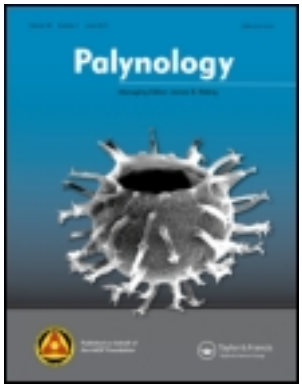

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Pollen and fungal remains as environmental indicators in surface sediments of Isla Grande de Tierra del Fuego, southernmost Patagonia

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Palynological studies have been performed in order to increase knowledge of relations between present vegetation and fungal biota. The analysis of modern analogues will help to improve the palaeoenvironmental reconstructions of fossil sequences from Isla Grande de Tierra del Fuego. A total of 24 fungal taxa have been found, described and illustrated. Surface samples were collected from the different vegetation communities developed on the island: steppe, *Nothofagus* forest–steppe ecotone and *Nothofagus* forest. The steppe is characterised by a predominance of Poaceae pollen accompanied by *Nothofagus* pollen (up to 30%) and spores of *Glomus* sp. In the forest–steppe ecotone, *Nothofagus* pollen frequencies rise up to 50% along with dwarf shrub heath communities and *Gaeumannomyces* species. In the forest unit, the percentage values of *Nothofagus* pollen surpass 50%. Among the fungal remains, fructifications of Microthyriaceae and dematiaceous spores such as *Alternaria* sp., *Dictyosporium* sp. and *Sporidesmium* sp. are present in forest samples and may be related to damp environments. Ascospores of the coprophilous *Sordaria*-type and *Sporormiella*-type appear to be common and are probably associated with livestock grazing. Fungal remains are very scarce in some of the samples obtained in mire environments. The ecological requirements of some of the fungi identified allowed inferences about the local conditions of the sampled site. This study demonstrates the palaeoenvironmental indicator value of fungal components and encourages further investigation of surface samples considering local habitat features to obtain a better understanding of local environmental conditions in the past.

Keywords: pollen; fungi; surface samples; modern analogues; vegetation; Tierra del Fuego

1. Introduction

The use of modern analogues for palaeoecological reconstructions is a useful approach to infer past conditions. Studies of pollen spectra produced by present vegetation units from surface samples constitute an essential step for the reconstruction of past vegetation communities from fossil pollen spectra (Birks and Birks 1980). In most cases, pollen records can be combined with other proxies. Among non-pollen palynomorphs (NPP), fungal remains are considered potential environmental indicators to assign specific ecological conditions. They provide an alternative source of information to supplement palynological analysis of Quaternary sediments. The relative abundance, host specificity and habitat preferences of fungi have significant implications in palaeoenvironmental studies. Due to a sporopollenin-like composition (a resistant material of pollen and spores) of the outer layer, most of the fungal material is well preserved and is not destroyed during chemical treatment of samples (Limaye et al. 2007). The recorded fungal spores in most cases are of strictly local occurrence. Their fossilisation occurs near the place where they are produced or are deposited at a short distance from the place where sporulation takes place (Medeanic and Silva 2010). The combined approach of data from modern pollen and fungal remains therefore allows for a better understanding of palaeoenvironmental conditions and reinforces the utility of modern analogues to constrain palaeoecological reconstructions (Limaye et al. 2007; Montoya et al. 2010).

Many studies of Late Cenozoic palaeoecological conditions from Isla Grande de Tierra del Fuego, southernmost Patagonia, have been largely based on palynological records (Markgraf 1983, 1991, 1993; Heusser 1989, 1990, 1998, 2003; Borromei 1995; Quattrocchio and Borromei 1998; Borromei and Quattrocchio 2001, 2008; Pendall et al. 2001; Mauquoy et al. 2004; Borromei et al. 2007, 2010; Candel et al. 2009; Markgraf and Huber 2010). However,

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detailed studies of present pollen deposition and its relation to modern vegetation and climate remain scarce (Heusser 1989; Trivi de Mandri et al. 2006; Musotto et al. 2009). Although several investigations have been carried out on fungal biodiversity in Tierra del Fuego (Arambarri and Gamundi 1984; Martínez et al. 2001; Ducid et al. 2005; Godeas and Arambarri 2007; Pancotto et al. 2010; Paredes et al. 2010), no one has focused on the study of fungal remains in surface samples. Analyses of fungal microfossils have been undertaken by Palamarczuk and Barreda (2000) and García-Massini et al. (2004).

The aim of this paper is to determine modern analogues from surface samples using palynological analysis (pollen and fungal remains) in order to increase the knowledge of present vegetation and fungal biota. The analysis of modern analogues will help to assist palaeoenvironmental interpretations of fossil sequences from Isla Grande de Tierra del Fuego.

2. Study area

Isla Grande de Tierra del Fuego (Figure 1), the largest island of the Fuegian Archipelago, is located at the southernmost extremity of South America at latitude 53–55° S and longitude 66–74° W. Much of the region is mountainous although altitudes do not exceed 500 m (except in the southern part where the Andes rise to near 2500 m; Heusser 1989).

The climate of Tierra del Fuego is cold-temperate and is influenced predominantly by the seasonal shifts of the Polar Front and the cyclonic activity related to the southern westerlies. Frequent heavy rainstorms strike the Pacific coastal sector and Patagonian Andes and become diverted south-eastwards by the axial trend of the Andes (Pisano 1977). Greater seasonal temperature extremes occur in the northeast of the island where average temperatures are between 11°C in January (summer) and 0°C in July (winter); in the south, temperatures are between 8° and 4°C, respectively (Heusser 1989). Prevailing winds originating from the W–SW are most frequent during spring and summer. Precipitation is regularly distributed throughout the year as a consequence of the year-round passage of humid and cold air masses crossing the mountain barriers, and decreases towards the north and east of the island. Snow occurs between April and November, and frozen ground may occur between April and September (Tuhkanen 1992).

Vegetation composition reflects the strong trans-Andean climatic and topographic gradient across Tierra del Fuego (Pisano 1977; Moore 1983; Tuhkanen et al. 1989–90) (Figure 1). Steppe in the north is followed southwards successively by deciduous beech forest, evergreen beech forest and Magellanic Moorland. Steppe of grassland, scrub and heath occupies the driest areas of the island where mean annual precipitations are less than 400 mm. Grasses include *Festuca gracillima* Hook. f. as the dominant species. Scrub is dominated by shrubby composites, *Lepidophyllum cupressiforme* (Lam.) Cass. in the north and *Chiliotrichum diffusum* (G. Forst.) Kuntze in the south. Dwarf shrub heath is typified by *Empetrum rubrum* Vahl ex Willd. (Heusser 1989). Contact of steppe with deciduous beech forest occurs through an ecotone with precipitation of 400–500 mm annually. Vegetation at lower altitudes is dominated by Subantarctic Deciduous Forest (Pisano 1977; Moore 1983). It is characterised by two species, *Nothofagus pumilio* (Poepp. & Endl.) Krasser ('lenga') and *Nothofagus antarctica* (G. Forst.) Oerst ('ñire'); the latter is present at all elevations on poorer and disturbed soils. Both *Nothofagus* species grow from sea level to the treeline (550–600 m a.s.l.) and become dominant where precipitation is between 400 and 800 mm/year. Towards the south and west of Fuegia, the annual precipitation rises to over 800 mm and the evergreen *Nothofagus betuloides* (Mirb.) Oerst ('guindo') becomes important in the forest. Initially, *N. betuloides* is intermingled with *N. pumilio* in an association which has been distinguished as mixed evergreen–deciduous forest which can be better considered ecotonal between the two life forms (Moore 1983). With increased precipitation, the Subantarctic Evergreen Forest develops and *N. betuloides* becomes dominant westwards and southwards into areas of up to at least 4000 mm annual precipitation. Communities occur either in pure stands or in association with *Drimys winteri* J.R. Forst. & G. Forst., *Maytenus magellanica* (Lam.) Hook. f. and abundant ferns and mosses (Moore 1983). Forest in both zones is often broken by scrub, heath and bog communities. Magellanic Moorland occurs beyond the forest along the exposed outermost coast under conditions of increased precipitation (5000 mm or more), high winds and poor drainage. Mostly treeless and tundra-like, the moorland is distinguished by a profusion of cushion bogs with distinctive species (*Astelia*, *Donatia*, *Gaimardia*, *Phyllachne*). Between the treeline and snowline, Andean Tundra develops. It is comprised of cushion heath (*Bolax gummifera* (Lam.) Spreng.), dwarf shrub heath (*Empetrum rubrum*) and meadow communities (Pisano 1977; Roig 1998; Heusser 2003).

