gr. *flava,* *Juncus pyrenaeus, Carex panicea, Cirsium rivulare* *Deschampsia cesppitosa,* *Succisa pratensis*	42º 37' 58'' N 0º 55' 12'' E
A-10	1910	Floating bog on a small pond	*Sphagnum* sp, *Carex lasiocarpa, Drosera longifolia, Menyanthes trifoliata, Molinia coerulea, Parnassia palustris*	42º 38' 17'' N 0º 55' 29'' E
A-7	1825	*Scirpus cespitosus* community and herb bogs	*Scirpus cespitosus, Molinia coerulea, Bartsia alpina, Deschampsia cespitosa, Equisetum fluviatile, Parnassia palustris, Pinguicula* sp.	42º 38' 46'' N 0º 55' 59'' E
A-6	1749	Fir forest within large granitic blocks	*Abies alba, Populus tremula, Vaccinium myrtillus*	42º 39' 46'' N 0º 55' 22'' E
A-26	1711	Open pine forest	*Pinus mugo* ssp.*uncinata, Vaccinium myrtillus, Deschampsia flexuosa, Hieracium cf. Prenanthoides, Melampyrum pratense.*	42º 39' 44'' N 0º 55' 14'' E
A-5	1644	Fir forest with *Rhododendron ferrugineum* on granitic soil	*Abies alba, Vaccinium myrtillus, Rhododendron ferrugineum, Calamagrostis arundinacea, Oxalis acetosella*	42º 39' 53'' N 0º 55' 13'' E
A-11	1561	Small stream within granitic boulders between old hayfields and forested patches	On both sides of the small stream: *Cardamine raphanifolia, Chaerophyllum hirsutum, Caltha palustris, Equisetum arvense, Holcus lanatus* Forest partch: *Corylus avellana, Betula pendula, Laserpitium latifolium, Lathyrus laevigatus, Pinus sylvestris, Prunella grandiflora,* Meadow: *Centaurea nigra, Agrostis tenuis, Asphodelus albus, Briza media, Carlina cynara, Scabiosa columbaria, Vicia orobus,*	42º 40' 28'' N 0º 54' 48'' E
A-27	1495	Birch forest with conifers at the shore of a river	*Betula pendula, Pinus sylvestris, Astrantia major* *Lathyrus laevigatus*	42º 40' 48'' N 0º 54' 57'' E
A-4	1447	Birch and pine forest colonizing a scree	*Betula pendula, Pinus sylvestris, Poa nemoralis* *Rubus idaeus, Dryopteris filix-mas*	42º 41' 53'' N 0º 54' 52'' E
A-28	1362	Young mixed forest close to a road	*Corylus avellana, Abies alba, Fraxinus excelsior* *Melica uniflora*	42º 41' 44'' N 0º 54' 41'' E
A-3	1328	Hazel forest on calcareous soil close to a road. Many oak leaves (*Quercus petraea*) on the ground. There is also open and marginal vegetation	*Corylus avellana, Carex ornithopoda, Fraxinus excelsior, Lonicera xylosteum*	42º 42' 7'' N 0º 54' 27'' E
A-2	1226	Riverine willow forest on peaty soil	*Salix purpurea, Equisetum arvense, Angelica razulii, Corylus avellana*	42º 40' 59'' N 0º 52' 29'' E

			Fraxinus excelsior, Knautia arvernensis	
A-29	1152	Abandoned terraces colonized by woody vegetation and some abandoned meadows around them. Close to a town	*Brachypodium sylvaticum* *Prunus avium, Corylus avellana, Fraxinus excelsior, Geum urbanum*	42º 41' 44" N 0º 52' 18" E
A-30	1096	Abandoned crops colonized by *Tilia platuphyllos* and *Prunus avium* forest	*Corylus avellana, Tilia platyphyllos, Galium odoratum, Geum urbanum, Prunus avium*	42º 41' 54" N 0º 50' 56" E
A-1	1027	Ash forest in the edge of a river, close to a town and a road	*Fraxinus excelsior, Corylus avellana, Brachypodium sylvaticum, Crataegus monogyna, Geranium robertianum*	42º 41' 55" N 0º 49' 17" E
A-31	994	Acidic pine wood with beech	*Fagus sylvatica, Pinus sylvestris, Abies alba, Fragaria vesca, Galium rotundifolium*	42º 43' 49" N 0º 46' 8" E
A-33	943	Old cultivated terraces colonized by mixed forest, on silicic soil	*Quercus petraea, Betula pendula, Fraxinus excelsior*	42º 43' 47" N 0º 43' 39" E
A-32	868	Mixed forest of alder and ash, with small streams	*Alnus glutinosa, Athyrium filix-femina, Carex flacca, Crepis paludosa, Filipendula ulmaria, Fraxinus excelsior, Mercurialis perennis*	42º 43' 56" N 0º 43' 14"

