The Vegetation of the Páramos of the Colombian Cordillera Oriental

by

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with 91 figures

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Aan de nagedachtenis van mijn vader

Aan mijn moeder

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*) The sequence of communities and syntaxa is based on physiognomy and does not reflect syntaxonomical rank or hierarchic position.

I. INTRODUCTION, GENERAL DATA AND METHODS

The name páramo was used since the early days of the Spanish conquest for the high, more or less open chilly areas of the northern Andes. The neotropical páramos are located in the humid tropical Andean mountains, and occur as an altitudinal belt between the uppermost forests and the perennial snow.

The following geobotanic and physiographic features characterize páramo plantcover. Zonal vegetation in these tropical mountains is dominated by bunchgrasses (*Calamagrostis*) and/or low bamboos (*Swallenochloa*), rosette plants and shrubs with small leaves. Caulescent stemrosettes of the Espeletiinae (Heliantheae, Compositae) are physiognomically the most characteristic element Azonal *Sphagnum* bogs and cushionbogs abound. The vascular flora belongs to the richest in genera and species of the high mountains in the world. Alpine rankers support zonal vegetation and histosoles are most common in azonal waterlogged areas.

Annual precipitation varies from 700 to more than 3000 mm. Mist and clouds are very frequent. Temperatures fluctuate very much in 24 hours.

Neotropical páramos are present in the northern Andes (Ecuador - Venezuela) with outliers towards Peru and Bolivia, and in Panamá and Costa Rica. Most of the páramos are located in Colombia; the Cordillera Oriental, the present study area is one of the main areas (Fig. 1). Páramo-like vegetation is further present on the summit of Cerro Neblina (Brasil-Venezuela) and on Itatiaia (Brasil), but here it is floristically different in many respects. A number of authors rank the open vegetation on the high equatorial mountains of Africa and Malesia also under páramos.

THE CORDILLERA ORIENTAL OF COLOMBIA: GENERAL DATA

Topography, geology, geomorphology and soils

Topography

The Colombian Cordillera Oriental extends between 1°N 76°30'W and 8° 30'N; its easternmost position is the Sierra Nevada del Cocuy at about 72°W. The main axis runs from the Macizo Colombiano in NNE direction and continues from the Cocuy area NNW to its norternmost point. The southern part of the Cordillera Oriental is generally low and poorly known. Numerous small páramo "islands" alternate with humid Andean forest along the crestline from south to north: e.g. Picos de la Fragua, Cerro Punta, Miraflores, C. Paramillo, C. Neiva and the highest island Cerro Leiva (3520 m). The Paso de las Cruces depression (1500-2000 m) is the lowermost pass across the Cordillera Oriental and is considered as an important pathway for the exchange of subandean and warm-tropical flora elements. The Páramo de Sumapaz and the Sierra Nevada del Cocuy and surrounding páramos are the main páramo islands above the 3500 m contourline. Smaller páramo islands are found on a parallel line to the NNE and include e.g. the páramos NW of Neusa, those E of Arcabuco and Villa de Leiva, the Páramo de la Rusia, and its northern extension the Páramo de Guantiva. Further to the north are the páramo islands of Almorzadero, Santurbán-Romeral, Cáchira and Jurisdicciones. On the Venezuelan border the island of Tamá is an eastern extension of the Santurbán páramos. Cerro Mina, NE of Ocaña, probably carries the northernmost páramo of the Cordillera Oriental.

The study area is located above the upper Andean forest line (c. 3300-3400 m;

range 3000-3500 m) and reaches up to the nival belt (c. 4800 m). The central ranges of the study area include some highland basins at an altitude of 2500-2600 m, e.g. the Sabana de Bogotá and the Sogamosa-Duitama high plain.
At present a permanent snowcap is found only on the high peaks of the Sierra Nevada del Cocuy. The recent snowcap is about at 4800 m, but glaciers reach as far down as 4400 m. Van der Hammen et al. (1981) charted the retreat of the snowline in this area since 1938. Seasonal snow at lower elevations is rare, but is reported occasionally. Peaks in the Sierra Nevada del Cocuy are higher than 4500 m, and some reach above 5000 m. The Ritacuba (5493 m) is the highest peak of the Cordillera Oriental.

The Nevado de Sumapaz (approximately 4250 m) and its surrounding páramos mark the southern boundary of the study area ($3^{o}55'$N). The summit of the Almorzadero (approximately 4375 m) is the northern limit of the study area ($7^{o}00'$N), which measures about 450 km 2 N - S by air, but varies considerably in width (25-75 km). Taking into consideration that the páramos are "islands" of various sizes, the total area under discussion measures about 10,000 km^2. The study area belongs to four "Departamentos" (Meta, Cundinamarca, Boyacá, Santander) and two "Intendencias" (Arauca, Casanare). For the boundaries of these political units reference is made to the "Atlas de Colombia" (3rd edition) and to the topographic maps (1:100,000 and 1:25,000), edited by the Instituto Geográfico "Agustin Codazzi", Bogotá.

Geology

While marine sediments were formed in the northern Andean geosyncline during most of the Cretaceous, continental sedimentation started around the Cretaceous-Tertiary transition. During the Upper Tertiary the Cretaceous and older Tertiary sediments became strongly folded and faulted, and finally the study area was uplifted to its present elevation. This probably happened during the early Pliocene.

According to the available geological maps (e.g. Arango et al., 1976) the greater part of the study area consits of Cretaceous sedimentary rocks, mainly sandstones and some shales. These include the older Villeta group, resp. formations Fómeque, Une, Chipaque (Hauterivien-Cenomanian) and the Guadalupe group, resp. formations Raizal, Pleaners, Tierna-Labor (Turonian - lower Maestrichtian). The northern part of the study area mainly consists of Palaeozoic and locally of Jurassic and Cretaceous sedimentary rocks. Here and there igneous rocks are present. In the southern páramos near Bogotá one finds outcrops of lower Tertiary age (Guaduas, Cacho and Bogotá formations) and Palaeozoic (partly calcareous) bedrock (Quetame, Farallones de Medina, Páramo de Palacio, Nevado de Sumapaz). Useful pertinent information is provided by Hettner (1892), Bürgl (1957), Irving (1971) and Mc Laughlin & Arce H. (1971).

The type and age of the rocks in the páramos visited is given below, mainly based on the geological maps obtained from Ingeominas, Bogotá, for which the help of Dr. A. Alvarez-Osejo and Dr. H. Duque-Caro is gratefully acknowledged.

Páramo de Sumapaz:

Mainly Cretaceous sandstone (Villeta and Guadalupe groups). On the eastern border limestones and lutites of the precretaceous Clarin group. The boundary between the two formations runs across the Laguna El Nevado and E of the Laguna Sitiales. Numerous fossil tabulate reefcorral species of *Chaetetes* (det. Dr. G. de Groot, Leiden) present in the calcareous rocks of the Nevado de Sumapaz suggest a carboniferous age. A collection of marine fossils collected with Mr. L. Carvajal was deposited in the museum of Ingeominas, Bogotá. The mountains E of the Chisacá lakes are of Lower Tertiary age.

Páramo de Cruz Verde, Páramo de Palacio-Chuza, Páramo de Guasca, Páramos NW of Neusa:

Sedimentary rocks of Lower Tertiary (Palaeocene to Oligocene) and Upper Cretaceous (Albian-Maestrichtian) age: e.g. Guadalupe group. Sandstones are predominant. A local limestone in the Páramo de Palacio is being mined.

Páramo de Tota and surroundings:

Cretaceous sedimentary rocks are present in most páramos. Upper Cretaceous (Albian-Maestrichtian) sandstones in the vicinity of the Páramo de La Sarna extend to the W. Locally, N and NW of the Lake Tota, there are Tertiary outcrops. Sedimentary rocks of Berriasian to Aptian age are found E of the headwaters of Rio Cusiana.

Páramo de la Rusia:

The triassic to Jurassic sedimentary rocks consisting of reddish sandstone and conglomerates, mainly belong to the Girón formation. The slopes inmediately W of Duitama consist of Tertiary rocks.

Páramo de Guantiva (southern part)

Reddish sandstones, lutites and conglomerates of the Girón formation are present in the southern part, including the headwaters of Q. Minas. The Cerro Pan de Azucar consists of Palaeozoic (Devonian-Permian) gneis and granites. W and NW of this peak is an area with intrusive and extrusive rocks of Triassic-Jurassic age. A narrow zone of (Lower) Cretaceous sandstone is found N of the Pan d'Azucar.

Páramo de Pisva and Chita:

Tertiary rocks on the Chicamocha side of the divide are bordered by a narrow zone of Upper Cretaceous sandstone striking N. The lowermost perhumid páramos of the Orinoco drainage basin consist of Lower Cretaceous bedrock (Triassic-Aptian).

Sierra Nevada del Cocuy:

The western dipslope of this range consists of Cocuy quartzite (Hettner 1892; Notestein & King, 1932) of Lower Cretaceous (Berriassian-Aptian) age. Near Patio Bolos lutites and calcareous layers were found with numerous plant fossils. A collection was deposited in the Museum of Ingeominas, Bogotá.

Páramo del Almorzadero:

Fieldstudies were only made in the southern calcareous part including the summit which mainly consists of rocks belonging to the Low Cretaceous Rosa Blanca formation. The greater part of the Páramo del Almorzadero is of Upper Jurassic age and consists of sandstones and conglomerates of the Girón formation.

Geomorphology

Though the páramo landscape was repeatedly glaciated during the Pleistocene (e.g. Van der Hammen 1974, 1979 and in numerous other publications), at present a snowcape is only present in the Sierra Nevada del Cocuy. During the Neoglaciation the snowline reached as low as 4250-4400 m in the Cocuy area, and the ice covered the area of the present superpáramo (Fig. 9), which then was located at a lower elevation. Steep ridges and crests as high as 4500 m remained free of snow and ice (Van der Hammen et al., 1981). At present these are overgrown with open *Calamagrostis* bunches and *Espeletia* stem rosettes, whereas moraines at the same elevation near the snowline are practically devoid of

vegetation. Gonzalez et al. (1965) and Van der Hammen et al. (1981) studied the glacial sequence and environmental history and recognized at least five (possibly six) drift bodies, all of which of Last Glacial (Fuquenian) and Holocene (Neoglacial) age.
During Neoglacial times a minor ice area must have been present on the Nevado de Sumapaz (Van der Hammen 1979[a]; Cleef et al., in press).

Various glacial features are found everywhere in the páramo belt, but they become less distinct near the forest line. The lower páramos longer remained free of ice and thus were longer subjected to weathering and erosion than the higher ones. As a result of glacial events various glacial and periglacial features, like moraines, boggy U-shaped valleys, tills, cirques, fluvioglacial deposits, tarns and glacial lakes behind moraine ramparts, polished bedrocks, roche moutonnée, erratic rocks, etc. are common features. Oppenheim (1940) gave a geomorphological description of the glacial evidence in the Páramo de Sumapaz. For the Sierra Nevada del Cocuy geomorphological descriptions were presented by Gonzalez et al. (1965) and Van der Hammen et al. (1981); the latter also presented an photographic map of the glacial morphological features.

