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Late and middle Pleistocene climatic change and forest development in Colombia: pollen record Funza II (2–158 m core interval)

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Abstract

A 586 m long core, Funza II, was recovered from the lake sediments of the high plain of Bogotá (Eastern Cordillera, Colombia, 2550 m alt.), which represent the bottom of a drained lake. Results of the palynological analysis of the interval 2–158 m with sample distances of 1 m are presented. Time control of the Funza II core is based on zircon fission-track datings of intercalated volcanic ash horizons. In addition, pollen record Funza II could be correlated in detail with pollen record Funza I, located at 1 km distance. The Funza I pollen record has been graphically correlated with the oxygen isotope record of ODP Site 677 (East Pacific). Oxygen isotope stages 19.1 to 3.0 have been tentatively recognized in the pollen record, indicating that the interval 158–2 m represents approximately the period of 735–28 ka. The average calculated time resolution is 4550 yr with considerable fluctuations depending changes in accumulation rate.

The interval 158–131 m core depth (estimated age 735–569 ka) shows warm climatic conditions most of the time and is tentatively correlated with the oxygen isotope stages 19.1 to 15.1. The pollen spectra have no direct modern analogues because of the absence of *Quercus* and related conditions. The upper forest line oscillated mainly from 2100 to 2700 m during most of the interval. The corresponding average annual temperature on the high plain is 6.5–11°C. The high plain was situated in the Andean forest belt most of the time. The upper limit of the subandean forest belt (*Acalypha*, *Alchornea*) was situated some hundreds of meters below the modern elevation. *Podocarpus* was most important in the lower part of the Andean forest belt. *Weinmannia* forest, the precursor of the modern *Weinmannietum*, included a substantial contribution of *Hedyosmum* as well as lower frequencies of *Myrsine* (= *Rapanea*) and *Eugenia*. A type of *Vallea*–*Miconia* forest, including low frequencies of *Ilex* and *Myrsine* (= *Rapanea*), could have occurred on the drier parts of the high plain. The lake was shallow most of the time, with local marsh vegetation of cyperaceous reed swamp and *Hydrocotyle*. *Myrica* thickets (*M. parvifolia*) and *Alnus* carr (swamp forest) covered the wet flats around the lake. *Myrica* (*M. pubescens*) and *Alnus* possibly contributed also with low frequency to the zonal Andean forest belt. Dwarf forest of *Polylepis*, *Myrica* and Compositae scrub occurred at the upper forest line.

The interval 131–100 m core depth (estimated age 569–350 ka) shows cold climatic conditions most of the time and is tentatively correlated with oxygen isotope stages 14.4 to 11.1. The upper forest line oscillated mainly from 1800 to 2500 m. The corresponding average temperature on the high plain is ca. 5–9.5°C. The high plain was situated in the grassparamo belt most of the time. Apart from Gramineae (e.g. *Calamagrostis*, *Chusquea*) and woody stem rosettes of *Espeletia* (Compositae) a variety of paramo herbs (*Valeriana*, Caryophyllaceae, *Geranium*, *Aragoa*, *Lycopodium*) were present with substantial frequencies, and abundant cushion bogs of *Plantago* were present. The water level in the lake was high and marsh vegetation limited. *Polylepis* dwarf forest occurred in the subparamo belt,

along with shrub of Compositae, *Hypericum* and Ericaceae. In the Andean forest belt *Vallea-Miconia* forest and *Weinmannia-Hedyosmum* forest were most important.

The interval 100–57 m core depth (estimated age 350–186 ka) shows warm climatic conditions most of the time and is tentatively correlated with the oxygen isotope stages 10.2 to 7.1. The upper forest line oscillated from 2000 to 2600 m in the first part and from 2600 to 2900 m in the last part of this interval. The corresponding average annual temperature is 6–10° and 10–12°C, respectively. The high plain was in the first part of this interval most of the time situated in the paramo and in the last part of this interval in the Andean forest belt. During this interval *Quercus* migrated into the area of the high plain. *Quercus* forests occurred in a wide altitudinal range (1000–2800 m) and constituted at first local patches of forest, but at the end of this interval zonal *Quercus* forests were a major part of the Andean forest belt. *Acalypha* and *Alchornea* reached higher elevations in the *Quercus* forests, and the upper limit of subandean forest rose to modern elevations. *Weinmannia* dominated in the *Weinmannia-Hedyosmum* forest type. At the end of this interval the contribution of *Vallea-Miconia* forest increased markedly and replaced *Weinmannia* forest. *Podocarpus*-rich forest occurred in the lower part of the Andean forest belt. *Alnus* carr and *Myrica* thickets were abundant around the lake, which was of a shallow type. Algae (*Botryococcus*) became very abundant from the beginning of this interval to the top of the record.

The interval 57–2 m core depth (estimated age 186–24 ka) shows for the first time in the record abundant presence of zonal *Quercus* forests. The composition of the Andean forest belt had changed dramatically. Based on arboreal percentages, climatic conditions seem warm most of the time, but the high frequency of *Quercus*, a wind-pollinated tree that produces large amounts of pollen, exaggerates real conditions. This interval is tentatively correlated with the oxygen isotope stages 6 to 3.0. The upper forest line oscillated from 2000 to 3000 m most of the time. The corresponding average annual temperature is 6–12.5°C. *Quercus* forests, resembling the modern *Saurauia-Quercus humboldtii* forest, and *Weinmannia-Hedyosmum* forest, resembling the modern *Weinmannietum*, dominated in the Andean forest belt. *Vallea-Miconia* forest probably resembled the modern *Xylosma-Duranta-Vallea* forest, but the latter is palynologically difficult to recognize. *Eugenia*, *Ilex* and *Myrsine* (= *Rapanea*) contributed substantially to this rather dry forest type of low stature. *Polylepis* dwarf forest was frequent at the forest line and possibly also in the paramo belt up to 4000 m. *Alnus* carr dominated completely the flat parts of the high plain. *Myrica* thickets and marsh vegetation diminished in the last part of this period. Sediment accumulation was very rapid (up to 60 cm per 1000 yr). Supposedly, erosion of the Tequendama Falls in the Bogotá River, the only outlet of the high plain, led to the final draining of the lake between ca. 28 and 22 ka.

The Andean biozones VI and VII are represented in this part of the record. Biozone VI (158–94 m core interval; estimated age 735–350 ka) is characterized by the presence of *Alnus* and absence of *Quercus*. Biozone VII (94–0 m core interval; estimated age 350–0 ka) is characterized by the presence of *Alnus* and *Quercus*, both from northern hemisphere origin.

1. Introduction

The high plain of Bogotá, at 2550 m alt. in the Eastern Cordillera of Colombia (Fig. 1A), represents the former bottom of a large Pleistocene lake (Van der Hammen and González, 1960), and is a tectonic-sedimentary basin. The sedimentary infill of this basin constitutes a continuous stratigraphic sequence with a thickness of ca. 600 m, covering at least the last 3 million years (Andriessen et al., 1993). The high plain is drained by the Bogotá River and its tributaries with one outlet, the Tequendama Falls.

The village of Funza lies more or less at the

location where the sedimentary sequence reaches maximum depth. Near this village the Funza I core was drilled in 1976, reaching a depth of 357 m. The results are presented in Hooghiemstra (1984, 1989). In 1988 another coring program was established to recover a new core from the sediment sequence near Funza. The Funza II site lies at ca. 1 km distance from the location of Funza I (Fig. 1B). This Funza II core reached a depth of 586 m. The lowest 15 cm of the core are made up of sandstone, suggesting that bedrock of Cretaceous and Tertiary sandstone was reached.

The present article presents the first full results of the 2–158 m interval of the Funza II core with

a sample distance of 100 cm. The interval 205–540 m is shown by Hooghiemstra and Cleef (submitted). Unfortunately, the interval 159–204 m was not recovered during coring due to technical problems, but this interval is well represented in the Funza I core (Hooghiemstra, 1984, 1989). Pollen analysis of the Funza II core with sample distances of 20 cm (ca. 1000 yr time resolution) will be presented later.

The present vegetational distribution of the Eastern Cordillera is presented in Fig. 2. A summary of the altitudinal distribution of the main vegetation belts is given. For more detailed information on the vegetation belts, the reader is referred to, e.g., Van der Hammen (1974), Cleef (1981), Cleef and Hooghiemstra (1984), Van der Hammen and Cleef (1986) and Hooghiemstra and Cleef (in press).

The Eastern Cordillera of the northern Andes rises up from the tropical lowlands, where rain forests, savannas, or xerophytic vegetation types dominate. The savanna area of the Llanos Orientales and the Orinoco lie northeast of this Cordillera; in the southeastern area rain forest is present. West of the Cordillera lies the Magdalena valley. In the Eastern Cordillera the warm tropical vegetation belt stretches from the lowlands to an altitude of ca. 1000 m. At about this elevation several “tropical” taxa, such as most Bombacaceae, disappear, whereas several other taxa are restricted to (parts of) this belt (e.g. *Byrsonima*, *Iriarte*, *Mauritia* and *Spatiphyllum*).

The next altitudinal zone is occupied by subandean forest (lower montane forest) from ca. 1000 to 2300 (2500) m. In the subandean vegetation belt the average annual temperature is from 22° to 13°C, and the annual rainfall is mostly between 1200 and 3000 mm. In the pollen diagrams this vegetation belt is represented by elements such as *Acalypha*, *Alchornea* and *Cecropia*. These genera are good pollen producers and they do not extend beyond the upper limit of the subandean forest belt. The same is true for many *Palmae*, *Hieronima*, *Ficus* and *Malpighiaceae*. From ca. 2300 (2500) to the upper forest limit at ca. 3200–3500 m elevation, lies the Andean forest belt (upper montane forest). The Andean forest belt has an average annual temperature of 9–16°C and an annual rainfall of 700–1400 mm in dry inter-Andean high plains and

adjacent valleys, and 1000–3000 mm on outer slopes of the high plain area. It is mostly characterized by forests of *Quercus* and *Weinmannia*. In the pollen diagrams other prominent taxa are *Alnus*, *Myrica*, *Podocarpus*, *Hedyosmum*, *Eugenia*, *Ilex*, *Juglans*, *Melastomataceae*, *Miconia*, *Myrsine* (= *Rapanea*), *Styloceras*, *Symplocos* and *Vallea*, although most of these genera are not restricted in their distribution to this vegetation belt.

The next altitudinal belt includes the high Andean dwarf forest (subalpine dwarf forest) and shrub formations, and the subparamo, extending from ca. 3200–3400 to 3600 m alt. It may be developed as a rather irregular belt, especially at its upper limit. It is characterized by such woody taxa as *Compositae*, *Ericaceae*, *Polylepis*, *Escallonia* and *Hypericum*. The forest trees of the genera *Quercus* and *Weinmannia* do not grow in this vegetation belt. It has an average annual temperature of 6–9°C and the annual rainfall is mostly 700–2500 mm. The grassparamo from ca. 3500 to 4000–4200 m consists mainly of grasses. Besides the grasses the most characteristic elements are woody stemrosettes of the genus *Espeletia*, and a number of herbaceous species such as *Gentiana*, *Halenia*, *Valeriana*, *Aragoa*, *Bartsia*, *Geranium*, *Plantago*, *Ranunculus*, *Paepalanthus* and *Lycopodium* (especially species with foveolate spores). The average annual temperature is 3–6°C, and the annual rainfall mostly 700–2500 mm. In the superparamo, extending from ca. 4000–4200 m upwards to the snowlimit, the vegetation becomes scarce and often patchy. *Espeletia* is mostly lacking. Characteristic elements are *Draba*, *Caryophyllaceae*, *Senecio niveo-aureus*, mosses and blue algae. The average annual temperature is 0–3°C and daily groundfrosts occur. The nival zone proper, principally devoid of vegetation, reaches from ca. 4500 to 4800 m alt. (locally somewhat higher) upwards. The highest parts of the Eastern Cordillera (ca. 5500 m alt.) may be covered permanently with snow.

2. Methods

2.1. Core recovery and sampling

The drilling was carried out by Ingeominas with Longyear equipment. The core was taken in

Fig. 1. (A) Map of Colombia and the area of the high plain of Bogotá in the Eastern Cordillera indicating the topography of the surrounding mountains.

intervals of 150 cm. The lithological description of the sediments is presented in Fig. 3. At each meter a sample of 3 cm³ was taken for palynological analysis. The samples were treated using the standard procedure of the Hugo de Vries-laboratory (the material was treated with a boiling 10% aqueous Na₄P₂O₇ solution, followed by acetolysis and a gravity separation by means of a bromoform-alcohol mixture with a specific gravity of 2.0). Exotic markers (*Lycopodium* spores) were added to calculate pollen concentrations. The samples were sealed in with paraffin wax and counted on

a Leitz microscope (magnification 400×–1000×). Each sample was counted until a pollen sum of at least 300 grains was reached. Elements included in the pollen sum are listed in Table 1.

