

UPPER PLEISTOCENE AND HOLOCENE CLIMATE AND  
VEGETATION OF THE "SABANA DE BOGOTÁ"  
(COLOMBIA, SOUTH AMERICA)

by

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## ABSTRACT

The uppermost 32 metres of a 266 metre core principally of lake sediments, Pleistocene and Holocene in age from the Sabana de Bogotá were analysed for its pollen content, at intervals of 10—15 cm. About seventy species, genera of families could be recognized, many of them for the first time. The rest of the core is being analysed and the results will be published later. The Sabana de Bogotá lies at an altitude of approximately 2560 metres above sea level,  $4\frac{1}{2}^{\circ}$ — $5^{\circ}$  North of the equator, and  $74^{\circ}$ — $74\frac{1}{2}^{\circ}$  West of Greenwich.

From the diagram it may be deduced that glacial and interglacial periods affected the tropics equally as Europe and North America. It also shows that the glacial periods were at the same time pluvials, and the interglacials interpluvials.

Curves for the real fluctuations of the tree-line, changes of annual precipitation and changes of temperature have been calculated (fig. 5). Temperatures during the high-glacial phases of the Würm glacial were  $\pm 8^{\circ}$  C lower than today, the altitude of the tree-line was some 1300 metres less than now and the snow-line showed an even greater difference (fig. 5).

Radiocarbon dates prove that the parts of the section considered to be respectively Holocene and later Würm-glacial really correspond to those ages. Moreover the temperature curve for the upper Pleistocene of the Sabana de Bogotá corresponds surprisingly well with that published by Emiliani for surface ocean water and by Gross for Europe (fig. 6).

With this knowledge it seemed fully justified to correlate also the older phases with the glacials and interglacials of Europe and North America, using principally the alpine nomenclature. The lowest part of the diagram seems to correspond to the end of Riss I (= Drenthe stadial), followed by the Riss I—II interstadial, and the Riss II (= Warthe stadial). Then follows the Riss-Würm interglacial, the Würm-glacial (subdivided by two long interstadials, together called Interpleniglacial), and the Holocene.

The more important conclusions of the present study are summarized in paragraph 12.

## 1. INTRODUCTION

The Sabana de Bogotá is an upland plain surrounded by mountains in the Eastern Cordillera of Colombia (South America), which has always been considered as the flat bottom of an old lake. Even the Chibcha-indians, who lived on the Sabana before the arrival of the Spaniards, had a legend, according to which the Sabana once became a lake. This legend also tells that the white skinned Chibcha-heroe Bochica, opened a way to the waters of the Sabana, which ran away through the present day outlet of the Tequendama waterfall.

When analysing provisionally some bore-hole samples from the young Sabana-formation, we realized that this formation, several hundreds of metres thick, consisted almost entirely of lake-sediments, all very rich in algae and pollen. So it seemed that here a complete, very thick, series of Pleistocene and probably even Pliocene sediments, developed in lake facies was present, giving the possibility of making a complete continuous pollen-diagram from the Upper Pliocene throughout the whole Pleistocene until recent, a case which would be almost unique in the world.

But the problem was how to get carefully collected continuous cores from this material. For this purpose a special boring was carried out, in the beginning of 1957 in the University-City, with the aid of the drilling equipment of the Hydrogeological department of the Geological Institute, taking continuous cores. At 203 metres below the surface the base of the lake-sediments, resting on tertiary red-mottled clays, was reached.

We now present the results of the pollen-analysis of the upper 33 metres of the section, comprising the Holocene and the Upper Pleistocene of the Sabana de Bogotá,  $4\frac{1}{2}^{\circ}$  North of the equator, at an altitude of 2560 metres.

At this point we would like to express our thanks to Dr. Enrique Hubach and Dr. Benjamín Alvarado, former directors of the Servicio Geológico Nacional and to Dr. Fernando Paba Silva, the present director, to have facilitated the realization of this study, and to Dr. Jaime Lopez Casas, former chief of the Department of hydrogeology of the Servicio Geológico Nacional, for his help in the technical execution of the boring.

We also wish to express our thanks to the Shell-Cóndor in Bogotá for providing several core-barrels and other accessories.

Schlumberger of Colombia were so kind to make the electric log without any cost.

Financial support was given by the glaciology commission of the International Geophysical year.

The C 14 analyses were carried out gratis, by Dr. H. Tauber of the Copenhagen laboratory, through the intermediary of Dr. Johs Iversen.

Mr. Juan B. Perico, laboratory assistant of the paleobotanical section, prepared all the samples, and did much valuable work on all our field excursions.

The collaborators of the Instituto de Ciencias, especially my friends Mr. Roberto Jaramillo and Mr. Jorge Hernández, contributed essentially to the

present study, determinating the recent plant collections, collaborating in the recent vegetation studies and facilitating the collection of recent pollen of specimens in the National Herbarium.

Mr. Erwin Kraus supplied many data, based on his observations, on the altitude of the snow-limit in different snow mountains, and was our guide and inestimable mountain companion in the Sierra Nevada de Santa Marta.

To all these friends and institutions without whose help we would not have been able to finish this study, our sincere thanks.

## 2. GEOGRAPHICAL POSITION AND GEOLOGICAL HISTORY OF THE "SABANA DE BOGOTÁ"

The "Sabana de Bogotá" is the largest one of several upland plains at an altitude of approximately 2560 metres above sea-level in the Eastern Cordillera of Colombia. Its geographical position (fig. 1) is approximately between  $4\frac{1}{2}^{\circ}$  and  $5^{\circ}$  north of the equator, and between  $74^{\circ}$  and  $74\frac{1}{2}^{\circ}$  West of Greenwich. The flat part of the Sabana de Bogotá has an area of 1400 km<sup>2</sup>, on which several important towns are situated, amongst them Bogotá, the capital of the country. The Sabana de Bogotá represents an almost completely closed basin, surrounded at all sides by mountains, and drained by the Bogotá river and its tributaries, with a single outlet in the south-west, vía Alicachín-El Charquito-Tequendama waterfall.

The present situation is logically the result of the geological history. Although the geology of the region is rather well known (Hubach, 1957; Bürgl, 1957; Van der Hammen, 1957), there still remain several structural problems to be resolved.

During the Cretaceous and the Lower Tertiary the actual Sabana de Bogotá was a part of the East Andean Geosyncline. During the Lower Cretaceous black marine shales were deposited, with some sandstone layers (Villeta formation). During the Upper Cretaceous the amount of sandstone increases, and the marine sedimentation closes with the sedimentation of respectively sandstone and siliceous rocks ("plaeners") and finally a frequently soft sandstone called Tierna-sandstone (Guadalupe formation).

The Tierna sandstone is of Lower Maestrichtian age. On top of this sandstone lies the Guaduas formation, also of Maestrichtian age, except the uppermost part, which is already Paleocene. The Guaduas formation presents principally a transitional to continental facies (grey shales and clays, sandstones and coals). Thus the geosyncline suffered a slight upheaval at the beginning of the Maestrichtian, or the sea retreated. Fresh movements took place in the beginning of the Paleocene, resulting in the sedimentation of sandstones (Cacho sandstone).

The Cacho sandstone forms the basal sandstone of the Bogotá formation, of Paleocene and Lower Eocene age. This Bogotá formation consists principally of red mottled clays and clay containing sandstones. In the middle part of the formation a coarse grained sandstone may be present, representing the base of the Lower Eocene (Lenguazaque sandstone). In the Tunjuelo valley, south of Bogotá, the Usme formation rests on top of the Bogotá formation and consists of a thick basal sandstone of probably Middle Eocene age, and a shale series with locally foraminifera of Upper Eocene and Lower Oligocene age. A sandstone with several coal layers, marks the beginning of the Middle Oligocene.

At the beginning of the Upper Oligocene, that part of the Eastern



Geosyncline which actually is the Eastern Cordillera, suffered orogenetic movements: a slight upheaval and probably folding (Van der Hammen, 1959). At that time the principal structural and morphological features of the Sabana began to develop. This development was completed during the Miocene, and the final upheaval took place probably in the beginning of the Pliocene. Then the Sabana was a composed, wide, deep and closed syncline valley. Several similar (but smaller) upland plains occur at approximately the same altitude in the central part of the Eastern Cordillera. This fact seems to indicate that there may be some major tectonic feature responsible for their formation, but we do not know what it is.

A geological section East-West through the Sabana de Bogotá is given in fig. 2. During the Pliocene and possibly the older Pleistocene, the Tilatá formation was deposited in valleys debouching into the proper Sabana, and near the base of the mountains which surround it. It consists of sand, gravel, loam and clay, and sometimes diatomite, volcanic ash and kaolin. Near the base of the formation fossil fruits of *Humiria cipaconensis* (Berry) Selling, were found (Hubach, 1957), indicating that the Cordillera was still much lower than to day. So it seems that the Eastern Cordillera suffered its principal upheaval after the deposition of the Tilatá formation. The formation did not suffer folding of any importance, but small faults are often present.

Probably during the whole Pleistocene and Holocene, the Sabana formation was deposited in what is now the truly flat part of the Sabana. It consists mainly of lake sediments, 200 to 400 metres thick.

Peat-layers are present at different depths, showing that the lake became partly a marsh at intervals. Only the uppermost metres of the Sabana formation do not consist of lake or marsh sediments, but of clays deposited by inundations during the wet seasons. These inundations, notwithstanding artificial drainage, still occur today in the lower parts of the Sabana. The contact of the lake deposits with the inundation clays coincides, as will be shown below, with the beginning of the improvement of the climate during the final part of the last glaciation.

It will be clear that in the course of the Quarternary and probably the last part of the Pliocene great quantities of rock were eroded by the Bogotá river and its tributaries, and deposited in the form of clay and sand in the Sabana-lake.

Thus naturally the mountains surrounding the Sabana were higher at the end of the Pliocene than that they are now. As it is important for our subject to know how much higher these mountains were in the past, we carried out the following calculation.

The area of the flat part of the Sabana de Bogotá is 1400 km<sup>2</sup>. The thickness of the sediments of the Sabana formation is not constant, but has an average of 300 metres. Thus the flat part of the Sabana contains 420 km<sup>3</sup> of material. The sediments in the somewhat higher valleys are not very thick, and the quantity of material deposited there may be estimated at 80 km<sup>3</sup>. So the total amount of sediments is approximately 500 km<sup>3</sup>.

The area exposed to erosion, that is to say the catchment-area of the Bogotá river less its sedimentation area (the flat part of the Sabana and the somewhat higher valley-plains), is approximately 2500 km<sup>2</sup>. Extending the 500 km<sup>3</sup> of material equally over this area, it would form a layer of 200 metres thick. Thus we may draw the conclusion that the mountains which surround the Sabana were somewhat less than 200 metres higher at the end of the Pliocene

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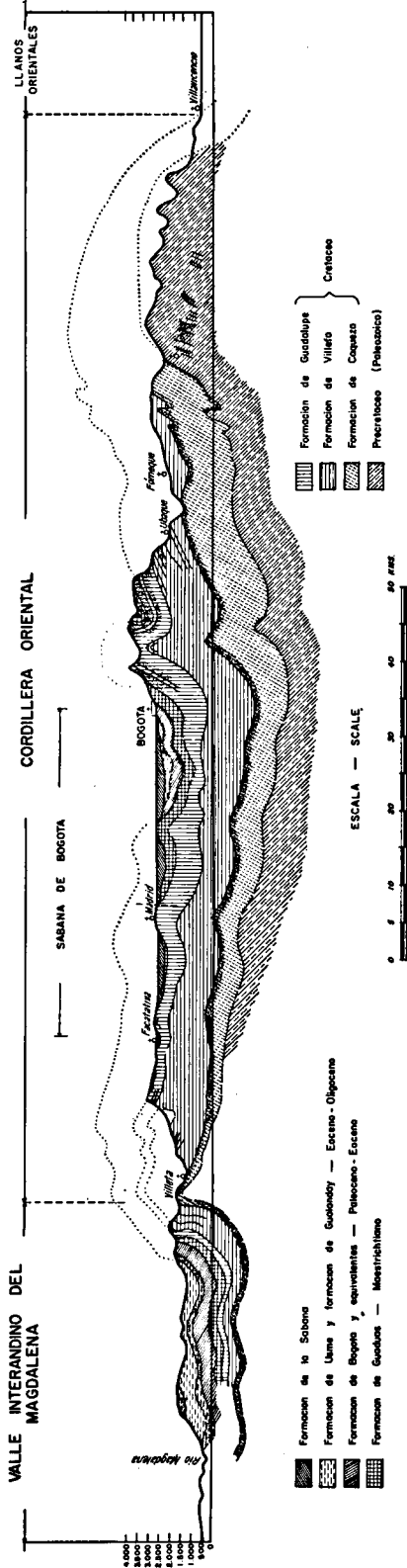


FIG. - 2

than nowadays. If the sedimentation time was 1 million years, then the average rate of sedimentation would be 2 cm in a century, or 20 cm in one thousand years. We will see below, that these figures are very near to the truth.

### 3. ACTUAL CLIMATE OF THE SABANA DE BOGOTÁ AND SURROUNDINGS

The Sabana de Bogotá lies  $4\frac{1}{2}^{\circ}$  lat. N. of the equator and at an altitude of 2560 m. These two factors determine its climate.

In order to be able to appreciate the Pleistocene and Holocene climatic changes, it is necessary to have a look at the actual climate of the entire department of Cundinamarca.

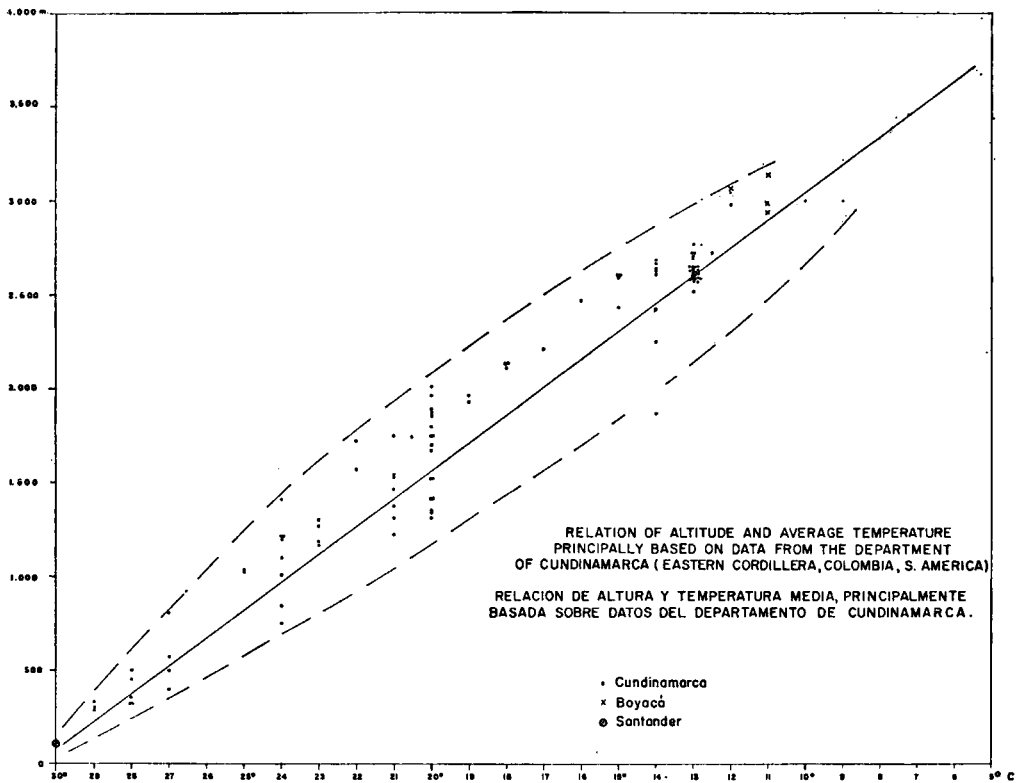


Fig. 3.

The centre of the department is occupied by the high plain of the "Sabana de Bogotá"; in the West it comprises part of the tropical Magdalena valley, to the East at first high mountains up to 4000 metres and then part of the tropical Eastern Plains (Llanos Orientales).

In order to know the relation of average temperature and altitude in Cundinamarca, we plotted more than 100 points in fig. 3. The points are relatively spread because of variable local conditions of each place (precipitation, wind), but nevertheless we see that the average clearly forms a straight



line. This line gives a theoretical temperature of  $0^{\circ}\text{C}$  at  $\pm 4540\text{ m}$ . The last mentioned altitude corresponds quite well with the snow-line in the Eastern Cordillera.

We may conclude from this curve, that the temperature lowers  $\frac{2}{3}^{\circ}\text{C}$  every 100 metres one rises in the Cordillera (provided that the local conditions do not change).

The climatology of Cundinamarca was treated extensively by Eidt (1952), who classified the climate of this department according to the system of Köppen. It would take us too far into detail here to discuss this; anyone interested may consult the mentioned study of Eidt.

We quote following facts, from the report by Eidt. On the Sabana de Bogotá two wet seasons may be differentiated, alternating with two dry seasons (see fig. 4a). The wet seasons fall in April-May and October-November. The average temperatures are lower during the dry months and higher during the wet months. This is mainly due to the fact that ground radiation during the

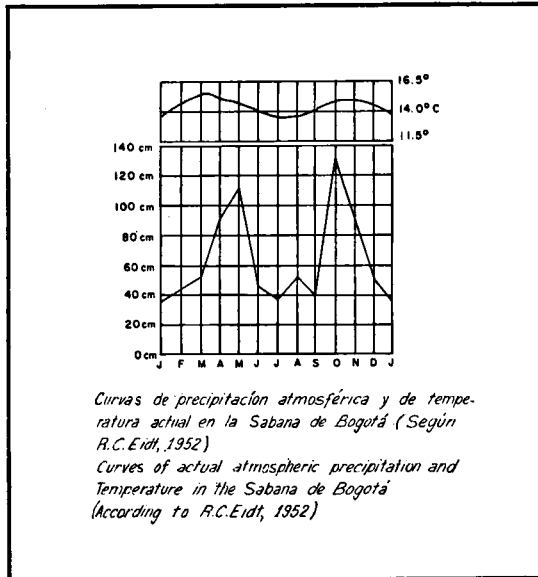


FIG. 4a

night is much greater if there is no overcast (night-frost sometimes occurs on the "Sabana de Bogotá" during the dry seasons).

Eidt gives the following explanation of the two wet seasons. "The department (of Cundinamarca) is situated in the zone where the trade winds of both hemispheres meet. In this zone the winds are frequently variable. The strong rains which fall in this zone are caused principally by the convergence, in such a way that while the sun passes from one tropic to the other every year, two periods of maximum rainfall occur: one when the sun moves northward, the other when the sun moves southward".

The general picture of four equivalent alternating dry and wet stations may change going westward or eastward from the Sabana. Westwards the June-September dry period may be much more pronounced than the other one,

and eastwards the December-February dry period may be much more pronounced.

While the total yearly rainfall on the "Sabana de Bogotá" is relatively low, it increases both towards the NW and towards the SE.

