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PALYNOLOGICAL DATA ON THE HISTORY OF TROPICAL SAVANNAS IN NORTHERN SOUTH AMERICA

BY

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SUMMARY

A number of pollen diagrams from the Llanos Orientales of Colombia and the Rupununi Savannas of Guyana show that the actual open savannas were preceded by a closed savanna woodland or dry forest with *Byrsonima* as principal pollen producer. Human influence during the last 3000 years was apparently an important factor in the extension of open savannas. Nevertheless, open savannas occurred also earlier in the Holocene. Even in approximately Late-Glacial time, open savanna sometimes extended temporarily at the expense of the dry forest or woodland. It seems that climatic and atmospheric influences (periods of very dry climate, lightning) were the cause of these extensions. The pollen diagrams suggest anyhow a very unstable equilibrium between the woody *Byrsonima* association and the herbaceous open savanna. In the North Rupununi Savannas dry forest dominated in most of what probably corresponds to Late-Glacial time.
Open savanna was common or dominating there during a shorter interval of the above-mentioned „Late-Glacial" and during most of the Holocene.

CONTENTS

INTRODUCTION

The question of the origin and history of tropical savannas is one of the most fascinating phytogeographical problems. Botanists, pedologists and geographers have brought forward different factors possibly causing or determining the existence of savannas. The most important are climate, soil, groundwater-level, fire, grazing animals and man. The discussion on what are the principal factors determining savannas is still going on. As far as we know, palynology has not yet been used as a tool for the elucidation of these problems. However, it is clear that pollen analysis could give directly factual data on the history of savannas, and indirectly influence ideas on the factors determining the existence of savannas. For that reason one of the authors went in Sept. 1958 to the Llanos Orientales of Colombia (fig. 1 and 2), together with Roberto Jaramillo and Jorge Hernandez, of the Instituto de Ciencias Naturales in Bogotá. An aluminium boat was provided by the Instituto de Ciencias for the special purpose of collecting sections for pollen analysis. Sections were collected at five different places, and a general survey was made of the vegetation surrounding the lakes. A collection of plants and recent pollen was made at the same time. The plants were determined by the two botanists mentioned above. In May 1964, one of us visited the Rupununi Savannas in Guyana, invited by Prof. Theo Hills of the „Mc Gill University Savanna Research Project". On that occasion four different sections were sampled for pollen. We were guided then by Mr. D. Frost and Mr. N. Sinha of the Mc Gill project.

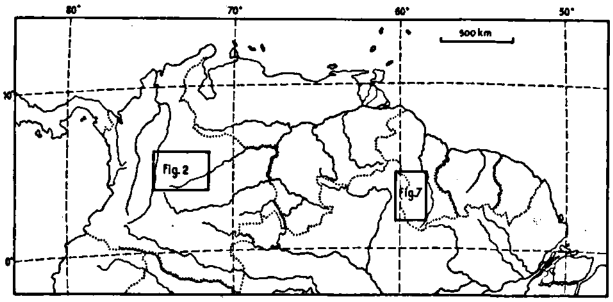

Fig. 1. Map of northern South America, indicating the areas of fig. 2 and 7, where the pollen sections were taken.

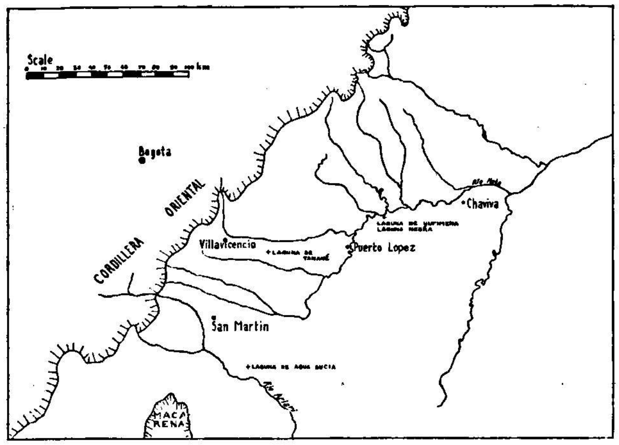

Fig. 2. Map (of part of the Llanos Orientales, Colombia), indicating the localities of the pollen sections.

The pollen analyses were principally made by one of the authors, while the C14 analyses were carried out by Dr. J. C. Vogel of the Laboratory of Groningen. These analyses were made possible by a grant of the Netherlands Foundation for Pure Scientific Research Z.W.O.

We wish to thank specially Dr. John Blydenstein and Dr. Gerardo Budowski of the „Instituto Interamericano de Ciencias Agricolas de la OEA" in Turrialba, for reading the manuscript and for valuable remarks and information.

For the pollen types mentioned in the diagrams, we may refer to van der Hammen (1963), but those types, that were not mentioned and illustrated before, are shown in two plates with photographs (fig. 16—23) of the present article.

The pollen diagrams that are presented here, give valuable data on the history of the savannas where the sections were collected. However, we fully realize that this is only the first step in deciphering of the rich archives buried in the savanna-lakes.

GEOLOGY AND RECENT VEGETATION

Short accounts of the savanna-vegetation of the Llanos Orientales of Colombia and the savannas of Guyana, are given in respectively Cuatrecasas (1958) and Fanshawe (1952). Here we will only mention a few important data, in as far as they are of relevance for the interpretation of the pollen diagrams. Some lists of genera, taken from the literature or observed near some of the sites of the pollen sections, will be added. As to the recent geology and geomorphology of the regions studied, a few relevant data will be mentioned. For further details we may refer to Goosen (1964a and b) for the Colombian Llanos, and to Bleackley (1962) and the still unpublished thesis (Mc Gill University) of N. Sinha for the Rupununi Savannas. The following description of the Colombian Llanos Orientales is principally according to Goosen (1964a). The Llanos may be subdivided into two main geomorphological-geological parts. The River Meta forms the boundary between these units (fig. 3). South of the Meta is the „altillanura", the „high plains", which are partly strongly dissected. These high plains may rise tens of metres above the rivers. Generally speaking, they are covered with forest south of the Ariari and Guaviare Rivers and with savanna north of that limit. North of the Meta is an alluvial overflow plain, partly covered with aeolian deposits (loess and river dunes; aeolian plain). It is principally covered with savanna.

In the area between Villavicencio, Puerto Lopez and San Martin, different terrace-levels may be distinguished, that are partly younger than the terrace of the high plains, and partly older than, or of the same age as the alluvial overflow plain. The age of the „high plain" terrace may be Lower Pleistocene, and that of the alluvial overflow plain and the terraces Middle to Upper Pleistocene (Goosen 1964a).

The actual river plain is always lower than the surface of the „alluvial overflow plain" and considerably lower than the surface of the „high plain".

Irregular inundations by river water occur here during the wet season. Inundations in the wet season occur in the „alluvial overflow plain" by the stagnation of rain water in the low depressions between the old levees. Inundations caused by the damming up of the water of the tributaries by the rising water of the main river in the wet season, increase towards the Venezuelan Llanos. The „high plains" are rather well drained, because of the type of sediments and the often deeply eroded drainage pattern. Poorer drainage may occur, where the plains are not highly dissected and at the same time covered with loess. It seems that the annual rainfall increases towards the East (towards the Cordillera) and towards the South. Open grasslands may exist on all the above-mentioned geomorphological units. They represent both „plateau grasslands" and „floodplain grass-lands". On the other hand, dense gallery forest or marsh forest may exist in the river valleys and in the smaller valleys and „caños", all over the area.

Between these extremes there are many vegetation

Fig. 3. View from the „Serrania de Manegua" (dissected „high plain", Alto Llano) northward over the Meta valley towards the „alluvial overflow plain". The site is between Puerto Lopez and Chaviva, Llanos Orientales.

types, intermediate between grass savanna and high forest. There is a grass savanna with irregularly distributed isolated small trees, what may be called a *Byrsonima-Curatella* savanna. Other woody genera often present are *Bowdichia, Palicourea, Cochlospermum,* etc. Shrubs or shrubby herbs often present are *Hyptis, Sida, Waltheria, Cordia, Pavonia, Grimaldia, Mimosa, Clitoria, Miconia* and *Tibouchina* (Cuatrecasas, 1958). Where the trees stand closer together, it may be called an open savanna woodland and finally a savanna woodland. In this last-mentioned type, the crowns already touch, but there is a ground cover of grasses. When it closes further, we might also speak of „dry tropical forest" or „very dry tropical forest". Parkland may also occur, when groups of trees („matas") occur in the grass savanna. At the border of these „matas" with the grass savanna we often find a transition zone with *Curatella.* Inside the „matas" many species of trees may occur, and according to the edaphic conditions (and probably also according to the history), species of the higher tropical forest may be present. It is known that on many places the grass savannas only maintain as such because of regular burning. If these places are not burnt anymore, the savanna is invaded by shrubs and small savanna trees. However, this is not known everywhere, and it seems that on other places such an invasion is extremely slow or does not occur at all. This may be the case on places which are inundated during many months of the year, and eventually also on certain places of old lateritic surfaces of the „Alto Llano" („high plain").

Anyhow, it is good to realize, that very little or nothing is known with certainty about this problem. On low inundatable places that are marshy or wet even during the dry season, the flora is different from that of the higher places. There are more hygrophilous plants, like species of *Utricularia, Polygala, Eriocaulon, Syngonanthus, Naiadothrix, Rynchospora, Fimbrystilis,* etc. (Cuatrecasas, 1958).

In the Rupununi Savannas the conditions show many similarities with the Colombian-Venezuelan Llanos (Bleackley, 1962). There is a higher, older surface, with locally remnants of an old lateritic soil, and lower savannas. The lowest areas are also inundated by the rivers in the wet season, while the others are only locally inundated by heavy rainfall. As to the vegetation types, these are also very similar to those of the Llanos. We cite the following general data, for the greater part also applicable to the Llanos, from Fanshawe (1952). The typical vegetation is the *Curatella-Byrsonima* association. Bunch-grass and sedges form the herb-layer, with *Trachypogon plumosus* as the dominant species. *Curatella americana, Byrsonima crassifolia, Byrsonima coccolobaefolia, Bowdichia, Antonia, Plumeria* and *Anacardium* are the commonest trees. Subshrubs and woody herbs include *Palicourea rigida, Byrsonima verbasciifolia, Tibouchina* and *Amasonia.* Fanshawe mentions as dominant community in the Rupununi Savannas the *Bowdichia virgilioides* faciation of this association. *Trachypogon* is again the dominant grass. The commonest trees are *Bowdichia, Curatella, Byrsonima crassifolia, Plumeria* and *Antonia.* He also mentions an other vegetation of grasses and sedges, replacing the bunch-grass-sedge community on the lowlands bordering the rivers. It is the *Mesosetum loliiforme* community, with *Mesosetum loliiforme* as the dominant grass.

