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THE PALEOBOTANICAL RECORD OF COLOMBIA: IMPLICATIONS FOR BIOGEOGRAPHY AND BIODIVERSITY¹

Henry Hooghiemstra,² Vincent M. Wijnnga,²
and Antoine M. Cleef²

ABSTRACT

Plant microfossil and macrofossil associations obtained from six dated sections from the area of the basin of Bogotá (2550 m, Eastern Cordillera, Colombia) show the evolution of the late Neogene Andean montane forest, triggered by the Andean orogeny. Progressive adaptation of warm tropical taxa to cool montane conditions, evolution of new neotropical montane taxa, and immigration of temperate Laurasian, Holarctic, and Austral-Antarctic elements gave shape to the present-day montane forest. Vegetational characteristics inferred from fossil plant associations reveal the altitude at the time of deposition. Neogene forests are floristically compared with contemporary forests at comparable altitudinal intervals in the surroundings of the Bogotá basin; however, the absence of taxa that had not yet arrived, or evolved, is most salient and shows that non-analogue plant communities are common.

The main phases of montane forest development are: (1) pre-uplift phase of the late Miocene with abundant lowland taxa with tropical or neotropical affinities (*Mauritia* Kunth, *Amanoa* Aubl., *Ceiba* Miller, and representatives of Humiriaceae); montane forest rich in Podocarpaceae (potentially including *Nageia* Gaertn., *Podocarpus* L'Hér., *Prumnopitys* Phil., and *Retrophyllum* C. N. Page) covered other previously uplifted areas in the region; (2) toward the early Pliocene the area was uplifted to ca. 1000 m; the relative proportion of temperate taxa of North American and southern South American stock increased and occupied the slopes of the low mountains; and (3) by the middle Pliocene uplift had proceeded to ca. 2000–2200 m and tropical lowland taxa, which are now restricted to altitudes below 1000 m, are no longer recorded in the fossil plant associations; the increase in the number of newly appearing montane taxa (*Myrica* L., *Turpinia* Vent., *Gunnera* L., *Bocconia* L., *Gaiadendron* G. Don f., *Daphnopsis* C. Martius, and *Monnina* Ruiz & Pav.) suggests a significant increase of diversity.

Until the late Pliocene there is little to no evidence for the existence of the páramo; taxa such as *Xyris* L., *Hypericum* L., *Carex* L., *Montia* L., and *Ranunculus* L. might have formed swamp or bog vegetation only. It is believed that these taxa colonized mountaintops with half-open vegetation; these areas extended when the mountains reached above upper forest line elevations.

The distribution areas of the endemic genera of the Espeletiinae largely coincide with the youngest parts (< 5 Ma) of the northern Andes. Changing climatic conditions forced individual plant species to migrate vertically. Composition of plant communities changed continuously and vegetation belts frequently were altitudinally squeezed or offered possibilities for expansion. This long process stimulated speciation and provoked sequential non-analogue vegetation types. Thus, the biodiversity hotspot of the northern Andes has a dynamic history.

Key words: Andean uplift, biome evolution, Colombia, Espeletiinae, montane forest, Neogene, páramo, phytogeography.

RESUMEN

Los microfósiles de plantas y asociaciones de macrofósiles obtenidos de seis secciones fechadas del área de la cuenca de Bogotá (2550 m, Cordillera Oriental, Colombia) demuestran la evolución del bosque andino del Neógeno tardío, accionado por la orogenia andina. La adaptación progresiva de taxones tropicales calidos hacia las condiciones frías montanas, la evolución de nuevos taxones neotropicales montanos y la migración de elementos templados laurásicos, holárticos y austral-antárticos dieron forma al bosque montano actual. Las características de la vegetación deducidas de las asociaciones de plantas fósiles revelan la altitud al momento de los depósitos. Los bosques neógenos se comparan florísticamente con bosques contemporáneos a intervalos altitudinales comparables en los alrededores de la cuenca de Bogotá; sin embargo, la ausencia de taxones que todavía no habían llegado, o desarrollado, es sobresaliente y demuestra que las comunidades de plantas no análogas son comunes.

Las fases principales del desarrollo del bosque montano son: (1) fase pre-levantamiento del Mioceno tardío con abundancia de taxones de las tierras bajas con afinidades tropicales o neotropicales (*Mauritia* Kunth, *Amanoa* Aubl., *Ceiba* Miller y representantes de Humiriaceae); un bosque montano rico en Podocarpaceae (potencialmente incluyendo *Nageia* Gaertn., *Podocarpus* L'Hér., *Prumnopitys* Phil. y *Retrophyllum* C. N. Page) cubría otras áreas previamente levantadas en la región; (2) hacia el Plioceno temprano el área se elevó ca. 1000 m; la proporción relativa de taxones templados de origen norteamericano y suramericano meridional aumentó y ocupó las vertientes de las montañas bajas; y (3) hacia el Plioceno medio, el

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levantamiento había llegado hasta ca. 2000–2200 m y taxones tropicales de las tierras bajas, que actualmente se restringen a las altitudes bajo los 1000 m, ya no se registran más en los registros fósiles de asociaciones de plantas; el aumento del número de taxones montanos nuevos (*Myrica* L., *Turpinia* Vent., *Gunnera* L., *Bocconia* L., *Gaiadendron* G. Don f., *Daphnopsis* C. Martius y *Monnina* Ruiz y Pav.) sugiere un aumento significativo de la diversidad.

Hasta el Plioceno tardío, hay poco a ninguna evidencia de la existencia del páramo; taxones como por ejemplo *Xyris* L., *Hypericum* L., *Carex* L., *Montia* L. y *Ranunculus* L. pudieron haber formado sólo vegetación de los pantanales o las turbas. Se cree que estos taxones colonizaron las cimas de las montañas con vegetación semi-abierta; estas áreas se extendieron cuando las montañas alcanzaron elevaciones sobre el límite superior del bosque.

Las áreas de distribución de los géneros endémicos de Espeletiinae coinciden en gran parte con las regiones más jóvenes (< 5 Ma) de los Andes del norte. Condiciones climáticas cambiantes forzaron a especies individuales de plantas a migrar verticalmente. La composición de las comunidades de plantas cambia continuamente y los cinturones de vegetación fueron comprimidos altitudinalmente o se ofrecieron posibilidades de expansión. Este largo proceso estimuló especiación y provocó tipos de vegetación secuenciales no análogos. Así el punto caliente de biodiversidad de los Andes del norte tiene una historia dinámica.

Increasing knowledge of the present-day flora and vegetation in the northern Andes promoted a simultaneous interest in its history. Paleocological, primarily palynological, studies of Neogene sediments have provided a general understanding of the composition of the flora in the past and its changes over time. Van der Hammen et al. (1973) demonstrated the influence of tectonics and climatic change on the development of the Andean forest. Since then, understanding of how and when the present-day Andean forest acquired its floristic composition has increased by integrating paleodata with information about the present-day Andean forest (Raven & Axelrod, 1974; van der Hammen, 1974; Simpson, 1975; Gentry, 1982; Cleef et al., 1983; van der Hammen & Cleef, 1986; van der Hammen, 1989; Simpson & Todzia, 1990; Hooghiemstra & Cleef, 1995; Hooghiemstra & van der Hammen, 2004).

This paper focuses on results obtained from plant macrofossils and fossil pollen from sediments located in the basin and surrounding areas of Bogotá, Eastern Cordillera of Colombia. Sites are sections from outcrops or deep bore holes and are all located at ca. 2550 m (Fig. 1). Fossil plant assemblages from the late Miocene (sites Salto de Tequenedama III; Wijninga, 1996a), early Pliocene (site Río Frío; Wijninga, 1996c), middle Pliocene (site Subachoque-39; Wijninga & Kuhry, 1990; site Facatativá-13; Wijninga, 1996b), and late Pliocene (site Guasca; Wijninga & Kuhry, 1993) present snapshots of the long-term paleocological development of the northern Andes (Table 1). Paleocological data are compared with present-day northern Andean flora in core Fuquene-2 (van Geel & van der Hammen, 1973) to shed light on speciation, migration, plant diversity, and phytogeographic composition (Cleef, 1979; Cuatrecasas, 1979; van der Hammen & Cleef, 1986; Luteyn, 1999). In addition, a synthesis of these data is presented to support our understanding of how evolution of the Neogene sedimentary environment and vegetation in northwestern Amazonia relates to the uplift of the northern Andes.

The objective of the present paper is to compare the paleobotanical evidence from the northern Andes with paleobotanical studies from Amazonian lowland sediments in order to reconstruct the evolution of the northern Andean biota. The phytogeographic composition of the fossil plant assemblages shows snapshots of a long process of gradual change. Uplift created large areas of habitat that had previously not existed regionally, offering new establishment possibilities for floral elements from different source areas. The biostratigraphic position of the recorded plant taxa is evaluated.

ALTITUDINAL ZONATION OF THE PRESENT-DAY NORTH ANDEAN VEGETATION AS A BASIS FOR PALEO- RECONSTRUCTIONS

The altitudinal zonation of the neotropical montane vegetation is primarily due to the effect of decreasing temperature with increasing elevation. Many studies have been dedicated to the composition and structure of the neotropical montane forest (e.g., Cuatrecasas, 1934; Grubb et al., 1963; van der Hammen & González, 1963; Vareschi, 1980; Cleef et al., 1983; Cleef & Hooghiemstra, 1984; Huber, 1986; Ulloa Ulloa & Jørgensen, 1993; Rangel, 1995; Rangel et al., 2003; Cleef et al., 2003). Cuatrecasas (1958) published an altitudinal zonation for the Colombian vegetation, later depicted by van der Hammen (1974) (Fig. 2). Their scheme of altitudinally arranged vegetation belts is used in this study, but new information from Wille et al. (2001) and Torres (2006) has been incorporated. This altitudinal zonation corresponds principally to the global vegetation zonation in high tropical mountains (Grubb, 1974, 1977) and is the basis for interpreting paleorecords in terms of uplift, climate change, and changing floristic compositions.

The following account of the present-day altitudinal vegetation distribution in the Eastern Cordillera of Colombia is needed to support the interpretation of

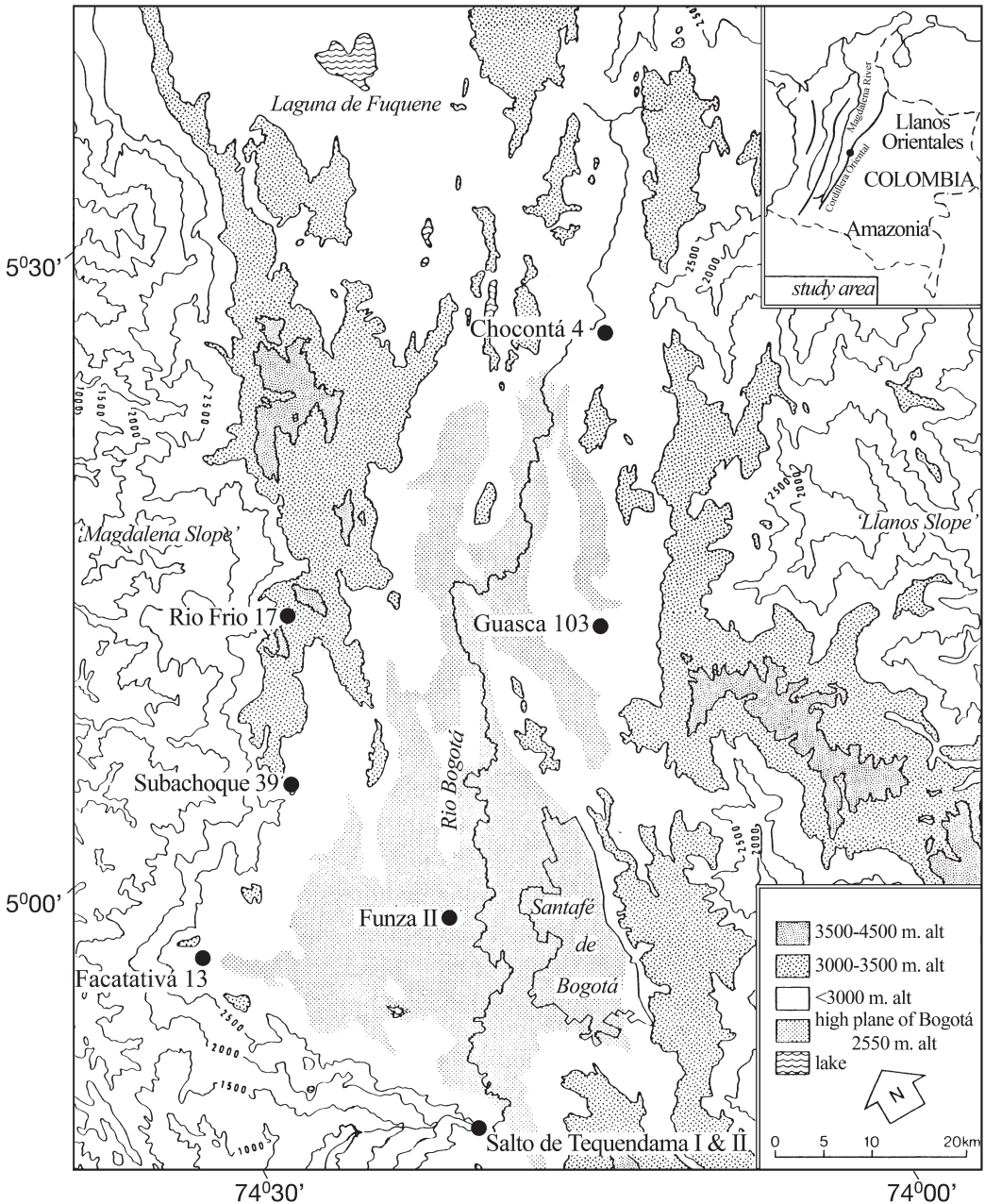


Figure 1. Map of the high plain of Bogotá, Colombia, and surroundings. Black dots indicate locations of sites (sections from outcrops and deep bore holes) with sediments of an age from late Miocene to late Pliocene. Modified after Hooghiemstra (1984), reprinted with permission from E. Schweizerbart'sche Verlagsbuchhandlung.