The annual precipitation on the Sabana de Bogotá is of 600—900 mm,

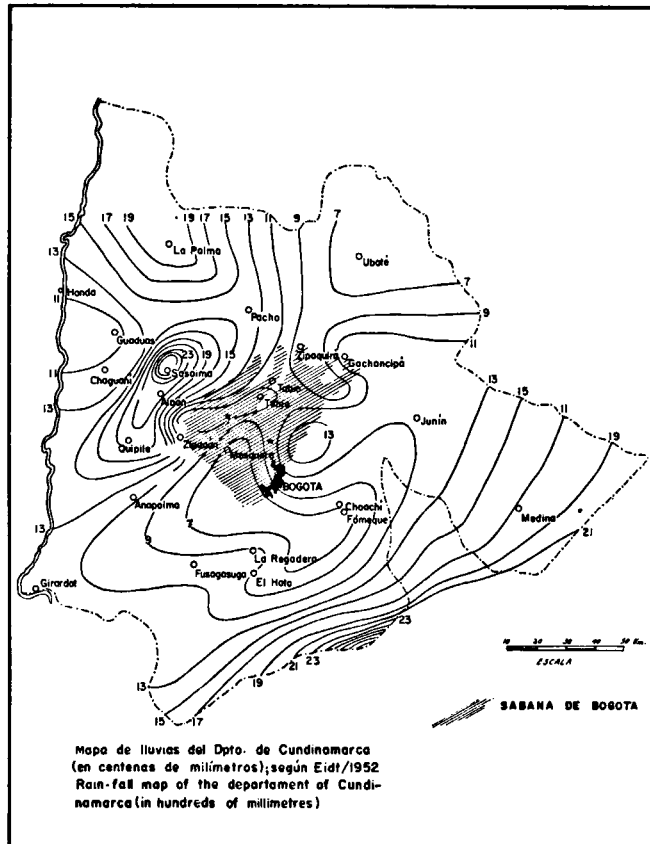


FIG. 4b.

with local maxima up till 1390 mm (near Bogotá). Going down from the Sabana towards the NW, the annual precipitation increases to 2850 mm in the region of Sasaima (fig. 4b).

The western border of the Sabana lies in the rainshadow of a hill range to the west and therefore it is the driest part of the region (xerophitic vegetation of Mosquera, etc.). In contrast to the west of this range, where the country slopes steeply toward warmer regions, there is a much greater rain fall.

These slopes are on many places almost continuously covered with fog-clouds, with a "greenhouse effect". This fact is the main reason for the difference of vegetation of these slopes with that on the slopes of the hills East of the Sabana: a clear difference exists between the *Weinmannietum* (relatively dry forests with higher temperature maxima and lower minima) and the *Quercetum* (relatively humid forests, or cloud-forests, with not so great temperature-differences).

#### 4. ACTUAL VEGETATION OF THE "SABANA DE BOGOTÁ" AND SURROUNDINGS

Although the specific content of the flora of the Eastern Cordillera is quite well known, real sociological vegetation studies were only published by Cuatrecasas (1934). As a matter of fact, as Cuatrecasas states himself, his observations are not complete. Nevertheless, if one considers the short time in which he realized his "observations", one cannot but admire profoundly this work, which in reality gives a wealth of data. We will use in the present study Cuatrecasas names and definitions. Those associations which were not studied by Cuatrecasas, and which nevertheless are of great importance for the study of vegetation history, were surveyed by Mr. Roberto Jaramillo, Mr. Jorge Hernández (both from the Instituto de Ciencias) and the author.

One may distinguish in the Eastern Cordillera the following major vegetation-belts.

Snow	
Meadows and "resulicaulon" of the andean "páramo"	4500 m
Dwarf-forest of the andean "páramo"	3200—3300 m
Andean forest	3000—3200 m
Subandean forest	± 2400—2500 m
Tropical forest	

Of these the uppermost three are of importance for the present study, and will be discussed more in detail. The andean forest includes the Weinmannion and the Quercion, which include the majority of the associations. The forest of the flat part of the Sabana de Bogotá, although related to the Weinmannietum, is a special association, as is the edaphically determined Alnetum.

The next higher belt (dwarf-forest of the andean paramo), includes the Vaccinion, and certain "derivations" of the Weinmannion. The highest belt (meadows and "rosulicaulon" of the andean paramo) includes the Espeletion.

It has to be kept in mind that the altitudinal limits of these belts may locally differ considerably according to the micro-climatical conditions. Thus the Weinmannion and Vaccinion may go up considerably higher in wind-protected valleys or slopes.

It is of importance to note, that there are many local variations in the associations, and that in the following short descriptions only some of the more important are mentioned.

The term "páramo" used here cannot be strictly defined; it is popularly used for the cold higher parts of the mountains. In the present study these are areas covered with meadows and resulicaulon, or with the dwarf-forest near the tree-line.

## ANDEAN-FOREST

*Weinmannietum tomentosae* (Cuatrecasas, 1934)

On the slopes of the mountains which form the eastern border of the "Sabana de Bogotá" and further East in the Cordillera, the most common original climax vegetation is a relatively high forest with *Weinmannia tomentosa* L.f. as a constant and frequently dominant species. On the lower parts of the slopes the original climax-vegetation was entirely or partly destroyed by the influence of man, but in various places at an altitude of 2800—3100 m it may still be intact over rather large areas.

The slopes covered with *Weinmannietum* have, as far as could be checked, a total annual precipitation of approximately 650—900 mm. The average year temperature lies between 9° and 14° C. There are two dry stations (December-March and June-September) and two wet stations (April-May and October-November).

Cuatrecasas mentions amongst others the following species from the *Weinmannietum* near Guasca:

<i>Weinmannia tomentosa</i>	<i>Hypericum goyanesii</i>
<i>Hesperomeles obtusifolia</i>	<i>Hypericum mexicanum</i>
<i>Hesperomeles goudotiana</i>	<i>Hypericum laricifolium</i>
<i>Drimys granatensis</i>	<i>Hypericum brathys</i>
<i>Clethra chrysoleuca</i>	<i>Berberis goudotii</i>
<i>Oreopanax discolor</i>	<i>Myrica parviflora</i>
<i>Clusia</i> sp. div.	<i>Pernettya pentlandii</i>
<i>Tibouchina grossa</i>	<i>Ribes columbianum</i>
<i>Bucketia glutinosa</i>	<i>Rubus floribundus</i>
<i>Vallea stipularis</i>	<i>Rubus loxensis</i>
<i>Gynoxis trianae</i>	<i>Rubus nubigenus</i>
<i>Baccharis floribundum</i>	<i>Salpichroa</i> aff. <i>diffusa</i>
<i>Diplostegium rosmarinifolium</i>	<i>Muehlenbeckia tamnifolia</i>
<i>Miconia eleaoides</i>	<i>Passiflora lanata</i>
<i>Miconia summa</i>	<i>Gaultheria coccinea</i>
<i>Miconia ligustrina</i>	<i>Gaultheria lanigera</i>
<i>Hypericum hartwegii</i>	<i>Diplostegium phyllicoides</i>
<i>Rapanea ferruginea</i>	<i>Valeriana oblongifolia</i>
<i>Senecio lanatus</i>	<i>Bomarea tomentosa</i>
<i>Viburnum suratense</i>	<i>Blechnum moritzianum</i>
<i>Vaccinium floribundum</i>	<i>Alsophila</i> sp.
<i>Gaultheria anastomosans</i>	<i>Lycopodium complanatum</i>
<i>Cavendishia cordifolia</i>	<i>Peperomia blanda</i>
<i>Macleania nitida</i>	<i>Pilea</i> aff. <i>jamesoniana</i>
<i>Ceratostema parvifolium</i>	<i>Cortaderia colombiana</i>
<i>Cavendishia guascensis</i>	<i>Chusquea tessalata</i>
<i>Miconia salicifolia</i>	<i>Tillandsia recurvata</i>
<i>Bejaria aestuans</i>	<i>Tillandsia turneri</i>
<i>Bejaria resinosa</i>	<i>Guzmania</i> sp.
<i>Aragoa abietina</i>	<i>Pleurothallis</i> sp.
<i>Arcytophyllum nitidum</i>	<i>Hymenophyllum</i> sp.
<i>Perilochroa lindenianum</i>	<i>Aetanthus mutisii</i>
<i>Gaylussacia buxifolia</i>	<i>Gaiadendron tagua</i>

At an altitude of 2600—2800 metres the vegetation is partly destroyed (recently or in the past) by man. The shrub and low forest vegetations of that altitude in general do not represent the original climax vegetation. Often different species of *Miconia* are very frequent in these secondary vegetations, and on other places *Alnus jorullensis* may become one of the important species, or several species of Ericaceae. An interesting species, both in the climax vegetation and the secondary ones, is also *Bocconia frutescens*.

Cuatrecasas describes from an altitude of 2650—2750 meters, near Bogotá, the "Consocietas of *Cordia lanata*", with *Cordia lanata* as the most constant plant, with the following species forming the majority: *Vallea stipularis*, *Palicourea lineariflora* and *P. angustifolia*, *Clusia*, *Baccharis floribundum*, *Stevia lucida*, *Piper croccatum*, *Oreopanax incisum*, *Miconia*, *Durantha mutisii*, *Solanum cornifolium*, *Cavendishia cordifolia*, *Lantana*, *Eupatorium*. Other important species are: *Alnus jorullensis* v. *ferruginea*, *Weinmannia tomentosa*, *Rapanea ferruginea*, *Croton bogotanum*, *Miconia* sp. div., *Bomarea frondea*, *Pteridium aquilinum* etc. Cuatrecasas considers this vegetation as very near to a climax.

It seems nevertheless to be difficult to reconstruct with certainty the vegetation of the lower parts of the slopes of the mountains surrounding the Sabana. Probably it was very similar, if not almost identical, with the *Weinmannietum tomentosae*, with the only differences being small changes in the frequency of several plants; *Alnus jorullensis*, *Vallea stipularis*, *Cordia lanata*, *Palicourea*, *Piper*, *Bocconia* and *Croton bogotanum* may have been more frequent, while other species like *Drimys*, *Ribes*, *Valeriana*, *Aragoa* etc. may have been less frequent or absent.

*Ilieto Valleetum Eugenetoso* (J. Hernández, inedited)

The truly flat part of the Sabana is occupied today almost completely by cultivated grassland. Nevertheless at a few places remnants of forest are present, especially near Suba. Together with Mr. Jorge Hernández we made the following observations and list of plants.

The dominant species are:

*Ilex kunthiana* and *Vallea stipularis*

Subdominant is: *Eugenia foliosa*

Moreover the following plants were found:

<i>Alnus jorullensis</i>	<i>Physalis peruviana</i>
<i>Symplocos</i> sp.	<i>Polygonum nepalense</i>
<i>Hesperomeles</i> sp.	<i>Muehlenbeckia</i> sp.
<i>Piper bogotense</i>	<i>Plantago</i> sp.
<i>Verbesina crassirama</i>	<i>Eupatorium fastigiatum</i>
<i>Polymnia pyramidalis</i>	<i>Peperomia</i> sp.
<i>Miconia reclinata</i>	<i>Baccharis floribunda</i>
<i>Senecio americanus</i>	<i>Rubus bogotensis</i>
<i>Cestrum buxifolium</i>	<i>Cynanchum</i> sp.
<i>Cestrum melanochoranthum</i>	<i>Borreria anthospermoides</i>
<i>Alchemilla</i> sp.	<i>Castilleja</i> sp.
<i>Salvia palaeifolia</i>	<i>Solanum caripense</i>
<i>Oxalis</i> sp.	<i>Nertera (Gomozia)</i> sp.

*Hydrocotyle* sp.  
*Salpichoa tristis*  
*Bomarea* sp.  
*Senecio formosus*  
*Prunus serotina*  
*Solanum nigrum*  
*Rhamnus goudotianus*

*Polypodium angustifolium*  
*Polypodium murorum*  
*Polypodium lanceolatum*  
*Dryopteris paleacea*  
*Rubus floribundus*  
*Rubus guianensis*  
*Rubus glaucus*

The differences of this association with the Weinmannietum may be due principally to soil and edaphic conditions.

The dominant and sub-dominant species *Ilex*, *Vallea* and *Eugenia* may occur much higher, practically up to the forest limit, but are in general rather scarce species of the Weinmannietum. In the flat part of the "Sabana de Bogotá" they become dominants, and Weinmannia is in general much scarcer, or may even be completely absent.

The annual average temperature of the flat part of the Sabana is about 13°—14° C, and the rainfall about 700—900 mm.

*Alnetum jorullensis* (J. Hernández, indedit)

On wet, easily flooded places in the flat part of the Sabana (old stream beds etc.), a peat-forming vegetation develops which is very similar to the Alnetum of the temperate zone of the Northern Hemisphere.

In the "Sabana de Bogotá" *Alnus jorullensis* var. *ferruginea* is the dominant species of this association.

The Alnetum must have been very common on the lower parts of the Sabana, inundated during the wet seasons. But to-day few remnants of this association are left.

*Alnus jorullensis* occurs in the Weinmannietum, up to altitudes of 3100 metres, and possibly even higher. In the Sierra Nevada del Cocuy we found *Alnus* at an altitude of 3500 m.

The following list of plants was made by Mr. Jorge Hernández and the author in a well preserved Alnetum North of Funza.

*Alnus jorullensis*  
*Miconia reclinata*  
*Eupatorium fastigiatum*  
*Cestrum buxifolium*  
*Cuphea racemosa*  
*Prunus serotina*  
*Epilobium* sp.  
*Jussiaea peruviana*  
*Prunella vulgaris*  
*Rubus floribundus*  
*Rubus nubigenus*  
*Rubus glaucus*  
*Borreria anthospermoides*  
*Lythrum maritimum*  
*Geranium* sp.  
*Baccharis revoluta*  
*Stachys* sp.

*Nertera granatensis*  
*Solanum nigrum*  
*Lachemilla aphanoides*  
*Lachemilla* cf. *mutisii*  
*Oxalis* sp.  
*Verbena* sp.  
*Polygonum hydropiperoides*  
*Calceolaria palustris*  
*Galium trianae*  
*Stellaria cuspidata*  
*Carex* spp.  
*Cortaderia* sp.  
*Scirpus californicus*  
*Cynanchum tenellum*  
*Polypodium angustifolium*  
*Blechnum* sp.  
*Dryopteris* sp.  
*Equisetum bogotense*

*Quercetum*

A *Quercetum* may be present in the Eastern Cordillera at altitudes between  $\pm 2500$  and  $\pm 3600$  metres. In the Cordillera immediately East of the Sabana de Bogotá it is completely absent, but it appears on the west flanks of the hill range which forms the western limit of the Sabana, with their rather steep slopes towards warmer regions. Here air streams from lower regions, saturated with water vapour are forced to rise up to the altitudes of the Sabana, resulting in a heavy almost continuous cloudiness and higher annual precipitation.

Also in the department of Boyacá (North of Cundinamarca) *Quercetum* occurs in many places, and may be found up to or possibly above an altitude of 3600 metres. The occurrence of *Quercetum* at such altitudes may be due to favorable local conditions, such as higher rainfall and higher average temperatures due to more frequent clouds and the attendant "greenhouse effect" (see paragraph 3).

Thus we see that one of the principal factors for the occurrence of a *Quercetum* instead of a *Weinmannietum* is a higher annual precipitation and a more continuous clouding. The soil seems to be of no influence in this case, as both the *Quercetum* and the *Weinmannietum* are found especially on sandstones.

The following more important genera and species were found by R. Jaramillo, J. Hernández, and the authors in the *Quercetum* near the limit of the departments of Boyacá and Santander.

<i>Quercus lindenii</i>	<i>Podocarpus</i> (scarce)
<i>Quercus humboldtii</i>	<i>Pilea</i> sp.
<i>Tibouchina lepidota</i>	<i>Soralea</i>
<i>Cinchona</i>	<i>Rhamnus</i>
<i>Carica</i>	<i>Siphocampylus</i>
<i>Gunnera</i>	<i>Piper</i>
<i>Weinmannia</i>	<i>Miconia</i>
<i>Bocconia</i>	<i>Berberis</i>
<i>Panopsis</i>	<i>Gaiadendron</i>
<i>Cedrela</i>	<i>Clethra</i>
<i>Hedyosmum</i>	<i>Palicaurea</i>
<i>Rapanea</i>	<i>Persea</i>
<i>Myrica</i>	etc.

A list of species, and genera made between 3060 and 3450 metres of altitude in the *Quercetum* on the Alto de Onzaga (Boyacá), is the following:

<i>Quercus lindenii</i> (dominant!)	<i>Cavendishia</i>
<i>Vaccinium</i>	<i>Clethra fimbriata</i>
<i>Vallea stipularis</i>	<i>Vernonia karstenii</i>
<i>Clusia</i> (sp.div.)	<i>Panopsis suaveolens</i>
<i>Weinmannia tomentosa</i>	<i>Eugenia</i>
<i>Rapanea guyanensis</i>	<i>Diplostegium</i>
<i>Rapanea ferruginea</i>	<i>Berberis</i>
<i>Schefflera</i>	<i>Symplocos</i>
<i>Macleanea</i>	<i>Rhamnus</i>
<i>Gaiadendron punctatum</i>	<i>Miconia</i> (2 spec.)
<i>Palicaurea</i>	<i>Oreopanax</i>

<i>Psychotria</i>	<i>Gaultheria</i>
<i>Persea mutisii</i>	<i>Brunellia</i>
<i>Viburnum</i>	<i>Podocarpus oleifolius</i>
<i>Symbolanthus</i>	<i>Compositae</i> indet.
<i>Bomarea</i>	<i>Myrsinaceae</i> indet.
<i>Hedyosmum bonplandianum</i>	<i>Myrtaceae</i> indet.
<i>Passiflora</i>	<i>Blechnum</i>
<i>Cestrum</i>	<i>Elaphoglossum</i>
<i>Aethanthus</i>	<i>Polypodium glaucophyllum</i>
<i>Thernstroemia</i>	<i>Polypodium</i> sp.

From this list it will be clear that the Quercetum and the Weinmannietum have many genera and species in common. Even *Weinmannia* (various species) is present in the Quercetum; but while *Quercus* is the dominant of the Quercetum, not a single *Quercus* is found in the Weinmannietum of the Sabana de Bogotá and surroundings.

#### DWARF-FOREST OF THE ANDEAN PARAMO

##### *Vaccinion floribundi* and related associations

Near the tree-line a transitional belt of dwarf forest may be present. This irregular belt may begin at 3000—3200 m and end at 3200—3300 m.

Cuatrecasas (1934) describes the *Vaccinion floribundi* from the Eastern Cordillera, with the following dominant species (shrubs or small trees).

<i>Vaccinium floribundum</i>	<i>Senecio lanatus</i>
<i>Hesperomeles obtusifolia</i>	<i>Weinmannia tomentosa</i>
<i>Clethra chrysoleuca</i>	<i>Hypericum laricifolium</i>
<i>Miconia eleaoides</i>	<i>Gaultheria anastomosans</i>
<i>Miconia summa</i>	<i>Tibouchina grossa</i>
<i>Hypericum hartwegii</i>	<i>Miconia salicifolia</i>

Almost identical or similar associations are found at altitudes up to 3600 metres or more, in small wind protected valleys, behind natural rock-walls etc. Associations of this type at altitudes between 3500—3600 m found by J. Hernández and the authors in "Páramo de Palacio", may contain as dominant species:

<i>Miconia summa</i>	<i>Diplostegium</i> sp.
<i>Hypericum</i> sp.	<i>Valeriana arborea</i>
<i>Vaccinium floribundum</i>	<i>Ribes</i>
<i>Aragoa</i>	<i>Berberis</i>

*Weinmannia* is practically absent.