Contributions on glacial and periglacial morphology of the Venezuelan páramos of the Sierra Nevada de Mérida were made by Schubert (1979). From 3600 m up to the snowline he observed needle ice, micro terrassettes, sorted and non-sorted stripes, sorted polygons and circles (structure soils, sensu Troll 1958) and an abundance of screes.

Furrer & Graf (1978) studied glacial and periglacial phenomena in the superpáramos of Ecuador. They illustrated the marked increase in height and width of the superpáramo zone in southern direction from the volcanoes of Cayambe, to the Cotopaxi and the Chimborazo.

Within the study area frost heaving is most common on bare ground in the superpáramo of the Sierra Nevada del Cocuy. Less evidence was obtained in the superpáramo of the Almorzadero and the Nevado de Sumapaz, due to the fact, that the corresponding lower superpáramos have a relatively dense vegetation cover. Permafrost, common in arctic-alpine areas, seems to be almost absent in equatorial mountains.
Quantitative data on weathering processes and denudation rates in the páramos of the study area are not available. In limestone areas, most of which are limited in size (e.g. Nevado de Sumapaz, summit and southern slope of the Almorzadero) karst phenomena were observed such as poljes and dolines, lost rivers, ponores, caves, etc.

Soils

At the time of the fieldwork (1972-73), little was known on the nature and genesis of the páramo soils. Local names were used by IGAC (1965) and Carrera et al. (1968) for the soils of the Rio Bogotá drainage basin, and descriptions and chemical analyses of profiles were presented. Names used in relation to soils of the páramos were e.g. "associación páramo" resp. "asociación Páramo-Usme-Guasca". In view of the scanty knowledge and the few publications available, it was decided to describe as simple as possible a number of soil scharacteristics that are of importance for the vegetation.

The following soil features were considered in each of the relevés.

1. The pH in the top soil, at a depth of about 10 cm (see introduction).
2. The lithologic composition (-texture) of the upper soil layer (A) (gravel, sand, silt, clay peat, gyttja).
3. Thickness of A-layer.
4. Colour of A-layer (with colour chart).

These are mentioned in the description of the communities resp. plant associations. Samples were collected for chemical and physical analyses. More detailed studies of the soil in relation to vegetation are now being made as part of the ECOANDES-project that includes also the páramos of the Sumapaz area and of the Cordillera Central.

Pedological data have been published by various authors and various classification systems (FAO, USDA, ORSTOM) are available. In this context only data will be mentioned, that have a direct bearing on the study area.
Faivre (in Duchaufour, 1977) described a zonal soil under zonal *Calamagrostis effusa* - *Espeletia* páramo on a moderately steep slope at 3700 m in the Páramo de Chisacá. This soil is classified as "alpine ranker" in the French classification system, as a "humic cambisol" in the FAO classification and as a "lithic humitropept" in the US classification system. The $A_0$of 30 cm consists for about 75% of organic matter and the low C/N ratio (of 15) indicates its origin in a vegetation rich in grasses.
Schnetter et al. (1976) determined a number of pedological characteristics in relation to vegetation in the Páramo de Cruz Verde, E of Bogotá. They found similar values, but also differences in C/N ratio in the dry season and the rainy seasons. C/N ratio varied under *Calamagrostis effusa* - bunchgrass páramo from 13 to 25. N increases in the dry season, while C decreases. C/N under *Diplostephium revolutum* shrub varied from 21 to 26.
Sturm (1978) presented some observations on soil flora and fauna and on decomposition processes in the Páramo de Monserrate, E of Bogotá. He summarized the results of previous pedological studies in the páramos near Bogotá and elsewhere in the páramos of the northern Andes. Páramo soils (of the lowermost part of the páramo belt) have in common:
1. relatively moderately to highly acid soils nad correspondingly low Ca lavels;
2. higher water capacity;
3. low free P-content;
4. relatively high content of K and N and reduced uptake of these elements by plants;
5. higher organic content than 10% in the toplayer;
6. hardly or no "podzolic" features (cryptopodzolic or andopodzolic).

Soils on limestone bedrock, e.g. On the superhumid Nevado de Sumapaz, have dark brownish clayey profiles with about the same pH values as in the super-páramo of the Sierra Nevada del Cocuy. At first sight, the calcareous nature seems to have little effect due to the humidity. Except for epilithic vegetation, there is hardly any botanical indication of the presence of calcareous parent rock.

An important observation is that many soils in the higher areas of the Cordillera Oriental contain volcanic ash from eruptions in the Cordillera Central, which were mainly deposited in the past 44,000 years (see e.g. Correal & Van der Hammen, 1977; Van der Hammen 1978. Schreve Brinkman; 1978, and Van der Hammen et al., 1980). In the Andean forest zone the ash added to the original surface (volcanic ashes, their weathering products, locally colluvial material and humus) may be as high as 2 meters or more, while 1.5 m is common. In the páramo the thickness of deposited material and (paleo)soils together rarely exceeds 1 m, but is generally thinner (Fig. 84). The upper recent soil is very dark to black, due to a high percentage of humus (see above: "black páramo soils"). The deposition of the ashes causes that in many places with concave topography the original rock or soil cannot be reached by the roots, and hardly effects the vegetation (except when the added material is thin).

In general, many soils in the páramos are inceptisols, which are slightly developed and relatively young; examples are orthents (alpine rankers), vitrandepts (vitrisols), cryandepts (andosols), and others (possibly pseudoalpine rankers, rendzines (?), calcimorf soils, etc.). Histosols (hydromorphic soils; gley, pseudogley) occur in very wet páramos, in peatbogs, swamps and mires.

Climate

Due to its geographical location on the northern hemisphere near the equator and at high altitude, the páramo climate in the study area is of the humic tropical diurnal type, cold at night and cool in the day time. It is classified as Csw (or Cws) in the Köppen system (see discussion in Eidt, 1968). In contrast to the climate in the southern puna, the páramo climate is basically humid. Lauer and Troll (in Lauer, 1979) reported 10-12 humid months. But the study area contains also dry páramos with only 8 to almost 9 humid months, which in the classification of Lauer & Troll are ranked as moist puna (7-10 humid months).

Information on the climate in the study area is scarce and is only available for some places near Bogotá and for the Páramo de Berlín (Santander) at 3230 m. Precipitation has been measured, especially in the southern part of the study area, but records are scarce or absent for the northern part. Meteorological data were obtained from the annual reports by

- Empresa de Acueducto y Alcantarillado de Bogotá, D.E.: Boletín Informativo Hidrometeorológico.
- Corporación autónoma regional de la Sabana de Bogotá y los valles de Ubaté y Chiquinquirá (CAR): Boletín estadístico de Hidrología y Meteorología.
- Servicio Colombiano de Meteorologia e Hidrología: Boletín Climatológico Mensual and Anuario Meteorológico.

As to the páramo climate in the study area, a number of climatic factors will be considered, the most important of which are precipitation and temperature. Some measurements were made on speed and direction of wind, cloudiness/sunshine, radiation, evaporation, relative humidity, and dew. The dependence of Bogotá on water from the páramos, has been conducive to the abundance of pluviometric data for the southern páramos.

Precipitation data were used for constructing climate diagrams. Extrapolation has been applied to arrive at a general idea of climate.
In contrast to Eidt (1968), a mean annual temperature of 0° C was assumed at 4800 m (climatic snowline) and a mean lap of 0.6°C for every 100 m of altitude. This method was preferred, as the páramo belt is close to the nival zone. Thus calculated temperatures (T) are about 1.2°C lower than the values obtained with the Eidt formula: $T = 30 - 6\ H$, where H is the height in km. This does not basically affect the shape of the presented diagrams. The calculated temperatures are indicated with an asterisk and a broken line in the diagrams of Fig. 3.
This value of 0.6°C/100 m is corroborated by calculations by Van der Hammen & Gonzáles (1960[a]) in Cundinamarca (2/3°/100 m) and by measurements during the ECOANDES transect study in the Buritaca trail, Sierra Nevada de S. Marta (0.56° C/100 m for the interval 1500-3300 m).
Snow (1976) mentioned a temperature decrease of 7°C/km, resp. 6°C/km between 5000 to 4000 and 4000 to 3000 m in the Colombian Andes. Unlike for higher latitudes, the mean annual temperatures near the Equator thus can be easily approximated and plotted in diagrams. These have been constructed for a number of selected puviometric stations in the páramo belt, in the vicinity of which field work was carried out (Fig. 3). Most precipitation values in the diagrams are above the temperatures curve during all the months of the year. Only in the

driest páramos a short period of waterdeficit may occur during one or two months. Werger (1973) summed up some restrictions for the application of climate diagrams, but for the scope of this study the diagrams are useful, especially for an ecological understanding of the different páramo vegetation types. For comparison, a typical dry puna diagram (Fig. 3p) is presented from Pampa Galeras in SW Peru as based on Tovar Serpa (1973). The zonal puna vegetation there consists of spaced bunchgrasses of *Festuca* associated with *Stipa*. In wet depressions there are cushionbogs with *Plantago rigida* and *Distichia muscoides*. About 35 out of approximately 150 vascular species in that area are also present in the Colombian páramos.

For the study area some values of meteorological factors given below have been obtained from data compiled by the Colombian services mentioned before. As a matter of fact, different combinations of these factors head to different páramo climates. Data for the superpáramo are not available.

Precipitation

Annual precipitation rates in the study area vary between 700 and 3000 mm. The highest precipitation with annual values up to about 3000 mm is found along the wet upper forest line on the humid side of the Cordillera (Figs. 3f and 4). With increasing elevation the precipitation rate drops (Figs. 3d,e,k; 4). The lowest values are from dry leeward subpáramos (Fig. 3a,i,m). There is one annual maximum of precipitation near the upper forestline on the wet side of the mountains, but there are two maxima on the dry side, Near the crestline intermediate conditions prevail (Fig. 3c,d,j,k,o).

Weischet (1969) reported on the character of the precipitation maxima in the Colombian Andes (including the southern part of the study area).

Temperature

Mean annual temperatures in the páramo belt vary from 13-14° C to 0° C. The precise position of the upper forest line is supposed to depend on the complex interrelation between temperature and moisture. Slight differences are found in the mean annual temperatures at equal elevation on the humid and the dry side of the Cordillera Central, and this may explain part of the asymmetrical distribution of plant species (Van der Hammen et al., ECOANDES report, in prep.). On the basis of the number of days with nightfrost and altitude, Lauer (1979[a], fig. 9) depicted the position of the humid equatorial páramos intermediate between Mexican and Peruvian high volcanoes.

Cloudiness & drizzle

Statistics on cloudiness are practically not available for the páramos in the study area. Cloudiness is highest in the wet season and this generally coincides with higher moisture conditions, as prevailing on the wet side of the mountains. Cloudiness maxima can be positively correlated with the presence of the forest line condensation belt and the upper condensation zone. In the early morning the páramos are generally free of clouds, but soon these rise from lower parts up to the páramo belt, which in the afternoon is mostly cloud covered and submitted to drizzle ("paramitos") and rain. According to Sturm (1978) this drizzle is practically not pluviometrically recorded. Much of the drizzle is intercepted by the numerous small leaves of woody species, as indicated by thick layers of pendulous epiphytic bryophytes dependent on atmospheric moisture. Interception rates are supposed to be considerably high. Only few observations have been made on this phenomenon in tropical mountain vegetation (e.g. Kerfoot 1968; Van der Hammen et al., in prep.). Pertinent data for the study area are lacking.

