

**Studies of vegetation, fire and climate dynamics during the late  
Quaternary as contribution towards conservation and management of the  
biodiversity hotspot „Mata Atlântica“ in southern Brazil**

**PhD Thesis**

submitted

at the Georg August University Göttingen,

Faculty of Biology

for the degree “Doctor of Philosophy (PhD) /Dr. rer. nat.”

in the Georg-August-University School of Science (GAUSS) Program

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Date of oral exam: 20/01/2011

To my lovely partner Marius and  
My dear parents Fredo and Erica

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## Acknowledgements

The time writing this thesis has been hard but it was a great phase of intensive learning. I have to thank all people who contributed to and were involved in the successful completion of the thesis. Funding was provided by Deutsche Forschungsgemeinschaft (DFG) project BE 2116/9-1.

First, I wish to thank my leading supervisor, Prof. Dr. Hermann Behling for giving me the opportunity to work in his department and for introducing me to the subject of Palynology. Further, I would like to thank my co-supervisor Prof. Dr. Erwin Bergmeier for his co-operation and help, as well as for his interest in the project. I would like to express my sincere gratitude to Sonia Fontana, Thomas Giesecke, Sander van der Kaars, Ellyn Cook, *Gerald Islebe* and Frank Schlütz for scientific discussions, critical comments about the work and productive collaboration while writing this *thesis*. Special thanks to all members of the department, especially to Ursula Grothmann for helping me with administrative issues and Jörg Christiansen for solving computer problems. At this point, I would like to thank Nele Jantz for the taking of pollen and spore pictures and Martin Zweigert for sample preparation in the laboratory.

Nicht zuletzt möchte ich den „Villa Hexen“ (Corinna Brunschön, Barbara Hermanowski, Lisa Schüler, Isabelle Matthias und Nele Jantz) für all die Unterstützung in den schwierigen Momenten, den Motivationsnachschieb und die unendliche Hilfe bei meiner Arbeit danken.

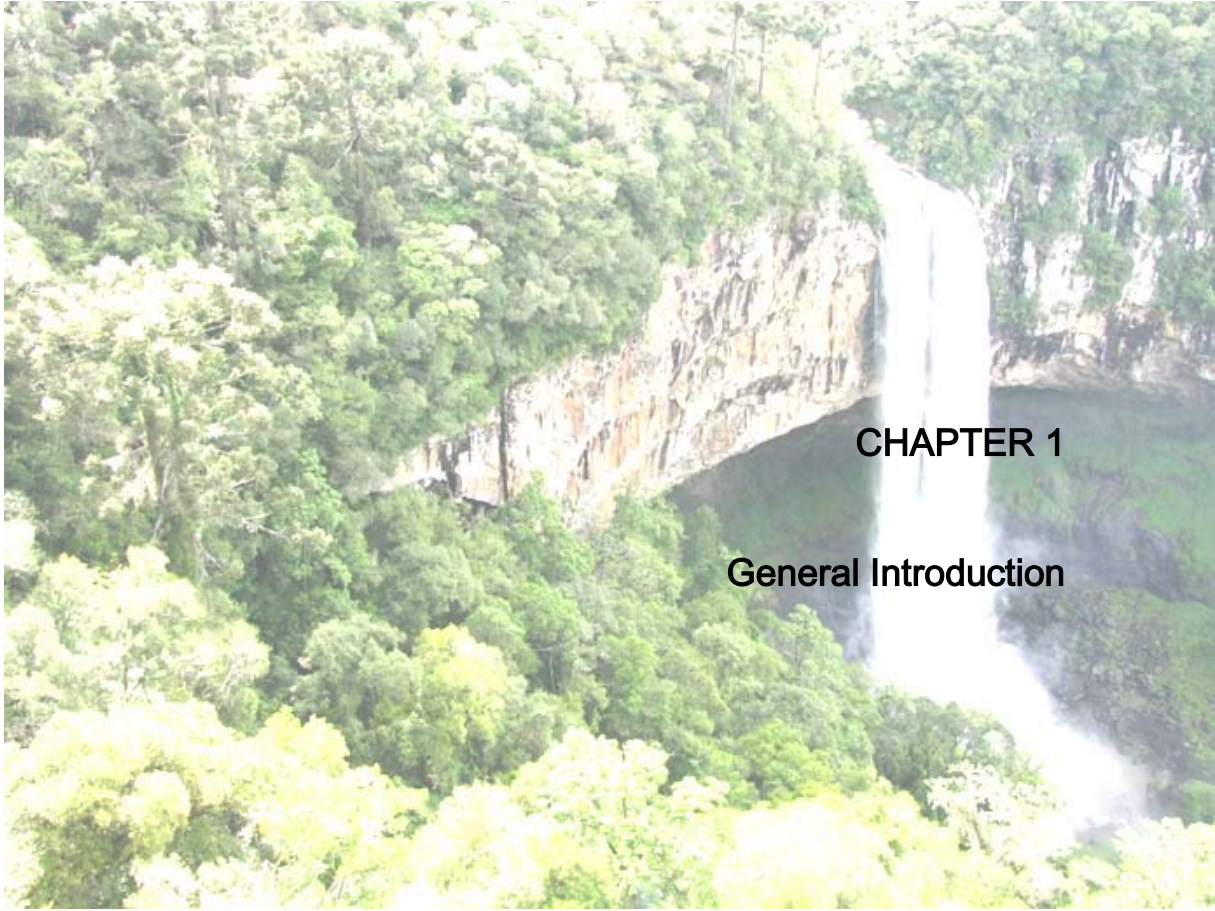
Agradeço ao meu pai por toda a ajuda em campo, como motorista e principalmente como guia. Aos meus colegas palinólogos Gisele L. de Lima, Renato B. Macedo, Rodrigo R. Cancelli, Andréia C. P. Evaldt e Prof. Soraia G. Bauermann, assim como à Renata I. Duzzioni, seu Weber e José Pedro P. Trindade pela grande ajuda durante os trabalhos de campo na Serra Geral e na Serra do Tabuleiro.

Em especial, agradeço à minha família pela força e apoio emocional, principalmente meus pais, grandes incentivadores, que sempre me encorajaram e ajudaram. Ao meu querido marido e companheiro Marius pelo carinho e paciência, bem como pela ajuda nas situações mais difíceis.

Muito obrigada!

## **Preface**

This PhD thesis, written as a cumulative work, has been accomplished at the Department of Palynology and Climate Dynamics at the University of Göttingen between March 2007 and December 2010. The thesis is composed of three different parts: a general introduction in Chapter 1, three independent articles presented in Chapter 2 to 4, and a synthesis in Chapter 5 integrating conclusions of the previous chapters together with a discussion. A fourth article in which the co-author Vivian Jeske-Pieruschka has written the palynological part on basis of data presented in Chapter 4 is attached in Appendix E. Tables and figures are inserted directly in the text following his statement on the text and enumerated separately for each chapter. Each article has been submitted separately for publication in international scientific journals and is arranged according to the layout of the journal. The reference style also follows the formatting rules of the designated journal except for Chapter 1. A summary of the thesis in English, German and Portuguese is given at the end. A complete list and some illustrations of identified pollen and spore types as well as complete pollen diagrams of the studied sediment records are included in the appendices.



## 1.1. The Atlantic Forest Biome

The mega-diverse country of Brazil encompasses six major biomes: Amazon, Cerrado, Caatinga, Atlantic Forest, Pantanal and Pampa (IBGE, 2004). The Atlantic Forest biome, considered one of the 25 global biodiversity hotspots (e.g. Myers *et al.*, 2000; Tabarelli *et al.*, 2005), comprises one of the most important tropical forests world-wide. It extends along the Brazilian Atlantic coast from north to south across several mountain ranges such as the Serra Geral and Serra do Tabuleiro (see 1.4.2, Fig. 5) and extends into the inland bordering Uruguay, northeastern Argentina and eastern Paraguay. The Atlantic Forest biome, situated in the most urbanized area of the country with more than 112 million inhabitants (Fundação SOS Mata Atlântica/INPE, 2009) continues to be under anthropogenic threat since European colonization around 1500 years AD (e.g. Morellato and Haddad, 2000). This biome, represented by only 7.6% of severely fragmented remaining areas (CN-RBMA, 1999), has already lost more than 90% of its original cover (Fig. 1). The Atlantic Forest biome represents therefore the most devastated vegetation of the country.

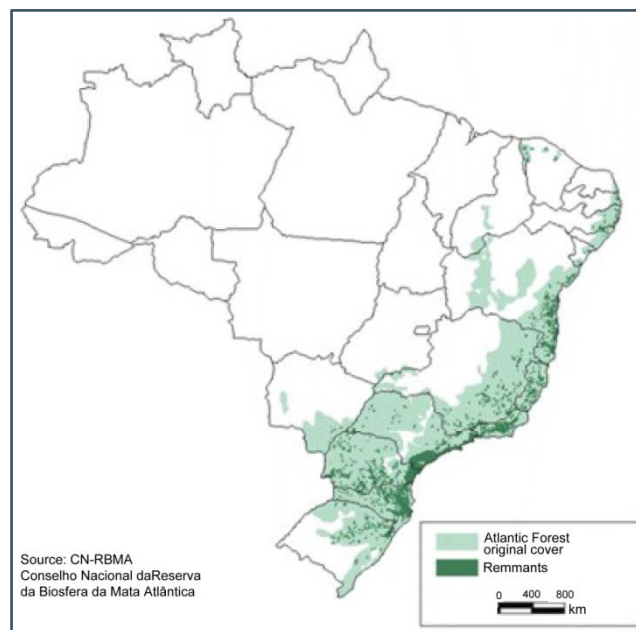


Figure 1. Map showing forest remnants of the Atlantic Forest original cover in Brazil.

([www.rbma.org.br/rbma/rbma\\_1\\_localizacao.asp](http://www.rbma.org.br/rbma/rbma_1_localizacao.asp))

The Atlantic Forest biome is composed of different vegetation types (Fig. 2) considered as associated ecosystems and thus forming contrasting landscapes. These ecosystems vary highly depending on the altitudinal gradient and associated temperature as well as on their proximity to the ocean, rainfall regime and edaphic properties (Raedig and Lautenbach, 2009). The different vegetation types belonging to the Atlantic Forest biome include Atlantic rainforest, open ombrophylous forest, *Araucaria* forest, Deciduous forest, Tropical semideciduous forest, pioneer vegetation formations and highland Campos. The vegetation types studied and discussed in this thesis are independent ecosystems and correspond to the highland Campos, *Araucaria* forest and Atlantic rainforest. They dominate the landscape of the southern Brazilian highlands and the escarpments, and overall picture a fascinating mosaic of subtropical grassland and forest ecosystems. The Atlantic Forest biome together with the Pampa biome, specifically the forest and grassland ecosystems associated with these two biomes in southern Brazil, were identified as priority areas for conservation and of extreme biological importance due to their high level of endemism and great biodiversity (Conservation International do Brasil, 2000). Although well documented, the Campos flora of the Atlantic Forest biome with 1161 vascular plant species (107 are endemic) (Boldrini *et al.*, 2009) still harbor undescribed species (Boldrini, 2009). Therefore, the biodiversity of southern Brazilian ecosystems is probably much greater than assumed so far.

The Campos vegetation has been used for pasture since European colonization. Since then, widespread deforestation and ecosystem alteration were the consequences of human activity in the *Araucaria* forests in the southern Brazilian highlands and the Atlantic rainforests on the slopes. Concerning land-use practices and climate change in the southern region of the Atlantic Forest biome and its associated ecosystems, palaeoenvironmental studies contribute significantly towards the understanding of vegetation dynamics and climate change. Thus, palynological studies can offer palaeoenvironmental information useful for the development of conservation and management strategies for these ecosystems, which are highly vulnerable to global change.

Two study sites on the Serra do Geral were chosen for palynological and charcoal analysis due to their locality relative to surrounding vegetation, which offer a great possibility to study the origin, dynamics and stability of grassland and forest ecosystems including human activities and fire history. In addition, the obtained information can also be compared to the results of previously accomplished palynological studies in the same region. The third study site on the Serra do Tabuleiro was chosen because of its special geographical position, namely the proximity to the coast and its isolation from other mountain ranges. That offers an excellent opportunity to study the development and history of Atlantic rainforest and *Araucaria* forest as well as fire events during the past.

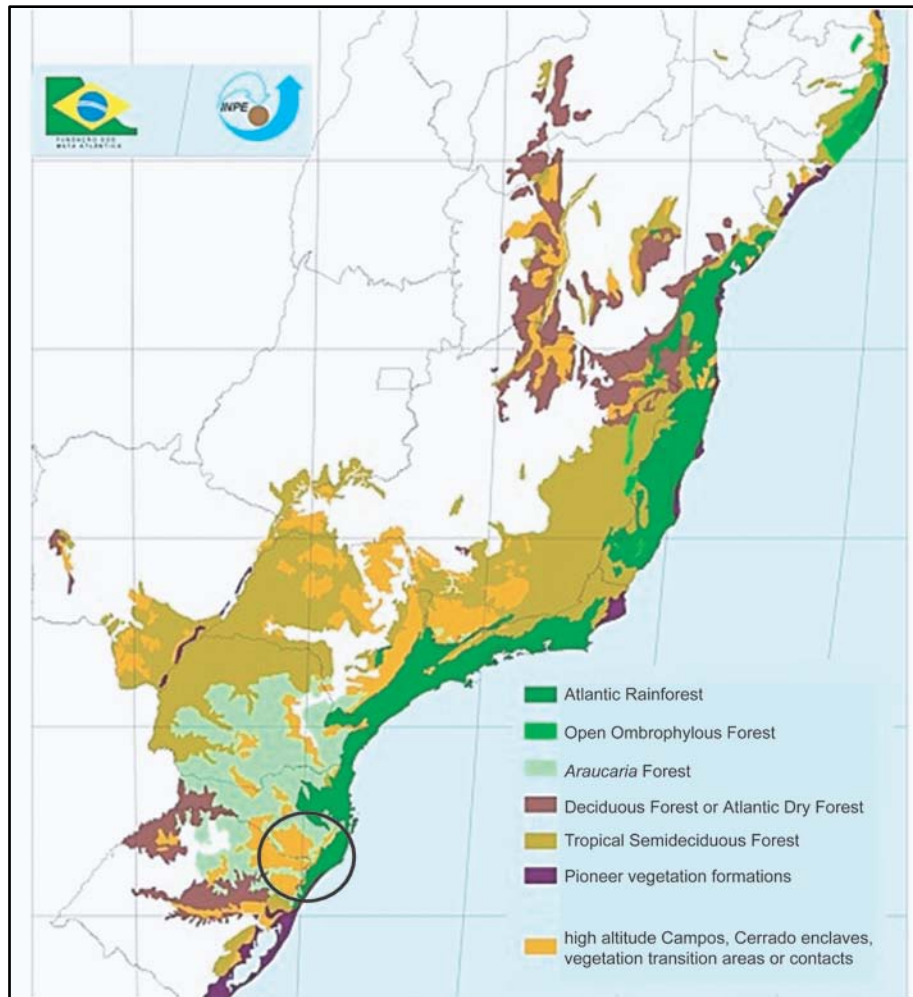


Figure 2. Different vegetation types of the Mata Atlântica Domain.

(source: Digitalização do Mapa de Vegetação do Brasil, FIBGE, 1993, escala 1:5:000.000 – Instituto Socioambiental/Fundação SOS Mata Atlântica) slightly modified. The circle on the map indicates the studied region.

([www.rbma.org.br/anuario/mata\\_02\\_eco\\_ssistema.asp](http://www.rbma.org.br/anuario/mata_02_eco_ssistema.asp))

## 1.2. Previous studies on the ecosystems of the Atlantic Forest Biome in southern Brazil during the late Quaternary

During the last few years, palaeoenvironmental studies of the Atlantic Forest biome were carried out for the southeastern (e.g. Behling and Lichte, 1997; Behling, 1998, 2002; Ybert *et al.*, 2003; Garcia *et al.*, 2004; Behling and Safford, 2010) and southern region of Brazil (e.g. Behling *et al.*, 1997; Behling and Negrelle, 2001; Lorscheitter, 2003; Cruz Jr. *et al.*, 2005, 2006; Leal and Lorscheitter, 2007; Oliveira *et al.*, 2008 a,b; Leonhardt and Lorscheitter, 2010). Nevertheless, studies on development and dynamics of the Atlantic rainforest ecosystem reaching into the full Glacial period still lack for southern Brazil. For the Santa Catarina lowlands, Behling and Negrelle (2001) documented initial Atlantic rainforest development after 12,300 yr BP (uncalibrated years before the



present) as part of a successional sequence and the appearance of a dense forest only after the marine regression at about 6100 yr BP. For Rio Grande do Sul, Lorscheitter (2003) indicated fossil evidence of some disperse Atlantic rainforest taxa at the beginning of the Holocene at about 10,000 – 8000 yr BP along the coastal plain and valleys. More recently, Leal and Lorscheitter (2007) propose a migration of Atlantic rainforest species from east to west on the lower slope of the Serra Geral, Rio Grande do Sul since 8800 yr BP.

For the southern Brazilian highlands Campos vegetation seems to be the predominant vegetation type during glacial times. The hypothesis of some authors about Campos vegetation as a relict from drier climatic conditions in the past (Rambo, 1956, 1994; Klein, 1960, 1975) has been confirmed by palynological studies in the last decades (Roth and Lorscheitter, 1993; Behling, 1995, 1997, 1998, 2002; Behling *et al.*, 2001, 2004; Leonhardt and Lorscheitter, 2010). Studies of late Quaternary palaeoenvironments in southern Brazilian grasslands, suggest initial *Araucaria* forest expansion after 2000 yr BP in Serra do Araçatuba (Behling, 2007) and about 2850 yr BP in Serra dos Campos Gerais (Behling, 1997), both in Paraná state. For the highlands of Santa Catarina state, Behling (1995) proposed first *Araucaria* forest expansion at about 3460 yr BP in Serra da Boa Vista and at about 2390 yr BP in Serra do Rio do Rastro. In Rio Grande do Sul, located further south of Santa Catarina, initial *Araucaria* forest expansion is documented for about 3950 yr BP in Cambará do Sul (Behling *et al.*, 2004) and after 4000 yr BP in São Francisco de Paula region (Leonhardt and Lorscheitter, 2010). Marked *Araucaria* forest expansion is reported for about 1400 cal yr BP (calibrated years before the present) in Paraná state (Behling, 1997, 2007) and since the last 1000 years for the highlands of Santa Catarina and Rio Grande do Sul states (Behling, 1995; Behling *et al.*, 2001; Behling *et al.*, 2004; Behling and Pillar, 2007). Although the early expansion of *Araucaria* forests occurred at different times, all interpretations suggest *Araucaria* forest initial expansion through migration from gallery forests along rivers and wet areas after mid-Holocene.

### 1.3. Aims of the work

At present, the remaining areas of Campos on the highlands represent remnants of early and widely expanded vegetation of glacial times that was gradually replaced by forest ecosystems during the late Holocene (see 1.2). However, on the highlands are also Campos areas of anthropogenic origin which resulted from the introduction of cattle after successive logging and burning. Despite a subtropical humid climate, which favors grassland replacement by forest (e.g. Lindman, 1906; Rambo, 1951; Klein, 1975), natural patches of grassland exist within the forest area (e.g. Klein, 1960; Hueck, 1966; Oliveira and Pillar, 2004). Still unclear and controversial is the reason of sharp borderlines which can be observed between forest and grassland (Fig. 3a). According to some authors, the natural

vegetation of Campos-*Araucaria* forest mosaics covering the highlands in southern Brazil and the marked borderline should be determined by grazing and fire regimes (e.g. Pillar and Quadros, 1997; Pillar, 2003; Overbeck *et al.*, 2007). For some regions on the southern Brazilian highlands, where regional economies are based on land use such as cattle farming and agricultural activities (Fig. 3b) together with silvicultural production (extensive *Pinus* plantations), a better understanding of past environmental changes is of crucial importance for predicting climatic and vegetational changes. Therefore, human activities and their possible role in the formation of Campos-*Araucaria* forest mosaics also need to be explored by mean of pollen and charcoal analysis.



Figure 3a shows an example for sharp borderline between Campos and *Araucaria* forest while figure 3b illustrates different forms of land use with *Pinus* sp. plantation back and in front rural agriculture.

The main goals of the present study are:

- a) To reconstruct vegetation development and dynamics, fire history and climate changes for the southeastern highlands of Rio Grande do Sul state and for the isolated Serra do Tabuleiro, Santa Catarina state during the late Quaternary;
- b) To investigate the origin, development and dynamics of the Campos-*Araucaria* forest mosaics ecosystems on the southern Brazilian highlands;
- c) To investigate the development and history of the Atlantic rainforest;
- d) To elucidate forest expansion in different time periods;
- e) To clarify if the present grasslands are natural or of anthropogenic origin and if the existence of isolated *Araucaria* forests originates from refugia of the last glacial period in the Serra do Tabuleiro coastal mountain range;
- f) To understand how the frequently observed sharp borderlines between Campos and *Araucaria* forest have been formed and how they are maintained;
- g) To examine and interpret the factors controlling the dynamic and stability of Campos-*Araucaria* forest mosaics;

- h) To discover since when and how strong grassland and forest ecosystems have been affected by human activities;
- i) To use this background information as important contribution for sustainable conservation and management of the species rich vegetation in southern Brazil;
- j) To connect these palaeoenvironmental studies with two other international research projects;
- k) To compare the results with other localities;

With the purpose of approaching these research questions, two sediment archives from the Serra Geral and one from the Serra do Tabuleiro have been studied by means of pollen and charcoal analysis. These sediment records were cored from bogs situated in the “Mata Atlântica” region. Therefore, these studies provide a basis to understand the development, stability and dynamics of modern ecosystems, including their biodiversity in space and time.

This study provides interpretations on palaeoecological changes and anthropogenic activities throughout the late Quaternary that could be integrated into two research projects. Part of this thesis (Chapter 2 and 3) is related to a research project titled „From Landscape to Ecosystem: Across-scales Functioning in changing environments (LEAF)” financed by the InterAmerican Institute for Global Change Research (IAI).

A smaller cooperation between the Department of Geosciences at the Universidade Federal de Santa Catarina, Brazil and the Department of Palynology and Climate Dynamics at the University of Göttingen about palaeoenvironmental characterization of the highlands of the Serra do Tabuleiro was funded by FAPESC – Fundação de Apoio à Pesquisa Científica e Tecnológica do Estado de Santa Catarina and resulted in two articles submitted to international journals (Chapter 4 and Appendix E).

## **1.4. Study region**

### **1.4.1. Location of the study sites**

The research was performed at three study sites in the southern Brazilian highlands, as shown by figure 4. The southern region of Brazil, covering 577.214 km<sup>2</sup>, corresponds to the smallest of the five regions of Brazil and encompasses the states of Paraná, Santa Catarina and Rio Grande do Sul. It borders Uruguay, Argentina and Paraguay to the west, the Central-West region and the Southeast region of Brazil to the North and the Atlantic Ocean to the east. The highlands of Rio Grande do Sul (Serra Geral) are located in the northeastern part of this state while the isolated Serra do Tabuleiro lies in the east of Santa Catarina state (Fig. 5).



Figure 4. Location of southern Brazil with indication of the study sites of this work: Ciama 2 (Ciama), São José dos Ausentes (SdA) and Rincão das Cabritas (RdC).

The first study area São José dos Ausentes (SdA) ( $50^{\circ}02'39.9''\text{W}$ ,  $28^{\circ}56'16''\text{S}$  at 1050 m a.s.l.) is situated between the village of Cambará do Sul and São José dos Ausentes. The second one, Rincão das Cabritas (RdC) ( $50^{\circ}34'22''\text{W}$ ,  $29^{\circ}28'35''\text{S}$  at 895 m a.s.l.), is situated in a rural area of São Francisco de Paula municipality. Both sites are located in the Serra Geral formation situated in the northeastern highlands of Rio Grande do Sul state. The escarpments of the Serra Geral mountain range, in the part of Rio Grande do Sul state, are situated at a distance of approximately 25 km from the coast (Itaimbezinho Canyon) and reaches an average elevation of 950 meters.

The third study site lies in the Ciama region ( $48^{\circ}52'5.33''\text{W}$ ,  $27^{\circ}53'48.46''\text{S}$ , at 860 m a.s.l.), on the highlands of the Serra do Tabuleiro, Santa Catarina state. The Serra do Tabuleiro is an isolated coastal mountain range reaching elevations up to 1260 m and is inserted into the State Park Serra do Tabuleiro. The Park was founded in 1975 and includes 9 municipalities close to the capital city of Florianópolis. With an area of 87.405 ha, it covers approximately 1% of the Santa Catarina state in southern Brazil, being the largest conservation unit in this State (Oliveira *et al.*, 2006).





Figure 5. Topographical map of Brazil (after Menegáz, 2006) showing the southern Brazilian highlands: Serra Geral and Serra do Tabuleiro (slightly modified).

#### 1.4.2. Geomorphology and soil

The southernmost highlands of southern Brazil, on the northeastern part of Rio Grande do Sul state, the so-called Serra Geral formation corresponds, in geomorphological terms to a plateau (Planalto Meridional). This geomorphological unit is formed by layers of basalt covering Jurassic/Cretaceous sedimentary rocks, the Botucatu formation. It is composed of base-rich basalt in the lower layers and acidic rocks mostly rhyolite and rhyodacite in the upper layers (IBGE, 1986).

Soil formation is affected by high precipitation rates under subtropical humid climate. According to the Soil Map of Brazil composed by the IBGE (Brazilian Institute of Geography and Statistics) and the EMBRAPA (Brazilian Agricultural Research Cooperation), humic cambisol and leptosols occur in the highlands (<http://mapas.ibge.gov.br/solos/viewer.htm>). A recent study on soils in

the Pró-Mata area, southern Brazilian highlands (Dümig, 2008), concludes that soils in grasslands of the region are more correctly termed andosols while umbrisols develops in the *Araucaria* forest.

The isolated mountain range of Serra do Tabuleiro is predominantly composed by granite intrusive rocks (Égas *et al.*, 2005) of approximately  $516 \pm 12$  Ma (Basei, 1985 in Tomazzoli *et al.*, 2005). Soils of the Serra do Tabuleiro are identified as cambisols and acrisols or lixisols (<http://mapas.ibge.gov.br/solos/viewer.htm>).

### 1.4.3. Climate

The climate of southern Brazil is influenced by the South Atlantic Anticyclone transporting equatorial warm and humid air masses from the tropical Atlantic Ocean over the continent during the whole year. This influence is weaker during the austral winter (June-August) and more frequent during the summer (December-February). Another atmospheric circulation also influences the climate of the southern Brazil mostly during the winter, the Polar Anticyclone with dry and cold air masses. These air masses formed in the Antarctic and its trajectory over the South-American continent provoke strong rainfall when it clashes with tropical warm and humid air masses (Nimer, 1989). The rainfall is also intensified by the elevation of air masses promoted by the relief that cause rain after their cooling and condensation. The amount of moisture depends on the proximity to the Atlantic Ocean and in consequence, precipitation reduces from the coast to inland (east-west).

The climate on the highlands of Rio Grande do Sul is subtropical humid, with high rainfall rates (up to ca. 2500 mm/year) distributed throughout the year without a pronounced dry period (Moreno, 1961). It is classified as wet mesothermic climate (Cfb, Köppen) and characterized by temperatures lower than 22°C in the warmest month and higher than 3°C in the coldest month. The winters are cold, with temperatures below 0 °C in cold winter nights and rare occurrence of snow at higher elevations; frosts are frequent. For the Santa Catarina highlands, the climate is also characterized as mesothermic Cfb (above 800 m a.s.l., Köppen) with high mean annual precipitation ranging from 1600 to 1800 mm/year, relatively uniformly distributed throughout the year.

Precipitation anomalies are associated with El Niño Southern Oscillation (ENSO) and La Niña events. Excessive rainfall events are related to El Niño whereas La Niña reduces rainfall in southern Brazil (Grimm *et al.*, 1998, 2000). Interannual variability of rainfall is also related to anomalies in sea surface temperature (SST), with increased (decreased) precipitation associated with warm (cold) deviation of SST in the southwestern Atlantic Ocean (Díaz *et al.*, 1998; Barros *et al.*, 2000).

#### 1.4.4. Current distribution of the vegetation

At present, a fascinating landscape formed by grassland-forest mosaics constitutes the highlands of southern Brazil (Fig. 6). These mosaics formed by large areas of subtropical grassland, so-called Campos, intercepted by patches of *Araucaria* forest, characterize the picture across the southern Brazilian highlands representing thus the landscape of the region (e.g. Klein, 1960; Rambo, 1994). Although *Araucaria* forest is the main vegetation type on the highlands forming Campos-forest mosaics, an exuberant forest ecosystem, the Atlantic rainforest, can be seen growing on the slopes of the coastal mountain ranges (Fig. 7).

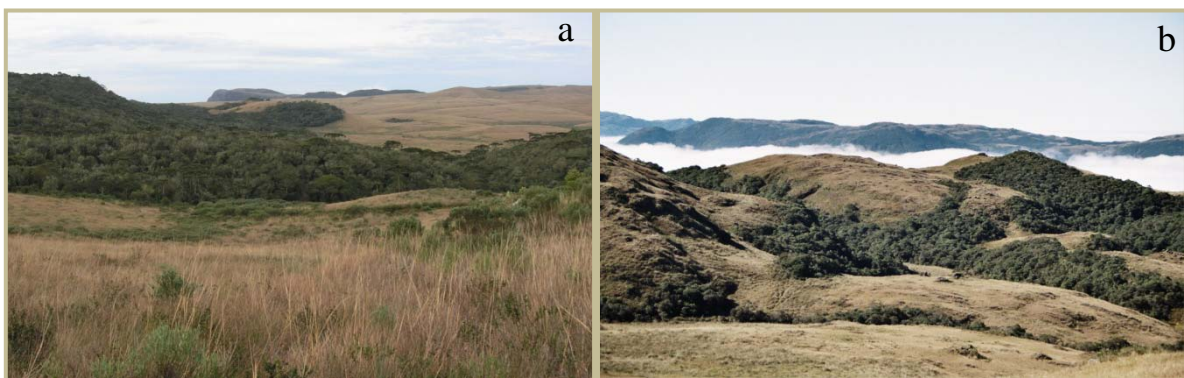


Figure 6. Mosaics of Campos-*Araucaria*-forest in the Serra Geral (a) and in the Serra do Tabuleiro (b).



Figure 7. Atlantic rainforest on the slopes of the coastal mountain range of Serra Geral (a) and of Serra do Tabuleiro (b).

The Campos ecosystem in the highlands of Rio Grande do Sul state is mainly composed of the plant families Poaceae, Asteraceae, Fabaceae, Cyperaceae and Apiaceae (Boldrini, 2009). Among the dominant Poaceae species, Boldrini (1997) identified *Andropogon lateralis*, *Axonopus siccus*, *Paspalum maculosum*, *Schizachyrium tenerum* and *S. spicatum* for well-drained and *Andropogon macrothrix* and *Paspalum pumilum* for poorly drained grasslands.

*Araucaria angustifolia* (Araucariaceae) is the most physiognomically important tree species of the *Araucaria* forest ecosystem on these highlands. The geographical distribution of *Araucaria*

*angustifolia* is in the southern states of Brazil that are Rio Grande do Sul, Santa Catarina and Paraná. The species also occurs isolated or in small populations in São Paulo, Rio de Janeiro and Minas Gerais state at higher elevations (Hueck, 1953) (Fig. 8). The *Araucaria* forest consists of species such as *Podocarpus lambertii* (Podocarpaceae), *Drimys* spp. (Winteraceae), *Mimosa scabrella* (Fabaceae), *Ocotea pulchella*, *O. puberula*, *Nectandra* spp. (Lauraceae), *Ilex paraguariensis*, *Ilex* spp. (Aquifoliaceae), *Matayba elaeagnoides*, *Cupania vernalis* (Sapindaceae) and various species of the Myrtaceae family (Reitz *et al.*, 1988). The slopes of the Serra Geral (Rio Grande do Sul state) are covered by Atlantic rainforest from the lower altitudes up to higher elevations where a gradual transition between the *Araucaria* forest and the Atlantic rainforest can be observed (Fig. 9).

The species-rich Atlantic rainforest is composed of numerous tree species with a predominance of Lauraceae (eg. *Ocotea* spp., *Nectandra* spp.) and Myrtaceae (eg. *Myrcia* spp., *Myrceugenia* spp., *Calypttranthes* spp., *Gomidesia* spp.). Other representative taxa are: *Alchornea* spp. (Euphorbiaceae), *Clethra scabra* (Clethraceae), *Weinmannia* spp. (Cunoniaceae), *Inga* spp. (Fabaceae), *Cedrela* spp., *Cabralea canjerana* (Meliaceae) as well as Mimosaceae (*Piptadenia*, *Parapiptadenia*, *Anadenanthera*). However, numerous lianas and epiphytes belonging to Bromeliaceae, Orchidaceae, Araceae, Cactaceae as well as pteridophytes are characteristic for the Atlantic rainforest ecosystem. A more extensive description of the Campos and forests of southern Brazil was published by Lindman (1906). The southern Brazilian vegetation has also been described in Rambo (1951, 1956), Klein (1960, 1975) and Hueck (1966). The two study sites on the Serra Geral, Rio Grande do Sul state, were covered by mosaics of natural Campos and *Araucaria* forest prior to the arrival of European settlers.



Figure 8. Original distribution of the *Araucaria*-forest in Brazil  
(<http://pt.wikipedia.org/wiki/Ficheiro:FlorestaOmr%C3%B3filaMista.jpg>).





Figure 9. Vegetational transition between two forest types: *Araucaria* forest and Atlantic rainforest on the upper slopes of the Serra Geral.

The present vegetation of the Serra do Tabuleiro in Santa Catarina state is composed of Atlantic rainforest on the slopes, *Araucaria* forest at higher elevations and Campos ecosystems at upper altitudes. This isolated coastal mountain range is inserted into the State Park Serra do Tabuleiro, which can be differentiated into five phytogeographic regions (Klein, 1981). In the eastern part, on the Quaternary sandy plain, coastal vegetation (so-called *restinga*) and mangroves occur. Atlantic rainforest is the dominating vegetation type in the Park, covering the lowland and the slopes. *Araucaria* forest and Campos occur at higher elevations. A comprehensive description of the recent vegetation of the park is given by Klein (1978, 1981).

## 1.5. Methods

### 1.5.1. Fieldwork

Two fieldwork periods during the time of 23.06.2007 until 04.07.2007 and from 06.11.2008 to 11.11.2008 were carried out on the highlands of Rio Grande do Sul and Santa Catarina state. During the first fieldwork period, one sedimentological record from a peat bog located on the northeastern highlands of Rio Grande do Sul was collected. Additionally, 18 surface soil samples were taken across a transect in an area covered by Campos and *Araucaria* forest in order to study the modern pollen rain in a grassland-forest-mosaic landscape. Furthermore, 20 pollen traps were installed in the Pró-Mata research area that also lies on the Rio Grande do Sul highlands. For the Santa Catarina highlands, 15 pollen traps were installed in the Serra do Tabuleiro. The peat record was sampled using a Russian corer. Each 50 cm long core section was sealed with split PVC tubes and wrapped with plastic film

before stored in a dark and cold room ( $\sim 4^{\circ}\text{C}$ ) until opened for sediment description and subsampling. The peat sediment and the transects of installed pollen traps as well as the collected surface soil samples are listed in Table 1.

Table 1. Collected samples and installed pollen traps during fieldwork.

Sample type	Sampling/installing date	Location	Elevation (m a.s.l.)	Coordinates (GPS)
Rincão das Cabritas (RdC) peat core	23.06.2007	São Francisco de Paula-Serra Geral	894	29°28.591`S 50°34.370`W 28°56`18.3``S
Surface soil samples (transect of 18 sites)	25.06.2007	São José dos Ausentes – Serra Geral	1053 - 1098	50°02`38.2``W to 28°56`09.3``S 50°02`26.7``W 27°54`01.2``S
Pollen traps (transect of 4 sites)	30.06.2007	Ciama –Serra do Tabuleiro	873 - 877	48°52`10.9``W to 27°54`00.1``S 48°52`10.1``W 27°49`13``S
Pollen traps (transect of 11 sites)	01.07.2007	Clino – Serra do Tabuleiro	1148 - 1186	48°53`28.8``W to 27°49`12.1``S 48°53`24.7``W 29°29`16.2``S
Pollen traps (transect of 20 sites)	03.07.2007	Pró-Mata – Serra Geral	900 - 935	50°13`0.1``W to 29°29`12.2``S 50°13`22.1``W

### 1.5.2. Analyzed sediment cores

The São José dos Ausentes (SdA) core has a length of 120 cm and was taken from a peat bog of ca. 30 m of diameter located at the border of a disturbed *Araucaria* forest island, surrounded by Campos (Fig. 10). It was collected by Hermann Behling and Soraia Girardi Bauermann on November 13<sup>th</sup> 2004 during fieldwork in southern Brazil. This peat core has an extrapolated age of 590 cal yr BP at 98 cm core depth. Furthermore, 18 surface soil samples were taken across a 340 m long transect (Fig. 11) in the research area of the peat core close to the village of São José dos Ausentes with the intention of studying the modern pollen rain of Campos-*Araucaria* forest ecosystems.



Figure 10. Cored peat bog situated between the village of Cambará do Sul and São José dos Ausentes on the Serra Geral, Rio Grande do Sul state. The studied peat at right side of the picture is bordered by a small, disturbed *Araucaria* forest island surrounded by Campos.



Figure 11. Surface soil transect in the same area of the sedimentary record to estimate the modern pollen rain of the two local vegetation types, Campos and *Araucaria* forest in order to holistically interpret the palaeodata from this locality.



The Rincão das Cabritas (RdC) core, reaching 281 cm length, was collected on June 23<sup>rd</sup> 2007 from a ca. 5000 m<sup>2</sup> bog situated within an *Araucaria* forest (Fig. 12). The base of the core is extrapolated to 16,700 cal yr BP.



Figure 12. Sampled peat within the rural property Rincão das Cabritas located on the Serra Geral, Rio Grande do Sul state.

The Ciama 2 core with a length of 169 cm was taken from a peat bog located in the Campos surrounded by Atlantic rainforest and *Araucaria* forest (Fig.12). Marcelo Accioly Teixeira de Oliveira and Hermann Behling took this sediment core during fieldwork on August 13<sup>th</sup> 2005. The extrapolated basal age at 168 cm core depth is 39,720 yr BP.



Figure 13. Peat bog cored by the Ciama area in the Serra do Tabuleiro, Santa Catarina state.

### 1.5.3. Laboratory techniques

Preceding sample preparation for pollen analysis, the lithology of each sediment core was described. Subsequently, subsamples were taken for pollen, charcoal and radiocarbon analysis. For the SdA sedimentary record, a total of 75 samples of 0.25-1 cm<sup>3</sup> were used for pollen and charcoal analysis. Samples were taken at 1 cm intervals between 0-32 cm, and every 2 cm between 33-120 cm core depth. For the RdC peat core, a total of 71 samples (0.25 -1 cm<sup>3</sup>) were taken at 4 cm intervals. At last, 83 volumetric subsamples (0.25 cm<sup>3</sup>) were taken every 2 cm along the Ciama 2 core, except between 0-8 cm core depth, i.e. 2 samples with interval of 4 cm. Differences in sampling intervals along each core are a result of different core lengths and depend on the sedimentation time that they encompass. The same analytical standard methods were applied for the surface soil samples (ca. 2 cm depth of soil and litter) as for the fossil pollen.

All samples were processed and prepared for pollen and charcoal analysis in the palynological laboratory with standard pollen analytical methods after Faegri and Iverson (1989). Prior to pollen preparation, samples were treated with hydrofluoric acid (HF) to digest siliceous matter as clay (sometimes containing layers of fine sand). One tablet of *Lycopodium clavatum* marker was added to each sample for determination of pollen and charcoal concentration (grains/cm<sup>3</sup>; particles/cm<sup>3</sup>) and accumulation rates (grains/cm<sup>2</sup>/year; particles/ cm<sup>2</sup>/year) (Stockmarr, 1971). Hydrochloric acid (HCl) was used to dissolve the carbonate present in the *Lycopodium* tablets. Subsequently, the samples were washed through nested metal screens with mesh size of 150 µm. Preceding acetolysis, which is applied for cleaning and to dye pollen, spores and palynomorphs, the samples were dehydrated with acetic acid (CH<sub>3</sub>COOH). Finally, the pollen residues were mounted in glycerin gelatin and searched for pollen grains under a light optical microscope and counted up to a minimum of 300 pollen grains at each level. Charcoal analysis is based on microscopic (5 – 150 µm) charred particles which were counted on the pollen-slides.

In total, 18 subsamples were taken from the cores and sent to radiocarbon dating through Accelerator Mass Spectrometry (AMS) at the Institute of Physics of the Erlangen-Nürnberg University, Germany. The resulting ages were converted into calibrated calendar years before present (cal yr BP) with CalPal (Weninger *et al.*, 2004) or using the software CALIB 6.0 (Stuiver and Reimer, 1993) applying the data set of SHCal04 (McCormac *et al.*, 2004) and of intcal09.14c (Reimer *et al.*, 2009). A chronological control is given for each sediment core through the radiocarbon ages that were used for constructing the age-depth models for the cores assuming an equal sedimentation rate. Table 2 shows radiocarbon dates for the São José dos Ausentes (SdA), for the Rincão das Cabritas (RdC) and for the Ciama 2 sediment archives.

Table 2. Radiocarbon dates from the studied sedimentary profiles.

Core name	Laboratory code	Sample depth (cm)	Sample type	Conventional age ( $^{14}\text{C}$ yr BP)	Calendar age (cal yr BP)
São José dos Ausentes (SdA)	Erl-11259	14	peat	-1424±37	0
São José dos Ausentes (SdA)	Erl-11260	26-30	wood	277±36	364±58
São José dos Ausentes (SdA)	Erl-11261	71	wood	451±37	507±18
Ricão das Cabritas (RdC)	Erl-12100	45	wood	704±42	612
Ricão das Cabritas (RdC)	Erl-15120	85	wood	1786±38	1641
Ricão das Cabritas (RdC)	Erl-11387	126	peat	2847±37	2892
Ricão das Cabritas (RdC)	Erl-12101	171	peat	5997±45	6769
Ricão das Cabritas (RdC)	Erl-12655	210	peat	10245±68	11877
Ricão das Cabritas (RdC)	Erl-12102	228	peat	12578±66	14806
Ricão das Cabritas (RdC)	Erl-11388	279	wood	13503±68	16679
Ciama 2	Erl-11255	34	peat	459±44	478
Ciama 2	Erl-12097	47	peat	3820±39	4129
Ciama 2	Erl-12656	61	peat	7327±45	8092
Ciama 2	Erl-11256	71	peat	10536±63	12545
Ciama 2	Erl-12657	83	peat	13399±72	15916
Ciama 2	Erl-12098	94	peat	19439±115	23126
Ciama 2	Erl-12099	122	peat	25380±152	-
Ciama 2	Erl-11257	167	peat	39407±681	-

#### 1.5.4. Identification of pollen and spores

Although pollen preservation and its accumulation can vary markedly depending on the sampled material, almost all counted levels had satisfactory or good pollen preservation and yielded sufficient pollen quantity to be counted. This was the case for the pollen amounts in the complete Rincão das Cabritas and Ciama 2 core as well as for the modern pollen rain in the surface soil samples. Samples below 58 cm core depth in the São José dos Ausentes core yielded low pollen quantities and had bad pollen preservation and were often sterile below 98 cm core depth and could not be counted. Pollen and spores were identified at magnifications of 400 and 1000 x, and counts reach to about 300 pollen grains of terrestrial flowering plants per sample. The identification of the diverse pollen and spore types was simplified by the use of the reference collection of the Department of Palynology and Climate Dynamics, University of Göttingen, together with morphological descriptions by Behling (1993) and Cancelli (2008). Occasionally, a precise identification was not possible. In this case, the word “type” was adopted referring to the most likely taxa. Pollen types that could not be identified were classified by morphological characteristics and included into the “Unknowns” group.

The number of identified pollen and spore taxa as well as the number of counted subsamples for each sedimentary record and surface soil samples is listed in Table 3.

Table 3. Number of identified pollen and spore types as well as number of counted subsamples for each sediment record. Total number indicates the sum of different identified pollen and spore found in all samples (see Appendix A).

Core name	Number of identified pollen taxa	Number of identified spore taxa	Number of counted sub-samples
São José dos Ausentes	170	16	43
Rincão das Cabritas	114	15	71
Ciama 2	155	16	83
Transect soil samples at São José dos Ausentes	82	10	18
<b>Total</b>	<b>241</b>	<b>49</b>	<b>215</b>

### 1.5.5. Calculation and data presentation

Pollen and spore data were used with the purpose of reconstructing past vegetation in the highlands of Rio Grande do Sul (Serra Geral) and of Santa Catarina (Serra do Tabuleiro). All identified pollen and spore types were grouped into different ecological groups (Campos, *Araucaria* forest, Atlantic rainforest, Aquatics, Tree ferns, Pteridophyta and Mosses). Pollen taxa that could not be included in any other vegetation type or have wider geographical distributions, were assigned to "Others". The classification of the pollen and spores in the respective vegetation types was based on the recent vegetation present in each study area (Appendix B). Pollen and spores were calculated as percentages of the pollen sum, which includes all different pollen types of grasses, herbs, shrubs and trees. Spores of pteridophyte and mosses as well as pollen grains of aquatic taxa were excluded from the total pollen sum. Fire event reconstructions are based on microscopic (5 – 150 µm) charred particles and are presented as concentration and influx rates in the pollen diagrams. Results of pollen and spore analysis together with charcoal data are presented as pollen diagrams in percentages of the total pollen sum, calculated and plotted using the software TILIA and TILIAGRAPH (Grimm, 1991). The zonation of the pollen records is based on marked changes in the pollen assemblages i.e. changes of the most important taxa and/or changes in the pollen composition reflecting vegetational changes. Zonation was also based on the cluster dendrogram calculated with CONISS (Grimm, 1987).

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**CHAPTER 2**

***Araucaria* forest dynamics in relation to fire frequency in southern  
Brazil based on fossil and modern pollen data**

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***Review of Palaeobotany and Palynology 160 (2010): 53-65***

## Abstract

To elucidate the relationship between forest dynamics and fire frequency, pollen percentages and charcoal amounts from a 120 cm long peat core and from samples of modern pollen rain were collected along a transect. The study site in southern Brazil is characterized by a species-rich mosaic of grassland-*Araucaria* forest. It is of crucial importance for management strategies for conservation to understand the development and maintenance of these vegetation mosaics including their sharp forest-grassland boundaries. During the late Holocene, considerable changes occurred in the area. From Anno Domini (AD) 1360 to 1410, the area was dominated by Campos (grassland) vegetation and fire was very common. From AD 1410 to 1500, *Araucaria* forest expanded and fire was less frequent. From AD 1500 to 1580, Campos grassland spread and the *Araucaria* forest ceased its development, apparently due to the increase of fire. From AD 1580 to 1935, after a decrease in fire frequency, *Araucaria* forest expanded again. From AD 1935 to the present, the *Araucaria* forest expanded while the Campos area decreased. Fire was very rare in this period. The results indicate a strong interaction of forest expansion, forming a mosaic of Campos and *Araucaria* forest, and the frequency of fire during the past 600 years. A possible collapse of the indigenous population following the post-Columbian colonization in southern Brazil after about AD 1550 may have caused a great reduction of fire frequency. The introduction of cattle (probably after AD 1780) and the resulting decrease of fire frequency might be the reason for forest expansion. Fire is probably the most important factor controlling the dynamics of the forest-grassland mosaics and the formation of sharp borders between these two vegetation types.

**Keywords:** Late Holocene, *Araucaria* forest, Campos-grassland, Fire, Human impact, Pollen analysis

## 1. Introduction

Nowadays, the southern highland region of Brazil is covered by a mosaic of grassland-forest vegetation, which is considered part of the Atlantic Forest Biome (IBGE, 2004). This peculiar vegetational formation is basically shaped by a mosaic of grassland, so-called Campos, and *Araucaria* forest with its distinct sharp boundary. Pillar and Quadros (1997) and Pillar (2003) affirmed that the natural vegetation mosaic of Campos-*Araucaria* forest in southern Brazil, including its boundaries, might be determined by grazing and fire regimes. Thus, palaeoenvironmental studies are important tools for confirming such affirmation. Knowledge of early fire activity is relatively well documented for the southern Brazil highlands where present day vegetation is still a mosaic of Campos and forest (Behling, 1997; Behling et al. 2007). The charcoal record from the last 42,840 yr BP documents that

natural grassland fires were rare during the glacial periods. Frequent fires during the mid Holocene, as well as the expansion of *Araucaria* forests together with lower fire frequencies during the late Holocene are good indicators of anthropogenic fire (Behling et al., 2004). The reduction of fire after 500 yr BP in the tropical Americas is synchronous with the indigenous population collapse following European conquest (Nevle and Bird, 2008). The landscape of grassland-forest mosaic in the southern Brazil uplands has been under human influence, first by pre-Columbian cultures using slash and burn activity. After the 19<sup>th</sup> century, European settlers caused deforestation due to intense colonization.

According to Behling (1993, 1995, 1998, 2002) Campos covered extensive areas on the highlands of southern Brazil during the last glacial until mid Holocene times, when *Araucaria* forest began to expand through migration from gallery forests along rivers and wetlands since ca. 3210 cal yr BP. A pronounced expansion of the *Araucaria* forest is reported for about 1400 cal yr BP in Paraná state (Behling, 1997, 2007) and for about 1000 cal yr BP in Santa Catarina state (Behling, 1995). In Rio Grande do Sul state, the initial expansion occurred about 4320 yr BP, being more pronounced since 1100 cal yr BP (Cambará do Sul record, Behling et al., 2004; Behling and Pillar, 2007). However, the history of the origin and dynamics of the *Araucaria* forest and Campos mosaic ecosystems is still not completely understood. Despite the very humid climate of present times, which favors replacement of grassland by forest, natural patches of grassland still exist within the forest area (Oliveira and Pillar, 2004; Overbeck et al., 2007). The reason for the sharp boundaries observed between the forest and grassland is also unclear. Therefore, past human activities and their possible role in the formation of Campos-*Araucaria* forest mosaics can be explored by applying both pollen and charcoal analyses.

Studies of late Quaternary palaeoenvironments of southern Brazilian highlands using palynological analysis have been published during the last few years (Behling and Pillar, 2007; Behling et al., 2001, 2004). However, studies using modern pollen rain data to help interpret fossil pollen records are lacking for the region. Surface soil samples collected along a transect through Campos vegetation and *Araucaria* forest can provide useful information on the interpretation of fossil pollen records from the same locality. Thus, changes in present and past vegetation are reflected in the pollen spectra. A floristic inventory can help to interpret pollen content in surface soil samples of the local area, which can indicate the presence of taxa in the area, or even their arrival from other areas. Surface sample data combined with core analysis are useful for interpreting modern vegetation in detail (Wright, 1967). Some authors have used modern pollen spectra to assist the interpretation of fossil pollen records e.g. in the Pampa grassland in Argentina (Stutz and Prieto, 2003), in Colombian Amazonas (Berrío et al., 2003) and in neotropical ecosystems of Bolivia (Gosling et al., 2009). Behling et al. (1997) investigated modern pollen rain in the lowlands of southern Brazil to determine the pollen spectra of the local vegetation (Atlantic rain forest). Behling et al. (2001) used modern pollen from



surface samples from São Francisco de Paula region, but they analyzed only 8 surface samples without any floristic inventory. Consequently, the necessity of studies including fossil pollen records and modern pollen combined with floristic inventories for the southern Brazil Campos is highlighted.

The aim of this study is to describe the origin and dynamics of the *Araucaria* forest during the early Holocene until present using palynological methods. This study also intends to investigate the relationship between fire frequency and forest expansion. Another significant aspect is to understand how the sharp borders between Campos and forest arise and which factors control and maintain them. Knowledge about the development and maintenance of these mosaics is essential for conservation management of these species-rich ecosystems of the Atlantic rain forest.

## **2. Environmental setting**

### ***2.1. Study area and climate***

The study area is situated in the northeastern highlands of the southernmost state of Brazil, Rio Grande do Sul (28°56'16'', 50°02'39.9''W) at a distance of approximately 9 km from the escarpment of the Serra Geral mountains range (Fig. 1). In geomorphological terms, it corresponds to the "Planalto Meridional". The studied peat bog is at 1050 m a.s.l., with a diameter of ca. 30 m at the border of a disturbed *Araucaria* forest island, surrounded by Campos. The special position of the bog in relation to these vegetation types offers an excellent opportunity to investigate the origin, dynamics and stability of this *Araucaria* forest, island including human activities.

The climate on the highlands of Rio Grande do Sul is classified by Moreno (1961) as subtropical humid (Cfb, Köppen). It is characterized by rainfall distributed throughout the year and temperatures lower than 22°C in the warmest month and higher than 3°C in the coldest month. The South Atlantic Anticyclone and the Polar Anticyclone with its origin in the Antarctic and its trajectory over the South-American continent, dominate the atmospheric circulation over southern Brazil (Nimer, 1989). Climate records from São Francisco de Paula, approximately 76 km south of the research area, show a rainfall of ca. 2500 mm/year with a January mean temperature of 18.3°C and July mean temperature of 9.9°C; frost is common and fog occurs on average 92 days/year (Moreno, 1961).

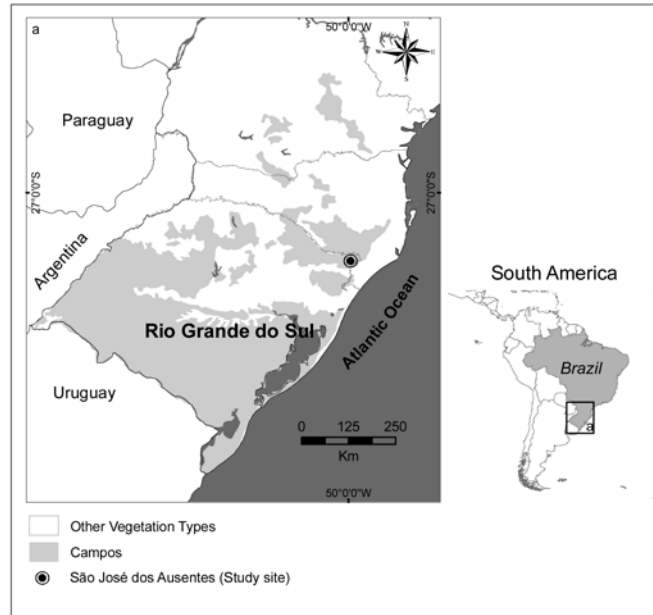


Figure 1. Map showing the Campos on the southern Brazil and the locality of the study area on the highlands of Rio Grande do Sul state.

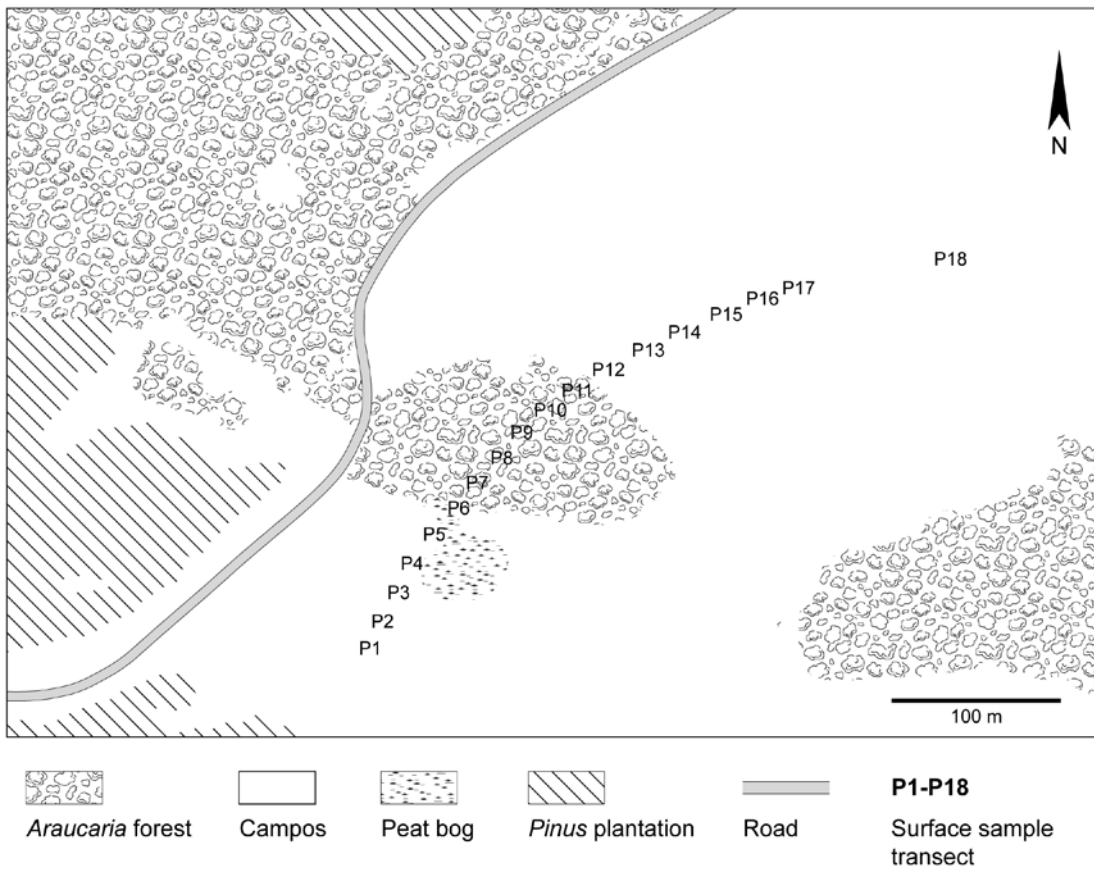


Figure 2. View of the studied area with the location of modern pollen surface sample sites P1 to P18 along the transect and the analyzed peat bog.

## 2.2. Modern vegetation

The species-rich Campos is the predominant vegetation type surrounded by islands of *Araucaria* forest. These forest patches are composed of species associated to *Araucaria angustifolia*, the dominant species: *Ocotea pulchella*, *O. puberula*, *Nectandra lanceolata*, *N. grandiflora* and *N. megapotamica* and diverse Myrtaceae like *Myrcia bombycina*, *Calypttranthes concinna*, *Myrceugenia euosma*, *Gomidesia sellowiana*, *Psidium cattleianum*, among others. Other dominant species are: Aquifoliaceae such as *Ilex paraguariensis* and *Ilex* spp., Sapindaceae such as *Matayba elaeagnoides* and *Cupania vernalis* and other species such as *Drimys brasiliensis*, *Podocarpus lambertii* and *Mimosa scabrella* (Reitz et al., 1988). The *Araucaria* forest vegetation is comparable to the Podocarpo *lambertii*-*Araucarietum angustifoliae* vegetation community described by Eskuche (2007). Boldrini (1997) identified *Andropogon lateralis* (Poaceae) as the dominant grassland species for the Campos in this region. However, *Schizachyrium tenerum*, *Paspalum plicatulum* and *Axonopus siccus* (all Poaceae) are also frequently found. Other grass species growing in this area are *Axonopus compressus*, *Bromus auleticus* and *B. brachyanthera*, forming a mosaic of C<sub>3</sub> and C<sub>4</sub> grasses. The Campos grasslands are also rich in Asteraceae, Cyperaceae and Leguminosae. Human induced fire is a common disturbance, and is responsible for changes in species composition.

## 3. Material and Methods

### 3.1. Sediment core and pollen analysis

The investigated core was sampled with a 50 cm long Russian corer and had a length of 120 cm. Each core section was wrapped in plastic film and stored under +4°C in dark conditions until analysis. Three subsamples of 2-3 g were used for radiocarbon dating by Accelerator Mass Spectrometry (AMS) at the laboratory of the University Erlangen-Nürnberg, Germany. A total of 75 volumetric samples of 0.25-1 cm<sup>3</sup> were used for pollen analysis. Samples were taken at 1 cm intervals: between 0-32 cm depth, and every 2 cm between 33-120 cm depth. They were prepared with standard pollen analytical methods applying hydrofluoric acid (HF) treatment and acetolysis (Faegri and Inversen, 1989). One tablet of *Lycopodium clavatum* (Stockmarr, 1971) was added to each sample in order to determine the pollen concentration (grains cm<sup>-3</sup>). Despite the unequal sedimentation rate, we used the radiocarbon ages to calculate the pollen accumulation rate (grains cm<sup>-2</sup> year<sup>-1</sup>). Subsequently, the samples were mounted in glycerin gelatin. A minimum of 300 pollen grains of terrestrial flowering plants were counted. Spores of Pteridophyta and mosses were excluded from the total pollen sum. Pollen and spore identification was based on comparison with reference slides available at the Department of Palynology and Climate Dynamics of the University of Göttingen and morphological descriptions by Behling (1993). The Melastomataceae group did not include Combretaceae pollen because of the absence of this family in the local vegetation, supported by the

floristic inventory data. The acetolysed *Lycopodium clavatum* marker were distinguished from the naturally occurring *L. clavatum* spores on the basis of the dark coloration and of its wrinkled aspect. Results of pollen and spore analysis are shown as pollen diagrams in percentages of the total pollen sum, which were created using the software TILIA and TILIAGRAPH (Grimm, 1991). Taxa were grouped into Campos, *Araucaria* forest, Atlantic rain forest, Others, Pteridophyta and Mosses. Local fire events were reconstructed based on microscopic ( $>5\mu\text{m}$ ) charred particles that were observed in pollen-slide preparation. Charcoal concentration (particles  $\text{cm}^{-3}$ ) and accumulation rate (particles  $\text{cm}^{-2} \text{year}^{-1}$ ) were calculated based on the known number of spores contained in a tablet of *L. clavatum* marker added previously in each sample. Five pollen zones were visually identified at depths where significant changes on pollen assemblages occurred: i.e. changes in presence or frequencies of the most important taxa and/or changes in the composition of the pollen assemblages, thus reflecting changes in composition of the different vegetation types.

### **3.2. Modern pollen rain**

In order to interpret the palaeo-data from the study area, the data obtained from soil surface samples, where the pollen rain reflected differences in present vegetation was used and analyzed according to the two different vegetation formations: Campos and *Araucaria* forest. Results were later compared with a floristic inventory carried out in the same area.

To estimate the modern pollen rain, a transect covering an area over 340  $\text{m}^2$  across Campos and *Araucaria* forest was established. 18 samples of 1-2 cm of surface soil were taken at 20 m intervals: 12 samples from Campos, five from *Araucaria* forest and one from a shallow lake (Fig. 2). The chemical treatment of the samples followed the same standard method used for sediment core samples (Faegri and Inversen, 1989). A volume of 2  $\text{cm}^3$  was used from each sample. Pollen, spores and charcoal particles were calculated as percentages of the pollen sum, including all terrestrial flowering plant taxa. The floristic inventory was carried out in January 2008. Plants were collected and identified to species level, when possible.

## **4. Results**

### **4.1. Stratigraphy of the core**

The sedimentological sequence observed in the São José dos Ausentes core shows eight distinct intervals (Table 1). The lower part (120-118 cm depth) consists of compact grey clay without organic matter. From 118 to 114 cm depth, the sediment is composed of clay with organic matter. The overlaying section (114-71 cm) consists of dark gray clay with organic material. Within this section, yellow sandy clay occurs between 96.5 and 95.5 cm and agglomerate sand between 82 to 81 cm. Between 71 and 46 cm the sediment is sandy and contains little clay. The following interval from 46 to

27 cm consists of almost decomposed organic matter with very fine, scarce sand. From 27 to 19.5 cm, the sediment consists of dark brown decomposed peat with only a few plant remains. Between 19.5 and 11 cm the sediment is composed of a compact decomposed peat layer with little plant fragments. The uppermost core section (11-0 cm) consists of decomposed organic matter, partly with plant fragments. The top (2-0 cm) is covered by *Sphagnum*.

