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Non-pollen palynomorphs from surface sediments along an altitudinal transect of the Venezuelan Andes

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ABSTRACT

Palynological studies including records of non-pollen palynomorphs (NPP) are uncommon in the Neotropics, in spite of their demonstrated usefulness in other regions. Modern analog studies to improve palaeoecological interpretations of NPP are even more scarce. Here, we report the NPP assemblages recorded in modern surface samples from an altitudinal transect of the Venezuelan Andes, ranging from about 2300 and 4600 m. We compared the assemblages with the results of previous pollen analyses of the same samples. The variables considered to explain NPP patterns along the transect are altitude and the local habitat of the sampling site ("sample type"). A total of 65 NPP taxa – classified into algal and zoological remains, and fungal spores – have been found. Unidentified taxa (23) have been named with a code, depicted and described for further reference. Fungal spores are well represented along the whole transect, whereas algal and zoological remains are absent or very scarce in the lower and the uppermost ranges. The altitudinal zonation of fungal spores matches with that of pollen and the corresponding vegetation belts, suggesting a close relationship. The known environmental requirements of some of the fungi identified allowed inferences on particular ecological features, in agreement with previous palynological interpretations. Both elevation and sample type are needed to explain the observed differences in the assemblages of the three groups, the elevation being more decisive for fungal spores and the local habitat of the sampling site for algal and zoological remains. The sample type effect is minimised when the NPP studied are considered altogether, thus increasing their usefulness as palaeoecological proxies. This study reinforces the utility of modern analog surveys of NPP with palaeoecological purposes and encourages further research, particularly in poorly known areas, as for example tropical regions.

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1. Introduction

The study of microfossils other than pollen and pteridophyte spores present in pollen slides, also called "non-pollen palynomorphs" (NPP), proved to be useful in palaeoecological interpretations (van Geel, 1986, 2001). NPP are of diverse origin, including fungal spores, algal remains, as well as plant and animal fragments of different nature. A common handicap in these studies is that the taxonomic identity of many NPP is not yet known, thus the indicator-species approach (Birks and Birks, 1990) is difficult to apply. This has lead to a classification system of NPP in morphological types using codes to name them, developed at the University of Amsterdam (Hooghiemstra and van Geel, 1998 and references therein). In this way, when a NPP type is identified, information from previous studies can be used for the environmental interpretation. This procedure has been applied successfully in many palaeoecological, palaeoenvironmental and palaeoanthropological studies (e.g. van Geel, 1976, 1978; van Geel et al., 1981, 1983, 1989, 1994, 1996; van Geel, 2001). The study of modern analogs is another useful approach for palaeoecological reconstructions. It is of increasing significance during the last few decades (Jackson and Williams, 2004). The idea is to associate the palynomorph content of surface samples to present-day environmental and biotic features, in order to infer past conditions from fossil assemblages, using the principle of uniformism. Despite some promising attempts (Grabandt, 1990; Rull and Vegas-Vilarrúbia, 2001), this approach has not yet been adequately tested in NPP studies. Another general handicap in both modern analog and palaeoecological studies is the choice of the best local habitat for sampling (sample type), in order to obtain accurate proxy representation (Medeanic, 2006; Rull, 2006).

In the Neotropical region, NPP studies are scarce, though several surveys have been conducted in Mexico (Almeida-Lenero et al., 2005), Brasil (Medeanic et al., 2003; Ledru et al., 2006; Medeanic, 2006), Colombia (van Geel and van der Hammen, 1978; Hooghiemstra, 1984;

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Kuhry, 1988; Grabandt, 1990), and Venezuela (Rull and Vegas-Vilarrúbia, 1997, 1999, 2001; Lovera and Cuenca, 2007; Rull et al., 2008). Besides identification issues, the lack of taxonomical and autoecological studies on potentially involved organisms is an added problem in this region. For example, Rull et al. (2008), working on the Venezuelan Andes, found a NPP indicator of the Younger Dryas chron (an event that has not been clearly recorded in the region, so far), that could not be related to any known organism and, hence, its palaeoenvironmental significance remains unknown. Another potential problem is that a number of studies assign some neotropical NPP types to the same taxa as recorded in temperate zones, which can be considered as doubtful (Ledru et al., 2006; Rull et al., 2008).

The aim of the present paper is to test the potential palaeoecological indicator value of modern NPP analogs in the Venezuelan Andes. The study uses the same altitudinal sampling transect from a previous modern analog survey on pollen and pteridophyte spores (Rull, 2006). In this way, besides the information that NPP may provide by themselves, the NPP record can be compared with pollen and altitudinal vegetation patterns, thus enhancing their interpretative usefulness.

2. Study area and methods

The sampling area is described in detail by Rull (2006); here a summary will be provided. The transect is in the Sierra de Santo Domingo, in the northernmost part of the Andes (Fig. 1). In this area, the montane Cloud Forest extends up to 3000 m, with 100–200 m local variation due to human activities. The Páramo ranges from this altitude to the snowline (4700 m), and its physiognomy is determined by the presence of the typical stem rosettes of *Espeletia* (Asteraceae). The transition between Cloud Forest and Páramo is not sudden but transitional, determining a narrow ecotone of one or a few hundred meters dominated by shrubs (Subpáramo or Páramo Shrubland). Similarly, the contact with the snowline shows a gradient from the densely vegetated Páramo to barren rocky environments, called Superpáramo or Desert Páramo, which extends between around 4000 and 4700 m altitude. Climatically, the upper and lower Páramo boundaries are characterised by respectively the 0 °C and 10 °C isotherms of annual average temperature (Monasterio and Reyes, 1980), and there is a fairly constant decrease of 0.6 °C/100 m altitude (Salgado-Labouriau, 1979). Total annual precipitation is not related to altitude, ranging from about 700 to 900 mm (Monasterio, 1980). Peat bogs are common in the whole range of the Venezuelan Páramos, while glacial lakes are especially abundant above 3500 m.

A total of 57 surface samples were taken from wet soils, moss polsters, lake shores and peat bog surface sediments, ranging from about 2300 to 4600 m altitude. Samples below ~3100 m are mostly from soils, bogs and mosses due to the scarcity of lakes at these elevations (Table 1). In the Páramo zone, most samples are from peat bogs, up to around 4100 m. In the Superpáramo, sample types are more varied, but mainly from mosses and bogs. This transect includes most of the sites cored in previous palaeoecological studies (Rull, 2006).

The samples were processed according to standard palynological procedures including KOH, HCl and HF digestions, and acetolysis (Faegri and Iversen, 1989). Slides were mounted with glycerine jelly. NPP abundance was expressed as percentage with respect to the pollen sum, which includes all pollen taxa apart from aquatic plants (Rull, 2006). NPP identification was made according to Bell (2005), Charman et al. (2000), Grabandt (1990), Hooghiemstra and van Geel (1998) and references therein, Jankovská (1990, 1991), Jankovská and Komárek (2000), Kuhry (1997), Rull and Vegas-Vilarrúbia (2001) and Vánky (1994). Diagrams were plotted with *psimpoll 4.10* and the different zonations were performed by "optimal splitting by information content" (OSIC), using the broken stick method to determine the significant number of zones (Bennett, 1996). Correspondence analyses (CA) and cluster analysis were performed with *MVSP 3.13*, after root-square transformation of percentages. Rare taxa were not downweighted. In the cluster analysis, the NPP were classified using the squared Euclidean distance and the minimum variance agglomerative method.

3. Results

A total of 65 NPP morphological types were recorded, including 38 forms of fungal spores, 10 forms of algal remains, and 17 forms corresponding to protozoans and diverse other zoological remains (Appendix A). Some of them have been identified to some extent.

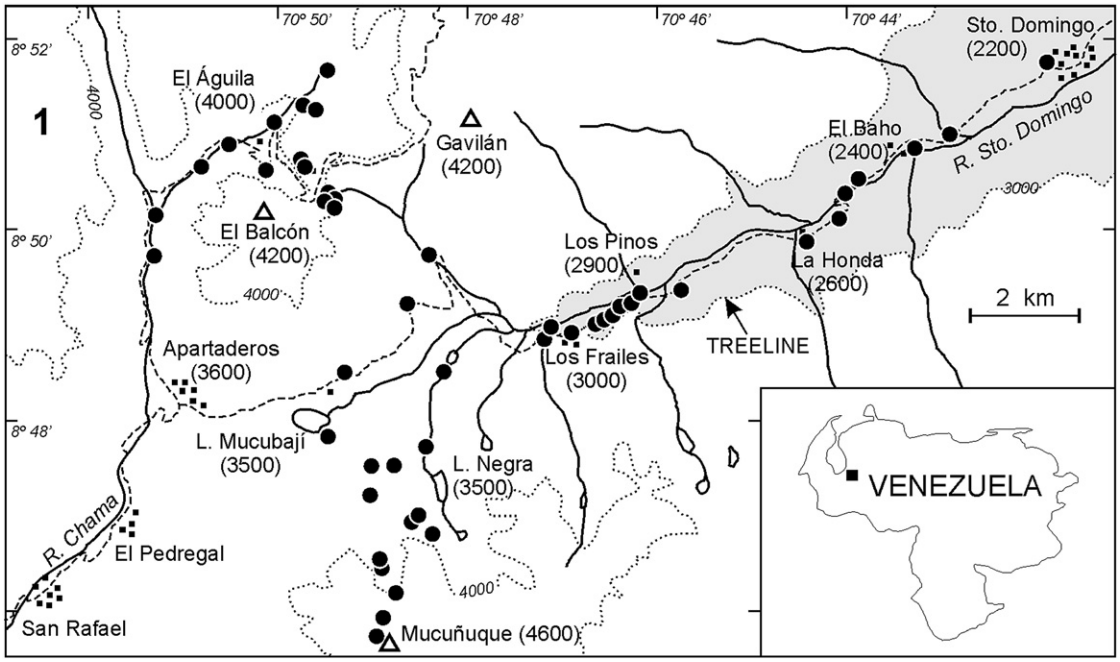

Fig. 1. Sketch map showing the sampling sites (black dots). The grey area corresponds to montane forests and the white area to Páramos *s.l.* (after Rull, 2006). Number 1 indicates the location of Laguna Verde Alta record (Rull et al., 2008), mentioned in the text. Altitudes are given in meters (m).