fossil assemblages in paleoaltitudes. Here we use the family level because a significant proportion of pollen- and macrofossil taxa were identified to that level. Moreover, given our objectives, Keizer's (2000) vegetation analysis of the Colombian Eastern Cordillera indicates that analysis at the family level is sufficient. During the Miocene and Pliocene, in-

dividual taxa may have had slightly different altitudinal ranges compared to today (Torres, 2006; Torres & Hooghiemstra, in prep.), but the large number of taxa used to infer paleoaltitudes and the relatively large envelope of uncertainty associated with the paleoaltitude estimates compensate for such potential taxa-specific errors.

Table 1. Site-specific data of sections and cores in and around the basin of Bogotá, Colombia, used in this study (see Fig. 1).

Site	Salto de								
	Tequendama I (section)	Tequendama II (section)	Río Frío 17 (section)	Subachoque 39 (section)	Facatativá 13 (section)	Guasca 103 (section)	Fuquene 2 (core)	Funza 1 (core)	Funza 2 (core)
Coordinates	4°50'N, 74°20'W	4°50'N, 74°20'W	5°14'N, 74°29'W	5°06'N, 74°29'W	4°57'N, 74°33'W	5°13'N, 74°15'W	5°27'N, 73°46'W	4°50'N, 74°12'W	4°59'N, 74°22'W
Modern altitude (m)	2450	2475	3165	2820	2750	2650	2580	2550	2550
Lithostratigraphy	Lower Tilatá Formation/ Tequendama Member	Lower Tilatá Formation/ Tequendama Member	Lower Tilatá Formation/ Tibagota Member	Lower Tilatá Formation/ Tibagota Member	Lower Tilatá Formation/ Tibagota Member	Upper Tilatá Formation/ Guasca Member	—	—	—
Depositional environment	stream deposit, river channel	floodplain, swamp	stream deposit, lake	floodplain deposit	peat, swamp, lake	swamp, lake	lake	swamp, lake, river deposits	swamp, lake, river deposits
Sample interval (m)	34.70–34.75/ 35.15–35.20	1.20–1.25	0.60–0.65	0.35–0.40	1.90–1.95	26.75–26.80	12–0	357–0	586–0
Sample material	peaty silt	peaty clay	silt	peaty silt	peat	peat	(peaty) clay, peat	clay, sandy clay, peat	clay, sandy clay, peat
Main macroremains	wood, cuticles	cuticles	seeds	wood	wood, cuticles	cuticles	—	—	—
Age (Ma)	± 17–11	± 17–11	5.3 ± 1	± 5–4	3.7 ± 0.7	± 3	ca. 32–0 ka	ca. 1.6 Ma–30 ka	ca. 3.2 Ma– 30 ka
No. of taxa included in percentage calculations	63	63	18	52	59	32	—	—	—
Biozone	I	I	II	II	II	III	VII	V, VI, VII	IV, V, VI, VII
Inferred paleoaltitude (m)	< 700 (± 500)	< 700 (± 500)	ca. 1000 (maximally ca. 1500)	1000 (± 500)	2000 (± 500)	2200 (± 500)	—	—	—
References	Wijninga, 1996a; 1996d	Wijninga, 1996a; 1996d	Wijninga, 1996c; 1996d	Wijninga & Kuhry, 1990; Wijninga, 1996d	Wijninga, 1996b; 1996d	Wijninga & Kuhry, 1993; Wijninga, 1996d	van Geel & van der Hammen, 1973	Hooghiemstra, 1984, 1989; Andriessen et al., 1993; Torres et al., 2005; Torres, 2006	Andriessen et al., 1993; Torres et al., 2005; Torres, 2006
Relevance	1	1	1	1	1	1	2	3	4

1. Paleoflora from which paleoaltitude has been inferred.

2. Modern flora used for comparison with paleofloras.

3. Pollen spectra reflect Quaternary setting after the upheaval of the Eastern Cordillera was completed.

4. Pollen spectra reflect late Pliocene and Quaternary setting after the upheaval of the Eastern Cordillera was completed.

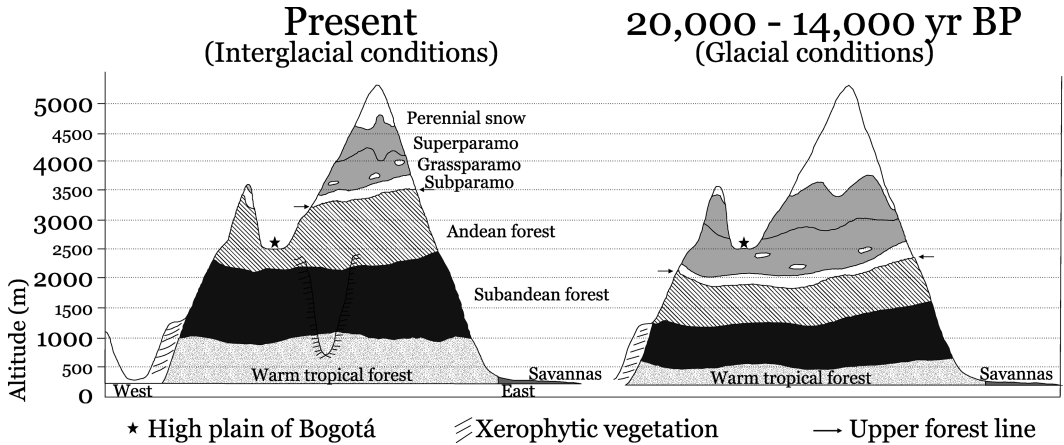


Figure 2. Schematic cross section through the Eastern Cordillera at the latitude of Bogotá. The altitudinal distribution of zonal vegetation belts for the present and the Last Glacial Maximum are shown. Xerophytic vegetation is mainly azonal and occurs in the interandean valleys. Its presence is shown because xerophytic elements are also present in the associations of paleofloras of this study. Modified after van der Hammen (1974), reprinted with permission from Blackwell Publishing.

The present-day tropical lowland belt extends from sea level to 1000–1200 m, and annual temperatures average 30°C at the lower altitudinal limit to 24°C at the upper altitudinal limit. The vegetation is principally characterized by arboreal representatives of the Anacardiaceae, Annonaceae, Apocynaceae, Arecaceae, Bombacaceae, Burseraceae, Caryocaraceae, Cecropiaceae, Clusiaceae, Euphorbiaceae, Humiriaceae, Lauraceae, Lecythidaceae, Leguminosae, Melastomataceae, Meliaceae, Moraceae, Myristicaceae, Rubiaceae, Sapotaceae, Sterculiaceae, Tiliaceae, and Vochysiaceae. Savanna vegetation is dominated by Poaceae and characterized by woody genera including Dilleniaceae, Malpighiaceae, and Rubiaceae. The most species-rich families include Fabaceae, Myrtaceae, Orchidaceae, Piperaceae, Rubiaceae, and Sapindaceae.

The present-day subandean forest belt (= lower montane forest belt) extends from 800–1200 to 2300–2500 m, and average annual temperatures are from 24°C at the lower altitudinal limit to 16°C at the upper altitudinal limit. Common arboreal taxa include representatives of the Araliaceae, Arecaceae, Brunelliaceae, Cecropiaceae, Clusiaceae, Cyatheaceae, Euphorbiaceae, Fabaceae, Fagaceae, Hippocastanaceae, Lauraceae, Malpighiaceae, Melastomataceae, Meliaceae, Proteaceae, Rubiaceae, Rutaceae, and Solanaceae. The most species-rich families include Leguminosae, Orchidaceae, Polypodiaceae, Rubiaceae, and Solanaceae.

The present-day Andean forest belt (= upper montane forest belt) extends from 2300–2500 to 3200–3300 m, and annual temperatures average 16°C at the lower altitudinal limit to 9°C at the upper altitudinal limit. The upper altitudinal limit reflects

the upper forest line. Palynological studies from deep cores from the basin of Bogotá show that during the Pliocene the upper forest line corresponded to a higher temperature than today (Hooghiemstra, 1984; Torres, 2006; Torres & Hooghiemstra, in prep.). Therefore, the Miocene-Pliocene temperature range may have been ca. 16°C to ca. 11°C. Common families are Aquifoliaceae, Araliaceae, Betulaceae, Caprifoliaceae, Chloranthaceae, Clethraceae, Clusiaceae, Cunoniaceae, Cyatheaceae, Elaeocarpaceae, Ericaceae, Euphorbiaceae, Fagaceae, Juglandaceae, Lorantheaceae, Melastomataceae, Myricaceae, Myrsinaceae, Myrtaceae, Arecaceae, Proteaceae, Rosaceae, Solanaceae, Symplocaceae, Theaceae, Thymelaeaceae, and Winteraceae. The most species-rich families include Asteraceae, Ericaceae, and Polypodiaceae.

The present-day subpáramo zone is immediately above the upper forest line and extends from 3200–3300 to ca. 3600 m, and annual temperatures average 9°C to 7°C at its upper limit. The lower part of the subpáramo belt is dominated by shrub and dwarf forest, whereas the upper part is characterized by dwarf shrub vegetation. The pollen record of Funza-2 shows that the subpáramo belt developed further during the late Pliocene (Torres, 2006; Torres & Hooghiemstra, in prep.). During the late Miocene and early Pliocene, the status of the subpáramo belt is uncertain and perhaps it had not developed into a discrete belt as it did during the Quaternary. Characteristic subpáramo taxa include Asteraceae, Clusiaceae, Ericaceae, Escalloniaceae, Melastomataceae, Myricaceae, Rosaceae, Rubiaceae, and Scrophulariaceae.

