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Investigations into the Late Pleistocene and Holocene history of vegetation and climate in Santa Catarina (S Brazil)

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Abstract. Palynological studies have been carried out on three highland peat bogs, and one situated on the Atlantic coastal plain. In the highlands, the late Pleistocene (14,000 - 10,000 uncal B.P.) vegetation was dominated by *campos* (grassland). Scattered stands of *Araucaria* forests were preserved in deep valleys. In the region of the sites at Morro da Igreja and Serra do Rio Rastro, the dominance of *campos* vegetation continued until about 1000 B.P. while at the Serra da Boa Vista site there was an expansion of Atlantic pluvial forest elements followed by *Araucaria* forests at the beginning of the Holocene. A general expansion of *A. angustifolia,* clearly related to a change towards an increasingly moist climate, can be dated to the present millenium. On the coastal plains, the late Pleistocene vegetation was dominated by Myrtaceae which were replaced by tropical taxa in the Holocene. The lowland profile (Poço Grande) also covers part of the upper Holocene, where the rich flora of the Atlantic pluvial forests can be characterized by taxa including *Alchornea*, Urticales and *Rapanea*. Close to the coring site, there was a repeated alternation between two different dune communities (4840 - 4590 B.P.), followed by a lake stage with aquatic plant succession (4590 - 4265 B.P.), plant communities dominated by *Rapanea* (4265 - 4230 B.P.) and the spread of *Alchornea* (4230 - 3525 B.P.). Late Pleistocene climate conditions (14,000 - 10,000 B.P.) can be described as cold and relatively dry, possibly including an equivalent of the Younger Dryas period. In the Holocene, there were changes from a warm and drier climate (10,000 - ~3000 B.P.) to a cool and more moist regime (ca. 3000 - ca. 1000 B.P.) and finally to a cool and very moist period (from around 1000 B.P.).

Key words: Brazil – Late Pleistocene – Holocene – *Araucaria* – Tropical forests – *Campos*

Introduction

Little is known about the history of Brazilian vegetation up to now, although there is a great need for more information. Many types of forests, such as rain forests and especially those of the coastal plains and the *Araucaria* forests, suffer severely from heavy and almost unlimited human exploitation. Palynological studies provide much needed information concerning the development and maintenance of such threatened vegetation types, which are in urgent need of protection. In addition, important questions such as how grassland can exist under present humid forest climate conditions (the *campos* problem; Hueck 1966), may be solved by palynological work on the problems of vegetation and climate development in southern Brazil.

At present, there are only a few palynological studies on the Quaternary of Brazil. In southern Brazil, palynological studies were first presented by Absy and Suguio (1975) and by Lorscheitter and Romero (1985). In the state of Santa Catarina, the present study is the first one. This is in contrast to the interest which has been focused on the history of southern Brazilian forests and grassland (Rambo 1951a, 1951b, 1953, 1954a, 1954b, 1956, 1957, 1960, 1961; Klein 1960, 1975, 1984; Smith 1962). However, these studies are based on biogeographical data only.

In Santa Catarina, some peat bogs exist in the highlands and on the coastal plain (Ule 1900; Grumpelt 1987). Most of them are severely influenced by fire or drainage. Therefore, it is rather difficult to search in the field for suitable deposits for palynological studies, although there are good opportunities for palynology.

The knowledge of the flora is far advanced. The work of P.R. Reitz and Dr. R.M. Klein done during the past 40 years has led to 140 of 220 families being completely studied.

In addition, the pollen morphological work on tree pollen taxa done during the last 20 years by Dr. O.M. Barth and her collaborators offers a good basis for the study of fossil pollen and spores.

Geographical situation

The state of Santa Catarina occupies an area of 95,985 km² (Fig. 1). The eastern part of the state consists mainly of the Atlantic lowland and the southern Brazilian highland. The highland is composed of the southern moun-

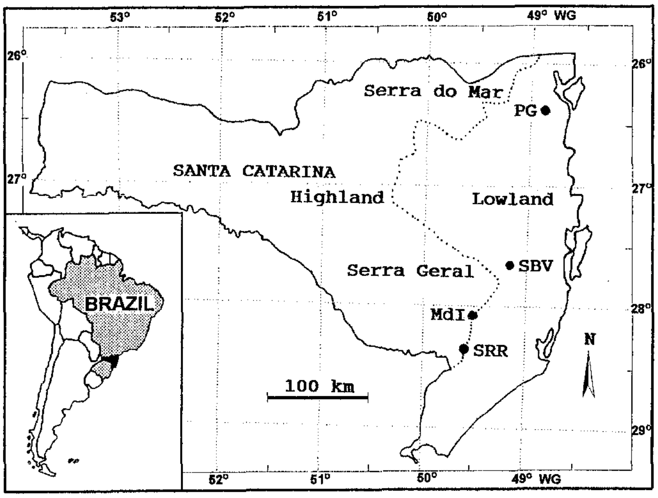


Fig. 1. Santa Catarina with the location of the peat bogs of Poço Grande (PG), Serra da Boa Vista (SBV), Morro da Igreja (MdI) and Serra do Rio Rastro (SRR). Dotted line: border between highland and lowland

tain ranges of the Serra do Mar (average elevation 900 - 1000 m a.s.l.) and the Serra Geral (average elevation 1200 - 1400 m a.s.l.) in the south.

The most northern part of the study area is situated on the coastal plain 20 km from the Atlantic coast (Fig. 1). The village of Poço Grande is situated 15 km south of the town Joinville. The core site (26°25' S, 48°52' W; 10 m a.s.l.), lies 800 m northwest of the end of the road to the Ranch Nutrimental.

The Serra da Boa Vista is part of the northeastern foothills of the Serra Geral. From the coast, the mountains gradually increase in altitude to the west. Here the investigated peat bog of Serra da Boa Vista (27°42' S, 49°09' W; 1160 m a.s.l.) is not far from the road BR 282, 10 km east of the village São Leonardo. The bog covers an area of 10 - 16 x 40 m and is situated on a small slope with a relatively steep east-west inclination behind a 3 m steep escarpment.

One of the highest parts of the Serra Geral, and therefore of the state of Santa Catarina is the Morro da Igreja (28°11' S, 49°52' W), 25 km southeast of the village Urubici. The peat bog (1800 m a.s.l.) is situated at the border of the São Joaquim National Park, 300 m west of the highest point. The bog occupies an area of 30 x 40 m on a western slope with a slight inclination, adjacent to the border line between the highland and the lowland.

The most southern part of the Serra Geral is the Serra do Rio Rastro. The peat bog investigated here is close to the road SC 438, 11 km west of the village Bom Jardim da Serra. The bog (28°23' S, 49°33' W; 1420 m a.s.l.) occupies an area of 50 x 50 m in a little shallow hollow, next to the steep escarpment.

Geology

The southern mountains of the Serra do Mar belong to the east Brazilian Shield. They are of Precambrian origin and form part of the highlands in northeast Santa Catarina. The mountains of the Serra Geral are part of the Paraná Basin which is filled with sediments up to a thickness of 2000 m. The lower 1000 m sediments are of Silurian age. Marine transgressions took place here during the Devonian and upper Carboniferous.

Gondwana coal occurs in thin layers that are overlain by sandy deposits of Permian and Triassic age. Extensive eruptions occurred at the end of the Mesozoic, resulting in a 1500 m deep lava deposit capping the coal and sand deposits. These basaltic formations formed large parts of the south Brazilian highland. In mid- and southeast Santa Catarina are the mountains of the Serra Geral. These have a steep escarpment parallel to the coast. The southern lowland consists of basaltic formations of Paleozoic and Mesozoic age, the middle and the northern Atlantic lowland of Precambrian crystalline rock formations. In the lowland basins, there are Quaternary sediments of fluvial and marine origin (Martin et al. 1988; Putzer 1969; Schobbenhaus 1984).

Climate

Compared with other regions of the country, southern Brazil has a constant warm and moist climate without marked dry periods. In the northern lowland and on the slopes of the Serra do Mar, the average annual precipitation is about 2200 mm. From north to south, the precipitation declines to 1400 mm. In the eastern highlands the average annual precipitation is about 1400 - 1800 mm, and in the south eastern highland the precipitation is less than 1400 mm. In the Atlantic coastal plain, the average annual temperature declines from +21°C in the north to +17°C in the south. In the highlands the average annual temperatures are between +14°C and +18°C, while in the upper region of the Serra Geral they decline from +14°C to below +12°C. Temperatures below zero are very rare in the lowland and only to be expected in the southern part. Nights in cold winters may have temperatures of -4°C to -8°C in the upper region of the Serra Geral (Atlas de Santa Catarina 1986; Nimer 1989).

Vegetation

According to Klein (1978), the potential native vegetation of east Santa Catarina is subdivided into five main zones each with subzones (Fig. 2).

The coastal vegetation (*Vegetação litorânea*) is situated within a narrow coastal strip, consisting of mangrove, beach and dune communities directly or indirectly influenced by the ocean.

The Atlantic pluvial forest (*Floresta Tropical Atlantica*) which is part of the *Mata Atlântica* in Santa Catarina, is subdivided into eight subzones (Fig. 2). That tropical forest appears in a 100 - 200 km broad strip from Natal to Porto Alegre along the Brazilian coast. The evergreen rain forest shows a very uniform structure with decreasing floral diversity towards the south (Klein 1961). Atlantic pluvial forest is found in Santa Catarina on the Serra Geral slopes up to 700 - 800 m and on the Serra do Mar at even higher altitudes. The 30 - 35 m high, very diverse, multi-layer forest is composed of characteristic taxa such as *Sloanea guianensis*, *Ocotea*

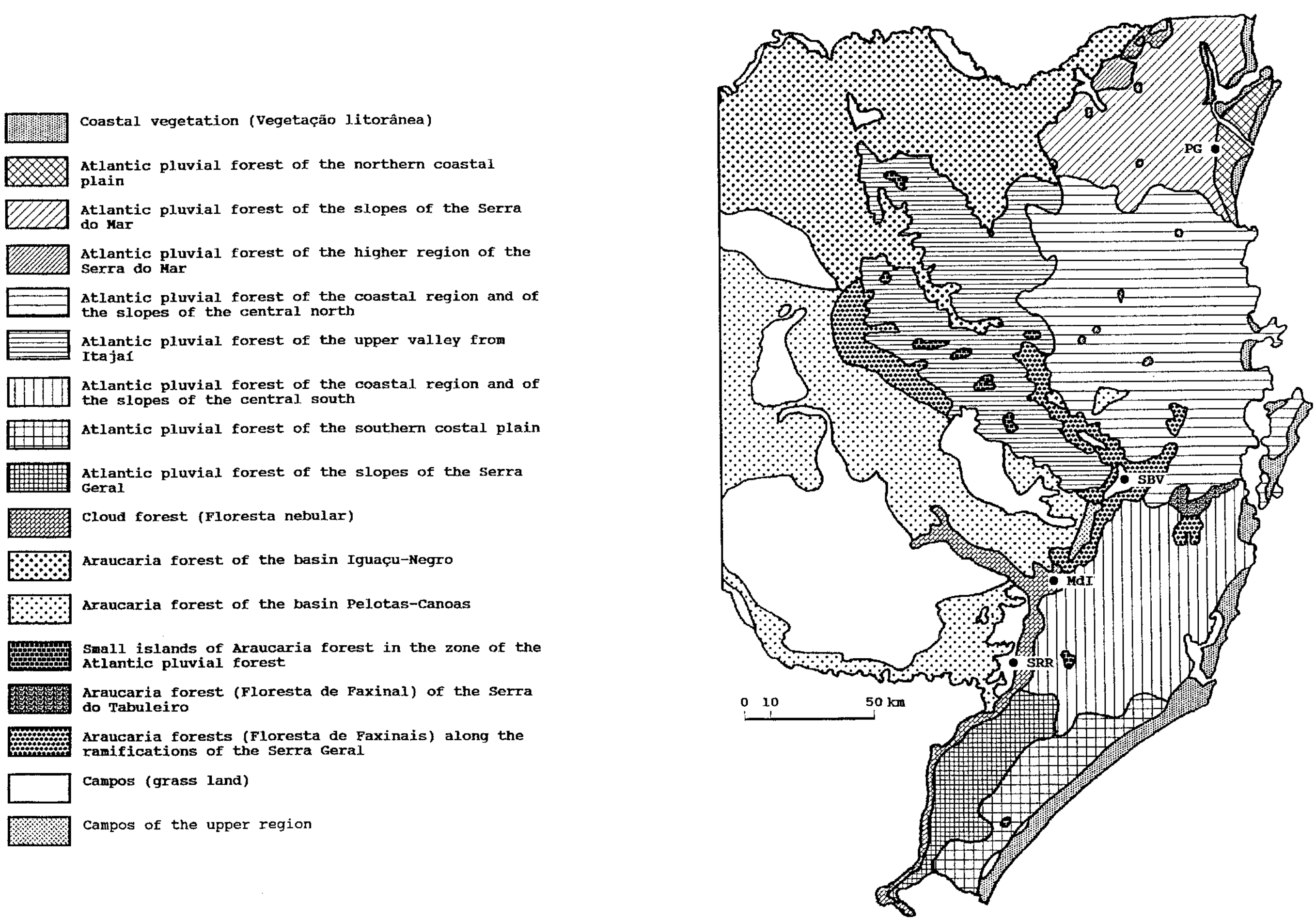


Fig. 2. Vegetation map of east Santa Catarina (according to Klein 1978) and with the location of the study area

sp., *Alchornea triplinervia*, *Ficus organensis* and *Euterpe edulis*. The rain forest is rich in lianas, tree ferns and epiphytes.

Along the coastal mountains of the Serra Geral, there is a cloud forest zone (*Floresta nebular*) at about 1200 m a.s.l. The dense forest is composed of medium high trees such as *Weinmannia humilis*, *Siphoneugena reitzii*, *Myrceugenia euosma*, *Drimys brasiliensis*, *Ilex microdonta* and *Berberis kleinii*. *Gunnera manicata* is a typical member of the cloud forest.

In the south Brazilian highlands, multi-layer *Araucaria* forests (*Florestas de Araucária*) dominate. In the states of São Paulo, Rio de Janeiro and Minas Gerais, only little islands of this forest exist (Hueck 1953). In eastern Santa Catarina, five subzones are significant with the most important species including *Araucaria angustifolia*, *Ocotea pulchella*, *Sloanea lasiocoma*, *Ilex paraguariensis* and *Mimosa scabrella*.

The *campos* (grassland) forms a mosaic with the *Araucaria* forests. The vegetation is mainly composed of Poaceae, Cyperaceae and Asteraceae. A "*campos limpo*" (clean grassland) and a "*campos sujo*" (dirty grassland) are distinguished. In the *campos sujos*, there is a shrub vegetation formed by Asteraceae (*Baccharis gaudichaudiana*, *B. uncinella*) and Apiaceae (*Eryngium* sp.). The *campos* of the upper region, which is found in the zone of the cloud forest (about 1600 m a.s.l.) can also be distinguished.

With the beginning of the intense colonization in Santa Catarina during the 19th and 20th centuries, large areas of the *Araucaria* forests and the Atlantic pluvial forests were cleared. Today it is difficult to say which area of the highland *campos* is natural and which is anthropogenic. Once, the Atlantic pluvial forest covered one third of Santa Catarina. Today only small remnants are left. In 1951, the cloud forest completely disappeared due to a nearby fire. During the last decades, some areas have been reafforested mainly with *Pinus elliottii* and *Eucalyptus*.

Material and methods

The profiles for the palynological work and radiocarbon dating were obtained on May 4th, 1989 (Serra do Rio Rastro), October 12, 1989 (Poço Grande), December 3rd, 1989 (Serra da Boa Vista), December 4th, 1989 (Morro da Igreja) and December 5th, 1989 (Serra do Rio Rastro). The upper parts of the profiles were mostly obtained in 20 cm long plastic boxes. The main parts of the profiles were taken with a Dachnowski corer.