Table 1
Sample types according to the altitudinal arrangement of vegetation.

	Soil	Moss	Bog	Lake	TOTAL
Superpáramo	1	4	7	3	15
Páramo	4	2	22	2	30
Subpáramo	1	2	0	0	3
Cloud Forest	5	0	4	0	9
Total	11	8	33	5	57

Among the unidentified forms, some could be assigned to previously described types of the Amsterdam classification and referred to the corresponding literature, while others have been described for the first time and named using a code with the prefix IBB — (Institut Botànic de Barcelona) and a sequential number.

The altitudinal distribution of the three NPP groups has been illustrated in Fig. 2. Fungal spores are present throughout the whole transect, showing their maximum values in the uppermost Cloud Forest and the Subpáramo (~2600–3000 m). The lower fungal spore values are around the middle of the Páramo zone (~3500–3800 m), and from these altitudes to the Superpáramo (up to 4600 m), percentages are intermediate. Algal and zoological remains show a different altitudinal pattern. These two types of NPP remains are very scarce or absent below ~3800 m, but show a pronounced increase above this altitude. Algae show their maximum values between 3900 and 4000 m (Páramo–Superpáramo transition), while zoological remains peak around 3900 m, decrease at the Páramo–Superpáramo transition, and increase again at the top of the transect. Concerning sample type, there is some differentiation regarding the different NPP abundances (Table 2): i) Algae are frequent and abundant in bog and lake samples, and scarce in moss polsters; ii) Zoological remains are also more frequent in bogs but interestingly absent in lake samples (except for the occurrence of *Neorhabdocoela* in one single sample, Fig. 4); and iii) Fungal spores are important in all sample types except for lake samples. All sample types have been productive for most of the NPP found, bogs being the sample type containing frequent and abundant representatives of all NPP groups, whereas moss samples are scarce in algal and zoological remains, and soil samples contain few zoological remains.

Algae are restricted between ~3300 and ~4100 m (Fig. 3). *Concentricystis* (which is also known in the literature as *Pseudoschizaea*) is included here because it is likely of algal origin (Milanesi et al., 2006), although the phylogenetic relationship has not yet been confirmed, thus supporting other opinions and nomenclature (Scott, 1992). *Concentricystis* has a low abundance in the sequence; it is only present in four samples from the Páramo zone and in three samples from the lower Subpáramo and Cloud Forest zones (between 3800 and 2800 m). From 3760 m upwards, several Chlorophyte taxa show a

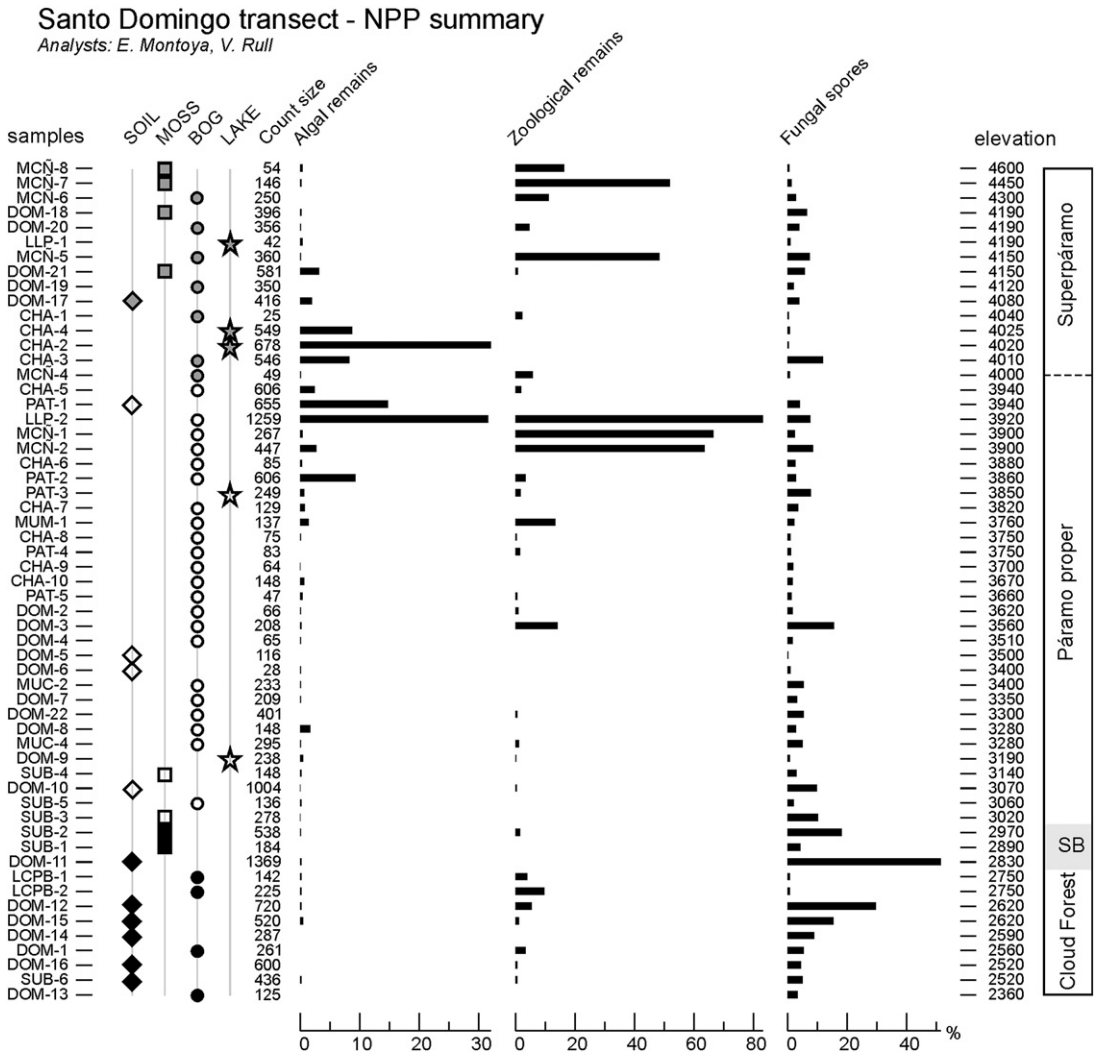

Fig. 2. NPP summary diagram. Percentages are based on pollen sum (see methods). The sample type (bog, lake, moss, and soil) is indicated at the left side of the diagram (black = Cloud Forest/Subpáramo, white = Páramo, grey = Superpáramo). The altitudinal vegetation patterns (Cloud Forest, Páramo, etc.) are indicated at the right column. SB = Subpáramo or Shrub Páramo.

Table 2
Dominance of the studied NPP categories depending on: 2A) sample type; and 2B) vegetation arrangement (numbers represent the samples where the NPP group was the dominant). SSP = Superpáramo; P = Páramo; SBP = Subpáramo; CF = Cloud Forest.

2A				
	Soil	Moss	Bog	Lake
Algae	2	1	3	2
Animals and others	0	1	11	0
Fungi	8	6	14	2
2B				
	SSP	P	SBP	CF
Algae	5	3	0	0
Animals and others	6	4	0	2
Fungi	5	15	3	7

short sequence until 4150 m, beginning with *Zygnema*-type and ending with *Spirogyra* (morphotype 1, see Appendix A), with *Pediastrum* and *Botryococcus* (two of the more frequent algae in palaeoecological studies) in an intermediate position between 3900 and 4000 m. Among the more abundant types, it is worth mentioning that *Botryococcus* and *Zygnema*-type are also present – though in very low values – at lower altitudes, whereas *Pediastrum* is absent. It is also noteworthy that algal types are common in lake samples and also occur in bog samples, but algae are absent or very scarce in soil and moss samples.

The altitudinal distribution of zoological remains is similar to the distribution of algae, except for the occurrence of *Assulina*, *Neorhabdocoela* and Acari in soil samples from the upper Cloud Forest zone (Fig. 4). Most zoological types are absent in the lower Páramo zone, appearing around 3500 m and extending to the top (4600 m), except for some types (*Centropyxis aculeata*-type, *Conochilus natans*-type and *Centropyxis cassis*-type), which occur until around 3900 m, and thus not reaching the Superpáramo. They are abundant in bog samples (Table 2), but they are also present in several moss samples.