APPENDIX II

Identified and classified morphotypes

Morphotype	Taxonomic group	Indicator value	References
Amphitrema flavum	Thecamoebida	Relatively wet conditions	Charman et al., 2000
Apiosordaria verruculosa	Ascomycota	Soilborne and coprophilous fungus Related to grazing pressure	Van Geel and Aptroop, 2006 Cugny et al., 2010; Ejarque et al., 2011
Arthrinium luzulae	Fungi	On *Luzula* (from Juncaceae present in Pyrenees)	Ellis, 1971
Assulina sp.	Thecamoebida	On mosses in relatively dry conditions	Charman et al., 2000
Asterosporium sp.	Ascomycota	Related to woody substrates	Cugny et al., 2010
Byssothecium spp.	Ascomycota	Saprobic or weak parasite	Van Geel and Aptroot, 2006
Callidina sp.	Rotifera	In peat bogs	Montoya et al., 2010
Centropyxis aculeata type	Thecamoebida		Charman et al., 2000
Cercophora-type	Ascomycota	Coprophilous fungus	Van Geel and Aptroop, 2006
cf. *Brachysporium bloxamii*	Ascomycota	On rotten wood and of several trees	Ellis, 1971
cf. *Brachysporium britannicum*	Ascomycota	On wood and bark of several trees	Ellis, 1971
cf. *Cirrenalia donnae*	Ascomycota	On *Abies* bark	Ellis, 1976
cf. *Endophragmiella* sp.	Ascomycota	Saprobic fungus	Ellis, 1976
cf. *Paratomenticola lanceolatus*	Ascomycota	On bark of *Berchemia* (Rhamnaceae)	Ellis, 1976
cf. *Pleurophragmium simplex*	Ascomycota	On partly decorticated dead stems of several plants	Ellis, 1971

cf. T-1106	Ascomycota		Gelorini et al., 2011
cf. *Trichocladium* sp.	Ascomycota	Saprobic fungus	Cugny et al., 2010
Chaetomium sp.	Ascomycota	On plant remains and on dung from undetermined origin	Van Geel et al., 2011
Chironomidae	Chironomidae		
Cladocera	Cladocera	Open, oligotrophic and acidic waters	Van Geel, 1976, 1978; Van Geel et al., 1983
Clasterosporium sp.	Ascomycota	On different plants, usually found on marshes and fens	Ellis, 1971
Coniochaeta cf. *ligniaria*	Ascomycota	On wood and dung from undetermined origin	Van Geel and Aptroop, 2006
Delitschia sp.	Ascomycota	Mostly coprophilous	Gelorini et al., 2011
Diporotheca sp.	Ascomycota		Gelorini et al., 2011
Fruit body (Different species)	Ascomycota	Unknown	
Glomus sp.	Glomeromycota	Micorrhizal fungi, indicative for soil erosion	Gelorini et al., 2011
HdV-18	Ascomycota		Van Geel et al., 1978
HdV-495	Fungi	Might be associated with epidermal remains of *Molinia* (Poaceae, present in Pyrenees forming wet meadows)	Hooghiemstra and van Geel, 1998 Marinas et al., 2009
HdV-65	Ascomycota	It probably prefers relatively mesotrophic conditions	Van Geel et al., 1978
IBB-18	Fungi	Unknown	Montoya et al., 2010
IBB-3	Ascomycota	Unknown	Montoya et al., 2010
IBB-42	Unknown	Unknown	Montoya et al., 2011
IBB-9	Ascomycota	Unknown	Montoya et al., 2011
Neorhabdocoela sp. (oocytes)	Turbellaria	Lacustrine, could be related to high lake levels	Rull et al., 2008
Neurospora crassa	Ascomycota	Could be indicator of	Van Geel and Aptroot, 2006