Poço Grande profile

The profile begins 5 cm below the turf. Due to a change in the ownership of the Ranch Nutrimental, the author was unable to finish coring.

0 - 50 cm	light grey brown fine detritus mud (16 - 50 cm darker), with wood, plant rootlets at 5 cm depth
50 - 78 cm	light brown, peaty detritus mud
78 -133 cm	dark brown to black, decomposed and unconsolidated carr peat, with wood; 82 - 92 cm: like 50 - 78 cm
133 -149 cm	transition to peaty detritus mud
149 -211 cm	grey fine detritus mud; 149 - 166 cm: some finely laminated peaty layers; 169 - 172 cm: brown peat layer
211 -243 cm	dark grey fine detritus mud
243 -310 cm	light brown fine sand
310 -320 cm	dark grey fine detritus mud; 318 - 320 cm: peaty layer
320 -468 cm	dark grey brown, peaty detritus mud, with wood
468 -587 cm	dark brown to black carr peat, with wood

Serra da Boa Vista profile

0 - 7 cm	brown, very weakly decomposed peat, with *Sphagnum*
7 - 25 cm	dark brown, decomposed peat, with some rootlets
25 - 41 cm	dark brown, compact, almost completely decomposed peat, with some rootlets
41 - 67 cm	dark grey to black, very compact, totally decomposed peat with fine sand; 50 - 52 cm: 1 cm thick lenses with a higher mineral content
67 -135 cm	dark grey brown, clayey fine sand, with wood
135 -140 cm	dark grey fine sand, poor in organic matter; rocky subsurface at 140 cm.

Morro da Igreja profile

0 - 16 cm	brown, very weakly decomposed peat with *Sphagnum*
16 - 31 cm	dark brown, decomposed peat, with some rootlets
31 - 43 cm	dark brown, compact, almost completely decomposed peat, with fine roots
43 -142 cm	black, very compact, totally decomposed peat, with some rootlets (at 70 cm depth)
142 -144 cm	transition to dark grey clayey fine sand; rocky subsurface at 149 cm

Serra do Rio Rastro profile

The water content in the upper part of the peat layer prevented the recovery of good material for examination. The profile begins below 30 - 40 cm thick moist *Sphagnum*.

0 - 8 cm	dark brown, weakly decomposed and unconsolidated peat, with roots and wood
8 - 30 cm	black, compact, almost completely decomposed peat, with rootlets
30 -159 cm	black, compact, totally decomposed peat, with some rootlets (at 80 cm depth)
159 -223 cm	dark grey, clayey fine sand, with wood; 162-223 cm: with small light-grey clayey stones; 193 - 197 cm: more peaty
223 -	clay on rocky subsurface

Laboratory work was carried out mainly according to Beug (1957). At first the samples were treated for one day (minimum) with 50% HF. The samples were not treated with KOH to allow for a good centrifugation. All the samples were acetolysed and mounted in a glycerin gelatin medium.

The largest part of about 270 different pollen and spore types were identified using the author's own reference collection containing about 1400 Brazilian taxa, and with south American published descriptions. For the latter pollen morphological descriptions and illustrations see Behling (1993).

The pollen counts are a minimum of 508 in the Poço Grande profile (average value of pollen and spores 1383), 979 in the Serra da Boa Vista profile (average value 3683), 1215 in the Morro da Igreja profile (average value 2353) and 1203 in the Serra do Rio Rastro profile (average value 5917). The pollen diagrams are based on the total sum of pollen (without spores). Pollen of aquatics which only display small values are included in the sum.

The pollen diagrams were drawn using an Atari ST 1040 computer and a Siemens HPGL A3 Plotter using the plotting program PPLOT 10 (Steffan and Dupont 1988). Four different broad hatchings were used for the pollen diagrams. In small hatched curves, the horizontal scale is magnified five times compared with very small hatched curves. Middle hatched curves are magnified ten times and broad hatched curves are magnified twenty times.

The pollen curves are grouped according to vegetation zones (*campos*, *Araucaria* forests, Atlantic pluvial forests, cloud forest, other types). This has been done except for the Poço Grande diagram, where the highland vegetation is poorly represented. Sometimes it was difficult to assign certain pollen types to a single vegetation zone. Pollen types of taxa which occur in more than one vegetation zone are listed according to their main distribution today. Taxa without such a main distribution are to be found among the category of "others". Less important, unknown and single finds of pollen and spores are not plotted in the diagrams.

Radiocarbon data

Radiocarbon dates were supplied by the Hanover 14C Laboratory (Niedersächsisches Landesamt für Bodenforschung), as set out in Table 1.

Table 1. Radiocarbon dates from the sites, in uncalibrated radiocarbon years

Poço Grande profile		
127 -132 cm	Hv 17559	3525 ± 175 B.P.
214 -219 cm	Hv 17560	4230 ± 185 B.P.
327 -332 cm	Hv 17561	4265 ± 190 B.P.
507 -514 cm	Hv 17562	4680 ± 150 B.P.
Serra da Boa Vista profile		
31 - 35 cm	Hv 17563	3460 ± 185 B.P.
45 - 50 cm	Hv 17564	6930 ± 195 B.P.
61 - 65 cm	Hv 17565	14,105 ± 510 B.P.
131 -135 cm	Hv 17566	13,905 ± 295 B.P.
Morro da Igreja profile		
40 - 44 cm	Hv 17557	60 ± 120 B.P.
140 -144 cm	Hv 17558	10,200 ± 275 B.P.
Serra do Rio Rastro profile		
74 - 79 cm	Hv 17554	2385 ± 225 B.P.
150 -155 cm	Hv 17555	6410 ± 190 B.P.
215 -220 cm	Hv 17556	11,210 ± 385 B.P.

Pollen analytical results and vegetation development

For comparison between fossil and modern pollen rain, an attempt has been made to study surface samples from the highland areas near to the core sites. Regrettably, they contained only small quantities of highly corroded pollen grains. However, the top pollen spectra of the Serra da Boa Vista and Morro da Igreja profiles are surface samples that appear to represent the pollen rain of the modern vegetation around the sites quite well.

The pollen diagrams have been zoned according to pollen stratigraphic criteria. Pollen zones (PZ) are units of the pollen diagram which reflect periods of stable conditions in the plant cover. Small changes within the PZ were used for defining subzones.

As the highland core sites are close together, vegetation developments seen in the pollen diagrams can be correlated with one another. Therefore a highland pollen zoning system beginning with PZ 1 is used. For the lowland type of vegetation development, a zonation beginning with PZ A is used. An attempt will be made to correlate both zonations with the help of radiocarbon dates.

Hiatuses are evident in some of the sequences and their duration is insufficiently known. Therefore interpretations of vegetation and climate development are necessarily preliminary. Parts of the profiles in which hiatuses may be expected are indicated with a question mark in Fig. 3.

Pollen diagram Serra da Boa Vista (Fig. 4)

The peat bog is situated in the *campos* zone. As well as the *campos* vegetation itself, the site is open to pollen transport from areas nowadays occupied by *Araucaria* forests, Atlantic pluvial forests and even from the cloud forest belt.

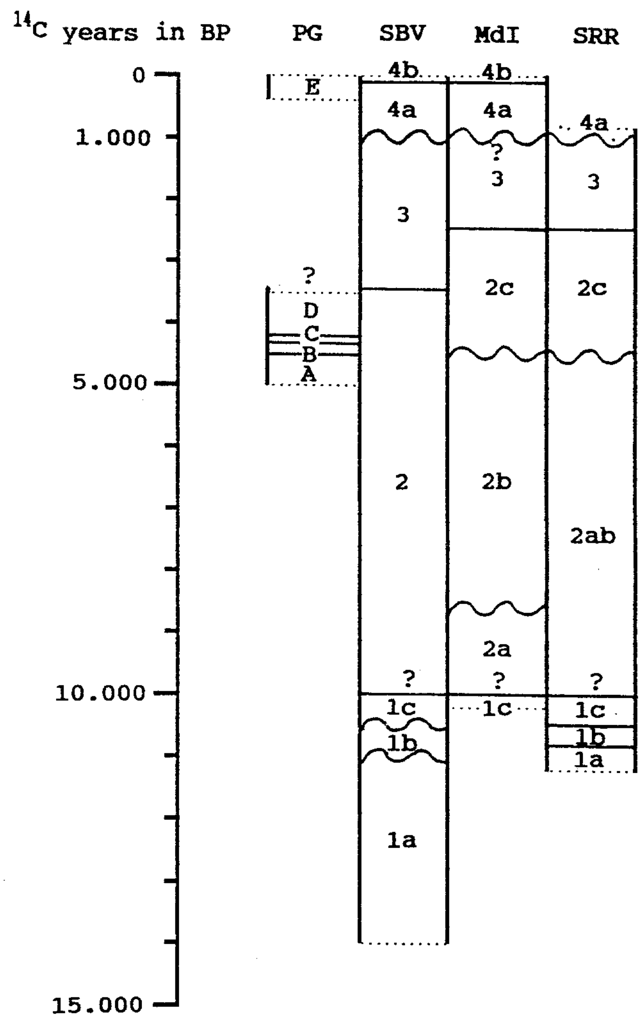


Fig. 3. Palynological and radiocarbon age correlations of the profiles Poço Grande (PG), Serra da Boa Vista (SBV), Morro da Igreja (MdI) and Serra do Rio Rastro (SRR)

PZ 1a Older campos zone (59 - 139 cm). Two radiocarbon dates give an almost identical age, namely 13,905 ± 295 B.P. (131 - 135 cm) and 14,105 ± 510 B.P. (61 - 65 cm).

In PZ 1a, the *campos* group is represented by about 90% of the total pollen, mainly by Poaceae (about 60%), Cyperaceae and Asteraceae (10% each), *Eryngium*-type, *Xyris*-type, *Eriocaulon/Paepalanthus* and *Plantago*. A dominant highland vegetation without forests can therefore be assumed for the late Pleistocene. High values of the Poaceae show the presence of *campos limpo*, and high values of *Eryngium* and *Baccharis*-type show the presence of *campos sujo*. Values of *Araucaria* forest taxa (*Mimosa scabrella*-type, *Ilex, Symplocos, Clethra* and the tree fern *Dicksonia sellowiana* are low. Obviously the typical members of *Araucaria* forests, as in this region today, were already represented in the late Pleistocene and have rarely occurred in the valleys.

Within the Atlantic pluvial forests group, the values of *Alchornea, Urticales, Celtis* and *Weinmannia*-type are low, while Myrtaceae values are high. *Didymopanax, Meliosma* and *Cecropia* occur in the final part of PZ 1a only. Several tropical taxa, which are not frost resistant, were probably unable to grow in the lowland during the time represented by PZ 1a. The appearance of a few tropical elements of the lowland of Santa Catarina, including *Alchornea*, Urticales and Palmae, is certain. At that time, Myrtaceae played an important role and obviously dominated the Atlantic coastal plain. The cloud forest, represented by small values of *Drimys brasiliensis, Mimosa taimbensis*-type and *Gunnera manicata*, were only poorly developed in PZ 1a and also in the following PZ.

Percentages of *Rapanea* ("others" group) are about 1%. *Rapanea* pollen grains are supposed to come from the lowland forests. Melastomataceae values are relatively high. Several taxa, which occur in *Araucaria* forests and in the Atlantic pluvial forests (*Allophylus, Matayba, Styrax, Lamanonia speciosa*-type, *Sebastiania commersoniana, S. brasiliensis*), are rarely represented. Pollen grains of *Alnus* and *Ephedra* were found in almost all pollen zones and they are supposed to derive from the Andes. Today, *Alnus* occurs in south America from the northern and middle Andean region to the southern tropics (Schmucker 1942). There are single pollen grains of *Ephedra tweediana*-type. Nowadays, *Ephedra tweediana* occurs in southern Rio Grande (Rambo 1954b).