Fungal spores are more diverse than algal and zoological remains, and show a more extended and continuous elevational distribution (Fig. 5). The zone boundaries obtained in this case almost coincide with the vegetation boundaries. In the Cloud Forest zone, the assemblage is dominated by *Coniochaeta* cf. *ligniaria* and IBB-31, with a significant contribution from *Cercophora*-type, Sordariales, IBB-32 and IBB-29. Other morphotypes such as Types 495, IBB-22, IBB-24 and IBB-6 occur in low frequencies. In the Páramo, these types decrease or disappear and are replaced by others, such as *Sporormiella*-type and Type 201, among the more abundant. *Sordaria*-type is present throughout the transect but in this part of the transect it reaches the maximum values.The Superpáramo is characterised by a

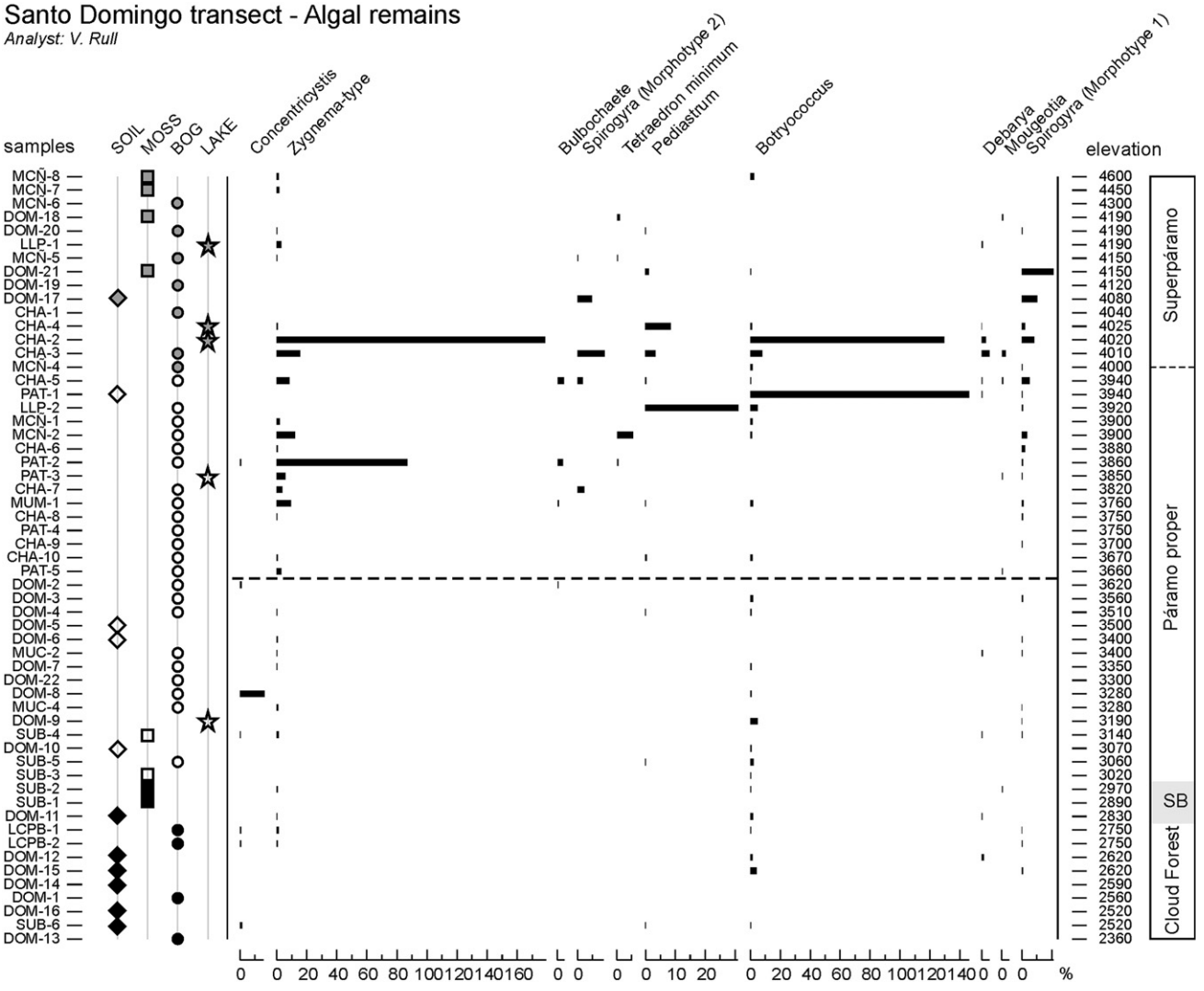

Fig. 3. Percentage diagram of algal remains, following the same representation patterns as in Fig. 2. The broken line indicates the zone boundaries using the OSIC zonation method (see Methods for details).

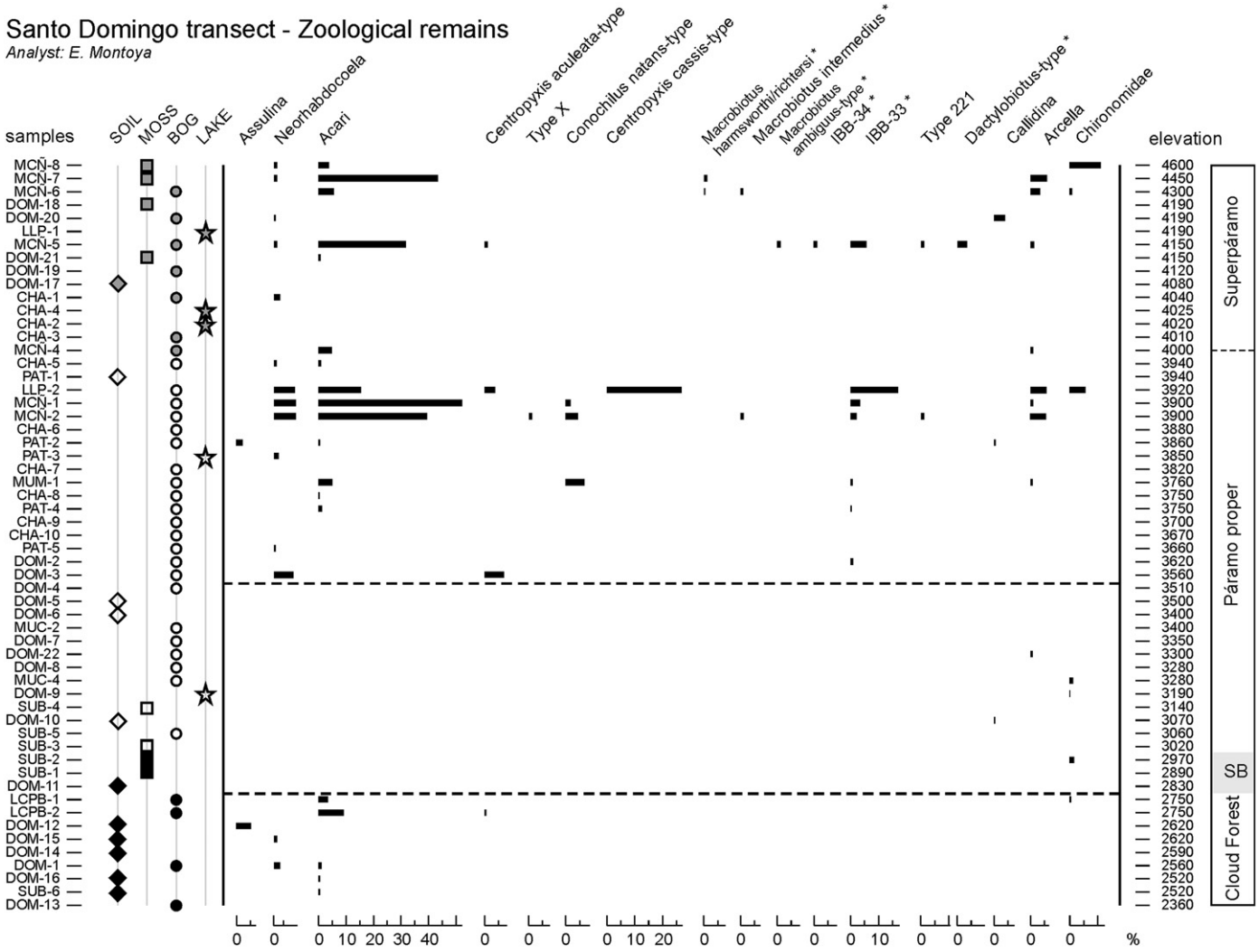

Fig. 4. Percentage diagram of zoological NPP, following the same representation patterns as in Fig. 2. The broken lines indicate the zone boundaries using the OSIC zonation method (see Methods for details). (*=Tardigrada egg morphotypes).

diversity decline due to the scarcity or absence of most of forest and Páramo types, except for *Sporormiella*-type and Type 201 which decrease compared to the Páramo zone, and IBB-15, which slightly increases. *Coniochaeta* cf. *ligniaria* also appears again at the top of the transect, but in a lower frequency than in the Cloud Forest zone.

The cluster analysis defined three main NPP groups with some subgroups (Fig. 6):

Group 1 includes 45 of the 65 identified NPP. All the zoological remains are present within this assemblage. Three well defined subgroups could be distinguished (excluding Acari from these subgroups):

Subgroup 1A represents NPP from the three established categories and is mainly formed by types present in few samples at low frequencies. Most of these types occur from ~3800 m upwards (Fig. 6B).