The present-day grasspáramo belt extends from ca. 3500 to ca. 4200 m, and annual temperatures average

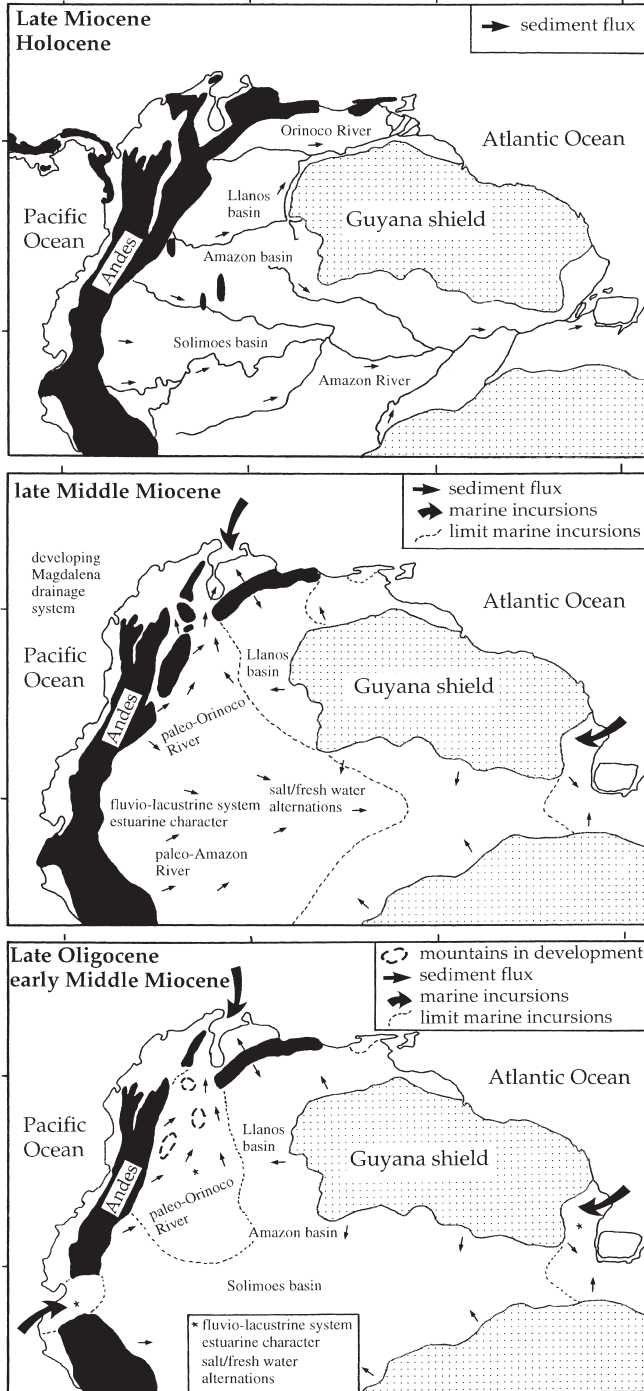


Figure 3. Paleogeographic maps of the (top) late Miocene to Present, (middle) late Middle Miocene, and (bottom) early Middle Miocene of northern South America. The development of the northern Andes, the separation of Chocó and Lower Magdalena rainforest areas from the main area of Amazonian rainforest, and the middle Miocene fluvio-lacustrine system in the present-day central Amazon basin is shown. During periods of high sea level stands, at various places in the present Amazon basin, mangrove vegetation developed under brackish water conditions (the extension of an inland sea is indicated by a dotted line). Between the late Miocene and the Quaternary, the modern Orinoco River system developed from the paleo-Orinoco River and the Amazon River developed as a transcontinental drainage system toward the Atlantic. Reprinted from Hooghiemstra & van der Hammen (1998), with permission from Elsevier. The Hooghiemstra & van der Hammen (1998) figure was created based on Hoorn et al. (1995).

7°C at the lower altitudinal limit to 3°C at the upper altitudinal limit. The vegetation is dominated by graminoid communities associated with stem rosettes of mainly *Espeletia* Mutis ex Bonpl. The most species-rich families in the subpáramo and grasspáramo belts are Asteraceae, Ericaceae, Poaceae, and Polypodiaceae.

The present-day superpáramo belt occurs above the grasspáramo and extends from ca. 4200 m up to the snowline at ca. 4800–5000 m. The annual temperature averages between 3°C and 0°C. The vegetation cover is scarce and patchy due to frequent frosts and unstable soil caused by frost heaving. The vegetation of this belt does not play a relevant role in estimating paleoaltitudes from paleofloras.

CHANGES OF THE PALEOENVIRONMENTAL SETTING OF NORTHERN SOUTH AMERICA SINCE THE MIOCENE

The geologic and paleogeographic history of the northern Andes is principally related to the relative motion of continental and oceanic plates. During the late Oligocene of northwest South America, the breaking up of the Farallón Plate in the Nazca and Cocos plates enhanced tectonic activity along the Pacific side of the continent and induced the uplift of the Andes (Wortel & Cloetingh, 1981; Wortel, 1984; Smith, 1985). Plate motions were also responsible for the closing of the Isthmus of Panama during the Pliocene (Keigwin, 1978, 1982; Duque Caro, 1990).

The uplift history of the three Cordilleras in Colombia stretches across the Neogene, but in many places uplift was most important during the period between the Oligocene and the Pliocene, with highest uplift rates during the Pliocene (van der Hammen, 1961; Harrington, 1962; van Houten & Travis, 1968; van der Hamen et al., 1973; Fabre, 1983; Kroonenberg et al., 1990; van der Wiel, 1991; Hoorn et al., 1995). Uplift in some parts of the Western Cordillera occurred during the Miocene. Parts of the Colombian Central Cordillera rose between 22 and 18 million years ago (Ma), whereas parts of the Eastern Cordillera were uplifted between 10 and 4 Ma. The Santander Massif of the Eastern Cordillera was uplifted between 16 and 12 Ma (Kroonenberg et al., 1990). In the Upper Magdalena Valley, the Garzón Massif was uplifted around 12 Ma, which resulted in a fundamental change in the Magdalena River's direction of flow (van Houten & Travis, 1968; van der Wiel, 1991; Guerrero, 1993; Flynn et al., 1994).

SHORT RECAPITULATION OF PALEOBOTANICAL EVIDENCE FOR UPLIFT FROM SITES IN LOWLAND AMAZONIA

Miocene and Pliocene sediments from exposures in river valleys in Colombian Amazonia showed pollen

records that could be dated based on biostratigraphy (Hoorn, 1993; Hoorn et al., 1995). Pollen records from these landlocked sites showed alternations between vegetation characteristic of inland wet forest, open vegetation of coastal plains (with abundant grasses and palms), and mangroves. These environmental changes strongly suggest that during those time intervals marine incursions were able to reach the area that is covered at present by the rainforests of northwest Amazonia. In particular, during periods with high sea-level stands, marine waters penetrated far into the Amazon basin, changing freshwater ecosystems (swamps and inundated forest) into brackish and saltwater ecosystems (mangroves) (Fig. 3). Because ecophysiological conditions during such changes would have been at extremes, during the Neogene a significant part of Amazonia had to have been repeatedly fully repopulated with a "new" ecosystem.

Uplift of the northern Andes is substantiated by a change in the drainage pattern: during the early Middle Miocene the Guayana Shield was the main source of sediment and the paleo-Orinoco River drained northward into Lake Maracaibo (mainly east-to-west flow direction in Fig. 3). During the late Miocene and Pliocene, the Andes gradually became the main source of sediment that substantiated the process of uplift (mainly a west-to-east flow direction). Closure of the Andean chain by the uplift of the Eastern Cordillera forced the paleo-Orinoco River to migrate eastward to its present-day position.

PALEOBOTANICAL EVIDENCE FOR UPLIFT FROM SITES IN THE HIGH ANDES

Fossil pollen and botanical macrofossils were studied in sediments from sections collected at six exposures at ca. 2550 m altitude in the surroundings of the present-day high plain of Bogotá (Fig. 1; Table 1). The fossil taxa were arranged according to their modern altitudinal distribution. Many taxa have altitudinal ranges in common and such ecological groups constitute vegetation belts, which are in fact abstractions. Modern altitudinal ranges are based on studies of the existing vegetation. The assignment of a fossil taxon to a particular ecological group is based on the principal altitudinal range of its present-day relatives. Every time slice shows the relative proportion of the phytogeographic source areas (Fig. 4; Appendix 1). The phytogeographic units are after van der Hammen and Cleef (1986) and Gentry (1986). Additional information on the phytogeographic distribution of the identified fossil taxa was obtained from Kappelle et al. (1992) and Mabberley (1993). The biostratigraphic range of selected pollen and macro-

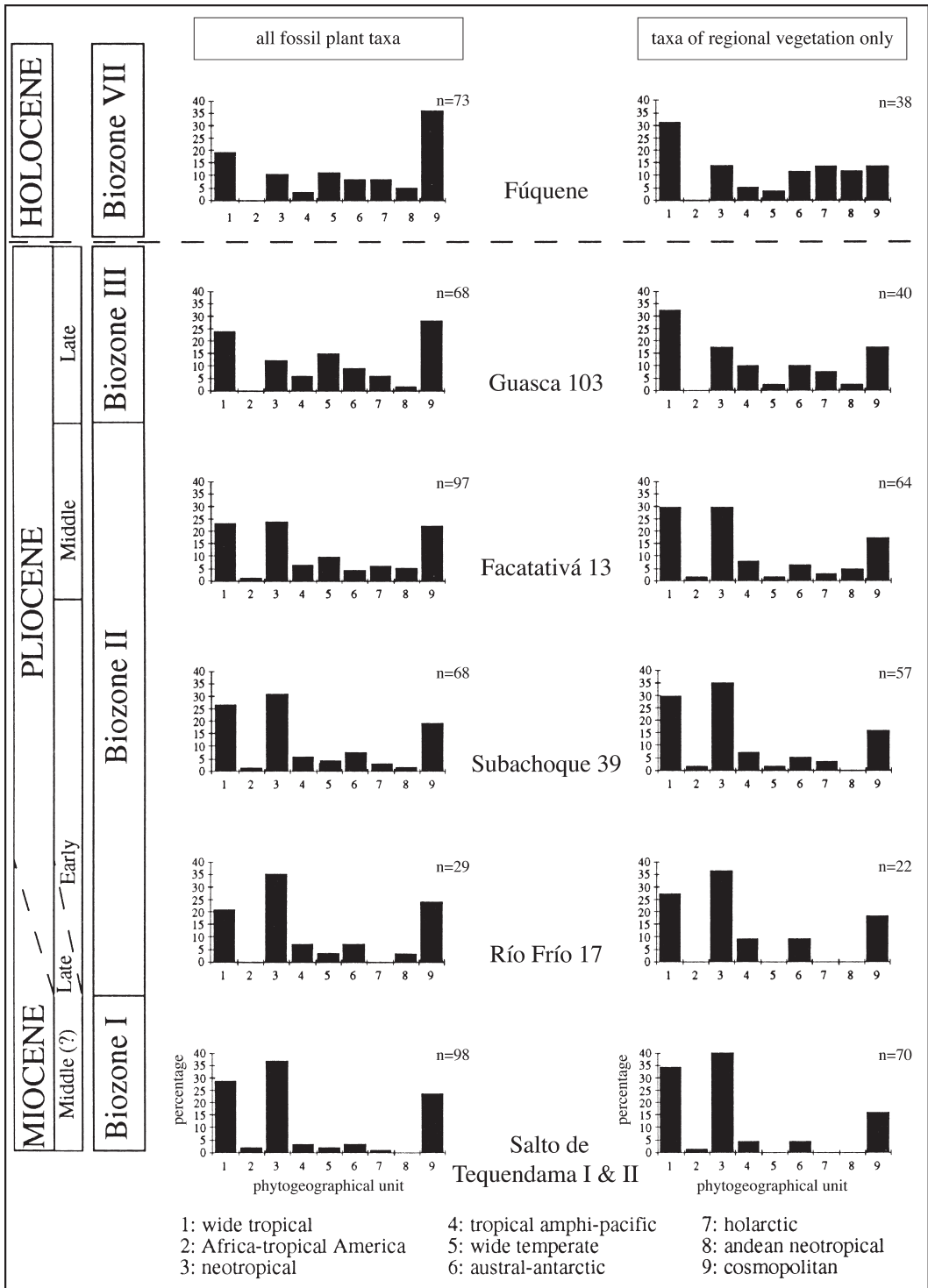


Figure 4. Phylogeographic composition of neogene fossil plant assemblages and paleofloras (only selected taxa are shown) from six sections located at the border of the basin of Bogotá, Colombia. Sections are arranged from the late Miocene (bottom) to the late Pliocene (top) and the present-day composition is shown above the dashed line for comparison. Percentage calculations are based on all identified fossil plant taxa (left), or on a selected group that represents the regional vegetation only. Plant assemblages representative for the Holocene are taken from core Fúquene-2 (van Geel & van der Hammen, 1973).

fossil taxa obtained from these Neogene sediment sequences is presented in Figure 5.

STATISTICAL ANALYSIS OF FOSSIL ASSEMBLAGES

Floristic similarity between fossil assemblages was statistically analyzed (cf. Graham, 1992). Data per ecological group and per section were not normally distributed using 95% confidence intervals (CI). Therefore, the nonparametric Kruskal-Wallis 1-sample test (Sokal & Rohlf, 1981) was chosen to evaluate the degree of dissimilarity between the fossil pollen spectra of sections Salto de Tequendama I and II, Subachoque 39, Facatativá 13, and Guasca 103. Pseudosignificance was expected because 85 individual comparisons were carried out. Pseudosignificance means that if for all tests a 95% CI is used, 5% of random data lie outside the 95% CI and decisions based on conventional levels of significance may be incorrect. Therefore, a more conservative approach was used that lowers the critical probability P for each individual comparison so that the probability of an erroneously rejected null hypothesis in the entire series of tests does not exceed the general critical alpha. The level of confidence for the individual comparisons was calculated as follows:

$$P = 1 - \sqrt[L]{1 - \alpha}$$

(L represents the number of comparisons)

In this case, the level of confidence is 0.0006.