The fossil pollen diagram was stratigraphically described only until 98 cm depth, which corresponds to the lowest counted sample. Samples below 98 cm core depth contained very badly preserved pollen grains or were sterile.

Table 1. Stratigraphic description of the São José dos Ausentes core.

Depth (cm)	Description
0 – 2	<i>Sphagnum</i> sp.
2 – 11	Dark brown, weakly decomposed peat with plant remains, less compact
11 – 19.5	Brown decomposed peat with few plant fragments, compact
19.5 – 27	Dark brown, decomposed peat with very few plant fragments
27 – 46	Dark brown-black almost decomposed peat, compact
46 – 71	Fine sand with very few clay
71 – 114	Dark gray clay with organic material, compact with fine sand, few white sandy small lenses
114 – 118	Dark grey-black, organic material with clay
118 – 120	Grey clay, compact

#### 4.2. Radiocarbon dates

Three subsamples of 2-3 g were used for radiocarbon dating by Accelerator Mass Spectrometry (AMS) at the laboratory of the University Erlangen-Nürnberg, Germany (Table 2). Radiocarbon dates were calibrated using the computer program CalPal ([www.calpal.de](http://www.calpal.de)). Radiocarbon dates were also calibrated with CALIB (<http://calib.qub.ac.uk/calib>), applying the data set of SHCal04 (McCormac et al., 2004), in order to calculate calendar ages. The core, with a length of 120 cm, has an extrapolated age of 590 cal yr BP at 98 cm depth. The sample at 14 cm depth, which is dated at -1424±37 <sup>14</sup>C yr BP, contains post-atomic-bomb carbon, corresponding to the modern age of approximately AD 1950.

Table 2. Radiocarbon dates for the São José dos Ausentes core.

Laboratory code	Depth (cm)	Sample type	<sup>14</sup> C yr BP	Calibrated age yr BP	Calibrated Calendar age Anno Domini (2 sigma at 95.4% prob.)
Erl-11259	14	peat	-1424±37	0	
Erl-11260	26-30	wood	277±36	364±58	1509-1700
Erl-11261	71	wood	451±37	507±18	1425-1620

### **4.3. Modern pollen rain transect**

The modern pollen diagram shows 20 pollen taxa and 8 spore types (Fig. 3) at the 18 sampled sites, which are arranged according to the vegetation types from southwest to northeast. A list of 107 different palynomorphs for these samples is given in Table 3. Comparing the results of the pollen rain data, the two vegetation types, Campos and *Araucaria* forest, have distinct pollen spectra, which can also be recognized by the floristic inventories of the study area. Pollen grains from Atlantic rain forest taxa that are found in the modern pollen rain and do not appear in the floristic inventory are probably wind-transported from nearby regions of Atlantic rain forest.

#### **4.3.1. Pollen representation of Campos vegetation**

Campos taxa predominate with frequencies ranging from 54% to 80% at sites 1 to 6 and ranging from 68% to 85% at sites 12 to 18. The pollen spectra of all 13 Campos sites are dominated by Poaceae (29-75%), Asteraceae subf. Asteroideae (3-22%) and *Baccharis* type (2-10%). Lower proportions of Cyperaceae pollen (0-9%) are found. Pollen of *Solanum* type appears scarcely with up to 1% in sample 6. *Araucaria* forest taxa, such as *Myrsine*, Myrtaceae, *Schinus*, Melastomataceae, *Mimosa scabrella* type, *Ilex*, *Weinmannia* type, *Araucaria angustifolia*, *Podocarpus* and *Clethra* type, are less frequent in Campos sites, representing pollen frequencies of less than 12% in each sample. Atlantic rain forest taxa are poorly represented with a highest value of 2% in samples 4 and 15. Pollen grains of the exotic species *Pinus*, which is originated from plantations near the study area, occur scattered along the transect. Spores of Pteridophyta, mainly *Blechnum imperiale* type (1-5%) and *Cyathea* type (1-6%) are relatively abundant in Campos sites. Spores of the tree fern *Dicksonia sellowiana* do not exceed 1% of the pollen rain in any samples. Moss spores represented by *Phaeoceros laevis* (0-1%) and *Sphagnum* (0-2%) occur sporadically in Campos sites. Carbonized particles are present in all surface samples, mostly in the samples 12 to 18, and occur in high frequencies ranging from 27,000 to 513,000 particles.

Table 3. List of identified pollen and spore taxa in the surface soil and litter samples from the São José dos Ausentes area. All taxa shown in the pollen diagram of Fig. 3 are in bold.

CAMPOS	<b>Solanum type</b>	<i>Symplocos lanceolata</i> type
Amarathaceae/Chenopodiaceae	<i>Vernonia</i> type	<i>Symplocos tenuifolia</i> type
<i>Ambrosia</i> type	<i>Zornia</i> type	<i>Tapirira</i> type
Apiaceae	ARAUCARIA FOREST	<i>Tetrorchidium rubrivenium</i>
<b>Asteraceae subf. Asteroideae</b>	<b><i>Araucaria angustifolia</i></b>	<i>Trema</i> type
Little Asteraceae	<i>Banara/Xylosma</i> type	OTHERS
<b><i>Baccharis</i> type</b>	<b><i>Clethra</i> type</b>	<i>Alnus</i>
<i>Borreria laxa</i>	<i>Cordia trichomata</i> type	<i>Caperonia</i> type
<i>Borreria</i> type	<i>Daphnopsis</i>	<i>Nothofagus dombeyi</i> type
Caryophyllaceae type	<i>Dodonaea</i>	<b><i>Pinus</i></b>
<i>Celosia</i> type	<i>Drimys brasiliensis</i>	<i>Typha</i>
<i>Chaptalia</i>	<b><i>Ilex</i></b>	UNKNOWN
Chenopodiaceae type I	<i>Lamanonia speciosa</i> type	Type 1 – Type 6
Cichorioidea	<i>Luehea</i> type	PTERIDOPHYTA
<b>Cyperaceae</b>	<b>Melastomataceae</b>	<b><i>Blechnum imperiale</i> type</b>
<b><i>Eryngium</i> type</b>	<b><i>Mimosa scabrella</i> type</b>	<i>Isoetes</i>
Fabaceae	<b><i>Myrsine</i></b>	<b><i>Lycopodium clavatum</i> type</b>
Fabaceae type II	<b>Myrtaceae</b>	<i>Lycopodium</i> sp.
<i>Gomphrenal Pfaffia</i> type	<b><i>Podocarpus</i></b>	Monolete echinate
<i>Hedyosmum brasiliense</i>	<i>Roupala</i> type	Monolete psilate
<i>Hydrocotyle</i> type	<b><i>Schinus</i> type</b>	<b>Monolete psilate &lt; 50 µm</b>
<i>Hypericum</i> type	<i>Sebastiania brasiliensis</i>	<b>Monolete verrucate &gt;50 µm</b>
<b>Iridaceae</b>	<i>Sebastiania commersoniana</i>	Monolete verrucate < 50 µm
<i>Jungial Holocheilus</i> type	<i>Styrax</i>	Monolete verrucate type I
Lamiaceae	<b><i>Weinmannia</i> type</b>	Pteridophyta type 7
Liguliflorae	<i>Zanthoxylum</i> type I	<i>Selaginella excurrens</i> type
<i>Ouratea</i> type	ATLANTIC RAIN FOREST	Trilete echinate
<i>Oxalis</i> type I	<i>Alchornea</i>	Trilete psilate
<i>Pamphalea</i>	<b>Arecaceae</b>	Trilete psilate type I
<i>Plantago australis</i> type	<i>Butia</i> type	TREE FERNS
<b>Poaceae</b>	<i>Celtis</i>	<i>Cyathea schanschin</i> type
<i>Polygala</i>	<i>Matayba</i>	<b><i>Cyathea</i> psilate type</b>
<i>Psychotria</i> type	Meliaceae	<b><i>Dicksonia sellowiana</i></b>
<i>Ranunculus bonariensis</i> type	<b>Moraceae/Urticaceae</b>	MOSSES
Rubiaceae	<i>Phrygilanthus acutifolius</i>	<b><i>Phaeoceros laevis</i></b>
<i>Salvia</i> type	<i>Prockia crucis</i> type	<b><i>Sphagnum</i></b>
<i>Senecio</i> type	<i>Salix humboldtiana</i> type	



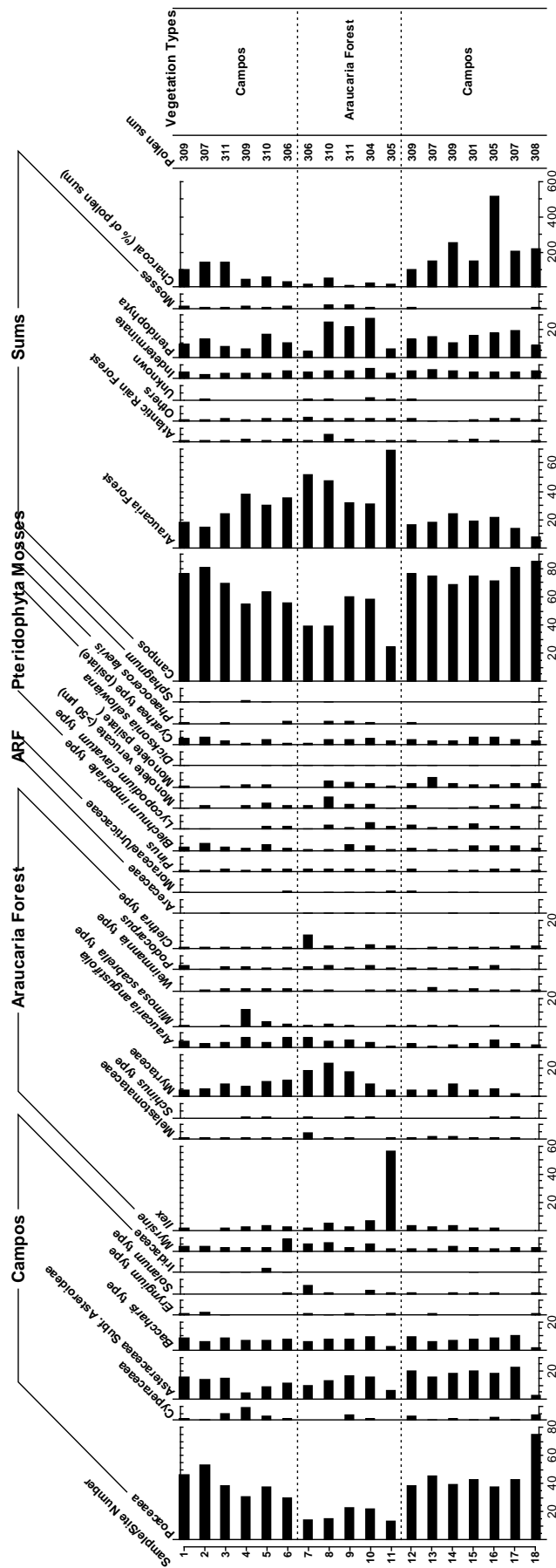


Figure 3. Diagram showing the percentage of pollen spectra from frequent and most important taxa grouped in Campos, Araucaria forest, Atlantic rain forest (ARF), Pteridophyta, Mosses and sums of the taxa.

### 4.3.2. Pollen representation of Araucaria forest vegetation

The lower representation of Campos taxa, varying between 24% and 60% at the forest sites 7 to 11, is attributed to the low pollen frequencies, especially of Poaceae (14-23%), Cyperaceae (0-4%) and Asteraceae subf. Asteroideae (6-17%). Pollen of *Solanum* type appears scarcely, but reaches 6% in sample 7. *Araucaria* forest taxa reach high values, between 31% and 70% mainly due to Myrtaceae (5- 23%) and *Myrsine* pollen (2- 6%). Pollen of *Clethra* type ranges from 0% to 10%. *Ilex* pollen appears in forest sites, but shows an extremely high value in the pollen rain relative to its abundance in the vegetation in sample 11 (56%). *Araucaria angustifolia* (1-7%) and *Podocarpus* pollen (0-3%) is widely dispersed throughout the transect. Pollen of *Mimosa scabrella* type appears in low proportions in forest sites. Pollen of Atlantic rain forest taxa is characterized by low representation at the sites 7 to 11, except for sample 8 with 5%. Pteridophyta spores are well represented (4-27%) in forest sites, mostly by *Lycopodium clavatum* type (0-5%), Monolete verrucate (>50µm) (0-7%) and Monolete psilate (<50µm) (0-5%). Spores of the moss *Phaeoceros laevis* (0-2%) are irregularly dispersed at the same sites. Charcoal is not abundant in the forest surface samples (11,000-49,000 particles).

### 4.4. Pollen-vegetation relationship

Floristic data from the present vegetation surrounding the peat bog was compared with the pollen rain data in order to establish modern pollen-vegetation relationships. The floristic inventory is summarized on Table 4 with species belonging to Campos and *Araucaria* forest vegetation. Each vegetation community (forest-grassland) contained taxa identified as component of the flora that are not represented in the modern pollen rain, such as species of the family Campanulaceae, Ericaceae, Hypoxidaceae, Juncaceae, Lithraceae, Orchidaceae and Verbenaceae present in the Campos flora and of the family Berberidaceae, Erythroxylaceae, Lauraceae as well as Rhamnaceae in the *Araucaria* forest. A total of 45 taxa are common for both the floristic inventory and the pollen rain. Since pollen grains from Poaceae and Cyperaceae cannot be morphologically distinguished so far, the real floristic diversity existing in the Campos cannot be shown based on modern pollen rain. It is also not possible to differentiate completely between the diverse pollen grains related to the Asteraceae family. The diversity of this family in south Brazil is very high (Matzenbacher, 2003), but the morphological diversity of its pollen grains is low (Cancelli, 2008). Therefore, some species are grouped into pollen types, which do not reflect the diversity of this family in comparison to the floristic composition. Nevertheless, some pollen types can be compared to some genera of the floristic inventory like *Baccharis*, *Chaptalia* and *Vernonia*. Possibly, the genus *Chevreulia* corresponds to the pollen type identified as "Little Asteraceae", due to its pollen morphological characteristic. The genus *Trichocline* is included in the group of *Jungia-Holocheilus* type based on pollen morphological similarities between these genera. For all other genera of Asteraceae present in Campos, the corresponding pollen grains

are possibly counted as Asteraceae subf. Asteroideae. As expected, most of the species and families growing on Campos are represented by pollen grains in the surface samples. Pollen grains of *Pfaffia*, *Eryngium*, *Hydrocotyle*, *Hypericum*, *Oxalis*, *Plantago australis*, *Polygala* and *Borreria* can be found, corresponding to the present Campos vegetation. Pollen grains belonging to the families of Cyperaceae, Fabaceae, Lamiaceae, Melastomataceae and Rubiaceae are also found.

Interesting is the number of different pollen grains corresponding to different genera listed in the floristic inventory belonging to *Araucaria* forest. The genera *Schinus*, *Lithraea*, *Ilex*, *Clethra*, *Myrsine*, *Podocarpus*, *Zanthoxylum*, *Xylosma*, *Solanum* and even species such as *Araucaria angustifolia* and *Mimosa scabrella* can be found within the pollen assemblages. The two species of Cunoniaceae, *Lamanonia ternata* and *Weinmannia paulliniifolia*, are probably counted as *Weinmannia* type, due to difficulties to distinguish these pollen grains. It is not possible to separate pollen grains of Myrtaceae and Melastomataceae into the different genera from southern Brazil. Thus, the diversity of these two families is not represented by their pollen grains. Results of the floristic inventory and surface soil samples collected along a transect across Campos-*Araucaria* forest show that the modern pollen rain is highly associated to species present in the two vegetation community types.

Table 4. List of *Araucaria* forest and Campos families and species resulting from floristic inventory in different randomly located sites at the *Araucaria* forest island and surrounding Campos.

Species from <i>Araucaria</i> forest	Species from Campos
Anacardiaceae	Amaranthaceae
<i>Lithraea brasiliensis</i> Marchand	<i>Pfaffia tuberosa</i> (Spreng.) Hicken
<i>Schinus polygamus</i> (Cav.) Cabrera	Apiaceae
Aquifoliaceae	<i>Eryngium horridum</i> Malme
<i>Ilex microdonta</i> Reissek	<i>Hydrocotyle exigua</i> (Urb.) Malme
<i>Ilex taubertiana</i> Loes.	Asteraceae
Araucariaceae	<i>Achyrocline satureioides</i> (Lam.) DC.
<i>Araucaria angustifolia</i> (Bertol.) Kuntze	<i>Baccharis erigeroides</i> DC.
Asteraceae	<i>Baccharis pentodonta</i> Malme
<i>Baccharis uncinella</i> DC.	<i>Baccharis trimera</i> (Less.) DC.
<i>Piptocarpha tomentosa</i> Baker	<i>Chaptalia runcinata</i> Kunth
<i>Vernonia discolor</i> (Spreng.) Less.	<i>Chaptalia integerrima</i> (Vell.) Burkart
Berberidaceae	<i>Chevreulia</i> sp.
<i>Berberis laurina</i> Billb.	<i>Eupatorium ascendens</i> Sch.Bip.
Clethraceae	<i>Eupatorium betonicaeforme</i> (DC.) Baker
<i>Clethra scabra</i> Pers.	<i>Eupatorium tanacetifolium</i> Gillies ex H.&A.
Cunoniaceae	<i>Gamochoaeta americana</i> (Mill.) Weddell
<i>Lamanonia ternata</i> Vell.	<i>Hypochaeris catharinensis</i> Cabrera
<i>Weinmannia paulliniifolia</i> Pohl	<i>Leptostelma</i> sp.
Erythroxylaceae	<i>Stevia lundiana</i> DC.
<i>Erythroxylum cuneifolium</i> (Mart.) O.E. Schulz	<i>Trichocline catharinensis</i> Cabrera

Euphorbiaceae	<i>Vernonia flexuosa</i> Sims
<i>Sapium glandulosum</i> (L.) Morong	Campanulaceae
Fabaceae	<i>Lobelia camporum</i> Pohl
<i>Mimosa scabrella</i> Benth.	<i>Wahlenbergia linarioides</i> (Lam.) DC.
Lauraceae	Cyperaceae
<i>Ocotea pulchella</i> (Nees) Mez	<i>Bulbostylis sphaerocephala</i> (Boeck.) C.B. Clarke
Melastomataceae	<i>Cyperus aggregatus</i> (Willd.) Endl.
<i>Miconia cinerascens</i> Miq.	<i>Cyperus hermaphroditus</i> (Jacq.) Standl.
<i>Miconia hiemalis</i> A. St-Hil. & Naudin ex Naudin	<i>Kyllinga odorata</i> Vahl
Myrsinaceae	<i>Rhynchospora barrosiana</i> Guagl.
<i>Myrsine coriacea</i> (Sw.) R.Br.	<i>Rhynchospora flexuosa</i> C.B. Clarke
<i>Myrsine lorentziana</i> (Mez) Arechav.	<i>Rhynchospora setigera</i> Griseb.
Myrtaceae	<i>Scleria sellowiana</i> Kunth
<i>Acca sellowiana</i> (O. Berg) Burret	Ericaceae
<i>Campomanesia xanthocarpa</i> O. Berg	<i>Gaylussacia brasiliensis</i> (Spreng.) Meisn.
<i>Myrceugenia euosma</i> (O. Berg) D. Legrand	Fabaceae
<i>Myrceugenia mesomischa</i> (Burret) D. Legrand & Kausel	<i>Adesmia tristis</i> Vogel
<i>Myrceugenia miersiana</i> (Gardner) D. Legrand & Kausel	<i>Lupinus rubriflorus</i> Planchuelo
<i>Myrcia hartwegiana</i> (O. Berg) Kiaersk.	Hypericaceae
<i>Myrcia retorta</i> Cambess.	<i>Hypericum connatum</i> Lam.
<i>Siphoneugena reitzii</i> D. Legrand	Hypoxidaceae
Podocarpaceae	<i>Hypoxis decumbens</i> L.
<i>Podocarpus lambertii</i> Klotzsch ex Endl.	Juncaceae
Rhamnaceae	<i>Juncus conglomeratus</i> L.
<i>Rhamnus sphaerosperma</i> Sw.	Lamiaceae
Rutaceae	<i>Rhabdocaulon gracilis</i> (Benth.) Epling
<i>Zanthoxylum rhoifolium</i> Lam.	Lythraceae
Salicaceae	<i>Cuphea glutinosa</i> Cham. & Schl.
<i>Casearia decandra</i> Jacq.	Melastomataceae
<i>Xylosma pseudosalzmanii</i> Sleumer	<i>Tibouchina gracilis</i> Cogn.
Solanaceae	Orchidaceae
<i>Solanum pabstii</i> L.B. Sm. & Downs	<i>Habenaria parviflora</i> Lindl.
<i>Solanum</i> sp.1	Oxalidaceae
Symplocaceae	<i>Oxalis lasiopetala</i> Zucc.
<i>Symplocos uniflora</i> (Pohl) Benth.	<i>Oxalis</i> sp.1
Winteraceae	Poaceae
<i>Drimys angustifolia</i> Miers	<i>Agrostis montevidensis</i> Spreng. ex Nees
<i>Drimys brasiliensis</i> Miers	<i>Andropogon lateralis</i> Nees
	<i>Axonopus argentinus</i> Parodi
	<i>Briza uniolae</i> (Ness) Ness ex Steud
	<i>Briza poaemorpha</i> (J. Presl) Henrard
	<i>Dichantelium sabulorum</i> (Lam.) Gould & C.A. Clark
	<i>Eragrostis airoides</i> Nees
	<i>Holcus lanatus</i> L.
	<i>Paspalum pumilum</i> Nees
	<i>Paspalum plicatulum</i> Michx.
	<i>Paspalum polyphyllum</i> Ness ex Trin
	<i>Paspalum maculosum</i> Trin.
	<i>Schizachyrium tenerum</i> Nees
	<i>Sporobolus camporum</i> Swallen

## Plantaginaceae

*Plantago australis* Lam.

## Polygalaceae

*Polygala pulchella* A. St.-Hill. & Moq

## Rubiaceae

*Borreria capitata* (R. & P.) DC.*Galianthe verbenoides* (Cham. & Schltld.) Griseb.*Galium humile* Cham. & Schltld.

## Verbenaceae

*Glandularia marrubioides* (Cham.) Tronc.**4.5. Description of the pollen diagram**

Samples from 58-98 cm depth in the section yielded low pollen quantities and had a bad pollen preservation. Samples below 98 cm depth were often sterile. As a result, a total of 43 samples could be counted. The pollen diagrams (Fig. 4 and 5) illustrate percentages of the dominant and most important taxa as well as charcoal data. A detailed pollen diagram (Fig. 4) shows 29 pollen and 8 spore types of more than 217 different pollen and spores types found in the core samples. A summary pollen diagram (Fig. 5) represents pollen taxa grouped into 3 vegetation types as well as other groups. "Others" corresponds to pollen grains of taxa that could not be included in any of the other vegetation types like *Pinus*. Pollen concentrations (34,150-553,000 grains cm<sup>-3</sup>) and pollen influx (1100-120,000 grains cm<sup>-2</sup>yr<sup>-1</sup>) are high and occur with some fluctuations in the studied core.

Zone SdA-I (98-87.5 cm, 555 - 493 <sup>14</sup>C yr BP, 2 samples) – is characterized by high pollen frequencies (78-85%) of Campos taxa, mostly Poaceae (17-47%), Cyperaceae (6-15%) and Asteraceae subf. Asteroideae (13-34%). Iridaceae pollen is frequent only in the lowermost sample (7%). Taxa of the *Araucaria* forest are less frequent (5-11%), represented mostly by pollen of *Myrsine* (0-5%), *Ilex* (0-1%), Melastomataceae (2-3%) and *Weinmannia* type (0-1%). At 98 cm depth, *Myrsine* and *Clethra* type appeared with only one pollen grain each and *Ilex* with 2 pollen grains. The Atlantic rain forest group is recorded in low percentages (3%), mainly represented by Arecaceae (1%) and Moraceae/Urticaceae (0-2%) pollen. Spores of Pteridophyta reach 21% in the lowermost sample, increasing to 73% in the following sample. This group is primarily represented by spores of *Blechnum imperiale* type (8-33%), Monolete psilate <50µm (6-22%), *Lycopodium clavatum* type (2-4%) and Trilete psilate >50µm (3-6%). Percentages of moss taxa are low (1-5%), being represented by spores of *Phaeoceros laevis* (1-2%) and *Sphagnum* (0-2%). The concentration (3500x10<sup>8</sup> particles cm<sup>-3</sup>) and accumulation rates (1100x10<sup>8</sup> particles cm<sup>-2</sup>yr<sup>-1</sup>) of carbonized particles were very high in the lowermost sample and lower in the upper sample (1050x10<sup>8</sup> particles cm<sup>-3</sup> and 3300x10<sup>7</sup> particles cm<sup>-2</sup>yr<sup>-1</sup>, respectively).

Zone SdA-II (87.5-53.5 cm, 493 - 385 <sup>14</sup>C yr BP, 3 samples) – pollen percentage values of Campos taxa decrease in this zone (42-76%). Among the herbaceous taxa, Poaceae pollen is

abundant (12-15%) and well represented in all samples. Pollen of Cyperaceae (1-5%), *Baccharis* type (1-2%) and Asteraceae subf. Asteroideae (15-30%) are also well represented. Pollen grains belonging to *Araucaria* forest taxa increase continuously from 24% to 38%, but decrease to 31% at the top of this zone. These higher values are mainly due to *Myrsine* (6-19%), *Ilex* (6-14%), Melastomataceae (4-6%), Myrtaceae (2-4%) and *Clethra* type (0-2%). Atlantic rain forest taxa increase from 10% to 17%, mostly represented by Areaceae (3-9%), *Butia* type (0-4%), *Symplocos laxiflora* type (1-3%), *S. tenuifolia* type (0-3%) and Moraceae/Urticaceae. Spores of Pteridophyta remain at very high percentages (68-93%), represented principally by *Blechnum imperiale* type (17-41%), Monolete psilate <50µm (17-42%) and Pteridophyta 7 spores (1-16%). Moss taxa, represented primarily by *Sphagnum* spores, increase up to 25% in the first part of the zone and decrease afterwards to 6% at the top. Carbonized particles continued to be frequent during this zone with concentrations ranging between  $7400 \times 10^7$  and  $2500 \times 10^8$  particles  $\text{cm}^{-3}$  and accumulation rates ranging between  $2300 \times 10^7$  and  $7900 \times 10^7$  particles  $\text{cm}^{-2}\text{yr}^{-1}$ .

Zone SdA-III (53.5-26.5 cm, 385 - 278  $^{14}\text{C}$  yr BP, 12 samples) – is characterized by an increase of Campos taxa from 72% to 82%. The most abundant pollen taxa are Cyperaceae (5-50%), Poaceae (12-30%) and Asteraceae subf. Asteroideae (3-30%). Moreover, pollen grains of *Baccharis* type (2-21%), *Eryngium* type (0-7%) and in minor proportions *Scutellaria* type, *Verbena* type and *Borreria* are also well represented. *Araucaria* forest taxa continued to decrease from 22% to 9%, reflected by low pollen percentages of *Myrsine* (1-6%), *Ilex* (0-4%), *Dodonaea* (first time), *Schinus* type, Myrtaceae, *Sebastiania commersoniana* type and *Weinmannia* type. Pollen of Melastomataceae group (0-10%) and *Mimosa scabrella* type (0-7%) show an increase of values only at the top of this zone. *Araucaria angustifolia* and *Podocarpus* pollen grains appear for the first time at 48 cm depth. Atlantic rain forest taxa decrease significantly from 6% to 2%, which is shown by pollen of Areaceae (0-2%), *Butia* type (0-2%), *Symplocos laxiflora* type and *S. tenuifolia* type. Abundances of Moraceae/Urticaceae pollen continue to be stable. Pteridophyta, mostly spores of *Blechnum imperiale* type (1-93%), *Lycopodium clavatum* type (1-14%), Trilete psilate (>50µm) (1-25%) and Monolete verrucate (>50µm) (0-28%), remain well represented and varied between 19% and 150%. Spores of Monolete psilate (<50 µm) (15-0%), as well as Pteridophyta 7 (9-0%), decrease to the top of the zone. Moss spores reach high values (7-61%) at the top of the zone, attributed to *Phaeoceros laevis* (3-40%) and *Sphagnum* spores (1-45%), both increasing significantly. The concentration ( $4300 \times 10^8$ - $1300 \times 10^8$  particles  $\text{cm}^{-3}$ ) and influx ( $1350 \times 10^8$ - $4,100,000$  particles  $\text{cm}^{-2}\text{yr}^{-1}$ ) of carbonized particles are very high during this period, but decrease gradually towards the top.

Zone SdA- IV (26.5-14.5 cm, 278 - 11  $^{14}\text{C}$  yr BP, 12 samples) – Campos taxa are represented in this zone by lower frequencies, between 24% and 55%, mainly because of lower values of Poaceae (5-12%), Cyperaceae (5-38%), Asteraceae subf. Asteroideae (3-10%) and *Baccharis* type (2-13%).

This zone is characterized by the high abundance of *Araucaria* forest taxa, which vary between 32% and 61%. Pollen percentages of *Myrsine* (7-27%), *Ilex* (0-3%), *Dodonaea* (4-15%), *Schinus* (1-4%), Myrtaceae (1-11%), *Araucaria angustifolia*, *Mimosa scabrella* type, *Sebastiania commersoniana*, *Weinmannia* type and *Clethra* type rise continuously. Also Atlantic rain forest taxa reach higher frequencies between 4% and 11%. Pollen percentage values of Arecaceae (0-2%), Moraceae/Urticaceae (0-2%) and *Alchornea* (0-2%) remain constant, while *Butia* type (0-3%) pollen grains become more frequent. Single *Pinus* pollen grains are found at 15 cm depth for the first time. Spores of Pteridophyta decrease significantly from 37% to 6%. Percentages of *Lycopodium clavatum* type spores account for 1% to 27%, whilst spores of *Blechnum imperiale* type decrease considerably (16-0%) and Trilete psilate (>50µm), Monolete psilate (<50µm) and Pteridophyta 7 show only minor representation. Moss spores are well represented (15-56%). *Phaeoceros laevis* spores decrease (10-0%), while *Sphagnum* spores increase constantly (13-55%). Values for concentration (1000x10<sup>8</sup>-800,000 particles cm<sup>-3</sup>) and influx (3,300,000-25,100 particles cm<sup>-2</sup>yr<sup>-1</sup>) of carbonized particles drop markedly during this zone.

Zone SdA-V (14.5-0 cm, 11 <sup>14</sup>C yr BP - modern, 14 samples) – the abundance of Campos taxa still decreases from 35% to 4%. The lower values are reflected mainly by Poaceae pollen (1-5%) and Cyperaceae pollen (0-3%), which are significantly reduced. Asteraceae subf. Asteroideae pollen is still relatively well represented (1-11%), while *Baccharis* type (0-21%) and the *Eryngium* type (0-3%) are more frequent than in the previous zone. Frequencies of all Campos taxa decline to the uppermost part of this zone, except for pollen of the *Verbena* type with 2% at 0 cm. *Araucaria* forest taxa continue to increase considerably, reaching frequencies up to 91%. The high values are expressed primarily by pollen of *Myrsine* (29-71%), *Schinus* (1-13%), Myrtaceae (4-15%) and with minor percentages by pollen of *Ilex*, *Sebastiania commersoniana*, *Weinmannia* type and *Podocarpus*. Pollen grains of Melastomataceae, *Dodonaea* and *Mimosa scabrella* type occurred with lower proportions than during the previous zone. Percentages of *Styrax* pollen as well as *Clethra* type pollen were very low and increase exceptionally in the upper part of this zone (0-12% and 0-8% respectively). *Araucaria angustifolia* pollen percentages (0-3%) increase continuously towards the top. Atlantic rain forest taxa decrease and vary from 6% to 0%. *Pinus* pollen become more frequent (0-1%), especially in the upper part of this zone. Spores of Pteridophyta decrease markedly from 7% to 0%. Almost all of the spore types are reduced to insignificant proportions, excluding Monolete psilate <50µm (0-1%). Also the proportion of moss spores (17-0%) is lower than in the previous zone due to the decline of *Sphagnum* spores from 17% to 0% and the absence of *Phaeoceros laevis* spores. Charcoal concentration (95,100-1600x10<sup>7</sup> particles cm<sup>-3</sup>) and charcoal influx (23,350-4,000,000 particles cm<sup>-2</sup>yr<sup>-1</sup>) is very low in this zone.





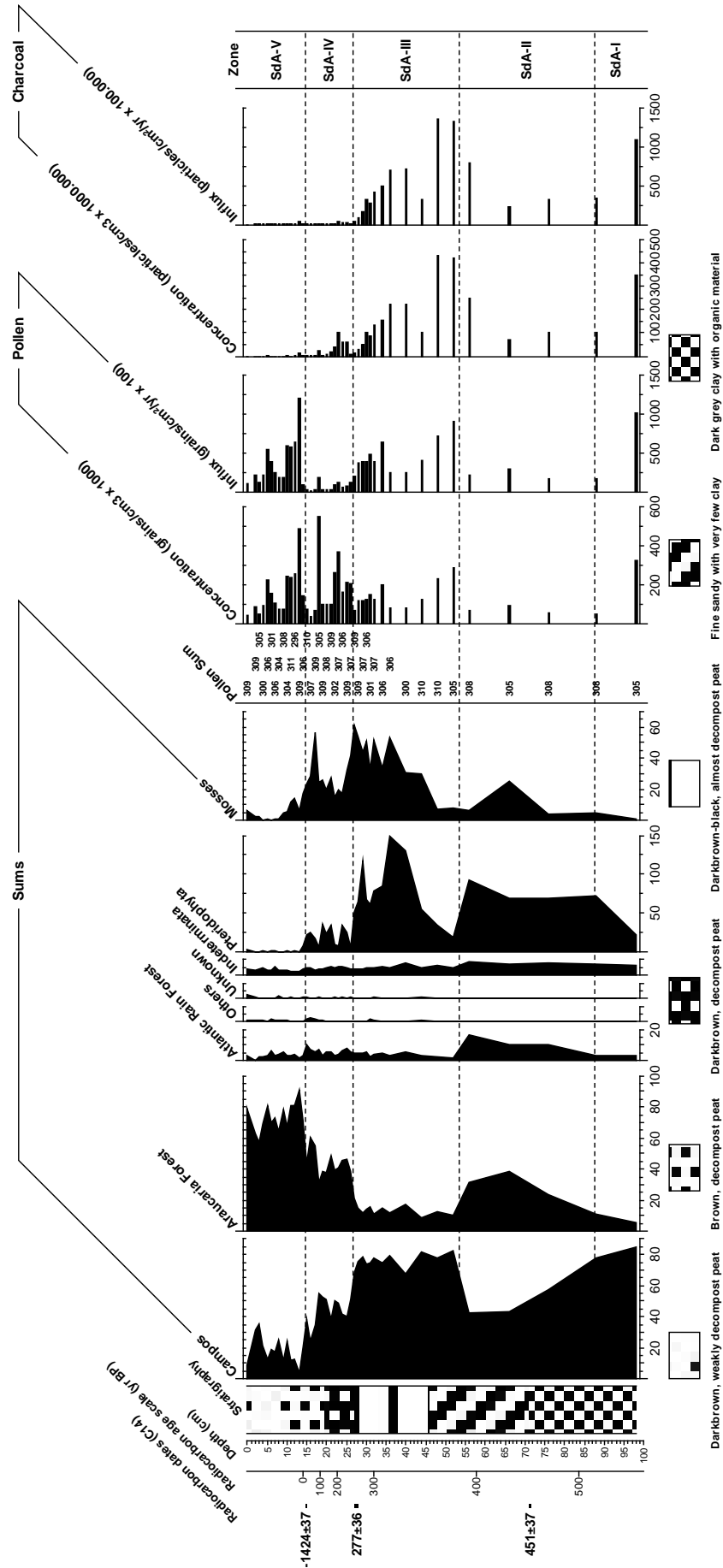


Fig. 5. Summary pollen percentage diagram of the core São José dos Ausentes with the AMS radiocarbon dates, age scale, stratigraphy, sums of vegetation groups, pollen and charcoal concentration as well as accumulation rates and pollen zones.

## 5. Interpretation and Discussion

### 5.1. Relationship between forest expansion and fire frequency

Pollen and charcoal results from the sedimentological record and surface soil samples together with the floristic inventory showed vegetation changes with forest expansion in relation to fire frequency. The fossil pollen record provided information on the *Araucaria* forest island dynamics as well as vegetational changes of Campos-*Araucaria* forest mosaics over the past 600 years.

During ca. 590 to 540 cal yr BP (AD 1360 to 1410; zone SdA-I), the area was dominated by Campos vegetation, mostly Poaceae, but also rich in other grassland species. Since this time, Campos was present in the area as demonstrated by the continuous presence of Campos taxa in the fossil spectra and similar percentage values to those of the modern spectra. The studied modern *Araucaria* forest island was very small or absent during this time period as reflected by *Ilex* and Myrtaceae, which are taxa commonly associated to this vegetation type as well as *Weinmannia*, *Myrsine* and Melastomataceae. Fire was very common as indicated by the high occurrence of charcoal particles in the lower most sample of the zone. It is possible that frequent fires did not allow the expansion and establishment of forests, despite the very humid conditions since about 1100 cal yr BP (e.g. Behling et al., 2004). It is also suggested that frequent fires during the wettest part of the Holocene were anthropogenic rather than natural fires (Behling et al., 2004). Iriarte and Behling (2007) found that the expansion of *Araucaria angustifolia* under wetter climatic conditions during the mid and late Holocene could be correlated to human occupation of the southern Brazilian highlands by the Taquara/Itararé Tradition. Archaeological sites also confirmed that the highlands of southern Brazil, including the studied region of São José dos Ausentes, were inhabited by the Taquara/Itararé Tradition from 2000 yr BP until 200 yr BP (Iriarte and Behling, 2007). In addition, the major expansion of *Araucaria* forest corresponded to this period of occupation (Bitencourt and Krauspenhar, 2006). Nevertheless, our data suggest that fire caused by indigenous people may have inhibited the expansion/development of the local *Araucaria* forest island at this period, even though a humid climate prevailed.

The formation or expansion of the small *Araucaria* forest island occurred during the following period from approx. 540 to 450 cal yr BP (AD 1410 to 1500), in zone SdA-II. The relatively high *Araucaria* forest values combined with high Atlantic rain forest values suggest the expansion of the forest, with taxa present in the modern pollen rain, mainly the pioneer tree *Myrsine* as well as species of *Ilex*, Melastomataceae, Myrtaceae and Arecaceae. The expansion of the Atlantic rain forest from the slopes to the upland is supported by pollen grains transported to the bog from the slopes of the plateau ca. 9 km away. The growth and expansion of the peat bog is supported by the increased occurrence of *Blechnum imperiale*, a fern that typically grows in shallow bogs, and by some

*Sphagnum* species as peat moss. Apparently, the formation and expansion of the small *Araucaria* forest island was strongly related to the decrease of fire frequency.

Between about 450 to 370 cal yr BP (AD 1500 to 1580; zone SdA-III), Campos vegetation increased in extent while the *Araucaria* forest island decreased in area. Within this time interval, the fossil samples shared some taxa that were also found in the surface samples, thus the gradual changes of the vegetation types can be interpreted on the basis of modern plant communities. The high number of carbonized particles of this period implies that fire was the main cause for the vegetational change. It is also interesting to note, that carbonized particles became frequent prior to the expansion of Campos, suggesting that fire was the most important factor leading this change. This assumption is also supported by high abundances of *Baccharis* and *Eryngium*, species common for frequently burned areas in Campos (Boldrini, 1997). *Eryngium horridum* has been characterized as a disturbance specialist profiting from frequent fires by population increase and higher reproductive output (Fidelis et al., 2008). The hornwort *Phaeoceros laevis* may be related to the frequent fires as well, as it occurs in open soil habitats.

From approx. 370 to 15 cal yr BP (AD 1580 to 1935; zone SdA-IV), the *Araucaria* forest island expanded, first Melastomataceae followed by *Myrsine*, which appears in secondary vegetation. *Myrsine* is known to be one of the most important pioneer species growing directly on grassland (Backes and Irgang, 2002). The pioneer tree *Dodonaea* and also species of Myrtaceae occurred with higher abundances. Based on the fossil pollen percentages and modern pollen rain, *Araucaria* forest spread and a progressive reduction of Campos taxa frequencies was recorded after AD 1580. It is worth noting that *Araucaria angustifolia* itself played only a minor role in the development of this forest island. Also during this period, a marked reduction of the fire frequency allowed the expansion of the *Araucaria* forest. The less frequent occurrence of *Blechnum imperiale* might be related to the partial expansion of the forest over shallow areas of the peat bog. The drastic decrease of fire frequency at about 370 cal yr BP (AD 1580) might be related to a possible collapse of the indigenous population by the post-Columbian colonization in southern Brazil. In this respect, Nevle and Bird (2008) showed for the Tropical Americas, that the forest regeneration from 1500 to 1750 AD is associated with the decline of anthropogenic fire due to the collapse of indigenous population after European arrival. The collapse of indigenous populations is also well known from the Andes (e.g. Behling et al., 1998; Niemann and Behling, 2008). The introduction of cattle by Jesuits in this region, probably after 270 cal yr BP (AD 1780) (Pillar and Quadros, 1997), together with the decrease in fire frequency might be a reason for the forest expansion. The introduction of cattle apparently caused no marked changes in the vegetation composition in accordance to the fossil pollen data during this period. Interpretation of the Cambará do Sul core by Behling et al. (2004) concluded that between AD 1520 and 1770 a warm period on the south Brazilian highlands arose based on an increase of *Weinmannia* type pollen

abundances. At the same time, the Little Ice Age occurred in the Northern Hemisphere. However, this phenomenon cannot be observed in our results on the basis of *Weinmannia* pollen frequencies, since they remain relatively constant during the whole 600 years period.

Marked changes in the local vegetation occurred in zone SdA-V, from approx. 15 cal yr BP (AD 1935) until present. The Campos area decreased markedly and the expansion of the *Araucaria* forest island occurred next to the coring site of the peat bog. Pollen percentages of Poaceae with mean values of 3% recorded at this time were very much lower than in any modern pollen rain sample. The low occurrence of *Podocarpus* and *Araucaria* in the fossil pollen record and the high abundance of these taxa on the modern pollen rain, suggests the current expansion/development of the *Araucaria* forest island. According to the core data, *Myrsine* showed a significant increase together with *Schinus* and Myrtaceae, while *Dodonaea* became less frequent. The highest occurrence of *Styrax*, a pioneer tree species, and *Clethra*, which occurs in secondary vegetation (Backes and Irgang, 2002), probably represents degradation of the forest due to logging, cattle grazing and trampling within the forest, during the last years. Also the high presence of Campos pollen grains (particularly Poaceae and Asteraceae) in the pollen rain of forest sites can be explained by the fact that the forest island is very degraded and regularly used by cattle. The evident expansion of this *Araucaria* forest island is clearly related to the marked decrease of fire frequency in the area during the past 70 years. It is known that fire has been frequent in the region since the late Holocene period (Behling et al., 2004), preventing *Araucaria* forest expansion over Campos and controlling vegetation changes mainly at the boundaries between the two vegetation types. Results of pollen and charcoal analysis on the Morro Santana in the Porto Alegre region (Behling et al., 2007) indicated the occurrence of a mosaic of forest-Campos vegetation under the influence of fire during the late Holocene period. A continuous forest expansion, especially the increase of *Myrsine*, was negatively correlated to charcoal concentration since 1930 AD (Behling et al., 2007). Pollen frequencies of *Pinus* in the core samples (up to 1%) and higher frequencies in surface soil samples (up to 2%, represented in all samples except one site) results from an effective dispersal from nonlocal plantations of this exotic species close to the study area. Immense areas have been changed in the last decades into different land use and plantation of exotic tree species like *Pinus* sp. (Overbeck et al., 2007). In order to protect these plantations, farmers avoid the occurrence of fires.

The constantly low presence of *Araucaria angustifolia* can be explained by deforestation for commercial interests, mostly between 1950 and 1970. This tree species has been explored regionally since the 19<sup>th</sup> century due to European settlers with an exploitation peak between 1920 and 1960 (Reitz et al. 1988). Another reason for the poor representation of *Araucaria angustifolia* could be due to physical characteristics of the pollen that reduce its flotation potential and thus, its dispersal abilities (Sousa and Hattemer, 2003).

### **5.2. Campos-*Araucaria* forest boundaries**

Even though the studied *Araucaria* forest island was a secondary forest with grasses and Asteraceae forbs growing in the substrate, which is atypical for a natural *Araucaria* forest, we could show that the forest is reflected in the Campos and the Campos in the forest by pollen assemblages that were distinct and always consistent according to the sampled site and to the vegetation type surrounding the surface soil samples. Furthermore, the results indicate that even small forest islands in a landscape of a grassland-forest mosaic are well reflected in the pollen rain and that possible reduction or expansion of forest areas during the past can also be well reflected by pollen deposition.

Despite the fact that modern climate favors the replacement of Campos by forest (Klein, 1960; Hueck, 1966; Rambo, 1951, 1956), a sharp boundary can be observed between the two vegetation types. The sharp borderline between Campos and *Araucaria* forest as well as local vegetational changes could be also detected and interpreted on the basis of modern vegetation communities, since soil surface samples showed many taxa occurring also in fossil samples. These boundaries could possibly be maintained by cattle, trampling and browsing on buds and plantlets of forest species growing directly in the Campos like *Myrsine*, *Schinus*, *Clethra*, that grow in degraded areas or *Styrax* and even *Araucaria angustifolia*, which are all pioneer species (Backes and Irgang, 2002). All these trees also appeared in the research area in the past. According to Overbeck and Pfdenhauer (2007) the pioneer tree species growing over Campos in southern Brazil usually do not tolerate fire; consequently, frequent fires should impede forest expansion. Despite being prohibited, fire is usually used to manage the area for cattle pastures, which is also the case at the study site. The distribution of carbonized particles in the surface samples indicates that fires occur frequently in the Campos area and are apparently absent in the small *Araucaria* forest area. Native pastures from Campos grasslands still represent the base for cattle farming with fire as a common tool in pasture management (Nabinger et al., 2000). Fossil evidence documents the presence of large grazing mammals in the region until 8000 BP (Kern, 1997 in Pillar, 2003), which may be responsible for the maintenance of grassland communities in the distant past. Later, after their extinction, induced fire could inhibit forest expansion. According to Overbeck et al. (2005, 2007) Campos is resilient to fire, being maintained by disturbance (fire and grazing). Fire intensity in Campos grassland is low (Fidelis, 2008). Due to lack of sufficient flammable biomass, fires in Campos generally cannot enter into the forest (Overbeck et al., 2005), suggesting that fire frequency is a regulator of forest expansion. Our results show that fires played a major role on the conservation of Campos-*Araucaria* forest mosaic in the study area. Moreover, local vegetation dynamics of Campos-forest mosaics has been influenced by anthropogenic fire during the past 600 years.

Hence, our results provide important information about local fire frequency that can also be used for regional interpretation. It is reasonable to indicate fire as a mechanism preventing forest

expansion and controlling the stability of the sharp boundaries between Campos-forest-mosaics. The suggestion of Pillar and Quadros (1997) and Pillar (2003) that the maintenance of these grassland-forest boundaries is determined by fire can be confirmed by this study. Oliveira and Pillar (2004), based on aerial photographs, observed that after exclusion of grazing and fire, a directional process on patches near to forest edges occurred with expansion of *Araucaria* forest over Campos.

Behling and Pillar (2007) showed the necessity of conservation and management strategies for Campos-*Araucaria* forest ecosystems. They also observed that the suppression of fire and grazing will lead to forest expansion over the Campos under the present humid climatic conditions. Additionally, Overbeck et al. (2007) pointed out the urgent need for more conservation units including Campos in southern Brazil. However, without human interference, like management strategies using grazing and/or fire, the maintenance of these biodiverse grasslands is not possible. Consequently, without human interventions these natural grasslands will change towards forest areas after a while depending on the proximity to forest borders. This is clearly demonstrated by this study.

## **6- Conclusion**

This study provides new results on the development and dynamics of the Campos-*Araucaria* forest mosaics on the southern Brazilian highland, as well as the role of fire during the last 600 years. We conclude that Campos was the dominant vegetation type before 600 cal yr BP in the study area. The expansion of *Araucaria* forests due to the very wet climatic conditions has been well documented for the southern Brazilian highlands (e.g. Behling et al., 2004). It is possible that frequent fires, probably caused by humans, have hampered the formation of *Araucaria* forest near the study site. However, the formation and expansion of an *Araucaria* forest island within the Campos area under very humid climatic conditions is apparently related to the decrease of fire frequency after 540 cal yr BP. The marked increase in fire frequency at about 460 cal yr BP stopped the forest expansion and thus promoted the Campos expansion. This leads to the conclusion that fire frequency is a very important factor controlling the dynamics and stability of Campos-*Araucaria* forest mosaics. A continuous decline of fire since 360 cal yr BP supports the forest expansion until today and might be associated to a collapse of the indigenous post-Colombian population in southern Brazil. The sharp boundaries between Campos and *Araucaria* forest could be maintained through the use of fire in combination with cattle.

## **Acknowledgements**

This research project was financially supported by the Deutsche Forschungsgemeinschaft (DFG). The fieldwork was supported partly by the Inter American Institut for Global Change Research (IAI). The IAI is also thanked for financing the radiocarbon dates. The authors thank, in particular, Dr.

Gerald Islebe, for comments and suggestions that helped to improve the manuscript. Special thanks to Sonia L. Fontana for valuable comments on the manuscript. We are also grateful to Anne Birgitte Nielsen and Lisa Schüler for reading the manuscript. We thank Barbara Hermanowski for graphical support and Renata Duzzioni for improving the map of study site. We are also thankful Angelo Schneider and Rafael Trevisan for help with taxonomy of grassland species as well as Soraia Bauermann for fieldwork support.

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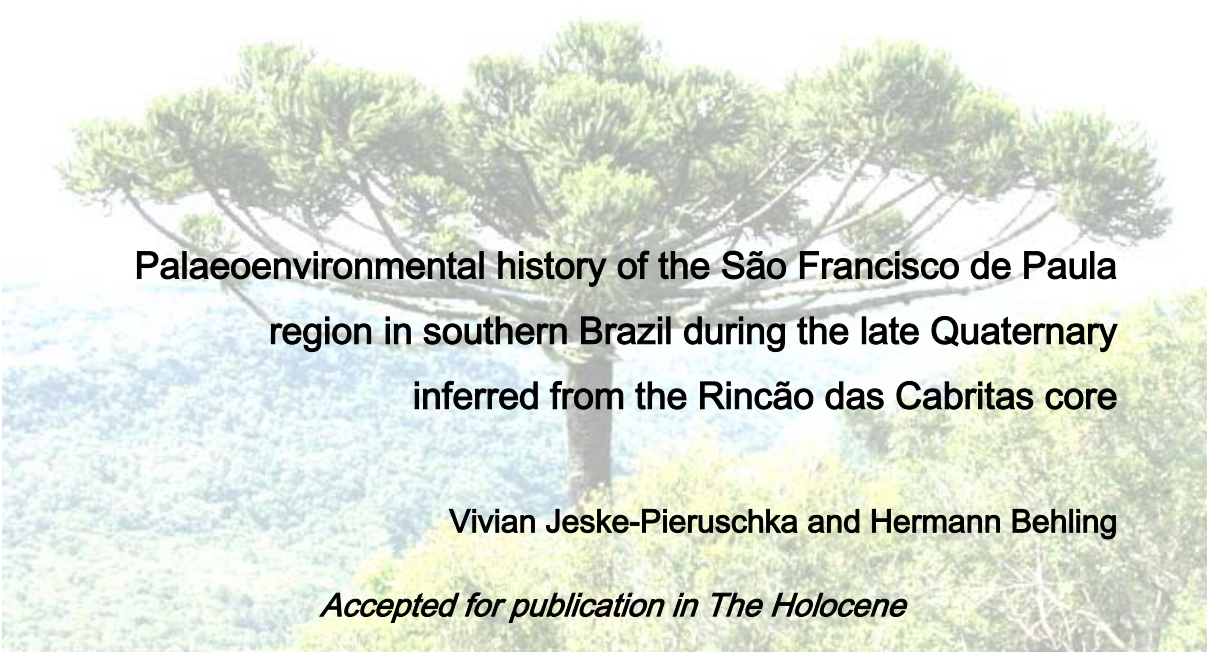


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## CHAPTER 3



**Palaeoenvironmental history of the São Francisco de Paula  
region in southern Brazil during the late Quaternary  
inferred from the Rincão das Cabritas core**

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*Accepted for publication in The Holocene*

## Abstract

We present new palaeoenvironmental data from a 281-cm-long sediment core studied by means of pollen and charcoal analyses from Rincão das Cabritas of the São Francisco de Paula area, which lies in the wettest region of southern Brazil at the present time. The high-resolution record, dated with 7 AMS dates, is spanning the last 16 700 cal. BP. The continuous presence of grassland vegetation (Campos) throughout the glacial period reflects cold and markedly drier climatic conditions than today. Nowadays, remote areas of Campos on the highlands represent remnants of an early and widely expanded vegetation of glacial times that was gradually replaced by forest ecosystems during the late Holocene. *Araucaria* forest began to develop after 3200 cal. BP, with its expansion over Campos starting at about 2950 cal. BP. This was probably due to the presence of a somewhat wetter climate after about 4600 cal. BP, which supported the initial development of forest ecosystems and allowed Atlantic rainforest to spread from the lower regions upwards to higher elevations. The maximum expansion of *Araucaria* forest took place during the last 1000 years, when it started to be the prevailing vegetation type. This vegetational change coincides with increased precipitation and continuously wetter climatic conditions since 1050 cal. BP. The reconstructed fire history indicates a presence of human related fires on the highlands from the late Pleistocene until the mid-Holocene. Fire activity was markedly reduced after about 3000 cal. BP when forest expanded continuously under regional wetter climatic conditions.

**Keywords:** Pollen analysis, *Araucaria* forest, Campos, vegetation history, climate dynamics, fire history, southern Brazil

## Introduction

Today, the highlands of southern Brazil are dominated by a mosaic of subtropical grassland (Campos) and *Araucaria* forest. Together with the Atlantic rainforest on the coastal mountain slopes, which is a hotspot of biodiversity (eg, Myers *et al.*, 2000; Tabarelli *et al.*, 2005), these ecosystems belong to the Atlantic Forest Biome (IBGE, 2004). The geographical distribution of *Araucaria angustifolia* trees is concentrated in the southern Brazilian highlands at altitudes above 500 m, but the species also occurs in smaller areas at higher altitudes in southeast Brazil (Hueck, 1953) (Fig. 1b).

The dominance of grassland vegetation under cold and dry conditions during glacial periods until the mid-Holocene has been recognized by several studies performed in the highlands of Rio Grande do Sul state during the last decades (eg, Roth and Lorscheitter, 1993; Behling *et al.*, 2001; 2004). Further north, on the highlands of Santa Catarina and Paraná state (Fig. 1a), evidence for Campos vegetation during the same periods is given by Behling (1995; 1997; 1998; 2002). During the Last Glacial Maximum (LGM) until late glacial, small populations of forest taxa were only present in

refugia situated in deep valleys or on the coastal slopes where sufficient humidity allowed their survival (eg, Behling *et al.*, 2004; Leonhardt and Lorscheitter, 2010). The initial development of the Atlantic rainforest on the lowlands and valleys of the highlands of Rio Grande do Sul state at the beginning of the Holocene is documented by Lorscheitter (2003). Its spreading in east-west direction since early Holocene is shown by Leal and Lorscheitter (2007). A similar trend for the initial development of the Atlantic rainforest under wetter climatic conditions at the beginning of the Holocene was recognized for the Serra do Tabuleiro in Santa Catarina state (Jeske-Pieruschka *et al.*, unpublished data). The first expansion of *Araucaria* forest in Rio Grande do Sul began at about 3950 yr BP in Cambará do Sul (Behling *et al.*, 2004) and after 4000 yr BP in the São Francisco de Paula region (Leonhardt and Lorscheitter, 2010). The onset of the *Araucaria* forest expansion in Santa Catarina occurred at about 3460 yr BP in Serra da Boa Vista and at about 2390 yr BP in Serra do Rio do Rastro (Behling, 1995). In Paraná, located north of Santa Catarina, the initial *Araucaria* forest expansion is documented after 2000 yr BP in Serra do Araçatuba (Behling, 2007) and at about 2850 yr BP in Serra dos Campos Gerais (Behling, 1997). For the Rio Grande do Sul, pronounced *Araucaria* forest expansion was recognized since 1060 yr BP in São Francisco de Paula (Behling *et al.*, 2001) and after 1140 yr BP for Cambará do Sul (Behling *et al.*, 2004). A marked expansion of *Araucaria* forest is reported since about 1000 yr BP in Morro da Igreja and Serra do Rio do Rastro, Santa Catarina state (Behling, 1995) and since about 1400 yr BP in Serra dos Campos Gerais, Paraná state (Behling, 1997).

The beginning of the *Araucaria* forest expansion occurred earlier further south, i.e. in Rio Grande do Sul state (*c.* 4000 yr BP) than in Santa Catarina (*c.* 3000 yr BP) and Paraná state (*c.* 2500 yr BP), both further north. In contrast to this, the marked *Araucaria* forest expansion occurred later in Rio Grande do Sul and Santa Catarina (last millennia) than further north. Although a climatic change to warmer and wetter conditions arose at the beginning of the Holocene, a long annual dry season may have hampered the initial forest expansion on the southern Brazilian highlands until mid-Holocene times (Behling, 2002). A marked forest expansion over Campos occurred only after about 1100 yr BP in the southernmost Brazilian highlands. Our question in this context is if the different times of forest expansion were related to regional climatic conditions and/or which other possible factors could have prevented a forest expansion on the highlands. The fact that this studied region has the highest annual precipitation rates of southern Brazil allows the investigation of vegetational changes advantageously. In this work, we present detailed data for the southernmost Brazilian highlands from a temporarily high resolution sedimentary record spanning the last 16 700 cal. BP. This represents the best dated core for the region so far. Therefore, this work provides the best detailed overview of vegetation dynamic, palaeoclimate and fire history of the São Francisco de Paula region. An inter-regional interpretation of environmental changes can be concluded from a comparison of these results.

## Environmental setting

### *Location*

The studied sedimentary record was collected from a peat bog (29°28'35''S, 50°34'22''W) situated in the rural property Rincão das Cabritas, approximately 5 km from the municipality of São Francisco de Paula in the southern Brazilian highlands (Fig. 1). The site is located on the eastern plateau of Rio Grande do Sul state, as part of the Serra Geral formation at a distance of *c.* 500 m from its escarpment. The Serra Geral corresponds to a geomorphological unit formed by layers of basalt covering Jurassic/Cretaceous sedimentary rocks, the Botucatu formation. It is composed of base-rich basalt in the lower layers and acidic rocks, mostly rhyolite and rhyodacite, in the upper layers (IBGE, 1986). The soil formation is affected by the high precipitation rates under subtropical humid climate. A study in the Pró-Mata area, southern Brazilian highlands (Dümig *et al.*, 2008) describes the occurrence of black-coloured, humus-rich soils in the São Francisco de Paula region, which can be classified as Andosols, Umbrisols and Cambisols.

The peat bog, which is surrounded by a forest, is situated in a basin of about 5000 m<sup>2</sup> at an altitude of 895 m a.s.l..

### *Modern vegetation*

Mosaics of Campos-*Araucaria* forest characterize the landscape of the highlands in Rio Grande do Sul state. The regional Campos ecosystem is mainly composed of Poaceae, Asteraceae, Fabaceae, Cyperaceae, Apiaceae and Verbenaceae (Boldrini, 2009). Large patches of *Araucaria* forest cover the region, therewith being the most representative forest formation. This forest type consists of species associated to *Araucaria angustifolia*, such as *Podocarpus lambertii*, *Drimys brasiliensis*, *Mimosa scabrella*, *Ocotea pulchella*, *O. puberula*, *Nectandra* spp., *Ilex paraguariensis*, *Ilex* spp., *Matayba elaeagnoides*, *Cupania vernalis* and different species of the Myrtaceae family (Reitz *et al.*, 1988). The slopes of the highlands are covered by Atlantic rainforest from the lower altitudes up to the top of the Serra Geral escarpment. At higher elevations, a gradual transition between these two forest types can be observed. The species-rich Atlantic rainforest is composed of numerous tree species with the predominance of Lauraceae (eg, *Ocotea* spp., *Nectandra* spp.) and Myrtaceae (eg, *Myrcia* spp., *Myrceugenia* spp., *Calyptanthes* spp., *Gomidesia* spp.). Other representative taxa are: *Alchornea* spp., *Clethra scabra*, *Weinmannia* spp., *Inga* spp., *Cedrela* spp., *Cabralea canjerana* as well as Mimosaceae (*Piptadenia*, *Parapiptadenia*, *Anadenanthera*). Furthermore, numerous lianas and epiphytes belonging to the plant families of Bromeliaceae, Orchidaceae, Araceae, Cactaceae as well as to the pteridophytes are characteristic for this ecosystem. A more extensive description of the Campos and forests of southern Brazil is published by Lindman (1906). The southern Brazilian vegetation has also been described in Rambo (1951; 1956), Klein (1960; 1975) and Hueck (1966).

The natural vegetation has been influenced anthropogenically since the occupation by the first inhabitants of São Francisco de Paula region, the Caaguaras Indians that lived in the highlands before the European colonization of southern Brazil. However, the Caaguaras Indians were decimated by disease and by the Bandeirantes (Portuguese colonial explorers in Brazil) about 1700 AD. At 1835 AD there was already a church but only at 1878 AD the city of São Francisco de Paula was established ([www.riogrande.com.br/municipios/saofranciscodepaula.htm](http://www.riogrande.com.br/municipios/saofranciscodepaula.htm)). Currently, land uses such as cattle farming and silvicultural production (extensive *Pinus* sp. plantations) form a big part of the local economy while other agricultural activities are less represented.

### ***Climate***

The present-day climate on the highlands of Rio Grande do Sul is subtropical humid, with high rainfall distributed throughout the year without a pronounced dry period (Moreno, 1961). It can thus be classified as wet mesothermic climate (Cfb, Köppen). According to Moreno (1961), São Francisco de Paula has the highest mean annual precipitation (*c.* 2500 mm per yr) and lowest mean annual temperature (14°C) of the state, with frequent frosts occurring in winter. The South Atlantic Anticyclone, transporting warm and humid air masses over the continent, dominates the atmospheric circulation over southern Brazil. The Polar Anticyclone with dry and cold air masses also influences the climate of the region provoking strong rainfall when it clashes with tropical warm and humid air masses (Nimer, 1989). Precipitation anomalies are associated with El Niño Southern Oscillation (ENSO) and La Niña events, where excessive rainfall is related to El Niño, whereas La Niña reduces rainfall in southern Brazil (Grimm *et al.*, 1998; 2000).