2.2. Time control

Several volcanic ash horizons were intercalated in the lake sediments, of which the zircon fractions have been dated by the fission-track method (Andriessen et al., 1993). One zircon sample is located in the core interval presented in this paper:

Fig. 1. (B) shows in detail the high plain of Bogotá with the location of the boreholes Funza I and Funza II. (After “Mapa de la Sabana de Bogotá”, 1:50,000; Instituto Geografico Agustín Codazzi, Bogotá, 1975).

the 67.76–67.79 m interval was dated 0.20 ± 0.12 Ma. The upper ca. 50 m of the Funza II core could be correlated with four other pollen records from the vicinity that cover the last

glacial–interglacial cycle, viz. the pollen records of CUX (Van der Hammen and González, 1960), Tarragona (Dueñas, 1979), Funza I (Hooghiemstra, 1984, 1989) and Fuquene III

Fig. 2. Altitudinal distribution of vegetation belts in the Eastern Cordillera of Colombia at present and during the last glacial maximum. Vertical shifts of the vegetation belts are mainly related to changes in temperature. After Van der Hammen, 1974.

Fig. 3. Lithological description of the interval 2–158 m of the Funza II core. (Description after S.R. Arevalo-Gamboa and I.D. Pinzon-Villazon. From G. Sarmiento-Perez, Ingeominas, Bogotá, internal document.)

(Van der Hammen and Hooghiemstra, in prep.). Graphic correlation of the Funza I arboreal pollen record with the oxygen isotope record of ODP core 677 (Shackleton and Hooghiemstra, unpubl. data; see also Hooghiemstra and Sarmiento, 1991; Hooghiemstra et al., 1993; Andriessen et al., 1993) showed a tentative land–sea correlation for the upper 300 m of the sediment sequence of Bogotá, representing the last ca. 1.2 Ma. Several zircon fission-track datings are included in this core interval. The 158–2 m interval of the Funza II core

is estimated to represent the period of ca. 735,000 (oxygen isotope stage 19) to ca. 26,000 yr B.P.

3. Results

3.1. Construction of the diagrams

The results of the pollen analysis are presented in a percentage diagram (Fig. 4). On the left hand

Fig. 3. (continued)

side two main diagrams present the downcore changes in the representation of four vegetation belts. From left to right are the subandean forest belt, the Andean forest belt, the subparamo vegetation belt and the grassparamo belt. In the first main diagram *Alnus* has been excluded from the pollen sum, while in the second one *Alnus* is included. *Alnus acuminata* produces large amounts of pollen and forms extensive (azonal) swamp forests (carr) around the former lake of Bogotá, but also occurs in (zonal) slope forests. The large

pollen production of the azonal *Alnus* forests, in combination with the relatively low pollen production of the other forest elements, possibly forms a disturbing factor in the estimation of shifts of the upper forest line. For this reason two ways of calculation were applied. The subandean and Andean forest belts together represent the upper forest line.

On the right hand side the curves of the individual taxa are represented based on the pollen sum (*Alnus* included). The zonation of the diagram is

Table 1

Pollen taxa included in the four recognized ecological (altitudinal) groups, constituting the "standard" pollen sum

Subandean forest elements

Acalypha, Alchornea, Cecropia

Andean forest elements

Alnus, Quercus, Podocarpus, Hedyosmum, Weinmannia, Vallea, Myrsine (= Rapania), Symplocos, Drimys, Ilex, Styloceras, Daphnopsis, Juglans, Bocconia, Melastomataceae, Miconia, Urticaceae–Moraceae, Pilea, Eugenia, Myrtaceae, Dodonaea, Gaillardendron, Myrica

Subparamo elements

Ericaceae, Hypericum, Compositae (subfamilies Tubuliflorae and Liguliflorae), Polyplepis–Acaena

Grassparamo

Gramineae

mainly based on the fluctuations in the main diagram. The numbers of the pollen zones follow the zonation used in Funza I (Hooghiemstra, 1984, 1989): pollen zones that correlate in time are assigned the same numbers; in core Funza I with a prefix F1 and in core Funza II with a prefix F2.

Descriptions of the pollen zones are provided in Appendix 1.

4. Vegetational and climatological reconstruction

The Funza II borehole lies more or less at the location where the sedimentary sequence reaches maximum depth, the present altitude of the surface sediments is 2550 m. Mountains that reach an altitude of 3000–3200 m are found ca. 20–25 km away from Funza, while mountains reaching 3600–3800 m altitude lie within a distance of 35–40 km. The vegetation on the surrounding mountains is the primary source of pollen for the lake sediments. Therefore, low percentages of open vegetation (paramo vegetation) indicate that the surrounding mountains were (almost) entirely covered with forest. Increasing values of elements characteristic for paramo vegetation correspond with a progressively downward shift of the upper forest line.

According to Hooghiemstra (1984), following the method of Van der Hammen and González (1960), the altitudinal forest line is characterized

by an arboreal pollen sum of 40% (calculations with *Alnus* included in the pollen sum). Van der Hammen and González (1960) calculated that at ca. 40% arboreal pollen and 20% Gramineae pollen, the level of the upper forest line lies at ca. 2550 m. When the percentage of Gramineae pollen reach values of ca. 40–45%, the boundary between subparamo and grassparamo lies at this level. Climatic humidity has some influence on the altitudinal level of the forest line, but the main determining factor is the prevailing annual temperature.

Table 2 gives the percentage of arboreal pollen at Funza (*Alnus* included in the pollen sum) and the corresponding altitudinal level of the upper forest line. The third column shows the corresponding estimated temperature at the elevation of Bogotá, based on a lapse rate of 0.66°C per 100 m forest line displacement and an annual average temperature of 9.5°C at the upper forest line.

4.1. Introduction to the vegetational reconstruction of the pollen zones F2-23 to F2-14 (period 735–333 ka)

The pollen zones F2-23 to F2-14 (core interval 158–100 m) are characterized by presence of *Alnus* and absence of *Quercus*, which does not appear below 94 m core depth. Therefore, this interval represents the upper part of biozone VI (Van der Hammen and González, 1960).

Alnus is a northern hemisphere genus which first arrived in South America across the Panamanian Isthmus, which came into existence some 5–4

Table 2

Basic relationship between arboreal pollen percentage (*Alnus* included in the pollen sum), altitudinal position of the upper forest line, and average annual temperature on the high plain of Bogotá (2550 m elevation)

Arboreal pollen (%)	Forest line (m)	°C at 2550 m
30	2000	6.2°
40	2550	9.9°
50	2700	10.9°
60	2900	12.2°
70	3100	13.5°
80	3300	14.8°

Fig. 4. Pollen percentage diagram of the 2–158 m interval of the Funza II core (Eastern Cordillera, Colombia, 2550 m alt.) analysed with 100 cm sample distance. Records of a number of selected pollen taxa are presented. The pollen zones are provisional and will be defined more precisely after time resolution has been increased. Time control is provided by a zircon fission-track date of an intercalated volcanic ash horizon (see also Fig. 5). Note the absence of *Quercus* below ca. 94 m core depth.

Fig. 4. Pollen percentage diagram of the 2–158 m interval of the Funza II core (Eastern Cordillera, Colombia, 2550 m alt.) analysed with 100 cm sample distance. Records of a number of selected pollen taxa are presented. The pollen zones are provisional and will be defined more precisely after time resolution has been increased. Time control is provided by a zircon fission-track date of an intercalated volcanic ash horizon (see also Fig. 5). Note the absence of *Quercus* below ca. 94 m core depth.

million years ago (Keigwin, 1978, 1982). *Alnus* forms carr vegetation on ill-drained flats around the lake and almost never occurs above the upper forest line. High pollen production of *Alnus* and eolian transport of pollen grains account for a high background effect in the pollen record: only percentages above 15–20% indicate local *Alnus*. According to Grabandt (1980, p. 143) *Alnus* belongs to the genera with highest effectiveness in pollen dispersal and she noted for *Alnus* the extreme *t/p* value of 0.2 (*t/p*: tree/pollen, indicating the relation between “real” vegetation cover and the contribution of vegetation concerned to the pollen rain). *Alnus* is in direct competition with *Myrica* swamp forest (*M. parvifolia*) on wet flats around the lake. Presence of shallow water aquatics, such as Cyperaceae, *Polygonum*, *Ludwigia*, *Hydrocotyle* and *Myriophyllum* alternated with the aquatic fern *Isoetes* that often occurs in deeper water of 5–10 m depth. Most of the time, high water levels in the lake corresponded to cool and glacial periods when evapotranspiration was relatively low.

When *Quercus* was absent, the upper limit of the subandean forest belt was at lower elevation than today, and the contribution of many arboreal elements was different from present-day conditions; such pollen spectra do not have modern analogues. However, altitudinal zonation and ecology of the Andean vegetation belts must have resembled late Quaternary conditions enough that an interpretation based on knowledge of present-day conditions can produce a reliable reconstruction of the vegetational and climatic history of this area.

Vallea, a semi-deciduous tree, at present occurs mostly in the drier forests covering the high plain and the surrounding hills. The appearance of *Alnus* at the beginning of biozone VI must have reduced the extension of *Vallea* forests and *Myrica* thickets around the lake. In the upper part of biozone VI, *Vallea* reached on the average higher frequencies again and possibly became more important as an element of the zonal forests. Apart from *Podocarpus*, the Andean forest belt contained an important contribution of *Weinmannia*, possibly in combination with *Vallea* under drier conditions and with *Hedyosmum* under more humid condi-

tions. At the forest ecotone and in the lower paramo belt the area covered by *Polylepis* woodland increased substantially. The woody shrubs of Ericaceae, *Hypericum*, Compositae and *Aragoa* are abundant in the second part (pollen zones F2-18 to F2-12) of this interval and reflect, upon the average, a low position of the upper forest line. A wider altitudinal range of the subparamo belt also could be hypothesized (under modern conditions ca. 300 m, viz. from ca. 3200–3500 m elevation).

Comparing the warm periods represented by the pollen zones F2-23 to F2-19 with those in the pollen zones F2-11 to F2-7, a higher representation of *Weinmannia*, *Myrsine* (= *Rapanea*) and *Miconia* is observed. This could point to a slowly rising upper forest line during the period 0.7–0.2 Ma.

Summing up, the following assumptions will be used in the interpretation of the pollen zones F2-23 to F2-14. The altitudinal differentiation of the paramo belt is comparable to modern conditions: the subparamo and grassparamo belts have an altitudinal range of ca. 300 and ca. 600 m, respectively. The upper forest line is assumed to have about the same altitudinal position, in relation to the thermal altitudinal gradient, as under modern conditions. Except for the absence of *Quercus*, the Andean forests were made up of basically the same floristic elements. Structure and stature of the Andean forests were comparable to modern conditions. The boundary between subandean and Andean forest belts was at a slightly lower elevation, possibly some 100–200 m, as compared to present day.

Pollen zone F2-23 (estimated period 735–725 ka)

Arboreal percentages of 45–54% (27–34% if *Alnus* is excluded from the pollen sum) indicate that the upper forest line was situated at 2600–2700 m elevation. In the Andean forests *Podocarpus*, *Hedyosmum*, *Weinmannia*, *Vallea* and *Miconia* were the most important elements, indicating the presence of *Weinmannia* forest and *Vallea*–*Miconia* forest. The subparamo belt was dominated by Compositae, whereas other subparamo taxa, such as *Hypericum* and Ericaceae, were almost absent. In open patches *Borreria* was present, an element always represented with low values in this habitat. The subparamo belt apparently had a narrow

altitudinal range and sparse *Polylepis* dwarf forest was present. The most important elements of the grassparamo are Gramineae, *Valeriana*, Caryophyllaceae, *Plantago*, *Lycopodium* fov. and Umbelliferae. The presence of Cyperaceae, *Hydrocotyle* and *Myriophyllum* indicate shallow water conditions under Andean forest conditions near the site. *Isoetes* prevailed in parts of the lake with deeper water. *Alnus* carr and *Myrica* thickets occurred on the wet flats bordering the lake. The sedimentary record shows lacustrine clays. The pollen concentration is $(67\text{--}150) \times 10^3$ pollen cm^{-3} .

Pollen zone F2-22 (estimated period 725–689 ka)

Arboreal percentages of 32–40% (10–25% if *Alnus* is excluded from the pollen sum) indicate that the forest line was situated at 2000–2100 m elevation. In the Andean forests *Podocarpus*, *Weinmannia*, *Hedyosmum* and *Vallea* were the most important elements. *Miconia* is almost absent, suggesting that the contribution of *Miconia* in these glacial uppermost continuous forests was low. This characteristic is valid for the period covered by the pollen zones F2-23 to F2-8. The most important elements of the subparamo are Compositae, Ericaceae and *Polylepis* dwarf forest. In the grassparamo belt Gramineae, *Valeriana*, Caryophyllaceae, *Lycopodium* fov., *Geranium*, *Aragoa* and Umbelliferae were most important.