The following important information on savanna species was kindly given to us by John Blydenstein and Gerardo Budowsky.

„*Byrsonima crassifolia* is characteristic of humid sites, occasionally inundated but never very deep or very long. It usually occurs as individual trees in open savanna and, if conditions are right, can form stands covering large areas. I found such stands more often in Venezuela, where the species also associated with *Curatella americana* to form the nucleus of a grove (see Blydenstein, 1962). It was not common in the southern area of the Colombian llanos, although occasionally conditions would be appropriate for limited stands to develop" (J. Bl.). „*Byrsonima crassifolia* is a good pioneer tree, of course very fire-resistant. But essentially as a pioneer, it is able to adapt itself and grow in all kinds of conditions. I have seen it on dry rocky slopes, on hard pans and even in areas flooded for short periods. The only thing it indicates is a special unfavourable biotic or soil condition, the latter usually connected with periods of drought, including physiological drought, such as resulting from occasional flooding. Savannas are also favoured by special edaphic and biotic conditions and are also fire- and drought-resistant, hence *Byrsonima* and savannas usually go together, but sometimes the special conditions are not the same and one may find one without the other. Moreover, when savannas are invaded by forests, *Byrsonima* may remain for tens of years (maybe hundreds) after savanna species have been exterminated" (G. Bud.).

As to the influence of fire, Dr. Budowsky thinks that the presence of lightning fires has often been underestimated for the tropical deciduous forest. He believes that one fire in an exceptionally dry year, every 20—30 years, is enough to favour savannas over forests.

GENERAL REMARKS ON THE POLLEN DIAGRAMS

After some experimentation with different kinds of representation of the pollen data of the savannas, we present here a type of diagram that seems most appropriate to show the relevant fluctuations of the pollen of the different groups of floral elements. The spectra of the general main diagram represent cumulatively the percentages of these groups, so that the total breadth (horizontal axis) represents the 100 % of the pollen grains counted (excluding spores and aquatic plants). At the right side we find the pollen of herbaceous plants, at the left the pollen of trees and shrubs. From right to left we find: Gramineae, Cyperaceae, other herbs, *Byrsonima* + *Curatella,* other forest elements, and *Mauritia* (see the general legend for the diagrams). In one case a special group was added for the Proteaceae. A total of 200 pollen grains

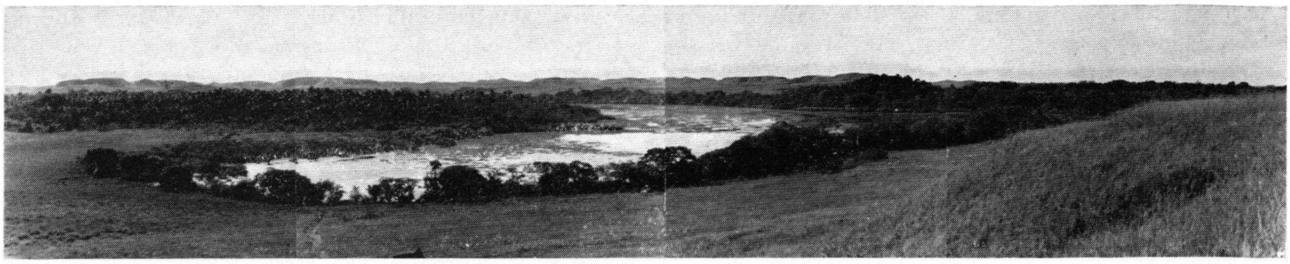

Fig. 4. Laguna de Agua Sucia (Llanos Orientales).

or more was used for all the spectra. Spores and aquatic plants are not included in the sum, but their percentages are, notwithstanding, calculated on the basis of that sum. In a few cases it was not possible to obtain a total of 200 grains, because the sample was very poor in pollen. The total used is then always mentioned in the diagram. We will see that this type of diagram permits us to appreciate easily the fluctuations between savanna and savanna woodland on the one hand, and between other forest and total savanna-vegetation on the other hand.

THE LLANOS ORIENTALES (COLOMBIA)

Fig. 1 gives the general situation of the area of fig. 2, where the locations of the pollen sections are indicated.

Laguna de Agua Sucia

The general situation of the lake, and the vegetation in its surroundings, is shown in the photo fig. 4 and the map fig. 5. The altitude is about 260 m above sea-level. It is situated in a small valley belonging to the incised drainage pattern of the „Alto Llano" (high plain), near to the place where it debouches into the valley of the Ariari River. It seems that the lake has been formed because the small valleys were dammed off by sedimentation of the Ariari in its own valley. Two other lakes in the map area have a similar position and seem to be caused by the same phenomenon.

The limit of the Ariari valley and the „Alto Llano" is indicated on the map by a thick line. In that valley there is rather high forest, with some herbaceous swamps or grass-lands. On the „Alto Llano" there is a grass-sedge savanna, and there is forest again in the deeper parts of the incised valleys. This forest meets downstream the forest of the river-valley, and resembles it very much there. In the upper part of the map, main source area for the pollen deposited in the open water of the lake, about 10 % of the surface is covered with forest, and about 90 % with open savanna. It is interesting to compare these values with the percentages of pollen in the uppermost sample of the lake. There is similarly about 10 % of forest elements, and about 90 % of open savanna elements.

The pollen rain of to-day in the lake represents therefore very well the actual coverage of these vegetation units in the dissected Alto Llano around it. We will see that a very good correspondence between pollen percentage and coverage of open savanna and forest was also found on other places (see the part on the

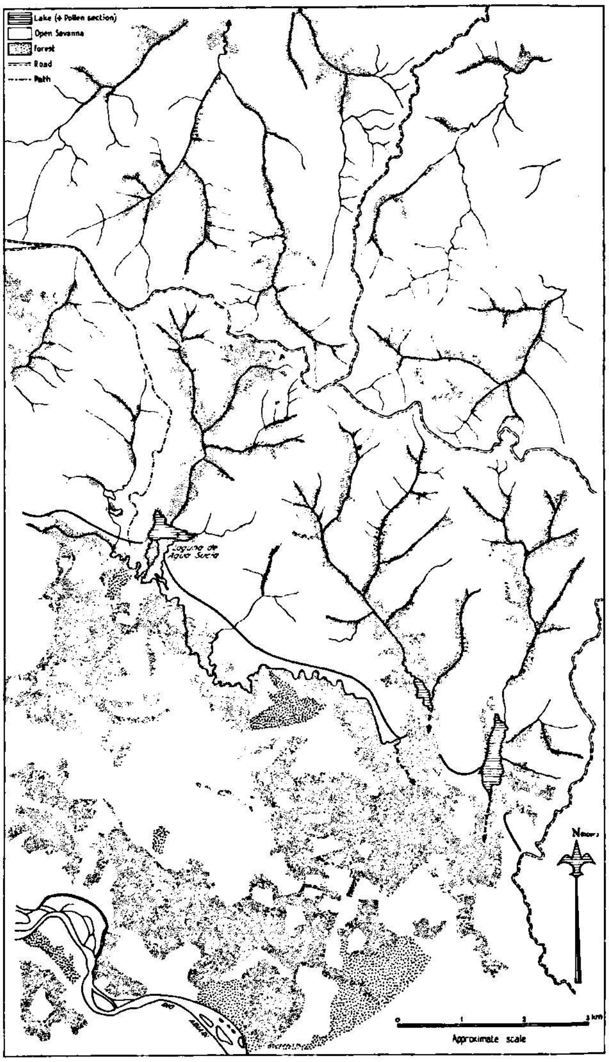

Fig. 5. Map of the area of Laguna de Agua Sucia, showing the actual distribution of savannas and forest. Prepared from aerial photographs by Anita van der Hammen-Malo.

Rupununi Savannas). Eliminating those spectra showing influence of local pollen deposited inside a swamp forest (see below), the diagrams give therefore most probably a very good reflection of the changes in the relation between savanna and forest that took place. In the valley immediately south of the lake (left background in the photograph fig. 4) there is dense forest, partly a *Mauritia* swamp forest ("Morichal"). The following list of genera was observed in this forest:

Mauritia	*Smilax*
Cyclanthus	Melastomataceae
Calathea	Myrtaceae
Costus	Cactaceae (epiphyt.)
Phyllodendron	*Croton*
Amyris	*Cochlospermum*
Dioscorea	*Duroia*
Heliconia	*Dichorisandra*
Spathiphyllum	*Montrichardia*
Pesopteris	*Mirosina*
Socratea	*Iriartea*
cf. *Euterpe*	*Mimosa*
Piper	*Pariana*
Ischnosiphon	*Cecropia*
Monstera	*Scheelea*
Pontederia	*Mucuna*
Dalbergia	*Paulinia*
Cephaelis	*Cissus*
Inga	Bignoniaceae
Triplaris	*Solanum*
Coccoloba	*Cestrum*
Ficus	

In the savanna on the slopes of the dissected „Alto Llano" (see photo fig. 4 foreground right and far background), we noted, besides the grasses and sedges (*Bulbostylis*):

Curatella	Myrtaceae
Byrsonima	Rubiaceae
Hyptis	*Calea*
Borreria	*Xyris*
Aneimia	

In the relatively wet zone (partly inundatable) immediately around the lake, the following genera or families were observed.

Utricularia	*Polypodium*
Lentibulariaceae (3 sp.)	Myrsinaceae
Siparuna	Apocynaceae
Adiantum	Orchidaceae
Bulbostylis	*Smilax*
Selaginella	Euphorbiaceae
Cuphea	Loranthaceae
Jussiaea	*Zygia*
Polygonum	*Erythroxylon*
Coccoloba	cf. *Dalbergia*
Rheedia	*Duroia*
Pariana	*Montrichardia*

In the water the following genera were observed:

Cabomba	*Pontederia*
Eichhornia	

The section was taken from a boat, with a Dachnovsky sonde (see for the exact location fig. 5), in water about 1m deep. At a depth of 5 m below the lake-bottom, sand was reached, and the sands could not be penetrated any deeper. The sediments consist of clays and intercalated peat-layers. The principal peat-layers were found at a depth of 35—65 cm and 240—290 cm. The pollen of the upper 350 cm was excellently preserved, the pollen of the lower part of the section (350 cm—500 cm) somewhat less well preserved. Four C14 analyses were made by Dr. J. C. Vogel of the Groningen Laboratory. Financial support for these analyses was given by the Netherlands Foundation for Pure Scientific Research Z.W.O. The place of the samples in the section is indicated on Plate I.