Subgroup 1B mainly includes fungal spores, but *Concentricystis* is also included. The maximum values of these types are found along intermediate elevations (2800–3300 m), though they are present until the lowest part of the transect (Fig. 6B).

Subgroup 1C includes a high number of zoological remains, although the three NPP categories are represented. Their maximum values are from ~3700 m upwards (Fig. 6B).

Group 2 is entirely formed by fungal spores; two subgroups could be distinguished:

Subgroup 2A includes 11 fungal spore types, the more abundant are *Cercophora*-type, Sordariales, IBB-31 and *Glomus*. These taxa are present in the lower part of the transect, being more abundant from 3000 m downwards.

Subgroup 2B includes only two fungal spore types wich are practically absent at intermediate elevations (between 3000 and 4000 m), and show their maximum values from 2800 m downwards (Fig. 6B).

Group 3 is the group less well defined; two subgroups could be differentiated (excluding *Pediastrum* from the subgroups):

Subgroup 3A only includes three fungal spore types, which are present along the whole transect, but with maximum values at the intermediate elevations (from around 3000 to 4000 m, Fig. 6B).

Subgroup 3B only includes two different algal types. Their maximum values are represented between 3800 and 4000 m (Fig. 6B).

Fig. 7A shows the arrangement of sampling sites in the space of the first two axes of the CA analysis, which account for 18% of the total variance. Axis 1 likely represents an altitudinal gradient with Cloud

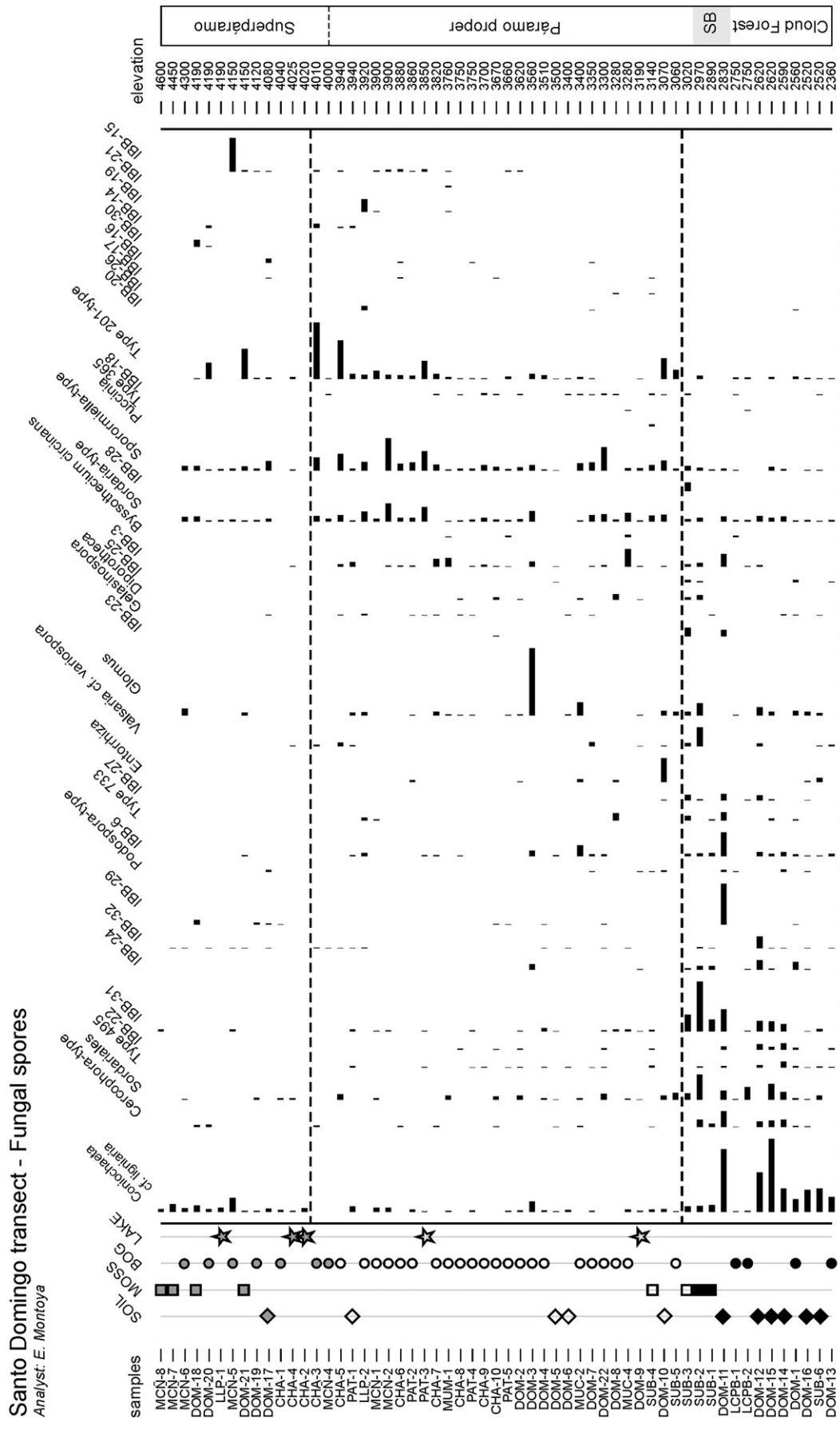

Fig. 5. Percentage diagram of fungal spores, following the same representation patterns as in Fig. 2. The broken lines indicate the zone boundaries using the OSIC zonation method (see Methods for details).

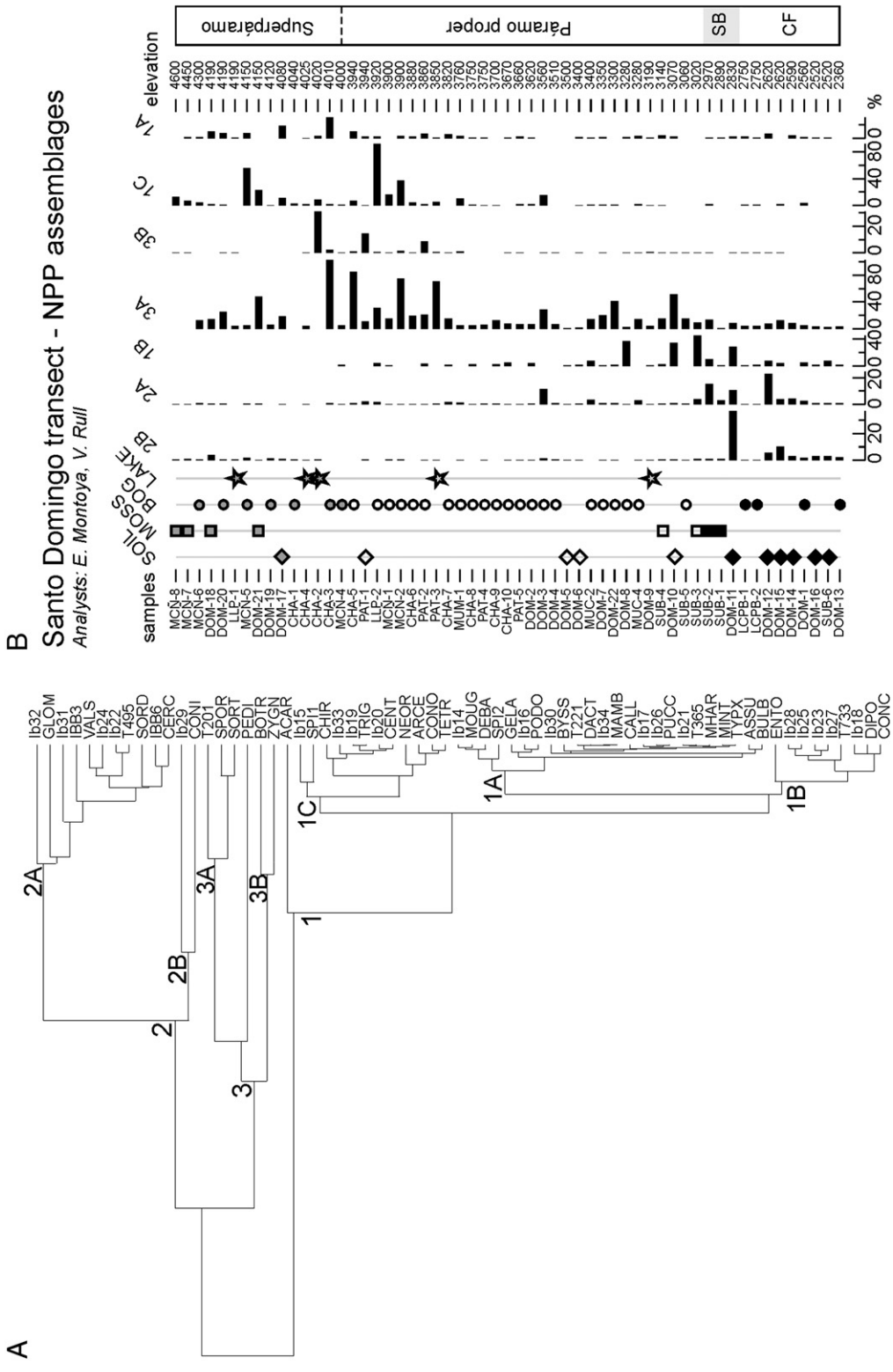

Fig. 6. NPP assemblages. 6A. Scatter plot using the cluster analysis results, based on minimum variance and squared euclidean distances. See acronyms in Appendix A. 6B. Percentage diagram of the assemblages obtained in cluster analysis, following the same representation patterns as in Fig. 2. CF = Cloud Forest.