Presence of *Isoetes* indicates that deeper water conditions prevailed locally. Marsh elements, such as Cyperaceae, *Myriophyllum* and *Sphagnum* occurred in shallow water. *Alnus* carr and *Myrica* thickets were probably absent on the high plain. The sedimentary record shows lacustrine clays. The pollen concentration is $(36\text{--}76) \times 10^3$ pollen cm^{-3} .

Pollen zone F2-21 (estimated period 689–660 ka)

Arboreal percentages of 38–66% (29–41% if *Alnus* is excluded from the pollen sum) indicate that the upper forest line was situated at 2600–2900 m elevation. In the Andean forest *Podocarpus*, *Hedyosmum*, *Weinmannia*, *Vallea* and *Miconia* were the most important taxa. The subparamo was dominated by Compositae, associated with Ericaceae and *Polylepis* dwarf forest. The most

important elements of the grassparamo are Gramineae, *Plantago*, *Valeriana*, Caryophyllaceae, *Geranium* and *Lycopodium* fov., and only recorded with low values at the base and top of this zone.

Alnus carr and *Myrica* thickets were abundant on the wet flats around the lake. The presence of marsh elements, such as Cyperaceae, *Hydrocotyle*, *Polygonum*, *Ludwigia* and *Myriophyllum* indicate shallow water conditions near the site. Very low presence of *Isoetes* corroborate this interpretation. The sedimentary record shows lacustrine clays. The pollen concentration is $(65\text{--}450) \times 10^3$ pollen cm^{-3} .

Pollen zone F2-20 (estimated period 660–622 ka)

Arboreal percentages of 25–30% (15–16% if *Alnus* is excluded from the pollen sum) indicate that the upper forest line was situated at 2000–2100 m elevation. In the Andean forest belt *Podocarpus*, *Hedyosmum*, *Weinmannia*, *Vallea* and *Miconia* were the most important elements, indicating the presence of *Weinmannia* type of forest and a *Vallea*–*Miconia* forest type. The subparamo was dominated by Compositae, but also Ericaceae and *Polylepis* dwarf forest was conspicuous. The most important elements of the grassparamo are Gramineae, *Jamesonia*, *Plantago* and *Lycopodium* fov., whereas *Valeriana*, Caryophyllaceae, *Geranium*, *Borreria* and *Aragoa* were less frequent.

Marsh elements are represented only by Cyperaceae, and increased frequency of submersed *Isoetes* vegetation indicates that on the average higher water levels prevailed. The algae *Botryococcus*, *Pediastrum* and *Coelastrum* are abundant in this period. *Alnus* carr was absent, and the observed *Myrica* vegetation was probably part of the zonal Andean forests. The sedimentary record shows lacustrine clays with intercalated small lenses of sand. The pollen concentration is $(65\text{--}180) \times 10^3$ pollen cm^{-3} .

Pollen zone F2-19 (estimated period 622–569 ka)

Arboreal percentages of 40–60% (18–39% if *Alnus* is excluded from the pollen sum) indicate that the upper forest line was situated at 2550–2800 m elevation. In the Andean forest belt *Podocarpus*, *Hedyosmum*, *Weinmannia*, *Vallea* and *Miconia* were the most important elements. Also *Myrsine*

(= *Rapanea*), *Symplocos*, *Eugenia* and *Ilex* occurred frequently. *Weinmannia* forest and a *Vallea–Miconia* type of forest were apparently present. The subparamo was dominated by Compositae, associated with *Hypericum*, Ericaceae and *Polylepis* dwarf forest. *Borreria* was continuously registered too. The most important taxa of the grassparamo are Gramineae, *Valeriana*, Caryophyllaceae, *Geranium*, *Plantago*, *Lycopodium* fov. and Umbelliferae.

Marsh elements are represented mainly by Cyperaceae and *Hydrocotyle*, associated with *Polygonum*, *Ludwigia*, *Myriophyllum* and *Sphagnum*, indicating shallow water conditions. Low representation of submersed *Isoetes* vegetation indicates that deep water conditions were locally almost absent. *Alnus* carr and apparently *Myrica* thickets were abundant on the wet flats around the lake. The sedimentary record shows mainly lacustrine clays, interrupted by a volcanic ash horizon at 140.70 m, a sand horizon around 135 m and some intervals with sandy clay. The pollen concentration is $(65–165) \times 10^3$ pollen cm^{-3} .

Pollen zone F2-18 (estimated period 569–510 ka)

Arboreal percentages of 13–20% (8–19% if *Alnus* is excluded from the pollen sum) with a peak of 40% indicate that the upper forest line was situated at 1800–1900 m elevation, with an oscillation to 2400 m. In the Andean forest belt *Weinmannia*, *Hedyosmum*, *Podocarpus*, *Vallea* and *Miconia* were the most important elements, indicating apparently the presence of abundant *Weinmannia* in the upper forest line (for the first time in the record) and *Vallea–Miconia* forest. The subparamo was dominated by Compositae, associated with *Hypericum* and Ericaceae and, for the first time in the record, fair presence of *Polylepis* dwarf forest around the forest–paramo ecotone. The most important elements of the grassparamo are Gramineae, *Plantago*, *Valeriana*, Caryophyllaceae, *Geranium*, *Lycopodium* fov. and Umbelliferae. *Borreria* was registered only two times, indicating bunchgrass paramo conditions. Some marsh vegetation was present, consisting of Cyperaceae and *Hydrocotyle*, indicating shallow water conditions. Submersed *Isoetes* vegetation

indicates that the water table was high on the average. *Myrica* thickets and *Alnus* carr were absent on the high plain, but *Plantago* was abundant around the site. The sedimentary record shows lacustrine clays, twice interrupted by horizons with sandy clay or sand, in which algae are absent. The pollen concentration is $(13–350) \times 10^3$ pollen cm^{-3} with a peak of 1.4×10^6 pollen cm^{-3} in the upper part of this zone.

Pollen zone F2-17 (estimated period 510–475 ka)

Arboreal percentages of 42–52% (19–40% if *Alnus* is excluded from the pollen sum) indicate that the upper forest line was situated most of the time at 2600–2800 m elevation. In the Andean forest belt *Podocarpus*, *Weinmannia*, *Hedyosmum*, *Vallea* and *Miconia* were the most important elements, indicating the presence of *Weinmannia* forest and for the first time clearly a *Vallea–Miconia* type of forest. The subparamo was dominated by Compositae, associated with *Hypericum*, Ericaceae and, at the end of the zone, also *Polylepis* dwarf forest. The most important elements of the grassparamo are Gramineae, *Valeriana*, Caryophyllaceae and *Plantago*, although registered with low frequencies due to the high altitudinal position of the grassparamo belt. In the upper part of the pollen zone conditions turn colder again as evidenced by the presence of *Borreria*, *Jamesonia*, woody subparamo elements and grassparamo elements.

Myrica thickets occurred frequently on the wet parts around the lake. In the beginning of this period Cyperaceae swamp, associated with *Hydrocotyle* and *Ludwigia*, was abundant on the location. Subsequently, *Alnus* carr expanded on the high plain and locally places with deeper water occurred with an abundance of *Botryococcus*. The sediment record shows lacustrine clays. The pollen concentration is low in the cyperaceous reed swamp vegetation (7.500 pollen cm^{-3}) but higher [$(60–225) \times 10^3$ pollen cm^{-3}] during the remaining part of this period, when *Alnus* carr dominated at the coring site.

Pollen zone F2-16 (estimated period 475–415 ka)

Arboreal percentages of 16–24% (8–12% if *Alnus* is excluded from the pollen sum) indicate

that the upper forest line was situated at 1800–2100 m elevation. In the Andean forest belt *Weinmannia*, *Hedyosmum*, *Podocarpus* and *Vallea* were the most important elements, whereas *Styloceras*, *Ilex*, *Symplocos* and *Myrsine* (= *Rapanea*) were associated *Weinmannia* forest in the upper Andean forest belt. *Polylepis* dwarf forest developed initially at and above the forest line. The subparamo was dominated by Compositae, *Hypericum*, and Ericaceae. Patches of *Polylepis* dwarf forest extended near the upper forest line. The most important elements of the grassparamo are Gramineae, *Jamesonia*, *Plantago*, *Valeriana*, Caryophyllaceae, *Geranium*, *Aragoa* and *Lycopodium* fov.

Submersed *Isoëtes* vegetation occurred frequently, and marsh elements such as Cyperaceae and *Hydrocotyle* were sparsely present, pointing to a high water level on the average. *Myrica* thickets and *Alnus* carr were absent on the high plain. The sediment record shows lacustrine clays. The pollen concentration is $(70\text{--}215) \times 10^3$ pollen cm^{-3} .

Pollen zone F2-15 (estimated period 415–350 ka)

Arboreal percentages of 15–49% (10–24% if *Alnus* is excluded from the pollen sum) indicate that the upper forest line oscillated from 1900 to 2600 m elevation. In the Andean forest belt *Podocarpus*, *Weinmannia*, *Hedyosmum*, *Vallea* and *Miconia* were the most important elements, associated with *Symplocos*, *Ilex*, Melastomataceae, *Eugenia* and *Myrica*. The subparamo was dominated by Compositae, *Hypericum* and Ericaceae. The most important elements of the grassparamo were Gramineae, *Jamesonia*, *Plantago*, *Valeriana* and *Lycopodium* fov.

Marsh elements, such as Cyperaceae, *Hydrocotyle* and *Myriophyllum* were frequent, whereas submersed *Isoëtes* vegetation, characteristic of deeper water conditions, was hardly present. Shallow water conditions on the average are inferred. *Myrica* thickets and *Alnus* carr occurred twice during this period on the high plain, documenting two oscillations with markedly warmer climatic conditions. The sedimentary record shows lacustrine clays. The pollen concentration is high in the first part of this interval (peak of 1.3×10^6

pollen cm^{-3}) when cyperaceous reed swamp occurred locally, and low $[(30\text{--}530) \times 10^3$ pollen $\text{cm}^{-3}]$ at the end of this interval when deeper water conditions became frequent.

Pollen zone F2-14 (estimated period 350–334 ka)

Increasing arboreal percentages of 23–44% (10–25% if *Alnus* is excluded from the pollen sum) indicate that the upper forest line was situated at 1800 m in the beginning of this period, and rose to 2500 m elevation at the end. In the (upper) Andean forest belt *Weinmannia* became dominant, although *Podocarpus*, *Hedyosmum* and *Vallea* were also frequent. It seems that from this period onward, *Weinmannia* forest was frequent at the upper forest line, alternating (locally) with *Polylepis* dwarf forest. The latter also occurred in the paramo belt. The increasing proportion of *Weinmannia* forest at the forest line probably caused an upslope shift in the ecological range of *Polylepis* dwarf forest. The contribution of *Vallea*–*Miconia* forest type in the Andean forest belt seems almost reduced during the pollen zones F2-18 to F2-12 (ca. 569–245 ka), while *Weinmannia* forest and *Podocarpus*-dominated forest at lower elevation, reached an optimal extension. The subparamo was dominated by Compositae, *Polylepis* dwarf forest and *Hypericum* and Ericaceae, *Borreria* was continuously present here. The most important elements of the grassparamo are Gramineae, *Jamesonia*, *Valeriana*, Caryophyllaceae, *Geranium*, *Aragoa*, *Plantago* and *Lycopodium*. From pollen zone F2-14 onward *Acalypha* and *Alchornea* became more frequent, suggesting that the boundary between the subandean and Andean forest belt reached slightly higher elevations than before. Pollen record Funza I shows that at this time *Quercus* reached the study area, but was at the beginning hardly recorded in the Funza II core. In summary, important changes in the composition of the zonal forests occurred during the period around 340 ka. The subandean forest belt reached slightly higher elevations, and *Weinmannia* became dominant at the upper forest line. *Quercus* forest migrated into the area and became established on the high plain, subsequently becoming an increasingly important component of the Andean forest belt. The *Vallea*–*Miconia* forest

became markedly less important, perhaps as a consequence of the expansion of *Weinmannia* and (later on) *Quercus* forests.

Marsh elements, such as Cyperaceae, *Hydrocotyle* and *Myriophyllum* were scarce, whereas submersed *Isoëtes* vegetation was common, indicating a high water level on the average. The alga *Botryococcus* became continuously abundant in the pollen record from this time onward. *Myrica* thickets were present on the high plain. At the end of this period the upper forest line reached the elevation of the high plain and *Alnus* carr extended on the wet flats along the lake. The sedimentary record shows lacustrine clays. The pollen concentration is very high (3×10^6 pollen cm^{-3}) in the first part of this pollen zone when, locally, cyperaceous reed swamp was replaced by *Isoëtes* vegetation in deeper water. In the later part of this period pollen concentrations reached $(35\text{--}155) \times 10^3$ pollen cm^{-3} .

