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A palynological record of Late Quaternary vegetational and climatic change in southeastern Brazil

De Oliveira, Paulo Eduardo, Ph.D.
The Ohio State University, 1992
A PALYNOLOGICAL RECORD OF LATE QUATERNARY
VEGETATIONAL AND CLIMATIC CHANGE IN
SOUTHEASTERN BRAZIL

DISSERTATION

Presented in Partial Fulfillment of the Requirements for
the Degree Doctor of Philosophy in the Graduate
School of The Ohio State University

By

Paulo Eduardo De Oliveira, B.S., M.S.

* * * *

The Ohio State University
1992

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Department of Zoology
A minha querida avó Francisca por ter me ensinado o amor pelas plantas, a
meus pais pelo amor, paciência e confiança em mim depositados, e à
natureza do Brasil, pela fonte de energia e inspiração, dedico este trabalho.
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275.

response to years of PO$_4$ fertilization: Kuparuk River, Alaska (68 N Lat.).
*Hydrobiologia* 240: 103-119.


FIELD OF STUDY

Major Field: Zoology.
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VEGETATIONAL AND CLIMATIC CHANGE IN 
SOUTHEASTERN BRAZIL 
By 
Paulo Eduardo De Oliveira, Ph.D. 
The Ohio State University, 1992 
Professor Paul A. Colinvaux, Adviser 

Two lake sediment sequences were retrieved from southeastern Brazil, with the objective of reconstructing the environmental history of the region, mainly the changes in vegetation and climate during the Late Quaternary. 

The first site, Lagoa da Serra Negra, occupies an almost circular basin on an ancient volcanic caldera at 1200 m elevation in western Minas Gerais. The second site, Lagoa dos Olhos occupies a small rectangular basin on the karst region of south central Minas Gerais, at 730 m elevation. 

The sediments, were analysed for pollen, plant and algal spores, diatoms, chlorophyll sedimentary units and were dated by the radiocarbon technique. The results indicate that very drastic vegetational changes occurred in the landscape of Minas Gerais during most of the last glacial period. A tropical coniferous forest, extensively dominated the landscape of western Minas Gerais, and possibly most areas above 800 m in southeastern Brazil, 

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prior to 40000 years BP (Before Present). This forest was characterized by the presence of two tropical gymnospermous taxa, *Araucaria* and *Podocarpus*. Also present in this forest were plants belonging to Myrtaceae, *Ilex*, *Symplocos*, *Rapanea* and *Drimys*. Presently, this type of forest is characteristic of moist regions with pronounced cooling in the winter. These conditions are characteristic of regions with latitudes higher than 24°S and in the high elevations of the mountain region of southeastern Brazil. Therefore, the existence of extensive *Araucaria* forests prior to 40000 years BP indicates pronounced temperature depression of ca. 7-9°C during the austral winter of western Minas Gerais during that time. Cooling and moist conditions were interrupted a number of times, thus allowing the expansion of semi-deciduous forests and cerrados to replace the cool and moist coniferous forests. However, there are no indications in the record for glacial aridity in any of the sites. Glacial cooling with concomitant increased moisture during the Late Quaternary of Minas Gerais is attributed to a northward 5° latitude displacement of the Atlantic Polar Front, which in the austral winter was positioned as far north as 18°S.
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INTRODUCTION

The results of Connell's studies (1978, 1979) on tropical diversity provided a mechanism through which some rich tropical ecosystems could maintain or augment diversity with disturbance regimes. These studies and the accumulating paleoecological evidence from the tropics brought to an end the long held belief in that tropical regions had remained unchanged in a benign environment for long periods of geological time (Flenley 1979, Colinvaux 1987). During the 1970's and early 1980's palynological evidence for climatic and vegetational changes during glacial times in the high mountain areas of South America (van Geel & van der Hammen 1973, van der Hammen 1974, Hooghiemstra 1984) started to accumulate. Information about the past climate of oceanic islands, i.e. Galapagos Archipelago (Colinvaux 1972), New Guinea (Flenley 1972), Malaysia (Flenley & Morley 1978) also became available. Previous to these developments, the palaeoecology of Africa had an earlier start, and provided proof of significant cooling and drying conditions there, during the time of glacial expansion in the northern hemisphere (Kendall 1969, Livingstone 1971, Coetzee 1967). The African data set prompted intensive efforts by biogeographers and geomorphologists, who started to search for evidence of ice age drying in the tropical regions of South America. The culmination of these efforts resulted in a congress led by biogeographers (Prance 1982), which compiled all the indirect evidence available to support the
then emerging Forest Refuge Hypothesis (Haffer 1969, 1974, Prance 1982). This hypothesis suggests that during the supposedly dry and cold climate of the last ice age tropical forests from the eastern Brazilian coast to the Isthmus of Panama retracted into refugia on high elevation areas, where orographic rains were able to maintain them as intact communities. According to Haffer (1969), the isolation of certain bird populations promoted allopatric speciation in the postulated isolated forest refugia. This argument was used by Haffer (1969) to explain the present disjunct distribution of some bird species over the Amazon basin. Disjunct distributions of angiosperms (Prance 1982), butterflies (Brown 1982) and other animal and plant groups were then used as indirect evidence for past forest refugia during the glacial maxima, when drier savanna supposedly expanded throughout most the continental area of South and Central America. The first palynological records from the South American tropical lowlands provided by Absy (1979) encompassed only the last 6000 years of the Holocene of the flooding valleys of Amazonian rivers. The results showed fluctuations in the Gramineae curve, indicative of fluctuating river levels, and brought no light on the problem as clearly stated by the author (Absy 1982). Recent palynological evidence from areas within the postulated Napo refuge in Ecuador (Liu & Colinvaux 1985; Bush et al. 1990) shows no evidence for the Refuge Hypothesis. A complete glacial sequence from the Isthmus of Panama (Bush & Colinvaux 1990) also provides no evidence for this hypothesis. These palynological investigations do show, however, the presence during glacial times of unexpectedly different tropical forests, composed of a mixture of elements from different biomes. These lowland mosaic forests, with no modern analogs, existed during a time when climate
was characterized by temperatures depressed as much as 9°C, when compared to present temperatures.

While tropical palaeoecological thought was revolving around the Refuge Hypothesis, a new line of thought was being developed by Davis (1981) that challenged old beliefs concerning stability of plant communities during glacial times. By examining 62 available pollen diagrams from the eastern United States covering the last 20000 years, Davis (1981, 1983a, 1983b, 1984) had shown that all present forest communities extending from Florida to Michigan have had very different histories since the time of maximum glaciation in North America. Tree taxa migrated at different rates following different routes. Davis's results clearly showed that the southward migration of the deciduous mixed mesophytic forests of eastern United States as intact and discrete plant communities advocated by Braun (1955) did not occur. Rather, the forests have been changing their floristic composition since the last glacial maximum. The ecological implications of these results are great and refer to the controversial nature of plant communities generated by the two opposing schools of thought, i.e. the Clementsian and Gleasonian points of view.

The Clementsian or the classic view of communities (Clements 1916) advocates that climax formations are capable of reproducing and repeating the stages of their development with great fidelity. Clements also suggested that the life-history of plant formations parallel that of an individual plant, thus suggesting that plant communities can be thought of superorganisms, or entities composed of many species with inherent properties (Colinvaux 1986). This particular view of plant communities suggests therefore that plant communities, regardless of its developmental or successional stage have very definite, and predictable floristic compositions.
The alternative view put forward by Gleason (1926) simply argues that plant communities can be thought of collections of individuals that share common environmental requirements. Floristic composition of a plant community under the Gleasonian point of view is explained as a consequence of accidental dispersal and a fluctuating environment. Furthermore, unlike the Clementsian point of view, Gleason's view of plant communities is that of unstructured collections of individuals (Ehrlich & Roughgarden 1987).

The individualistic view of communities of Gleason (1926) found strong support in the late 1970's when the results of the large palynological data set available for North America and Europe was analysed. Gleason's individualistic concept of communities reemerged when Davis (1981) stated that "the history of spread of trees northward during the present interglacial leads inevitably to an individualistic view of plant communities. " There was no evidence in the pollen diagrams analyzed by Davis for the Clementsian superorganismic view of communities (Clements 1916).

During the rediscovery of Gleason's point of view, supported by the palynological record of temperate forests, and the continuing debate over the existence of tropical forest refuges, a new line of research became increasingly important in North America and Europe. Concerns about possible drastic future global environmental changes led to the increased interest by paleocologists in producing Climatic Models, which based on former climatic changes, attempt to infer the future climate of the Planet. Climate modelers (Peterson et al. 1979; Kutzbach & Street-Perrott 1985; Kutzbach 1987) all face the problem of producing models that appear to have very little predictive power for lowland
South America and other tropical regions of the Southern Hemisphere. This is clearly understood by the climate modelers as consequence of inexistence of paleocological data from these areas. The lack of paleoecological data from non-Andean South America is great. In a review of the Holocene climatic history of South America by Markgraf & Bradbury (1982), the only record from Brazil, a country with 47.7 % of the total land surface of South America, was the short Holocene sequence of Absy (1979). Seven years later, another review of the palaeoecological information from South America by one of the authors (Markgraf 1989), the same sequence of Absy (1979) appears as the only one available for Brazil.

The present research was designed to test current palaeoecological hypothesis and to provide two additional records from the late Quaternary of Brazil. Under study is the southeastern region of Brazil, an area palaeoecologically less known than that of the Amazon. Two sites were selected based on lake characteristics, location, as well as their geographical position in relation to the principal plant formations of southeastern Brazil.
The Hypotheses

The primary objective of this research is to test the following hypotheses:

**Hypothesis 1. Tropical forests took refuge at higher elevations during the time of maximum glaciation in the northern hemisphere. This allowed the expansion of semi-arid vegetation in southeastern Brazil during a supposedly dry climate.**

The choice of sites of this study is suitable to the testing of this hypothesis. The first site, Lagoa da Serra Negra, a lake at 1200 m elevation and the second site, Lagoa dos Olhos, at 730 m, are located outside the main centres of proposed forest refuges in southeastern Brazil: the Atlantic rainforest and the central Brazil forest refuges (fig. 1) proposed by Prance (1982) after examining the distribution of certain neotropical woody angiosperm taxa in Brazil. The refuge hypothesis (Haffer 1969, 1974; Prance 1982) predicts that during the last glacial maximum in the north (ca. 18000 yr BP) most of the southeastern Brazil landscape was covered by semi-arid vegetation of the caatinga type, i.e. thorn-scrub and xeromorphic vegetation presently found in semi-arid regions of northeastern Brazil, or cerrado vegetation. Therefore, presence of tropical forests or any other type of vegetation typical of humid climates in the sites during the time of maximum glaciation would inevitably falsify this hypothesis.

**Hypothesis 2. Tropical forest communities are stable through time.**

There are two opposing views on the stability of tropical forests. Supporters of the Refuge Hypothesis advocate the maintenance of forests in
Fig. 1. Location of study sites in relation to proposed Late-Pleistocene tropical forest refuges for central and coastal Brazil, based on the distribution of neotropical angiosperm taxa (Prance 1982). (Modified from Prance 1982).
refuge, with stable floristic compositions, i.e. rainforest communities retracted to hilltops as intact and discrete communities. The other point of view, for which the evidence is very strong, refers to the ephemeral nature of communities, as demonstrated by Davis (1980, 1983a, 1983b).

Hypothesis 3. Expansion of *Araucaria* forests occurred in southeastern Brazil during times of cooling of the last ice age.

This hypothesis can be stated as follows: during the time of the last glaciation in the northern hemisphere, there was widespread temperature depression in continental Brazil. This cooling favored the expansion of the southern *Araucaria* forests, which reached the mountains of southeastern Brazil, forming a continuous coniferous belt. This hypothesis was indirectly suggested by Dansereau (1957) and was formally presented by Ab'Saber (1982), who suggested the expansion of *Araucaria* reached latitudes as far north as 18°S during the last glacial maximum. If this hypothesis is supported by the pollen records, this would imply that the present disjunct *Araucaria* forest islands of São Paulo, Minas Gerais and elsewhere in southeastern Brazil may represent relics of a continuous forest belt that existed during the last glacial maximum.

Hypothesis 4. Climatic changes in southeastern Brazil and southern South America were synchronous in the last ice age.

If Late Quaternary cooling occurred in southeastern Brazil, it had somehow to be associated with changes in the climate of southern South America, since cold polar air surges into Brazil originate in the higher latitudes of that continent (Nimer 1989a). These cold air surges into Brazil today during
the winter are responsible for the maintenance of the cool and wet climate of the present contiguous *Araucaria* forest region (Nimer 1989). Intensification or interruption of this system in the past, would have drastic consequences for the vegetation of southern and southeastern Brazil.
THE STUDY SITES

Two sediment sequences were obtained from two locations in the state of Minas Gerais, southeastern Brazil. The first site, Lagoa da Serra Negra, is located in the westernmost section of the state and is part of the Central Brazilian Plateau. Lagoa dos Olhos, the second site, is located in the municipality of Lagoa Santa, central Minas Gerais, 38 km north of the capital city Belo Horizonte.

Site A. Lagoa da Serra Negra

This lake presently occupies a considerable area of the large caldera, named Serra Negra (Plate I), which was formed during the extensive late Mesozoic volcanism of southern Brazil (Gomes et al. 1990). The caldera lies between 18°55' and 19°00' S; 46°45' and 46°57' W and has an approximate external diameter of 12 x 15 km (Maio 1987). Lagoa da Serra Negra was most likely formed by collapse of the terrain due to dissolution of underground carbonatite (Barbosa et al. 1970), presently under 200 m of a laterite crust (Gomes et al. 1990). The present shallow lake occupies a 2.5 x 4 km basin. Since 1989, the site was visited three times, during both the dry and wet seasons and no apparent difference in lake level was observed. Residents of the area claim that to their knowledge the lake has never dried out. Altitude of
Plate I. Aerial view of the Serra Negra caldera. The schematic representation of the caldera below indicates the location of Lagoa da Serra Negra. (Picture on Plate I, shown in Maio (1988), by Prospec S.A. 1965, available at DNPM-Belo Horizonte, Minas Gerais)
the inner crater rim varies from 1250-1273 m above sea level. Elevation at the lake is 1170 m (Barbosa et al. 1970). Lake depth in most of its area is 50 cm but a 6 m deep hole is found at its northern edge, where coring was performed. The site is ideal for palynological studies because of the large diameter of the caldera, and its internal drainage system, thus rendering characteristics of a giant trap for regional pollen. Recent Landsat imagery (Plate II) shows extensive agricultural activities in the crater, responsible for the great load of sediments being deposited into the lake.

Geology and Climate

Ringlike structures or dykes, surround the crater and are composed of Precambrian/Cambrian quartzite rocks (Fig. 2). Two exposures of alkaline rocks occur in the north part of the caldera, which is drained northwards by two streams, not in contact with the lake (Barbosa et al. 1970).

The climate of the Serra Negra site is classified as Aw according to the Köppen classification system, a climate characteristic of tropical savanna regions, i.e. warm and seasonally dry in the winter and moist and warm in the summer. Average annual rainfall is 1600 mm, which is unevenly distributed throughout the year. Spring and summer months (September to February) account for 80 % of that amount. Mean annual temperature is 21.9°C. Mean temperature of the coldest month (June) is 18.8°C, whereas the warmest month (October) has a mean temperature of 24°C. Lowest and highest temperature values have averages of 15.2°C and 27.4°C, respectively (Source: Meteorological Station Estação Auxiliar de Patrocínio, Instituto de Meteorologia, 5º Distrito).
Plate II. Landsat imagery of the Serra Negra caldera taken in 1989. The white and dark polygonal fields represent areas of agricultural activities, mainly coffee plantations.
Plate II.
Fig. 2. Geological map of the Serra Negra volcanic structure. The caldera rim is composed of Pre-Cambrian/Cambrian quartzite rocks. Lagoa da Serra Negra lies on a 200 m deep lateritic crust (T1). The outlet stream flows northward towards the village of São João da Serra Negra. Alkaline rocks (du) are found in the northern section of the caldera. (From Barbosa et al. 1970).
Fig. 2.
Vegetation

Cerrado (savanna) is the most abundant type of plant formation in the region, although Cerradão (forest-like or tall cerrado) is widespread on many areas. Both cerrado and Cerradão are present as fragments of the original vegetation on areas of the caldera. Seasonal semi-deciduous tropical forest predominates on the outer caldera slopes where rich volcanic soil prevails. A transition from this type of forest to gallery forest occurs on the waterlogged soils adjacent to the lake and accompanying the northward flowing outlet stream. Most of the semi-deciduous forest, cerrado and Cerradão, formerly found within the caldera, have been replaced by coffee plantations. The extent of deforestation and intensity of agricultural activities within the Serra Negra caldera can be visualized by comparing the aerial photograph taken in 1965 (Plate I) to the July 20, 1989 Landsat imagery of the site (Plate II).

Typical elements of the seasonal semi-deciduous forest found on the slopes and hills of the Serra Negra are: *Andira* sp (Fabaceae), *Aspidosperma polyneuron* (Apocynaceae), *Bowdichia virgilioides* (Fabaceae), *Cabralea cangerana* (Meliaceae), *Cariniana estrellensis* (Lecythidaceae), *Cedrela fissilis* (Meliaceae), *Chorisia speciosa* (Bombacaceae), *Erythrina falcata* (Fabaceae), *Hymenaea courbaril* (Caesalpinioideae), *Luehea divaricata* (Tiliaceae), *Machaerium* sp (Fabaceae), *Nectandra* sp. (Lauraceae), *Piptadenia communis* (Mimosaceae). On the external slopes of the caldera, from the base to the rim, there is a gradual replacement of semi-deciduous forest taxa by cerrado (savanna) elements. Sections of forest reoccur in the center of the caldera on the northern lake margin. At this particular location, there is a patch where cerrado and seasonal tropical forest taxa coexist side-by-side. Cerrado elements found at edge of lake are: *Caryocar brasiliensis* (Caryocaraceae),
Qualea grandiflora (Vochysiaceae), Kielmeyera coriacea (Clusiaceae), Kielmeyera sp (Clusiaceae). Other members of Vochysiaceae, especially Vochysia thyrsoidea and other species of Vochysia are more common on the higher and drier soils of the caldera. Other cerrado elements also occurring in the better drained soils of the crater are: Jacaranda decurrens (Bignoniaceae), Lafoensia densiflora (Lythraceae), Palicourea rigida (Rubiaceae), Pouteria sp. (Sapotaceae), Psidium sp. (Myrtaceae), Solanum grandiflorum (Solanaceae), Stryphnodendron adstringens (Mimosaceae), many Compositae herbs and grasses. Aquatic plants cover large areas of the lake, especially Eichhornia azurea (Pontederiaceae). Around the edge of the lake, Juncus sp. (Juncaceae), Ludwigia cf. brasiliense (Onagraceae), Polygonum hydropiperoides (Polygonaceae), Pontederia sp. (probably P. lanceolata) are commonly found. On the flooded flat edges of the lake, many specimens of Drosera sp. (Droseraceae), are invariably found submersed under a thin lamina of water. Floating islands of grasses with associated Blechnum (Blechnaceae) plants are commonly dispersed throughout the lake.

Site B. Lagoa dos Olhos

This small lake, occupies a somewhat rectangular basin of 1 x 0.25 km, located within the karst region of central Minas Gerais at 19°38'S  43°54'W, elevation 730 m. The lake basin has a small outlet stream and is located 1 km southwest of the larger renowned lake Lagoa Santa (Plate III). Because there is no cyclic changes in water level of Lagoa Santa, Kohler (1978) defines it as a pseudo-karst lake. Therefore, the same term can be applied to Lagoa dos
Plate III. Aerial photograph of Lagoa dos Olhos (indicated by arrow on the left hand corner of the photograph) and Lagoa Santa (large triangular shaped lake), surrounded by city of Lagoa Santa, south central Minas Gerais.
Plate III.
Olhos, because it also does not show any considerable water level changes found in the true karst lakes of this region.

Geology and Climate

The basic rock matrix in the region of Lagoa Santa is gneiss of Archean age (Schobbenhaus et al. 1984) overlaid by calcareous rocks, and by phyllite, a metamorphic rock, which is found exposed in various locations (Kohler 1978). Dissolution of the underneath calcareous rocks has been suggested for the origin of the Lagoa Santa (Kohler 1978). It is very likely that Lagoa dos Olhos also represents a dissolution basin.

Average annual rainfall of the area is 1381 mm, most of which occurs during the spring and summer months. Highest precipitation values occur in January with the lowest rainfall values in August. Approximate number of rainy days is 105. Average annual temperature is 20.8°C. Average of high temperature values is 27.2°C and average for the minimum temperature values is 15.4°C. Record high temperature is 35°C and record low is 2°C. (Kohler & Malta 1991; Kohler 1978).

Vegetation

The original vegetation around Lagoa Santa, and consequently around Lagoa dos Olhos, was systematically eliminated since the time of the floristic survey by Warming (1892, 1902) when a semi-deciduous forest was present on the southwestern and western margins of Lagoa Santa, whereas cerrado was found mainly on its eastern margin. This suggests that the modern vegetation of the region, prior to interference by European settlers on the landscape, was composed of a mosaic of seasonal forests and cerrado. Some of the important
tree taxa found in the primary forests by Warming were: *Acacia polyphylla* (Mimosaceae), *Astronium fraxinifolium* (Anacardiaceae), *Cassia ferruginea* (Caesalpinioideae), *Cedrella fissilis* (Meliaceae), *Chorisia speciosa* (Bombacaceae), *Hymenaea stilbocarpa* (Caesalpinioideae), *Copaifera langsdorfii* (Caesalpinioideae), *Machaerium angustifolium* (Fabaceae), *Melanoxylum brauna* (Caesalpinioideae), *Protium heptaphyllum* (Burseraceae), *Tapirira guianensis* (Anacardiaceae), *Vochysia tucanorum* (Vochysiaceae), and many others. Warming (1892) indicated that the forests of the Lagoa Santa region had variable floristic compositions in different areas although the families Papilionaceae, Caesalpinioideae and Myrtaceae were the most diversified and abundant in any of his surveys.
THE STUDY SITES IN RELATION TO THE PRESENT VEGETATION AND CLIMATE OF SOUTHERN AND SOUTHEASTERN BRAZIL

The vegetation between the two sites under study is a mosaic composed of various plant formations, principally cerrado with its various physiognomic categories and seasonal or semi deciduous tropical forest. From Lagoa dos Olhos towards the Atlantic coast, there is a clear transition to moist evergreen tropical rainforests. To the south, lies the domain of seasonal, semi-deciduous forests and in the states of Paraná, Santa Catarina and Rio Grande do Sul, the contiguous mixed coniferous forests of Araucaria. To the north, lies the central Brazil core area of cerrado (fig. 3,4).