Sunshine

Duration of sunshine (in hours) is monthly recorded in a number of páramos near Bogotá. For example, in the lowermost bamboo páramo or wet upper Andean forest of Chingaza and Chuza were recorded about 773 to 972 hours of sunshine in 1971, against 1432 hours in La Regadera at 3050 m in the dry valley between Usme and Chisacá and 1473 hours at the Represa de Neusa at about 3100 m. The two last stations are located in the upper Andean forest belt. The bamboo-bunchgrass-páramo station Palacio-Guasca at 3760 m recorded an annual mean of 1080 (985-1127) hours of sunshine from 1972 to 1974.

Radiation

Radiation increases with elevation and is highest in dry tropical high mountains. Ultraviolet waves contribute more at these high altitudes than at sea level. Intensity of radiation is controlled by frequent fog, and contrary to summer conditions in alpine belts at higher latitudes, the duration of radiation is limited to 12 hours per day in the páramos in the dry season. Incoming radiation is mainly converted into heat by the soil surface and the plantcover. Part of it is reflected by plants, which have developed various protection and/or reflecting structures: e.g. several types of adpressed indumentum, silvery leaves, brittle brilliant leaves, brownish-glaucous or reddish leaves. Apparently correlated with elevation and climate, an array of different morphological structures was observed, which will be dealt with in detail in future studies. Nightly long wave (re-)radiation is strongest under clear skies in the dry high páramo, and surface cooling causes nightfrosts. Radiation is quantified in the study area as follows:

- Páramo de Cruz Verde at 3480 m: 0.18-0.51 cal. cm^2. min. on Nov. 5, 1971 under clouded sky between 10 a.m. and 4 p.m. (Schnetter et al., 1976)
- Represa del Neusa at 3100 m: yearly average 345 (129-629) cal. cm^2/day. For 1969 120.564 cal. cm^2 were recorded.

Evaporation

Evaporation records are scarce in the study area. The annual mean as deduced from the data of different stations near Bogotá is about 400-600 mm in the lower bamboo páramo and 700 - 1000 mm in the lower bunchgrass páramos. In the extremely dry Páramo de Berlín near Bucaramanga, annual evaporation varies even between 1200 and 1400 mm (1973-1974).

Relative humidity

Mean values of relative humidity are usually highest in the lower páramos and vary from 10 to 30 and up to 100%. Condensation belts are characterized by persistence of fog, and, consequently, by permanently high levels of relative humidity.

Wind

Wind is generally strongest in the highest parts, where wind action on plants can be observed. Local diurnal upslope and downslope compensation winds seem to be predominant. N-E tradewinds are active most of the year. Near the wet and clouded upper forestline the windflow is slight: only about 1 - 2 m. sec (Chuza; Chingaza stations).
Stormy upslope compensation winds seem to be an exception. We only experienced these during the night and early morning on e.g. Febr. 25, 1972 at 3700 m near Belén and on March 1, 1973 at 4300 m in the Páramo de Cóncavo, Sierra Nevada del Cocuy.

Condensation belts

Since the study of precipitation in relation to elevation in the Colombian Andes by Weischet (1969), later confirmed by Guhl (1974), Lauer (1979) paid attention to the unequal spatial distribution of humidity in the Mexican mountains and in the Ecuadorian Andes. Condensation zones have also been recognized in the study area, especially on the wet side of the mountains: 1) the forestline condensation zone (or "2ª Cinturón de nubes ecuatoriales" of Guhl 1974), and 2) the upper condensation belt (or Guhl's "3ª Cinturón de nubes ecuatoriales") in the lowermost superpáramo between 4100 and 4300 m.

Condensation zones are characterized by high moisture conditions, i.e. higher precipitation and relative humidity, more cloudiness and fog, and reduced sunshine, radiation, windspeed, and evaporation. In the study area also the presence of woody plants in zonal vegetation with larger leaves, and a marked increase in the bryophyte cover are characteristic. The daily temperature amplitude is less extreme than outside the condensation zone and is indicated as oligothermic by e.g. Troll (1968). It allows the growth of woody species at elevations above 4000 m. Gradstein et al. (1977), Cleef (1978) and Cuatrecasas & Cleef (1978) pointed to the botanical richness of condensation zones, especially the uppermost one. It is assumed that such limited areas of favourable temperature and moisture conditions must have been of fundamental importance to the survival of a large number of hygrophytic species during arid (and cold) Pleistocenic periods. According to Weischet (1969) and this is confirmed by the precipitation data for the study area, the rainfall decreases with the height in the páramo belt. The precipitation maximum appears to be located near the wet upper forest line (Fig. 3f,3g,4). Altitudinal positions and temperature and moisture characteristics of condensation zones will be quantified in the future as part of the current ECOANDES project. At this moment mainly physiognomical and floristic evidence is available in regard to the condensation zones in the study area.

Meso- and microclimate directly affecting plant growth have been studied by Schnetter et al. (1976), Sturm (1978) and Rangel et al. (in prep.). The last author collected these in different altitudinal zones. Interesting microclimatic studies demonstrating the importance of rosettes and tussocks in páramo environment were carried out in the Venezuelan Mérida páramos by Vareschi (1953), Smith (1974), Larcher (1975), Hedberg & Hedberg (1979), Monasterio (1979) and Azócar & Monasterio (1979). The last mentioned authors and Walter & Medina (1969) studied *Polylepis sericea* dwarfforest. Hedberg & Hedberg (1979) measured daily temperature variation in *Plantago rigida* bog and in *Hypericum laricifolium* shrub.

Pāramo flora

The neotropical pāramo flora has been studied since its first plants were described by von Humboldt & Bonpland in 1805. In the course of the last century contributions were made by Mutis, Triana, Weddell, Mitten, Hampe, Spruce, Nylander, and numerous other botanists. In this century and up to the present many new taxa of the pāramo flora have been bescribed and many taxonomists actively study this rich flora.
Botanical exploration of the pāramos has not yet been completed and it is to be expected that still many new endemic taxa will be described in the future. Obviously, continued botanical exploration of the pāramos will also contribute to our knowledge of plantgeography and of natural resources.

Local regional and "national" checklists, catalogues and floras have advanced the study of pāramo plants. However, a systematic treatment within the framework of a flora project covering most neotropical pāramos, at least fron northern Peru (Chachapoyas) up to Costa Rica and the Cordillera de la Costa, Venezuela, is the optimal approach and deserves attention. An attempt will be made to review the present taxonomical knowledge of the major taxonomic groups of the pāramo flora.

Vascular plants

The vascular pāramo flora is well known in comparison with other groups as bryophytes, lichens, algae and fungi. More than 300 native vascular genera are present in the pāramos of the northern Andes. About 260 of them are found in the pāramo belt of the Colombian Cordillera Oriental, an area which contains about 700 species (Cleef 1979a; Van der Hammen & Cleef, in press). Together with the flora of the puna of northern Argentina (Cabrera 1958), the vascular flora of the study area belongs to the richest in genera and species of the high mountains of the world. Fig. 5 shows the qualitative and quantitative composition of the vascular pāramo flora of the study area for families and genera. For comparison, similar data have been included for the Argentinan puna (Cabrera 1958), the "afro-alpine" belt on the equatorial East African Mountains (Hedberg 1965), and for the "tropic-alpine" belt of Mt. Wilhelm (4510 m), Papua New Guinea (J.M.B. Smith 1977). Only the families are shown that are present in the pāramos of the study area. As in other temperate areas, the Compositae and Gramineae are represented by far the most genera. The tropical character is proved demonstrated by the presence of numerous genera of the Orchidaceae, Melastomataceae, Piperaceae, Bromeliaceae, Xyridaceae, etc. Bromeliaceae are almost limited to the neotropics and Melastomataceae only here are adapted to supra forest-line habitats.
Among others, J. Cuatrecasas contributed to the knowledge of the vascular pāramo flora in numerous publications. Soon forthcoming is his monographic treatment of the Espeletiinae (Heliantheae, Compositae), species of which are undoubtedly most characteristic for the north Andean pāramos.

A number of vascular genera is in need of systematic study or revision. Alphabetically according to family these are; *Ilex, Callitriche, Arenaria, Hypochoeris, Hieracium, Senecio s.l., Lucilia, Gynoxys, Draba, Carex, Eleocharis, Scirpus* subgenus *Isolepis, Gaultheria, Plutarchia, Gentianella, Halenia, Agrostis, Bromus, Calamagrostis, Festuca, Muhlenbergia, Poa, Altensteinia* s.l. *Lupinus. Lachemilla, Rubus, Hesperomeles, Ribes, Castilleja, Bartsia* and *Valeriana*. For most of these genera cytologic research in combination with experimental breeding under controlled conditions is required to determine the exact systematic position Preliminary results of a cytologic inventory are promising (H. 't Hart, unpubl.; E.G.B. Kieft, unpubl.).

Musci

The present knowledge of the moss flora of the páramos is illustrated by the checklist of páramo mosses from Venezuela and Colombia by Griffin (in prep.), containing about 180 genera and 380 species.

Acrocarpous mosses are prominent in the open páramo. Their abundance generally increases with altitude and aridity. The most common genera of the páramos include: *Breutelia*, *Campylopus* (Florschütz & Florschütz-de Waard 1974, Frahm & Cleef, in prep.), *Leptodontium*, and *Sphagnum*. Species of *Chorisodontium* (Frahm & Cleef, in prep.), *Racomitrium crispulum* and *Rhacocarpus purpurascens* abound especially on the humid side of the mountains and within the reaches of the condensation belts. *Kingiobryum* is the only endemic genus described from the páramos (Robinson 1967, Zander & Cleef, in press). The most recent work on Colombian mosses is that of Robinson (1967). In addition to checklists published for other tropical Andean countries, Florschütz-de Waard & Florschütz (1979) presented a list of Colombian moss species.

Hepaticae

In nearly all altitudinal zones of the páramo belt, possibly the upper superpáramo excepted, liverworts are conspicuous elements of the páramo vegetation, in some places even dominating the vegetation. *Stephaniella paraphyllina*, and *Gongylanthus liebmannianus* are characteristic for the open dry zonal bunchgrass páramo and *Jamesoniella rubricaulis*, *Isotachis multiceps*, *Riccardia* spp. and *Jensenia erythropus* for the (zonal) bamboo páramo. Species of *Ricardia* mainly abound in páramo bogs, mostly on decaying *Sphagnum* or vascular cushionplants, but they are also common on peaty soil. *Anastrophyllum* spp., *Adelanthus lindenbergianus*, *Lepidozia macrocolea*, *Kurzia verrucosa*, *Leptoscyphus cleefii* and species of *Plagiochila* are also common in boggy habitats. Together with mosses they play an important role in the succession of *Sphagnum* bogs, especially in the bamboo páramos. *Symphyogyna sinuata* is typical for tall Cyperaceae reedswamps containing species of *Carex* and *Cyperus*, *Marchantia plicata* for the same Cyperaceae reedswamps, as well as for the different types of *Calamagrostis ligulata* mire and *Montia* springs. *Isotachis serrulata* is practically the only species dominant in submerged communities in streams the high páramo. This species is also present together with submerged bryophytes, associated with species of *Isoetes* sect. *Laeves* in cold páramo lakes. *Herbertus subdentatus* and *H. acanthelius* cause the characteristic reddish hue to the (lower) superpáramo vegetation in the upper condensation zone of the Nevado de Sumapaz (Van Reenen, in press).