4.2. Introduction to the vegetational reconstruction of the pollen zones F2-13 to F2-2 (period 333–24 ka)

Quercus (oak) immigrated into the area about 650,000 yr after *Alnus* (alder), and for a last time the aspect of the forests of the northern Andes changed drastically. The precursors of the present-day *Saurauia-Quercus humboldtii* forest probably had floristic affinities with the *Weinmannia* forests. Species of *Hedyosmum*, *Brunellia*, *Hesperomeles* and *Vallea* are common elements of both types of forest. It is striking that some taxa with pioneer qualities are represented. *Cecropia* is represented again from pollen zone F2-13 onward during the first pollen zones which represent the establishment of *Quercus*. *Dodonaea* re-appeared later, viz. in pollen zone F2-12, and it is remarkable that its major oscillations are more or less correlated with lower peaks of the *Myrica* record, which suggests rather unstable slope communities with *Myrica pubescens* as the prominent element of recovering forest, and *Dodonaea viscosa* colonizing the open areas. *Dodonaea* is a general pioneer of open ground and often colonizes, together with *Myrsine* (= *Rapanea*), former eroded paramo ground, preceding the establishment of other Andean forest

elements. At present *Dodonaea* is mainly observed on the climatologically dry side of the mountains from about sea level up to about 3000 m elevation.

All palynologically recognizable elements of the modern Andean forest were present from now on in the area of the high plain of Bogotá, and the subsequent adaptation and further regional speciation of *Quercus* in the area must have mainly taken place in the last part of the record. This accounts for the presence of different species of *Quercus* in Colombia.

Oreopanax-Cordia lanata forest is palynologically difficult to identify. It contains many palynologically well recognizable taxa in common with the high plain forest and the *Weinmannietum*, whereas other characteristic elements are palynologically hard to identify, or were only scarcely represented. In the vegetational reconstruction, therefore, in general no reference is made to this type of forest, which does not imply that the *Oreopanax-Cordia lanata* forest type was absent at that time.

Pollen zone F2-13 (estimated period 333–303 ka)

Arboreal percentages of 29–65% (16–35% if *Alnus* is excluded from the pollen sum) indicate that the upper forest line was situated at 2300–2700 m elevation. In the upper Andean forest belt *Weinmannia* was dominant and *Vallea-Miconia* forest was almost absent. Forest with an important contribution of *Podocarpus* occurred in the lower part of the Andean forest belt. The subparamo was dominated by Compositae, associated with *Hypericum*, Ericaceae, *Aragoa* and *Polylepis* dwarf forest. The most important elements in the lowermost grassparamo are *Jamesonia*, *Valeriana*, Caryophyllaceae, *Plantago*, *Lycopodium*, *Geranium* and Umbelliferae. *Rumex* increased in frequency in the paramo belt.

Marshes with Cyperaceae, *Hydrocotyle*, *Ludwigia*, *Polygonum* and *Myriophyllum* occurred in shallow water, several times interrupted by periods with extensive carr of *Alnus* and *Myrica* thickets. Presence of submersed *Isoëtes* vegetation, pointing to high water levels, alternated with *Alnus* carr on wet flats around the lake. The sedimentary record shows lacustrine clays. The pollen concentration is $(60\text{--}525) \times 10^3$ pollen cm^{-3} .

Pollen zone F2-12 (estimated period 303–245 ka)

Arboreal percentages of 28–55% (12–19% if *Alnus* is excluded from the pollen sum) indicate that the upper forest line was situated at 2000–2200 m elevation. In the upper Andean forest belt *Weinmannia* forest was dominant with extensions of *Polylepis* dwarf forest in the grassparamo. Other Andean forest elements were *Podocarpus*, *Hedyosmum*, *Vallea* and *Miconia*. The first occurrence of *Quercus* as a permanent element in the Andean forest belt is registered in this period. The subparamo was dominated by Compositae, *Hypericum*, *Aragoa* and Ericaceae, probably with patches of *Polylepis* dwarf forest. The most important elements in the grassparamo belt are Gramineae, *Plantago*, *Lycopodium* fov., *Valeriana*, Caryophyllaceae and *Geranium*.

Alnus carr and vegetation of *Myrica* thickets were absent on the high plain. Marsh vegetation with Cyperaceae, *Hydrocotyle* and *Sphagnum* was present and submersed *Isoetes* vegetation was scarce. The sedimentary record shows lacustrine clays. The pollen concentration varies during this period between 600×10^3 and 60×10^3 pollen cm^{-3} .

Pollen zones F2-11 to F2-9 (estimated period 245–186 ka)

Arboreal percentages of 41–75% (17–47% if *Alnus* is excluded from the pollen sum) indicate that the upper forest line oscillated from 2600 to 2900 m elevation. In the (lower) Andean forest belt *Podocarpus* became a very important element. In the upper Andean belt *Weinmannia* forest was dominant, associated with *Hedyosmum*, *Myrsine* (= *Rapanea*), *Ilex*, *Juglans* and *Eugenia*. At the end of this period, when *Quercus* forest increased rapidly in the Andean forest belt, *Vallea* replaced *Weinmannia* for a considerable part, apparently leading again to the presence of *Vallea*–*Miconia* forest. *Borreria* may have been prominent in open patches of this forest and in the open subparamo. *Myrica* must also have contributed to this zonal forest belt. The subparamo was dominated by Compositae, associated with *Hypericum*, Ericaceae and *Polylepis* dwarf forest. The most important elements in the grassparamo are Gramineae, *Plantago*, *Lycopodium* fov., *Valeriana*, Caryo-

phyllaceae, *Geranium* and Umbelliferae. Abundant *Alnus* carr was present on the wet flats around the lake. *Myrica* thickets also occurred frequently. Shallow water conditions are evidenced by the presence of cyperaceous reed swamp with *Ludwigia*, *Hydrocotyle* and *Sphagnum*, and intermittently, the presence of other shallow water aquatics, such as *Azolla* and *Myriophyllum*. The sedimentary record shows lacustrine clays. The pollen concentration is $(35\text{--}270) \times 10^3$ pollen cm^{-3} .

Pollen zone F2-8 (estimated period 186–128 ka)

Arboreal percentages of 15–25% (7–15% if *Alnus* is excluded from the pollen sum) indicate that the upper forest line was situated at 1800–1900 m elevation. In the Andean forest belt forest elements of the previous zone are reflected at large distance; *Podocarpus*, *Vallea*, *Hedyosmum*, *Weinmannia*, *Quercus* and *Miconia* were the most important elements. The low altitudinal position of the Andean forest belt hampers a more detailed conclusion about the composition of forest types. The subparamo was initially made up of *Hypericum*, Compositae, Ericaceae and *Polylepis* dwarf forest. *Hypericum* apparently appeared on moist grounds on flats around the lake. The most important elements of the lower grassparamo were Gramineae, *Jamesonia*, *Lycopodium*, *Plantago*, *Valeriana*, Caryophyllaceae, *Geranium*, *Aragoa* and Umbelliferae.

Submersed *Isoetes* vegetation was common, whereas marsh vegetation, including Cyperaceae, *Polygonum*, *Hydrocotyle* and *Sphagnum*, in shallow water was scarce; high water levels prevailed. The sedimentary record shows lacustrine clays, interrupted by a narrow horizon with sandy clay, corresponding to a drop in the marsh vegetation and in the abundance of algae. The pollen concentration is $(35\text{--}150) \times 10^3$ pollen cm^{-3} .

Pollen zone F2-7 (estimated period 128–92 ka)

Arboreal percentages of 47–77% (25–59% if *Alnus* is excluded from the pollen sum) indicate that the upper forest line was situated at 2700–3200 m elevation. In the (upper) Andean forest belt *Quercus* and *Weinmannia* forests were common,

whereas *Vallea-Miconia* forest with *Borreria* occurred in the (lower) parts of the Andean forest belt. A variety of other arboreal genera were associated with the latter forest type, such as *Myrsine* (= *Rapanea*), *Symplocos*, *Ilex*, *Juglans* and *Eugenia*. Also *Drimys* occurred again as a forest element. Substantial representation of subandean forest elements, such as *Acalypha*, *Alchornea* and Urticaceae–Moraceae indicates that the upper boundary of this belt reached close to the high plain, possibly to ca. 2400 m elevation. From pollen zone F2-7 onward, the contribution of *Miconia* to the Andean forest increased markedly. Also the contribution of *Quercus* increased considerably from pollen zone F2-7 (last part of pollen zone F2-8) onward, suggesting that the combination of *Quercus* and *Miconia* led to a new forest type with strong possibilities for competition. The *Quercus* records in the Funza I and Funza II cores start at 92 (99) m and 84 (89) m core depth, respectively. A marked increase, however, is noted at 68 m and 58 m core depth, respectively. This difference in registration indicates that the first patches of *Quercus* forest apparently were of local importance, and *Quercus* formed extensive zonal forests since pollen zone F2-9 (corresponding to oxygen isotope stage 7.1; ca. 200,000 yr B.P.). This observation explains a seeming contradiction that was noticed by Helmens and Kuhry (1986) and Hooghiemstra (1988). The Funza pollen records apparently register the first local presence of *Quercus* forest on the high plain at ca. 320 ka. The Laguna de Agua Blanca pollen record at 3250 m elevation and at some 30 km distance to the high plain, did not record the first azonal presence of *Quercus* and apparently registered only the presence of zonal *Quercus* forest on the mountains surrounding the high plain since ca. 200,000 yr B.P.

The subparamo was dominated by Compositae, *Hypericum*, Ericaceae and *Polylepis* dwarf forest. The most important elements in the grassparamo are Gramineae, *Valeriana*, Caryophyllaceae, *Plantago*, *Lycopodium* and Umbelliferae.

Isoetes was almost absent whereas marsh vegetation, consisting of cyperaceous reed swamp and *Hydrocotyle*, *Ludwigia*, *Myriophyllum* and *Azolla*, indicates shallow water conditions. *Myrica* thickets occurred on the wet parts of the high plain, and

Alnus carr was abundant on the wet flats along the lake. The sedimentary record shows lacustrine clays. The pollen concentration is $(33\text{--}280) \times 10^3$ pollen cm^{-3} .

Pollen zone F2-6 (estimated period 92–84 ka)

Arboreal percentages of 23–39% (17–29% if *Alnus* is excluded from the pollen sum) indicate that the upper forest line was situated at 2000–2300 m elevation. In the (upper) Andean forest belt *Quercus* and *Weinmannia* forests were most important, and in the lower part of this forest belt *Podocarpus* and *Vallea-Miconia* forests occurred. The subparamo was dominated by *Aragoa*, Compositae, *Hypericum* and *Polylepis* dwarf forest, associated with lower presence of Ericaceae. The most important elements in the grassparamo are Gramineae, *Valeriana*, Caryophyllaceae, *Plantago* and *Lycopodium*, along with *Geranium* and *Rumex*.

Myrica thickets and *Alnus* carr were absent on the high plain; these genera must have contributed to the zonal Andean forests. *Isoetes* vegetation was abundant whereas marsh vegetation of Cyperaceae, *Hydrocotyle*, *Polygonum* and *Sphagnum* was rare, indicating a high water level during this period. Algae of the genus *Botryococcus* were markedly abundant. The sedimentary record shows lacustrine clays. The pollen concentration is low, $(41\text{--}99) \times 10^3$ pollen cm^{-3} .

Pollen zone F2-5 (estimated period 84–73 ka)

Arboreal percentages of 55–79% (37–59% if *Alnus* is excluded from the pollen sum) indicate that the upper forest line was situated at 2700–3100 m elevation. In the Andean forest belt zonal *Quercus* forest was apparently not frequent, but *Weinmannia* forest (including *Hedyosmum*, *Podocarpus* and Urticaceae, indicative of more humid climate) and drier *Vallea-Miconia* forest were common. Arboreal taxa from the subandean forest belt, such as *Acalypha*, *Alchornea* and Urticaceae–Moraceae show substantial presence in the surroundings of the high plain, indicating that the uppermost subandean forests reached to at least 2400 m. Because of its high altitudinal position the subparamo belt is not well documented, but *Hypericum* and Compositae seem the most important elements. The main elements in the

grassparamo are Gramineae, *Valeriana*, Caryophyllaceae, *Plantago* and *Lycopodium*.

Marsh elements such as Cyperaceae, *Polygonum*, *Hydrocotyle* and *Myriophyllum* were common and indicate shallow water conditions. This interpretation is corroborated by the low presence of submersed *Isoetes* vegetation. Great parts of the wet flats around the lake were covered by *Alnus* carr and *Myrica* thickets. The algae *Botryococcus*, *Pediastrum* and *Coelastrum* were extremely abundant. The sedimentary record shows lacustrine clays. The pollen concentration is $(80\text{--}180) \times 10^3$ pollen cm^{-3} .