Col. 27—GrN-4416 — Laguna de Agua Sucia, peat, 50—60 cm . . . . . . 2160 ± 50 yrs.
Col. 26—GrN-3601 — Laguna de Agua Sucia, peat, 60—70 cm . . . . . . 2340 ± 90 yrs.
Col. 28—GrN-4213 — Laguna de Agua Sucia, peat, 250—260 cm . . . . . . 3830 ± 60 yrs.
Col. 30—GrN-3522 — Laguna de Agua Sucia, peat, 270—280 cm . . . . . . 4110 ± 70 yrs.

The diagram (Plate I) shows a number of marked changes, subdividing it into a number of pollen zones. We indicate these zones provisionally with the letters V, W, X, Y, and Z (see the table on p. 76). The C14 dates enable us to calculate a rate of sedimentation for the different parts of the diagram, and so we may calculate the approximate age of the zone-limits. Between the two principal peat-layers the average rate of sedimentation was 10 cm in 80 years. Boundary Y/Z is then appr. 2500 yrs old, X/Y appr. 3000 yrs, W/X appr. 3700 yrs.

If we accept the same rate of sedimentation for the lower part of the diagram, then we find an age of appr. 5100 yrs.

It seems therefore that zones W and X together exactly correspond in time to pollen zone VII of the Eastern Cordillera, and zones Y and Z to pollen zone VIII. In the table (on p. 76) we give all these data mentioned above, with the principal characteristics of the pollen zones.

There is a very strong increase of Gramineae in the upper 10—15 cm of the section, probably corresponding approximately to the last 400 years. The peat-layer from 35—65 cm corresponds in time appr. to 2300—1400 yrs B.P., and the one from 240—290 cm appr. to 4200—3700 yrs B.P.

The thin peat-layer from about 190—200 cm corresponds appr. to 3250 yrs B.P. The upper two peat-layers correspond to times of a relatively low lake-level. It is not quite certain that the lowest peat-layer represents a lower lake-level than before. If the clays below it are also lake-sediments, as seems probable, this was certainly so. The pollen rain in the peat-layers was apparently influenced by the local swamp-vegetation that sometimes spread over the area of the lake. The high *Mauritia* and *Hedyosmum* maxima seem to represent such local influences. The apparently „abnormal" minima of the herbs in zone Z seem to be caused exclusively by these local maxima. Some of the separate curves show characteristic forms, but often it is not yet known what this means.

Anacolosa only appears in the interval 130—180 cm; *Celtis* is only well represented in zone Y and the beginning of zone Z; there is a maximum of *Virola*

Prov. pollen zones Llanos Orientales	Depth in section Laguna de Agua Sucia	Principal characteristics	Calculated age	Corresponding pollen zones Cordillera Oriental
Z	0—90 cm	Percentage of herbs higher than in Y. *Byrsonima* very low (35—65 cm peat-layer).		
			2500	VIII
Y	90—160 cm	Percentage of herbs higher than in X. *Byrsonima* lower than in X.		
			3000	
X	160—240 cm	Very low percentage of herbs. Very high percentage of *Byrsonima.*		
			3700	VII
W	240—420 cm	Percentage of herbs very high. Perc. of *Byrsonima* very low (240—290 cm peat-layer).		
			5100	
V	420—(480) cm	Herbs lower and *Byrsonima* higher than in W.		VI

in the beginning of zone Y; there is a maximum of *Jussiaea* in the first part and in the last part of zone W, etc.

It is very interesting to compare this section with the one from Laguna de la Herrera, a lake at 2550 m altitude in the Sabana de Bogotá (van der Hammen & Gonzalez, 1965a). The lake is situated in an old stream-valley related to the Balsillas River. The sedimentation in the lake started around 5100 B.P., about the beginning of the pollen zone VII. There is also a peaty layer, corresponding to a low lake-level during the interval about 2000—2200 B.P. These facts seem to be caused in both lakes by contemporaneous, similar phenomena. Both lakes may have been dammed off by an increased river sedimentation in the time near or shortly before 5100 B.P., and both lakes suffered from a short period of dry climate around 2000—2200 B.P.

The calculated ages enable us to correlate zones W and X with the Subboreal of Europe and zones Y and Z with the Subatlantic.

We will now try to translate the pollen diagram into a history of vegetation in the area around the lake during the last about 5500 years.

We see that at the end of zone V (corresponding probably to the end of the Atlantic) there is a strong decrease of *Byrsonima*, and an increase of Gramineae, apparently interrupted only by the local maximum of *Mauritia*. There may have been in the surroundings of the lake equal areas of the coverage of open savanna and savanna trees. During zone W time (corresponding in all probability to the first part of the Subboreal), the lake seems to have dried out sometimes during the dry seasons. This at least would explain that the pollen grains are somewhat corroded in some of the samples. The open savanna strongly increased in the area, and the savanna trees were very few in general. It seems that at least some 80 % of the area occupied by savanna-vegetation was covered with open savanna, where *Byrsonima* was rare. This is a rather surprising fact, that cannot be changed fundamentally, even if we accept a (difficult to imagine) certain local influence of Gramineae and Cyperaceae.

During zone X time (corresponding to the last part of the Subboreal), there is a strong increase of savanna trees (*Byrsonima*), and a corresponding decrease of open savanna. Not taking into account the short period of increase of herbs (during the dry time of low lake-level around 3250 B.P.), we may say that the area was almost entirely occupied during that zone by a savanna woodland or a very dry type of forest. There must have been very little, if any, open savanna.

During zone Y time (corresponding to the beginning of the Subatlantic) there is a decrease of savanna trees (*Byrsonima*) and an increase of open savanna. At the same time there is an increase of the forest trees. The total impression is that the forest in the immediate vicinity of the lake extended at the cost of the savanna, but that at the same time savanna woodland was partly replaced by open savanna. It is interesting to note that at the base of zone Y small black particles, probably of charcoal, were present in the sediment (see Plate I). It may be therefore that fire (natural or otherwise) caused the elimination of part of the savanna trees, while the climate apparently became wetter.

During zone Z time the savanna trees (*Byrsonima*) were further eliminated, and at the same time the open savanna increased. During the dry period that starts around 2200 B.P., it seems that the level of the lake became so low that it was partly invaded by marsh forest, and peat was formed. When the lake-level rose again, the marsh forest disappeared too. Then we can see that the open grass savanna extended

further rapidly at the cost of all other vegetation elements, reaching a proportion of 90 % of open savanna to 10 % of forest, the actual situation now.
Resuming the above and accepting the probable correlations, we may give the following possible reconstruction of events. At the beginning of the Subboreal the climate became so dry that open savanna prevailed in the area around the lake. Towards the second part of the Subboreal the climate became somewhat wetter, so that the open savanna changed into a savanna woodland or dry forest with much *Byrsonima*. At the beginning of the Subatlantic the climate became somewhat wetter, so that the forest extended in the area around the lake, but fires increasingly destroyed the savanna trees, so that the savanna woodland was replaced by open savanna. The open grass savanna extended finally at the cost of all other vegetation types to its actual extension of 90 % of the surface, because of the influence of man during the last hundreds of years.

Laguna de Yurimena and Laguna Negra

The lake of Yurimena is shown in the photo fig. 6. The Laguna Negra is much smaller and situated a little to the west of the other one. Both are connected by a low marshy zone, and together they form part of an old arm of the River Meta, that actually has its course not far north of the site. The altitude of the lakes is about 160 m above sea-level. At the north side of the Laguna de Yurimena is a dense forest, which is part of the vegetation of the Meta valley. Along the other side however, there is only a very narrow strip of forest, and behind it, at a terrace-level of some 5—10 m higher, open savanna. In the forest the following genera or families have been found.

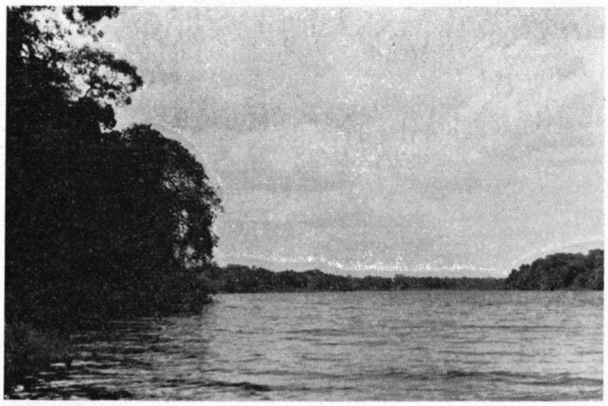

Fig. 6. Laguna de Yurimena (Llanos Orientales).

Coccoloba
Ravenala
Ficus
Scheelea
Hirtella
Jacaranda
Piptadenia
Renealmia
Diefenbachia
Cecropia
Swartzia
Aiphanes
Melastomataceae
Burseraceae
Monstera
Pariana
Mauritia
Tabebuia
Dendropanax
Xylopia
Cissus
Dalbergia
Combretum
Socratea
Phyllodendron
Mirosina
Calathea
Strychnos
Inga
Warczewiczia
Costus
Ochnaceae
Entadopsis
Spathiphyllum
Sapotaceae
Eschweilera
Mimosaceae

3 m of sediment (clay and sandy clay) was collected with the Dachnovsky sonde from the Laguna de Yurimena (from a boat, through about 1 m of water). 1.2 m of sediment was collected in the Laguna Negra, also below 1 m of water.
The diagrams (Plates II and III) are considerably different from the diagram of Laguna de Agua Sucia, because of its situation in a river-valley. The percentage of forest is therefore much higher.
The rise of Gramineae is most clearly marked (in both diagrams) at a depth of resp. 70 (Yurimena) and 50 cm (Negra), and the fall of Gramineae in the last sample. It seems to represent a relatively recent temporary strong extension of the savanna. It is difficult to know whether this was on the nearby terrace or in the river-valley. It is possible that this upper part of the sections corresponds to zone Z.
At a depth of about 230 cm in the Laguna de Yurimena there seems to be a boundary that has a number of characteristics in common with the boundary of zones X/Y of the diagram of Laguna de Agua Sucia. There is an increase of forest, and a decrease of *Byrsonima*; somewhat later there is also an increase of Gramineae, and *Byrsonima* disappears. Moreover the *Anacolosa*-curve of Yurimena and Agua Sucia is very much the same, in relation to this boundary. It is interesting that at this same level in Yurimena, a temporary increase of river-influence is indicated by the curves for *Myrica*, *Podocarpus* and *Alnus* and probably also of the Ericaceae. The pollen of these elements must have come from the Cordillera, transported by the river.
There are a number of interesting characteristics of this diagram, which are not yet understood. One example is the maximum of both *Byrsonima* and Chenopodiaceae-type between about 70 and 170 cm (however, the maximum of this part of the Chenopodiaceae-curve corresponds with a secondary minimum of the corresponding part of the *Byrsonima*-curve).