The results of the Kruskal-Wallis tests are shown in Table 2. The tropical lowland taxa assemblages differed significantly in all sections. For the subandean-tropical lowland and Andean-subandean assemblages, site Salto de Tequendama II differed significantly from all other sites. Additionally, for the Andean-subandean assemblage, site Facatativá 13 differed significantly from site Guasca 103. For the Andean assemblage, sites Salto de Tequendama I and II differed significantly from each other as well as from all the other sections. For the subpáramo assemblages, both sites Salto de Tequendama I and Subachoque 39 differed significantly from Facatativá 13 and Guasca 103. The general decrease in floristic affinity between the studied associations is consistent with the decreasing age of these associations. This trend shows that each flora is slightly different in floristic composition from its neighboring floras.

PALEO-PHYTOGEOGRAPHY

The fossil floras from sites in the Bogotá area show a gradual change in plant composition from the late Miocene to late Pliocene. The late Miocene warm tropical lowland taxa are subsequently replaced by taxa with pre-montane and ultimately montane affinities (Figs. 4 and 5). During the late Miocene to late Pliocene, the following trends in the phytogeographic composition of the floras can be observed (Fig. 4): (1) the percentage of wide tropical taxa decreased slightly, (2) neotropical elements decreased markedly, (3) the percentage of cosmopolitan taxa increased; (4) Andean neotropical taxa were present from the middle Pliocene onward, and (5) wide temperate taxa increased significantly. During the late Miocene, Amazonian-centered families made up the majority of the local forest taxa (Fig. 6). Toward the late Pliocene, the proportion of this group gradually decreased. Laurasian elements showed the opposite pattern (van der Hammen & Cleef, 1983), whereas the proportion of Andean-centered taxa remained approximately the same. The calculated similarity values reveal the degree of floristic affinity between the associations (Table 2). The general observation is that calculated values of floristic affinity decline with an increasing difference in age between the floras.

Van der Hammen et al. (1973) used the successive immigration of temperate arboreal taxa, such as *Alnus* Mill., *Hedyosmum* Sw. (not strictly temperate), *Myrica* L., and *Quercus* L., to construct a biostratigraphic framework. He established seven biozones for the sediments in the study area (Table 3) (cf. Kuhry & Helmens, 1990; van der Hammen & Hooghiemstra, 1995; Wijninga, 1996d; van der Hammen & Hooghiemstra, 1997; Torres & Hooghiemstra, in prep.).

UPLIFT OF THE NORTHERN ANDES EVIDENCED BY
PALEOBOTANICAL DOCUMENTS FROM LOW AND
HIGH ALTITUDES

In the Bogotá area, middle Miocene sediments show dominant warm lowland taxa, whereas late Miocene and Pliocene sediments show increasing proportions of taxa associated with high-elevation vegetation (Table 4; Figs. 4 and 5). This trend in vegetation change is primarily explained in terms of a gradual

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Phytogeographic relationships of the identified taxa are according to van der Hammen & Cleef (1986), Maberly (1993), and Kappelle et al. (1992). The neotropical and Andean neotropical groups have no taxa in common. (cf. genus name = sp. ined., cf. genus name; aff. genus name = sp. ined., aff. genus name). Modified after Wijninga (1996d).

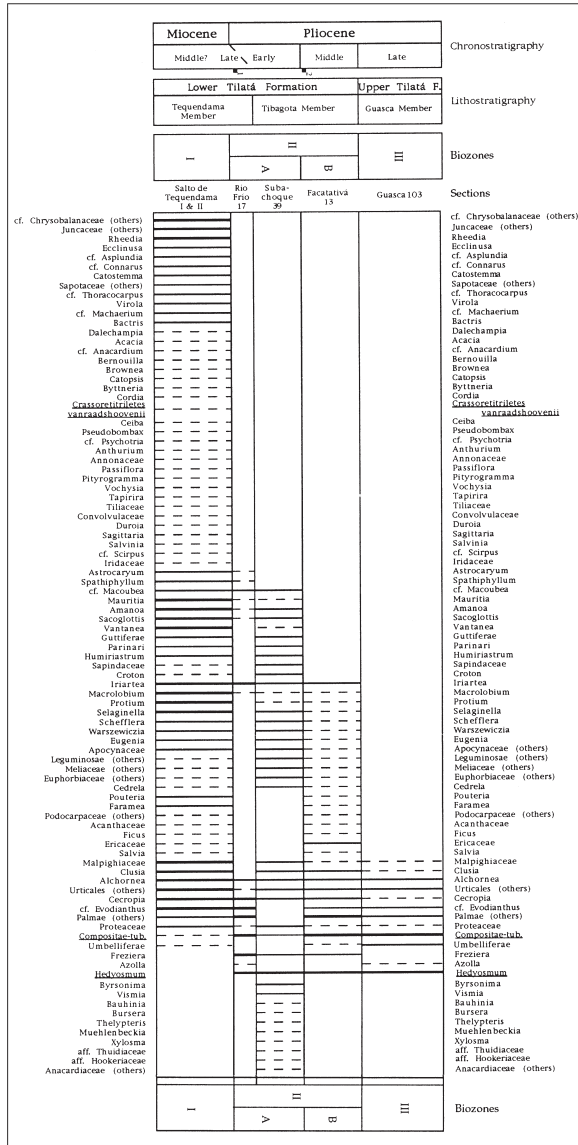


Figure 5. Biostratigraphic range of fossil plant taxa in sections Salto de Tequendama-I and II, Río Frío-17, Subachoque-29, Facatativá-13, and Guasca-103. Marker taxa for biozones (see Table 3) are underlined. Time control: 1 = 5.3 ± 1 Ma; 2 = 3.7 ± 0.5 Ma. Percentages (thick lines $\geq 10\%$; thin lines = $10\%–1\%$; dashed lines $\leq 1\%$) are based on average representation in the pollen or macrofossil diagrams of the respective paleofloras (Wijninga, 1996d).

increase in the elevation of the sedimentary environment and thus reflects a decrease in temperature. However, a temperature decrease is also expected at the transition from the late Pliocene to early Pleistocene, when temperatures decreased on a global scale and the period of Pleistocene ice ages started (e.g., Lohman & Carlson, 1981; Kennett, 1995; Shackleton, 1995). Despite this cooling trend, paleoclimatic studies show that low latitude sea surface temperature showed much less variation, generally in

the range of 3°C (Savin et al., 1975; Savin, 1977; Shackleton, 1982; Tiedemann et al., 1994). We therefore assume that Neogene temperatures in montane equatorial South America were maximally 3°C higher than at present. A maximum difference of 3°C corresponds to a 500 m maximum shift of the altitudinal vegetation belts when the modern temperature gradient of $6^{\circ}\text{C}/1000$ m is applied (Meyer, 1992; Witte, 1994). This potential temperature shift does not explain the difference between present-day altitude

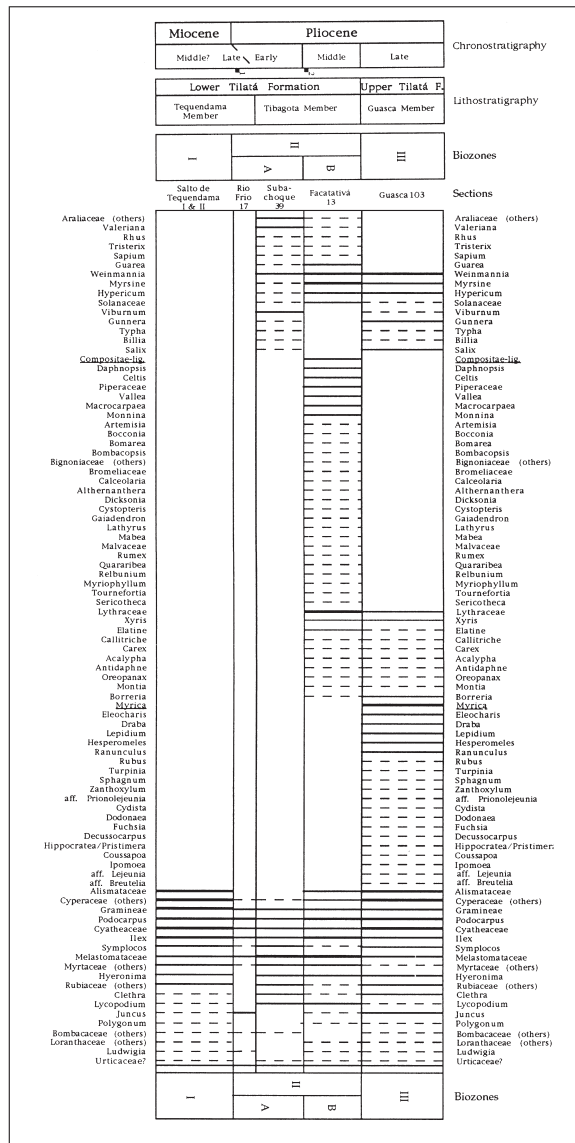


Figure 5. Continued.

and inferred paleoaltitude of sections Salto de Tequendama-I, Salto de Tequendama-II, Río Frío-17, and Subachoque-39. As a consequence, the change in vegetation and the inferred temperature decrease must have been primarily caused by tectonic uplift. When uplift was quantified and plotted against time, the Pliocene was identified as the period with main uplift (Fig. 7).

From the late Miocene onward, a period of approximately 2 to 3 million years elapsed before the area of sedimentation was uplifted to altitudes equivalent to the present-day lowermost limit of the Andean forest belt (2300–2500 m). During this time

span, the montane forest evolved. The rate of development in the study area may have been accelerated by the presence of montane forest in other areas. Several middle to late Miocene pollen records from northwestern South America show pollen grains of Podocarpaceae. Podocarpaceae pollen grains may potentially belong to *Nageia* Gaertn., *Podocarpus* L'Hér. ex Pers., *Prumnopitys* Phil., and/or *Retrophyllum* C. N. Page (Lorente, 1986; Hoorn, 1993, 1994a, 1994b; Behling, 1996; Wijninga, 1996a). In the northern Andes, representatives of the Podocarpaceae occur mainly as single trees or as groups of trees in the Andean upper montane rain forest; at

Table 2. Results of the Kruskal-Wallis 1-sample test applied to the floral assemblages of five sections from the area of Bogotá: Salto de Tequendama I and II, Subachoque 39, Facatativá 13, and Guasca 103; sections are dated from middle Miocene to late Pliocene, respectively. Individual significance level, $P = 0.0006$; global significance level, $\alpha = 0.05$. Significant scores are in bold; — = no data available. Results show floristic dissimilarity between five sections for five different ecological assemblages, ranging from tropical lowland to subpáramo.

	S. de Tequend. II	Subachoque 39	Facatativá 13	Guasca 103
Tropical lowland assemblages				
S. de Tequendama I	0.0000	0.0000	0.0000	0.0000
S. de Tequendama II		0.0000	0.0000	0.0000
Subachoque 39			0.0000	0.0000
Facatativá 13				0.0000
Subandean-tropical lowland assemblages				
S. de Tequendama I	0.0000	0.0104	0.0051	0.8114
S. de Tequendama II		0.0002	0.0000	0.0000
Subachoque 39			0.0008	0.3717
Facatativá 13				0.1524
Andean-subandean assemblages				
S. de Tequendama I	0.0000	0.3207	0.0018	0.0602
S. de Tequendama II		0.0000	0.0000	0.0000
Subachoque 39			0.2072	0.0148
Facatativá 13				0.0000
Andean assemblages				
S. de Tequendama I	0.0000	0.0000	0.0000	0.0000
S. de Tequendama II		0.0000	0.0000	0.0000
Subachoque 39			0.5002	0.3100
Facatativá 13				0.4646
Subpáramo assemblages				
S. de Tequendama I	—	0.5949	0.0000	0.0000
S. de Tequendama II		—	—	—
Subachoque 39			0.0002	0.0003
Facatativá 13				0.3703

present Podocarpaceae have been removed in most forests to produce timber. Stands of *Podocarpus*-dominated forest have been reported from, among others, the Mérida Andes ca. 2500 m (Vareschi, 1980), the Serranía de Perija between 3300 and 3500 m (J. O. Rangel, personal communication), and near Loja, Ecuador, in the Podocarpus National Park. The lowermost part of the Funza-2 pollen record (Torres, 2006; Torres & Hooghiemstra, in prep.) shows that before 2 Ma Podocarpaceae were more abundant in equatorial montane forests. Patches of modern Podocarpaceae-dominated forest may represent the last relicts of the original montane forest. Podocarpaceae-dominated forest was more common before the immigration of arboreal elements from northern and southern latitudes and before warm neotropical taxa adapted to cool and cold conditions. The late Miocene evidence of Podocarpaceae pollen grains points to the existence of montane forest, although it has to be stressed that only a few modern species of Podocarpaceae occur as rare trees scattered over the lowlands

of Amazonia and in the Chocó biogeographic region along the Pacific coast of Colombia (Rangel, 2004). According to W³ TROPICOS (2006), *Podocarpus magnifolius* J. Buchholz & N. E. Gray is recorded from Panama to the Bolivian Amazon and in Colombia and Venezuela up to ca. 2000 m in the lower montane rain forest belt.