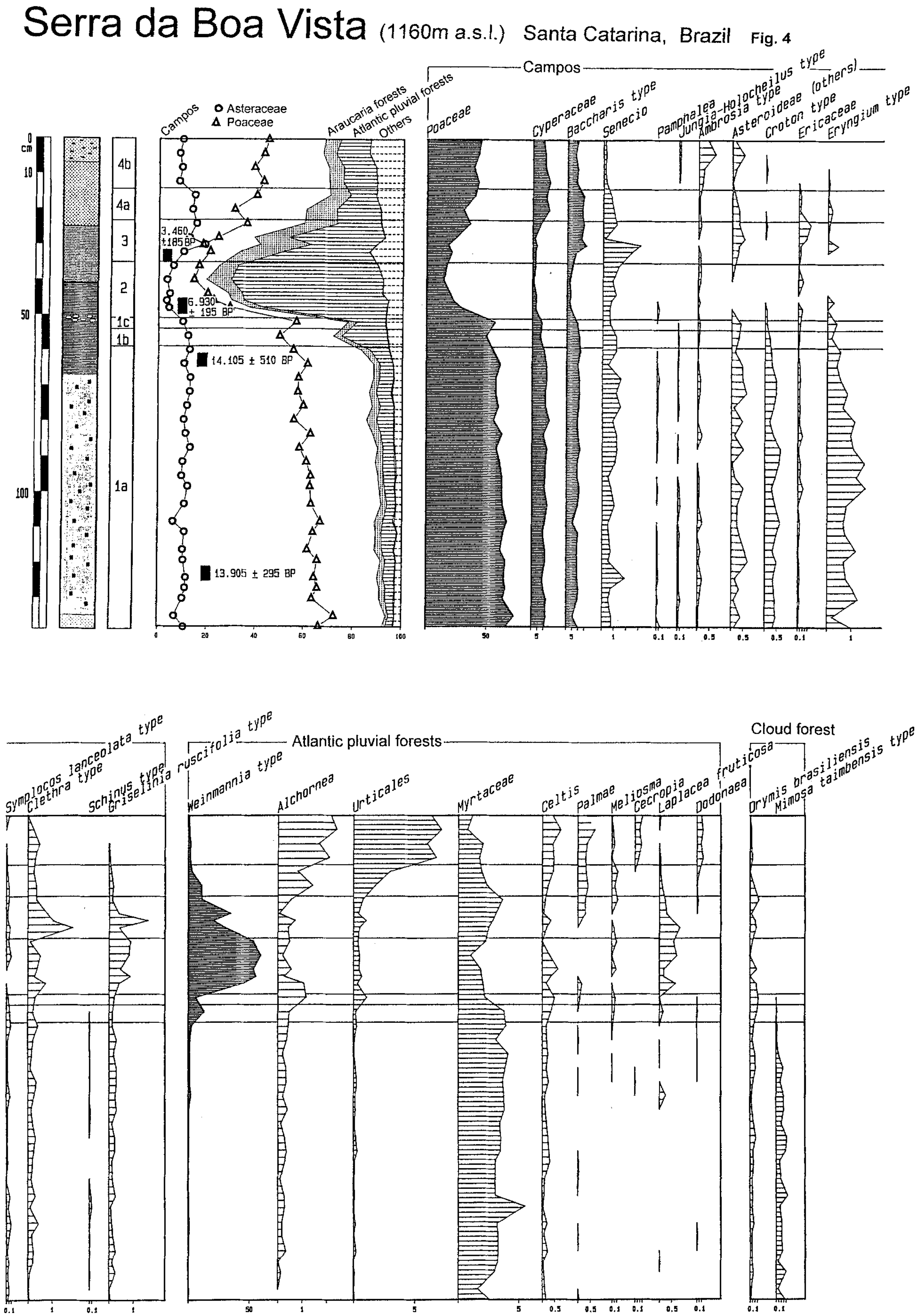
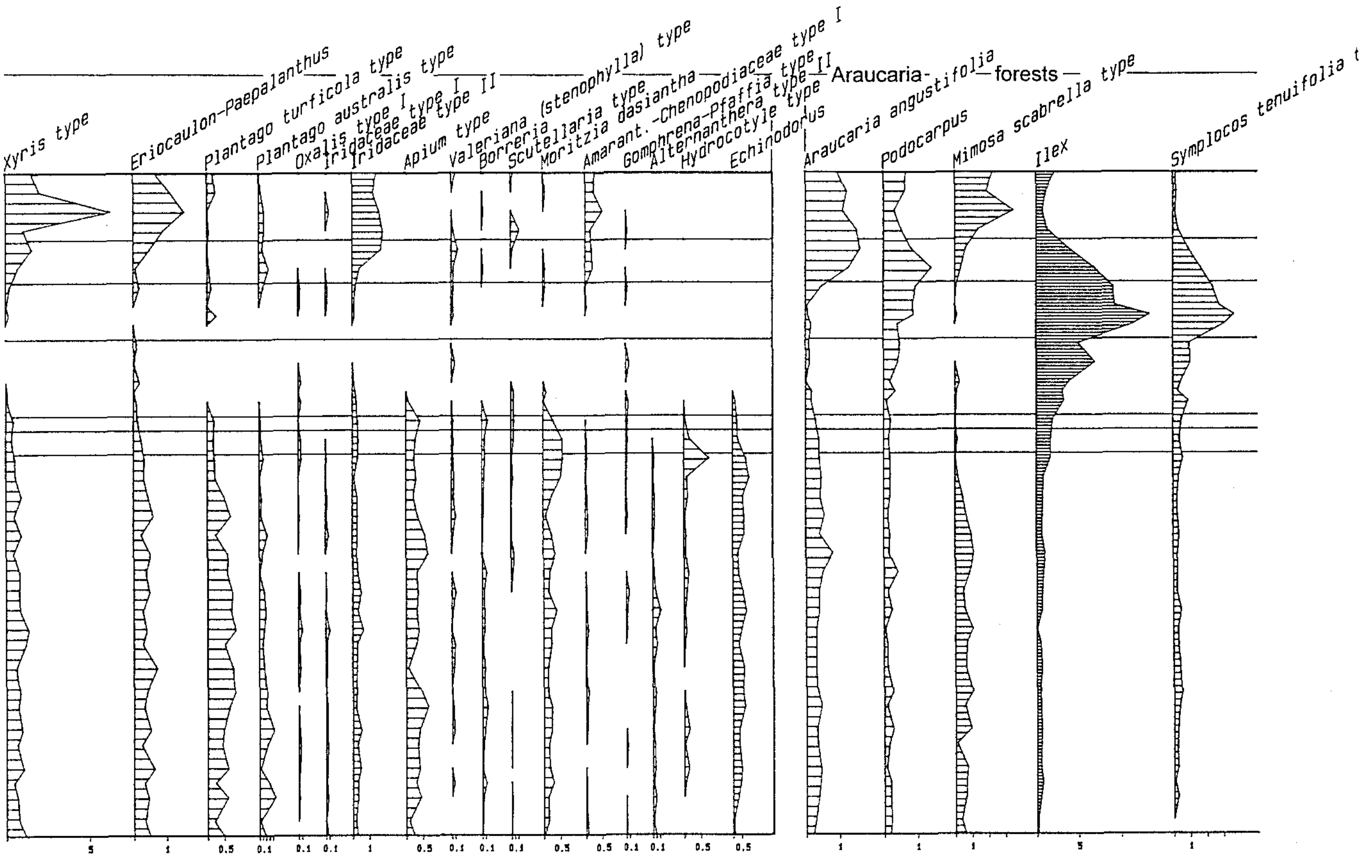
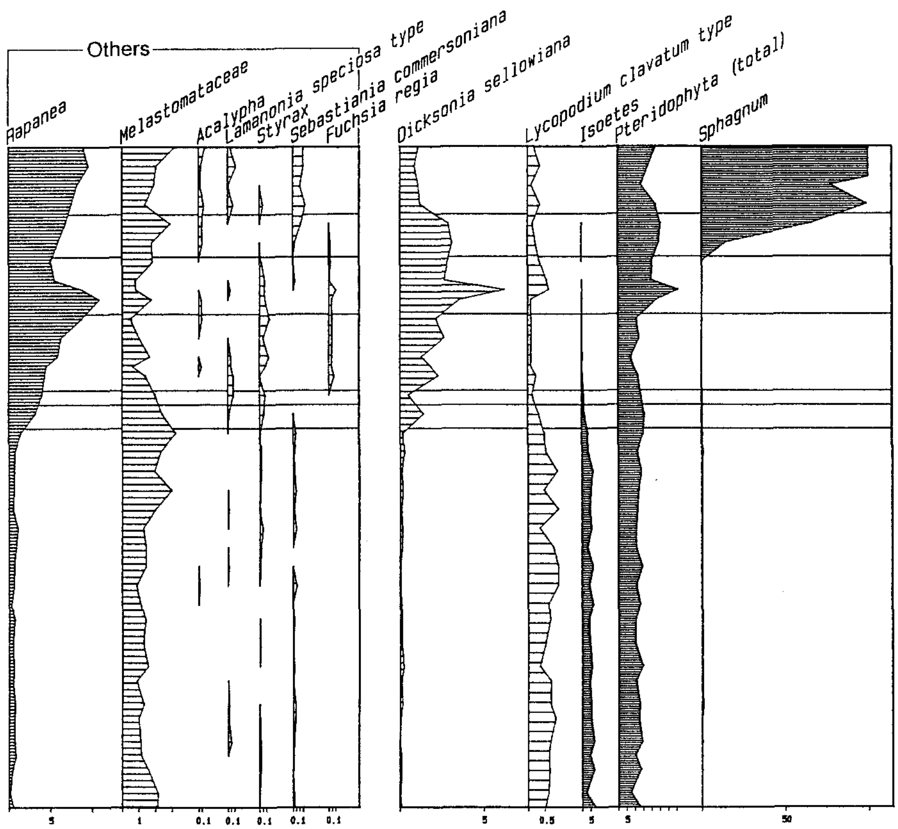


Fig. 4. Pollen diagram Serra da Boa Vista





analys: H. Behling

Zone boundary 1a/1b: Decrease of Poaceae and increase of *Weinmannia*-type.

PZ 1b Middle campos zone (54 - 59 cm). This PZ (and PZ 1c, too) is represented by one spectrum only, making the interpretation very tentative. The percentages of the *campos* vegetation taxa (mainly Poaceae) decrease. Percentages of *Weinmannia*-type (14%), *Laplacea fruticosa, Ilex, Rapanea, Styrax* and *Dicksonia sellowiana* are slightly higher than in the previous PZ while the values of *Araucaria angustifolia, Podocarpus* and *Symplocos tenuifolia*-type remain stable. The minor expansion of forests was possibly caused by better climatic conditions that are reflected in the especially high values of *Weinmannia* (in this case mainly *W. paulliniifolia*, a member of the Atlantic pluvial forest).

Zone boundary 1b/1c: Increase of Poaceae and decrease of *Weinmannia*-type.

PZ 1c Younger campos zone (51 - 54 cm). There is no radiocarbon date, but by assuming a constant sediment accumulation rate, the PZ can be dated at approximately 10,000 to 10,500 B.P. The *campos* representation (mainly Poaceae) is higher than before. Values of *Weinmannia*-type (10%), *Laplacea fruticosa* and *Dicksonia sellowiana* decrease and percentages of *Ilex* and *Rapanea* increase. Percentages of *Alchornea* and Urticales are higher than in the previous PZ. This may indicate a decrease in temperature, and the retreat of the taxa of higher altitudes (*Weinmannia, Laplacea fruticosa*). Taxa of lower altitudes (*Alchornea,* Urticales, *Ilex, Rapanea*) were able to continue to maintain their distribution.

Zone boundary 1c/2: Decrease of Poaceae and a corresponding increase of *Weinmannia*-type.

PZ 2 Weinmannia zone (35 - 51 cm). The increase of the *Weinmannia*-type curve compared with that of the *campos* vegetation indicates that a thorough afforestation had taken place by 6930 ± 195 B.P. For that level, an age near to the Pleistocene-Holocene boundary was expected. For an explanation, one may point to a hiatus or to an extremely low sedimentation rate.

PZ 2 is characterized by high percentages of the Atlantic pluvial forest taxa with domination by *Weinmannia paulliniifolia*, and by low *campos* values (20% - 25%). Most curves of the *campos* members are discontinuous (except Poaceae, Cyperaceae, *Baccharis*-type and *Senecio*). It is probable that the *campos* was dominant only in the higher region of Serra da Boa Vista. Among the *Araucaria* forest taxa, the values of *Araucaria angustifolia* decrease. *Ilex* values increase and the values of *Podocarpus*, *Symplocos tenuifolia*-type and *Clethra*-type are slightly higher than in PZ 1. This indicates a minor expansion of *Araucaria* forests. Frequent occurrences of *Griselinia ruscifolia*-type pollen grains may be mentioned. The semi-parasite *G. ruscifolia* is associated with *Araucaria angustifolia* and other tree taxa (Klein 1971).

Atlantic pluvial forest elements are seen in the values of *Weinmannia*-type which increase up to 50% which means that *W. paulliniifolia* occurred during this time in the forests from low altitudes up to the *campos* belt. *Laplacea fruticosa* also expanded into higher regions than today. Myrtaceae values continue to decrease. After their first rise in the PZ 1c, the values of *Alchornea* and Urticales are low. *Alchornea* and Urticales taxa probably occurred farther away from the Serra da Boa Vista. In the group of "others", the curve of the pioneer *Rapanea* continuously increases. This demonstrates the expansion of forests in the highlands. Pollen grains of *Fuchsia regia* found here for the first time indicate that forests occurred near to the core site.

Zone boundary 2/3: Increase of Poaceae and a strong decrease of *Ilex* and *Symplocos tenuifolia*-type.

PZ 3. Ilex-Symplocos zone (23 - 35 cm). At a depth of 31-35 cm, the beginning of PZ 3 has been dated to 3460 ± 195 B.P. The values of the *campos* members increase considerably, which indicates a spreading of the campos zone compared with the forest, probably caused by colder climate conditions. *Araucaria* forest taxa such as *Ilex, Symplocos tenuifolia*-type, *Clethra*-type and *Griselinia ruscifolia*-type display their highest representation here. Most probably under the colder climate conditions, *Araucaria* forests were better able to grow in favourable localities, such as valleys and slopes that were previously occupied by *Weinmannia* (PZ 2).

Within the group of Atlantic pluvial forest taxa, it is difficult to explain the increase of *Weinmannia*-type. It may be caused either by the colder climate or by the low competitive pressure from *Ilex*, *Symplocos* and *Clethra*. *Alchornea* and Urticales values remain low. Myrtaceae and Palmae are more frequent than in the previous PZ. Low *Fuchsia regia* values and an increase of *Rapanea* percentages point to a spreading of highland forests at the end of PZ 3.

Zone boundary 3/4a: The *Araucaria angustifolia* curve exceeds 1%.

PZ 4a. Older Araucaria forest zone (14 - 23 cm). The representation of the *campos* group increases continuously. Poaceae and Cyperaceae values are higher than in PZ 3. Spores of *Sphagnum* increase for the first time in this zone, suggesting a strong expansion of *Sphagnum* across the peat bog. For the first time, there is an increase of the *Araucaria angustifolia* curve, although the values remain smaller than 2% (*Araucaria* values reach 10% in the region of Morro da Igreja and Serra do Rio Rastro, see Figs. 5 and 6). This is followed by a change in the *Araucaria* forest composition indicated by a rise of *Podocarpus* (maximum values 1.4%) and of the *Mimosa scabrella*-type curve, and by a decrease of *Ilex* and *Symplocos tenuifolia*-type. Among the Atlantic pluvial forest members, the curves of *Alchornea* and Urticales strongly increase. The first pollen grains of *Didymopanax* and *Virola oleifera* have been found here. Myrtaceae values are lower than in PZ 3 and the curve of *Weinmannia*-type continuously decreases. This is followed by an expansion of important rain forest taxa, which probably came from eastern valleys and from the upper valleys of the river Itajaí on the northwest side, and migrated towards the Serra da Boa Vista.

Zone boundary 4a/4b: Decrease of the *Araucaria angustifolia* curve.

PZ 4b. Younger Araucaria forest zone (0 - 14 cm). PZ 4b strongly indicates human influence. Pollen grains of *Pinus* (0 - 8 cm depth) come from very modern plantations. PZ 4b therefore does not represent more than about 100 years. *Campos* values are still high. The *Xyris*-type curve has a remarkable maximum. Values of *Eriocaulon-Paepalanthus* are high. Decreased values of *Araucaria, Ilex, Symplocos tenuifolia*-type and *Dicksonia* (group of *Araucaria* forests) and highest values of *Alchornea* and Urticales (important members of the Atlantic pluvial forests) give evidence of a major expansion of Atlantic pluvial forest and also of a deforestation of *Araucaria* forest. The percentages of *Celtis*, Palmae and *Cecropia* are also somewhat higher than before. *Laplacea fruticosa* and *Weinmannia*-type values are very low and the first pollen grains of *Hyeronima* were found. Obviously, the important rain forest species reached their present distribution very recently.

Pollen diagram Morro da Igreja (Fig. 5)

The studied peat bog is situated in the *campos* of the upper region at an altitude of 1800 m a.s.l. This vegetation is therefore largely represented in the diagram by its pollen rain. There is less evidence of the *Araucaria* forests, the Atlantic pluvial forests and the cloud forest. The cloud forest is close to the bog on the steep slopes.

PZ 1c Younger campos zone (142 - 144 cm). The profile starts at 10,200 ± 275 B.P. PAZ 1c covers only one sample. The situation of the vegetation corresponds with PZ 1c in the Serra do Rio Rastro profile. The percentage of *campos* taxa is 86%. The small Poaceae value (35%) is especially striking. This indicates that the site was even more forested than the Serra do Rio Rastro (the same situation as today).

Zone boundary 1c/2a: Decrease of the Myrtaceae curve and increase of *Alchornea* and Urticales.

PZ 2a. Late campos zone I (124 - 142 cm). Assuming a constant rate of sedimentation, the beginning of PZ 2a is about 10,000 B.P. PZ 2a is characterized by higher values of *Araucaria* elements. The percentage of *campos* taxa decreases from 85% to 70%, mainly due to the decrease of Poaceae. This must have been caused by the expansion of forests. The values of *Eryngium*-type, *Xyris*-type, *Eriocaulon-Paepalanthus* and *Plantago turficola*-type are high. These herbaceous taxa must have been widespread in the *campos* of the upper region. Higher percentages, especially of *Araucaria angustifolia, Mimosa scabrella*-type and *Dicksionia sellowiana,* provide evidence for a minor expansion of *Araucaria* forests but, at that time, only in this area under study. This was probably an expansion out of the deep valleys of the mountainous region of Morro da Igreja. In the Holocene, there was a significant change in the Atlantic pluvial forests (decrease of the Myrtaceae curve, increase of *Alchornea* and Urticales curves). The Myrtaceae were replaced by *Alchornea*, Urticales and other new immigrant species (*Tetrorchidium rubrivenium*) and many tropical taxa (Palmae, *Meliosma, Didymopanax*). The increase in the values of *Weinmannia*-type (in this case mainly *W. humilis*) and *Gunnera manicata* provide evidence for the formation of the cloud forest at that time. Of the group "others", only *Rapanea* has high values.

Zone boundary 2a/2b: Decrease of *Araucaria angustifolia* values.

PZ 2b. Late campos zone II (100 - 124 cm). Characteristic for this PZ is an increase in percentages from *campos* taxa (higher values of Poaceae) and the small decrease in *Araucaria* forest values. *Araucaria angustifolia* and *Podocarpus* may have retreated to the moist valleys. The *Celtis* and Palmae values of the Atlantic pluvial forests are remarkably higher than in the previous PZ. The first pollen grains of *Hyeronima* appear in this PZ. In the cloud forest group, the *Weinmannia*-type values decrease. The percentages of *Gaultheria ulei* are higher.