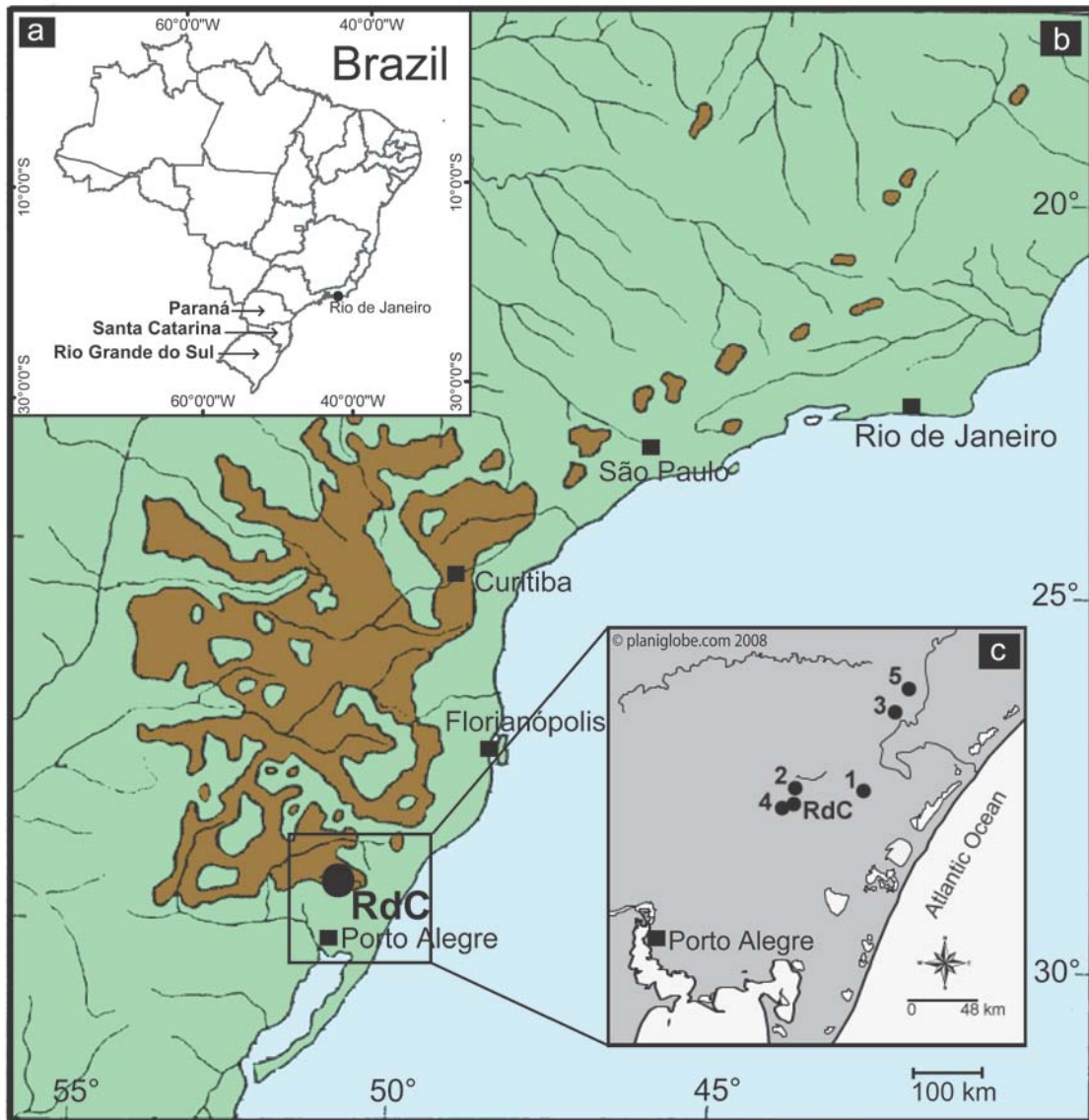


Figure 1. (a) The states of southern Brazil, (b) distribution of *Araucaria angustifolia* in Brazil (after Hueck, 1953), slightly modified and (c) the position of the Rincão das Cabritas (RdC) core together with the other studies performed in the region of São Francisco de Paula and the highlands of Rio Grande do Sul state: (1) Aparados da Serra (Roth and Lorscheitter, 1993), (2) Fazenda do Pinto (Behling *et al.*, 2001), (3) Cambará do Sul (Behling *et al.*, 2004), (4) Alpes de São Francisco (Leonhardt and Lorscheitter, 2010) and (5) São José dos Ausentes (Jeske-Pieruschka *et al.*, 2010).

## Methods

The core has a length of 281 cm and was sampled with a Russian corer from the deepest part of the bog. Seventy-one volumetric subsamples of 0.25 -1 cm<sup>3</sup> were taken every 4 cm along the core for pollen and charcoal analysis. Each subsample was prepared applying hydrofluoric acid treatment and acetolysis (Faegri and Iversen, 1989). In order to calculate pollen and charcoal concentration, one tablet of *Lycopodium clavatum* marker was added to each sample (Stockmarr, 1971). Subsequently, the samples were mounted in glycerin gelatin and counted up to a minimum of 300 pollen grains each. The identification of the diverse pollen and spore types was simplified by the use of the reference collection of the Department of Palynology and Climate Dynamics, University of Göttingen together with morphological descriptions of Behling (1993) and Cancelli (2008). The acetolysed *Lycopodium clavatum* marker was distinguished from the naturally occurring *L. clavatum* spores on the basis of the dark coloration and of its wrinkled aspect. For calculations and plotting of pollen, spore and charcoal results, we used the programs TILIA and TILIAGRAPH (Grimm, 1991). Pollen and spores were calculated as percentages of the pollen sum, which included different taxa of grasses, herbs, shrubs and trees and excluded aquatic taxa and pteridophytes. All terrestrial and aquatic taxa were grouped into different ecological groups. Pollen taxa that could not be included in any other vegetation type or had a wider geographical distribution were included into "Others". The zonation of the pollen record is based on marked changes in the pollen assemblages and the cluster dendrogram calculated with CONISS (Grimm, 1987). The charcoal analysis is based on microscopic (5 – 150 µm) charred particles which were counted on the pollen-slides.

Seven sub-samples were sent to radiocarbon dating by Accelerator Mass Spectrometry (AMS) at the Institute of Physics of the Erlangen-Nürnberg University, Germany. An age-depth model was established using linear interpolation between calibrated ages, which was used to describe the pollen diagrams.

## Results

### *Lithology*

The 281-cm-long sediment core from Rincão das Cabritas (RdC) consists of light brown clay in the lower core section (281-224 cm). From 224 to 7 cm core depth, the sediment is composed of decomposed peat. The overlaying section (7-0 cm depth) consists of weakly decomposed peat. A detailed description of the stratigraphic changes in the core is shown in Table I and Figure 4.

Table I. Sediment description of the Rincão das Cabritas core from the São Francisco de Paula region, southern Brazil.

Depth (cm)	Sediment description
0 – 7	Weakly decomposed peat with <i>Sphagnum</i> spp.
7 – 30	Decomposed peat with fine roots
30 – 87	Dark brown decomposed peat rich in fine roots
87 – 123	Black highly decomposed peat with many roots and plant remains
123 – 224	Dark brown strongly decomposed peat with clay
224 - 281	Light brown clay with little organic matter

### Chronology

The chronology for the core Rincão das Cabritas (RdC) was obtained from seven AMS radiocarbon dates (Table II). The calibration of the radiocarbon dates was performed using the software CALIB 6.0 (Stuiver and Reimer, 1993) applying the data set of SHCal04 (McCormac *et al.*, 2004) to the date of 10 245 <sup>14</sup>C yr BP and of intcal09.14c (Reimer *et al.*, 2009) for the two older radiocarbon dates. A median probability was adopted for each calibrated age range. The base of the core is extrapolated to be of an age of 16 700 cal. BP, indicating that the sediment reaches back to the end of the full glacial period. The depth vs. age relationship (Fig. 2) suggests an irregular sediment accumulation through time. During the period between about 16 700 and 14 800 cal. BP, sedimentation rates are high (*c.* 0.272 mm/yr). Sedimentation rates are low (*c.* 0.061 – 0.116 mm/yr) from approximately 14 800 until 3000 cal. BP. Since about 3000 cal. BP, sedimentation rates are increasing (*c.* 0.328 – 0.673 mm/yr).

Table II. Radiocarbon dates for Rincão das Cabritas core.

Laboratory code	Sample depth (cm)	Sample type	Conventional age ( <sup>14</sup> C yr BP)	Age range <sup>a</sup> (cal. yr BP)	Med. Prob. (cal. yr BP)
Erl-12100	45	wood	704±42	558 – 670	612
Erl-15120	85	wood	1786±38	1534 - 1734	1641
Erl-11387	126	peat	2847±37	2783 - 2995	2892
Erl-12101	171	peat	5997±45	6659 - 6894	6769
Erl-12655	210	peat	10 245±68	11 409 – 12 149	11 877
Erl-12102	228	peat	12 578±66	14 239 – 15 170	14 806
Erl-11388	279	wood	13 503±68	16 369 – 16 902	16 679

<sup>a</sup> Range at standard deviation of 2  $\sigma$ , 95.4% probability

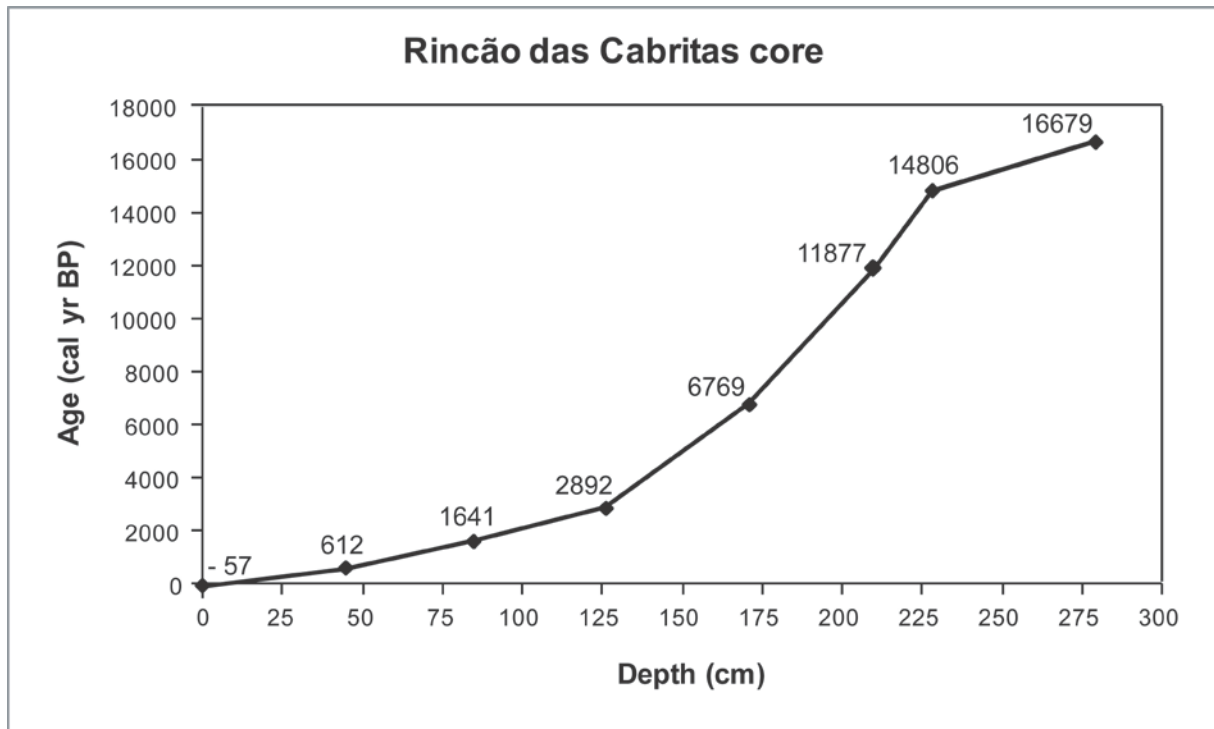


Figure 2. Depth age curves for the Rincão das Cabritas core. All ages are in calibrated radiocarbon dates (cal. yr BP).

#### **Description of the pollen diagram**

In total, 114 identified pollen and 23 different spore taxa were recorded in 71 sediment samples. Pollen types that could not be identified were classified by morphological characteristics and included into “Unknowns”. Most frequent and important pollen and spore types are shown in the percentage pollen diagram (Fig. 3). Figure 4 displays a summary percentage diagram of the grouped taxa into different vegetation types together with pollen and charcoal concentration.

Zone RdC-I (280-230 cm, 13 520 – 12 600 yr BP or 16 700 – 14 900 cal. BP, 13 samples) is dominated by high percentages (82-92%) of Campos taxa, primarily Poaceae (44-67%), Cyperaceae ( $\leq 4\%$ ), *Plantago* ( $\leq 11\%$ ), Apiaceae ( $\leq 9\%$ ), *Eryngium* type ( $\leq 10\%$ ) and Asteraceae ( $\leq 19\%$ ). Pollen of forest taxa is less represented with values of up to 6% for the *Araucaria* forest and up to 2% for the Atlantic rainforest group. This zone contains very low pollen abundances of *Myrsine*, Myrtaceae, *Mimosa scabrella* type, *Podocarpus*, *Ilex*, *Araucaria angustifolia*, *Clethra* type, *Weinmannia* type, *Celtis* and Moraceae/Urticaceae (each  $>3\%$ ). The aquatic group is represented by pollen of *Myriophyllum* type, *Echinodorus* and *Hydrocotyle* type, which account for 0.3 - 4%. Pteridophyta, mostly spores of *Isoetes* (up to 5%), are well represented and vary between 2 and 9%. Moss spores occur in very low proportions ( $<0.7\%$ ). Pollen concentrations are low ( $300 \times 10^6 - 800 \times 10^6$  grains/cm<sup>3</sup>) whereas concentrations of carbonized particles are high ( $13\,000 \times 10^9 - 120\,000 \times 10^9$  particles/cm<sup>3</sup>).

Zone RdC-II (230-186 cm, 12 600 – 7600 yr BP or 14 900 – 8700 cal. BP, 11 samples) is characterized by high percentages of Campos taxa (88-91%) and low percentages of *Araucaria* forest taxa (2-4%) and Atlantic rainforest taxa (1-3%). Pollen percentages of Poaceae, Cyperaceae and some Asteraceae taxa increase, whereas *Plantago*, Apiaceae and *Eryngium* type decrease. Pollen of *Myriophyllum* type has one maximum of 4% at the bottom of the zone, but decreases to 0% towards the top. The last pollen of *Echinodorus* was recorded at the end of this zone while *Hydrocotyle* type pollen is absent. The Tree ferns group occurs with low amounts ( $\leq 1.3\%$ ). Pteridophyta spores remain at the same level (3-8%) but proportions of *Isoetes* decrease to 0%. Mosses are represented by increasing values of *Sphagnum* (2-10%) and *Phaeoceros laevis* (0.3-13%). Concentrations of pollen ( $400 \times 10^6 - 1500 \times 10^6$  grains/cm<sup>3</sup>) and of microscopic charred particles ( $170\,000 \times 10^9 - 480\,000 \times 10^9$  particles/cm<sup>3</sup>) show higher values.

Zone RdC-III (186-126 cm, 7600 – 2900 yr BP or 8700 – 2950 cal. BP, 15 samples) shows a slight decrease in Campos taxa from 86% to 60%, mostly due to decreasing pollen frequencies of Poaceae and *Plantago*. The *Araucaria* forest group is represented by increasing values of *Myrsine* (1-8%) and Myrtaceae (0.3-4%), while pollen percentages of other *Araucaria* forest taxa continue to be low. Atlantic rainforest taxa also reach higher values, mostly due to increasing pollen percentages of *Weinmannia* type (0-11%) and *Alchornea* (0.3-3%). Melastomataceae pollen abundances increase compared to the previous zone. Proportions of Aquatic taxa ( $\leq 0.3\%$ ) and *Isoetes* spores ( $\leq 0.3\%$ ) are very low. The Tree ferns and Pteridophyta groups show an increasing trend from 0% to 3% and from 2% to 11%, respectively. Spores of *Sphagnum* increase markedly at the beginning (up to 36%), but decline towards the top of the zone, while percentages of *Phaeoceros laevis* spores remain at relatively high proportions. Pollen concentrations are lower with values between  $170 \times 10^6$  and  $600 \times 10^6$  grains/cm<sup>3</sup> whereas charcoal concentrations continue to be high ( $130\,000 \times 10^9$  and  $340\,000 \times 10^9$  particles/cm<sup>3</sup>).

Zone RdC-IV (126-62 cm, 2900 – 1160 yr BP or 2950 - 1050 cal. BP, 16 samples) is marked by a strong decrease in Campos taxa from 19% to 3%, reflected by a sharp decline of Poaceae with values between 2 and 9% and low pollen percentages of Asteraceae and other grassland taxa. Pollen of forest taxa increase considerably, reaching proportions up to 63% for the *Araucaria* forest and up to 49% for the Atlantic rainforest group. Pollen percentages of the *Araucaria* forest group increase (*Myrsine*, Myrtaceae, *Ilex*, *Araucaria angustifolia*, *Lamanonia speciosa* type, *Drimys brasiliensis* and *Griselinia ruscifolia* type). Pollen frequencies of *Weinmannia* type increase highly up to 44% while percentages of *Alchornea* and Melastomataceae decrease in this zone. The Tree ferns group increases in this zone up to 16%, due to higher proportions of Cyatheaceae and *Dicksonia sellowiana* spores. Abundances of Pteridophyta spores continue to increase (8-31%), whereas the Moss group decreases markedly ( $\leq 3\%$ ) due to low values of *Sphagnum* and *Phaeoceros laevis* spores. Values of

pollen concentration are higher ( $140 \times 10^6 - 1750 \times 10^6$  grains/cm<sup>3</sup>) whereas the ones of charcoal concentration are markedly lower ( $4700 \times 10^9 - 29\,000 \times 10^9$  particles/cm<sup>3</sup>).

Zone RdC-V (62-0 cm, 1160 yr BP – present or 1050 cal. BP - present, 16 samples) is characterized by high percentages of *Araucaria* forest taxa (36-64%) and decreasing values of Atlantic rainforest taxa (42-13%). Campos taxa increase continuously from 13 to 42%. Pollen concentrations are high ( $1500 \times 10^6$  grains/cm<sup>3</sup>) at the beginning of the zone and very low ( $23 \times 10^6$  grains/cm<sup>3</sup>) in the upper part. Values of charcoal concentration remain low ( $370 \times 10^9 - 18\,000 \times 10^9$  particles/cm<sup>3</sup>). This zone is divided into two subzones. Subzone RdC-Va (62-6 cm, 1160 – 45 yr BP or 1050 – 30 cal. BP, 14 samples) shows a further increase in pollen percentages of *Myrsine* (up to 50%) and *Clethra* type, while other *Araucaria* forest taxa decrease slightly or remain at the same proportions. The same can be observed in subzone RdC-Vb (6-0 cm, 45 yr BP – present or 30 cal. BP - present, 2 samples), except for pollen frequencies of *Myrsine* which decrease and for Myrtaceae and *Mimosa scabrella* type which increase towards the top. Pollen abundances of *Weinmannia* type decrease continuously until the top of the core (38-9%). *Alchornea* pollen reaches higher values up to 7% at subzone RdC-Va, but decreases in the next subzone. *Pinus* pollen appears for the first time at the upper part of subzone RdC-Va and is represented, together with *Trema* type, by higher percentages in the subsequent subzone. In subzone RdC-Va, pollen of Campos taxa are present with low percentages only, whereas pollen of Cyperaceae and some Asteraceae taxa increase in the upper part of this subzone and continue to increase in the following subzone. Tree fern taxa decrease compared to the previous zone, but spores of Cyatheaceae increase slightly in subzone RdC-IVb. The Pteridophyta group is represented by increasing values of Monolete psilate <50µm, Monolete psilate >50µm, *Blechnum imperiale* type and *Osmunda* spores in subzone RdC-Va. The increasing trend continues in the following subzone, including spores of *Lycopodium clavatum* type and *Selaginella excurrentis* type, only Monolete psilate <50µm decreases. The Moss group increases and is relatively well represented in both subzones with *Sphagnum* reaching values up to 19%.





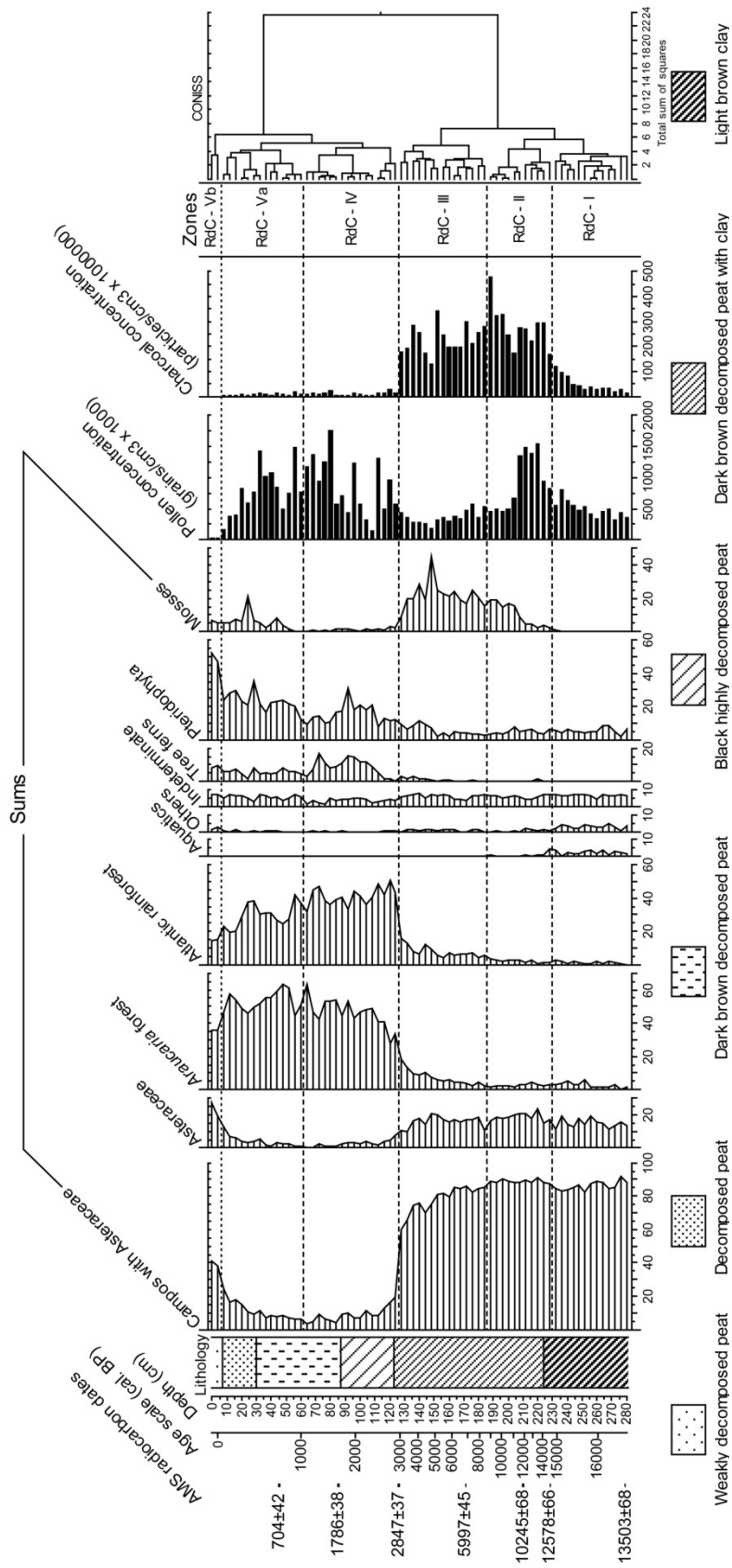


Figure 4. Sums of vegetation groups together with pollen and charcoal concentrations, as well as the cluster analysis dendrogram and the stratigraphy of the RdC core are summarized in the diagram.



## Interpretation and discussion

### *Last glacial (13 520 – 12 600 yr BP or 16 700 – 14 900 cal. BP; Zone I)*

During the recorded full glacial and late glacial period, the landscape was dominated by grassland formed by forbs and graminoids, mostly Poaceae, *Plantago*, Apiaceae, *Eryngium*, different Asteraceae and other plants that are characteristic for open vegetation. Some Myrtaceae may represent shrubs growing in the grassland at this period. According to Schüler and Behling (2011a, 2011b), Poaceae species of grasslands during glacial times on the southern Brazilian highland can probably be seen as a mixture of Pampa (found further South in the lowlands of southern South America) and high elevation grassland (Campos de Altitude) vegetation (found further North in the higher mountains of southern and southeastern Brazil). A few forest taxa and tree ferns were present in small populations probably on the lower slopes with sufficiently retained moisture or as gallery forest along rivers or streams at lower elevations. Among the *Araucaria* forest taxa were *Mimosa scabrella*, *Podocarpus*, *Araucaria angustifolia* and *Clethra*, whereas *Weinmannia*, *Celtis* and Moraceae/Urticaceae belong to Atlantic rainforest. The presence of *Isoëtes*, which is commonly found in seasonally wet to aquatic habitats and of aquatic taxa as *Myriophyllum*, *Echinodorus* and *Hydrocotyle* suggests local shallow water conditions in the studied basin during this period. Furthermore, the occurrence of some Cyperaceae and Eriocaulaceae confirms local water saturation.

The dominance of grassland reflects dry and cold climatic conditions in the region during the later part of the full glacial and late glacial. The rainfall of nowadays about 2500 mm per yr in São Francisco de Paula region (Moreno, 1961; Nimer, 1989) must have been markedly reduced during late glacial times. However, sporadic strong rainfall may have provided the local prerequisites for shallow water in the basin. Environmental reconstructions by different authors have been consistent by suggesting that grassland dominated the highlands of Rio Grande do Sul state during glacial times under cold and relatively dry climate and that some *Araucaria* forest taxa were present only in refugia, such as in deep valleys or on coastal slopes with sufficient moisture (Roth and Lorscheitter, 1993; Behling *et al.*, 2004; Leonhardt and Lorscheitter, 2010). Vegetation development and climate change on the highlands of southern Brazil shown by palynological studies performed on different sites are summarized in Table III.

Pollen data from São Francisco de Paula (Leonhardt and Lorscheitter, 2010) point to the presence of a local shallow lake between 25 000 and 16 000 yr BP, whereas data from Cambará do Sul (Behling *et al.*, 2004) indicates for a local permanent shallow lake before 26 900 yr BP and a non-permanent lake until 10 120 yr BP. Our results show that a local shallow lake existed before 12 600 yr BP which became a peat bog afterwards.

**Late glacial to early Holocene (12 600 – 7600 yr BP or 14 900 – 8700 cal. BP; Zone II)**

The São Francisco de Paula region continues to be characterized by a treeless landscape with Campos as the predominant vegetation community. A small number of forest taxa represented by *Myrsine*, *Podocarpus*, *Ilex*, *Lamanonia speciosa*, *Clethra*, *Weinmannia*, *Celtis*, Moraceae/Urticaceae and *Alchornea* indicate the existence of some trees in protected areas of drought. These can have been refugia with sufficient moisture at lower elevations in valleys or on the slopes. Some of the tree species such as *Myrsine*, *Ilex*, *Lamanonia speciosa*, *Weinmannia*, Moraceae/Urticaceae and *Alchornea* may reflect a first forest movement from the lower slopes to higher elevations of the Serra Geral, which can have been favored by warmer and wetter conditions after the late glacial period. The presence of some dispersed Atlantic rainforest taxa at the beginning of the Holocene at about 10 000 – 8000 yr BP along the coastal plain and valleys of the Serra Geral is documented by Lorscheitter (2003). More recently, Leal and Lorscheitter (2007) propose the spreading of Atlantic rainforest from east to west since 8800 yr BP based on a sediment profile from the lower northeast slope of the Serra Geral. After *c.* 12 600 yr BP, the continuous bog formation began with the local occupation of *Sphagnum* as a peat moss and *Blechnum imperiale* as a fern growing on the site. The presence of *Sphagnum* combined with the almost disappearance of aquatic taxa and *Isoëtes* point to periods of pronounced drought, but sufficient local humidity. The increase of Poaceae together with the decrease of *Plantago*, Apiaceae, *Eryngium*, Eriocaulaceae and possible absence of *Araucaria angustifolia* (no pollen grains) indicate for longer dry periods. According to Hueck (1966), *Araucaria angustifolia* can neither endure annual precipitation levels lower than 1000 mm nor long dry seasons.

Extensive Campos vegetation points to regionally dry climatic conditions extending from the late glacial to the early Holocene. The results of research by other authors have been consistent with respect to dry climatic conditions in the region during this period. According to Behling *et al.* (2004), climate was dry with annual long dry period from 10 120 to 3950 yr BP and markedly drier than today from 7500 to 4000 yr BP (Behling *et al.*, 2001). However, for Leonhard and Lorscheitter (2010), the climate was warm and dry between 9700 and 6500 yr BP. On the other hand, Roth and Lorscheitter (1993) propose a warmer and wetter climate at the beginning of the Holocene at about 11 000 yr BP and according to Leonhard and Lorscheitter (2010), it was warm and moist from 11 000 to 9700 yr BP. However, dry climatic conditions are also confirmed by other studies, which show the dominance of Campos vegetation on the highlands of Santa Catarina (Behling, 1995) and Paraná state (Behling, 1997).

**Early- to mid-Holocene (7600 – 2900 yr BP or 8700 – 2950 cal. BP; Zone III)**

Campos vegetation composed mostly of Poaceae and Asteraceae continues to prevail in the region. Forest indicators as the pioneer taxa *Myrsine*, *Lamanonia speciosa* and *Alchornea* (Backes

and Irgang, 2002; 2004) as well as *Weinmannia*, Myrtaceae and Cyatheaceae point to a continuous spreading of forest from the lower to the upper part of the slopes and an initial *Araucaria* forest development. At this period, the peat bog became completely developed. It was mostly dominated by *Sphagnum* but consisted also of other bog vegetation taxa, such as some Cyperaceae and Eriocaulaceae as well as *Blechnum imperiale*.

Campos vegetation remained the predominant ecosystem on the highlands under dry climatic conditions during the early Holocene. However, a moderate and wetter climate since the mid-Holocene allowed for gradual forest spreading from the lower regions of the Serra Geral upwards to higher elevations. The increasing frequency of moist forest taxa, such as *Myrsine*, Myrtaceae, *Lamanonia speciosa*, *Weinmannia* and Cyatheaceae as well as of bog taxa such as *Blechnum imperiale*, *Osmunda* and *Sphagnum* indicate for a slightly wetter climate after about 4250 yr BP. Increased moisture levels after 4000 yr BP correlate with an increasing humidity reported from Cambará do Sul (Behling *et al.*, 2004) with a first *Araucaria* forest expansion. Similar conditions with small areas of *Araucaria* forest are shown for the São Francisco de Paula region (Behling *et al.*, 2001). For the same region, Leonhardt and Lorscheitter (2010) suggest a gradual increase of humidity between 6500 and 4000 yr BP and an *Araucaria* forest expansion under moister climatic conditions between 4000 and 2000 yr BP. Additionally, a wet climate since 4000 yr BP has been recorded for the southern Brazilian coastal lowland (Cordeiro and Lorscheitter, 1994). In respect of climatic improvement towards warmer-wetter conditions in the Holocene, Roth and Lorscheitter (1993) show a significant forest expansion over Campos, which is related to a mild and humid phase.

#### **Late Holocene (2900 – 1160 yr BP or 2950 – 1050 cal. BP; Zone IV)**

The *Araucaria* forest expansion in the region began at approximately 2900 yr BP. It is reflected by an increase in arboreal pollen taxa frequencies, such as *Myrsine*, Myrtaceae, *Ilex*, *Araucaria angustifolia*, *Lamanonia speciosa*, *Drimys brasiliensis* and *Griselinia ruscifolia*. At the same time, the establishment of the Atlantic rainforest on the upper part of the slopes is suggested by the presence of *Weinmannia* together with other tree taxa and tree ferns belonging to this ecosystem. It is worth noting that *Weinmannia* increased exactly simultaneously with the abrupt decrease of Poaceae. This does not account for an almost disappearing of Campos vegetation or a replacement of this vegetation community by forest, but most probably reflects the presence of *Weinmannia* pollen in the sediment. Therefore, a high pollen production of *Weinmannia* does not represent its dominance in the landscape but is more owed to its local presence. Despite of a higher sediment deposition, an expected low pollen concentration since about 3000 cal. BP was not encountered in our results (Fig. 4). It is possible that a greater pollen production of forest compared to Campos taxa has led to higher pollen concentration rates. A vegetation change from a grassland landscape to a forested ecosystem since

3000 cal. BP is shown in the pollen diagrams (Fig. 3 and 4). The shift of the forest around the bog supports the idea that higher pollen concentrations are caused by a higher pollen production of forest taxa. It is unclear why *Sphagnum* has declined during this period and the reasons for desiccating the peat bog. It may be possible that the peat bog was reduced and substituted by the surrounding vegetation formed by *Araucaria* forest and some Atlantic rainforest taxa which were temporarily more widespread in the *Araucaria* forest since the last 3000 years.

Forest covered the study site during this period, thus pointing to a climatic amelioration to wetter conditions. The *Araucaria* forest development began at about 3950 yr BP in Cambará do Sul, but its expansion and the replacement of Campos took place much later, after 1140 yr BP (Behling *et al.*, 2004). This results differs from our that demonstrate a continuously expansion of *Araucaria* forest in São Francisco de Paula region since the mid-Holocene, after *c.* 2900 yr BP. Evidence for a moister mid- to late Holocene, which lead to the initial expansion of *Araucaria* forest, is also given by other studies that have been carried out on the highlands of Santa Catarina (Behling, 1995) and Paraná state (Behling, 1997; 2007), situated further north.

#### ***Last millennium (1160 yr BP – present or 1050 cal. BP – present-day; Zone V)***

The replacement of Campos by forest ecosystems continued until the last millennium, although the Atlantic rainforest seems to have declined in the São Francisco de Paula region. This reduction is primarily indicated by the decrease of *Weinmannia* and the tree fern family of Cyatheaceae. The reduction of the Atlantic rainforest reflects a vegetational change caused by the expansion of the *Araucaria* forest in the region. The latter became the main vegetation type on the highlands forming Campos-forest mosaics. Local *Araucaria* forest expanded increasingly since the last 1000 years, thereby leading to a vegetational change also on the upper part of the Serra Geral close to its slopes that became a transition zone between Atlantic rainforest and *Araucaria* forest since then. During the last millennium, the bog regenerated and was covered by *Sphagnum* and other plants characteristic for bog communities, such as *Blechnum imperiale*, *Osmunda* and *Phaeoceros laevis*. However, the peat bog has been influenced by human activities over the last decades. This is reflected by a continue increase of *Blechnum imperiale*, *Osmunda*, *Lycopodium clavatum*, *Selaginella excurrens* and some Cyperaceae that suggest a bog growth within the forest due to opening of the forest since *c.* 1890 AD. A bog expansion could also have been promoted by the accumulation of water in the basin, which then allowed the emergence of bog taxa adapted to high moisture levels.

Climatic conditions continued to become wetter during the last 1000 years with an increased precipitation that coincides with the maximum forest expansion. This is consistent with Behling *et al.* (2004) who documented the wettest period without a marked annual dry season since 1140 yr BP and noted a replacement of Campos by *Araucaria* forest in Cambará do Sul. Furthermore, Behling *et al.*

(2001) recorded a forest expansion since 1060 yr BP. However, they suggest an expansion of *Araucaria angustifolia* trees only since 850 yr BP in the São Francisco de Paula region under climatic conditions similar to the modern climate. These interpretations, proposing a much later forest expansion than indicated from the results presented here, could be explained by the extensive use of Campos areas as a natural pasture with distant patches of disturbed *Araucaria* forest at the study site. A study on the dynamics of a small *Araucaria* forest island in the region showed its development and expansion associated to fire frequency after 490 yr BP (Jeske-Pieruschka *et al.*, 2010). A pronounced *Araucaria* forest expansion is reported since about 1000 yr BP in Santa Catarina state (Behling, 1995) and since about 1400 yr BP in Paraná state (Behling, 1997).

The first occurrence of *Pinus* at *c.* 1890 AD points to an ecosystem disturbance by the introduction of these exotic trees. The reduced arboreal taxa reflect continuing but decreasing disturbance with the expansion of shrubs. This is evidenced by the increase of Asteraceae since the end of the 19th century. Also, disturbance indicators such as *Mimosa scabrella* and *Trema* increased over the past 60 years. Disturbance of the native vegetation, resulting in a forest opening, can be related to human activities, such as the introduction of cattle by Jesuits probably during the early 18th century (Pillar, 2003) and the exploitation of *Araucaria angustifolia* by European settlers since the 19th century (Reitz *et al.*, 1988).

Table III. Survey of major vegetational changes and climatic variabilities recorded for the highlands of southern Brazil since the late Pleistocene.

Site	Chronology				
	late Glacial	early and mid-Holocene	late Holocene		
Paraná	12 500-9700 yr BP Serra dos Campos Gerais <sup>1</sup> 24°40'S, 50°13'W; 1200 m a.s.l.	Campos vegetation; scattered stands of forest trees in valleys at lower elevations; cold and dry	9700-2850 yr BP Campos vegetation; Atlantic rainforest expansion in the valleys; warm and dry	2850-1550 yr BP Campos vegetation; <i>Araucaria</i> forest expansion and migration to the highlands; cooler and somewhat wetter	Since 1550 yr BP marked expansion of <i>Araucaria</i> forest; wettest climate without strong annual dry season
	Serra do Araçatuba <sup>2</sup> 25°55'S, 48°59'W; 1500 m a.s.l.	14 900-12 950 cal yr BP Campos vegetation; cold and dry	12 950-2050 cal yr BP Campos vegetation; slightly forest expansion to higher elevations; warm and relatively dry	After 2050 cal yr BP <i>Araucaria</i> forest expansion; wetter conditions	
Santa Catarina	Morro da Igreja <sup>3</sup> 28°11'S, 49°52'W; 1800 m a.s.l.	Before 10 200 yr BP Campos vegetation; small <i>Araucaria</i> forest stands in deep valleys; cold and relatively dry	10 000-3000 yr BP Campos vegetation; beginning of <i>Araucaria</i> forest expansion; warm and dry	3000-1000 yr BP Campos vegetation; forest retraction; cool and moister	Since 1000 yr BP Campos retraction; great expansion of <i>Araucaria</i> forest; cool and very moist
	Serra do Rio Rastro <sup>3</sup> 28°23'S, 49°33'W; 1420 m a.s.l.	Before 11 200 yr BP Campos vegetation; cold and relatively dry	10 800-10 500 yr BP Campos vegetation; warmer and moister 10 500-10 000 yr BP cold and relatively dry 10 000-3000 yr BP warm and drier	3000-1000 yr BP Campos vegetation; first <i>Araucaria</i> forest expansion; cool and moister	Since 1000 yr BP Campos retraction; great expansion of <i>Araucaria</i> forest; cool and very moist
Serra da Boa Vista <sup>3</sup> 27°42'S, 49°09'W; 1160 m a.s.l.	14 000-10 800 yr BP Campos vegetation; cold and relatively dry 10 800-10 500 warmer and moister 10 500-10 000 yr BP cold and relatively dry	10 000-3000 yr BP expansion of Atlantic rainforest followed by <i>Araucaria</i> forest; warm and less dry	3000-1000 yr BP Atlantic rainforest retraction and <i>Araucaria</i> forest expansion; cool and moister	Since 1000 yr BP Campos expansion; forest retraction; cool and very moist	

<sup>1</sup>Behling (1997); <sup>2</sup>Behling (2007); <sup>3</sup>Behling (1995).

Site	Chronology				
	Pre-LGM, LGM and post-LGM	late Glacial	early and mid-Holocene	late Holocene	
Parque Nacional Aparados da Serra <sup>4</sup> 29°25'S, 50°15'W ~1000 m a.s.l.		Before 10 500 yr BP Campos vegetation; existence of <i>Araucaria</i> forest refuges; semi-arid	About 10 500 yr BP Campos vegetation; <i>Araucaria</i> forest expansion from refuges; warmer and wetter	Significant forest expansion over Campos; mild humid phase	
Fazenda do Pinto <sup>5</sup> 29°24'S, 50°34'W 900 m a.s.l.			7500-4000 yr BP Campos vegetation; dry	After 4000 yr BP Campos; small areas of <i>Araucaria</i> forest; wetter conditions	Since 1100 yr BP <i>Araucaria</i> forest expansion; modern climate
Cambará do Sul <sup>6</sup> 29°03'09''S, 50°06'04W; 1040 m a.s.l.	42 850-41 500 yr BP Campos vegetation; small populations of forest trees on the coastal slopes; dry and cold; somewhat wetter than during the LGM and the late Glacial	26 900-10 100 yr BP Campos vegetation; small populations of <i>Araucaria</i> forest and Atlantic rainforest trees on the coastal slopes; seasonal climate with a long annual dry period	10 100-4000 yr BP Campos vegetation; <i>Araucaria</i> forest taxa migrated into the study region; expansion of the Atlantic rainforest on the coastal slopes; warm and dry; seasonal climate with a dry season of about 3 months	4000-1150 yr BP Campos vegetation; <i>Araucaria</i> forest expanded along streams; wetter climate with higher rainfall rates and a shorter annual dry season	Since 1150 yr BP strong expansion of <i>Araucaria</i> forest replacing Campos; permanently wet without seasonality; AD 1520-1770 a warm period during the Little Ice Age
	Alpes de São Francisco <sup>7</sup> 29°29'35''S, 50°37'18''W; 911 m a.s.l.	25 000-12 500 yr BP Campos vegetation; forest taxa in refuges; regional cold and dry after 16 000 yr BP more arid	14 000-12 500 yr BP Campos vegetation; forest taxa restricted to refuges; cold and semi-arid conditions 12 500-9700 yr BP slight migration of arboreal taxa from refuges; warm and moist	9700-6500 yr BP reduction of Campos; forest in refuges; warm and dry 6500-4000 yr BP forest migration from refuges; gradual increase of humidity	4000-2000 yr BP <i>Araucaria</i> forest spread; moister climate
Rincão das Caritas 29°28'35''S, 50°34'22''W; 895 m a.s.l.	16 700-14 900 cal. BP Campos vegetation; forest taxa in small populations on the lower slopes; cold and markedly drier than today with sporadic strong rainfall	14 900-8700 cal. BP Campos vegetation; first forest movement from the lower slopes to higher elevations; warmer-wetter conditions after the late Glacial	8700-2950 cal. BP Campos vegetation; continuous spreading of forest to the upper part of the slopes and initial <i>Araucaria</i> forest development; dry conditions during the early Holocene and wetter after about 4600 cal. BP	2950-1050 cal. BP begin of <i>Araucaria</i> forest expansion; establishment of the Atlantic rainforest on the upper part of the slopes; wetter conditions	Since 1050 cal. BP maximum of forest expansion; continuously wetter conditions with increased precipitation and without long periods of drought

Landscape and vegetational changes with regional climate

Rio Grande do Sul

<sup>4</sup>Roth and Lorscheitter (1993); <sup>5</sup>Behling et al. (2001); <sup>6</sup>Behling et al. (2004); Leonhardt and Lorscheitter (2010).

### ***Climate as the main limiting factor for forest expansion***

The interpretations regarding the first development and expansion of the *Araucaria* forest over Brazilian southernmost highlands after 4000 yr BP under wetter conditions (Behling *et al.*, 2001; Behling *et al.*, 2004; Leonhard and Lorscheitter, 2010) are consistent with our results (see Table III). Palaeoenvironmental records confirmed a marked *Araucaria* forest expansion in the São Francisco de Paula region since about 1000 years, which can be correlated with an increased precipitation and the absence of longer dry periods (Behling *et al.*, 2001, Behling *et al.*, 2004). Hence, the fact that a pronounced expansion of *Araucaria* forest covering Campos on the highlands of Rio Grande do Sul was very late, although small forest populations were already present there, can be explained with higher precipitation rates and a lack of drought since the last 1000 years. Therefore, the evidences point to climate, *i.e.* higher rainfall distributed throughout the year, as the most important factor controlling the *Araucaria* forest expansion on the highlands of southern Brazil. For Leonhard and Lorscheitter (2010), a humid but warmer climate was responsible for limiting the expansion of forest since 2000 yr BP because it affected the reproductive capacity of *Araucaria* forest taxa. We do not consider, however, that the climate has become warm to such an extent, that it served as a potentially limiting factor for forest expansion. Our results rather show an increase of taxa belonging to this ecosystem since at least 2600 yr BP, including *Araucaria angustifolia* itself. However, we have to consider this possibility, as we used percentage data for reconstructing environmental history instead of concentration data as did Leonhard and Lorscheitter. Similar observations have been made by Silva *et al.* (2009). They suggest that *Araucaria angustifolia* can have growth limitations under lower precipitation and higher temperature levels. Hence, the evidences show that future climate changes will strongly influence *Araucaria* forest ecosystems.

Regional environmental differences such as soil depth, edaphic properties, local drainage and topography have also to be considered as possible limiting factors of forest expansion in different times. According to Dümig *et al.* (2008), development and permanence of Andosols is favored by grassland vegetation and the loss of its andic properties caused by forest expansion due to crystallization of Al and Fe oxides. The authors show also that variations of soil properties of the Brazilian southernmost highlands occur in different vegetation types. However, according to them these do not control the expansion of *Araucaria* forest into grassland.

Another explanation for forest expansion taking place in different times could be anthropogenic activity, such as induced fires and forest exploitation. It is known from different studies that Campos areas have been subjected to fires in order to manage pastures for cattle farming (eg, Nabinger *et al.*, 2000; Overbeck *et al.*, 2005; Behling and Pillar, 2007). More recently, Jeske-Pieruschka *et al.* (2010) demonstrated that *Araucaria* forest dynamics are strongly influenced by fire frequencies. We do not think, however, that these human interferences served as a substantially



important cause of limiting *Araucaria* forest expansion but that they can rather be seen as a mechanism preventing forest expansion and controlling its stability.

### ***Fire history***

Results of the charcoal record show a rising trend of micro-charcoal fragments at the end of the late glacial period. Higher concentrations of charred particles from the end of the late glacial (12 650 yr BP) until the mid-Holocene (3000 yr BP) suggest that fire activity was very common in the region. Fires of anthropogenic origin at the beginning of the Holocene in Paraná state (Behling, 1997) and after 7400 yr BP in Rio Grande do Sul state (Behling *et al.*, 2004), suggest an early human occupation of the southern Brazil highlands at different time periods. It may be possible that Amerindians have caused these fires at the transition of the Pleistocene to Holocene in the studied region. According to Prous and Fogaça (1999), the Uumbu and Humaitá tradition occupied the southern Brazil at *c.* 8000 yr BP. On the other hand, because of the small size of the sedimentary charcoal particles (mostly <50µm), wind-transportation from distant and over-regional fire events cannot be excluded.

### **Conclusions**

New palaeoecological interpretations for the São Francisco de Paula region are presented in this work based on the results of the RdC pollen and charcoal record. The investigated core, spanning the last 13 520 yr BP (16 700 cal. BP), provides specific information about the origin and history of the mosaic of grassland and *Araucaria* forest and its expansion during late Quaternary in the São Francisco de Paula region. During the recorded glacial period, the landscape was completely covered by grassland under cold and dry climatic conditions. Some forest taxa and tree ferns were only present in refugia on coastal slopes or as part of the gallery forest along rivers or streams with sufficiently retained humidity. The existence of a local shallow lake before 12 600 yr BP (14 800 cal. BP), as well as similar interpretations of other researches in the same region, lead to the conclusion that a dry and cold climate with sporadic strong rainfall prevailed in the region throughout this period. The lake began to fill up after *c.* 12 600 yr BP (14 800 cal. BP) and became a fully developed peat bog afterwards. The São Francisco de Paula region then continued to be characterized by a treeless landscape with Campos as the predominant vegetation community from the late Pleistocene to the mid-Holocene, thus pointing to dry climatic conditions. Over the last 4250 yr BP (4600 cal. BP), a wetter climate allowed the initial *Araucaria* forest development and a continued spreading of Atlantic rainforest from the lower to the upper parts of the slopes. The development of *Araucaria* forest began after 3100 yr BP (3200 cal. BP). However, its expansion started only about 2900 yr BP (2950 cal. BP). Climate became increasingly wetter since 1160 yr BP (1050 cal. BP),

resulting in continuously forest expansion over Campos ecosystems. *Araucaria* forest spread progressively since the last 1000 years, thereby suppressing the Atlantic rainforest along the upper slopes and forming Campos-forest mosaics on the highlands. Climate seems to be the most important factor limiting *Araucaria* forest expansion on the highlands of southern Brazil. The disturbance of the native vegetation, resulting in forest opening, can be related to human practices since the end of the 19th century. Higher concentrations of micro-charred particles from the late Pleistocene to the mid-Holocene point to frequent fires in the region during this time, thus probably indicating human occupation on the southern Brazil highlands.

### Acknowledgements

Our thanks go to the owner of Rincão das Cabritas, Victor Umann for permitting us to conduct fieldwork in his property. We would like to thank our field collaborators, especially Renato Backes Macedo and Rodrigo Rodrigues Cancelli for assistance with coring. We thank Dr. Gerald Islebe for the review of the manuscript, and Dr. Sonia Fontana for providing constructive comments on the manuscript. Thanks are also to Nele Jantz for reading the English text. The Deutsche Forschungsgemeinschaft (DFG) funded this research (BE 2116/9-1). The Inter American Institute for Global Change Research (IAI) is gratefully acknowledged for financial support for radiocarbon dating and part of the fieldwork.

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## CHAPTER 4

**New insights into vegetation, climate and fire history of  
southern Brazil revealed by a 40,000 years-old  
environmental record from the State Park  
Serra do Tabuleiro**

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*Submitted to Vegetation History and Archaeobotany*

## Abstract

The present study reveals palaeoenvironmental changes in the coastal southern Brazilian highlands during the last 39,720 B.P. by the means of pollen, charcoal and multivariate data analyses. The isolated mountain range of Serra do Tabuleiro corresponds to the southern distribution limit of many tropical species and is therefore sensitive to climate change. Palaeoenvironmental reconstructions from the Ciama 2 core at 860 m a.s.l. indicate that *Campos* (subtropical grassland) covered extensive areas on the highlands throughout the recorded glacial period, thus suggesting cold and dry climatic conditions. The initial development of the Atlantic rainforest occurred after the glacial period, while plant diversity increased only from the beginning of the Holocene due to climate change to warmer and wetter conditions. The development of Atlantic rainforest over the slopes started at about 10,400 cal B.P., when *Campos* retracted. Multivariate data analysis showed a change of vegetation dynamics after 11,200 cal B.P. with initial development of the Atlantic rainforest continuing until the mid-Holocene. Major vegetation changes, with a further expansion of the Atlantic rainforest and the initial development of the *Araucaria* forest on the higher regions of the Serra do Tabuleiro, occurred during the late Holocene after about 3600 cal B.P.. These changes reflect higher precipitation levels without an annual dry season. Multivariate data analysis reveals a clearly directional change of vegetation dynamics corresponding to the progressive expansion of the Atlantic rainforest from 3850 to 1600 cal B.P.. A second directional change of vegetation dynamics occurred from 320 to 160 cal B.P. (A.D. 1630 to 1790) with a further development of the Atlantic rainforest and the replacement of *Campos* by *Araucaria* forest. Thereafter, an ecosystem disturbance, which resulted in forest opening, took place. Palaeofires, which were probably caused by Amerindians, were common from ca. 10,400 until 3600 cal B.P.. During the late Holocene, fires occurred less frequently. Fire events during the Holocene were of mostly anthropogenic origin, as the climate was wet in the early/mid-Holocene and even wetter during the late Holocene.

**Keywords:** Late Quaternary, *Campos*, Atlantic rainforest, *Araucaria* forest, Southern Brazilian climate, fire history, Serra do Tabuleiro

## Introduction

The “Mata Atlântica” is described as a hotspot of biological diversity (e.g. Myers et al. 2000; Tabarelli et al. 2005) and is known to be highly vulnerable to global change. Unfortunately, the Mata Atlântica ecosystems, which are very rich in species and have a high level of species endemism, are under continuous threat by human activity since the European colonization at A.D. 1500 (e.g. Morellato and Haddad 2000). During the past years, investigations using pollen data were carried out

in southern (e.g. Behling and Negrelle 2001) and southeastern Brazil (e.g. Behling and Lichte 1997; Behling and Safford 2010; Garcia et al. 2004; Ybert et al. 2003), where the Atlantic rainforest occurs. Palynological studies can offer palaeoenvironmental information, which is useful for the development of conservation and management strategies.

Here, we provide the first available record of palynological and charcoal data for the late Quaternary in the isolated coastal mountain range of Serra do Tabuleiro, in the state of Santa Catarina, southern Brazil. The State Park Serra do Tabuleiro is part of the Atlantic Forest Biome (IBGE 2004), the so-called “Mata Atlântica” with *Campos* (subtropical grassland) and *Araucaria* forest on the highlands and Atlantic rainforest covering the lowland and the slopes. The species diversity of trees, shrubs, epiphytes and lianas of the Atlantic rainforest gradually decreases towards the south. The Serra do Tabuleiro represents the southern distribution limit of many tropical species and is thus an important phytogeographical divisor (Klein 1962, 1981). Past vegetation and climate dynamics have been studied by Behling (1995, 1997b, 2007) and Behling et al. (2001, 2004) in the southern Brazilian highlands. However, with the exception of Behling et al. (2004), who reported environmental changes over a time frame of 42,840 B.P. for the Cambará site in the southernmost highland in Rio Grande do Sul State, studies including the glacial period are still scarce for the entire southern Brazil highland region. Thus, our study, covering the last 39,720 B.P. years of vegetation, climate and fire history in Santa Catarina state, located about 175 km to the north from Cambará site, will contribute to a better understanding of palaeoenvironmental changes and human activities in a very sensitive climatic region in South America.

In this study, we focus on the development and dynamics of *Campos*, *Araucaria* forest and Atlantic rainforest, and the inferred climatic change in the isolated Serra do Tabuleiro. This study helps to answer the question if this coastal mountain range was a refugium for forest taxa originating from *Araucaria* forest and Atlantic rainforest during the LGM period. Another goal is to detect the effect of future climate changes on the dynamics of grassland vegetation and different forest ecosystems. The significance and influence of fire in the last 39,720 years and the human impact during the past will be addressed as well.

## **Regional setting**

### ***The study area***

The State Park Serra do Tabuleiro was established in 1975 and covers an area of 87,405 ha, being the largest conservation unit in Santa Catarina State (Oliveira et al. 2006). As part of the park, the investigated peat bog (27°53′48.46″S, 48°52′5.33″W) is situated in the Ciama region (860 m a.s.l., Fig. 1). It is located in a small area of *Campos* (subtropical grassland), which is surrounded by forest. Currently, the distribution of *Araucaria* forest in the park is restricted to the Ciama region and its



surrounding areas. Due to the proximity to the coast and its isolation from other mountain ranges, the site is adequate to record the development and dynamics of *Campos*, *Araucaria* forest and Atlantic rainforest, as well as the fire history of the region.

Nowadays, the local population continues to use the land on which they lived before establishment of the park on 1975. Forest exploitation on the Serra do Tabuleiro, mainly by logging of *Araucaria angustifolia* and *Ocotea porosa* (Klein 1981) began in the early 20<sup>th</sup> century due to the establishment of the Ciama sawmill. In the 1950s a road was constructed in the region to facilitate transport of timber. The capital Florianópolis was founded by the first Portuguese settlers in the 17<sup>th</sup> century and later, in the 18<sup>th</sup> century, a new wave of Portuguese settlers colonized the coast more extensively. The first German and Italian settlers arrived in the 19<sup>th</sup> century ([www.angelfire.com/al/Geografia/sc.html](http://www.angelfire.com/al/Geografia/sc.html)).

### **Modern vegetation**

From the coastline to the upper part of the Serra do Tabuleiro at 1200 m a.s.l., five different phytogeographic units can be observed (Klein 1981). In the eastern part, coastal vegetation (so-called *restinga*) and mangroves occur on a Quaternary sand plain. Atlantic rainforest is the dominating vegetation type on the slopes. Cloud forest grows at altitudes from 700 to 900 m. *Araucaria* forest and *Campos* can also be found at higher altitudes. Water supply for Florianópolis and other surrounding cities comes from streams and rivers which rise at higher altitudes. At present, large areas of natural vegetation can still be found within the park. Local vegetation in the Ciama area consists of secondary vegetation. The area is a transition zone of Atlantic rainforest and *Araucaria* forest with small patches of *Campos*. It was not clear to what extent these grassland patches were natural or anthropogenic. The *Araucaria* forest is composed of *Araucaria angustifolia*, diverse Myrtaceae and other tree species such as *Calyptanthes concinna*, *Siphoneugena reitzii*, *Myrciaria tenella* and *Mimosa scabrella*. *Ocotea porosa*, *O. puberula*, *Lamanonia speciosa*, *Weinmannia pauliniaefolia*, *Drimys brasiliensis*, *Vernonia discolor*, *Piptocarpha angustifolia*, *Ilex* spp. and *Dicksonia sellowiana* appear associated with *Araucaria* forest along the upper slopes. Characteristic for the transition between the *Araucaria* forest and the Atlantic rainforest are *Clethra scabra*, *Gomidesia sellowiana*, *Myrsine* spp., *Symplocos* spp., *Clusia criuva*, *Merostachys ternata*, *M. speciosa* and *Chusquea* spp.. Some species from the Atlantic rainforest can also be found, such as: *Alchornea triplinervia*, *Hyeronima alchorneoides*, *Cryptocarya aschersoniana*, *Ocotea* spp., *Nectandra rigida*, *Aspidosperma olivaceum*, *Tapirira guianensis* and *Sloanea guianensis*. Numerous lianas and epiphytes belonging to Bromeliaceae, Orchidaceae, Araceae, Cactaceae, as well as pteridophytes, are typical for the Atlantic rainforest ecosystem. *Campos* vegetation is formed by forbs and graminoids, mostly by Poaceae, Cyperaceae, Fabaceae, Verbenaceae and Asteraceae (Klein 1978, 1981).

### ***Climate***

The climate is characterized as mesothermic (Cfa under 800 m a.s.l. and Cfb above 800 m a.s.l., Köppen) without a dry season. Rainfall is uniformly distributed throughout the year with the average annual precipitation varying between 1600 and 1800 mm/year. Average annual temperatures vary greatly according to the relief: lower regions and the coast have higher temperatures than the highlands, which can reach temperatures below 0 °C in cold winter nights. Climate records from Florianópolis in the lowland show a January mean temperature of 24°C and a July mean temperature of 16°C ([www.inmet.gov.br/html/clima.php](http://www.inmet.gov.br/html/clima.php)). However, moderate summers and cold winters are characteristic for the highlands, while hotter and longer summers characterize the coastal area (due to subtropical latitudes) and further west (due to lower altitudes and continentality). The study site is located in an area, which is mostly influenced by the warm and humid Tropical Atlantic Air Masses and by the cold and dry Polar Atlantic Air Masses. The first ones, occurring during the whole year, are formed over the Atlantic Ocean and occur more frequent during summer (Nimer 1989). The second ones are initially dry, due to the extreme cold climate of Antarctica where they are formed. They become moister only after passing over the Atlantic Ocean. These two types of air masses mostly influence the weather across the continent during winter. In spring, the Equatorial Continental Air mass can provoke lightning and thunder storms.

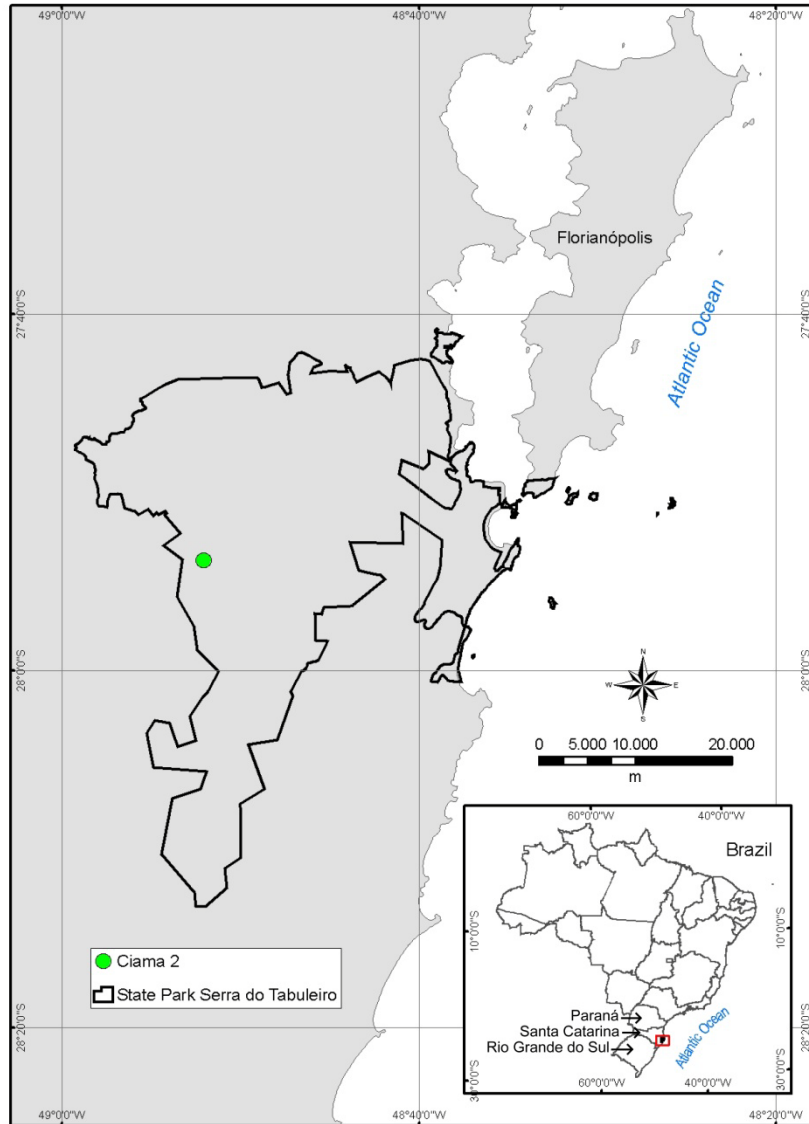


Figure 1. Map of the study area, showing the location of the State Park Serra do Tabuleiro and Ciama 2 (the studied peat bog).

Elaboration Renata I. Duzzioni.

## Material and Methods

### *Fieldwork and subsampling*

A sediment core (169 cm long) was obtained in 2005 using a Russian corer. Each sealed 50 cm long core section was transported to the laboratory and stored under dark and cold conditions until it was opened for sediment description and subsampling. A total of 83 volumetric subsamples (0.25 cm<sup>3</sup>) were used for pollen and charcoal analysis. Subsamples were taken every 2 cm except between 0-8 cm core depth, where two subsamples were taken at an interval of 4 cm. Eight subsamples were sent to the AMS Radiocarbon Laboratory at the University Erlangen-Nürnberg, Germany for <sup>14</sup>C AMS

dating. The age-depth model was constructed through linear interpolation between the radiocarbon ages by considering an equal sedimentation rate. The resulting ages were converted to calibrated calendar years before present using the software CALIB 5.0 (Stuiver and Reimer 1993). We applied the data set of SHCal04 (McCormac et al. 2004) for the ages in the Holocene period as well as for the multivariate data analysis and of IntCal04 (Reimer et al. 2004) for the ages in the Pleistocene period. For each calibrated age range a median probability was adopted.