3. Materials and methods

Fourteen surface soil samples were collected from the steppe, forest–steppe ecotone and forest (Figure 1, Table 1). All samples were processed for palynological analysis according to standard techniques

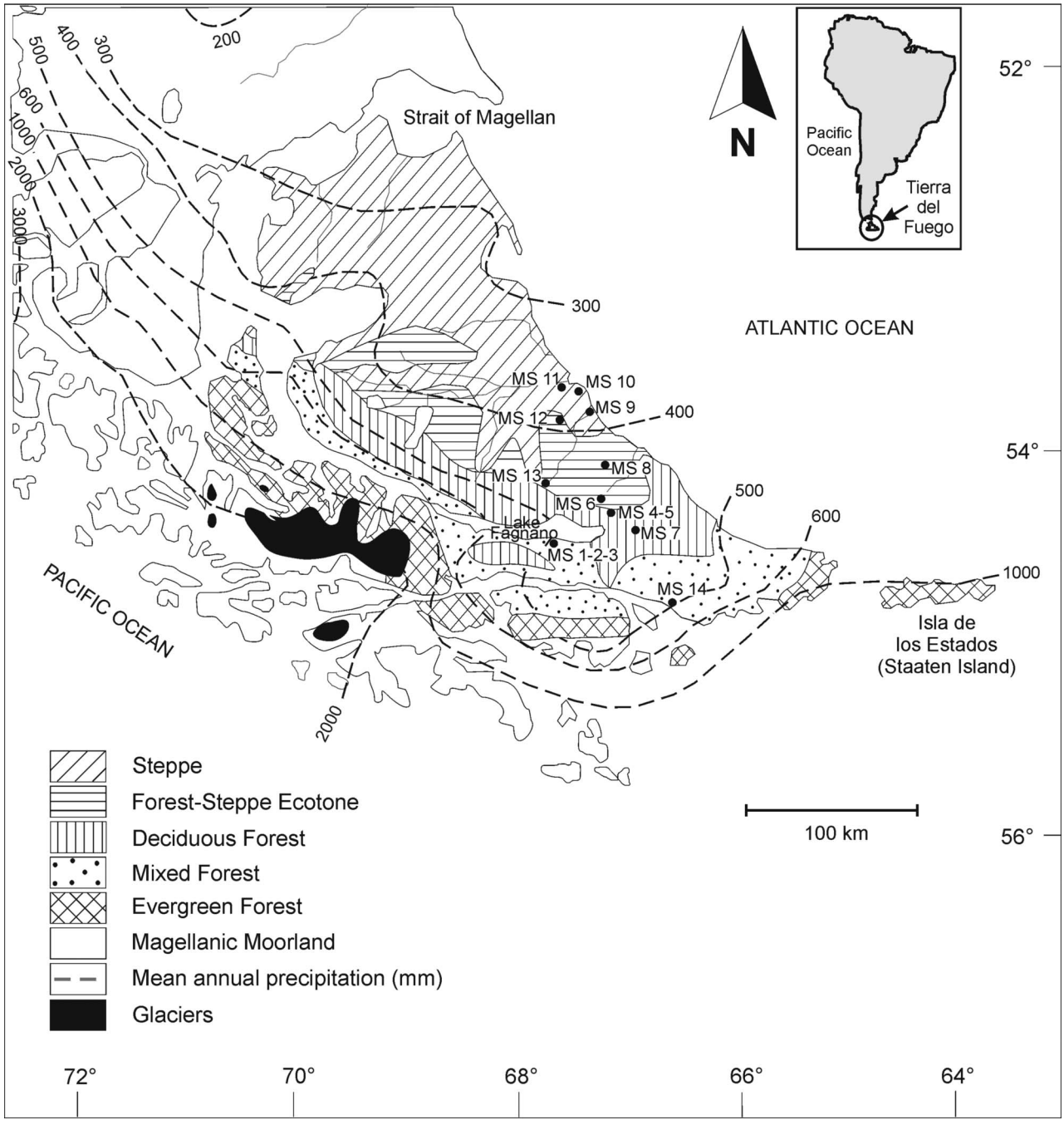

Figure 1. Location map of Isla Grande de Tierra del Fuego showing vegetation units (Tuhkanen, 1989–1990), annual precipitation (mm) and the sampled sites (1–14).

(Faegri and Iversen 1989). Exotic spores (*Lycopodium*) were added to allow calculation of palynomorph concentration per gram of dry weight of sediment (Stockmarr 1971). The palynological slides are housed in the Laboratory of Palynology, Universidad Nacional del Sur, Bahía Blanca, Argentina coded UNSP followed by the nature of the sampling site: MS (surface samples).

Frequencies (%) of trees, shrubs and herbs were based on counts between 200 and 450 pollen grains. Pollen of aquatic plants and cryptogams were calculated separately and related to the sum of terrestrial pollen. Modern pollen data are plotted in Figure 2, showing the main pollen taxa percentages; other herbs include taxa with low values, such as Polygonaceae and *Ribes*. An unconstrained cluster analysis using the

Table 1. Latitude, longitude, altitude, vegetation and environment at sampling sites in the study area. Note: the samples have been arranged according to their occurrence in vegetation units.

Sample code	Latitude (°S)	Longitude (°W)	Altitude (m a.s.l.)	Vegetation and environment	Vegetation units
MS 1	54.36552	67.46266	120	*Nothofagus pumilio* and *Nothofagus antarctica* forest/ *Sphagnum* bog	
MS 2	54.36542	67.46276	120	Within the *N. pumilio* and *N. antarctica* forest, edge of *Sphagnum* bog	
MS 3	54.36548	67.46267	120	Within the *N. pumilio* and *N. antartactica* forest, edge of *Sphagnum* bog	
MS 4	54.28175	67.11379	101	Open *N. pumilio* and *N. antarctica* forest	*Nothofagus* forest
MS 5	54.24015	67.14243	183	Sedges in openings of the *N. pumilio* and *N. antarctica* forest	
MS 6	54.24023	67.14216	187	Stands of *N. pumilio* and *N. antarctica*	
MS 7	54.33185	67.00418	202	Open *N. pumilio* and *N. antarctica* forest and *Sphagnum* bog minerotrophic sector	
MS 9	53.59061	67.26430	29	Herbaceous communities	
MS 10	53.54498	67.36084	7	Sedge and herb communities	Steppe
MS 11	53.53419	67.41395	27	Shrub, herb and sedge communities	
MS 8	54.16305	67.12301	152	Grass meadows and shrubs, edge ecotone/stand *Nothofagus* forest	
MS 12	54.02537	67.40479	18	Shrubs, herbs and *N. pumilio* and *N. antarctica* forest, edge ecotone/steppe	Forest–steppe ecotone
MS 13	54.20419	67.50173	84	Shrubs, herbs and *N. pumilio* and *N. antarctica* forest, edge ecotone/steppe	
MS 14	54.58087	66.44187	36	*Donatia–Astelia* cushion bog	Moorland–forest

Cavalli-Sforza and Edwards Distance (TGView 2.0.2, Grimm 2004) was applied to distinguish the vegetation units based on taxa that reached percentages of $>1\%$ of the sum of terrestrial pollen.

Following Heusser (1998), *Nothofagus betuloides*, *N. pumilio* and *N. antarctica* are shown collectively as '*Nothofagus dombeyi* type' given the difficulty in species separation. Another special case is *Empetrum rubrum* and Ericaceae which are morphologically similar, so the latter is included together with *E. rubrum*.

Some of the genera and species of fungi have been unequivocally assigned to modern taxa based on information provided in the current literature. The informal 'Type' denomination is used to label fungal remains which have biological affinity with modern taxa. Unidentified fungal forms were labelled as Type A, Type B and so on. All unidentified spores with 2 or more transversal septa were labelled as multiseptate. Fructifications of Microthyriaceae include cf. *Microthyrium fagi*, cf. *Trichothyrites* sp. and fruitbody indet. 1. *Alternaria* sp. comprises *Alternaria* sp. A and *Alternaria* sp. B. Fungal descriptions were made according to Elsik et al. (1983).

Frequencies (%) of fungal remains (Figure 3) were calculated outside the total pollen sum in order to infer accurate local environment for each sampling site. All identified taxa of fungi are represented in Table 2. The most common fungi are shown in Plates 1 and 2. Frequency (%) and concentration values of modern fungal and pollen data are plotted in Figure 4.

4. Results

The unconstrained cluster analysis of the pollen record provides evidence that the principal vegetation units are strongly correlated with the vegetation communities developed in the island: steppe, forest–steppe ecotone and *Nothofagus* forest (Figure 2).

4.1. Steppe

4.1.1. Pollen

Poaceae reaches its highest values (37.7–60.5%, mean: 47%) in the steppe samples, accompanied by *Empetrum*/Ericaceae (1.5–5.2%, mean: 3.9%) and

Table 2. Taxonomic variety of fungal remains from the different vegetation units (steppe, forest–steppe ecotone and forest) in Isla Grande de Tierra del Fuego: + (present), − (absent). Note: the species have been arranged according to their occurrence in vegetation units.