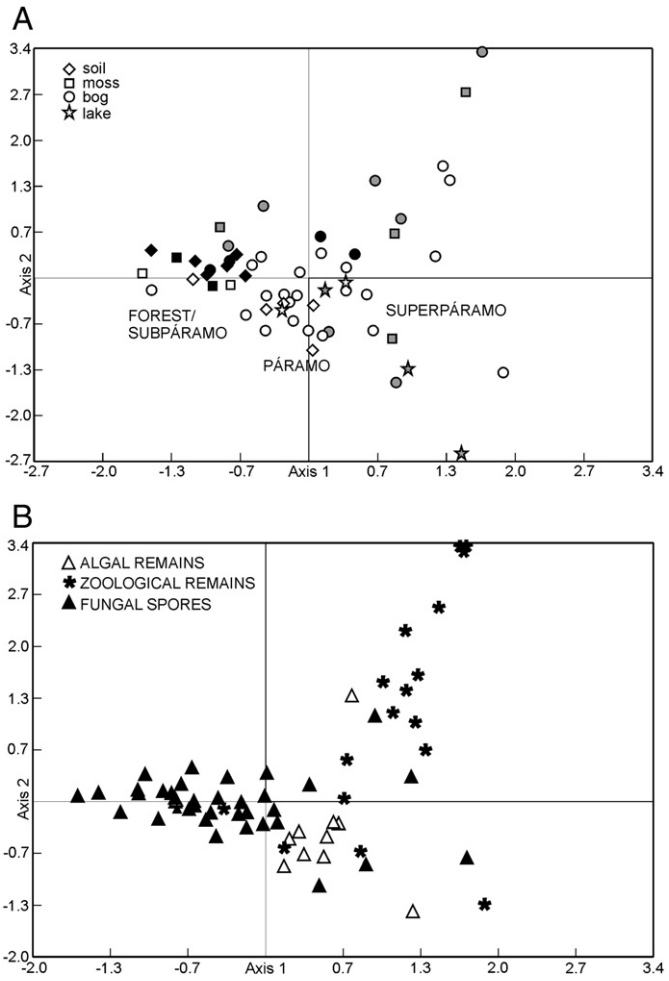

Fig. 7. Ordination analyses. A) Sample ordination analysis. Scatter plot using the first two CA axes. Samples are differentiated according to two criteria: sample type (see legend) and vegetation type (black = Cloud Forest/Subpáramo, white = Páramo, grey = Superpáramo). B) NPP ordination analysis. Scatter plot using the first two CA axes. NPP are differentiated according to their taxonomic origin.

Forest/Subpáramo samples at the left side, Superpáramo samples at the right, and Páramo proper samples in between. However, six samples deviate from this pattern. This is the case in one Páramo sample (LLP-2) that lies in the Superpáramo region (Fig. 7A). This sample, however, is from a bog at 3920 m elevation, which is very close to the Páramo–Superpáramo boundary. Also, two Cloud Forest/subpáramo bog samples (LPCB-1 and LPCB-2) are within the Superpáramo and Páramo regions, respectively. Despite their elevation (2750 m) below the regional upper Cloud Forest limit, these bogs are in an area where human activities have significantly lowered the treeline. The vegetation now consists of open Páramo vegetation. Finally, two bog samples (CHA-1 and DOM-19) and one moss (DOM-18) Superpáramo sample fall within the Cloud Forest domain. In this case, there are no apparent environmental features that distinguish these samples from others taken at Superpáramo elevations. The Pearson product-moment correlation coefficient between axis 1 and altitude is $r = 0.417$, which is significant at $p < 0.001$. Axis 2 could be related to sample type, possibly linked to water content, as all lake samples are within the negative side, while most soil and moss samples are at the positive side. The dispersion along axis 2 increases with altitude, indicating that the effect of sample type is larger at higher than at lower altitudes.

Fig. 7B shows the arrangement of the NPP types in the space of the first two axes of the CA analysis. Although some of them deviated from the general rule, they form three clear groups according to their taxonomic origin. Fungal spores are widespread along axis 1, but they occur mostly at medium to lower elevations. Algal and zoological remains lie mostly at intermediate to high values, respectively. With respect to axis 2, fungal spores show little dispersion as compared to other NPP types. This axis clearly seggregates algal (mostly negative) from zoological remains (mostly positive) at the right side of the plot.

4. Discussion

The main environmental variables tested in this study are altitude and sample type. In a previous study, altitude was found to be the main environmental feature needed to interpret pollen and pteridophyte spore presence and abundance along the same transect (Rull, 2006). The record of pollen and pteridophyte spores was linked with the distribution of pollen and spore producing plants but in the case of NPP, the situation is somewhat different, as is discussed below. The discussion is organised according to the different NPP groups found.

4.1. Algal remains

The maximum abundance of this group, as a whole, occurs around the transition between Páramo and Superpáramo vegetation belts in different sample types (wet soils, bogs and lake sediments; Fig. 2), suggesting a major influence of elevation. However, the abundance of each NPP type differs according to both altitude and sample type (Fig. 3), which points towards an influence of this factor at individual NPP level (Fig. 7B). For example, the influence of altitude is especially significant in *Spirogyra* morphotype 1, which is almost restricted to the Superpáramo and increases with elevation until about 4200 m (Fig. 3). Contrastingly, *Spirogyra* morphotype 2 occurs in bog and soil samples but not in lake sediments (Fig. 3). *Botryococcus* is abundant in lakes and soils but not in bogs, whereas *Pediastrum* and *Zygnema*-type have their maxima in bogs and lakes. Previous palaeoecological studies in the northern Andes have documented the same or similar algal remains and have interpreted them in palaeoenvironmental terms. In the Venezuelan Andes, Salgado-Labouriau and Schubert (1977) used *Botryococcus* and zygospores of Zygnemataceae as indications of warmer climates, while Rull and Vegas-Vilarrúbia (1993) emphasised that habitat preference (i.e. littoral vs. pelagic conditions) would be more determinant. In a neighbouring area (Fig. 1), Rull et al. (2008) suggested that the *Pediastrum–Botryococcus* alternation would be the reflection of colder–warmer climates in the Superpáramo belt. The results of the present work do not support evident climatic (i.e. altitudinal) differences for these NPP, as habitat peculiarities (i.e. sample type) seem to play a role. In the Colombian Andes, van Geel and van der Hammen (1978) linked *Debarya* with cool climates and *Mougeotia*, *Spirogyra* and *Zygnema*-type with Páramo conditions, and that conclusion is supported by the results of our Venezuelan transect study.

4.2. Zoological remains

The maximum abundance of these NPP as a group occurs in the uppermost Páramo and Superpáramo samples (Fig. 2), and therefore elevation is a factor to be taken into account. However, maximum abundances occur almost always in bog samples and never in lakes (Table 2), indicating that sample type should also be considered (Fig. 7B). Individually, some interesting relationships can be established. For example, the maximum around 3900 m is mainly due to Acari remains and coincides with a maximum of *Isoëtes* (Rull, 2006), an aquatic fern living on flooded bogs and shallow waterbodies. The association of Oribatid mites and aquatic macrophytes is well known elsewhere (Erikson, 1988), and has also been documented in the Venezuelan Páramos (Rull and Vegas-Vilarrúbia, 1997). Testate amoebae show very different patterns as *Assulina* is scarce and

present in the Cloud Forest and Páramo belts, while *Arcella* was recorded almost only in Páramo and Superpáramo belts, reaching the uppermost levels (Fig. 4). Grabandt (1990) found a similar distribution for *Arcella* in the Colombian Andes. Other important types are *Neorhabdocoela* and the different Tardigrada egg morphotypes (Fig. 4). In this study, *Neorhabdocoela* peaks around the Páramo–Superpáramo transition in bog samples. Rull et al. (2008) suggested that increases in *Neorhabdocoela* oocites could be related to higher lake levels but this is not supported here; a more detailed study of the different lacustrine sub-environments would be necessary to test this hypothesis. In general, Tardigrada eggs have been found at high latitudes and at low-latitude high altitudes, usually under cold climates, in shallow permanent oligotrophic and acidic water bodies (Jankovská, 1990, 1991; Kaczmarek et al., 2008). According to Cromer et al. (2008), this is because these environments provide better preservation conditions, but a bias in sampling efforts should also be considered. For example, in the present study, most of the six classes of these eggs were found in bog samples and none of them was recorded in lake sediments (Fig. 4).