Zone boundary 2b/2c: Decrease of *Eryngium*-type curve and small decrease of *Gunnera manicata* values.

PZ 2c. Late campos zone III (76 - 100 cm). This PZ is characterized by an increase of the values of the upper region *campos* taxa and by changes in the *campos* vegetation. There is an increase in Poaceae and a decrease in Asteraceae values. *Jungia-Holocheilus, Trixis, Oxalis* and *Alstroemeria* show their highest values and their greatest expansion. Values of *Eryngium*-type and *Eriocaulon/Paepalanthus* show a strong decrease. The *Sphagnum* curve has its highest point (there are no high values of *Sphagnum* at that time in other studied bogs), followed by a very high maximum of *Plantago turficola*-type (15%). *Araucaria* forest taxa values are generally unchanged compared to the previous PZ. The percentages of the Atlantic pluvial forests decrease from 12% to 7%, caused by the corresponding increase of the *campos* taxa values. In the cloud forest group of taxa, *Weinmannia*-type values are higher. *Gunnera manicata* is less frequent. Among the "others", In PZ 2c, two pollen grains of *Notofagus dombeyi*-type were found (further finds include a single pollen grain in the profile Morro da Igreja, PZ 3; two in Serra do Rio Rastro, PZ 3; and two in Serra da Boa Vista, PZ 4a). The south American distribution of *Notofagus* is in the southern Andes (Schmucker 1942). These pollen grains must have been transported over more than 2000 km.

Zone boundary 2c/3: High values of Poaceae, *Weinmannia*-type, *Mimosa scabrella*-type, low values of *Gunnera manicata* and *Eryngium*-type.

PZ 3. Late campos zone IV (43 - 76 cm). The *campos* of the upper region is dominant (especially indicated by the increase of the Poaceae values). The cooler climate may have caused an expansion of the *campos* area into the 1800 m high Morro da Igreja. Several curves (*Pamphalea, Trixis, Eriocaulon-Paepalanthus*) fade out. *Croton* and *Lycopodium clavatum*-type values increase and the first pollen grains of Ericaceae and *Trifolium* appear. This indicates an important change in the *campos* vegetation. With the very low values of *Eryngium*-type and

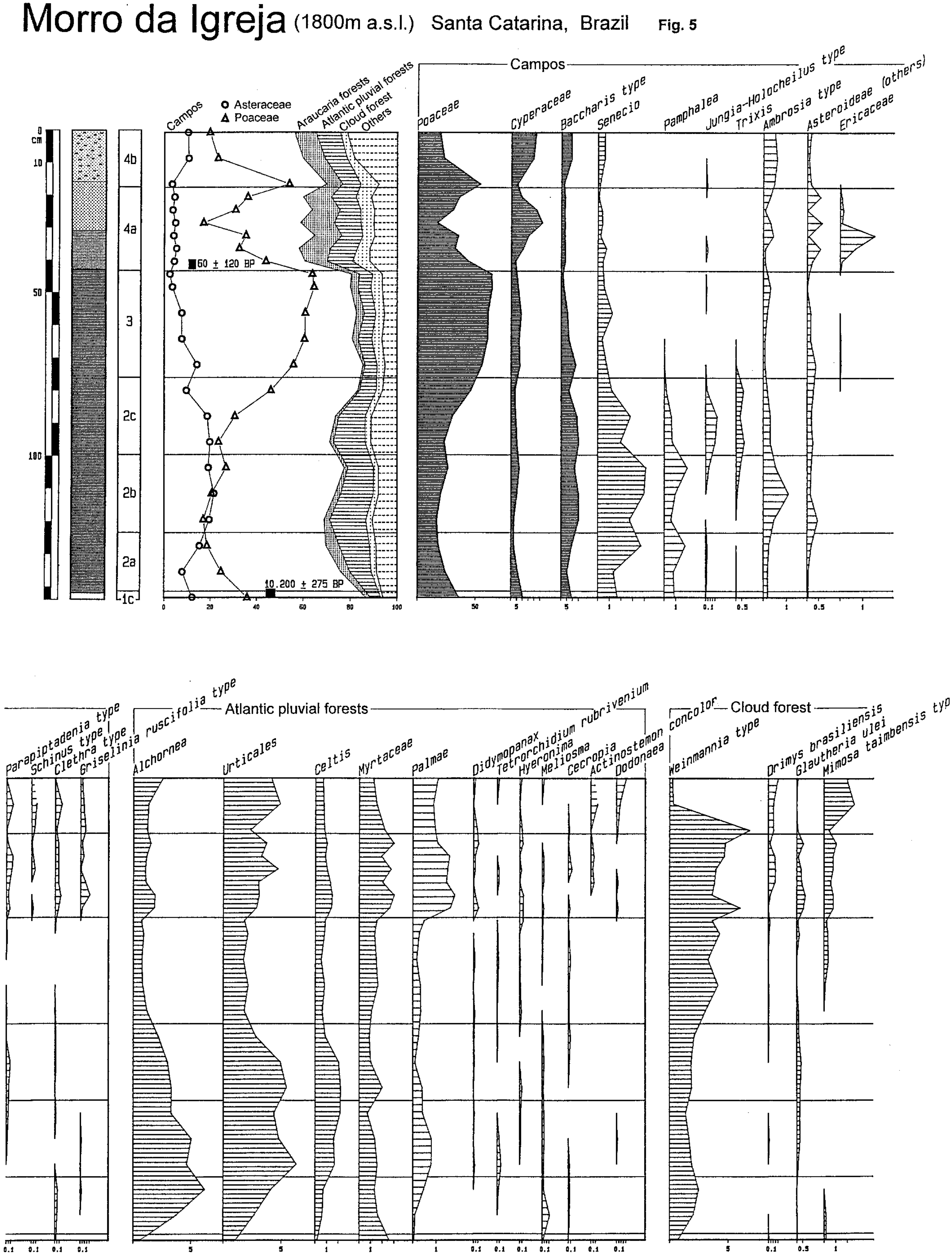
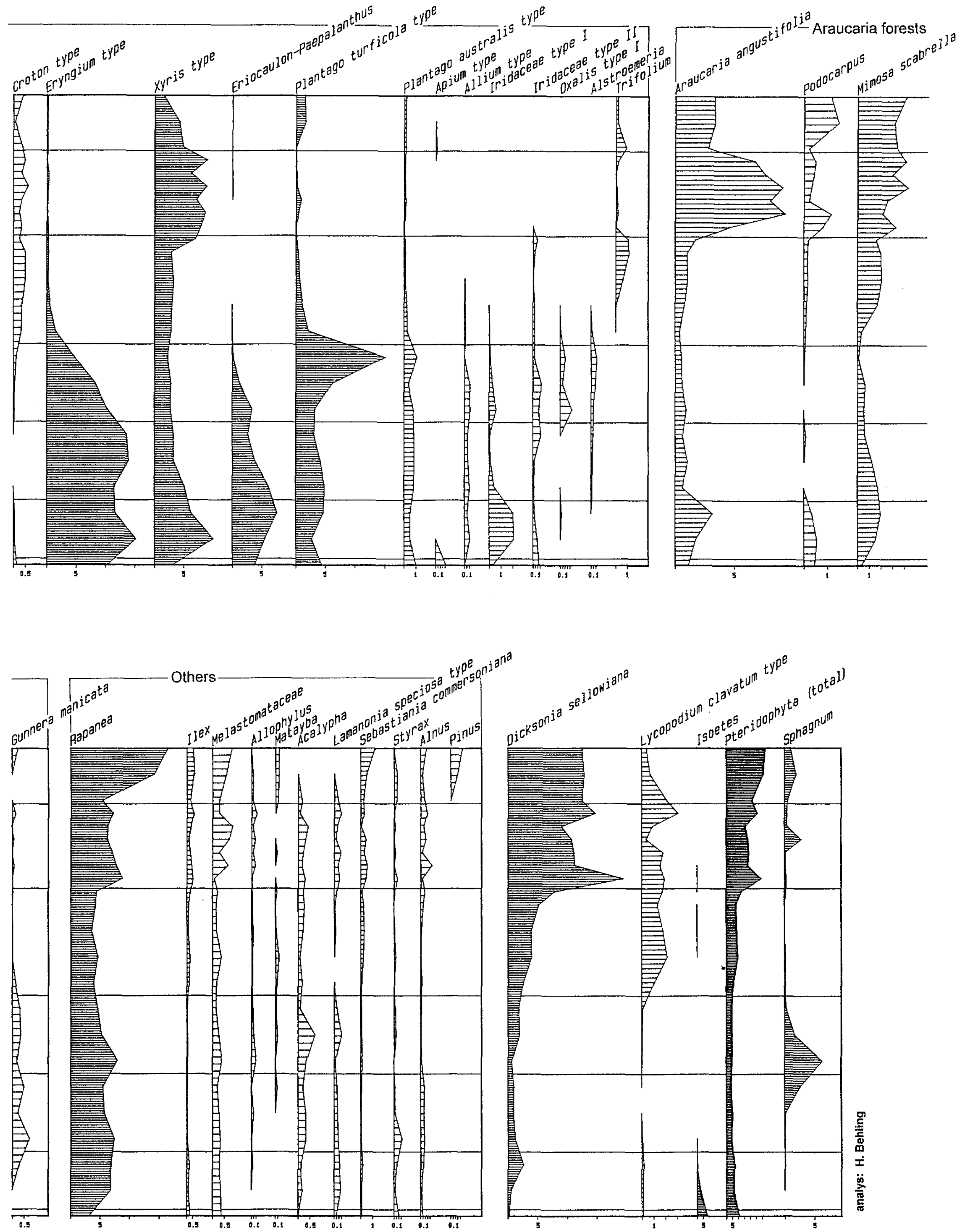


Fig. 5. Pollen diagram Morro da Igreja


Croton type
Eryngium type
Xyris type
Eriocaulon-Paepalanthus
Plantago turficola type
Plantago australis type
Apium type
Allium type
Iridaceae type I
Iridaceae type II
Oxalis type I
Alstroemeria
Trifolium
Araucaria forests
Araucaria angustifolia
Podocarpus
Mimosa scabrella
Gunnera manicata
Others
Rapanea
Ilex
Melastomataceae
Allophylus
Matayba
Acalypha
Lamanonia speciosa type
Sebastiania commersoniana
Styrax
Alnus
Pinus
Dicksonia sellowiana
Lycopodium clavatum type
Isoetes
Pteridophyta (total)
Sphagnum
analys: H. Behling

the high values of Poaceae, the *campos* can be characterized as "*campo limpo*". *Mimosa scabrella*-type and *Dicksonia sellowiana* curves increase. Curves of *Podocarpus* and *Araucaria angustifolia* are still more or less on the same level. It is probable the there was only a moderate expansion of *Araucaria* forests at that time. Higher values of *Weinmannia*-type provide evidence of a more important expansion of *W. humilis* in the cloud forest.

Zone boundary 3/4a: Strong increase of the *Araucaria angustifolia* curve.

PZ 4a. Older Araucaria forest zone (17 - 43 cm). The radiocarbon date at the beginning of the PZ is 60 ± 120 B.P. Present-day plant roots have probably influenced this radiocarbon age and therefore it is not possible to date the beginning of the PZ. In relation to the sedimentation rate determined from PZ 4b, it will probably not be older than 1000 years. Characteristic for PZ 4a is the large expansion of *Araucaria* forests (mainly *A. angustifolia*) combined with the return of the *campos* (especially the Poaceae value). The percentages of *A. angustifolia* increase from 1% to 10%. With this remarkable expansion of *Araucaria*, we have an expansion of the accompanying taxa (*Podocarpus, Mimosa scabrella*-type, *Schinus*-type, *Parapitadenia*-type, *Clethra*-type, *Griselinia ruscifolia*-type, *Dicksonia sellowiana*). Palmae with their highest values in this PZ were more frequent in the Atlantic pluvial forests. Among the cloud forest taxa, the values of *Weinmannia*-type, *Mimosa taimbensis*-type, *Drimys brasiliensis* and *Gaultheria ulei* are higher than in PZ 3. In the group "others", there are high values of *Rapanea*, suggesting that in the highland there was an expansion of this pioneer taxon.

Zone boundary 4a/4b: Decrease of the *Araucaria angustifolia* curve.

PZ 4b. Younger Araucaria forest zone (0 - 17 cm). This PZ covers approximately only the last 100 years. This is evident from strong signs of human impact. The percentages of *Araucaria angustifolia* are only 3% (after 10% in PZ 4a), which is a result of severe logging of *Araucaria*, and caused *Podocarpus, Mimosa scabrella* and especially *Rapanea* to become more frequent in the *Araucaria* forests. The high maximum of Poaceae at the beginning of PZ 4b may be caused by the cutting down of *Araucaria*. Values of *Dicksonia sellowiana* are still continuously high. Between 8 and 16 cm, we note a complete decrease of the *Weinmannia*-type values, most probably caused by a big fire in 1951 in which large areas of the cloud forest on the Serra Geral were destroyed (Klein 1978). The fire evidently favoured the expansion of *Mimosa taimbensis*. In this PZ, there are (as in the Serra da Boa Vista profile) pollen grains of *Pinus* (0 - 8 cm depth) and a single pollen grain of *Zea mays* (8 cm depth).

Pollen diagram Serra do Rio Rastro (Fig. 6)

This peat bog has the same general geographical situation and vegetation as Morro da Igreja, but is located 400 m lower in altitude.

PZ 1a. Older campos zone (197 - 216 cm). The profile starts at 11,210 ± 385 B.P. The PZ is characterized by the high percentages of the *campos* taxa (about 93%), mainly represented by Poaceae (55%), Cyperaceae (15%), Asteraceae (10%), *Eryngium*-type, *Xyris*-type, *Eriocaulon-Paepalanthus* and *Plantago*. This is similar to the findings from the Serra da Boa Vista. *Araucaria* forest taxa are represented by very low values of *A. angustifolia*, *Podocarpus*, *Mimosa scabrella*-type, *Schinus*-type and *Dicksonia sellowiana*. These pollen grains were probably transported over a long distance and it is probable that *Araucaria* forests did not exist then in the area under study. For species characteristic for the Atlantic pluvial forests, only the Myrtaceae show high values. The *Weinmannia*-type, in this case mainly *W. humilis* of the cloud forest, and the *Mimosa taimbensis*-type have low values. Therefore, the cloud forest at the end of the late Pleistocene was poorly represented or absent in the region. In the group of "others", the percentages of *Rapanea* are about 1%. *Rapanea* at that time seemed to have occurred only in the lowland.

Zone boundary 1a/1b: Slight increase of the *Alchornea* and Urticales curve.

PZ 1b. Middle campos zone (186 - 197 cm). The interpolated age of this PZ is 10,500 to 10,800 B.P. *Alchornea*, Urticales, *Celtis* and Myrtaceae display higher values than before. A slight expansion of these taxa probably took place in the Atlantic pluvial forests, caused by better climatic conditions. The Myrtaceae maximum (one sample) is not significant. In the diagram from the Serra da Boa Vista, there is a high Myrtaceae maximum, without changes in the other pollen curves in PZ 1c.

Zone boundary 1b/1c: Slight decrease of the *Alchornea* and Urticales curves.

PZ 1c. Younger campos zone (159 - 186 cm). Values of Atlantic pluvial forest taxa are lower. It is more or less the same situation as in PZ 1a. The first pollen grains of *Gunnera manicata*, associated with the cloud forest, appear in this PZ.

Zone boundary 1c/2a: Decrease of the Myrtaceae curve and increase of the *Alchornea* and Urticales curves.