Cerrado

The word cerrado has various meanings in Brazil and its closest equivalent in English is the term savanna (Eiten 1972). However, due to the distinct floristic, physiological and structural characteristics of the Brazilian cerrados, this term should be preferentially used to distinguish them from the African savannas. As defined by Eiten (1972), in its wide sense, cerrado s.l. (sensu lato) is a phytogeographical province, with its core area in central Brazil. In this area cerrado s.l. is composed of a rich mosaic of plant associations, varying from forest-like to grassland vegetation. In its restricted sense or cerrado s. str. (sensu stricto) (Goodland 1969), it refers to a type of
Fig. 3. Simplified map of the Brazilian vegetation. The core area of cerrado (s.l.) is located in central Brazil, although cerrado vegetation is found as islands in Amazonia, southern and southeastern Brazil (From Romariz 1974).
Fig. 4. Simplified map of the vegetation of southern and southeastern Brazil (modified from Hueck 1966). The location of the study sites is indicated by star signs.
xeromorphic and floristically diverse plant association, composed of closely spaced trees. This particular association constitutes one of the five cerrado categories (Eiten 1963, 1972, 1986; Goodland 1969). The other cerrado categories are: Cerradão, a tall arboreal forest-like association with a closed or semi-closed canopy, which normally reaches 6-18 m in height. Campo-Cerrado or savanna-like cerrado, is characterized by the presence of medium sized trees (3-6 m) scattered on the landscape, which is dominated by grasses and other herbs. Campo sujo, is an association composed of herbs, woody plants, small shrubs and occasionally small trees, whereas Campo Limpo, is a steppe-like plant association composed primarily of grasses and other herbs. According to Eiten (1972) typical arboreal genera of the cerrado s.l. are: *Anacardium* (Anacardiaceae), *Andira* (Fabaceae), *Annona* (Annonaceae), *Aspidosperma* (Apocynaceae), *Bowdichia* (Fabaceae), *Byrsonima* (Malpighiaceae), *Caryocar* (Caryocaraceae), *Copaifera* (Caesalpiniaceae), *Diospyros* (Ebenaceae), *Curatella* (Dilleniaceae), *Dimorphandra* (Caesalpiniaceae), *Diospyros* (Ebenaceae), *Hancornia* (Apocynaceae), *Lafoensia* (Lythraceae), *Luehea* (Tiliaceae), *Kielmeyera* (Clusiaceae), *Protium* (Burseraceae), *Qualea* (Vochysiaceae), *Vochysia* (Vochysiaceae), *Roupala* (Proteaceae), *Salvertia* (Vochysiaceae) and others. In general terms, the core area of cerrado is located in central Brazil (fig. 3), where mean annual precipitation values range from 1000 to 2000 mm, which are unevenly distributed throughout the year. Precipitation is concentrated in the summer, whereas winters are exceptionally dry. Number of dry months can be as many as five in certain areas of the core region of cerrado. Winter average temperatures in central Brazil are normally above 15°C (Nimer 1989a; Nimer 1989b; Nimer & Brandão 1989).
The Atlantic Rain forest

This forest once formed a contiguous forested corridor along the Brazilian coast, from 30°-60°S (Hueck 1978). Presently, only fragments of primary forests can be found, especially in São Paulo, Paraná, southern Bahia and Espírito Santo. The Atlantic forest in its primary conditions is composed of an emergent tree layer composed of large evergreen trees that can reach up to 40 m in height. According to Hueck 1966, Joly 1975, important arboreal genera in the Atlantic rain forests are: *Alchornea* (Euphorbiaceae), *Anacardium* (Anacardiaceae), *Apuleia* (Caesalpiniaceae), *Cabralea* (Meliaceae), *Caesalpinia* (Caesalpiniaceae), *Cariniana* (Lecythidaceae), *Cecropia* (Moraceae), * Cedrela* (Meliaceae), * Centrolobium* (Fabaceae), * Chorisia* (Bombacaceae), * Copaifera* (Caesalpiniaceae), * Dalbergia* (Fabaceae), * Didymopanax* (Araliaceae), * Enterolobium* (Mimosaceae), * Euplassa* (Proteaceae), * Jacaranda* (Bignoniaceae), * Lecythis* (Lecythidaceae), * Luehea* (Tiliaceae), * Machaerium* (Fabaceae), * Melanoxylon* (Caesalpiniaceae), * Nectandra* (Lauraceae), * Ocotea* (Lauraceae), * Parapiptadenia* (Mimosaceae), * Pouteria* (Sapotaceae), * Protium* (Burseraceae), * Pseudobombax* (Bombacaceae), * Pterogyne* (Caesalpiniaceae), * Roupala* (Proteaceae), * Schizolobium* (Caesalpiniaceae), * Tabebuia* (Bignoniaceae), * Tapirira* (Anacardiaceae), * Vochysia* (Vochysiaceae) and many others.

The climate of the region of the Atlantic forest is characterized, in general terms, by an absence of a dry season. Precipitation values range from 1500-4000 mm annually and winter average temperatures are normally above 15°C (Nimer 1989a).
Seasonal semi-deciduous tropical forests

These forests, in their primary and undisturbed state in central and southeastern Brazil, are characterized by large and tall emergent trees, forming an upper canopy averaging 30 m in height (Waibel 1948). A second arboreal layer is present at 15 m, whereas the shrub layer is one to two meters tall. Important tree genera in these forests are: *Apeiba* (Tiliaceae), *Apuleia* (Caesalpiniaceae), *Aspidosperma* (Apocynaceae), *Balfourodendron* (Rutaceae), *Bathysa* (Rubiaceae), *Bowdichia* (Fabaceae), *Cedrela* (Meliaceae), *Chorisia* (Bombacaceae), *Daphnopsis* (Thymelaeaceae), *Enterolobium* (Mimosaceae), *Hymenea* (Caesalpiniaceae), *Luehea* (Tiliaceae), *Mabea* (Euphorbiaceae), *Nectandra* (Lauraceae), *Schinus* (Anacardiaceae), *Tabebuia* (Bignoniaceae), *Vochysia* (Vochysiceae) and others. Important genera of shrubs of these forests are: *Campomanesia* (Myrtaceae), *Eugenia* (Myrtaceae), *Faramea* (Rubiaceae) among many others. On the Central Brazilian Plateau, prior to deforestation, this type of tropical forest was very widespread and occupied the large river valleys and the humid mountain slopes (Waibel 1948, James & Faissol 1956).

The climate of the semi-deciduous tropical forest region is characterized by a dry season of 1 to 3 months, average annual rainfall of 1500 mm, and winter temperatures ranging from 10 to 15°C (Hueck 1966; Nimer 1989a; Nimer 1989b; Nimer & Brandão 1989).

*Araucaria* forests

The Brazilian pine tree, *Araucaria angustifolia*, forms when mature a large corymbose canopy (see Appendix B), which bestows to this forest a distinct and readily recognized physiognomy. One characteristic of mature
Araucaria forests that sets them apart from other tropical forests is the presence of a monospecific emergent tree layer, i.e. composed only of Araucaria angustifolia which can reach 30-40 m in height. This characteristic can lead the untrained visitor to view it as a low-diversity forest. The understory of this forest type, on the contrary, is highly diversified and composed of several types of associations, which vary according to the geographical location of the forest and its particular successional stage (Klein 1975). Important elements of this forest and their respective families, according to Klein (1975) are: Apuleia leiocarpa (Caesalpiniaceae), Aspidosperma olivaceum (Apocynaceae), Aspidosperma polyneuron (Apocynaceae), Casearia decandra (Flacourtiaceae), Cedrela fissilis (Meliaceae), Copaifera trapezifolia (Caesalpiniaceae), Clethra scabra (Clethraceae), Drimys brasiliensis (Winteraceae), Ilex paraguariensis (Aquifoliaceae), Ilex theezans (Aquifoliaceae), Lythraea brasiliensis (Anacardiaceae), Merostachys multitiramea (Poaceae = Gramineae), Myrciaria delicatula (Myrtaceae), Ocotea porosa (Lauraceae), Ocotea pulchella (Lauraceae), Parapiptadenia rigida (Mimosaceae), Podocarpus lambertii and Podocarpus sellowii (Podocarpaceae), Schinus therebinthifolius (Anacardiaceae), Siphoneugenia reitzii (Myrtaceae), Sloanea monosperma (Elaeocarpaceae), Styrax leprosus (Styracaceae), Symplocos celsatrinea, Symplocos itatiaiae, Symplocos nitidiflora, Symplocos uniflora (Symplocoaceae), Weinmannia paullinietolia (Cunoniaceae) and many other taxa. Tree ferns, usually present in the understory of this forest type belong to the families Dicksoniaceae and Cyatheaceae. In the aluvial Araucaria forest, common taxa are Podocarpus lambertii, Drimys brasiliensis, many elements of the Lauraceae, Sebastiana and other genera of the Euphorbiaceae, as well as the palm Arecastrum.
romanzoffianum, and the tree *Erythrina crista-galli*. In the montane *Araucaria* forests of Paraná, Santa Catarina and Rio Grande do Sul, the following taxa are common: *Ilex paraguariensis*, *Nectandra megapotamica*, *Ocotea porosa*. According to Veloso et al. (1991) *Podocarpus lambertii* and *Drimys brasiliensis* are important elements of the *Araucaria* forests of the southernmost states located at elevations higher than 1000 m.

The southernmost limit of this forest lies in the mountains of northern Rio Grande do Sul at approximately 30°S. From this latitude to 24°S the forest was continuous in its distribution. Most of this continuous forest area is now fragmented as a result of the intensive logging. The altitudinal distribution of the *Araucaria* forest is a function of the latitude. For example, in its southern limit (Rio Grande do Sul) this forest is found at altitudes varying as low as 400 m, whereas in Paraná, the northern limit of the contiguous forest, it is found in elevations up to 800 m (Hueck 1966, 1978; Romariz 1974). Beyond its northern limit at 24°S as a contiguous formation, *Araucaria* forests are found as scattered islands in the states of São Paulo, Minas Gerais, Rio de Janeiro and Espírito Santo, reaching latitudes as far north as 20°S (fig.4). In this region, the *Araucaria* forest islands, are found at higher altitudes (lower latitudes) of southeastern Brazil, more specifically on the Serra da Mantiqueira, Serra do Mar and Serra dos Orgãos. The altitudinal limit for these forest islands varies from 1000 m in São Gotardo, Minas Gerais (Hueck 1966) to 2000 m in Passa Quatro, Minas Gerais (Brade 1948). In Campos do Jordão, São Paulo, large *Araucaria* trees are found up to 1900 m in elevation (Mondanesi 1988).

*Araucaria angustifolia* requires average summer temperatures of 20-21°C and winter average temperatures ranging from 10 to 11°C, for optimum growth (Rizzini 1971). In southern Brazil only slight differences in climate are
found, which varies as a function of elevation. In regions 500-800 m in
elevation, winters are short with an average temperature lower or equal to
15°C, whereas summers with average temperature higher or equal to 20°C are
long and humid (Leite & Klein 1990). Areas higher than 800 m, are
characterized by longer winters (average winter temperature lower or equal to
15°C) and short summers and no dry season. Both regions have effectively no
dry season. Climatic maps of southern Brazil (Nimer 1989a) show that the core
area of the contiguous Araucaria forest lies within the 13°C average isotherm
for July, the coldest month. Number of days per year with frost in this area
varies from 5 to 30. Precipitation values within the total contiguous Araucaria
forest area vary from 1400 to 2450 mm, but are never lower than 1000 mm
annually (Hueck 1966). Climatologically, the areas of contiguous Araucaria
forest of southern Brazil show great similarities to the high elevation areas of
southeastern Brazil, where scattered Araucaria forest islands are found. For
example, In Campos do Jordão and Itatiaia (alt. 1600-2200), mean annual
temperatures range from 11.5 to 13.6°C. In both localities, number of days with
frosts are 46 and 56, respectively. Thus, the existance of Araucaria forests on
high elevations of lower latitudes is possible by maintenance of a moist
temperate-like climate in those areas. Climate limits for present day Araucaria
forests in both southern and in to locations of southeastern Brazil are
summarized on Table 1.
Table 1. Climate limits for present day *Araucaria* forests in southern and southeastern Brazil. Two southeastern sites, Campos do Jordão and Itatiaia represent two regions where the distribution of *Araucaria* is disjunct. Although the elevational range for *Araucaria* forests in most of its contiguous area in southern Brazil is 400-800 m, this forest is also found in altitudes higher than 800 m in this region. (From Nimer 1989a)

<table>
<thead>
<tr>
<th></th>
<th>Southern Brazil</th>
<th>Campos do Jordão, S. Paulo</th>
<th>Itatiaia, Rio de Janeiro/Minas Gerais</th>
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<td>ca. 23°S</td>
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<tr>
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<td>Annual average</td>
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<td>temperature °C</td>
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<td>11</td>
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<tr>
<td>Number of days with frost per year</td>
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<td>46</td>
<td>56</td>
</tr>
<tr>
<td>Annual precipitation (mm)</td>
<td>1400-2450</td>
<td>1563</td>
<td>2359</td>
</tr>
</tbody>
</table>
General climatic patterns of southeastern Brazil

The climate of southeastern Brazil is directly influenced by the presence of the subtropical anticyclone over the south Atlantic, the southern subtropical jet stream, and the polar air masses generated by the polar anticyclone of the higher latitudes of the southern hemisphere (Hastenrath 1985, Nimer 1989a, Rasool 1984).

The south Atlantic Anticyclone is a permanent high pressure system, which generates counterclockwise winds. During the austral winter (June-August), this high pressure system generates easterly winds, thus maintaining good weather in southeastern and central Brazil. GOES satelite photographs of South America usually show the conspicuous absence of clouds in most of Brazil during the winter months (Plate IV). Central Brazil, the core area of cerrados, has long winters characterized by the presence of warm and dry easterly winds. In Brasília, number of dry months are as many as five (Nimer & Brandão 1989), when relative humidity can reach very low values.

A very different climatic scenario prevails during the summer months. GOES satelite images of South America during the summer normally show increased cloud cover, over most of Brazil (Plate IV). This increased cloud cover and consequently rainfall, is a consequence of the southward migration of the Intertropical Convergence Zone (ITCZ) that occurs during the austral summer months (Hastenrath 1985, Nimer 1989a, Nimer & Brandão 1989). According to Hastenrath & Lamb (1977), the ITCZ reaches its southernmost position in March. GOES satellite image for summer circulation depicted in Plate IV shows the southernmost positioning of the ITCZ in March 1991, when southeastern Brazil, especially São Paulo experienced very severe flooding...
Plate IV. GOES satellite images of South America, showing general circulation in a winter day (left), when most of Brazil lacks cloud cover due to presence of easterly winds generated by the South Atlantic Anticyclone and absence of the Atlantic Polar frontal system. The approximate location of the present study sites are indicated by the two white dots, labelled SN (Serra Negra) and OL (Lagoa dos Olhos). The image on the right represents general circulation in March, when the ITCZ reaches its southernmost position (Hastenrath & Lamb 1977). GOES satellite images purchased at INPE-Cachoeira Paulista, São Paulo.
Plate IV.
conditions. Summer rains in southeastern Brazil are also a consequence of the mixing of dry Atlantic polar air with lower temperatures, with the warm and humid winds generated by the Atlantic anticyclone (Hastenrath 1985, Nimer 1989a). There is consistent decrease in number of dry months towards southern Brazil, which lacks a distinct dry season.

The subtropical westerly jet stream of the southern hemisphere is best developed during the austral winter and it can be best observed over the Australian and New Zealand region (Hastenrath 1985). However, in some years, this phenomenon becomes intensified in South America, when its strong westerly winds bring storms and high rainfall to southeastern Brazil. In 1983, this phenomenon became very intensified during the winter (Plate V), and showed some relationship to the El Niño phenomenon of that year (see below).

Of all the secondary circulation phenomena, the one of great importance to the present research is the South Atlantic Polar Frontal system, especially during the winter months of the southern hemisphere. This system refers to the cold air masses (Polar Pacific and Polar Atlantic) originating in the antarctic continent, which frequently advance into continental Brazil in its route towards the equator.

Originally the movement of the polar air masses follows two main routes determined by orography (Nimer 1989a). The first route follows the western side of the Andes along the Chilean coast, through which the Polar Pacific air mass brings frequent cold as well as light rains to coastal and central Chile, respectively (James 1939). The second route lies east of the Andes. When the second route is taken by the polar air masses, effects on climate are felt not only along the eastern side of the Cordillera but also in Brazil. An intricate sequence of events described in Nimer (1989a) determines which routes are
taken by the the cold polar air in its movement towards the equator. During the austral summer months, polar air moves into the continent following primarily the western route because the Pacific anticyclone is weakened and distant from the south american mainland. In the winter months, however, this anticyclone moves closer to the western coast of the continent, thus blocking the northward migration of the now stronger Polar Pacific air mass. This blockage forces polar air to take the eastern route, which it does after crossing over the southernmost section of the Cordillera. After passing across to the eastern side of the Cordillera, the cold polar air now becomes the Polar Atlantic frontal system, as it is intensified by thermal differences possessed by the tropical Atlantic air masses, which dominate the eastern section of the continent. The Polar Atlantic air mass in its movement towards the equator is broken into two main routes (Coyle 1940, Nimer 1989a) as it encounters the mountain chains of southern and southeastern Brazil. The western or continental route passes through the lowlands of the Chaco region leading to the interior of the continent and the second route follows primarily the the Brazilian coast with eventual dissipation of its strength in the Atlantic Ocean. According to Nimer (1989a) when the oceanic route is taken, the incident polar air reaching lower latitudes are eventually overpowered by the NE winds generated by the Atlantic anticyclone.

A strong equator-pole thermal gradient in the winter months favors the powerful incurrence of the Atlantic Polar air mass into Brazil (Nimer 1989a). Polar air can occasionally reach northern Mato Grosso in the winter when the continental western route is taken by the Atlantic Polar air mass. During abnormally cold winters, when this frontal system is greatly intensified, polar air reaches the Amazon basin bringing about significant temperature depression. According to Coyle (1940), this phenomenon widely referred to "friagem" in
Amazonia has claimed many lives among local inhabitants, when the
temperature can reach values as low as 10°C. It is also mentioned by the
author that for a long period of time, it was believed that the "friagem" was a
result of incurrence of cold Pacific air over the Andes and consequently into
central Amazonia. The polar nature of the "friagem" was indicated by James
(1939) on his maps of the migration of the polar air towards the equator.
Normally in the winter, this polar frontal system originating in northeastern
Argentina moves on northwards into Rio Grande do Sul, Santa Catarina,
Paraná, São Paulo, after which it starts to deflect eastwards towards Rio de
Janeiro, Espirito Santo and southern Bahia.

During the autumn months, this system can reach latitudes above the
Tropic of Capricorn, but the southern displacement of the ITCZ does not allow
incurrence of polar air to the lower latitudes. In the summer the Atlantic Polar
frontal system is restricted to its eastern or oceanic route. According to Monteiro
(1969), the most conspicuous position of this frontal system, in the winter, is
located at the border of Santa Catarina and Rio Grande do Sul. The region
including the northeastern, central and southern Parana, Santa Catarina and
Rio Grande do Sul are constantly under its influence, even in the summer
months (Monteiro 1969, Nimer 1989b). The northernmost limit of this system is
located in northern Paraná. Monteiro 's (1969) analysis of the percentual
participation of the different air masses in the winter for the latitudes between
28° and 32° S indicates that the polar air mass and the Polar Atlantic front
average 85% of the participation in the climate, which is influenced by the
intertropical system by only 15%. The climate at latitude of the states of São
Paulo and Rio de Janeiro, is characterized by a 50% participation of the polar
system. The polar air participation in the climate of the southern Brazilian
region, i.e., the states of Paraná, Santa Catarina and Rio Grande do Sul, is the sole factor determining the absence of a dry season. Rainfall is well distributed in this area all over the year (Nimer 1989a, 1989b; Monteiro 1969, Simões 1954).

Examples of winter temperature depression due to incurrence of polar air into southern Brazil are given by Monteiro (1969). In the winter of 1957, the following minimum temperature values for different localities were observed: Curitiba, -3°C; Porto Alegre, 2°C; Santa Catarina/Rio Grande do Sul border, -2°C; São Paulo, 3°C. Other exceptionally cold winters mentioned by Nimer (1989a) occurred in 1933, 1945, 1947 and 1955 with the following minimum temperatures in some southern locations: Guarapuava (Paraná) alt. 1116 m, -8.4°C; Palmas (Paraná) alt. 1090 m, -10°C; Xanxerê (Santa Catarina), -11.6°C.

El Niño Southern Oscillation and its effects in Brazil

The El Niño Southern Oscillation phenomena (ENSO) have been described in detail by various authors (see Kousky et al. 1984 for references). There appears to exist a strong correlation between increased rainfall in southern Brazil (Rasool 1984, Kousky et al. 1984) concomitant with ENSO events in western South America. A series of GOES satellite images taken during the El Niño phenomenon of 1983, shown on Plate V, indicate a prolonged blockage of the polar front in southern Brazil, which could not trespass the 20°S latitude. The region north of the blockage line remained under the influence of the warm and dry winds generated by the Atlantic anticyclone. The persistence of the polar front at this latitude produced
Plate V. GOES satellite images of the 1983 El Niño event. This sequence of photographs encompasses the period of June 10 (photo 83:161:15:17) to June 13, 1983 (photo 83:164:15:17). The increased cloud cover off the coast of Ecuador clearly shown on the bottom right photograph represents the cumulus-nimbus clouds related to the abnormally warm surface waters of the Pacific. The diagonal cloud line extending across the continent and conspicuously intensified over southern Brazil represents the position of a stationary Polar Atlantic Front (Suguio & Tessler 1989; Suguio & Tessler 1991). (Satellite photographs by INPE-Cachoeira Paulista, São Paulo)
Plate V.
abnormally high rainfall values for the southern states, including São Paulo, in synchrony with abnormally low values in central Brazil and in Amazonia (Kousky et al. 1984). Recently, this phenomenon which was observed in 1983 in Brazil, has been advocated by Martin et al. (1991, 1992) as a possible mechanism explaining the controversial and still debatable ice-age aridity in Amazonia.
FIELD METHODS AND MATERIALS

A 1.80 m long sediment core was retrieved from the deepest section of Lagoa dos Olhos at 3 m depth. A 7.82 m sediment sequence was retrieved from Lagoa da Serra Negra at the deepest point of the lake at 6 m depth. The sediments were secured with a modified Livingstone piston core sampler (Colinvaux 1986), operated from a wooden platform held by two inflatable boats. Coring operation was terminated whenever a dense layer of sediments or any other materials prevented further penetration. Core sections were sealed with corks at both ends and with fiberglass and duct-tape and transported to The Ohio State University, where they were stored in the dark at 4°C.

Surface sediment samples were collected in an undisturbed area adjacent to the coring site in both lake basins for use as modern analogs. In subsequent visits to Serra Negra and Lagoa dos Olhos, soil samples were collected under different vegetation types to provide further information on the modern pollen spectra of the area. Identification of fossil pollen taxa was facilitated by access to the tropical pollen reference collections of Dr. P. Colinvaux, containing ca. 3000 tropical angiosperm taxa, Dr. M.L. Salgado-Labouriau at the Universidade de Brasília, and Dr. M.L. Absy at INPA (Manaus). In addition, a modern reference pollen slide collection of approximately 500 taxa, present in the different forests of Minas Gerais and adjacent to the sites,
was prepared from catalogued specimens from the Missouri and New York Botanical Gardens herbaria. Extraction of pollen from herbarium materials followed the methodology described in Salgado-Labouriau (1973).
LABORATORY METHODS AND MATERIALS

Before opening, cores were x-radiographed with a Norelco MG-150 X ray unit on a 1:1 scale. This was done initially to determine if the original stratigraphy was perturbed during transportation of the sediments from the sites to the laboratory. Areas of the stratigraphic column showing reworking of the sediments were not sampled for any of the analysis. Furthermore, x-radiography can reveal important stratigraphic characteristics of the sediments, such as mineral laminations and other types of markers that can have paleoenvironmental significance.

All cores were opened with a router and their surfaces cleaned with a spatula for description according to texture, type and color by comparison with a Munsell Soil Chart. The cores were subsampled for pollen, loss on ignition (L.O.I.) at 550°C, chlorophyll, diatoms, and C14 analysis. A total of eleven sediment samples from Lagoa da Serra Negra and six from Lagoa dos Olhos were submitted to Beta Analytics Inc. for radiocarbon dating.

The methodology used in the L.O.I. determinations are described in Bengtsson & Enell (1986). Briefly, 0.5 cc sediment samples were weighed and combusted at 105°C for 24 hours, reweighed, and ignited at 550°C for 1 hour and reweighed for estimates of organic matter lost at 550°C.

A total of 65 sediment samples and 2 surface samples from Lagoa da Serra Negra were analysed palynologically, whereas those numbers for Lagoa
dos Olhos are 32 and 2, respectively. The technique used follows the methodology presented in Faegri & Iversen (1966, 1989): KOH, acetolysis (9 parts acetic anhydride : 1 part concentrated \( \text{H}_2\text{SO}_4 \)) for 5 min and 48% HF (1 hour boiling and 2 h cold in fresh acid). One tablet of exotic *Lycopodium clavatum* spores, containing 11300 ± 300 spores, was added to each sample to access pollen concentration (Stockmarr 1971). The residue was stained with 2% safranin solution and mounted in glycerine. Because the samples from Lagoa da Serra Negra had an overrepresentation of pollen of aquatic plants, a total of 300 terrestrial grains, including Gramineae and Cyperaceae, was counted at 10 cm depth intervals. For Lagoa dos Olhos, a total of 200 grains, excluding Alismataceae pollen, was counted at 5 cm depth intervals along the sediment sequence. The lower number of pollen counted, in the sediments of the latter lake, is due to the fact that the only aquatic pollen type that appeared to be found in large quantities was that of Alismataceae. Percentage and concentration values of spores and algal cells were obtained from the following calculations sums: \( \Sigma \) pollen + \( \Sigma \) spores (for spores); \( \Sigma \) pollen + \( \Sigma \) algal zygospores (for algae) (Berglund 1986).