4.3. Fungal spores

The evident and continuous gradient of these spores along the transect, independent from sample type (Fig. 5), suggests that altitude is the main environmental feature that controls their distribution (Fig. 7B). Furthermore, the corresponding fungal spore zonation and pollen zonation suggest a close relationship, probably because flowering plants create the habitats for various saprophytic and parasitic fungi. This is manifest, for example, in the lower zone, corresponding to the Cloud Forest and Subpáramo belts, dominated by ligneous plants, where *Coniochaeta* cf. *ligniaria* and *Cercophora*-type – two taxa typical of environments with abundant decaying wood; van Geel et al., 2003; van Geel and Aptroot, 2006 – are dominant. Likewise, the frequent occurrence of *Glomus*, though in low frequencies, is also noteworthy as this is a mycorrhizal fungus commonly associated to the roots of trees and shrubs (van Geel et al., 1989). The highest abundance of *Glomus*, however, occurs in one single sample (DOM-3) within the Páramo belt. This sample was taken in a bog near a *Pinus* plantation, which could explain the high abundance of this mycorrhizal fungus. In the Páramo belt, *Sporormiella*-type and *Sordaria*-type are almost continuously present. Both genera have been described as coprophilous (van Geel and Aptroot, 2006), and often related with the presence of large herbivores (van Geel et al., 2003; Raper and Bush, 2009). In our transect *Sporormiella*-type and *Sordaria*-type are linked with the abundance of herbaceous vegetation and both fungal spore types are probably associated with grazing (Almeida-Lenero et al., 2005). Most fungal spore types found in the Superpáramo belt were unknown morphotypes, so environmental information could not yet be obtained. However, their record at higher elevations might be useful for future palaeoecological interpretations.

In this study, both altitude and sample type are linked to NPP assemblages. This is manifested in the low correlation of CA axis 1 with sample elevation and the high dispersion of the different sample types along CA axis 2 (Fig. 7A). Some interaction exists between these two variables, as they are not totally independent. For example, soil and moss samples predominate below ca. 3200 m, whereas lake sediment samples extend from around 3800 m upwards. Bog samples are more or less widespread, but they are more frequent between 3000 and 4000 m. At higher elevations, moss surface samples are more frequent again, while no soil samples were collected. These patterns are determined by the availability of the different habitats at different altitudes, which is mainly due to climatic, geomorphological and vegetation features. In this sense, due to the relationship observed between algal and zoological remains and sample type, it can be suggested that local conditions of sample locations (such as pH, dissolved oxygen, macrophyte presence, etc.) probably influence the NPP distribution. On the other hand, although the human impact at these locations is practically absent, the distribution of lower vegetation belts could be disturbed by human activities, as is the case of *Pinus* plantation named above. Therefore, when using the results of the present study for palaeoenvironmental interpretations, all these factors should be considered.

In spite of this apparently similar influence of altitude and sample type on NPP groups, the NPP assemblages found by cluster analysis show a genuine elevational pattern (Fig. 6). Assemblages 2A and 2B only include fungal spores, and are clearly related to the Cloud Forest–Subpáramo belt; assemblage 1B characterises the Cloud Forest–Páramo transition; assemblage 3A is widespread along the whole transect but peaks around the Páramo proper–Superpáramo transition; assemblage 3B (*Botryococcus* and *Zygnema*-type) is also characteristic of this transition; and assemblages 1C and 1A are typical of the higher elevations, within the Superpáramo belt. The combination of the fungal spores gradient with a clear altitudinal pattern (Fig. 5) with the higher abundance of algal and zoological remains — more affected individually by local conditions (Fig. 7B) – at upper levels (Figs. 3 and 4) – minimises the influence of sample type. Thus, the representation of the NPP assemblages (Fig. 6B) is mainly linked to the altitudinal gradient and, therefore, useful to interpret past records in terms of altitudinal (and indirectly, climate) shifts.

5. Conclusions

Sixty-five different NPP types – classified as algal and zoological remains, and fungal spores – have been identified in an altitudinal transect in the Venezuelan Andes mountains. Among the environmental variables considered, altitude was found to be important for the observed differences in the NPP assemblages, whereas sample type and probably water body characteristics also influence algal and zoological remains distribution. In the case of fungal spores, the relationship with altitude is clearly linked to the altitudinal vegetation patterns, in agreement with the previously studied pollen record. The sample type effect is minimised when the NPP studied are considered altogether, and grouped into 7 assemblages by cluster analysis. In this way, their usefulness as palaeoecological proxies is maximised. This study reinforces the utility of modern analog studies for NPP as a complement of traditional pollen surveys. Besides the altitudinal patterns, which can provide general palaeoenvironmental information, the influence of sample type on NPP assemblages can be useful to derive inferences on *in situ* ecological characteristics. Further studies based on NPP distribution considering local habitat features will surely improve the accuracy of the present results. The study of modern sedimentation of these microremains with palaeoecological purposes is thus encouraged, particularly in poorly known areas, as tropical regions.

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Appendix A

Name, acronym used for the ordination analyses and brief description of the non-pollen palynomorphs (NPP) types recorded in the present study. Illustrations of non-identified NPP (IBB types) and Tardigrada eggs are attached.

A.1. Algal remains

Concentricystis: CONC. Classified by Christopher (1976), also known as *Pseudoschizaea* (Scott, 1992). They have been related to freshwater marshes (Rossignol, 1962; Milanesi et al., 2006).

Zygnema-type (HdV.213 and HdV.314): ZYGN. Classified by van Geel et al. (1981, 1989), Bakker and van Smeerdijk (1982) and Kuhry (1997). Heterogeneous group of hyaline, spheroidal and flattened spores from different species. The occurrence suggests stagnant, shallow, mesotrophic to eutrophic, open water.

Bulbochaete: BULB. Classified by van Geel and van der Hammen (1978).

Spirogyra morphotype 2 (HdV.132): SPI2. Classified by Pals et al. (1980) and van der Wiel (1983). Reticulate *Spirogyra* spores.

Tetraedron minimum (HdV.371): TETR. Classified by Bakker and van Smeerdijk (1982). Indicative for eu- to mesotrophic conditions of open freshwater.

Pediastrum: PEDI. See, e.g., Jankovská and Komárek (2000) and Komárek and Jankovska (2001). *Pediastrum* species seem to be indicative of a wide range of environmental responses, such as change in erosion at the catchment, turbidity, water chemistry, nutrient status and pH (Batten, 1996). The range of responses may be due to the fact that in palynological records often different *Pediastrum* species are lumped together (van Geel, 2001).

Botryococcus: BOTR. See, e.g., Jankovská and Komárek (2000). Modern *Botryococcus* occurs in temperate and tropical regions, and is known to tolerate seasonally cold climates. It generally lives in freshwater fens, temporary pools, ponds and lakes, where it may form a thick surface scum, but considerable abundances in variable salinity habitats are also known (Batten and Grenfell, 1996).

Debarya (HdV.214): DEBA. Classified by van Geel et al. (1989) and observed in the initial phase of sandy pools (Ellis-Adam and van Geel, 1978), but also in Colombian Andes lake deposits (van Geel and van der Hammen, 1978).

Mougeotia (HdV.133): MOUG. Classified by Pals et al. (1980). Van Geel and Grenfell (1996) showed an example of a short successional phase in which *Mougeotia* zygospores played a pioneer role after a local rise of the water table in a Holocene northwest European raised bog.

Spirogyra morphotype 1 (HdV.130): SPI1. Classified by Pals et al. (1980), van der Wiel (1983) and van Geel et al. (1983). Psilate *Spirogyra* spores. Species of *Spirogyra* are common in stagnant, shallow water.

A.2. Zoological remains

Assulina (HdV.32): ASSU. Identified and illustrated by van Geel (1978). The occurrence of this oligotraphentous thecamoeba has been related to a low-nutrient situation and, although they are probably the most common genus in all studies, they appear more abundant in intermediate to relatively dry locations (Charman et al., 2000).

Neorhabdocoela (HdV.353): NEOR. Classified by van Geel et al. (1981). Its morphology suggests a cocoon of the non-parasitic flatworm order Rhabdocoela (Class Turbellaria). The cocoons usually appear broken.

Acari (HdV.36): ACAR. Classified by van Geel (1976) as various types of animal remains that may be part of mites.

Centropyxis aculeata-type: CENT. Illustrated by Charman et al. (2000). Mostly associated with aquatic habitats (De Graaf, 1956) or very wet conditions (Warner, 1987).

Type-X: TYPX. Recorded by Grabandt (1990). It has been found in Colombian Andes sediments and tentatively related to *Hyalosphenia* sp. (Testate Amoebae). Both in Venezuelan (the present study) and Colombian Andes it was found in very low frequencies.

Conochilus natans-type: CONO. Illustrated by van Geel (2001). Resting eggs of rotifers are of regular occurrence in lake deposits.

Centropyxis cassis-type: TRIG. Illustrated by Charman et al. (2000). According to De Graaf (1956) this taxon is typical of hygrophilous, submerged and wet mosses.

Macrobiotus harmsworti/richtersi (Plate II): MHAR. Classified by Jankovská (1991).

Macrobiotus intermedius (Plate II): MINT. Classified by Jankovská (1991).

Macrobiotus ambiguus-type (Plate II): MAMB. Unidentified microfossil remains which could proceed from Tardigrada egg remains. It has been tentatively related in this study with *Macrobiotus ambiguus* egg remains (Jankovská, 1991).

Tardigrada IV (IBB-34; Plate II): Ib34. Unidentified microfossil remains which could proceed from Tardigrada egg remains.

Tardigrada II (IBB-33; Plate I): Ib33. Unidentified microfossil remains which could proceed from Tardigrada egg remains. It has been tentatively related in this study with *Macrobiotus* sp. Type 3 egg remains from Jankovská (1990).

Type 221: T221. Classified by van Geel et al. (1989). Hyaline microfossils probably of invertebrate origin, that are of regular occurrence in samples from sandy pool deposits.