##### *Polylepietum*

A special type of dwarf-forest is the *Polylepietum*, found often in patches at altitudes rather far above the local forest-limit. This association may sometimes be a true high forest, with trees up to 7—10 m and more. The following list of species was made by R. Jaramillo, J. Hernández and the authors of a *Polylepietum* on moraine soil at an altitude of 3400 m in "Páramo de Guantiva".



<i>Polylepis boyacensis</i> (dominant)	<i>Syphocampylus columnae</i>
<i>Hypericum mexicanum</i>	<i>Gaylussacia buxifolia</i>
<i>Hypericum</i> sp.	<i>Bidens rubifolia</i>
<i>Senecio</i>	<i>Befaria</i>
<i>Arcythophyllum</i>	<i>Bomarea</i>
<i>Clethra</i>	<i>Chusquea</i>
<i>Vallea stipularis</i>	<i>Espeletia verrositae</i>
<i>Aragoa</i>	<i>Espeletia glandulosa</i>
<i>Weinmannia</i>	<i>Niphogeton</i>
<i>Miconia</i>	<i>Halenia</i>
<i>Bucquetia</i>	<i>Cerastium</i>
<i>Berberis</i>	<i>Paepalanthus</i>
<i>Vaccinium</i>	<i>Ranunculus</i>
<i>Ilex</i>	<i>Geranium</i>
<i>Gynoxis</i>	<i>Eryngium</i>
<i>Macleanea rupestris</i>	<i>Excremis</i>
<i>Hesperomeles</i>	<i>Rubus</i>
<i>Symplocos</i>	<i>Blechnum</i>
<i>Pernetia prostrata</i>	<i>Jamesonia</i>
<i>Gaultheria</i>	<i>Elaphoglossum</i>
<i>Tibouchina</i>	

In the Sierra Nevada del Cocuy we found a Polylepietum, developed as a real forest, up to 4000 metres.

#### *Escallonietum*

In the "Ciénaga del Visitador" (Páramo de Guantiva) another type of dwarf forest, 2.5 m high, on peaty soil (marsh vegetation) was found, at an altitude of 3300 metres. The following list of species was made by R. Jaramillo, J. Hernández and the authors from this Escallonietum:

<i>Escallonia myrtilloides</i> (dominant)	<i>Niphogeton</i>
<i>Eupatorium fastigiatum</i> (codominant)	<i>Halenia</i>
<i>Senecio subruncinatus</i>	<i>Cortaderia</i>
<i>Hypericum struthoeolaefolium</i>	<i>Cyperaceae</i>
<i>Hypericum</i> sp.	<i>Geranium</i>
<i>Galium</i>	<i>Xyris</i>
<i>Paepalanthus</i>	<i>Cerastium</i>
<i>Vicia andicola</i>	<i>Lycopodium</i>
<i>Puya</i>	<i>Festuca</i>
<i>Gentiana</i> (2 spec.)	

In places with open water:

<i>Potamogeton</i>	<i>Marsilia</i>
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#### MEADOWS AND "ROSULICAULON" OF THE ANDEAN PARAMO

From 3200 or 3300 m upwards (in the Eastern Cordillera near Bogotá) large areas are occupied by associations in general characterized by the abundant occurrence of different species of *Espeletia*. In the lower part of this belt, besides the grasses, small shrubs are still abundant, like *Hypericum*,

*Gaultheria*, *Pernettya*, *Vaccinium*, *Arcytophyllum*, *Diplostegium*, etc.; but in the higher parts the grasses, specially *Calamagrostis* and *Chusquea*, soon become the dominants.

#### *Espeletietum*

Quatrecasas (1934) gives the following list of species from his *Espeletietum argenteae calamagrostiosum* from the "Páramo de Guasca" (3300—3460 m).

<i>Espeletia argentea</i>	<i>Senecio formosus</i>
<i>Espeletia grandiflora</i>	<i>Halenia asclepiadea</i>
<i>Gaultheria anastomosans</i>	<i>Bartschia pedicularioides</i>
<i>Diplostegium phyllioides</i>	<i>Alchemilla galloides</i>
<i>Hypericum laricifolium</i>	<i>Elaphoglossum caulolepis</i>
<i>Pernettya pentlandii</i>	<i>Jamesonia glutinosa</i>
<i>Arcytophyllum aristatum</i>	<i>Lupinus paniculatus</i>
<i>Gaultheria mutisiana</i>	<i>Geranium multiceps</i>
<i>Niphogeton glaucescens</i>	<i>Azorella multifida</i>
<i>Lobelia tenera</i>	<i>Paepalanthus karstenii</i>
<i>Cosmos chrysanthemifolius</i>	<i>Acaena cylindrostachya</i>
<i>Ranunculus peruvianus</i>	<i>Halenia pauana</i>
<i>Rhizocephalum candolei</i>	<i>Rhynchospora ruiziana</i>
<i>Castratella piloselloides</i>	<i>Orthosanthus ocisapunga</i>
<i>Erigeron hybridus</i>	<i>Cerastium caespitosum</i>
<i>Hypochaeris sessiliflora</i>	<i>Calamagrostis effusa</i>
<i>Eryngium humile</i>	<i>Festuca</i> sp.
<i>Paepalanthus ensifolius</i>	<i>Paspalum humboldtianum</i>

Peat bogs are very abundant in the Espeletion belt, and *Sphagnum* covers large tracts of the ground. In the higher parts of this belt in the "Páramo de Palacio", with many peat-bogs, the following plants are abundant:

<i>Calamagrostis</i>	<i>Stachys</i>
<i>Chusquea</i>	<i>Bomarea</i>
<i>Festuca</i>	<i>Lachemilla</i>
<i>Geranium</i>	<i>Ranunculus</i>
<i>Halenia</i>	<i>Paepalanthus</i>
<i>Gentiana</i>	<i>Jamesonia</i>
<i>Bartschia</i>	<i>Blechnum</i>
" <i>Valeriana</i> " <i>stenophylla</i>	<i>Elaphoglossum</i>
<i>Valeriana</i> sp.	<i>Polypodium</i>
<i>Rhizocephalum</i>	<i>Sphagnum</i>

Although no *Isoetes* was found, spores of this plant are very common in the same sites.

#### *Acaenetum*

A very curious association, with *Acaena cylindrostachya* as the dominant species is found in páramos above the Quercetum forest-limit in Boyacá (Alto de Onzaga, Páramo de Guantiva, etc.). We also found it in the Sierra Nevada del Cocuy up to an altitude of more than 4000 m, and in the Sierra Nevada de Santa Marta up to an altitude of 4300 m.

Although *A. cylindrostachya* may be present in the páramos above the upper limit of the Weinmannietum around Bogotá, the Acaenetum seems to be lacking in this region.

The Acaenetum is mostly found on rocky soil with very little humus, and in some cases seems to be related with cattle grazing and dunging. Nevertheless it presents a natural association in the majority of the cases. The following list of this Acaenetum was made on the Alto de Onzaga (department of Boyacá), at an altitude of approximately 3450 metres.

<i>Acaena cylindrostachya</i> (dominant)	<i>Geranium</i>
<i>Acaena elongata</i>	<i>Miconia</i>
<i>Orthosanthus chimboracensis</i>	<i>Senecio</i>
<i>Arcythophyllum nitidum</i>	<i>Clethra</i>
<i>Hypericum mexicanum</i>	<i>Gaultheria</i>
<i>Excremis coartata</i>	<i>Weinmannia</i> (dwarf-form)
<i>Paepalanthus</i>	<i>Pernettya</i>
<i>Espeletia</i>	<i>Hypericum</i>
<i>Carex</i>	<i>Lycopodium</i>
<i>Lachemilla</i>	<i>Festuca</i>
( <i>Castilleja</i> )	<i>Calamagrostis</i>
( <i>Befaria</i> )	<i>Jamesonia</i>

Sometimes *Espeletia* may become more abundant, without changing the specific composition, and in that case the association could be called an Espeletietum acaenosum. But in general the Espeletias are scarce, or completely lacking.

Exact meteorological data are not available for the altitudes higher than 3300 metres in the Eastern Cordillera. Espinosa (quoted in Cuatrecasas 1934) indicates for Ecuador average monthly temperatures which oscillate between 6.5° C (3600 m) and 2.9° C (4450 m); absolute mínima of 1.5° C (3600 m) and absolute máxima of 16° C (3600 m); daily oscillation of 15° C. In Cotopaxi the annual precipitation is, according to the same author, 1071 mm, with 234 rain days. The relative humidity varies between 80 and 90.

We made in April 1958 during 8 days the observation in "Páramo de Palacio", at an altitude of 3650 m, of 4° C at 8.°° P.M. and the same temperature at 7.°° A.M. 6.5° C average temperature at 3600 m (in Ecuador) closely corresponds with our altitude-temperature relation for Cundinamarca (fig. 3) but 2.9° at 4450 m seems to be too high a temperature for our region.

## 5. TREE-LINE AND SNOW-LINE

Under tree-line (or "altitudinal forest limit") we will understand here the upper, principally closed, limit of the  $\pm$  3—5 metres or more high uppermost zone of the forest and dwarf forest belt. For this limit are not taken into account higher isolated stations of forest or dwarf forest in small wind protected valleys etc. The tree-line in the surroundings of the Sabana de Bogotá lies at 3200—3300 metres. In Páramo de Palacio (in the Eastern Cordillera, east of the Sabana de Bogotá) it lies at  $\pm$  3250 metres. On the western slopes of the Sierra Nevada de Cocuy (dry!) the tree-line was found at approximately 3300 metres, but on the eastern flanks (wet!) at 3500 metres or more. On the Alto de Onzaga (with an apparently high annual precipitation and frequently clouded), the forest-limit lies at 3500—3600 metres (Quercetum!).

In the Central Cordillera on places with a more humid climate, the tree-line lies at 3800 metres (Nevado del Tolima; Cuatrecasas, 1934). On the slopes of the Nevado del Huila, where it rains all the year round, without a pronounced dry season, the tree-line lies even at 3900 metres (Erwin Kraus, personal communication); and there are indications that forest may even occur up to 4000 metres. Small patches of dwarf forest may still be found several hundreds of metres higher up.

From the data mentioned above it will be clear that the tree-line depends principally on two factors:

- 1° Temperature (altitude)
- 2° Humidity (amount of annual precipitation and its distribution during the year; "greenhouse-effect" of a continuous overcast).

Another factor is wind, but it has only local importance, as this factor is of almost equal effect in all more extensive páramo regions (forest or dwarf forest in wind-protected valleys far above the tree-line; lack of forest vegetation on windswept tops below the forest-limit).

One could express it in the following way:

The highest tree-line in the Colombian Andes lies at 3900(—3800) metres, and the lowest at 3200(—3000) metres (desert or semi-desert conditions are not taken into account). Local differences in altitude of the tree-line, between those two values, depend on annual precipitation and distribution of this precipitation during the year. If the annual precipitation reaches maximum values and there is no marked dry season, the tree-line reaches its highest limit (3800—3900 m). Where the annual precipitation is low and there are one or two pronounced dry seasons, the tree-line is reduced to its lowest level (3200—3000 m).

These variations may be due to the fact that areas having a higher annual precipitation and no marked dry season, show higher average annual temperatures. In such places the predominance of overcast skies prevents heat losses by ground radiation ("greenhouse effect") which more than compensates the lower insolation.

In those regions of the country where certain species of *Quercus* are present (*Quercus* is a relatively young immigrant and apparently has not reached its maximum area), the difference between the 1° and 2° conditions may be indicated by different forest types. In the first case (cloud-forest!) a Quercetum (or a related association) is present, and in the second case a Weinmannietum (or related association).

We will take the maximum altitude of the cloud forest (Quercetum or related associations) at 3800 (to 3900 metres, and the minimum altitude of the relatively dry forest (Weinmannietum etc.) in the "Sabana de Bogotá" (actual conditions) at 3200 m ( $\pm$  800(700—900) mm annual precipitation and two pronounced dry stations).

The combination of a major quantity of annual precipitation, the absence of one or two pronounced dry seasons and of a more continuous low overcast, will be indicated here and in the following, with the term "humidity" or "humid climate". The contrary will be indicated with the term "relative dryness" or "dry climate".

Several species of the humid forest are characterized by a greater leaf-surface ("esclero meso-microfilas") and several species of the relatively dry forest by a smaller leaf surface ("esclero micro-nanofilas").

The snow-line in the Eastern Cordillera lies at 4500 m or higher. Erwin Kraus (personal communication) measured 4520 metres on several occasions on the west flank of the Nevado del Cocuy (Laguna de la Sierra), without any change between 1938 and 1943. On other places in the same Nevado he found different values and a general retiring of the snow-line (and glaciers). We give his observations here in tabular form. All the observations were made on the West flank of the Nevado del Cocuy.

	1938	1942	1943	1946	1948
Laguna de la Sierra	4520	4520	4520	4550	4600
Pan de Azúcar	4500	4650		4740	4720
Ritacuva		4690			
Cerros de la Plaza			4640	4780	
Pico del Castillo			4600	4650	
Northern area				4660	

The following additional measurements were made by the authors in 1959

Cerros de la Plaza	4425 m, 4390 m and 4325 m
Pan de Azúcar	4325 m

The retirement of the snow-line between 1938 and 1948 is probably an effect of a minor climatic fluctuation which cannot have exercised in the course of a few decades any important influence on the position of the tree-line. We therefore took the average of all the data obtained by Kraus in the Sierra Nevada del Cocuy between 1938 and 1948 and by us in 1959. This average is 4570 metres. The theoretical altitude given by the line representing the relation of altitude and average temperature (fig. 3) for 0° C, is approximately 4550 metres. Moreover we know that the Nevado del Sumapaz (in the extreme SE of Cundinamarca), which lost its snow-cap some decades ago, has an altitude of 4560 metres. If we take into account all these data, we may conclude that a theoretical snow-line at 4550 metres for the central part of Cundinamarca (Sabana de Bogotá and surroundings) seems to be a most trustworthy figure.

In the region of the Nevados of the Central Cordillera, where the tree-line lies at 3800 (or even at 3900) metres, the snow-limit may lie considerably lower.

Mr. Erwin Kraus provided us with the following observations:

In 1943 the snow-line on the Nevado del Tolima was found on the NE flank at 4200 m, on the SW flank at 4150 m and on the W flank 4150 m. (Quatrecasas mentions approximately 4500 m on the E flank in 1934).

In 1943 the snow-line on the Nevado de Santa Isabel was found on the W flank at 4200 m and in the same year on the W flank of the Nevado del Ruíz at 4200.

In 1940 the snow-line on the W flank of the Nevado del Huila (tree-line at 3900!) was found at 4100 metres, and in 1944 also at 4100 m.

The average of these figures for the West-flank of the Central group of Nevados of the Cordillera Central is 4150 metres. The average for the East flank (based on two observations only made in 1934 and 1943 on the Nevado del Tolima) is 4350 m; the tree-line on this flank lies according to Quatrecasas at 3800 m.

It is interesting that this last mentioned figure corresponds very closely with the Espeletia-limit on the Nevado del Tolima, given by Quatrecasas (1934), at 4320 m. It seems probable to us that the snow-line continuously retires and advances, and may be dependent on small-range solar cycles. The average

extension of the eternal snow would then coincide in certain regions with the upper Espeletia-limit, visible during the years of minimal extension.

From the above we may now draw the following conclusions.

By the influence of greater or lesser "humidity", the snow-line fluctuates between approximately 4550 metres (in the surroundings of the "Sabana de Bogotá") and 4150 metres (central group of Nevados of the Central Cordillera, West flank). As the tree-line depends on the same influence, we may say that a tree-line of 3200 metres corresponds to a snow-line of 4550 metres, and a tree-line of 3900 metres to a snow-line of 4150 metres.

The theoretically highest forest-limit would correspond to the line, where, with a still greater humidity, forest-limit and snow-line meet. This theoretical line may lay at approximately 4000 metres.

## 6. RECENT POLLEN-DEPOSITION

The recent deposition of atmospheric pollen in the Sabana de Bogotá and surroundings, is treated by Van der Hammen & Perico (1960). Recent pollen was caught on glass slides with glycerine jelly, exposed one or two weeks each and during a whole year at six different stations. Summing the total pollen deposition of one year in each of these stations and calculating the percentages in the same way as done for the fossil spectra of the diagram, general pollen-spectra were obtained. These pollen-spectra are almost all rather heavily influenced by the extense meadows of human origin of the Sabana de Bogotá, or in general, by the destruction of the forest by man. For that reason the percentage of Gramineae is in general much higher than would correspond to the same site with a natural, not destroyed, vegetation.

The most interesting spectrum, and the less influenced by human action is the one of a station at 3450 metres altitude in the "Páramo del Alto de la Viga", east of Bogotá. It shows the following percents:

Gramineae		51.5 %
<i>Alnus</i>	3.6 %	
<i>Podocarpus</i>	0.4 %	
<i>Miconia</i>	4.3 %	
<i>Bocconia</i>	0.6 %	
<i>Hedyosmum</i>	23.5 %	
<i>Weinmannia</i>	0.1 %	
<i>Myrica</i>	9.9 %	
Urticaceae	5.7 %	
<i>Drimys</i>	0.2 %	
<i>Rapanea</i>	0.2 %	
<hr/>		
Total of forest plants		48.5 %
<hr/>		
Total		100 %

The most interesting results of this spectrum are the almost 50 % of pollen of forest-plants, including a percentage of *Hedyosmum* as high as 23.5 %, at a site approximately 250 metres above the closed tree-line in an extense páramo-area. As we will see below, almost identical spectra are to be found in the Pleistocene part of the pollen diagram.

Another very interesting fact is shown by the spectrum from the station in the Alnetum near Subachoque. Although the station was placed in the centre of the forest, completely surrounded by the highly pollen producing *Alnus* trees, the influence of the culture meadows which surround this patch of forest is clearly visible in the 38 % of the Gramineae.

Even greater is this influence in the pollen spectrum from the forest near Suba, with almost 80 % of Gramineae. The dominating trees of this forest, with an evidently very low pollen production (*Ilex*, *Vallea*, *Eugenia*) are represented only by a few percent. *Alnus*, hardly present in the vegetation, is represented by almost 10 %.

In the midst of the culture meadows, in the pollen station of the "Ciudad Universitaria", the Gramineae show 80 %, culture trees (*Acacia*, *Eucalyptus*) 8 %, and trees from the natural vegetation (only to be found in the hills which surround the Sabana, the nearest at 3.5 km distance) 12 %.

A rather high percent of *Weinmannia* (16 %) was only found in the station near La Cita, at an altitude of 2880 metres, surrounded by partly destroyed Weinmannietum. Apparently the small pollengrains of this common tree are not transported very far by the wind. Culture influence is apparently still rather strong at this site (56 % of Gramineae), and so it is at another pollen station (in a patch of forest in a partially culture landscape at 3330 metres near the "Páramo del Alto de la Viga", which showed 78 % of Gramineae.