		local fires	
Pediastrum sp.	Chlorophyta	Different types of freshwater Possible relationships with cold climes	Komárek and Jankovská, 2001 Rull et al., 2008
Pleospora-type	Ascomycota	On different plant remains	Van Geel and Aptroot, 2006
Podospora sp.	Ascomycota	Coprophilous Indicates local presence of herbívores	Van Geel and Aptroot, 2006 Ejarque et al., 2011
Sordaria-type	Ascomycota	Coprophilous Indicates local presence of herbivores	Van Geel and Aptroot, 2006 Ejarque et al., 2011
Sporormiella sp.	Ascomycota	Coprophilous Indicates local presence of herbivores	Van Geel and Aptroot, 2006 Ejarque et al., 2011
Trichodelitschia sp.	Ascomycota	Coprophilous Indicates local presence of herbivores	Bell, 2005 Ejarque et al., 2011
Valsaria spp.	Ascomycota		Van Geel and Aptroot, 2006

Identified and classified morphotypes

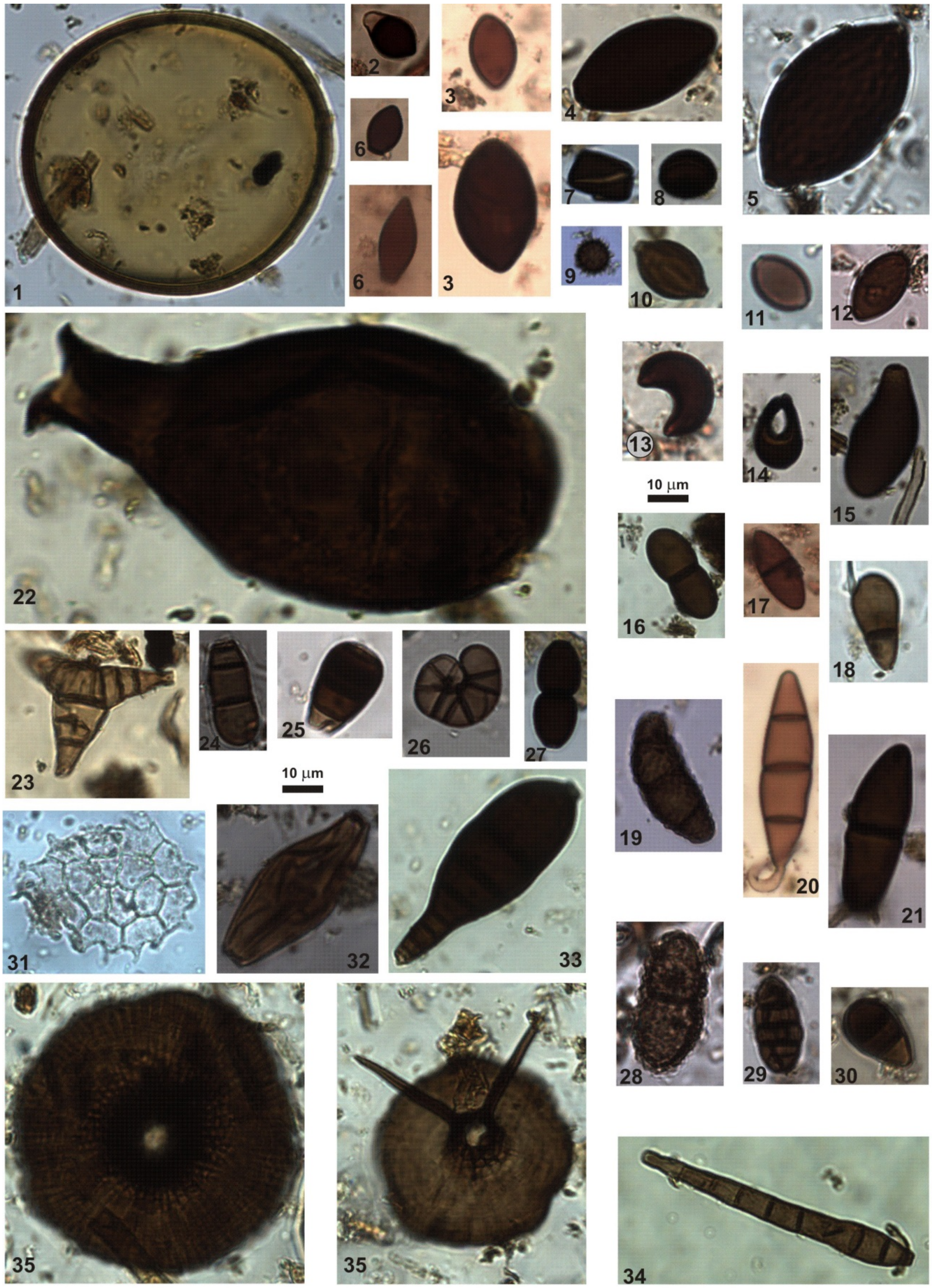


Plate I: 1. *Glomus* sp.; 2. *Apiosordaria verruculosa*; 3. *Sordaria*-type; 4. *Podospora* sp.; 5. IBB-9; 6. *Cercophora*-type; 7. *Sporormiella* sp.; 8. *Coniochaeta* cf. *ligniaria*; 9. HdV-495; 10. *Neurospora crassa*; 11. *Chaetomium* sp.; 12. IBB-3; 13. IBB-18; 14. *Arthrinium luzulae*; 15. HdV-65; 16. *Delitschia* sp.; 17. HdV-18; 18. cf. *Trichocladium* sp.; 19. *Byssothecium* spp.; 20. cf. *Pleurophragmium simplex*; 21. UG-1106; 22. IBB-42; 23. *Asterosporium* sp.; 24. cf. *Brachysporium bloxamii*; 25. cf. *Endophragmiella* sp.; 26. cf. *Cirrenalia donnae*; 27. *Trichodelitschia* sp.; 28. *Valsaria* spp. ; 29. *Pleospora*-type; 30. cf. *Brachys-porium britannicum*; 31. *Pediastrum* sp.; 32. *Diporotheca* sp.; 33. *Clasterosporium* sp.; 34. cf. *Paratomenticola lanceolatus*; 35. Fruitbody (Ascomycete).