Earlier uplifted areas in the environs of the basin of Bogotá are the Garzon, Quentame, and Santander massifs, and the Central Cordillera. All of these may have been populated by some type of early Andean forest and may have been the sources for a newly developing flora and vegetation in the newly uplifted mountain areas. Taxa already adapted to cool climatic conditions may have accelerated the formation of monodominant upper montane forest in the area under study.

Forty taxa of the modern páramo belt have been recorded in the fossil assemblages. Among these taxa are *Xyris* L., *Miconia* Ruiz & Pav., *Eleocharis* R. Br., and *Scirpus* L., which are shared with lowland savanna flora (Cleef et al., 1993). *Xyris* probably originated

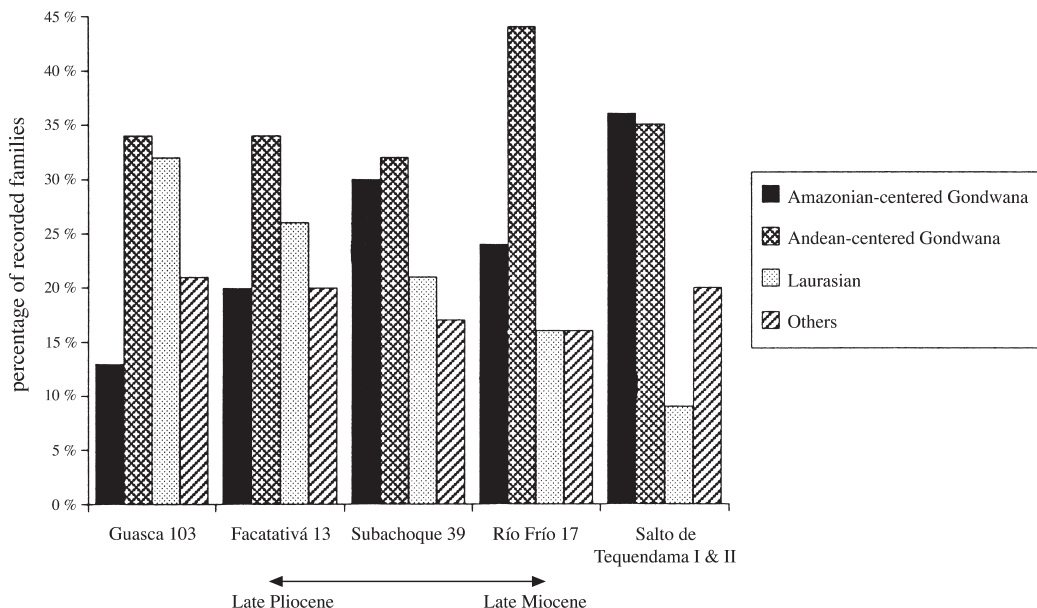


Figure 6. Relative contribution of Amazonian-centered Gondwanan, Andean-centered Gondwanan, and Laurasian families to the composition of the fossil plant assemblages of sections Salto de Tequendama-I and II (Middle Miocene), Río Frío (late Miocene to early Pliocene), Subachoque-39 (early Pliocene), Facatativá-13 (middle Pliocene), and Guasca-103 (late Pliocene). Modified after Wijninga (1996d).

from the open warm tropical lowlands and underwent gradual adaptation to cool climatic conditions during the uplift of the Eastern Cordillera. Finally, *Xyris* became part of the páramo vegetation. However, plant macroremains, of *Xyris* in particular (Wijninga, 1996b), indicate swamps are present in the different forest belts. This does not exclude their former occurrence in exposed mountain savannas as suggested by Cleef et al. (1993). *Miconia* is mainly an important component of the understory of (successional) lowland and montane rain forest. Wijninga (1996b) identified remains of Pliocene seeds to the taxonomic levels of the Miconieae and *Miconia*. It is difficult to assess whether species of *Eleocharis* and *Scirpus* in the northern Andes are from tropical or temperate origin.

In addition, other characteristic taxa of modern subpáramo and grasspáramo, such as *Acaena* Mutis ex L., *Polylepis* Ruiz & Pav., *Aragoa* H.B.K., *Arcytophyllum* Willd. ex Schult., *Bartsia* L., Caryophyllaceae, *Clinopodium* L. (= *Satureja*), *Eryngium* L., *Plantago* L., and *Puya* Molina, were absent during the Pliocene. Van der Hammen and Cleef (1986) postulated the presence of a hypothetical “pre-páramo” (i.e., an open type of vegetation occurring locally on exposed hilltops before the final uplift of the Eastern Cordillera) and also a “proto-páramo” (i.e., early páramo vegetation with characteristic páramo taxa, but still poor in species). The suggested local presence of late Miocene open vegetation on hilltops may represent pre-páramo vegetation (Biozone I; Grubb, 1971; Wijninga, 1996a). The fossil

Table 3. Main characteristics of northern Andean Biozones I to VII (after van der Hammen et al., 1973). Biozones IV to VII also follow from cluster analysis of the pollen assemblages of the Funza-2 record (Torres, 2006; Torres & Hooghiemstra, in prep.).

Biozone	Age	First appearance date/Taxon dominance
Biozone I	middle to late Miocene	abundant <i>Mauritia</i> , <i>Iriartea</i> , Bombacaceae
Biozone II	early Pliocene	start of the record of <i>Hedyosmum</i>
Biozone III	late Miocene	start of the record of <i>Myrica</i>
Biozone IV	middle Pliocene	abundant <i>Borreria</i>
Biozone V	late Pliocene	abundant <i>Juglans</i> and <i>Plantago</i>
Biozone VI	early Pleistocene	start of the record of <i>Alnus</i>
Biozone VII	middle Pleistocene	start of the record of <i>Quercus</i>

Table 4. Continued.

	Salto de Tequendama I	Salto de Tequendama II	Río Frío 17	Subachoque 39	Facatativá 13	Guasca 103
Subandean forest	<i>Alchornea</i>	<i>Alchornea</i>	<i>Alchornea</i>	<i>Alchornea</i>	<i>Acalypha</i>	<i>Acalypha</i>
bell-tropical	Apocynaceae (others)	Apocynaceae (others)	Arecaceae (others)	Apocynaceae (others)	<i>Alchornea</i>	<i>Alchornea</i>
lowland taxa	Arecaceae (others)	Arecaceae	Urticales	<i>Bauhinia</i>	Apocynaceae	Arecaceae
(0–2300 m)	Burseraceae/Sapotaceae	<i>Cordia</i> ²		<i>Cecropia</i>	Arecaceae	<i>Cecropia</i> ²
	<i>Cecropia</i>	<i>Farama</i>		<i>Cedrela</i> -type	<i>Cecropia</i> ¹	<i>Hyeronima</i>
	<i>Cedrela</i>	Malpighiaceae		Euphorbiaceae (others)	<i>Cedrela</i>	Malpighiaceae
	<i>Cordia</i> ²	cf. Rubiaceae		<i>Guarea</i> -type	<i>Farama</i>	Meliaceae
	<i>Croton</i>	<i>Schefflera</i> ²		<i>Hyeronima</i>	<i>Ficus</i> ²	Rubiaceae
	cf. Euphorbiaceae	Urticales (others)		Fabaceae (others)	<i>Guarea</i>	<i>Salix</i>
	Fabaceae (others)			Malpighiaceae	<i>Hyeronima</i>	Urticales (others)
	Fabaceae			Meliaceae (others)	<i>Fabaceae (others)</i>	
	<i>Farama</i>			<i>Paraprotium</i> -type	<i>Mabea</i>	
	<i>Hyeronima</i>			<i>Rhus</i>	Malpighiaceae ²	
	Malpighiaceae			Rubiaceae (others)	Meliaceae	
	Meliaceae (others)			Sapindaceae	<i>Rhus</i>	
	Rubiaceae (others)			<i>Sapium</i>	Rubiaceae-type	
	Sapindaceae			<i>Schefflera</i>	Rubiaceae	
	<i>Schefflera</i>			Urticales (others)	<i>Sapium</i>	
	Urticales (others)			<i>Vismia</i>	<i>Tournefortia</i>	
	<i>Warszewiczia</i>			<i>Warszewiczia</i>	Urticales (others)	
				<i>Zanthoxylum</i> ²	<i>Warszewiczia</i>	

Table 4. Continued.

Tropical low land taxa (0–1000 m)	Salto de Tequendama I	Salto de Tequendama II	Río Frío 17	Subachoque 39	Facatativá 13	Guasea 103
	<i>Acacia</i>	<i>Amanoa</i>	<i>Amanoa</i>	<i>Amanoa</i>	Bignoniaceae	Bombacaceae
	<i>Amanoa</i>	Annaceae ²	<i>Astrocaryum</i>	Anacardiaceae ²	<i>Bombacopsis</i>	
	<i>Astrocaryum</i>	<i>Bacris</i>	Bombacaceae	Bombacaceae	<i>Iriartea</i>	
	<i>Bernoullia</i>	Bombacaceae (others)	<i>Ilex</i>	<i>Bursera</i> ²	<i>Macrobium</i> ²	
	Bombacaceae (others)	<i>Byttneria</i>	<i>Iriartea</i>	<i>Byrsonima</i>	<i>Pouteria</i> ²	
	<i>Brownea</i>	<i>Catostemma</i>	cf. <i>Macoubea</i>	<i>Humiriastrum</i>	<i>Protium</i> ²	
	<i>Byttneria</i>	<i>Celba</i>	<i>Macrobium</i>	<i>Iriartea</i>	<i>Quararibea</i>	
	<i>Catostemma</i>	<i>Clusia</i> ²	<i>Mauritia</i>	cf. <i>Macoubea</i>	<i>Trichantera/Branaisa</i> ²	
	<i>Celba</i>	<i>Eugenia</i> ²	<i>Spathiphyllum</i>	<i>Macrobium</i>		
	cf. <i>Chrysobalanaceae</i>	<i>Ficus</i>		<i>Mauritia</i>		
	cf. <i>Connarus</i>	<i>Humiriastrum</i>		cf. <i>Sacoglottis</i>		
	<i>Dalechampia</i>	<i>Ilex</i>				
	<i>Duroia</i> ²	<i>Iriartea</i>				
	<i>Ecclinusa</i>	cf. <i>Machaerium</i>				
	<i>Eugenia</i>	cf. <i>Macoubea</i>				
	<i>Ficus</i>	<i>Macrobium</i>				
	<i>Humiriastrum</i>	<i>Mauritia</i>				
	<i>Ilex</i>	<i>Pouteria</i>				
	<i>Iriartea</i>	<i>Protium</i> ²				
	cf. <i>Machaerium</i>	cf. <i>Psychotria</i>				
	<i>Macrobium</i>	<i>Spathiphyllum</i>				
	<i>Mauritia</i>	<i>Tapiria</i>				
	<i>Pouteria</i>	Tiliaceae ²				
	<i>Protium</i>	<i>Virola</i> ²				
	<i>Pseudobombax</i>	<i>Warszewiczia</i> ²				
	<i>Rheedia</i>					
	Sapotaceae (others)					
	<i>Spathiphyllum</i>					
	<i>Tapiria</i>					
	<i>Virola</i>					
	<i>Vochysia</i> ²					

¹ Poaceae may reflect mainly local vegetation (and are excluded from the percentage calculations and statistical analysis elsewhere in this paper).² Taxa with low frequency (omitted from the statistical analysis elsewhere in this paper).