Sampling interval in the Lagoa dos Olhos sequence was also decreased to compensate for the shorter sequence obtained and to increase resolution of the analysis. Pollen, spores and algal remains were counted at 600-1000 x magnification with a Leitz Ortholux light microscope. Identification of the different pollen types was accomplished by using published pollen keys and descriptions of Absy (1979), Heusser (1971), Hooghiemstra (1984), Kuhry (1988), Markgraf & D'Antoni (1978), Roubik & Moreno (1991) and Salgado-Labouriau (1973). Photomicrographs were taken of the different pollen types, algal remains and palynomorphs present, with an Olympus C35AD camera.
attached to the microscope. The photomicrographs accompanied by morphological descriptions of the pollen, spores and palynomorphs encountered in the analysis are given in Appendix A. Both pollen concentration and percentage values were calculated by the MacPollen program (Eisner & Sprague 1988).

Analysis of sedimentary chlorophyll units or SPDU (Sedimentary Pigment Degradation Units) was slightly modified from Wetzel & Likens (1979) and Bengtsson & Enell (1986). Samples containing 0.5 cc were mixed in a 90% acetone, homogenized with a Vortex vibrator and stored in the dark at 4°C for 24 hours, with occasional mixing with the Vortex vibrator. The samples' absorbance within the wavelength range of chlorophyll absorbance, i.e. from 664 to 667 nm, is determined spectrophotometrically, and later compared to the absorbance of a blank sample containing only 90% acetone solution. The concentration of the pigment is then accomplished by using the calculations given in Wetzel & Likens (1979). SPDU can be used to infer former trophic conditions and lake level variations (Carpenter & Leavitt 1991, Frost 1984, De Oliveira 1985).

Diatom valves were extracted from 0.5 cc sediment subsamples by elimination of the organic component with a strong oxidant (concentrated HNO₃). After restoring pH to neutrality, a small amount of the residue was then applied to a glass coverslip. The coverslip was dried under low heat in a hot plate and finally inverted on glass slide containing Hyrax Mounting Medium. Analysis of the diatoms were performed under 1000 x magnification. Identification of the specimens was accomplished by using the following references: Carter & Denny (1982, 1987), Frenguellli (1933,1953), Hustedt
(1930, 1936, 1952a, 1952b, 1955, 1965), Patrick & Reimer (1966, 1975) and
Schmidt (1874-1959).
SEDIMENT CHRONOLOGY AND STRATIGRAPHY
OF LAGOA DA SERRA NEGRA

A total of 11 sediment subsamples have been radiocarbon dated by Beta Analytic Inc. and the results are shown in Table 2. The C\textsubscript{14} dates clearly indicate a very slow sedimentation in the last 40000 years at Lagoa da Serra Negra (fig. 5). Similarly low sedimentation rates have been reported from a closed basin lake at 720 m altitude in the Serra do Carajás, eastern Brazilian Amazonia, where a radiocarbon age of 28660 ±450 years B.P. was obtained at the third meter of the sediment column (Absy et al. 1991).

The sample obtained at 5.58 m has yielded a radiocarbon age of 30980 ±710 years BP which is in disagreement with the dates obtained for other samples of the stratigraphic unit. Because radiocarbon ages beyond the limit of the method are already encountered in the third meter of the stratigraphic sequence of Serra Negra, it is highly probable that the unexplained younger date of the sample collected at 5.58 m must be a consequence of contamination, or other source of error during the preparation of the sample. Therefore, this date is ignored, and the last date for this sequence within the limits of the C\textsubscript{14} method remains that of depth 2.39 m, i.e. 39930 years B.P.

The sediment sequence retrieved from Lagoa da Serra Negra was 7.82 m long and a detailed description of its stratigraphy is shown on fig. 6. The lake sediments are composed mainly of very dark gyttja which is predominant in the
Table 2. Radiocarbon dating of sediment samples from Lagoa da Serra Negra. Sample 53329 (depth 0 m) represents a wood fragment from a former tree trunk, immediately above the water surface.

<table>
<thead>
<tr>
<th>Beta Analytic Code</th>
<th>Depth (m)</th>
<th>C(^{14}) dating (years BP)</th>
<th>C(^{13}/C^{12})</th>
<th>C(^{13}) adjusted age (years BP)</th>
</tr>
</thead>
<tbody>
<tr>
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<td>-28.5 0/00</td>
<td>120+-50</td>
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<td>53312</td>
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<td>1180+-70</td>
<td>-20.6 0/00</td>
<td>1250+-70</td>
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<tr>
<td>53313</td>
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<td>4970+-90</td>
<td>-23.1 0/00</td>
<td>5000 +-80</td>
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<td>14280+-90</td>
<td>-21.2 0/00</td>
<td>14340+-90</td>
</tr>
<tr>
<td>53315</td>
<td>2.39</td>
<td>39890+-530</td>
<td>-22.5 0/00</td>
<td>39930+-540</td>
</tr>
<tr>
<td>53316</td>
<td>3.39</td>
<td>&gt; 42000</td>
<td>-28.9 0/00</td>
<td>&gt; 42000</td>
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<tr>
<td>53317</td>
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<td>&gt; 41000</td>
<td>-29.6 0/00</td>
<td>&gt; 41000</td>
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<tr>
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<td>&gt; 44050</td>
<td>-29.8 0/00</td>
<td>&gt; 44000</td>
</tr>
<tr>
<td>53319</td>
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<td>&gt; 39860</td>
</tr>
<tr>
<td>53320</td>
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<td>31020+-710</td>
<td>-27.5 0/00</td>
<td>30980+-710</td>
</tr>
<tr>
<td>53321</td>
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<td>&gt; 46220</td>
<td>-27.4 0/00</td>
<td>&gt; 46180</td>
</tr>
<tr>
<td>53322</td>
<td>7.76</td>
<td>&gt; 39920</td>
<td>-29.6 0/00</td>
<td>&gt; 39850</td>
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</tbody>
</table>
Fig. 5. Sedimentation rate curves for Lagoa da Serra Negra (top) and Lagoa dos Olhos (bottom).
Fig. 6. Sediment stratigraphy of the 7.82 m long sequence from Lagoa da Serra Negra.
Fig. 6.
first 5 meters. A transition to clayey sediments starting at 5.38 m leads to very dense clay and finally to gravel at the bottom of the stratigraphic column at 7.82 m. At 0.26-0.35 m and 1.26-1.36 m, many fragments of small stems and of grass-like leaves were found interspersed among organic black gyttja. Small amounts of quartz particles and of other minerals are found mixed with the black gyttja matrix from 1.59 to 2.56 m. Examination of these sediments under a stereomicroscope suggests these particles to be derived from quartzite rock, which is the predominant rock type of the Serra Negra caldera (Barbosa et al. 1970). X-ray radiography and visual analysis of the sediments indicated that from 2.56 to 3.54 m, the stratigraphic sequence is rather different than the previous section due to the conspicuous presence of areas of high concentration of quartzite particles. These particles form well-defined laminae especially at 2.56-2.61 m, 2.98 m, and 3.30-3.52 m, although very faint laminae are found throughout from 2.56 to 3.54 m. From 3.54 to 4.54 m, the sediment sequence is homogeneous and composed of black gyttja with interspersed quartzite fragments but without distinct laminations. From 4.54 to 5.38 m the sediment column is again characterized by the presence of various laminations of quartzite derivatives among gyttja. Clay rich sediments are found from 5.38 to the bottom of the stratigraphic unit.

Percent dry weight, L.O.I and SPDU profiles are given on fig.7. The percent dry weight profile shows high values from 5-7.82 m, intermediate and oscillating values from 5-1.20 m and lowest values in more recent sediments. This pattern is common in deep sequences and is usually attributed to compaction of the sediments (Bengtsson & Enell 1986). Increased percent dry weight can also be a reflection of the sediment type found as denser sediments
Fig. 7. Percentage dry weight, Loss on Ignition at 550°C, and sedimentary chlorophyll units profiles for Lagoa da Serra Negra.
Fig. 7.
composed of clay and quartzite minerals are more abundant at the bottom of the Serra Negra sequence. L.O.I. values range from 6 to 31%, although the profile obtained shows the majority of these values ranging from 10-20%. SPDU (units per gram of organic weight) oscillate after 14340 years B.P or 1.57 m. SPDU are found only in trace amounts from 1.84 to 3.35 m but are present with oscillating values from 3.35 m to the bottom of the Serra Negra stratigraphic unit.
SEDIMENT CHRONOLOGY AND STRATIGRAPHY
OF LAGOA DOS OLHOS

Six sediment samples from Lagoa dos Olhos were submitted for radiocarbon dating by Beta Analytic Inc. and the results are presented on Table 3.

Sedimentation rates shown on fig. 5, indicate that in the Lagoa dos Olhos, they range from 0.022 to 0.89 mm/year. Those values are closely comparable to those obtained at the Lagoa da Serra Negra.

Fig. 8 shows the stratigraphic sequence of the 1.80 m core retrieved from Lagoa dos Olhos. The first 0.21 m of this sequence is composed of very dark grayish brown gyttja. At 20 cm depth, there is a well defined transition to black gyttja, which extends to 1.16 m. After this point, the black gyttja is replaced by very dark gray clay, which extends to 1.59 m. A distinct layer of quartz particles is found from 1.59 to 1.61 m. and a mixture of gyttja and a few quartz particles occur from 1.61 m to 1.64 m. From this point to the bottom of the sediment sequence at 1.80 m nodular black gyttja occurs interspersed with fewer quartz particles.

Fig. 9 shows the % dry weight, % L.O.I. and SPDU profiles for the sediments of Lagoa dos Olhos. The percent dry weight profile of the sediments reach high values at both the top and bottom portions of the stratigraphic unit, i.e. from 0.05-0.15 m and from 1.21-1.82 m. This can be explained by the high
Table 3. Radiocarbon dating of sediments from Lagoa dos Olhos.

<table>
<thead>
<tr>
<th>Beta Analytic Code</th>
<th>Depth (m)</th>
<th>( C^{14} ) age (years BP)</th>
<th>( C^{13}/C^{12} ) adjusted age(yr BP)</th>
</tr>
</thead>
<tbody>
<tr>
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<td>-21.1 0/00 930±70</td>
</tr>
<tr>
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<td>0.85</td>
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<td>-23.5 0/00 2760±90</td>
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<td>6710±140</td>
<td>-20.3 0/00 6790±140</td>
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<tr>
<td>53328</td>
<td>1.68</td>
<td>15530±110</td>
<td>-18.9 0/00 15630±110</td>
</tr>
<tr>
<td>35394</td>
<td>1.77</td>
<td>19410±160</td>
<td>-18.3 0/00 19520±160</td>
</tr>
</tbody>
</table>
Fig. 8. Sediment stratigraphy of Lagoa dos Olhos. Sediments containing sand grains are predominant at the deeper sections of the stratigraphic unit.
Fig. 9. Percentage dry weight, percent L.O.I. (Loss on Ignition at 550°C), and SPDU (sedimentary chlorophyll units) profiles for Lagoa dos Olhos.

<table>
<thead>
<tr>
<th>Depth (cm)</th>
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<tbody>
<tr>
<td>0</td>
</tr>
<tr>
<td>% Dry Weight</td>
</tr>
<tr>
<td>% L.O.I. (Loss on Ignition at 550°C)</td>
</tr>
<tr>
<td>S.P.D.U. (Chlorophyll units)</td>
</tr>
</tbody>
</table>

Radiocarbon dating (years B.P.)

- 19520±110
- 15630±70
- 6960±70
- 2760±70
- 930±70
- 6790±10
- 15630±110
- 19520±160

Stratigraph
concentration of an inorganic matrix at both ends of this sequence. Percent L.O.I., although lower than the values obtained at Serra Negra, also shows a certain degree of constancy ranging from 7 to 15%, with an average value of 9.55%. SPDU are found only in trace amounts from 19520 to ca. 6000 years BP, but a gradual increase in the chlorophyll concentration occurs after ca. 6000 yr BP, and maximum values are reached after ca.1320 yr BP. This SPDU maximum is followed by a generalized decline in recent times in the Lagoa dos Olhos. This lake is presently an oligotrophic lake which is consistent with the trace amount of chlorophyll found in its modern surface sediments.
THE PALAEOECOLOGICAL RECORDS

The palynological profiles of Serra Negra and Lagoa dos Olhos sediments were divided into eight and five discrete zones respectively, by visual inspection based on concentration and percentage values of the taxa found. Within some of these zones oscillations of some taxa are frequent, as past environmental changes in the two areas under study appear to be very complex.

The Serra Negra record

The pollen, spore and algal percentage profiles of Lagoa da Serra Negra are shown on fig. 10. Pollen concentration curves for some of the taxa represented in percentage diagram are given on fig. 11, whereas pollen cumulative concentration and total pollen concentration values for Serra Negra are shown on fig. 12. Both the percentage and concentration diagrams are composed of selected taxa for simplification of the analysis.

Zone SN1 (7.20-7.82 m)

This zone is characterized by very low percentage and concentration values of Araucaria, Podocarpus, Xylosma, Ilex, Sebastiana and Esenbeckia pollen. The latter taxon is included in the "Other forest trees" category of the pollen diagram. Since ponding of the lake, concentration values of Gramineae
Fig. 10. Percentage diagram of selected pollen, spores and algal spore taxa of Lagoa da Serra Negra. The + sign shown on profiles of some taxa indicates values equal or lower than 2%.
Drimys
Acalypha
Alchornea
Anacardiaceae
Cellia
Copaifera
Mimosaceae
Melastomataceae
Meliaceae
Patagonula
Piperaceae
Proteaceae
Rapanese
Rubiaceae
Sapindaceae
Sebastiana
Solanaceae
Urticaceae/Moraceae
other tropical forest trees
Burseraceae
Byronima
Compositae (Asteraceae)
Cyperaceae
Gramineae (Poaceae)
Loranthaceae
other cerrado trees
Palmae (Arecaceae)
Mauritia
herbs
Aquatics
Fig. 10 (continued).
Fig. 11. Concentration diagram of selected pollen, spores and algal spore taxa of Lagoa da Serra Negra. The + sign shown on profiles of some taxa indicates values equal or lower than 2%. 

Stratigraphy

Radiocarbon dating (years BP)

Depth [m]

- Araucaria
- Podocarpus
- Myrtaceae
- Ilex
- Ericaceae
- Symplocos
- Xylosma
- Melastomataceae
- Ranaea
Fig. 11 (continued).
Fig. 12. Total pollen concentration and cumulative pollen concentration profiles of Lagoa da Serra Negra.
and Cyperaceae start to decrease gradually, indicating a reduction in the herbaceous layer, in which there is a reduced contribution of Compositae. The percentage pollen diagram shows the predominance of Myrtaceae and Melastomataceae, among the arboreal taxa in this zone. However, their concentration values are also very low. The spore diagram starts at 7.82 m with high concentration and percentage values of Sphagnum, monolete psilate spore (cf. Blechnum type (Blechnaceae)/Polypodiaceae), monolete verrucate (cf. Polypodiaceae) and trilete spores, although these taxa rapidly decrease during this period. Among the aquatic plants there is a predominance of Myriophyllum, but Pontederiaceae, Drosera (Droseraceae), Polygonum (Polygonaceae) and Ludwigia (Onagraceae) are also well represented. With the exception of Myriophyllum, all the latter taxa are represented in the aquatics sum in the diagram. Reasonably high values of chlorophyll (SPDU) occur at the onset of ponding of the lake. Algal spores present suggest increased humidity, allowing the expansion of this shallow system on the flattened topography of the Serra Negra crater. The pollen and spore assemblages of this zone strongly suggest cooling and rather humid conditions supporting a myrtaceous and melastomataceous shrub vegetation with sparse trees of Araucaria, Podocarpus, ilex, in the caldera. It is probable that the reduced pollen percentage and concentration values in this zone (fig. 11) is an artifact created by the overwhelming abundance of Sphagnum and other spores and herbs. High humidity and pronounced cooling are suggested by Myriophyllum, aquatics, chlorophyll levels and high concentration of algal spores. Presently, Myriophyllum is abundant in lakes of higher southern latitudes in Brazil (Lindman 1906, Jolly 1976), although occasional occurrences were reported in São Paulo (Usteri 1911) and Minas Gerais (Warming 1892). One modern
vegetation analog for this zone is probably the dwarf shrub vegetation of the high mountains of southeastern Brazil. For example, at ca. 2300 m in Itatiaia, Rio de Janeiro, the landscape is characterized by the overwhelming presence of dwarf shrubs of Melastomataceae, Myrtaceae, Compositae, Ericaceae. Sedges and grasses and sparse small trees are also part of the vegetation at high elevations of Itatiaia (Wettstein 1970). Present climate of this vegetational zone in Itatiaia (Nimer 1989) is: annual mean temperature, 11.5°C; July mean temperature, 6.4°C; annual precipitation, 2560 mm (Nimer 1989a).

One radiocarbon date from zone SN1 (Table 2) is beyond the limit of the C\textsuperscript{14} method, therefore the duration of this period cannot be presently be determined.

**Zone SN2 (6.20-7.20 m)**

During this period, the previous vegetation loses *Araucaria* and *Podocarpus*. The arboreal taxa *Xylosma* and Myrtaceae attain their greatest percentage and concentration values at the onset of this stage, following the decline in *Araucaria* and *Podocarpus*. Initially, Gramineae percentage and concentration levels are low but this taxon attains high values following the decline in Myrtaceae. The oscillations in forest taxa can be interpreted as consequence of gradual warming and a more seasonal climate with relatively warmer, longer dry seasons. This replaced a climate that was sufficiently cold and humid to maintain sparse trees of *Araucaria* and *Podocarpus*. Another hypothesis for the loss of *Araucaria*, a pioneer species, is that the forest had reached maturity and its loss could be explained by its inability to regenerate under its own shade in mature forests (Rizzini 1971). In addition, some successional *Araucaria* forests are characterized by a numerical predominance
of Myrtaceae (Leite & Sohn In Press, In: Leite & Klein 1990). It has been observed by Mori et al. (1983) that in some wet forests of eastern Brazil this family often possesses the highest number of species, individuals and total basal area. Increased values of Myrtaceae in the understory of forests where the emergent layer is composed of Araucaria are presently observed in many forests of southern Brazil. Another aspect of zone SN2 is the increased percentage and abundance of Xylosma after the Araucaria and Podocarpus decline. Presently in southern Brazil the flacourtiaaceous genus Xylosma is represented by understory trees reaching up to 15 in height in both Araucaria and Atlantic forests, as indicated by the herbarium collections of the Universidade Federal do Paraná. There is an increase in the Melastomataceae and Compositae pollen concentrations during the rise of Xylosma, which suggests this particular forest to be experiencing some successional event.

The most likely climatic scenario during this period is that of increasing drying conditions, which were responsible for the successional changes observed in the pollen diagram. Reduced precipitation after this short expansion of Xylosma, is suggested by the loss of algal spores and increased monolete psilate spores. It is quite probable that during this time, lower precipitation values caused a contraction of the swamp, whose wet sections became rapidly colonized by ferns. Chlorophyll values gradually decrease during this phase, going from 2.60 units during the Xylosma peak to 0.64 units at the end of Zone SN2, thus providing more evidence for the contraction of the swamp. A radiocarbon date greater than 46180 yr BP is available for the depth of 6.63 m.
Zone SN3 (5.14-6.20 m)

The early stages of this pollen zone are characterized by the presence of pollen of *Araucaria*, *Podocarpus*, *Schinus*/*Anacardium* (Anacardiaceae), *Lithraea* (Anacardiaceae), *Astronium* (Anacardiaceae), *Alchornea*, *Rapanea*, Ericaceae, high concentrations of Myrtaceae and Melastomaceae. Presently these taxa are found in the cold and moist *Araucaria* forests of the southern Brazilian Plateau, at latitudes of 23-30°S, thus suggesting reoccurrence of pronounced cooling, in conjunction with high humidity levels in this zone. The landscape was probably forested with a mosaic of temperate *Araucaria* forest taxa coexisting with elements from other tropical forests (*e.g.* *Astronium* and *Alchornea*).

A very slow climatic change begins to occur when Burseraceae pollen appears in the sediments at 5.78 m. At 5.68 m, *Podocarpus* pollen reaches its highest concentration and percentage values since the onset of the lake, but at 5.48 m, its decline is followed by a sharp increase in Burseraceae pollen. Synchronous with the Burseraceae peak there is also an overall decrease in other humid forest taxa, *i.e.* *ilex*, Myrtaceae, *Rapanea*. In addition, loss of most algal taxa and sharp decrease in monolette psilate and *Sphagnum* spore concentrations are also observed at this point. The Burseraceae increase is also synchronous with increase in Urticaceae/Moraceae, Gramineae and Compositae, thus suggesting expansion of successional vegetation. In general, pollen and spores were not well preserved in the sediments following this phase at 5.14 m, where the sediments are characterized by an overwhelming abundance of *Botryococcus* and few grains of Urticaceae/Moraceae, Burseraceae, Myrtaceae and Compositae. All the evidence implies a return at the end of this zone to a climate with a longer dry season and warmer winters.
Zone SN4 (4.80-5.14 m)

This zone represents the establishment of the climatic conditions that started in the middle of the previous zone. The presence of *Sebastiana*, *Astronium*, Palmae, *Luehea* (Tiliaceae), Compositae, Melastomataceae and Myrtaceae pollen indicates a period when seasonal semi-deciduous forest becomes established in the caldera of Serra Negra. Gramineae pollen concentration values are slightly lower than previously, thus suggesting a reduced herbaceous layer. Chlorophyll achieves its maximum levels during this phase and fern spores start a gradual rise towards the end of this period. The climate of Zone SN4 is therefore characterized by higher humidity levels when compared to the previous stage (Zone SN3).

Zone SN5 (3.00-4.80 m)

This zone is characterized by the overall highest percentage and concentration values of cold forest taxa: *Podocarpus*, *Araucaria*, *Ilex*, Myrtaceae, *Rapanea*, Melastomataceae, together with Solanaceae and Compositae. Also well represented during this period are Ericaceae, and the arboreal taxa *Symplocos*, *Drimys*, *Xylosma*, *Celtis*, *Esenbeckia* and *Daphnopsis*. The latter two taxa are represented in the "Other forest taxa" curve. Few typical cerrado (savanna) arboreal taxa occur within this zone, e.g. *Lafoensia* (Lythraceae). Cooling is also suggested by the presence of *Debarya* spores. This alga spore appears for the first time in the diagram during this phase. *Debarya* as well as *Zygnema* and *Mougeotia* spores occur frequently in cold to cool paramo or subparamo climate in Colombia and are frequently used as reliable indicators of former cooler conditions during the Quaternary (van Geel 1976; van Geel & van der Hammen 1978, Mondanesi 1988).
This stage represents the largest and possibly the longest expansion of cold moist *Araucaria -Podocarpus* forest in the Serra Negra region. Presently in southern and southeastern Brazil, this type of forest is restricted to areas with average winter temperatures lower than 15°C and absence of a dry season (see Table 1).

Three samples from this period were submitted to radiocarbon dating, yielding C\(^13\) adjusted ages greater than 42000 yr BP at 3.39 m, greater than 41000 yr BP at 3.84 m and greater than 44000 yr BP at 4.24 m. Because of the age of those samples is greater than the effective range of the standard radiocarbon method (Birk & Birks 1980), the duration of this period cannot be asessed.

The pollen diagram of Zone SN5 does not suggest floristic constancy during this period. Oscillation of concentration and percentage values of some taxa suggest this forest cold has contracted and expanded a number of times in the past. For instance, *Araucaria* concentration values show six oscillations, although *Podocarpus* appears to be more stable during this period. Oscillating values are also found in Gramineae and Cyperaceae concentration curves. The trilete spore curve appears to oscillate in close synchrony with the *Podocarpus* curve, thus suggesting that ferns played a considerable role in the composition of the herbaceous layer of those cold forests. This idea is also supported by the higher concentration levels of monolet psilate spores during this period. The compiled pollen, spore and algal evidence suggest that this period represents the coldest time in the Serra Negra region prior to 40 000 years BP.

The end of this zone shows abrupt changes in stratigraphy, when quartz laminations become very conspicuous in the x-radiographs of the sediments, especially in depth interval of of 3.30 to 3.52 m. This change in stratigraphy is
synchronous with the sharp decline in *Araucaria* and *Podocarpus* forest elements. The increased concentration in quartz particles is likely to be a consequence of increased weathering as the forest cover of the area dwindled.