	Vegetation units		
Fungal remains	Steppe	Forest-steppe ecotone	*Nothofagus* forest
Arthrinium puccinioides	+	−	+
Glomus sp.	+	−	−
Sordaria-type	+	+	+
Sporormiella-type	+	+	+
Tetraploa aristata	+	−	−
Uredinales-type	+	−	+
Type 370 (Hooghiemstra 1984)	+	+	−
Type B	+	−	+
Type C	+	−	−
Type D	+	−	−
Type E	+	+	+
Type F	+	+	−
Type H	+	+	+
Type I	+	−	−
Dictyosporium sp.	−	+	+
Gaeumannomyces sp.	−	+	+
Microthyriaceae	−	+	+
Sphaerodes sp.	−	+	−
Alternaria sp.	−	−	+
Endophragmia sp.	−	−	+
Sporidesmium sp.	−	−	+
Xylariales-type	−	−	+
Type 364 (Hooghiemstra 1984)	−	−	+
Type A	−	−	+
Type G	−	−	+
Total sum of taxa	14	10	17

Asteraceae subf. Asteroideae (0.4–5.3%, mean: 2.9%). *Nothofagus dombeyi* type reaches 21.8–33% (mean: 26.6%) and *Misodendrum*, a mistletoe on *Nothofagus*, records low frequency values (<5%). Other herbs and shrubs (*Acaena*, Apiaceae, Asteraceae subf. Cichorioideae, *Berberis*, Brassicaceae, Caryophyllaceae, *Gentiana*, *Gunnera*, Ranunculaceae, *Rumex*) are also present with low frequencies (<5%). *Azorella* peaks at 11.8% in sample MS 11 and Solanaceae pollen reaches 12.6% in sample MS 10. Among the wetland taxa, Cyperaceae registers high values in samples MS 10 (8.8%) and MS 11 (29.3%). Total pollen concentration values are low, varying between 33,535 and 156,793 grains/gram contributed mainly by Poaceae (14,391–94,851 grains/gram). The *Nothofagus* concentration shows the lowest values throughout the pollen spectra (11,050–34,198 grains/gram).

4.1.2. Fungal remains

Chlamydospores of the arbuscular mycorrhizal fungus *Glomus* sp. (*fide* van Geel 2001) (1.3–16.2%, mean: 6.5%) are restricted to all the steppe samples, while Type C (33%), Type D (16.8%), Type I (96.1%) and *Tetraploa aristata* Berk. & Broome (3.2%) are only recorded in steppe samples. Type H spores are abundant in samples MS 9 (60%) and MS 10 (13.4%). *Sordaria*-type (*fide* van Geel et al. 2003) (0.3–6.7%) and *Sporormiella*-type (*fide* van Geel et al. 2003) (0.3–9.5%) are present in all the samples. Type 370 (*fide* Hooghiemstra 1984) and Uredinales-type register percentages of <10%. Meanwhile, multiseptate spores, Type B, Type E, Type F and *Arthrinium puccinioides* Kunze & Schmidt appear with low frequencies (<5%). Total fungal concentration values range between 23,000 and 100,013 fungal remains/gram.

4.2. Forest–steppe ecotone

4.2.1. Pollen

Relatively high percentages of *Empetrum*/Ericaceae (41.4–46.9%, mean: 41.4%) and low values of Poaceae (3.3–17.5%, mean: 10.4%) characterise the ecotone samples. *Nothofagus dombeyi* type pollen varies between 31.4% and 47.8% (mean: 39.6%). *Misodendrum* is present with low values (<1%). Among the herbs and shrub taxa, Asteraceae subf. Asteroideae (6%), *Rumex* (3%), Apiaceae (2.5%), Caryophyllaceae (2%) and *Berberis* (2%) are recorded. Total pollen concentration values vary between 241,037 and 298,049 grains/gram, contributed mainly by *Empetrum*/Ericaceae (113,302–131,344 grains/gram). *Nothofagus* concentration values vary between 99,590 and 115,467 grains/gram.

4.2.2 Fungal remains

The fungal spores Type E (38.5–40.7%), hyphopodia of *Gaeumannomyces* sp. (7.4–44.9%) and Type 370 (*fide* Hooghiemstra 1984) (6.4–14.8%) show the highest frequency values. Spores Type F (11.1%), *Dictyosporium* sp. (*fide* Bianchinotti and Sánchez 2007) (5.6%) and Type H (7.4%) are also present. Ascospores of *Sphaerodes* sp. (*fide* Borel et al. 2001) (6.4%) are only recorded in sample MS 13. The record of *Sordaria*-type (3.8–7.4%) and *Sporormiella*-type (3.7%) is similar to that of steppe samples. Fungal fructifications of Microthyriaceae are found in low frequencies (<2%). Total fungal remains concentration values vary between 38,970 and 56,290 fungal remains/gram.

4.3. Nothofagus forest

4.3.1. Pollen

Nothofagus dombeyi type is dominant throughout the forest samples with percentages varying between 72%

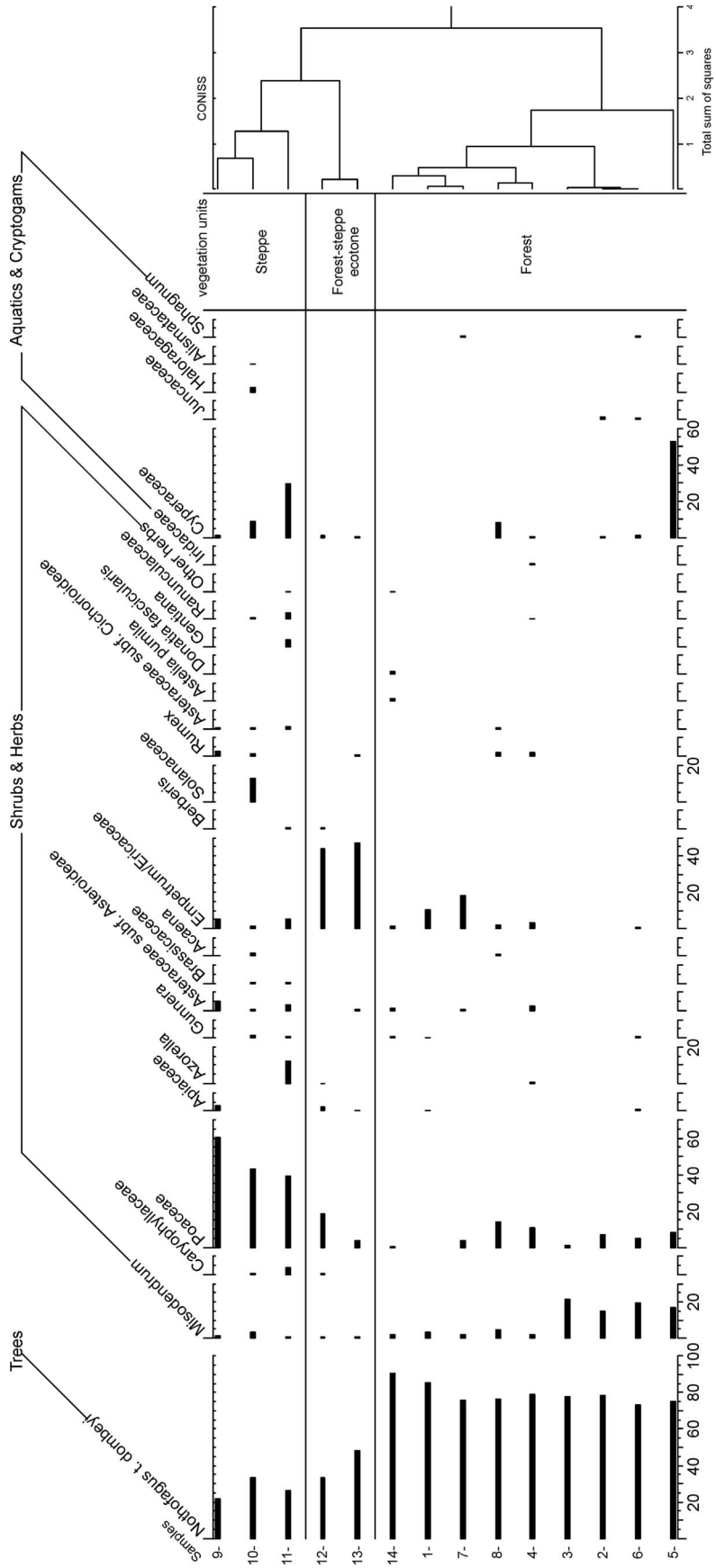

Figure 2. Modern pollen frequency diagram (%) showing vegetation units. Surface samples collected at sites are indicated by number.