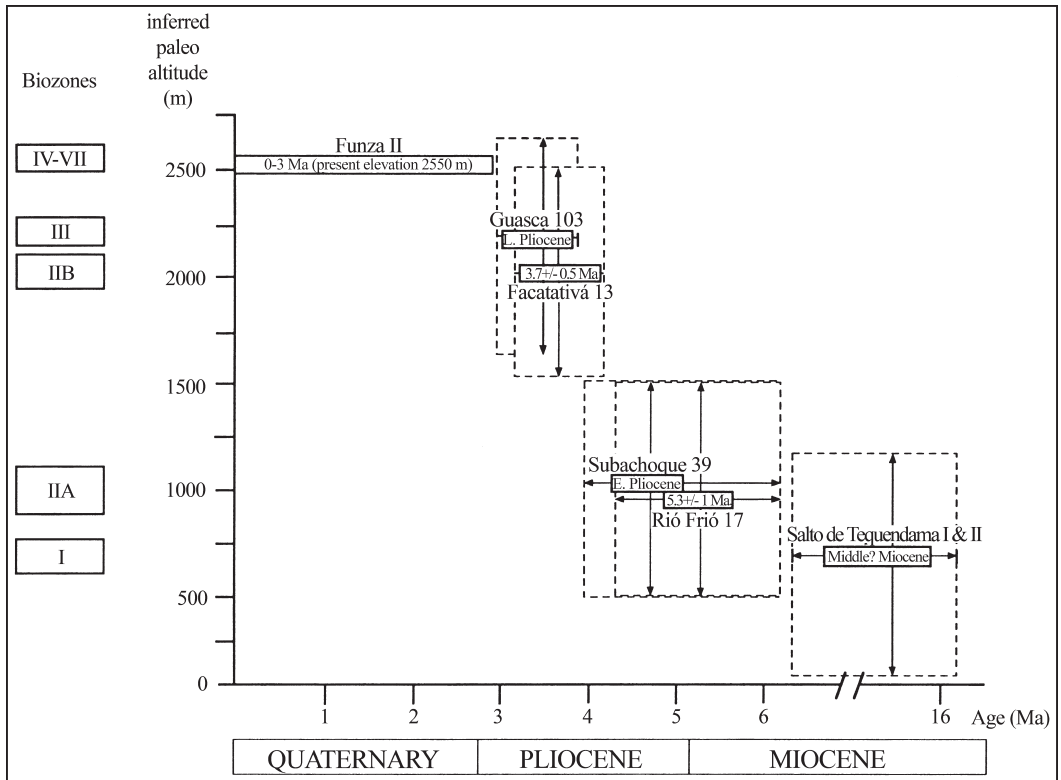


Figure 7. Main chronological, biostratigraphic, paleoenvironmental, and paleoaltitudinal properties of the five sections from exposures in the outer valleys of the basin of Bogotá, Colombia, representing the middle Miocene to late Pliocene. Elevation of past depositional environments was estimated by comparing paleofloras with present-day equivalents. Sediments were dated by fission track dating of intercalated volcanic ashes. Sections make a diagonal in this age vs. paleo-altitude diagram, indicating uplift of the Eastern Cordillera during the late Miocene and Pliocene. Vertical arrows correspond to an estimated uncertainty of ca. 3°C. The basin of Bogotá itself started to accumulate sediments when the Andes had reached its present-day elevation, which is reflected by the position of Funza-2 pollen spectra. For Biozones see Table 3. Modified after Wijninga (1996d).

assemblages discussed here (Biozone II to Biozone III) do not show evidence for the existence of protopáramo vegetation. The first possible record of protopáramo or páramo-like vegetation is from the late Pliocene (Biozone IV; van der Hammen et al., 1973; Helmens & van der Hammen, 1994; Torres & Hooghiemstra, in prep.).

Despite the fact that the uplift of the Eastern Cordillera ceased by the end of the Pliocene, the floristic composition of the Andean forest was subject to change up to the late Quaternary. Throughout this period, forest types without modern analogues developed, existed for a while, and became further modified by new migrants, such as *Alnus* and *Quercus* (van der Hammen & González, 1964; van der Hammen et al., 1973; van der Hammen, 1974; Hooghiemstra, 1984; Hooghiemstra & Cleef, 1995; van't Veer & Hooghiemstra, 2000). The latest chronology of the sediments of the basin of Bogotá comes from astronomical tuning of the arboreal pollen

record, and consequently first appearance dates from van't Veer and Hooghiemstra (2000) have been corrected (Torres, 2006; Torres & Hooghiemstra, in prep.; Torres et al., in prep.).

Toward the late Pliocene, the fossil floras show at the family level an enrichment of taxa with a Laurasian affinity, and taxa with an Amazonian-centered affinity became less important. These trends are in accordance with the change from tropical lowland environments to Andean forest conditions. The slight decrease in the percentage of Andean-centered elements could be caused by the fact that in the montane forest these families represent predominantly epiphytic and understory shrubs (Gentry, 1982), which are generally underrepresented in the fossil record.

THE DYNAMIC PÁRAMO ARCHIPELAGO AND SPECIATION

During the Quaternary the upper forest line migrated between ca. 2000 m (during the coldest

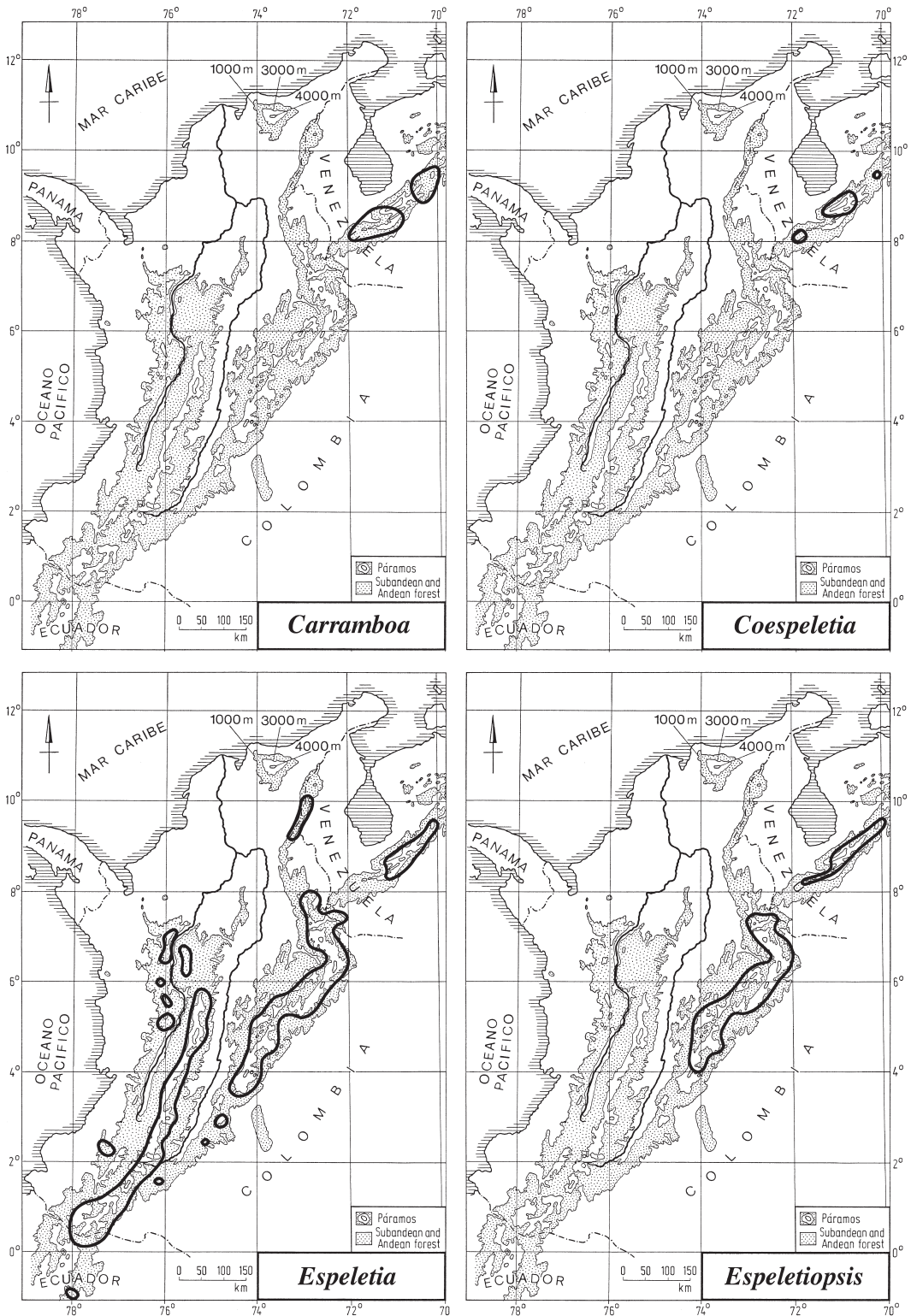


Figure 8. Maps showing the distribution of eight genera belonging to the Espeletiinae (Asteraceae). All genera are endemic to the northern Andes, and many distribution areas coincide with the geologically youngest parts of the Andes.