Pollen zone F2-4 (estimated period 73–50 ka)

Arboreal percentages of 39–62 (72)% [22–47 (55)% if *Alnus* is excluded from the pollen sum] indicate that the upper forest line oscillated from 2400 to 2800–2900 m elevation. In the Andean forest belt *Quercus* forest, *Weinmannia* forest [including a substantial contribution of *Hedyosmum*, *Eugenia*, *Miconia* and *Myrsine* (= *Rapanea*)], and *Vallea*–*Miconia* forest were present. *Podocarpus* was mainly frequent at lower elevation in the Andean forest belt. The arboreal taxa of the subandean forest belt, *Acalypha* and *Alchornea*, were present with markedly high frequency. Wide altitudinal distribution of *Quercus* forests in the lower subandean forest belt to the upper Andean forest belt, for the first time in the record, could have facilitated an upward shift of those subandean forest elements. This situation under modern conditions is reported from the Magdalena slopes, northwest of Bogotá. The subparamo was dominated by Compositae, with important contribution of *Hypericum*, Ericaceae and *Aragoa*. *Polylepis* dwarf forest also occurred. The most important elements in the grassparamo are Gramineae, *Valeriana*, Caryophyllaceae, *Plantago* and *Lycopodium*.

Submersed *Isoetes* vegetation increased in frequency and several important marsh elements, such as Cyperaceae and *Myriophyllum* became markedly less abundant, indicating a higher water level than during the previous pollen zone. The altitudinal level of the upper forest line permitted the occurrence of *Alnus* carr on the high plain. However, limited presence of ill-drained areas

around the lake because of the high water level must have limited the expansion of *Alnus* carr. *Myrica* was possibly part of the zonal Andean forest and also occurred as thickets on the high plain. The presence of algae in the lake reduced abruptly and only *Botryococcus* was continuously present. The sedimentary record shows lacustrine clays. The pollen concentration shows two minima of $(19\text{--}26) \times 10^3$ pollen cm^{-3} , corresponding to intervals with low presence of *Alnus*, strongly suggesting that during these short intervals *Alnus* carr was locally absent. A maximum of 27×10^4 pollen cm^{-3} in between these two maxima corresponds to higher arboreal percentages (higher inferred temperature) and a brief lower water level, based on an increase of marsh vegetation and a modest increase of *Alnus* carr. At the end of the zone the pollen concentration increased to 145×10^3 pollen cm^{-3} , coinciding with a marked increase of *Alnus* carr.

Pollen zone F2-3 (estimated period 50–24 ka)

From the arboreal percentages of 47–72 (82)% [31–55 (65)% if *Alnus* is excluded from the pollen sum] it is inferred that the upper forest line oscillated from 2600 to ca. 2900 m elevation. During a short period the upper forest line descended to an elevation of 2400 m. In the Andean forest belt *Quercus* forest had reached a dominant position for the first time in the record. Associated elements of the modern *Saurauia*–*Quercus humboldtii* forest (with an altitudinal range of 2340–2800 m), such as *Weinmannia*, *Vallea* and Cyatheaceae were also present with substantial frequencies in this period. *Weinmannia* forest, and in the first part of the zone *Vallea*–*Miconia* forest, contributed substantially to the Andean forest belt. A number of subandean forest elements reached their upper limit in the zone with *Quercus* forest, a situation that apparently also occurred in this period. *Acalypha* and *Alchornea* occurred with high frequencies and possibly reached elevations of ca. 2200 m in the *Quercus* forest. *Weinmannia* forest was common, including a substantial contribution of *Hedyosmum* and *Podocarpus*, but *Vallea*–*Miconia* forest had a reduced distribution in the upper part. *Quercus* forest with a high pollen production apparently replaced forest types with a lower pollen pro-

duction that previously dominated in the (upper) Andean forest belt, such as *Vallea–Miconia* forest, including associated pollen producers such as *Ilex*, *Juglans* and several arboreal Melastomataceae. This change in the composition of the Andean forest belt explains the markedly high arboreal pollen percentages under climatologically temperate conditions. The replacement of traditional forest types by *Quercus* forest caused a substantial competition and re-arrangement of the most important forest types for yet another time in the long and dynamic history of the Andean forest. Simple deduction of the altitudinal position of the upper forest line from arboreal percentages is not adequate in this period.

The subparamo was dominated by Compositae and *Hypericum*, associated with *Polylepis* dwarf forest and Ericaceae. The most important elements in the grassparamo were Gramineae, *Valeriana*, *Plantago*, *Lycopodium* and Caryophyllaceae.

Cyperaceous reed swamp and *Alnus* carr became very abundant on the extensive wet flats around the lake. The water level must have lowered substantially, giving way to a wide distribution of *Alnus* carr, interspersed with *Myrica* thickets on wet ground. Submersed *Isoetes* became less important. It seems that the lake was draining, which happened in the period of 27,000–22,000 yr B.P. Extraordinary rates of sediment accumulation, mainly consisting of clay but sometimes interrupted by coarse gravel in the Funza I core, are indicative of an intensive erosion process that finally eroded the outlet of the lake at Tequendama Falls. The sediment record shows lacustrine clays. The pollen concentration is $(30\text{--}190) \times 10^3$ pollen cm^{-3} .

The start of a transition to cold climatic conditions is recorded in the uppermost sample of the Funza II core. The upper part of the Funza I record also shows this transition to the last glacial maximum, and documents an even longer interval of this transitional phase. The Funza records do not show the history from the last glacial maximum to the Holocene. For this period one must refer to, e.g., the pollen record of Laguna de Fuquene, located at the same elevation some 50 km north of this site (Van Geel and Van der Hammen, 1973).

5. Discussion

5.1. Comparison between the Funza I and Funza II pollen records

Fig. 5 shows the correlation of the pollen records Funza I (Hooghiemstra, 1984) and Funza II (this study). In addition, the tentative correlation with the deep-sea oxygen isotope stratigraphy is indicated. After the high-resolution analysis of the pollen record is completed, an updated match with the ODP 677 record will be presented.

By comparison of the pollen records Funza I (Hooghiemstra, 1984) and Funza II (this study) the following remarks can be made. In the summary diagrams, pollen zones 8 and 6 show lower arboreal values in Funza II than in Funza I. This difference is caused by the records of *Alnus* and *Quercus*, which represent to a considerable extent an azonal signal. The role of *Quercus* is analyzed in a separate paper (Van 't Veer et al., in press) and it will be shown that the “warm” aspect of the uppermost 50 m of the record is attributed to an inadequate interpretation of the pollen record. The high *Polylepis* percentages between pollen zones 18 and 12 are characteristic in both records.

Concerning the major arboreal elements of the forest belts it can be noted that most taxa recorded in the Funza II and Funza I core show a very similar tendency over the pollen zones 23 to 2, viz. *Podocarpus*, *Hedyosmum*, *Myrsine* (= *Rapanea*), *Symplocos*, *Ilex*, *Styloceras*, *Juglans*, *Miconia*, *Gaiadendron*, *Myrica*, *Acalypha* and *Alchornea*. Markedly lower percentages are recorded in parts of the Funza II record for *Weinmannia*, Melastomataceae, Urticaceae–Moraceae, *Eugenia* and *Cecropia*, whereas *Vallea* and Myrtaceae show higher percentages in Funza II than in Funza I. The difference concerning *Weinmannia* and *Vallea* could be related to identification problems of both pollen types but first statistical analysis of the pollen spectra (Van 't Veer, unpubl. data) do not agree for this hypothesis. The difference between the records of *Eugenia* (Myrtaceae) and the group Myrtaceae p.p. is a matter of absolute size of the pollen grains: *Eugenia* are small grains (14–21 μm ; Hooghiemstra, 1984), whereas the larger grains are recorded as Myrtaceae p.p. A slightly different

Fig. 5. Correlation of the pollen records Funza II (this study) and Funza I (Hooghiemstra, 1984, 1989). Correlating pollen zones in both records have the same numbers, with a prefix *F1* (Funza I) or *F2* (Funza II). Depth and age of pollen zone boundaries are indicated. A tentative correlation with the deep-sea oxygen isotope stratigraphy has been indicated. Ages of oxygen isotope stages are after Imbrie et al. (1984).

interpretation during routine analysis accounts easily for this difference in percentages. Also the difference in the record of the Melastomataceae in the cores Funza II and Funza I is a matter of absolute size of pollen grains. *Miconia* (Melastomataceae) grains are mostly smaller than 19 μm , whereas grains of other Melastomataceae genera are larger (see Hooghiemstra, 1984). This difference, however, is not as distinct as suggested by the pollen keys.

Funza I shows stronger alternations between swamp elements (*Myriophyllum* and *Ludwigia*) and *Isoetes* than Funza II, indicating that the water level changed more at site Funza I. Site Funza I was probably situated nearer to deeper parts of the lake. A maximum of Cyperaceae in the pollen zones 21 and 17 is recorded in both cores, indicating that considerable areas on the high plain were simultaneously covered by cyperaceous swamps. The algae *Pediastrum* and *Coelastrum* are less common in the Funza II core, on the average. Considerable differences in individual pollen zones can be noted; compare, e.g., *Pediastrum* in pollen zone 14. The fluctuations in both cores in the records of *Botryococcus* correlate well.

5.2. Time control

Time control of the Funza records needs some discussion. Eight horizons with intercalated volcanic ash, between 506 m and 67 m core depth, have been dated by fission-track dating using zircon (Andriessen et al., 1993) providing an absolute time frame. The dates at 270 m, 250 m, and 239 m core depth show ages of 0.53 ± 0.15 , 0.27 ± 0.11 and 0.26 ± 0.18 Ma, respectively. Based on climatostratigraphical arguments, these dates are assumed too young, although from a technical point of view there are no objections (see the discussion in Andriessen et al., 1993). The dating at 67 m core depth of 0.20 ± 0.12 Ma is in good agreement with the general climatostratigraphy of this area.

Pollen record Funza II is correlated in detail with pollen record Funza I, located at a distance of ca. 1 km. The immigration of *Alnus*, for example, occurs in both cores at 257 m core depth. Pollen record Funza I has been graphically

matched with the oxygen isotope record of core ODP 677 (Shackleton and Hooghiemstra, unpubl. data; Hooghiemstra and Sarmiento, 1991; Hooghiemstra et al., 1993). The fission-track time control of the lowermost four dates of Funza II match well with the ODP 677 time control. The characteristic climatic cycles of the last 1 Ma (especially oxygen isotope stage 22) matched in good agreement. Therefore we conclude that the three fission-track dates between 239 and 277 m core depth are not correct probably due to inadequate volcanic ash samples. It needs to be mentioned that the Eastern Cordillera is not volcanic and only distal airborne tephra from the Central Cordillera could be used (Andriessen et al., 1993).

5.3. Immigration of *Quercus*: forest changes

The appearance of *Quercus* in the area of Bogotá is the most salient feature in this upper part of the pollen record. *Quercus* reached South America by crossing the Panamanian landbridge and the recent distribution map of *Quercus* in Colombia (Lozano and Torres, 1974) shows a pathway southwards along the Western and Central Cordillera. Latitudinal migration was maximal at lower elevation (ca. 1000–1800 m) and at several places vertical expansion apparently took place. On the Magdalena slope of the Eastern Cordillera the distribution of *Quercus* forest is discontinuous (Lozano and Torres, 1974; Rangel, pers. commun.). On the eastern slopes of the Eastern Cordillera, facing the llanos, no *Quercus* forests have been recorded. Near the western edge of the high plain of Bogotá most *Quercus* forest is found from 2300 to 2800 m. On the eastern slopes of the Central Cordillera *Quercus* forests occur from ca. 2500 m to 3100 m (Cuatrecasas, 1934; Cleef et al., 1983), whereas further north, in Boyacá, *Quercus* forests may be found up to 3500 m elevation. It is hypothesized that, especially in the Eastern Cordillera, under natural conditions, *Quercus* is still in a phase of expansion and a well balanced equilibrium between presence and ecological conditions is lacking. The fact that only the *Quercus* record of the Funza I data set showed a chaotic response in the frequency analysis to climatic

change (Hooghiemstra et al., 1993) corroborates this assumption.