**Zone SN6 (3.00m - 39930 yr BP; 3.00-2.39 m)**

This stage is initiated by the return of a more seasonal forest with an open canopy composed of Burseraceae with a well developed herbaceous layer of Compositae, Cyperaceae and Gramineae. This latter taxon has a clear increase in its concentration curve at this stage. Also present during this period are pollen belonging to *Copaifera*, *Sebastiana*, *Didymopanax*, *Erythrina*, *Tabebuia*, *Daphnopsis*. The latter tree taxa are represented in the pollen diagram by the "Other forest taxa" curve, but all are elements of present day seasonal semi-deciduous forests of central Brazil. The climate in this zone is again likely to be more seasonal, *i.e.* with a longer dry season and similar to that found presently in central Brazil. Increased drying is also indicated by the initial low concentration values of aquatic pollen, monolete and trilete spores. Increased seasonality is also suggested by the increase in quartz particles in the sediments at the end of this zone.

During this zone, chlorophyll reaches its lowest values, being found only in trace amounts. In summary, the initial part of this period represents a transition from the previous cold and wet climate supporting forests presently found in subtropical areas of higher southern latitudes or elevation, with no distinct dry season, to a seasonal climate supporting a semi-deciduous forest. The latter forests are presently found in areas with long dry winters and rainy summers, especially in central Brazil.
Zone SN7 (39930 yr BP - 14340 yr BP ; 2.39-1.58 m)

There is evidence for a period of glacial cooling, during this stage, which is provided by the pollen assemblage at 2.39 m, with a radiocarbon age of 39930 yr BP. During the initial phase of this period, the pollen assemblages show increase in the concentration of *Araucaria*, *Podocarpus*, *Ilex* and Ericaceae pollen, together with other moist tropical forest elements such as *Daphnopsis* and *Sebastiana*. This pollen assemblage is indicative of a mosaic forest containing a mixture of cold and warm loving taxa. At 2.20 m (ca. 34000 yr BP), a short dry phase occurs as indicated by the decrease of moist forest taxa, decrease in aquatics, and correspondent increase in Gramineae. However, cooling appears to have continued as indicated by increase in levels of *Debarya* spore, and the maintenance of *Araucaria* and *Podocarpus*. This implies that some humidity was still available in the region to support them. At 2.09 m (ca. 30453 yr BP), Gramineae still predominate in the counts, although moist forest taxa like *Erythrina* and *Podocarpus* are still present. Cool and moist conditions return to the region at 1.89 m (ca. 24134 yr BP) with *Araucaria*, *Podocarpus*, *Daphnopsis* and *Alchornea*. At 1.79 m (ca. 20975 yr BP) there is a decline in these elements and in other arboreal genera, as well as in aquatic plants. These changes occur synchronously with an increase in herbaceous taxa, e.g. Compositae, Gramineae and Cyperaceae. Cooling and wet conditions reappear immediately before 14340 yr BP (1.58 m) with an increase in *Araucaria*, *Podocarpus*, Myrtaceae, Melastomataceae, Palmae and aquatic plants at 1.61 m (ca. 15280 yr BP). Generally, the period from 39930 to 14340 years BP can be summarized as a time when pronounced glacial cooling was permeated with moist and drier phases, forcing oscillations in the vegetation.
Zone SN8 (14340 yr BP to Present; 1.58-0 m)

The pollen spectrum at this level is composed of increased percentage values of *Podocarpus*, Ericaceae, Melastomataceae and Myrtaceae. Also present are *Drimys*, *Hedyosmum*, and the savanna element *Ayenia* (Sterculiaceae). The latter taxon is represented in the "Other cerrado taxa" curve. This spectrum suggests that intensity of glacial cooling declines sometime after 14340 yr BP (1.58 m depth) as indicated by a sharp decline in *Podocarpus*, and other cold-loving taxa. Depth of 1.31 m, ca. 10000 years represents the last known occurrence of *Araucaria* in Serra Negra.

At 1.06 m (5000 yr BP) the sediments are characterized by the presence, in lower percentage and concentration values, of *Podocarpus*, Palmae, Anacardiaceae, Melastomataceae, Mimosaceae, Myrtaceae, as well as high concentration and percentage values of Gramineae and Cyperaceae.

After 5000 years BP, there is an increased contribution of savanna elements represented by *Cuphea*, *Qualea*, Mimosaceae (cf. *Stryphnodendron*). Also represented are semi-deciduous forest taxa. The pollen data suggests that since 5000 years BP the climate of Serra Negra has been characterized by reduced precipitation, and higher temperatures, allowing it to support cerrado and semideciduous forests in a two season climate. After 5000 yr BP there is faster sedimentation rate when compared to the previous sections of this sediment sequence, for depth 0.69 m yields a radiocarbon age of 1250 years BP.

At certain shallow areas of the lake one finds today many tree stumps emerging out of the water. A radiocarbon dating for one of these samples was 120+-50 yr BP. This information, when combined with the pollen spectra of surface samples and the pollen assemblages for the topmost samples of the
stratigraphic sequence, indicates that during the late Holocene, the Serra Negra region has supported both savanna and seasonal forests with many elements still present in the adjacent areas. The tree stumps are indicative of a much larger gallery forest that existed adjacent to the lake and along the northward flowing stream. Old residents of the village of São João da Serra Negra, located outside the caldera, confirmed the presence of forest / savanna mosaic in the caldera prior to recent development.
The record of Lagoa dos Olhos

The pollen, spores and algal percentage profiles of Lagoa dos Olhos are shown in fig. 13. Concentration diagram for taxa shown on percentage curves is shown on fig. 14. Pollen concentration and cumulative concentration curves are shown on fig. 15.

Zone OL 1 (19520-ca. 13685 yr BP; 1.80-1.59m)

The pollen profile of this period is characterized by high concentration and percentage values of Podocarpus, Rapanea, Caryocar (Caryocaraceae), Compositae, Gramineae and Cyperaceae. Also present, but in very low concentration and percentage values are Araucaria, Hedyosmum (Chloranthaceae), Myrtaceae and Solanaceae. Trilete spores as well as algal zygospores belonging to Cosmarium, Mougeotia, Spyrogyra and Debarya are also very abundant. At the onset of this period the vegetation immediate to Lagoa dos Olhos was a mosaic forest without presently known modern analogs in Brazil. The pollen assemblage suggests a Podocarpus - Caryocar forest with an open canopy and well developed herbaceous layer characterized by grasses and possibly Compositae herbs. It is not possible here to discern arboreal from non-arboreal Compositae pollen. Although arboreal taxa of Compositae, e.g., Piptocarpha, Baccharis and Moquinia are commonly found in the forests of southern and southeastern Brazil, Compositae pollen is interpreted here as derived from herbaceous plants.

An alternative interpretation for the high representation of Podocarpus pollen in this zone can be suggested. Due to its airborne characteristics, the presence of this taxon could represent long distance transport from distant moist forests. In a year-long pollen rain survey conducted in a cerrado area of central
Fig. 13. Percentage diagram of selected pollen, spore and algal spore taxa of Lagoa dos Olhos. The + sign shown on profiles of some taxa indicates values equal or lower than 2%.
Euplatta
Roupala
Sapindaceae
Sebastiana
Copaifera
Urticaceae/Moraceae
Mimosaceae
other tropical forest trees
Palmae (Arecaeae)
Solanaceae
Mauntia
Byrsonima
Caryocar cf. brasiliensis
other cerrado trees
Compositae (Asteraceae)
Cyperaceae
Gramineae (Poaceae)
herbs
Alismataceae
Aquatic plants
Fig. 13 (continued).
Fig. 14. Concentration diagram of selected pollen, spore and algal spore taxa of Lagoa dos Olhos. The + sign shown on profiles of some taxa indicates values equal or lower than 2%.
other herbs
Alismataceae
other aquatics
damaged/unidentified

Monolete verrucate
Monolete psilate
Trilete

Trilete verrucate
Selaginella

Trilete echinate
Fig. 14 (continued).
Fig. 15. Total pollen concentration and cumulative pollen concentration profiles of Lagoa dos Olhos.
Brazil by Salgado-Labouriau (1973) *Podocarpus* pollen was found only once in very low quantities. In addition, analyses of surface sediment pollen spectra of Lagoa dos Olhos and surrounding lakes lack *Podocarpus* pollen. During Zone OL1, *Podocarpus* pollen reached values of ca. 15000 grains per cubic centimeter of lake sediments, thus indicating that parent trees had to be growing adjacent to the lake basin. More surprising than the concentration values of *Podocarpus* are the values for *Caryocar* pollen in this zone, which are as high as ca. 10000 grains/cc. Because *Caryocar* is pollinated by bats (Prance 1990), the probability of its pollen ever reaching lake basins is very small. This has been observed at Lagoa da Serra Negra, where *Caryocar* trees are presently found in the northern edge of Lagoa da Serra Negra and yet no pollen belonging to this taxon can be found in the lake's surface sediments. Therefore, the high representation of both *Caryocar* and *Podocarpus* in Zone OL1 must indicate that an extensive *Podocarpus-Caryocar* forest existed adjacent to Lagoa dos Olhos from 19520 to ca. 13685 years BP. The present day distribution of *Caryocar* in Brazil, suggests this taxon to be tolerant of cooling since its found in latitudes as high as 25°S in southern Brazil (Prance 1990), well within the present phytogeographical province of *Araucaria* forests.

The pollen spectra of this period suggests, therefore, that the climate of Zone OL1 is characterized by a pronounced regional temperature depression associated with high humidity. Lower temperatures are also suggested by the increased concentration of the algae *Debarya*, *Zygmena* and *Mougeotia*. Despite the suggested high levels of humidity for this zone, Lagoa dos Olhos at this period was likely to be a marsh as indicated by the high concentration of pteridophyton trilete spores as well as by a relative abundance of pollen of Pontederiaceae and *Monnina* (Polygalaceae). Marshy conditions with
concomitant reduced light penetration is also supported by the lack of diatoms and reduced values of SPDU. The *Podocarpus* forest existed for approximately 3890 years, at a time that can be described as the coldest glacial time of Lagoa dos Olhos region. A clear transition to drier conditions at 15630 yr BP (1.68 m) is indicated by a gradual decrease in concentration and percentage values of *Podocarpus*, *Rapanea*, Gramineae, Compositae, Palmae, *Hedyosmum*, fern and algal spores in contrast with the gradual increase in *Caryocar* pollen. Increased concentration of charcoal occurs at the end of this period suggesting an increase in frequency of local fires. The change to a drier climate and consequently to a *Caryocar* cerradão (tall cerrado forest) with a reduced grassy layer at the end of this zone is also suggested by the sediment stratigraphy. At 15630 yr BP the sediment stratigraphy shows increased concentration of sand particles. A well defined 2 cm thick sand layer occurs at 1.61-1.59 m (ca. 13685 yr BP), thus suggesting increased drying conditions and a more open vegetation. Chlorophyll concentration, which until this particular point in time, was found in trace amounts, reaches an absolute zero value, when the marsh probably became drier. It is important to note that during this drier climate, cerrado pollen is found together with pollen of taxa found in moister forests, e.g. *Celtis* (Ulmaceae), *Sebastiana* (Euphorbiaceae) and *Xylosma* (Flacourtiaceae).

**Zone OL2 (ca. 13685- 6790 yr BP ; 1.59 m-1.43 m)**

During this phase the *Caryocar* cerradão reaches its maximum at 1.50 m (ca. 9300 yr BP) and the Gramineae, Cyperaceae and Compositae curve reach their lowest values since the onset of the record. This suggests that a closed
Caryocar canopy was attained in Zone OL2. During this time total pollen concentration is low when compared to the previous period. High concentration of charcoal suggests the occurrence of natural fires at 1.45 m (ca. 7500 yr BP) and a possible increase in the duration of the dry season in the area of Lagoa dos Olhos during this phase. This interpretation is also suggested by a decrease in Rapanea and Podocarpus percentages. There is a pronounced decline in algal spore percentages during this period, also suggestive of contraction of the lake induced by a longer dry season. Chlorophyll units reach an absolute zero value, although it is found in trace amounts towards the end of this period.

Zone OL3 (6790 - yr BP- ca. 4000; 1.43 - 1.15 m)

Initially this zone is characterized by an increase in Celtis, Alchornea and Myrtaceae pollen, suggesting that a successional moist forest occupied the area as the Caryocar forest retracted. This successional forest was likely to have had an open canopy, which could have favored the herbaceous layer composed of grasses and some Compositae plants. The concentration diagram shows increased values of Gramineae and lower values for Compositae during this period. Since the onset of this period, there is gradual rise in pollen of aquatic plants (Utricularia, Hydrocotyle, Umbelliferae, Alismataceae), Myrtaceae, Roupala, Celtis, and lower percentage and concentration values of Caryocar, whose pollen is no longer present at 1.30 m depth. However, at 1.25 m (ca. 5000 yr BP) although present in low concentration and percentage values, Podocarpus and Caryocar pollen cooccur again, together with Xylosma, Hedyosmum, Casearia and Alchornea. This zone also marks the beginning of the Alismataceae rise.
The end of this period at 1.15 m (ca. 4000 yr BP) is marked by even higher humidity values as moist tropical forest elements become more prevalent in the area as shown by the increase in *Cabralea* (Meliaceae), *Hedyosmum*, *Styrax* (Styracaceae), *Sapindaceae* (cf. *Matayba*), *Sebastiana* and *Urticaceae/Moraceae* pollen. The total pollen spectrum at this zone is suggestive of an open forest with well developed herbaceous layer composed of Gramineae, under a climate gradually becoming moister.

**Zone OL4. (ca. 4000 yr BP-1320 yr BP; 1.15-0.80 m)**

Pronounced changes during this period occur in the pollen, spore, algal concentration and percentage diagrams as well as in the Chlorophyll profile and sediment stratigraphy. This zone also marks the onset of the diatom record of Lagoa dos Olhos (fig. 16). The diatom record in this zone is suggestive of higher lake levels, which favored the development of planktonic taxa, e.g. *Melosira transitus*, the most abundant taxon of the diatom record. Epiphytic taxa (*Eunotia* and *Pinnularia*) are also present suggesting increased availability of surface for attachment, usually provided by macrophytes. Increased lake levels are also suggested by the Alismataceae, aquatic plants (sum of *Eriocaulaceae*, *Eryngium* and *Monnina*) curves, which reach their maximum values during this period.

The previous successional forest of Zone OL3 undergoes great changes in floristic composition during this period. At 1.00 m (ca. 2520 yr BP) a short-lived cool and moist climate favored the presence of *Araucaria* in a forest containing *Euplassa* (Proteaceae), *Xylosma*, *Esenbeckia*, *Myrtaceae*, *Rapanea*, *Cecropia* as well as *Caryocar* trees. This ephemeral cooling with increased moisture is likely to be the result of increased winter precipitation with
Fig. 16. Diatom percentage diagram of Lagoa dos Olhos.
slightly depressed temperatures. It is precisely at this point, i.e. 1.00 m depth (ca. 2500 yr BP) that the diatom record begins, thus suggesting increase lake levels. Starting at 0.95 m this forest loses Araucaria and other moist forest indicators disappears from the record. This is followed by an increase in Cecropia at 0.90 m, followed by a peak of Bathysa, which is represented in the diagram by the "Other Tropical Forest Trees" category at 0.95 m. The increase in Cecropia is interpreted as a return of a moist climate and its replacement by Bathysa, an arboreal taxon presently found in the Atlantic rain forests, is likely to represent a successional event. The increase in Urticaceae/Moraceae, is highly suggestive of increased successional events in the forests at the end of this zone. Other arboreal taxa found at the end of this zone are Ilex, Esenbeckia (Rutaceae), Sebastiana, Xylosma, Rapanea, Celtis and others.

The sedimentary Chlorophyll profile begins to rise at 1.10 m (ca. 2500 yr BP), and reaches its maximum values at 0.75 m (ca. 1212 yr BP). The diatom record which started during this phase at 1m is characterized by a predominance of the plantkonic taxa Melosira transitus, Melosira granulata and various epiphytic species of Eunotia, Pinnularia and Gomphonema, thus suggesting higher lake levels during zone OL4. Higher lake levels during this time also favoured the predominance of Botryococcus over other algal taxa, eg. Zygnema, Spyrogyra and Mougeotia, which are abundant in shallow pools (Bold et al. 1980).
Zone OL5 (ca. 1320 years BP - Present; 0.80 m-Present)

The most conspicuous change in the pollen profile during this stage is the increased importance of Myrtaceae and Ilex. Alismataceae is present throughout this phase but in lower percentage and concentration values. The pollen assemblages encountered during this phase are suggestive of mesophilous tropical forest and cerrado, which appear to have coexisted as they do presently, during most of the Holocene. At 0.10 m (ca. 250 yr BP), there is a single occurrence of a Zea grain (monoporate, annulate, psilate, > 120 um), probably representing the beginning of agriculture by European settlers in the area. Despite the presence of a single occurrence of Zea, the pollen evidence from Lagoa dos Olhos does not suggest disturbance of forest by agricultural practices. It is highly probable that the vegetation surrounding Lagoa dos Olhos has remained undisturbed by until settlement by Europeans. The Chlorophyll curve together with diatom analyses in the sediments strongly support this view. Both indicators suggest increased oligotrophic conditions as opposed to eutrophic conditions usually encountered in lakes in areas with agricultural activities and other types of disturbances.

Total pollen and cumulative pollen concentration attain their lowest values during the Holocene (fig. 15). In addition, a Cerrado-forest mosaic appears to have existed throughout the Holocene. Both sources of information suggest that the present two-season climate, with pronounced drying in the winter and elevated precipitation in the summer, conducive to the maintenance of the forest-mosaic vegetation of central Minas Gerais has persisted in this area during the last 6000 years.
SYNTHESIS OF THE LATE QUATERNARY HISTORY OF MINAS GERAIS AND ITS RELATION TO THE PALAEORECORDS OF SOUTH AMERICA

The 7.82 m record of Serra Negra is beyond the limits of the radiocarbon dating technique after the fourth meter. Nevertheless, it provides evidence for three periods of intense cooling and high humidity levels prior to 40000 yr BP (zones SN1, SN3 and SN5) intercalated by two periods of increased seasonality, most likely to represent longer and warmer winters (dry season) in zones SN2 and SN4.

The most pronounced cooling as well as increased humidity levels in the history of western Minas Gerais occurred at Zone SN 5 (radiocarbon dating greater than 41000 and 42000 yr BP), when the landscape was characterized by trees of *Araucaria*, *Podocarpus*, *Myrtaceae*, *Ilex*, *Symplocos*, *Drimys*, *Melastomataceae* (trees and shrubs). This period shows various oscillations of *Gramineae* and *Cyperaceae*, although *Compositae* was always present in the herbaceous layer of this forest or in canopy gaps. The oscillation in the *Araucaria* curve is more likely to indicate forest successional events as this taxon is a pioneer tree in gaps, and does not regenerate in the shady environment of its own canopy (Klein 1960, Rizzini 1971). Optimum growth average winter and summer temperatures for *Araucaria angustifolia* are 10-11°C and 20-21°C, respectively (Rizzini 1971). Presently, the main area of
contiguous distribution of this taxon lies within the 13°C average isotherm line in southern Brazil (Nimer 1989a). The geographical area within this isotherm has presently a mean annual temperature of 16-18°C. Therefore, an average winter and summer temperature depression of 6-7°C and 3°C, respectively, is suggested for these cold periods in the region of Serra Negra, Minas Gerais. However, if the *Araucaria* forest island region of Campos do Jordão, São Paulo is used as a modern analog, the suggested temperature depression is even more pronounced. As discussed previously, Campos do Jordão has mean July temperature of 8.9°C and average annual temperature of 13.6°C (Table 1). Present day Serra Negra is characterized by average July temperature of 18.8°C and mean annual temperature of 22°C. This implies that cooling prior to 40000 yr BP in Serra Negra could have been characterized by a 9-10°C reduction in average July temperature, and 6°C reduction in annual average temperature.

The period of early cooling in Serra Negra probably correlates to the last world-wide glaciation after 80 000 years BP (Prell & Kutzbach 1987) which favoured extensive glaciations in Argentina and Chile (Mercer 1976), and in the Andes of Ecuador (Clapperton 1987) and Peru (Wright 1983).

Radiocarbon dating of the subsequent zones is possible from the third meter towards modern sediments of the Serra Negra sequence, when ages fall within the limits of the C14 method. From 39930 to 20000 yr BP the climate in Serra Negra is generally cool and moist with drier or more seasonal climate at ca. 30000 and 20000 years BP. Reduced humidity occurs from 30000-34000 yr BP although conditions were still satisfactory to maintain some cold and moisture-loving taxa in the caldera. Some climatic records available for the tropics during this period suggest maximum glacier advances with synchronous
temperature depression between 33000-25000 yr BP in Colombia (van Geel & van der Hammen 1973, van der Hammen 1974; Hooghiemstra 1984). More evidence for this pronounced cooling was possible with the discovery of fossilized *Podocarpus* wood dated at 33000 and 26000 yr BP (Liu & Colinvaux 1985), *Drimys* logs at 30000 and 26000 yr BP (Bush et al. 1990) in the present Amazonian forest region of the eastern flanks of the Ecuadorian Andes (elev. 1000 m). Polleniferous sediments found in the same sites, also indicate a major descent of high elevation forest elements into the lowland forests of Ecuadorian Amazon at that time. The authors suggest a temperature depression of at least 7°C for this period. Therefore, 7-9°C temperature depression suggested for Serra Negra for some periods within the interval of 39930 to 14340 yr BP, is comparable to the values suggested by Bush et al. (1990), Liu and Colinvaux (1985) for Ecuador.

At ca. 24134 yr BP there is reoccurrence of cold and moist conditions in Serra Negra. Increased seasonality occurs again at ca. 20975 yr BP with continuing lower temperatures. At ca. 20000 yr BP there is an ephemeral period of drier conditions at Serra Negra followed by a return of cool and wet climate. This particular point in time marks the onset of the palaeoecological record of Lagoa dos Olhos. The record of this latter lake starts at 19520 yr BP, when a cooler climate supported a forest-savanna mosaic, with no modern analogs. This cooling at 20000 yr BP appears to be a widespread climatic phenomenon in South America. Mercer (1976) reports glacial expansion in Chile at 21000, 19000 and 18000 yr BP (18000 yr BP) and Heusser (1989) indicates that in Chile the coldest time, with a correspondent 9°C temperature depression, occurred at 20000 yr BP. A cooling of similar magnitude (7-8°C) is reported for the High Plains of Bogotá at 19500-22500 yr BP (Kuhry 1989).
Extensive glaciation for the southern Andes at 18000 - 20000 yr BP is suggested by Rabassa & Clapperton (1990). Cooling persisted at Lagoa dos Olhos from 19520 until ca.13685 yr BP. This climatic scenario appears to be in agreement with that of a generalized cooling in the southern hemisphere at 16000 yr BP (Heusser 1989, p.62). At ca. 13685-6000 yr BP there is increased seasonality with concomitant extension of the dry season and reduced cooling as a Caryocar savanna replaces the Pocarpus -Caryocar mosaic forest that existed previously. This increased seasonality is present, although not as obvious, in the Serra Negra diagram, where oscillating levels of Araucaria and Podocarpus, suggested their persistence although in reduced numbers, in the Serra Negra caldera. Cooling associated with moist conditions in Serra Negra occurs at 10000 yr BP, when the last occurrence of Araucaria is reported.

Drying (two-season climate with increased dry season) is greatest at ca. 9300 years BP at Lagoa dos Olhos. From 6000-present the general climate is that of a two season climate, with warm and moist summers and dry winters.

However, a radiocarbon date of 5000 +- 80 yr BP is available for the depth of 1.06 m at Serra Negra, possessing a pollen assemblage suggesting a brief reoccurrence of colder and moister climates. Ledru (1991) suggests that the period between 4500-5500 yr BP for the adjacent Serra do Salitre represent an arid climate with a very long dry season. Her conclusion is based primarily on the high percentage of Gramineae pollen (80%), with consequently decreased percentage of arboreal taxa, although it stated that the arboreal pollen at this stage belong to Podocarpus, Palmae, Anacardiaceae, Melastomataceae, Mimosaceae and Myrtaceae, which are found in lower percentages. The correspondent pollen assemblage for Serra Negra indicates the percentage values for Gramineae of 38%, Podocarpus 2.11%, Myrtaceae
5.8 %, Melastomataceae 1.84 %, Palmae 6.33 %, Drimys 0.26 %. This is in total disagreement with Ledru's (1991) climatic interpretation for 5000 yr BP. One problem of using Gramineae as the sole taxon for interpreting climatic change refers to the effect of lake morphology on the pollen signal. Ledru's lake, Lagoa Formosa is actually a grassy swamp. According to Barbosa et al. (1970), who studied the geology of this region, the name Lagoa Formosa is actually a misnomer and the word alagadiço or swamp is best to describe that site (Barbosa et al. 1970, p. 142, foto 2). Landsat imagery as well as aerial photographs of both Serra Negra and Serra do Salitre indicate that Lagoa Formosa is never a true lake even in the wettest months. Thus, a slight increase in the dry season is sufficient to produce a intensified pollen signal where the swamp grasses are likely to be overrepresented. Lagoa da Serra Negra, on the contrary, is a true lake, with a catchment area 4-5 times larger than that of the Formosa swamp. Because the Serra Negra caldera, with an external diameter of 12x15 km, has a completely internal drainage, the pollen signal of the sediments is more indicative of the regional vegetation. Therefore the climate at 5000 years BP for the region is best indicated by the Serra Negra sediments, suggesting marginally moist and cool conditions in the winter although a marginally dry season was longer than previously.