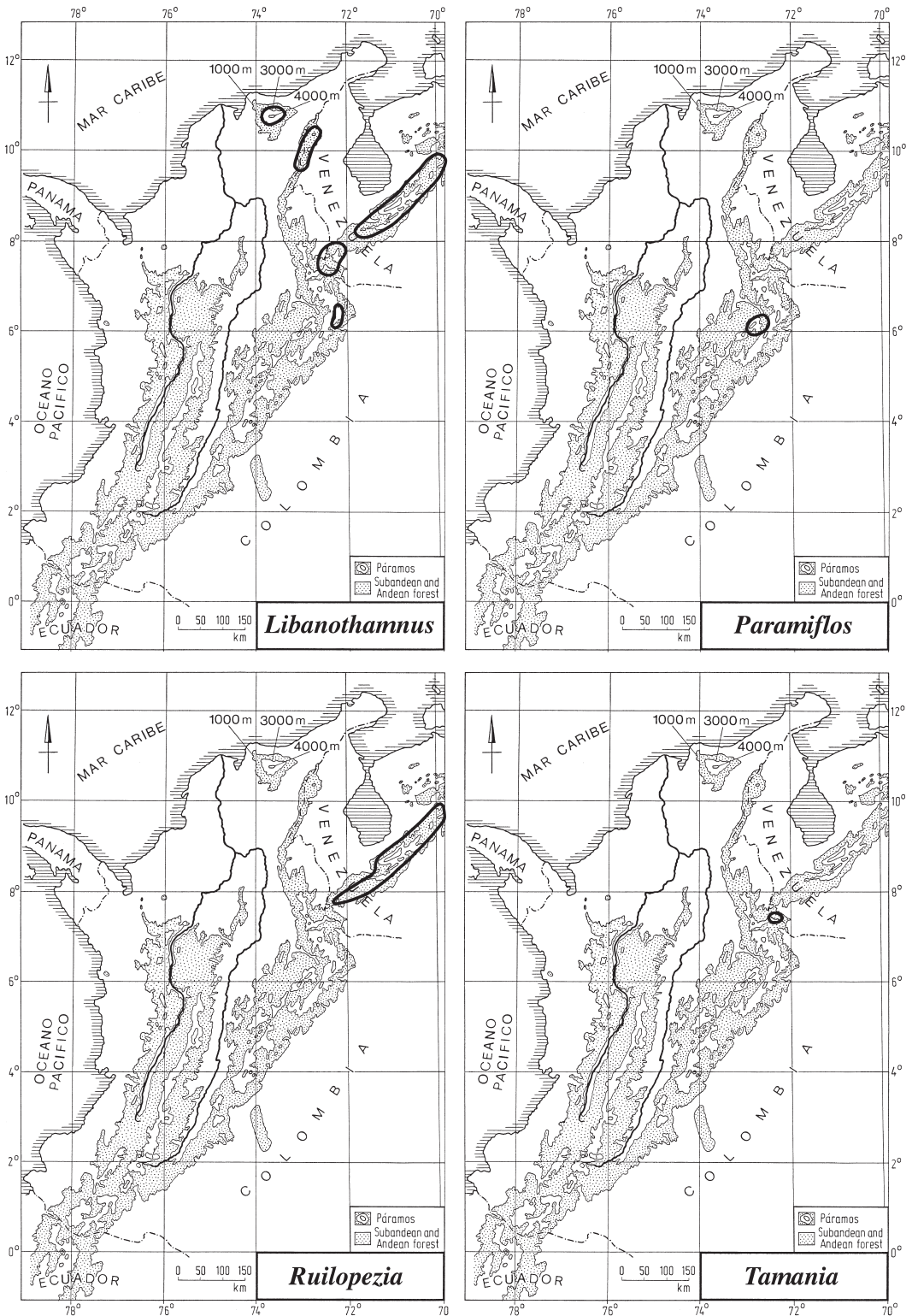


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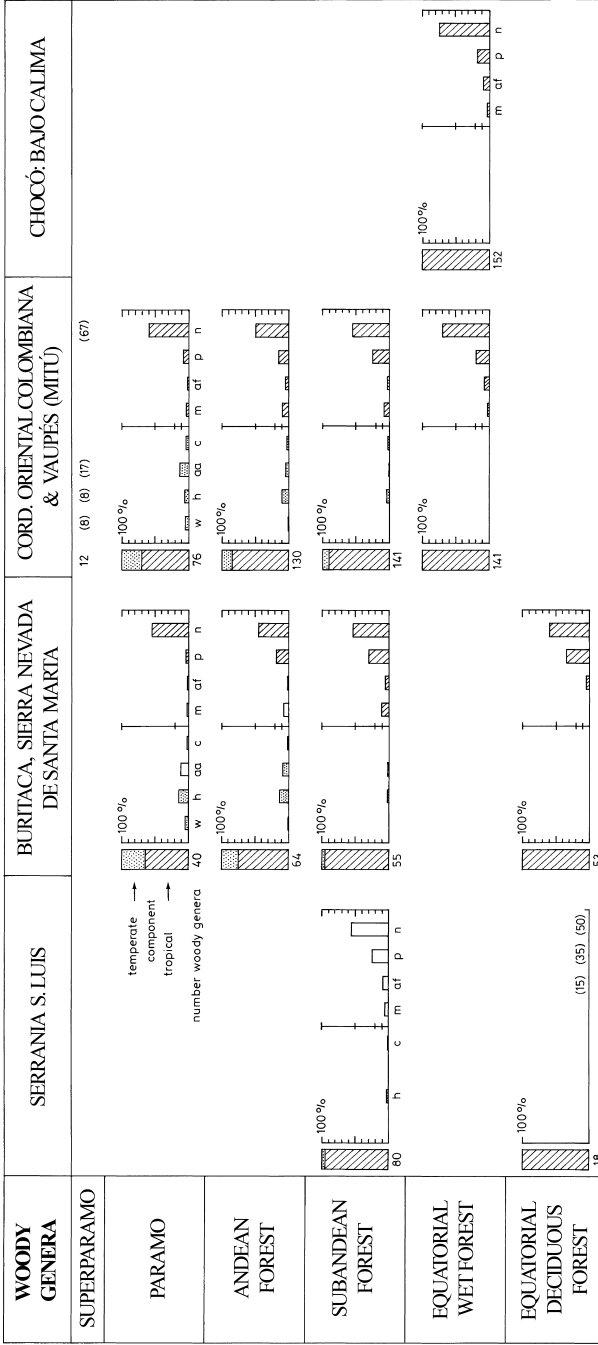


Figure 9. Representation of geographic elements of woody genera for six different vegetation belts in northern Andean and adjacent lowland vegetation showing the adaptation of neotropical lowland taxa to cool climatic conditions. Data are specified (from left to right) for the Serrania San Luis (Venezuela) (subandean forest (1200–1500 m) and deciduous forest (700–1200 m) after Steyermark (1975)); the Buritaca area in the Sierra Nevada de Santa Marta (páramo (> 3300 m), and subandean forest (1300–2500 m) based on Rangel & Jaramillo (1984); Barranquilla (dry deciduous lowland forest after Dugant (1941); Vaupés (lowland rainforest of Amazonia near Miti-Caruru, after Cuatrecasas (1958)); the Eastern Cordillera of Colombia (Andean forests after van der Hammen & Jaramillo (unpublished data), and páramos after Cleef (1979) with corrections); and Chocó (Bajo Calima) (lowland rainforest of Amazonia near Trojita-La Brea, after Cuatrecasas (1958)). The bar to the left of each graph shows the number of woody genera and the proportion of tropical and temperate taxa. Phylogeographic elements: n = neotropical; p = pantropical; af = African and American; m = southeast Asian and American; c = cosmopolitan; aa = Austral-Antarctic; h = Holarctic; w = wide temperate. Numbers in parentheses show representation (percentages) of floral elements based on a low total number of genera. After Cleef, unpublished data.

episodes of glacials) and ca. 3200–3400 m (during the warmest episodes in interglacials) (e.g., van der Hammen, 1974; Hooghiemstra, 1984; van't Veer & Hooghiemstra, 2000; Wille et al., 2001). As a consequence, the area covered with páramo vegetation has changed accordingly, from many small areas at mountaintops during interglacial periods (high position of the upper forest line) to large united areas during glacial periods (low position of the upper forest line) (van der Hammen, 1974; van der Hammen & Cleef, 1986). The series of ice ages during the Quaternary caused these altitudinal migrations to repeat many times, potentially leading to a relevant mechanism of speciation.

Cuatrecasas (1979) studied species diversity and distribution areas of the Espeletiinae (Asteraceae). He identified the northern part of the Eastern Cordillera of Colombia (i.e., the Cocuy area and the area north of Chicamocha Valley up to the Mérida Andes) as the area with the highest number of species. The Espeletiinae include the genera *Carramboa* Cuatrec., *Coespeletia* Cuatrec., *Espeletia* Mutis ex Bonpl., *Espeletiopsis* Cuatrec., *Libanothamnus* Ernst, *Paramiflos* Cuatrec., *Ruilopezia* Cuatrec., and *Tamania* Cuatrec. The genera *Espeletia* and *Espeletiopsis* are exclusive to the Colombian and Venezuelan parts of this area, while the genus *Coespeletia* is exclusive to the Venezuelan part of this area. These genera comprise morphologically and ecologically diverse plants and occur in the altitudinal range between 2500 and 4500 m (Rauscher, 2002). Figure 8 shows distribution maps of the genera of the Espeletiinae and shows this area as the center of origin of this taxonomic group (cf. van der Hammen & Cleef, 1986). Notably, the area of highest diversity among Espeletiinae is also the place where the northern Andes is youngest, geologically speaking. According to Luteyn (1999), Colombia has ca. 45 species of *Espeletia* and ca. 16 species of *Espeletiopsis*. Venezuela has ca. 15 species of *Espeletia*, ca. 5 species of *Espeletiopsis*, and ca. 6 species of the genus *Coespeletia*. Many of these taxa show a very limited distribution area and sometimes are restricted to a single mountaintop (Luteyn, 1999). On the Quaternary time scale, the Holocene is among the periods during which distribution areas have a minimal surface. Placing the recent anthropogenic pressure on the páramo ecosystem in this context, many species are relatively close to extinction.

The Andean uplift played a major role in the development and distribution of the present-day northern Andean flora. Numerous neotropical lowland taxa adapted to the cool climatic conditions at high elevation. Additionally, the Andes served as a route for temperate taxa to migrate from temperate latitudes to cool tropical montane areas. The result of these two

phenomena can be seen in the present-day composition of the flora of the Colombian montane forest and páramo. Figure 9 supports this view as it shows the representation of geographic elements of woody genera for five different main vegetation belts in northern Andean and adjacent lowland vegetation. At high elevations, temperate taxa are abundant while at low elevations neotropical and pantropical taxa are abundant. A minority of Holarctic elements appear below the Andean forest belt.

DISCUSSION AND SYNTHESIS

During the late Miocene (Biozone I), the area of the present-day Bogotá basin was a lowland riverine environment (ca. 700 m elevation) dominated by tropical lowland taxa which, at present, are found in the modern várzea forest of the Amazon basin. This “pre-uplift” vegetation principally consisted of taxa with a wide tropical or neotropical origin (e.g., Bombacaceae, Cyclanthaceae, Humiriaceae, *Iriartea* Ruiz & Pav., *Mauritia* L. f., Melastomataceae, and *Parinari* Aubl.). Amazonian and Andean-centered families were predominant. Trees of Podocarpaceae, accompanied by *Symplocos* Jacq., *Clethra* L., and probably *Weinmannia* L., apparently were constituents of the Neogene montane forests found on elevated areas near the study area.

By the late Miocene to early Pliocene (Biozone IIA), the proportion of tropical lowland taxa had decreased from 75% (Biozone I) to ca. 60%. The share of taxa from present-day Andean and subandean vegetation belts increased from 5% (Biozone I) to 20%. During Biozone IIA, the proportion of Laurasian families increased from 10% to ca. 23%. These changes in the floral composition show a transition from tropical lowland to subandean forest and suggest the local uplift of the Eastern Cordillera to ca. 1000 m elevation. Some tropical lowland taxa, such as Humiriaceae, *Mauritia*, and *Parinari*, persisted in areas, such as valleys, that were still below 1000 m elevation. A number of present-day montane taxa, including those of neotropical origin (e.g., *Billia* Peyr., *Freziera* Sw. ex Willd., *Myrsine* L., and *Xylosma* G. Forst.), appeared for the first time in the study area, indicating a more diverse subandean and apparently Andean forest.

During the middle Pliocene (Biozone IIB), the floral composition was still characterized by a dominance of taxa with a tropical affinity, whereas only 25% of the taxa had either tropical amphipacific, wide temperate, Austral-Antarctic, Holarctic, or Andean neotropical affinities. Based on the affinity of their taxa, the floras of Biozones IIA and IIB are very similar. Alternatively, a comparison between floral composition has been

made on the basis of plant affinity to present-day altitudinal vegetation belts. Around 50%–60% of the Pliocene taxa also belong to present-day subandean and Andean vegetation belts. In contrast to a comparison based on phytogeographic composition, the difference in floral composition between Biozones IIA and IIB is now significant. The characteristics of the vegetation suggest that the area had reached an altitude of ca. 2000 m. Prominent taxa in the montane forest included trees of Podocarpaceae, as well as *Hedyosmum* Sw., *Ilex* L., *Myrsine* L., and *Weinmannia* L. Taxa that first appeared in the studied sequence are *Alternanthera* Forssk., Asteraceae (Liguliflorae), *Bocconia* Plum ex L., *Borreria* G. May, *Calceolaria* L., *Callitriche* L., *Daphnopsis* Mart., *Gaiadendron* G. Don., *Elatine* L., *Montia* L., *Myrica* L., *Quararibea* Aubl., *Sericotrocha* Rafin., *Vallea* Multis ex L. f., and *Xyris* L. The majority of these taxa are predominant in the present-day Andean forest and páramo vegetation (van der Hammen & Cleef, 1986; Cleef et al., 1993).

During the late Pliocene (Biozone III), continued uplift increased elevation to ca. 2600 m. About 40% of the fossil flora taxa have a tropical affinity and 35% have a temperate affinity. The Amazonian-centered families and the Andean-centered and Laurasian elements contribute 18% and 60%, respectively, to the paleoflora. The main forest taxa, including *Alchornea* Sw., *Hedyosmum* Sw., *Myrica* L., Podocarpaceae; *Weinmannia* L., *Hesperomeles* Lindl., *Myrica* L., *Rubus* L., and *Turpinia* Vent., are recorded for the first time. The composition of the late Pliocene Andean forest differs from that of the late Quaternary Andean forest. Notable is the absence of *Alnus* Mill., *Juglans* L., and *Quercus* L., which immigrated into the area during the Pleistocene. The contribution of *Hedyosmum*, *Myrica*, and Podocarpaceae to the Andean vegetation cover was apparently higher in the late Pliocene than in the Quaternary (Wijninga & Kuhry, 1993). It is possible that the late Pliocene forest had a more open character locally (in the area of the high plain of Bogotá), perhaps related to a dynamic river valley environment (Hooghiemstra, 1984; Torres et al., 2005). To some extent, the above-mentioned characteristics of this early Andean forest are already apparent during the middle Pliocene (Biozone IIB) and prevail until the early Pleistocene.

During the Quaternary, repeated climate change forced main vegetation belts to migrate altitudinally along mountain slopes. Combining the palynological information from ecotone forests (e.g., van der Hammen, 1974; van't Veer & Hooghiemstra, 2000) with the dynamics at lower elevations (Wille et al., 2001), we concluded that the subandean forest belt was maximally squeezed, during glacial periods in particular, from the present-day ca. 1300 m vertical

extension (ca. 1000–2300 m) to ca. 600 m vertical extension during the Last Glacial Maximum (LGM) (ca. 800–1400 m). Other vegetation belts lost less of their vertical expansion during the LGM: tropical lowland forest lost 200 m (0–300 m LGM expansion) and Andean forest lost 300 m (1400–2000 m LGM expansion). The páramo belt kept the same altitudinal extension (2000–3000 m) during the LGM as today, but this belt in particular gained much surface when it moved to lower elevations. In consequence, Quaternary dynamics were highest in the páramo belt. This reconstruction is consistent with the observation that the high mountain flora, in particular, reached a high level of diversity. In the Espeletinae group, highest diversity occurs in the area where the uplift history is youngest (Cuatrecasas, 1979), suggesting that in the northern Andes the dynamic Quaternary environment has contributed positively to the present-day high level of plant diversity.