Another aspect of discussion concerns the age of immigration of *Quercus*. Helmens and Kuhry (1986) studied a 13 m long core from Paramo de Agua Blanca. Using a combination of two radiocarbon dates for the upper 3.20 m of the borehole, and pollen concentration values for the remaining lower part of the pollen record, the Paramo de Agua Blanca I section was estimated to represent the last 0.45 Ma. A calculated pollen influx of $1310 \text{ pollen cm}^{-2} \text{ yr}^{-1}$ was assumed to be constant over the whole section. In this section, the beginning of a continuous record of *Quercus* at 7 m core depth was thought to register the moment of immigration of this genus into the area. According to this pollen density time frame (Middeldorp, 1984, 1986), the first appearance of *Quercus* in the Paramo de Agua Blanca I section occurred at about 0.2 Ma. This date seems in disagreement with the age of 0.34 Ma, based on the absolute time frame of Funza II in combination with the correlation between Funza II, Funza I and the ODP 677 oxygen isotope record (Andriessen et al., 1993; Hooghiemstra and Sarmiento, 1991). Better inspection of the Funza I and the new Funza II pollen record, however, makes clear that there is no discrepancy in age, but a difference in registration between these pollen records. Funza I registers the first *Quercus* pollen at 100 m core depth, shows a more or less continuous record from 92 m onward, and a record with substantial values from 68 m onward. Funza II registers the first *Quercus* pollen at 89 m core depth, shows a more or less continuous record from 82 m onward (245 ka), and a record with substantial values from 67 m onward (200 ka). It becomes now clear that *Quercus* must have arrived on the slopes of the Magdalena valley, close to the high plain, around 340 ka. First records of *Quercus* pollen apparently represented long distance transport from the Magdalena valley. Around 245 ka *Quercus* reached the high plain and must have occurred in small patches of forest on the slopes around the lake. It took apparently some 50 ka before *Quercus* forest expanded over the surrounding slopes of the high plain to form around 200 ka zonal *Quercus* forests, contributing substantially to the Andean forest

belt. It is plausible that the Paramo de Agua Blanca record at 3250 m elevation and at ca. 30 km distance from the central part of the high plain, did not register the first local patches of oak forest on the high plain and records *Quercus* from the moment that oak forest is an important part of the zonal forest belt.

5.4. Pollen concentration and pollen density dating

The agreement in age of the moment that *Quercus* formed zonal forests, around 200 ka, is noteworthy. The assumption of Helmens and Kuhry (1986) that the calculated pollen influx of $1310 \text{ pollen cm}^{-2} \text{ yr}^{-1}$ for the upper part of their record is also valid for at least the middle part of the core seems correct. They justify the continuous validity of their pollen influx value by arguing that part of a glacial–interglacial cycle is included in their calculations. Possible errors due to changes from forest vegetation to paramo vegetation should have been reduced in this way. The pollen concentration diagram of core Funza II (Fig. 6) shows that there is little or no relation between the pollen concentration and the period of time represented. Application of the pollen density method (Middeldorp, 1984, 1986) to the Funza II core, with the aim to improve on a linear interpolation between dated horizons, seems invalid. The assumptions of the method apparently are not met, a feature which seems plausible.

The pollen concentration diagram of Funza II (Fig. 6) shows that boundaries between pollen zones, based on the pollen percentage diagram, are often at places where a marked change in the pollen concentration takes place. Frequently, presence or absence of vegetation of local importance, such as *Alnus* carr or *Plantago rigida* cushion bogs, can be identified as a major reason. General conclusions concerning the pollen concentration values during glacial and interglacial periods, however, can not be inferred.

5.5. Implications for relation $AP\%$ –elevation upper forest line

A perusal of the main pollen diagram shows markedly high arboreal pollen percentages in the

Fig. 6. Pollen concentration diagram of the 2–158 m interval of the Funza II core (Eastern Cordillera, Colombia, 2550 m alt.) analysed with 100 cm sample distance. Pollen concentration records are presented of the total number of taxa included in the pollen sum, and specified for the four ecological–altitudinal groups that make up the pollen sum.

uppermost 30 m of the record. This interval represents the period of ca. 80–25 ka of the last glacial and, compared to older parts of the pollen record, rather high temperatures for glacial conditions are suggested. The relationship between arboreal pollen percentage and altitudinal position of the upper forest line apparently needs some adjustment for the period when *Quercus* forests became abundant in the region. *Quercus* is an anemophilous genus and produces large quantities of pollen (Grabandt, 1980). *Quercus* probably replaced during the last 200 ka mainly taxa such as *Podocarpus* and *Weinmannia* which produce markedly less pollen. In this respect it is important to note that neither in pollen record Laguna La Cocha-1 (Hooghiemstra et al., unpubl. data) from southern Colombia is the relationship as given in Table 2 valid. The pollen record of this lake, at 2820 m elevation and ca. 300 m below the upper forest line, shows ca. 15–35% arboreal pollen in Holocene times. According to Table 2 20–25% more arboreal pollen should be expected for this elevation. This low arboreal pollen percentage for a situation at 300 m below the upper forest line is explained by the composition of the Andean forest belt. Good anemophytic pollen producers, such as *Quercus* and *Myrica*, are rare or absent in the direct vicinity of Laguna La Cocha, and Andean forests contain mainly *Miconia* and *Weinmannia*, which produce considerably less pollen.

The uppermost 100 m of pollen record Funza I was recently re-examined using different pollen sums (Van 't Veer and Hooghiemstra, unpubl. data). Using a pollen sum from which *Alnus* and *Quercus* are excluded, the relationship of Table 2 led to results that are comparable to several other records from this region, e.g., the records CUX (Van der Hammen and González, 1960), Tarragona (Dueñas, 1979), Fúquene III (Van der Hammen, unpubl. data), Fúquene II (Van Geel and Van der Hammen, 1973) and Funza IIA (Mommersteeg, Ran, Van 't Veer and Hooghiemstra, unpubl. data). It is concluded that, depending on the abundance of *Quercus* in the regional Andean forest belt, the values of Table 2 need some correction. More data are published in the framework of the high-resolution pollen analy-

sis of the upper 90 m of the Funza II core (Ran and Mommersteeg, unpubl. data) elsewhere.

5.6. Time resolution

The present study shows over the core interval 158–2 m an average calculated time resolution of ca. 4500 yr. Substantial difference between pollen zones is noticed depending on the sediment accumulation rate. During glacial conditions time resolution ranges from 19,000 yr (pollen zone F2-20) and 14,500 yr (pollen zone F2-8) to 3933 yr (pollen zone F2-18) and 1142 yr (pollen zone F2-6) per meter of sediment. During interglacial conditions time resolution ranges from 5833 yr (pollen zone F2-17) and 4833 yr (pollen zone F2-21) to 3272 yr (pollen zone F2-7) and 2269 yr (pollen zone F2-9 to 11) per meter of sediment. Fine-resolution pollen analysis with sample distances of 20 cm is in progress, leading to a minimum time resolution of 4000 yr and an maximum of 250 yr. Frequency analysis of climatic change at frequencies of the precession band (18–21 kyr) and even higher (15–10 kyr band) become possible and will provide an important data set to evaluate the evolution of orbital forcing during the middle and late Quaternary.

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Appendix 1—description of the pollen zones F2-23 to F2-3 (158–2 m core interval of the Funza II pollen record)

Pollen zone F2-23 (158–155.5 m)

Pollen zone F2-23 is characterized by relatively high values (45–53%) of arboreal pollen. The main constituents are *Alnus* (25–29%), *Podocarpus* (4–8%), *Hedyosmum* (2%), *Weinmannia* (4–1%), *Vallea* (3–2%), *Miconia* (2–1%) and *Myrica* (6–8%). Subparamo elements are dominated by Compositae (11–12%) with low values of *Polylepis/Acaena* (2–1%). Gramineae reach values of 41–32%. Paramo taxa are represented with low values, *Plantago* reaches its highest values (2–3%). Aquatics, represented by Cyperaceae (7–4%), *Hydrocotyle* (4–2%), *Myriophyllum* (0.5–1%) and *Isoetes* (21–5%) show a decreasing trend. Ferns are mainly represented by monolete spores (9–4%). The alga *Botryococcus* reaches values of 31–37%.

Pollen zone F2-22 (155.5–152.5 m)

Pollen zone F2-22 is characterized by relatively low values (33–43%) of arboreal pollen. It differs from pollen zone F2-23 by lower percentages of arboreal pollen, and higher values of Gramineae, subparamo elements, and grassparamo elements. All arboreal taxa present contribute with lower values, *Alnus* (23–25%), *Podocarpus* (6–3%), *Hedyosmum* (3–0.5%), *Weinmannia* (1.5–1%), *Vallea* (3–0.5%) and *Myrica* (4–2%). The subparamo elements are dominated by Compositae (14–21%) with some *Polylepis-Acaena* (3–1%) and Ericaceae (1%). Gramineae reach values of 37–48%. Paramo elements are represented mainly by *Plantago* (2.5–3%), with low values of *Valeriana* (1–0.5%), Caryophyllaceae (0.5–2%) and *Lycopodium* fov. (fov.: species with foveolate spores) (2–0.5%). Aquatics are primarily represented by Cyperaceae (6–3%) and *Isoetes* (47–8%). Of the Ferns only monolete spores are noteworthy (8–9%). The alga *Botryococcus* has values of 28–8%.

Pollen zone F2-21 (152.5–146.5 m)

Pollen zone F2-21 is characterized by relatively high values (43–67%) of arboreal pollen. This zone differs from the previous zone by higher values of *Alnus*, *Podocarpus*, *Juglans*, *Miconia*, *Myrica*, Cyperaceae and *Hydrocotyle* and by the lower values of Gramineae, *Polylepis/Acaena*, Ericaceae, Compositae, *Valeriana*, Caryophyllaceae, *Plantago*, *Lycopodium* fov. and *Isoetes*. The main elements of the Andean forest belt are *Alnus* (51–24%), *Podocarpus* (16–5%), *Myrica* (10–3%), *Hedyosmum* (4–0%), *Weinmannia* (0.5–2%), *Vallea* (0.5–3%), *Juglans* (0–1%) and *Miconia* (0.5–1%). The subparamo elements are still dominated by Compositae (18–4.5%). Gramineae reach values of 26–45%. Paramo elements are scarcely represented. Of the aquatic taxa only Cyperaceae reach relatively high values (18–6%). Ferns are mainly represented by monolete spores (12–1.5%). The alga *Botryococcus* reaches values of 150–4%.

Pollen zone F2-20 (146.5–144.0 m)

Pollen zone F2-20 is characterized by relatively low arboreal pollen values (26–36%). This zone differs from pollen zone F2-21 by the lower percentages of *Alnus*, *Podocarpus*, *Vallea*, *Miconia*, *Myrica*, Cyperaceae and *Ludwigia* and the higher values for Gramineae, Compositae, *Weinmannia*, *Lycopodium* fov., *Isoetes* and the spiky appearance of the curves for the algae *Botryococcus* and *Coelastrum*. The main arboreal contributors are *Alnus* (13–24%), *Podocarpus* (5–4%), *Hedyosmum* (1–2%), *Weinmannia* (2–4%), *Vallea* (1–0.5%) and *Myrica* (2–4%). The paramo elements are represented by Gramineae (58–45%), Compositae (14.5–16%) *Plantago* (1–2%) and *Lycopodium* fov. (1–1.5%). Aquatics are represented by Cyperaceae (11–3%) and *Isoetes* (10–4%). Ferns are represented by *Jamesonia* (1.5–4%) and monolete spores (4–10%). The algae show maxima in a spiky record, *Botryococcus* of 55%, *Pediastrum* of 30% and *Coelastrum* of 87%.

Pollen zone F2-19 (144.0–130.5 m)

Pollen zone F2-19 is characterized by the relatively high values (36–60%) of arboreal pollen. This zone differs from pollen zone F2-20 by higher values of *Alnus*, *Podocarpus*, *Hedyosmum*, *Vallea*, *Myrsine* (= *Rapanea*), *Symplocos*, *Ilex*, *Miconia*, Urticaceae/Moraceae, *Eugenia*, *Myrica*, *Acalypha*, *Alchornea* and *Hypericum*, and lower values of Gramineae, *Pediastrum* and *Coelastrum*. Of the arboreal pollen all of the following taxa contribute to the relatively high values: *Alnus* (20–41%), *Podocarpus* (4.5–12%), *Hedyosmum* (1–4%), *Weinmannia* (1–4%), *Vallea* (1–6%), *Miconia* (0–2%), *Myrica* (2–6%), *Myrsine* (= *Rapanea*) (0–1%), *Ilex* (0–2%) and Urticaceae (0–1%). The subparamo elements are dominated by Compositae (7–21%) with low values of *Polylepis-Acaena* (0.5–1.5%), Ericaceae (0.5–1.5%) and *Hypericum* (0–1.5%). Of the paramo taxa *Plantago* (0.5–3%) and *Lycopodium* fov. (0.5–2%) are present. Gramineae have values of 28–41%.