### ***Pollen and charcoal analysis***

Standard pollen preparation procedures with hydrofluoric acid (HF) and acetolysis followed Faegri and Iversen (1989). One tablet of *Lycopodium clavatum* spores was added to each subsample to be able to calculate pollen and charcoal concentrations and accumulation rates (Stockmarr 1971). All *L. clavatum* spores that occur naturally in the area could be differentiated from the acetolysed *L. clavatum* marker due to the dark coloration and the wrinkled aspect of the latter. The pollen residues were mounted in glycerin gelatin and each sample was counted up to at least 300 pollen grains. Pollen and spores were identified using the reference slides available at the Department of Palynology and Climate Dynamics of the University of Göttingen and morphological descriptions by Behling (1993) and Cancelli (2008). The pollen sum, which includes all terrestrial taxa, as well as pollen percentages and concentration, were calculated and plotted in TILIA and TILIAGRAPH (Grimm 1991). The zonation of the pollen diagrams (C2-I – IV) was based on the cluster analysis using CONISS (Grimm 1987). The charcoal analysis was based on microscopic charred particles (5 – 150 µm) which were counted on the pollen-slides.

### ***Multivariate analysis***

Principal coordinates analysis (PCoA) of the counted pollen data set (total of 83 subsamples as units and 120 taxa as variables) was used as ordination method applied to Chord distances between subsamples. All analyses were performed using the MULTIV 2.5 software (Pillar 2006). Aquatic and non-identified pollen grains, as well as all spores, except the tree fern ones, were excluded prior to analysis in order to avoid the interference of local indicators in the results. All taxa present in at least two subsamples were included. Pollen sums were square root transformed before calculating the distances to reduce the importance of dominant taxa. The ordination analysis represents past vegetation dynamics from 39,720 to -55 B.P. (A.D. 2005). In addition, we analyzed the vegetation trajectory during the recorded Pleistocene period to the mid-Holocene and over the Holocene. To verify local fire events, correlations between taxa and the concentration of charred particles were performed for the Pleistocene and Holocene period.

## Results

### Lithology

The 169 cm long sediment core consists of seven distinct units (Fig. 2). The sediment is composed of light-brown very sandy clay with organic material and small granite stones at the bottom (169-142 cm). From 142 to 70 cm core depth, the sediment consists of brown clay with organic material. Within this section, small amounts of sand and small granite stones occur between 142 and 120 cm. The following interval from 70 to 45 cm is composed of black clay with few fine roots. Between 45 and 25 cm, the sediment contains dark-brown decomposed peat with some fine roots and from 25 to 17 cm, the sediment contains light-brown decomposed peat with many fine roots. The overlying section (17-7 cm) consists of brown, decomposed peat rich in fine roots. In the upper part of the core (7-0 cm), there is a layer of weakly decomposed peat with *Sphagnum* sp. covering the top.

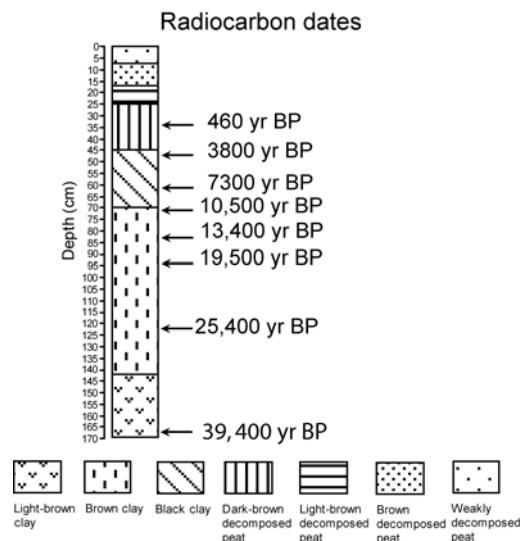


Figure 2. Lithology and location of dated subsamples on the Ciama 2 sediment core. (uncalibrated years B.P.).

### Radiocarbon dating and chronology

The chronology of the sediment sequence is constructed from eight accelerator mass spectrometry (AMS) radiocarbon dates (Tab. 1). The extrapolated basal age at 168 cm core depth corresponds to 39,720 B.P.. Based on the radiocarbon dates, a continuous sedimentation with no gaps is suggested for the recorded glacial and Holocene periods. Pollen of *Pinus* occurs in the subsamples between 14 and 0 cm core depth, which would be after 160 cal B.P. (approximately A.D. 1790) indicating a complete core until modern times. The age vs. depth relationship (Fig. 3) shows that sedimentation rates were relatively constant through time until 34 cm core depth, when the sedimentation rate increases. Around this point the sedimentological composition changes from clayey

sediment to almost decomposed peat after 45 cm core depth and to weakly decomposed peat after 7 cm core depth. As expected, pollen concentration rates decreases significantly during this period.

Table 1. Radiocarbon ages and calibrated ages of organic matter from Ciama 2 core.

Sample	Depth (cm)	Age ( <sup>14</sup> C year B.P.)	Age range* (cal year B.P.)	Med. Prob. (cal year B.P.)	Calibration curve
Erl-11255	34	459 ± 4	328 - 534	478	SH cal
Erl-12097	47	3820 ± 39	3981 - 4284	4129	SH cal
Erl-12656	61	7327 ± 45	7981 - 8179	8092	SH cal
Erl-11256	71	10,536 ± 63	12,240 - 12,786	12,545	Int cal
Erl-12657	83	13,399 ± 72	15,528 - 16,341	15,916	Int cal
Erl-12098	94	19,439 ± 115	22,661 - 23,596	23,126	Int cal
Erl-12099	122	25,380 ± 152	too old for calibration		
Erl-11257	167	39,407 ± 681	too old for calibration		

\* Range at standard deviation of 2 sigma at 95.4% probability

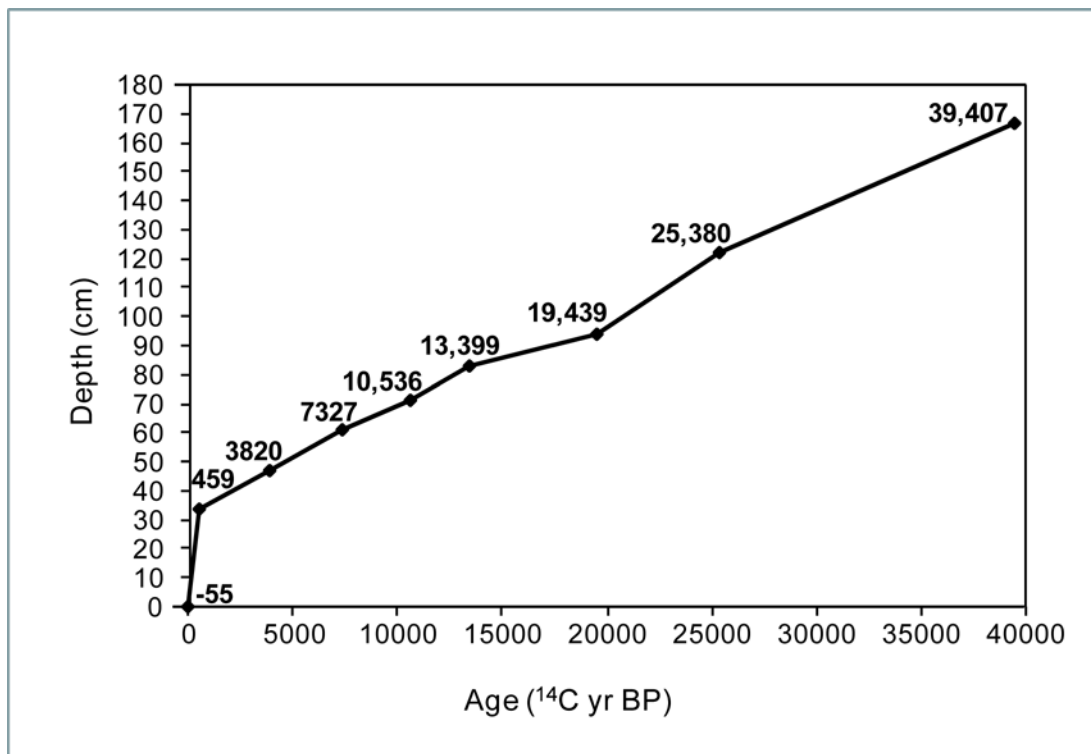


Figure 3. Radiocarbon ages from Ciama 2 core plotted against depth (cm).

### ***Palaeoecological record***

The pollen diagram (Fig. 4) illustrates the percentages of the dominant and most important taxa out of 200 different pollen and spore types found in the core subsamples. A summary pollen diagram (Fig. 5) represents the pollen taxa grouped into different vegetation types, as well as the charcoal data. Based on important changes in the pollen assemblages and on the result of the cluster analysis, four pollen zones have been distinguished (C2-I to C2-IV) (Tab. 2). Pollen concentrations vary between  $61 \times 10^7$  and  $4,800 \times 10^7$  grains/cm<sup>3</sup> and pollen influx varies between 43,700 and 4,600,000 grains/cm<sup>2</sup> yr.

Zone C2-I (39,720 - 17,800 B.P.) is divided into two subzones (Ia and Ib) due to slight changes in pollen composition. Zone C2-I is characterized by high percentages of *Campos* taxa (69-90%), consisting primarily of Poaceae (49-75%) and minor pollen proportions of Cyperaceae, different Asteraceae, *Eryngium* type, Apiaceae, *Xyris*, Iridaceae and *Plantago*. Atlantic rainforest taxa are relatively constant (5-23%) and are represented mostly by pollen of Myrtaceae, *Weinmannia* type, *Myrsine* and Melastomataceae. Less frequent (1-5%) are taxa of the *Araucaria* forest, represented by pollen of *Ilex*, *Mimosa scabrella* type and *Podocarpus*. A single *Araucaria angustifolia* pollen grain was counted at 142 cm core depth, but single pollen grains were also found at 152, 166 and 168 cm core depth not included in the pollen sum, as found in an additional scanning process. The tree ferns group reaches up to 8%, principally due to the rise of spores of Cyatheaceae. Pteridophyta, with values between 4% and 15%, are mainly represented by spores of *Blechnum imperiale* type, Monolete psilate <50µm, *Selaginella excurrens* type and *Isoetes*. Moss spores are poorly represented by low percentages of *Sphagnum* (0-1%). Concentrations of carbonized particles ( $960 \times 10^{10}$  -  $32,250 \times 10^{10}$  particles/cm<sup>3</sup>) and influx ( $31 \times 10^7$  -  $1500 \times 10^7$  particles/cm<sup>2</sup>yr) are constantly low during this period.

The lower subzone, C2-Ia (39,720 - 32,500 B.P.), shows higher values (up to 5%) for the *Araucaria* forest group, mainly due to *Ilex* pollen which decreases during the subsequent subzone. The subzone C2-Ib (32,500 - 17,800 B.P.) shows a slight increase in pollen diversity. Pollen of *Ouratea* type, *Trema* type and *Dodonaea* type (not shown in the diagram) appears for the first time in the Atlantic rainforest group. Likewise, pollen of the *Clethra* type (not shown in the diagram) as part of the *Araucaria* forest group, and spores of the tree fern *Dicksonia sellowiana* can be found for the first time. The proportions of tree ferns taxa and the other Pteridophyta spores decrease in this subzone.

In zone C2-II (17,800 - 9900 B.P.) the percentages of *Campos* taxa increase slightly from 84% to 90%, dominated by Poaceae pollen (65-78%). Pollen of Cyperaceae, *Eryngium* type, Apiaceae, Iridaceae and *Plantago* decreases in abundance to  $\leq 2\%$ . A slight decrease of percentages of the Atlantic rainforest group can be noted. *Alchornea* pollen percentages increase to the top of this zone up to 3%. The *Mimosa taimbensis* type occurs until 86 cm core depth. Abundances of *Araucaria* forest taxa decrease to 0%. Tree fern spores are represented by decreasing percentages, mainly by low

values of Cyatheaceae (<4%). The Pteridophyta group remains stable but abundances of spores of *Blechnum imperiale* type and of *Isoetes* drop at the top of this zone. Mosses are basically represented by *Sphagnum* spores (0-3%). Charcoal concentration ( $2000 \times 10^{10}$  –  $30,000 \times 10^{10}$  particles/cm<sup>3</sup>) and charcoal influx ( $38 \times 10^7$  –  $1000 \times 10^7$  particles/cm<sup>2</sup>yr) continues to be low during this zone.

Zone C2-III (9900 - 3300 B.P.) shows a decrease in *Campos* taxa (80- 63%), attributed mainly to lower percentages of Poaceae pollen (65-40%). Pollen abundances of Asteraceae subf. Asteroideae increase up to 10% and those of Apiaceae up to 5%. *Eryngium* type reaches its highest values (8%) in this zone. A marked increase of abundances of the Atlantic rainforest taxa from 12% to 28% can be noted. It is mainly due to the increase in *Weinmannia* type pollen to 14% at the top of this zone. Pollen percentages of *Myrsine*, Melastomataceae and *Alchornea* and, with lower values, of Moraceae/Urticaceae, *Celtis* and *Trema* type also increase. Myrtaceae pollen frequencies slightly decrease (4-1%). Much less frequent are taxa of the *Araucaria* forest (<2%). Tree fern taxa increase to 7%, with higher proportions of Cyatheaceae and lower frequencies of *Nephelea setosa* and *Dicksonia sellowiana*. The group of Pteridophyta is well represented with values between 6% and 16%, mainly composed of spores of Monolete psilate <50 µm. Spore abundances of *Blechnum imperiale* type increase up to 7% at the top of this zone. Abundances of spores of *Selaginella excurrens* type decrease strongly (7-0%). Mosses proportions increase slightly up to 5%, represented by spores of *Sphagnum* and *Phaeoceros laevis* (not shown in the diagram). Values for concentrations ( $33,000 \times 10^{10}$ -  $115,000 \times 10^{10}$  particles/cm<sup>3</sup>) and influx ( $1100 \times 10^7$  –  $4500 \times 10^7$  particles/cm<sup>2</sup>yr) of carbonized particles increase markedly in this zone.

Zone C 2-IV (3300 B.P. to the present) is also divided into two subzones (IV-a and IV-b). A strong decrease from 61% to 26% in *Campos* taxa, reflected mostly by the decrease of Poaceae pollen (31-7%), characterize this zone. Abundances of Cyperaceae pollen increase markedly compared to the previous zone and reaches values of 21%. Pollen frequencies of Heliantheae type also increase (up to 8%) whereas Apiaceae pollen percentages decrease strongly, reaching a maximum value of 1%. Pollen abundances of *Eryngium* type decreases continually from 6% at the first part of the zone to 0%, but increases towards the top of the core up to 3%. Abundances of Atlantic rainforest taxa show a further increase with values between 30% and 54%, as pollen percentages of Myrtaceae (2-22%) and *Weinmannia* type (8-37%) rise. Moraceae/Urticaceae pollen frequency increases again slightly (4%), while pollen percentages of Melastomataceae and *Alchornea* decrease. The *Araucaria* forest group shows a notable increase from 1% to 24 %, mostly due to values of *Mimosa scabrella* type pollen (0.3-20%). Percentages of *Araucaria angustifolia* pollen increase considerably up to 4%, but decline towards to the top of this zone. Abundances of tree fern taxa increase up to 10%, but decrease further to a minimum of 1%. Pteridophyta spores reach very high proportions up to 121% at 24 cm depth, but decrease strongly to a minimum of 5% at 4 cm core depth.



Spores of *Lycopodium clavatum* type (0-6%) increase, whilst spores of *Selaginella excurrens* type and *Isoetes* are only found sporadically during this period. Mosses are mainly represented by *Sphagnum* spores (0.3-5%). Concentration ( $50,000 \times 10^{10}$  particles/cm<sup>3</sup>) and influx ( $2000 \times 10^7$  particles/cm<sup>2</sup>yr) of carbonized particles are very high only in the lowermost part of the zone and decrease significantly towards the top of the core ( $200 \times 10^{10}$  particles/cm<sup>3</sup> and  $150 \times 10^7$  particles/cm<sup>2</sup>yr, respectively).

The deepest subzone, C2-IVa (3300 - 290 B.P.), shows an increase in *Baccharis* type, *Eupatorium* type, *Senecio* type, *Calea* type, *Pluchaeae* type and *Xyris* pollen frequencies. The opposite trend can be observed for the following subzone C2-IVb (290 B.P. to the present). Cyperaceae pollen abundances increase markedly compared to the previous subzone (up to 21%). Pollen percentages of Myrtaceae (2-11%) increase again during the subzone C2-IVa and reach maximum values of 22% in the next subzone C2-IVb. Abundances of *Weinmannia* type pollen increase strongly with proportions up to 37% at C2-IVa, but decrease to 8% in the following subzone. Compared to the previous subzone, *Lamanonia speciosa* type, *Celtis*, *Symplocos lanceolata* type, *Ouratea* type and *Trema* type pollen occur with higher proportions in subzone C2-IVb. *Ilex* and *Mimosa scabrella* type pollen percentages increase in subzone C2-IVa and continue to increase in subzone C2-IVb. *Podocarpus* pollen frequencies decrease to 0% in subzone C2-IVb. *Pinus* pollen reaches amounts of 1% at the top of the core. Cyatheaceae spores decrease in abundance compared to the previous subzone. Proportions of *Blechnum imperiale* type (up to 58%) and Monolete psilate <50 µm (up to 50%) reach high values in subzone C2-IVa, but decrease significantly in the subsequent subzone.

Table 2. Pollen zones of the Ciama 2 core, showing the depth, the converted radiocarbon ages and the number of subsamples of each pollen zone.

Zone	Depth (cm)	Age range ( <sup>14</sup> C year B.P.)	Age range (cal year B.P.)	No. of subsamples
C2-Ia	168 - 145	39,720 - 32,500		12
C2-Ib	145 - 91	32,500 - 17,800		27
C2-II	91 - 69	17,800 - 9900	21,200 - 10,400	11
C2-III	69 - 45	9900 - 3300	10,400 - 3600	12
C2-IVa	45 - 23	3300 - 290	3600 - 300	11
C2-IVb	23 - 0	290 - -55	300 - -55	10

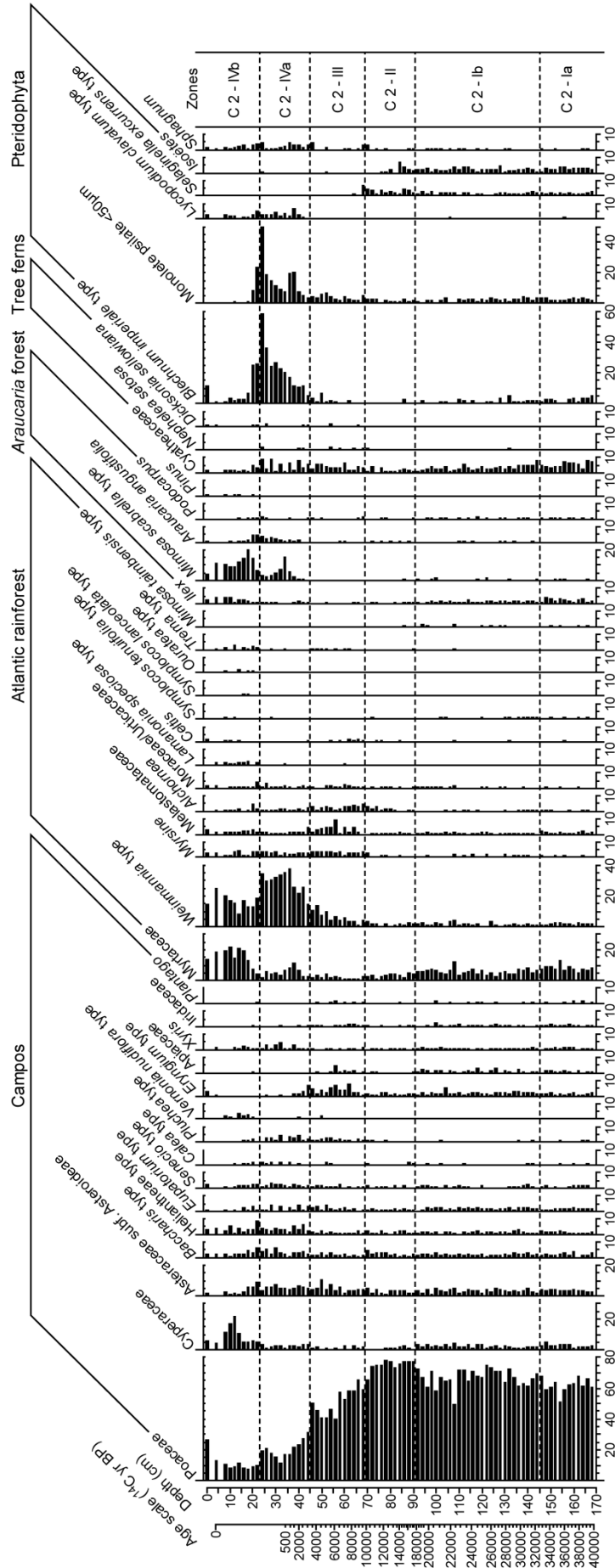


Figure 4. Pollen diagram for the Ciama 2 core, showing percentages of the major and significant taxa, grouped into Campos, Atlantic rainforest, Araucaria forest, Tree ferns and Pteridophyta based on the total pollen sum.



### **Multivariate analysis**

The complete trajectory of pollen composition changes over the last 39,720 B.P. is shown in the ordination diagrams (Fig. 6a, b). Axes 1 and 2 explain 58% of the total variation in the data set with 120 taxa and 83 subsamples. A random phase, with slight changes in vegetation occurs during the glacial period until 12,680 B.P. (13,470 cal B.P.) with *Campos* as the dominating vegetation type in the system. Non-directional changes in the pollen composition dynamics at the small temporal scale and a directional trend at the large scale during the end of the Pleistocene (12,680 B.P. or 13,470 cal B.P.) until mid-Holocene (3560 B.P. or 3850 cal B.P.) can be observed in Fig. 6b. The replacement of the initially predominant *Campos* (Fig 6a, on the right-hand side) by forest vegetation (Fig 6a, on the left-hand side) occurs only after 3850 cal B.P., when Atlantic rainforest and *Araucaria* forest expands. Changes in the pollen composition along a time trajectory from 39,720 until 3560 B.P. (3850 cal B.P.) are depicted on a separate ordination (Fig. 6c, d), in which the two main axes account for 35% of the total variation. During the period from 39,720 until 12,680 B.P. (13,470 cal B.P.), corresponding to the pollen zones C2-I – II, the system is dominated by *Campos*, represented primarily by Poaceae (Fig. 6c). Some taxa belonging to the *Araucaria* forest, like *Ilex* and Myrtaceae, are present, but slightly decrease during this period. Myrtaceae may also correspond to species that occur in the *Campos* vegetation, which can be seen on the right-hand side in Fig. 6c, together with the groups of Cyperaceae and Apiaceae. Subsequent to phases of randomness, an evident change in the vegetation dynamics occurs after 10,780 B.P. (11,200 cal B.P.), corresponding to the pollen zone C2-III. The vegetation is characterized by increased quantities of forest taxa, such as *Alchornea*, *Myrsine*, *Weinmannia* and Melastomataceae, which represent the Atlantic rainforest (Fig. 6c, on the left). Another ordination exploring the period of 8930 B.P. (9510 cal B.P.) to -55 B.P. (A.D. 2005) (Fig. 6e, f) reveals the vegetation dynamics over the Holocene period and corresponds to the pollen zone C2-IV. The main ordination axes account for 47.6% and 12.6%, respectively, for the first and second axes. Three phases of strong directionality of vegetation change occur. The first significant directional change in the pollen composition appears between 3560 until 1490 B.P. (3850 until 1600 cal B.P.), when vegetation changes from predominant open vegetation, such as *Campos* (Fig. 6e, on the right), to more arboreal (Fig. 6e, on the left). The Atlantic rainforest expands, mostly represented by *Weinmannia*, whereas the *Araucaria* forest starts to develop, as it is reflected by *Araucaria angustifolia* pollen grains (Fig. 6e). The second directional change follows a random phase and takes place from about 310 until 160 B.P. (A.D. 1630 to 1790). During this phase, a further development of the Atlantic rainforest and the *Araucaria* forest occur, which replaces the *Campos*. This is represented by the taxa *Lamanonia speciosa*, Myrtaceae, *Symplocos tenuifolia*, *S. lanceolata* and *Ouratea* (Fig. 6e, on the left). Also, *Araucaria* forest is well represented in the diagram by taxa such as *Mimosa scabrella*, *Ilex* and *A. angustifolia*. From 5 to -55 B.P. (A.D. 1940 to 2005), subsequent to the spatial expansion of the

forest, a sharp change in pollen composition takes place, with a tendency towards a pollen composition of *Campos* vegetation.

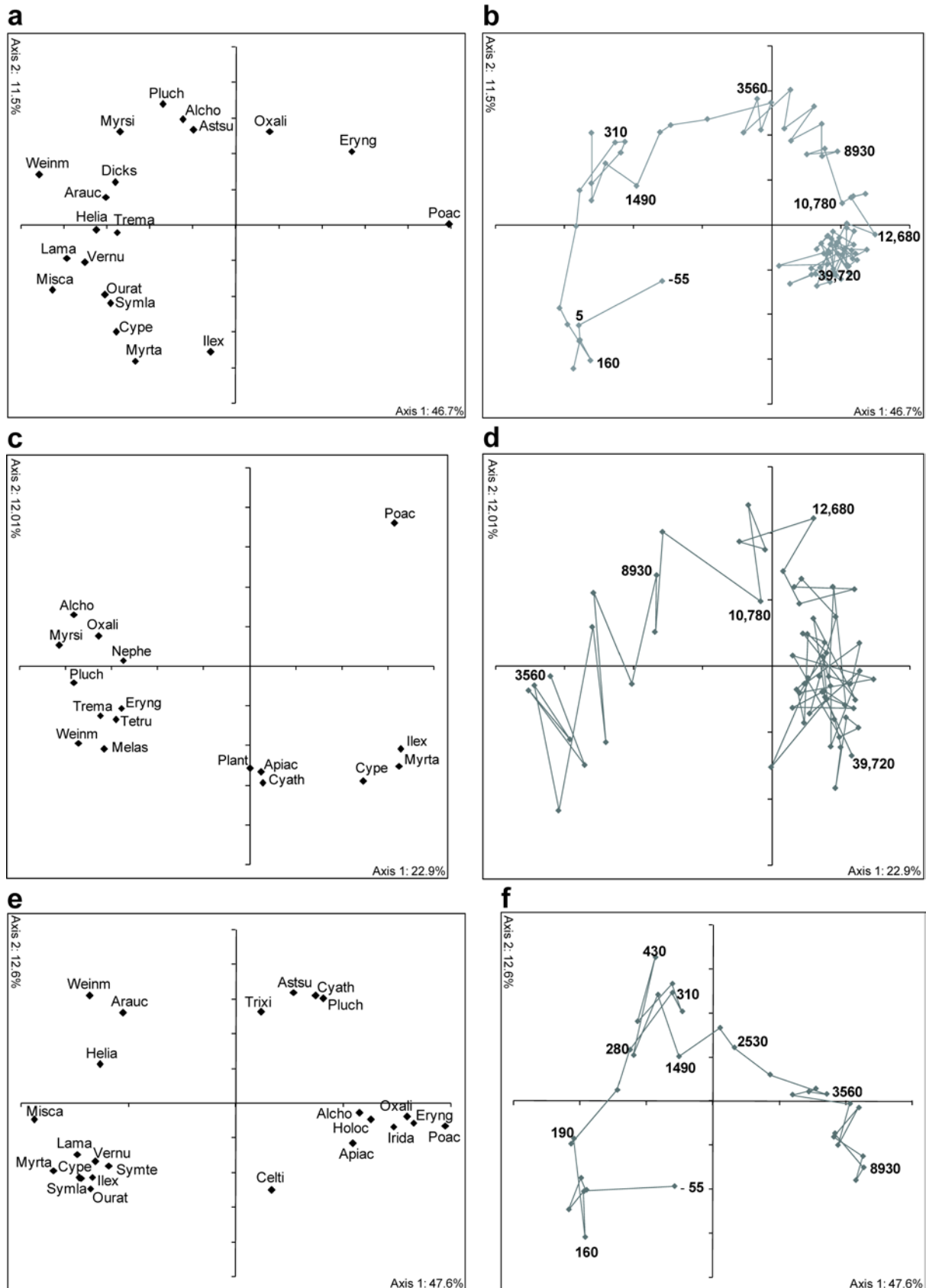


Fig. 6 Ordination diagrams using Principal Coordinate Analysis (PCOA) applied to chord distances

between sampling units from the Ciama 2 core. Pollen data were previously transformed by the square root. The complete vegetation trajectory for the last 39,720 B.P. is mapped in the diagrams (a) and (b) with 83 sampling units and 120 taxa including counted pollen types and tree fern spores. Sampling units are identified by age (radiocarbon years). Other separated ordinations using the same method map the trajectory over the Pleistocene until mid-Holocene in (c) and (d), with 62 sampling units and 102 taxa, and over the complete Holocene in (e) and (f), with 33 sampling units and 87 taxa. Only taxa with the highest correlation ( $-0.5 \leq r \leq 0.5$ ) are shown in positions proportional to their correlation level to the each ordination axis in (a), (c) and (e). Taxa abbreviations are in Table 3.

Table 3. Abbreviations of the pollen taxa shown in the ordination diagrams.

Abbreviation	Pollen and spore taxa	Abbreviation	Pollen and spore taxa
Alcho	<i>Alchornea</i>	Myrsi	<i>Myrsine</i>
Apiac	Apiaceae	Myrta	Myrtaceae
Arauc	<i>Araucaria angustifolia</i>	Nephe	<i>Nephelea setosa</i>
Atsu	Asteraceae subf. Asteroideae	Ourat	<i>Ouratea</i> type
Celti	<i>Celtis</i>	Oxali	<i>Oxalis</i> type
Cyath	Cyatheaceae	Plant	<i>Plantago</i>
Cype	Cyperaceae	Pluch	Plucheae type
Dicks	<i>Dicksonia sellowiana</i>	Poac	Poaceae
Eryng	<i>Eryngium</i> type	Symla	<i>Symplocos lanceolata</i> type
Helia	Heliantheae type	Symte	<i>Symplocos tenuiflora</i> type
Holo	<i>Holocheilus</i> type	Tetru	<i>Tetrorchidium rubrivenium</i>
Ilex	<i>Ilex</i>	Trema	<i>Trema</i> type
Irida	Iridaceae	Trixi	<i>Trixis</i> type
Lama	<i>Lamanonia speciosa</i> type	Vernu	<i>Vernonia nudiflora</i> type
Melas	Melastomataceae	Weinm	<i>Weinmannia</i> type
Misca	<i>Mimosa scabrella</i> type		

## Interpretation and Discussion

### *Palaeoecological reconstruction for the pre-LGM (Last Glacial Maximum) and LGM period*

Grassland predominated throughout the pre-LGM and LGM period from 39,720 B.P. until 21,200 cal B.P. (pollen zone C2-I). The vegetation was mainly composed of grasses (Poaceae) and different forbs of the Asteraceae family, but also of Cyperaceae, Apiaceae and other plants characteristic for grassland ecosystems. Some species of Myrtaceae, placed in the Atlantic rainforest group, probably belonged to the grassland vegetation during the recorded last glacial. They might have been shrub species (e.g. *Campomanesia* spp.) that grew in open grassland vegetation at this time. During the pre-LGM and LGM period, the Atlantic rainforest was represented by low frequencies of *Weinmannia*, *Myrsine*, Melastomataceae, *Alchornea*, Moraceae/Urticaceae, *Celtis*, *Symplocos tenuifolia* and *Mimosa taimbensis*. Small populations of arboreal taxa probably occurred on the slopes of the mountain range at lower elevations or even formed small gallery forests along rivers or streams in the lowland, thereby creating refugia. It might be possible that these taxa existed in deep valleys of the Serra do Tabuleiro or in areas with well-drained soils because of the retained humidity. The proximity to the Atlantic Ocean could have positively influenced the southward migration of forest taxa from the north due to moderate and moister conditions in the coast. The coastal mountain range of Serra do Tabuleiro was no glacial refugium for forest taxa during the LGM. Some (sub-) tropical forest species such as *Roupala*, *Drimys brasiliensis*, *Mimosa taimbensis*, *Sebastiania commersoniana* (not shown in the pollen diagram) and *Symplocos lanceolata* were not present during the LGM period. Other sensitive arboreal species such as *Alchornea* and *Myrsine* were represented by diminished abundances, sometimes with only one pollen grain in the whole period. These slight differences in the pollen spectra reflect colder and drier climatic conditions for the LGM in comparison to the pre-LGM on the Serra do Tabuleiro. Only a few pollen grains of *Araucaria angustifolia* and *Podocarpus* during the last glacial period suggest the presence, probably in scattered patches, of these trees in the lower regions of the Serra do Tabuleiro. When taking *Araucaria angustifolia* as an indicator species for moist and cold forest, because it can neither tolerate temperatures lower than  $-10^{\circ}\text{C}$  nor an annual precipitation lower than 1400 mm (Hueck 1966), climate was cold on the Serra do Tabuleiro during the last glacial. With respect to palaeoclimate, Behling and Negrelle (2001) propose an annual average cooling of  $5^{\circ}$  to  $7^{\circ}\text{C}$  for the LGM period in the southern Brazilian lowland.

Dry and cold climate conditions appeared in the region during the pre-LGM and LGM period (pollen zone C2-I). According to Behling et al. (2004), climate in the southern Brazilian highlands was dry and cold during the pre-LGM, but even drier and colder during the LGM. Other authors agree that cold and dry conditions prevailed during the last glacial (e.g. Behling 1998; Behling et al. 2005; Leal and Lorscheitter 2007; Leonhard and Lorscheitter 2010). Additional information on a late Pleistocene dry period comes from a geomorphic study in the northern highlands of Santa Catarina state (Oliveira

et al. 2008). The authors suggest a warming and drying phase for the pre-LGM in relation to the previous period and cold and drier climatic conditions for the LGM.

The multivariate analysis of the pollen data indicates a predominance of *Campos* taxa during the palaeovegetational trajectory spanning over glacial times (from 39,720 to 12,680 B.P. or 13,470 cal B.P.; pollen Zone C2-I-II). As indicated by a random phase, only little changes in pollen composition that does therefore not reflect marked changes in vegetation dynamics prevailed during the last glacial period. Steady cold climatic conditions at this time may have produced just small-scale compositional changes in the highlands.

#### ***Palaeoecological reconstruction for the late glacial period***

The slight decrease of Atlantic rainforest taxa such as *Weinmannia*, *Myrsine*, *Symplocos tenuifolia* and *Mimosa taimbensis* signalize that a dry phase lasted throughout the pollen zone C2-II (21,200 to 10,400 cal B.P.). Forest taxa, such as *Ilex*, together with Cyperaceae and tree ferns (Cyatheaceae), decreased during this period, thus indicating drier conditions. This hypothesis is also supported by the increase of Poaceae. However, a dry phase from 21,200 to 10,400 cal B.P. cannot be recognized in the ordination diagrams, as Poaceae were the dominant taxon in the system throughout the last glacial stage. Roth and Lorscheitter (1993) proposed drier conditions before the Holocene for the Aparados da Serra region in the southern Brazilian highlands. They record a reduced forest cover and an expansion of grassland. Thus, our results for the Ciama 2 profile corroborate these and other previous findings (Behling 1995; Behling et al. 2004; Oliveira et al. 2008) which indicate mostly drier conditions for the late glacial period.

#### ***Palaeofires***

Charcoal particles were relatively rare during glacial times. They can be interpreted as wind-blown from fire events over distant localities, assuming that natural fires were very unlikely in these highland environments at glacial periods. Local palaeofires could not be detected based on the concentration of charred particles, as the counted particles sizes (5 – 150 µm) were mostly too small to give certainty about this. The sedimentary charcoal fragments (<50 µm) indicate distant or over-regional fire events. In addition, results of unexpected correlations between pollen taxa and charcoal concentration (Tab. 4) during the Pleistocene (pollen zone C2-I and C2-II) support the assumption that fire was almost absent during glacial periods on the Serra do Tabuleiro. Forest taxa, such as *Weinmannia*, show a highly positive correlation with charcoal concentration, while Poaceae as a *Campos* taxon and *Blechnum imperiale* as a fern that grows in peat bogs are negatively correlated to charcoal concentration.



Table 4. Pollen taxa with the highest positive or negative correlations with charcoal concentration during the Pleistocene and for the Holocene period. All pollen taxa found in at least 50% of the subsamples were used for the analysis.

Pleistocene 39,720 – 10,200 <sup>14</sup> C years		Holocene 9600 <sup>14</sup> C years until present	
Taxa	<i>r</i>	Taxa	<i>r</i>
<i>Weinmannia</i> type	0.57396	Poaceae	0.75412
<i>Alchornea</i>	0.36713	<i>Eryngium</i> type	0.65964
Asteraceae subf. Asteroideae	0.35346	Melastomataceae	0.50486
<i>Baccharis</i> type	0.33598	Cyperaceae	-0.43453
<i>Myrsine</i>	0.27903	<i>Blechnum imperiale</i> type	-0.45904
<i>Holocheilus</i> type	0.27424	<i>Araucaria angustifolia</i>	-0.46249
Iridaceae	0.25451	<i>Ilex</i>	-0.4772
<i>Blechnum imperiale</i> type	-0.34302	<i>Lamanonia speciosa</i> type	-0.48713
Poaceae	-0.40661	Heliantheae type	-0.50711
		Myrtaceae	-0.5557
		<i>Lycopodium clavatum</i> type	-0.58425
		<i>Weinmannia</i> type	-0.58822
		<i>Mimosa scabrella</i> type	-0.61206

#### ***Palaeoecological reconstruction for the early/mid-Holocene***

The beginning of the Holocene was characterized by an increase in tree pollen frequencies like *Weinmannia*, *Myrsine* and *Alchornea*, thus reflecting the early development of Atlantic rainforest from the lowland over the slopes. Between 10,400 and 3600 cal B.P. (zone C2-III), *Campos* taxa, such as some Asteraceae, *Eryngium*, Apiaceae, Iridaceae and *Plantago*, as well as forest taxa, such as Melastomataceae, Moraceae/Urticaceae, *Celtis* and *Trema*, rose in abundance simultaneously with tree ferns, thereby indicating a climatic improvement to wetter and warmer conditions. This vegetational change, implying forest development/expansion, but also reflecting the maintenance of a forest-grassland mosaic could be due to an increase in precipitation in the Pleistocene/Holocene transition. The multivariate analysis gives clear evidence for a marked change on vegetation dynamics after 11,200 cal B.P.. Better climatic conditions with higher humidity permitted a forest development, which is indicated by a large-scale directional trend during the end of the Pleistocene (13,470 cal B.P.) until the mid-Holocene (3850 cal B.P., Figure 6c, d). Forest taxa, such as *Alchornea*, *Myrsine*, *Weinmannia* and Melastomataceae, increased during this transition period, thus suggesting the expansion of Atlantic rainforest.

The results indicate that, allowed by warmer and wetter climatic conditions, Atlantic rainforest likely extended over the coastal slopes. A similar climatic trend has been observed on the eastern side

of Morro de Itapeva (southeastern Brazil) in the early Holocene, whereas dry conditions prevailed in the highlands (Behling 1997a). A pollen profile of São Francisco de Paula, on the eastern plateau of southern Brazil (Serra Geral), indicates that temperature and moisture increased at the beginning of the Holocene (Leonhard and Lorscheitter 2010). The pollen record from Serra Velha on the lower slope of the Serra Geral about 330 km south from Ciama 2 site shows the occurrence of Atlantic rainforest taxa at about 8800 and 5000 B.P., indicating the migration of tropical species from an eastern to a western direction since the early Holocene (Leal and Lorscheitter 2007). However, Behling (1995) demonstrated for the southern Brazil highlands that *Campos* vegetation continued to prevail until ca. 1000 B.P. on Morro da Igreja and Serra do Rio do Rastro, while an expansion of Atlantic rainforest taxa followed by *Araucaria* forest occurred at the beginning of the Holocene in the Serra da Boa Vista. The latter site is located 50 km inland from the Atlantic Ocean and approximately 35 km from the Ciama 2 site, which in turn is situated just 25 km away from the coast. The proximity of this site to the Atlantic Ocean may have provided higher moisture influenced by the warm and humid Tropical Atlantic Air Mass.

In the southern Atlantic lowland, Atlantic rainforest started to develop after 12,300 B.P. as a part of a successional sequence. However, a dense forest grew only after the marine regression at about 6100 B.P. (Behling and Negrelle 2001). A wet climate has been recorded since 4900 cal B.P. for the southeastern (Ybert et al. 2003) and about 4000 B.P. for the southern (Cordeiro and Lorscheitter 1994) Brazilian coastal lowland.

Drier conditions and a longer annual dry season are reported for the early- and mid-Holocene for southern (Behling 1997b, 2002, 2007; Behling et al. 2001, 2004) and southeastern Brazil (Garcia et al. 2004). However, these studies cover sites that are more inland than Ciama 2. Our results from the Serra do Tabuleiro, which is located much closer to the Atlantic Ocean, indicate humid conditions throughout the whole Holocene.

#### ***Palaeoecological reconstruction for the late Holocene***

From 3600 cal B.P. until present (zone C2-IV), we observe a continuous development/expansion of Atlantic rainforest, and *Araucaria* forest began to develop and expand as well. At this time, the study bog was covered by *Sphagnum* and *Blechnum imperiale*.

The establishment of a forest environment throughout the late Holocene (3600 to 300 cal B.P.; zone C2-IVa) is indicated by the decrease of Poaceae, some Asteraceae, Apiaceae, *Eryngium* and other *Campos* taxa, whereas Myrtaceae and *Weinmannia* highly increased. *Araucaria* forest began to develop at approximately 2160 cal B.P. and reached its maximum expansion after 300 cal B.P. (A.D. 1650) in the study area. Hence, a pronounced development of the *Araucaria* forest happened much later in the Serra do Tabuleiro than in the Serra Geral further south, and just in the

northwestern part of the park. The isolated occurrence of *Araucaria* forest and its very late expansion despite of favorable climatic conditions suggest that the Serra do Tabuleiro was not a refugium for *Araucaria* forest taxa during glacial times.

Three evident directional changes of vegetation dynamics, corresponding to the pollen zone C2-IV, happened over the Holocene trajectory (9510 cal B.P. to the present). From 3850 to 1600 cal B.P., Atlantic rainforest continued to expand, mostly due to *Weinmannia* and Myrtaceae, while the *Araucaria* forest group started to develop mainly with the pioneer taxa *Mimosa scabrella* and *Araucaria angustifolia*. Forest development and expansion was probably related to increased moisture levels during this period. Pollen data from other sites in the southern Brazilian highlands are consistent in suggesting that forest expansion started in the mid-Holocene and reached its expansion maximum after 1500 cal B.P. (Behling 1995, 1997b, 2007; Behling et al. 2004).

The continuous forest development during the late Holocene indicates an amelioration of climate towards moister conditions. Higher precipitation levels without a major annual dry season that allowed marked forest expansion since mid/late Holocene times were also inferred by Behling (1997b) at Serra dos Campos Gerais for the last 1500 B.P. and by Behling (2007) at Serra do Araçatuba after 2000 B.P., both in Paraná state. For Santa Catarina (Behling 1995) and the Rio Grande do Sul highlands (Behling et al. 2001), the major *Araucaria* forest expansion occurred later than in Paraná (situated further northern than Santa Catarina), i.e. during the last 1000 B.P., thus under modern climatic conditions. A comparison with a high-resolution oxygen and carbon stable isotope record of cave calcite from Caverna Botuverá, at a distance of 80 km from the Ciama 2 site, reveals that the local temperature can be affected by the summer monsoonal precipitation and winter extra tropical circulation patterns (Cruz Jr. et al. 2005, 2006). Negative  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values in this speleothem record indicate that increased rainfall coincided with a marked forest expansion over the Serra do Tabuleiro at the mid-Holocene. Behling et al. (2004) suggest a warmer phase during the Little Ice Age for the southern Brazilian highlands based on the increase of *Weinmannia* type pollen frequencies. This finding is consistent to our data, in which we found an increase of certain woody taxa that are characteristic of moister and warm conditions, such as *Weinmannia*. The Little Ice Age is known as a period of cooling in Europe between about A.D. 1200 and 1700.

#### ***Vegetation changes and ecosystem disturbance during the last centuries***

Major changes in forest composition occurred in the last 360 years (pollen zone C2-IVb). A further, third expansion of Atlantic rainforest from the slopes to the upland is revealed by an increase of different pollen types. Ecosystem disturbance is indicated by the increase of *Trema* and *Mimosa scabrella*, coinciding with the decrease of *Araucaria angustifolia* and *Podocarpus*. Both, *Trema* and *Mimosa scabrella*, are known as pioneer species that establish after disturbance, thus representing

forest exploitation by European settlers and logging in the last years. An abrupt decrease of *Blechnum imperiale* after 260 cal B.P. (A.D. 1690) also indicates bog disturbance.

After the change of the predominant *Campos* vegetation to a forest system, another directional change in vegetation dynamics occurred from 320 to 160 cal B.P. (A.D. 1630 to 1790). During this period, a further expansion of Atlantic rainforest and *Araucaria* forest, thereby replacing *Campos*, took place, which can be observed by the increased abundances of *Lamanonia speciosa*, Myrtaceae, *Symplocos tenuifolia*, *S. lanceolata*, *Ouratea*, *Mimosa scabrella*, *Ilex* and *Araucaria angustifolia*. Later, ecosystem disturbance occurred, resulting in forest opening. The disturbance of this native forest on the Ciama region can be related to Portuguese settlers from the coast, which might have exploited the forest throughout the 17<sup>th</sup> and 18<sup>th</sup> centuries. From A.D. 1940 to 2005, a strong directional phase in vegetation dynamics revealed by changes in pollen composition indicates a tendency of *Campos* vegetation returning on the Ciama area. The higher occurrence of Poaceae at the top of the subzone C2-IVb may indicate the opening of the forest due to human activity. Ecosystem disturbance has also taken place by the construction of a road for timber transport by the company Ciama in the 1950s. With successive timber exploitation and burning, open areas were created, which due to cattle grazing were converted into anthropogenic *Campos* (Klein 1981).

#### ***Fire events during the Holocene***

The charcoal records suggest that fire was very common in the region from ca. 10,400 until 3600 cal B.P.. It is likely that Amerindians may have caused these fires. Prous and Fogaça (1999) provide evidence for human presence in Minas Gerais, central Brazil, at the end of the Pleistocene (between 12,000 and 11,000 B.P.). The authors also pointed out that human occupation in southern Brazil can be recorded since ca. 8000 B.P., when the Uumbu and Humaitá cultures arrived. Available evidence suggest that fires of anthropogenic origin can be dated back to the beginning of the Holocene in Paraná state (Behling 1997b) and to after 7400 B.P. in Rio Grande do Sul state (Behling et al. 2004). Human induced fires continued to be common in the Serra do Tabuleiro as indicated by the high occurrence of charred particles during late Holocene. Results of correlation analyses between pollen taxa and charcoal concentrations during the Holocene (pollen zone C2-III and C2-IV) show a strong positive correlation of Poaceae with charred particles, while forest elements as *Mimosa scabrella*, *Weinmannia* and Myrtaceae show a strong negative correlation with charcoal concentration (Table 4). These results indicate that fires occurred locally or regionally during the Holocene. However, it would be reasonable to interpret these fires during the Holocene as to be of anthropogenic origin, as climate was moist in the early/mid Holocene and more humid during the late Holocene.

### **Conservation strategies**

The remaining areas of natural *Campos* at the higher elevations of the State Park Serra do Tabuleiro will probably disappear in the future due to progressive forest expansion over *Campos* under modern, humid climatic conditions (e.g. Hueck 1966; Lindman 1906; Rambo 1956). Nonetheless, this biodiverse ecosystem can be maintained by human interference, such as the promotion of fire and grazing (Behling et al. 2007; Jeske-Pieruschka et al. 2010; Overbeck et al. 2005; Pillar 2003; Pillar and Vélez 2010). Preservation of the restricted areas of *Campos* in the park by the creation of natural pasturelands would be a better management strategy than the use of fire due to the negative effects of frequent burnings.

Observations of *Araucaria* forest replacing *Campos* areas are also recorded by Hueck (1953), Klein (1960) as well as Oliveira and Pillar (2004). Furthermore, the first two authors notice that the Atlantic rainforest restricts both, the *Campos* and the *Araucaria* forest, in its ongoing vegetation succession.

Here we provide evidence for a progressive replacement of *Campos* and *Araucaria* forest by Atlantic rainforest in the southern Brazilian highlands if climate will become warmer under the effects of global change. Frequent frost during the winter months nowadays continues to limit the survival of the tropical species on the highlands. Contrary to this, if climate becomes drier and/or longer periods of drought become more frequent, both ecosystems, the *Araucaria* forest as well as the Atlantic rainforest will show a hindered development due to water deficits. To sum up, future climate changes will play a crucial role in vegetation composition and dynamics in the subtropical southern Brazilian highlands.

### **Conclusions**

The pollen and charcoal record from the Serra do Tabuleiro indicates cold and dry conditions during the last glacial period from 39,720 B.P. until 21,200 cal B.P. After the LGM, from ca. 21,200 cal B.P., there is evidence of dry conditions lasting until 10,400 cal B.P. A treeless landscape continues to dominate under cold and dry climates throughout the last glacial period until 13,470 cal B.P.. Scattered trees probably grew only at lower altitudes, e.g. in the lowlands. The Serra do Tabuleiro was no refugium for forest taxa during the glacial times. Only few tree species were present in small populations in the lower regions during this period. A climatic amelioration towards warmer and wetter conditions during the transition from the Pleistocene to the Holocene period provided adequate conditions for the initial colonization of the slopes by trees at about 10,400 cal B.P., with tropical species migrating from the lowland and the coast over the slopes. Extensive areas of *Campos* vegetation existed on the Serra do Tabuleiro until the mid-Holocene, when a wetter climate with no long dry period arose. Due to this climatic improvement since ca. 3600 cal B.P., the predominant

*Campos* vegetation was replaced by a forest ecosystem. First ecosystem disturbances occurred between A.D. 1630 and 1790 and resulted in a forest opening, probably due to forest exploitation by the first European settlers. Forest clearance and tropical deforestation with the tendency of *Campos* returning to the studied area occurred since the early 20<sup>th</sup> century. Local palaeofires did probably not occur during glacial times, whereas fires that were probably caused by Amerindians were common during the early- and mid-Holocene on the Serra do Tabuleiro.

The findings of the Ciama 2 core provide an important contribution to the understanding of vegetation changes in relation to future climate changes in the important tropical forest of the Brazilian coast. Accordingly, we attempt to encourage environmentalists to create management strategies for the conservation of the State Park Serra do Tabuleiro.

### Acknowledgments

The authors are grateful to Renata Duzzioni for elaborating the study site map. We thank Nele Jantz and Alessandra Fidelis for an English revision of the manuscript. The authors thank Gisele Leite de Lima for valuable information that helped to improve the article. Funding for the project was provided by the Deutsche Forschungsgemeinschaft (DFG) (BE 2116/9-1). Part of fieldwork expenses and radiocarbon dating were financially supported by Fundação de Apoio à Pesquisa Científica e Tecnológica do Estado de Santa Catarina (FAPESC) (Grant CON08857/2007-9) and by the Inter-American Institute for Global Change Research (IAI) CRN-2005 (U.S. NSF Grant GEO-0452325).

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## CHAPTER 5

### Synthesis

## 5. Synthesis

Palaeoenvironmental changes from subtropical southern Brazil highlands were interpreted for the late Quaternary from three pollen and charcoal records. In Santa Catarina state in the Serra do Tabuleiro, palaeoenvironmental reconstruction is based on palynological, charcoal and multivariate data analyses of the Ciama 2 core for the last 39,720 yr BP. In Rio Grande do Sul state for the Serra Geral, a broad view on vegetation, fire and climate dynamics is given by the Rincão das Cabritas (RdC) record over the last 16,700 cal yr BP. The São José dos Ausentes (SdA) core documents the local development and dynamics of a grassland-forest mosaic as well as the role of fire and anthropogenic impact on the Serra Geral for the last 600 years. A summary of the articles presented in this thesis will be given for the recorded late Pleistocene and Holocene periods.

### 5.1. Late Pleistocene period

The environments of the southern Brazil highlands continue to be scarcely investigated for the Pleistocene period, i.e. extending into the full glacial period. An issue of growing significance is the reconstruction of the vegetation types belonging to the Atlantic Forest biome today that includes Campos, *Araucaria* forest and Atlantic rainforest. Thus, palynological and charcoal results from the Ciama 2 core, spanning the last 39,720 yr BP and from Rincão as Cabritas (RdC) core, covering the last 16,700 cal yr BP, provide important information for understanding the development and dynamic of these ecosystems.

#### 5.1.1. Pre-Last Glacial Maximum

According to the Ciama 2 high-resolution pollen record (Chapter 4), the highlands on the isolated Serra do Tabuleiro in Santa Catarina were covered by extensive grassland vegetation from 39,720 until ca. 26,000 yr BP. The landscape on the highlands was composed mostly by grasses (Poaceae) and different forbs of the Asteraceae family, but also by Cyperaceae, Apiaceae and other plants characteristic for grassland ecosystems. The rare occurrence of forest taxa such as *Weinmannia*, *Myrsine*, *Alchornea*, Moraceae/Urticaceae, *Celtis* and *Symplocos tenuifolia* reflects the existence of Atlantic rainforest taxa probably in deep protected valleys of the Serra do Tabuleiro, on its slopes at lower elevations or even in areas along rivers or streams in the lowland forming refugia. Only a few single arboreal pollen grains of *Araucaria angustifolia* and *Podocarpus* represent its scattered presence in the lower regions of the Serra do Tabuleiro during this period. A treeless scenario on the

highlands during the recorded glacial period suggests dry and cold climate conditions in the region. The charcoal records indicate no or only rare fires on the Serra do Tabuleiro during this period.

### 5.1.2. Last Glacial Maximum

Pollen data from the Ciama 2 record reveal a treeless landscape on the Serra do Tabuleiro during the Last Glacial Maximum (LGM) that culminated at about 21,000 years ago. Although the highlands of southern Brazil continues to be characterized by widespread grasslands since the pre-LGM period, some differences in pollen spectra could be identified for the LGM period. Forest taxa such as *Araucaria angustifolia*, *Roupala*, *Drimys brasiliensis*, *Mimosa taimbensis*, *Sebastiania commersoniana* and *Symplocos lanceolata* among others were not present during this period. Arboreal taxa such as *Myrsine* and *Alchornea* were represented by diminishment or even with only one pollen grain during this period. Extensive grassland vegetation with dominance of Poaceae and absence or reduction of some forest taxa during the LGM reflects colder and drier climatic conditions on the Serra do Tabuleiro than before.

The Rincão das Cabritas pollen and charcoal record, which was collected from a peat bog in the São Francisco de Paula region, allows detailed palaeoenvironmental reconstruction over the last 16,700 cal yr BP, reaching the later part of the full Glacial period (Chapter 3). During the recorded glacial times between 16,700 and 14,900 cal yr BP, the highland region was dominated by an open vegetation composed mostly of Poaceae together with other graminoids and forbs. This grassland landscape reflects cold and markedly drier climatic conditions in the region than today throughout glacial times. The presence of some aquatic taxa such as *Isoëtes*, *Myriophyllum*, *Echinodorus* and *Hydrocotyle* suggest local shallow water condition in the studied basin. A few arboreal taxa and a few tree ferns were only present in small populations where sufficient retained humidity allowed its growth as on the lower slopes or as gallery forest along rivers or streams at lower elevations. Nevertheless, the occurrence of *Mimosa scabrella*, *Podocarpus*, *Clethra* and *Araucaria angustifolia* itself, evidence the existence of *Araucaria* forest taxa and the occurrence of *Weinmannia*, *Celtis* and Moraceae/Urticaceae confirm the presence of Atlantic rainforest taxa in the region at glacial times, probably in refugia of the lowlands.

The highlands of southern Brazil were covered by grassland vegetation that dominated on the Serra do Tabuleiro and the Serra Geral throughout glacial times under cold and dry climatic conditions. The presence of some disperse Atlantic rainforest taxa and scattered *Araucaria angustifolia* and *Podocarpus* pollen grains, reflect the existence of forest taxa in refugia on the slopes of these two coastal mountain ranges during this period. The low number of microscopic charred

particles in the Ciama 2 and Rincão das Cabritas charcoal records suggest that fire was rare on the Serra do Tabuleiro and on the Serra Geral during the LGM period.

### 5.1.3. Late Glacial

Results of pollen and multivariate data analyses of the Ciama 2 record (Chapter 4) reveal a dry phase lasting from 21,200 to 10,400 cal yr BP in the Serra do Tabuleiro region interpreted from a decrease of moist forest taxa like *Weinmannia*, *Myrsine*, *Symplocos tenuifolia*, *Mimosa taimbensis*, *Ilex* and tree ferns (Cyatheaceae). Thus, due to very low occurrence of arboreal taxa and the dominance of Poaceae indicating extensive grassland vegetation, the climate on the highlands continued cold after the LGM. Interpretations from the Ciama 2 core also show that isolated *Araucaria* forest areas on the Serra do Tabuleiro were originated from small populations on the lower slopes with sufficiently retained humidity or even from gallery forest along rivers or streams at lower elevations. Therefore, the Serra do Tabuleiro coastal mountain range was not a refugium for forest taxa during the last glacial period. Charcoal records of the Ciama 2 core document that palaeofires were rare or almost absent in these highland environments during glacial times.

Palaeoenvironmental results of the Rincão das Cabritas record confirmed a continuous presence of extensive grassland vegetation during the late Glacial, suggesting dry climatic conditions on the southernmost Brazilian highlands (Chapter 3). The investigated peat core from the São Francisco de Paula region, which has the highest annual precipitation rates of the whole southern Brazil today, indicates a regional markedly reduced mean annual precipitation with longer annual dry periods during the late glacial to the early Holocene (14,900 – 8700 cal yr BP). Periods of pronounced droughts are also suggested by the almost disappearance of aquatic taxa and bog formation with local occupation of *Sphagnum* and the fern *Blechnum imperiale* after 14,900 cal yr BP. A small number of arboreal taxa indicates the existence of some scattered trees of the *Araucaria* forest and of the Atlantic rainforest in protected areas with sufficient moisture at lower elevations in valleys or on the slopes. Results of the charcoal records show a rising trend of micro-charcoal fragments about 14,950 cal yr BP suggesting the occurrence of fire in the Serra Geral.

A grassland vegetation composed mostly by Poaceae continues to prevail on the Serra do Tabuleiro and the Serra Geral during the late Glacial suggesting dry and cold climatic conditions. Environmental interpretation of Ciama 2 core indicate drier conditions since the LGM until the beginning of the Holocene on the Serra do Tabuleiro, while the Rincão das Cabritas suggests longer dry periods in the Serra Geral lasting from the late Glacial to the early Holocene. Charcoal particles are relatively rare in the Serra do Tabuleiro during glacial times suggesting almost no fire events over

there. For the Serra Geral, however, fires were indicated by increased proportions of charcoal particles since the late Glacial.

## 5.2. Holocene period

The Holocene, starting ca. 11,500 years ago, is divided into three periods: early, mid- and late Holocene. Palynological and charcoal results from the three investigated sedimentary records, Ciama 2, Rincão das Cabritas (RdC) and São José dos Ausentes (SdA), reveal marked and rapid changes in vegetation composition related to climatic and man induced changes over the Holocene.

### 5.2.1. Early Holocene

Although the highlands of the Serra do Tabuleiro continue to be dominated by grassland vegetation since glacial times, initial development of the Atlantic rainforest starting about 10,400 cal yr BP is traced by the Ciama 2 pollen record (Chapter 4). The studied palaeoecological record reveals increasing pollen frequencies of forest taxa (*Weinmannia*, *Myrsine*, *Alchornea*, Melastomataceae, Moraceae/Urticaceae, *Celtis* and tree ferns) at the beginning of the Holocene reflecting first development of Atlantic rainforest from the lowland onto the slopes. Campos and forest taxa increased together with tree ferns after 10,400 cal yr BP indicating a climatic change to wetter and warmer conditions. Results of the multivariate data analysis also evidence better climatic conditions with higher humidity allowing forest development after 11,200 cal yr BP and a change on vegetation dynamics with Atlantic rainforest spreading over the slopes until mid-Holocene. Fire events on the Serra do Tabuleiro since ca. 10,360 cal yr BP are supposed to be of anthropogenic origin based on evidence on human occupation on the southern Brazilian highlands already in the early Holocene.

In the São Francisco de Paula region, Campos vegetation composed mostly of Poaceae and Asteraceae remained the predominant ecosystem during the early Holocene under dry climatic conditions (Chapter 3). Nevertheless, some forest taxa (*Myrsine*, *Ilex*, *Lamanonia speciosa*, *Weinmannia*, Moraceae/Urticaceae and *Alchornea*) may represent first forest arrival from the lower slopes to higher elevations of the Serra Geral favored by warmer-wetter conditions after the late Glacial period. After 8700 cal yr BP, a continuous spread of the Atlantic rainforest from lower to the upper part of the slopes is indicated by *Weinmannia*, *Alchornea* and Cyatheaceae, and initial *Araucaria* forest development on the highlands by *Myrsine*, *Lamanonia speciosa* and Myrtaceae. The peat bog fully developed during this period primarily filled by *Sphagnum*. Fires were frequent during the early Holocene in the studied region.

Extensive grassland vegetation continued to prevail on the upper parts of the Serra do Tabuleiro and the Serra Geral during the early Holocene. However, climatic improvement to warmer-wetter conditions after glacial times allows a slight initial *Araucaria* forest development on the highlands and Atlantic rainforest expansion on the slopes of both mountain ranges. The reconstruction of fire history indicates occurrence of fires on the southern Brazilian highlands during this period.

### 5.2.2. Mid-Holocene

Palaeoenvironmental interpretation of the Ciama 2 pollen record indicates a continuous presence of extensive areas of Campos vegetation on the Serra do Tabuleiro until mid-Holocene (Chapter 4). Only after ca. 3600 cal yr BP the predominant Campos vegetation was replaced by a forest ecosystem, when wetter climatic conditions with no long dry period arose. The results of multivariate data analysis show an evident directional change in vegetation dynamics from 3850 to 1600 cal yr BP indicating continued expansion of Atlantic rainforest and initial development of *Araucaria* forest in the higher regions of the Serra do Tabuleiro. Fire events, probably caused by Amerindians occupying this region, were common during the mid-Holocene.

Results from the Rincão das Cabritas core indicate a vegetational change from extensive Campos into forest on the southernmost highlands of Brazil during the mid-Holocene (Chapter 3). Forest coverage during this period reflects climatic changes to wetter conditions. The increasing frequency of moist forest taxa such as *Myrsine*, Myrtaceae, *Lamanonia speciosa*, *Weinmannia* and Cyatheaceae as well as bog taxa such as *Blechnum imperiale*, *Osmunda* and *Sphagnum* indicate that climate became slightly wetter after about 4600 cal yr BP. *Araucaria* forest began to develop after 3200 cal yr BP but its expansion over Campos started only about 2950 cal yr BP. A continuous expansion of *Araucaria* forest in São Francisco de Paula region since the mid-Holocene is evidenced by an increase in arboreal pollen frequencies such as *Myrsine*, Myrtaceae, *Ilex*, *Araucaria angustifolia*, *Lamanonia speciosa*, *Drimys brasiliensis* and *Griselinia ruscifolia*. Moderate and wetter climate since mid-Holocene allowed gradual forest spreading from the lower regions of the Serra Geral upwards to higher elevations. The establishment of the Atlantic rainforest on the upper part of the slopes is suggested from the presence of *Weinmannia* together with other tree taxa and tree ferns belonging to this ecosystem since the last 3000 years. Higher amounts of charred particles until mid-Holocene (3060 cal yr BP) suggest that fires were very common in the region and were probably caused by humans that occupied the southern Brazil highlands.