CONCLUSIONS

- Differences in the composition of fossil plant associations recovered from sediments in the area of the Bogotá basin form a series from middle Miocene to late Pliocene and reflect changing climatic conditions that result primarily from the Pliocene tectonic uplift of the Eastern Cordillera.
- Global temperature change during the Neogene, estimated at 3°C, may explain at most one third of the difference in inferred paleoaltitude, and hence the difference in floristics between the oldest and youngest fossil plant assemblages.
- The fossil plant assemblages show that the late Miocene vegetation was dominated by taxa with a wide tropical or neotropical distribution. Early montane forest seems to have been relatively rich in Podocarpaceae. During the Pliocene, the diversification of the forests gradually increased. Taxa with a cosmopolitan, wide temperate, tropical amphipacific, or Holarctic distribution enhanced the diversity of the montane forest. During the same time span, the number of Amazonian-centered families decreased in favor of families of Laurasian origin.
- Although reconstructed forest types are non-analogues, to a certain extent they can be compared to their modern homologues, taking into consideration the absence of taxa that immigrated into the study area at a later time.
- Although in some parts of the Eastern Cordillera uplift had already started in the middle Miocene, the area of Bogotá remained below 700 m altitude until the late Miocene.
- From the middle Pliocene onward, the number of Holarctic and Asia-derived (e.g., *Trigonobalanus* Forman, *Symplocos* Jacq.) taxa increased. This indicates the importance of the northern migration route via the Panamanian isthmus for plant taxa. Migration from southern South America possibly occurred before the late Neogene. A substantial number of Austral-Antarctic taxa arrived in the northern Andean montane rain forest biome before immigration from the Northern Hemisphere took place, but in the present-day flora there are fewer immigrants from the south than from the north.

- Based on the studied fossil plant assemblages, the first records of páramo-like vegetation are from the late Pliocene, confirming earlier conclusions by van der Hammen et al. (1973).
- Mainly during the Quaternary, climate change forced vegetation belts to migrate vertically. During this process, vegetation belts were repeatedly squeezed in altitudinal extension and afterward expanded again, causing populations to be repeatedly isolated and remerged. In the northern Andes, high diversity correlates strongly with a dynamic environment in which migration and isolation played key roles.

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Appendix 1. Checklist of identified pollen taxa, their phylogeographic relationships, and their absence/presence in the studied pollen and macrofossil floras. Sites: S. de T. I/II = Salto de Tequendama I/II (middle Late Miocene); Río F 17 = Río Frio-17 (early Pliocene); Subach. 39 = Subachoque-39 (early Pliocene); Faca. 13 = Facatativá-13 (middle Pliocene); Guasca 103 (late Pliocene). Modern phylogeographic units: 1 = wide tropical; 2 = tropical Africa-America; 3 = neotropical; 4 = tropical amphipacific; 5 = wide temperate; 6 = austral-antarctic; 7 = holarctic; 8 = andean neotropical; 9 = cosmopolitan. (cf. genus name = sp. ined., cf. genus name). Appendix modified after Wijninga (1996d).

Taxon	Phyt. unit	S.de T. I/II	Río F 17	Subach. 39	Faca. 13	Guasca 103
<i>Acacia</i> Miller	1	x				
<i>Acalypha</i> L.	1				x	x
Acanthaceae	1	x			x	
<i>Alchornea</i> Sw.	1	x	x	x	x	x
Alismataceae	9	x			x	x
<i>Amanoa</i> Aubl.	3	x	x	x		
Anacardiaceae	1			x		
<i>Anacardium</i> L. cf.	3	x				
Annonaceae	1	x				
<i>Anthurium</i> Schott.	3	x				
<i>Antidaphne</i> Poeppig & Endl.	3				x	x
Apiaceae	9	x			x	x
Apocynaceae	1	x		x	x	
Araliaceae	1			x	x	
Arecaceae (Palmae)	1	x	x		x	x
<i>Artemisia</i> L.	7				x	
<i>Asplundia</i> Harling cf.	3	x				
Asteraceae - liguliflorae	9	x			x	
Asteraceae - tubuliflorae	9	x	x	x	x	x
<i>Astrocaryum</i> G. Meyer	3	x	x			
<i>Azolla</i> Lam.	9		x			x
<i>Bactris</i> Jacq. Ex Scop.	3	x				
<i>Bauhinia</i> L.	1			x		
<i>Bernouillia</i> Oliver	3	x				
Bignoniaceae	1				x	
<i>Billia</i> Peyr.	3			x		x
<i>Bocconia</i> L.	4				x	
<i>Bomarea</i> Mirbel	8				x	
Bombacaceae	1	x	x	x		x
<i>Bombacopsis</i> Pittier	3				x	
<i>Borreria</i> G. Meyer	6					x
Bromeliaceae	3				x	
<i>Brownea</i> Jacq.	3	x				
<i>Bursera</i> Jacq. ex L.	3			x		
<i>Byrsonima</i> Rich. ex Kunth	3			x		
<i>Byttneria</i> Loeffl.	1	x				
<i>Calceolaria</i> L.	1				x	
<i>Callitriche</i> L.	5				x	x
<i>Carex</i> L.	5				x	x
<i>Catopsis</i> Griseb.	3	x				
<i>Catostemma</i> Benth.	3	x				
<i>Cecropia</i> Loeffl.	3	x	x	x	x	x
<i>Cedrela</i> P. Browne	3	x		x	x	
<i>Ceiba</i> Miller	1	x				
<i>Celtis</i> L.	7				x	
Chrysobalanaceae cf.	1	x				
<i>Clethra</i> L.	4	x		x	x	x
<i>Clusia</i> L.	3	x		x	x	x
Clusiaceae s.l. (Guttiferae)	9	x		x		
Convolvulaceae	9	x				
<i>Connarus</i> L. cf.	1	x				
<i>Cordia</i> L.	1	x				
<i>Coussapoa</i> Aubl.	1					x
<i>Crassoretitriletes</i>	1	x				
<i>Croton</i> L.	1	x		x	x	

Appendix 1. Continued.

Taxon	Phyt. unit	S.de T. I/II	Rio F 17	Subach. 39	Faca. 13	Guasca 103
Cyatheaceae	1	x	x	x	x	x
<i>Cydista</i> Miers	3					x
Cyperaceae	9	x	x	x	x	x
<i>Cystopteris</i> Bernh.	7				x	
<i>Dalechampia</i> L.	1	x				
<i>Daphnopsis</i> C. Martius	3				x	
<i>Decussocarpus</i> Laubenf.	1					x
<i>Dicksonia</i> L'Hér.	4				x	
<i>Duroia</i> L.f.	3	x				
<i>Ecclinusa</i> C. Martius	3	x				
<i>Eleocharis</i> R. Br.	9					x
Ericaceae	9	x			x	
<i>Eugenia</i> L.	1	x		x	x	
Euphorbiaceae cf.	9	x		x	x	
<i>Evodianthus</i> Oersted. cf.	3	x	x		x	
Fabaceae	9	x		x	x	
<i>Faramea</i> Aubl.	3	x			x	
<i>Ficus</i> L.	1	x			x	
<i>Freziera</i> Willd.	8		x	x	x	
<i>Fuchsia</i> L.	6					x
<i>Gaiadendron</i> G. Don f.	8				x	
<i>Guarea</i> Allam ex L.	2			x	x	
<i>Gunnera</i> L.	6			x		x
<i>Hedyosmum</i> Sw.	4	x	x	x	x	x
<i>Hesperomeles</i> Lindley	8					x
<i>Hippocratea</i> L./ <i>Pristimera</i> Miers	1					x
<i>Humiriastrum</i> (Urban) Cuatrec.	3	x		x		
<i>Hyeronima</i> Allemão	3	x		x	x	x
<i>Hypericum</i> L.	5			x	x	x
<i>Ilex</i> L.	9	x	x	x	x	x
<i>Ipomoea</i> L.	1					x
<i>Iriartea</i> Ruiz & Pavón	3	x	x	x	x	
Iridaceae	9	x				
Juncaceae s.l.	9	x				
<i>Juncus</i> L.	5	x	x		x	x
<i>Lathyrus</i> L.	7				x	
<i>Lepidium</i> L.	9					x
Loranthaceae	9	x			x	x
<i>Ludwigia</i> L.	9	x	x		x	x
<i>Lycopodium</i> L.	9	x		x	x	x
Lythraceae	9				x	x
<i>Mabea</i> Aubl.	3				x	
<i>Machaerium</i> Pers. cf.	3	x				
<i>Macoubea</i> Aubl. cf.	3	x	x	x		
<i>Macrocarpea</i> (Griseb.) Gilg	8				x	
<i>Macrolobium</i> Schreber	3	x	x	x	x	
Malpighiaceae	1	x		x	x	x
Malvaceae	9				x	
<i>Mauritia</i> Kunth	3	x	x	x		
Melastomataceae	1	x	x	x	x	x
Meliaceae	1	x		x	x	
<i>Monnina</i> Ruiz & Pavón	3				x	
<i>Montia</i> L.	5				x	x
<i>Muehlenbeckia</i> Meissner	6			x		
<i>Myrica</i> L.	7				x	x
<i>Myriophyllum</i> L.	9				x	
<i>Myrsine</i> L.	1			x	x	x
Myrtaceae	1	x	x	x	x	x
<i>Oreopanax</i> Decne. & Planchon	3				x	x
<i>Paraprotium</i> -type Cuatrec.	3			x		

Appendix 1. Continued.

Taxon	Phyt. unit	S.de T. I/II	Rio F 17	Subach. 39	Faca. 13	Guasca 103
<i>Parinari</i> Aubl.	1	x		x		
<i>Passiflora</i> L.	3	x				
Piperaceae	1				x	
<i>Pityrogramma</i> Link	2	x				
Poaceae	9	x	x	x	x	x
Podocarpaceae	6	x			x	x
<i>Podocarpus</i> L'Hér. ex Pers.	6	x	x	x	x	x
<i>Polygonum</i> L.	5	x			x	x
<i>Pouteria</i> Aubl.	1	x			x	
<i>Protium</i> Burm.f.	1	x			x	
<i>Pseudobombax</i> Dugand	3	x				
<i>Psychotria</i> L. cf.	1	x				
<i>Quararibea</i> Aubl.	3				x	
<i>Ranunculus</i> L.	5					x
<i>Rheedia</i> L.	2	x				
<i>Rhus</i> L.	7			x	x	
Rubiaceae	9	x		x	x	x
<i>Rubus</i> L.	5					x
<i>Rumex</i> L.	5				x	
<i>Sacoglottis</i> C. Martius	3	x	x	x		
<i>Sagittaria</i> L.	9	x				
<i>Salix</i> L.	7			x		x
<i>Salvia</i> L.	7	x			x	
<i>Salvinia</i> Séguier	1	x				
Sapindaceae	1	x		x		
<i>Sapium</i> P. Browne.	3			x	x	
Sapotaceae	1	x				
<i>Schefflera</i> Forster & Forster f.	3	x		x	x	x
<i>Scirpus</i> L. cf.	9	x				
<i>Selaginella</i> Pal.	9	x		x	x	
<i>Sericotheca</i> Rafin.	3				x	
Solanaceae	9			x	x	x
<i>Spathiphyllum</i> Schott	3	x	x			
<i>Sphagnum</i> L.	9					x
<i>Symplocos</i> Jacq.	4	x	x	x	x	x
<i>Tapirira</i> Aubl.	3	x				
<i>Thelypteris</i> Schmidel	5			x		
<i>Thoracocarpus</i> Harling cf.	3	x				
Tiliaceae	9	x				
<i>Tournefortia</i> L.	1				x	
<i>Trichantera</i> Kunth / <i>Bravaisia</i> D.C.	3				x	
<i>Tristerix</i> Mart.	3			x	x	
<i>Turpinia</i> Vent.	4					x
<i>Typha</i> L.	9			x		x
Urticaceae	9				x	x
Urticales	9	x	x	x	x	x
<i>Valeriana</i> L.	5			x	x	
<i>Vallea Mutis</i> ex L. f.	8				x	
<i>Vantanea</i> Aubl.	3	x		x		
<i>Viburnum</i> L.	7			x		x
<i>Virola</i> Aubl.	3	x				
<i>Vismia</i> Vand.	3			x		
<i>Vochysia</i> Aubl.	3	x				
<i>Warszewiczia</i> Klotzsch	3	x		x	x	
<i>Weinmannia</i> L.	6			x	x	x
<i>Xylosma</i> Forster f.	1			x		
<i>Xyris</i> L.	1				x	x
<i>Zanthoxylum</i> L.	1			x		x