Gradstein et al. (1977) reported 62 genera of liverworts native to the Colombian páramos. From this list should be omitted *Arachniopsis*, *Pallavicinia* and *Leucosarmentum*; specimens brought then to these genera are now considered to belong to resp. *Telaranea*, *Jensenia* and *Bonneria*. Among the genera to be added to this list are: *Andrewsianthus*, *Eopleurozia* and *Nardia*. During the last 10 years contributions to the knowledge of Colombian liverworts were made by Dr. S.R. Gradstein and his students (Division of Cryptogams, Utrecht University). Revisions were prepared for the high Andean species of *Radula* (Jans 1979), *Jensenia* (Van der Gronde 1980), *Frullania* subg. *Chonanthelia* (Haarbrink, in press), and *Herbertus* (Van Reenen, in press).

Lichenes

About 50 genera of macrolichens have been recorded for the Colombian páramos (Sipman & Aguirre, in prep.). Included are *Neuropogon* and *Umbilicaria*

which had not been previously reported for Colombia.
According to H.J.M. Sipman (pers. comm.), part of the lichen flora is of tropical origin, e.g. *Heterodermia, Cora,* Stictaceae and a number of parmeliaceous genera; most genera are wide-temperate in distribution, e.g. *Stereocaulon, Thamnolia.* Holarctic (e.g. *Cetraria, Alectoria, Bryoria)* and genera of austral-antarctic affinity (e.g. *Cladia, Neuropogon, Pseudocyphellaria)* are present in more or less equal generic proportions. Remarkable is the amphi-pacific distribution, e.g. in *Anzia, Glossodium, Oropogon.*
Since Nylander (1863), few systematic studies were made on páramo lichens. During the last years, however, the attention of lichenologists for the neotropical mountains increased considerably. For the Colombian Andes and more in particular the present study area, Sipman & Cleef (1979) reported on *Cladonia* subgenus *Cladina.* Sipman (1980) studied high Andean members of the *Everniastrum* complex, and in addition to several new species he described a new and apparently endemic genus *Cetrariastrum. Stereocaulon* and *Leprocaulon* have been studied by Boekhout (in prep.). A checklist of Colombian macrolichens is being prepared by Sipman & Hekking.

Algae

Algae are abundantly present in het humid páramos of the study area. Conspicuous is the presence of lilac *Aphanocapsa gervillei* (Hass.) Rabenh. (Cyanophyta) in humid glaciersand in the superpáramo of the Sierra Nevada del Cocuy (det. Dr. G.H. Schwabe). This pioneer species had been recorded already for the high Alps and Surtsey (G.H. Schwabe, in litt.).
Dr. A.J. Dop (formerly Free University of Amsterdam) identified part of the collected fresh-water algae, some of which are of interest for (paleo-)ecological studies. Three main groups were reported by Dop (in litt.):

1. Cyanophytae: Haptophytic and pleustophytic *Stigonema* spp. (3440-4335 m): e.g. *Stigonema ocellatum* Thuret, *S. tomentosum* (Kütz.) Hieron.; *S. flexuosum* W. & G.S. West; *Nostoc* sp.
2. Rhodophytae: Haptophytic *Batrachospermum* sp. (3450-3800 m) in running and stagnant water.
3. Chlorophytae: predominantly members of the Conjugales and (cf.) *Microspora, Mougeotia, Spirogyra* and *Zygnema* are the most common genera of the Conjugales. Generally they form thick masses floating just below the surface in pools and streams. Van Geel & Van der Hammen (1978) reported on fossil Zygnemataceae, Oedogoniaceae and Desmidiaceae in Pleistocene and Holocene lake sediments in the high Colombian Cordillera Oriental. *Chaetophora pissiformis* was found in a páramo stream at 3460 m (Roth.) C.A. Agardh.

Dr. Dop also identified *Vaucheria* cf. *dichotoma* (Xanthophyceae), from páramo streams and seepages. Diatoms were found associated with or dominant in pioneer habitats, especially *Navicula* sp. Three characeous species *(Nitella acuminata* A. Braun ex Wallm., *N. clavata* Kütz. em. R.D. Wood, *N. flexilis* (L.) C. Agardh) were collected in the study area; probably they are most common in deep páramo lakes.

In summary, it is clear that a systematic inventory of algae and other limnological research has only just started in the páramos. On this taxonomic group West (1914) is the main reference for the study area. In addition, for Venezuelan páramo lakes reference is made to Gessner (1955) and Weibezahn & Cressa (1979).

Macrofungi

According to Dennis (1970) rather few endemic genera of macrofungi are known from the Venezuelan páramos. Most of them were found in bamboo habitats It is possible that the same holds true for the Colombian páramos, which are generally more humid with bamboo as a common feature.
Though some haphazard observations on macrofungi were maded during the present study, most of them in boggy habitats; e.g. *Scutellinia* spp. (Pezizales) with its bright red discs ; only little material was collected and sent to Dr. K. Dumont (NY) for identification.
Dumont et al. (1978) recently started with "Flora de hongos de Colombia". A number of contributions have been published, mainly in Caldasia. Recently, Boekhout (in prep.) collected macrofungi in the zonal bunchgrass páramo of the volcanoes S. Rosa and S. Isabel, from the forestline up to 4600 m, during an ECOANDES transect study in that area in 1980. Species of lichenized *Omphalina* are most common on bare ground in the high páramo. *Lycoperdon* sp. was frequent there in grazed *Lachemilla orbiculata* vegetation and also in the study area. Species of *Scutellinia* and *Cystoderma* were collected. In conclusion, inventory of the macrofungi had just started in the Colombian páramos.

Phytogeography

Phytogeographic aspects have already received special attention in some earlier papers (Cleef 1978, 1979[b]; Van der Hammen & Cleef, in press). The main reason is that such studies on the phytogeographic relations of the páramo flora and vegetation may yield more qualitative and quantitative information, e.g. for an inventory of local and allochtonous elements (Cleef 1979[b]). In connection with historical data (Van der Hammen 1979[b] van der Hammen & Cleef, in press) these studies may shed more light on the origin of the early páramo flora (about 2.5-3 millions of years ago), and on its successive enrichment by subsequent immigration, evolution, and speciation caused by the repeated fragmentation and isolation of Pleistocene páramo biota.

Analysing the present geographical distribution of the endemic vascular genera on the páramos of the Colombian Cordillera Oriental the present author (Cleef 1979[b]) distinguished primarily between (local) tropical and (allochtonous) temperate components.
The local t r o p i c a l component is subdivided into:
- neotropical element dominated by genera with a tropical-Andean distribution. The endemic páramo element is part of it.
- wide tropical element defined as proper to cool, as well as to warm tropical areas of at least two continental regions, either America and Africa and Asia/Australia, or all three of them. Taxa belonging to this elements have a similar distribution in páramos and savannas.

The allochtonous t e m p e r a t e component is subdivided into:
- holarctic element, which comprises all kinds of northern immigrants, widely distributed in the temperate holarctic (e.g. *Pleurozium schreberi*) or restricted to cold arctic-alpine areas (e.g. *Alectoria*).
- austral-antarctic element, which is geographicall broadly defined (Cleef 1979[b]).
- wide temperate element, whose distribution extends to nearly all temperate and cold regions of the world.

Finally, the (sub-)cosmopolitic element combines more or less the taxa with distribution areas of both the tropical and the temperate component.

In about 260 vascular genera Cleef (1979[b]) found equal proportions of the tropical and the temperate component. For the pâramo element, the other neotropical element and the wide tropical element, the proportions are resp. about 8, 33, and 10%. The holarctic and austral-antarctic element are present in about the same proportions, resp. 11 and 9%; the wide temperate element attains about 20% and the (sub-)cosmopolitic element about 8%.

This subdivision into geographical flora elements has also been used for vascular pâramo and for superpâramo species in the study area (Van der Hammen & Cleef, in press) it was further applied to the non-vascular pâramo flora and to dominant taxa in the vegetation types of the study area in order to obtain a first impression of main geographic affinities.

As a consequence of current monographic systematic studies, we know that high tropical mountains in America, Africa and Australasia have a considerable number of species of bryophytes and lichens in common.

Genetic phytogeographic flora elements have not been recognized in our studies, because the precise areas of origin of many vascular and non-vascular genera of the pâramo have not been well established.

Botanical exploration

The history of scientific botany in the Colombian high Andes began in the early years of the last century, when Mutis and von Humboldt & Bonpland collected and described the first pâramo plants in the vicinity of Santafé de Bogotâ in the "Virreynato de Nueva Granada", under Spanish government at that time.
In the middle of the 19th century, collectors amongst others Purdie, Triana, Lindig and Kalbreyer were active.
Since the first decennia of this century, collecting activities in the high parts of the Cordillera Oriental were strongly renewed, e.g. by Killip & Smith, Troll, Pérez-Arbelaez, Cuatrecasas, García-Barriga.During world-war II, members of the US Chinchona expedition, with Fosberg, Little jr., Haught, Fassett and others, collected in the pâramos throughout the study area.
In the years after the founding of the Herbario Nacional Colombiano (1931) and the Instituto de Botânica of the Universidad Nacional (1938) headed by Pérez-Arbelaez, the staff members substantially supported collecting activities in the pâramos of the study area, e.g. H. García-Barriga, J. Cuatrecasas, L. Uribe-Uribe, L.E. Mora-Osejo, R. Jaramillo-Mejía, M.T. Murillo, J.M. Idrobo-Munoz, A. Fernandez-Pérez, P. Pinto-Escobar, G. Huertas & L. Camargo, E. Forero-Gonzâlez, G. Lozano-Contreras, S. Díaz-Piedrahita, O. Rangel-Churio, J. Aguirre-Ceballos.

Below follows a listing of the pâramos of the Cordillera Oriental, where botanical exploration not or hardly has been carried out:
- pâramos E of Neiva: Cordillera de los Picachos,
- southern part of the Pâramo de Sumapaz,
- the Farallones de Medina,
- the pâramos above Villa de Leiva,
- the northern part of the Pâramo de Guantiva,
- the pâramos between Pisva and Tota,
- the pâramos between Tamâ and the Cocuy,
- the Cordillera de los Cobardes (if it supports pâramos),
- the northernmost pâramos of the Cordillera Oriental (N of the Tibû pipeline),
- all wet forestline pâramos.

For collecting localities of the present author, reference is made to Appendix 3.