Laguna de Tanané

The section was taken in a relatively small lake, from a boat. The altitude of the site is about 320 m above sea-level. There was 55 cm of clay on top of the hard whitish clay and the coarse pebbles of a terrace. Only these upper 55 cm of clay contained pollen. There was a remnant of forest at one side of the lake, but the remaining shore was open savanna, with amongst others *Curatella*, *Mimosa*, *Croton*, *Xyris*, Melastomataceae and *Dicromena*. In the forest the following genera were observed.

Anona	*Maximiliana*
Eugenia	cf. *Jessenia*
Hirtella	*Jacaranda*
Myrcia	Marcgraviaceae
Rauwolfia	*Ficus*
Ravenala	*Bellucia*
Piper	*Selaginella*
Pariana	*Duroia*
Tococca	*Vismia*
Mauritia	

The diagram (Plate III) shows a high to very high percentage of Gramineae. A temporary increase of „forest" is caused by a maximum of the *Bactris* type. There is no doubt that there was dominantly open grass savanna during most of the time that the 55 cm of clay were deposited. It seems probable that this whole section corresponds to the later part of zone Z of Laguna de Agua Sucia.

Section Rio Meta near Puerto Lopez

A very short section of only about 18 cm was taken from the sediments of the eroded side of the bed of the River Meta, near Puerto Lopez, at the site of the ferry-boat over the River Meta (altitude about 200 m above sea-level). They represent sediments, deposited during high-water-level, and the site is only in the order of 1 m higher than the dry-season-level of the river. The section was taken by hand, from a big block of clay, broken from the eroded side. The sample distance is only 2 cm. The samples were taken crossing a continuous layer of big fragments of charcoal, that indicated a level of severe burning. It was hoped to find a reflection in the pollen diagram of the effect of this burning and the following regeneration of the vegetation. The charcoal was analysed in the C14 Laboratory of Groningen by Dr. J. C. Vogel; it was paid with a grant for this purpose from the Netherlands Foundation for Pure Scientific Research Z.W.O. The result follows here.

Col. 37—GrN-4385 — Charcoal from the young sediments of the River Meta near Puerto Lopez (Llanos Orientales) .... 165 ± 40 yrs (A.D. 1785 ± 40).

The burning seems to be related with a time of increased colonization of the Llanos, towards the end of the 18th century. The actual vegetation on the recent river sediments at the Puerto Lopez side of the river, is a rather dense forest. The diagram (Plate III) shows a strong dominance of forest elements in the part below the charcoal-layer. The charcoal-layer is immediately followed by a violent maximum of the Gramineae. The open vegetation was then apparently invaded again by elements of the high forest, but also by *Byrsonima*.
It is quite clear in this case, that man destroyed the forest in this area by fire, and that the result was an extension of savanna-vegetation in part of the area.

THE RUPUNUNI SAVANNAS (GUYANA)

Fig. 1 gives the general situation of the area of fig. 7, where the sites of the pollen sections are indicated. These sections are all in the North Rupununi Savannas. There is some 1600 mm of annual rainfall in the area. The Takutu River is low in September-April, and highest in June (about 9 m of difference in level).

Lake Moriru

The general situation of the lake, and the vegetation in its surroundings, is shown in the photos fig. 9, 10 and 11, and the map fig. 8. The altitude is approximately 360 feet (110 m) above sea-level.
When we collected the section, with the Dachnovsky sonde, the lake-level was very low, so that we could take the samples rather far towards the centre.
The samples were collected down to a depth of 6.5 m. The bottom of the deposit was not reached, as no more rods were available.
The lake is situated on the northernmost extensions of the Rupununi Savannas, near the southernmost hills of the Pakaraima Mountains. The Ireng River passes 2 km west of the lake. Some 17 % of the map area (fig. 8) is covered with forest, the rest (about 83%) is open savanna and savanna trees. This corresponds again very well to the uppermost pollen spectrum of the diagram (Plate IV), with 20 % of pollen of forest elements and 80 % of savanna elements (15 % pollen of savanna trees and 65 % of elements of the open savanna). Two C14 analyses were made by Dr. J. C. Vogel of the Groningen Laboratory; they were paid from a grant for this purpose of the Netherlands Foundation of Pure Scientific Research Z.W.O. The results follow below.

B.G.15—GrN-4581 — Lake Moriru; humic clay from a depth of 105—115 cm.... 6,060 ± 95 yrs.
B.G.16—GrN-4526 — Lake Moriru; humic clay from a depth of 165—195 cm .... 7,285 ± 75 yrs.

From the first-mentioned date it is possible to calculate the average rate of sedimentation for the upper 115 cm of the section as 1.9 cm per 100 years. Between 115 and 185 cm it is 5.7 cm per 100 years. These values will be used, together with the direct C14 results, to give an estimate of the age of the zone boundaries. The first one will be used for the upper part, the second for the lower part of the section. It is interesting to note that a similar slowing down of the sedimentation rate was found in the uppermost part of the sediments of Laguna de Agua Sucia. Nevertheless, as the clay between 200 and 500 cm is very much compacted, the cipher of 5.7 cm per 100 years may be too high for this interval; a second set of possible ages is therefore given for this interval in a table (see p. 81).
The diagram gives the longest continuous record actually known from a savanna, and has a special interest because it seems to reach back into the last glacial period. It is however much less detailed than the diagram from Laguna de Agua Sucia, where the rate of sedimentation was about 4 times that of the

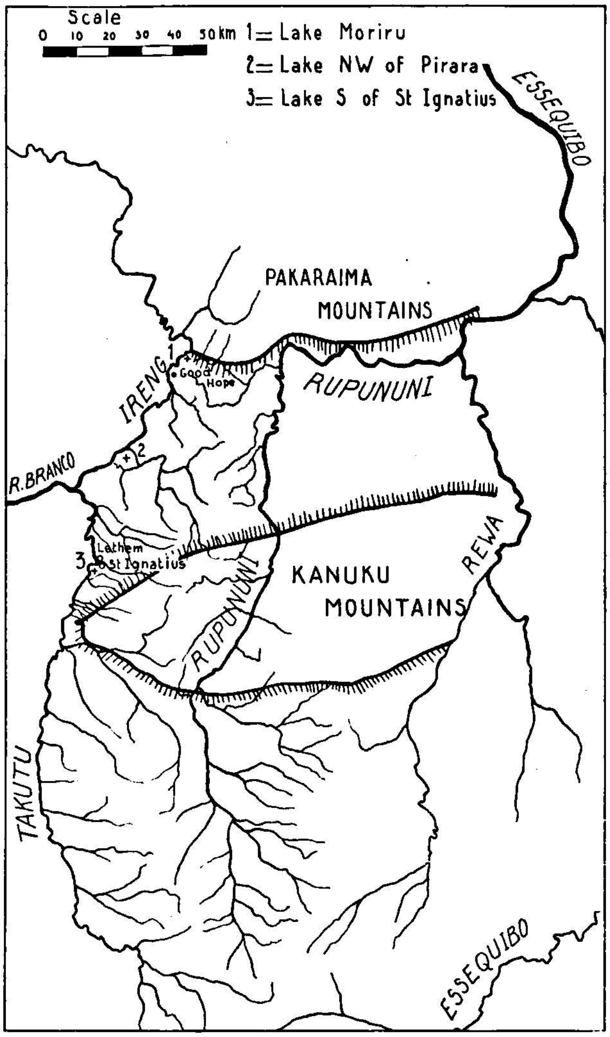

Fig. 7. Map of the Rupununi Savannas (Guyana), indicating the localities of the pollen sections.

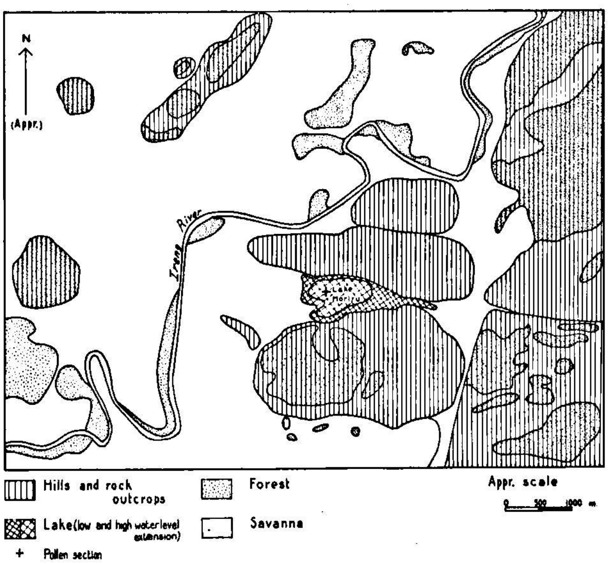

Fig. 8. Map of the area of Lake Moriru, north of Good Hope (Rupununi Savannas).

Fig. 9. Lake Moriru, looking northward.

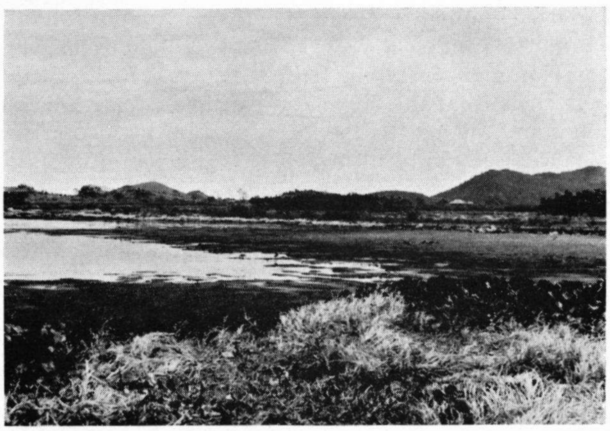

Fig. 10. Lake Moriru, looking southward.