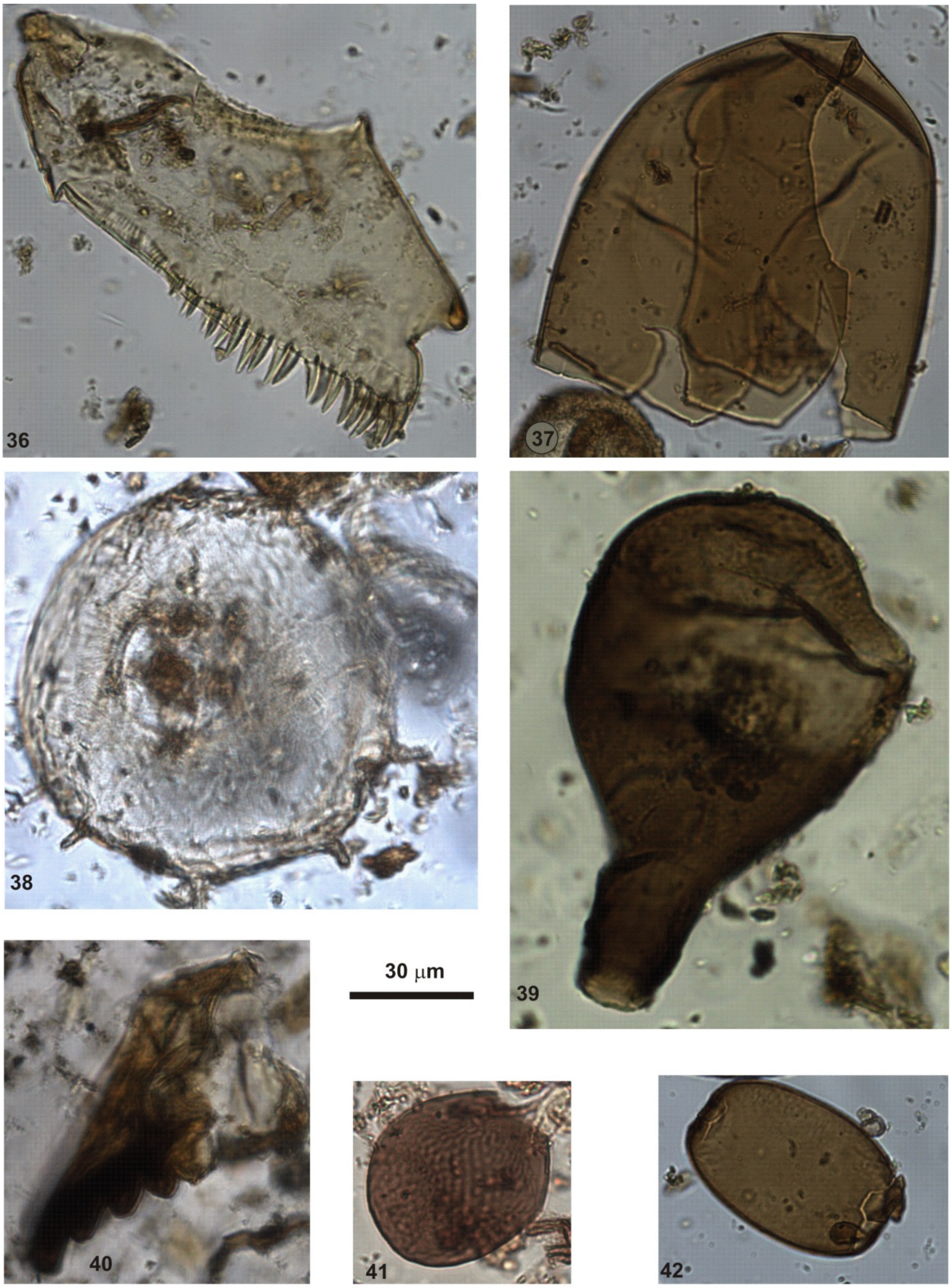


Plate II (Zoological remains): 36. Cladocera. Mandibles; 37. *Neorhabdocoela* sp. oocytes (Turbellaria); 38. *Centropyxis aculeata*. Individual (Thecamoebida); 39. *Callidina* sp. Eggs (Rotifera); 40. Chironomidae. Mandibles; 41. *Assulina* sp. Individual (Thecamoebida); 42. *Amphitrema flavum*. Individual (Thecamoebida).