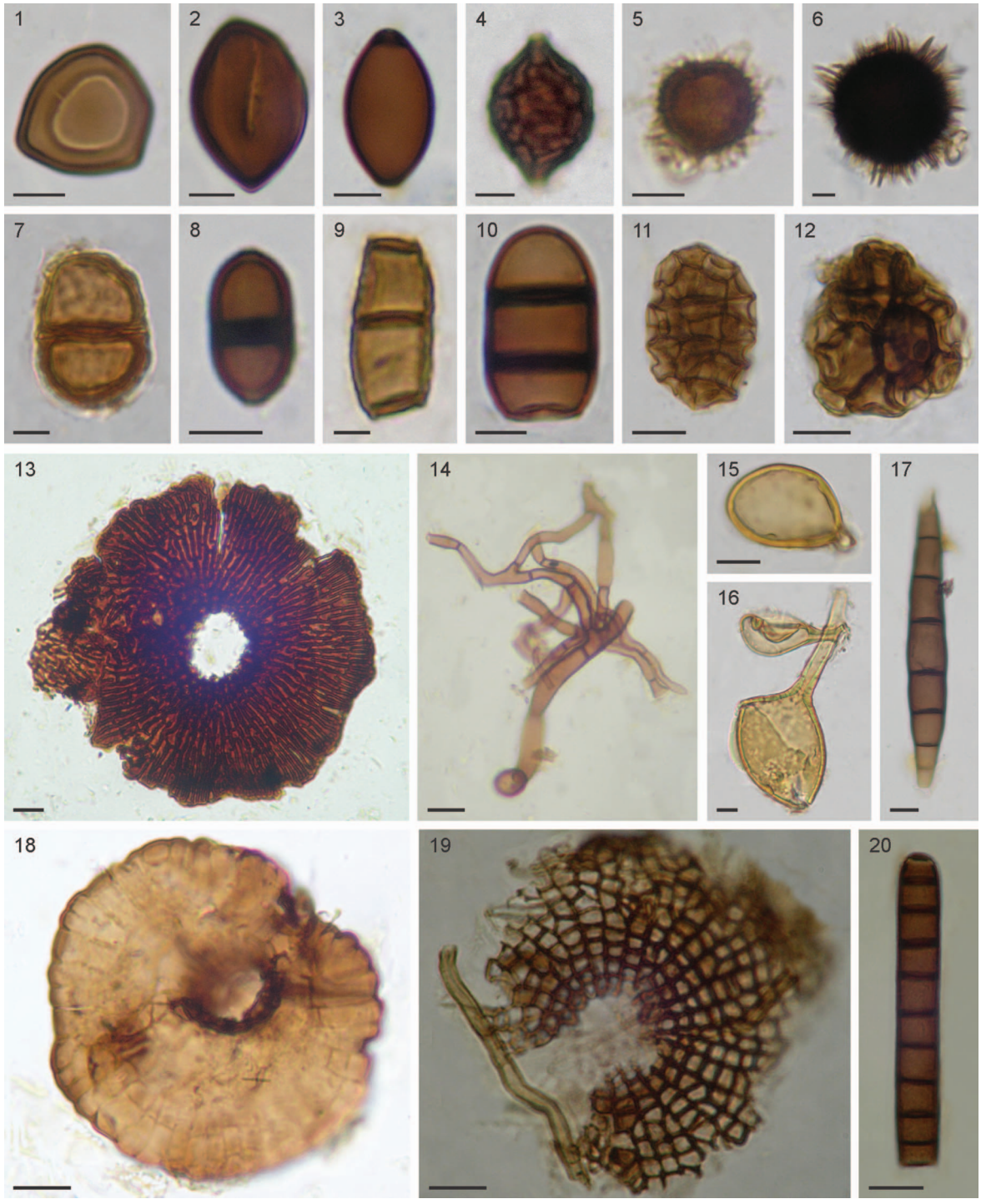

Plate 1. Fungal remains found in surface samples. Figure 1. *Arthrinium puccinioides*, UNSP MS 3196: X45. Figure 2. Xylariales-type, UNSP MS 3163: V38/2. Figure 3. *Sordaria*-type, UNSP MS 3164: T32/4. Figure 4. *Sphaerodes* sp., UNSP MS 3183: V50. Figure 5. Type 370 (*fide* Hooghiemstra 1984), UNSP MS 3182: N33. Figure 6. Type G, UNSP MS 3163: V33/3. Figure 7. Type A, UNSP MS 3184: S31/1. Figure 8. Type B, UNSP MS 3184: V29. Figure 9. Type C, UNSP MS 3197: Y38/2. Figure 10. Unidentified multiseptate spore, UNSP MS 3163: Z39. Figure 11. Type 364 (*fide* Hooghiemstra 1984), UNSP MS 3163: P34. Figure 12. Type D, UNSP MS 3197: W40. Figure 13. cf. *Microthyrium fagi*, UNSP MS 3163: Z47/3. Figure 14. Probably mycelia of the Microthyriaceae fruitbodies, UNSP MS 3163: X36. Figures 15, 16. *Glomus* sp., (15: UNSP MS 3196: V33; 16: UNSP MS 3196: R29). Figure 17. *Sporidesmium* sp., UNSP MS 3182: X39. Figure 18. cf. *Trichothyrites* sp., UNSP MS 3163: Q34. Figure 19. Fruitbody indet. 1, UNSP MS 3193: S31. Figure 20. *Endophragmia* sp., UNSP MS 3193: U42. Scale bars: 1–10 = 5 μm; 11–20 = 10 μm.

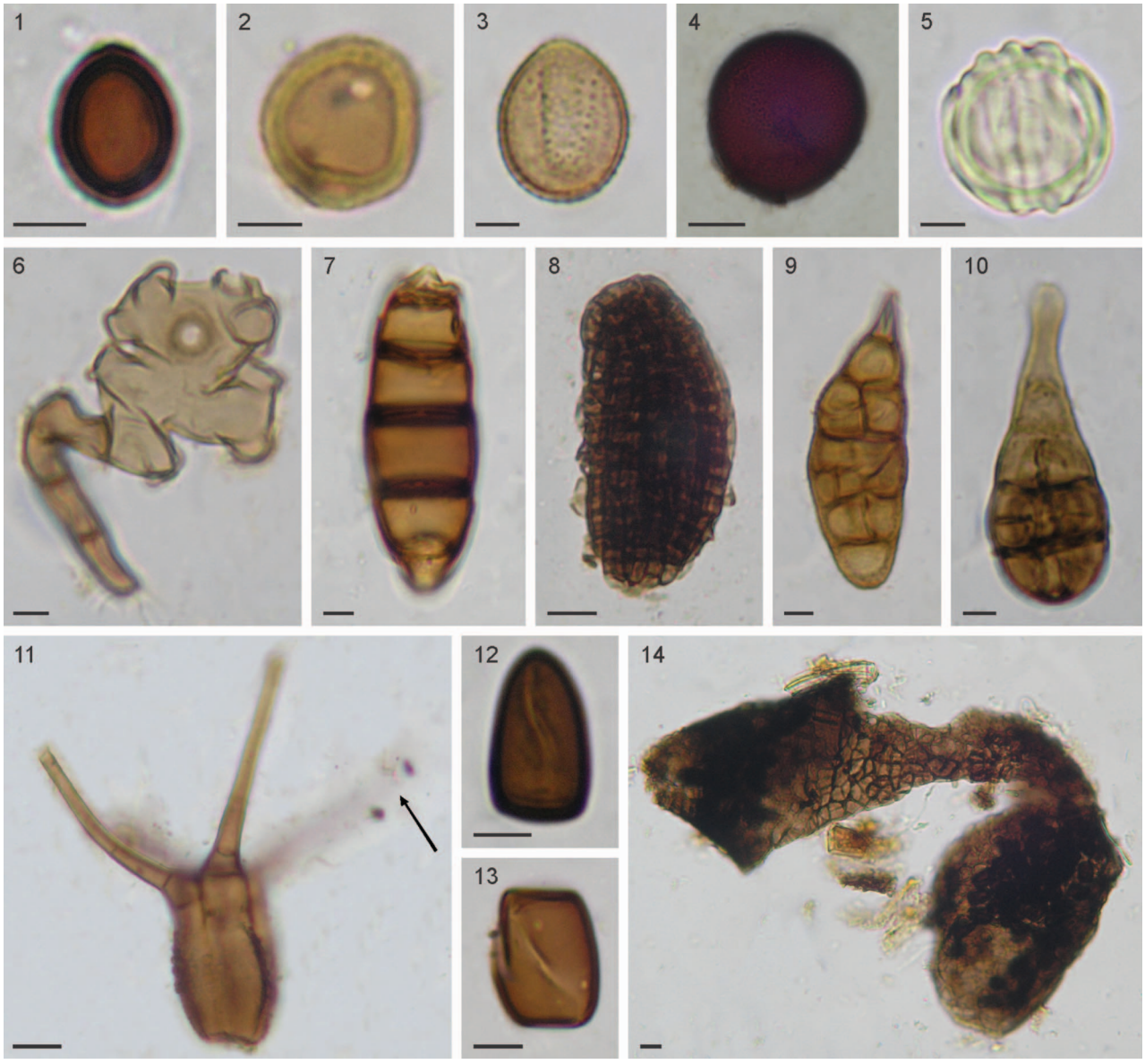

Plate 2. Fungal remains found in surface samples. Figure 1. Type E, UNSP MS 3163: X28/1. Figure 2. Uredinales-type, UNSP MS 3181: Y39. Figure 3. Type H, UNSP MS 3196: X40. Figure 4. Type F, UNSP MS 3199: V40. Figure 5. Type I, UNSP MS 3196: Y48. Figure 6. *Gaeumannomyces* sp. hyphopodium, UNSP MS 3182: S35/2. Figure 7. Unidentified multiseptate spore, UNSP MS 3163: Y41. Figure 8. *Dictyosporium* sp., UNSP MS 3164: Z40. Figure 9. *Alternaria* sp. A, UNSP MS 3163: P41. Figure 10. *Alternaria* sp. B, UNSP MS 3182: P47. Figure 11. *Tetraploa aristata*, UNSP MS 3199: V42/2, arrow shows an appendage in high focus. Figures 12, 13. Separate ascospore-cells of *Sporormiella*-type (12: UNSP MS 3184: L38/3; 13: UNSP MS 3164: T41). Figure 14. Broken fruitbody with ascospores of *Sporormiella*-type, UNSP MS 3184: M37. Scale bar is 4 μm except in photos 4, 8, 11 and 14 where the scale bar is 10 μm.