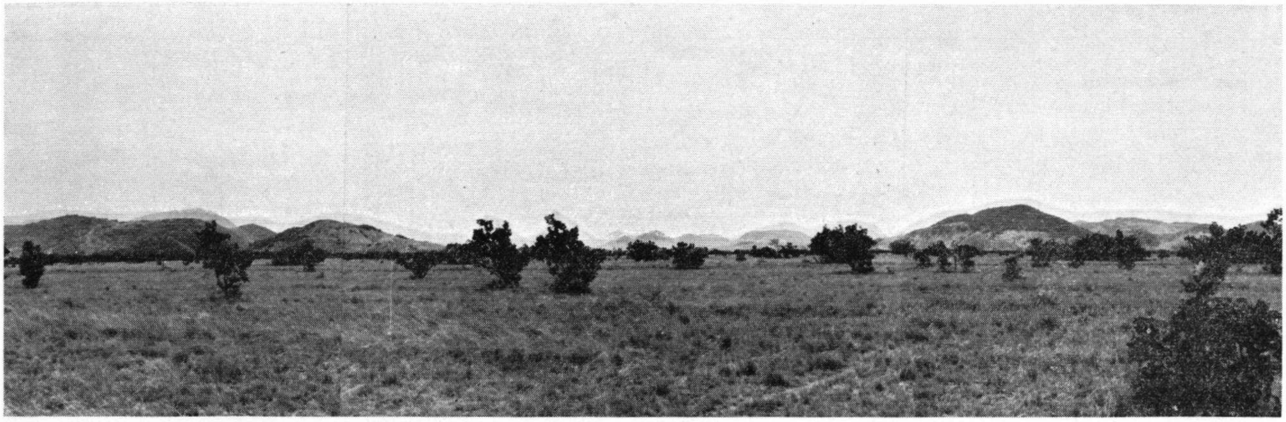

Fig. 11. View of Rupununi Savannas near Lake Moriru.

corresponding (uppermost) part of the diagram of Lake Moriru, and where the sample distances could be much smaller.

We distinguished provisionally 8 zones in the diagram (Plate IV), indicated with the letters a, b, c, d, e, f, g and h. Zone h seems to correspond in time to zones Y and Z of Laguna de Agua Sucia, and zone g seems to correspond in time to zones W and X together.

In the table (see p. 81) we give the zones, their depth in the section, their principal characteristics and their provisional correlation with the zones of Laguna de Agua Sucia (Llanos Orientales) and the zones of the Cordillera Oriental.

For details on the zones of the Cordillera Oriental and on the Late-Glacial subdivision, we may refer to van der Hammen & Gonzalez (1960 a, 1960b, 1965b), van der Hammen & Vogel (1966) and Gonzalez, van der Hammen & Flint (1965).

It is clear, that the correlation with the Late-Glacial zones and the ages in the lower part of the section are hypothetical, until direct C14 evidence proves or disproves them. Nevertheless, the C14 dates, in the upper part at least, make it highly probable that the lower part as a whole is Late-Glacial to Late-Pleniglacial.

We may resume the above in the following, partly tentative reconstruction of the vegetation history. During the end of the Pleniglacial and the early Late-Glacial, the area was occupied by a savanna woodland or dry forest, with patches of open savanna. Sometimes there was a short temporary increase of open savanna. Finally, approximately during Younger Dryas or Allerød time (about 11,000—10,000 B.P. or 12,000—11,000 B.P.), there was a somewhat longer period of open savanna, when there was a strong decrease of *Byrsonima*. Immediately after that, approximately during the beginning of the Holocene or during Younger Dryas time, there was an almost closed dry forest or savanna woodland. At the beginning of zone d, the open savanna extends again at the cost of the woodland. During the first part of the Holocene, there is a further increase of open savanna and a changing proportion of open savanna and woodland, but during the later Holocene (the last 5000—6000 years) the open savanna completely dominates in the area. Around 3000 B.P. there is a marked increase of Gramineae. The upper recent time shows an increase of Cyperaceae and a slight increase of *Byrsonima*.

Interesting are the very high percentages of Cyperaceae at 85 and 185 cm, dated approximately 5000 and 7500 B.P. They might represent intervals with a low lake-level and/or a dry climate.

Lake SW of St. Ignatius Mission

The general situation of the lake and the vegetation in its surroundings, is shown in the photo fig. 13 and the map fig. 12. The altitude of the site is about 330 feet (100 m). The lake apparently is a part of an old course of the Takutu River. It is totally surrounded bij an orchard savanna (*Byrsonima-Curatella*), but at only a 100 m distance of the gallery forest of the Takutu River. The pollen section was taken near the eastern end of the lake, in a marshy „shrub" of *Montrichardia* and some trees. The top of the sediments was higher than the lake-level, and it seemed that locally some erosion had taken place. The diagram (Plate V) includes another group, of Proteaceae, as the pollen of this family is very frequent in this particular section. We believe that it may represent a locally frequent element of the savanna trees. The diagram shows, like most other diagrams, a rather recent increase of the open savanna elements. Before that, the savanna trees seem to have covered a greater part of the surface. Nevertheless, there is another phase of more open savanna, reflected in the lowest part of the diagram. It is not certain how much time the section does represent, but it will not be more than a few thousands of years (corresponding eventually to zones Z or Y and Z of Laguna de Agua Sucia).

Lake NW of Pirara

The situation of the lake and the vegetation around it are shown in the photo fig. 15 and the map fig. 14. The altitude of the site is about 320 feet (97 m). The distance from the lake to the river is 3 km, and there is no forest in the vicinity. The area is occupied by open grass savanna and „orchard savanna" (*Curatella-Byrsonima*). The section consists of about 1 m of

Provisional pollen zones Lake Moriru		Some characteristics of pollen zones, and depth in section	Approximate calculated age B.P.	Correlation with provisional pollen zones of Laguna de Agua Sucia	Possible correlation with the pollen zones of the Cordillera Oriental		
h		0—55 cm. High Gramineae percentages (rise at the beginning, decrease at the end).	3000	Z Y	VIII		
g		55—85 cm. Rising Gramineae percentages. A high top of Cyperaceae, at the base of this zone, seems to indicate temporary relatively dry conditions.	5000	X W	VII		
f		85—125 cm. Rise of „other herbs", followed by a rise of Cyperaceae. Immediately below, definite fall of *Byrsonima.*		V	VI		HOLOCENE
e		125—200 cm. Gradual rise of Gramineae. At the base a very high peak of Cyperaceae, probably indicating temporary relatively dry conditions.	7500		VI		
d		200—260 cm. Rising herb percentages and falling *Byrsonima* curve.	8700—10,000		V	V IV	
c		260—340 cm. *Byrsonima*, very high percentages. (Probably no open savanna in the vicinity). (Boundary: Sudden fall of herbs, sudden rise of *Byrsonima*).	10,000—11,000		IV	III	
b		340—385 cm. High percentages of herbs (High peak of Cyperaceae near the top).	11,000—12,000		III	II	LATE-GLACIAL
a	2	385—580 cm. Byrsonima, high percentages; herb percentages relatively low (mainly Gramineae), but higher than in zone C. Peaks of Gramineae at 475 and 535 cm.	appr. 14,000?		II I	I	
	1	580—640 cm. As zone a2, but with relatively high percentages of *Ouratea.*					PLENI-GLA-CIAL

clay, resting on sand with small pebbles. The diagram (Plate V) clearly reflects the actual situation in its upper part. There is a complete dominance of the pollen of grasses and sedges, up to 98 %. This upper part is preceded by a part where the *Byrsonima* pollen shows a higher percentage, while *Jussiaea* and Compositae were also higher. It seems that the fall of *Byrsonima* and certain herbs may have been caused by an increased effect of burning in the area. They were replaced by Cyperaceae, that contain several genera (*Bulbostylis*, etc.) which are considerably fire-resistant. The lowermost sample shows a higher percentage of Gramineae again, but it is not clear if this is of local origin (beginning of sedimentation in the lake) or not. The section might eventually correspond in time to that SW of St. Ignatius.

Quatata

In the area of the Nappi head, north of Quatata Fort, a section was collected in a pit for water in a small marshy valley, occupied by open grass savanna, but possibly occupied formerly by a *Mauritia* swamp. The material consisted of 170 cm of black to grey clay, resting on coarse sand.

Unfortunately only the uppermost two samples contained sufficient pollen for analysis. The uppermost sample (near the surface) contained (132 grains counted):

Gramineae	77 %	Palmae	13 %
Cyperaceae	4 %	Lecythidaceae	1 %
Compositae	1 %	*Ilex*	1 %
Byrsonima	2 %	*Mauritia*	4 %

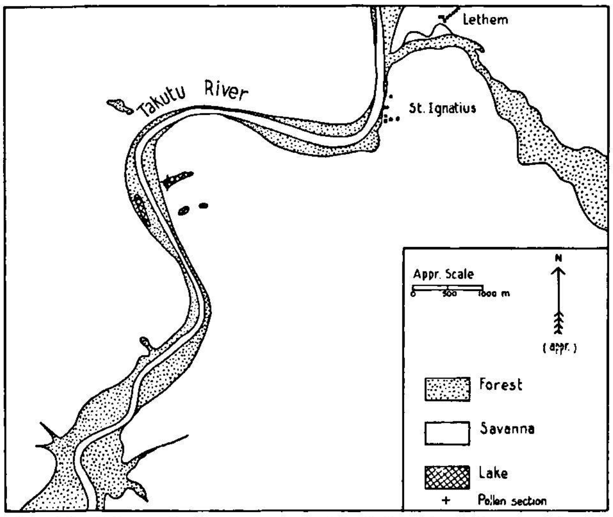

Fig. 12. Map of the area south of St. Ignatius, with the place of the pollen section.

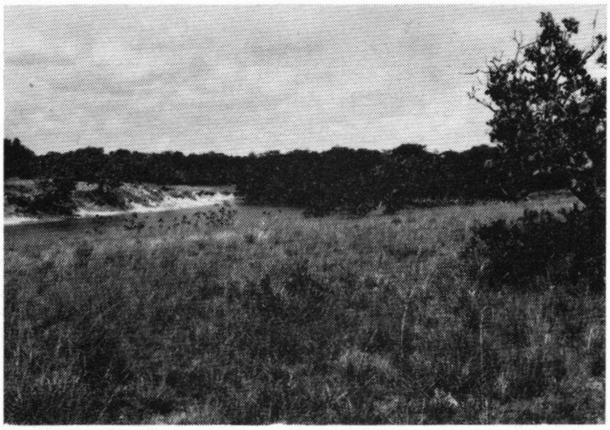

Fig. 13. The Lake SW of St. Ignatius, near the Takutu River (Rupununi Savannas).

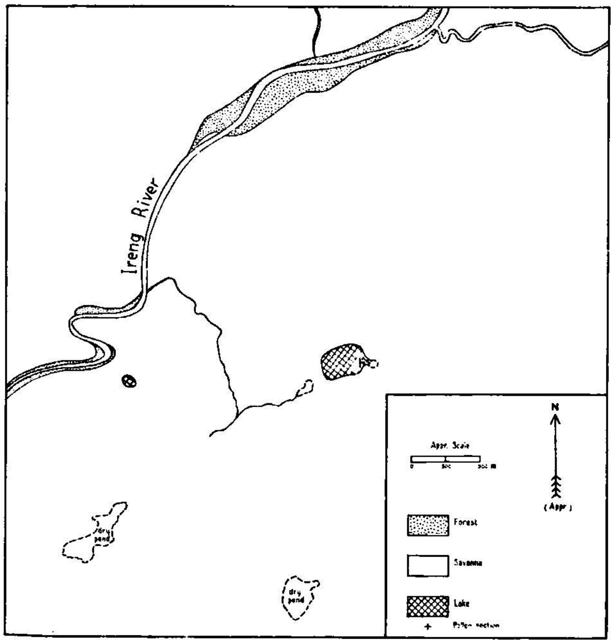

Fig. 14. Map of the area around the Lake NW of Pirara.