PZ 2ab. Late campos zone I/II (110 - 159 cm). A radiocarbon date from close to the base of PZ 2ab (150 - 155 cm) was 6410 ± 190 B.P. The limit of PZ 1c/2ab marks the change from the Late Pleistocene to the Holocene (see radiocarbon date of profile Morro da Igreja). For that level, an age about 9000 B.P. had been expected. An extremely low sedimentation rate or a hiatus of more than 2000 years may have caused this difference (see also the profile from Serra da Boa Vista). Characteristic of PZ 2ab are the significant changes in the Atlantic pluvial forests and in the *campos*, but without change of the *campos* values. Poaceae values are still continuously high, but the Cyperaceae values show a strong decrease. *Eryngium*-type values are increased. The *campos sujo* appears to have been more strongly developed. *Senecio*, *Jungia/Holocheilus*-type, *Trixis*, Cichorioideae, other Asteroideae, *Cuphea urbaniana, Vicia/Lathyrus,* *Alstroemeria* and *Oxalis* have their highest values. They were all very common at that time in the *campos*. In comparison to Morro da Igreja and Serra da Boa Vista, *Pamphalea*, *Jungia-Holocheilus*-type, *Trixis* and Cichorioideae were more frequently found in the *campos*. Indicators of *Araucaria* forest, as at Morro da Igreja, are absent. In the Atlantic pluvial forests, the change is expressed by a decrease of Myrtaceae values and an increase of *Alchornea*, Urticales and *Celtis*. It is the same situation as that described for Morro da Igreja. High values of *Gunnera manicata* combined with continuous low values of *Weinmannia*-type show a small representation of the cloud forest. In the group of "others", only the *Rapanea* curve increases. These pollen grains are apparently from the lowland.

Zone boundary 2ab/2c: Slight increase of the *Weinmannia*-type curve, decrease of the *Eryngium*-type curve and slight decrease of the *Gunnera manicata* curve.

PZ 2c. Late campos zone III (76 - 110 cm). Most of the percentages of *campos* Asteraceae taxa are lower than in the previous PZ. Only *Pamphalea* has very high percentages, frequently with a maximum of 25%. Values of *Gunnera manicata* are lower and those of *Weinmannia*-type are higher.

Zone boundary 2c/3: Higher values of *Weinmannia*-type, slight increase of the *Araucaria angustifolia* values, low values of *Gunnera manicata*.

PZ 3. Late campos zone IV (7 - 76 cm). Sediments of the PZ 2c/3 boundary were dated to 2385 ± 225 B.P. and sediments at the beginning of PZ 3 in profile Serra da Boa Vista to 3460 ± 195 B.P. This discrepancy cannot be explained yet; more investigations and radiocarbon dates are necessary. Characteristic for PZ 3 is the slight increase of the *Araucaria* forest percentages (1% to 5%) and a slight decrease of the *campos* taxa percentages (89% to 83%). *Eryngium*-type values continuously decrease and *Xyris*-type increases steadily. For the first time, we see high values of *Sphagnum*. The values of *Araucaria angustifolia* and *Mimosa scabrella*-type rise. At that time, *Araucaria* forest may have developed along the rivers as small gallery forests. Within the group of the Atlantic pluvial forests, values of *Alchornea* decrease, and those of Urticales increase. The cloud forest taxa values decrease (especially *Weinmannia humilis*). In the group "others", the *Rapanea* curve rises. *Sebastiania commersoniana* is found more frequently. This species probably also occurred in gallery forests along rivers in the highlands.

Zone boundary 3/4a: Strong increase of the *Araucaria angustifolia* curve.

PZ 4a. Older Araucaria forest zone (0 - 7 cm). The profile only contains a small part of this PZ. From PZ 3 to PZ 4a we see a change from high to low Poaceae values and from low to high *A. angustifolia* values. These striking changes are the same as in the profile from Morro da Igreja.

Pollen diagram Poço Grande (Fig. 7)

The area under study is situated in the Atlantic pluvial forest zone of the northern coastal plain, 20 km from the Atlantic Ocean. This zone, the zone of the Atlantic pluvial forest on the slopes of the Serra do Mar and the coastal vegetation zone (Vegetação litorânea) strongly influence the pollen rain. Pollen transport from the highland vegetation is low.

According to the radiocarbon dates, the profile for Poço Grande covers only part of the upper Holocene. By extrapolation, the profile starts at 4840 B.P. Sediments between 580 and 133 cm seem to have accumulated continuously. Sediments between 243 and 310 cm (PZ C) were quickly deposited. In the lower part of PZ E, obviously a hiatus or a relatively great increase of growth has to be taken into consideration. The upper part of PZ E might be very young, possibly only a few centuries old.

PZ A (472 - 580 cm). Sediments from 507 - 514 cm were dated to 4680 ± 150 B.P. PZ A is characterized by strong changes of values of two dune plant communities of which one is typical of stable Tertiary dunes (Myrtaceae) and the other of slightly moving dunes (Palmae, *Ilex*, *Weinmannia*-type, *Schinus*-type).

Myrtaceae values increase, forming a first maximum (85%). They later decrease accompanied by an increase of the curves of Palmae (10%), *Ilex* (7%), *Weinmannia*-type (20%) and *Schinus*-type (1%). This change takes place repeatedly. The above pollen types may derive from two different dune plant communities. According to Klein (1978), the Myrtaceae *Eugenia catharinae, E. umbelliflora, Gomidesia palustris* and *Myrcia multiflora* var. *glaucescens* existed on stable Tertiary dunes as low and dense communities. *Butia capitata* var. *odorata* (Palmae), *Ilex dumosa, Psychotria alba, Schinus terebinthifolius, Guapira opposita, Rapanea parvifolia* and *Gomidesia palustris* (Myrtaceae) colonise slightly moving dunes. It is therefore possible that numerous Myrtaceae pollen grains from stable Tertiary dunes and many pollen grains of Palmae, *Ilex* and the *Schinus* type originated from moving dunes. The *Weinmannia*-type curve indicates that these pollen grains spread from plants on moving dunes. This probably represents *W. paulliniifolia*, which today is widely distributed in the coastal vegetation.

Pollen grains of aquatics indicate low water level (*Echinodorus*) or a higher one (*Cabomba*). High Cyperaceae values point towards open locations. Water level changes in the low plain were possibly indirectly influenced by ocean level changes. According to Fairbridge (1962) and Bigarella (1965), there was a rise of the ocean level by +1.5 m to -3.5 m a.s.l. between 4800 and 4600 B.P. A low ocean level probably led to stronger drainage of the low plain.

The vegetation development can be explained as follows: sinking water levels indicated by a decrease of *Echinodorus* values at the beginning of PZ A caused the expansion of Tertiary dune plants, especially the Myrtaceae. Open locations were colonized by Cyperaceae (small Cyperaceae values). After the decrease of Myrtaceae values, the values of slightly moving dune

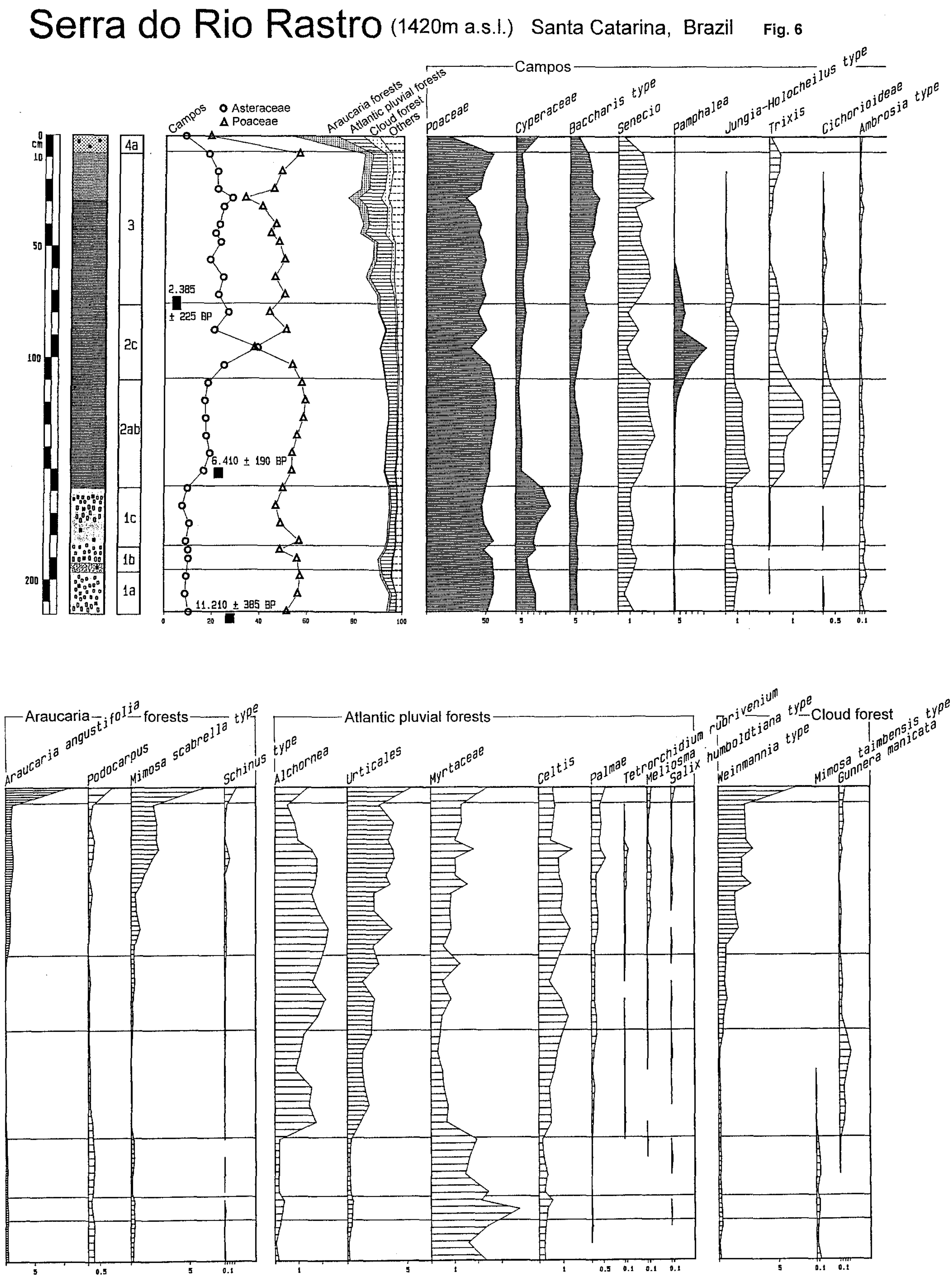
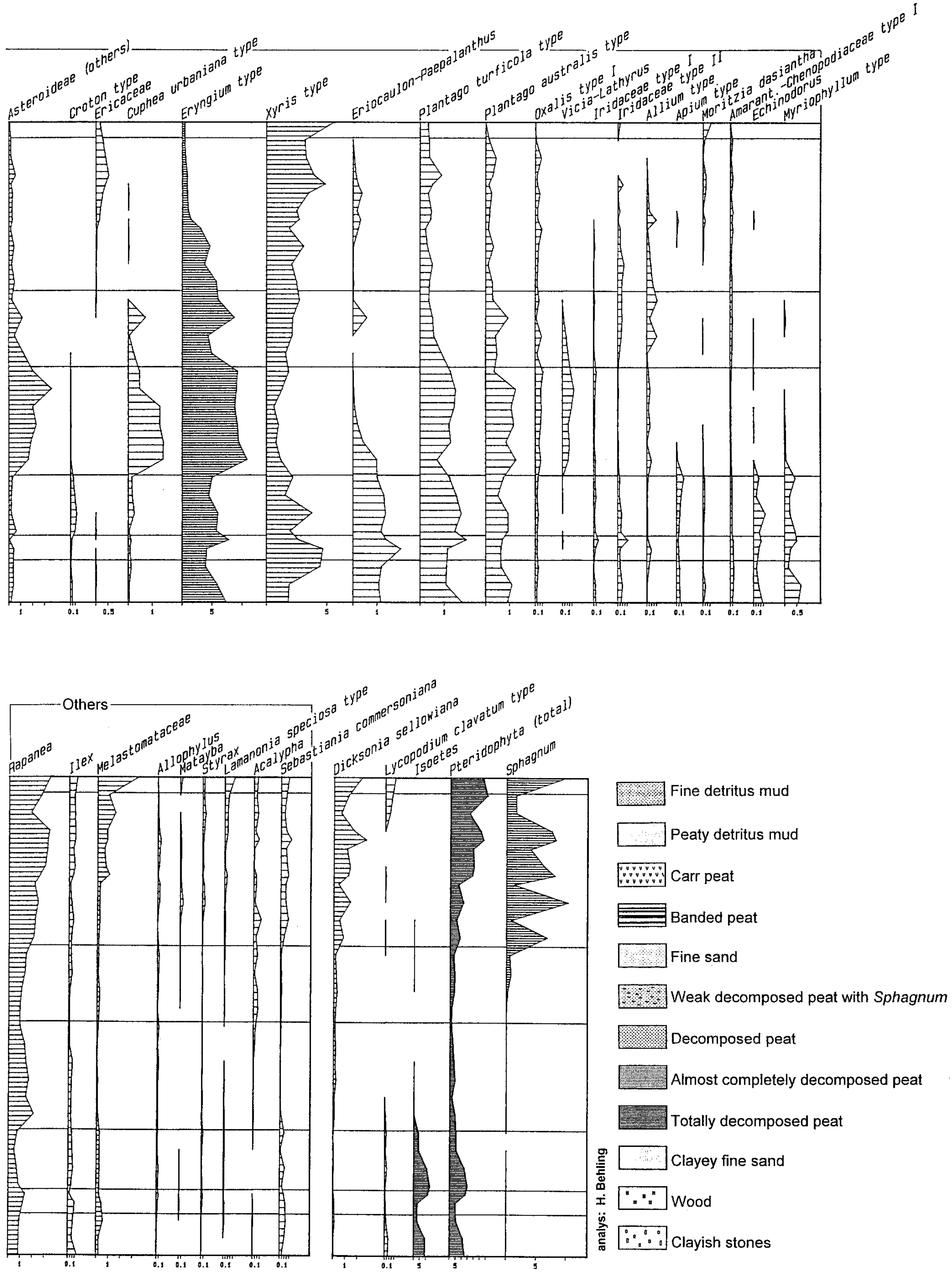


Fig. 6. Pollen diagram Serra do Rio Rastro


Asteroideae (others)
Croton type
Ericaceae
Cuphea urbaniana type
Eryngium type
Xyris type
Eriocaulon-Paepalanthus
Plantago turficola type
Plantago australis type
Oxalis type I
Vicia-Lathyrus
Iridaceae type I
Iridaceae type II
Allium type
Apium type
Moritzia dasiantha
Amarant.-Chenopodiaceae type I
Echinodorus
Myriophyllum type
Others
Rapanea
Ilex
Melastomataceae
Allophylus
Matayba
Styrax
Lamanonia speciosa type
Acalypha
Sebastiania commersoniana
Dicksonia sellowiana
Lycopodium clavatum type
Isoetes
Pteridophyta (total)
Sphagnum
Fine detritus mud
Peaty detritus mud
Carr peat
Banded peat
Fine sand
Weak decomposed peat with Sphagnum
Decomposed peat
Almost completely decomposed peat
Totally decomposed peat
Clayey fine sand
Wood
Clayish stones
analys: H. Behling