Páramo vegetation

Previous investigations

In the beginning of last century von Humboldt gave the first impression and scientific description of the páramo vegetation and its environment, based on his travels in the northern Andes. Cleef (1978) listed the authors of publications dealing with the ecology and vegetation of the neotropical páramos until 1975. During the last 5 years, the interest in the páramos has strongly increased, as indicated by the number of papers on its vegetation and ecology (mentioned in Cleef, 1981[b]), by a special páramo session of the International Symposium of Tropical Ecology in Panamá in March 1977, and by the first Seminario del Medio Ambiente Páramo, held in November 1978 in Mérida, Venezuela (Salgado-Labouriau (ed.) 1979).

With respect to the Colombian páramo vegetation, Dr. J. Cuatrecasas in 1934 presented the first plant-sociological data in his classic account: "Observaciones Geobotánicas en Colombia". Contributions to the knowledge of the Colombian páramo vegetation were made by Fosberg (1944) and Cuatrecasas (1954, 1958), who proposed the altitudinal subdivision of the páramo belt. Further contributions were made by Cuatrecasas (1968), Espinal & Montenegro (1963), Van der Hammen & Gonzalez (1963), Lozano & Schnetter (1976), Gradstein et al. (1977), Cleef (1978, 1979a), Sturm (1978) and Van der Hammen et al. (1981). Important work was also done by staff and students of the Department of Biology (Universidad Nacional, Bogotá) in fieldcourses, e.g. in the Páramo de Pisva (Rangel (ed.) 1976).

These studies on páramo vegetation can be divided into two groups:

(1) local studies: e.g. in the Páramo de Cruz Verde (Lozano & Schnetter 1976), Monserrate (Sturm 1978), and in the Parque Los Nevados, Cordillera Central (Cleef et al., in press).

(2) regional studies, based on fieldwork in a geographically larger area of Colombian páramos. For example: Fosberg (1944), Cuatrecasas (1954, 1958, 1968) and Cleef (1978, 1979[b], the present study).

The present study

From November 1971 up to July 1973 fieldwork (sponsored by WOTRO) was carried out in the Colombian Cordillera Oriental between the Sierra Nevada del Cocuy and the Nevado de Sumapaz, and in March and April 1977 additional fieldwork was carried out in the Sierra Nevada del Cocuy (with R. Jaramillo-Mejía & T. van der Hammen), near Neusa, Cundinamarca (with S. Díaz-Piedrahita) and in the Páramo de Sumapaz in the Chisacá, Andabobos and Rabona areas (with T. van der Hammen). In November 1978 the páramo vegetation of the southern slope of the Páramo del Almorzadero was studied (with J. Aguirre Ceballos & H. Hooghiemstra) and in the same month the zonal páramo vegetation was surveyed in the headwaters of the Quebrada Chuza and Río Guandoque near Bogotá during a phytosociological fieldcourse (for students, given in collaboration with staffmembers of the Universidad Nacional). The present vegetation study covered 8 cross-sections or transects, shown on the map (Fig. 2).

In some of the páramos visited by the author at that time no previous botanical exploration had been carried out. These areas include the Nevado de Sumapaz (about 4250 m) and the headwaters of Río Sitiales with many lakes; the Peña de

Arnical and surroundings, North of Vado Hondo and East of the Tota lake; the southern part of the Páramo de Guantiva, NW of Belén including the Pan de Azucar (4270 m), the highest peak; the Páramo Cóncavo and valley of the Quebrada Los Osos in the Sierra Nevada del Cocuy (with T. van der Hammen) and the calcareous summit area (4375 m) of the Páramo del Almorzadero. In the southern part of the Cordillera Oriental the Huila slope of Cerro Punta was explored up to the wet forest line (2760 m) just below the highest peak.

The páramos studied in the Cordillera Oriental of Colombia thus extend from the Páramo del Almorzadero in the north to the Nevado de Sumapaz in the south. For the sake of comparison some additional trips were made to adjacent páramos in the northern Andes and Central America. Observations and phytosociological records were made in the páramos of the volcano Puracé (1972, with A. Fernandez Pérez) and in the Parque Los Nevados (ECOANDES project 1980) both located in the Cordillera Central of Colombia, and in the Sierra Nevada de S. Marta (ECOANDES project 1977). Some data were collected in the humid subpáramo in Costa Rica (1973, with L. Fournier), in the dry subpáramo on the Avila above Caracas (1977, with O. Huber), and in the Venezuelan Sierra Nevada de Mérida (1972, 1978). Also the "zacatonales" (grasslands), dominated by bunches of *Calamagrostis tolucensis* (HBK) Trin. and *Festuca tolucensis* HBK on the high Mexican volcanoes Popocatepetl and Iztaccihuatl, on the boundary of the tropics, were visited with C. Delgadillo M. (1973).

Morphological characters of páramo vegetation

Studies on the structure and texture of the vegetation of the Colombian Andes were already made in 1934 by Cuatrecasas. In fact, interest in the structure of the vegetation was first aroused in the tropical Andes by von Humboldt in the beginning of last century. Later, e.g. Beard (1955, 1973), Vareschi (1966, 1980), Hallé et al. (1978) and Roth (1980) made substantial contributions, mainly based on studies in the American tropics.

Cuatrecasas (1934) in his classic study mainly follows Del Villar (1929). The socalled "simorfias" of Del Villar are based on the physiognomic concepts of von Humboldt and Grisebach. Cuatrecasas (1934, 1968) adapted these to the páramo vegetation of the study area, and thus distinghuished a number of basic forms. Some of the most characteristic are e.g. "caulirrósula" and "cryptolignum". Woody monocaulous composite rosettes, e.g. "caulirrósula", are only present in the equatorial high mountains of Africa and S. America, where they evolved independently by adaptive evolution.

Textural characteristics studied by Cuatrecasas (1934, 1968) include:

1) Leaf size. according to Raunkiaer (1916):
   - leptophyllous (<25 mm^2)
   - nanophyllous (25-225 mm^2)
   - microphyllous 225-2025 mm^2)
   - mesophyllous (2025-18.225 mm^2)
   - macrophyllous (18.225-164.025 mm^2)
   - megaphyllous (>164.025 mm^2)
2) Leaf consistency. Cuatrecasas (1934) divided this character into three classes:
   - sclerophyllous or coriaceous
   - subcoriaceous or cartilaginous
   - herbaceous
3) Leaf indumentation: a number of different xeromorphic characteristics were used: pubescent, villose, tomentose, lanate, hispidous,

pulverulent and scabrous; in addition, pubescent nerves or ciliate margins and the position of the indumentation on one or both sides of the leaves. Occasionally the leaf colour was noted.

4) Other leaf conditions: grasses were subdivided into 1) revolutifolious species, with inrolled leaves, determining zonal bunch grass páramos; 2) planifolious species, with flat leaves, predominant in the lower part of the superpáramo (e.g. *Poa, Agrostis foliata*). *Poa* cf. *pauciflora* has complicated leaves.
5) Characteristics of the tomentum of young twigs.

Cuatrecasas (1934) determined these morphological characters for each plant species and summarized the data in "biotypological spectra". In conclusion he presented an altitudinal outline for climax-vegetation in all zones from tropical lowlands up to the snowline, both for the Cordillera Central and for the Cordillera Oriental of Colombia. For the latter , in the highest reaches of which the study area is situated, Cuatrecasas (l.c.) demonstrated the presence of predominantly macro- and mesophyllous subandean forests ("*Ingion*") at 1500 m up to nano- and leptophyllous subpáramo thickets at 3400 m. The proportion of sclerophyllous leaves of these forests increases with altitude from 23% in the "*Ingion*" to 56% in the "*Cordietum*" near Bogotá (2650 m), to 80% in the microphyllous "*Weinmannion*" (2900-3100 m) and up to 100% in forestline thickets at about 3300 m.

To define morphological characters reference is made to general concepts as recently summarized by Barkman (1979). Leafsize, however, follows the classic subdivision of Raunkiaer (1916), which is not quite consistently quoted by Barkman (1979) as he adds the bryophyllous class (0-4 mm^2) which is in fact a finer subdivision of the leptophyllous class.
Comparison of the leaf size spectra becomes difficult as various authors applied different size classes, e.g. Vareschi (1966), Werger & Ellenbroek (1978) and Barkman (1979). Camerik & Werger (1981) studied leaf sizes of the evergreen summit vegetation of Itatiaia, Brasil, and applied size classes that nearly coincide those of Raunkiaer for the lepto-, nano- and microphyllous categories. My results (Fig. 86) are directly comparable to those in studies on the tropical Andes by Cuatrecasas (1934), Grubb et al. (1963), Lozano & Torres (1965, 1974), and Rangel & Aguirre (in prep.). For other textural characteristics, Cuatrecasas (1934) has been followed.

In an earlier study (1978), I presented a summarized inventory of prominent páramo in relation to altitudinal zones. The present study provides more details for both the atmospherical dry and humid side of the Cordillera (Fig. 6), but the "life forms" discussed in the earlier study are now called "growth forms" in agreement with the concepts explained by Barkman (1979). The present author believes, however, that life forms and growth forms in the high tropical mountains cannot be distinctly separated in a satisfactory way. Some authors even do not make distinction between them. Aspects of both growth form (morphological aspects) as well as life form (ecological aspects) are closely interwoven in the plants of these habitats and result in clearly distinct forms. It is a matter of arbitrary emphasis to decide to call it growth form or life form.

In the most fundamental morphological system for waterplants (Luther, 1949) a distinction is made between: 1) haptophytes, 2) rhizophytes, and 3) planophytes (including pleustophytes). Den Hartog & Segal (1964) is followed for outlining growth forms of vascular species in aquatic environment. Their system is based on that of Du Rietz (1921, 1930) and Luther (1949), and is worked out here for rhizophytes and pleustophytes. In absence of Podostemonaceae in our study area, haptophytes are only represented by benthic algae and bryophytes.
In the páramo belt have been recognized:
- rhizophytes:
  1) isoetids: *Isoetes* spp., *Limosella australis*

2) elodeids: *Potamogeton* spp.
3) myriophyllids: *Myriophyllum elatinoides*
4) callitricheids is used instead of batrachiids, because native species of *Ranunculus* subg. *Batrachium* are virtually absent in the Neotropics. Species of *Callitriche*, *Hydrocotyle ranunculoides* and *Elatine* cf *chilensis* may belong to this group. Species of the two last genera are also named amphiphytes by Iversen (1936).

- pleustophytes:
1) ceratophyllids: *Utricularia obtusa* is the only species belonging to this group. (*Ceratophyllum* is absent in neotropical waterbodies).
2) lemnids: *Lemna minor, Azolla filiculoides.*

The relation to the environmental conditions is also expressed by such terms as amphiphytes, helophytes and pleustophytes, which are also used in this paper.

Physiognomical systems for defining páramo vegetation, e.g. by Fosberg (1967) and Mueller-Dombois & Ellenberg (1974), will be worked out in future studies. An example of zonal lower páramo vegetation was given by Sturm (1978). Following Raunkiaer's plant life forms (in the revised version of Ellenberg & Mueller-Dombois 1967) Sturm developed spectra for the Monserrate páramo at about 3230 m above Bogotá: zonal dwarfshrub páramo is dominated by (sclero-)nanophanerophyta, and the lower grasspáramo by caespitosa hemicryptophyta. Rosette species (nanophanerophyta) are prominent with a cover of 20-30%. Macrophanerophytes, geophytes, therophytes and thallophytes are scarce or absent.