Several of the conclusions drawn from these recent pollen spectra will be used below for the interpretation of the diagram.

## 7. THE BORING, THE CORES AND THE SEDIMENTS

In the beginning of 1957 the first part of the boring was carried out with a small mining equipment. The exact site is indicated in fig. 1; the elevation is approximately 2560 metres above sea-level. Cores with a diameter of 1 inch were taken continuously, and drawn up every 1 to 1.5 metre approximately. Coring was done dry, without the use of water or mud. In this way a complete section was recovered, from a depth of 2.5 metres down to a depth of 32.2 metres. From 30 metres down to 212 metres a second boring was carried out, at a few metres distance from the first hole, with a "Portadrill" equipment, and coring continuously with a core-barrel of 2 inches inner diameter.

In order to collect from the uppermost 2.5 metres, and moreover obtain material for C14 analysis, a hole was excavated at the boring-site, 2 × 2 metres wide, and 4 metres deep. Besides a continuous series of samples for pollen analysis, four C14 samples were collected, of which the uppermost three consisted of charcoal.

There was no loss of cores, but the cores were compressed, in the core-barrel, during the time of coring, to more or less half of their original length.

For each core the exact amount of compression was measured, in order to know the real interval of the samples for pollen-analysis taken from these cores.

The real sample interval used (see pollen diagram) was 7.5 or 15 cm in the uppermost 2.3 metres, 10 cm (or in some cases a little less) from 2.3 to 5.5 metres, and 15 cm from 5.5 to 32.2 metres.

Only the uppermost 32.2 metres (first boring; C. U. X.) have yet been

analysed, and the diagram corresponds to that part. The diagram of the continuation of this section (second boring; C. U. Y.) will be analysed and published later.

We will now give a short description of the sedimentary succession of boring C. U. X. (see the stratigraphical column of the pollen-diagram).

The top 0.20 m is a layer of a very recent man-made fill of sand and brick. Below this the uppermost natural sediments consist of a rather dark grey clay with reddish brown veins, until a depth of 0.85 m. At this level a rather sharp contact is present with the under-lying layer. This consists of grey yellowish clay, with yellowish brown veins, and extends from 0.85—2.35 m; charcoal particles occur especially from 1.65—2.00 m.

From 2.35—2.65 m depth a humic gray clay with charcoal particles is present. Then from 2.65 to 3.05 m a yellowish grey clay, and from 3.00—3.45 m a strongly humic blackish clay.

The sediments mentioned above contain abundant pollen, but algae like *Botryococcus* and *Pediastrum*, which form an important part of the sediments below a depth of 3.45 m, were only found occasionally.

The explanation is, that the Sabana lake dried up at the moment represented by the 3.45 m horizon. But sedimentation went on by means of intermittent inundations during the wet seasons (which still occur to-day in certain parts of the Sabana. We will call these clays "inundation-clays".

From 3.45 to 22.25 m a continuous series of lake-sediments is present. These sediments are mainly lake-clays (or clay-gyttjas) with a rather high content of algae (especially *Botryococcus* and *Pediastrum*), fine plant-detritus and pollen; diatoms are present at various depths (5.70, 12.90, 18.45, 18.75, 19.05 and 19.65 m).

From 22.25—24.00 m a peat layer is present. This peat contains a little clay; algae are absent.

From 24.00—29.00 m a continuous series of lake-clays (or clay-gyttjas) is present again, of the same type as those present above the peat layer. Diatoms were found at 24.85, 28.30, 28.60 and 29.00 m.

From 29.00 to 31.00 m a black humic layer is present, partly peaty, and with a clay content much higher than the peat layer at 24.00 m. A few algae were found in some samples, and from 30.50—30.85 m a small layer of diatomite is intercalated; this diatomite contains also volcanic ash.

From 31.00 m downwards to the deepest point of boring C. U. X. (32.20 m) a layer of fine grained clayey sand is present; while the uppermost 0.60 m of this layer do not contain algae nor *Isoetes* spores, the rest contains some algae and an increasing percentage of *Isoetes*. So we have to conclude that the main part of the fine-sand layer is a lake-deposit.

## 8. DESCRIPTION OF THE SPECIES

As many of the species mentioned in the diagram represent first records as fossil pollen grains, we will describe them here shortly, and give a photograph of each. In addition, a few details will be given about the aspect, the habitat and ecological conditions of the species, genus or family.

### *Quercus* (Pl. I, 1—7)

Pl. I, 1: C. U. X., No. 183; Pl. I, 2: C. U. X., No. 183; Pl. I, 3: C. U. X., No. 37; Pl. I, 4: C. U. X., No. 37; Pl. I, 5: C. U. X., No. 179b; Pl. I, 6: C. U. X., No. 179b; Pl. I, 7: C. U. X., No. A-150.



Tricolporate, scabrate (inord.).  $\pm$  28—48 micron. Different types may be distinguished, but the specific determination is difficult. Pl. I, 1: corresponds to the type of *Quercus lindenii* A. D. C.

Dominant in the Quercetum, often representing cloud-forest.

*Podocarpus* (Pl. I, 8—9)

Pl. I, 8: C. U. X., No. 184-A; Pl. I, 9: C. U. X., No. 159.

Vesiculate,  $\pm$  55—82 micron. Different types may be distinguished, but the specific determination was impossible. There is one relatively small type (55—70 micron; Pl. I, 8) and another relatively large ( $\pm$  82 micron; Pl. I, 9). The large type is the dominant in the samples C. U. X., No. 146—153 and the small type is in general the more common in the other samples.

*Podocarpus oleifolius* D. Don (with pollen grains of the small type), is an element of the Quercetum in Boyacá, up to at least 3500 metres. Other species are found in different associations.

*Hedyosmum* (Pl. II, 10—12)

Pl. II, 10: C. U. X., No. 88; Pl. II, 11: C. U. X., No. 88; Pl. II, 12: C. U. X., No. 87.

Inaperturate (?), Clavate.  $\pm$  30—48 micron. (Some small irregular grooves in one area of the pollengrain).

*Hedyosmum bonplandianum* H. B. K. is a woody climber of the Quercetum in Boyacá; but *Hedyosmum* is equally found in the Weinmannietum and in associations of the temperate and tropical belts. The pollen production is very great (anemophilous).

*Myrica* (Pl. II, 13—14)

Pl. II, 13: C. U. X., No. 184-A; Pl. II, 14: C. U. X., No. 184-A.

Triporate, psilate,  $\pm$  25—40 micron; pores with annulus; "granulate" zone around the pores.

There are two important species, *M. parviflora* and *M. pubescens*. We tried to differentiate the two species by means of size-statistics, but without success.

Trees or shrubs, common both in the Quercetum and the Weinmannietum and related associations.

*Styloceras* (Pl. II, 15—16)

Pl. II, 15: C. U. X., No. 150; Pl. II, 16: C. U. X., No. 179b.

Periporate, reticulate,  $\pm$  40—50 micron. The muri are one or two granula wide. Number of pores  $\pm$  12—25.

*Styloceras laurifolium* (Willd.) H. B. K. is a tree of the andean forest in general.

*Bocconia* (Pl. II, 17)

Pl. II, 17: PV 4a II.

Periporate, reticulate,  $\pm$  30—40 micron. Number of pores  $\pm$  6. *Bocconia frutescens* L. is a very common tree or shrub of the andean forest in general.

*Juglans* (Pl. III, 18—20)

Pl. III, 18: C. U. X., No. 201; Pl. III, 19: C. U. X., No. 201; Pl. III, 20: PV 9a II.

Periporate (heteropolar), psilate,  $\pm$  35—55 micron. Pores on the equator

(like a stephanoporate grain) and on one of the hemispheres. There are several species of *Juglans*, trees, which are apparently not very common in the andean forest.

*Weinmannia* (Pl. III, 21)

Pl. III, 21: C. U. X., No. 177.

Tricolporate, micro (intra ?) reticulate, 11—15 micron.

*Weinmannia tomentosa* L. f. is a very common tree of the Weinmannietum and related associations of the Eastern Cordillera. Several species are also found in the Quercetum. Certain species may be found even considerably above the "tree-line".

*Rapanea* (Pl. III, 22—23)

Pl. III, 22: C. U. X., No. 124; Pl. III, 23: C. U. X., No. 132.

Stephanocolpate (4 furrows), psilate,  $\pm 25$ —30 micron. Polar area large. (Sometimes tricolpate).

Several species, which are trees or shrubs, are frequent in the andean forest.

*Symplocos* (Pl. III, 24)

Pl. III, 24: C. U. X., No. 142.

Tricolporate, foveolate (-psilate),  $\pm 40$ —45 micron. Furrows very short (in polar view the grains seem to be triporate). Small transversal furrows, not always visible.

Shrubs or small trees of the andean forest.

*Drimys* (Pl. III, 25; Pl. IV, 26)

Pl. III, 25: C. U. X., No. 132; Pl. IV, 26: C. U. X., No. 70.

Tetrads, reticulate  $\pm 45$ —50 micron. The separate grains are monoporate.

*Drimys granatensis* L. f., a relatively common tree, especially in the higher zone of the andean forest.

*Ilex* (Pl. IV, 27—31)

Pl. IV, 27: C. U. X., No. 183; Pl. IV, 28: C. U. X., No. A-154; Pl. IV, 29: C. U. X., No. A-154; Pl. IV, 30: C. U. X., No. 184-A; Pl. IV, 31: C. U. X., No. 184-A.

Tricolpate, clavate,  $\pm 30$ —40 micron. The species are difficult to differentiate on base of the pollen. Pl. IV, 28 is the type of *Ilex kunthiana*. Trees and shrubs of the andean forest. Certain species may be found considerably higher than the "tree-line".

*Miconia* (Pl. IV, 32—33)

Pl. IV, 32: C. U. X., No. 183; Pl. IV, 33: C. U. X., No. 183.

Heterocolpate, psilate,  $\pm 13$ —19 micron.

There are many species in the andean forest (and also in the tropical belt), which cannot be differentiated on the basis of their pollen. Several species grow even considerably above the "tree-line". Morphologically it is not possible to differentiate the pollen grains of the genus *Miconia* from the majority of the other Melastomataceae. We differentiated them on the basis of their size: all the species of *Miconia* from our region we know, are less than 19 micron in diameter (in general between 13 and 17 micron), while the other Melastomataceae of our region are more than 19 micron.

## Urticaceae (Pl. IV, 34—36; Pl. XIV, 117)

Pl. IV, 34: C. U. X., No. 184 A; Pl. IV, 35: C. U. X., No. 184-A; Pl. IV, 36: C. U. X., No. 50; Pl. XIV, 117: C. U. X., No. 183.

Triporate or diporate, psilate or scabrate,  $\pm$  12—25 micron. *Pilea* is diporate-scabrate (Pl. IV, 36). The stephanoporate type (Pl. XIV, 117) is also found.

Several genera (amongst others *Phenax* and *Pilea*) are herbaceous or shrubby, common in the zone of the Andean forest (and lower).

*Alnus* (Pl. IV, 37—39)

Pl. IV, 37: C. U. X., No. 154; Pl. IV, 38: C. U. X., No. 154; Pl. IV, 39: C. U. Y., No. inferior.

Stephanoporate, psilate,  $\pm$  25—35 micron. Arcs from pore to pore.

*Alnus jorullensis* is the dominant species of the Alnetum, and is moreover found in the entire belt of the andean forest, both in the Weinmannietum and in the Quercetum. We observed this species up till 3500 metres in the Sierra Nevada del Cocuy. The species is a great pollen-producer (anemophilous).

*Gramineae* (Pl. V, 40)

Pl. V, 40: C. U. X., No. 37.

Monoporate, psilate (-scabrate), 20—90 micron. Pore with a clear annulus. The pollengrains of the common páramo grasses, like *Calamagrostis*, *Festuca*, etc., are smaller than 45 micron. The pollen-grains of the genus *Chusquea*, common in the Páramo, the higher zone of the Weinmannietum and the transitional zone, have sizes between 44 and 55 micron. Moreover some rather large pollengrains ( $\pm$  80 micron) were found in some of the Würm-glacial samples of the section C. U. X., which possibly are of Maize. If this is right, then it would be the proof of the existence of primitive races of Maize in Colombia, before the arrival of agriculture.

*Acaena* (Pl. V, 41—43)

Pl. V, 41: C. U. X., No. 179b; Pl. V, 42: C. U. X., No. 179b; Pl. V, 43: C. U. X., No. 179b.

Tricolpate; scabrate,  $\pm$  psilate or irregular ( $\pm$  rugulate-verrucate);  $\pm$  30—45 micron. Pores with protuberant operculum. Furrows very short with transversal furrows.

*Acaena cylindrostachya* (a herb) and *Acaena elongata* (a dwarf-shrub), are locally common in the paramo belt. Although it is difficult to separate the two species always with certainty on the basis of their pollen, it has to be noted that the majority of the grains found, belong to *A. cylindrostachya*. The pollen grains of *Polylepis*, a tree found in isolated patches of forest at great altitude (up till 4000 metres in the Sierra Nevada del Cocuy), are very similar, but are larger and have a somewhat different sculpture. We found *Acaena cylindrostachya* up to an altitude of  $\pm$  4300 m in the Sierra Nevada de Santa Marta, and *Acaena elongata* up to an altitude of  $\pm$  3850 m.

## Melastomataceae (Pl. V, 44—45)

Pl. V, 44: C. U. X., No. 183; Pl. V, 45: C. U. X., No. 183.

Heterocolpate, in general psilate,  $\pm$  19—30 micron. (*Miconia* is smaller, see above).

The Melastomataceae are shrubs or trees, very common in the Andean

forest (and also in the tropical belt). Several species grow considerably higher than the proper forest-limit. There is also a little herb, *Castratella*, common in the high paramo. For that reason we did not include the Melastomataceae in the forest. Only the genus *Miconia* could be included (differentiation on the basis of size, see above).

*Aragoa* (Pl. V, 46)

Pl. V, 46: C. U. X., No. 178b.

Tricolpate; sculpture very typical; perforations, connected one with another by "channels", which leave radially from each one of the perforations. Size of the pollengrains variable,  $\pm 40$  micron.

The species of *Aragoa* are shrubs of the open paramo, up to altitudes of at least 4000 m. They also grow in the upper transitional zone of the andean forest, and in isolated patches of forest in the open paramo.

Ericaceae (Pl. V, 47—49)

Pl. V, 47: C. U. X., No. 183; Pl. V, 48: C. U. X., No. 183; Pl. V, 49: C. U. X., No. 183.

Tetrads; psilate, foveolate-fossulate;  $\pm 30$ —45 micron.

Numerous genera and species, trees, shrubs and dwarf-shrubs, in the andean forest and in the paramo. They are specially common in the upper transitional zone of the forest.

*Geranium* (Pl. VI, 50—52)

Pl. VI, 50: C. U. X., No. 21; Pl. VI, 51: C. U. X., No. 32; Pl. VI, 52: C. U. X., No. 21.

Tricolpate; clavate-reticulate;  $\pm 60$ —85 micron. Furrows short and more or less irregular, sometimes resembling pores. Clavae sometimes joining to form a reticulum more or less complete. There are several species, all herbaceous and principally of the open paramo. Sometimes also in marshy zones of the forest belt.

*Valeriana* (Pl. VII, 53—54)

Pl. VII, 53: C. U. X., No. 88; Pl. VII, 54: C. U. X., No. 86.

Tricolpate; (micro-) echinate;  $\pm 40$  micron. It is possible to distinguish various groups of species, on the basis of the size of the pollen-grains and the size of the columellae and spines. In the diagram all were taken together.

They are herbs of the open paramo. There is only one shrub or tree (*Valeriana arborea*), which grows in isolated patches of dwarf-forest above the proper forest-limit, but the pollen of this species is easily determinable, and grains of this species were not found in the section C. U. X.

*Polygonum* (Pl. VII, 55—56)

Pl. VII, 55: C. U. X., No. 88; Pl. VII, 56: C. U. X., No. 141.

Periporate, reticulate,  $\pm 50$ —65 micron. The pores in lumina of the reticulum; tectate. These grains are of the *Persicaria*-type.

There are several species of *Polygonum* of the *Persicaria*-type of pollen in our region. All are herbaceous, and they grow in the paramo and in the forest belt.

## Caryophyllaceae (Pl. VII, 57—58)

Pl. VII, 57: C. U. X., No. 184-A; Pl. VII, 58: C. U. X., No. 37.

Periporate,  $\pm$  psilate,  $\pm$  15—40 micron. Columellae relatively large. It may be possible to make generic determinations, but we did not attempt to do so.

The Caryophyllaceae are herbaceous plants of the paramo and the forest-belt.

*Gentiana* (Pl. VIII, 59—61)

Pl. VIII, 59: C. U. X., No. PV 9a II; Pl. VIII, 60: C. U. X., No. PV 9a II; Pl. VIII, 61: C. U. X., No. 142.

Tricolporate, psilate or striate,  $\pm$  40—50 micron. Columellae large. *Gentiana corymbosa* is one of the striate species. Specific determination is in some cases possible.

The Gentianas are herbs, of different sizes, of the open paramo.

*Plantago* (Pl. VIII, 62—63)

Pl. VIII, 62: C. U. X., No. A-159; Pl. VIII, 63: C. U. X., No. 124.

Periporate, verrucate,  $\pm$  25—35 micron. The pores are not very well delimited. Two different types are found, one with very clear and high warts, and another with not very clear and lower warts. The specific determination could not be realized with certainty. There are various types of *Plantago* in our area, partly herbaceous and partly somewhat woody. They are locally very abundant in the open paramo. Some may be found in the forest belt, where the forest has been destroyed by man.

*Jussiaea* (Pl. IX, 64)

Pl. IX, 64: C. U. X., No. 183.

Triplicate; psilate, or  $\pm$  undulated ( $\pm$  verrucate) and irregularly foveolate;  $\pm$  60—110 micron. Pores more or less of the *Oenothera* type, but less prominent and less protuberant.

Plants frequently of humid soil or marsh, at different altitudes.

*Gaiadendron* (Pl. IX, 65)

Pl. IX, 65: C. U. X., No. 154.

Syncolporate, psilate, scabrate,  $\pm$  20—24 micron. Shape triangular with strongly concave sides. Furrows joined at the poles, without a triangular area. Plant of the andean forest.

*Eugenia* (Pl. IX, 66)

Pl. IX, 66: C. U. X., No. 32.

Syncolporate, psilate, micro-verrucate,  $\pm$  20—40 micron. Shape more or less triangular. Furrows joined at the poles, in a triangular area.

Trees of the andean forest. Subdominant of the "Ilieto Valleatum Eugenetoso".

## Myrtaceae (Pl. IX, 67)

Pl. IX, 67: C. U. X. No. 32.

Syncolpate, psilate scabrate,  $\pm$  25 micron. The pollen grain of the photograph may be an *Eugenia* or another Myrtaceae. These grains were joined with those of *Eugenia* (which form the majority) in one curve for the Myrtaceae.

## Monocotyledoneae (Pl. IX, 68—69)

Pl. IX, 68: C. U. X., No. 37; Pl. IX, 69: C. U. X., No. 32.

Monocolpate, reticulate,  $\pm$  30—55 micron. Muri composed of joined or separated granules. There are different types, but the majority of the grains included in the curve are of the type of Pl. IX, 68.