The landscape of the Serra do Tabuleiro and the Serra Geral has changed from a dominating grassland vegetation into a more forested ecosystem since the mid-Holocene. Continuous expansion of Atlantic rainforest over the slopes reaching higher elevations and *Araucaria* forest development on

the highlands indicate a wetter climate. Fire events still occurred frequently on the highlands of southern Brazil during mid-Holocene times.

### 5.2.3. Late Holocene

Palaeoecological data from the investigated Ciama 2 record suggests a continuous development/expansion of Atlantic rainforest since 3600 cal yr BP, while *Araucaria* forest began to develop and expand over the Serra do Tabuleiro (Chapter 4). *Araucaria* forest began to develop approximately 2010 yr BP and reached its maximum of expansion in the study area only after 290 yr BP (1650 AD). Multivariate data analysis reveals a clearly directional change in vegetation dynamics corresponding to progressive expansion of Atlantic rainforest from 3850 to 1600 cal yr BP, when the ecosystem changed from an almost treeless to a more forested landscape. A second directional change in vegetation dynamics occurred from 320 to 160 cal yr BP (1630 to 1790 AD) with further expansion of Atlantic rainforest and *Araucaria* forest replacing the Campos. A vegetational change to forest environment throughout the late Holocene with marked forest development and expansion was probably related to increased moisture, i.e. higher precipitation levels without a major annual dry season since about 3600 cal yr BP. Wetter climatic conditions during the late Holocene suggest that common fires on the Serra do Tabuleiro were mostly of anthropogenic origin during this period.

For the São Francisco de Paula region, replacement of Campos by forest ecosystems continued into the last millennia (Chapter 3). From 1050 cal yr BP onwards, *Araucaria* forest reaches its maximum of expansion turning into the main vegetation type in the northeastern highlands of Rio Grande do Sul and forming a mosaic of Campos-*Araucaria* forest. A vegetational change on the upper part of the Serra Geral also happened since the last 1000 years, where a transition zone between Atlantic rainforest and *Araucaria* forest can be observed since then. Although small forest populations were already present there, the maximum of forest expansion occurred only after continuously wetter climatic conditions with increased precipitation and absence of a pronounced dry season during the past 1000 years. Thus, it is reasonable to interpret climate as the main limiting factor for forest expansion on the southern Brazilian highlands. Anthropogenic fires on the São Francisco de Paula region decreased markedly after about 3000 cal. BP when forest expanded continuously under regionally wetter climatic conditions.

Despite higher rainfall rates distributed throughout the year and a lack of annual dry periods on the southern Brazilian highlands since the past 1000 years, the pollen and charcoal record of São José dos Ausentes shows *Araucaria* forest expansion only after 450 cal yr BP (1500 AD) related to a decrease in fire frequency. Frequent fires were mostly of anthropogenic origin during the past 1000 years, when the climate became more humid. The investigated sediment record provides new insight



into the strong relation between *Araucaria* forest development, dynamic and fire frequency on the southern Brazilian highlands as well as the role of fire and human impact on the Campos-*Araucaria* forest mosaics during the past 600 years (Chapter 2). Before 540 cal yr BP (1410 AD), the area next to the studied peat bog of São José dos Ausentes was dominated by Campos vegetation and fire was very common. The studied modern *Araucaria* forest island must have been very small or still not existent during this time. Afterwards, *Araucaria* forest expanded and fire was less frequent. A marked reduction of the fire frequency after about 370 cal yr BP (1580 AD) allowed further expansion of *Araucaria* forest but its maximum of expansion occurred in the area only during the past 70 years and can be clearly related to the decrease of fire frequency. The expansion of *Araucaria* forest under modern wet climatic conditions has been hindered by frequent fires probably caused by indigenous population in southern Brazil near the study site of São José dos Ausentes.

The late Holocene period is characterized by marked forest expansion replacing Campos ecosystems on the southern Brazil highlands due to increasingly wetter conditions together with the absence of long annual dry periods. Another important factor controlling forest expansion over the highlands is the frequency of fires.

### 5.3. Conservation

#### 5.3.1. Human impact on the grassland and forest ecosystems during the last centuries

Results from the three studied pollen and charcoal records provide evidence for ecosystem disturbance through time. Data from the São José dos Ausentes core reveal human related fires inhibiting greater *Araucaria* forest expansion over Campos since the past 600 years on the study site (Chapter 2). Pre-Columbian cultures living in the region before European arrival caused fires by hunting and slash and burn practices. Forest degradation and deforestation is related to intense European colonization in southern Brazil later than the 19th century. According to the fossil and modern pollen results, the present *Araucaria* forest island remains to be very degraded and regularly used by cattle since 1935 AD.

Palynological data from Rincão das Cabritas record indicate disturbance of native vegetation by post-Colombians resulting in forest opening since the end of the 19th century (Chapter 3). Human impact on the forest ecosystems since around 1890 AD can be associated with the introduction of cattle by Jesuits probably in the early 18th century and wood exploitation by European settlers since the 19th century.

Pollen and charcoal data from Ciama 2 core reveal marked changes in the original vegetation caused by anthropogenic activities during the past centuries (Chapter 4). First intense ecosystem

disturbance occurred between 1630 and 1790 AD due to forest exploitation by the first European settlers. Forest clearance and tropical deforestation still happen in the Serra do Tabuleiro region since the early 20th century. Forest exploitation on the Serra do Tabuleiro, mainly due to logging of *Araucaria angustifolia* and *Ocotea porosa*, began in the early 20th by the Ciama sawmill. In the 1950s a road was constructed in the region to facilitate timber transport. For the State Park Serra do Tabuleiro, the local population continues to use the land in which they had been living before the establishment of the park in 1975 AD. As a result, territorial conflicts involving farmers and environmental organizations are frequent. Natural vegetation has been removed for agriculture and pasture since then with subsequent growth of secondary vegetation.

### 5.3.2. Campos-*Araucaria* forest mosaics and its sharp borderline

Nowadays most of the extensive remaining areas of Campos vegetation on the southern Brazil highlands are relicts from glacial climate conditions. This grassland ecosystem continues to be suppressed by forest expansion since mid-Holocene times (see 5.2.2) when the climate became more humid. The development of Campos-*Araucaria* forest mosaics and their sharp borderlines can be explained by forest expansion over Campos since mid-Holocene, when a vegetational change from completely open vegetation to a more forested landscape happened. The investigated record of São José dos Ausentes (Chapter 2) clearly demonstrates high fire frequency as a mechanism preventing forest expansion and controlling the formation and stability of the sharp border between Campos-forest ecosystems. Results of the three records studied in this thesis show that fire has been frequent on the southern Brazilian highlands since early Holocene. Therefore, it is reasonable to assume fire as an important factor preventing forest expansion and controlling the formation of the sharp border between Campos-*Araucaria* forest since the marked forest expansion during mid-Holocene. At present, despite its prohibition, fire is used to manage the area for cattle pastures on the highlands with burns over Campos that normally do not enter the forest. Cattle farming with extensive native pastureland continue to be part of the economy for some regions on the southern Brazilian highlands, like in the São Francisco de Paula region. Thus, cattle could also prevent forest expansion and manage the boundaries between grassland and forest by trampling and eating buds or seedlings of pioneer tree species growing directly over Campos. Hence, the sharp borderlines between Campos and *Araucaria* forest could be maintained by pastures, i.e. cattle and by the use of fire. Nevertheless, the use of Campos as natural pasture seems to be a better alternative than fire to maintain Campos ecosystems and the beautiful highly biodiverse vegetation mosaics including their sharp borderline on the highlands. Overall, pastureland instead of induced fire will be the better manage for ecosystem maintenance and conservation due to the negative effects of frequent burns such as carbon dioxide

emissions, uncontrolled fires and biodiversity loss along a longer time line. However, without human interference such as management strategies using grazing or fire, conservation and maintenance of Campos ecosystems is not possible and its complete replacement by forests in the future can not be avoided.

### 5.3.3. Impact of climate changes on forest ecosystems

Climate change during the transition from the Pleistocene to the Holocene period as recorded from Rincão das Cabritas and Ciama 2 core, allowed initial colonization of the escarpments of Serra Geral and Serra do Tabuleiro by trees, with tropical species migrating from the lowland and the coast over the slopes. The representation of forest taxa by identified pollen in these fossil sediments indicates its presence in the lowlands already during glacial times. Pollen data from Rincão das Cabritas and Ciama 2 core reveal development and expansion of Atlantic rainforest from the lower slopes to higher elevations together with initial *Araucaria* forest development on the highlands only after climate improvement to wetter conditions during mid-Holocene. Atlantic rainforest spread from north to south and from east to west i.e. from the coastal plain to the slopes of Serra Geral and Serra do Tabuleiro. Largest populations of *Araucaria* forest distributed further north apparently spread from north to south due to moister conditions. However, small populations represented by scattered trees in regional refugia during dry climate may reflect *Araucaria* forest expansion from lower to higher elevations. There is sufficient evidence to suggest marked *Araucaria* forest expansion only after a climate improvement with increased rainfall and lack of longer periods of drought on the southern Brazilian highlands as demonstrated by the Rincão das Cabritas and Ciama 2 core.

Palaeoenvironmental interpretation for the Serra Geral and Serra do Tabuleiro suggest continuous replacement of *Araucaria* forest by Atlantic rainforest in the southern Brazil highlands if the climate continues to become warmer than present-day. The floristic composition of the Atlantic rainforest can not withstand frost, which occurs frequently on the highlands in the winter months today. Hence, the current climate is still too cold in the southern Brazil highlands for these tropical species. Contrariwise, under the effects of global warming, a rapid vegetational change with expansion of Atlantic rainforest ecosystem in the highlands suppressing Campos-*Araucaria* forest mosaics may happen. If periods of prolonged drought become more frequent in southern Brazil due to global change, the *Araucaria* forest vegetation will suffer water deficit as it requires high precipitation rates to survive. Longer periods of drought will also hinder the development and expansion of Atlantic rainforest with its tropical species adapted to and dependent on high humidity. Hence, future climate changes will play a crucial role in vegetational dynamics on the southern Brazil highlands.

Each of these ecosystems, Campos, *Araucaria* forest and Atlantic rainforest, belongs to the same biome, although they are distinct from each other. Thus, due to their different vegetational composition and species richness, they should be preserved for biodiversity maintenance.

## Summary

The Atlantic Forest biome, with less than 8% of severely fragmented remnants, represents the most devastated vegetation of Brazil. This biome is composed of different associated vegetation ecosystems such as Atlantic rainforest covering the slopes of the Brazilian coastal mountain ranges and mosaics of Campos-*Araucaria* forest shaping the highlands of southern Brazil. A sharp borderline between Campos and *Araucaria* forest can often be observed in these highland landscapes. Palaeoenvironmental and palaeoclimate studies carried out in remaining areas of Atlantic rainforest and Campos-*Araucaria* forest mosaics provide important information for understanding the development, stability and dynamics of these biodiverse ecosystems. Knowledge of development and dynamics of these highly vulnerable ecosystems is essential to afford management strategies for their conservation and maintenance. Two sediment archives from the Serra Geral and one from the Serra do Tabuleiro have been studied by means of pollen and charcoal analysis resulting in a broad view on vegetation, fire and climate dynamics on the southern Brazilian highlands during the late Quaternary.

The landscape on the southern Brazilian highlands was covered by extensive grassland vegetation before and during the Last Glacial Maximum (LGM), reflecting cold and dry climatic conditions throughout glacial times. Some scattered fossil pollen grains of forest taxa indicate existence of forest in refugia at protected sites in lower elevations and/or on the slopes of the Serra Geral and Serra do Tabuleiro during this period. Fire events were rare in these highland environments during glacial periods. Extensive grassland vegetation continues to prevail on the Serra Geral and the Serra do Tabuleiro during the late Glacial, suggesting dry and cold climatic conditions. After the LGM, longer dry periods from the late Glacial to the early Holocene were recorded for the Serra Geral and the Serra do Tabuleiro. Fire events in the Serra Geral are indicated by increased proportions of charred particles since the late Glacial. In the Serra do Tabuleiro, however, palaeofires were almost absent. Although Campos vegetation remained the predominant ecosystem on the Serra Geral and the upper part of the Serra do Tabuleiro during the early Holocene, a climatic change to warmer/wetter conditions allowing forest development was recognized at the beginning of the Holocene. Initial development of forest ecosystems over the slopes of the Serra Geral and Serra do Tabuleiro was promoted by higher moisture since then. Fire events occurred during the early Holocene in both highlands. A vegetational change from extensive Campos into a forested landscape has been taking place since mid-Holocene on the southern Brazilian highlands. Campos replacement by forest ecosystems is related to climatic amelioration since mid-Holocene. Wetter climate allowed continuous expansion of Atlantic rainforest over the slopes reaching higher elevations and initial *Araucaria* forest development on the highlands. Fire events were common until mid-Holocene times on these highlands. Replacement of Campos by forest ecosystems continues during the late Holocene on the

southern Brazil highlands reflecting increasingly wetter conditions with no long annual dry period. Atlantic rainforest expanded onto the slopes to higher elevations while *Araucaria* forest spread progressively on the highlands forming grassland-forest mosaics. Frequent fires on the Serra Geral and Serra do Tabuleiro were mostly of anthropogenic origin during late Holocene when the climate became more humid. The frequency of fires can be considered as an important factor preventing forest expansion and controlling the formation and stability of the sharp border between Campos-forest ecosystems. A different option for the preservation of Campos-*Araucaria* forest mosaics could be through natural pasturelands, which would be a better management strategy than the use of fire due to the negative effects of frequent burns.

Palynological and charcoal interpretations of the three studied peat records indicate human impact on the grassland and forest ecosystems during the past. The results indicate marked changes in the original vegetation caused by anthropogenic activities since the arrival of Europeans. Nonetheless, future climate change will strongly affect vegetation composition and dynamic on the subtropical southern Brazilian highlands. The Atlantic rainforest will expand progressively over the highlands suppressing *Araucaria* forest and Campos vegetation under the effects of global warming. The unique landscape of southern Brazil highlands and its escarpments will also change if climate becomes drier or longer periods of drought become more frequent, which will severely influence vegetation composition due to the high humidity dependence of these subtropical species. During the past century, the human and economic losses caused by “natural” disasters have increased also in southern Brazil showing the importance of global change not only for the country’s economy but also for the perpetuation of these original ecosystems.

## Zusammenfassung

Das Atlantische Regenwaldbiom, von dem in heutiger Zeit nur noch weniger als 8% in äußerst stark fragmentierten Resten erhalten geblieben ist, stellt die am stärksten zerstörte Vegetation Brasiliens dar. Verschiedene Vegetationsökosysteme gehören zu diesem Biom, wie beispielsweise der Atlantische Regenwald an den Hängen der brasilianischen Küstengebirge und Campos-Araukarienwald-Mosaik im südbrasilianischen Hochland, wobei letztere häufig durch eine scharfe Grenze zwischen Campos und Araukarienwald gekennzeichnet sind. Studien zur Paläoumwelt und Paläoklima der verbliebenen Teile des Atlantischen Regenwaldes und der Campos-Araukarienwald-Mosaiken liefern wichtige Informationen zum Verständnis der Entwicklung, Stabilität und Dynamik dieser artenreichen Ökosysteme. Das Wissen über die Entwicklung und Dynamik dieser stark bedrohten Ökosysteme ist für das Erstellen von Managementstrategien hinsichtlich ihrer Erhaltung unerlässlich. Zwei Sedimentarchive von der Serra Geral und eines von der Serra do Tabuleiro wurden mittels Pollen- und Holzkohleanalyse untersucht und erlauben einen detaillierten Überblick über die Vegetations-, Feuer- und Klimadynamik im südbrasilianischen Hochland während des Spätquartärs.

Vor und während des letzten glazialen Maximums (LGM) war die Landschaft im südbrasilianischen Hochland von ausgedehnter Graslandvegetation bedeckt, was auf kalte und trockene klimatische Bedingungen in dieser Region während der letzten Eiszeit hinweist. Vereinzelt auftretender subfossiler Pollen unterschiedlicher Waldtaxa deutet auf ihre Existenz in Refugien an geschützten Standorten in tieferen Lagen und/oder an den Hängen der Untersuchungsgebiete hin, und nur sehr selten kam es zu Feuerereignissen in den Hochlandgebieten während der letzten Eiszeit. Auch während des Spätglazials waren ausgedehnte Grasländer die vorherrschende Vegetation der Serra Geral und Serra do Tabuleiro, was auf das Andauern trockener und kalter klimatischer Bedingungen hinweist. Für die Serra Geral und die Serra do Tabuleiro konnten längere Trockenperioden vom Spätglazial bis zum frühen Holozän nachgewiesen werden. Erhöhte Holzkohleanteile weisen auf Feuerereignisse in der Serra Geral seit dem Ende der letzten Eiszeit, während in der Serra do Tabuleiro Feuerereignisse selten waren. Im frühen Holozäns ist weiterhin Camposvegetation das vorherrschende Ökosystem der Serra Geral und in höheren Lagen der Serra do Tabuleiro, jedoch zeichnet sich eine Änderung zu wärmeren und feuchteren klimatischen Bedingungen zu Beginn des Holozäns ab, welche die Entwicklung von Waldvegetation ermöglichte. Die Entwicklung von Waldökosystemen an den Hängen der Serra Geral und Serra do Tabuleiro wurde seitdem durch höhere Feuchtigkeit vorangetrieben. Feuerereignisse traten während des frühen Holozäns in den Regionen beider Hochländer auf. Ein Wechsel vom vorherrschenden Campos hin zu einer Waldlandschaft fand im südbrasilianischen Hochland seit dem mittleren Holozän statt. Ein feuchteres Klima erlaubte eine kontinuierliche Ausbreitung des Atlantischen Regenwaldes über die

Gebirgshänge bis in höhere Lagen, und die erste Entwicklung von Araukarienwald im Hochland. Feuerereignisse waren bis zum mittleren Holozän in diesen Hochlandgebieten verbreitet. Die fortlaufende Verdrängung von Campos durch Waldökosysteme im späten Holozän auf dem südbrasilianischen Hochland deutet auf zunehmend feuchtere Bedingungen ohne jährliche lang andauernde Trockenperioden hin. Atlantischer Regenwald breitet sich weiter an den Hängen bis in höhere Lagen aus, während sich der Araukarienwald sukzessiv über das Hochland verbreitet und Grasland-Wald-Mosaik entstehen lässt. Häufige Feuerereignisse im späten Holozän auf der Serra Geral und Serra do Tabuleiro waren meist anthropogenen Ursprungs, als das Klima feuchter wurde. Die Häufigkeit von Bränden kann hier sowohl als wichtiger Faktor zur Verhinderung der Waldausbreitung angesehen werden, also auch als Steuerelement der Entwicklung und Stabilität der scharfen Grenze zwischen Grasland und Waldökosystemen. Hinsichtlich der Erhaltung der Campos-Araukarienwald-Mosaik ist eine natürliche Beweidung eine mögliche Managementstrategie, die auch dem Einsatz regulierter Brände aufgrund deren negativen Auswirkungen vorzuziehen wäre.

Interpretationen der drei durch Pollen- und Holzkohleanalyse untersuchten Moorkerne weisen auf von Menschen verursachte Auswirkungen auf die Grasland- und Waldökosysteme in der Vergangenheit hin. Die Ergebnisse zeigen starke Veränderungen der ursprünglichen Vegetation verursacht durch anthropogene Aktivitäten seit Ankunft der Europäer. Dennoch werden zukünftige Klimaveränderungen die Zusammensetzung und Dynamik der Vegetation im subtropischen südbrasilianischen Hochland stark beeinflussen. Unter dem Einfluss der globalen Erwärmung wird der Atlantische Regenwald sich zunehmend über das Hochland ausbreiten und den Araukarienwald und die Camposvegetation unterdrücken. Die einzigartige Landschaft des südbrasilianischen Hochlands und seiner Hänge wird ebenfalls starken Veränderungen unterzogen werden. Denn falls das Klima trockener werden oder es häufiger zu längeren Trockenperioden kommen sollte, wird die Vegetationszusammensetzung stark beeinflusst werden aufgrund eines Feuchtigkeitsdefizits der stark feuchtigkeitsabhängigen subtropischen Arten. Vermehrt auftretende Naturkatastrophen im Verlauf des letzten Jahrhunderts verursachten verheerende menschliche und wirtschaftliche Verluste auch in Südbrasilien, welche die Bedeutung der globalen Veränderungen nicht nur für die Landwirtschaft, sondern auch für den Fortbestand dieser natürlichen Ökosysteme verdeutlichen.



## Resumo

O bioma Mata Atlântica representa hoje a vegetação mais devastada do Brasil, apresentando menos de 8% de área remanescente que se encontra severamente fragmentada. É composto por diferentes ecossistemas associados: a Mata Atlântica cobrindo as encostas das serras costeiras brasileiras e os mosaicos vegetacionais que são constituídos de floresta com Araucária ocorrendo juntamente com os Campos nas terras altas do sul do Brasil. Um nítido limite entre o campo e a floresta com Araucária pode ser freqüentemente observado nestas paisagens de mosaico. Estudos paleoambientais e paleoclimáticos realizados em áreas remanescentes da Mata Atlântica e em mosaicos de floresta com Araucária e Campos fornecem informações importantes para compreender o desenvolvimento, estabilidade e dinâmica destes ecossistemas altamente biodiversos. O conhecimento sobre o desenvolvimento destes ecossistemas altamente vulneráveis é essencial para contribuir no planejamento de estratégias para o seu manejo, conservação e preservação. Dois perfis sedimentares da Serra Geral e um da Serra do Tabuleiro foram estudados por meio de análise palinológica e de carvão, resultando em uma visão ampla da dinâmica vegetacional, do clima e ocorrência do fogo nas terras altas do sul do Brasil durante o Quaternário Tardio.

A paisagem nas regiões mais elevadas da Serra Geral e da Serra do Tabuleiro antes e durante o Último Máximo Glacial (UMG), se caracterizava por extensivas formações campestres, refletindo a vigência de clima frio e seco perdurando desde os tempos glaciais. A ocorrência de alguns poucos grãos de polen fósseis indicam a presença de táxons florestais em refúgios, como locais protegidos nas baixas altitudes e/ou nas encostas durante estes períodos. O fogo ocorreu muito raramente nas áreas mais elevadas dessas duas Serras durante os períodos glaciais. Extensas áreas de vegetação campestre continuam a prevalecer sobre a Serra Geral e a Serra do Tabuleiro durante o Glacial tardio, sugerindo condições climáticas frias e secas. Prolongados períodos de seca que se estenderam desde o período Glacial tardio até o Holoceno inferior foram registrados para a Serra Geral e para a Serra do Tabuleiro. A ocorrência de fogo na Serra Geral é indicada pelo aumento na proporção de partículas carbonizadas desde o Glacial tardio. Para a Serra do Tabuleiro, no entanto, evidências para a ocorrência de fogo durante o período da última glaciação foi praticamente ausente. Apesar da vegetação campestre continuar a prevalecer na Serra Geral e nas regiões mais elevadas da Serra do Tabuleiro durante o Holoceno inferior, houve uma mudança nas condições climáticas mais quentes e úmidas que permitiu o desenvolvimento florestal no início do Holoceno. O desenvolvimento de ecossistemas florestais sobre as encostas de ambas as Serras foi favorecido pelo aumento de umidade desde então. Foi registrada a ocorrência de fogo durante o Holoceno inferior nas duas Serras do sul do Brasil. Uma mudança vegetacional de extensas áreas campestres para uma paisagem mais florestal ocorreu desde o Holoceno médio nas áreas estudadas. A substituição dos Campos como vegetação predominante por ecossistemas florestais está

relacionada à melhora do clima desde o Holoceno médio. Um clima mais úmido permitiu a contínua expansão da Mata Atlântica sobre as encostas, atingindo assim altitudes mais elevadas e propiciando o desenvolvimento inicial da floresta com Araucária nas regiões mais altas. Evidências da ocorrência freqüente de fogo foram registradas até o Holoceno médio em ambas as Serras. A substituição de Campos por ecossistemas florestais continuou durante o Holoceno superior, refletindo condições cada vez mais úmidas sem períodos anuais prolongados de seca. A Mata Atlântica continuou a expandir sobre as encostas atingindo altitudes cada vez mais elevadas, enquanto que a floresta com Araucária expandiu progressivamente sobre o planalto formando mosaicos de floresta e Campos. A ocorrência freqüente de fogo foi principalmente de origem antrópica durante o Holoceno tardio, quando o clima se tornou ainda mais úmido. A freqüência de fogo pode ser considerada como um importante fator impeditivo para a expansão da floresta, pois controla a formação e a estabilidade dos limites entre os ecossistemas florestais e campestres. Outra alternativa para preservar os mosaicos de floresta com Araucária e Campos poderia ser através de pastagens naturais, que seria uma melhor estratégia de manejo do que o uso de fogo, devido aos efeitos negativos das freqüentes queimadas.

Interpretações palinológicas e de carvão dos três testemunhos sedimentares indicam o impacto humano sobre os ecossistemas de campo e floresta durante o passado. Os resultados indicam mudanças marcantes na vegetação original causados por atividades antrópicas desde a chegada dos europeus. No entanto, as futuras mudanças climáticas irão influenciar fortemente a composição e dinâmica da vegetação subtropical das terras altas do sul do Brasil. A Mata Atlântica irá expandir progressivamente sobre o planalto suprimindo a floresta com Araucária e a vegetação campestre sob os efeitos do aquecimento global. A paisagem única dessas duas Serras do sul do Brasil incluindo suas encostas, também irá mudar se o clima ficar mais seco ou se longos períodos de seca se tornarem mais freqüentes, os quais influenciarão severamente a composição da vegetação devido à elevada dependência de umidade dessas espécies subtropicais.

# Appendix A

Complete list of identified pollen and spore types of the São José dos Ausentes (SdA), Rincão das Cabritas (RdC) and Ciama 2 records as well as of the surface soil samples (soil SdA)

## Remarks

- Indeterminate spores are abbreviated in the list as monolete ML for Monolete and TL for trilete followed by morphological characteristic or type.
- Systematic classification of Angiosperms family was based on Souza, V.C., Lorenzi, H., 2005. *Botânica sistemática: guia ilustrado para identificação da famílias de Angiospermas da flora brasileira, baseado em APG II*. Instituto Plantarum: Nova Odessa, São Paulo.
- Systematic classification of tree ferns was based on Smith, A.R., Pryer, K.M., Schuettpelz, E., Korall, P., Schneider, H., Wolf, P.G., 2006. A classification for extant ferns. *Taxon* 55, 705-731.

Pollen taxa	Family	SdA	Soil SdA	RdC	Ciama 2
<i>Acaena</i> type	Rosaceae	X			X
<i>Acalypha</i>	Euphorbiaceae	X		X	X
<i>Actinostemon concolor</i>	Euphorbiaceae	X			
<i>Alchornea</i>	Euphorbiaceae	X	X	X	X
<i>Allium</i> type	Alliaceae				X
<i>Allophylus</i>	Sapindaceae	X		X	X
<i>Alnus</i>	Betulaceae	X	X	X	X
<i>Alseis floribunda</i> type	Rubiaceae	X			X
<i>Alstroemeria</i>	Alstroemeriaceae				X
<i>Alternanthera</i> type I	Amaranthaceae			X	X
<i>Alternanthera</i> type II	Amaranthaceae				X
Amaranthaceae/Chenopodiaceae			X	X	X
<i>Amaryllis</i>	Amaryllidaceae			X	X
<i>Ambrosia</i> type	Asteraceae	X	X	X	X
Anacardiaceae type I		X			
Anacardiaceae type II		X			
Anacardiaceae type III		X			
Apiaceae		X	X	X	X
Apiaceae type I		X			
Apiaceae type II		X			
<i>Apium</i> type	Apiaceae				X
Apocynaceae		X			
<i>Araucaria angustifolia</i>	Araucariaceae	X	X	X	X
Arecaceae		X	X	X	X
Arecaceae type I		X			
Arecaceae type II		X			
Asteraceae sub. Asteroideae		X	X	X	X
<i>Baccharis</i> type	Asteraceae	X	X	X	X
<i>Banara/Xylosma</i> type	Salicaceae	X	X	X	X
<i>Bathysa</i>	Rubiaceae	X			
<i>Begonia</i>	Begoniaceae				X
<i>Bernardia pulchella</i> type	Euphorbiaceae	X			X
Bignoniaceae		X			
<i>Borreria</i> type	Rubiaceae	X	X	X	X
<i>Borreria laxa</i>	Rubiaceae	X	X		
<i>Bougainvillea</i>	Nyctaginaceae			X	X
Bromeliaceae		X			X

Pollen taxa	Family	SdA	Soil SdA	RdC	Ciama 2
<i>Buddleia</i> type	Scrophulariaceae	X			X
<i>Butia</i> type	Arecaceae	X	X		
<i>Calea</i> type	Asteraceae			X	X
<i>Caperonia</i> type	Euphorbiaceae	X	X		
Caryophyllaceae type			X		
<i>Cassia racemosa</i> type	Fabaceae(Caesalpinioideae)				X
<i>Cecropia</i>	Urticaceae				X
<i>Cedrela fissilis</i> type	Meliaceae			X	
<i>Celosia</i> type	Amaranthaceae	X	X	X	X
<i>Celtis</i>	Cannabaceae	X	X	X	X
<i>Chaptalia</i> type	Asteraceae	X	X		
Chenopodiaceae(Amaranthaceae)		X	X		
<i>Chevreulia</i> type	Asteraceae				X
Cichorioideae type I	Asteraceae	X	X		
Cichorioideae type II	Asteraceae	X			
<i>Clethra</i> type	Clethraceae	X	X	X	X
<i>Coccocypselum</i>	Rubiaceae				X
Convolvulaceae		X			
<i>Cordia trichomata</i> type	Boraginaceae		X		X
<i>Croton</i>	Euphorbiaceae			X	X
Cucurbitaceae type		X		X	
<i>Cupania</i>	Sapindaceae	X		X	X
<i>Cuphea</i>	Lythraceae	X		X	X
Cyperaceae		X	X	X	X
<i>Daphnopsis</i> type	Thymelaeaceae	X	X	X	
<i>Daphnopsis</i> type II	Thymelaeaceae				X
<i>Dasyphyllum</i> type	Asteraceae				X
<i>Didymopanax (Scheffera)</i>	Araliaceae	X		X	X
<i>Diodia alata</i>	Rubiaceae	X			
<i>Dodonaea</i> type	Sapindaceae	X	X		X
<i>Dodonaea</i> type I	Sapindaceae	X			
<i>Drimys brasiliensis</i>	Winteraceae		X	X	X
<i>Echinodorus</i>	Alismataceae			X	X
<i>Ephedra</i>	Ephedraceae			X	X
Ericaceae		X			X
Eriocaulaceae				X	X
<i>Eryngium</i> type	Apiaceae	X	X	X	X

Pollen taxa	Family	SdA	Soil SdA	RdC	Ciama 2
<i>Esenbeckia</i>	Rutaceae			X	
<i>Eupatorium</i> type	Asteraceae			X	X
<i>Euphorbia</i> type	Euphorbiaceae			X	X
<i>Euphorbia</i> type I	Euphorbiaceae	X			
<i>Euphorbia</i> type II	Euphorbiaceae	X			
<i>Euphorbia</i> type III	Euphorbiaceae	X			
<i>Euphorbia papillosa</i> type	Euphorbiaceae	X		X	X
<i>Euplassa</i> type	Proteaceae				X
<i>Euterpe</i> type	Arecaceae	X			
Fabaceae		X	X	X	X
Fabaceae type I		X			X
Fabaceae type II		X	X		X
Fabaceae type III		X			X
Fabaceae type IV		X			X
Fabaceae type V		X			X
Fabaceae type VI		X			X
Fabaceae type VII		X			
<i>Faramea</i> type	Rubiaceae	X			
<i>Fuchsia</i>	Onagraceae	X			
<i>Gallesia</i>	Phytolaccaceae				X
<i>Genipa</i> type	Rubiaceae	X			
<i>Gomphrena/Pfaffia</i> type	Amaranthaceae	X	X	X	X
<i>Gordonia fruticosa</i>	Theaceae			X	X
<i>Griselinia ruscifolia</i> type	Griselinaceae			X	X
<i>Hedyosmum brasiliense</i>	Chloranthaceae		X		X
<i>Heimia</i>	Lythraceae	X			
<i>Heliantheae</i> type	Asteraceae			X	X
<i>Hoffmannia peckii</i>	Rubiaceae				X
<i>Holocheilus</i> type	Asteraceae			X	X
<i>Hydrocotyle</i> type	Araliaceae	X	X	X	X
<i>Hyeronima</i>	Phyllanthaceae	X			X
<i>Hypericum</i> type	Hypericaceae	X	X	X	X
<i>Hypochaeris</i> type	Asteraceae			X	X
<i>Hyptis</i> type	Lamiaceae	X			
<i>Ilex</i>	Aquifoliaceae	X	X	X	X
Iridaceae		X	X	X	X
<i>Jungia/Holocheilus</i> type	Asteraceae	X	X		

Pollen taxa	Family	SdA	Soil SdA	RdC	Ciama 2
<i>Lamanonia speciosa</i> type	Cunoniaceae		X	X	X
Lamiaceae		X	X	X	X
Ligulifloraea type	Asteraceae	X	X		
Little Asteraceae ( <i>Chevreulia</i> type)	Asteraceae	X	X		
Loranthaceae		X			X
<i>Ludwigia</i>	Onagraceae			X	X
<i>Luehea</i> type	Malvaceae	X	X	X	X
<i>Lupinus</i> type	Fabaceae (Papilionoideae)	X			
Malvaceae		X		X	
<i>Mandevilla</i> type	Apocynaceae				X
<i>Matayba</i>	Sapindaceae	X	X	X	X
Melastomataceae		X	X	X	X
Meliaceae		X	X	X	
<i>Meliosma</i>	Sabiaceae	X		X	X
Menispermaceae	Fabaceae (Mimosoideae)	X			
Mimosaceae	Fabaceae (Mimosoideae)			X	
<i>Mimosa</i>	Fabaceae (Mimosoideae)				X
<i>Mimosa</i> type	Fabaceae (Mimosoideae)	X		X	
<i>Mimosa</i> type I	Fabaceae (Mimosoideae)	X		X	
<i>Mimosa</i> type II	Fabaceae (Mimosoideae)			X	X
<i>Mimosa</i> type III	Fabaceae (Mimosoideae)			X	X
<i>Mimosa</i> type IV	Fabaceae (Mimosoideae)	X			
<i>Mimosa</i> type VIII	Fabaceae (Mimosoideae)	X			
<i>Mimosa</i> P4 type I	Fabaceae (Mimosoideae)	X			X
<i>Mimosa</i> P4 type II	Fabaceae (Mimosoideae)				X
<i>Mimosa</i> P8	Fabaceae (Mimosoideae)	X			
<i>Mimosa</i> P16	Fabaceae (Mimosoideae)	X			X
<i>Mimosa</i> <i>invisa</i> type	Fabaceae (Mimosoideae)	X		X	X
<i>Mimosa</i> <i>scabrella</i> type	Fabaceae (Mimosoideae)	X	X	X	X
<i>Mimosa</i> <i>taimbensis</i> type	Fabaceae (Mimosoideae)				X
Moraceae/Urticaceae		X	X	X	X
<i>Mutisia</i> type	Asteraceae				X
<i>Myrica</i>	Myricaceae				X
<i>Myriophyllum</i> type	Haloragaceae			X	X
<i>Myrsine</i> ( <i>Rapanea</i> )	Myrsinaceae	X	X	X	X
Myrtaceae		X	X	X	X
<i>Nothofagus dombeyi</i> type	Fagaceae		X		

Pollen taxa	Family	SdA	Soil SdA	RdC	Ciama 2
Nyctaginaceae					X
<i>Ocotea</i> type	Lauraceae	X			X
Orchidaceae					X
<i>Oreopanax fulvum</i> type	Araliaceae			X	X
<i>Ouratea</i> type	Ochnaceae		X		X
<i>Oxalis</i> type I	Oxalidaceae	X	X	X	X
<i>Oxalis</i> type II	Oxalidaceae				X
<i>Pamphalea</i> type	Asteraceae	X	X		X
<i>Passiflora</i>	Passifloraceae			X	
<i>Paullinia</i> type	Sapindaceae				X
<i>Pera</i> type	Euphorbiaceae				X
<i>Pfaffia gnaphalioides</i>	Amaranthaceae			X	
<i>Phaseolus</i> type	Fabaceae (Papilionoideae)	X			
<i>Phrygilanthus acutifolius</i>	Loranthaceae	X	X	X	X
<i>Phyllanthus</i> type	Phyllanthaceae	X			
<i>Phyllanthus stipulatus</i> type	Phyllanthaceae				X
<i>Phyllocarpus</i> type	Fabaceae(Caesalpinioideae)	X			
<i>Pinus</i>	Pinaceae	X	X	X	X
<i>Piper</i>	Piperaceae			X	
<i>Piptadenia</i> type	Fabaceae (Mimosoideae)	X		X	X
<i>Plantago</i>	Plantaginaceae			X	X
<i>Plantago australis</i> type	Plantaginaceae	X	X		
<i>Pluchea</i> type	Asteraceae			X	X
Poaceae		X	X	X	X
<i>Podocarpus</i>	Podocarpaceae	X	X	X	X
Polemoniaceae		X			
<i>Polygala</i>	Polygalaceae	X	X	X	X
<i>Polygonum</i>	Polygonaceae			X	X
Polygonaceae		X			
<i>Potamogeton</i> type	Potamogetonaceae			X	
<i>Pouteria garderana</i>	Sapotaceae			X	X
<i>Prockia crucis</i> type	Salicaceae	X	X	X	X
<i>Prunus</i> type	Rosaceae	X		X	
<i>Psychotria</i> type	Rubiaceae	X	X		
<i>Psychotria alba</i> type	Rubiaceae				X
<i>Psychotria birotuba</i> type	Rubiaceae	X			
<i>Quercus</i> type	Fagaceae	X			



Pollen taxa	Family	SdA	Soil SdA	RdC	Ciama 2
<i>Ranunculus bonariensis</i> type	Ranunculaceae	X	X	X	X
<i>Relbunium (Galium)</i> type	Rubiaceae	X			
Rhamnaceae				X	
<i>Rhamnus</i> type	Rhamnaceae	X			X
<i>Richeria australis</i> type	Phyllanthaceae	X			
Rosaceae type I		X			
Rosaceae type II		X			
Rosaceae type III		X			
<i>Roupala</i> type	Proteaceae		X	X	X
Rubiaceae		X	X	X	X
<i>Rubus</i> type	Rosaceae	X			
<i>Salix humboldtiana</i> type	Salicaceae	X	X	X	X
<i>Salvia</i> type	Lamiaceae	X	X	X	X
<i>Salvia</i> type I	Lamiaceae	X			
Sapotaceae		X			X
<i>Schinus</i> type	Anacardiaceae	X	X	X	X
<i>Schinus</i> type I	Anacardiaceae	X			
Scrophulariaceae		X			
<i>Scutellaria</i> type	Lamiaceae	X		X	X
<i>Sebastiania</i> type	Euphorbiaceae	X			
<i>Sebastiania brasiliensis</i> type	Euphorbiaceae	X	X	X	X
<i>Sebastiania commersoniana</i> type	Euphorbiaceae	X	X	X	X
<i>Sebastiania schottiana</i> type	Euphorbiaceae	X			X
<i>Securidaca</i> type	Polygalaceae	X		X	X
<i>Senecio</i> type	Asteraceae	X	X	X	X
<i>Sloanea</i> type	Elaeocarpaceae	X			
Solanaceae					X
<i>Solanum</i> type	Solanaceae	X	X	X	X
<i>Styrax</i>	Styracaceae	X	X	X	X
<i>Symplocos</i> type	Symplocaceae	X			
<i>Symplocos lanceolata</i> type	Symplocaceae	X	X	X	X
<i>Symplocos laxiflora</i> type	Symplocaceae	X			
<i>Symplocos nitens</i> type	Symplocaceae	X			X
<i>Symplocos tenuifolia</i> type	Symplocaceae	X	X	X	X
<i>Tapirira</i> type	Anacardiaceae	X	X		X
<i>Tetrorchidium rubrivenium</i>	Euphorbiaceae	X	X		X
Thymelaceae type					X

Pollen taxa	Family	SdA	Soil SdA	RdC	Ciama 2
Tiliaceae		X			
<i>Trema</i> type	Cannabaceae	X	X	X	X
<i>Trichocline</i> type	Asteraceae	X			
<i>Trixis</i> type	Asteraceae	X		X	X
Tubulifloraea type (Asteroideae)	Asteraceae	X			
<i>Typha</i>	Typhaceae		X	X	
Urticaceae P2			X		
Urticaceae P3		X			
<i>Utricularia</i>	Lentibulariaceae			X	
<i>Valeriana</i> type I	Valerianaceae	X		X	X
<i>Valeriana</i> type II	Valerianaceae				X
Verbenaceae		X			
<i>Verbena</i> type	Verbenaceae	X			X
<i>Verbena isabellii</i>	Verbenaceae	X			
<i>Vernonia</i> type	Asteraceae	X	X		
<i>Vernonia nudiflora</i> type	Asteraceae			X	X
<i>Vicia/Lathyrus</i> type	Fabaceae (Papilionoideae)	X		X	
<i>Virola</i> type	Myristicaceae				X
<i>Weinmannia</i> type	Cunoniaceae	X	X	X	X
<i>Xyris</i>	Xyridaceae	X		X	X
<i>Zanthoxylum</i> type I	Rutaceae	X	X	X	X
<i>Zanthoxylum</i> type II	Rutaceae	X		X	
<i>Zornia</i> type	Fabaceae (Papilionoideae)	X	X	X	X
<i>Alsophyla</i> type	Cyatheaceae	X			
<i>Alsophila elegans</i> type	Cyatheaceae				X
<i>Anthoceros punctatus</i>	Anthocerotaceae	X		X	
<i>Blechnum imperiale</i> type	Blechnaceae	X	X	X	X
Cyatheaceae				X	X
<i>Cyathea</i> type	Cyatheaceae		X		
Spore taxa	Family	SdA	Soil SdA	RdC	Ciama 2
<i>Cyathea schanschin</i> type	Cyatheaceae	X	X		X
<i>Dicksonia sellowiana</i>	Dicksoniaceae	X	X	X	X
<i>Gymnogramma</i> type	Pteridaceae	X		X	
<i>Hymenophyllum</i> type	Hymenophyllaceae	X			
<i>Isoetes</i>	Isoetaceae		X	X	X
<i>Lycopodium</i> sp.	Lycopodiaceae		X	X	X
<i>Lycopodium alopecuroides</i> type	Lycopodiaceae	X		X	X

Spore taxa	Family	SdA	Soil SdA	RdC	Ciama 2
<i>Lycopodium cernuum</i> type	Lycopodiaceae	X		X	X
<i>Lycopodium clavatum</i> type	Lycopodiaceae	X	X	X	X
<i>Marattia</i>	Marattiaceae			X	X
Monolete type I		X			
Monolete type II		X			
Monolete type III			X		
Monolete echinate			X		
Monolete foveolate				X	
Monolete psilate >50µm			X	X	X
Monolete psilate <50µm			X	X	X
Monolete verrucate <50µm		X	X	X	X
Monolete verrucate >50µm		X	X	X	X
<i>Nephelea setosa</i>	Cyatheaceae	X			X
<i>Osmunda</i>	Osmundaceae	X		X	
<i>Phaeoceros laevis</i>	Anthocerotaceae	X	X	X	X
Pteridophyta type 1					X
Pteridophyta 3		X			X
Pteridophyta 6					X
Pteridophyta 7		X	X		
<i>Selaginella</i>	Selaginellaceae	X			X
<i>Selaginella excurrens</i> type	Selaginellaceae	X	X	X	X
<i>Sphagnum</i>	Sphagnaceae	X	X	X	X
Trilete type I		X			
Trilete type II		X			
Trilete type III			X		
Trilete echinate type I		X	X		X
Trilete echinate type II					X
Trilete foveolate					X
Trilete psilate			X		X
Trilete psilate >50µm		X		X	X
Trilete psilate <50µm		X		X	
Trilete reticulate					X
Trilete scabrate					X
Trilete verrucate				X	X
Trilete verrucate >50µm		X			
Trilete verrucate <50µm		X			

# Appendix B

Complete list of pollen and spore types counted in the sedimentary records and soil samples grouped into different ecological groups

## Remarks

- Indeterminate spores are abbreviated in the list as monolete ML for Monolete and TL for trilete followed by morphological characteristic or type.
- Systematic classification of Angiosperms family was based on Souza, V.C., Lorenzi, H., 2005. Botânica sistemática: guia ilustrado para identificação da famílias de Angiospermas da flora brasileira, baseado em APG II. Instituto Plantarum: Nova Odessa, São Paulo.
- Systematic classification of tree ferns was based on Smith, A.R., Pryer, K.M., Schuettpelz, E., Korall, P., Schneider, H., Wolf, P.G., 2006. A classification for extant ferns. *Taxon* 55, 705-731.

List of all pollen and spore taxa found in the São José dos Ausentes (SdA) core grouped into the main vegetation formations.

Campos	<i>Acaena</i> type, <i>Alseis floribunda</i> type, <i>Ambrosia</i> type, Apiaceae, Apiaceae type I-II, Asteraceae sub. Asteroideae, <i>Baccharis</i> type, <i>Borreria</i> type, <i>Borreria laxa</i> , <i>Celosia</i> type, <i>Chaptalia</i> type, Chenopodiaceae, Cichorioideae type I-II, Cucurbitaceae type, <i>Cuphea</i> , Cyperaceae, <i>Diodia alata</i> , Ericaceae, <i>Eryngium</i> type, <i>Euphorbia</i> type I-III, <i>Euphorbia papillosa</i> type, Fabaceae, Fabaceae type I- VII, <i>Faramea</i> type, <i>Genipa</i> type, <i>Gomphrena/Pfaffia</i> type, <i>Heimia</i> , <i>Hydrocotyle</i> type, <i>Hypericum</i> type, <i>Hyptis</i> type, Iridaceae, <i>Jungia/Holocheilus</i> type, Lamiaceae, Liguliflorae type, Little Asteraceae, <i>Lupinus</i> type, Malvaceae, <i>Oxalis</i> type I, <i>Pamphalea</i> type, <i>Phaseolus</i> type, <i>Phyllocarpus</i> type, <i>Plantago australis</i> type, Poaceae, <i>Polygala</i> , Polygonaceae, <i>Psychotria</i> type, <i>Psychotria birotuba</i> type, <i>Ranunculus bonariensis</i> type, <i>Relbunium</i> type, Rubiaceae, <i>Salvia</i> type, <i>Salvia</i> type I, <i>Scutellaria</i> type, <i>Securidaca</i> type, <i>Senecio</i> type, <i>Solanum</i> type, <i>Trichocline</i> type, <i>Trixis</i> type, Tubuliflorae type, <i>Valeriana</i> type I, Verbenaceae, <i>Verbena isabellii</i> , <i>Verbena</i> type, <i>Vernonia</i> type, <i>Vicia/Lathyrus</i> type, <i>Xyris</i> , <i>Zornia</i> type
<i>Araucaria</i> forest	<i>Araucaria angustifolia</i> , <i>Banara/Xylosma</i> type, Bromeliaceae, <i>Buddleia</i> type, <i>Clethra</i> type, <i>Daphnopsis</i> type, <i>Dodonaea</i> type, <i>Dodonaea</i> type I, <i>Fuchsia</i> , <i>Ilex</i> , <i>Luehea</i> type, Melastomataceae, <i>Mimosa scabrella</i> type, <i>Myrsine</i> , Myrtaceae, <i>Ocotea</i> type, <i>Phyllanthus</i> type, <i>Piptadenia</i> type, <i>Podocarpus</i> , <i>Prunus</i> type, <i>Schinus</i> type, <i>Schinus</i> type I, Scrophulariaceae, <i>Sebastiania</i> type, <i>S. brasiliensis</i> type, <i>S. commersoniana</i> type, <i>S. schottiana</i> type, <i>Sloanea</i> type, <i>Styrax</i> , <i>Weinmannia</i> type, <i>Zanthoxylum</i> type I-II
Atlantic rainforest	<i>Acalypha</i> , <i>Actinostemon concolor</i> , <i>Alchornea</i> , <i>Allophylus</i> , Anacardiaceae type I-III, Apocynaceae, Arecaceae, Arecaceae type I-II, <i>Bathysa</i> , Bignoniaceae, <i>Butia</i> type, <i>Celtis</i> , Convolvulaceae, <i>Cupania</i> , <i>Didymopanax</i> , <i>Euterpe</i> type, <i>Hyeronima</i> , Loranthaceae, <i>Matayba</i> , Meliaceae, <i>Meliosma</i> , Menispermaceae, Moraceae/Urticaceae, <i>Phrygilanthus acutifolius</i> , <i>Prockia crucis</i> type, <i>Rhamnus</i> type, <i>Salix humboldtiana</i> type, Sapotaceae, <i>Symplocos</i> type, <i>S. lanceolata</i> type, <i>S. laxiflora</i> type, <i>S. nitens</i> type, <i>S. tenuifolia</i> type, <i>Tapirira</i> type, <i>Tetrorchidium rubrivenium</i> , <i>Trema</i> type, Urticaceae P3
Other environment	<i>Alnus</i> , <i>Bernhardia pulchella</i> type, <i>Caperonia</i> type, <i>Mimosa</i> type, <i>Mimosa</i> type I, <i>Mimosa</i> type IV, <i>Mimosa</i> type VIII, <i>Mimosa</i> P4 type I, <i>Mimosa</i> P8, <i>Mimosa</i> P16, <i>Mimosa invis</i> type, <i>Pinus</i> , Polemoniaceae, <i>Quercus</i> type, <i>Richeria australis</i> type, Rosaceae type I-III, <i>Rubus</i> type, Tiliaceae
Unknown pollen type	C3 type I-III, C3P3 type I-XI, C4 type, Type 8, Type 11, Inaperturate type, Reticulate type
Pteridophyta	<i>Alsophila</i> type, <i>Blechnum imperiale</i> type, <i>Cyathea schanschin</i> type, <i>Dicksonia sellowiana</i> , <i>Gymnogramma</i> type, <i>Hymenophyllum</i> type, <i>Lycopodium alopecuroides</i> type, <i>L. cernuum</i> type, <i>L. clavatum</i> type, ML type I-II, ML verrucate <50µm, ML verrucate >50µm, <i>Nephelea setosa</i> , <i>Osmunda</i> , Pteridophyta type 3, Pteridophyta type 7, <i>Selaginella</i> , <i>Selaginella excurrans</i> type, TL type I-II, TL echinate type I, TL psilate >50µm, TL psilate <50µm, TL verrucate >50µm, TL verrucate <50µm
Moss	<i>Anthoceros punctatus</i> , <i>Phaeoceros laevis</i> , <i>Sphagnum</i>

List of all pollen and spore taxa found in the surface soil samples content from São José dos Ausentes study area grouped into the main vegetation formations.

Campos	Amarathaceae/Chenopodiaceae, <i>Ambrosia</i> type, Apiaceae, Asteraceae sub. Asteroideae, <i>Baccharis</i> type, <i>Borreria</i> type, <i>Borreria laxa</i> , Caryophyllaceae type, <i>Celosia</i> type, <i>Chaptalia</i> type, Chenopodiaceae, Cichorioideae type I, Cyperaceae, <i>Eryngium</i> type, Fabaceae, Fabaceae type II, <i>Gomphrena/Pfaffia</i> type, <i>Hedyosmum brasiliense</i> , <i>Hydrocotyle</i> type, <i>Hypericum</i> type, Iridaceae, <i>Jungia/Holocheilus</i> type, Lamiaceae, Ligulifloraea type, Little Asteraceae, <i>Oxalis</i> type I, <i>Pamphalea</i> type, <i>Plantago australis</i> type, Poaceae, <i>Polygala</i> , <i>Psychotria</i> type, <i>Ranunculus bonariensis</i> type, Rubiaceae, <i>Salvia</i> type, <i>Senecio</i> type, <i>Solanum</i> type, <i>Vernonia</i> type, <i>Zornia</i> type
<i>Araucaria</i> forest	<i>Araucaria angustifolia</i> , <i>Banara/Xylosma</i> type, <i>Clethra</i> type, <i>Cordia trichomata</i> type, <i>Daphnopsis</i> type, <i>Dodonaea</i> type, <i>Drimys brasiliensis</i> , <i>Ilex</i> , <i>Lamanonia speciosa</i> type, <i>Luehea</i> type, Melastomataceae, <i>Mimosa scabrella</i> type, <i>Myrsine</i> , Myrtaceae, <i>Podocarpus</i> , <i>Roupala</i> type, <i>Schinus</i> type, <i>Sebastiania brasiliensis</i> type, <i>S. commersoniana</i> type, <i>Styrax</i> , <i>Weinmannia</i> type, <i>Zanthoxylum</i> type I
Atlantic rainforest	<i>Alchornea</i> , Arecaceae, <i>Butia</i> type, <i>Celtis</i> , <i>Matayba</i> , Meliaceae, Moraceae/Urticaceae, <i>Ouratea</i> type, <i>Phrygilanthus acutifolius</i> , <i>Prockia crucis</i> type, <i>Salix humboldtiana</i> type, <i>Symplocos lanceolata</i> type, <i>S. teinuifolia</i> type, <i>Tapirira</i> type, <i>Tetrorchidium rubrivenium</i> , <i>Trema</i> type, Urticaceae P2
Other environment	<i>Alnus</i> , <i>Caperonia</i> type, <i>Nothofagus dombeyi</i> type, <i>Pinus</i> , <i>Typha</i>
Unknown pollen type	C3 type, C3P3 type I-IV, Echinete type
Pteridophyta	<i>Blechnum imperiale</i> type, <i>Cyathea</i> type, <i>C. schanschin</i> type, <i>Dicksonia sellowiana</i> , <i>Isoetes</i> , <i>Lycopodium</i> sp., <i>L. clavatum</i> type, ML type III, ML echinate, ML psilate >50µm, ML psilate <50µm, ML verrucate <50µm, ML verrucate >50µm, Pteridophyta type 7, <i>Selaginella excurrens</i> type, TL type III, TL echinate type I, TL psilate
Moss	<i>Phaeoceros laevis</i> , <i>Sphagnum</i>

List of all pollen and spore taxa found in the Rincão das Cabritas (RdC) core grouped into the main vegetation formations.

Campos	<i>Alternanthera</i> type I, Amaranaceae/Chenopodiaceae, <i>Amaryllis</i> , <i>Ambrosia</i> type, Apiaceae, Asteraceae sub. Asteroideae, <i>Baccharis</i> type, <i>Borreria</i> type, <i>Calea</i> type, <i>Celosia</i> type, <i>Croton</i> , <i>Cuphea</i> , Cyperaceae, Eriocaulaceae, <i>Eryngium</i> type, <i>Eupatorium</i> type, <i>Euphorbia papillosa</i> type, Fabaceae, <i>Gomphrena/Pfaffia</i> type, Heliantheae type, <i>Holocheilus</i> type, <i>Hypericum</i> type, <i>Hypochaeris</i> type, Iridaceae, Lamiaceae, <i>Oxalis</i> type I, <i>Pfaffia gnaphalioides</i> , <i>Plantago</i> , <i>Pluchea</i> type, Poaceae, <i>Polygala</i> , <i>Ranunculus bonariensis</i> type, Rubiaceae, <i>Salvia</i> type, <i>Scutellaria</i> type, <i>Securidaca</i> type, <i>Senecio</i> type, <i>Solanum</i> type, <i>Trixis</i> type, <i>Valeriana</i> type I, <i>Vernonia nudiflora</i> type, <i>Vicia/Lathyrus</i> type, <i>Xyris</i> , <i>Zornia</i> type
<i>Araucaria</i> forest	<i>Araucaria angustifolia</i> , <i>Banara/Xylosma</i> type, <i>Clethra</i> type, <i>Daphnopsis</i> type, <i>Drimys brasiliensis</i> , <i>Griselinia ruscifolia</i> type, <i>Ilex</i> , <i>Lamanonia speciosa</i> type, <i>Mimosa scabrella</i> type, <i>Myrsine</i> , Myrtaceae, <i>Oreopanax fulvum</i> type, <i>Podocarpus</i> , <i>Prunus</i> type, Rhamnaceae, <i>Roupala</i> type, <i>Schinus</i> type
Atlantic rainforest	<i>Acalypha</i> , <i>Alchornea</i> , <i>Allophylus</i> , Arecaceae, <i>Bougainvillea</i> , <i>Cedrela fissilis</i> type, <i>Celtis</i> , <i>Cupania</i> , <i>Didymopanax</i> , <i>Esenbeckia</i> , <i>Gordonia fruticosa</i> , <i>Luehea</i> type, <i>Matayba</i> , Meliaceae, <i>Meliosma</i> , Moraceae/Urticaceae, <i>Passiflora</i> , <i>Phrygilanthus acutifolius</i> , <i>Piper</i> , <i>Salix humboldtiana</i> type, <i>Sebastiania brasiliensis</i> type, <i>S. commersoniana</i> type, <i>Styrax</i> , <i>Symplocos lanceolata</i> type, <i>S. tenuifolia</i> type, <i>Trema</i> type, <i>Weinmannia</i> type, <i>Zanthoxylum</i> type I-II
Other environment	<i>Alnus</i> , Cucurbitaceae type, <i>Ephedra</i> , <i>Euphorbia</i> type, Malvaceae, Melastomataceae, Mimosaceae, <i>Mimosa</i> type, <i>Mimosa</i> type I-III, <i>Mimosa invisa</i> type, <i>Pinus</i> , <i>Piptadenia</i> type, <i>Pouteria gardnerana</i> , <i>Prockia crucis</i> type
Aquatic	<i>Echinodorus</i> , <i>Hydrocotyle</i> type, <i>Ludwigia</i> , <i>Myriophyllum</i> type, <i>Polygonum</i> , <i>Potamogeton</i> type, <i>Typha</i> , <i>Utricularia</i>
Unknown pollen type	C3P3 psilate group, C3P3 reticulate group, C3P3 scabrate, C3P3 type, C3 psilate, C3 reticulate
Tree fern	Cyatheaceae, <i>Dicksonia sellowiana</i>
Pteridophyta	<i>Blechnum imperiale</i> type, <i>Gymnogramma</i> type, <i>Isoetes</i> , <i>Lycopodium</i> sp., <i>L. alopecuroides</i> type, <i>L. cernuum</i> type, <i>L. clavatum</i> type, <i>Marattia</i> , ML foveolate, ML psilate >50µm, ML psilate <50µm, ML verrucate <50µm, ML verrucate >50µm, <i>Osmunda</i> , <i>Selaginella excurrens</i> type, TL psilate >50µm, TL psilate <50µm, TL verrucate
Moss	<i>Anthoceros punctatus</i> , <i>Phaeoceros laevis</i> , <i>Sphagnum</i>

List of all pollen and spore taxa found in the Ciama 2 core grouped into the main vegetation formations.