Aquatics are represented by Cyperaceae (1.5–8%), *Hydrocotyle* (0.5–1.5%) and *Isoetes* (0.5–34%). Of the ferns *Monoletes* reach relatively high values (3–10%), while *Cyathea* (0–1.5%), *Jamesonia* (1–3%) and *Lophosoria* (0–1%) are present throughout the zone with low values. Of the algae *Botryococcus* reaches values of 7–130%, *Pediastrum* 0–2.5% and *Coelastrum* 0–7%.

Pollen zone F2-18 (130.5–116.5 m)

Pollen zone F2-18 is characterized by relatively low arboreal pollen values (12–41%) and relatively high Gramineae values (34–65%). This zone differs from the previous zone by higher values of Gramineae, *Polylepis-Acaena*, *Hypericum*, Compositae, *Weinmannia*, *Valeriana*, Caryophyllaceae, *Plantago*, *Lycopodium* fov. and *Isoetes*, and lower values of *Alnus*, *Podocarpus*, *Vallea*, *Myrica* and *Botryococcus*. To the arboreal pollen contribute *Alnus* (22–3%), *Podocarpus* (0.5–6%), *Hedyosmum* (0–3%), *Weinmannia* (0.5–7%), *Vallea* (0.5–3%), *Ilex* (0–1%), *Miconia* (0.5–1.5%) and *Myrica* (0.5–6%). The subparamo taxa are dominated by Compositae (11–29%) with relatively high values of *Polylepis/Acaena* (0–9%), Ericaceae (0–2%) and *Hypericum* (0–5%). Paramo elements are dominated by *Plantago* (2–10%), with the presence of *Valeriana* (0–3%), Caryophyllaceae (0–3%), *Geranium* (0–0.5%), *Aragoa* (0–0.5%) and *Lycopodium* fov. (0.5–2%). Aquatics are represented by Cyperaceae (0.5–10%), *Hydrocotyle* (0–2%), *Myriophyllum* (0–2%) and *Isoetes* (2–19%). Ferns are represented by monolete spores (1.5–20%), *Jamesonia* (0–5%) and *Cyathea* (0–4%). Of the algae *Botryococcus* is present throughout the zone (0.5–43%), while *Pediastrum* (43%) and *Coelastrum* (6%) show a spike.

Pollen zone F2-17 (116.5–110.5 m)

Pollen zone F2-17 is characterized by relatively high values of arboreal pollen (34–53%). This zone differs from pollen zone 18 by higher values of *Alnus*, *Podocarpus*, *Hedyosmum*, *Vallea*, *Miconia*, Melastomataceae, *Eugenia*, *Myrica*, Ericaceae, Umbelliferae, Cyperaceae, *Jamesonia*, and *Botryococcus*, and lower values of Gramineae, *Polylepis-Acaena*, *Hypericum*, *Weinmannia*, *Valeriana*, Caryophyllaceae, *Plantago* and *Isoetes*. In the first half of the zone especially *Vallea* (7–1%), *Miconia* (7–0.5%), Melastomataceae (1.5–0.5%), *Eugenia* (1.5–0%) and Myrtaceae (0.5–0%) contribute to the Andean forest belt, while in the upper half of the zone *Alnus* (11–38%) is the main contributor. Other arboreal taxa are *Podocarpus* (2–5%), *Hedyosmum* (1–3%), *Weinmannia* (1.5–3%) and *Myrica* (7–2%). In the first half of the zone also the subparamo elements have lower values than in the upper half of the zone: Compositae (3–27%), *Polylepis-Acaena* (0–3%), Ericaceae (0–4%) and *Hypericum* (1–2%). Gramineae reach values of 51–23%. Paramo elements are hardly present. Aquatics are dominated by Cyperaceae (707–9%) which have a huge peak in the lower half of the zone. *Isoetes* (1–8%) and *Hydrocotyle* (0.5–3%) are also present. The ferns *Cyathea* (0–1%), *Jamesonia* (0–7%), *Lophosoria* (0–0.5%), monolete spores

(3–16%), and the alga *Botryococcus* (3–110%) increase in the upper half of the zone.

Pollen zone F2-16 (110.5–105.5 m)

Pollen zone F2-16 is characterized by relatively low values (27–16%) of arboreal pollen and relatively high values of the subparamo taxa. This zone differs from the previous zone by higher values of Gramineae, *Polylepis-Acaena*, *Valeriana*, *Aragoa*, *Plantago*, *Lycopodium* fov. and *Isoetes*, and lower values of *Alnus*, *Podocarpus*, *Vallea*, *Miconia*, Melastomataceae, *Myrica*, Cyperaceae, and *Botryococcus*. The arboreal taxa are *Alnus* (12–9%), *Podocarpus* (2–0.5%), *Hedyosmum* (2–1%), *Weinmannia* (2–3%), *Vallea* (0–1%), *Ilex* (0–0.5%), *Styloceras* (0–0.5%) and *Myrica* (2–1%). The subparamo elements are dominated by Compositae (14–22%) with some *Polylepis-Acaena* (6–1%), Ericaceae (0.5%) and *Hypericum* (1–4%). The paramo elements are mainly represented by *Valeriana* (3–0.5%), *Plantago* (0.5–3%), *Geranium* (0.5–0%) and *Aragoa* (0.5%). Gramineae reach values of 50–57%. *Isoetes* is the main aquatic representative (12–4%), with low values for *Hydrocotyle* (1–0.5%) and Cyperaceae (1–0.5%). The ferns are mainly monolete spores (9.5–3.5%) and *Jamesonia* (5–0.5%) with lesser amounts of *Cyathea* (1–0%). The alga *Botryococcus* decreases from 130 to 4%.

Pollen zone F2-15 (105.5–100.5 m)

Pollen zone F2-15 is characterized by relatively high values of arboreal pollen (21–50%). This pollen zone differs from pollen zone F2-16 by higher values of *Alnus*, *Podocarpus*, *Vallea*, *Ilex*, *Miconia*, Melastomataceae, *Eugenia*, *Myrica* and Cyperaceae, and lower values of *Polylepis-Acaena*, Compositae, *Hedyosmum*, *Weinmannia*, *Valeriana*, Caryophyllaceae, *Geranium*, *Aragoa*, *Plantago*, *Lycopodium* fov., *Isoetes* and monolete spores. Arboreal taxa are *Vallea* (1.5–5%), *Ilex* (0–1%), *Miconia* (0–2%), Melastomataceae (0–0.5%), *Eugenia* (0–0.5%), *Myrica* (1–8%), *Hedyosmum* (2–1%), *Weinmannia* (3–1%), *Alnus* (12–32%) and *Podocarpus* (2–0.5%). Of the subparamo elements Compositae have values of 7–18%, *Polylepis-Acaena* 3–0.5%, Ericaceae 0–2.5% and *Hypericum* 0.5–3.5%. Gramineae show values of 34–69%. Of the paramo elements only *Plantago* is clearly present (5–1%). Aquatics are dominated by *Isoetes* (22–1%) in the lower half of the zone, while in the upper part Cyperaceae (1.5–45%) dominate. *Hydrocotyle* (0.5–2.5%) and *Myriophyllum* (0.5–1.5%) have low values. Ferns are mainly present in the lower half of the zone and in the uppermost sample, represented by monolete spores (9–1%) and *Jamesonia* (0–7%). The alga *Botryococcus* shows the same pattern as the ferns with values of 1–53%.

Pollen zone F2-14 (100.5–93.5 m)

Pollen zone F2-14 is characterized by relatively low values (24–44%) of arboreal pollen. This zone differs from pollen

zone F2-15 by higher values of *Polylepis-Acaena*, Ericaceae, *Weinmannia*, *Acalypha*, *Alchornea*, *Valeriana*, Caryophyllaceae, *Geranium*, *Aragoa*, *Lycopodium* fov., Umbelliferae, *Isoetes*, monolete spores and *Botryococcus*, and lower values of *Hypericum*, *Miconia* and Cyperaceae. The main arboreal taxa are *Alnus* (15–26%), *Podocarpus* (1–4%), *Hedyosmum* (0.5–2%), *Weinmannia* (0.5–8%), *Vallea* (0.5–1%), *Miconia* (0–1%), *Eugenia* (0–1%) and *Myrica* (1.5–6%). The subparamo elements are dominated by Compositae (12–21%) with a relatively high abundance of *Polylepis-Acaena* (1.5–5%). Ericaceae (4.5–0.5%) and *Hypericum* (2–0%) are more common in the lower half of the zone. Gramineae have values of 41–48%. The paramo taxa are mainly represented by *Plantago* (0.5–2.5%) and *Lycopodium* fov. (0.5–9%), the latter showing a clear maximum in this zone. Aquatics are dominated by *Isoetes* (3.5–24%) with lower values of Cyperaceae (7–0%). Ferns are mainly represented by monolete spores (19–4%) and *Jamesonia* (5–1%), both having higher values in the lower part of the zone. The alga *Botryococcus* has values of 27–260%.

Pollen zone F2-13 (93.5–87.5 m)

Pollen zone F2-13 is characterized by relatively high values (30–66%) of arboreal pollen occurring in two peaks. In this zone the first occurrence of *Quercus* pollen grains is recorded. This zone differs from the previous zone by higher values of *Alnus*, *Juglans*, *Myrica*, Cyperaceae and *Hydrocotyle*, and lower values of Gramineae, *Lycopodium* fov., *Weinmannia* and *Isoetes*. Arboreal taxa are *Alnus* (18–47%), *Weinmannia* (1.5–6%), *Podocarpus* (5–2%), *Hedyosmum* (2–0.5%), *Vallea* (0–1%), *Ilex* (0–0.5%), *Juglans* (0.5–0%), *Miconia* (0–1%), *Eugenia* (0.5–0%) and *Myrica* (2–7%). The main constituent of the subparamo is Compositae (20–10%), while *Polylepis-Acaena* (1–4%), Ericaceae (0.5–3%) and *Hypericum* (0–1%) have lower percentages. Gramineae occur with values of 21–44%. The paramo taxa are represented by low percentages. Of these taxa *Lycopodium* fov. (0.5–3%) and *Plantago* (0.5–1%) reach highest values. Aquatics are dominated by *Isoetes* (1.5–12%) and Cyperaceae (13–2.5%), while *Hydrocotyle* (0.5–2%) contributes to a lesser extent. Ferns are still dominated by monolete spores (6–15%) and *Jamesonia* (0.5–5%). *Lophosoria* (0–1%) increases somewhat. Of the algae *Botryococcus* shows values of 43–420% and *Coelastrum* has a small spike of 4%.

Pollen zone F2-12 (87.5–81.5 m)

Pollen zone F2-12 is characterized by somewhat lower values of arboreal pollen (25–55%). This zone differs from pollen zone F2-13 by higher values of Gramineae, *Polylepis-Acaena*, *Weinmannia* and *Botryococcus*, and lower values of Ericaceae, *Alnus*, *Podocarpus*, *Myrica* and Cyperaceae. Arboreal taxa are *Alnus* (15–45%), *Podocarpus* (1–3%), *Hedyosmum* (0.5–2%), *Weinmannia* (4–8%), *Vallea* (0.5–2%), *Miconia* (0–1%), *Eugenia* (0–0.5%) and *Myrica* (1–7%). The subparamo elements are dominated by Compositae (12–17%) with some *Polylepis-Acaena* (1.5–6%). Gramineae show values of 28–55%.

Paramo elements are present in low values, *Valeriana* 0.5–1%, Caryophyllaceae 0–1%, *Plantago* 0.5–2% and *Lycopodium* fov. 0.5–2%. Aquatics are dominated by *Isoetes* (1–20%) and Cyperaceae (2.5–7%), with low values of *Hydrocotyle* (0.5–2%). Ferns are dominated by monolete spores (3.5–13%). *Jamesonia* has low values (0.5–2%). The alga *Botryococcus* shows a spiky appearance with values between 46 and 2000%.

Pollen zones F2-11 to F2-9 (81.5–55.5 m)

With the present resolution of 1 m sample distance we are not able to identify the correct location of pollen zone F2-10. Pollen zones F2-11 to F2-9 are characterized by relatively high values (38–76%) of arboreal pollen in a sawtoothed appearance. In this part the continuous recording of *Quercus* starts. Pollen zones F2-11 to F2-9 differ from pollen zone F2-12 by higher values of *Alnus*, *Podocarpus*, *Hedyosmum*, *Vallea*, *Myrsine* (= *Rapanea*), *Symplocos*, *Ilex*, *Juglans*, *Miconia*, Urticaceae–Moraceae, *Eugenia*, *Myrica*, *Acalypha*, *Alchornea*, *Hydrocotyle* and Cyperaceae, and lower values of Gramineae, *Polylepis-Acaena*, Caryophyllaceae and *Isoetes*. Arboreal pollen taxa are *Alnus* (19–56%), *Quercus* (0–6%), *Podocarpus* (3–11%), *Weinmannia* (6–0.5%), *Vallea* (0.5–5%), *Myrsine* (= *Rapanea*) (1–0%), *Ilex* (1–0%), *Miconia* (0.5–2.5%), Urticaceae (0–1.5%), *Hedyosmum* (0.5–6%), *Eugenia* (1–0%), *Myrica* (1–6.5%), *Symplocos* (0–0.5%) and *Juglans* (0–0.5%). The subparamo elements are dominated by Compositae (5–16%). *Polylepis-Acaena* has values of 0–4%, Ericaceae of 0–2% and *Hypericum* of 0–3%. The paramo elements have low percentages. Gramineae have values of 16–48%. Of the aquatics Cyperaceae increase throughout the zones (2–17%), while *Isoetes* (1–18) decreases with a sudden rise at the uppermost sample. *Hydrocotyle* reaches somewhat higher values (0–3%). The main constituent of the ferns is monolete spores (2–11%), with low values (0–3%) of *Jamesonia*. Of the algae *Botryococcus* has values of 11–480%, *Pediastrum* of 0–4% and *Coelastrum* of 0–11%.