These grains correspond probably to herbs of the paramo, but it has not been possible to determine the genera.

## Cyperaceae (Pl. IX, 70—71)

Pl. IX, 70: Secc. L. H. C.; Pl. IX, 71: Secc. L. H. C.

Monoporate (-periporate), psilate (-scabrate). Size variable. Pore-limits irregular.

Very frequent herbs of the paramo and in marshes, but there are also species in the andean forest, etc.

## Compositae (Tubuliflorae) (Pl. IX, 72—74)

Pl. IX, 72: Secc. L. H. C.; Pl. IX, 73: Secc. L. H. C.; Pl. IX, 74: C. U. X. No. 171c.

Tricolpate, echinate,  $\pm$  25—45 micron. Frequently with transversal furrows. Spines long (photo 72 and 74) or short (photo 73). Generic determination could not be carried out.

Herbs, shrubs and trees, very common at all altitudes.

## Compositae (Liguliflorae) (Pl. XIV, 116)

Pl. XIV, 116: Secc. L. H. C.

Fenestrate, echinate,  $\pm$  40—50 micron. Generic determination has not been possible. These pollen grains are very rare.

## Umbelliferae (Pl. X, 75—76)

Pl. X, 75: C. U. X., No. 183; Pl. X, 76: C. U. X., No. 154.

Tricolpate, psilate, micro-reticulate. Size variable. Shape elongated.

In general herbs, frequent in the paramo, but also several species in the forest-belt.

*Hydrocotyle*-type (Umbelliferae) (Pl. XIV, 115)

Pl. XIV, 115: C. U. X., No. A-159.

Tricolpate,  $\pm$  reticulate,  $\pm$  25—35 micron. Small transversal furrows. Exine clearly thicker in the polar areas, with well defined columellae.

This type corresponds to *Hydrocotyle*, herbs of marshy areas or humid soil in the andean forest belt (and lower).

*Rumex* (Pl. X, 77—79)

Pl. X, 77: C. U. X., No. 150; Pl. X, 78: C. U. X., No. 150; Pl. X, 79: C. U. X., No. 183.

Tricolpate (or pericolpate); more or less clear finely reticulate;  $\pm$  30—40 micron. Sometimes a specific determination is possible: *Rumex tolimensis* (photo 79). Probably the majority of the grains of *Rumex* found, belong to this species of giant herb of the high paramo.

*Borreria* (Pl. X, 80—81)

Pl. X, 80: C. U. X., No. 183; Pl. X, 81: C. U. X., No. 37.

Stephanocolpate, reticulate,  $\pm$  45 micron. Furrows very short, number approximately 8. Reticulum composed of big separated granules.

Herbs of the andean forest belt (and lower).

*Borreria anthospermoides* to which correspond the grains found, is a species frequent in the Alnetum of the Sabana de Bogotá.

## Coniferae — type A and B (Pl. X, 82—83)

Pl. X, 82: C. U. X., No. 15; Pl. X, 83: C. U. X., No. A-159.

Grains more or less inaperturate, micro-granulate. Type A: size very variable, the specimen of photo 82 is of 75 micron. Type B: more or less 45 micron (but also variable).

These types are very similar to certain species of *Juniperus*, but might also belong to other genera of the Coniferae (*Araucaria* ?) etc. The correct determination has not been possible for the lack of sufficient material for comparison.

This type of conifers does not exist actually in Colombia (the only native Coniferae genus is *Podocarpus*; *Juniperus* is found in North America, and apparently also in Central America. Other conifers of this type occur in the flora of Chile and Patagonia.

We hope to be able to determine the genus of these types of Coniferae when we obtain sufficient material for comparison. At any rate they represent elements which existed until in the Upper Pleistocene in Colombia, but extinguished here when the Holocene began.

*Ranunculus* (Pl. XI, 84—85)

Pl. XI, 84: C. U. X., No. 201; Pl. XI, 85: C. U. X., No. 200.

Syncolpate ( $\pm$  spirals etc.), scabrate—micro echinate,  $\pm$  25—35 micron. Exine relatively thick, columellae clearly visible (in *Paepalanthus* the exine is very thin). The majority of the grains correspond to *R. peruvianus*, a frequent herb of the high paramo.

Chenopodiaceae — *Amaranthus*-type (Pl. XI, 86)

Pl. XI, 86: C. U. X., No. A-187.

Periporate, psilate, 30—35 micron. Number of pores more than 50. Columellae clearly visible, but not so well defined as in the Caryophyllaceae. These pollengrains may be of Chenopodiaceae or of the *Amaranthus*-type of the Amaranthaceae, but seem to correspond better to *Amaranthus*.

*Panopsis* (Pl. XI, 87—88)

Pl. XI, 87: C. U. X., No. 157; Pl. XI, 88: C. U. X., No. A-176.

Triporate, scabrate and foveolate,  $\pm$  25—30 micron. Shape  $\pm$  triangular. Trees of the andean forest.

*"Valeriana" stenophylla* (Pl. XI, 89—91)

Pl. XI, 89: C. U. X., No. 34; Pl. XI, 90: C. U. X., No. 10; Pl. XI, 91: C. U. X., No. 32.

Stephanocolp(or)ate, striate (and reticulate);  $\pm$  45 micron. There are always 6 furrows, which are placed in pairs (the two furrows of each pair are nearer to each other than to the other furrows) (it may therefore appear that the grains are tricolp(or)ate operculate).

Small herb of the high paramo.

We found these very typical pollen grains in the sediments of the Sabana de Bogotá (and in several paramo-lakes of the Eastern Cordillera), before we knew the plant. Later we found the plant in the Páramo de Palacio, but it was not possible to determine it in Colombia, as no comparable material was present in the National Herbarium. Dr. A. Fernández was so kind to determine it in the U. S. A., where he found identical material described by Killip (Journ. Wash. Acad. Sc. 18; 1928) as *Valeriana stenophylla*. While there is no doubt that the plant has been described as *Valeriana stenophylla*, we like to express our doubt that the classification in the genus *Valeriana* or even in the same family is correct for the reasons given below.

The pollen-grains of the genus *Valeriana*, including also other genera of the Valerianaceae, like *Phyllactis*, are all very similar tricolpate, (micro-) echinate, and completely different from the type of "*Valeriana*" *stenophylla*. For this reason it seems to be impossible to us that this species has some near relationship with the genus *Valeriana* or *Phyllactis*. The pollen-type of "*Valeriana*" *stenophylla* seems to be more related to that of *Rhizocephalum* (Campanulaceae), although there are important differences.

#### Malvaceae (Pl. XII, 92—93)

Pl. XII, 92: C. U. X., No. 166; Pl. XII, 93: C. U. X., No. 166.

Periporate, echinate,  $\pm$  50—75 micron.

The pollen grains of Malvaceae found are all of one type, and are especially frequent in the Riss-glacial part of the section.

In the Sierra Nevada del Cocuy we found, from 3800 m upward (observed until 4200 m, but probably they grow still higher), with a maximum development and frequency at 4000 m, small Malvaceae which were determined as *Malvastrum acaule* (Cav.) Gray. The type of pollen of this plant corresponds exactly to the fossil grains.

The high percentage found in sample 210 (Riss-glacial), which would in that case correspond to an altitude of 4000 m under present-day conditions, indicates that the vegetation-zones were some 1400 m lower than today. This corresponds very well to the value that derived from the curves of fig. 5 which show that the tree-line was 1300 m lower. Thus we have a good proof of the accuracy of these curves, and especially for the minimum temperature during the Riss-glacial.

#### *Tricolporites* "type C" (Pl. XII, 94)

Pl. XII, 94: C. U. X., No. 72-A.

Tricolp(or)ate, micro-echinate, (-scabrate),  $\pm$  15—20 micron. Furrows sometimes hardly visible. Pores perfectly round and with a very thin annulus. Thickness of the exine  $\pm$  1—1.3 micron. The small spines are in general smaller than 1 micron, but in rare cases may be 1 micron or a little more.

Grains of this type were found in many samples of section C. U. X. (see the curve in the diagram). Nevertheless it has not yet been possible to determine the natural genus.

#### *Stephanoporites* "type D" (Pl. XII, 95—96)

Pl. XII, 95: C. U. X., No. 124; Pl. XII, 96: C. U. X., No. 124.

Stephanoporate, echinate,  $\pm$  35—40 micron. Spines  $\pm$  1—2 micron.



Number of pores  $\pm 6$ . Pores provided with an annulus. Thickness of the exine  $\pm 2$  micron. Columellae clearly visible.

This type was found fairly frequently in section C. U. X. (see the curve of the diagram), but we have not yet been able to determine the species. These grains resemble somewhat those of *Nothofagus*, but the apertures are perfectly round and the spines are longer, etc. There seems to be also a certain similarity with *Picrodendron* (Erdtman, 1952).

*Thalictrum* (Pl. XII, 97—98)

Pl. XII, 97: C. U. X., No. 27; Pl. XII, 98: C. U. X., No. 27.

Periporate, psilate-scabrate,  $\pm 25$  micron. Pores with granules. The number of pores varies between 6 and 9. Climbing herb of the andean forest-belt.

*Evolvulus*-type (Pl. XIII, 99)

Pl. XIII, 99: C. U. X., No. 88.

Pericarpate, psilate (apparently with a tectum with small perforations).  $\pm 35$  micron. Columellae clearly visible. Exine relatively thick (2—3 micron). Herb of open parts in the forest belt.

Solanaceae (Pl. XIII, 100—101)

Tricolpate, psilate,  $\pm 25$ —30 micron. With transversal furrows. Solanaceae grow at nearly all altitudes.

Polygalaceae (Pl. XIII, 102—104)

Pl. XIII, 102: C. U. X., No. 183; Pl. XIII, 103: C. U. X., No. 141; Pl. XIII, 103: C. U. X., No. A-183.

Stephanocolp(or)ate (or fenestrate, cf. Iversen, 1950), foveolate,  $\pm 35$ —50 micron, with  $\pm 10$ —12 furrows. Transversal (equatorial) furrow.

The majority of the grains we found correspond probably to the genus *Moninna*, shrubs of the andean forest.

*Hypericum* (Pl. XIII, 105)

Pl. XIII, 105: C. U. X., No. A-183.

Tricolp(or)ate, reticulate,  $\pm 25$ —35 micron. Reticulum very fine. Equatorial part of the furrows very typical.

Shrubs, very common in the open paramo, in the dwarf forest and in the uppermost part of the forest belt.

As we did not distinguish these grains in the first analyses we made, we do not present a curve for *Hedyosmum* in the diagram. Nevertheless, a large part of the grains represented in the curve for the "tricolp(or)ate indet.", belong to *Hypericum*.

*Dodonaea* (Pl. XIII, 106)

Pl. XIII, 106: C. U. X., No. 25.

Tricolpate, micro rugulate-micro reticulate,  $\pm 34$ —45 micron. Pores somewhat protuberant. Thickness of the exine 3—3.5 micron. Furrows narrow; pores large with costae pori.

Small shrub, frequent in zones of destroyed forest and in savannas, between 1500 and 3000 m altitude.

## Malpighiaceae (Pl. XIII, 107)

Pl. XIII, 107: C. U. X., No. 185.

Periporate,  $\pm$  psilate,  $\pm$  38 micron. Exine thick ( $\pm$  4—5 micron). Two grains were found, one in sample 185 and another in sample 86. The Malpighiaceae are trees and shrubs of lower belts, but a few representatives of the genus *Stygmaphyllon* grow higher: *S. bogotense* up to  $\pm$  2100 m and *S. ruzianum* up to  $\pm$  2800 m. Their presence might be due to long-distance transportation.

*Cuphea* (Pl. XIII, 108)

Pl. XIII, 108: C. U. X., No. 43.

Syncolporate, striate,  $\pm$  23 micron. Shape  $\pm$  triangular with convex sides. Pores protuberant. Our grains are of the type of *Cuphea dipetala*, with which they correspond in all details. The pollengrains of *Cuphea serpyllifolia* are considerably different, as they are not striate.

Woody herbs of the andean forest belt (and lower).

*Gunnera* (Pl. XIV, 112)

Pl. XIV, 112: C. U. X., No. A-183.

Tricolpate, micro-reticulate,  $\pm$  35—40 micron. Intercolpia salient (and furrows sunk).

Plants of humid sites and marshes in the forest belt. *Gunnera magellanica* is a species of the high paramo of the Central Cordillera.

*Oenothera* (Pl. XIV, 113)

Pl. XIV, 113: C. U. X., No. 163-A.

Triporate,  $\pm$  psilate,  $\pm$  70 micron. Pores larger and more salient than in *Jussiaea*, of the *Oenothera*-type.

*Oenothera multicaulis* is a herb of the higher part of the forest belt and grows even in the paramo.

Amaranthaceae (*Alternanthera*-type) (Pl. XIV, 114)

Pl. XIV, 114: C. U. X., No. A-172.

Fenestrate, scabrate (-micro echinate),  $\pm$  15—25 micron. This is the *Alternanthera*-type.

Herbs of all zones, except the paramo.

*Fuchsia* (Pl. XIV, 109)

Diporate, psilate,  $\pm$  80 micron. Large pores of the *Oenotheraceae* type. The grain of photo 109 corresponds very well to *Fuchsia hartwegii*.

Herbs and small shrubs of the open paramo and of the higher part of the forest belt. Also found in lower belts.

*Cordia lanata* (Pl. XIV, 110)

Pl. XIV, 110: C. U. X., No. A-175.

Reticulate,  $\pm$  45—50 micron. Typus pollinis is not clear, possibly triporate, but the pores are badly defined. Muri of the reticulum composed of large separate granules.

The pollen type of *Cordia lanata* is very different from other species of *Cordia*, like *Cordia alliodora*, which are tricolporate and frequently micro-echinate.

*Cordia lanata* is a tree of the andean forest belt.

*Daphnopsis*-type (Pl. XIV, 111)

Pl. XIV, 111: C. U. X., No. 12.

Periporate, sculpture  $\pm$  Croton-type (forming a reticulum, possibly scabrate on the muri),  $\pm$  35—40 micron.

*Daphnopsis bogotensis* is a shrub of the andean forest belt.

*Dacrydium*-type (Pl. XV, 118)

Pl. XV, 118: Secc. C. U. P., No. 2.

Two pollen grains very similar to the type of *Dacrydium guillauminii*, of  $\pm$  67 micron, were found one in sample No. 2 of the section C. U. P., and the other in sample No. A-159 of the section C. U. X. The first is of Würm-glacial age, and the second of Riss II — glacial age. The presence of *Dacrydium* during the Pleistocene in Colombia, would mean that this genus had a much wider distribution than to-day, because at present it grows only in the southernmost part of the South American continent.

## Podocarpaceae — "type E" (Pl. XV. 119)

Pl. XV, 119: C. U. X., No. 124.

Vesiculate, circular air-sack,  $\pm$  80 micron. This pollen grain is a representative of the Podocarpaceae, may be *Dacrydium* or *Podocarpus*.

This seems to be at least a species not known in the actual flora of Colombia. For the lack of sufficient material for comparison we were not able to determine this grain more exactly. One specimen was found.

*Mutisia*

(C. U. X., No. 86)

Tricolporate, scabrate-echinate  $\pm$  65 (—95) micron. Transversal furrows and costae transversales. Exine thick, columellae large and well defined. "Spines" very low and with a broad base.

Climber of the andean forest.

*Aetanthus*

(C. U. X., No. 18)

Syncolpate, scabrate,  $\pm$  40—65 micron. Shape triangular with concave sides. Several species are found in the higher part of the forest belt, and even in the Paramo.

*Ribes*

(C. U. X., No. 31)

Periporate, psilate,  $\pm$  35 micron. Pores provided with operculum ( $\pm$  5—6 pores?). This type corresponds to the pollen in a slide of recent material of *Ribes bogotanus*. Other slides with recent material of *Ribes* show the well known *Ribes*-type, where every two pores are connected by zones where the exine is very thin.

Shrub or small tree of the patches of dwarf forest in the high paramo.

*Croton*

(C. U. X., No. 30a)

Inaperturate, sculpture  $\pm$  "Croton-type",  $\pm$  50—75 micron. The type of pollen we found is a *Croton* corresponding to the species *Croton bogotanus*, which has a clear clavate sculpture, being different from the other species.

*Croton bogotanus* is a species of the andean forest.

*Berberis*

(C. U. X.)

Very irregular, but apparently syncolpate; foveolate;  $\pm$  45—70 micron. Shrub of the dwarf-forest and the paramo.

*Jamesonia* (Pl. XVI, 120—121)

Pl. XVI, 120: C. U. X., No. 158-A; Pl. XVI, 121: C. U. X., No. 158-A.

Trilate, psilate (sometimes some slight undulations or a few pits may be present),  $\pm$  45—80 micron. Exosporium very thick on the sides and thinner towards the angles; the proper angles are salient. (The outer layer of the exosporium loosens easily, and is not present in fossil state).

A curious fern, very abundant in the high paramo.

*Lycopodium* (foveolate) (Pl. XVI, 122)

Pl. XVI, 122: C. U. Y., (base).

Trilete, foveolate on the distal side,  $\pm$  45—60 micron. Species of *Lycopodium* which have spores of this type, are especially abundant in the high paramo.

*Lycopodium* (reticulate) (Pl. XVI, 123)

Pl. XVI, 123: C. U. Y. (base).

Trilete, reticulate on the distal side, and on the proximal side a more or less incomplete reticulum. Muri very high. Size of spores  $\pm$  40—60 micron.

Species of *Lycopodium* which have spores of this type, are abundant in the high paramo, and also in the forest belts.

## Cyatheaceae-type (Pl. XVI, 124)

Pl. XVI, 124: C. U. X., No. A-150.

Trilete, psilate, 35—60 micron. Exosporium relatively thin to intermediate. Tetrad-mark with or without a "margo". Shape more or less triangular with strongly rounded angles; sides flat, or slightly concave.

It seems that the spores we found of this type, belong principally to certain genera of the Cyatheaceae.

*Hymenophyllum*-type (Pl. XVI, 125)

Pl. XVI, 125: C. U. X., No. 179b.

Trilete,  $\pm$  scabrate — micro gemmate — micro clavate — micro echinate,  $\pm$  45—65 micron. Arms of the tetrad-mark very characteristic, reaching the limit between the distal and proximal side, and frequently opening towards their ends.

Ferns common in different vegetation belts, including the paramo (*Hymenophyllum calodictyon*, up to 3600 m).

*Hemitelia* (Pl. XVI, 126)

Pl. XVI, 126: C. U. X., No. 66.

Trilete, psilate,  $\pm$  45 micron. Shape very characteristic, exosporium with cavities, a big one in the middle of each side. We only found one grain, which was probably brought by long distance transportation (altitude of the genus up to 2100 m).

*Verrutrilletes* "type F" (Pl. XVII, 127)

Pl. XVII, 127: C. U. X., No. 142.

Trilete, verrucate-gemmate,  $\pm$  60—70 micron. Sculpture elements transparent. The determination has not yet been possible.

*Verrutrilletes* "type G" (Pl. XVII, 128)

Pl. XVII, 128: C. U. X., No. 199.

Trilete, verrucate,  $\pm$  50—60 micron. The warts cover completely both the distal and the proximal side. The determination has not yet been possible.