Morphotypes codified using the IBB system

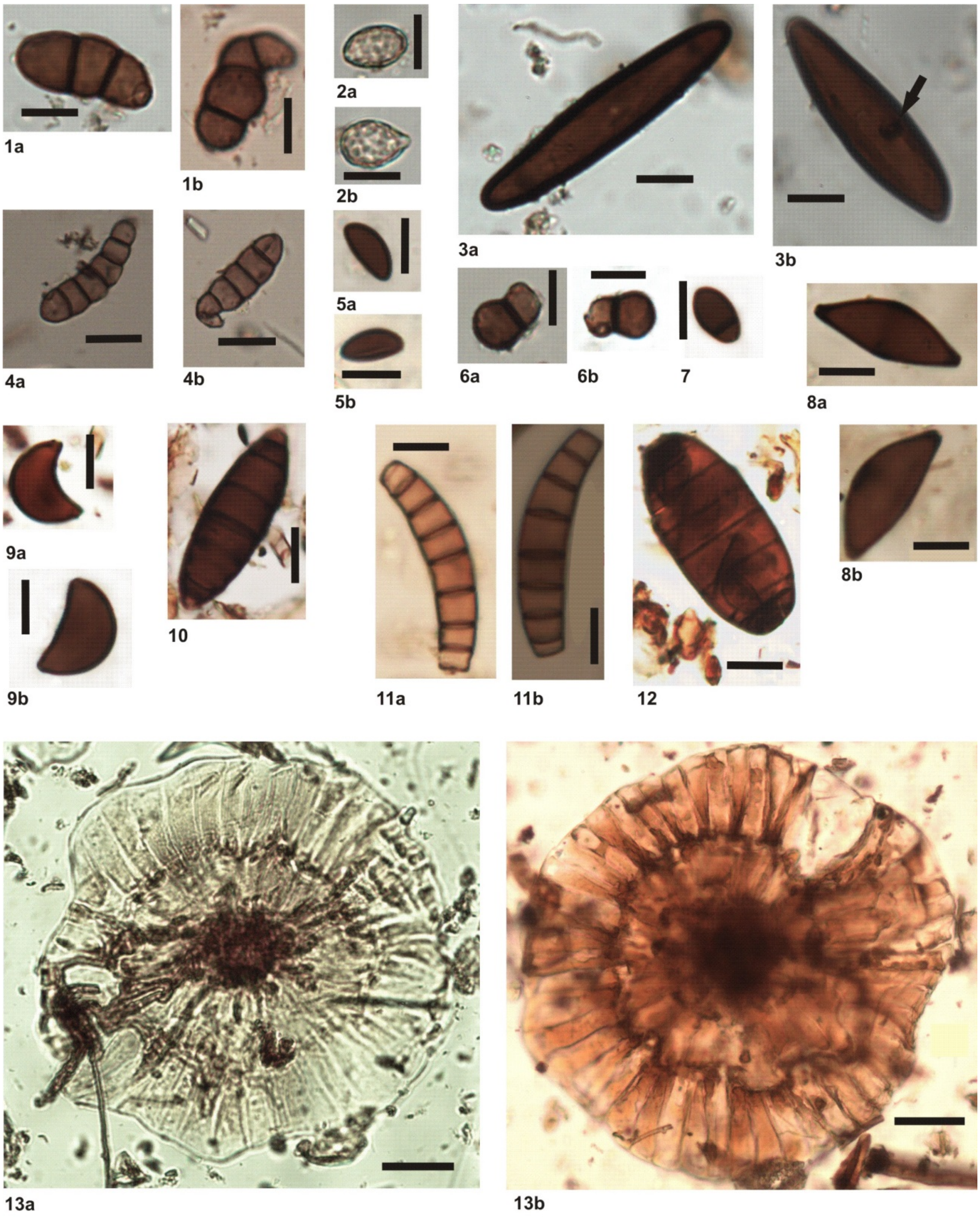


Plate III: Not identified morphotypes, named with the IBB code. White bar is 10 µm, except on pictures 13a and 13b where it is 30 µm:

1a-1b: IBB-265; 2a-2b: IBB-266; 3a-3b: IBB-264; 4a-4b: IBB-267; 5a-5b: IBB-259; 6a-6b: IBB-263; 7: IBB-256; 8a-8b: IBB-261; 9a-9b: IBB-260; 10: IBB-257; 11a-11b: IBB-262; 12: IBB-258; 13a-13b: IBB-255.

Descriptions of the unknown morphotypes (Plate III):

IBB-255 (Picture 13a-13b): Microfossil circular with unknown origin, 165.9-233.7 µm in diameter; formed by two concentric circles showing transverse grooves converging in a darker central zone.

IBB-256 (7): Ascospores ellipsoid, asymmetrically two-celled 9-11x5.4-8.4 µm, one cell large, dark and thick-walled; other cell, small, hyaline thin-walled with an apical pore.

IBB-257 (10): Conidia fusiform, eight-celled, 27.9-40.1x9.6-12.1 µm, gradually decreasing in size towards the ends of the conidia, smooth and thick-walled, apical cells hyaline with darker septa.

IBB-258 (12): Conidia ellipsoid to cylindrical with truncate ends, eight-celled, 32.9-46.4x14.4-21.1 µm, thick-walled, decreasing in size from the center of the conidia, apical cells clearer, showing a zigzag structure throughout the conidia.

IBB-259 (5a-5b): Ascospores ellipsoid to inequilateral, one-celled, 10-12.4x4.8-5.9 µm, smooth and thick-walled, showing a longitudinal germ slit running about 3/4 of the spore-length in the flattened side.