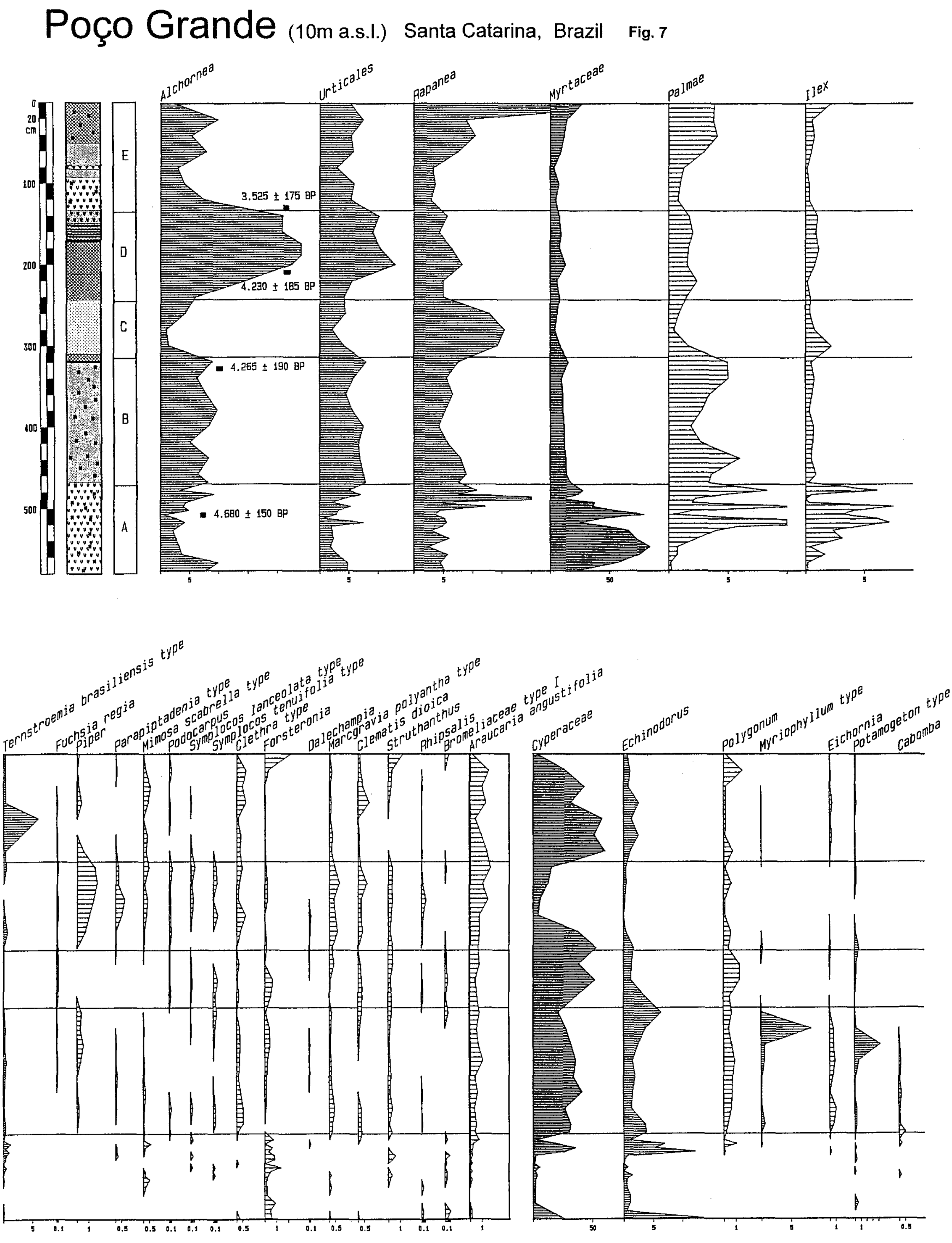
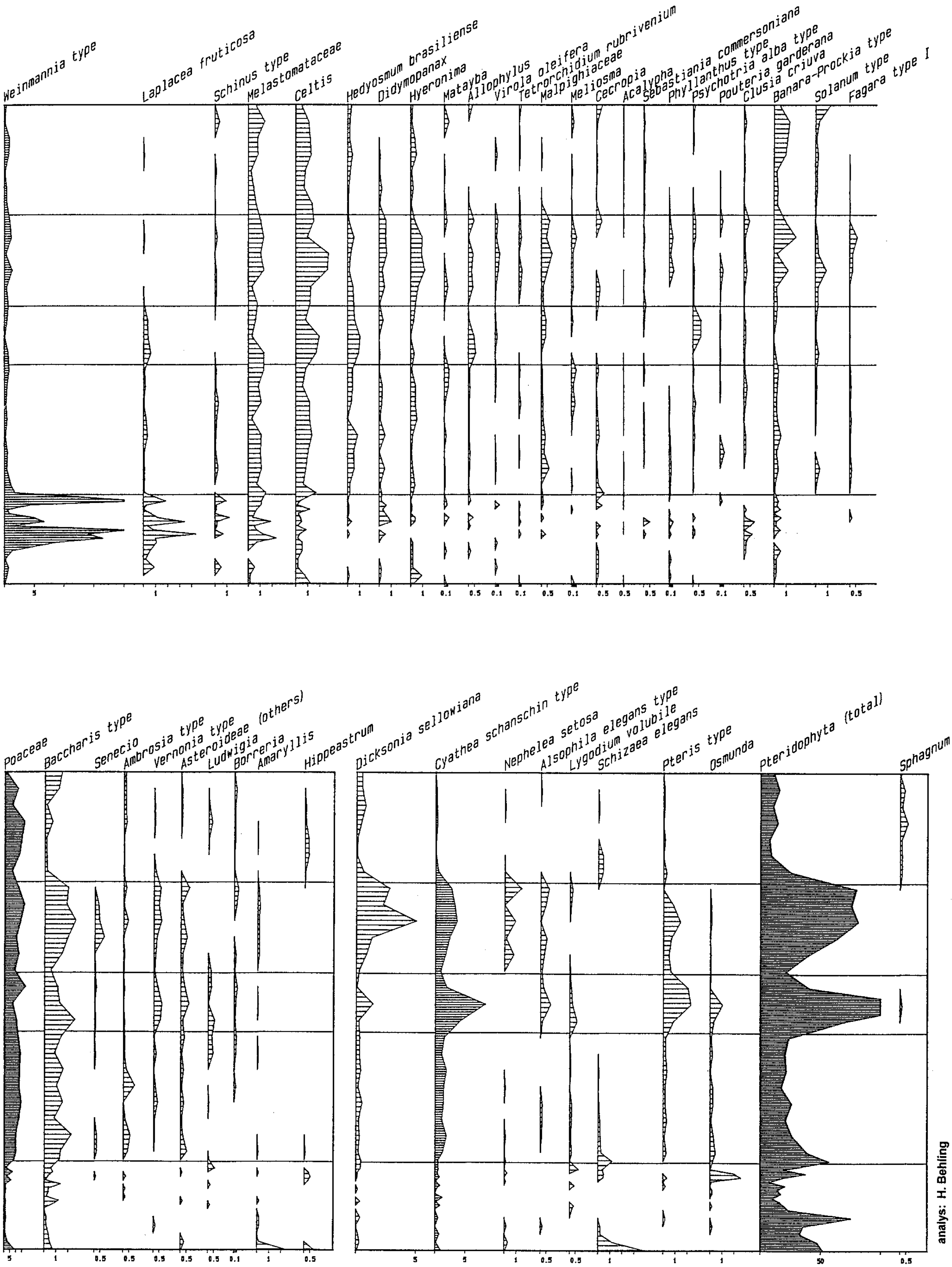


Fig. 7. Pollen diagram Poço Grande



Weinmannia type
Laplacea fruticosa
Schinus type
Melastomataceae
Celtis
Hedyosmum brasiliense
Didymopanax
Hyeronima
Matayba
Allophylus
Virola oleifera
Tetrorchidium rubrivenium
Malpighiaceae
Meliosma
Cecropia
Acalypha
Sebastiania commersoniana
Phyllanthus type
Psychotria alba type
Pouteria garderana
Clusia criuva
Banara-Prockia type
Solanum type
Fagara type I
Poaceae
Baccharis type
Senecio
Ambrosia type
Vernonia type
Asteroideae (others)
Ludwigia
Borreria
Amaryllis
Hippeastrum
Dicksonia sellowiana
Cyathea schanschin type
Nephelea setosa
Alsophila elegans type
Lygodium volubile
Schizaea elegans
Pteris type
Osmunda
Pteridophyta (total)
Sphagnum
analys: H. Behling

taxa increased. Perhaps the Myrtaceae became more dominant then. This change in the high values of stable Tertiary dune taxa to the moving dune taxa is repeated twice. Among the moving dune taxa the values of *Rapanea* are higher (11%) and *Weinmannia*-type values lower (7%). The cause of this change is not explained yet.

Following this, there are again higher *Echinodorus* and Cyperaceae values in the upper section of PZ A, evidence of higher water levels and a development of open sites with Cyperaceae. With the further decrease of Myrtaceae values, *Rapanea* has a maximum of 20%. There was possibly a short strong expansion of *Rapanea*, before the other moving dunes taxa spread again.

At the end of PZ A, there is a decrease of values of the moving dune taxa. Caused by higher water levels (pollen grains of *Cabomba* are more frequent), dunes were presumably flooded. This is possible due to the slightly wavy relief in the low plain with a maximum of 2 - 3 m between crest and valley.

Atlantic pluvial forests are mainly represented in the pollen spectrum by *Alchornea,* Urticales, *Rapanea,* Myrtaceae, Palmae, *Hedyosmum brasiliense, Virola oleifera, Tetrorchidium rubrivenium,* Malpighiaceae and *Meliosma*. These forests on some higher locations at the low plain border were probably of some importance. The pioneer, *Alchornea triplinervia* var. *janeirensis* may have been significant on suitable locations by the coastal plain. *Didymopanax, Hyeronima, Matayba* and *Allophylus* are found mainly in Atlantic pluvial forests on slopes of the Serra do Mar (shortest distance is 15 km). Relatively high values of *Laplacea* suggest that these taxa grew on moving dunes. Today, *Laplacea fruticosa* occurs frequently on slopes at 500 - 900 m a.s.l. (Reitz et al. 1978).

Pollen grains of the liana *Forsteronia* were frequently found. Single pollen grains of Menispermaceae, *Marcgravia polyantha*-type, *Dalechampia* and *Clematis dioica* were also found. Among tree ferns of the Atlantic pluvial forests, which in PZ A have only low values, there is *Cyathea schanschin*-type and *Alsophila elegans*-type. *C. schanschin* occurs in coastal slope forests. Epiphytes are represented by Bromeliaceae types I, II and *Rhipsalis*. The highland vegetation is poorly represented by pollen grains such as *Araucaria angustifolia* and *Dicksonia sellowiana*.

Zone boundary A/B: Decrease of the values of *Weinmannia*-type, *Ilex* and Palmae.

PZ B (314 - 472 cm). The beginning of PZ B is estimated at 4590 B.P. The end of PZ B is dated to 4265 ± 190 B.P. Characteristics of the PZ are the high values of *Alchornea*, Urticales, *Rapanea* and relatively high values of water plants. The profile contains fresh water deposits.

During the time covered by the first part of PZ B, the pollen curves of aquatics are relatively low, and the presence of *Cabomba* indicates higher water levels. There was probably a water-lily zone with *Cabomba*, and a zone with *Potamogeton*. In the shallow water, a zone with *Myriophyllum* and *Eichhornia* was formed, and by the shore a Cyperaceae zone and a zone with *Polygonum* and *Echinodorus*, corresponding to aquatic plant communities described by Reitz (1961). In the upper part of the PZ, there is a maximum of the *Potamogeton* type, followed by a *Myriophyllum* and finally of *Echinodorus*. These changes suggest a process of aquatic plant succession. Of interest is a single *Nuphar* pollen grain; *Nuphar* is not mentioned in the flora of Santa Catarina.

Compared with PZ A, pollen grains of Tertiary dune taxa occur in small amounts only. Taxa that existed at high water levels in the low plain were hardly able to exist. Possibly the few pollen grains, coming form the dune vegetation of the coast, are due to long distance transport.

Pollen grains of *Alchornea*, Urticales, *Rapanea* and Myrtaceae are (except Palmae) equally represented compared with PZ A. It is possible that *Rapanea* and *Alchornea triplinervia* var. *janeirensis* formed a low shrub area on higher places behind the aquatic plant zones, followed by tall rain forest species. In this PZ the lianas *Cardiospermum* and *Sicyos* (both one pollen grain) are new. The tree fern *Cyathea schanschin* is found more frequently. Percentages of *Araucaria angustifolia* are higher in PZ B (almost 1%). This points to an expansion of *Araucaria* in the highlands. *Dicksonia sellowiana* values remain low.

Zone boundary B/C: Strong increase of the *Rapanea* curve.

PZ C (243 - 314 cm). According to the radiocarbon dates obtained for PZ B and D, the PZ C characterized by high values of *Rapanea* lasted for only a short period. Values of *Echinodorus* decrease and of Cyperaceae increase. At the same time, the *Rapanea* curve increases to 15%. Decreasing water level evidently caused a spread of Cyperaceae and *Rapanea*. *R. ferruginea* appears to be quite important in the recolonization of secondary forests on the coastal plains (Klein 1980). Among the tree ferns, the curve of *Cyathea schanschin*-type has its largest maximum at 8%, while other fern spore percentages are important. *Araucaria angustifolia* values are still high. *Dicksonia sellowiana* has high values in the mid PZ C.

Zone boundary PZ C/D: Strong increase of the *Alchornea* curve and decrease of the *Rapanea* curve.

PZ D (133 - 243 cm). This PZ is characterized by high values of *Alchornea*. The increase of the *Alchornea* curve was dated to 4230 ± 185 B.P. The percentages of *Rapanea* decrease to 5% and those of *Alchornea* increase to 24%. *Alchornea* obviously expanded more than *Rapanea* which suggests the development of dense forest near the site (low Cyperaceae values). *Didymopanax, Hyeronima, Virola oleifera* and Malpighiaceae are represented by higher values. Percentages of tree fern and other fern spores continue to be high, but are lower than in PZ C. In the upper section of PZ D, percentages of *Araucaria angustifolia* increase to nearly 2% and *Dicksonia sellowiana* values have a maximum of 5%. That points to a major expansion of *Araucaria* forest in the highlands.

Zone boundary D/E: Decrease of the *Alchornea* curve.

PZ E (0 -133 cm). The beginning of PZ E is dated to 3525 ± 175 B.P. By interpolation (based on dates for PZ A and PZ B) an age of 4030 B.P. was expected. The difference of 500 years probably points to a hiatus or disturbed sedimentation. This is also suggested by abrupt changes of values of *Alchornea*, and also of numerous ferns and Cyperaceae. We have no radiocarbon dates for the middle and upper part of PZ E. It is possible that these deposits originated from the last centuries, because the top pollen spectra appear to indicate human influence. Thus, there may be a hiatus of more than 2000 years.

High Cyperaceae values suggest the existence of places without forest in the low plain. Remarkable are the low values of tree ferns and other ferns in comparison to PZ D. *Araucaria angustifolia* values are still high, but low in the top sample. Values of *Dicksonia sellowiana* are still low. In the top pollen spectra, the values of *Alchornea* decrease while these of *Rapanea* increase. This is perhaps caused by the cutting down of *Alchornea* and other trees leading to an expansion of *Rapanea*. The Ranch Nutrimental and neighbouring areas were extensively drained. Perhaps that increased the expansion of *Rapanea* too.

Discussion

Climate indicators

Some pollen and spore types can be used as indicators of climatic conditions. *Gunnera manicata* is sensitive to severe frosts. Mild winters permit a greater expansion of this species into the higher parts of the cloud forest. *Laplacea fruticosa* is found frequently on mountain slopes at elevations between 500 and 900 m a.s.l. (Reitz et al. 1978). A warmer climate would permit an expansion of this species into higher regions as well.

Indicators of a cold climate cannot be derived directly from the present vegetation. However, it is possible to identify indirect indicators of cold conditions by the values of some pollen and spore types during the Late Pleistocene and Holocene. Higher percentages of *Croton*-type, *Lycopodium clavatum*-type and *Isoëtes* (submerged and terrestrial) in the Late Pleistocene and low percentages in the Holocene may indicate a colder climate. The Morro da Igreja region is of special significance. Due to an elevation of 1800 m a.s.l, cold climate indicators are more obvious in this diagram. The higher values of *Croton*-type and *Lycopodium clavatum*-type may also indicate a colder climate.