*Triletes* "type I" (Pl. XVII, 129)

Pl. XVII, 129: C. U. X., No. 176.

Trilete; muri irregular, the majority of them not connected, and following an undulant and irregular course;  $\pm$  60—70 micron.

These spores are similar to those of *Ophioglossum*.

*Triletes* "Type H" (Pl. XVII, 130)

Pl. XVII, 130: C. U. X., No. 132.

Trilete, with large verrucae, which principally are placed at the sides, with  $\pm$  2 on each side; size of spores  $\pm$  55—80 micron. The determination has not yet been possible.

*Triletes* "type J" (Pl. XVIII, 131)

Pl. XVIII, 131: C. U. X., No. A-176.

Trilete, sculpture difficult to describe, on the distal side  $\pm$  rugulate-fossulate; size of spores  $\pm$  60 micron. Exosporium relatively thick. The determination has not yet been possible.

*Triletes* "type K" (Pl. XVIII, 132)

Pl. XVIII, 132: C. U. X., No. A-176.

Trilete. Small and large "foveolae" on the distal side; size  $\pm$  65 micron. Exosporium very thick. This type is very similar to *Lophosoria*.

*Verrumonoletes* (Pl. XVIII, 133—134)

Pl. XVIII, 133: C. U. X., No. 132; Pl. XVIII, 134: C. U. X., No. 27.

Monolete, verrucate. Size very variable. All the spores of this type were joined in one group in the diagram. They are probably all Polypodiaceae.

*Psilamonoletes* (Pl. XVIII, 135—136)

Pl. XVIII, 135: C. U. X., No. 158-A; Pl. XVIII, 136: C. U. X. No. A-184.

Monolete, psilate. Size very variable. All the spores of this type were joined in one group of the diagram. They are probably all Polypodiaceae.

*Isoetes* (Pl. XVIII, 137)

Pl. XVIII, 137: C. U. X., No. A-154.

Monolete. Outer part of the exosporium transparent, being like a wide sack, with a type of "skirt" at one side. Size  $\pm$  40—50 micron. Surface smooth or undulated.

Plants of the bottom of lakes and of marshes and bogs in the high paramo.

## 9. DESCRIPTION AND INTERPRETATION OF THE DIAGRAM \*)

## GENERAL OBSERVATIONS AND INTERPRETATIONS

From the cores, samples were taken for pollen-analysis every 10 or 15 centimetres, and these samples prepared, first with the modified Erdtman-method (KOH and acetolysis), as described by Faegri & Iversen (1950). Then, those samples which contained clay or sand were treated a few minutes with HF, and subsequently gravitative separation was carried out in a mixture of bromoform and alcohol with a specific gravity of 2.

Between 200 and 300 pollen grains of those species included in the pollen-sum which formed the basis of percent-calculations were counted in each sample. Pollen grains of the following plants were included in this sum:

Gramineae	<i>Juglans</i>
<i>Acaena</i>	<i>Weinmannia</i>
<i>Alnus</i>	<i>Rapanea</i>
<i>Podocarpus</i>	<i>Symplocos</i>
<i>Quercus</i>	<i>Drimys</i>
<i>Hedyosmum</i>	<i>Ilex</i>
<i>Myrica</i>	<i>Miconia</i>
<i>Styloceras</i>	Urticaceae
<i>Bocconia</i>	<i>Vallea</i>

The percentages of the pollen grains of the other plants were calculated on the basis of the sum.

For the construction of the diagram, the principles for the type proposed by Iversen for the representation of Late-glacial vegetation-changes were put in practice.

The breadth of the diagram represents the 100 % of the pollensum. From the right to the left the percentages of the most important elements (anemophilous) of the open vegetation are represented (striped and hatched), summing one on top of the other. From the left to the right the percentages of the more important forest elements are represented by separated curves. For *Alnus* an open square-symbol was used, for *Quercus* a closed square, for *Podocarpus* a closed circle, and for the total of the remaining forest-elements a cross. Although the last two symbols are used also for other trees (not to be found in Colombia), we preferred to use these simple ones instead of more complicated types, which make the reading of the diagrams more difficult.

If we exclude desert or semi-desert-type vegetation (which may be recognized by the occurrence of various typical species, not present in our section), then the open vegetation (Gramineae + *Acaena*) indicates high andean vegetation-types (open "paramo" vegetation; Espeletion). The forest elements together represent the Andean forest (including the dwarf-forest of the andean paramo near the altitudinal limit of the forest, and partly the isolated patches still higher up on protected sites).

The pollen-rain which fell on the Sabana-lake was provided principally by the vegetation of the surrounding mountains. These mountains rise up to an altitude of approximately 3200—3300 metres (or even higher in more distant mountains). So, a percentage of only a few percent of open vegetation (Gramineae + *Acaena*) will indicate that the slopes of these mountains were entirely or almost entirely covered with forest (original present-day con-

\*) for the diagram see annexes

ditions). When the percentage of open vegetation becomes a little higher, then this open vegetation must have made its appearance on the tops of the mountains, and when it increases more, the altitudinal limit of the forest must have come further down. As isolated patches of forest are still present high above the continuous closed forest limit (and as the slopes of the mountains towards the Sabana with its many small valleys have many protected sites), the percentages of open vegetation might only in extreme cases have reached a percentage near 100, even when the closed forest limit was already far below the Sabana de Bogotá.

Thus it will be clear that the curve of Gramineae + *Acaena* is an excellent indicator of the relative fluctuations of the forest-limit.

Besides the important fluctuations of the open-vegetation curve, important changes in the quantitative composition of the forest are visible in the diagram. Especially *Quercus* is significant: it sometimes reaches high values, and sometimes reaches zero. As we saw above, the Quercetum indicates here a wetter climate, with less pronounced dry seasons, higher annual precipitation and more continuous cloud covering. When *Quercus* disappears in the diagram, the curve for the rest of the forest elements, including *Weinmannia* (but not including *Alnus* and *Podocarpus*) go on or show higher percentages.

Although many of these elements may occur also in the Quercetum, the relation of the *Quercus* curve to this curve of the rest of the forest elements will give us an idea of the fluctuations of annual atmospheric precipitation.

During the driest periods the Sabana-lake dried partly out, the deposition of lake-sediments being replaced by peat formation or river sedimentation (inundation clays). Then local vegetation becomes more important and fluctuations of humidity seem to be indicated by relative fluctuations of the *Alnus* curve and the curve for the total of the rest of the forest elements.

The *Podocarpus* curve shows characteristic maxima and minima at certain intervals, but no special climatic conditions could be deduced from it up till the present, as the different species have rather different ecological conditions, and no specific determination could be carried out.

The curve of the open vegetation (fluctuations of the tree-line) and the curve of the relation of *Quercus* to the total of the rest of the forest elements (fluctuations of annual atmospheric precipitation etc.) could be converted from relative into more exact ones, and out of both a temperature curve could be calculated; they are treated separately in the next paragraph.

In the paragraphs 4 and 5 we saw that, when the annual precipitation is higher than at the present day near Bogotá, the tree-line lies higher. This factor is very important, as then the curve for the fluctuation of the tree-line is not only determined by temperature but also by the changes of annual precipitation (see the next paragraph).

In general (but not always in minor details) the *Quercus* curve is high in the intervals of the diagram where the Gramineae + *Acaena* curve is high. Thus we may say that, in general, the cold phases were considerably colder than the open-vegetation curve seems to indicate.

#### THE GENERAL DIAGRAM

The uppermost three metres of the section consist of inundation clays. The diagram of this part shows in general low percentages of Gramineae, and alternating tops of *Alnus* and *Myrica*. It seems logical to refer this part

of the diagram to the Holocene. The Radiocarbon dates verified this assumption (see paragraph 11). In the uppermost spectra the Gramineae curve is much higher, corresponding to the destruction of the forest by man. A more detailed description of the diagram of the uppermost 4 metres is given in paragraph 11.

From 3 to 8 metres the Gramineae (and see also *Acaena*) are high, although with several fluctuations. *Quercus* is also present with rather high percentages; it is not present above sample 12. A little later the Sabana lake dried up (3.5 metres level). We interpreted this part of the diagram as the last high glacial part of the Würm-glaciation (Pleniglacial II), which according to recent Radiocarbon dates lasted in Europe from  $\pm 28,000$  BC —  $\pm 14,000$  BC. A Radiocarbon date from the 340 cm level confirms this interpretation (see paragraph 11). It is interesting to observe here, that several of the spectra, with a high percent of *Hedyosmum*, are almost identical (not taking into account the presence of *Quercus*) with the year spectrum of the atmospheric pollen station at 3450 metres in the "Páramo del Alto de la Viga" (see paragraph 6).

From 8—11.5 metres and from 14—15.5 metres the diagram shows intermediate climatic conditions. These two intervals are separated by the interval between 11.5 and 14 metres, which shows colder conditions, although a little milder than during the high glacial phase (see the temperature curve and paragraph 10). The interpretation as Würm interstadials ("Interpleniglacial", van der Hammen, 1957) seems now quite logical.

From 15.5—19.5 metres, another very cold interval is present, again with high *Quercus* values. We interpret this interval as representing the first high glacial phase of the Würm glaciation (Pleniglacial I).

The interval from 19.5—22.2 metres shows less cold conditions, but nevertheless colder than interstadial.

From 22.2—24 metres the lake had disappeared partly, and peat was formed. *Quercus* is absent or very low: the climate dry. The Gramineae curve is very low in the lower and in the upper part of this interval, but higher in the middle part. We interpret this interval as Riss-Würm interglacial. Sedimentation must have been much slower during this interval. There seems to be a somewhat colder interval in the interglacial, showing moreover the highest *Podocarpus* values of the whole diagram. From 24—29 metres a much colder interval showing partly high glacial conditions, is present. It consists again of lake sediments. We interpret this interval as Riss glacial II (= Warthe stadial).

From 29—31 interstadial conditions prevail again. The lake dried again partly up during that time, and peat was formed. Our interpretation of this interval is Riss I—II interstadial. In the lower part was deposited some volcanic ash which came probably from volcanic eruptions in the Central Cordillera.

The lowermost part of the diagram, from 31 to 32.2 metres shows high glacial conditions again. But *Quercus* is absent or very low. The climate was dry and very cold. We interpret this part of the diagram as the last part of the Riss glacial I (= Drenthe stadial). This last part of the Riss I was apparently dry, just as the last part of the last high glacial phase of the Würm glacial.

#### THE SEPARATE CURVES

Separate curves for all the recognized genera and families are drawn to the right of the general diagram. For the description of the pollen



grains, and data on the ecological conditions of the plants they represent, see paragraph 8. Immediately at the right of the general diagram, the curves for the types included in this diagram (pollen sum) are to be found. Separate curves are given for all the elements which constitute together the curve of the "total forest elements (less *Alnus*, *Quercus* and *Podocarpus*)". Then follows a list of figures, representing the number of pollen grains included in the sum of calculation of each sample. Then follow the three climatic curves (real fluctuations of tree-line, "humidity" or annual atmospheric precipitation, and temperature). A detailed description of these curves is given in paragraph 10. To the right of the third one of these curves follows again a list of figures, representing the total number of pollen grains counted in each sample.

Then follow the curves of those pollen-types not included in the general diagram nor in the sum of calculation. They represent genera or families which are herbaceous, or partly herbaceous and partly shrubs or trees.

The curves of the spores begin with *Jamesonia*. After the curve of *Isoëtes*, the diagram ends with a curve of the pollen-density, expressed in "number of grains per slide of  $22 \times 22$  mm".

The interpretation of all these separate curves will not present any difficulties, with the aid of the geographical or sociological data given in paragraph 8.

One of the most surprising curves of the diagram is the curve for *Acaena*. The bulk of the pollengrains included in this curve belong to the species *Acaena cylindrostachya*. As we saw before (paragraph 4), this paramo-species is in general not very common, and even in those regions with a strong local development of an Acaenetum, it is only represented by one or a few percent in the pollen flora of recent lake sediments (van der Hammen & Gonzalez, 1960b).

Under actual conditions the occurrence of an Acaenetum seems locally to be connected with cattle grazing and dunging, and it is not found in the paramo-belt above the Weinmannietum in the surroundings of Bogotá, but especially in the paramo-belt above the Quercetum and related associations. In the Sierra Nevada del Cocuy *Acaena* is found considerably abundant on old moraines etc., on sites where the humus-layer is absent or very thin. During the Würm-glacial, in the Sabana de Bogotá, when Quercetum took the place of the interglacial Weinmannietum, the Acaenetum must have occupied considerable surfaces above the tree-limit, as relatively high percentages of *Acaena* are found in all the samples corresponding to that time. Also very interesting is the curve of the Malvaceae, which were only found in the Riss-glacial I. They belong to a species which we recently found at an altitude of approximately 4000 m in the Sierra Nevada del Cocuy (*Malvastrum acaule*). The presence of these pollengrains is another proof of the very low Riss I temperatures (see also paragraph 8 and 10).

## 10. THE TEMPERATURE AND PRECIPITATION CURVES

The curve of the Gramineae + *Acaena* in the diagram indicates logically the relative fluctuations of the tree-line. As many of the forest elements included in the pollen sum occur still in patches of forest or dwarf forest above the proper tree-line, becoming gradually scarcer with the altitude, the

above mentioned curve is naturally gentle and will not show a sharp break when the proper "tree-line" passes the Sabana level.

It is now possible to convert this relative curve in a curve indicating absolute values in metres of displacement of the tree-line. This was realized in the following way.

A recent pollen spectrum from "Páramo Alto de la Viga" (calculated on the basis of a year-long aerial pollen collection, see paragraph 6) gave 51.5 % of Gramineae, at 3450 metres above sea-level or approximately 250 metres above the local tree-line. In a pollen diagram of lake sediments of "Laguna de la América", Páramo de Palacio (van der Hammen & Gonzalez, 1960a), the spectrum No. 51 (just below the uppermost 2 spectra with human influence), shows 49 % of Gramineae, at 3500 metres above sea level or approximately 250 metres above the local tree-line.

So we find that three different sources (one of atmospheric pollen one of a region with *Weinmannietum* and a local tree-line of 3250 metres and one of a region with *Quercetum* and a local tree-line of 3550 metres) give almost identical informations: approximately 50 % of Gramineae corresponds to a site approximately 250 metres above the local tree-line.

Another datum may be found in the diagram from the Sabana de Bogotá. The sample 1d, just below the samples with a growing human influence, shows 8 % of Gramineae. As the local tree-line near Bogotá is 3250 metres, and the level of the Sabana approximately 2600 metres, we may conclude that 8 % of Gramineae corresponds to a site 550 metres below the local tree-line. As the Gramineae + *Acaena* curve is gentle, for reasons exposed above, we may now, on the basis of the two data calculated above, calculate how many percents of Gramineae correspond to each 100 metres of displacement of the tree-line.

We take 52 % of Gramineae 250 metres above the local tree-line, and 8 % of Gramineae 550 metres below the local tree-line. So we have 44 % of Gramineae for a displacement of 800 metres, or 5.5 % for every 100 metres of displacement.

In this way we have converted the relative curve in a curve showing absolute values in metres of displacement of the tree-line (see the main diagram). The error of this curve will probably be not greater than  $\pm 50$  metres. For the Sabana de Bogotá we cannot trace the exact curve further when the Gramineae curve is lower than 8 % (or the forest limit higher than 3250 metres): as the highest tops of the mountains which form the proper limits of the Sabana have approximately an altitude of 3200—3300 metres, a discontinuity in the curve may be expected when these mountains become totally covered with forest.

Let us now consider the precipitation curve. We have seen above, that the relative amount of *Quercus* increases when the climate becomes wetter. At the same time the local forest limit becomes higher. So there exists a relation between the relative amount of *Quercus* and the altitude of the local forest limit.

The precipitation curve of the diagram, based on the relation of *Quercus* to the total forest elements less *Alnus* and *Podocarpus* ("*Quercus*-ratio"), is again a relative curve. We will now try to convert it in a curve showing absolute values, expressed in the altitude of the corresponding tree-line under actual temperature conditions. We may approach this problem from two different sides, theoretically and based on actual observations.

Theoretically the highest *Quercus*-ratio in the diagram would correspond to the highest possible tree-line in the Eastern Cordillera. Thus a *Quercus*-ratio of 84 % would correspond to a tree-line of  $\pm 3800$  metres. On the other hand the *Quercus*-ratio is 0 % near Bogotá, where the tree-line lies at  $\pm 3200$ — $3250$  metres. Thus 600 metres of displacement of the tree-line under actual temperature-conditions would correspond to 84 % change in *Quercus*-ratio, this is 14 % for every 100 metres.

The actual observations are the following. In the "Laguna de los bobos" we found in spectrum 4 (just below the level where human influence starts) a *Quercus*-ratio of 50 %. The actual tree-line lies there at  $\pm 3550$  metres (van der Hammen & Gonzalez, 1960b). In the "Laguna de la América" ("Páramo de Palacio"), with an actual tree-line of 3250 metres, a *Quercus*-ratio of 2.5 % was found in spectrum 51 (van der Hammen & Gonzalez, 1960a). In the atmospheric pollen spectrum from "Páramo del Alto de la Viga", with a local tree-line of  $\pm 3200$  metres, a *Quercus*-ratio of 0 % was found.

The theoretical calculations and the actual observations are in very satisfactory agreement:

Tree-line	Theoretical <i>Quercus</i> -ratio	Observed <i>Quercus</i> -ratio
3200 m	0	0
3250 m	6 %	2.5 %
3550 m	49 %	50 %

Here again, the limit of error is small, at any rate less than  $\pm 25$  metres. Thus we may convert the *Quercus*-ratio curve in a curve indicating the theoretical altitude of the tree-line due to "humidity" (supposing actual temperature conditions).

The curve for the real fluctuations of the tree-line is the result of two factors: temperature changes and "humidity" changes. In order to obtain a temperature curve we have to eliminate from this curve the influence of the "humidity" changes. Thus for every point of this curve we have to add to the corresponding real altitude of the forest limit the number of metres indicated by the corresponding point of the converted *Quercus*-ratio curve. In this way we obtain a curve indicating the imaginary position of the tree-line if it were only affected by temperature fluctuations. The possible error of this curve will not be greater than  $\pm 75$  metres. This curve may now easily be converted with the aid of the graph of fig. 3. From this graph, based on a great number of observations on the present-day relation of altitude and average year temperature in the Eastern Cordillera (principally department of Cundinamarca), it appears that the temperature decreases rather consistently  $\frac{2}{3}^{\circ}\text{C}$  for every 100 metres of altitude (see paragraph 3). A tree-line of 3200 metres, the actual tree-line near Bogotá, corresponds then logically to the actual average year temperature of the Sabana de Bogotá,  $14^{\circ}\text{C}$ ; and for every 100 metres lowering of the imaginary tree-line  $\frac{2}{3}^{\circ}\text{C}$  lower.

The value of  $\frac{2}{3}^{\circ}\text{C}$  per 100 metres is a fairly exact value. As a matter of fact, temperature — altitude relations of different sites of observation in the Eastern Cordillera lie often outside the line of the graph of fig. 3, but this is only due to local geographical climatological conditions which may differ considerably in a mountain range. But as we are considering climatic fluctuations on one and the same site, this factor has no influence on our

curve. For that reason no error is taken into account for the last conversion. The limits or error of the temperature curve will then be  $\frac{75}{100} \times \frac{2}{3} = \pm 1\frac{1}{2}^{\circ}\text{C}$ .