Páramo fauna

An excellent general outline regarding the páramo fauna was recently published by Sturm (1978). It will not be attempted to list all species of animals in the study area, but a short outline of the most conspicuous groups will be given.

Tropical American grasslands only support few endemic grazing vertebrat in comparison with those in tropical Africa. This also applies to the páramo belt of the study area, in which only two large herbivorous species of deer are known: *Odocoileus virginianus goudotii* Gayl & Gervais ("venado grande") and *Mazama rufina bricenii* Thomas ("venado soche"). These species are being hunted, and they have become rather scarce.

Bears (*Tremarctos ornatus* (F. Cuvier)) mainly enter the páramos in the dry season. Their diet here consists of the soft parts of bromeliaceous rosettes of *Puya* and *Greigia*. Another, but common omnivorous species hiding on screes and other rocky areas is *Nasuella olivaceae* (Gray), known as "guache" (Cundinamarca/ Meta or "tinajo" (Boyacá). This raccoon species was observed up to the boundary of the lower superpáramo at 4300 m in the Sierra Nevada del Cocuy.

Small grazing vertebrates with a distinct impact on the páramo vegetation are common, e.g. the rodents as *Sylvilagus brasiliensis meridensis* Thomas ("conejo") and *Cavia porcellus anolaimae* J.A. Allen ("curí"). *Sylvilagus* is present everywhere up to 4600 m, judging from the excrements. *Cavia* is mainly restricted to páramo mires and *Sphagnum* bogs, where it forages mainly on sedges. *Cavia* is found between 2000 and 3800 m. Another rodent, *Stictomys taczanowskii* Thomas ("borugo" or "lapa") has only been observed in the lower pármos.

Among the avifauna may be mentioned ducks, snipes, hummingbirds, and birds of prey (Olivares 1969, 1973). Ducks (*Anas* spp.) are common on the large páramo lakes, but generally in small numbers. Humming birds (Trochilidae) are present throughout the páramo belt up to 4300 m. They are common in shrubby páramo

*) Data on vertebrates were kindly provided by Dr. Jorge Hernandez Camacho, head of the research division of INDERENA, Bogotá.

vegetation, visiting the flowers of *Espeletia, Senecio, Pyua, Castilleja* and the red flowering species of *Bartsia*. It is possible that pollination of the purple-reddish and the yellow-greenish species of *Bartsia* is different. Reddish flowering sprecies of *Bartsia* pollinated by the hummingbird, seem to be predominant on the clouded side of the mountains, whereas mainly insect pollinated green-yellowish flowering species are predominant in the dry bunchgrass páramos Hedberg et al. (1979, 1980) studied the yellow and white to pink flowering species of *Bartsia* in the afro-alpine flora, but made no reference to bird pollination.

Snakes are reported by Sturm (1978) from the subpáramo. Lizard species are common in the atmospherical dry páramos up to about 4300 m. They are scarce in the bamboo páramos, however.

Amphibians are common except in the superpáramo; they are found in bogs, mires and on other humid and wet ground. They hide in rosettes of Bromeliaceae, in shrubs, under tussocks and in the dense mantle of marcescent dry leaves of the Espeletiinae.

In many páramos the trout, *Salmo gairdnerii*, has been introduced. The effect of the presence of trouts on the páramo freshwater ecosystem is unknown (to the author).

Gastropods, especially Bulimulidae, are common in the zonal grass páramo, especially on humid thin soil (community 13[a]). Breure (1976 and pers.comm.) supposes that they feed on raw litter. *Plekocheilus (Aeropictus) succinoides* (Petit) is the most common species in the study area. According to Breure (1976) the ssp. *succinoides* is found from the Sabana de Bogotá (2600 m) up to about 3600 m, and the ssp. *cleeforum* in the high bamboo-bunchgrass páramo between 3800 and 4000 m in the Páramo de Sumapaz. Species of Bulimulidae were recently also collected up to about 4400 m in the humid lower superpáramo (Breure & Eskens, in press; ECOANDES report 1980, in prep.). Small fresh-water bivalves are common in páramo lakes, in mire and under flush vegetation. Specimens were identified as *Sphaerium lauricochae* Philippi (det. J.G.J. Kuijper). Previously they were only known from high Andean lakes in Bolivia and Peru. Aquatic fauna further includes species of *Gammarus* and Hirudinae (leeches), which are common up to 4400 m.

Butterflies are common in the páramos of the study area, but most of them are small and inconspicuous, except for *Eupyra ducalis* Maassen (det. Dr. R. de Jong, Leiden), which was commonly observed on the disc flowers of *Espeletia* spp. together with bumblebees.

Ants (Formicoidea) only have been observed in the lowermost páramos mainly on the dry side of the mountains.

Grasshoppers (Orthoptera) are locally common up to higher areas. Native species of cockroaches (Blattoidea, *Dysdercus*) are common under stones and boulders up to 4500 m, together with small black beetles (Carabidae). The ecology of insects in alpine environments was studied by Mani (1962) and Franz (1980), and their conclusions may also apply to the study area. Worms (Lumbricidae) are common in humid páramo soils up to 4300 m. According to Sturm (1978) they are less important to the páramo ecosystem than they are to ecosystems in temperate areas. Among the mesofauna, Enchytraeidae are apparently most active in humic páramo soils.

Interesting studies on the ecology of the páramo fauna in the study area, especially of invertebrates, were recently made by Sturm (1978, 1979) and Rangel & Bernal (1980). Janzen et al. (1976) studied insects by means of sweep samples along elevational transects in Venezuela and Costa Rica.

Land use and human impact

Shifting cultivation frequently in combination with stock farming is most common in the pâramos of the study area. Most of these agricultural activities are concentrated on the dry side of the mountains. The other side is less densely populated due to the high humidity. Most ranches ("finca/finquita ") are located in the subpâramo, and they are of subeconomic size. The farmers, mainly from indian descendence, are very poor. The way in which they are selfsupporting is impressive and deserves respect. Partly, as a result of their struggle for existence, native pâramo shrub and timberline forests disappear at an alarming speed. Native timber (e.g. *Polylepis*) is used for the construction of fenceposts, for ranches and as fuel. The walls of the highest located small ranches are still made from *Espeletia*-stems (e.g. *Espeletia lopezii*, *E. grandiflora*) and these are thatched with *Calamagrostis effusa* bunches. The highest dwellings just reach the lower grasspâramo at 3500-3550 m, but on the dry side of the Sierra Nevada del Cocuy they are found locally up to 3950 m. This is exceptional for the Cordillera Oriental, but common in the Cordillera Central, e.g. in the Parque Los Nevados. Large-scale habitation and agricultural activities in the lower pâramos are of recent time, and are believed to have begun after the arrival of the conquistadores.

Originally, and before the Conquest, most of the study area belonged to the territory of the Chibchas. The Laches and Tunebos tribes controlled the northern part of the study area; the latter still live here. The Sutagaos lived in the Pâramo de Sumapaz. According to Dr. G. Correal-U. (pers. comm.), in pre-Colombian times the natives visited the highest peaks only to bury their prominent dead. Legends are related to sacred places as the Lagunas de Siecha in the Pâramo de Palacio and the Filo Sitiales in the Pâramo de Sumapaz. The names of these pâramos indicate the nearness to heaven.

With regard to crop and herding, some remarks will be made with respect to the impact of these activities on the vegetation of the study area. The main crop is potatoes, with two crops per year. One of the products are the delicious small tubercules of the race "papa criolla". Onions, *Tropaeolum tuberosum* R. & P. ("cûbios"), *Oxalis tuberosa* Savign.("îbias") and aromatic weeds are grown too. Tubers are the most important food source for all Andean people (Barclay 1962, Murra 1979, Wagner 1979, Troll 1968). Chuñu, a technique to preserve tubers by dehydration, as practized on the Peruvian and Bolivian altiplano is not applied in the study area. In the atmospherically driest lowermost pâramos wheat is grown. According to Notestein & King (1930) wheat grows up to 3700 m, and potatoes and onions up to 4200 m.

The cycle in shifting cultivation seems to take about 6-7 years in the lower pâramo, and is dependant on the recourses of the peasant. After burning and ploughing the original pâramo vegetation, potatoes are planted. After the harvest, the soil is left fallow; regeneration to pâramo vegetation starts with *Rumex acetosella* L., later followed by other species. In the following years the number of species increases. After a few years *Hypericum juniperinum* shrub replaces the initial *Rumex acetosella* in some places. In the final stage, the number of species slowly decreases when the area is invaded by Espeletiinae and bunchgrasses.

Cattle, horses, donkeys and sheep were introduced by the Spaniards. Camellidae (*Lama*, *Vicuña*) thriving in the puna of Peru and Bolivia are absent in the study area. Sheep are locally common in dry pâramos up to 4500 m whereas cattle, horses and mules may be found moving freely in many pâramos. Most of the plant cover in the wetter and steeper places is undisturbed, as in the whole superpâramo.

In the dry season the pâramo vegetation may be set afire to stimulate regrowth of tussocks and bamboos, which are preferred by cattle. Burning caused by lightning is a rare event and has never been observed during the field survey.

Recuperation of the vegetation after fire takes years, as was demonstrated by Janzen (1973) for subpáramo bush and bamboos in Costa Rica. Growth of *Espeletia grandiflora* was determined by Sturm (1978) at 3,5-3,9 cm/year. Tussocks, rosette plants and bamboos are well adapted to damage by occasional fire. Further data on the effect of fire on páramo vegetation are scarce. Most research on the impact of fire on neotropical grasslands was carried out in savannas (e.g. San José & Medina 1975).

Growth of páramo plants is marked by low speed. Primary production in páramo vegetation is low, as is the case in all high mountains in the world. Cardozo & Schnetter (1976) estimated production equal or higher than in temperate areas, but their study concerned the lower part of the páramo belt. Decomposition is also slow due to low temperatures, a humid climate and absence of larger decomposer insects as ants, termites and wood-boring beetles.

As a result of repeated burning and overgrazing, tussocks and bamboos disappear, leaving a low herbaceous mat, with short grasses (*Agrostis trichodes A.* spp., *Paspalum bonplandianum*), rosaceous species (*Lachemilla* spp., *Acaena* spp.) and other low herbs (*Eryngium humile, E. humboldtii, Bidens triplinervia, Hypochoeris sessiliflora, Siegesbeckia orientalis, Jaegeria hirta,* etc.). Alien species may be found also, simply as a result of the intense and diverse impact on the land. Frequent species are *Holcus lanatus L., Digitalis purpurea L., Rumex acetosella L., Juncus effusus L., Anthoxanthum odoratum L., Gnaphalium purpureum L., Rumex obtusifolius L., Achillea millefolium L., Ulex europaeus L.,* etc. (Over-)grazing, manuring, trampling and burning due to extensive, and locally intensive farming is most common in the lowermost (bunchgrass) páramos. This mismanagement of the páramo vegetation has its effect on the water supply of lower areas. The páramo belt is indispensable for the water supply (drink-water, irrigation) of the lower areas (Guhl 1968), especially the bamboo páramo. Schnetter et al. (1976) demonstrated that the watercapacity of (azonal) *Diplostephium revolutum* shrub is at least 12x more than in a *Calamagrostis effusa-Spiranthes vaginata* community. In the Cordillera Oriental for instance, the subandean and andean forest belt has the densest population, which depends on fresh water from the páramo belt. In combination with some agricultural activities, obtaining and storing drinkwater is the most important use of the páramo belt. The conservation of the natural páramo vegetation and an optimal management is the first condition for maintaining reliable water resources.