Campos	<i>Allium</i> type, <i>Alseis floribunda</i> type, <i>Alstroemeria</i> , <i>Alternanthera</i> type I-II, Amarathaceae/Chenopodiaceae, <i>Amaryllis</i> , <i>Ambrosia</i> type, Apiaceae, <i>Apium</i> type, Asteraceae sub. Asteroideae, <i>Baccharis</i> type, <i>Borreria</i> type, <i>Calea</i> type, <i>Celosia</i> type, <i>Chevreulia</i> type, <i>Coccocypselum</i> , <i>Croton</i> , <i>Cuphea</i> , Cyperaceae, <i>Dasyphyllum</i> type, Ericaceae, Eriocaulaceae, <i>Eryngium</i> type, <i>Eupatorium</i> type, <i>Euphorbia papillosa</i> type, Fabaceae, Fabaceae type I-VI, <i>Gomphrena/Pfaffia</i> type, <i>Heliantheae</i> type, <i>Hoffmannia peckii</i> , <i>Holocheilus</i> type, <i>Hypochoeris</i> type, Iridaceae, Lamiaceae, <i>Mutisia</i> type, Orchidaceae, <i>Oxalis</i> type I-II, <i>Pamphalea</i> type, <i>Phyllanthus stipulatus</i> type, <i>Plantago</i> , <i>Pluchea</i> type, Poaceae, <i>Polygala</i> , <i>Psychotria alba</i> type, <i>Ranunculus bonariensis</i> type, Rubiaceae, <i>Salvia</i> type, <i>Scutellaria</i> type, <i>Securidaca</i> type, <i>Senecio</i> type, Solanaceae, <i>Solanum</i> type, <i>Tetrorchidium rubrivenium</i> , <i>Trixis</i> type, <i>Valeriana</i> type I-II, <i>Verbena</i> type, <i>Vernonia nudiflora</i> type, <i>Xyris</i> , <i>Zornia</i> type
Araucaria forest	<i>Araucaria angustifolia</i> , <i>Banara/Xylosma</i> type, <i>Buddleia</i> type, <i>Clethra</i> type, <i>Daphnopsis</i> type II, <i>Euplassa</i> type, <i>Griselinia ruscifolia</i> type, <i>Ilex</i> , <i>Mimosa scabrella</i> type, <i>Ocotea</i> type, <i>Oreopanax fulvum</i> type, <i>Podocarpus</i> , <i>Rhamnus</i> type, <i>Roupala</i> type, <i>Schinus</i> type
Atlantic rainforest	<i>Alchornea</i> , <i>Allophylus</i> , Arecaceae, <i>Begonia</i> , <i>Bougainvillea</i> , Bromeliaceae, <i>Cecropia</i> , <i>Celtis</i> , <i>Cordia trichomata</i> type, <i>Cupania</i> , <i>Didymopanax</i> , <i>Dodonaea</i> type, <i>Drimys brasiliensis</i> , <i>Gordonia fruticosa</i> , <i>Hyeronima</i> , <i>Lamanonia speciosa</i> type, Loranthaceae, <i>Luehea</i> type, <i>Mandevilla</i> type, <i>Matayba</i> , Melastomataceae, <i>Meliosma</i> , <i>Mimosa taimbensis</i> type, Moraceae/Urticaceae, <i>Myrsine</i> , Myrtaceae, Nyctaginaceae, <i>Ouratea</i> type, <i>Paullinia</i> type, <i>Pera</i> type, <i>Phrygilanthus acutifolius</i> , <i>Salix humboldtiana</i> type, <i>Sebastiania brasiliensis</i> type, <i>S. commersoniana</i> type, <i>S. schottiana</i> type, <i>Styrax</i> , <i>Symplocos lanceolata</i> type, <i>S. nitens</i> type, <i>S. tenuifolia</i> type, <i>Tapirira</i> type, <i>Trema</i> type, <i>Virola</i> type, <i>Weinmannia</i> type, <i>Zanthoxylum</i> type I
Other environment	<i>Acaena</i> type, <i>Acalypha</i> , <i>Alnus</i> , <i>Bernhardia pulchella</i> type, <i>Cassia racemosa</i> type, <i>Ephedra</i> , <i>Euphorbia</i> type, <i>Gallesia</i> , <i>Hedyosmum brasiliense</i> , <i>Hypericum</i> type, <i>Mimosa</i> , <i>Mimosa</i> type II-III, <i>Mimosa</i> P4 type I-II, <i>Mimosa</i> P16, <i>Mimosa invisita</i> type, <i>Myrica</i> , <i>Pinus</i> , <i>Piptadenia</i> type, <i>Pouteria garderana</i> , <i>Prockia crucis</i> type, Sapotaceae, Thymelaceae type
Aquatic	<i>Echinodorus</i> , <i>Hydrocotyle</i> type, <i>Ludwigia</i> , <i>Myriophyllum</i> type, <i>Polygonum</i>
Unknown pollen type	C3P3 type I- X, C4 type I-II, Clavate type, Pilate type
Tree fern	<i>Alsophila elegans</i> type, Cyatheaceae, <i>Cyathea schanschin</i> type, <i>Dicksonia sellowiana</i> , <i>Nephelea setosa</i>
Pteridophyta	<i>Blechnum imperiale</i> type, <i>Isoetes</i> , <i>Lycopodium</i> sp., <i>L. alopecuroides</i> type, <i>L. cernuum</i> type, <i>L. clavatum</i> type, <i>Marattia</i> , ML psilate >50µm, ML psilate <50µm, ML verrucate >50µm, ML verrucate <50µm, Pteridophyta type 1, Pteridophyta type 3, Pteridophyta type 6, <i>Selaginella</i> , <i>Selaginella excurrens</i> type, TL echinate type I-II, TL foveolate, TL psilate, TL psilate >50µm, TL reticulate, TL scabrate, TL verrucate
Moss	<i>Phaeoceros laevis</i> , <i>Sphagnum</i>



# Appendix C

**Photo gallery:** Illustration of some pollen and spores types

<b>Pollen type (taxon)</b>	<b>Family</b>	<b>Natural occurrence</b>	<b>Photo</b>
<i>Acaena</i> type	Rosaceae	Uncertain environment	1
<i>Acalypha</i>	Euphorbiaceae	Uncertain environment	2
<i>Alchornea</i>	Euphorbiaceae	Forest	3
<i>Allophylus</i>	Sapindaceae	Forest	4
<i>Alnus</i>	Betulaceae	Other environment	5
<i>Alseis floribunda</i> type	Rubiaceae	Grassland	6
<i>Alsophila elegans</i> type	Cyatheaceae	Forest	7
<i>Alstroemeria</i>	Alstroemeriaceae	Grassland	8
<i>Alternanthera</i> type II	Amaranthaceae	Grassland	9
Amaranthaceae/Chenopodiaceae		Grassland	10
<i>Amaryllis</i>	Amaryllidaceae	Grassland	11
<i>Ambrosia</i> type	Asteraceae	Grassland	12
<i>Anthoceros punctatus</i>	Anthocerotaceae	Bog environment	13
Apiaceae		Grassland	14
<i>Araucaria angustifolia</i>	Araucariaceae	Forest	15
Arecaceae		Forest	16
<i>Baccharis</i> type	Asteraceae	Grassland	17
<i>Banara/Xylosma</i> type	Salicaceae	Forest	18
<i>Begonia</i>	Begoniaceae	Forest	19
<i>Bernardia pulchella</i> type	Euphorbiaceae	Uncertain environment	20
<i>Blechnum imperiale</i> type	Blechnaceae	Bog environment	21
<i>Borreria</i> type	Rubiaceae	Grassland	22
Bromeliaceae		Forest	23
<i>Buddleia</i> type	Scrophulariaceae	Forest	24
<i>Calea</i> type	Asteraceae	Grassland	25
<i>Cecropia</i>	Urticaceae	Forest	26
<i>Celtis</i>	Cannabaceae	Forest	27
<i>Chevreulia</i> type	Asteraceae	Grassland	28
<i>Clethra</i> type	Clethraceae	Forest	29
<i>Croton</i>	Euphorbiaceae	Grassland	30
<i>Cupania</i>	Sapindaceae	Forest	31
<i>Cuphea</i>	Lythraceae	Grassland	32
Cyperaceae		Grassland	33
<i>Cyathea schanschin</i> type	Cyatheaceae	Forest	34
<i>Daphnopsis</i> type	Thymelaeaceae	Forest	35
<i>Dasyphyllum</i> type	Asteraceae	Grassland	36
<i>Dicksonia sellowiana</i>	Dicksoniaceae	Forest	37
<i>Didymopanax (Schefflera)</i>	Araliaceae	Forest	38
<i>Dodonaea</i> type	Sapindaceae	Forest	39
<i>Drimys brasiliensis</i>	Winteraceae	Forest	40

Pollen type (taxon)	Family	Natural occurrence	Photo
<i>Echinodorus</i>	Alismataceae	Aquatic	41
<i>Ephedra</i>	Ephedraceae	Other environments	42
Ericaceae		Grassland	43
Eriocaulaceae		Bog environment	44
<i>Eryngium</i> type	Apiaceae	Grassland	45
<i>Eupatorium</i> type	Asteraceae	Grassland	46
Fabaceae		Grassland	47
<i>Faramea</i> type	Rubiaceae	Grassland	48
<i>Gomphrena/Pfaffia</i> type	Amaranthaceae	Grassland	49
<i>Gordonia fruticosa</i>	Theaceae	Forest	50
<i>Griselinia ruscifolia</i> type	Griselinaceae	Forest	51
<i>Gymnogramma</i> type	Gymnogrammaceae	Forest	52
<i>Hedyosmum brasiliense</i>	Chloranthaceae	Other environment	53
<i>Heimia</i>	Lythraceae	Grassland	54
<i>Hoffmannia peckii</i>	Rubiaceae	Grassland	55
<i>Holocheilus</i> type	Asteraceae	Grassland	56
<i>Hydrocotyle</i> type	Araliaceae	Aquatic	57
<i>Hyeronima</i>	Phyllanthaceae	Forest	58
<i>Hypericum</i> type	Hypericaceae	Grassland	59
<i>Hypochaeris</i> type	Asteraceae	Grassland	60
<i>Ilex</i>	Aquifoliaceae	Forest	61
Iridaceae		Grassland	62
<i>Isoëtes</i>	Isoetaceae	Other environment	63
<i>Lamanonia speciosa</i> type	Cunoniaceae	Forest	64
<i>Ludwigia</i>	Onagraceae	Aquatic	65
<i>Luehea</i> type	Malvaceae	Forest	66
<i>Lycopodium alopecuroides</i> type	Lycopodiaceae		67
<i>Mandevilla</i> type	Apocynaceae	Forest	68
<i>Marattia</i>	Marattiaceae	Forest	69
<i>Matayba</i>	Sapindaceae	Forest	70
Melastomataceae		Uncertain environment	71
<i>Meliosma</i>	Sabiaceae	Forest	72
<i>Mimosa</i>	Fabaceae	Uncertain environment	73
<i>Mimosa scabrella</i> type	Fabaceae	Forest	74
<i>Mimosa taimbensis</i> type	Fabaceae	Forest	75
Moraceae/Urticaceae		Forest	76
<i>Myriophyllum</i> type	Haloragaceae	Aquatic	77
<i>Myrsine (Rapanea)</i>	Myrsinaceae	Forest	78
Myrtaceae		Forest	79
<i>Ocotea</i> type	Lauraceae	Forest	80

Pollen type (taxon)	Family	Natural occurrence	Photo
<i>Oreopanax fulvum</i> type	Araliaceae	Forest	81
<i>Osmunda</i>	Osmundaceae	Peat environment	82
<i>Ouratea</i> type	Ochnaceae	Forest	83
<i>Oxalis</i> type I	Oxalidaceae	Grassland	84
<i>Phaeoceros laevis</i>	Anthocerotaceae	Bog environment	85
<i>Phrygilanthus (Notanthera) acutifolius</i>	Loranthaceae	Forest	86
<i>Pinus</i>	Pinaceae	Other environment	87
<i>Piptadenia</i> type	Fabaceae	Uncertain environment	88
<i>Plantago</i>	Plantaginaceae	Grassland	89
<i>Pluchea</i> type	Asteraceae	Grassland	90
Poaceae		Grassland	91
<i>Podocarpus</i>	Podocarpaceae	Forest	92
<i>Polygala</i>	Polygalaceae	Grassland	93
<i>Polygonum</i>	Polygonaceae	Aquatic	94
<i>Prockia crucis</i> type	Salicaceae	Uncertain environment	95
<i>Ranunculus bonariensis</i> type	Ranunculaceae	Grassland	96
<i>Relbunium (Galium) type</i>	Rubiaceae	Grassland	97
<i>Rhamnus</i> type	Rhamnaceae	Forest	98
<i>Richeria australis</i> type	Phyllanthaceae	Uncertain environment	99
<i>Roupala</i> type	Proteaceae	Forest	100
Rubiaceae		Grassland	101
<i>Salix humboldtiana</i> type	Salicaceae	Forest	102
<i>Salvia</i> type	Lamiaceae	Grassland	103
<i>Schinus</i> type	Anacardiaceae	Forest	104
<i>Scutellaria</i> type	Lamiaceae	Grassland	105
<i>Sebastiania brasiliensis</i> type	Euphorbiaceae	Forest	106
<i>Sebastiania commersoniana</i> type	Euphorbiaceae	Forest	107
<i>Securidaca</i> type	Polygalaceae	Grassland	108
<i>Selaginella excurrens</i> type	Selaginellaceae	Bog environment	109
<i>Solanum</i> type	Solanaceae	Grassland	110
<i>Sphagnum</i>	Sphagnaceae	Bog environment	111
<i>Styrax</i>	Styracaceae	Forest	112
<i>Symplocos lanceolata</i> type	Symplocaceae	Forest	113
<i>Symplocos tenuifolia</i> type	Symplocaceae	Forest	114
<i>Tapirira</i> type	Anacardiaceae	Forest	115
<i>Tetrorchidium rubrivenium</i>	Euphorbiaceae	Uncertain environment	116
Thymelaceae type		Uncertain environment	117
<i>Trema</i> type	Cannabaceae	Forest	118
<i>Trixis</i> type	Asteraceae	Grassland	119
<i>Valeriana</i> type I	Valerianaceae	Grassland	120

<b>Pollen type (taxon)</b>	<b>Family</b>	<b>Natural occurrence</b>	<b>Photo</b>
<i>Verbena</i> type	Verbenaceae	Grassland	121
<i>Verbena isabellii</i>	Verbenaceae	Grassland	122
<i>Vernonia nudiflora</i> type	Asteraceae	Forest	123
<i>Vicia/Lathyrus</i> type	Fabaceae	Grassland	124
<i>Weinmannia</i> type	Cunoniaceae	Forest	125
<i>Xyris</i>	Xyridaceae	Grassland	126
<i>Zanthoxylum</i> type II	Rutaceae	Forest	127

Plate 1

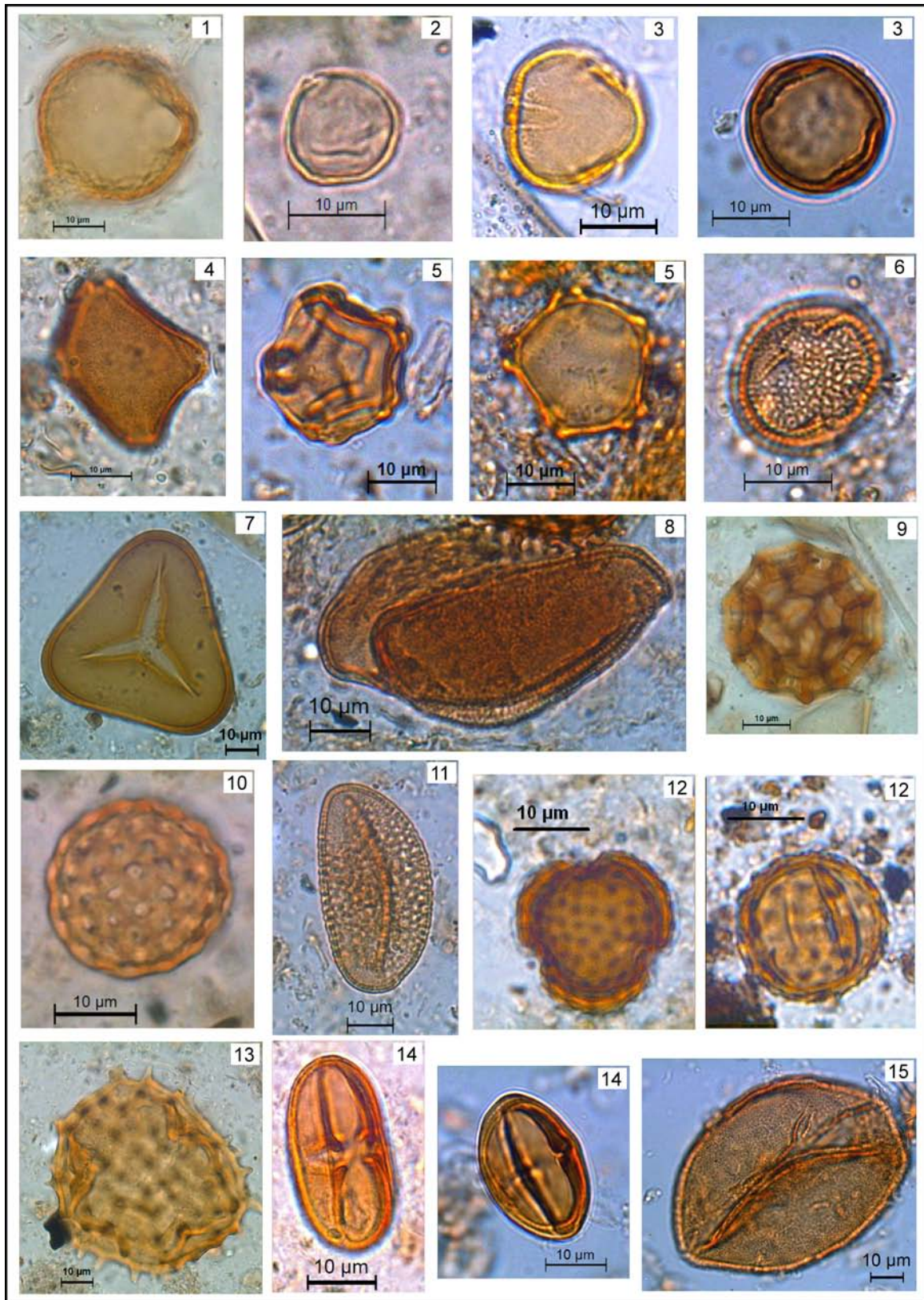




Plate 2

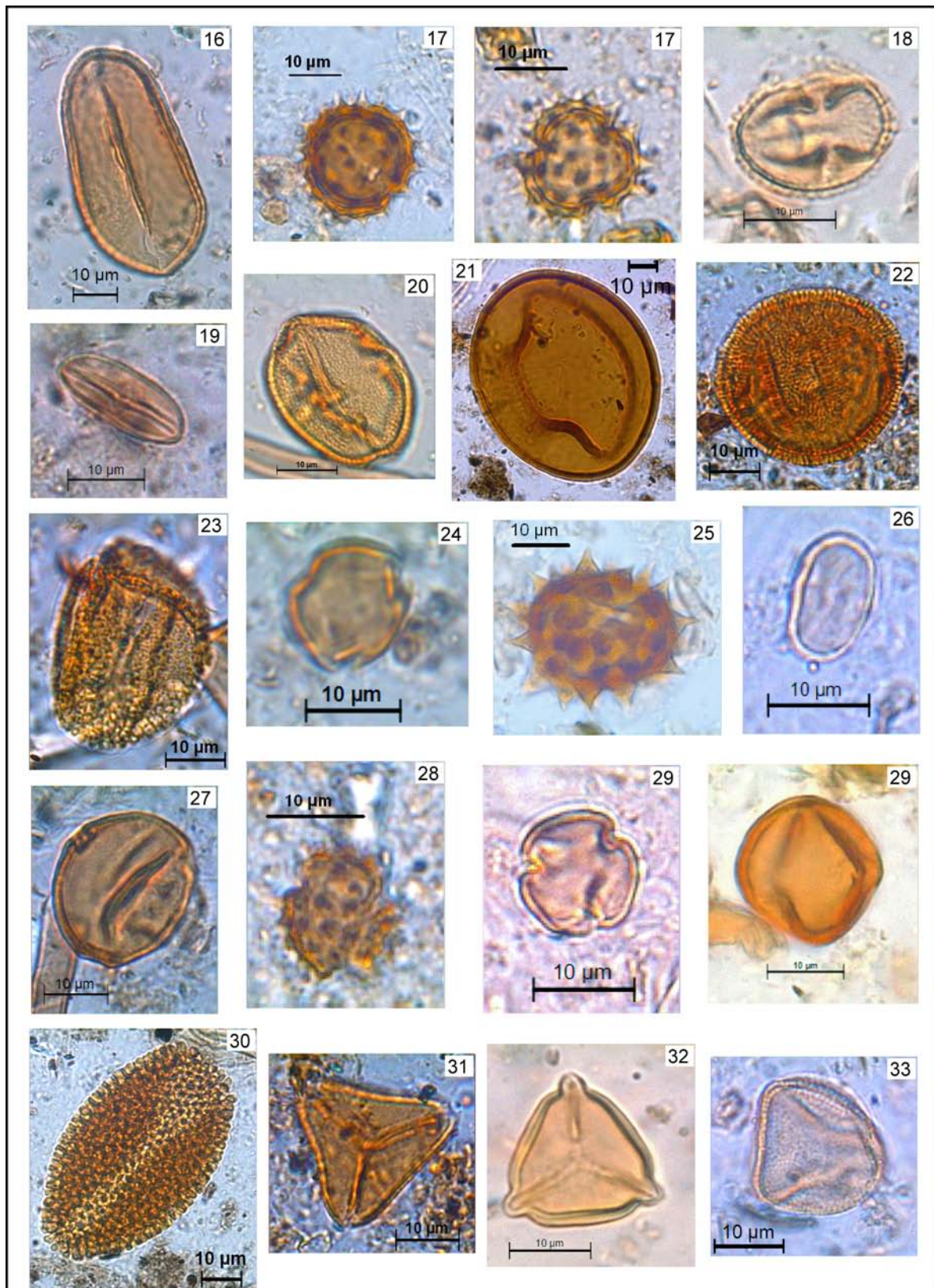




Plate 3

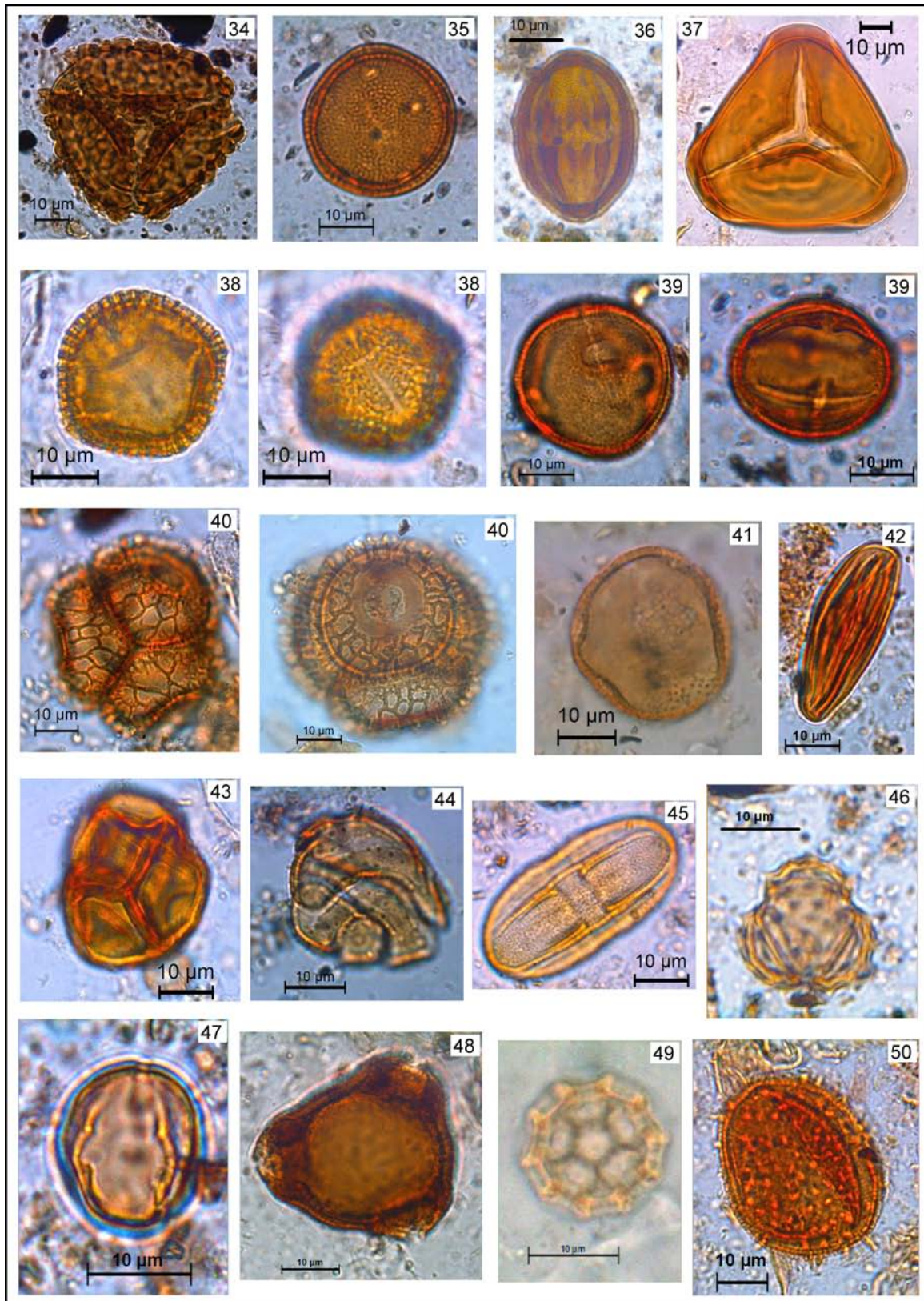




Plate 4

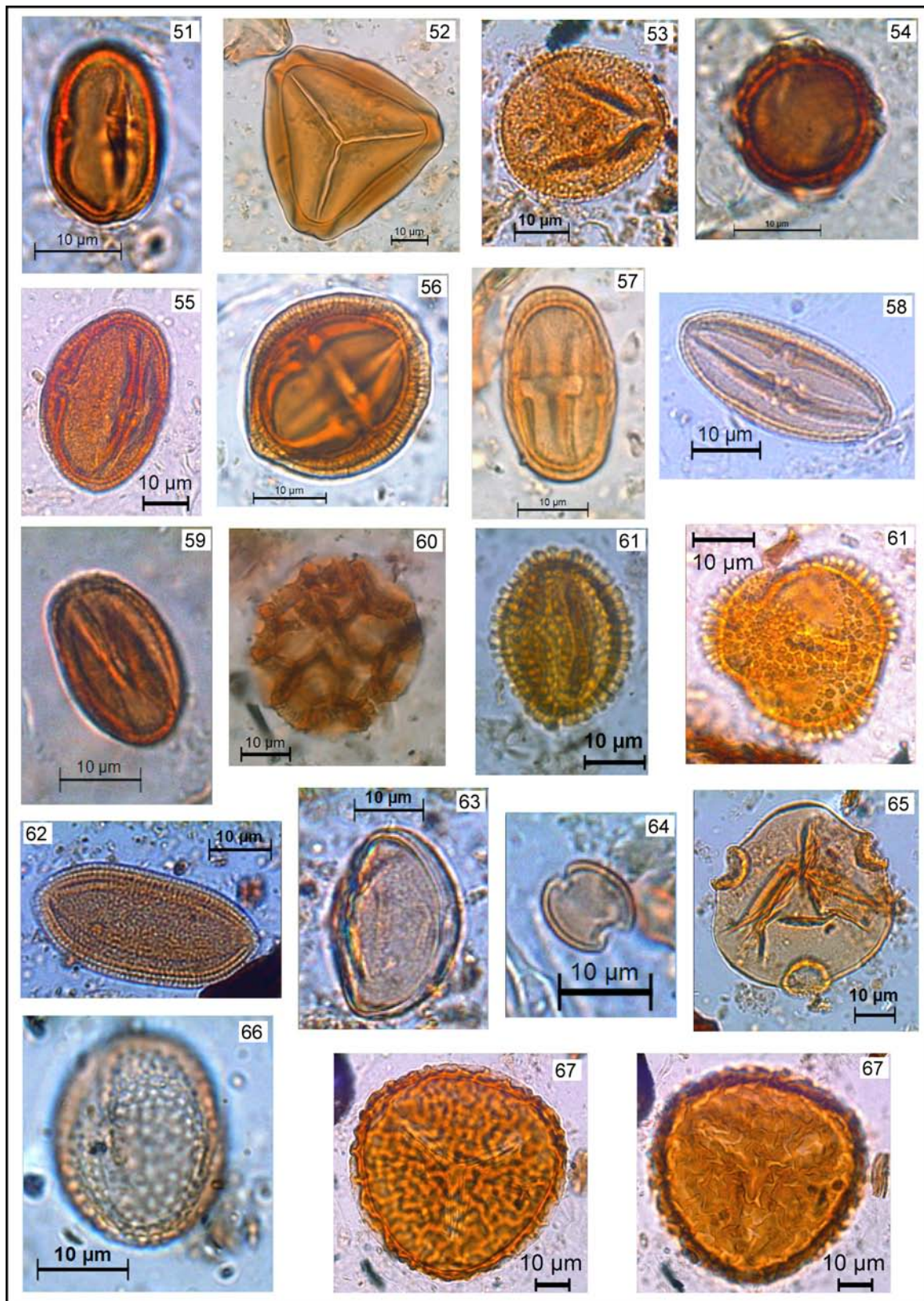




Plate 5

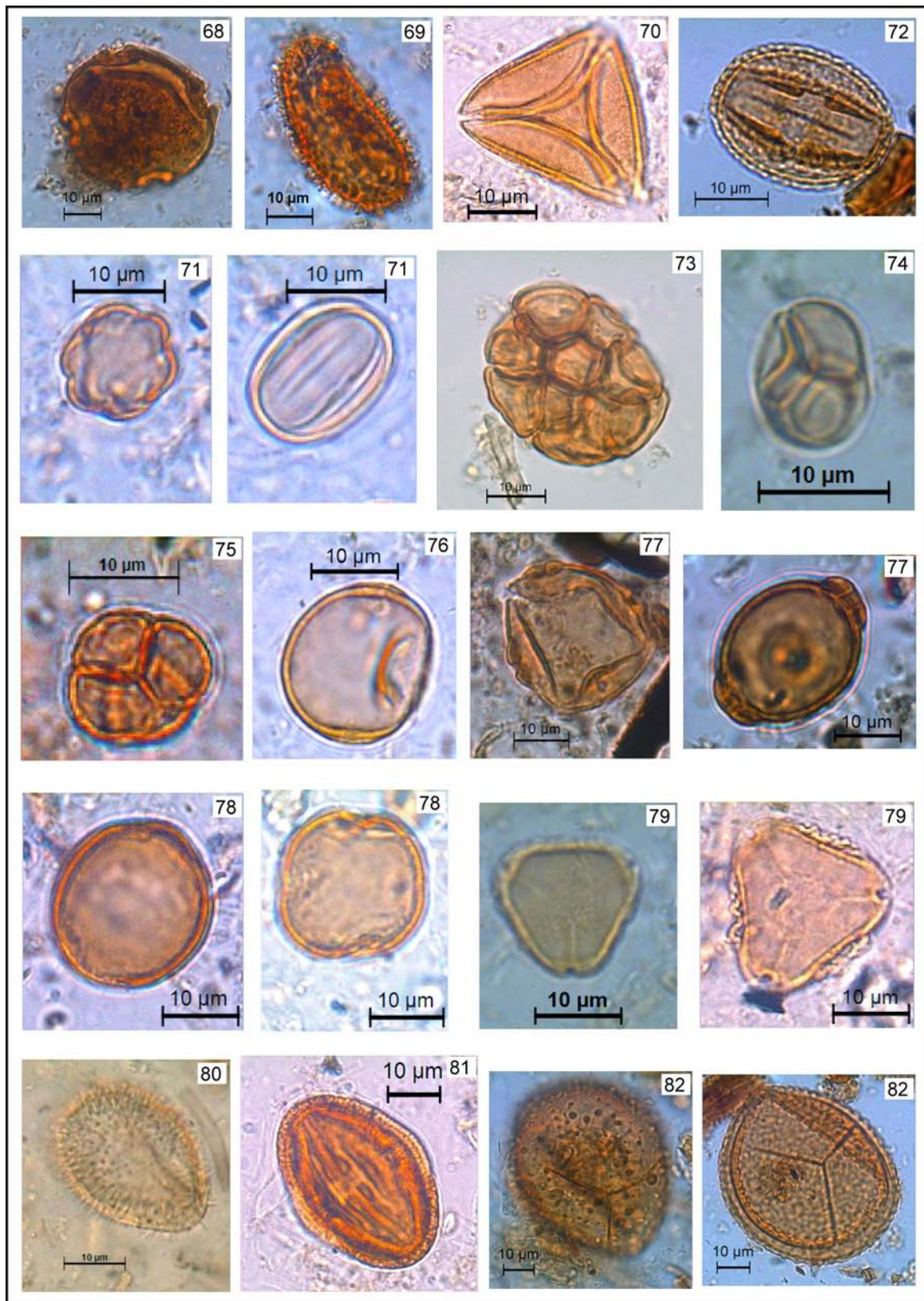




Plate 6

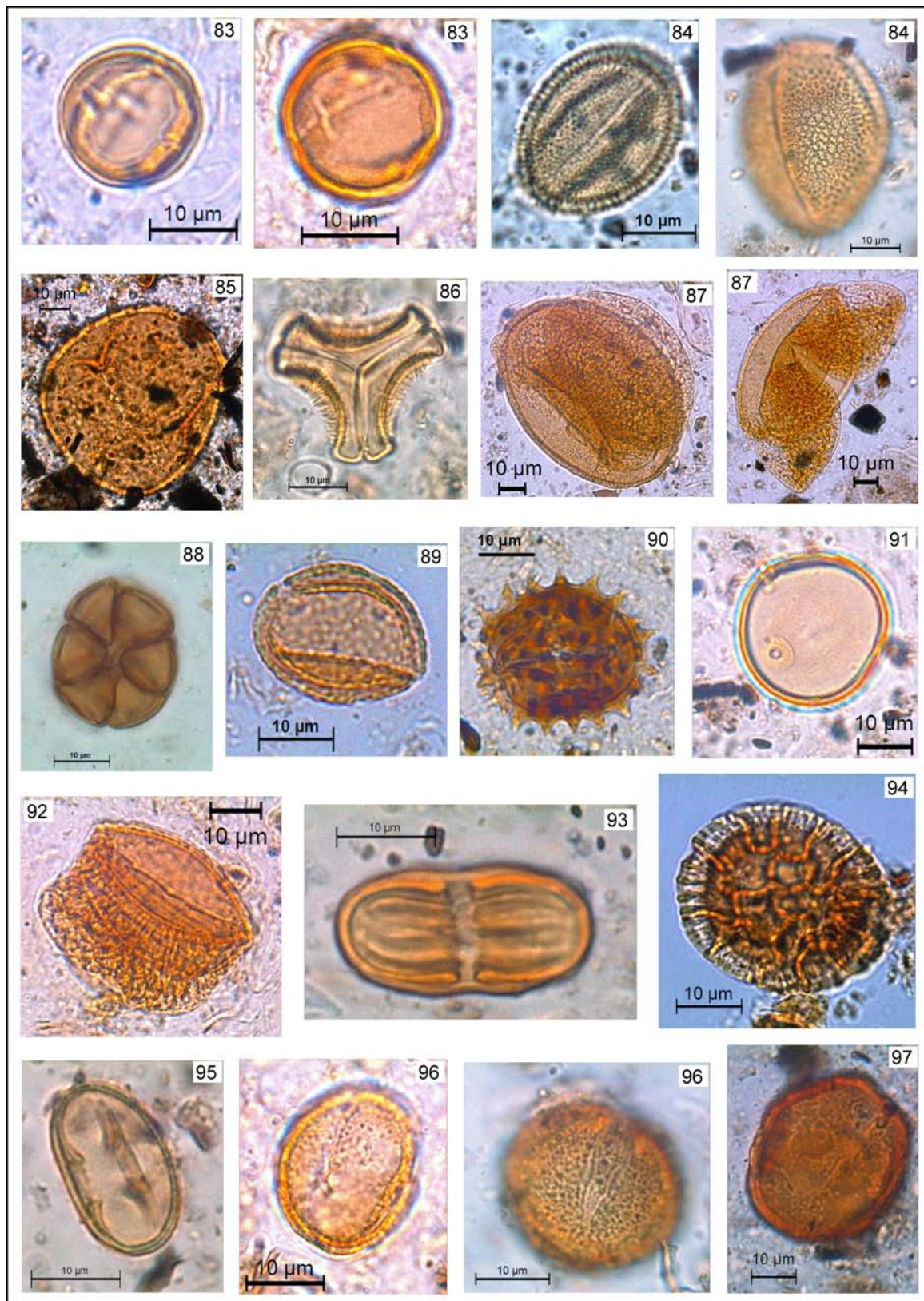




Plate 7

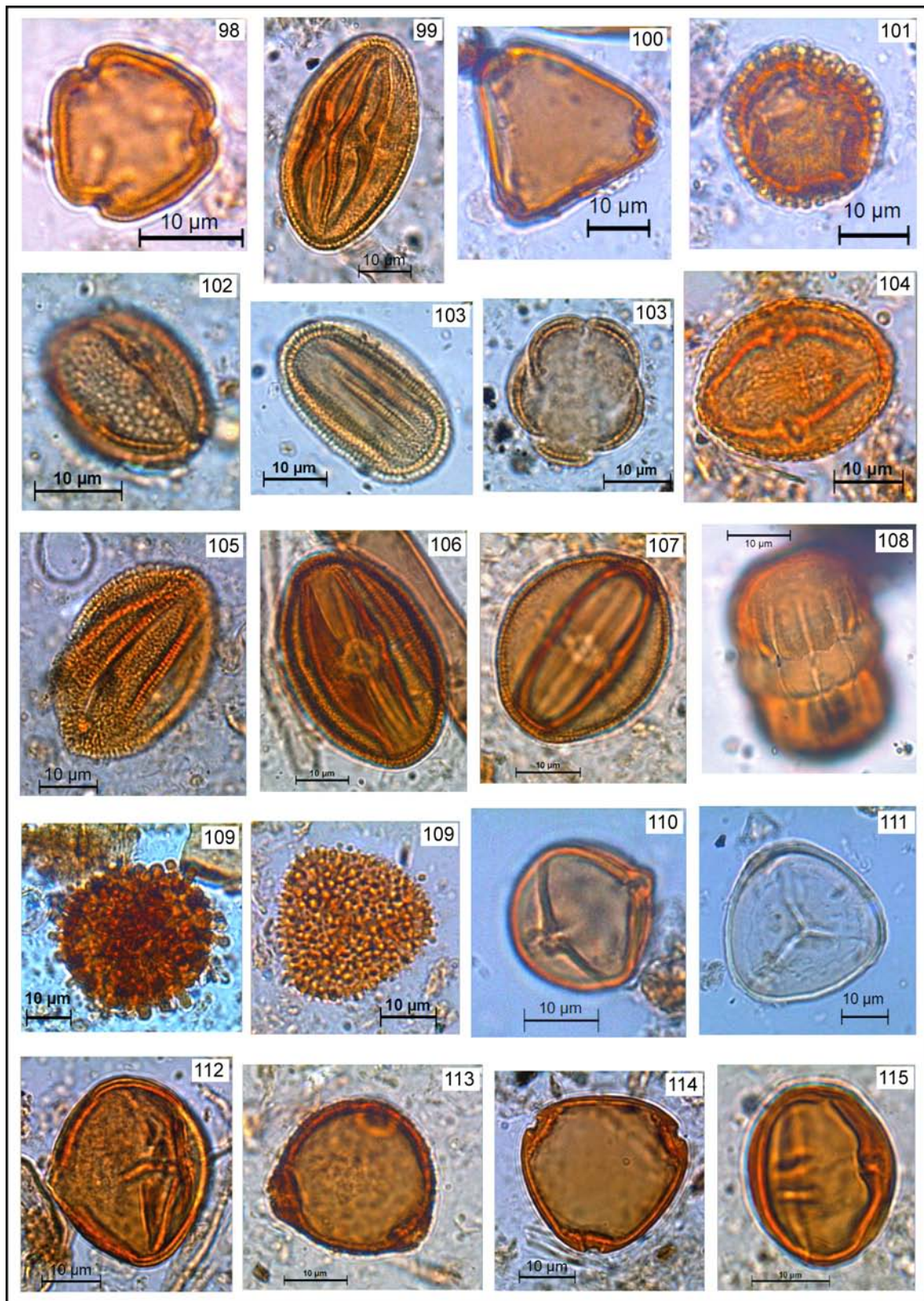
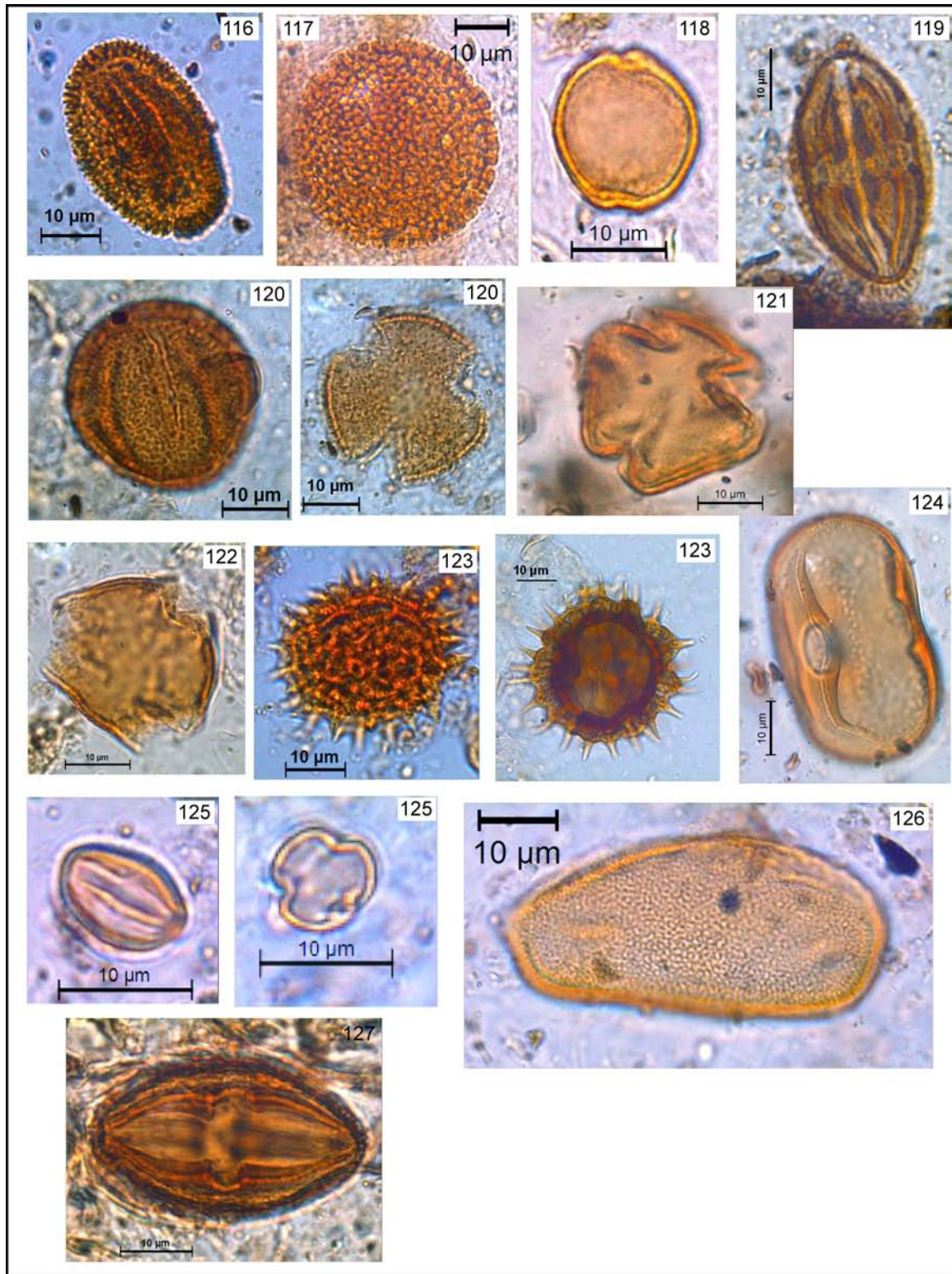




Plate 8



# Appendix D

Complete pollen diagrams of the sedimentary records

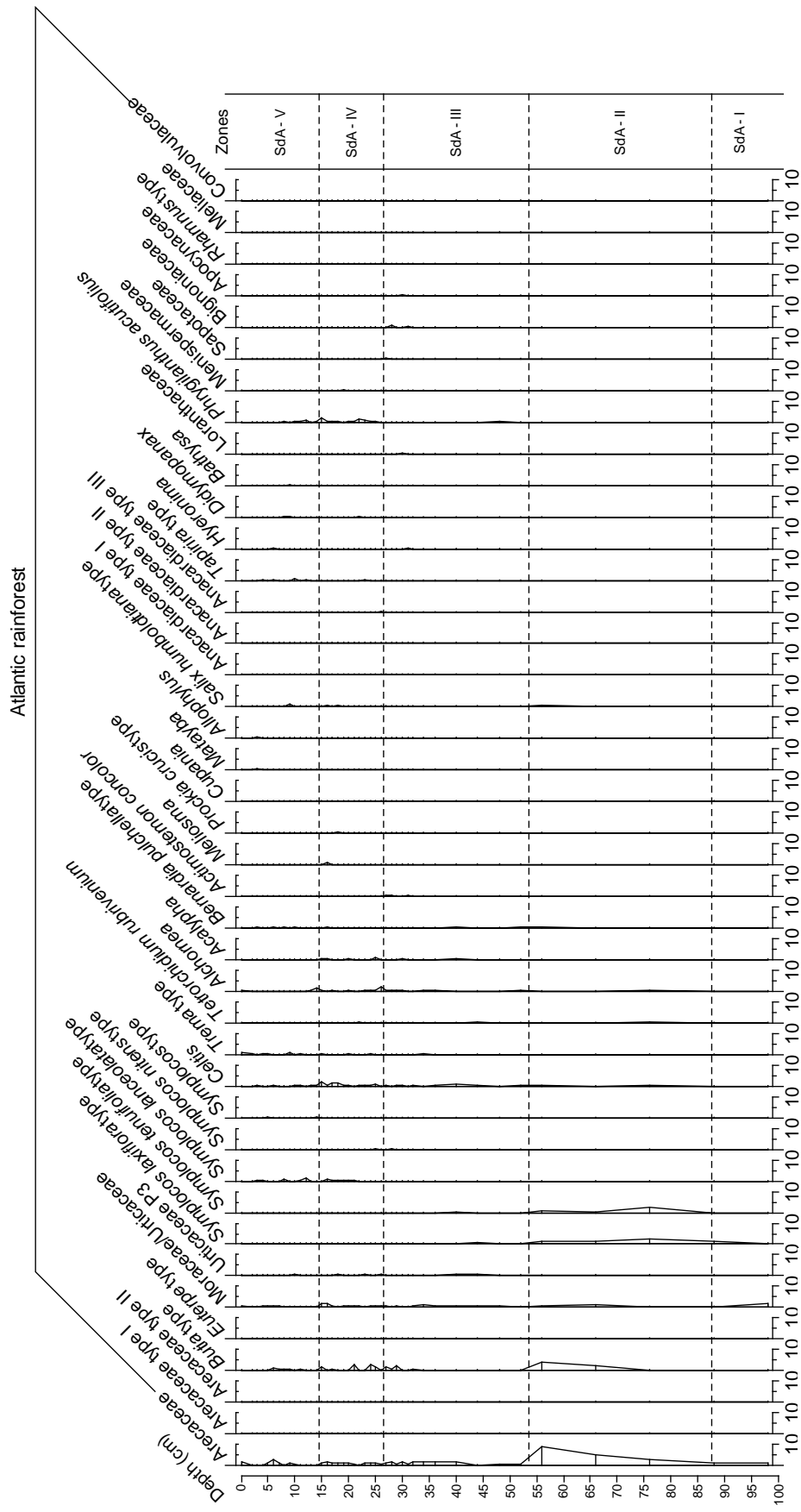




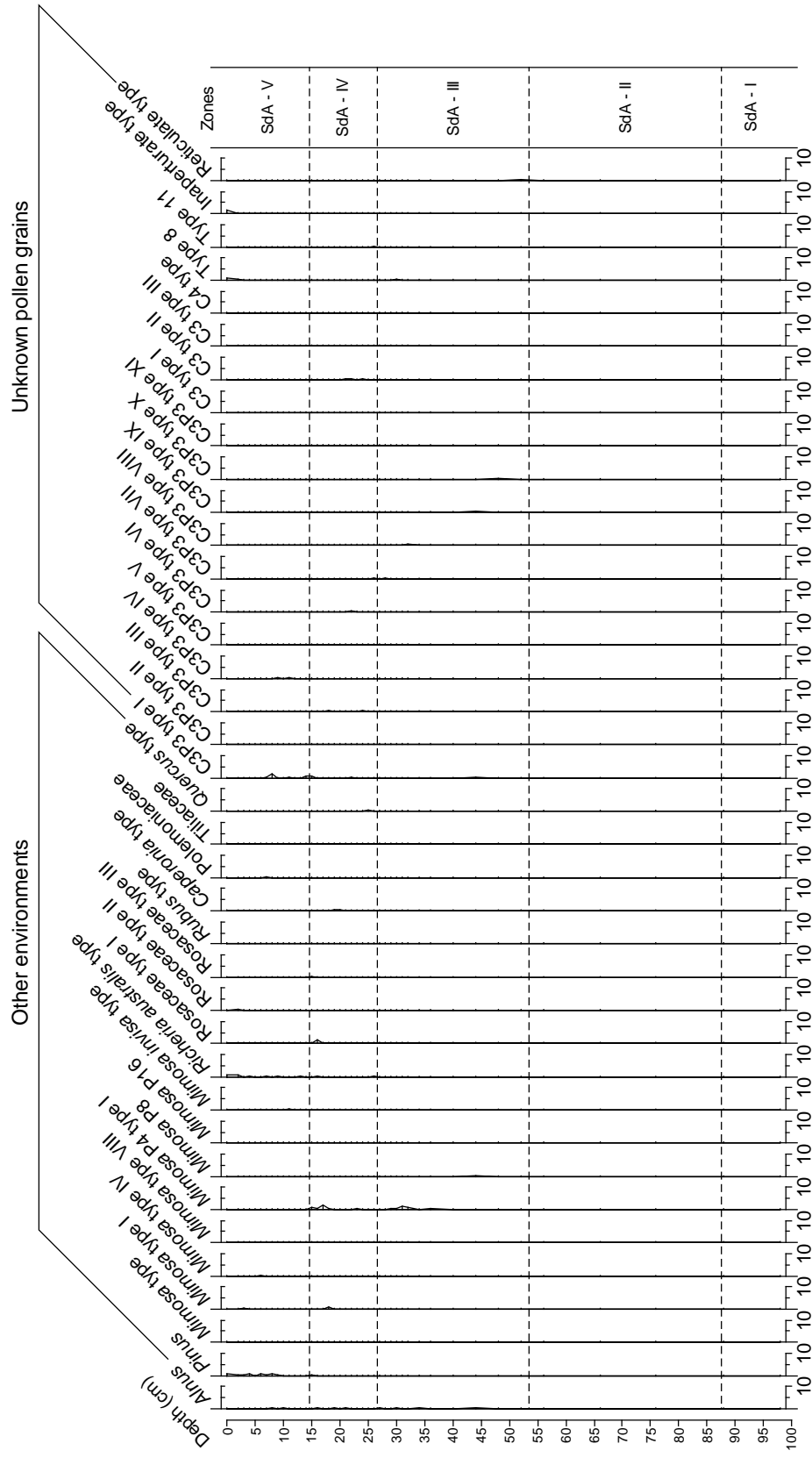
Continued (2).



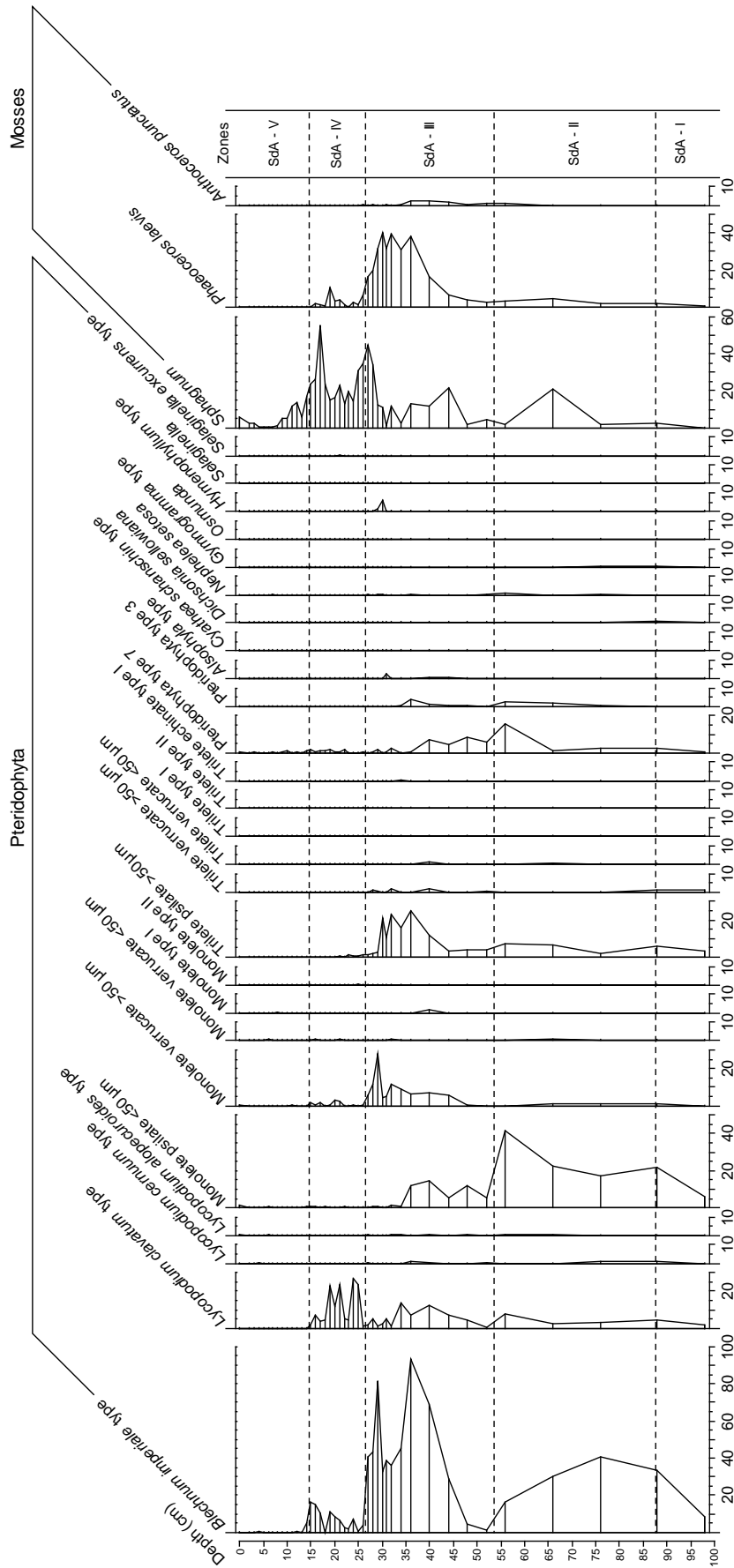




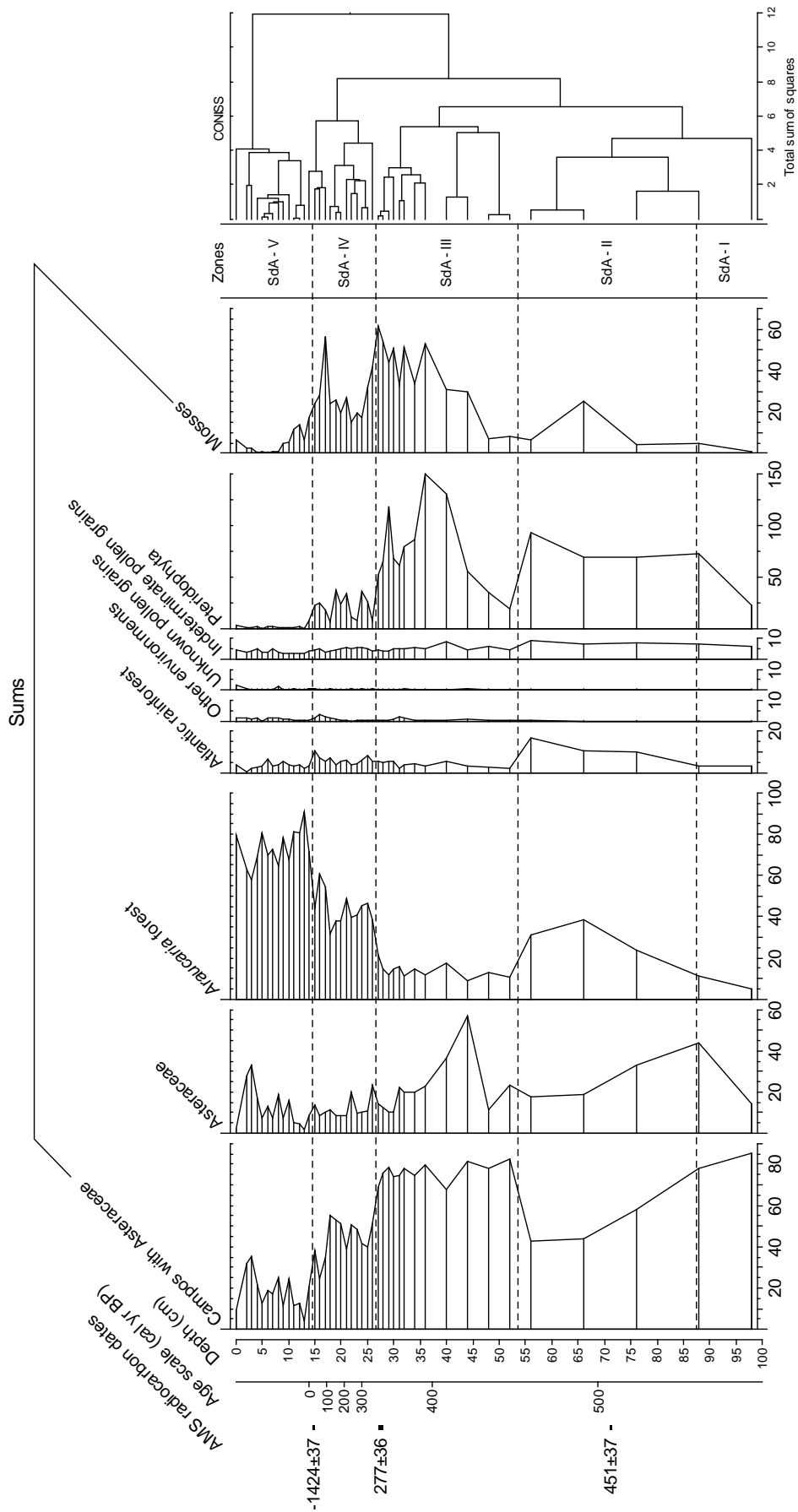
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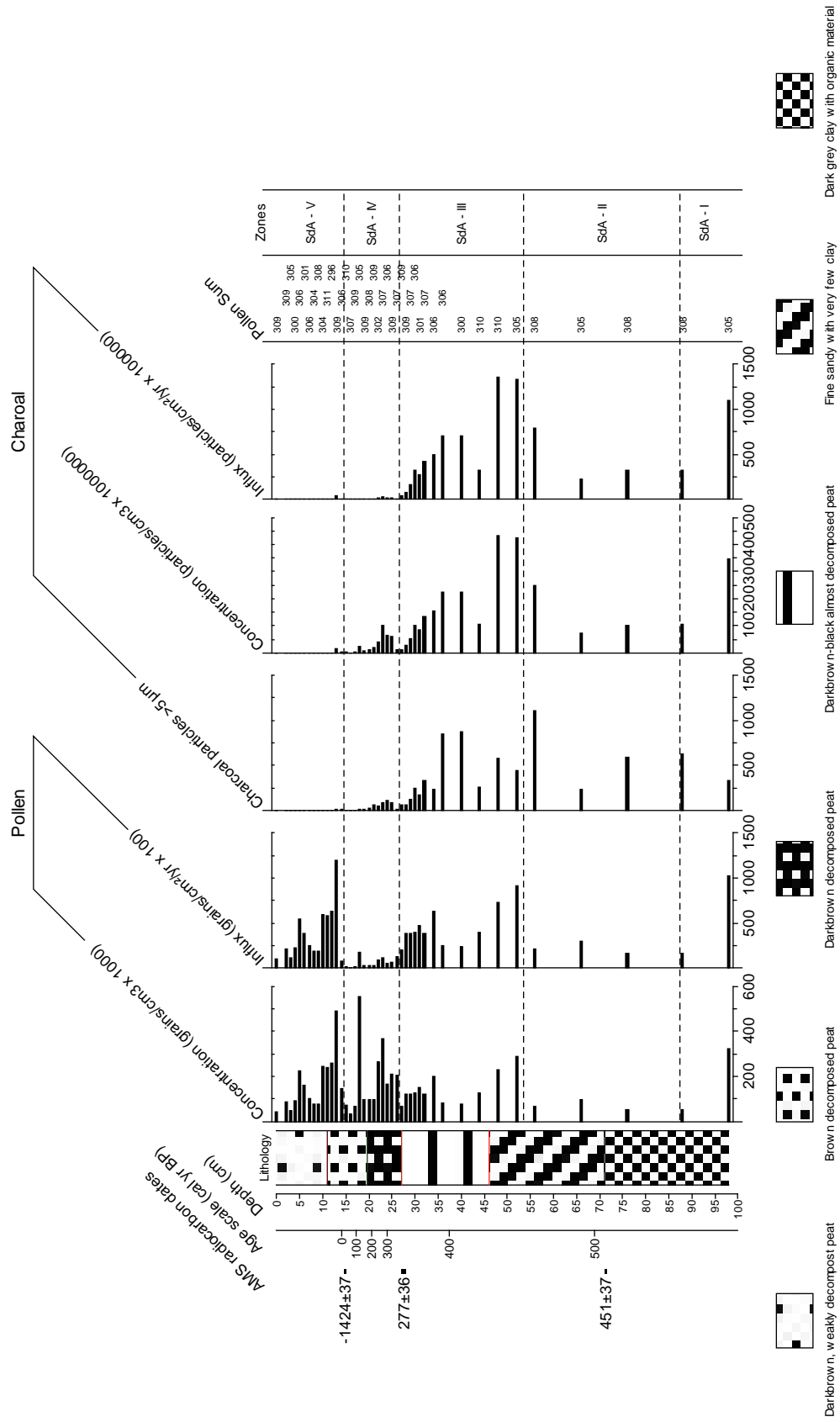
Continued (5).



Continued (6).