Support for the cooling at 5000 yr BP of Serra Negra is found elsewhere in southern South America. A return to slightly colder conditions (temperature 2°C lower than present) with consequent expansion of the Patagonian forest at 5500 yr BP has been reported in southern Chile by Paskoff (1977). However, with the exception of Podocarpus, which is found in low percentage (0.52 %), this cooling is not found in Lagoa dos Olhos. This low percentage of this taxon may not be significant, since this taxon is wind dispersed and also a good
pollen producer (Flenley 1979). The pollen diagram of Lagoa dos Olhos at 5000 yr BP is suggestive of a semi-deciduous forest with open canopy and increased herbaceous layer. It is very probable that this slight difference in temperature at 5000 year BP is due to the orographic difference between the two sites. The Serra Negra lake is located at 1200 m elevation, and altitude of 1273 m is reached by the inner rim of the caldera, whereas Lagoa dos Olhos stands at 730 m. This difference in altitude could account for a slight difference in temperature, and consequently in the regional pollen spectra.

It's important to mention that the climate at 5000 yr BP could have never been arid. There is no moment in the climatic history of the last 40000 years of western and Central Minas Gerais, that can be described as arid. Increased drying, however, has been reported a number of times. This drying has to be understood in terms of more seasonal conditions, which are typically found in present day central Brazil, i.e. long dry season (3 to 5 months) and humid summer and spring.

In summary, the pollen data from both sites of this study indicate that from 5000-Present the climate is similar to the present in both areas i.e. a two-season climate, with long dry season in the winter months and increased precipitation in the summer. This climate has favored the expansion of the semi-deciduous forest/savanna mosaic presently found in both western and central Minas Gerais.
TESTING OF THE HYPOTHESES

Hypothesis 1. Tropical forests took refuge at higher elevations during the time of maximum glaciation in the northern hemisphere. This allowed the expansion of semi-arid vegetation in southeastern Brazil during a supposedly dry climate.

The pollen evidence from both Serra Negra and Lagoa dos Olhos does not support this hypothesis. The record of Lagoa da Serra Negra, shows no evidence for any kind of semi-arid vegetation during the coldest glacial time. Instead, forest and herbaceous vegetation have expanded and contracted a number of times from 39930 to ca. 20000 years BP in this region. At Lagoa dos Olhos, the change in vegetation was gradual and consistent until time of maximum drying at ca. 9260 years BP. Because both sites lie outside the proposed central and coastal Brazil forest refuges of Prance (1982), the refuge hypothesis predicts the presence of either savanna or caatinga (semi-arid vegetation) in these two regions during the last glacial maximum. The Caryocar-Podocarpus forest present at Lagoa dos Olhos from 19520 to ca. 13685 yr BP represents a cold cerradão, or forest-like savanna with presently no modern analogs. Semi-arid climate did not exist in either area during the last 20000 years. Even during times of reduced precipitation and increased seasonality, enough moisture was still available to support humid-forest taxa on the
landscape. Pollen histories from the supposed late Pleistocene Napo refuge
area in Ecuador (Liu & Colinvaux 1985; Bust et al. 1990) as well as from the
Chiriqui refuge of Panama (Bush & Colinvaux 1990) have also shown no
evidence for the Refuge Hypothesis. Rather, they show increased seasonality
and temperature depression, favoring the expansion of forests of different
compositions in the lowlands and no evidence for Pleistocene savannas was
found by the authors. Although decreased precipitation was caused by
increase in seasonality (longer dry and warm winters), there was enough
moisture to maintain lowland taxa in these colder forests. The results from
southeastern Brazil falsify the forest refuge hypothesis with basically the same
arguments as do the paleorecords from proposed refuge areas in Panama and
Ecuador.

Falsifying the Late Quaternary Refuge Hypothesis by means of
biochemical biological clocks has been accomplished (Heyer & Maxson 1982,
In : Meyers & Giller 1988). Dating of speciation, of some animal taxa found in
some postulated Amazonian refuges, provided Miocene or Oligocene ages for
certain Amazonian speciation events, whereas Lynch (In : Meyers & Giller
1988) obtained Pliocene to Oligocene dates for speciation of certain frog
species found in proposed refuges of Amazonia.

Haffer (1990) has recently modified the time scale of the original
argument, in an attempt to save his hypothesis, by suggesting that the
supposed refuges can be older than Late Quaternary. The forest refuges
proposed by Haffer (1969) have been thought of as a specific Late-Quaternary
phenomenon, since this hypothesis was put forth by the author (Prance 1982,
Brown 1982, Ab'Saber 1982). However, Haffer (1990) recently stated: "
ecological refugia probably formed during many periods of the geological past,
and therefore, the refuge concept does not exclusively refer to the Quaternary period. As a Late-Quaternary phenomenon, there is presently no evidence from any part of the tropics for the presence of forest refuges. On the contrary, enough evidence already exists in the literature to reject the Refuge Hypothesis.

Hypothesis 2. Tropical forest communities are stable through time.

The pollen histories of both Serra Negra and Lagoa dos Olhos, strongly reject this hypothesis. Forest composition in both forests, has changed extensively in the past. The forest adjacent to Lagoa dos Olhos were characterized by mosaic assemblages from 19520 to ca. 9300 yr BP. During this period cerrado, cold-forest taxa, and tropical rain forest taxa coexisted in a Caryocar-Podocarpus forest. Presently this combination of taxa is not reported from any location in Brazil. The present southern limit of Caryocar lies within the area of the Araucaria forests in eastern Paraná (Prance 1990). Its occurrence there, however, is limited to cerrado islands with well defined boundaries (Leite & Klein 1990). Because Caryocar is primarily pollinated by bats (Prance 1990), its high pollen concentration values in the Lagoa dos Olhos diagram are indicative of Caryocar trees adjacent to the lake. The same conclusion is valid for Podocarpus, which although possessing anemophilous pollen, is found in high concentrations in the diagram.

Although the Serra Negra pollen record rejects this hypothesis, this site does not appear to be as suitable to its testing as the record of Lagoa dos Olhos. This is probably a consequence of the morphometric characteristics of the Serra Negra caldera. Presently, different plant formations can colonize its inner area, and the resulting pollen signal in surface sediment is composed of a
mixture of elements from these plant formations, thus not allowing for their discrimination into assemblages. However, prior to 40000 years BP, its pollen record does suggest the presence of three main episodes (zones SN2 to SN4) of very cold and moist forests, with alternating and oscillating compositions.

The data presented here strongly suggests maximum forest disequilibrium during times of intensified temperature depression. Similar conclusions have been reached for the late Quaternary forests of Ecuador (Liu & Colinvaux 1985; Bush et al. 1990) and Panama (Bush & Colinvaux 1990).

Hypothesis 3. Expansion of *Araucaria angustifolia* forests occurred in southeastern Brazil during times of cooling of the last ice age.

The pollen from Serra Negra supports the expansion hypothesis whereas the evidence from Lagoa dos Olhos rejects it. There were multiple expansions of this taxon in Serra Negra during the last 39000 years, which are not represented in the Lagoa dos Olhos diagram since its paleorecord only encompasses the last 20000 yr BP. The Pleistocene/Holocene boundary of this latter site is characterized by the presence of a cool *Podocarpus* forest lacking *Araucaria*. The long record from Serra Negra, on the other hand shows oscillating values of *Araucaria* pollen, which was present in the forests of the caldera from 39990 to 10000 yr BP. The Serra Negra diagram indicates that the greatest expansion of *Araucaria* in southeastern Brazil occurred prior to 40000 years BP, when average winter temperatures were 7-9°C lower than present. By using the conservative value of 7°C for winter temperature depression for Serra Negra (prior to 40000 yr BP), lapse rate of 0.6°C per 100 m rise in elevation (Flenley 1979, Bush et al. 1990), present day July average
temperature (18.8°C) the following vegetational change is likely to have occurred: the *Araucaria* forest belt had descended to 800 m elevation (400 m forest belt descent). This period prior to 40000 years BP, probably marked a time when a continuous *Araucaria* forest belt existed in the mountain region of southeastern Brazil, with altitudes higher than 800 m. After this period, this forest type has contracted to the higher elevation (>1200 m) areas of southeastern Brazil, which are climatically conducive to their maintenance. This hypothesis is supported by the record of Lagoa dos Olhos (730 m elevation), which has shown only sporadic occurrences of *Araucaria* pollen in very low percentage and concentration values, thus indicating its origin in distant forests.

The late Pleistocene/Holocene boundary at Lagoa dos Olhos is marked by the presence of cool and moist *Podocarpus* forest lacking *Araucaria*. A possible hypothesis for the lack of *Araucaria* forests during the late Pleistocene to early Holocene of Lagoa dos Olhos, is that this taxon was already restricted to altitudes higher than 1000 m at the latitude of Lagoa dos Olhos, at that time. This would explain the presence of *Araucaria* in Lagoa da Serra Negra (elev. ca. 1170-1270m) when the cold late-Pleistocene forest of Lagoa Santa had a predominance of *Podocarpus*.

**Hypothesis 4. Climatic changes in southeastern Brazil and southern South America were synchronous in the last ice age.**

The long pollen record of Serra Negra indicates that maximum temperature depression, accompanied by moist conditions, occurred prior to 39930 yr BP. A temperature depression of ca. 7°C (a conservative estimate) in the average temperature of the month of July is suggested, based on the present geographical position of contiguous *Araucaria* forest, present climate of
southeastern Brazil, and growth requirements of this taxon. This climatic scenario appears to be in agreement with the paleocological evidence from southern South America. Mercer (1976) reports that the most extensive glacier advancement both in Argentina and Chile during the last glaciation occurred before 56000 yr BP. Likewise, coldest glacial times prevailed in Serra Negra prior to 40000 yr BP, whereas oscillating cold/moist and warm/dry conditions prevailed from 30000 to 20000 yr BP. Depressed temperatures and high humidity characterize also the climate of Lagoa dos Olhos at 19520 yr BP. This is in close agreement with reoccurrence of cooling at 20000 yr BP reported by Heusser (1989) at higher latitudes of the south american continent. Extensive ice fields are also reported at 20000 yr BP on both sides of the Andes and in Patagonia (Mercer 1984; Rabassa & Clapperton 1990). This major period of glacier formation in South America is synchronous with the greatest expansion of the Laurentide ice sheet in Illinois at 19000-20000 yr BP (Frye & Willman 1973, In Mercer 1976). The period of 19500 to 22500 yr BP also marks extensive glaciation in the Andes of Colombia (Kuhry 1989). At ca. 10000 yr BP, conditions are cool and moist in Serra Negra, and significantly drier in Lagoa dos Olhos. Cooling at this time is also reported for the Lake District of Chile by Heusser (1984). In summary, the pollen record from southeastern Brazil appears to be in much agreement with glacial and palynological records from higher latitudes of the south american continent.

As in Serra Negra, coldest times of the last glaciation in southern South America were synchronous with high humidity levels. During the austral winter at high latitudes, the climate is cold and moist due to equatorward shift of the westerly circulation. Summer rains, in the higher latitudes of South America,
are directly dependent on the southward movement of the subtropical high pressure system (Pittock 1980 In Markgraf 1989).

The maintenance of *Araucaria* forests in southern Brazil is primarily controlled by the cool and moist climate maintained by the constant surge of polar air from southern South America. The present northernmost limit of contiguous *Araucaria* forest lies at 23°S (Tropic of Capricorn) close to the border of São Paulo and Paraná (Leite & Klein 1990). The pollen diagram of Serra Negra clearly suggests that both the northern limits of the Atlantic polar front and of the *Araucaria* forests, were both displaced as far north as 18°S latitude, especially prior to 40000 year BP and numerous time during the period from ca. 39900 to ca. 10000 yr BP. This implies a total northward displacement of the Atlantic polar frontal system of approximately 5° of latitude. A similar magnitude of northward displacement (5-6°) for the southern polar front during the Wisconsin Glacial age has been advocated by Paskoff (1970), Hastenrath (1971), Caviedes (1972) and Suzuki (1973).
CONCLUSIONS

The following conclusions can be drawn from the paleoecological analyses of the sediments of Lagoa da Serra Negra and Lagoa dos Olhos:

1. The palynological record of Lagoa da Serra Negra provides evidence for three periods of intense cooling, synchronous with high levels of humidity, prior to 40000 yr BP (zones SN1, SN3 and SN5). The pollen assemblages suggest expansion of *Araucaria* forests in these zones, when average winter temperature were 7-9°C lower than presently. By using the conservative estimate of 7°C, lapse rate of 0.6°C per 100 m elevation, and the present annual and winter average temperatures of the Serra Negra region, the palaeoecological data suggest that the cool and moist *Araucaria* forests had descended to 800 m elevation during times of Late Pleistocene glacial cooling. This large expansion of *Araucaria* forests is likely to have formed a continuous belt over most of southeastern Brazil prior to 40000 yr BP. Since that time, the *Araucaria* forests have been retracting to the higher elevations of this area, thus accounting for its present disjunct distribution.

2. Expansion of *Araucaria* forests in Serra Negra during times of lowered winter temperatures and increased moisture, is likely to be a consequence of a
5° northward displacement of the Atlantic polar frontal system. Presently, this system has its average northernmost limit in the winter at 24°S. A similar magnitude of northward displacement (5-6° C) for the southern polar front during the Wisconsin Glacial age has been advocated by various authors (Paskoff 1970; Hastenrath 1971; Caviedes 1972; and Suzuki 1973).

3. The period of 39930 to ca. 20000 yr BP was characterized by general cool and moist climate, with oscillating dry and warmer phases. Drier or more seasonal climate, i.e. two-season climate, was present especially at 30000 and 20000 yr BP.

4. These drier phases were characterized, however, by the presence of sufficient levels of humidity to maintain moist forest taxa on the Serra Negra landscape.

5. The record from Lagoa dos Olhos starts at 19950 yr BP. The pollen assemblage at the onset of this record is indicative of a forest-savanna mosaic with presently no modern analogs in Brazil. The paradoxical nature of this plant association is due to the coexistence at this time of numerous *Podocarpus* and *Caryocar* trees. This unusual forest type existed during a time, which was characterized by widespread atmospheric cooling in South America.

6. Cooling, as indicated by the presence of *Podocarpus* pollen in the sediments of Lagoa dos Olhos, lasted from 19950 to until ca. 13685 yr BP.
7. Increased seasonality, with concomitant extension of the dry season and reduction in winter cooling is suggested for Lagoa dos Olhos at ca. 9300 yr BP, when the *Podocarpus*-*Caryocar* forest looses the former taxon. This climatic scenario is also suggested for western Minas Gerais, when *Araucaria* ceases to exist on the Serra Negra caldera after 10000 yr BP.

8. A brief cooling period occurs at Serra Negra at 5000 yr BP, when *Podocarpus* pollen reappears in the sediments associated with *Drimys*. However, this cold climate was marginally dry, thus allowing Gramineae and Cyperaceae to be well represented in the pollen diagrams. Seasonal forest taxa, e.g. *Tabebuia*, *Erythrina* also occur during this time indicating that enough moisture was still available for their maintenance during this phase.

9. There is no evidence for the Late-Pleistocene Forest Refuge Hypothesis during the Late-Quaternary vegetational history of western and eastern Minas Gerais. There is no moment in the climatic history of the last 40000 years of this region that can be described as arid. The supposed caatinga vegetation expansion proposed by Ab'Saber (1982) and others who advocated the Refuge Hypothesis did not expand into western and eastern Minas Gerais during the time of the last glacial maximum in the northern hemisphere.

10. The results of the present study clearly indicate that tropical forest communities are not stable through time. Similarly to the results
obtained by Davis (1980, 1983a, 1983b, 1984) for the temperate forests of eastern United States, there is strong evidence in the pollen diagrams of the present study for Gleason's individualistic view of plant communities.

11. Because there is now direct and strong evidence refuting the Late-Pleistocene Forest Refuges in most of the neotropical landmass, new hypothetical mechanisms attempting to explain the origin of the high biodiversity of this area must take into consideration the drastic climatic and vegetational changes that have occurred there during the last glacial cycle.
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APPENDIX

Morphological description of pollen types

Introduction

The objective of this section is to provide a concise photographic documentation of the identified pollen, spores and palynomorphs encountered in this study. However, a small number of taxa mentioned in the text were not photographed.

Identification of pollen, spores types was controlled by comparing fossil types with collections of recent pollen and spores at the following Palynology laboratories and their respective institutions: Dr. P. A. Colinvaux-The Ohio State University, Dr. M.L. Salgado-Labouriau- Universidade de Brasília and Dr. M.L.Absy- INPA (Manaus). Identification of fossil pollen was supplemented by collecting pollen from cerrado, Atlantic and Araucaria forest taxa in the following herbaria: New York Botanical Garden, Missouri Botanical Garden, Museu de História Natural e Jardim Botânico-UFMG (Belo Horizonte) and INPA (Manaus).

Many descriptions are based on one or few grains. Shape of pollen grains have been determined by following the size classes in Salgado-Labouriau (1973) which are function of the polar axis divided by the equatorial
axis lengths (P/E): 0.50 peroblate; 0.50-0.74 oblate; 0.75-0.87 suboblate; 0.88-0.99 oblate-spheroidal; 1.00 spheroidal; 1.01-1.14 prolate-spheroidal; 1.15-1.33 subprolate; 1.34-2.00 prolate; 2.00 perprolate.

The specimens encountered were photographed with Kodak T-Max 125 ASA. Magnification of the photomicrographs ranges from 400 to 1000 x.

Abbreviations used:
Amb= contour of the grains in polar view.
C3P0 = tricolpate pollen grain
C3P3 = tricolporate pollen grain
cf. = Latin confer = compare
e.g = Latin exempli gratia = for example
EV= equatorial view
M: magnification
NYBG= New York Botanical Garden
PV= polar view
um = micrometer

Descriptions

Type 1-6: *Podocarpus* (Podocarpaceae). Plate VI.
**Type 7-13:** *Araucaria* (Araucariaceae). Plate VI.
Inaperturate, intectate, spheroidal grain. Ornamentation composed of fine
columellae. Grain very fragile. Under prolonged acetolysis treatment the thick
exine (2-3 um) usually separates from the intine (types 9-13). Grains 32 (without

**Type 14-15:** *cf. Xyris* (Xyridaceae). Plate VII.
Monocolpate grain with microreticulations, and provided with baculate muri, 18-

**Type 16:** *cf. Palmae*. Plate VII.
Elliptical, monocolpate, micro-reticulate, 37 x 23 um. M: 1000 x. Ref.: Erdtman
(1952).

**Type 17:** *cf. Amaryllidaceae*. Plate VII.

**Type 18-20:** *Palmae (Arecales)* *cf. Euterpe*.
Plate VII.
Monocolpate, reticulate, sulcus wider at both extremities and as long as grain.
Type 19, 41 x 21 um; type 20, 35 x 20 um. M: 1000 x. Ref.: Markgraf & D'Antoni

**Type 21:** *Palmae (Arecales)*. Plate VII.
Monocolpate, micro-reticulate, elliptical grain, 42 x 20 um. M: 1000 x. Ref.: Erdtman

**Type 22:** *Cabomba* (Nymphaeaceae). Plate VII.

**Type 23-25:** *cf. Palmae (Arecales)?* Plate VII.
Grains circular in PV, with wide colpus, grains psilate, 22-23 x 17-18 um. PV.

**Type 26-27: Monocolpate, psilate. Plate VII.**
Grains 24-25 um x 15 um. Grains show a certain affinity with the *Syagrus comosa* (Palmae, Arecaceae) type. Magnification for type 26 is 1000 x and for 27 is 400 x.

**Type 28: *Astrocaryum* (Palmae = Arecaceae). Plate VIII.
Grain tricotomocolpate, triangular in PV, micro-reticulate, 31 x 33 um. M: 1000 x. Ref.: Erdtman (1952)

**Type 29: Xyridaceae/Pontederiaceae. Plate VIII.**
Grains dicolpate, psilate, exine 1 um thick, grains usually 21-22 x 12 um. M: 1000 x. Ref.: Erdtman (1952).

**Type 30-35: Pontederiaceae. Plate VIII.**
Mono-dicolpate grains, tectate, columellate, 45-65 x 18-23 um. Type 34 is echinate. Two genera can be discerned, *Pontederia* (Type 30-33) and *Eichhornia* (Type 34-35). M: 1000 x. Ref.: Roubik & Moreno (1991), Erdtman (1952).

**Type 36: Monocolpate, reticulate. Plate VIII.**
Microspinate grain, 35 x 25 um. Shows affinity to Pontederiaceae. Occurred in Lagoa da Serra Negra, at depth of 1.61 m. M: 1000 x.

**Type 37: Monoporate. Plate VIII.**
Grain more or less spheroidal, spinulose, pore somewhat annulate (?), 18 x 16 um. This type shows a certain affinity to Lemnaceae. M: 1000 x. Ref.: Heusser (1971), Erdtman (1952).
Type 38-41: Gramineae (Poaceae). Plate VIII.

Family with a very homogeneous pollen type (Salgado-Labouriau 1973), *i.e.* monoporate, occasionally diporate (type 39). Sexine usually psilate, granulate, occasionally reticulate. Other ornamentations are known to occur (Salgado-Labouriau & Rinaldi 1990). Types 38-40 have a certain affinity to the woody bamboos due to their dimensions (> 40 um), robust annulus and presence of a granular exine lacking infrategillar bacula (Salgado-Labouriau & Rinaldi 1990).

Type 42: *Zea* (Gramineae, Poaceae). Plate VIII.

This type is separated from other grasses based on the dimensions of the polar diameter. Diameter of *Zea* ranges from 85-125 um (Salgado-Labouriau 1973). Type 42 has a diameter of 102 um. One single occurrence at 0.10 m of Lagoa dos Olhos. M: 1000 x. Ref.: Salgado-Labouriau (1973), Salgado-Labouriau & Rinaldi (1990).

Type 43-48: Cyperaceae. Plate IX.

Pollen mono-periporate, tectate. Apertures are actually poroids. Exine psillate, baculate. Variable in shape (usually pear-shaped) and size. Type 44, 30 x 19 um; type 45, 37 x 37 um; type 46, 24 x 20 um; type 47, longest axis 33 um. M: 1000 x. Ref.: Erdtman (1952), Salgado-Labouriau (1973), Roubik & Moreno (1991).

Type 49-50: *Cecropia* (Moraceae). Plate IX.

Diporate, bilaterally symmetrical, psilate to slightly granulate grains, 10 x 6-7 um in EV. Amb circular. M: 1000 x. Ref.: Barth *et al.* (1975), Hooghiemstra (1984).
Type 51-55: Urticaceae/Moraceae. Plate IX.

Type 56. Ficus (Moraceae). Plate IX.

Type 57: Diporate, reticulate. Plate IX.
Large, conspicuous pores. Grain robust, 31 x 26 um. This type has some affinity with Ananas (Bromeliaceae) (see Salgado-Labouriau 1973, p. 59). One single occurrence in Lagoa dos Olhos, at 0.45 m. M: 1000 x.

Type 58: Dicolporate, psilate. Plate IX.
Grain small, 11 x 14 um. One single occurrence in Lagoa dos Olhos at 0.75 m. M: 1000 x.

Type 59: Diporate, scabrate. Plate IX.
Grain small, 18 x 15 um, pores large and protruding. This type shows some affinity to Onagraceae (type 20, Hooghiemstra 1984). M: 1000 x.

Type 60: cf. Bromeliaceae. Plate IX.

Type 61: Dicolporate (dicolpate ?). Plate IX.
Grain small, 10 x 6 um. Unknown affinity.