Annual precipitation in the *Araucaria angustifolia* area is only exceptionally below 1400 mm, and never drops below 1000 mm (Hueck 1966). High values of *Araucaria* indicate a very moist climate. This also applies to *Dicksonia sellowiana*, which grows in moist habitats (Sehnem 1978). *Xyris* appears in very moist locations (Klein 1978), but some species of *Xyris* also grow on bogs.

Species of the genus *Eryngium* are found in moist and often in dry places (Mathias et al. 1972). In parts of pollen diagrams in which there are very high percentages of moisture indicators (*Araucaria angustifolia, Dicksonia sellowiana, Xyris*), the *Eryngium*-type values are low. Therefore, it is probable that *Eryngium*-type pollen will increase under dry climatic conditions.

Table 2. Pollen and spore types which are possible indicators of climatic change in the highland diagrams; the percentage ranges in the pollen diagrams are given in parentheses

Pollen or Spore Type	% Representation	Indication of increased representation
1. Indicators of temperature change		
Gunnera manicata	(0 - 0.7%)	colder
Laplacea fruticosa	(0 - 0.8%)	colder
Fuchsia regia	(0 - 0.2%)	colder
Croton-type	(0 - 0.7%)	colder
Lycopodium clavatum-type	(0 - 3.1%)	colder
Isoëtes	(0 - 13.4%)	colder
2. Indicators of moisture change		
Araucaria angustifolia	(0 - 10.8%)	wetter
Xyris-type	(0 - 8.7%)	wetter
Dicksonia sellowiana	(0 - 19.4%)	wetter
Eryngium-type	(0 - 15.0%)	drier

Some of these climate indicators are only represented by small records in the diagrams, and their presence cannot be used as good evidence for changes. This is valid for *Gunnera manicata* in the Serra da Boa Vista diagram and for *Laplacea fruticosa* in Morro da Igreja and Serra do Rio Rastro. The values of *Croton*- and *Lycopodium clavatum*-types in the Serra do Rio Rastro diagram are also almost all below 0.25%. The percentages of *Gunnera manicata*, *Laplacea fruticosa* and *Croton*-type are small (at most 0.7% and 0.8% respectively), but large counts were made from the highland profiles, on average 3984 pollen and spores per sample, so the values should be reliable.

The presence of *Fuchsia* and of high tree fern values in the diagrams is important for climatic interpretation. In his climate classification Köppen (1900) selected *Fuchsia* as a characteristic plant for the C6-climate (*Fuchsia* climate). The C6-climate is described by him as a temperate climate, with little frost, warmest month below 22 C, and all months are rainy and have a long summer vegetation period. In an improved classification of C6-climate, Troll (1970) selected tree ferns (Cyatheaceae) as characteristic plants and called the C6-climate a tree fern climate. This C6-climate is now called Cfa-climate. The presence of *Fuchsia* or high tree fern values indicate these climatic conditions.

The expansion of the Atlantic pluvial forests within the climatic zone of south Brazil or in higher regions of the Serra Geral reflect climatic changes.

The above mentioned indicators mainly permit an interpretation of the highland climate. For the lowland, high values of tree ferns (*Cyathea schanschin*-type) are a good indicator of a moist climate. Clear indicators for temperature changes could not found.

Climate development in the highlands

Due to the small distances between the study areas, the same climatic development can be expected. Therefore, the highland pollen diagrams are comprehensively interpreted, as follows.

In PZ 1 the climate indicators provide evidence of cold and drier conditions. There is some evidence of a warmer climate (PZ 1b) followed by a colder one (PZ 1c) mainly based on the expansion of the Atlantic pluvial forests (higher values of *Weinmannia*-type in the diagram from Serra da Boa Vista, *Alchornea* and Urticales in Serra do Rio Rastro). However, the climatic interpretation of PZ 1b and 1c is based on a few pollen spectra only.

In PZ 1a the high percentages of *Isoëtes* (5.4% in the profile from Serra da Boa Vista, 7.2% in Serra do Rio Rastro), *Croton*- and *Lycopodium clavatum*-types (0.4% respectively 0.6% in Serra da Boa Vista), the absence of pollen grains of *Gunnera manicata* and only a few pollen grains of *Laplacea fruticosa* (Serra da Boa Vista) indicate a cold climate. PZ 1a is the coldest period and tropical elements are only represented in small amounts. During the winter months, there was probably frequent frost in the lowlands and hard frost in the highlands. Relatively high values of *Eryngium*-type (5.7% in the profile from Serra do Rio Rastro and 0.9% in Serra da Boa Vista) and the relatively low values of *Xyris*-type (2.7% in the profile from Serra do Rio Rastro and 0.8% in Serra da Boa Vista) suggest a relatively dry climate. According to the curves of moisture indicators, precipitation may have been below present values.

In PZ 1b, in the Serra da Boa Vista diagram, the values of *Isoëtes* (1.6%), *Lycopodium clavatum*-type (0.3%) and *Croton*-type (0.2%) are lower than in PZ 1a. Taxa of the Atlantic pluvial forest zone (higher values of *Weinmannia*-type and *Laplacea fruticosa*) were able to spread into higher regions of the Serra da Boa Vista. This points to slightly warmer conditions. The slightly higher values of *Alchornea* and Urticales in the diagram from Serra do Rio Rastro provides further evidence, but this small expansion into the Atlantic pluvial forest zone was not very important. High values of *Xyris*-type and lower ones of *Eryngium*-type in Serra do Rio Rastro in the first section of PZ 1b point to a moister climate, and in the second section (both curves go the other way) to a drier one. Higher percentages of *Dicksonia sellowiana* (1.4% against 0.1% in PZ 1a in the Serra da Boa Vista diagram) suggest an increase of moisture.

In PZ 1c, the decrease of *Weinmannia*-type values in the diagram from Serra da Boa Vista (retreat of forests in the higher region) can be interpreted as a change to a colder climate. The values of *Isoëtes*, *Lycopodium clavatum*-type and *Croton*-type decrease continuously. A small percentage of *Dicksonia sellowiana* (0.5%) indicates a slightly drier climate. Higher *Isoëtes* values in Serra do Rio Rastro once more point to a cold climate, as in PZ 1a. The percentages of *Eryngium*-type and *Xyris*-type are nearly as high as in PZ 1a and indicate relatively dry conditions.

In PZ 2, in the Serra da Boa Vista diagram, the expansion of the Atlantic pluvial forests (*Weinmannia paulliniifolia*) in the higher region, and higher values of *Laplacea fruticosa* point to a very warm phase in the Holocene. The values of *Dicksonia sellowiana* are slightly higher in relation to the diagrams from Morro da Igreja and Serra do Rio Rastro, followed by more moisture on the Serra da Boa Vista. Serra da Boa Vista is located at a border of a zone of higher precipitation. Due to higher *Dicksonia sellowiana* values and the presence of *Fuchsia regia* pollen grains at PZ 2, the climate of PZ 2 can be classified as C6- or Cfa-climate.

In PZ 2a in the Morro da Igreja diagram, high percentages of *Xyris*-type (8%) and an increase of *Dicksonia sellowiana* values (2.6%) point to a moister period, for which there is no evidence in the Serra do Rio Rastro results. The precipitation, in view of the high *Eryngium* percentages (13.4%), was not very high but it was obviously sufficient for a small expansion of *Araucaria angustifolia*. The increase of *Gunnera manicata* values (0.3%) suggest warmer conditions.

In PZ 2b in the Morro da Igreja diagram, the highest *Gunnera manicata* percentages (0.5%), high *Eryngium*-type values (13%) and small percentages of *Xyris*-type (3.8%) mark this PZ as the warmest and driest period of the Holocene. Despite the high altitude, cold climate indicators are only represented in small amounts.

In PZ 2ab in the Serra do Rio Rastro diagram, *Gunnera manicata* has here the highest values (at the most 0.5%). There are high percentages of *Eryngium*-type (9.4%) and small ones of *Xyris*-type (1.1%) marking this PZ as the driest Holocene phase.

In PZ 2c in the Morro da Igreja and Serra do Rio Rastro diagrams *Gunnera manicata* percentages (0.3% in the Morro da Igreja profile; 0.1% in Serra do Rio Rastro) are lower than in PZ 2b and PZ 2ab. This indicates a slight decrease of temperature. In the diagram from Serra do Rio Rastro, the values of *Xyris*-type increase, but not in the diagram from the Morro da Igreja. Values of *Eryngium*-type values do not increase rapidly as in the diagram from the Serra do Rio Rastro and they continuously decrease in Morro da Igreja. This evidence indicates that the climate in PZ 2c was not as dry as it was during the previous PZ.

In PZ 3, compared with PZ 2, the values of *Gunnera manicata* are lower (only 0.1%) in the Morro da Igreja and Serra do Rio Rastro diagrams. In Morro da Igreja, the values of *Croton*- and *Lycopodium clavatum*- types rise (0.4 and 1.6% respectively). *Campos* values are higher, too. This indicates that the conditions were cooler, especially at the 1800 m high Morro da Igreja. At Serra da Boa Vista the retreat of the Atlantic pluvial forests (decrease of *Weinmannia*-type values) points to the beginning of a period of cooler climate. During the middle part of PZ 3, the values of *Laplacea fruticosa* and *Fuchsia regia* decrease, and *Lycopodium clavatum*-type increase. Consequently, the cooler climate affected this area at a later phase. The moisture indicators point to a more moist climate compared with PZ 2. Obviously there are differences between the study areas. Whereas in the diagram of Morro da Igreja the curve of *Xyris*-type is still unchanged, the *Dicksonia sellowiana* curve shows an even increase. In the diagram from Serra do Rio Rastro, the curves of *Dicksonia* and of *Xyris*-type point to repeated change of moisture. There are high values of *Dicksonia sellowiana* in the Serra da Boa Vista diagram and a maximum (6.2%) at the beginning of PZ 3. That points to a more moist climate compared to the region of Morro da Igreja and Serra do Rio Rastro.

In PZ 4a, the abrupt increase of *Xyris*-type percentages (8.5% in the profile from Morro da Igreja and 5.6% in Serra do Rio Rastro), the increase of *Araucaria angustifolia* and *Dicksonia sellowiana* percentages (9.3% and 19.4% respectively in the profile of Morro da Igreja; 10.8% and 2.3% respectively in Serra do Rio Rastro) provide evidence for very moist conditions. A C6- or Cfa-climate on the highland (Morro da Igreja and Serra do Rio Rastro is present with the high values of *Dicksonia sellowiana*.

In PZ 4b, this human influenced PZ provides evidence of a continuously cool climate with a tendency to being slightly warmer and relatively moist, but a somewhat drier climate than in PZ 4a. In the diagram from Morro da Igreja there is a decrease in *Croton*-type values (by 0.4% in PZ 4a and 0.3% in PZ 4b) and an increase of *Gunnera manicata* values (0.3% in the top sample), which suggest a warmer climate. Although in the diagram of Morro da Igreja the *Dicksonia sellowiana* values are high, the curve of *Xyris*-type shows a continuous decrease. The curve for *Eryngium*-type is unchanged. In the diagram from Serra da Boa Vista, *Xyris*- type values show a very strong increase (6.3%) and later a strong decrease (1.6%). A tendency toward a drier climate can be assumed. In the Serra da Boa Vista diagram, relatively low values for *Dicksonia sellowiana* are probably the result of human disturbance.

Table 3. Survey of climate history - highlands

Radiocarbon age	PZ	Climate
14,000 -10,800	1a	cold and relatively dry
10,800 -10,500	1b	warmer and moister
10,500 -10,000	1c	cold and relatively dry
10,000 - ~2900	2	very warm and drier (PZ 2, Serra da Boa Vista: less dry than in Morro da Igreja and Serra do Rio Rastro (PZ 2a, Morro da Igreja: more moist)
	2c	less warm and less dry
~2900 -~1000	3	cool and moister
~1000 - 100	4a	cool and very moist
100 - 0	4b	tendency towards a warmer and drier climate

Climate development in the lowlands

In the Poço Grande diagram, only *Cyathea schanschin-type* can be used as an indicator for moisture. This tree fern probably grew on slopes close to the coast. The percentages of *C. schanschin*-type (0.5%) are small in PZ A and point to a little moisture. In PZ B, the higher values of *Cyathea* (1.7%) suggest a small increase in moisture. For the time represented by PZ C and PZ D, the relatively high values (maximum is 8% in PZ C) indicate higher moisture in the Atlantic coastal plain. At the time of PZ E, the small values of *C. schanschin*- type suggest low moisture.

In PZ D, the percentages of *Dicksonia sellowiana* (maximum 5%) are very high. This indicates a moist climate in the nearby highlands at the time of PZ D.

Table 4. Survey of climate history - lowlands

Radiocarbon age	PZ	Climate
4840 - 4590	A	drier
4590 - 4260	B	slightly moister
4260 - 3525	C-D	moister
? - 0	E	drier

The history of campos vegetation

In the southern Brazilian highlands, there is a sharp border between forest and *campos*. How can the *campos* vegetation withstand the competitive expansion of the *Araucaria* forests under the present forest climate conditions?

According to Hueck (1953, 1966) there is no indication of former forest growth in the *campos*, such as old forest soils or burnt horizons. The first European colonists found large *campos* areas in the 18th century. According to Hueck's interpretation, the *campos* with *Araucaria* forests is a retrogressive vegetation zone, which survived after changes from steppe climate to temperate forest climate. Rambo (1956, 1960) and Klein (1960) consider the advance of *Araucaria* forests into the *campos* to be an incomplete migration. The cause of this vegetation shift at the cost of the *campos* areas was caused by increased precipitation in the recent past.

The pollen analytical results suggest that the present-day *campos* is a relict of the late Pleistocene with a cold and relatively dry climate (PZ 1), and the older Holocene with a warm and dry climate (PZ 2). Only for a relatively short time did the expansion of *Araucaria* forests cause a reduction of the *campos* zone (in PZ 4). These results are similar to the interpretations of Hueck (1953, 1966), Rambo (1956, 1960) and Klein (1960), but we must inspect the study regions separately because of their different geographical and climatic situations.

In the Serra da Boa Vista highland border at the beginning of the Holocene, there was an expansion of Atlantic pluvial forest elements (*Weinmannia paullinii-*

folia) with some delay by *Araucaria* forest elements (*Ilex*). This was the result of the warmer climate. This expansion caused a reduction of the campos zone. During PZ 3 (Fig. 8) the campos vegetation was again widespread due to a cooler climate.

In the region of Morro da Igreja, there was higher precipitation (high mountains) causing an expansion of the *Araucaria* forests and a slight reduction of the *campos* of the upper region (PZ 2a). The cooler climate after PZ 3 also caused an expansion of the *campos* of the upper region (Fig. 8).

In the study area of Serra do Rio Rastro, the reduction of *campos* took place as late as in PZ 4a (Fig. 8). The same probably also happened in a large area of the highlands, because here and in the Morro da Igreja region there was a great expansion of *Araucaria* forests accompanied by a strong reduction in extent of the *campos* within more or less the last 1000 years (PZ 4a).