As native fish species are almost absent in the páramo belt trouts (*Salmon gairdnerii*) have been introduced in many places. They have moved to other páramo lakes and streams and multiply rapidly. They provide an excellent source of protein rich food for the páramo peasants. Superpáramo lakes and lakes surrounded by deep bamboo-*Sphagnum* bogs apparently are not or less suitable for trouts.

Mining is fortunately restricted, e.g. limestone in the Páramo de Palacio for cement. It is recommended that areas of high biological and environmental importance (e.g. Sierra Nevada del Cocuy and the calcareous peaks of the Nevado de Sumapaz, Almorzadero, Farallones de Medina, Tamá) should be spared as much as possible and that INDERENA (the Colombian National Institute for the development of the renewal of natural resources and envinronment) will continue to develop an active policy for establishing National Parks.

General data on the ecology in the páramo and puna were provided by Barclay (1962), Murra (1979) and Flores-Ochoa (1979); by Wagner (1979) for the Venezuelan Mérida páramos. Ellenberg (1979) provided an interesting outline of man-made ecosystem succession and land use in the Ecuadorian and Peruvian Andes.

Evolution and Quaternary history of páramo climate and vegetation

The evolution of flora and vegetation of the high Tropical Andean páramo ecosystems has recently been reviewed by Van der Hammen & Cleef (in press), on the basis of information obtained in the Colombian Cordillera Oriental, a key area for the páramos in the northern Andes. A general outline of that study will be presented here. In addition, some new pollendiagrams (to be published in the near future), covering the Late Glacial and Holocene history of the Páramo de Sumapaz, will be briefly discussed. This large high páramo extends to about 150 km S of Bogotá and was previously not included in palynological studies by Van der Hammen and coworkers.

The very origin of the páramo flora and vegetation lays in the Tertiary, when a non-forest vegetation covered hilly, tropical lowland and low mountains with some kind of upland savanna. Savannas are very old, the upland savannas must have been present at least in non-zonal habitats on the Venezuelan Tepuis, at that time possibly the only high mountains in northern S. America. In lower areas these upland savannas mainly contained local tropical elements, especially those which still are common in open savanna and savanna bush. The Tepuian and Amazonian savannas, at present with a limited distribution depending on the presence of special edaphic conditions, stand out by a number of endemic plant taxa. This indicates their long existence under repeated or permanent isolation by neotropical forests (Steyermark 1966, Huber 1978, Schultes 1944, Van der Hammen 1974). Phytogeographic analysis of the modern páramo flora show that the Tepuis hardly contributed to its present composition.

The Tertiary tropandean hills and low mountains thus were gradually covered by local savanna and forest species from the surrounding lowlands. It is supposed that open vegetation persisted locally on the rising Andean mountains. Such patches on hilltops or ridges are determined by edaphic factors, whereas zonal open vegetation may be caused by local arid climate. Even today natural (half-) open vegetation is found under such special conditions in the Andean forest belt. This is confirmed by a number of vascular páramo taxa of the (neo)tropical element growing in lowland savannas. Tropical plants in these uplifted "prepáramo" habitats became adapted to lower temperatures, and forest species to open environment. This is suggested by the pollendiagram Tequendama (probably Lower Pliocene) from the Tilatá formation on the present high plain of Bogotá (Van der Hammen, et al. 1973).

Essential for adaptation of plantspecies to lower temperatures is the crossing over the lower nightfrost line, today reaching down to about 2200-2300 m. The "proto-páramo" developed somewhere above the nightfrost line since the Middle Pliocene and contained Compositae and Gramineae. Among the oldest elements in the proto-páramo are *Valeriana, Plantago, Myriophyllum, Polylepis, Aragoa,* Ericaceae, *Symplocos, Myrica, Miconia, Ilex,* cf. *Hydrocotyle, Jamesonia, Hymenophyllum* and *Hypericum*. Also recorded were: *Myrica, Polygonum, Borreria* and *Jussiaea (Ludwigia)*, taxa which at present only just reach the lowermost limit of the páramo belt. Their presence indicates higher annual mean temperatures in the lower parts of the proto-páramo. *Valeriana,* Ranunculaceae, *Myrica* are northern immigrants; *Hydrocotyle, Myriophyllum* and *Plantago* entered from the adjacent southern Andean mountains. The other taxa largely originated in local tropical or gondwanic areas.

During the Early Pleistocene, between about 3.5 and 1 million years ago, new taxa became added, e.g. Caryophyllaceae, *Geranium, Lycopodium, Isoetes,* and *Sphagnum*, later followed by *Gentianella (G. corymbosa* type*), Lysipomia,* and *Acaulimalva,* nearly all of allochtonous origin. Meanwhile, the forest line moved to a higher position, thus enclosing a páramo belt with a vascular flora that begins to resemble the present one in composition. As from the Middle and Upper Pleistocene some 15 to 20 major glacial/interglacial cycles - palynologically determined - must have had a strong influence on the evolution and speciation of flora and fauna. Depending on the climate the Pleistocenic upper forest line moved from low (10% of the time) and intermediate (40%) positions up to the same or locally higher (50%) level than at present. Moderate temperatures and high humidity alternated with low temperatures and low humidities, and due to the upward moving upper forestline and snowline the former páramo ecosystems never seem to have reached complete stability (Van der Hammen 1979[b]). The Cocuy island (including for half of the total time mentioned the Almorzadero, S. Urbán and Romeral páramos) has never been in direct contact with the southern Sumapaz island. Distribution and speciation patterns of modern páramo plants reflect this separation, and speciation in isolation continues here up till now (Van der Hammen & Cleef, in press).

More information is available on the history of Last- and Late Glacial times (Van der Hammen & González 1960, Van Geel & Van der Hammen 1973, Schreve-Brinkman 1978, Van der Hammen 1979). Between 44,000 and 21,000 B.P., during the maximum extension of the Cocuy glaciers, *Polylepis quadrijuga* forests were abundantly present near Lake Fúquene (2650 m). This humid period was followed by a dry and colder bunchgrass páramo phase, which lasted up to 14,000 B.P. The *Ditricho-Isoetion* in the Last Glacial Lake Fúquene was replaced in the Holocene by *Potametea* communities. In the cold and arid last phase of the Upper Pleni-Glacial, the drying-out lake must have been bordered by high sedge communities belonging to the *Galio-Gratiolion*. In the same interval Cyperaceae were also present on the Laguna Ciega (3500 m) on the W slope of the Sierra Nevada del Cocuy (Van der Hammen et al. 1981).
The Late Glacial climate became warmer and wetter, and was interruped by the Ciega and the El Abra stadials.

During the Andean pollenzones V and VI, corresponding to the European Boreal and Atlantic (7500-5000 BP), the páramos of the study area were smaller than today as a result of slightly higher forest line. The climate became colder again in the Andean pollenzone VIII (corresponding to the European Subatlantic), the humidity increased and the páramo-forest line moved to its present position. This movement was only interrupted by the Neoglacial period in recent time, which may have caused local changes of the vegetation. Pollendiagrams reflecting Late Glacial and Holocene conditions in the study area were published for the Páramo de Palacio (Van der Hammen & González, 1960[b]), the Páramo de Guantiva (Van der Hammen 1962, Van der Hammen & González 1965) and the Sierra Nevada del Cocuy (González et al. 1965, Van der Hammen et al. 1981).

During the present survey in the Páramo de Sumapaz a number of sections were sampled in transect 8 (Fig. 2) running E-W across the Nevado de Sumapaz; El Triangulo (4100 m), the Laguna La Guitarra (3425 m), the Laguna La Primavera (3550 m), the watershed at Cuchilla La Rabona (4000 m), Andabobos (3750 m) and the Laguna Gobernador (3800 m). Mr. L. Carvajal (Bogotá) and Mr. S. Villalba (Lagunitas, Sumapaz) assisted with the sampling in the Páramo de Sumapaz. Pollen analyses were carried out by Mr. G. Noldus (La Primavera, El Triangulo, La Rabona), Mr. J. Martinez-Rea (Andabobos), Mrs. A. Meier & Mr. M. Lebouille (La Guitarra) and Mr. G.B.A. van Reenen (Gobernador). Mr. H. Hooghiemstra rendered assistence in pollen identification.
Publication of the Sumapaz pollendiagrams is planned for the near future.

Evidence of the Late Glacial is present in the lake sections of Andabobos and Gobernador. During the El Abra stadial (11,000-10,000/9500 B.P.) both lakes were located in open grass páramo just as today. As from the time of Andean pollenzone V (corresponding to the European Boreal) Compositae and *Hypericum* subpáramo thickets extended upslope while the upper forest line continued to move upward. The Andean pollenzone VIa (corresponding to the European early Atlanticum) was warmer than at present, but there is no evidence that both lakes on the W slope and the Laguna La Primavera on the E slope were ever reached by the upward moving humid Andean forest, principally made up of *Weinmannia*, *Alchornea*, Melastomataceae and palms, probably *Ceroxylon*. An apparently colder interval is dated at 6290 ($\pm$ 70) B.P. (GrN-9333 - Col 274), and was named the Sitiales phase

(Fig. 7). Later, this was followed by a general amelioration of the climate and an increase of the subpâramo shrub and/or dwarfforests with *Hypericum* (probably *H. laricifolium*, Compositae (probably *Gynoxys*, *Ageratina*, *Diplostephium*, *Senecio*) and Ericaceae (probably *Gaultheria ramosissima*, *Vaccinium floribundum*) enclosing the hills bordering these lakes.

The early part of a cold phase is dated at 4700 (± 150) BP (GrN-9331 - Col 272) in the Laguna La Primavera, a date very near to the European Atlantic-Subboreal boundary. As from that time the pâramo climate became colder and the possible combination with an increased humidity caused the open pâramo to replace the forest line shrubs. *Plantago rigida* cushion bogs began to develop in the highest parts (Cuchilla La Rabona; 5090 ± 25 BP. (GrN 8457 - Col 266)) and *Sphagnum* bogs in the lower part of the pâramo belt. There is ample evidence now that the development of most pâramo bogs started about 5,000 years ago. Some *Hypericum* and composite shrub was in the vicinity of the Laguna La Primavera. From the base of zone VIII corresponding to the European Subatlantic onwards, dated at 2920 (± 130) BP (GrN-9332 - Col 273) the climate became definitely colder and wetter in de Laguna La Primavera area and approached present conditions. Open zonal grass pâramo probably containing bamboos (*Swallenochloa*), largely determined the aspect up to recent time. In the lake La Primavera the *Ditricho-Isoetion* developed again (*Isoetes andicola*, *I. karstenii*, *I. palmeri*, *I. glacialis* are found at present).