Pollen zone F2-8 (55.5–51.5 m)

Pollen zone F2-8 is characterized by low values of arboreal pollen (15–22%); all arboreal species show lower values. This pollen zone differs from the previous one by higher values of Gramineae, Ericaceae, *Hypericum*, Compositae, *Valeriana*, *Plantago*, *Lycopodium* fov. and *Isoetes*, and lower values of *Alnus*, *Quercus*, *Podocarpus*, *Hedyosmum*, *Weinmannia*, *Vallea*, Urticaceae–Moraceae, *Eugenia*, *Myrica*, *Acalypha*, *Alchornea* and Cyperaceae. The arboreal taxa are *Alnus* (13–8.5%), *Quercus* (0.5–1.5%), *Podocarpus* (0.5–2.5%), *Hedyosmum* (0.5%), *Weinmannia* (0.5–2%), *Vallea* (1–1.5%), *Ilex* (0–0.5%), *Miconia* (0–2%) and *Myrica* (1–3.5%). Gramineae have values of 66–36%, *Hypericum* 3.5–20% and Compositae 13–21%. The paramo taxa *Valeriana* (0.5–2%), *Plantago* (0.5–3.5%) and *Lycopodium* fov. (1–3%), are present. The aquatics show highest values in the lower part of the zone, dominated by *Isoetes* (17–6%) and Cyperaceae (8.5–0.5%). Of

the ferns monolet spores (4–5%) show lower values than in the previous zone, while *Cyathea* (0–2%) and *Jamesonia* (4–1.5%) show somewhat higher values. The alga *Botryococcus* has values of 18–82%.

Pollen zone F2-7 (51.5–40.5 m)

Pollen zone F2-7 is characterized by relatively high values (47–77%) of arboreal pollen. Pollen zone F2-7 differs from pollen zone F2-8 by higher values of *Alnus*, *Quercus*, *Podocarpus*, *Hedyosmum*, *Weinmannia*, *Vallea*, *Myrsine* (= *Rapanea*), *Ilex*, *Miconia*, *Melastomataceae*, *Urticaceae*–*Moraceae*, *Eugenia*, *Myrica*, *Acalypha*, *Alchornea*, *Cyperaceae*, monolet spores and algae, and lower values of *Gramineae*, *Ericaceae*, *Hypericum*, *Valeriana*, *Plantago*, *Lycopodium* fov., *Isoetes*, and *Jamesonia*. *Gramineae* decrease in value (9–29%), as well as subparamo elements *Hypericum* (4.5–0.5%) and *Ericaceae* (1–0.5%). The arboreal taxa are *Alnus* (19–49%), *Quercus* (1–9.5%), *Podocarpus* (1.5–5%), *Hedyosmum* (0.5–4%), *Weinmannia* (0.5–4%), *Vallea* (7–2%), *Myrsine* (= *Rapanea*) (0–1.5%), *Symplocos* (0.5–0%), *Ilex* (0.5–1.5%), *Miconia* (0.5–7%), *Melastomataceae* (0–1%), *Urticaceae* (1–0%), *Eugenia* (1.5–0%), *Myrica* (1.5–8%) and the subandean forest species *Acalypha* (1.5–0%) and *Alchornea* (0–1%). The paramo elements have decreased to very low values. The aquatic *Cyperaceae* reach values of 1–16%. The ferns are dominated by monolet spores (4–12%), with some *Jamesonia* (0.5–1.5%). Of the algae *Coelastrum* (685–0%) has a peak in the lower part of the zone, followed by a peak in *Pediastrum* (71–2%), while *Botryococcus* (23–300%) has its highest values in the upper part of the zone.

Pollen zone F2-6 (40.5–33.5 m)

Pollen zone F2-6 is characterized by relatively low values (24–44%) of arboreal pollen. This zone differs from pollen zone F2-7 by higher values of *Gramineae*, *Polylepis*–*Acaena*, *Hypericum*, *Valeriana*, *Caryophyllaceae*, *Plantago*, *Lycopodium* fov., *Isoetes*, *Sphagnum*, *Cyathea*, *Jamesonia*, and monolet spores, and lower values of *Alnus*, *Podocarpus*, *Vallea*, *Myrsine* (= *Rapanea*), *Ilex*, *Miconia*, *Myrica* and algae. Arboreal taxa are *Alnus* (7–19%), *Quercus* (2.5–7%), *Podocarpus* (7–0.5%), *Hedyosmum* (0.5–2%), *Weinmannia* (2.5–6%), *Vallea* (1.5–5.5%), *Myrsine* (= *Rapanea*) (0.5–1%), *Miconia* (0.5–4%), *Melastomataceae* (0.5–1%), *Urticaceae* (0–2%) and *Myrica* (1–3.5%). The subandean forest elements *Acalypha* (0–2%) and *Alchornea* (0–1.5%) are present. The subparamo elements are dominated by *Compositae* (11–20%), with relatively high values of *Polylepis*–*Acaena* (1–4%), *Hypericum* (2–5%) and *Ericaceae* (0–1.5%). *Gramineae* have values of 40–56%. The main constituents of the paramo taxa are *Valeriana* (0.5–2%), *Caryophyllaceae* (0.5–1.5%), *Plantago* (0–3%) and *Lycopodium* fov. (0–1.5%). Of the aquatics *Isoetes* (5–33%) increases and takes over dominance of *Cyperaceae* (1–7%). At the top of the zone there is an increase in *Hydrocotyle* (0–2%). Ferns are mainly represented by monolet spores (3–6%) and *Jamesonia*

(0.5–1.5%). Of the algae *Botryococcus* has fluctuating high values (150–380%), *Pediastrum* increases (0–176%) and *Coelastrum* (0–285%) has a peak at the uppermost sample.

Pollen zone F2-5 (33.5–29.5 m)

Pollen zone F2-5 is characterized by relatively high values (55–77%) of arboreal pollen. This zone differs from the previous zone by higher values of *Alnus*, *Hedyosmum*, *Vallea*, *Miconia*, *Urticaceae*–*Moraceae*, *Eugenia*, *Myrica*, *Acalypha*, *Alchornea*, *Myriophyllum* and *Cyperaceae*, and lower values of *Gramineae*, *Polylepis*–*Acaena*, *Ericaceae*, *Compositae*, *Quercus*, *Weinmannia*, *Valeriana*, *Caryophyllaceae*, *Plantago*, *Lycopodium* fov., *Isoetes*, and *Jamesonia*. The arboreal taxa are *Alnus* (29–56%), *Quercus* (3.5–1%), *Podocarpus* (1–4%), *Hedyosmum* (0.5–3%), *Weinmannia* (3.5–1.5%), *Myrsine* (= *Rapanea*) (1–0%), *Vallea* (2–6%), *Juglans* (1–0%), *Miconia* (2–7%), *Melastomataceae* (1.5–0.5%), *Urticaceae* (0–2%), *Pilea* (0.5–0%), *Eugenia* (0.5%) and *Myrica* (3–5%). The subandean forest species *Acalypha* (4–0%) and *Alchornea* (1.5–1%) are present. The values of *Gramineae* (11–26%) have diminished, as well as the percentage subparamo elements which is dominated by *Compositae* (4–13%) with some *Hypericum* (1.5–2.5%). The paramo elements are a little lower. Aquatics are mainly represented by *Cyperaceae* (6–21%) with some *Isoetes* (0.5–1.5%), *Myriophyllum* (0.5–1.5%), *Hydrocotyle* (1–0.5%), *Polygonum* (0–0.5%) and a single occurrence of *Ludwigia*. Ferns are very low, only monolet spores (3–8%) are noteworthy. Of the algae *Pediastrum* (1100–1%) has a peak at the lower part of the zone, *Botryococcus* has fluctuating high values (83–340%) and *Coelastrum* (68–3%) decreases.

Pollen zone F2-4 (29.5–17.5 m)

Pollen zone F2-4 is characterized by relatively high values (38–71%) of arboreal pollen in a fluctuating curve. This zone differs from pollen zone F2-5 by higher values of *Gramineae*, *Ericaceae*, *Compositae*, *Quercus*, *Podocarpus*, *Myrsine* (= *Rapanea*), *Ilex*, *Valeriana*, *Lycopodium* fov., *Isoetes*, *Sphagnum*, *Cyathea*, *Jamesonia*, and monolet spores, and lower values of *Alnus*, *Weinmannia*, *Miconia*, *Urticaceae*–*Moraceae* and *Botryococcus*. Arboreal taxa are *Alnus* (19–31%), *Miconia* (1–4.5%), *Quercus* (2–12%), *Myrsine* (= *Rapanea*) (0–2%), *Drimys* (0.5–0%), *Ilex* (0–1.5%), *Podocarpus* (0.5–7%), *Hedyosmum* (1.5–6%), *Weinmannia* (0.5–5%), *Vallea* (1.5–6.5%), *Styloceras* (0–0.5%), *Melastomataceae* (0–1%), *Urticaceae* (0–1%), *Eugenia* (0–1%) and *Myrica* (2–7%). Of the subandean forest elements *Acalypha* (0–1%) has decreased a little while *Alchornea* (0.5–2.5%) reaches somewhat higher values. The subparamo elements all reach somewhat higher percentages: *Compositae* 5.5–20%, *Hypericum* 4.5–1%, *Ericaceae* 0.5–2.5% and *Polylepis*–*Acaena* 0.5–2%. *Gramineae* reach values of 17–45%. Of the paramo elements *Valeriana* (0–2%), *Plantago* (0–1.5%) and *Lycopodium* fov. (0–1.5%) are noteworthy, while *Rumex* (0–8%) has a peak in the upper part of the zone. The aquatics are dominated by *Cyperaceae* (1–19%)

and *Isoetes* (0.5–12%), with some *Hydrocotyle* (0.5–3%) and *Sphagnum* (0–2%). The ferns are dominated by monolete spores (4–15%). *Cyathea* (0.5–6%) and *Jamesonia* (0.5–8%). Of the algae *Botryococcus* reaches values of 14–130%, *Pediastrum* of 0–83% and *Coelastrum* of 0–21%.

Pollen zone F2-3 (17.5–2 m)

Pollen zone F2-3 is characterized by relatively high values (44–79%) of arboreal pollen. This zone differs from the previous zone by higher values of *Alnus*, *Quercus*, *Podocarpus*, *Weinmannia*, *Vallea*, *Miconia*, *Acalypha*, *Alchornea*, *Hydrocotyle* and *Myriophyllum*, and lower values of Compositae, Cyperaceae and *Jamesonia*. The arboreal taxa are *Alnus* (22–48%), *Quercus* (2–18%), *Podocarpus* (0.5–10.5%), *Hedyosmum* (0.5–4.5%), *Weinmannia* (0.5–5%), *Vallea* (10–0.5%), *Myrsine* (= *Rapanea*) (2–0%), *Miconia* (7–0%), *Eugenia* (1–0%) and *Myrica* (0.5–6%). The subandean forest elements *Acalypha* (0–1.5%) and *Alchornea* (0–2%) are clearly present. The subparamo elements are dominated by Compositae (16–4.5%) with some *Hypericum* (0.5–7.5%), *Polylepis-Acaena* (0.5–4%) and Ericaceae (0.5–1%). Gramineae reach percentages of 7–44%. Of the paramo elements *Valeriana* (0–1%), *Plantago* (0–2%) and *Lycopodium* fov. (0–1.5%) are noteworthy. Of the aquatics Cyperaceae (8–0.5%) decrease throughout the zone, while *Hydrocotyle* (0.5–4%) increases. *Isoetes* is present with values of 1–9% and *Myriophyllum* with values of 0–2%. The ferns are still dominated by monolete spores (3–14%) with clear presences of *Cyathea* (1.5–3.5%) and *Jamesonia* (1–6%). Of the algae *Botryococcus* (12–1240%) increases in the upper part of the zone, *Pediastrum* reaches values of 37–30% and *Coelastrum* hardly occurs.

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