Type 62: Dicolporate, syncolporate. Plate IX.
Grains 21 x 14 um, pores protruding. Unknown affinity. M: 1000 x.
Type 63-64: *Forsteronia* (Apocynaceae). Plate X.

Type 65-66: *Urticaceae/Moraceae*. Plate X.
Triporate, psilate grains, radially symmetric, 19 x 20 um (type 65) to 13 x 12 um in diameter (type 66). M: 1000 x. Ref.: Hooghiemstra (1984).

Type 67: *Celtis* (Ulmaceae). Plate X.

Type 68-74: *Symplocos* (Symplocaceae). Plate X.
Grains tricolporate, appearing triporate in PV, exine clavate, some are spinulose (type 73), 19-30 x 17-30 um in PV. M: 1000 x. Ref.: Salgado-Labouriau (1973), Absy (1975).

Type 75, 78-79: *Ludwigia =Jussiaea* (Onagraceae). Plate X.

Type 76-77: *Ayenia* (Sterculiaceae). Plate X.

Type 80, 82: *Onagraceae*. Plate XI.
Tricolporate, psilate, very robust grain, pores strongly protruding, 48 um diameter. This type possibly belongs to *Ludwigia*. M: 1000 x. Ref.: Roubik & Moreno (1991).
Type 81: *Posoqueria* (Rubiaceae). Plate XI.

Type 83-84: Triporate (Tricolporate ?) reticulate. Plate XI.
Grains robust, distinctly baculate, 37-38 um diameter. M: 1000 x.

Type 85, 87: Tricolporate, verrucate. Plate XI.
Grains robust, 42-43 um diameter. M: 1000 x.

Type 86: Tricolporate, micro-reticulate. Plate XI.
Grains tectate, with triangular amb, pores circular and very distinct. Colpi very short and indistinct, thus rendering the grain a triporate appearance, 19 -20 um in PV. M: 1000 x.

Type 88: *Erythrina* (Papilionaceae). Plate XI.

Type 89: *Helicteres* (Sterculiaceae). Plate XI.

Type 90-97: *Peixotoa /Banisteriopsis* (Malpighiaceae).
Plate XII.
Type 98-103. *Myriophyllum* (Haloragaceae).

Plate XIII.

Grains are stephanoporate, with circular amb. Pore number varying from 3 (type 98) to 6, most commonly 4 (types 100, 101, 103). Type 102 is pentaporate. Sexine twice as thick as the nexine, tectate. Aspidote grains with simple aperture., 20-25 um diameter. Ref.: Praglowski (1970).

Type 104: Tetraporate, reticulate. Plate XIII.

Pores large. Grain 23 x 20 um. One single occurrence in Lagoa da Serra Negra at 1.16 m. M: 1000 x.

Type 105-106: Periporoidate. Plate XIII.

Grains micro-reticulate, baculate, subcircular, 4-6 poroids, 19-22 um diameter. These types show a possible affinity to Cyperaceae.

Type 107: *Alnus* (Betulaceae). Plate XIII.

Tetraporoidate, aspidote, psilate grains, with arci connecting the appertures. Diameter in PV 18 um. Although this taxon is presently not native to Brazil, it has been found in Holocene sediments from Amazonia (Absy 1979) and Quaternary sediments from southeastern Brazil (Absy 1975). One single occurrence in Lagoa dos Olhos at 1.65 m. M: 1000 x. Ref.: Erdtman (1952); Absy (1975, 1979).

Type 108: Tetraporate (Tetracolporate ?). Plate XIII.

Psilate spheroidal grain with distinct elliptical pores., 15 x 14 um in EV. M: 1000 x.
Type 109, 111-112: *Alisma / Echinodorus / Sagittaria* (Alismataceae). Plate XIII.

Type 110: Tetraporate, echinate. Plate XIII.
Grain zonoaperturate. Exine thick, pores large, circular to elliptical. M: 1000 x.

Type 113: *cf.* Cyperaceae. Plate XIII.

Type 114-116: *Alisma / Echinodorus / Sagittaria* (Alismataceae). Plate XIV.
Same morphological characters found in types 109, 111-112. Type 114 has a diameter of 12 um. Type 115, 32 x 37 um. Type 116 is reticulate, baculate, with small spines, 20 um diameter. M: 1000 x. Ref.: Hooghiemstra (1984), Erdtman (1952).

Type 117, 120: Chenopodiaceae/Amaranthaceae. Plate XIV.

Type 118: Periporate *cf.* Malpighiaceae (?). Plate XIV.
Grain with circular amb, exine thick, 6 pores present. Grain 24 x 21 um. Very indistinct colpi present. This type appears to have a certain affinity to the *Hirea / Peixotoa* (Malpighiaceae). M: 1000 x.
Type 119: Periporate, annulate. Plate XIV.
Grain distinctly baculate, micro-reticulate, 6 pores present. Exine 1 um thick., 20-19 um diameter. One single occurrence in Lagoa da Serra Negra at 7.32 m. M: 1000 x.

Type 121: cf. Typha (Typhaceae). Plate XIV.

Type 122: Monoporate, echinate. Plate XIV.
Ulcerate grain with conspicuous echinae, 20 x 20 um. One single occurrence in Lagoa da Serra Negra at 7.10 m. M: 1000 x.

Type 123: Periporate, baculate. Plate XIV.
Grain with various annulate pores, sexine with reticulate pattern, 24 x 23 um. M: 1000 x.

Type 124, 134: Malvaceae. Plates XIV and XVI.

Type 125: Periporate, granulate. Plate XIV.

Type 126: Monoporate, echinate. Plate XV.
Grains with baculate exine possessing a possible affinity with Typha. Grains 21-25 um diameter. M: 1000 x.
Type 127-128: *Mauritia* (Palmae = Arecaceae).

**Plate XV.**

Type 129-132: Alismataceae. **Plate XV.**

Type 133: Malvaceae. **Plate XV.**
Grain spheroidal to prolate, with large echinae, grain probably periporate, pores indistinct, 55 x 36 um (measurement from only one grain). Exine tectate, echinae on raised structures. M: 1000 x. Ref.: Hooghiemstra (1984), Erdtman (1952).

Type 134: see Type 124, Plate XIV.

Type 135: Malvaceae, *cf. Pavonia* ?. **Plate XVI.**

Type 136: Malvaceae. **Plate XVI.**

Type 137: *Polygonum* (Polygonaceae). **Plate XVI.**
Pollen grains periporate, reticulate, heterobrochate, amb circular, spheroidal, 48 um diameter. M: 1000 x. Ref.: Roubik & Moreno (1991),

**Type 138: Malvaceae. Plate XVI.**
Pollen grains spheroidal, echinate, periporate, 45-50 um diameter. M: 400 x.

**Type 139: cf. Pfaffia (Amaranthaceae). Plate XVI.**

**Type 140: Gomphrena (Amaranthaceae). Plate XVI.**

**Type 141: Alternanthera (Amaranthaceae). Plate XVI.**
Pollen grains fenestrate, with a polyhedral shape and containing 12 pores. One pore is found in each lumen. Muri supported by one row of columellae. Diameter of grains in the sediments range from 16 to 20 um. M: 1000 x. Ref.: Hooghiemstra (1984), Salgado-Labouriau (1973).

**Type 142-144: Eriocaulon (Eriocaulaceae). Plate XVII.**

**Type 145-155: Compositae (Asteraceae). Plate XVII.**
No attempt was made here to distinguish the different types of this family with the exception of *Elephantopus /Elephantopsis* type (Type 156-158, Plate XVIII). The Compositae micrographs depicted on Plate XVII represent the most common types of that family, found in the sediments of Lagoa da Serra Negra and Lagoa dos Olhos. Some Compositae types found in the sediments were
not photographed. Dimmension of the grains here shown are: type 146, 30 x 37 um; type 147, 27 um diameter; type 148, 23 um; type 149, 25 x 26 um (excluding echinae); type 150, 31 x 32 um (including echinae); type 152, 24 x 25 um (excluding echinae); type 153, 27 um diameter (excluding echinae); type 154, 3 um diameter, type 155, 36 um diameter (excluding echinae).

**Type 156-158: *Elephantopus* /*Elephantopsis* (Compositae = Asteraceae). Plate XVIII.
Pollen grains fenestrate, with three lumina, each containing an indistinct pore. The reticulate sexine containing small spines can be seen in low magnification. Diameter of grains varying from 38 to 40 um. M: 1000 x. Ref.: Salgado-Labouriau (1973), Roubik & Moreno (1991).

**Type 159-160: *Daphnopsis* (Thymelaeaceae).
Plate XVIII.

**Type 161: Loranthaceae (Loranthaceae type I).
Plate XVIII.

**Type 162-163: Loranthaceae (Loranthaceae type II).
Plate XVIII.

**Type 164: Loranthaceae ? Plate XVIII.
Syncolpate, psilate pollen grain, 32 x 30 um. M: 1000 x.
Type 165: Syncolpate, granulate. Plate XVIII.
Pollen grain, 25 um diameter. This type appears to have some affinity to Loranthaceae, Proteaceae and possibly Myrtaceae. One single occurrence in Lagoa dos Olhos at 0.55 m. M: 1000 x.

Type 166: Syncolpate, psilate. Plate XVIII.
Pollen grains very small (13-14 um diameter), subspheroidal. There is an apparent affinity to Myrtaceae. One single occurrence at Lagoa dos Olhos at 1.35 m (mid Holocene).

Type 167: Sapindaceae. Plate XVIII.
Syncolporate, psilate, isopolar grain, 21 x 21 um. M: 1000 x.

Type 168-172, 174: Myrtaceae. Plate XVIII.
Grains with a characteristic triangular to subtriangular amb, exine psilate to slightly granulate. Some grains have short colpi (Type 169) whereas others are syncolpate (Types 170-172, 174). Diameter in PV ranging from 15 to 22 um. M: 1000 x. Ref.: Salgado-Labouriau (1973), Hooghiemstra (1984).

Type 173: Matayba (Sapindaceae). Plate XVIII.

Type 174-177: Myrtaceae. Plate XVIII.

Type 178: Cupania (Sapindaceae). Plate XVIII.
Pollen grains with a triangular amb, syncolporate, sexine with microreticulations visible only under immersion, 17-25 um PV diameter. M: 1000 x.

**Type 179-180: Sapindaceae. Plate XIX.**

**Type 181: Sapindaceae, cf. Cupania ?. Plate XIX.**
Syncolporate, micro-reticulate grain, 22 um diameter. Exine baculate. M: 1000 x.

**Type 182-183: Roupala (Proteaceae). Plate XIX.**

**Type 184-185: Proteaceae. Plate XIX.**
Pollen grains triporate, triangular amb (with sides straight), exine distinctly reticulate, 24-27 um PV diameter. Type 185 (one single occurrence) has a diameter of 3 um. M: 1000 x. Ref.: Erdtman (1952).

**Type 186, 187: Euplassa (Proteaceae). Plate XIX.**

**Type 188: Tricolporate, granulate. Plate XIX.**
Grain with triangular amb (sides slightly concave), colpi short, pores large and ellipsoidal, 22 x 26 um diameter. This type shows a certain affinity to *Couepia* type (Salgado-Labouriau 1973, p. 63). M: 1000 x.

**Type 189-190: cf. Chrysobalanaceae. Plate XIX.**
Suboblate grains with triangular amb (sides straight to slightly concave), tricolporate. Sexine granulate to striate-reticulate, 20-38 um PV diameter.
Type 191: Tricolporate. Plate XIX.
Grain psilate to granulate, pores protruding, 19-18 um. Grain not examined in EV. M: 1000 x.

Type 192: Proteaceae (?). Plate XIX.
Triporate, micro-reticulate grain, 20 x 19 um in PV. M: 1000 x.

Type 193-195,198: Cuphea (Lythraceae). Plate XIX.
Very distinct pollen grains. Grains with triangular amb, angulaperturate, syncolporate, sexine striate, 18-26 um PV diameter. M: 1000 x.

Type 196: Cuphea thymoides (Lythraceae). Plate XIX.
Very distinct type characterized by the presence of 2-3 pseudocolpi, 2 circular protruding pores. Sexine striate (striations visible only under immersion). Only one occurrence. Grain 29 x 20 um in EV. M: 1000 x.

Type 197: Cuphea ? Plate XIX.
Grain tricolporate, non-syncolporate. There is a strong affinity to Cuphea due to the presence of few striations of the sexine. M: 1000 x.

Type 198: see Type 193. Plate XIX.

Type 199-200: Lafoensia (Lythraceae). Plate XX.
Grain not examined under PV. Salgado-Labouriau (1973) reports triangular amb and reticulations, which are visible with magnification equal to or higher than 1200 x. M: 1000 x. Ref.: Salgado-Labouriau (1973), Erdtman (1952).
Type 201: *Chrysophyllum* (Sapotaceae). Plate XX.
Tricolporate, exine 1 um thick, sexine psilate, prolate grain, 21 x 14 um.

Type 202-203, 205: *Tabernaemontana* (Apocynaceae).
Plate XX.
Pollen grains tricolporate, distinctly zonorate (with a continuous equatorial oral zone), sexine granulate., circular amb, 28-52 x 24-36 um in EV. M: 1000 x.

Type 204: Zonorate, psilate, cf. Burseraceae. Plate XX.
Pollen grains with a narrow equatorial oral zone. Grains C3(P3?) showing a possible affinity to *Tabernaemontana* type. This type has been identified by M.L. Absy, INPA, as belonging to Burseraceae. Dimensions of this type are: 40-42 x 24-26 um in EV. M: 1000 x.

Type 205: see Type 202. Plate XX.

Type 206: Burseraceae, cf. *Protium* (?), Sapotaceae ?.
Plate XX.

Type 207-208, 210: *Trattinickia/Tetragastris* (Burseraceae). Plate XX.
Tricolporate grains, sexine psilate to slightly striate, micro-reticulate., triangular amb (sides straight to slightly concave), exine thick (1-2 um), pore large and lalongate. Grains 21-30 x 20-21 um in EV, 20-21 um PV diameter. M: 1000 x.
**Type 209: Tricolporate, granulate. Plate XX.**
Grains with exine granulate to slightly micro-reticulate, pores circular.
Dimensions in EV are 39 x 27 um, not examined in PV. One single occurrence.
M: 1000 x.

**Type 211: Tricolpate, microechinate. Plate XXI.**
Grain characterized by the presence of very small spines widely dispersed on the sexine, exine 1 um thick, prolate, 17 x 15 um EV, 17-20 um PV. This type shows some affinity to *Pisonia* (Nyctaginaceae) (see Salgado-Labouriau 1973, Markgraf & D'Antoni (1978).

**Type 212: cf. Cariniana (Lecythidaceae). Plate XXI.**
Tricolporate (pores appearing to be poroids) micro-reticulate, tectate, colpi narrow and long, 30 x 34 um in EV. This grain resembles somewhat those belonging to the *Lecythis* type, which includes *Bertholletia* and *Gustavia*. M: 600 x. Ref.: Erdtmann (1952), Ledru (1991).

**Type 213: Tricolporate (Tricolpate ?). Plate XXI.**
Grains psilate, prolate, 30 x 36 um EV. Unknown affinity. M: 600 x.

**Type 214: Tricolporate (Tricolpate ?). Plate XXI.**
Grain prolate, sexine slightly striate, appearing to have poroids instead of pores associated with colpi, 27 x 29 um in EV. M: 1000 x.

**Type 215: Tricolporate, granulate (psilate ?). Plate XXI.**
Grain not well preserved appearing to have a granulate sexine, pores indistinct, 25 um in PV. M: 1000 x.

**Type 216: Tricolpate (tricolporate ?), psilate. Plate XXI.**
Grains small, 18 x 14 um. Circular pore-like structures could be present.
Type 217: Tricolpate (tricolporate ?). Plate XXI.
Grains 20 x 31 um in EV, micro-reticulate. Unknown affinity. M: 1000 x.

Type 218: Tricolpate, granulate. Plate XVI.
Grain 25 x 15 um in EV. Unknown affinity. M: 1000 x.

Type 219-220: Tricolpate reticulate. Plate XXI.
Grain 30-32 x 17 um in EV. Unknown affinity. M: 1000 x.

Type 221: Tricolpate, reticulate. Plate XXI.
Grain 35 x 22 um EV, strongly reticulate, baculate.. Unknown affinity. M: 1000 x.

Type 222: Tricolpate, reticulate. Plate XXI.
Grain 24 x 16 um, exine with very small bacula. Unknown affinity. M: 1000 x.

Type 223-224: Tricolporate, psilate. Plate XXI.
Grains prolate, psilate, tectate, amb triangular convex, pores not very distinct, appearing to be slightly lalongate. Grains 16-17 x 12-13 um in EV. This type shows some affinity to Myroxylon (Fabaceae) shown in Ledru (1991).

Type 225: Tricolporate, psilate. Plate XXI.
Grains small, 15-16 x 14 um in EV, pores not very distinct, showing some affinity to the previous types (222-223). M: 1000 x.

Type 226: Tricolporate, psilate. Plate XXI.
Grains 17 x 8 um, pores circular.

Type 227: Tricolporate, psilate. Plate XXI.
Grains prolate, 11-12 x 9 um, pores distinct and circular. Like types 222-223, this type also shows a possible affinity to Myroxylon (Fabaceae) (see Ledru 1991). M: 1000 x.
Type 228: Caesalpiniaceae (cf. Schizolobium)?

Plate XXII.

Type 229: Escallonia (Escalloniaceae). Plate XXII.
Tricolporate, psilate, exine 2 um thick, subprolate to spheroidal, amb circular, colpus equatorially constricted with costae colpi (presence of thickening of endexine delimiting colpi), 18 x 17 um EV, 17 um PV diameter. M: 1000 x. Ref.: Markgraf & D'Antoni (1978).

Type 230: Tricolporate, granulate. Plate XXII.
Grains oblate-spheroidal, 22 x 24 um in EV, with very indistinct pore. Sexine granulate to slightly striate. M: 1000 x.

Type 231: Tricolporate, psilate. Plate XXII.
Grain small, 16 x 16 um EV, 15 x 15 um PV, pores very indistinct. M: 1000 x.

Type 232: Ouratea (Ochnaceae). Plate XXII.

Type 233: Tricolporate, psilate, cf. Escallonia.

Plate XXII.
Type morphologically very similar to Escallonia (type 228). Grain 17 x 18 um EV, 18 x 19 um PV. M: 1000 x.

Type 234: Tricolporate, granulate-psilate. Plate XXII.
Grain prolate 20 x 18 um EV, 17-19 um PV, sexine baculate, pore distinct and lalongate appearing operculate. Exine 2 um thick. M: 1000 x.
Type 235: *Curatella* (Dilleniaceae). Plate XXII.

Type 236: *cf. Cochlospermum* (Cochlospermaceae).
Plate XXII.

Type 237: *cf. Fabaceae* (Papilionaceae). Plate XXII.

Type 238: *cf. Fabaceae* (Papilionaceae). Plate XXII.

Type 239-240: Tricolporate, psilate. Plate XXII.
Grains prolate, 18-19 x 15-17 um EV, 15 x 15 um PV, pore lalongate. M: 1000 x.

Type 241: Tricolporate, psilate. Plate XXII.
Grains slightly granulate, prolate, 17 x 12 um, pore indistinct. M: 1000 x.

Type 242: Tricolporate, micro-reticulate. Plate XXII.
Grain prolate, 20 x 15 um EV, exine baculate, pores annulate (?). M: 1000 x.

Type 243: Tricolporate, micro-reticulate, *cf. Fabaceae*?
Plate XXII.
Grain prolate, 29 x 18 um EV, pores distinct, colpi long and narrow. M: 1000 x.
Type 244: Tricolporate, micro-reticulate. Plate XXII.
Pollen grain small, prolate, 19 x 14 um EV, exine tectate. M: 1000x.

Type 245: Tricolporate, psilate. Plate XXII.
Grain prolate, 23 x 20 um EV, pore distinct and lalongate. M: 1000 x.

Type 246: Tricolporate, psilate. Plate XXII.
Grain prolate to subspheroidal, 22 x 19 um EV, circular amb, 19 x 18 um PV. This type appears to be syncolporate. Unknown affinity. M: 1000 x.

Type 247: Balfourordendron (Rutaceae). Plate XXIII.

Type 248: cf. Balfourordendron? (Rutaceae). Plate XXIII.
Grain with morphology similar to that of previous type, however, this type is larger and more prolate, 27 x 19 um. M: 1000 x.

Type 249: Tricolporate, granulate. Plate XXIII.
Grain prolate-spheroidal, 20 x 18 um in EV. Colpi long, widest at equator, pores lalongate and very conspicuous. Sexine baculate. M: 1000 x.

Type 250: Tricolporate, granulate. Plate XXIII.
Grain spheroidal, 17 x 18 um EV, 18 um PV. Colpi very narrow and inconspicuous. One single occurrence. M: 1000 x.

Type 251, 253: Xylosma (Flacourtiaceae). Plate XXIII.

Type 252: cf. Xylosma (Flacourtiaceae)? Plate XXIII.
Grain with morphology very similar to that of Xylosma, but differs from it when PV is examined. Dimensions for this type are: 17 x 15 um EV, 15 um PV.
diameter. This type was found in a Serra Negra sediment sample, where
*Xylosma* pollen was abundant. M: 1000 x.

**Type 254: Tricolporate reticulate. Plate XXIII.**
This type shows a certain resemblance to *Xylosma* type, however, it appears to possess costae colpi. Dimensions for this type are: 21 x 14 um EV (prolate). M: 1000 x.

**Type 255: Tricolporate reticulate. Plate XXIII.**
Grain subspheroidal, 19 x 18 um EV, 18 x 17 um PV. Pores distinct, ellipsoidal, sexine baculate. M: 1000 x.

**Type 256: *Banara* (Flacouriaceae). Plate XXIII.**

**Type 257: cf. *Zanthoxylum/Pilocarpus* (Rutaceae) Plate XXIII.**

**Type 258: cf. *Prunus* (Rosaceae). Plate XXIII.**

**Type 259: Tricolporate reticulate. Plate XXIII.**
Grain subspheroidal, 16 x 15 um EV, 17 x 16 um PV. Reticulations forming wide lumina. Exine baculate. M: 1000 x.

**Type 260: cf. Rosaceae. Plate XXIII.**
Grain tricolporate reticulate-striate, spheroidal, 14 x 14 um, sexine baculate.
Type 261: Tricolporate reticulate. Plate XXIII.
Grains small, subspheroidal, 14 x 12 um EV, 14 x 13 um PV. Sexine baculate. M: 1000 x.

Type 262: Tricolporate reticulate. Plate XXIII.
Grain showing a strong affinity to the previous type. Dimensions for type 262 are: 16 x 16 um EV, 16 x 16 um PV. M: 1000 x.

Type 263-266: Alchornea (Euphorbiaceae). Plate XXIV.
Grains spheroidal to subspheroidal, scabrate to micro-reticulate, amb circular. The triangular internal outline of these grains in PV is due to the unequal thickening of the exine (Salgado-Labouriau 1973). Pores lalongate, operculate. Dimension for types shown on Plate XXIV are: type 263, 20 x 18 um EV, 19 x 19 um PV; type 264, 19 x 18 um EV, 19 x 19 um PV; type 265, 25 x 22 um EV; type 266, 26 x 25 um. Magnification of types 263-266 is 1000 x.

Type 267: Tricolporate (tricolpate ?), scabrate. Plate XXIV.
Grain prolate, 20 x 16 um EV, exine tectate. M: 1000 x.

Type 268-269: Triporate, micro-reticulate, cf. Xylosma ? Plate XXIV.
Grain prolate 18 x 10 um, pores circular and distinct. Grain not examined in PV, thus affinity with Xylosma cannot be ascertained. Type 269 is subprolate, 19 x 15 um EV, PV not examined. M: 1000 x.

Type 270: Tricolporate, scabrate. Plate XXIX.
Grain prolate, 24 x 17 um EV, colpi narrow and long, pores indistinct. M: 1000 x.
**Type 271**: *Patagonula* (Boraginaceae). Plate XXIV.
Grains tricolporate, oblate-spheroidal, 19-20 x 21-22 um EV, sexine with vestigial spines. The grain depicted in Markgraf & D'Antoni (1978), Plate 11, fig. 99 and identified as *Patagonula americana* is heterocolpate and does not correspond to Erdtman's description of this type. *Patagonula americana* pollen obtained from herbarium material at the New York Botanical Garden have the same morphology as described in Erdtman (1952). M: 1000 x.