and 90.6% (mean: 78.7%). *Misodendrum* fluctuates between 21.6% and 1.7% (mean: 9.6%) and records the highest values in those samples located within the forest (samples MS 2, MS 3, MS 5 and MS 6) (Table 1). Among the herbaceous and shrub taxa, Poaceae (up to 13.8%, mean: 5%) and *Empetrum*/Ericaceae (up to 18.3%, mean: 4%) register low values. Despite the Cyperaceae pollen peak in samples MS 5 (52.8%) and MS 8 (8.4%), the record of wetland taxa throughout the forest samples is low. Other taxa (*Acaena*, Apiaceae, Asteraceae subfam. Asteroideae, Asteraceae subfam. Cichorioideae, *Gunnera*, Ranunculaceae, *Rumex*) are present with low frequencies (<3%). The record of *Astelia* (1.7%) and *Donatia* (1.3%) is observed in the sample from a cushion-type bog (sample MS 14) (Table 1). Total pollen concentration

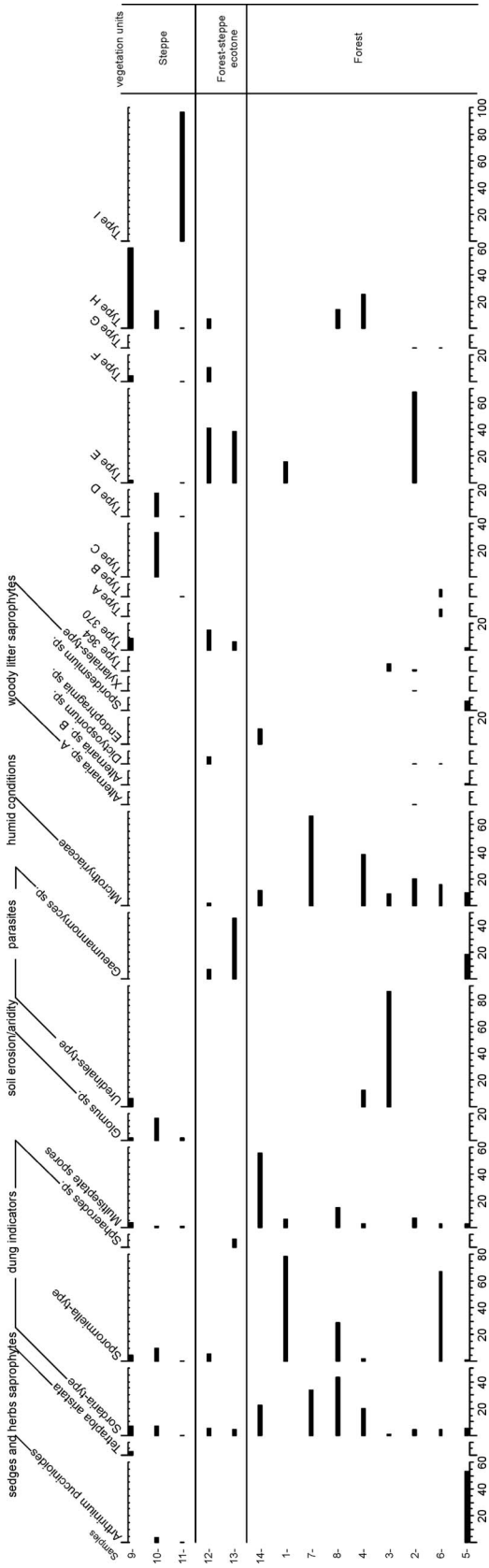

Figure 3. Modern fungal remains frequency diagram (%). Surface samples collected at sites are indicated by number.

values are high (50,882–535,725 grains/gram), contributed mainly by *Nothofagus dombeyi* type (38,715–421,884 grains/gram).

4.3.2. Fungal remains

Fungal fructifications of Microthyriaceae (mean: 18.7%) characterise most of the samples. *Sordaria*-type (mean: 14.7%) and *Sporormiella*-type (mean: 19.7%) are relatively important. Spores such as *Alternaria* sp., *Dictyosporium* sp., Xylariales-type and Type G are registered with low values (2%). Hyphopodia of *Gaeumannomyces* sp. (18.1%) and spores of *Arthrinium puccinioides* (53.5%) and *Sporidesmium* sp. (6.9%) are present in sample MS 5, while spores of Type A (5.7%) and Type B (4.9%) appear in sample MS 6. Both samples are located within the forest. *Endophragmia* sp. (11.1%) is found in a sample from a cushion-type bog (sample MS 14). Multiseptate spores show a higher percentage (mean: 10%). Uredinales-type (MS 3: 85.5%), Type E (MS 2: 68%, MS 1: 15.6%) and Type 364 (*fide* Hooghiemstra 1984) (MS 3: 5.2%, MS 2: 0.4%) are recorded in those samples collected from the forest–mire environment (Table 1). Type H records a significant contribution in samples MS 4 (25%) and MS 8 (14.3%) from open forest and at the edge of the forest, respectively (Table 1). Total fungal concentration values are high (219,139–570,593 fungal remains/gram) in the samples located within the forest (samples MS 2, MS 3, MS 5 and MS 6) and the total concentration values are lower (2,985–89,287 fungal remains/gram) in those samples collected in more open forest environments (samples MS 4 and MS 8) (Table 1). Meanwhile, fungal forms are very scarce (664–53,573 fungal remains/gram) in some of the samples obtained in mire environments (MS 1, MS 7 and MS 14) (Table 1).

5. Discussion

The palynological record reveals that steppe vegetation is dominated by grasses (Poaceae) associated with herbs and shrubs. Pollen data also show the relative preponderance of *Nothofagus* in the steppe where frequency values do not surpass 20–30%. Caryophyllaceae, Brassicaceae and *Gentiana* pollen typified open herb communities. Peak amounts of local taxa such as *Azorella*, Solanaceae and Cyperaceae reflect the local conditions related to the sampled steppe sites (Table 1). *Azorella*, a typical non-graminoid species, characterises the lowlands in the steppe with soils that are undergoing enhanced erosion (Heusser 2003). The record of Solanaceae pollen may be related to livestock grazing and *Rumex* pollen, an introduced taxon, indicates vegetation disturbance including logging,

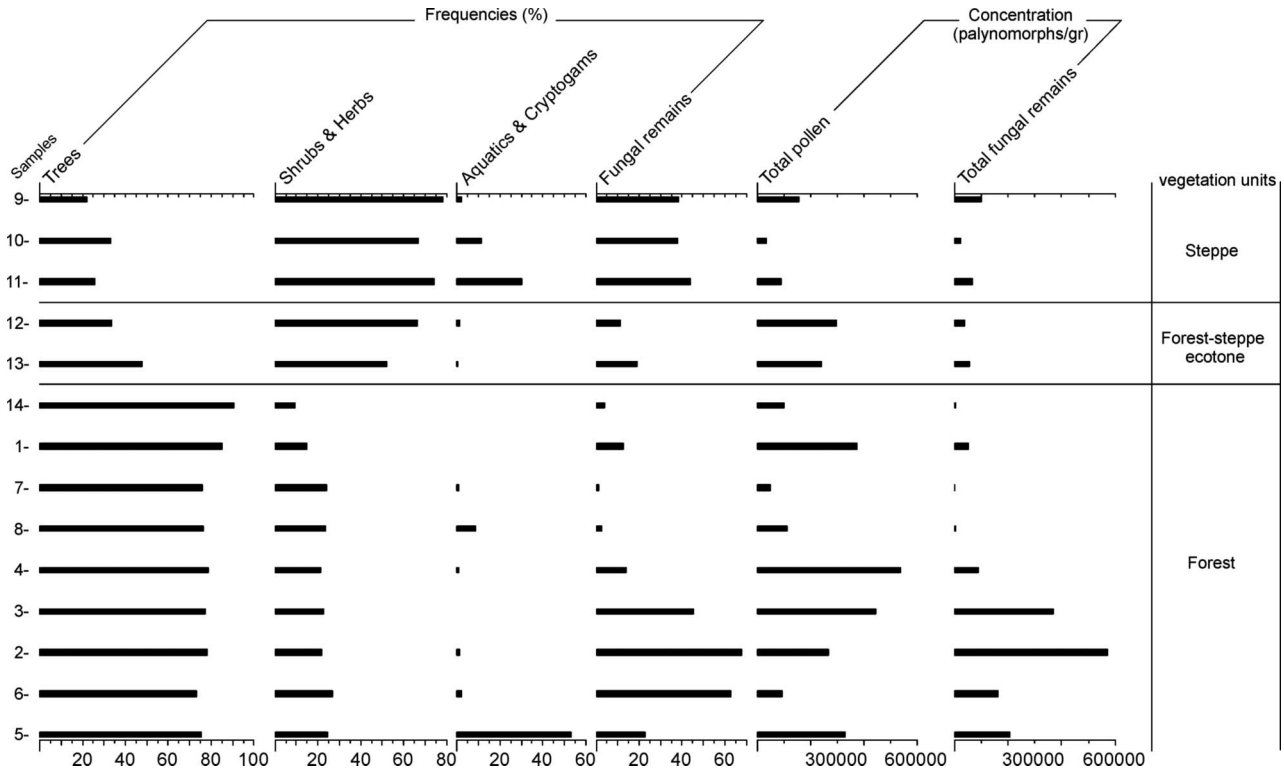

Figure 4. Modern pollen and fungal remains frequencies (%) and concentration values. Surface samples collected at sites are indicated by number.