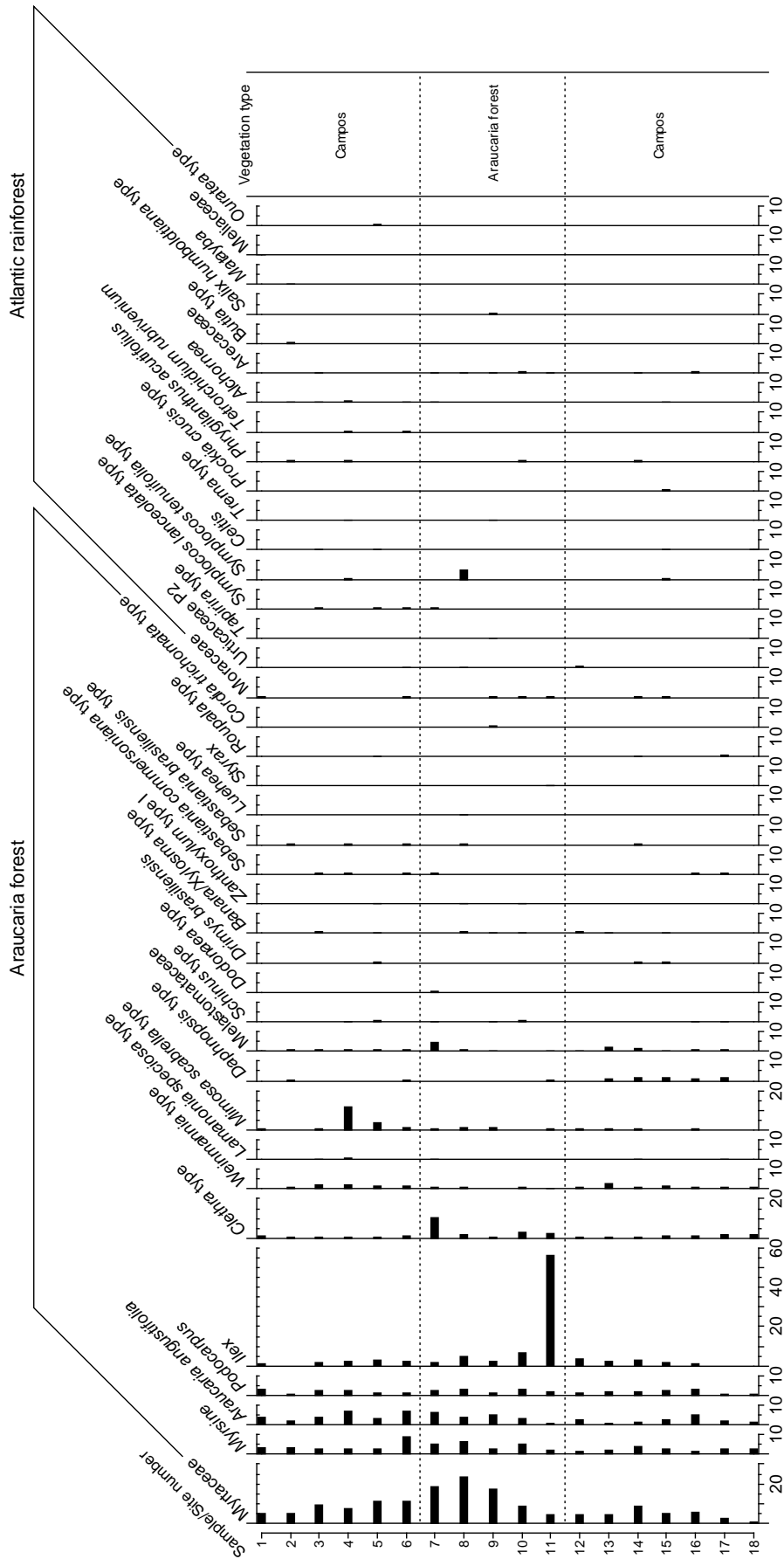


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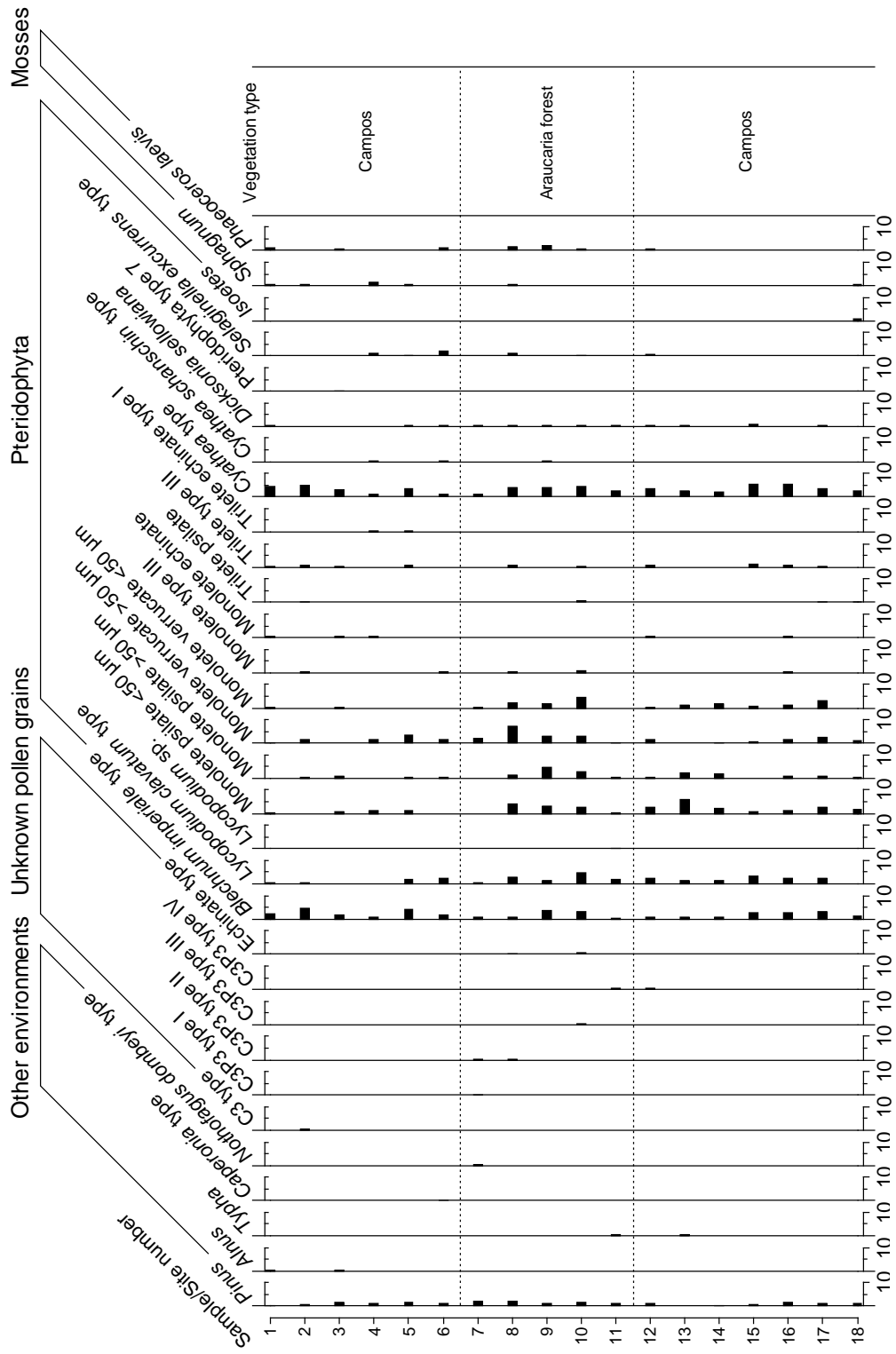
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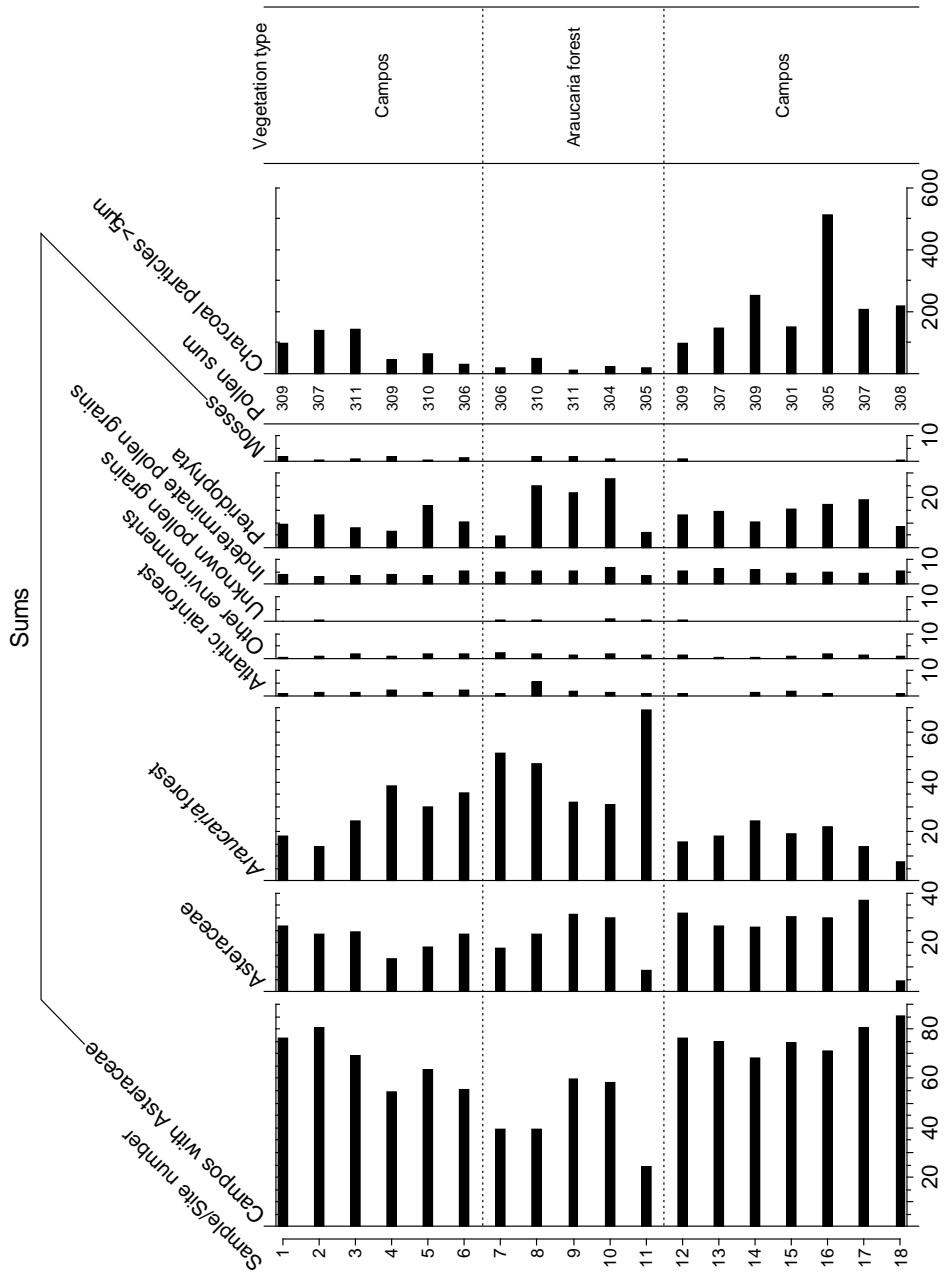


Continued (2).



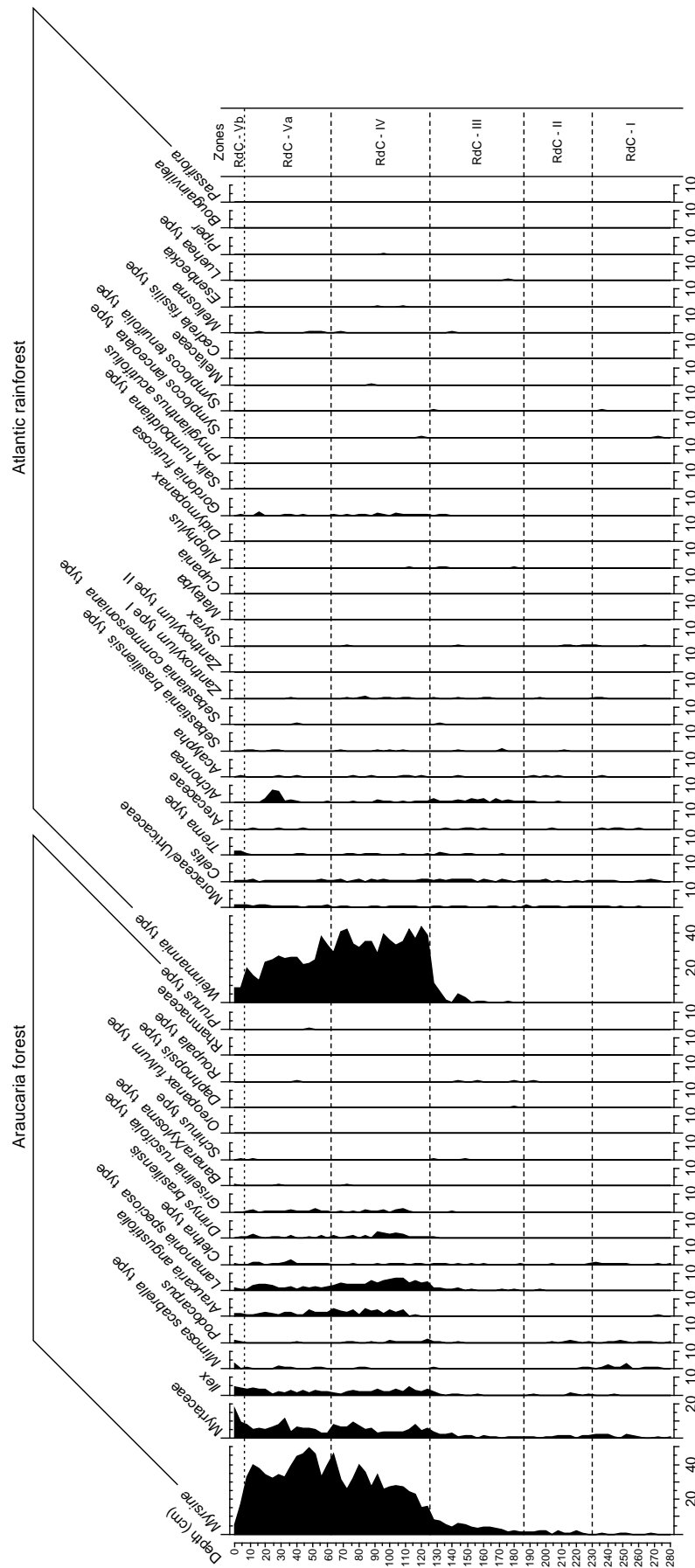


Continued (3).

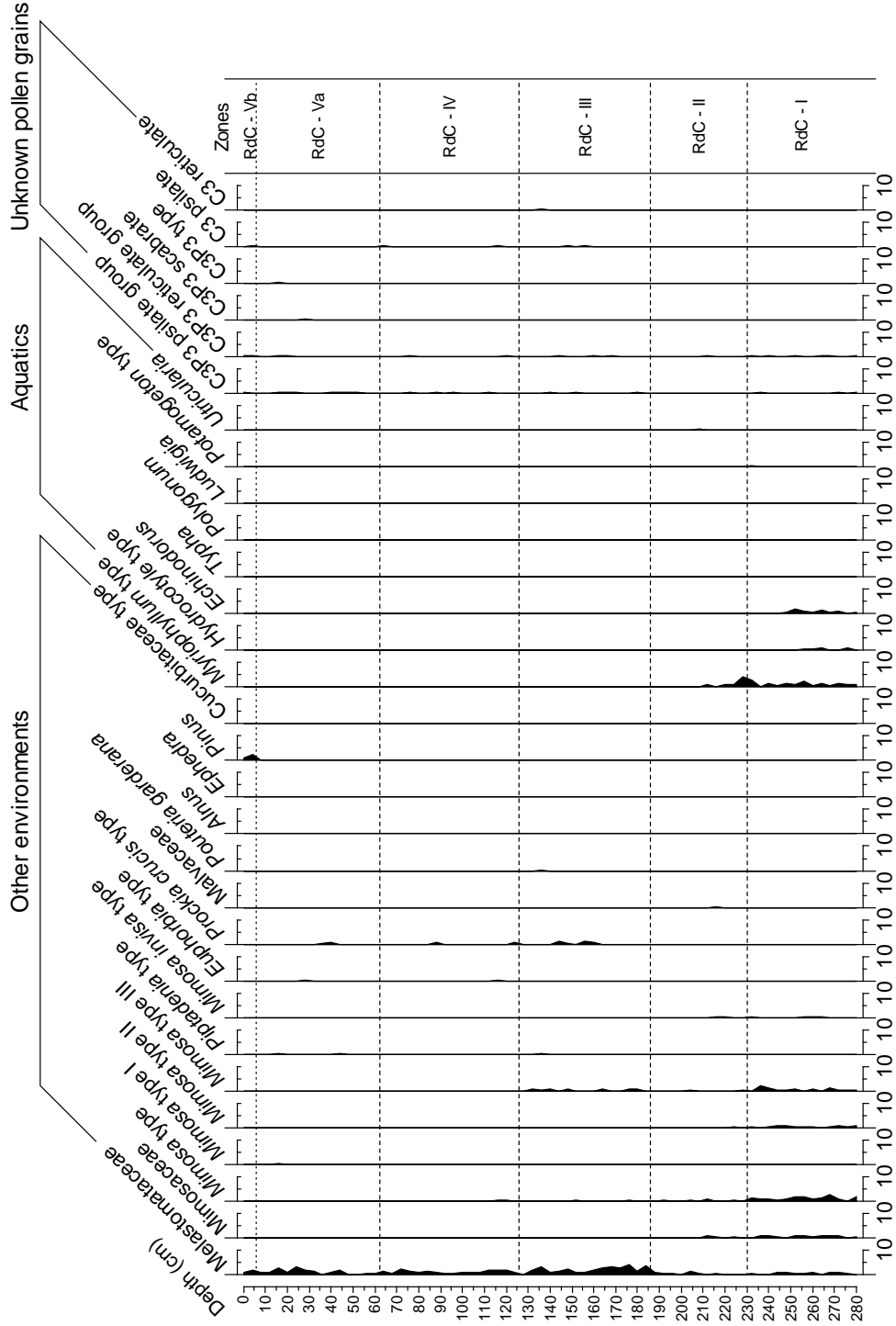


Continued (4). Charcoal presented as % of pollen sum.

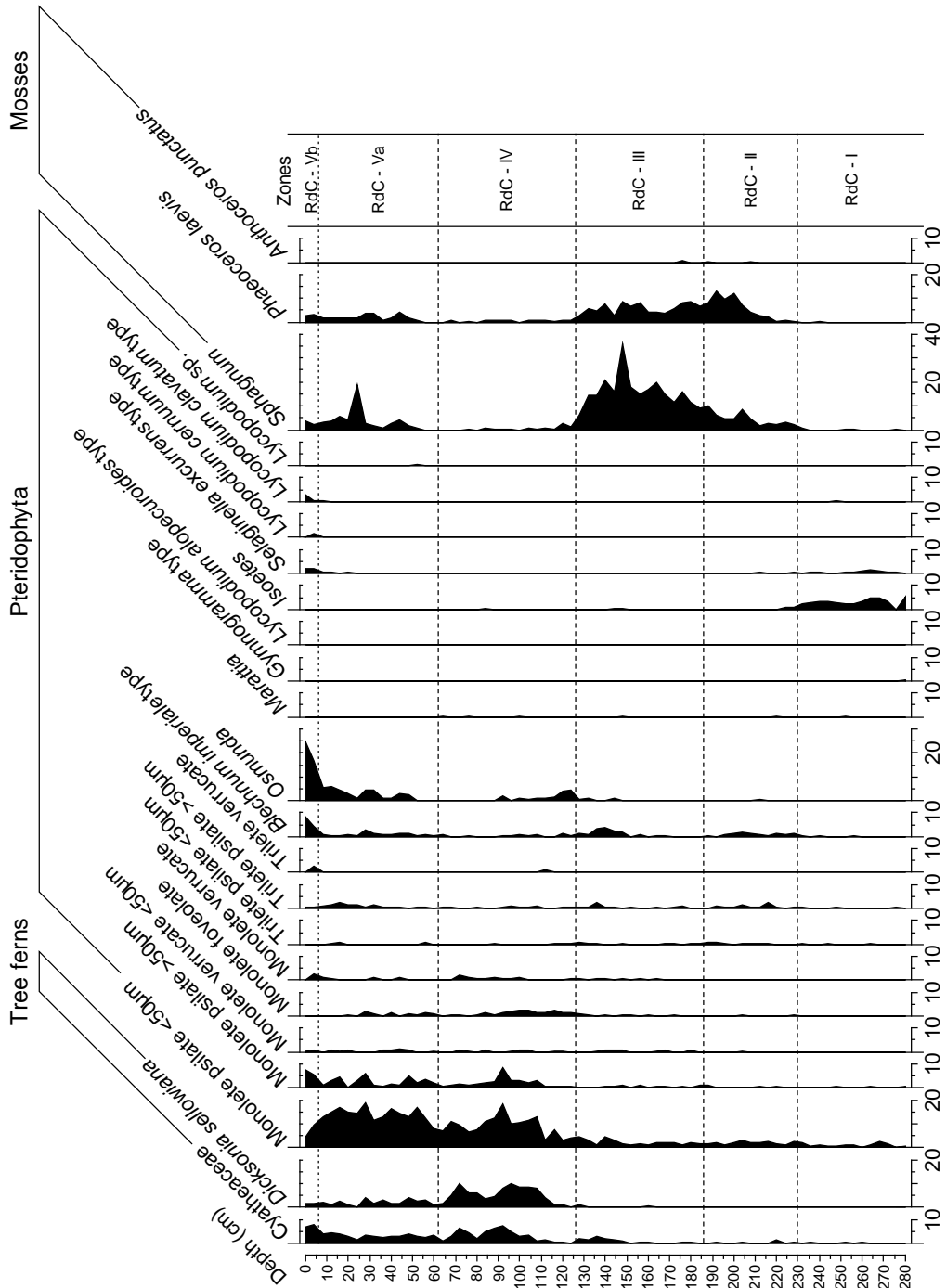




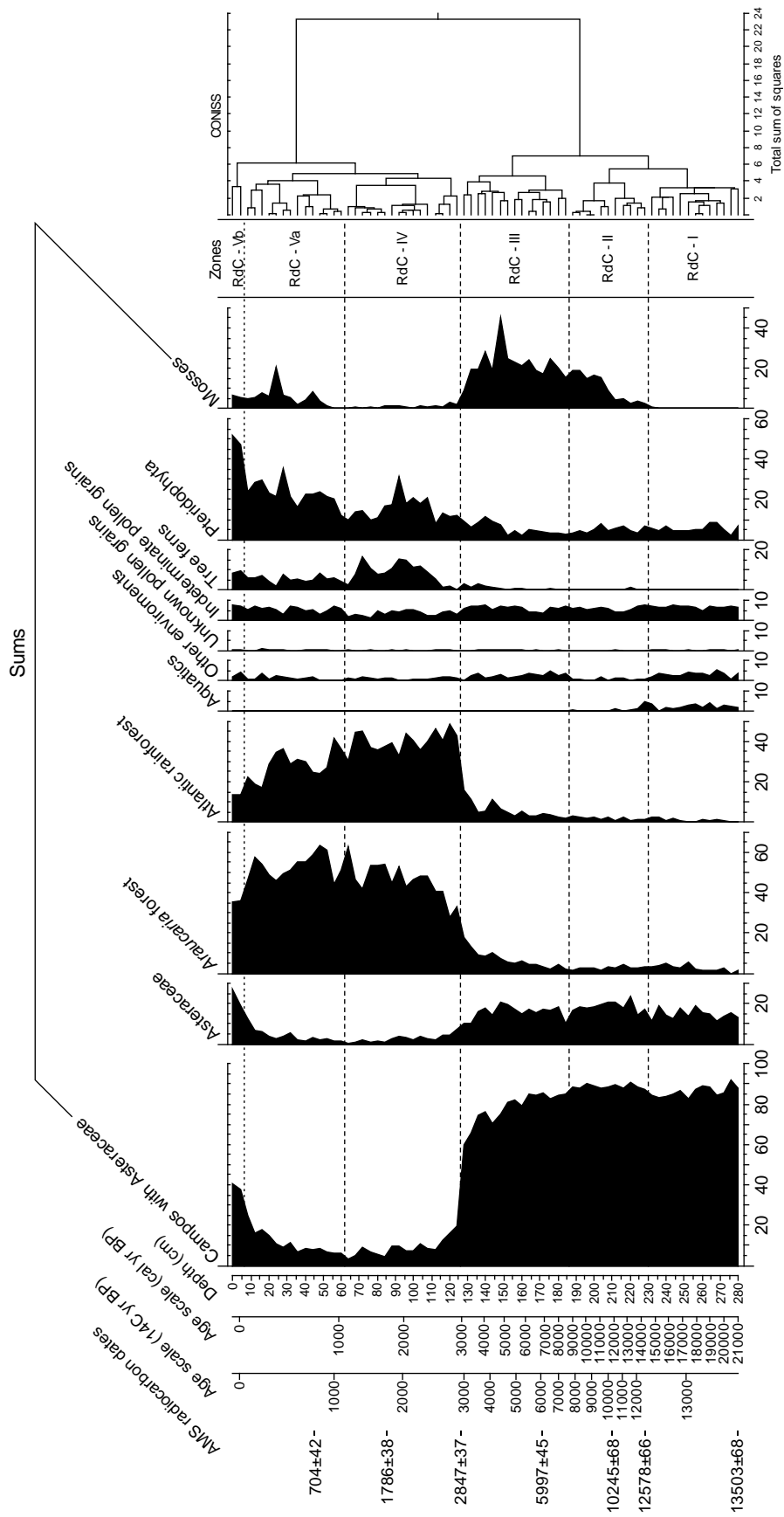
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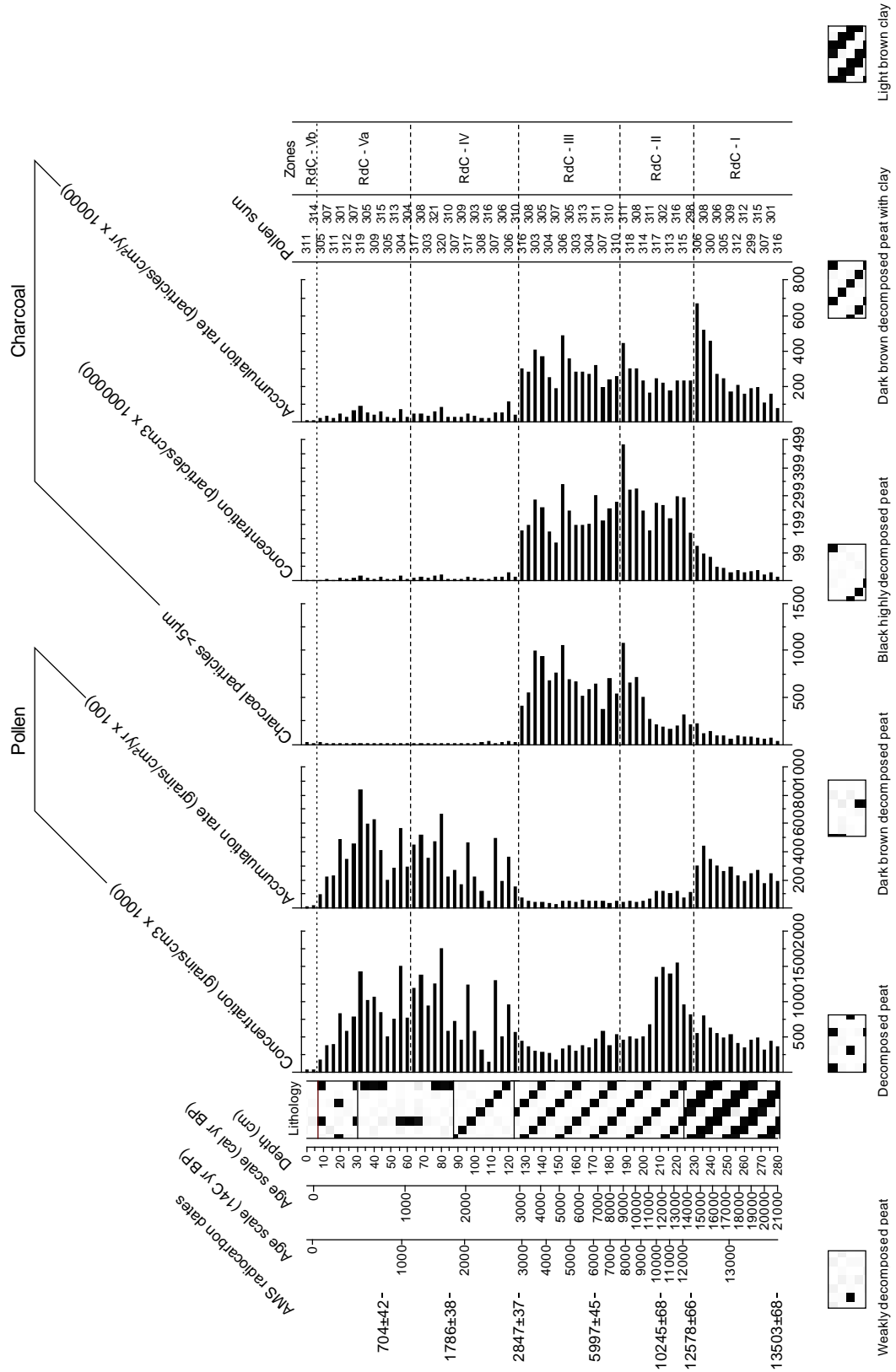
Continued (3).



Continued (4).

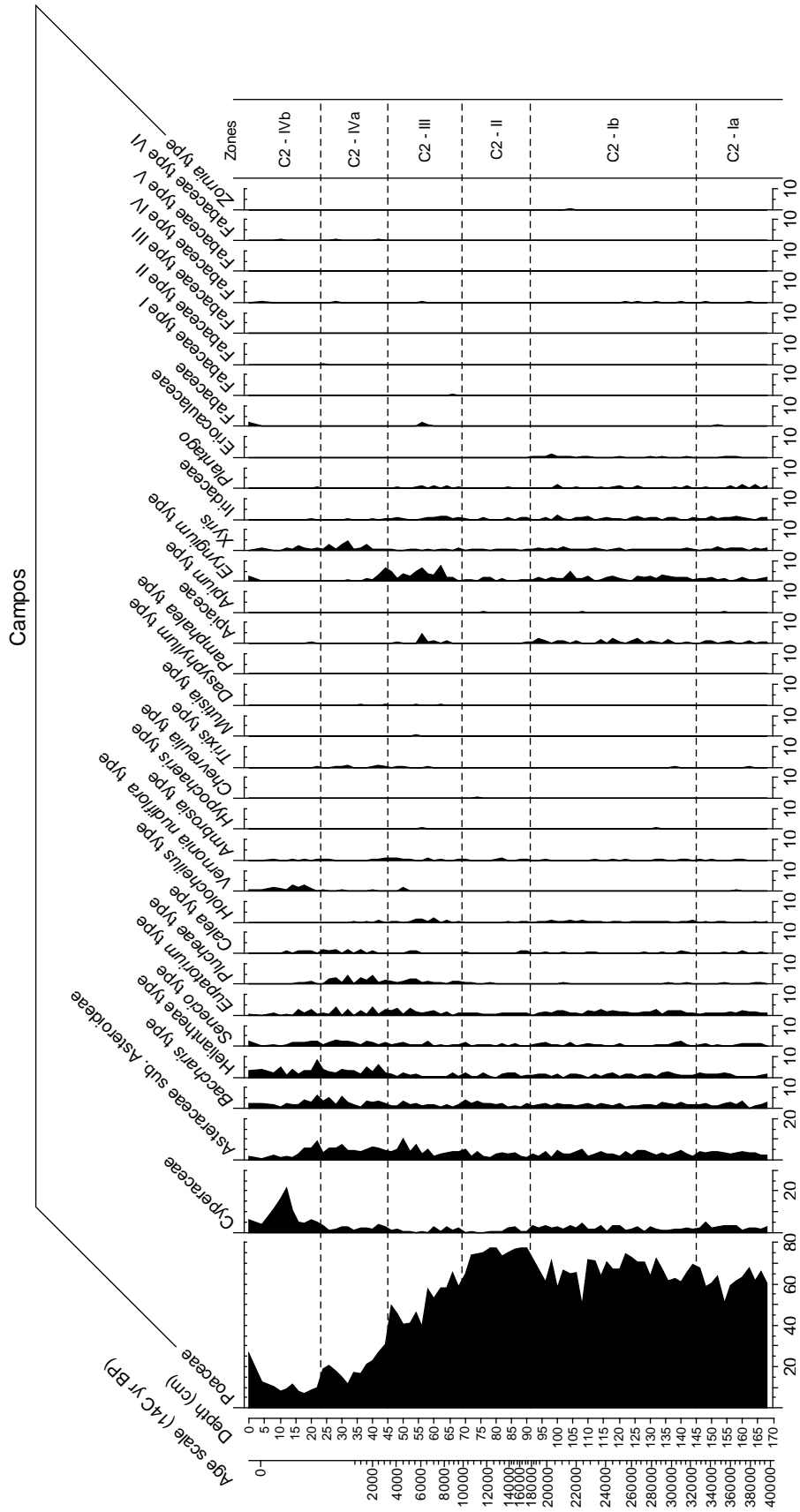


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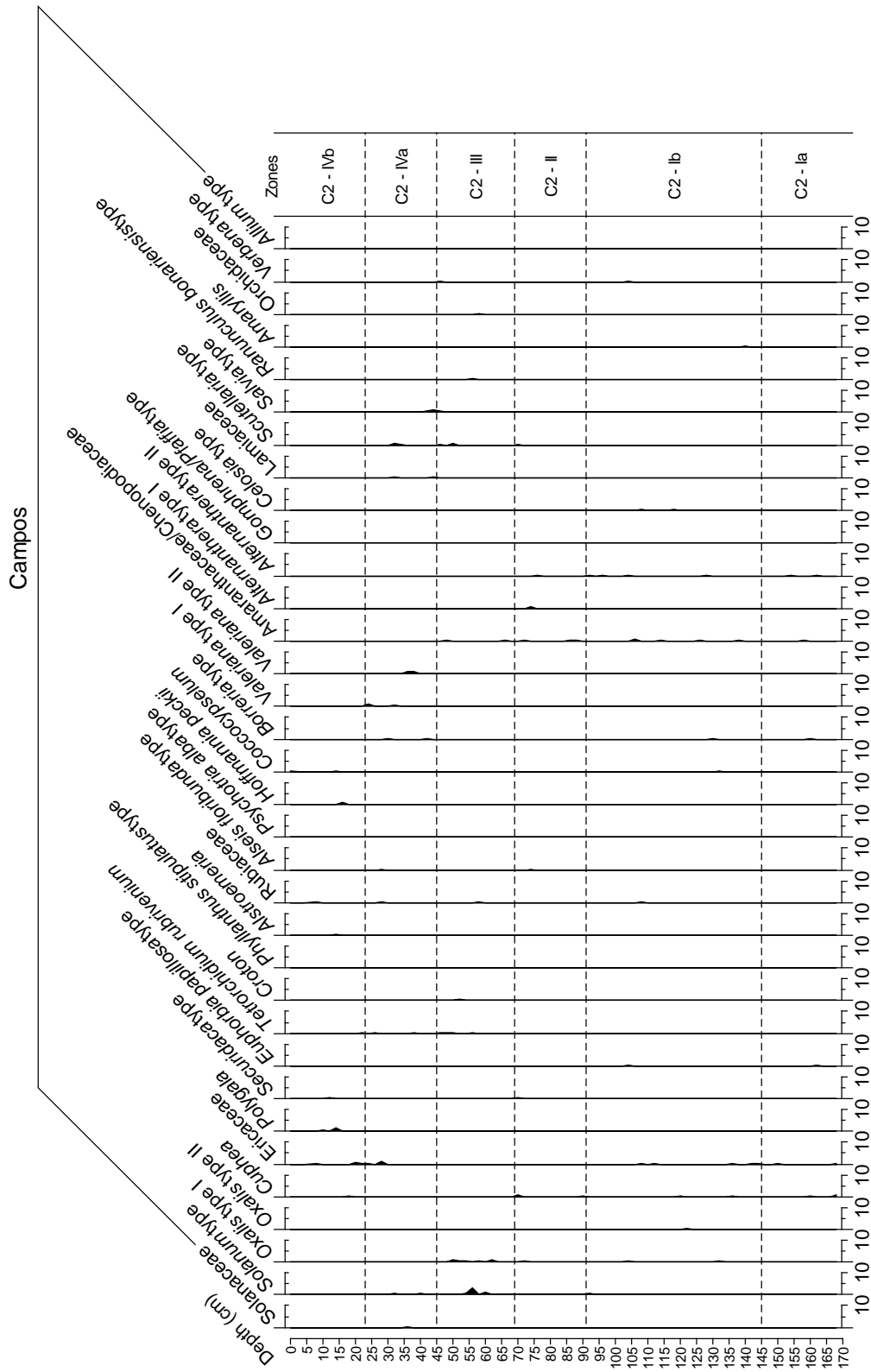


Continued (6).



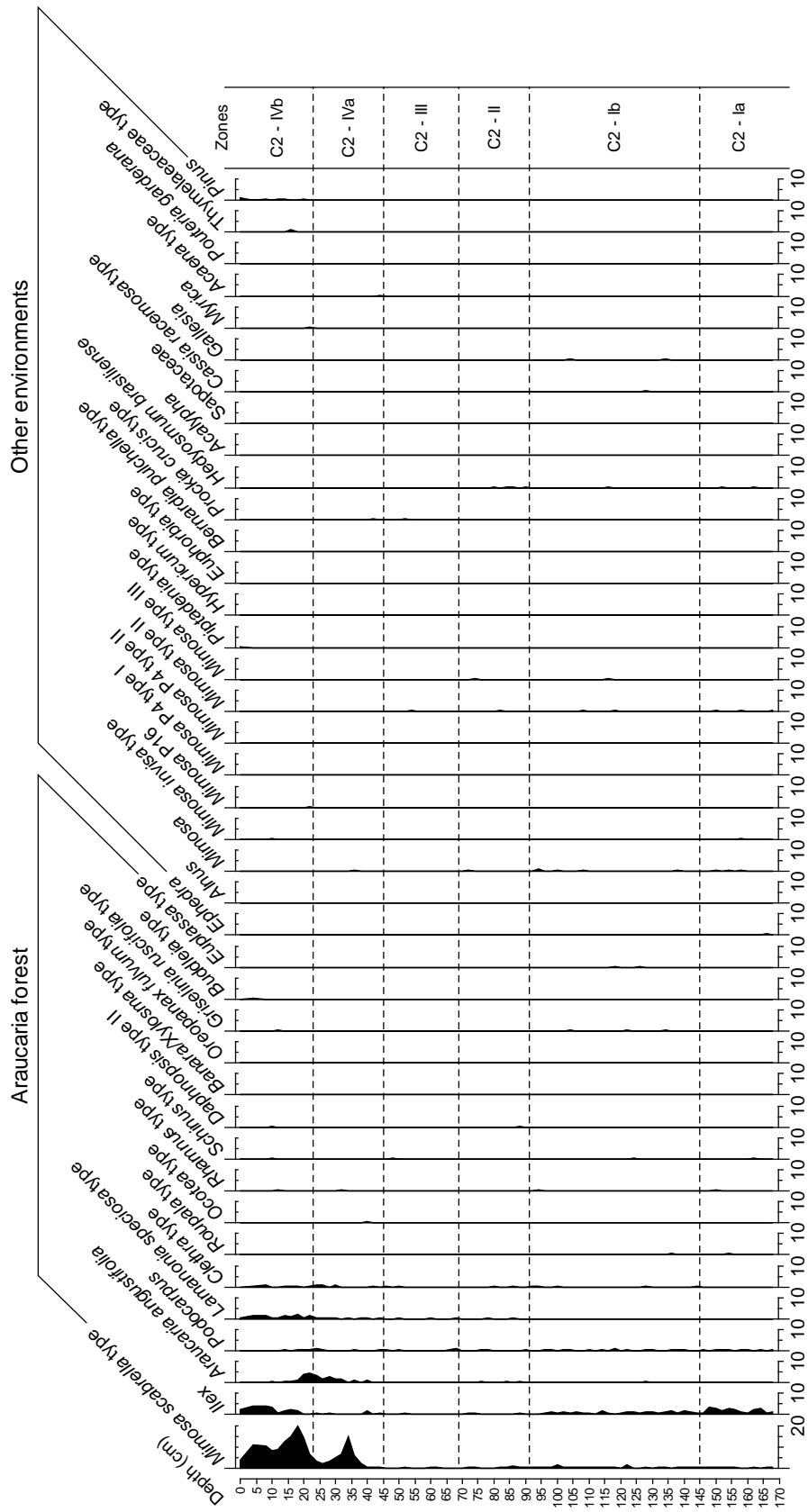


Pollen percentage diagram of the Ciama 2 record (1).

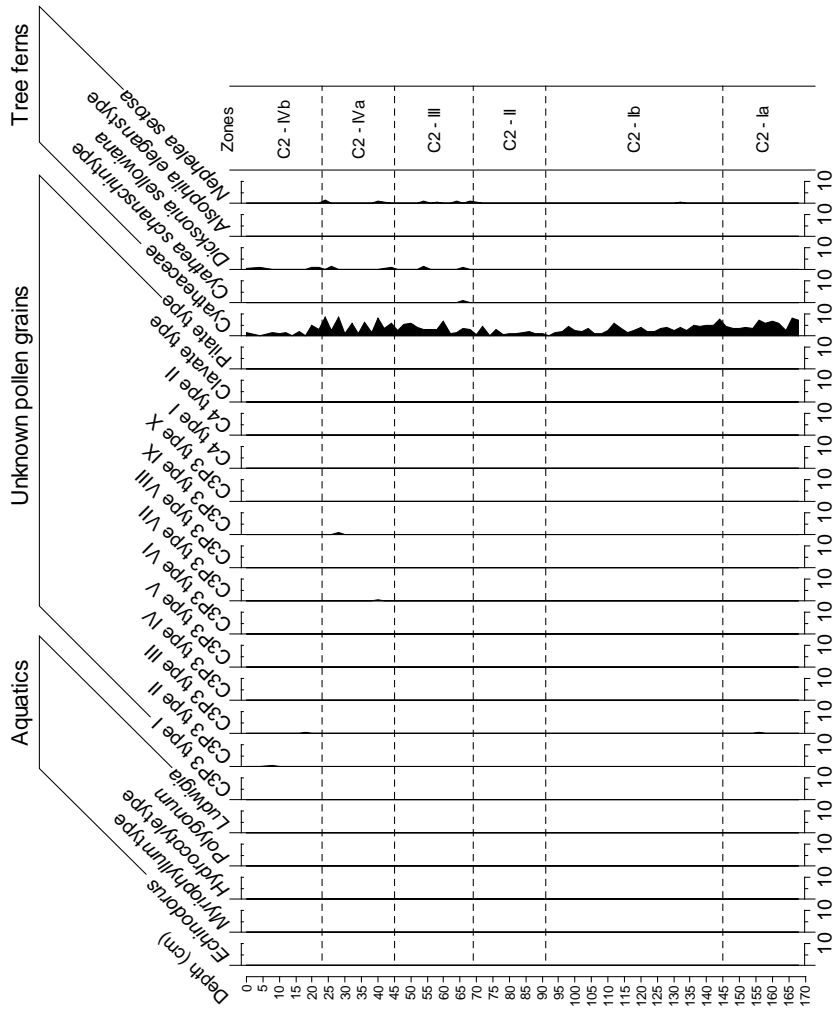


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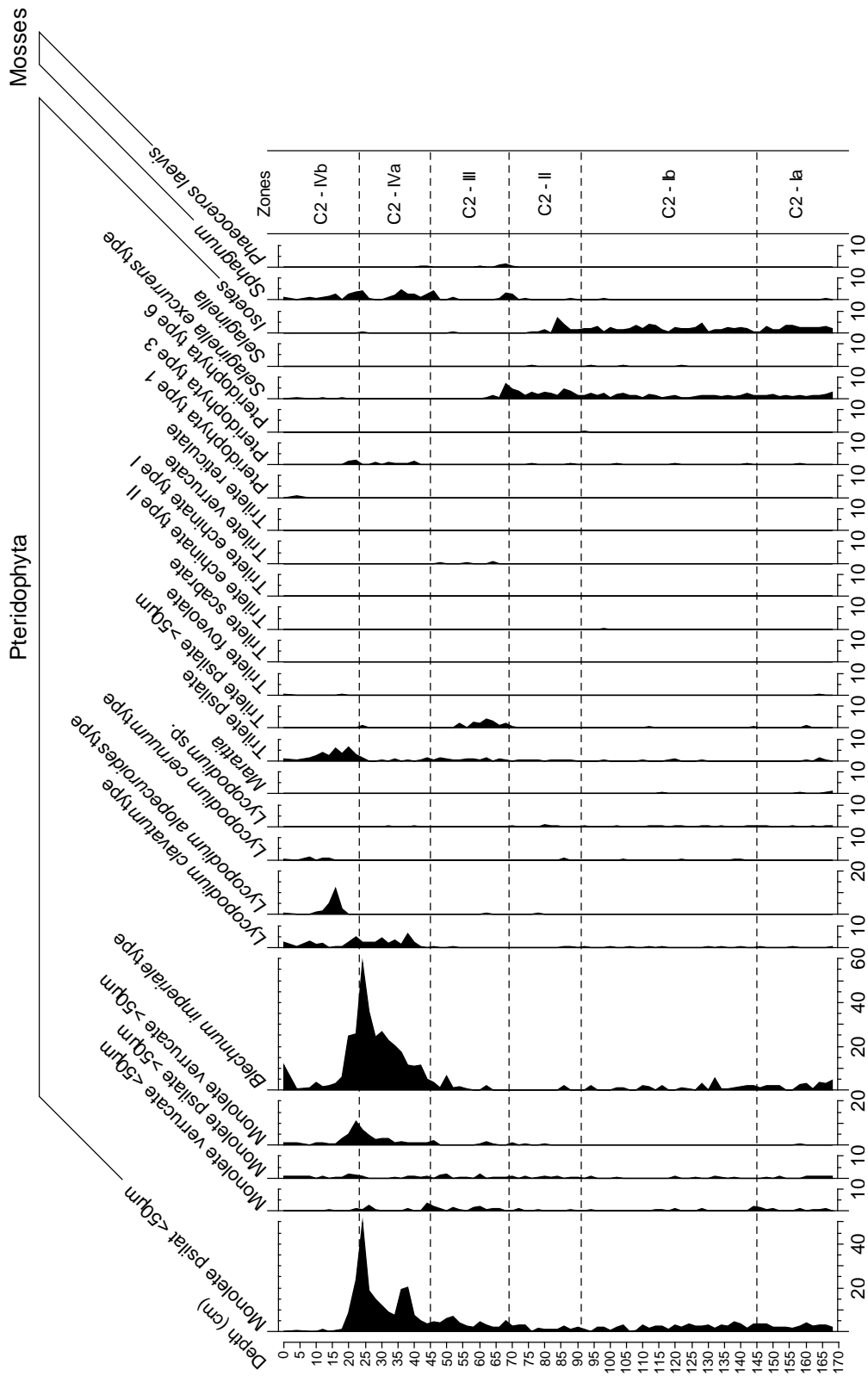




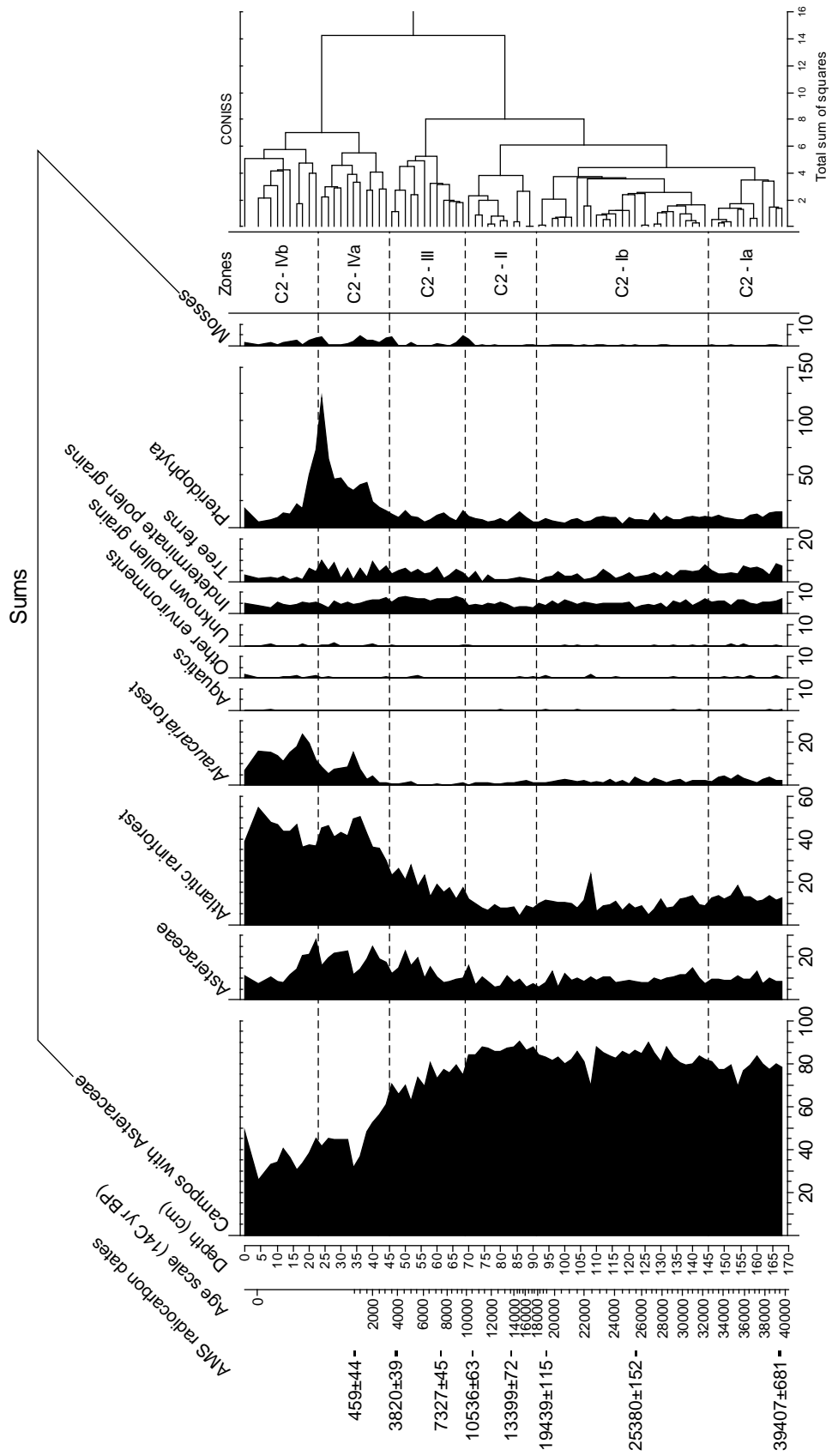
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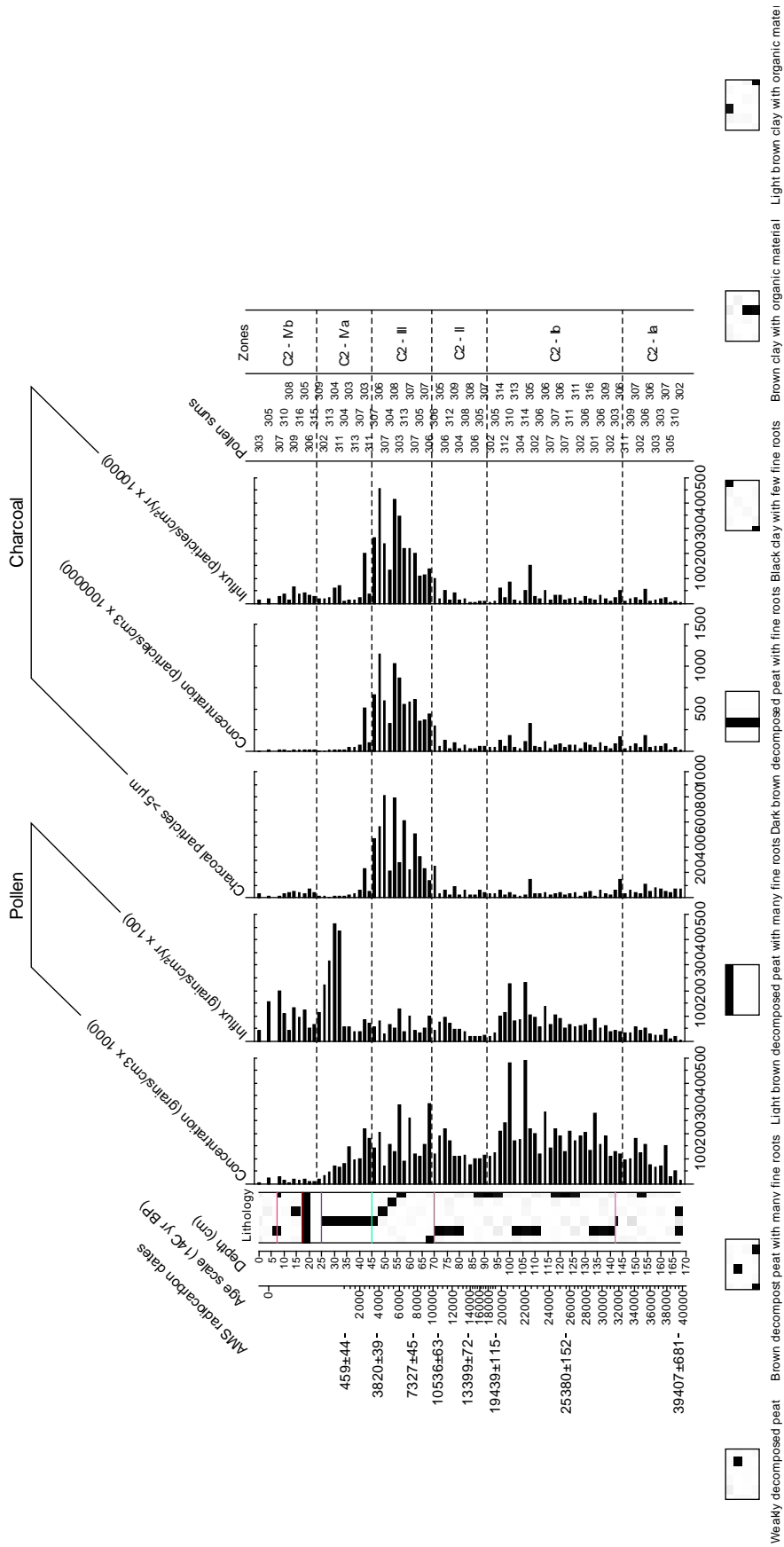
Continued (5).



Continued (6).



Continued (7).



Continued (8).



# Appendix E

Upper Pleistocene to Holocene Peatland Evolution in Southern  
Brazilian Highlands as Depicted by Radar Stratigraphy,  
Sedimentology and Palynology  
(*Quaternary Research, in review*)

## **Upper Pleistocene to Holocene Peatland Evolution in Southern Brazilian Highlands as Depicted by Radar Stratigraphy, Sedimentology and Palynology**

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### **Abstract**

Paleoenvironmental interpretation of proxy data derived from peatlands is largely based upon an evolutionary model for ombrotrophic bogs, in which peat accumulates in still environments. Reports on proxies obtained from minerotrophic fens, where hydrologic inputs are variable, are less common. In this study, a highland peatland in Southern Brazil is presented through geophysical (GPR), sedimentological, palynological and geochronologic data. The radar stratigraphic interpretation suggests a relatively complex history of erosion and deposition at the site since at least the beginning of marine isotopic stage 3 (MIS-3) interstadial. In spite of this, radar stratigraphic and palynologic interpretations converge, suggesting that the minerotrophic fen is a source of proxies. Electromagnetic (EM) reflections tend to group in clusters that show lateral coherence and correlate with different sediment types. Evidence in the literature suggests that minerotrophic fens would predominate in Brazilian highland mires, probably associated with a complex local sedimentary history that needs to be accounted for.

### **Keywords**

Radar Stratigraphy, Peatlands, Clastic Inputs, Palynology, Quaternary, GPR

## 1. Introduction

Peatlands in Brazil occupy an estimated area of  $1.5 \times 10^4$  km<sup>2</sup> (IPS, 2011), which corresponds to about 0.2% of the country's land surface. Reported Brazilian peatlands occur mainly in flood plains, valleys and valley heads, either in lowlands or highlands, and most of the mires are considered to be minerotrophic fens, because typical ombrotrophic bogs (*raised bogs*) are unknown (Franchi et al. 2006). The associated peat deposits are mainly used as sources of raw material for gardening, and as data sources for Quaternary palynological studies (Franchi et al. 2003; Behling et al. 2004). Despite their scientific interest, very little information is published in Brazil about peat stratigraphy, evolution and classification (e.g. Roth and Lorscheitter, 1993).

In the Northern Hemisphere, where ombrotrophic raised bogs are the most studied type of mire, peatland stratigraphy is considered to be a proxy climate record (e.g. Blackford, 2000; Barber et al., 2003), as climate has a direct influence on peat humification rates, bulk density and associated water content (Blackford & Chambers, 1995). Studies on minerotrophic fens are less common, but evidence suggests that peat humification rates tend to decrease with time in fens (Yu et al., 2003), contrary to humification rates in ombrotrophic bogs where the input of stable organic matter tends to increase over time (Clymo, 1984). Moreover, hydrologic inputs are variable in fens, as compared to bog hydrology and peat accumulation rates depend on fluctuating water level responses to storm events (Hughes, 2000). As a result, fen stratigraphy often displays inorganic sediments mixed with peat deposits (Doolittle and Butnor, 2009).

Ground penetrating radars (GPR) have been used to study a wide range of depositional environments (Jol and Smith, 1991; van Dam and Schlager, 2000). Radar stratigraphic interpretation is based on the definition of sedimentary-radar facies that result from the distribution and configuration of radar reflections (Baker and Jol, 2007). Because changes in bulk density and organic matter content create strong GPR reflections (Warner et al. 1990), GPR surveys in peatlands are useful for detecting the interface between the peat deposits and the underlying inorganic sediments (Jol and Smith, 1995; Slater and Reeve, 2002). In addition, due to the dependence of peat stratigraphy on climate and humification rates, GPR data allow depicting the inner peat structures, because variations in bulk density cause changes in pore water content and create significant reflectors (Theimer et al., 1994). Thus, GPR data may be used to interpret the evolutionary history of peat deposits (Kettridge et al., 2008; Comas and Slater, 2009).

This study uses a set of complementary methodologies to highlight the use of Brazilian highland mires as sources of stratigraphic data. The study relies on the application of radar (GPR) stratigraphy (e.g. Neal, 2004) and pollen proxy analysis (e.g. Behling, 1993), to assist in paleoenvironmental interpretation. Because of the conceptual proximity between radar and seismic stratigraphies (Baker, 1991), particularly in relation to the definition and interpretation of bounding

surfaces, groups of radar reflections (radar facies units) are considered as allostratigraphic units, enabling the genetic interpretation of the associated deposits (Catuneanu et al., 2009). The results indicate that Brazilian mires are important sources of Quaternary stratigraphic information.

## 2. The study site

The study site is located at 860 m above sea level in one of the residual plateaus that characterize the Serra do Tabuleiro range (Fig. 1), which has altitudes ranging from 850 to 1,240 m a.s.l. Due to the altitude and the atmospheric Atlantic humidity, the climate is classified as wet mesothermic with relatively mild summers (Köppen's "Cfb" type). The mean annual temperature is 20°C and precipitation is well distributed throughout the year, ranging from 1,600mm to 1,800mm. Tropical and subtropical vegetation coexist in the study area, and natural grasslands are frequent on the summits of the range mountains (Klein, 1978).

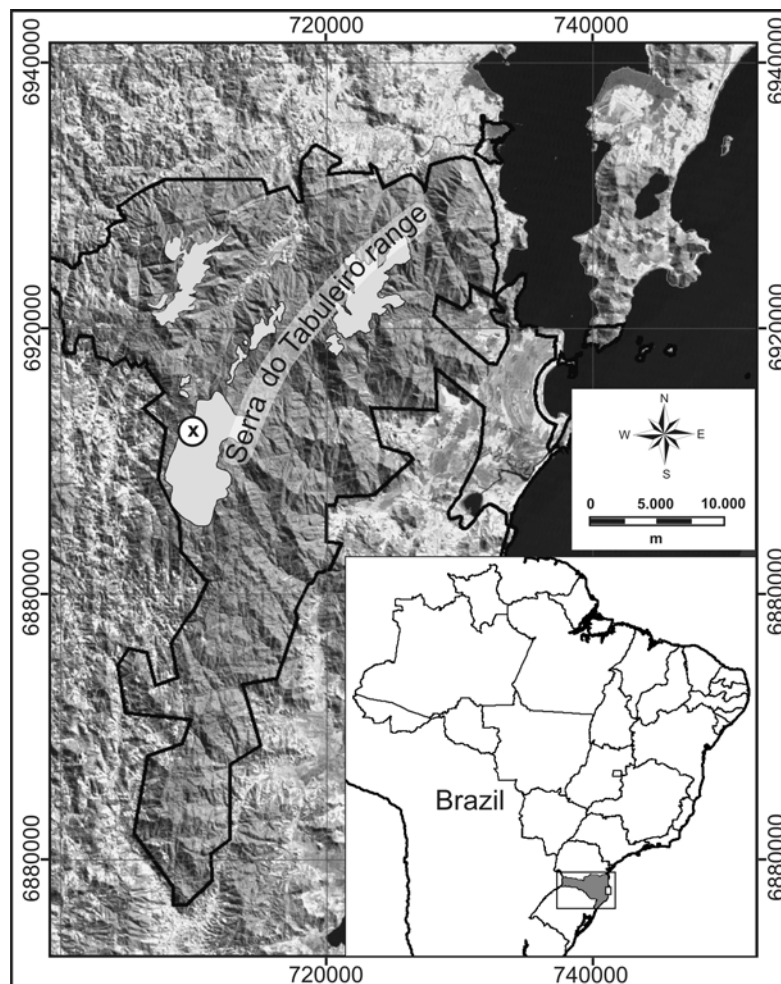


Figure 1: Study site location in the Serra do Tabuleiro range (open circle), Santa Catarina State, Southern Brazil. The light shaded areas in the range indicate the residual plateaus where highland mires occur.

The Serra do Tabuleiro range is predominantly composed of Proterozoic ( $516 \pm 12$  Ma) sienogranites and accessory monzogranites (Zanini et al. 1997). The most commonly reported structures are sub-vertical faults and joints that roughly coincide with the location of peat mires at the heads of the local drainage network (Fig.2).

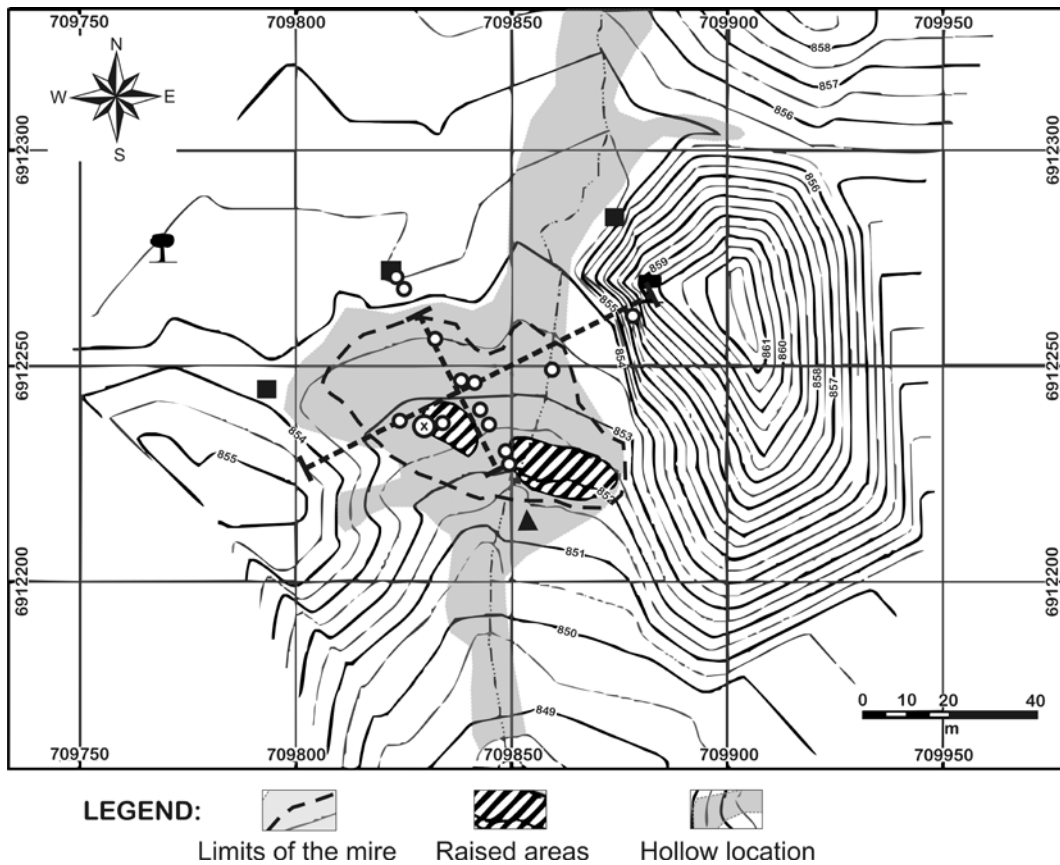


Figure 2: Study site topography and orthogonal distribution of GPR profiles (dashed lines). The mire deposits occupy an area of about 2.600 m<sup>2</sup>, inside a valley head hollow. Open circles indicate location of manual drills for sampling. The big circle with an x inside indicates the location of a core sampled for palynology. Floating peat mats occur near the downslope border of the mire, forming local raised areas (hachured).

### 3. Methods

Due to the reduced depth of the peat deposits, as compared to those reported in Brazilian lowlands, GPR surveys using a 400-MHz antenna were performed along the perpendicular lines illustrated in Fig.2. Data acquisition was conducted with common offset surveys. GPR measurements were made by a GSSI system consisting of a single transmitting and receiving antenna that was dragged along the ground. Horizontal distances were recorded with a survey wheel. Subsurface-radar-wave velocity was determined by direct measuring distances to peat horizons and to underlying inorganic materials, in relatively undisturbed core samples (Morton et al., 2009), in order to estimate

two-way travel-times (TWT). The resulting average velocity of radar pulses in the peat was 0.03827 m/ns, and a relative dielectric constant ( $\epsilon_r$ ) value of 61.43 was calculated. This value is consistent with average values of  $\epsilon_r$  reported for peat materials, which range from 52.4 to 70.4 (Slater and Reeve, 2002), and enabled the association of radar reflection clusters to the detailed peat stratigraphy. The optimal vertical resolution of the 400-MHz GPR antenna is estimated at 0.024 m (2.4 cm), based upon the nominal center frequency of the transmitting antenna. The sampling time window was 120 ns, which provides a maximum study depth of 2.2962 m, assuming that  $\epsilon_r$  remains constant with depth. The system was set to acquire data at a rate of 25 scans per meter; with 512 samples per scan. The data was processed with RADAN 6.5 software and included: a) signal-saturation correction, in order to suppress low-frequency noise; b) application of manual gain, to consider signal decay at later times, while preserving relative amplitudes; c) time-domain frequency filtering, to remove ambient and systematic noises; d) Kirchhoff 2-D variable velocity migration, to correctly position subsurface reflections in the plane of the survey by collapsing the hyperbolic diffractions; e) topographic correction, by moving traces by an appropriate TWT, using ReflexW 5.0 software.