Fig. 15. Lake NW of Pirara (Rupununi Savannas).

The sample at a depth of 20 cm contained (141 grains counted):

Gramineae	90 %
Byrsonima	1 %
Palmae	1 %
Mauritia	8 %

A sample at 40 cm contained only 16 grains of Gramineae and 1 of *Byrsonima*. We may conclude, that the area (lying in the area where the old laterites are near or at the surface) was occupied principally by open savanna during the time that the uppermost part of the section was deposited. It is not known how much time this part represents, but it should be at least several hundreds of years.

CONCLUSIONS

Many of the data on the history of the savannas, obtained from the pollen diagrams, will need further confirmation from other places before they may be generalized. Nevertheless, there are certain facts that seem sufficiently clear to justify already some general conclusions.

Both in the Llanos Orientales (Agua Sucia) as in the Rupununi Savannas (Moriru), open savannas existed already during at least several thousands of years before the present. This savanna-vegetation was preceded by a dry forest (or closed savanna woodland), with *Byrsonima* as the most common high pollen producer.

The appearance of open savanna areas in the Agua Sucia region happened around 3000 B.P. There are strong indications that it was at least partly caused by man (felling and burning). There are indications for an earlier period of open savannas in the Agua Sucia region, between 5000 and 4000 B.P. Local influence on the pollen spectra (eventual seasonal short period of drying up of the lake) may suggest that more open savanna was present than actually was the case. Nevertheless, a drier period with a part of the area covered with open savanna, seems to be an inevitable conclusion.

In the Moriru area (Rupununi Savannas), the time of closed dry forest or closed savanna woodland with *Byrsonima* as the dominant high pollen producer, lies as far back as some 9,000—10,000 years. Before that date dry forest dominated, but as far as the record reaches (possibly into the full Würm-Glacial), there were temporary phases of some extension of open savanna areas. An especially marked extension of open savanna took place approximately during Younger Dryas or Allerød time. Between about 9,000—10,000 and 5,000 before present, the proportion of dry forest (or savanna woodland) and open savanna is changing repeatedly. There is no proof of human action in the area at that time. From 5000 B.P. on, and especially in the last 3000 years, the open savanna dominated in this area.

The pollen diagrams from the Meta valley seem to indicate that both human action and changing edaphic factors (inundation, change of river course) were important factors determining the local fluctuation of forest and open savanna. Open grass savanna (eventually caused by felling and burning by man) may be first invaded by savanna trees (*Byrsonima*), and then be replaced by a type of „gallery forest". Two diagrams of the Meta valley show an increase of forest and a decrease of open grass savanna in recent time, while at the same time in the savanna areas proper the open grass savannas increase. Excluding the river valleys, or those savannas that are under heavy influence of river inundations, we believe that the available pollen analytical data show that a dry forest or a closed savanna woodland was once the climax vegetation in many actual savanna areas. Human action was important in the formation of open grass savanna out of this forest. Nevertheless, it seems that natural causes, such as periods of very dry climate and lightning, may have had (and eventually locally still have) a similar, semi-permanent or temporary effect on this dry forest.

We do not know what was the precise composition (qualitative and quantitative) of the savanna woodland that is reflected in the pollen diagrams as high percentages of *Byrsonima.* It may have been extensive dense stands of *Byrsonima crassifolia,* as mentioned by Blydenstein (see p. 73). It may also be that the vegetation was composed of a greater number of co-dominating, but very little pollen producing woody species. Although we cannot yet determine with certainty all the species of *Byrsonima* on the basis of their pollen morphology, it is certain that several species are represented in the pollen spectra.

All the pollen diagrams strongly suggest a very unstable equilibrium between the *Byrsonima* association and the open herbaceous savanna. This equilibrium was apparently influenced by changes of climate, lightning fire and in later time by man-made fire.

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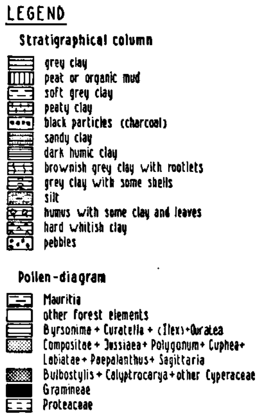
Legend for all Plates (except Plate I)



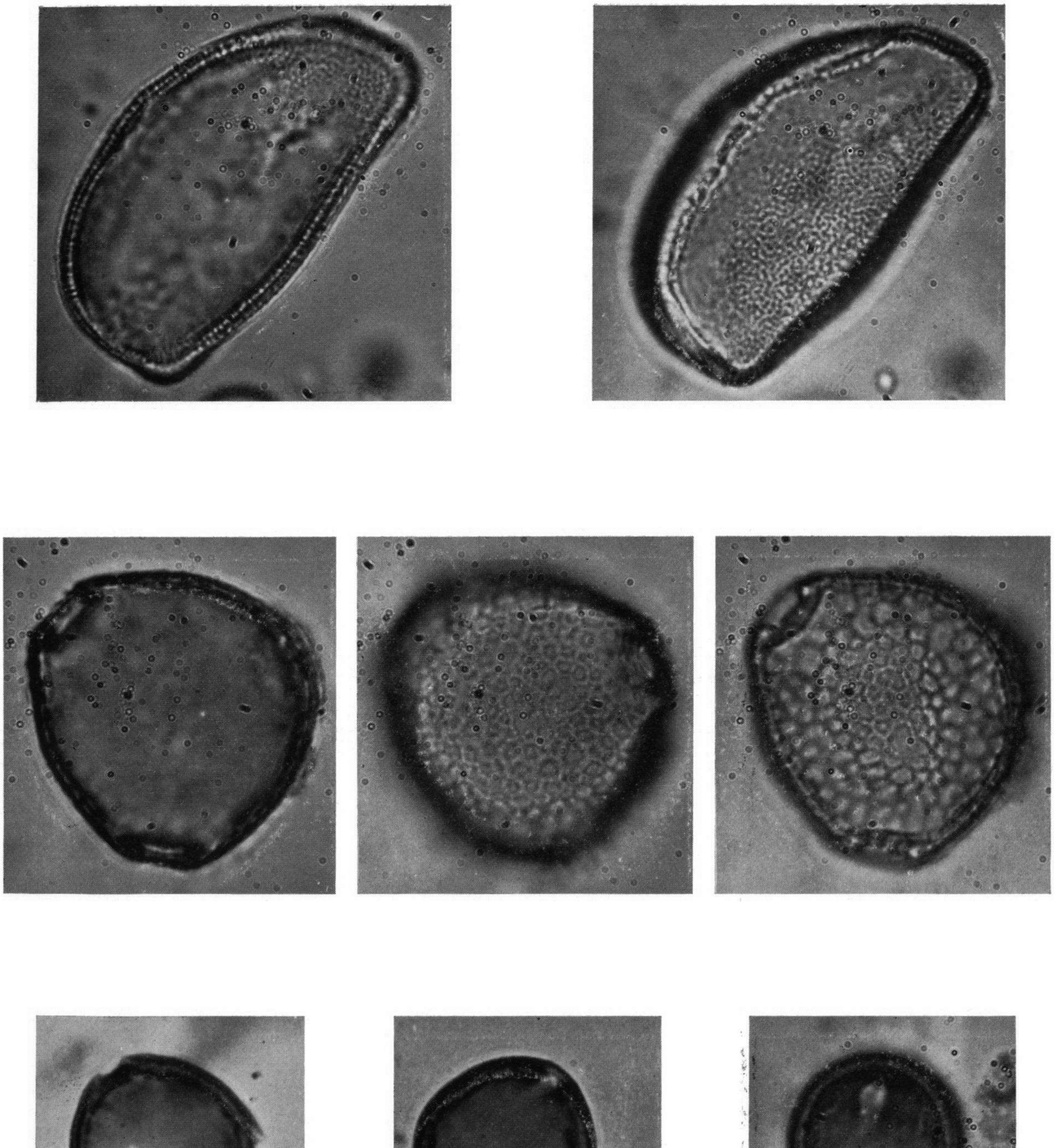


Fig. 21. Xyris.

Fig. 22. Duroia.

Fig. 23. Ouratea.