fire and grazing (Mancini 2009). Sedges (Cyperaceae) develop in locally wet settings such as flat-lying areas of slow-moving drainage into the steppe. Among the fungal remains that characterise the steppe samples, the record of spores of *Glomus* sp., *Tetraploa aristata*, Type C and Type D are restricted to this environment. The occurrence of *Glomus* sp. is indicative of active soil erosion processes in the catchment area (Medeanic and Silva 2010) and correlates well with decreases in soil moisture levels (Chmura et al. 2006). Its presence is a good indicator of soil conditions associated with aridity and stressed environments (Limaye et al. 2007). The abundance of *Glomus* spp. in steppe samples has been related to various species of Poaceae in Tierra del Fuego (Mendoza et al. 2002). *Tetraploa aristata* has been recorded on more than 120 plant species, in particular on senescent culms of Poaceae and Cyperaceae as a major saprophytic fungus (Tanaka et al. 2009). This species is present in one sample (MS 9) dominated by grassland communities (Table 1). *Sordaria*-type and *Sporormiella*-type are almost continuously present in all the surface samples. Both genera have been described as coprophilous, and the record of the ascospores are indicative of dung produced by herbivorous animals (López-Sáez and López-Merino 2007) probably linked with grazing (Montoya et al. 2010). The register of spores of coprophilous fungi indicates that herbivorous grazers are present, but whether these are wide-ranging domesticates such as sheep and cows from the farms or wild herbivores such as *Lama guanicoe* ('guanaco') and hare is open for debate.

The samples from the *Nothofagus* forest–steppe ecotone are characterised by relatively high frequencies of *Nothofagus* pollen (30–50%) along with dwarf shrub heath (*Empetrum*/Ericaceae) and herb (Poaceae) communities. Fungal remains are represented by the records of *Gaeumannomyces* species. Their characteristic lobed hyphopodia correlate well with the local occurrence of sedges and grasses. *Gaeumannomyces* species are parasitic on roots, crowns and lower stems and leaf sheaths of Poaceae and Cyperaceae (Walker 1980; Limaye et al. 2007). Also, dematiaceous spores of *Dictyosporium* sp. occur in leaves and soil organic matter in terrestrial habitats (Raja et al. 2007). The *Sphaerodes* sp. ascospores recorded in the present study are similar to the spores of a coprophilous species, *S. fimicola* (Hansen) P. Cannon & D. Hawksw. (Cannon and Hawksworth 1982). *Sphaerodes fimicola* has been recorded on hare and sheep

dung (Saccardo 1883; Zhang and Blackwell 2002) and also on Poaceae (Farr and Rossman 2011). This fungal spore recorded in an ecotone sample is linked with the open herb vegetation and is probably associated with livestock grazing. Spores such as Type 370 (*fide* Hooghiemstra 1984), Type F and Type I have been recorded only in the steppe and/or ecotone samples (Table 2), and may be related to drier climate conditions.

All the forest samples were collected in the deciduous beech forest constituted by *Nothofagus pumilio* and *Nothofagus antarctica*. The forest unit is recognised in the pollen spectrum when the *Nothofagus* percentage values surpass 50%. The highest values (22%) of *Misodendrum* pollen recorded in the samples taken within the forest suggest that stands of forest are *in situ* and very close to the sampled site (Figure 2, Table 1). *Misodendrum punctulatum* DC is the most abundant mistletoe in the subantarctic forests and mainly infects the two deciduous *Nothofagus* species: *N. pumilio* and *N. antarctica* (Tercero-Bucardo and Kitzberger 2004). This mistletoe is the only wind-dispersed hemiparasitic species and seed dispersion occurs over a short distance from the seed source (<10 m) (Tercero-Bucardo and Rovere 2010). *Misodendrum punctulatum* may develop earlier in faster-growing hosts in lower elevation sites of *N. antarctica* habitats than in the higher elevation, hasher subalpine habitat of *N. pumilio* (Tercero-Bucardo and Kitzberger 2004). Low-frequency values of *Misodendrum* ($<5\%$) are registered in samples from open forest stands, forest–steppe ecotone and steppe (Figure 2, Table 1). In the samples from open forest stands, low values of *Misodendrum* pollen are associated with high *Nothofagus* pollen frequencies pointing to extra-local forest establishment (200 m to 2 km distant from the pollen source, *sensu* Prentice 1985). In those samples from the ecotone and the steppe, low frequencies of *Misodendrum* are associated with low values of *Nothofagus* pollen implying regional forest locations (2–200 km from the pollen source, *sensu* Prentice 1985). Only one sample (MS 14) has been collected from a cushion-type bog at Moat site, located in moorland–forest vegetation on the southeastern coast of Tierra del Fuego (Figure 1). This sample records *Donatia* and *Astelia* pollen, principal components of cushion bogs. The development of grass (Poaceae) and sedge (Cyperaceae) vegetation are linked with openings in the forest (Figure 2, Table 1). Heaths of *Empetrum rubrum* are found in Fuego-Patagonian steppe, forming dense carpets of dwarf shrubs over acid, permeable, often rather shallow soils in which clay is absent (at least in the upper horizons; Moore 1983), growing on wind-exposed sites under low levels of precipitation (below 200 mm) (Markgraf and Huber 2010). However, high percentages of *E. rubrum* can also reflect disturbance related to human activity. Studies of grass steppes in Tierra del Fuego suggest that litter removal by grazing causes an increase in cover of *E. rubrum* in sectors where this species is a common element (Quintana 2009). In addition, *E. rubrum* is found within the deciduous forest zone in association with *Sphagnum* bogs growing on dry hummocks and covering tracts of poorly drained lowland in the mires (Moore 1983). These two habitats are well represented in the samples collected from the ecotone (samples MS 12 and MS 13) and forest units (samples MS 1 and MS 7) (Table 1). According to Markgraf and Huber (2010), the ecological interpretation of *Empetrum* in fossil pollen records can be ambiguous and could be related to local environmental conditions such as presence or absence of local bog indicators.

The presence of fructifications of Microthyriaceae characterises the forest vegetation unit and suggests damp environments. Microthyriaceae are epiphyllous fungi and their occurrence is correlated with moist, humid climates and heavy rainfall, considered essential for their abundance and rapid spread (Limaye et al. 2007). *Alternaria* species are common saprophytes found on many kinds of plants (Ellis 1971). These fungi have been recorded on soils of *Nothofagus* forests in Tierra del Fuego (Martinez et al. 2001). Spores of *Alternaria* sp. are present in the samples collected within the forest (MS 2 and MS 5). *Endophragmia* species have been recorded on decaying leaves and stems (Ellis 1976). *Endophragmia* sp. appears in sample MS 14 from a cushion-type bog. Spores Type 364 (*fide* Hooghiemstra 1984) have been registered in the mire samples (MS 2 and MS 3, Table 1) and may be linked with minerotrophic sectors of the mire where vegetation is dominated by sedges and herbs (Birks and Birks 1980). The saprotrophic dematiaceous spores of *Sporidesmium* sp. often occur on woody substrates or on decaying plant tissues from moist habitats (Gulis and Marvanová 1999). This fungal spore is recorded only in a sample (MS 5, Table 1) collected within the forest under locally more humid conditions. Spores of *Dictyosporium* sp. are also found in forest samples. A species of *Dictyosporium* has been found on dead wood of *Nothofagus pumilio* (Bianchinotti and Sánchez 2007). Dematiaceous spores of *Arthrinium puccinioides* correlate well with the occurrence of Cyperaceae pollen. According to Saccardo (1886) and Ellis (1971), this fungus grows on dead leaves of various species of Cyperaceae. It is registered in the samples of forest (MS 5) and steppe (MS 10 and MS 11) sites linked with sedge communities (Table 1). Xylariales are saprophytic fungi mostly on woody substrates (Brundrett et al. 1996). This fungal type is recorded only in a forest sample (MS 2). Uredinales-type and

the informal types such as multiseptate spores and Type B were recorded in some samples from forest and steppe sites. Rust fungi (formerly Uredinales) are obligated parasites of a wide range of plants. The spores Type E and Type H appear in some samples from all the vegetation units and Type A is present in one sample from a forest site (Table 2).