We have now at our disposal three curves (see the main diagram):

1°. Real fluctuations of the tree-line (expressed in metres).  
2°. Fluctuations of "humidity" (principally annual atmospheric precipitation) (expressed in metres of fluctuation of the tree-line as a result of "humidity" only).

3°. Temperature fluctuations (expressed in  $^{\circ}\text{C}$ ).

If we consider the three curves together, it will be clear at one glance that they are congruent in major features: when the temperature decreases, the "humidity" increases. There is no doubt that the glacials are at the same time pluvials, and the interglacials are interpluvials (see also: Maarleveld & van der Hammen, 1959). But in minor details we see that often minor fluctuations of humidity have no relation with minor fluctuations of temperature.

As a fall of temperature will lower the tree-line, and a simultaneous increase of humidity will rise the tree-line, these two factors are opposed, and the real forest limit was lowered less during the glacials than would have been expected from temperature fluctuation only.

But it has not to be forgotten that the fluctuations of the snow-line followed the temperature fluctuations (or the increasing humidity during the glacials lowered the snow-line even somewhat more than would have been expected from temperature fluctuations only). The result was, that the snow-line and the tree-line were much nearer to each other during the glacials than during the interglacials, and may have been even in contact on especially wet places (this is almost the case in the present on the Nevado del Huila, in the Central Cordillera, with an extremely humid climate all the year round (see paragraph 5).

The maximal decreases of average year temperature during the coldest phase of the Würm-glacial lie between  $7^{\circ}$  and  $8^{\circ}\text{C}$  ( $-8\frac{2}{3}^{\circ}\text{C}$ ) lower than to-day. These temperatures are  $2^{\circ}\text{C}$  lower than those calculated by Wilhelmly (1956). Minimum Würm temperatures found by Emiliani (1955) for Caribbean and equatorial atlantic surface ocean water, are approximately  $6^{\circ}$ — $8^{\circ}\text{C}$  lower than to-day. They are in perfect agreement with our data from the equatorial Andes.

The Riss I glacial temperatures in our curve are even lower than the Würm glacial ones (see below).

The Würm glacial snow-line, taking into account a temperature decrease of  $8\frac{2}{3}^{\circ}\text{C}$ , must have been at least 1300 metres lower than to-day in the Eastern Cordillera. But the pluvial climate must have lowered the snow-line even more: the snow-line was 1300 metres lower than the snow-line of to-day in areas with an equal annual atmospheric precipitation as during the Würm temperature minima in the Sabana de Bogotá. The three temperature minima of the Würm-Pleniglacial II give the following data:

Temperature minimum ( $^{\circ}\text{C}$ lower than today)	Theoretical altitude of the tree-line according to "humidity" only	Lowering of snow-line, according to temperature decrease only
1° minimum $8\frac{2}{3}^{\circ}\text{C}$	$\pm 3550\text{ m}$	$\pm 1300\text{ m}$
2° minimum $8^{\circ}\text{C}$	$\pm 3700\text{ m}$	$\pm 1225\text{ m}$
3° minimum $\pm 7.5^{\circ}\text{C}$	$\pm 3550\text{ m}$	$\pm 1135\text{ m}$

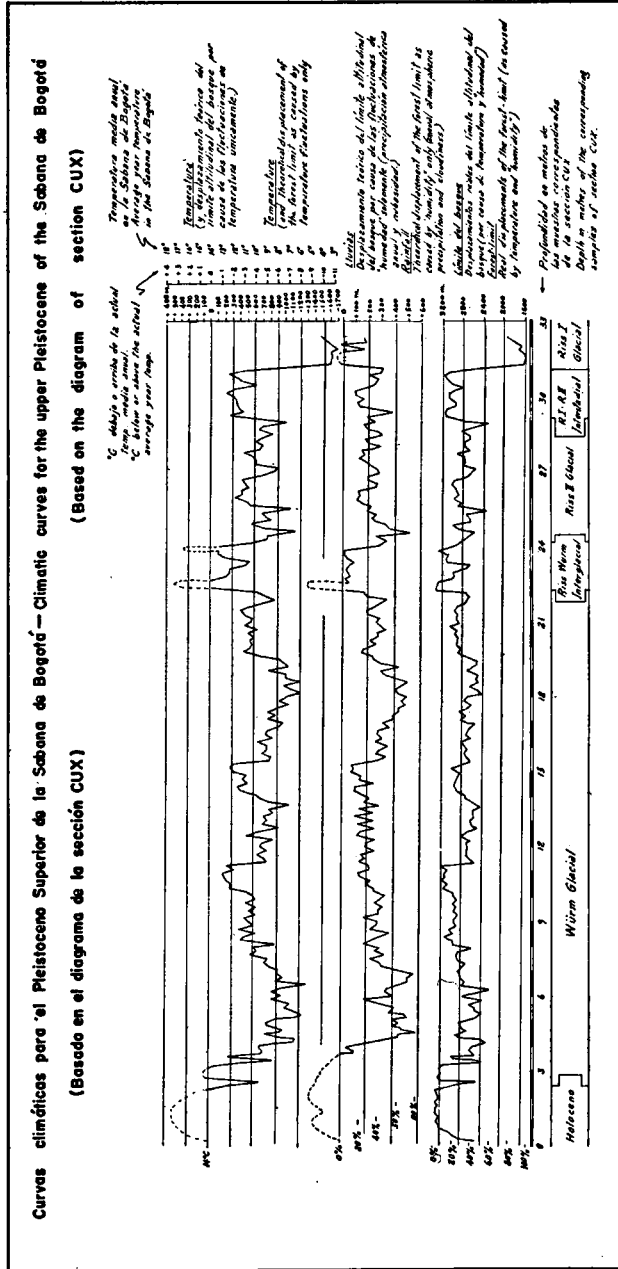


FIG. 5

If we suppose that the actual tree-line ("humidity") — snow-line relation is approximately a straight line (which is suggested if we plot these relations, given in paragraph 5), and this line passes through the two points corresponding to the relation of: tree-line 3900 m, snow-line 4150 m and tree-line 3200 m, snow-line 4550 m, then we find the following data for the Würm glacial temperature minima:

	Theoretical altitude of tree-line according to humidity only	Theoretical altitude of snow-line according to "humidity" only
1° minimum	3550 m	4350 m
2° minimum	3700 m	4250 m
3° minimum	3550 m	4350 m

For the lowest Würm glacial snow-lines in the Sabana de Bogotá we find then:

1° minimum	4350 — 1300 = ± 3050 metres
2° minimum	4250 — 1225 = ± 3025 metres
3° minimum	4350 — 1135 = ± 3215 metres

For the Riss I glacial temperatures of our curve we find a minimum temperature of 11° C lower than to-day, corresponding to a lowering of the snow-limit of 1650 metres. The theoretical tree-line according to humidity only has a value of 3380 metres, which would correspond to-day to a snow-line of 4450 metres. We find then the lowest "Riss I" snow-line at 4450 — 1650 = 2800 metres.

These data on the Würm and Riss glacial position of the snow-line in the area of the Sabana de Bogotá correspond very well with the altitude of observed glacial phenomena, taking into account that valley-glaciers in some cases may have advanced some 100 metres lower than the actual snow-line. Near La Calera (in the mountains East of Bogotá), important remnants of moraines are found at ± 2700 metres, and glacial U-shaped valleys (in some places combined with moraines) are found in the hills sloping towards the Sabana in several places, showing that glaciers came down to approximately 2700 metres.

Very clear and fresh glacial phenomena can be observed in many places around the Sabana de Bogotá (and in general in the Eastern Cordillera) from 3000 metres upward. Especially around 3200 metres important moraines are found in many places of the Eastern Cordillera. In Northern Boyacá we could recognize the following important terminal moraine-levels: 3400 metres, 3200 metres and 3050 metres. Further down, partly destroyed moraines are present between 2750 and 2800 metres.

It is interesting to observe that the real tree-line during the Würm-glacial temperature minima in the area of the Sabana de Bogotá was relatively close to the snow-line. We find the following values:

Snow-line	Real tree-line	Vertical distance
1° minimum 3050	2250	± 800 m
2° minimum 3025	2400	± 625 m
3° minimum 3215	2400	± 815 m

For the Riss I temperature minimum we find:

2800	1700	± 1100 m
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At present this distance, in the central part of the Eastern Cordillera, is approximately 1350 metres.

It is very interesting that the interstadial maximal temperatures are only 1.5–2° C lower than to-day, although during the major part of the interstadial, prevailed a temperature between 3° and 4° C lower than to-day. But the interstadials were much wetter (Quercetum) than the interglacials; on the other hand, this "humidity" meant that the tree-line could rise still nearer to the present-day one, being only some 300–200 metres lower, and in an extreme case it even reached the same altitude for a very short time. While in the area of the Sabana de Bogotá the glaciers disappeared completely during the interstadials, they probably maintained themselves in those times in Northern Europe as a still considerable mass of ice. May be this fact was the reason that the temperature in Europe during some interstadials could not rise so high as in our equatorial region.

As we cannot calculate any data when the real tree-line becomes higher than 3200 metres (see above), no estimations can be made on the position of the tree-line during the Holocene. Moreover, influence of local vegetation in the sediments above 350 cm (inundation clays) makes it very difficult to carry out any calculations on the temperature fluctuations of both Late-glacial and Holocene. Fortunately we have good records of the Late-glacial and Holocene climatic history from lake sediments of Páramo de Palacio, in the mountains NE of Bogotá (van der Hammen & Gonzalez, 1960a). The following data were obtained, calculated in exactly the same way as exposed above:

The tree-line during the optimal temperature conditions of the Holocene, was 300–400 (occasionally even 500) metres higher than to-day (in Páramo de Palacio, where the tree-line lies actually at 3250 metres, it reached approximately 3550–3650 metres; occasionally it even reached 3750 metres during a short time).

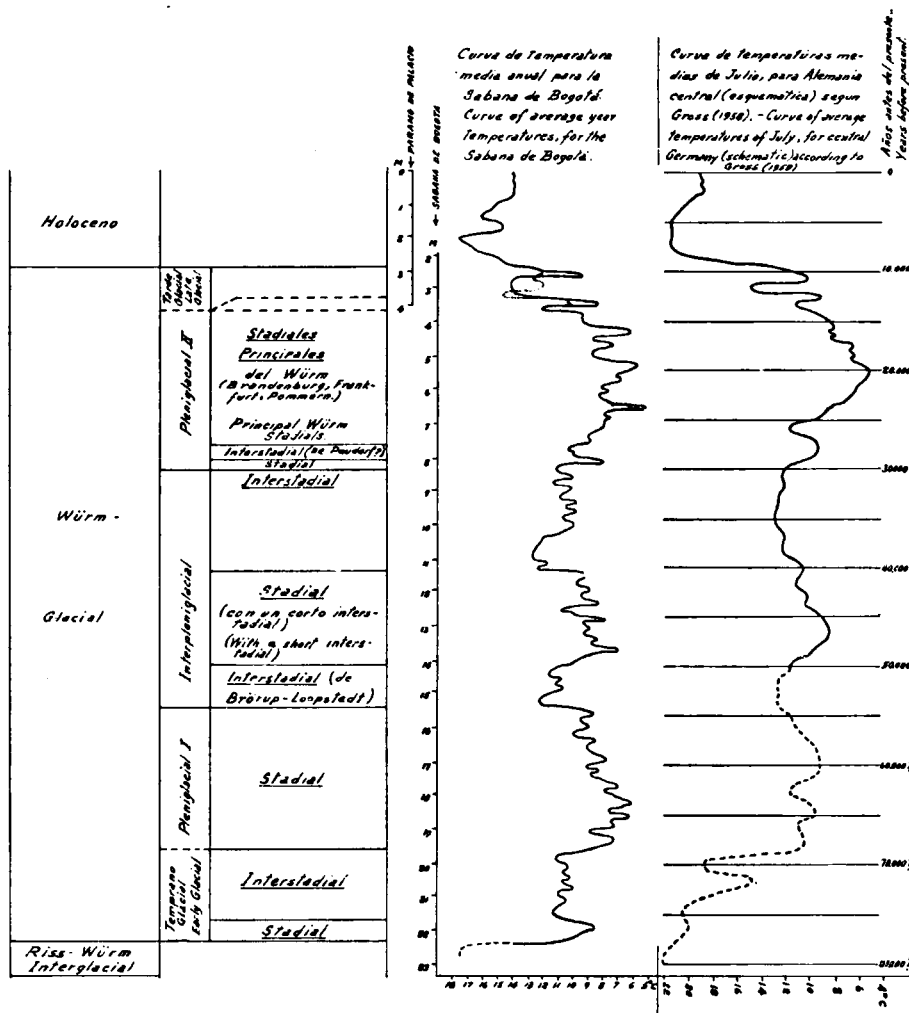
This datum is in perfect agreement with data from the Alps, where the timber-line was 300–400 metres higher than to-day during the Subboreal (Lüdi, 1955). Deevey & Flint (1957) calculate from these alpine data a temperature of 2°–3° C above the present. Our data give exactly the same temperature difference:  $3 \times \frac{2}{3}^{\circ} \text{C} = 2^{\circ} \text{C}$  and  $5 \times \frac{2}{3}^{\circ} \text{C} = 3\frac{1}{3}^{\circ} \text{C}$ .

It is very interesting to realize that during this time of optimal climatic conditions, the Páramo regions (Espeleton) disappeared almost completely in the mountains around the Sabana de Bogotá.

The climatic curves of the Sabana de Bogotá are represented on a smaller scale in fig. 5.

A somewhat simplified temperature-curve, based on the analysis of the Sabana de Bogotá, completed with the Late-glacial and Holocene curve of Páramo de Palacio, is given in fig. 6, compared with Gross's partly dated curve for the European Upper Pleistocene (Gross, 1958). The two curves are strikingly similar, especially in the dated and better known part of the Gross-curve. There is also a great similarity with the curve of Emiliani (1955), so that the interpretation of our curve and diagram seems to be well substantiated. It is important to realize in this respect, that any displacement of one of the two curves is impossible and absurd, as one of them would end in the future instead of in the present. The C 14 dates of the Holocene also make such a displacement impossible. With these facts, the possibility is excluded that the climatic changes in South America occurred somewhat later or earlier than in Europe. They also definitely exclude polar movements,

etc., as the explanation of the pleistocene climatic changes. These problems of the correlation of glacials and pluvials were also considered, with the same result, by Flint & Gale (1958) and Maarleveld & van der Hammen (1959). The Riss-Würm interglacial is represented in our diagram (and curves)



Curva de temperatura del Pleistoceno Superior y del Holoceno de los Andes ecuatoriales (Sabana de Bogotá), comparada con una curva para el Pleistoceno Superior de Europa de H. Gross.

Temperature curve of the upper Pleistocene and Holocene of the equatorial Andes (Sabana de Bogotá), compared with a curve for the upper Pleistocene of Europe of H. Gross.

FIG. 6

with apparently much too short an interval. This is certainly due to the fact, that the Sabana lake became dry (or was at any rate much smaller) during that time. Peat was formed, but the peat formation stopped or was

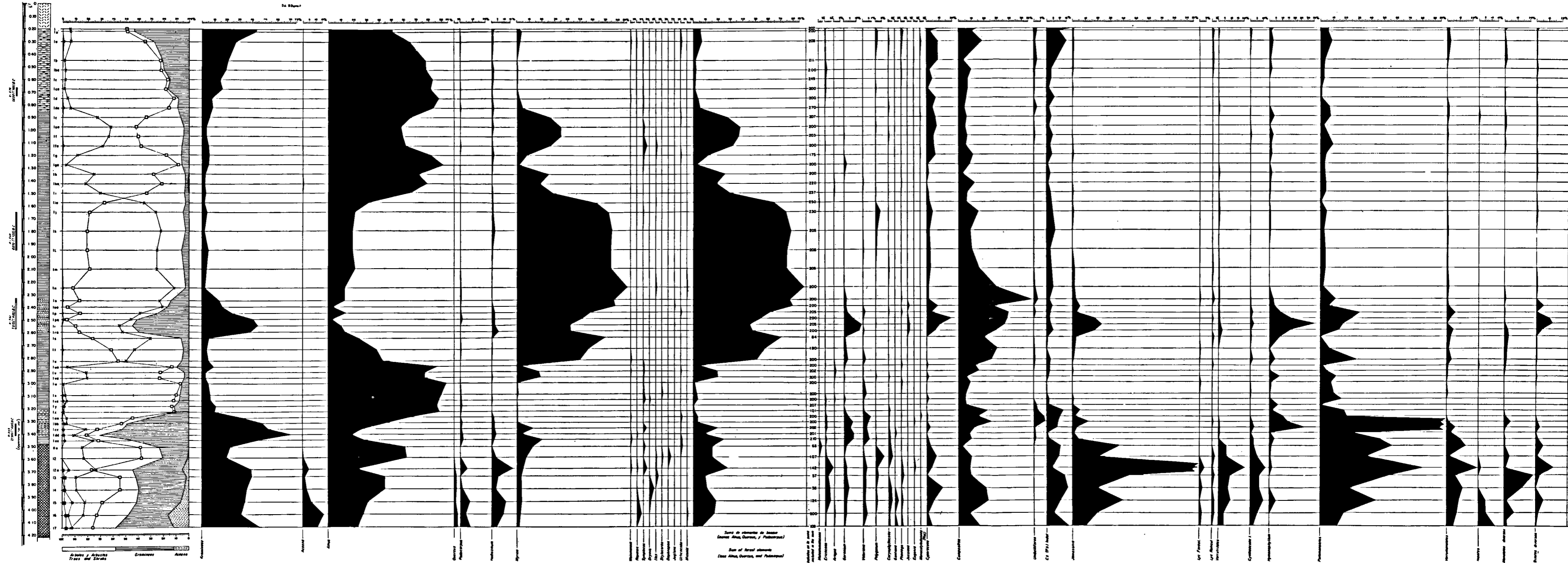


# SABANA DE BOGOTA

Sección CUX, parte superior Section CUX, upper part  
 (Bogotá, Ciudad Universitaria) (Bogotá, University Park)

ANAL Thomas von der Haumen  
 Enrique González

24 34 cm



- Arcilla lúmina (Lime clay)
- Arcilla Ch<sub>2</sub>
- Arcilla de espasa y grilla azules (Lime clays and clay-grilles)
- Pedregosa
- Cuarzo
- Aluv
- Suma de otros elementos de arena (Sum of other sand elements)

FIG - N° 7

Suma de elementos de arena  
 (Sand elements)

Suma de otros elementos de arena  
 (Sum of other sand elements)

Suma de otros elementos de arena  
 (Sum of other sand elements)

very slow during the driest and warmest parts, when the Sabana was covered with forest.

The data we calculated on the altitude of the tree-line and the altitude of the snow-line during the different phases of the Upper Pleistocene and the Holocene, were used to draw maps of the vegetation zones and the extension of the eternal snow of the Sabana de Bogotá and surroundings in those times. These maps were drawn using contour lines, and possible changes in altitude of the indicated limits because of local circumstances (as for instance in valleys the tree-line will be higher and the snow-line lower), were not taken into account. These maps are represented in Plates XLI—XLV.