Due to the significant content of siliciclastic sediments at the site, radar stratigraphic analysis was performed by defining radar facies units (Baker, 1991; Neal 2004), which consist of clusters of radar reflections with particular configurations. The data interpretation followed the same principles and terminology (Supplementary Fig. 1) as those used in sequence stratigraphy (Fig. 3). Depositional trends such as progradation, retrogradation, aggradation and truncation were defined through the consideration of hypothetical sedimentation rates and base-level change rates (Catuneanu et al., 2009). The interpretation technique accepts that the physical mechanisms that produce sedimentary units are scale independent (Neal, 2004).

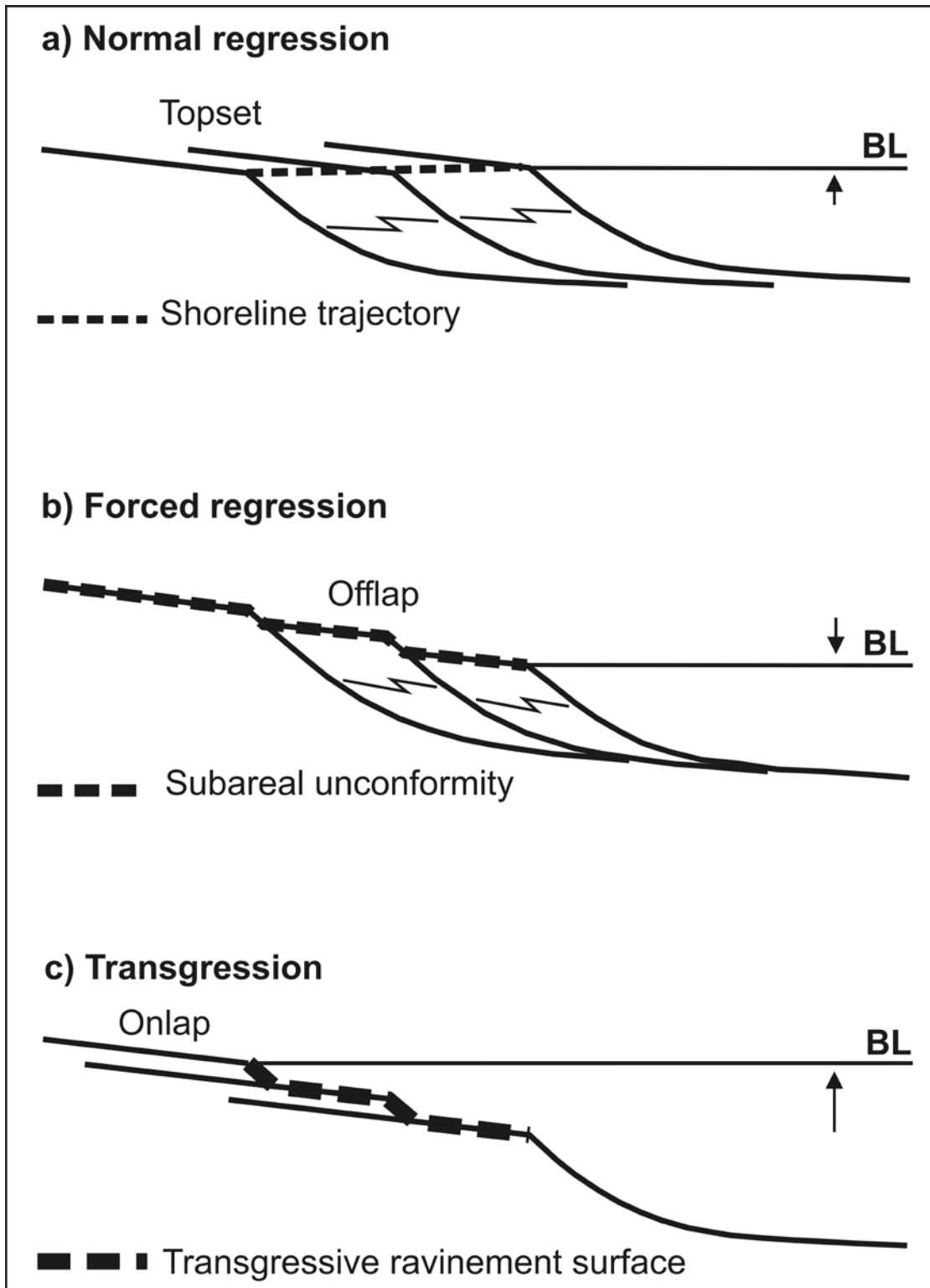


Figure 3: Genetic types of deposits, after Catuneanu et al. (2009, p.3): a) normal regression; progradation is driven by sediment supply, b) forced regression, progradation is driven by base-level fall; c) transgression; retrogradation is driven by base-level rise. Possible types of shoreline trajectories are indicated, according with rising or falling base level changes.

Samples were taken at specific depth ranges for sedimentologic analysis, according to the distribution of radar reflection clusters. Shallow materials composed of vegetal tissues from the first 30 to 40 cm were not sampled for sedimentology. Due to the site's relatively high content of siliciclastic deposits (15% to 70%), grain-size analyses were conducted on 45 samples, according to standard procedures with pipetting and dry sieving (Oliveira and Lima, 2004). The results are displayed on ternary plots (Fig. 5), which accounts for 100% of the mineral fraction only, as the organic matter was previously eliminated by oxidation. Materials were classified according to Flemming (2000), for muds, and according to Folk (1974), for samples with gravel content above 5%. Subsamples were taken using steel rings from a Russian corer, which is supposed to reduce core sediment deformation (Morton et al., 2009). Bulk density was determined by oven drying and weighing, using the Brazilian standard thermogravimetric method (Embrapa, 1979). The moisture content of subsamples was determined by weighing and drying: the samples were dried until their mass is constant, and the change in mass is interpreted as the evolved moisture. Due to the variety of materials in the mire deposits, including organic and mineral layers, the organic matter content of the samples was analyzed with the Walkley-Black acid digestion method, using chromic acid to measure the oxidizable organic carbon.

A 170-cm long sediment core was sampled for independent pollen analysis with a 50-cm long Russian corer. Each core section collected was sealed in plastic bags and stored under cool (ca. +4 °C) and dark conditions. 35 samples were taken at intervals of 4 to 6 cm along the core. For pollen analysis, samples of 0.25 cm<sup>3</sup> were prepared with standard pollen analysis methods, using hydrofluoric acid (HF) treatment and acetolysis (Faegri and Inversen 1989). To determine the pollen concentration (grains/cm<sup>3</sup>), one tablet of exotic *Lycopodium clavatum* spores was added to each sample. Subsamples were counted up to a minimum of 300 pollen grains. Pollen and spore identification was conducted using reference slides available at the Department of Palynology and Climate Dynamics of the University of Göttingen, in conjunction with pollen morphological descriptions (Behling, 1993). TILIA software was used to plot the pollen and spore data as percentages of the total pollen sum. The graphic representation of results was obtained using TILIAGRAPH software, and cluster analysis was achieved using CONISS software (Grimm, 1987, 1991).

Radiocarbon ages of peat and wood samples were determined at the Center for Applied Isotope Studies, at the University of Georgia (USA) and at the Institute of Physics of the Erlangen-Nürnberg University (Germany). Optic stimulated luminescence (OSL) ages were obtained at the Laboratory of Glass and Dating at the College of Technology of São Paulo (FATECSP - Brazil). Measurements were recorded with a model 1100-series automated TL/OSL system, of Daybreak Nuclear and Medical Systems Inc. The MAR protocol was adopted, using the total regeneration method. All the aliquots (with the exception of the natural aliquots) are bleached to near zero by



sunlight exposure during 16 hours and then given laboratory doses. Preheating was made at 25°C, to obtain the best reproductive paleodoses. The annual dose rate was obtained by Gamma spectroscopy, using a NaI (TI) detector. Annual doses were evaluated by U, Th and K-40 contents in each sample. A value of 15% water content was adopted. The paleodose values were obtained by direct comparison of the natural OSL with the ones resulting from artificial irradiations. The location of samples used for dating is illustrated in Fig. 2, Fig. 4 and Fig 6.

## 4. Results

### 4.1. Radar stratigraphy and sedimentology

The configuration and distribution of radar reflections in the survey plane (Fig. 4) enables the individualization of different radar packages (Neal, 2004; Hugenholtz et al., 2007) (Fig. 4.B), the assemblage of which led to a division of the mire deposits into four radar zones (Fig. 4.A): zone 1 (Z1); zone 2 (Z2); zone 3 (Z3); and zone 4 (Z4).

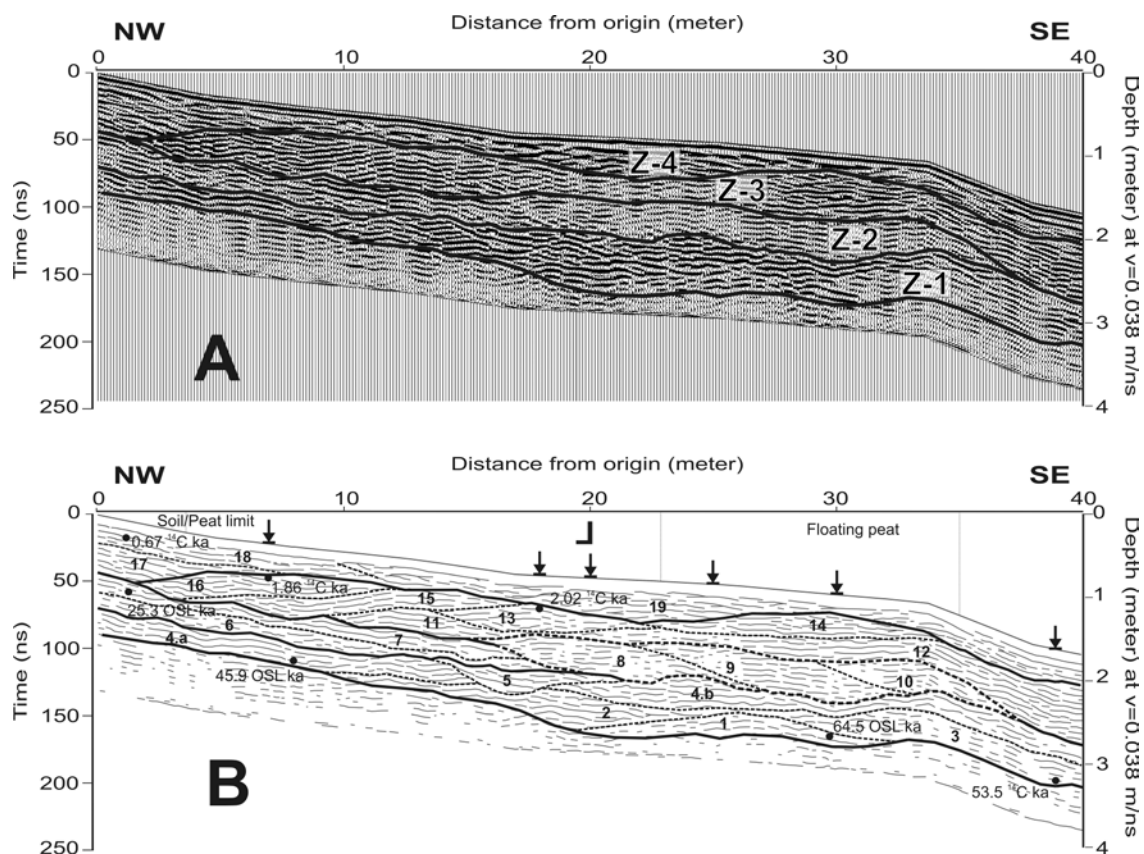


Figure 4: NW to SE 400 MHz radar reflection section. A: Distribution of radar reflections along the section, with indication of the four radar zones. B: Radar stratigraphic interpretation. Numbers indicate stratigraphic order of observed radar packages. Some radiocarbon and luminescence dates are plotted. Vertical arrows indicate position of manual drillings and the inverted L marks the point where section crosses the NE-SW section illustrated in Figure 6. Note vertical exaggeration.

Reflectors from the six packages defined for Z1 are continuous to moderately continuous and have the section's highest relative amplitude. The apparent external form of radar packages in Z1 has the highest variation (Pks. 1 to 5). In Z2, two of the five packages are in the form of sheet drapes (Pks. 6, 7), and radar package 7 displays truncation features at its upper boundary (Fig. 4.B). The other three radar packages of Z2 (Pks. 8, 9, 10) are in the form of lenses, where reflectors become weak and are predominantly discontinuous. Dip of reflectors attains the section's lowest values in these packages. The apparent offlapping of radar packages 8, 9 and 10 indicates a progradation of about 20 meters (Fig. 3). Z3 is composed of six radar packages. Four of them (Pks. 11, 13, 15, 16) are set in apparent retrogradation at the section's NW portion. Z4 is composed of three radar packages (Pks. 17, 18, 19) (Fig. 4.B). Package 19 differs from all of the others in Z4 because of its oblique relationship between relatively high amplitude reflectors. Ground truth information obtained by field descriptions and samplings is summarized in Table 1.

Table 1: Field and laboratory characteristics of the sediments per radar zone.

<b>Table 1: General field and laboratory characteristics of the sediments per radar zone.</b>							
<b>Radar Zone 4 (Z4)</b>							
<i>Colors (code)</i>	<i>Colors (name)</i>	<i>Residuals</i>	<i>Fabric</i>	<i>von Post</i>	<i>Carbon (%)</i>	<i>Bulk Density (g.cm<sup>3</sup>)</i>	<i>Water Content (%)</i>
10 YR 2/1	Black	vegetal (80%)	vertical	h <sub>3</sub>	n/a	0.06	87.62
10 YR 4/2	Dark grayish brown	vegetal (90%)	vertical	h <sub>2</sub>	n/a	0.19	84.19
<b>Radar Zone 3 (Z3)</b>							
<i>Colors (code)</i>	<i>Colors (name)</i>	<i>Residuals</i>	<i>Fabric</i>	<i>Von Post</i>	<i>Carbon (%)</i>	<i>Bulk Density (g.cm<sup>3</sup>)</i>	<i>Water Content (%)</i>
7.5 YR 2.5/1	Black	n/a	massive	h <sub>8</sub> to h <sub>9</sub>	51,0	0.17	82.18
10 YR 2/1	Black	n/a	massive	h <sub>8</sub> to h <sub>9</sub>	34,0	0.26	76.13
<b>Radar Zone 2 (Z2)</b>							
<i>Colors (code)</i>	<i>Colors (name)</i>	<i>Residuals</i>	<i>Fabric</i>	<i>von Post</i>	<i>Carbon (%)</i>	<i>Bulk Density (g.cm<sup>3</sup>)</i>	<i>Water Content (%)</i>
7.5 YR 3/1	Very dark gray	fine gravel	conglomeratic	h <sub>3</sub>	36,7	0.41	62.95

10 YR 2/2	Very dark brown	gravel and vegetal (1%; 1 mm)	inclined to horizontal	h <sub>2</sub> to h <sub>3</sub>	n/a	0.37	65.74
10 YR 3/1	Very dark gray	gravel and vegetal (1%; 2 mm)	horizontal	h <sub>2</sub> to h <sub>3</sub>	n/a	0.39	57.50
10 YR 4/2	Dark grayish brown	vegetal (5 to 10%; 2 to 4 mm)	horizontal	h <sub>2</sub> to h <sub>3</sub>	16,8	0.35	61.30
10 YR 5/2	Grayish brown	none (mineral mud layer)	not observed	n/a	15,2	0.54	44.20
<b>Radar Zone 1 (Z1)</b>							
<b>Colors (code)</b>	<b>Colors (name)</b>	<b>Residuals</b>	<b>Fabric</b>	<b>von Post</b>	<b>Carbon (%)</b>	<b>Bulk Density (g.cm<sup>3</sup>)</b>	<b>Water Content (%)</b>
2.5Y 6/3	Light yellowish brown	gravel and vegetal remnants (< 1%)	conglomeratic	n/a	3,2	0.65	47.20
2.5Y 7/3, 7.5 YR 3/1	Pale yellow, Black	fine gravel, A horizon pedorelicts (1%)	conglomeratic	n/a	2,2	0.67	42.20
5Y 8/2	Pale yellow	fine gravel	conglomeratic	n/a	1,5	1.28	26.37

With the exception of the three uppermost packages in Z2 (Pks. 8, 9, 10) (Fig. 4.B), the materials in all the radar packages in Z2 and Z1 contain a high proportion of sands and fine gravel (Fig. 5). Sands are also present in shallower materials from Z3. As expected from the application of the Flemming diagram for muddy sediments, materials tend to group in several textural classes (Fig. 5.A), which enables facilogic analysis (Flemming, 2000; Oliveira and Lima, 2004). Clustering is also noted in the diagram of Folk (Fig. 5.B).

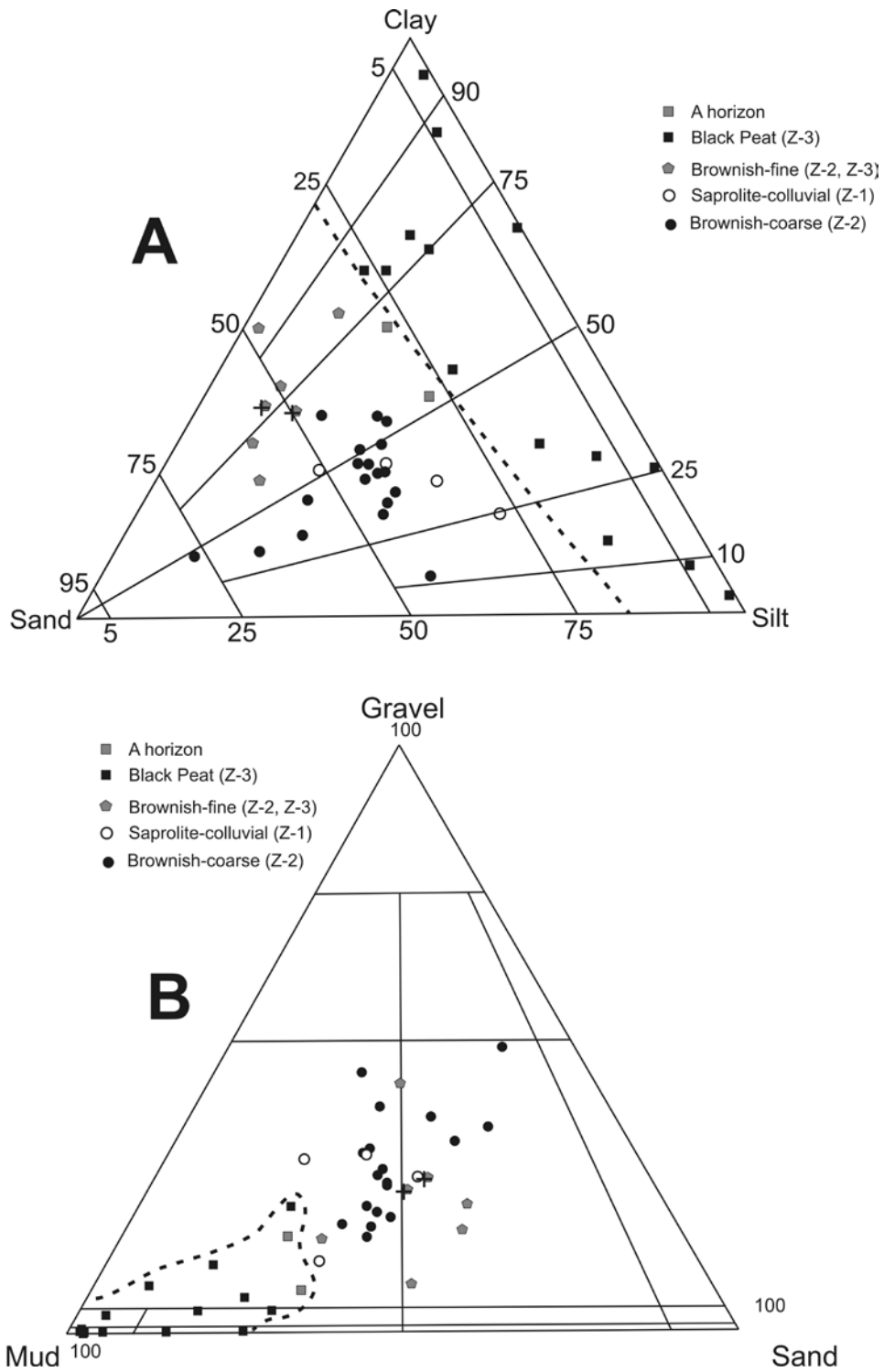


Figure 5: Ternary diagrams for textural classification, according to A: Flemming (2000) and B: Folk (1954; 1980). The dashed line divides characteristic black peat samples from mixed material samples. Correspondence between materials and radar zones is indicated by the legend. Two samples marked with a cross correspond to mineral muds which occur mixed with Z-3 organic muds.

Samples from Z1 plot around the center of the Flemming diagram, together with about half of the samples from Z2 and samples from two packages of Z3 (Pks. 12, 15) (Fig. 5.A and Fig. 4.B). Samples from Z1 and Z2 had more than 10% gravel content and less than about 50% of mud in the mineral portion, as did materials from the above mentioned packages of Z3. All samples taken from the other packages of Z3 had more than 70% mud, in which organic remains predominate. The upper radar package of Zone Z4 was not analyzed, since its materials are mainly composed of vegetal tissue (Table 1). As a result, the definition of radar zones, such as assemblages of radar packages (Fig. 4), corresponds to the general stratigraphy of the mire, representing depositional units that have particular sedimentologic characteristics and allostratigraphic significance.

The first unit (Z1), which is close to the weathered bedrock, has textures that range from extremely silty sandy mud to very silty sandy mud, according to Flemming (Fig. 5.A). Most of the samples classify as gravelly mud, according to Folk (Fig. 5.B). Wood particles were found together with centimetric gravels in this unit, which samples plot around the center of textural diagrams, as is commonly observed in samples from colluvial deposits. The second unit (Z2) is composed of materials that vary along the section. In the first 20 meters of the section (the NW side), the materials classify as slightly muddy sands to sandy muds, according to Flemming's, and as gravelly muds, according to Folk's. The coarser samples of Z2 contain higher proportions of sands (75% - 95%) and gravels than sediments from Z1 (Fig. 5.A and 5.B). In the SE portion of the section (Fig. 4.B), Z2 radar packages 8, 9 and 10 coincide with brownish muds, in which the samples range from clayey sandy mud to extremely clayey sandy mud. The upper half of the section (units Z3 and Z4) is composed of typical peat material, although the clastic content is still significant (45% in average) in Z3. Z3 deposits are classified as the peat catotelm, while those of Z4 as the acrotelm. Colluvium and humic A horizons occur at the NW extremity of the section, associated respectively with radar packages 17 and 18.

The radar stratigraphy and sedimentology of the site suggest a relatively complex local history of erosion and deposition, associated with the accumulation of peat deposits, which had been mixed at some levels with sands and gravels. Radiocarbon and luminescence ages for samples of the mire radar zones are shown in Table 2. Their ages span a period ranging at least from the beginning of marine isotopic stage 3 (MIS 3) (64 ka) to historic times (0.4 ka).

Table 2: Radiocarbon and stimulated optical luminescence ages of the study samples. The shaded lines in  $^{14}\text{C}$  dates mark samples which were taken from the core used for palynology (see location in Figure 6). Note radar stratigraphy at the first column.

Radar Zone	Sample code	Depth (cm)	Method	$\delta^{13}\text{C}$ (‰)	Age (years B.P.)	Age range* (cal year B.P.)
Z4	UGAMS-5970	20	Liquid scintillation	-21.5	400 ± 20	327 – 493
Z4	UGAMS-5969	20	Liquid scintillation	-23.7	670 ± 25	556 – 651
Z3	UGAMS-5968	35	Liquid scintillation	-20.5	1,860 ± 25	1,626 – 1,822
Z3	UGAMS-5967	40	Liquid scintillation	-18.6	2,020 ± 30	1,827 – 1,992
Z4	Erl-11255	34	AMS	-20.0	459 ± 44	328 - 534
Z3	Erl-12097	47	AMS	-18.8	3,820 ± 39	3981 - 4284
Z3	Erl-12656	61	AMS	-17.2	7,327 ± 45	7981 - 8179
Z3	Erl-11256	71	AMS	-26.5	10,536 ± 63	12,240 - 12,786
Z2	Erl-12657	83	AMS	-26.5	13,399 ± 72	15,528 - 16,341
Z2	Erl-12098	94	AMS	-28.1	19,439 ± 115	22,661 - 23,596
Z2	Erl-12099	122	AMS	-27.2	25,380 ± 152	too old for calibration
Z2	Erl-11257	167	AMS	-28.9	39,407 ± 681	too old for calibration
Z1	UGAMS-5144	210	AMS	-28.6	53,560 ± 1,450	too old for calibration

\* Range at standard deviation of 2 sigma, at 95.4% probability. Calibration curve for holocenic samples: SH cal. Calibration curve for pleistocenic samples: Int cal.

**Radiocarbon dates.** Shade : subsamples taken from pollen core sample

Radar Zone	Sample code	Depth (cm)	Annual dose (mGy/year)	Accumulated dose OSL (Gy)	OSL age (years)
Z2	LVD-2551	140	2,512 ± 181	63.58	25,300 ± 3,100
Z1	LVD-2550	84	2,223 ± 118	102.06	45,900 ± 4,700
Z1	LVD-2439	175	2,190 ± 129	141.23	64,500 ± 7,000
Z1	LVD-2438	120	2,625 ± 168	260.99	99,400 ± 11,300
Z1	LVD-2440	190	1,907 ± 109	304.60	159,700 ± 17,100

**Luminescence dates.**

## 4.2 Mire palynology

Long before the use of GPR at the mire, a sedimentological record for palynological analysis was incidentally sampled at the location where radar packages 8, 9 and 10 occur (Fig. 4), crossing the Z2, Z3 and Z4 radar stratigraphic units (Fig. 6).

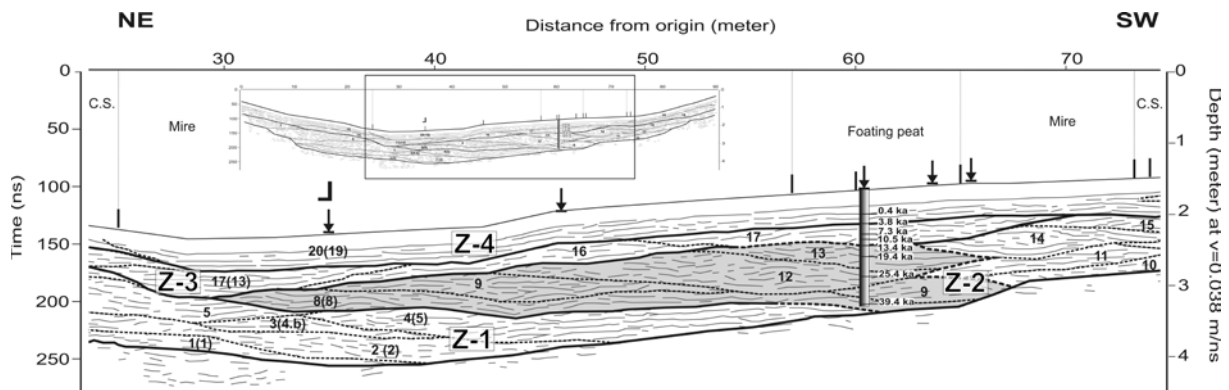


Figure 6: NE to SW 400 MHz interpreted radar reflection section. The number of radar packages differs from that in Figure 4, due to variation of the stratigraphic set. The brownish muddy materials of Z2 are marked with a gray shade and correspond to packages 8, 9, 12 and 13, at this section. Note position of the core sampled for palynology, together with radiocarbon ages. Vertical arrows indicate position of manual drillings. The inverted L marks the point where the section crosses the NW-SE section. The legend “C-S” refers to “colluvial slope”. Inset indicates position of the figure respective to surveyed section and topography. Note vertical exaggeration.

Radiocarbon ages obtained from the 170-cm long core range from  $39,407 \pm 681$   $^{14}\text{C}$  yr BP to  $459 \pm 49$   $^{14}\text{C}$  yr BP, encompassing a period between the Late Pleistocene (MIS-3) and historic times (see Table 2). Pollen data from this core can be subdivided into four pollen zones (Fig. 7 and Fig. 8).





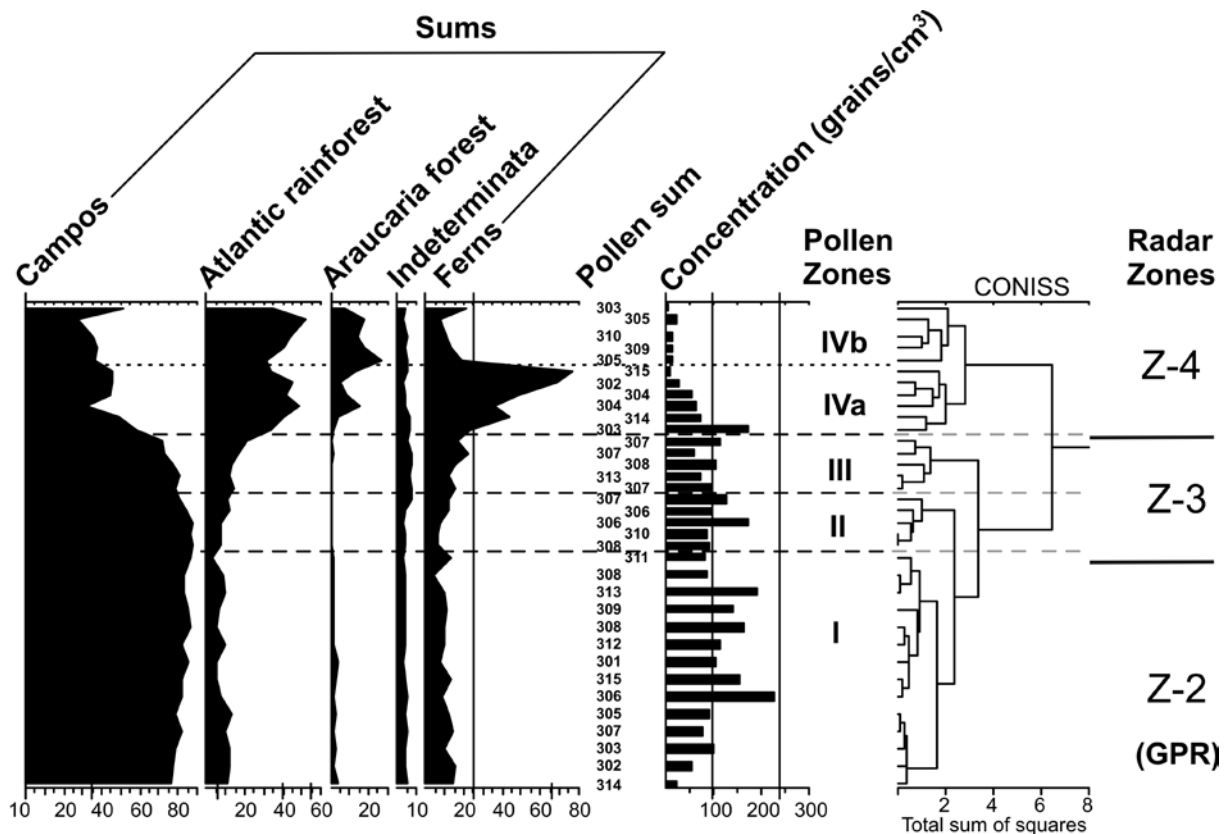


Figure 8: Summary pollen percentage diagram. Pollen concentration data are shown, together with pollen zones and CONISS cluster analysis dendrogram. Correspondence between pollen zones and radar zones is indicated.

Zone I (164-84 cm; 38,470-14,100  $^{14}\text{C}$  yr BP; 14 samples) is characterized by a very high representation of *Campos* pollen (77-90%), which consists primarily of Poaceae (61-77%), with lower proportions of Asteraceae, Cyperaceae, *Eryngium* type, *Xyris*, Iridaceae and Eriocaulaceae. Atlantic rainforest pollen is relatively stable at 4% to 13%, while taxa of the *Araucaria* forest are much less frequent. Ferns (3% and 14%) are mainly represented by spores of Cyatheaceae, *Blechnum imperiale* type, Monolete psilate, *Selaginella excurrens* type and *Isoetes*.

Pollen zone II (84-64 cm; 14,100 - 8290  $^{14}\text{C}$  yr BP; five samples) shows a slight increase in *Campos* taxa percentages, reflected mostly by Poaceae pollen (65-78%), with a decrease in other grassland pollen. A slight decrease in Atlantic rainforest is noted primarily by lower frequencies of Myrtaceae pollen (1-4%), Moraceae/Urticaceae and Arecaceae. *Araucaria* forest species are found in only very low percentages. The ferns group also shows a decrease from 12% to 4%, mainly influenced by lower values of Cyatheaceae, *Blechnum imperiale* type and *Isoetes*.

Pollen zone III (64-44 cm; 8,290 – 3,050  $^{14}\text{C}$  yr BP; five samples) displays an increase in Atlantic rainforest species from 13% to 23% attributed to the increase in pollen percentages of *Weinmannia* type, *Myrsine* and Melastomataceae. *Araucaria* forest taxa are poorly represented. A

decrease in *Campos* taxa (80% to 69%) is mainly due to variances in Poaceae pollen (58-41%). There is an increased proportion of Asteraceae and *Eryngium* type pollen. There is an increase in the ferns group (12% and 22%), mainly represented by spores of Cyatheaceae, *Dicksonia sellowiana* type, *Blechnum imperiale* type and Monolete psilate. The opposite was found for spores of the *Selaginella excurrens* type, which decrease noticeably. *Sphagnum* spores increase slightly up to the top.

Pollen zone IV (44-0 cm; 3045 <sup>14</sup>C yr BP to the present; 11 samples) is characterized by a further increase in Atlantic rainforest taxa, which reach values between 34% and 53%, mainly influenced by variations in the pollens of Myrtaceae (2-22%) and *Weinmannia* type (8-35%). *Araucaria* forest taxa show a notable increase from 1% to 26%, represented mainly by higher frequencies of *Ilex* (up to 4%) and *Mimosa scabrella* type pollen (1-20%). *Araucaria angustifolia* pollen percentages also increase up to 4%, but drop towards the top of this zone. Poaceae pollen decreases as an important *Campos* element from 27% to 7%. Pollen abundances of Cyperaceae increase while those of the *Eryngium* type decrease continuously. Fern taxa reach very high proportions (77%), but decrease to a minimum of 7% at a depth of 4 cm. *Sphagnum* spores are well represented and vary between 0.3% and 3%. This zone is divided into two subzones. Subzone IVa shows an extremely high proportion of fern taxa (23% to 77%), represented mainly by *Blechnum imperiale* type and Monolete psilate. Subzone IVb is characterized by a marked decrease in fern taxa from 21% to 7%, as indicated by low proportions of Cyatheaceae, *Blechnum imperiale* type, Monolete psilate, Monolete verrucate and *Lycopodium clavatum* type. The representation of *Pinus* pollen reaches 1% at the top of the core.

## 5. Interpretation

### 5.1. Geochronology and radar stratigraphic interpretation

According to the OSL and <sup>14</sup>C dates (Table 2), the first unit (Z1) (Fig. 4) had accumulated during a period that coincides on average to the first half of the MIS-3 interstadial. Ages range from 64 ka to 45 ka. Older ages occur in two OSL dates, probably as a result of partial reworking of older pleistocenic sediments by overland flow pulses. Z1 deposits are associated with relatively concentrated fluid-sediment mixtures that were carried from adjacent slopes to a hollow, where typical colluvium was preserved (Oliveira and Lima, 2004). Z1 radar packages have variable geometries: sheet drapes (Pk. 4.a and 4.b); wedge (Pk. 3), lenses (Pk. 1, 2) and trough (Pk. 5) (Fig. 4.B), which is interpreted as evidence of a variable depositional pattern. The Z1 upper radar package (Pk. 5) trough geometry suggests the existence of low sediment concentration flows towards the end of the period (the first half of MIS 3), associated with channelized overland flows (Bertrand and Texier 1999). The origin of Z1 deposits is attributed to an environment with relatively open vegetation, which was associated with sporadic storm flows that would have eroded and transported surface materials along the valley head.

Overlying deposits from the Z2 unit have OSL and  $^{14}\text{C}$  ages that range from 39 ka to 13 ka (Table 2), thus extending from the second half of the MIS-3 interstadial to the tardiglacial. As a result, most Z2 deposits were formed during a period of lowering global temperatures, which includes the MIS-2 last glacial maximum (LGM) (Aharon and Chappell, 1986). Sandy and gravelly, roughly stratified muds are understood to be the source of the strong relatively continuous GPR reflections at the NW side of the section, where radar packages (Pks. 6, 7) have sheet drape geometry (Fig. 4). At the section's SE side, Z2 lenticular radar packages 8, 9 and 10 are set in offlap and have terminations of individual reflections downlapping at the base. This configuration indicates that muds from radar packages 8, 9 and 10 were deposited in progradation, probably under the influence of a lowering local base-level change, in the lentic environment of shallow ponds. The overall configuration of the Z2 reflectors coincides with the forced regression pattern of sedimentation from sequence stratigraphy (Fig.3.B). Even the predicted sub-aerial unconformity may be noted, at the top of radar package 7, at the NW portion of the section (Fig. 4.B). This depositional pattern is consistent with an environment where MIS-2's lower global temperatures would cause a decrease in average precipitation and evaporation rates. The lower temperatures may have induced, however, a local excess of precipitation over evaporation, forcing the accumulation of ground water (Oliveira et al., 2008) and explaining the formation of the shallow pond. The increasing dryness would cause lowering local base-level changes, creating the Z2 shallow pond deposits. Intense storms would thus trigger overland flows on adjacent slopes (Dietrich and Dunne, 1993), creating the alluvial deposits at the section's NW portion. Probably under the influence of this local hydrology, the Z1 colluvial depositional pattern changed in the alluvial deposits of Z2, which were created in a more watery local environment, around an evolving shallow pond. Later, during the LGM, a shift towards the terrestrealization (Shotik, 1992) of the site led to silting of the shallow pond, in a process that persisted until tardiglacial times (Table 2 and Fig. 4).

Z3 deposits have  $^{14}\text{C}$  ages that encompass the entire Holocene (from 10 ka to 1.8 ka) (Table 2). Peat deposits predominate and Z3 materials are classified as the mire catotelm (Charman, 2002). Some of the radar packages, however, coincide with layers of inorganic sediments (Pks. 12 and 15), mixed with catotelm materials, as would be expected in minerotrophic fens (Doolittle and Butnor, 2009). Radar packages 13, 15 and 16 are set in retrogradation, at the NW half of the section, near the mire's border (Fig. 4.B). Terminations of reflectors occur in onlap at the base of these packages, and in toplap at their top. The overall configuration and sedimentology are interpreted as evidence of a period with a wetter climate (such as the early Holocene), during which peat began to accumulate. Interpretation of a local rising base-level for the period is supported by the onlapping of radar packages at the NW portion of the section, which could be a consequence of rising water tables. Once again, an interesting coincidence between sequence stratigraphy and radar stratigraphic interpretation is noted, as this configuration coincides, at the site scales, with the transgression depositional pattern

illustrated in Fig.3.c. Shallow waterlogged ground materials could induce pulses of overland flow, explaining the overall configuration of radar packages in Z3 and the origin of the siliciclastic sediments of radar packages 12 and 15, which have been mixed with typical peat deposits (Fig. 4.B).

The Z4 deposits are predominantly made of vegetal tissues that constitute the site acrotelmic horizon (Pk.19). Their  $^{14}\text{C}$  ages are historic (Table 2). Reflectors are generally disposed in onlap retrogradation, apparently overlaying a humic A horizon (Pk. 18), at the peatland's NW border (Fig. 4.B). A colluvial layer (Pk. 17) overlies radar package 16 (from Z3) in progradation, with reflectors disposed in downlap, indicating the apparent flow direction respective to the plane of survey.

The association of the radar stratigraphic and sedimentologic data allows distinguishing 8 radar facies in the mire, which are summarized in Table 3 (see also Supplementary Table). Evidence suggests an evolutionary scenario in which the mire was formed by a succession of erosive and depositional events that seem to be associated with the forcing signal of Upper Pleistocene and Holocene global climate changes. The high content of siliciclastic deposits (15% to 70%) in the peat explains the coincidence between the detailed stratigraphic description and laterally coherent GPR reflections, probably as a result of associated pore water-content variations induced by changes in bulk density (Theimer et al. 1994) (Supplementary Fig. 2).

Table 3: Interpretation of radar-sedimentary facies, according to radar zones and radar packages characterization. Field and laboratory characteristics are also taken into account. Shading is intended to stress radar zones and the 8 defined facies.

Radar Zones	Radar Packages	Radar reflection characteristics, sediments and faciologic interpretation
Z4	Pk-19	External form of package in sheet-drape. Reflections are wavy and their terminations are concordant, at the upper boundary, and onlap at the lower boundary. Average dip of reflections is 5°. - Vegetal horizon, associated with oblique to sub-parallel low amplitude relative reflections. <b>Interpretation:</b> acrotelm accumulation.
Z4	Pk-17, Pk-18	Lenticular packages. Reflections are wavy to sigmoidal. Their terminations are concordant at the upper and lower boundaries. Average dip of reflections is 4.5°. - Soil horizon and colluvial deposits, associated with moderately continuous sub-parallel high to low relative amplitude reflections. <b>Interpretation:</b> local deposition and pedogenesis on adjacent slopes.
Z3	Pk-11, Pk-13, Pk-14, Pk-16	Lenticular packages predominate. Reflections are wavy and sigmoidal (Pk-16). Terminations are concordant at the upper

		<p>boundary and concordant, or downlap, at the lower boundary. Average dip of reflection is 3.5°.</p> <p>- Black muds associated with moderately continuous sub-parallel high relative amplitude reflections. <b>Interpretation:</b> locally reworked peat catotelm. Development of the mire under rising water tables.</p>
Z3	Pk-12, Pk-15	<p>Packages have sheet drape external form, with wavy reflections, which terminations are concordant or toplap at the upper boundary. Terminations are concordant or onlap at the lower boundary. Average dip of reflections is 4°.</p> <p>- Inorganic sandy muds associated with moderately continuous low to high relative amplitude reflectors. <b>Interpretation:</b> local alluvial input among peat deposits.</p>
Z2	Pk-8, Pk-9, Pk-10	<p>All packages are lenticular. Reflections are wavy. Their terminations are concordant at the upper boundary and vary (downlap, concordant, onlap) at the lower boundary. Average dip of reflections is 2°.</p> <p>- Brownish mud deposits associated with moderately continuous to discontinuous low relative amplitude reflections. Lenses are mutually disposed in offlap. <b>Interpretation:</b> shallow silting pond, under lowering base-level change.</p>
Z2	Pk-6, Pk-7	<p>External form of packages: sheets. Reflections are wavy and have concordant (Pk-6) and truncated (Pk-7) terminations at the upper boundary. They are concordant or downlap at the lower boundary. Dip attains 7° in Pk-7.</p> <p>- Alluvial deposits associated with continuous to moderately continuous high relative amplitude reflections. <b>Interpretation:</b> flash flows on slopes.</p>
Z1	Pk-4.a, Pk-4.b, Pk-5	<p>Sheet, sheet drape and trough external forms. Wavy and sigmoidal reflections, which terminations in toplap or in truncation at the upper boundary of packages. Reflection terminations are concordant or onlap (Pk-5) at the lower boundary of packages. Average dip of reflections is 3°.</p> <p>- Alluvial-colluvial deposits associated with continuous to moderately continuous high relative amplitude reflections. <b>Interpretation:</b> fan-like and cut and fill deposits.</p>
Z1	Pk-1, Pk-2, Pk-3	<p>Packages present lenses and wedge external forms. Reflections are wavy and sub-parallel. Their terminations are predominantly concordant at the upper boundary, and onlap at the lower boundary. Average dip of reflections is 4°.</p> <p>- Colluvial-alluvial deposits associated with low to high relative amplitude reflections in the form of lenses. <b>Interpretation:</b> high sediment concentration flows on bare slopes.</p>
<p>Shading is intended to highlight radar zones and the 8 defined radar-sedimentary facies.</p>		

## 5.2. Paleoenvironmental interpretation and mire classification

Deposits from the first radar stratigraphic unit (Z1) are not covered by the palynologic record (Fig. 6). However, the interpretation for Z1 would indicate that the valley head was covered by relatively open savanna-type vegetation, which would favor the hyperconcentrated flows able to create colluvial deposits during the first half of MIS 3 interstadial, between 64 ka to 45 ka. Towards the end of that period, a radar package with trough geometry suggests the action of low concentrated channelized flows (Fig.4).

Pollen Zone I coincides with Z2 materials (Fig. 8), corresponding to a period between 39.4 ka to 13.4 ka. The predomination of grass pollen in pollen Zone I (Fig. 7 and Fig. 8), mainly from the Poaceae family, together with other families, indicates a grassland ecosystem (*Campos*), in which small populations of trees and tree ferns (Cyatheaceae) grew in refuges with sufficient moisture. Evidence of the existence of local shallow ponds is indicated by *Isoetes*, which are commonly found in seasonally wet to aquatic habitats. A treeless landscape, however, suggests a dryer and colder climate on the site's highland during the period. According to the radar stratigraphic interpretation, flash floods would have produced alluvial deposits in the vicinity of a shallow silting pond, between the second half of MIS-3 and MIS-2. The radar stratigraphic and palynological interpretations converge, given that the treeless, dry, cold and seasonally wet environment depicted by palynology is a scenario consistent with the action of flash floods and the silting of shallow ponds. The occurrence of waterlogged soils is also supported by the pollen record, which may be better explained, for the drier and colder climate trend of the period, by a local excess of precipitation over evaporation. Pollen Zone II (13.4 ka to 7.3 ka) essentially coincides with the lower half of the Z3 radar zone (Fig.8), and documents a still drier climate between the late-glacial and early Holocene, as suggested by an increase of Poaceae combined with a decrease of arboreal taxa and fern families, such as *Blechnum imperiale*, which grows in bogs (Fig.7 and Fig. 8). Nevertheless, local humidity may have favored development of *Sphagnum*, such as peat moss, and *Selaginella excurrens*, which grows on wet ground. Slightly higher proportions were found of *Weinmannia*, *Myrsine* and *Alchornea*, which represent Atlantic rainforest taxa, and probably grew in refugia or in areas with sufficient humidity. This interpretation conflicts with the local wetter climate interpretation advanced by radar stratigraphy, although increasing temperatures and evaporation rates from the period could explain both the existence of *Sphagnum* and the development of the black peat materials in the record, probably as a consequence of an increase in ground-water saturated areas around valley heads and topographic hollows (Dietrich and Dunne, 1993). Pollen Zone III coincides with the upper half of radar zone Z3 and indicates a period of milder and moister climatic conditions (8.3 ka to 3.0 ka), which promoted development of the Atlantic rainforest at the study site (Fig. 8). Wetter conditions are suggested by the increase of forest taxa as well as by increases of the tree ferns Cyatheaceae and *Dicksonia*

*sellowiana* type. Otherwise, Poaceae decreased during this period. The interpretation is consistent with the development of the typical peat catotelm of Z3, and also explains the retrogradation pattern of some of the Z3 radar packages, at the NW side of the section (Fig. 4), where sediments would accumulate because of rising ground water tables. Pollen zone IV's coincides with radar zone Z4 (Fig. 8) and displays forest expansion and replacement of the *Campos* vegetation. Atlantic rainforest continued to expand upland over the range; while *Araucaria* forest began to develop on the heights of the Serra do Tabuleiro, around the study site. Since the mid-late Holocene, Poaceae decreased markedly, whereas arboreal taxa increased for the Atlantic rainforest and for the *Araucaria* forest. This change to a forest ecosystem may be related to the wetter conditions found since the mid/late Holocene. During this time, the mire was covered partly by *Sphagnum*. The division into two subzones is due to variations in pollen composition, which indicate changes in vegetation dynamics, related to ecosystem disturbances caused by human occupation (Fig. 7). This scenario explains the eventual reworking of peat and adjacent soil materials by storm flows, even in the Late Holocene, as a result of the natural evolution of the fen, under the influence of overland flow pulses at the valley head.

Since classification of highland Brazilian peatlands is still a line of open investigation (Franchi et al., 2006), radar stratigraphy, sedimentology and palynology suggest that the study mire better classifies as: 1) a valley head *mire*, in terms of its geomorphology, and 2) a particular case of *minerotrophic soligenous peatland*, in terms of its hydromorphologic evolution (Charman, 2002). As a result, *fen* (minerotrophic) characteristics predominate at the study site (Hughes, 2000).

## 6. Final remarks

As far as we know, this is the first highland peatland complex described and classified in Brazil on the basis of its stratigraphy. The study shows an intimate relationship between geomorphology, stratigraphy and local or global environmental changes, which also explains the site's relatively complex history of erosion and deposition, which was depicted by radar stratigraphy. Despite the common gaps that characterize Quaternary continental deposits, the record is relatively continuous and application of GPR stratigraphy allows conducting an evolutionary interpretation of the site, with the aid of sedimentology, geochronology and palynology.

Our results demonstrate a case of minerotrophic peatland in which GPR methodology was used to produce a direct correlation between the inner organization of peat deposits and clusters of EM reflections. The reflections tended to group in several packages, which correlate with different sediment types, probably as a result of sharp reductions in volumetric moisture content at the interface between organic and mineral sediments, creating significant EM wave reflections (Kettridge et al., 2008). Indeed, water content variation along the profile (Supplementary Fig. 2) largely exceeds the range of moisture content changes to which GPR is reported to be sensitive (larger to 3%) (Theimer et

al., 1994). The lateral coherence of reflections found in the study is thus a direct result of the minerotrophic evolutionary trend at the site, where interstratifications of siliciclastic and organic sediments caused variations of bulk density and moisture content along the profile (Comas et al., 2005). The overall stratigraphy of the mire coincides with the assemblage of the individual radar packages in radar zones, depicting the underlying mineral sediments (Jol and Smith, 1991), the catotelm and acrotelm (Warner et al., 1990).

At the local scale, stratigraphic and palynologic interpretations converge, as illustrated by the existence of a shallow pond at the study site that was still evolving during the LGM. Evidence of this local wetness is partially supported by the occurrence of *Isoetes*, at the base of shallow pond muddy deposits in Z2, which coincides with pollen zone I. *Isoetes*, also known as quillworts, evolve mostly in clear ponds and slow-moving streams. This relative local dampness during the LGM may be explained as a side-effect of temperatures lower than those found today, which would also cause a relative excess of precipitation over evaporation (Oliveira et al., 2008).

The paleoenvironmental evolution depicted by the study record coincides with isotopic evidence of changing atmospheric circulation and convective activity during the Late Pleistocene, which seems to be associated with precessional increases of South American summer monsoon precipitation in Southern Brazil (Cruz et al., 2009). However, the eventual effect of cyclonic storms associated with South Atlantic polar fronts, which would be strengthened during periods of lower global temperatures, would also help to explain: a) the patchy pattern of erosion and deposition and; b) the palynologic evidence of lower temperatures and higher dryness at the study site in this Atlantic range.

The depositional patterns depicted by radar stratigraphy and the high content of siliciclastic deposits associated with the peat are strong evidence of the minerotrophic origin of the mire, which is strongly controlled by the geomorphological setting. Similarly, palynologic accounts of Brazilian highland peats (Roth and Lorscheitter, 1993; Behling, 1995, 1997a, 1997b) often report the existence of sand in peat basal layers, although few studies have quantified this (Roth and Lorscheitter, op. cit.). Siqueira (2006), for instance, shows that significant sand content may occur along the entire peat deposit, justifying her proposal to integrate sedimentology and palynology for improved paleoenvironmental interpretation.

Together with the view that highland ombrotrophic raised bogs are unknown in Brazil (Franchi et al, 2006), evidence in the literature suggests that the clastic inputs that are common in minerotrophic fens would tend to predominate in the evolution of Brazilian mires, associated with a complex local sedimentary history that needs to be accounted for. Indeed, because palynology requires a record ideally accumulated under the Northern Hemisphere ombrotrophic bog model (Clymo, 1984), the supposition that Brazilian highland mires are characteristically ombrotrophic is



common, in spite of geomorphological and stratigraphical evidence to the contrary (e. g. Roth and Lorscheitter, 1993). This would also explain why there are few studies on pollen deposition associated with flowing waters (Bauermann et al., 2002). Application of GPR surveys to peat stratigraphy allows using Brazilian minerotrophic *fen* deposits as a source of paleoenvironmental interpretation, integrating both stratigraphy and palynology and opening a wide range of paleoenvironmental studies.

## 7. Acknowledgments

This project was partially undertaken at the Departamento de Geofísica – IAG – USP, São Paulo. Funding was provided by CNPq – Conselho Nacional de Desenvolvimento Científico e Tecnológico (research grant number 152377/2007-7), and by FAPESC – Fundação de Apoio à Pesquisa Científica e Tecnológica do Estado de Santa Catarina (research grant number CON08857/2007-9). We would like to thank Dr. Soraia Girardi Bauermann for her kind and useful critics. We would also like to thank Dr. Xavier Comas and Dr. Paulo César Fonseca Giannini, whose careful and generous reviews greatly contributed to this manuscript.

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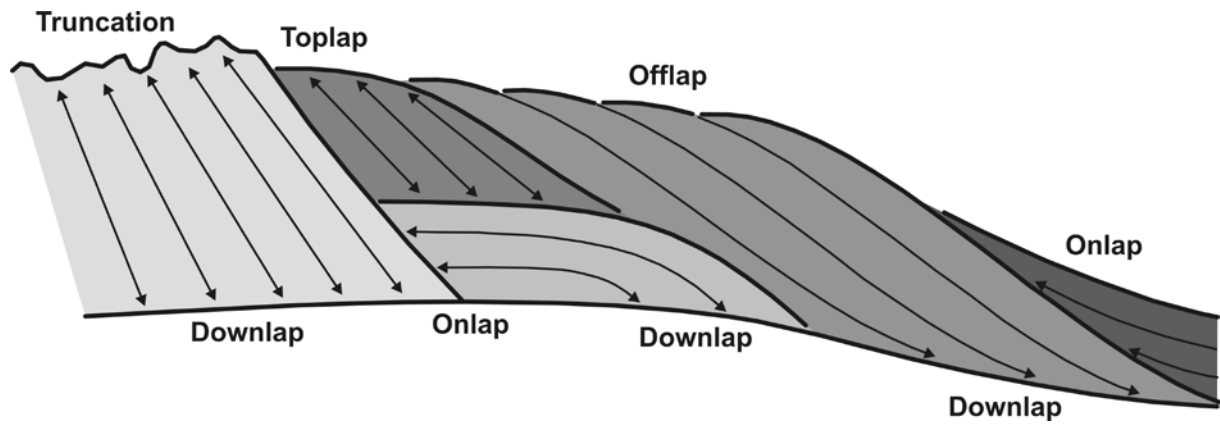
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Supplementary Material



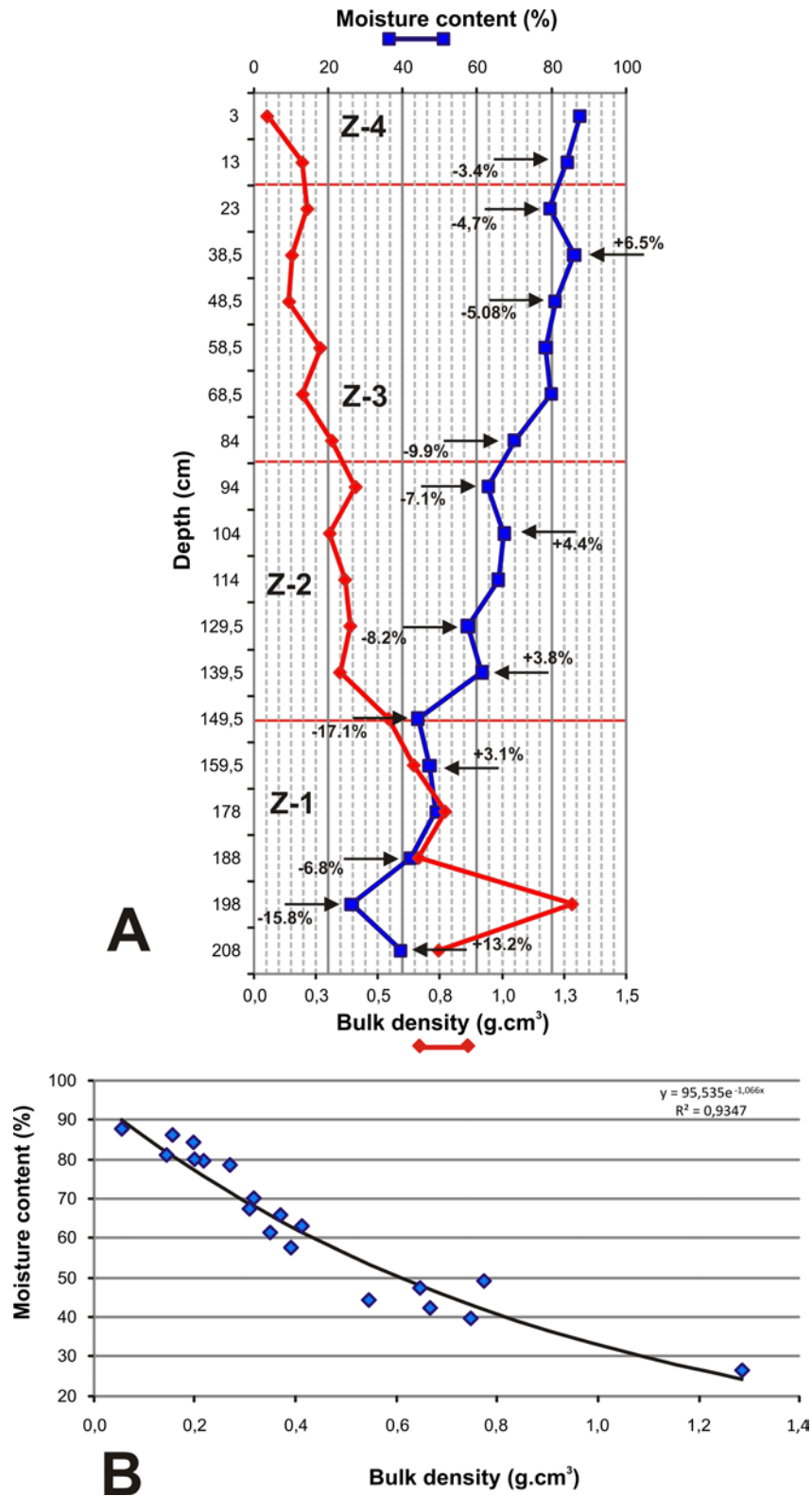
Supplementary Figure 1: Types of stratal terminations, after Catuneanu (2002 - Journal of African Earth Sciences 35, 1-43).

Supplementary Table: Geometry of radar surfaces, external form of radar packages and configuration of radar reflections (shape, dip, relationship, continuity). Radar packages are numbered in accordance with stratigraphic superposition and organized by radar zones, as in Figure 4.

Radar Zone	Package Number	Package upper boundary	Package lower boundary	Package external form	Shape of reflections	Dip	Relationship among reflections	Continuity of reflections
Z4	19	concordant	onlap, local downlap	sheet drape	wavy	2 to 8 degrees	oblique to subparallel	continuous to moderately continuous
Z4	18	concordant	concordant	lens	wavy	2 to 7 degrees	subparallel	moderately continuous
Z4	17	toplap to concordant	concordant to downlap	lens	sigmoidal	2 to 7 degrees	subparallel	moderately continuous
Z3	16	toplap to concordant	concordant to downlap	lens	sigmoidal	2 to 7 degrees	subparallel to oblique	moderately continuous
Z3	15	concordant to toplap	concordant	sheet drape	wavy	2 to 5 degrees	parallel to tangential	moderately continuous
Z3	14	concordant	concordant	lens	wavy	1 to 5 degrees	subparallel	moderately continuous
Z3	13	concordant	downlap	lens	wavy	1 to 5 degrees	subparallel	moderately to discontinuous
Z3	12	concordant	onlap to concordant	sheet drape	wavy	0 to 8 degrees	subparallel	moderately continuous
Z3	11	concordant	concordant	sheet drape	wavy	2 to 5 degrees	subparallel	continuous to moderately continuous
Z2	10	concordant	onlap to	lens	wavy to	0 to 8	subparallel	discontinuous

			downlap		sigmoidal	degrees		
Z2	9	concordant to truncated	concordant	lens	wavy	0 to 4 degrees	subparallel	moderately continuous
Z2	8	concordant	concordant to downlap	lens	wavy	horizontal	subparallel	moderately to discontinuous
Z2	7	truncated	concordant	sheet	wavy	2 to 12 degrees	subparallel	continuous to moderately continuous
Z2	6	concordant	concordant to downlap	sheet	wavy	1 to 4 degrees	subparallel	moderately continuous
Z1	5	concordant to toplap	onlap to downlap	trough	sigmoidal	1 to 5 degrees	tangential	moderately continuous
Z1	4b	toplap to concordant	concordant	sheet drape	wavy	0 to 6 degrees	subparallel	continuous to moderately continuous
Z1	4a	toplap to truncated	concordant	sheet	wavy	1 to 6 degrees	subparallel	continuous to moderately continuous
Z1	3	toplap to concordant	onlap to concordant	wedge	wavy	2 to 8 degrees	subparallel	discontinuous
Z1	2	concordant to truncated	onlap	lens	wavy	2 to 6 degrees	subparallel	continuous to moderately continuous
Z1	1	concordant	onlap to downlap	lens	convex	0 to 4 degrees	subparallel	discontinuous

Radar packages are numbered in accord with stratigraphic superposition and organized by radar zones, as in Figure 4.



Supplementary Figure 2: Moisture content and bulk density across the mire materials (A). Radar Zones are indicated. Arrows point to focus where variation of moisture content exceeds the range of moisture content changes to which GPR is reported to be sensitive (larger to 3%), either by an increase (+) or a decrease (-) relative to the immediate previous depths. B: bulk density and moisture content correlation.

# CURRICULUM VITAE

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## PERSONAL DATA

**Full name:** Vivian Luciana Jeske-Pieruschka

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## PRACTICAL EXPERIENCE

- 2007-2010 DFG project at the University of Göttingen: Studies of vegetation, fire and climate dynamics during the late Quaternary as contribution towards conservation and management of the biodiversity hotspot „Mata Atlântica“ in Southern Brazil.
- 2005-2006 Scientific Graduate Assistant at the chair of special botany and mycology (University of Tübingen) within the scope of the DFG projects „Diversity and potential of use of arbuscular mycorrhiza in the tropical montane rain forest of Southern Ecuador“ and „AM fungal diversity in a Montane forest of Ethiopia with special emphasis in Nurse tree effect“.
- 2002 Scientific Student Assistant working at the Centre for Plant Molecular Biology and Developmental Genetics (University of Tübingen) on the DFG project "Molecular analysis of sterol-biosynthesis-mutants of *Arabidopsis thaliana*"

## EDUCATION

- 2007 – 2011 **PhD-Program** (Biology) at the University of Göttingen, Albrecht-von-Haller Institute of Plant Sciences, Department of Palynology and Climate Dynamics.
- 2001 – 2005 **Graduation in Biology** (Diplom) at the University of Tübingen  
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- 2001 Successfully passed "Deutschen Sprachprüfung für den Hochschulzugang für ausländische Studienbewerber" (DSH, german language test for foreign study applicants) at the University of Tübingen.
- 2000 – 2001 Participated in an exchange program between the University of Tübingen and the Pontifical Catholic University of Rio Grande do Sul.
- 2000 Scholarship from the Research Foundation of the State of Rio Grande do Sul (FAPERGS).
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Göttingen, den 25.08.2011