In general, fungal frequencies in the palynological record are more variable than pollen frequencies (Figure 4); a possible explanation is that they are more sensitive to local conditions. High fungal diversity is recorded both in the steppe and forest samples (Table 2). The steppe samples show high frequencies of fungi but low concentration values of total fungal remains. The samples collected within the forest register the highest total concentration values of fungi and they decrease in samples located in the open forest stands. According to Promis et al. (2010), the microclimate in the interior of *Nothofagus pumilio* forest is generally more dark, windless, cooler and humid than outside the forest. These conditions are favourable for the development of fungi. Furthermore, the wood of *N. pumilio* found in the forest floor or submerged in bodies of water is considered a good substrate for growth and sporulation of Hyphomycetes (Godeas and Arambarri 2007). In the samples collected in the *Nothofagus* forest, dominated by woody plants, *Alternaria* sp., *Sporidesmium* sp. and *Dictyosporium* sp. (three typical taxa of environments with abundant decaying wood) are dominant.

Meanwhile, fungal remains are very scarce and their taxonomic variety are restricted in some of the samples obtained in mire environments (MS 1 and MS 14, Figure 3). The anaerobic soil and stagnant flood conditions found in mires probably inhibit the activity of microorganisms, which otherwise would produce the decomposition of dead plant material (Roig 2001). The decreased presence of fungi under flooded conditions observed in the present study is consistent with the hypothesis that fungi are less prevalent in inundated soils (Unger et al. 2009). Another cause of fungal growth inhibition could be the low levels of nitrogen in a bog, particularly when the material is formed predominantly by species of *Sphagnum* (Roig 2001).

6. Conclusions

The following conclusions can be drawn from our analysis of surface samples.

(1) The pollen spectra obtained from surface-soil samples reflect the principal units of vegetation found in the island: steppe, forest–steppe ecotone and *Nothofagus* forest.
(2) The fungal assemblages are taxonomically diverse and are represented in a wide range of habitats. In this sense, the local conditions of sampled sites (such as local vegetation, pH, dissolved oxygen, humidity, stagnant flooding, soil conditions, etc.) probably influences the distribution of fungi.
(3) Spores of *Glomus* sp. and *Tetraploa aristata* are restricted to the steppe samples, and could be related to drier climate conditions.
(4) Most fungal taxa recorded in the ecotone samples are also found in the forest and steppe environments.
(5) Fructifications of Microthyriaceae and spores of *Alternaria* sp., *Dictyosporium* sp., *Endophragmia* sp. and *Sporidesmium* sp. are present in forest samples. These fungal spores may be linked with damp environments.
(6) Ascospores of the coprophilous *Sordaria*-type and *Sporormiella*-type appeared to be of common occurrence and are probably associated with livestock grazing.
(7) The highest total concentrations of fungi are obtained within the forest and the lowest in the mires (stagnant flood conditions) and more open forest environments (drier conditions). Meanwhile, the total concentration values of fungi are low in both steppe and forest–steppe ecotone units.
(8) Most informal fungal types (Type A to Type I) found in the samples were unknown morphotypes, so environmental information could not be obtained. However, their record at different environments within the steppe, ecotone and forest might be useful for future palaeoecological interpretations.
(9) This study reinforces the utility of fungal remains as an additional source of information to complement traditional pollen analysis. Further research based on the identification of fungal components and their distribution considering local habitat features will be useful for future studies of fossil pollen/non-pollen microfossils in the area.

7. Descriptions and illustrations of fungal material

A total of 24 different fungal forms were recognised. The informal forms that have not been unequivocally assigned to any known taxa are described as Types (Type A to Type I).

PHYLUM GLOMEROMYCOTA C. Walker & A. Schüssler

Fam. Glomaceae Pirozynski & Dalpé

Glomus sp. (Plate 1, figures 15–16)

Spores subspherical, aseptate, pale yellow-brown, thick-walled, 27–55 × 22–42 μm; wall ornamented with perforations distributed irregularly, 1–2 μm thick; subtending hyphae 6–50 μm long, 5–6 μm wide at the apex, 5–8 μm at the base. Studied material: UNSP MS 3196: V33, R29.

Comments. Spores of *Glomus* sp. were recorded by van Geel (2001). *Glomus* is an endomycorrhizal fungus occurring on the roots of a variety of host plants.

PHYLUM ASCOMYCOTA Cavalier-Smith

Family Magnaporthaceae P.F. Cannon

Gaeumannomyces sp. (Plate 2, figure 6)

Hyphopodia brown, 20–28 × 20–24 μm, with blunt lobes and a prominent central clear pore 3 μm diam.; wall less than 1 μm thick. Runner hypha, 0–2 septate, brown, 20–26 μm long, 4–5 μm wide. Studied material: UNSP MS 3182: S35/2, S43/2.

Comments. Hyphopodia are regularly found as palynomorphs. The material here described is close to *G. graminis* in the morphological features of the lobed hyphopodia (*fide* Walker 1980). *Gaeumannomyces graminis* is a cosmopolitan fungus and has been recorded on roots, culms and leaf sheaths in various species of Poaceae (Farr and Rossman 2011). It has been reported in Valdivia and the Región de la Araucanía, Chile by Mujica et al. (1980) and Oehrens (1961), among others. This material is also similar to hyphopodia of *Gaeumannomyces caricis*, but the latter shows hyphopodia with pronounced and sharp lobes. *Gaeumannomyces* cf. *caricis* has been recorded in peat deposits of Tierra del Fuego, Argentina (Mauquoy et al. 2004: type 126, plate 5, figure 1).

Family Microthyriaceae Saccardo

cf. *Microthyrium fagi* Ellis 1977 (Plate 1, figure 13)

Circular fruiting bodies formed by a single layer of elongate-lobulate cells, radially arranged, dark brown, with a lobulate margin, 95–130 × 93–125 μm. Ostiole circular, central, 15–24 × 15–20 μm, surrounded by a ring of thick-walled cells. Studied material: UNSP MS 3163: Z47/3, Y37/2, T30, R43.

Comments. These ascomata resemble that described and illustrated by Arambarri and Gamundi (1984, plate 1, figure 2) in general morphology, size range and in the presence of rows of hyphae that branch dichotomously. *Microthyrium fagi* has been recorded on dead leaves of *Nothofagus pumilio* in Tierra del Fuego and Neuquén, Argentina (Arambarri and Gamundi 1984). They also look similar to ascoma designated as Type I by García-Massini et al. (2004), but this specimen has anastomosing hyphae.

cf. *Trichothyrites* sp. (*fide* Rosendahl 1943) (Plate 1, figure 18)

Ascoma circular, formed by two layers, pale brown, lobed margin, 63 × 57 μm; cells of upper layer thick-walled, cells of lower layer thin-walled. Neck short, raised. Ostiole circular, central, 10 μm diam.; one cell elonged into a short setae. Studied material: UNSP MS 3163: Q34.

Comments. This ascoma resembles that designated as *Trichothyrites* sp. 1 by García-Massini et al. (2004, plate 3, figure D), but differs for its lobed margin. *Trichothyrites* sp. 1 has a psilate margin.

Fruitbody indet. 1 (Plate 1, figure 19)

Ascoma circular, formed by a single layer of rectangular cells, thick-walled and radially arranged, dark brown, 62 μm diam.; ostiole circular, central, 16 μm; walls about 1 μm thick. Studied material: UNSP MS 3193: S31.

Comments. The material could not be assigned to any genus because margins of ascoma are in poor condition.

Family Sporormiaceae Munk

Sporormiella-type (*fide* van Geel et al. 2003) (Plate 2, figures 12–14)

Spores cylindrical, pluricellular, dark brown, with transverse to oblique septa, smooth, easily splitting in separate cells. Terminal cells half-ovoid, 11–13 × 6–7 μm; central cells more or less cylindrical, 10–11 × 7–9 μm, each cell with an elongated germ slit, oblique to the longitudinal axis. Studied material: UNSP MS 3184: M37, L38/3, K39.

Comments. Only fragments of entire spores were observed, but separate cells showed enough characters for their identification. A broken ascoma was found in one sample. Separate spore cells of *Sporormiella*-type were distinguished by Davis et al. (1977) and by van Geel et al. (2003), among others. Most *Sporormiella* species are coprophilous, the presence of these spores is associated with the dung of herbivores.

Order Melanosporales Zhang & Blackwell

Family Ceratostomataceae G. Winter

Sphaerodes sp. (*fide* Borel et al. 2001) (Plate 1, figure 4)

Spores citriform, straight, 0-septate, dark brown, thick-walled, reticulate, 18–20 × 12–16 μm, with a strongly umbonate germ pore at each end, 1.5–2.0

μm diam.; wall about 1 μm, ornamented with an irregular, polygonal reticulum, lumina 1–4 μm diam., muri ca. 1 μm. Studied material: UNSP MS 3183: Y28/1, V50, T45, Q47, H41.

Order Sordariales Chadefaud ex Hawksworth & Eriksson

Family indet.