1250 ×

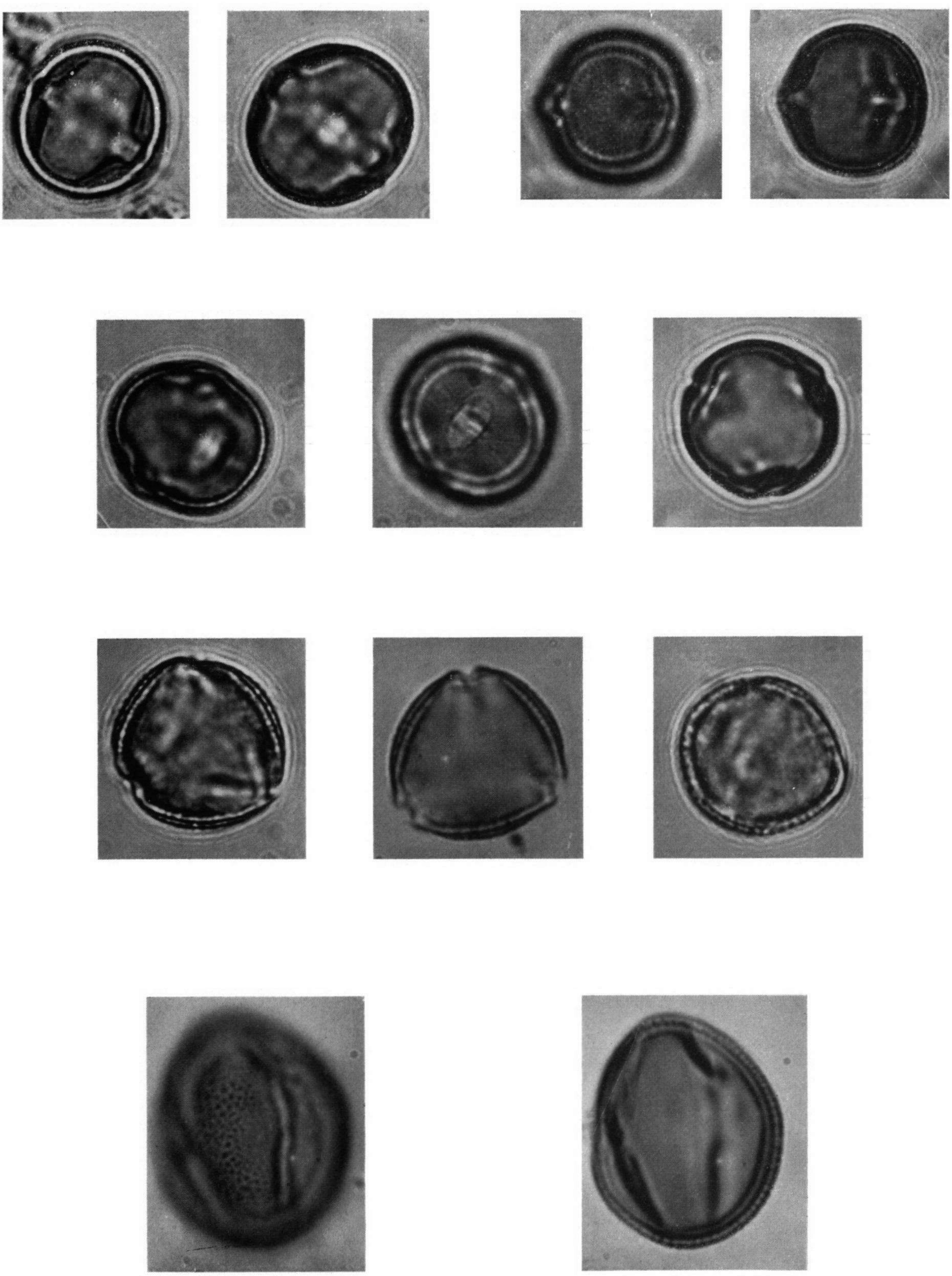


Fig. 16. Byrsonima densa.

Fig. 17. Byrsonima schomburgkiana.

Fig. 18. Byrsonima coriacea var. spicata.

Fig. 19. Vismia.

Fig. 20. Curatella.