**Type 272**: Tricolporate, reticulate. Plate XXIV.
Grain prolate, 19 x 16 um EV. M.: 1000 x.

**Type 273**: Tricolpate (tricolporate ?) psilate.
Plate XXIV.

Grain prolate, 19 x 15 um EV, 15 x 15 um PV. M: 1000 x.

**Type 274**: Tricolpate, psilate to micro-reticulate.
Plate XXIV.

Grain prolate, 20 x 16 um. M: 1000 x.

**Type 275**: Tricolpate, psilate to micro-reticulate.
Plate XXIV.

Grain subprolate, 16 x 15 um EV, 17 x 17 um PV diameter.

**Type 276**: Tricolpate, micro-reticulate. Plate XXIV.
Grain prolate, 22 x 18 um EV. M: 1000 x.

**Type 277**: Tricolpate, granulate. Plate XXIV.
Grain prolate-spheroidal, circular amb, 17 x 17 um PV. M.: 1000 x.

**Type 278**: Tricolpate (tricolporate ?), psilate.
Plate XXIV.

Grain prolate-spheroidal, 21 x 20 um EV, fossaperturate, colpi short and wide. M: 1000 x.
Type 279: Tricolpate reticulate. Plate XXV.
Grain prolate, 21 x 15 um EV. M: 1000 x.

Type 280: Tricolpate, psilate. Plate XXV.
Grain prolate-spheroidal, 17 x 15 um EV. M: 1000 x.

Type 281: Tricolpate, psilate. Plate XXV.
Grain spheroidal, 16 x 16 um EV, 15 x 15 um PV.

Type 282, 285: Tricolpate, psilate. Plate XXV.
Grains prolate-spheroidal to spheroidal, 13-15 x 12-15 um EV, triangular amb.
Grain appearing syncolpate in PV. Pore lalongate, colpi wide. M: 1000 x.

Type 283: Tricolpate, psilate. Plate XXV.
Grain oblate-spheroidal, 14 x 15 um EV. M: 1000 x.

Type 284: Tricolpate, psilate. Plate XXV.
Grain prolate-spheroidal, 15 x 14 um EV, pore circular, exine 0.5 um thick.
M: 1000 x.

Type 286: Tricolpate, psilate. Plate XXV.
Grain showing a strong affinity to types 282 and 285, but differing from both
types by the absence of wide colpi. Pore lalongate. Dimensions for this type
are: 16 x 15 um EV (prolate spheroidal), 16 x 15 um PV. M: 1000 x.

Type 287: Tricolpate, psilate. Plate XXV.
Grain not well preserved, spheroidal, 15 x 15 um EV, 15 x 15 um PV. Pore
lalongate. M: 1000 x.

Type 288: cf. Acaiypha (Euphorbiaceae). Plate XXV.
Grain tricolporate, spheroidal, 14 x 14 um EV, pores protruding, colpi very fine.
Type 289: Tricolporate (tricolpate ?), psilate.  
Plate XXV.
Grain prolate-spheroidal, 13 x 12 um EV, pore circular, although not very distinct. M: 1000 x.

Type 290: Acalypha (Euphorbiaceae). Plate XXV.
Grain tricolporate, oblate-spheroidal, 10 x 11 um EV, psilate, pores distinctly protruding. M: 1000 x.

Type 291: Acalypha (Euphorbiaceae). Plate XXV.
Grain tetracolporate, pores protruding, 16 x 16 um P. M: 1000 x.

Type 292: cf. Acalypha (Euphorbiaceae). Plate XXV.
Grain tricolporate, psilate, oblate-spheroidal, 14 x 16 um EV, 15 x 15 um PV. M: 1000 x.

Type 293: cf. Pera (Euphorbiaceae). Plate XXV.

Type 294: Pera glabrata (Euphorbiaceae). Plate XXV.
Pollen from herbarium specimen (NYBG) and depicted here for comparison with fossil specimens. Grain subprolate to spheroidal, 15-16 x 13-15 um EV, circular amb (ca. 15 um PV), micro-reticulate, pore circular. M: 1000 x.

Type 295-296: Byrsonima (Malpighiaceae). Plate XXV.

Type 297: Tricolporate, psilate. Plate XXV.
Grain subprolate, 15 x 13 um EV, pore lalongate. M: 1000 x.

Type 298: Tricolporate, psilate. Plate XXV.
Grain prolate-spheroidal, 16 x 14 um EV, pore lalongate.
Type 299: Tricolporate, psilate. Plate XXV.
Grain subprolate, 15 x 13 um EV, pore lalongate and inconspicuous. M: 1000 x.

Type 300: Mabea (Euphorbiaceae). Plate XXVI.

Type 301: Tricolporate, psilate. Plate XXVI.
Grain showing a certain affinity to Euphorbiaceae (cf. Sebastiana ?). Grain prolate, psilate to slightly striate, 33 x 20 um EV, exine tectate. M: 1000 x.

Type 302: Erythroxylum (Erythroxylaceae). Plate XXVI.

Type 303: cf. Styrax (Styracaceae)? Plate XXVI.

Type 304: cf. Styrax (Styracaceae)? Plate XXVI.
Grain subprolate, 31 x 26 um EV, reticulate, pore lalongate, syncolporate (?) in PV. Ref.: Salgado-Labouriau (1973).

Type 305: Styrax (Styracaceae). Plate XXVI.

Type 306: Tricolporate, psilate. Plate XXVII.
Grain prolate, 15 x 11 um EV, pore lalongate. M: 1000 x.

Type 307: Tricolporate, psilate. Plate XXVII.
Grain subprolate, 16 x 12 um EV, pore lalongate. M: 1000 x.
Type 308: Tricolporate, psilate. Plate XXVII.
Grain subprolate, 20 x 15 um EV, 13 x 15 um PV, colpi narrow and long, pore indistinct. M: 1000 x.

Type 309: Tricolporate, psilate. Plate XXVII.
Grain prolate-spheroidal, 16 x 14 um EV, 13 x 14 um PV, pore lalongate. M: 1000 x.

Type 310: Tricolporate, psilate. Plate XXVII.
Grain subprolate, 19 x 15 um EV, pores indistinct. M: 1000 x.

Type 311: Bowdichia (Fabaceae). Plate XXVII.

Type 312: Tricolporate, psilate. Plate XXVII.
Grain prolate, 19 x 12 um EV, 12 x 12 um PV. M: 1000 x.

Type 313: Antonia (Loganiaceae). Plate XXVII.
Grain subprolate, 18 x 15 um EV, 17 x 17 um PV, amb circular, more or less fossaperturate, sexine micro-reticulate. Pores circular. M: 1000 x. Ref.: Salgado-Labouriau (1973).

Type 314: Tricolporate, psilate. Plate XXVII.
Grain prolate, 24 x 14 um EV, spore lalongate. M: 1000 x.

Type 315: Casearia (Falcourtiaceae). Plate XXVII.

Type 316: cf. Casearia (Flacourtiaeae) ? Plate XXVII.
Grain tricolporate, psilate, prolate, 19 x 12 um EV, 12 x 12 um PV. Coastae colpi present, pore lalongate. M: 1000 x.
Type 317: Tricolporate, psilate. Plate XXVII.
Grain prolate, 21 x 9 um EV. Unknown affinity. M: 1000 x.

Type 318: cf. Lathyrus (Fabaceae = Papilionaceae).
Plate XXVII.
Grain prolate, rounded polar area, psilate, 30 x 18 um EV, pore lalongate M: 600 x. Ref.: Heusser (1971).

Type 319: Tricolporate, psilate. Plate XXVII.
Grain prolate, 16 x 11 um EV, exine tectate. M: 1000 x.

Type 320-324, 327: Andira / Machaerium / Dalbergia.
Plate XXVII.

Type 325: Tricolporate, psilate. Plate XXVII.
Grain prolate, 15 x 11 um EV. M: 1000 x.

Type 326: Tricolporate, reticulate. Plate XXVII.
Grain prolate-spheroidal, 16 x 15 um EV, pore lalongate. This type appears to have a certain affinity to Andira / Machaerium / Dalbergia type. M: 1000 x.

Type 328: Andira / Machaerium / Dalbergia.
Plate XXVII.
Grain subprolate, 20 x 17 um EV, sexine reticulate, pore lalongate and very conspicuous, pore 6 x 8 um, exine 1.5 um thick. M: 1000 x. Ref.: Salgado-Labouriau (1973).

Type 329: Andira / Machaerium / Dalbergia.
Plate XXVII.
**Type 330:** *Andira /Machaerium /Dalbergia*.

**Plate XXVII.**

**Type 331:** *Emmotum* (Icacinaceae). **Plate XXVII.**

**Type 332:** Tricolporate, psilate. **Plate XXVII.**
Grain subprolate, 17 x 13 um EV, psilate, fossaperturate, tectate exine, pores rectangular. M: 1000 x.

**Type 333:** *Tapirira (cf. T. guianensis)* (Anacardiaceae)

**Plate XXVIII.**
Pollen grains tricolporate, prolate spheroidal, 23 x 21 um EV, sexine distinctly striate, colpi long and narrow. Striations parallel to colpi. M: 1000 x. Ref: This taxon has been identified, after examination of reference slide of *Tapirira guianensis* pollen, obtained at NYBG Herbarium.

**Type 334-335,337:** *Lithraea* (Anacardiaceae).

**Plate XXVIII.**
Grains prolate spheroidal to subprolate, 25-27 x 21-25 um EV, amb circular to slightly triangular. Sexine reticulate, heterobrochate, brochi mostly elongate and arranged in striations, which are not as conspicuous as in *Tapirira*. M: 1000 x. Ref: Heusser (1971).
Type 336: *cf. Lithraea* (Anacardiaceae). Plate XXVIII.
Grain poorly preserved, but showing a certain affinity to *Lithraea*, *e.g.* presence of striations and reticulations, heterobrochi, and similar pore structure. Grain subprolate, 7 x 20 um EV. M: 1000 x.

Type 338-339, 341: *Anacardium / Schinus* (Anacardiaceae). Plate XXVIII.

Type 340, 342, 343: *Astronium* (Anacardiaceae).
Plate XXVIII and XXIX.

Type 344, 346: *Luehea* (Tiliaceae). Plate XXIX.

Type 345: *Luehea divaricata* (Tiliaceae). Plate XXIX.

Type 347-348: *Herrania* (Sterculiaceae). Plate XXIX.
Tricolporate, reticulate, subprolate to spheroidal, 22-30 x 22-25 um EV, homo-heterobrochate, brochi wide, pores circular. M: 1000 x.

**Type 349: Tricolporate, reticulate.** **Plate XXIX.**
Grain subprolate, 32 x 27 um EV, exine semi-tectate, baculate, colpi wide and long. M: 1000 x.

**Type 350: Tricolporate, micro-reticulate.** **Plate XXIX.**
Grain prolate-spheroidal, circular amb, 22 x 21 um EV, 21 x 21 um PV, colpi wide and long, pores operculate ?. Mag: 1000 x.

**Type 351-354: Sapium (Euphorbiaceae).** **Plate XXX.**

**Type 355: Sebastiana (cf. S. brasiliensis) (Euphorbiaceae).** **Plate XXX.**

**Type 356-360: Sebastiana (cf. S. schottiana) (Euphorbiaceae).** **Plate XXX.**

**Type 361: cf. Sebastiana (Euphorbiaceae).** **Plate XXX.**
Grain tricolporate, reticulate, prolate, 26 x 18 um EV. This type possesses some affinity to Euphorbiaceae, e.g. presence of a thick exine, fine striations, amb distinctly fossaperturate. M: 1000 x.
Type 362: *Sebastiana (cf. S. bidentata)* (Euphorbiaceae)  
Plate XXX.  
Grain oblate-spheroidal, 28 x 29 um EV, 28 x 27 um PV, micro-reticulate, slightly striate, exine 2.5-3 um thick, poles with a conspicuous depression. Amb triangular, strongly fossaperturate. M: 1000 x. Ref: Reference material from NYBG Herbarium.

Type 363: *Esenbeckia* (Rutaceae). Plate XXXI.  
Tricolporate, reticulate to slightly striate, pore lalongate, exine tectate, baculate. Grain prolate-spheroidal 32-33 um x 28-29 um EV, 26-27 um PV. Exine 2.5-3 um thick. Pollen morphology of *Esenbeckia* shows a remarkable similarity to those found in the Anacardiaceae. This is not surprising since both families belong to the Order Sapindales (Cronquist 1988). M: 1000 x. Ref.: Reference material from NYBG Herbarium.

Type 364: Tricolporate, scabrate. Plate XXXI.  
Grain examined only in PV. Syncolporate, pores appear operculate, 28 x 27 um PV. M: 1000 x.

Type 365: Tricolporate, reticulate. Plate XXXI.  

Type 366: *Didymopanax* (Araliaceae). Plate XXXI.  
Type 367: *Bathysa Augusta* (Rubiaceae). Plate XXXI.
Tricolporate, reticulate, heterobrochate, brochi become larger away from the apertures, pores somewhat annulate, exine baculate. Grains prolate-spheroidal, 23-25 x 21-22 um EV, 24-26 um PV. Ref.: Reference material from NYBG Herbarium.

Type 368: *cf. Apeiba* (Tiliaceae) Plate XXXI.
Tricolporate, reticulate, colpi very short and narrow. Grain oblate, 20 x 28 um EV, not examined in PV. M: 1000 x. Ref.: reference material collected from *Apeiba* spp., deposited at the NYBG Herbarium.

Type 369: Tricolporate, reticulate. Plate XXXI.
Grain spheroidal, 23 x 23 um EV, 26 x 25 um PV, pores distinctly lalongate. Exine thick, sexine conspicuously spinulose.

Type 370: Tricolpate (tricolporate ?) reticulate. Plate XXXI.
Grain examined only in PV, 25 x 25 um PV. M: 1000 x.

Type 371: Tricolporate, reticulate. Plate XXXI.
Grain examined only in PV, 22 x 22 um PV. M: 1000 x.

Type 372: Tricolporate, psilate. Plate XXXII.
Grain prolate-spheroidal, 16 x 15 um EV, 16 x 15 um PV. Pore very indistinct. M: 1000 x.

Type 373: Tricolporate, psilate. Plate XXXII.
Grain syncolporate, prolate, 18 x 13 um EV, amb circular, 18 x 18 um PV. M: 1000 x.

Type 374: Tricolporate, granulate. Plate XXXII.
Amb circular, 28 x 27 um PV, pore lalongate, exine tectate, baculate. Grain syncolporate. M: 1000 x.
Type 375: Tricolpate (tricolporate ?), psilate.
Plate XXXII.
Grain examined only in PV, 20 x 19 um PV. Grain distinctly syncolporate. M: 1000x.

Type 376: cf. Toullicia (Sapindaceae). Plate XXXII.
Tricolporate, psilate, suboblate, 21 x 18 um EV, 22 x 22 um PV, syncolporate.
Colpi wide, pore circular. M: 1000 x. Ref.: Reference material from NYBG herbarium.

Type 377: Tetracolporate (tetracolpate ?), psilate.
Plate XXXII.
Grain examined only in PV, 20 x 20 um. M: 1000 x.

Type 378: Tricolpate (tricolpate ?), psilate.
Plate XXXII.
Grain examined only in PV, 13 x 13 um. M: 1000 x.

Type 379: Tricolporate, psilate. Plate XXXII.
No measurements are available for this type. Pores are indistinct.

Type 380: Tricolpate (tricolporate ?), psilate.
Plate XXXII.
Grain examined only in PV, 15 x 13 um PV. M: 1000 x.

Type 381: Tricolporate, psilate. Plate XXXII.
Grain spheroidal, 16 x 16 um EV, pores indistinct. M: 1000 x.

Type 382: Tricolporate, reticulate. Plate XXXII.
Grain oblate-spheroidal, 22 x 24 um EV, 26 x 23 um PV, colpi wide. M: 1000 x.

Type 383: Tricolporate, psilate. Plate XXXII.
Grain subprolate, 18 x 14 um EV. M: 1000 x.
Type 384: Syncolpate, tectate. Plate XXXII.
Grain 32 x 29 um, exine thick. M: 1000 x.

Type 385: Grain with unknown morphology.
Plate XXXII.
Star-shaped grain, tetracolporate (?), 19 x 15 um, pores indistinct. M: 1000 x.

Type 386, 388: Solanaceae. Plate XXXIII.
Tricolporate, sexine psilate, pores lalongate. Grain subprolate to prolate-spheroidal, 19-22 x 16-20 um Ev, amb circular, 18-20 um PV diameter. Pores lalongate, forming a continuous ring on the equator. M: 1000 x.

Type 387, 390: Erythroxylum (Erythroxylaceae).
Plate XXXIII.

Type 389: Cestrum (Solanaceae). Plate XXXIII.

Type 391, 393: Jacaratia (Caricaceae). Plate XXXIII.

Type 392: Tricolporate, psilate. Plate XXXIII.
Grain oblate-spheroidal, 28 x 29 um Ev, 28 x 28 um PV. Sexine micro-reticulate (to granulate ?). Pores operculate. M: 1000 x.
Type 394: **Tricolporate, micro-reticulate. Plate XXXIV.**
Grain subprolate, 37 x 28 um EV, costae colpi, pores lalongate and appearing somewhat operculate. M: 1000 x.

Type 395-397: **Justicia (Acanthaceae). Plate XXXIV.**

Type 398: **Hydrocotyle (Umbelliferae=Apliceae). Plate XXXIV.**
Tricolporate, scabrate, pore lalongate, exine conspicuously thicker at the poles (< um thick). Grains prolate, 22 x 14 um EV. Colpi as long as grain. M: 1000 x.

Type 399-400: **Umbelliferae = Apliceae (cf. Eryngium) Plate XXXIV.**
Tricolporate, micro-reticulate to scabrate, costae colpi distinct, colpi long and narrow, exine thicker at the poles. Grain perprolate, 31-37 x 15-18 um EV. M: 400 x.

Type 401: **Umbelliferae = Apliceae. Plate XXXIV.**

Type 402: **Umbelliferae = Apliceae. Plate XXXIV.**
Type 403: *Eryngium* (Umbelliferae = Apiaceae).

**Plate XXXIV.**
Tricolporate, granulate, pores lalongate, distinctly zonorate, costae colpi, exine thicker at the poles. Grain prolate, 28 x 15 um EV. M: 1000 x.

Type 404: Tricolporate, micro-reticulate. **Plate XXXIV.**
Grain prolate, 27 x 13 um EV. Exine slightly thicker at the poles. M: 1000 x.

Type 405: Umbelliferae (Apiaceae) ? **Plate XXXIV.**

Type 406: Umbelliferae (Apiaceae) ? **Plate XXXIV.**
Tricolporate, psilate, colpi narrow and long as grain. Pores lalongate, zonorate (?). Grain perprolate, 24 x 11 um EV. Presence of a distinct an equatorial depression in the EV outline of this type. Exine slightly thicker at the poles. M: 1000 x.

Type 407: Tricolpate (tricolporate ?), psilate.

**Plate XXXIV.**
Grain prolate, 30 x 21 um EV. Pores not distinct, appearing tricolpate. M: 1000 x.

Type 408, 410: *Copaifera* (Caesalpinioideae).

**Plate XXXIV.**
Tricolporate, psilate, oblate spheroidal, 18 -19 x 20-22 um EV, 20 x 22-23 um PV. Amb triangular, sides of the triangle straight (type 408) to concave (type 410). Grains sometimes syncolporate (type 410). A distinct 8-shaped structure around the pores is observed in EV. M: 1000 x.

**Type 409:** Tricolporate, psilate. Plate XXXIV
Grain suboblate, 20 x 23 um EV, amb triangular, 15 x 15 um PV. Pores indistinct. M: 1000 x.

**Type 410:** see Type 408. Plate XXXIV.

**Type 411:** Tricolporate, reticulate. Plate XXXV.
Grain prolate-spheroidal, 16 x 15 um EV, circular amb, 15 x 15 um PV. Exine distinctly baculate, pores lalongate. M: 1000 x.

**Type 412-413:** Connarus (Connaraceae). Plate XXXV.

**Type 414:** Tricolporate, reticulate. Plate XXXV.
Grain suboblate, 17 x 20 um EV, amb subtriangular, 20 x 18 um PV. Pore lalongate, operculate (?) when seen in PV. Exine appearing tectate, baculate. M: 1000 x.

**Type 415:** cf. Cleome (Capparidaceae, Cleomaceae) Plate XXXV.

**Type 416:** Tricolporate, reticulate. Plate XXXV.
Grain spheroidal, 15 x 15 um Ev, amb circular, 15 x 15 um PV. Pores somewhat lalongate, exine baculate. M:: 1000 x.
Type 417: *cf. Vismia* (Clusiaceae = Guttiferae).

Plate XXXV.

Type 418: *Qualea* (Vochysiaceae). Plate XXXV.
Tricolporate, sexine reticulate to slightly striate, pores lalongate, colpi wide and as long as grain. Grains suboblate to oblate-spheroidal, 21-30 x 25-34 um EV, exine thicker at apertures (2.5 um) than at poles (1.5 um). Type 418 d, e, belong to a different specimen of the same taxon. M: 1000 x. Ref.: Erdtman (1952), Ledru (1991).

Type 419-421: *Vochysia* / *Salvertia*. (Vochysiaceae).
Plate XXXV.
Tricolporate, striate, pores lalongate, colpi wide with distinct thickenings (incrassate at apertures) which are found in most taxa of the Vochysiaceae and clearly seen in type 420 b. Grains prolate to spheroidal, 26-47 x 34-35 um EV. Examination of reference material from herbaria suggests that it might be possible to separate *Vochysia* from *Salvertia* pollen by size. *Salvertia* pollen appears at first sight to be larger than those of *Vochysia*. M: 1000 x. Ref.: Erdtman (1952).

Type 422: Tricolporate, psilate. Plate XXXV.
Grain prolate, 29 x 18 um EV. Slight striations of the exine, pore structure and presence of exine thickenings in colpi suggests an affinity to Vochysiaceae. M: 1000 x.
Type 423-424, 426: Caryocar (Caryocaraceae).

Plate XXXVI.

Type 425: Tricolporate, reticulate. Plate XXXVI.
Grain prolate, 30 x 21 um EV, pore lalongate, exine thicker at poles. M: 1000 x.

Type 426: see Type 423. Plate XXXVI.

Type 427: Tricolporate, psilate (Solanaceae ?).
Plate XXXVI.
Tricolporate, psilate, colpi constricted at the equator, pores conspicuously protruding. Grain prolate, 41 x 25 um EV. M: 1000 x.

Type 428: Tricolporate, psilate. Plate XXXVI.
Grain prolate, 38 x 24 um EV, pore circular, exine tectate. M: 1000 x.

Type 429: cf. Bignoniaceae ? Plate XXXVI.
Tricolpate (tricolporate ?), psilate , colpi constricted at equator. Grain not examined in PV. Grain prolate, 35 x 23 um EV. M: 1000 x.

Type 430: Tricolporate , micro-reticulate. Plate XXXVI.
Grain prolate, 29 x 21 um EV, costae colpi, exine 1 um thick and 2.5 um thick at poles, pore rectangular and indistinct. M: 1000 x.

Type 431-432: Bignoniaceae. Plate XXXVII.
Type 433: Tricolporate, reticulate. Plate XXXVII.
Grain examined only in PV, 18 x 18 um PV. Sexine distinctly reticulate.
M: 1000 x.

Type 434: Tricolporate, striate-reticulate. Plate XXXVII.

Type 435: cf. Chorisia (Bombacaceae)? Plate XXXVII.
Tricolporate, reticulate, large lumina of irregular shape. Amb circular, 41 x 41 um. Grain not examined in EV. This taxon is described by Markgraf & D'Antoni (1978) as tricolpate, whereas Salgado-Labouriau (1973) describes it as tetrapentacolporate. M: 1000 x. Ref.: Salgado-Labouriau (1973). Examination of reference material from NYBG indicates this taxon to be colporate.

Type 436: Tricolporate, baculate. Plate XXXVII.
Grain distinctly reticulate, with bacula and clavae in areas away from apertures. Grain examined only in PV, amb somewhat triangular, 26 x 26 um. A certain affinity to Bombacaceae is present. M: 1000 x.

Type 437: Eriotheca (Bombacaceae). Plate XXXVII.
Grains with distinct triangular amb, sides of the triangle straight. Grain tricolporate, 30 x 30 um PV, colpi very short, strongly reticulate, lumina of different shapes and sizes. Type Eriotheca is distinguished from Bombacopsis and Pseudobombax by the absence of equatorial caps. M: 1000 x. Ref.: Salgado-Labouriau (1973), Roubik & Moreno (1991).