Sordaria-type (*fide* van Geel et al. 2003) (Plate 1, figure 3)

Spores ellipsoidal, 0-septate, dark brown, smooth, 18–20 × 10.5–12 μm, monoporate, pore slightly umbonate, 1.5–2.0 μm diam.; wall less than 1 μm thick, thickened and darkened around the apical pore. Studied material: UNSP MS 3164: T32/4, 3182: X30.

Comments. Similar spores were recorded by van Geel et al. (2003). These ascospores are probably produced by various species belonging to the (mostly coprophilous) Sordariales (van Geel et al. 2003), and their presence is considered a good indicator of grazing activities (López-Sáez and López-Merino 2007).

Family Xylariaceae Tulasne & Tulasne

Xylariales-type (Plate 1, figure 2)

Spore ellipsoidal, 0-septate, dark-brown, smooth, 19 × 13 μm, with a linear furrow reaching the ends of the spore; wall ca. 1 μm thick. Studied material: UNSP MS 3163: V38/2.

Comments. Similar spores were described by Borel et al. (2001: Type Xylariaceae, plate 4), but they are larger (34–35.5 × 19–22.4 μm) and the furrow occupies about two-thirds of the spore length.

Mitosporic fungi

Alternaria sp. A (Plate 2, figure 9)

Spore obclavate, muriform, with 6 transverse septa and irregularly spaced longitudinal septa, constricted at septa, pale brown, punctate, 41 × 13 μm, wall 1 μm thick, with an apical scar of 2 μm diam. Studied material: UNSP MS 3163: P41.

Comments. This spore is close to that described from upper Pleistocene–Holocene deposits from Arroyo Chasicó basin, Buenos Aires, Argentina by Borel et al. (2001: *Alternaria* 1, plate 6, figure A), but differs for its smaller size. Also, *Alternaria* 1 (54 × 18 μm) is 7-septate whereas the present species is 6-septate.

Alternaria sp. B (Plate 2, figure 10)

Spore obclavate, muriform, rostrate, with 4 transverse septa and inconspicuous longitudinal septa, constricted at septa, pale brown, punctate to smooth in the rostrum, 38 × 15 μm; wall less than 1 μm thick. Studied material: UNSP MS 3182: P47.

Comments. This spore is close to those described by Borel et al. (2001, plate 6, figure B) as *Alternaria* 2, but they are greater (46–51 × 13 μm) and have punctate walls.

Arthrinium puccinioides Kunze & Schmidt 1823 (Plate 1, figure 1)

Conidia rectangular to pentagonal, 0-septate, dark-brown, smooth, 15–13 × 15–12 μm, wall ca. 1 μm thick. Studied material: UNSP MS 3196: X45, 3182: Y23, X23/2, N44.

Comments. These spores are similar to those described by Ellis (1971, plate 413, figure B). *Arthrinium puccinioides* have been recorded on dead leaves of various species of Cyperaceae (Ellis 1971; Saccardo 1886). It has been reported in Tierra del Fuego (Ellis 1971).

Dictyosporium sp. (*fide* Bianchinotti and Sánchez 2007) (Plate 2, figure 8)

Spores cylindrical, multicellular, cheiroid, pale to dark brown, smooth, consisting of seven or more rows of cells, which are more or less straight, not constricted at septa, 49–70 × 22–37 μm; wall less than 1 μm thick. Studied material: UNSP MS 3163: P41, 3164: Z40, R36, L47/2, 3184: G38/2.

Endophragmia sp. (Plate 1, figure 20)

Conidium cylindrical, truncate at the base, rounded at the apex, 9-septate, not constricted at septa, dark brown, apex lighter, 58 × 7 μm; wall punctate, less than 1 μm thick, with a basal scar. Studied material: UNSP MS 3193: U42.

Comments. This material is close to *Endophragmia alternata* Tubaki & Saito, but differs for its punctate wall (Matsushima 1975).

Sporidesmium sp. (Plate 1, figure 17)

Conidia obclavate, 7–8 septate, constricted at septa, brown, with lighter end cells, smooth, 107–123 × 15–17 μm; wall ca. 1 μm thick. Studied material: UNSP MS 3182: X39, G45.

Comments. The material could not be assigned to any species because the ends of the conidia are broken. *Sporidesmium* is a saprophyte commonly associated with dead wood of various trees (Ellis 1971, 1976).

Tetraploa aristata Berkeley & Broome 1850 (Plate 2, figure 11)

Conidia short cylindrical, appendaged, muriform, brown, clearly verrucose, 38–48 × 20–25 μm, consist of 4 columns of 9–12 μm wide, 5-celled, each row ending in a setose appendage. Appendages pale brown, lighter at the apex, smooth, 30–58 μm long, wider at the base, apex truncate, 3.0–3.5 μm wide at the apex, 5 μm at the base, with 1–3 septa at 10 to 17.5 μm intervals. Studied material: UNSP MS 3199: V42/2, U24, K35/1.
Comments. The ornamentation is variable; sometimes it is restricted to the basal cells and in others covers all the main body of the conidia. *Tetraploa aristata* is an ubiquitous cosmopolitan fungi (Tanaka et al. 2009). It has been recorded in Tierra del Fuego (Cannon et al. 1989).

Type 364 (*fide* Hooghiemstra 1984) (Plate 1, figure 11)

Spores cylindrical, muriform, consisting of 6 rows of cells which are more or less straight and located in 2 planes, brown, smooth, 32–41 × 20–22 μm, with one pore in each cell, 1 μm diam., wall less than 1 μm thick. Studied material: UNSP MS 3163: P34, 3181: M43.
Comments. The range of spore size in Type 364 described by Hooghiemstra (1984) varied over the range 23–28 × 16–18 μm.

PHYLUM BASIDIOMYCOTA R.T. Moore
Order Pucciniales Clements & Shear
Family Pucciniaceae Chevallier
Uredinales-type (Plate 2, figure 2)

Spores spherical, 0-septate, pale brown, minutely spinose, 11–14 × 7–11 μm, with two or three pores; wall 1–2 μm thick. Studied material: UNSP MS 3181: Y39, W31/2, V28, V34/4.
Comments. These spores show features of uredospores, one of the spores produced by rust-fungi. Rusts are the largest group of phytopathogenic fungi. They parasite a wide range of plants including various ferns, conifers and angiosperms (Aime 2006).

Indeterminated fungal spores
Type A (Plate 1, figure 7)

Spores cylindrical, 1-septate, constricted or not at septa, pale brown, punctate to reticulate, 22–24 × 15 μm, diporate, pores located one in each cell, 1 μm diam.; wall 1–2 μm thick. Studied material: UNSP MS 3184: S31/1, O25/3.

Type B (Plate 1, figure 8)

Spores cylindrical, 1-septate, dark-brown, smooth, 10.5–13 × 5 μm; wall 0.8–1.0 μm thick. Studied material: UNSP MS 3184: K43, V29.

Type C (Plate 1, figure 9)

Spores cylindrical, 3-septate (?), only the medium septum well preserved, not constricted at septa, brown, punctate, 12–14 × 5–8 μm; wall ca. 1 μm thick. Studied material: UNSP MS 3197: Z38, Y38/2, R39, R39/3.

Type D (Plate 1, figure 12)

Spores globular, multicellular, brown, smooth, 31–34 × 28 μm, consisting of 13 or more cells located in 2 planes, individual cells spherical-polygonal, irregularly arranged, 6–13 μm diam., wall less than 1 μm thick. Studied material: UNSP MS 3197: W40, Y38/4.

Type E (Plate 2, figure 1)

Spores spherical to subspherical, 0-septate, dark-brown, smooth, 6–9 × 6–7 μm; wall ca. 1 μm thick. Studied material: UNSP MS 3163: Z35, Y47/4, Y37/2, X28/1.

Type F (Plate 2, figure 4)

Spores spherical, 0-septate, dark-brown, punctate, 31–34 × 28–29 μm, monoporate, pore about 2 μm diam., sometimes absent; wall 1–2 μm thick. Studied material: UNSP MS 3199: V40, W40.

Incertae sedis
Type 370 (*fide* Hooghiemstra 1984) (Plate 1, figure 5)

Spores spherical, aseptate, dark brown, spinose, 9 μm diam., wall 1 μm thick; spines slender, 0.5–3.0 μm long. Studied material: UNSP MS 3182: N33, 3183: S30, O49, 3199: U29.

Type G (Plate 1, figure 6)

Spores spherical, 0-septate, dark-brown, spinose, 20–25 μm diam., spines uniformly distributed, up to 5 μm long. Studied material: UNSP MS 3163: V33/3, 3184: E33/4.

Type H (Plate 2, figure 3)

Spores spherical, 0-septate, pale brown, spinose, 15–16 × 13 μm; spines less than 1 long, wall 0.75 μm thick. Studied material: UNSP MS 3196: X40, 3195: Z28, Z29, T33.

Type I (Plate 2, figure 5)

Spores spherical, 0-septate, hyaline, 14–15 μm; wall with superficial ridges, 2 μm thick; ridges 1.5–2.0 μm wide forming helices all over. Studied material: UNSP MS 3196: Y48, W48.

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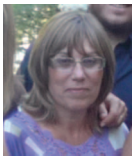

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