IBB-260 (9a-9b): Ascospores crescent-shaped, once-celled, 15-18.2x8.2-9.6 µm, thick-walled with apical pores. This morphotype resembles *Arthrinium curvatum*, but we didn’t observe its characteristic lateral germ slit.

IBB-261 (8a-8b): Ascospores fusiform, one-celled, 25-28.3x10-12.4 µm, thick-walled, showing a darker strip perpendicular to the equatorial axis of the spore.

IBB-262 (11a-11b): Conidia allantoidal, eight-celled, 33-45.3x6.8-7.9 µm, thick-walled, hyalines, slightly constricted at the septa. Cells almost square decreasing in size towards the apical zones.

IBB-263 (6a-6b): Ascospores, unequally and asymmetrically 2(-3)-celled, 12-15.8x5.6-8 µm, rounded and smooth: one cell large, dark and thick-walled; other cell smaller, hyaline and thin-walled.

IBB-264 (3a-3b): Ascospores cylindrical to fusiform, with rounded ends, one-celled, 41.9-55.1x9.6-12.4 µm, smooth and very thick-walled with central pore (indicated with an arrow). In some cases the ends are slightly constricted.

IBB-265 (1a-1b): Conidia, unequally 3 (-4)-celled, 16.5-24.4x8.5-12.1 µm, smooth, thick-walled, constricted at the septa, where the wall is thicker, apical cell paler.

IBB-266 (2a-2b): Basidiospores amygdaloid to ellipsoid, 11-13.5 x 7.3-8.9 µm, thin-walled, strongly ornamented and warty, hyaline and showing and *apiculus* or *hilar appendage*.

IBB-267 (4a and b): Conidia, unequally five (or six)-celled, 20.5-26.4 x 5.4-7.8 µm, smooth, thick walled, slightly constricted at the septa, with slightly tapering ends.