1250 ×

POLLEN PHOTOS

PLATE I **LAGUNA DE AGUA SUCIA**

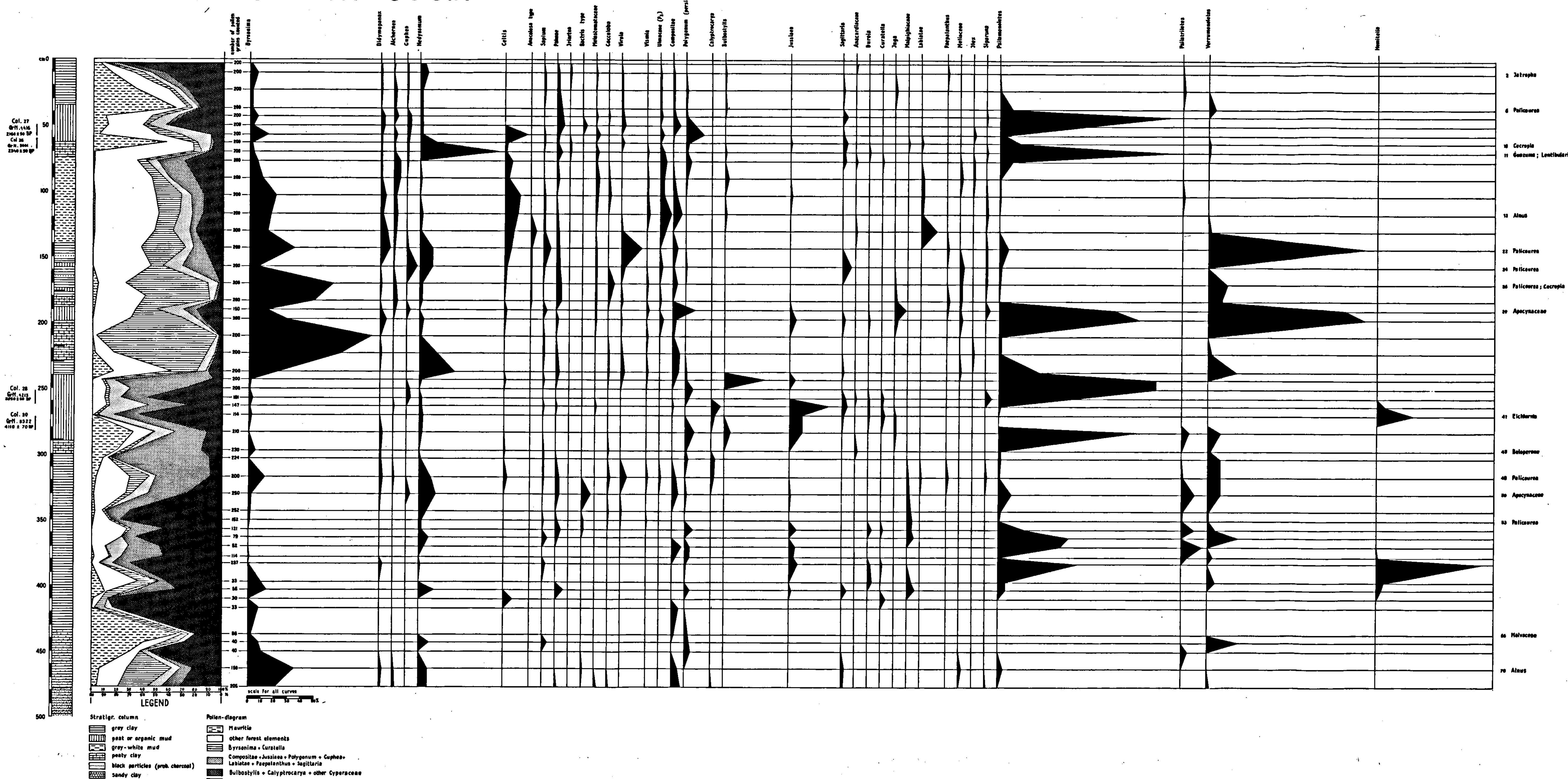


PLATE II

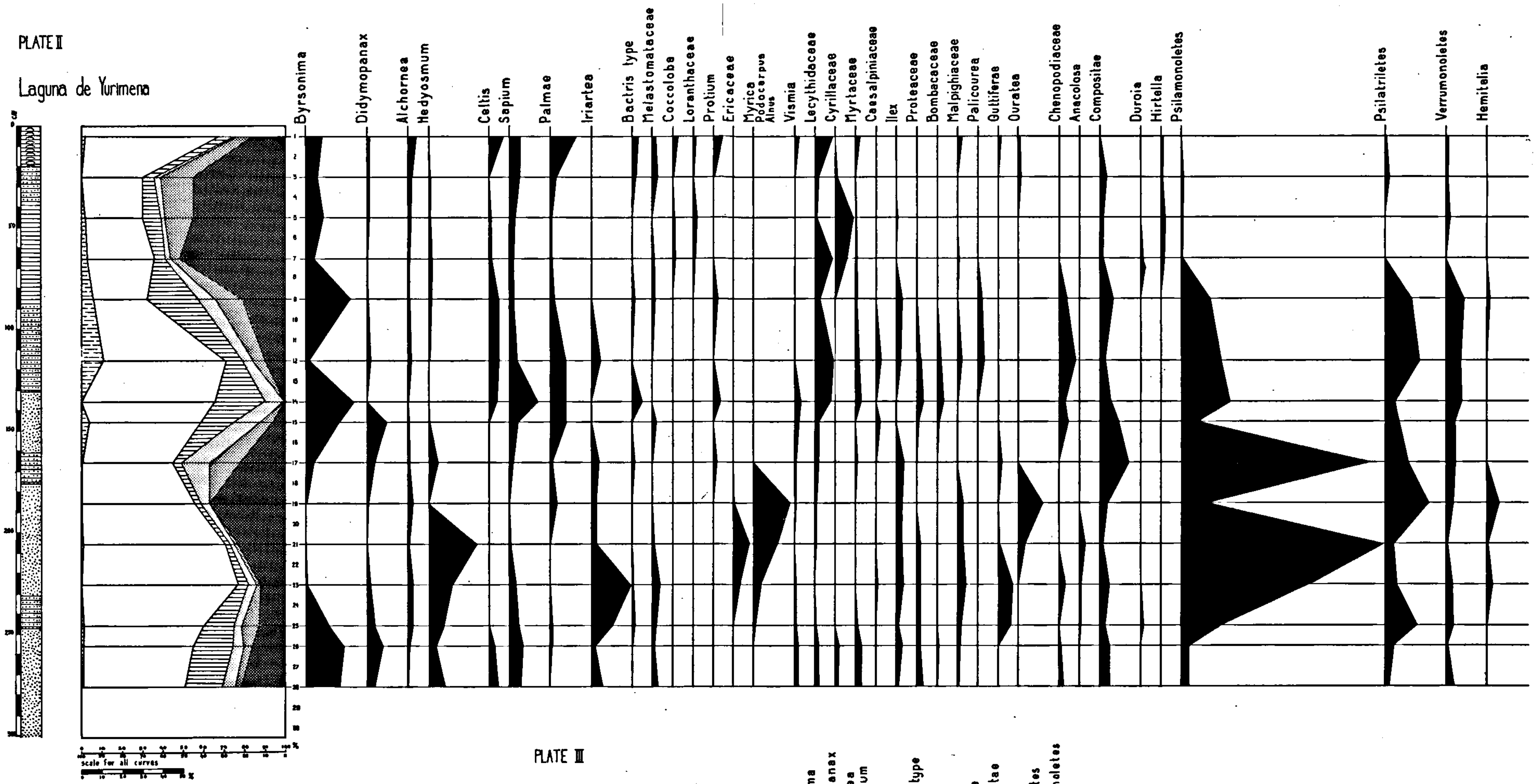


PLATE III

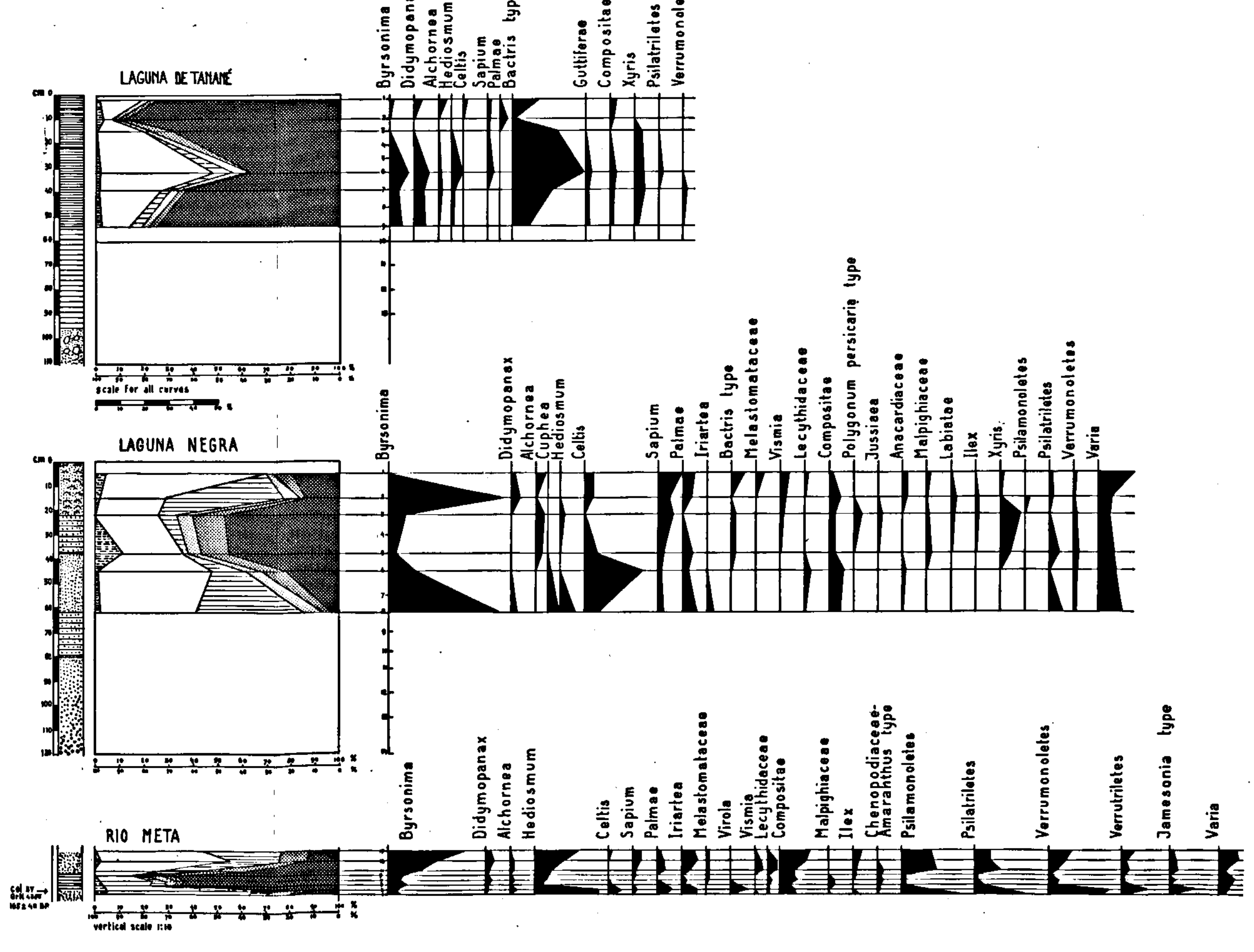
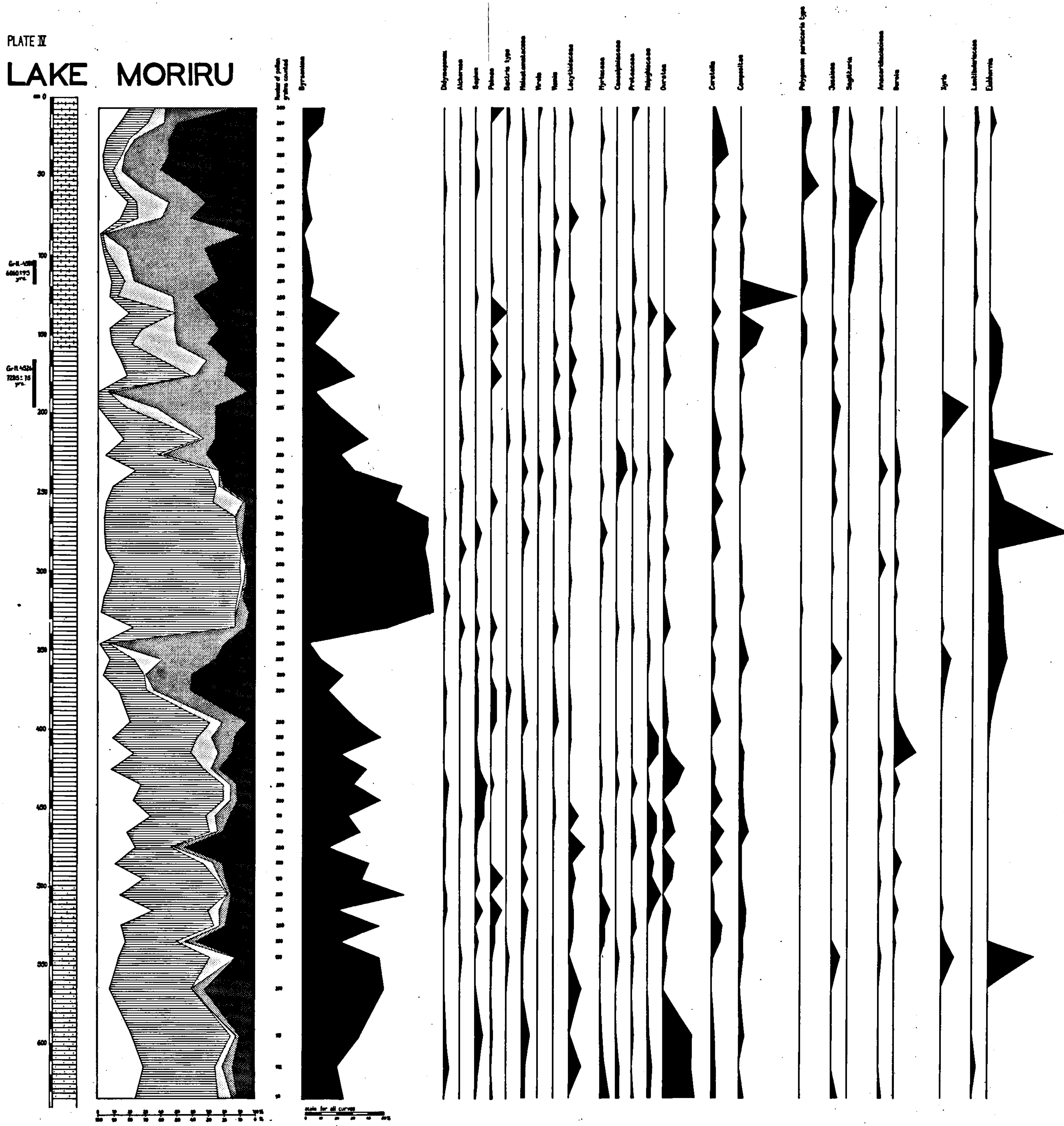


PLATE IV

LAKE MORIRU



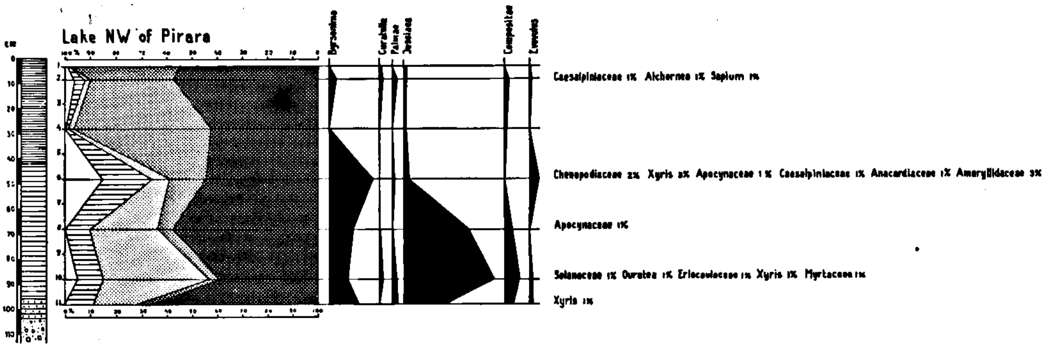
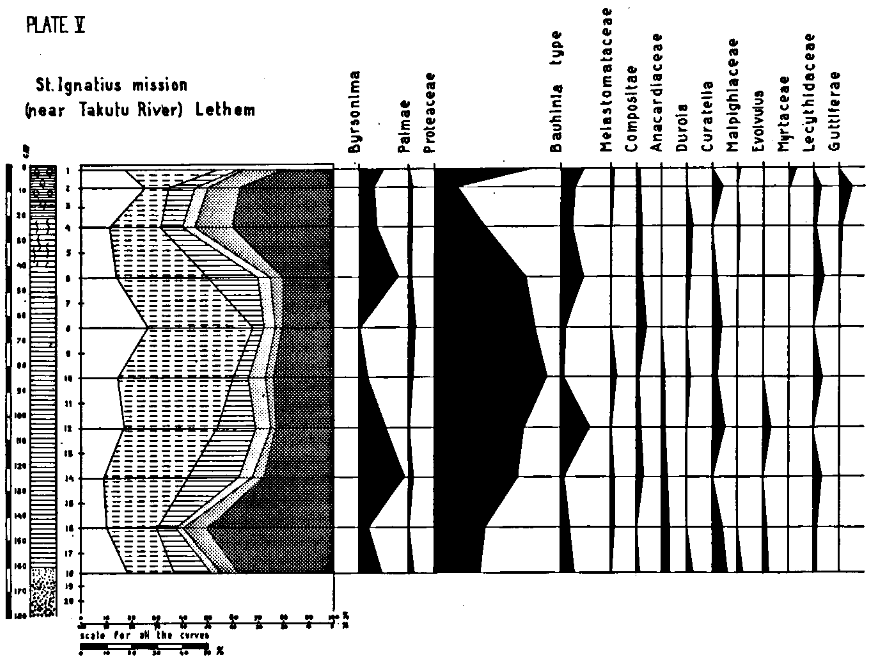

Lake NW of Pirara
Caesalpiniaceae 1% Alchornea 1% Sapium 1%
Chenopodiaceae 2% Xyris 2% Apocynaceae 1% Caesalpiniaceae 1% Anacardiaceae 1% Amaryllidaceae 3%
Apocynaceae 1%
Solanaceae 1% Ouratea 1% Eriocaulaceae 1% Xyris 1% Myrtaceae 1%
Xyris 1%

PLATE V


St. Ignatius mission
(near Takutu River) Lethem
Byrsonima
Palmae
Proteaceae
Bauhinia type
Melastomataceae
Compositae
Anacardiaceae
Durola
Curatella
Malpighiaceae
Evolvulus
Myrtaceae
Lecythidaceae
Guttiferae
scale for all the curves