Type 438: Pseudobombax / Bombacopsis (Bombacaceae).
Plate XXXVII.
Only fragments of this type have been encountered during this study. The colporate structure as well as sections of the reticulate pattern of the sexine can
be best seen in fig. 438 a, whereas one equatorial cap is shown on the right-hand side of fig. 438 b. Longest axis of this grain was 70 um. M: 1000 x.

**Type 439-441: Ilex (Aquifoliaceae). Plate XXXVII.**

**Type 442: Tricolporate, baculate. Plate XXXVII.**
Grain examined only in PV, 30 x 21 um PV, sexine densely baculate, aperture operculate. M: 1000 x.

**Type 443: Tricolpate (tricolporate ?) densely baculate.**

**Plate XXXVII.**
Grain with morphological features poorly preserved. Apertures indistinct, sexine densely baculate. Grain subprolate, 43 x 35 um EV. M: 1000 x.

**Type 444: Baculate grain, tricolpate ? Plate XXXVII.**
Folded grain, indistinct apertures (tricolpate ?), densely baculate. Grain subprolate, 32 x 24 um EV. M: 1000 x.

**Type 445: Maytenus (Celastraceae). Plate XXXVIII.**
Tricolporate, reticulate, homobrochate, exine semi-tectate, baculate. Grain spheroidal, 20 x 20 um Ev, circular amb, 20 x 20 um PV. Pore indistinct, although there is a distinct lalongate opening of the colpi at equator. M: 1000 x.

**Type 446: Tricolporate, reticulate. Plate XXXVIII.**
Grain oblate-spheroidal, 26 x 29 um EV, amb circular, 25 x 26 um PV. Colpi wide and fusing in the polar area. Sexine reticulate with some very small echinate. Pore indistinct. M: 1000 x.
Type 447: Tricolporate, reticulate. Plate XXXVIII.

Type 448-449: Tricolporate, reticulate, echinate. Plate XXXVIII.

Type 450: Tricolporate, reticulate. Plate XXXVIII.
Grain prolate-spheroidal. No measurements are available for this type. M: 1000 x.

Type 451: Tricolporate ?, echinate. Plate XXXVIII.
Grains tricolporate (?) but pores indistinct. Sexine with well spaced echinae. Grain subprolate, 22 x 17 um EV, amb circular, 19 x 18 um PV. M: 1000 x.

Type 452: Tricolporate, reticulate. Plate XXXVIII.

Type 453: Tricolporate, reticulate. Plate XXXVIII.
Grain prolate-spheroidal, 21 x 19 um EV, amb circular, 20 x 20 um. Pore very indistinct (tricolpate ?). M: 1000 x.

Type 454: Arrabidea (Bignoniaceae). Plate XXXVIII.
Tricolpate, exine tectate, baculate, colpi constricted at the equator, sexine micro-reticulate. Grain subprolate, 25 x 20 um EV, 26 x 25 um PV. M: 1000 x.
Type 455: Bignoniaceae. Plate XXXIX.
Tricolpate, sexine micro-reticulate, 23 x 19 um PV. M: 1000 x.

Type 456-458: cf. Tecoma / Tabebuia (Bignoniaceae).
Plate XXXIX.

Type 459: Tricolporate? Plate XXXIX.
Grain examined only in PV (tricolpate ?), sexine with well spaced echinae.

Type 460: Tricolporate? reticulate. Plate XXXIX.
Grain only seen in PV, 34 um PV diameter. M: 400 x.

Type 461-462: cf. Anemopaegma (Bignoniaceae).
Plate XXXIX.

Type 463: cf. Bignoniaceae. Plate XXXIX.
Type 464: Tricolpate (tricolporate ?). Plate XXXIX.
Grain examined only in PV. Measurements not available for this type. Sexine reticulate. M: 1000 x.

Type 465: Bignoniaceae. Plate XXXIX.

Type 466-467: Hancornia (Apocynaceae). Plate XL.

Type 468: Aspidosperma (Apocynaceae). Plate XL.
Grain seen only in EV, tricolporate, 34 x 29 um EV., costae colpi very conspicuous. Type 468c represents a PV of a different specimen of the same taxon, for which no measurements are available. M: 1000 x. Ref.: Salgado-Labouriau (1973), Roubik & Moreno (1991).

Type 469: Tricolpate (tricolporate ?). Plate XL.
Grain examined only in PV, tricolporate (tricolporate ?), psilate, colpi narrow and reaching polar area, where they almost meet. No measurements are available for this taxon.

Type 470-471, 475: cf. Cabralea (Meliaceae).
Plate XL.
Type 472, 476: cf. *Trichilia* (Meliaceae). Plate XL.
Tetracolporate, psilate, amb circular of the external outline, whereas the internal outline is squared. Grains prolate, 20-25 x 15-21 um EV. M: 1000 x.

Type 473: Tetracolporate, psilate (*cf. Meliaceae* ?).
Plate XL.
Grain examined only in EV, sexine psilate, pore lalongate and very distinct. No measurements are available for this type. M: 400 x.

Type 474: Meliaceae. Plate XL.
Tetracolporate, transversal colpi present, colpi narrow and long, pores distinct and circular. Grain subprolate, 14 x 12 um EV, 11 x 11 um PV. M: 1000 x.

Type 477: 5-colporate (colporate ?), reticulate. Plate XL.
Grain prolate, 23 x 17 um EV, densely baculate, colpi narrow and indistinct, pores also indistinct. M: 1000 x.

Type 478: Tetracolporate, baculate. Plate XL.
Grain prolate-spheroidal, 18 x 16 um EV, 18 x 17 um PV, exine thicker at the poles. M: 1000 x.

Type 479: Tetracolporate, psilate. Plate XL.
Grain prolate, colpi short and narrow, exine thick. No measurements are available for this type. M: 1000 x.

Type 480: 5-6 colpate, baculate. Plate XL.
Grain poorly preserved, colpi indistinct. No measurements are available for this type. M: 1000 x.

Type 481: cf. *Meliaceae*. Plate XL.
Tetracolporate, psilate, prolate-spheroidal, 16 x 15 um EV, amb circular,
15 x 14 um. M: 1000 x.

**Type 482: Trichilia (Meliaceae). Plate XLI.**

**Type 483-484: Rapanea (Myrsinaceae). Plate XLI.**

**Type 485, 487: cf. Cedrella (Meliaceae) ?. Plate XLI.**

**Type 486: Cedrella (cf. C. fissilis ). (Meliaceae).**
Plate XLI.
Tetracolporate, sexine psilate to granulate, pore distinctly circular with surrounded by exine thickening (annulus ?). Grain prolate-spheroidal, 26 x 25 um EV, 24 x 24 um PV. M: 1000 x. Ref.: Reference material from NYBG Herbarium, Roubik & Moreno (1991), Markgraf & D'Antoni (1978).

**Type 488: Tetracolporate, reticulate. Plate XLI.**
Grain oblate-spheroidal, 21 x 22 um EV, 23 x 23 um PV. Sexine reticulate, heterobrochate, densely baculate. Pore lalongate. M: 1000 x.

**Type 489: Melastomataceae /Combretaceae.**
Plate XLI.
Type 490-492: Tetracolpate (colporate ?, psilate.

Plate XLI.

Grains flattened and examined only in PV. Type 490, 20 x 14 um PV; type 491, 25 um PV diameter; type 492, 22 x 21 um PV. M: 1000 x.

Type 493: Melastomataceae/Combretaceae ?

Lithraceae ? Plate XLI.

Grain oblate-spheroidal, 17 x 18 um EV, tetracolporate, heterocolpate, with pores rectangular with lateral projections towards the center. M: 1000 x

Type 494: Diplusodon (Lythraceae). Plate XLI.

Tetracolporate, heterocolpate (presence of three pseudocolpi), sexine psilate to granulate, pores rectangular. Grains prolate-spheroidal, 20 x 19 um EV, 17 x 17 um PV. Colpi are longer almost fusing in the polar area. Grains appear somewhat more robust than the melastomataceous type. M: 1000 x.

Ref.: Reference material from Diplusodon sp. (Lythraceae) obtained at the NYBG Herbarium.

Type 495-496: Borreria Rubiaceae). Plate XLI.


Type 497: Pentaporate (cf. Symphonia /Tovomita , Clusiaceae = Guttiferae ?). Plate XLII.


Type 498: Pentaporate. Plate XLII.

Grain flattened allowing examination only of PV, 34 x 22 um PV. Sexine scabrate to micro-reticulate. M: 1000 x.
Type 499-501: Labiatae = Lamiaceae (*cf. Hyptis*)

Plate XLII.

Type 502-503: *Diodia / Richardia* (Rubiaceae).

Plate XLII.
Stephanocolpate (+-12 colpate), reticulate, exine semi-tectate, sexine baculate. Grains observed only in PV, 34-38 um PV diameter. M: 1000 x. Ref.: Roubik & Moreno (1991), Salgado-Labouriau (1973) and *Richardia* reference material from NYBG Herbarium.

Type 504: Rubiaceae. Plate XLII.
Grain stephanocolpate (6-colpate), exine semi-tectate, sexine baculate. Grain examined only on PV, 27 x 23 um PV. M: 1000 x.

Type 505: *cf. Labiatae = Lamiaceae*. Plate XLII.
Grain stephanocolpate (7-colpate), sexine micro-reticulate. Grain subprolate, 20 x 17 um EV, amb circular, 20 x 17 um PV. M: 1000 x.

Type 506, 511: Lentibulariaceae. Plate XLII.
Stephanocolpate (9-colpate), amb circular, 28 x 28 um PV. Colpi fused at the equator. M: 630 x (type 511), 1000 x (type 506). Ref.: Heusser (1971).

Type 507: *Utricularia* (Lentibulariaceae). Plate XLII.
Type 508-510: *Monnina / Polygala* (Polygalaceae).

Plate XLII.


Type 511: see Type 506. Plate XLII.

Type 512: *Drimys* (Winteraceae). Plate XLIII.


Type 513-515: Ericaceae. Plate XLIII.


Type 516: *Mimosa* (Mimosaceae). Plate XLIII.


Type 517-518: *Mimosa* (Mimosaceae). Plate XLIII.


Type 519-522, 528: Mimosaceae. Plate XLIII.

Pollen grains united in polyads, containing 5-28 cells. Each cell 3-8 porate, pores not distinct. Tetrad diameter of the specimens found in this study range from 22-50 um. Type 528 shows affinity to *Newtonia* (Caesalpiniaceae). M: 1000 x. Ref.: Salgado-Labouriau (1973), Roubik & Moreno (1991).

**Plate XLIII.**

Type 525-526: *Drosera* (Droseraceae). **Plate XLIII.**
Pollen grains united in tetrads, individual grains stephanoporate, pores indistinct, conspicuously echinate. Tetrads 44-45 x 50-60 um. M: 1000 x (type 525), 400 x (type 526).


**Plate XLIII.**

Type 528: see Type 519. **Plate XLIII.**

**Type 529-530: Bauhinia** (Caesalpiniaceae).

**Plate XLIV.**

Type 531: Tricolpate, micro- reticulate. **Plate XLIV.**
Pollen grain appearing tricolpate, examined only in PV, 23 x 23 um PV. M: 1000 x.
Type 532: Tricolpate, micro-reticulate. Plate XLIV.
Grain prolate, sexine micro-reticulate. No measurements are available for this type. M: 1000 x.

Type 533-534: Tricolpate, reticulate. Plate XLIV.
Grains prolate, 30-32 x 26-28 um EV, some echinae are found on the sexine. M: 1000 x.

Type 535: Inaperturate, baculate. Plate XLIV.
Grain 25 x 20 um. M: 1000 x.

Type 536: Inaperturate (?), baculate. Plate XLIV.
Grain densely baculate, central area broken. Grain subspheroidal 24 x 23 um. M: 1000 x.

Type 537: *Hedyosmum* (Chloranthaceae). Plate XLIV.

Type 538: Inaperturate, echinate. Plate XLIV.
Grain 17 x 16 um. M: 1000 x.

Type 539: Inaperturate ?, clavate. Plate XLIV.
Grain 20 x 25 um. M: 1000 x.

Type 540: Inaperturate, clavate. Plate XLIV.
Grain 14 x 14 um. M: 1000 x.

Type 541: Pentacolpate?, baculate. Plate XLIV.
Grain 21 x 21 um, syncolpate? M: 1000 x.

Type 542: Inaperturate gemmate (pollen ?).
Plate XLIV.
Grain 24 um in diameter. M: 1000 x.
Type 543: Inaperturate, echinate. Plate XLIV.
Grains small, 15 x 12 um. M: 1000 x.

Type 544: Inaperturate, echinate. Plate XLIV.
Echinae regularly distributed on sexine. Grains 19-21 um in diameter.
M: 1000 x.

Type 545: Tricolporate, reticulate. Plate XLIV.
Grain oblate, 20 x 36 um EV, densely clavate. M: 1000 x.

Type 546-547: Sphagnum (Sphagnaceae). Plate XLV.

Type 548: Anthocerus. (Anthocerotaceae) /Selaginella (Selaginellaceae)/Hymenophyllum. (Hymenophyllaceae).
Plate XLV.
Spore trilete, echinate, amb more or less circular or subtriangular convex, 38 x 30 um. M: 1000 x. Ref.: Hooghiemstra (1984).

Type 549: Selaginella (Selaginellaceae). Plate XLV.

Type 550: Trilette spore. Plate XLV.
Spore, 45 x 45 um diameter. M: 1000 x.

Type 551: cf. Selaginella (Selagniellaceae) Plate XLV.
Trilette, echinate spore, 39 x 34 um equatorial diameter. M: 1000 x.

Type 552: Lycopodium (Lycopodiaceae). Plate XLV.
Type 553: *cf. Lophosoria* (Lophosoriaceae). Plate XLV.

Type 554: *cf. Lycopodium* (Lycopodiaceae) ?
Plate XLV.
Trilete spore, 43 x 44 um equatorial diameter. M: 1000 x.

Type 555: *Dicksonia* (Cyatheaceae, Dicksoniaceae).
Plate XLV.

Type 556: *cf. Cyatheaceae*. Plate XLV.
Trilete verrucate, 33 x 32 um, amb triangular convex, laesura with distinct margo. M: 1000 x. Ref.: Absy (175), Heusser (1971).

Type 557: *Cyathea* (Cyatheaceae). Plate XLVI.
Spore trilete, amb subtriangular convex, 45 x 43 um equatorial diameter, laesura extending almost to the equator, no margo present. M: 1000 x. Ref.: Hooghiemstra (1984).

Type 558, 560: *cf. Lycopodium* (Lycopodiaceae) ?
Plate XLVI.
Trilete spore, amb triangular convex, 30-51 x 28-52 um equatorial diameter, sclerine very thick, margo more or less distinct. M: 1000 x. This type shows a certain affinity to *L. cernuum* type, which has a developed margo. Ref.: Hooghiemstra (1984).

Type 559: Trilete spore. Plate XLVI.
Spore trilete, amb triangular convex, 30 x 21 um, no margo. M: 1000 x.
Type 560: see Type 558. Plate XLVI.

Type 561: Trilete verrucate. Plate XLVI.
Trilete spore, amb triangular convex., 50 x 45 um. M: 1000 x.

Type 562-563: Trilete spore. Plate XLVI.
Trilete spore, circular amb, 33-35 um, , sclerine thick. M: 1000 x.

Type 564: cf. Lycopodium (Lycopodiaceae). Plate XLI.
Trilete spore, amb triangular convex, 30 x 29 um. M: 1000 x.

Type 565: Trilete verrucate. Plate XLVI.
Amb circular, no measurements are available for this type.
M: 1000 x.

Type 566: Trilete spore. Plate XLVI.
Amb triangular, 38 x 38 um, with sides more or less straight, laesura undulated, no margo present. M: 1000 x.

Type 567: cf. Sphagnum (Sphagnaceae)? Plate XLVI.
Trilete spore, amb subtriangular-circular, 36 x 35 um, faint margo present.

Type 568-569: cf. Lycopodium (Lycopodiaceae)? Plate XLVI.
Spore trilete, amb subtriangular concave to straight sides, 1-35 x 35-36 um.
M: 1000 x.

Type 570, 572: Asplenium (Polypodiaceae) / Blechnum (Polypodiaceae= Blechnaceae). Plate XLVII.

Type 571: Monolete spore Plate XLVII.
Monolete spore laterally plane-convex, amb elliptical, 37 x 23 um, with irregular verrucae. M: 1000 x.
Type 573-575: Monolete psilate. Plate XLVII.
This type is also found in Blechnum (Blechnaceae = Polypodiaceae) and other taxa. M: 1000 x. Ref.: Hooghiemstra (1984).

Type 576: Trilete spore. Plate XLVII.
Amb circular, 45 x 48 μm, laesura lacking margo. M: 1000 x.

Type 577: cf. Adiantum (Polypodiaceae). Plate XLVII.

Type 578: Trilete spore. Plate XLVII.
Amb triangular, 61 x 62 μm. M: 1000 x.

Type 579: Trilete spore. Plate XLVII.
Amb triangular, 33 x 33 μm, laesura large. M: 1000 x.

Type 580: Trilete spore. Plate XLVII.
Triangular amb, 54 x 57 μm, sclerine thick, laesura with a faint margo. M: 630 x.

Type 581-583, 596: Zygnema (Zygnemataceae, Chlorophyceae). Plate XLVIII.

Type 584, 588, 589: Mougeotia (Zygnemataceae, Chlorophyceae). Plate XLIII.
Type 585-586: *Pediastrum* (Hydrodictyaceae).

Plate XLIII.
Colonic green alga of the division Chlorophycophyta (Bold *et al.* 1980). The colony (coenobium) is a flat plate. The preservation and resistance to biodegradation of *Pediastrum* colonies in palynological analyses is "one of the puzzles of palynology" according to Traverse (1988). The same specimen was photographed at 1000 x (type 585) and 400 x (type 586).

Type 587: Fungal spore. Plate XLIII.
M: 1000 x.

Type 588-589: see Type 584. Plate XLVIII.

Type 590: *Scenedesmus* (Scenedesmaceae, Desmidiaceae). Plate XLVIII.
Alga consisting of a four-celled colony, with spinelike processes (Bold *et al.* 1980), 18 x 15 um. M: 1000 x.

Type 591: *Debarya* (Zygnemataceae). Plate XLVIII.
The specimens of this taxon found in the Pleistocene sediments of Lagoa da Serra Negra and Lagoa dos Olhos are usually spheroidal, 34-40 um diameter. The *Debarya* zygospore has a sharply defined equatorial line of weakness, which causes the zygospore to split in two symmetrical halves. This taxon is very important in paleocological analyses of sediments, for it has been shown by the authors referenced below to be a reliable indicator of cooling. M: 1000 x.

Type 592: Fungal spore. Plate XLVIII.

Type 593: Unknown palynomorph. Plate XLVIII.
M: 400 x.
Type 594: Unknown palynomorph. Plate XLVIII.
M: 1000 x.

Type 595: *Pseudoschizaea* spore. Plate XLVIII.
Spores described in Pleistocene and Holocene sediments of Israel and Pleistocene sediments of Alabama by Christopher in 1976 (Mondanesi 1988). This type as reported by Mondanesi (1988) was very common in her Late-Quaternary peat from Campos do Jordão, São Paulo.

Type 596: *Zygema* (Zgnemataceae). Plate XLVIII.
See type 582.

Type 597: *Cosmarium* (Desmiaceae) ? Plate XLVIII.
Star-shaped palynomorph, 17 x 15 um, cell wall with no ornamentation. M: 1000 x.

Type 598: *Spyrogyra* (Zygnemataceae). Plate XLVIII.
Spore oval to ellipsoidal, with more or less pointed ends, 45 um long. M: 630 x. Ref.: van Geel & van der Hammen (1978).

Type 599: *Botryococcus* (Botryococcaceae). Plate XLVIII.
Colonia algae, of irregular size. Due to the differential rate of fragmentation in different colonies diameter varies from 20 to 80 um. M: 400 x. Ref.: Hooghiemstra (1984).

Type 600: Fungal spore. Plate XLVIII.
M: 400 x.

Plate XLVIII.
Type 601 depicts the hardened alveolar material termed massula (Bold et al. 1980), protecting the internal microscopores. Various glochidia or arm-like extensions with a conspicuous anchor-shaped structure at the end, extend from
the massulae. The glochidia represent an adaptation that allows attachment of t microsporic to megasporic massulae (Bold et al. 1980). Diameter of Azolla massulae in the present study varied from 150-195 um. Ref.: Bertelsen (1972), Markgraf & D'Antoni (1978). Fig. 602 shows a glochidium, 40 um long.

Fig. 603: Melosira transitus. (Bacillariphycaceae).

Plate XLIX.

Cylindric cells forming a chain. This taxon is characterized by the presence of small hairlike spines connecting the frustules and by the fine striae visible at the ends of the cell. The specimen depicted is 17 um wide and 38 um long. M: 1000 x. Ref.: Carter & Denny (1987).

Fig. 604: Valve view of Melosira transitus. Plate XLIX.

Diameter of valve, 20 um. M: 1000 x.

Fig. 605: General view of diatom rich sediments.

Plate XLIX.

This figure illustrates the overwhelming abundance of Melosira transitus valves in most of the Lagoa dos Olhos sediment samples (see diatom profile of Lagoa dos Olhos. The large pennate diatom is Pinnularia maior. M: 600 x.

Fig. 606: Pinnularia tropica (Bacillariphycaceae).

Plate XLIX.


Fig. 607-608: Pinnularia stauroptera (Bacillariphycaceae).

Plate XLIX.

Pennate diatoms, 106-110 x 11-12 um. M: 1000 x. Ref.: Reference material from the Diatom Herbarium of the Academy of Natural Sciences of Philadelphia.
Fig. 609: *Navicula pseudocari* (Bacillariophyceae).

Plate XLIX.

Length 55 um, breadth 6 um, striae 16 to many in 10 um. Ref.: Frenguelli (1942).

Fig. 610: *Eunotia zygodon* (Bacillariophyceae).

Plate XLIX.

Taxon characterized by the undulated dorsal margin. Length 80 um, breadth 16 um, striae 12-14 in 10 um. Ref.: Schmidt (1874-1959).

Fig. 611: *Eunotia* sp. (cf. *Eunotia incisa*)

(Bacillariophyceae). Plate XLIX.

Breadth 48 um, breadth 10 um. M: 1000 x.

Fig. 612: *Eunotia zygodon* var. *elongata*

(Bacillariophyceae). Plate XLIX.

Length 104 um, breadth 11 um, striae 10-12 in 10 um. M: 1000 x.

Ref.: Schmidt (1874-1959).

Fig. 613: *Eunotia* sp. (Bacillariophyceae). Plate XLIX.

Length, 59 um, breadth 7 um. M: 1000 x.

Fig. 614-615: *Coscinodiscus* sp. (Bacillariophyceae).

Plate XLIX.

Diameter of valve 10-26 um. This taxon was only encountered in the sediments of Lagoa da Serra Negra. Ref.: Hustedt (1930).

Fig. 616-617: *Actinella gulanensis* (Bacillariophyceae).

Plate XLIX.

Taxon with conspicuous spines on the valve margins. Length, 48-70 um. Fig. 617 represents a teratological form of this taxon. M: 1000 x.

Ref.: Schmidt (1874-1959).
Fig. 618: Plant tissue remains. Plate L.
Common palynomorph in the sediments of Lagoa dos Olhos. Dimension of the remains depicted are 39 x 40 µm. M: 1000 x.

Fig. 619: Leaf epidermal remains. Plate L.

Type: 620-622: Echinate palynomorph (Cosmarium ?).

Plate L.
Zygospore (?) 57-65 x 50-65 µm. M: 1000 x.

Fig. 623: Inaperturate, densely echinate palynomorph.

Plate L.
Ellipsoidal palynomorph, 48 x 25 µm. M: 1000 x.

Type 624: Unknown palynomorph. Plate L.

Type 625: Monoporate (?) palynomorph. Plate L.
Ellipsoidal palynomorph, 42 x 30 µm, reticulate, baculate. M: 1000 x.

Type 626: Subspheroidal inaperturate palynomorph.

Plate L.
Micro-reticulate, baculate, with thick cell wall. Palynomorph subspheroidal, 39 x 40 µm. M: 1000 x.

Type 627-628: Rectangular to ellipsoidal palynomorph.

Plate L.
Cell wall with pits to psilate, 29-48 x 26-27 µm. M: 1000 x.
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Plate VIII. Pollen types 28-42.
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