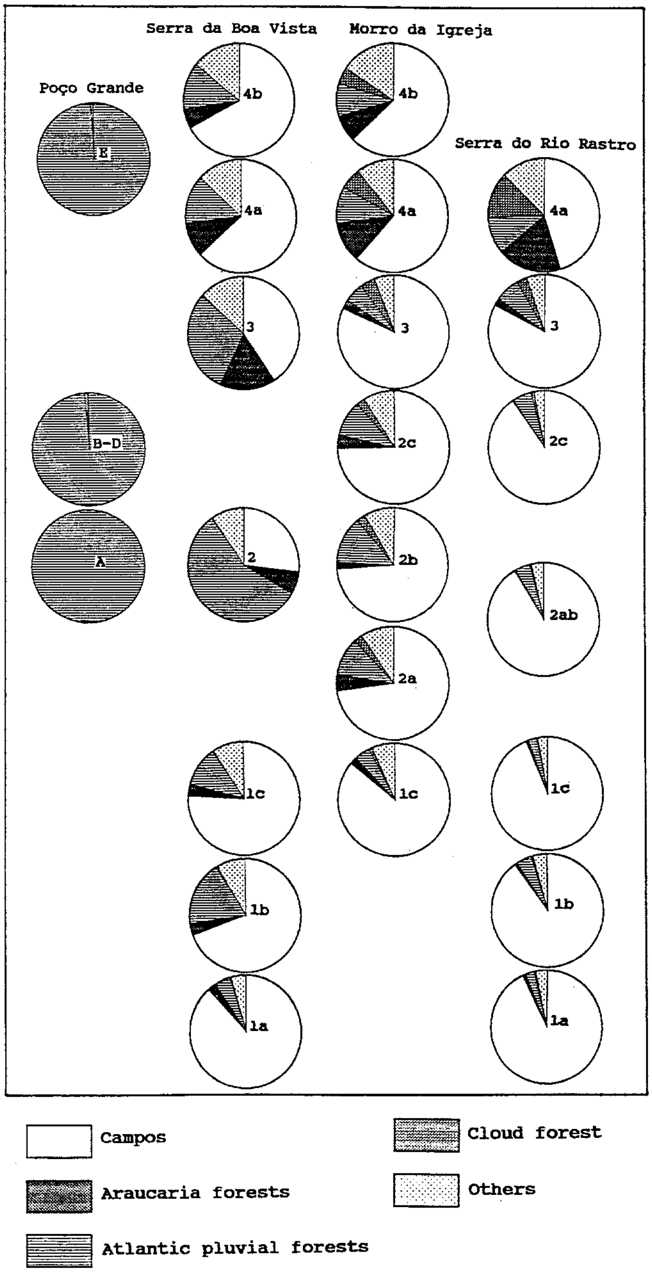


Fig. 8. Relative parts of vegetation zones (average values) from the PZ of Poço Grande, Serra da Boa Vista, Morro da Igreja and Serra do Rio Rastro

In the absence of human influence and under the present climatic conditions a total colonization of *campos* areas by *Araucaria* forests and, in suitable regions, Atlantic pluvial forests is possible. The intensification of the current relatively dry conditions would, however, slow forest expansion or even reverse this trend and favour *campos* vegetation expansion.

The history of Araucaria forests

According to the pollen records, small *Araucaria* forests probably existed during the Late Pleistocene in protected highland valleys with sufficient moisture. *Araucaria* percentages of 1% in PZ 1c and about 3% in PZ 2a in the diagram from Morro da Igreja (at the beginning of the Holocene, if there is not a hiatus) support this conception. *Araucaria* may have persisted in deep valleys in the mountain region between 14,000 and 10,000 B.P. even if the climatic conditions of the glacial maximum are unknown.

At the time represented by PZ 1, a cold and relatively dry climate in the highlands prevented a greater expansion of *Araucaria angustifolia*, and in PZ 2 an even drier climate prevailed. Only in PZ 3 (with the exception of the minor expansion in the Morro da Igreja region in PZ 2a) was there a minor expansion resulting in small gallery forests along rivers. The first general major expansion of *Araucaria* was in consequence of a very moist climate in PZ 4 (Fig. 8).

The colonization of the *campos* areas by *Araucaria* was clearly caused by an increase of precipitation. According to Hueck (1966) the precipitation in the *A. angustifolia* area today is only exceptionally below 1400 mm and never below 1000 mm. Under present conditions *A. angustifolia* is a pioneer species, which is spreading into the *campos* (Reitz and Klein 1966).

The beginning of the *Araucaria* spread which was caused by an increase in moisture between 8000 and 10,000 B.P. (Ab'saber 1977) could not be confirmed in the study areas. In this connection, an expansion of *Araucaria angustifolia* in southeast Brazil during the last glacial cycle (De Oliveira 1992), between 12,000 and 11,000 B.P. and between 10,000 and 8500 B.P. (Ledru 1993) is interesting. No *Araucaria* exist today in this area.

Migrations of Atlantic pluvial forests

According to Ab'saber (1977), the Atlantic pluvial forests survived in "moist islands", (refuges) between São Paulo and Espírito Santo during the glacial periods. The present investigation could not determine if rain forests had been preserved in refuges on the Atlantic coast, as presented by Ab'saber (1977) or if the rain forest zone had shifted to the north, or both.

Data presented here revealed that during the Late Pleistocene (at 14,000 B.P.), the Atlantic pluvial forest taxa were only very rarely represented (*Alchornea*, Urticales, Palmae). Tropical elements, which already existed from 14,000 B.P. in climatically favourable locations, possibly survived the last glacial period, if they did not migrate from far away to Santa Catarina during the time between the last glacial maximum and about 14,000 B.P. Tropical taxa may have been situated more to the north on the Brazilian Atlantic coast.

After the end of the Late Pleistocene, more elements of Atlantic pluvial forests (*Meliosma, Cecropia, Didymopanax*) have migrated into the southern lowland. Others appeared for the first time in the Holocene, such as *Hyeronima* and *Tetrorchidium rubrivenium*). The warm phase (PZ 2) may have induced a rapid expansion of tropical taxa into the southern lowland.

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Appendix

List of pollen and spores found

Abutilon/Malvastrum-type (Malvaceae)
Acacia (Mimosaceae)
Acaena/Polylepis-type (Rosaceae)
cf. Acanthaceae (Acanthaceae)
Acalypha (Euphorbiaceae)
Actinostemon concolor (Euphorbiaceae)
Alchornea (Euphorbiaceae)
Allium-type (Liliaceae)
Allophylus (Sapindaceae)
Alnus (Betulaceae)
Alseis floribunda-type (Rubiaceae)
Alsophila elegans-type (Cyatheaceae)
Alstroemeria (Amaryllidaceae)
Alternanthera-type I (Amaranthaceae)
Alternanthera-type II (Amaranthaceae)
Amaranthaceae/Chenopodiaceae-type I
Amaranthaceae/Chenopodiaceae-type II
cf. Amaryllidaceae
Amaryllis (Amaryllidaceae)
Ambrosia-type (Asteraceae)
Anemia (Schizaeaceae)
Anemia phyllitides-type (Schizaeaceae)
Anogramma-type (Pteridaceae)
Anthoceros punctatus (Anthocerotaceae)
Apiaceae
Apium-type (Apiaceae)
Apocynaceae-type
Araucaria angustifolia (Araucariaceae)
Aspidosperma
Other Asteroideae (Collective group, Asteraceae)
Baccharis-type (Asteraceae)
Banara/Xylosma-type (Flacourtiaceae)
Begonia (Begoniaceae)
Berberis kleinii (Berberidaceae)
Bernhardia pulchella-type (Euphorbiaceae)
Blechnum imperiale-type (Blechnaceae)
Bomarea-type (Amaryllidaceae)
Borreria (Rubiaceae)
Bougainvillea glabra (Nyctaginaceae)
Bromeliaceae-type I
Bromeliaceae-type II
Buddleia-type (Loganiaceae)
Byttneria (Sterculiaceae)
Cabomba (Nymphaeaceae)
Cardiospermum (Sapindaceae)
Caryophyllaceae
Casearia catharinensis (Flacourtiaceae)
Casearia decandra (Flacourtiaceae)
Caperonia-type (Euphorbiaceae)
Cecropia (Moraceae)
Cedrela fissilis-type (Meliaceae)
Celosia-type (Amaranthaceae)
Celtis (Ulmaceae)
Chamissoa-type (Amaranthaceae)
Chaptalia (Asteraceae)
Chrysophyllum dusenii (Sapotaceae)
Chrysophyllum marginatum (Sapotaceae)
Chrysophyllum viride-type (Sapotaceae)
Cichorioideae (Collective group, Asteraceae)
Clethra type (Clethraceae)
Clematis dioica (Ranunculaceae)
Clusia criuva (Guttiferae)
Coccocypselum (Rubiaceae)
Cordia trichomata-type (Boraginaceae)
Croton-type (Euphorbiaceae)
Cupania (Sapindaceae)
Cuphea urbaniana-type (Lythraceae)
Cyathea schanschin-type (Cyatheaceae)
Cyperaceae
Dalechampia (Euphorbiaceae)
Daphnopsis (Thymelaeaceae)
Daphnopsis beta-type (Thymelaeaceae)
Dicksonia sellowiana (Cyatheaceae)
Didymopanax (Araliaceae)
Dioclea (Papilionaceae)
Dodonaea (Sapindaceae)
Dorstenia (argentata) (Moraceae)
Drimys brasiliensis (Winteraceae)
Echinodorus (Alismataceae)
Eichornia (Pontederiaceae)
Ephedra (Ephedraceae)
Ephedra tweediana-type (Ephedraceae)
Ericaceae
Eriocaulon-Paepalanthus (Eriocaulaceae)
Eryngium-type (Apiaceae)
Euphorbia (*papillosa*) type (Euphorbiaceae)
cf. Euphorbiaceae-type I
cf. Euphorbiaceae-type II
Euplassa (Proteaceae)
Fagara-type I (Rutaceae)
Fagara-type II (Rutaceae)
Forsteronia (Apocynaceae)
Fuchsia regia (Onagraceae)
Gaultheria ulei (Ericaceae)

Geranium (Geraniaceae)
Gomphrena/Pfaffia-type (Amaranthaceae)
Griselinia ruscifolia type (Cornaceae)
Guapira (Nyctaginaceae)
Gunnera manicata (Gunneraceae)
Gymnogramma-type (Pteridaceae)
Hedyosmum brasiliense (Chloranthaceae)
Hippeastrum (Amaryllidaceae)
Hirtella hebeclada (Chrysobalanaceae)
Hydrocotyle-type (Apiaceae)
Hyeronima (Euphorbiaceae)
Hygrophila (Acanthaceae)
Hymenophyllum-type (Hymenophyllaceae)
Ilex (Aquifoliaceae)
Inga-type (Mimosaceae)
Iridaceae-type I
Iridaceae-type II
Isoëtes (Isoëtaceae)
Jacobina/Justica-type I (Acanthaceae)
Jacobina/Justica-type II (Acanthaceae)
Jungia/Holocheilus-type (Asteraceae)
Labiatae
Lamanonia speciosa-type (Cunoniaceae)
Laplacea fruticosa (Theaceae)
Linum (Linaceae)
Lophosoria quadripinnata (Cyatheaceae)
Ludwigia (Onagraceae)
Luehea (Tiliaceae)
Lycopodium sp. (Lycopodiaceae)
Lycopodium alopecuroides (Lycopodiaceae)
Lycopodium cernuum-type (Lycopodiaceae)
Lycopodium clavatum-type (Lycopodiaceae)
Lygodium volubile (Schizaeaceae)
Malpighiaceae
Malvaceae
Mandevilla-type (Apocynaceae)
Marattia verschaffeltiana-type (Marattiaceae)
Marcgravia polyantha-type (Marcgraviaceae)
Matayba (Sapindaceae)
Melastomataceae
Meliosma (Sabiaceae)
Menispermaceae
Mimosa invisa-type (Mimosaceae)
Mimosa scabrella-type (Mimosaceae)
Mimosa taimbensis-type (Mimosaceae)
Mimosa-type I (Mimosaceae)
Mimosa-type II (Mimosaceae)
Mimosa-type III (Mimosaceae)
Moritzia dasiantha (Boraginaceae)
Mucuna altissima (Papilionaceae)
Myriophyllum type (Haloragaceae)
Myrtaceae
Nephelea setosa (Cyatheaceae)
Notofagus dombeyi-type (Fagaceae)
Nuphar (Nymphaeaceae)
Ocotea-type (Lauraceae)
Orchidaceae
Oreopanax fulvum-type (Araliaceae)
Osmunda (Osmundaceae)
Ouratea type (Ochnaceae)
Oxalis-type I (Oxalidaceae)
Oxalis-type II (Oxalidaceae)
Palmae
Pamphalea (Asteraceae)
Papilionaceae-type I
Papilionaceae-type II
Papilionaceae-type III
Papilionaceae-type IV
Parapiptadenia-type (Mimosaceae)
Pavonia (engleriana)-type (Malvaceae)
Pera obovata-type (Euphorbiaceae)
Petunia-type (Solanaceae)
Pfaffia gnaphalioides (Amaranthaceae)
Phaeoceros laevis (Anthocerotaceae)
Phrygilanthus acutifolius (Loranthaceae)
Phyllanthus caroliniensis-type (Euphorbiaceae)
Phyllanthus-type (Euphorbiaceae)
Pinus (Pinaceae)
Piper (Piperaceae)
Piptadenia-type (Mimosaceae)
Plantago australis-type (Plantaginaceae)
Plantago turficola-type (Plantaginaceae)
Poaceae
Podocarpus (Podocarpaceae)
cf. Polemoniaceae
Polygala (Polygalaceae)
Polygonum (Polygonaceae)
Potamogeton-type (Potamogetonaceae)
Pouteria garderana (Sapotaceae)
Pouteria venosa (Sapotaceae)
Prockia crucis-type (Flacourtiaceae)
Pseudobombax grandiflorum (Bombacaceae)
Psychotria alba-type (Rubiaceae)
Psychotria barbiflora-type (Rubiaceae)
Pteridophyta-type 1 at Pteridophyta type 7
Pteris-type (Pteridaceae)
Rabdadenia pohlii (Apocynaceae)
Ranunculus bonariensis-type (Ranunculaceae)
Rapanea (Myrsinaceae)
Rhamnus-type (Rhamnaceae)
Rhipsalis (Cactaceae)
Richeria australis-type (Euphorbiaceae)
Roupala-type (Proteaceae)
Salix humboldtiana-type (Salicaceae)
Salvia type (Labiatae)
Sapium glandulatum (Euphorbiaceae)
Schinus-type (Anacardiaceae)
Schizaea attenuata (Schizaeaceae)
Schizaea elegans (Schizaeaceae)
Scutellaria-type (Labiatae)
Sebastiania brasiliensis (Euphorbiaceae)
Sebastiania commersoniana (Euphorbiaceae)
Sebastiania schottiana-type (Euphorbiaceae)
Securidaca-type (Polygalaceae)
Selaginella decomposita (Selaginellaceae)
Selaginella excurrens-type (Selaginellaceae)
Senecio type (Asteraceae)
Serjania (Sapindaceae)
Sickingia sampaioana-type (Rubiaceae)
Sicyos (bryoniaefolius)-type (Cucurbitaceae)
Solanum-type (Solanaceae)
Sphagnum (Sphagnaceae)

Struthanthus (Loranthaceae)
Styrax (Styracaceae)
Symplocos lanceolata-type (Symplocaceae)
Symplocos laxiflora-type (Symplocaceae)
Symplocos nitens (Symplocaceae)
Symplocos tenuifolia-type (Symplocaceae)
Ternstroemia brasiliensis-type (Theaceae)
Tetrorchidium rubrivenium (Euphorbiaceae)
Trichocline (Asteraceae)
Trifolium (Papilionaceae)
Trixis (Asteraceae)
Type 1 at type 23
Typha domingensis (Typhaceae)
Urticales-type (Urticaceae, Moraceae, *Trema*)
Urvillea (Sapindaceae)
Utricularia (Lentibulariaceae)
Valerianaceae
Valeriana (stenophylla)-type (Valerianaceae)
Vantanea compacta (Humiriaceae)
Verbena isabellii (Verbenaceae)
Verbena-type (Verbenaceae)
Vernonia-type (Asteraceae)
Vicia-Lathyrus (Papilionaceae)
Virola oleifera (Myristicaceae)
Wahlenbergia-type (Campanulaceae)
Weinmannia type (and *Sloanea*) (Cunoniaceae)
Xyris (Xyridaceae)
Zea mays (Poaceae)
Zornia latifolia-type (Papilionaceae)