Dactylobiotus-type (Plate II): DACT. Unidentified microfossil remains which could proceed from Tardigrada egg remains. It has been tentatively related in this study with *Dactylobiotus* sp. egg remains (Kaczmarek et al., 2008); also of similar morphology to *Macrobiotus* sp. Type 2 egg remains from Jankovská (1990). *Dactylobiotus luci* was identified by Kaczmarek et al. (2008) and related to permanent marsh pools with acid pH from high altitudes of tropical African mountains.

Callidina (HdV.37): CALL. Classified by van Geel (1978), van Geel et al. (1981) and Kuhry (1985). This rotifer occurs in pools and peat bogs. *Callidina* is a terrestrial form that sometimes remains dormant for the greater part of the year in a desiccated condition, but becomes active, immediately when moistened by rain water.

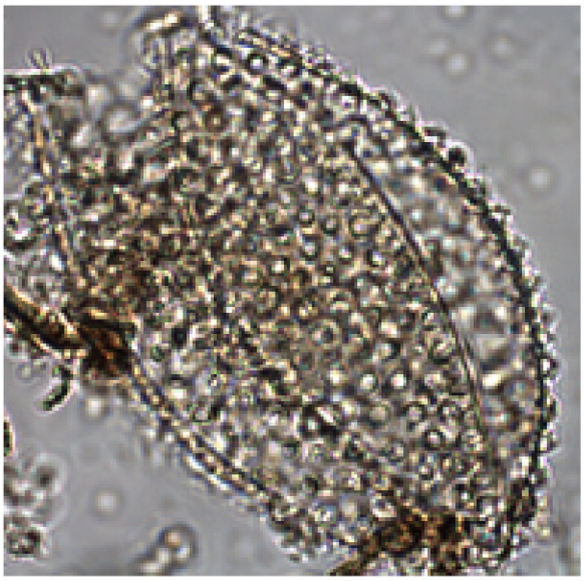
Arcella (HdV.352): ARCE. Classified by van Geel et al. (1981) and Kuhry (1997). Taxa from the genus *Arcella* often appear at the wetter end of sampled gradients (Charman et al., 2000).

Chironomidae: CHIR. Heterogeneous group which represent several types of animal remains (mainly mandibles) that may be part of Chironomidae.

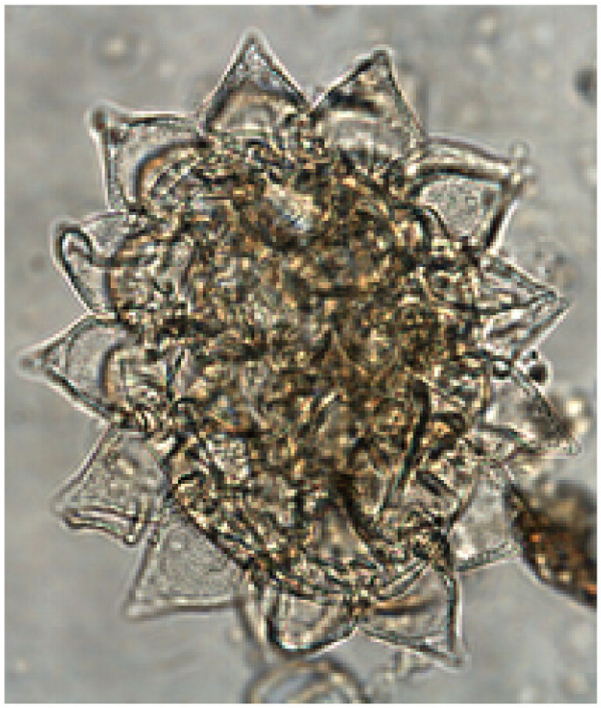
A.3. Fungal spores

Most ecological remarks are based on northwest European records.

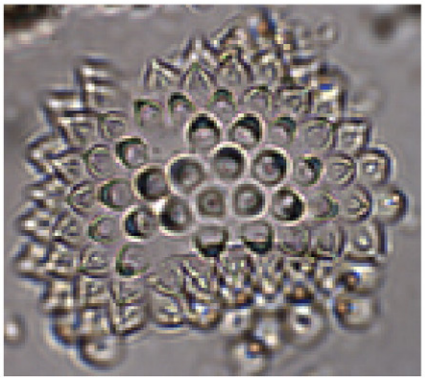
Gelasinospora (HdV.1): GELA. Classified by van Geel (1978) and Garneau (1993). *Gelasinospora* species are mainly fimicolous, but also carbonicolous and lignicolous. Previous studies of Holocene peats have revealed that maxima in the frequency of *Gelasinospora* sp. occur in highly decomposed peat formed under relatively dry, oligotrophic conditions.



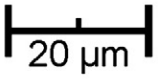
Dactylobiotus-type

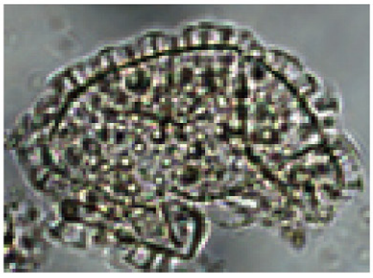


Macrobiotus harmsworti/richtersi



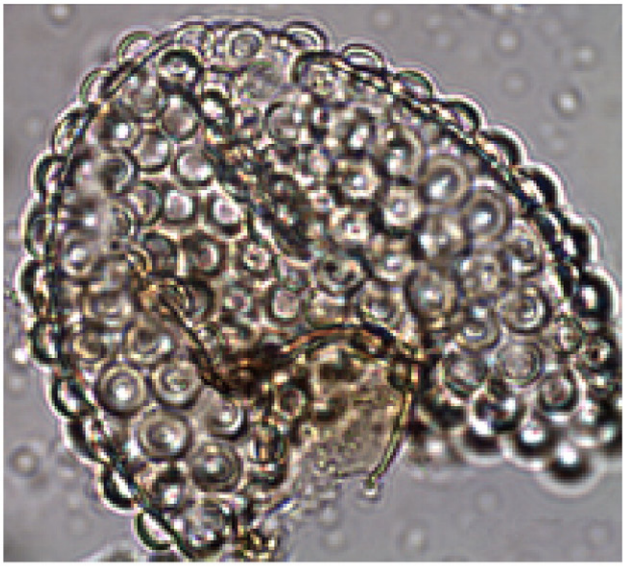
Macrobiotus ambiguus-type





Macrobiotus intermedius

IBB-33



IBB-34

Plate I: Illustrations of the different Tardigrada eggs morphotypes found. Non-identified types are now described and named with IBB prefix.

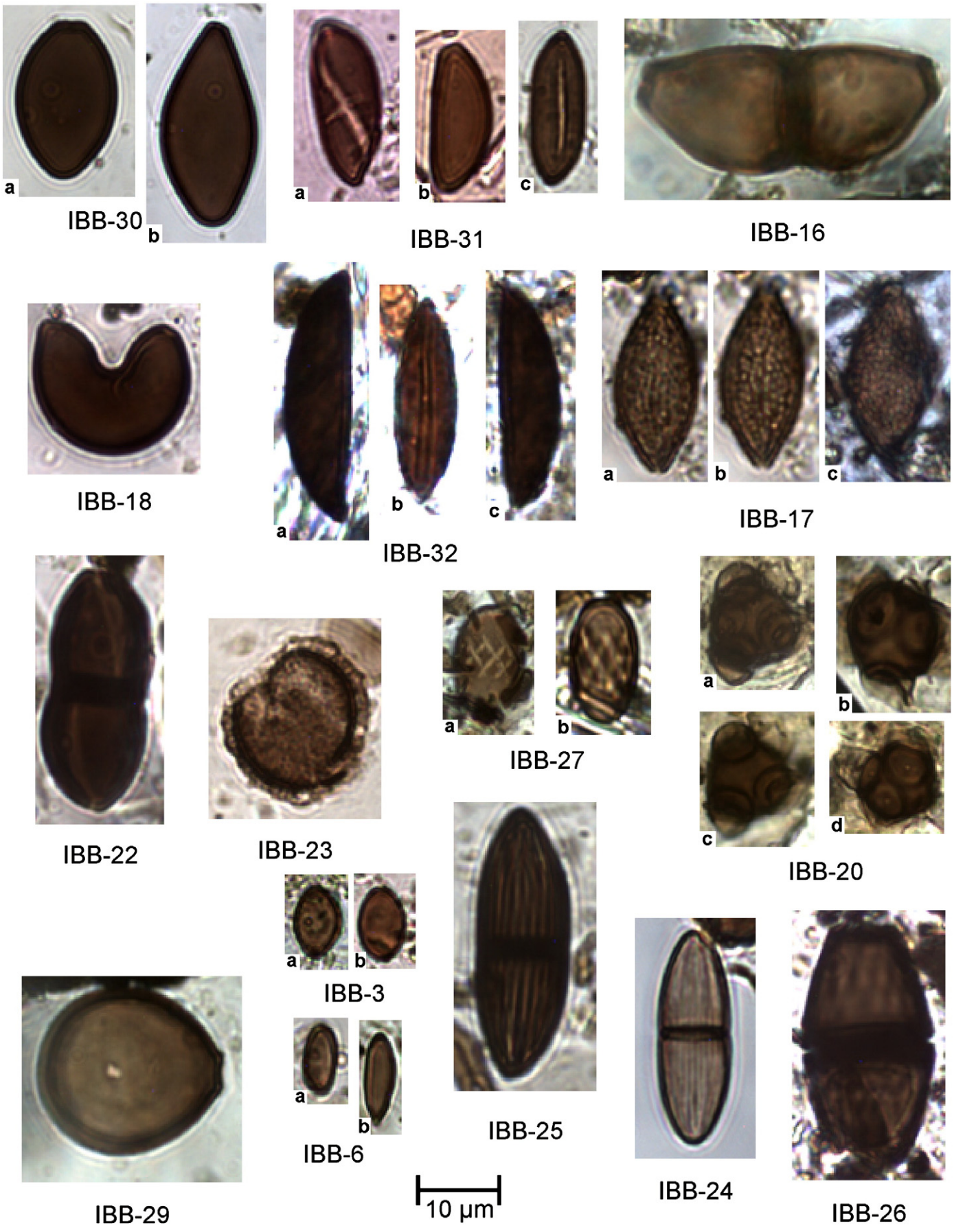


Plate II: Illustrations of some non-identified NPP, now described and named with IBB prefix.