## 11. THE RADIOCARBON DATES AND THEIR INTERPRETATION

In order to establish if our interpretations and correlations with the European and North American Upper Pleistocene and Holocene climatic phases were right, a number of samples for C 14 analysis was collected. For that reason a hole was dug at the site of the bore-hole C. U. X., of 2 × 2 metres wide, and 4 metres deep. In the walls of that hole there were several horizons containing small charcoal particles, from which samples were collected. A sample was also taken from a layer of humic clay near the bottom of the hole.

Fig. 7 shows a diagram of the upper part of section C. U. X. in a more detailed way than in the complete diagram, with the position of the samples dated by C 14 analysis. The samples were dated, through the intermediary of Dr. Johs Iversen, by Dr. Tauber in the Copenhagen laboratory.

We list the dated samples below (the depth of some of the samples differs in a few centimetres with their place indicated in diagram fig. 7, because of posterior pollen correlation of these samples with the pollen section).

K - 576 - Col. 25 - Charcoal. Section X, Sabana de Bogotá (Colombia, South America).	
Depth 75 cm .....	1650 ( $\pm$ 160) A.D.
K - 560 - Col. 9 - Charcoal. Section X, Sabana de Bogotá (Colombia, South America).	
Depth 170—205 cm .....	6070 ( $\pm$ 120) B.C.
K - 561 - Col. 10 - Charcoal. Section X, Sabana de Bogotá (Colombia, South America).	
Depth 235—265 cm .....	7010 ( $\pm$ 400) B.C.
K - 568 - Col. 11 - Humic clay. Section X, Sabana de Bogotá (Colombia, South America).	
Depth 230—345 cm .....	21900 ( $\pm$ 600) B.C.

Fig. 8 shows another diagram, from the section C. U. P., taken only some 500 metres South of Section X. From this section two samples were analysed in the Copenhagen laboratory, both from the peat layer between 440 and 460 cm; their position is indicated in the diagram. The results were the following:

K - 536 - Col. 2a - Peat. Section C. U. P., Sabana de Bogotá (Colombia, South America).	
Depth 450—460 cm .....	> 34000 yrs.
K - 538 - Col. 2b - Peat. Section C. U. P., Sabana de Bogotá (Colombia, South America).	
Depth 440—450 cm .....	> 34000 yrs.

We will now consider the interpretation of the dated diagrams.

The lower part of the diagram of fig. 7, from 425 cm to 335 cm was interpreted as representing the last part of a cold phase thought to be the Würm (Weichsel). The date  $\pm$  21900 ( $\pm$  600) B. C. seems to confirm this interpretation. Nevertheless, it seems that it is some thousands of years too old. The reason could be the redeposition of older material, derived from interstadial or interglacial peat-beds eroded at the shore of the lake when

the water-level dropped (section C. U. P.). Only future C 14 analysis may resolve this problem definitely. Until then we will have to take into account the possibility that this sample is in reality several thousands of years younger than indicated by the present analysis.

The part of the diagram from 245 cm to the surface was interpreted as Holocene. This is confirmed by the three available dates: 7010 ( $\pm 400$ ) B. C., 6070 ( $\pm 120$ ) B. C. and 1650 ( $\pm 160$ ) A. D. In this part of the diagram important changes in the forest composition are registered, principally determined by the species: *Alnus* and *Myrica*. They seem to indicate wetter and drier periods. When *Alnus* dominates, the Sabana de Bogotá must have been subjected to longer and more frequent inundations during the year, whereas when *Myrica* dominates the contrary seems to have occurred. If this is right, then we may distinguish the following climatic phases (see fig. 7):

- VIII - Wet phase (20—85 cm)
- VII - Dry phase (85—115 cm)
- VI - Wet phase (115—155 cm)
- V - Dry phase (155—235 cm)

The fact that a little below the limit V—VI a date of 6070  $\pm 120$  B. C. was found, strongly suggests that this limit corresponds to the limit Boreal-Atlantic in Europe, which has a date of  $\pm 5500$  B. C.

This suggests that also the other pollen-analytical limits could correspond to the European zones: limit VI—VII with the Atlantic-Subboreal limit, and limit VII—VIII with the Subboreal-Subatlantic limit. The date 1650 ( $\pm 160$ ) A. D. at  $\pm 20$  cm above the limit VII—VIII, although younger than expected, is not in contradiction with this supposition (see below).

The following correlation seems therefore to be very well possible:

Sabana de Bogotá	Europe
VIII - Wet phase	Subatlantic
VII - Dry phase	Subboreal
VI - Wet phase	Atlantic
V - Dry phase	Boreal

The interpretation of the part of the diagram between 335 cm and 235 cm is more difficult. This part is at any rate younger than 21900 ( $\pm 600$ ) B. C. and the uppermost part is 7010 ( $\pm 400$ ) B. C. The last mentioned date was obtained from charcoal particles picked out of the interval 233—257 cm, but the bulk of the particles was collected between 234 and 236 cm. The date 7010 ( $\pm 400$ ) B. C. is a date that indicates that we are in a zone that corresponds to the European Preboreal.

Somewhat below this last mentioned horizon (234—236 cm), between 245 and 260 cm, a Gramineae maximum is present, and the presence of certain pollen species (*Valeriana*, *Aragoa*) also indicates a colder climate.

Thus it seems most probable to correlate the 245—260 cm cold interval with the Younger Dryas time, and the 230—245 cm interval, a period of gradual amelioration of the climate, with the European Preboreal.

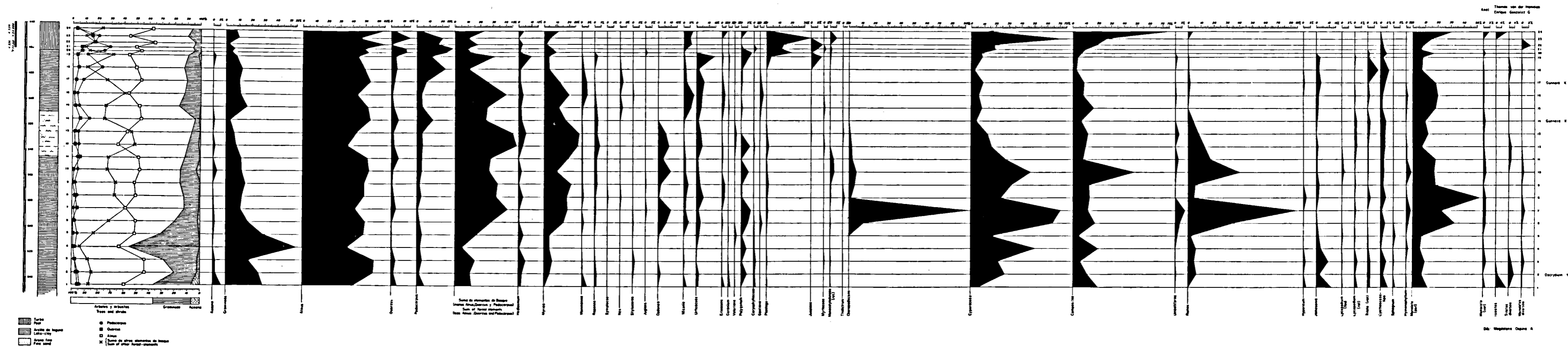
If the above mentioned interpretations are right, then the 260—285 cm interval might be interpreted as Alleröd-interstadial, with a drier climate than the remaining 285—330 cm interval.

This last-mentioned interval will have to represent then at least the part of the Late-glacial before the Alleröd.

SECCION "CUP"

Ciudad Universitaria - Puerta calle 45

Fig. - Nº 8



Then the problem arises: why is the Gramineae-percentage so low, while this pollen reaches more than 40 % during Younger Dryas time?

The solution might be the following. The climate during the last part of the last glaciation was becoming gradually drier (the Sabana lake was drying out, and its surface was lower than 2556 metres), but still considerably wetter than during the lower Holocene, and consequently the tree-line was still lying higher than today. When the climate ameliorated still further, a dense Alnetum was formed on the marshy lake bottom. This situation continued until at the beginning of the Alleröd-time the climate became definitely warmer and drier (*Myrica* dominance). Then, during Younger Dryas time the climate went colder, but remained dry. The possibility also exists that the sedimentation of the 330—355 cm interval, deposited immediately after the place where the section was taken ran dry, was extremely slow or that even a small hiatus may be present (small cracks, formed apparently by a drying out of the humic clay, were observed).

At any rate it is clear that local conditions influenced the picture given by the diagram, after the lake disappeared (at 355 cm), resulting first in a rather high Gramineae percentage and then, when the climate became a little more favorable (so that *Alnus* could grow on the place), in an abnormally high *Alnus* percentage.

The following zones may now be distinguished in the diagram, with their probable or possible correlation with European zones, C 14 dates and probable or possible ages of their limits. The zone numbers refer to the Sabana de Bogotá only, and the fact that they partly coincide with the numbers of the European zones, eventually even combined with a time correspondence, is incidental.

Although there is still much to be proved in detail, the general picture seems to be clear: a correlation of the climatic phases of the Holocene (and possibly also of the Late-glacial) of the Sabana with the European and North American ones seems to be perfectly possible, and the zone limits seem to be synchronous (at least those limits where C 14 dates a little above or below these limits are available).

In the great cycle Glacial—Interglacial the climate in Europe and northern North America was respectively dry and wet, but in the Sabana de Bogotá, near the equator, respectively wet and dry. In the minor climatic changes of the Holocene this reversal of climatic conditions seems not to be present: both in Europe etc. and synchronously in the Sabana de Bogotá we find the same well-known alternation of dry-wet-dry-wet. An interesting point still to discuss is the increase of Gramineae in zone VIII, from a depth of 70 cm upwards. This increase is not accompanied by "cold" species, but by certain species like *Plantago*. This increase cannot be due to a considerably colder climate (today the slopes of the mountains surrounding the Sabana are covered, or were covered in historical time, almost completely by forest up to  $\pm$  3200 m), nor to an excessively dry climate (climatic savanna), as we are in a relatively wet period, and the foregoing drier periods do not show such a savanna vegetation.

Hence it must be the effect of human agriculture. Agriculture was practised by the Chibcha indians before the arrival of the Spaniards; the latter found therefore a type of park-landscape, so that they called the plateau: Sabana de Bogotá. But from the foregoing it will be clear that this was an anthropogene savanna; before the advent of agriculture the Sabana de Bogotá was

		Zones in the Sabana de Bogotá	C 14 dates	Climate	Vegetation (Sabana de Bogotá)	Possible or probable correlation with the european climatic phases.	Possible age of zone-limits.
		HOLOCENE		VIII	1650 ± 160 A.C.	Wet (and a little colder?).	<i>Alnus</i> dominant. The Gramineae increase gradually, starting a little after the beginning of this period, being the result of increasing agriculture.
VII				Relatively dry.	<i>Alnus-Myrica</i>	Subboreal	3000 B.C.
VI					<i>Alnus</i> dominant	Atlantic	5500 B.C.
V	6070 ± 120 B.C.			Dry	<i>Myrica</i> dominant	Boreal	6600 B.C.
IV	7010 ± 400 B.C.			Dry Relatively cold, gradually becoming warmer.	<i>Myrica</i> dominant (Gramineae more frequent than in the succeeding phase but less frequent than in the preceding).	Preboreal	8100 B.C.
III				Dry cold	„Parklandscape“ <i>Myrica</i> dominant amongst the trees. Gramineae frequent.	Younger Dryas time	8900 B.C.
II				Dry Warmer than the succeeding and preceding phases.	<i>Myrica</i> dominant ( <i>Alnus</i> still frequent in the lower part).	Alleröd interstadial?	9900 B.C.
I				Wet and Cold	<i>Alnus</i> dominant		14000 or 16000 B.C. ?
WURM GLACIAL					21900 ± 600 B.C. ? (probably too old)	Wet and Cold	<i>Alnus</i> in general dominant. <i>Quercus</i> frequent, but gradually disappearing in the uppermost part. Gramineae and <i>Acaena</i> frequent. Sabana de Bogotá covered with a lake, which is drying up towards the end of this phase.
Pleiglacial II							

covered with dense forests. Remnants of these forests are still to be found in patches of Alnetum at different sites, and especially in the little pollen producing *Ilex-Vallea-Eugenia* forest near Suba. The beginning of intensive agriculture on the Sabana de Bogotá can now be dated, with the aid of a C 14 date as 1650 ( $\pm 160$ ) A. D., that is somewhat after the arrival of the Spaniards. The radiocarbon date of this sample may be too young, perhaps by the influence of small rootlets which from the nearby surface might have penetrated in the charcoal particles without being observed. The rate of sedimentation from the dated level upwards increased considerably, probably because of the increase of the frequency of the inundations for the reason of the destruction of the forests both on the Sabana itself and on the surrounding mountains.

Let us now turn to the diagram of section C. U. P. (fig. 8). The section was taken some 500 metres south of section C. U. X., near the entrance of the Ciudad Universitaria. The upper part (not represented here) is of Holocene age, then follows from 440—460 cm a peat-layer, and then lake-sediments alternating with thin peaty layers until 620 cm, representing a lake-shore facies. From 620 cm down pure lake-clays are present. Two C 14 samples were taken from the peat layer (Col. 2a and 2b) and analysed in the Copenhagen laboratory (see above); both samples are more than 34.000 years old.

The interpretation of the diagram presents serious problems, probably mainly because it represents a shore-facies, while in the diagram C. U. X. the sediments older than 21.900 B. C. (?) are represented by pure lake sediments.

The diagram shows a continuous rather low *Quercus*-curve, a rather high percentage of *Alnus*, a *Podocarpus*-curve which shows rather high percentages in the uppermost part, and a high percentage for the rest of the forest elements. Except in the lowermost parts, the Gramineae and *Acaena*-percentage is relatively low.

A great part of the "rest of the forest-elements" consists of *Myrica*; this plant forms the absolute dominant of the same group in the Holocene inundation clays, and is relatively scarce in lake sediments.

As the sediments of this section are shore-sediments, we will have to abstract this local influence if we want to compare this section with the lake sediments of section C. U. X. If we do so, then all the other curves will rise, amongst them the *Quercus*, *Podocarpus* and Gramineae curves. The whole picture will then be that of an interstadial, and there seems no other place in the diagrams of section C. U. X. where the diagram of section C. U. P. fits reasonably, as somewhere in the interval between 8 and 11.5 metres. This interval was interpreted as corresponding to a Würm-interstadial, and so we see that a date of  $> 34.000$  fits very well in this picture.

In view of the above mentioned facts it will be clear that on the C. U. P. site some five metres of sediments, representing the cold last part of the Würm, are lacking. The interstadial sediments lie there at least some 4.5 metres higher than 500 metres to the north. Perhaps tectonic movements were responsible for this fact. This seems not to be impossible, but we cannot yet give a definite answer to this question.

## 12. CONCLUSIONS

The more important conclusions of the present study may be summarized as follows:

1°. The tropics were equally effected by important temperature fluctuations, glacial and interglacial, as the Northern temperate-regions.

2°. The average year temperatures during the coldest phases of the Würm-glacial in the Andes of equatorial South America, were approximately 8° C lower than today. During the warmest phases of the interglacials these temperatures were about 2°—3° C higher than today. These values are not essentially different from those calculated for Europe, and those found by Emiliani for surface ocean water. During the Riss I glacial, temperatures were apparently 11° C lower than today.

3°. The glacials of the tropics are also periods with a major annual atmospheric precipitation, that is to say pluvials. The interglacials of the tropics are thus periods with lowered annual atmospheric precipitation, that is to say interpluvials.

4°. Minor fluctuations of the annual atmospheric precipitation occur during the glacials, partly independent of the minor temperature fluctuations. The late Würm and the late Riss I were relatively dry periods.

5°. The fluctuations of the tree-line, at least in the equatorial Andes, did not depend only on temperature fluctuations, but also on fluctuations of the annual precipitation. A lower temperature caused a downward shift of the tree-line, but a higher annual precipitation forced it upward. For that reason the lowerings of the tree-line during glacial—pluvial phases were less than would correspond to the decrease of temperature only.

6°. On the basis of the temperature curves for the Upper Pleistocene and Holocene and combined radiocarbon dates, it may be said that the glacials and interglacials, and also the interstadials and probably the minor climatic fluctuations of the Holocene, of equatorial South America, are perfectly contemporaneous and may directly be correlated with the ones known from the temperate regions of the Northern hemisphere (see fig. 6).

7°. The snow-line and the tree-line during the three glacial maxima (temperature minima) of the last portion of the Würm-glacial (Pleniglacial II), were situated approximately as follows:

Snow-line	Tree-line
Minimum 1° — 3050 m	2250 m
Minimum 2° — 3025 m	2400 m
Minimum 3° — 3215 m	2400 m

For the Riss I glacial maximum the figures are:

2800 m	± 1700 m
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And the present day conditions:

4550 m	3200 m
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8°. In the Late glacial and Holocene of the Sabana de Bogotá eight zones (numbered I—VIII) may be distinguished. In so far as C 14 dates are available, the zone limits seem to coincide very well with european zone limits. The succession of dry-wet-dry-wet during the Holocene in the Sabana de Bogotá seems to correspond very well with the european Boreal-Atlantic-Sub-boreal-Subatlantic succession.

9°. During the wet and cold glacial phases *Quercus* was one of the most common trees on the slopes of the mountains which surround the Sabana de Bogotá. During the drier and warmer interglacials the Quercetum was almost entirely replaced by a Weinmannietum or similar associations.



10°. The following major subdivisions of the Upper Pleistocene (and Holocene) could be recognized in the Sabana de Bogotá (see also point 6): Holocene (with 5 zones); Late-glacial; Würm-glacial: Pleniglacial II, Interpleniglacial (including two interstadials separated by a cold phase), Pleniglacial I; Riss-Würm interglacial; Riss-glacial: Riss II (= Warthe), Riss I—II interstadial, Riss I.

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## ERRATA

	<b>Dice</b>	<b>Debe decir según M.N.</b>
471	54 Montuledo	Montludo
475	57 Río Toran	Río Torón
479	57 Grábere	Crabere
482	55 Pt. de la Hourquette	Pt. de la Hurqueta
484	55 P. Maubermé	P. Mauberme
488	55 Pt. d'Orle	Pt. de Orlá
489	54 P. du Pt. d'Orle	P. del Pt. de Orlá
480	47 Areño 2532 altitud	2522 Altitud
472	55 L. Layo	L. Layó
468	53 Mina Margerita	Margarita
469	49 Beños	Benos (según nomenclátor)
"	" Begos	Begós " "
472	48 Arros	Arrós " "
473	48 Moncarbau	Montcorbán " "
4°18'	42°38' Gregüeña	Cregüeña
4 17	42 37 Valibierna	Vallibierna
4 31	42 36 Cota 2951	En M.N. hay dos cotas superiores a 3.000 metros.
4 34	42 38 Montarto 2820 altitud	2830 Altitud
4 37	42 36 El Colomes	Colomé
4 30	42 39 Las Losas	Las Llosas
4 34	42 41 Río de Valartías	Río Balartias
4 39	42 40 Río Garóna de Ruda	Río de Ruda
4 32	42 42 Garús	Garós (según nomenclátor)
4 32	42 44 Candalías	Campalías