Plate III: Illustrations of some non-identified NPP, now described and named with IBB prefix.

Coniochaeta cf. *ligniaria* (HdV.172): CONI. Classified by van Geel et al. (1983). This type is common on dung and wood but is also of regular occurrence in soil surface samples from a Roman Period settlement site with strong evidence for a high population density of domesticated animals (van Geel et al., 2003).

Cercophora-type (HdV.112): CERC. Classified by van Geel et al. (1981, 1983) and van der Wiel (1983). *Cercophora* species are coprophilous or occur on decaying wood, on clumps and on other herbaceous stems and leaves and can be used as indicators for (extra) animal dung in the surroundings of the sample site (van Geel and Aptroot, 2006). There are different morphotypes within this taxon.

Sordariales: SORD. See Bell (2005). Included several morphotypes within this order but without genus identification.

Type 495 (HdV.495): T495. Classified by van Smeerdijk (1989). Globose fungal spores with evenly distributed spines.

Podospora-type (HdV.368): PODO. Classified by van Geel et al. (1981). Van Geel and Aptroot (2006) suggest a relationship between increased occurrence and the presence of man or domesticated animals (providing dung as a substrate).

Type 733 (HdV.733): T733. Classified by Bakker and van Smeerdijk (1982). Globose microfossils which occur in mesotrophic conditions.

Entorrhiza (HdV.527): ENTO. Classified by van Geel et al. (1983). *Entorrhiza* species occur as parasites on a variety of plants (Vánky, 1994).

Valsaria cf. *variospora* (HdV.140): VALS. Classified by van Geel et al. (1983) and van der Wiel (1983). Ascospores of this type were recorded in peat deposits formed under wet eutrophic conditions.

Glomus (HdV.207): GLOM. Classified by van Geel et al. (1989). *Glomus* species with their globose chlamydospores have a vesicular–arbuscular endomycorrhizal relationship with flowering plants and occur on the roots of local vegetation. In lake deposits the occurrence of chlamydospores points so soil erosion in the catchment area (Anderson et al., 1984).

Diporotheca (HdV.143): classified by van Geel et al. (1986, 1989) and van der Wiel (1983). Spores were regularly recorded in Holocene deposits formed in eutrophic to mesotrophic conditions. Representatives of Diporothecaceae often have specific parasite–host relationships (van Geel and Aptroot, 2006).

Byssothecium circinans (HdV.16): BYSS. Recorded by van Geel (1978) and identified by van Geel and Aptroot (2006). The species is a saprobe or weak parasite on woody substrates.

Sordaria-type (HdV.55): SORT. Classified by van Geel (1976) and van Geel et al. (1983). Most *Sordaria* species are coprophilous (van Geel and Aptroot, 2006).

Sporormiella-type (HdV.113): SPOR. Classified by Ahmed and Cain (1972) and van Geel et al. (2003). *Sporormiella* species are mainly coprophilous. Separate spore cells of *Sporormiella*-type were distinguished by Davis et al. (1977) and by van Geel et al. (2003) who concluded that the spores are a reliable proxy for faunal biomass.

Puccinia (HdV.529): PUCC. Classified by van Geel et al. (1983). Many of the species in this genus are plant pathogens.

Type 365 (HdV.365): T365. Classified by van Geel et al. (1981). Fungal spores with rounded protuberances.

Type 201-type (HdV.201): T201. Classified by van Geel et al. (1989) and Kuhry (1997). Type 201 was described as fungal spores (conidia?) 7–10 septate, often broken off at one or both ends. For the present study there are different morphotypes included in Type 201 (HdV.201).

IBB-3 (Plate III): IBB3. Ascospores fusiform, 9.9–13.3 × 6.4–8.6 μm, with an apical pore.

IBB-6 (Plate II): IBB6. Fungal spores ellipsoidal to cylindrical, 10.6–14.7 × 5.2–6.5 μm, with a soft longitudinal germ slit.

IBB-14 (Plate I). Ib14. Ascospores one-septate 34.3–47 × 13.3–25.4 μm, constricted at the septum. Usually one cell larger than the other one. An outer, light-coloured wall showing an irregular pattern of longitudinal furrows and ridges up to ca. 2.7 μm high.

IBB-15 (Plate I): Ib15. Ascospores lemon-shaped, 37–49 × 23–30 μm, with two different protruding pores, in apical and subapical positions, ca. 2 and 4.8 μm in diameter. Wall thickened around the pores.

IBB-16 (Plate III): Ib16. Ascospores one-septate, 37.7–52.3 × 14.3–22.3 μm, constricted at the septum. Originally the spores may have been 3-septate, with hyaline, thin-walled (not-preserved) end cells.

IBB-17 (Plate III): Ib17. Ascospores fusiform, 20.1–24.1 × 9.9–12.6 μm, with two apical pores and a reticulate surface. IBB-17 spores are present in many samples along the transect, but always in low frequency.

IBB-18 (Plate III): Ib18. Fungal spores kidney-shaped, 19.3–23.1 × 9.6–16.8 μm, with apical pores. Present in several samples in very low frequency.

IBB-19 (Plate I): Ib19. Ascospores one-septate fusiform, 66–73.3 × 7.9–10.6 μm, slightly constricted at the septum. One cell somewhat shorter than the other. Wall showing a regular pattern of longitudinal narrow ridges and furrows.

IBB-20 (Plate I): Ib20. Fungal spores formed by a circular dark cell, ca. 11.2–15 μm in diameter, with (normally five) hyaline additional cells, up to 8.7 μm in diameter.

IBB-21 (Plate I): Ib21. Globose microfossils of unknown origin, 54.5–98.3 μm in diameter; wall showing dark appendages, 2.1–3.3 μm in diameter, some of those connected by black lines. IBB-21 type often appears broken and is present only in sample MUM-1. The presence of IBB-21 within the animal assemblage is noteworthy (Fig. 7B). Although its morphology did not reveal its nature, the position in the CA analysis could suggest an animal origin.

IBB-22 (Plate III): Ib22. Ascospores one-septate, 26.7–31 × 10.9–11.9 μm, constricted at the septum. Each cell showing an S-shaped furrow. It has been tentatively related in this study with *Delitschia* genus spores.

IBB-23 (Plate III): Ib23. Spores globose, 13.9–20.2 μm in diameter, showing a thicker internal wall and a slightly undulating outer wall.

IBB-24 (Plate III): Ib24. Ascospores one-septate, fusiform, 28.3–38.3 × 9.7–9.5 μm, constricted at the septum, with a variable number of longitudinal furrows.

IBB-25 (Plate III): Ib25. Ascospores one-septate, 28.2–38.9 μm, with many longitudinal light-coloured furrows. Present at low frequencies in several samples. It was found in Colombian Andes sediments and tentatively identified as *Neurospora* sp. (Hooghiemstra, 1984).

IBB-26 (Plate III): Ib26. Ascospores one-septate, slightly fusiform, 31.7–32 × 15.4–15.5 μm, strongly constricted at the septum, probably originally 4-celled. With (8–) 10 longitudinal dark furrows. Present in several samples in very low frequency.

IBB-27 (Plate III): Ib27. Ascospores ellipsoidal, 16.6–20.3 × 9.3–11.8 μm, with (6–) 8 oblique light furrows. Hooghiemstra (1984) found this morphotype also in Colombian Andes sediments and tentatively identified it as *Spirotremesporites ecuatorialis.*

IBB-28 (Plate I): Ib28. Fungal remains (conidia or chlamydospores?) 3-septate, 51.6–70.5 × 9.4–11.2 μm, each dark cell ca. 13.4–24.6 μm long. End cell rounded. Basal cell paler (thinner-walled) and narrow.

IBB-29 (Plate III): Ib29. Fungal spores globose, 22–29.3 μm in diameter, with a protruding pore 2.3–6 μm wide.

IBB-30 (Plate III): Ib30. Fungal spores pyriform, 21.4–30.4 × 10.9–18.6 μm, truncate at one end.

IBB-31 (Plate III): Ib31. Ascospores fusiform 17.9–20–29.4 × 6–9) μm, one side flattened and bearing a longitudinal or sometimes S-shaped slit. Wall paler around the apices. It has been tentatively related in this study with *Rosellinia* genus spores.

IBB-32 (Plate II): Ib32. Ascospores fusiform, dark brown, 27.4–37.2 × 8–9.9 μm, one side flattened and bearing a longitudinal slit.

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