The stability of the vegetation, especially in the high pâramos, was again affected by the Neoglacial, the Little Ice Age; c. 1500-1800 A.D. Superpâramo moraines of the Corralitos stade mark the Neoglacial ice extension in the Sierra Nevada del Cocuy. Such moraines have not been observed on the steep slopes of the Nevado de Sumapaz (c. 4250 m). Palynological indications, however, of the nearby melting ice are found in the pollendiagram El Triangulo, based on the analysis of submerged lake sediments under the *Isoetetum karstenii* (rel. 271). The lower part of the diagram apparently represents upper superpâramo conditions with Caryophyllaceae and species of *Draba*. After a *Hedyosmum* pioneer phase, the upper Andean forest rapidly returned to its present location and composition. The site is simultaneously reached by composite shrub of the lower superpâramo line (*Senecio vernicosus*, *Loricaria complanata*). *Plantago rigida*, *Gentiana sedifolia* and *Hypericum lancioides* indicate the establishment of the perhumid upper condensation belt on this peak.

MATERIAL AND METHODS

General concepts

For the main goal of the present study - to present an inventory description of the modern vegetation of the pâramos of the Colombian Cordillera oriental - the Zürich-Montpellier method of phytosociology has been applied, however, with some slight adaptations that will be discussed later.

Vegetation study according to the Zürich-Montpellier method includes sampling of representative homogeneous (in composition and structure) stands of a certain minimum size for similar and different vegetation types. The plots are usually selected on physiognomic and floristic criteria throughout the study area. Sampling was carried out at different elevations and in different cross-sections of the pâramo belt of the study area. The large number of relevés reduces the subjective element in the synthetic procedure. Heterogeneous plots were avoided (see Werger 1973).
For the present study a relevé included: 1) making an inventory of all plant species, except inconspicuous terrestric algae, microlichens and fungi, and 2) estimating the percentage of (canopy) cover for each species.
The relevés are presented in tables in the usual phytosociological way, which allows the recognition of vegetation units. The units or vegetation types are ranked in a hierarchic system, based on floristic criteria. Only in cases where the vegetation was exceptionally poor in species, additional ecological criteria have been used. The Zürich-Montpellier method was used, because reliable results have been obtained using this method in other parts of the world. In the tropics, this method has mainly been applied to open or semi-open tropical vegetation (e.g. Duvigneaud 1949, Van Donselaar 1965, Werger 1973, Van Zinderen Bakker & Werger 1974, Ruthsatz 1977). Whether the Zürich-Montpellier method can be applied to open or semi-open tropical vegetation is no longer relevant. Remains the discussion whether this approach is suitable for zonal tropical forests with their complex structure and their abundance of species (Van Donselaar 1965). Few examples of the classification of zonal tropical forests are available (Schnell 1952, Mullenders 1954; Schmitz 1962, 1971; Sprangers & Bulasubramanian 1978; Van der Werff 1978).The present author agrees with Werger (1977),that a reliable floristic classification of zonal tropical primary forests according to the Zürich-Montpellier principles is well possible. This is based on the results of the first preliminary tables for the ECOANDES transect studies in zonal forests along slopes in the Colombian Andes (Van der Hammen & Jaramillo, in prep.; Rangel et al., in prep.; Cleef, unpubl.).
Technical descriptions of the Zürich-Montpellier approach of phytosociology were provided by Braun-Blanquet (1964), Mueller-Dombois & Ellenberg (1974), Werger (1973, 1974) and Westhoff & Van der Maarel (1973).

Although many azonal pâramo communities are dominated by one species, their definition is entirely determined according to the Zürich-Montpellier approach. In Europe simply structured communities are often studied according to the methods of the Scandinavian (Uppsala) School. In this study these methods have not been considered, however, since throughout the Zürich-Montpellier approach was found to give satisfactory results as regards the classification of the communities.

Field methods and materials

Thorough knowledge of the flora is indispensable for any botanical

environmental study, especially for vegetation studies according to floristic principles. In absence of flora works for the study area collection of every unknown species in relevés is the only way to solve the identification problems of inventoried taxa. After a short training in the taxonomy of Colombian bryophytes in Utrecht by the late Dr. P.A. Florschütz and Dr. S.R. Gradstein, Dr. R. Jaramillo M. introduced the author in the vascular páramo flora near Bogotá in November and December 1971. Additional pertinent information was further provided by staff members of the Instituto de Ciencias Naturales headed by Dr. A. Fernandez-Pérez at that time.
Relevés (records or sample plots) of the páramo vegetation were gathered in a number of E-W running cross-sections or transects through the study area (Fig. 2).
These transects are located in (from N to S):
1) Páramo del Almorzadero
2) Sierra Nevada del Cocuy
3) Páramo de Guantiva (southern part) -Páramo de Pisva - Chita
4) Páramo de la Rusia - Páramos de Tota - Vado Hondo/Peña de Arnical
5) Páramos NW of Neusa - Páramo de Palacio - Guasca - Chuza.
6) Páramo de Cruz Verde
7) Páramo de Chisacá
8) Páramo de Sumapaz: S. Juan - la Rabona - Nevado de Sumapaz.
It was attempted to cover both the humid and the dry sides of the Cordillera. Usually vegetation studies were conducted near the upper forestline, at middle elevations in the grasspáramo and in the reaches of the highest (snowcapped) peaks. Some of the selected cross sections (e.g. 3,4,5) continue downslope with transects (no. 13,14,15 in Grabandt 1980) of previous studies of the Andean forests on slopes and foothills conducted in 1967 by Prof. Dr. Th. van der Hammen and Dr. R. Jaramillo Mejía (in prep.). Mrs. R.A.J. Grabandt (in prep.) presently studies the relationship between recent pollenrain and páramo vegetation in the eight selected páramo transects.

For general transport a Nissan jeep (4 wheel drive) was used as far as conditions allowed. Further transport to the selected campsites was on horseback or just by walking. Camp equipment, plant collections and other sampled materials were transported by mules. Usually the jeep driver and a local guid accompanied the expedition. Only two small sleeping tents (type Capriola, Slee BV, Utrecht) were used and a small shelter for storing food and kitchen tools.
Elevation was determined by aneroid reading of a Thommen (0-5000/6000 m) altimeter. Altitudes were regularly checked at the Instituto Geográfico "Agustín Codazzi" (2560 m), Bogotá and also by other points of known altitude according to official topographic maps. The mean daily variation of elevation according to the altimeter for a given site in the páramo belt amounts to about 35 m (exceptionally up to 50 m) and was occasionally also recorded by a barograph. The compass (Bézard model UBK/3, Lufft G.m.b.H., Stuttgart) used included a clinometer. The topographic base maps (1:25.000 and 1:100.000) were obtained from the Instituto Geográfico "Agustín Codazzi". Aerial photographs of the selected expedition areas were studied before leaving, especially from areas not yet covered by maps. Botanical collections were preserved during the evening and stored in plant presses (vascular species) or in aluminium boxes. The drying process was later performed in the Instituto de Ciencias Naturales in Bogotá.
About 600 relevés of páramo vegetation were gathered in the study area during 1971-73 and later during short visits in 1977 and 1978. The original reference numbers of the relevés are used. Nearly all plot areas 1 - 424 were almost completely inventoried, making botanical collections of nearly all unknown species (reference number Cleef et al. 1-10.430). Vouchers are deposited in COL (completely) and U. In most cases specimens were also deposited in local herbaria by residing specialists, which are summed up later.
The sample plots were layed out in open páramo vegetation of different

physiography and included open zonal and azonal habitats as defined by Walter (1954) and Mueller-Dombois & Ellenberg (1974). The term zonal vegetation is interpreted here in its widest sense and comprises mesic to xeric habitats on level and sloping ground at the base or on tops of slopes. Minimal area and plot size were tested out during 1971 in some communities of the zonal and azonal páramo vegetation near Bogotá. In general the plot size used in the present study was strongly dependent on the structure of the vegetation and agrees roughly with values summarized in Westhoff & Van der Maarel (1973, table I) and Vareschi (1989). All plots selected were square or rectangular in shape. When all plant species present in the sample plot were recorded, part of them with their reference number, the canopy cover in % was estimated for each species by taking its global circumference as limit. As a rule lower values generally result of estimating the real cover of each plant species. But this is an almost impossible, time consuming task, which is hardly worthwhile, especially when the phytosociological survey covers a large area in a semi--detailed way as in the case of the present study area, which ranges over 10,000 km^2. In dense spherical shaped, lepto- or nanophyllous shrub or in dense bunch grassland differences between canopy cover and real cover are hardly existing. In rare hypericaceous shrub (e.g. *Hypericum lancioides*, *H. trianae*, etc.) or isoetid vegetation (e.g. *Isoetetum karstenii typicum*) real cover may be about half of the canopy cover. In general terms estimates of canopy cover obviously are usually somewhat higher than real cover. The discrepancy between these two parameters is strongly determined by species--bound characteristics like leaf-form and -size, leaf-packing and canopy arrangement. On the other hand environmental variables, which are site-determined also have their impact on this, so that the ratio between canopy and real cover may differ between the populations of one species growing on different sites. Cover was estimated for all species together forming vegetation layer i.e. the total cover estimated for the relevé may in that case amount to more than 100%. Obviously the total canopy cover in one stratum however was never more than 100%, even though species may have interlocking canopies. This holds for each layer. Mainly because of further mathematic elaboration of data for e.g. studies on recent pollendeposition and its relation with fossil evidence, the canopy cover of each of the"modern"species was estimated in % as accurate as possible. Between about 20 and 80% however, cover was estimated in intervals of 5% (e.g. 20 - 25 - 30 - (33 1/3) - 35 - 40 - 45 etc.), since it is extremely difficult to establish more exact values in this traject. Cover of less than 1% was listed as " 1". For the sake of comparison it seems an advantage that all records were made by the same investigator.

Abundance was estimated only when cover was less than 5%, and usually less than 1%. Presence of numerous specimens of a given species is indicated by adding a "+" to the cover %. Sociability was not recorded. Cover values recorded in this way may be easily translated in any phytosociological scale and further worked up in quantitative studies. Airborn pollen was gathered in about 400 relevés by collecting some 10-15 random samples of the bryophyte layer (or upper soil layer in lake and ponds). These are currently under study (Grabandt, in prep.).

A number of additional observations was made in each sample plot. Recorded were cover (in %) and height (in cm/m) of main constituing"growth forms": e.g. shrub, herbs, grasses, bamboos, stemrosettes, bryophytes, lichens and algae. Further the approximate size of the whole phytocoenosis sampled was estimated and if time allowed a line transect of this and adjacent vegetation was surveyed and depicted. Such drawings contribute to knowledge about borders in vegetation and visualize structure and (in part) texture characters of the vegetation type(s) under study.

The actual phreatic level, the presence or temporarily absence of lateral water supply or depth of the standing waterbody were recorded. Soil depth, texture and thickness of the various layers were determined with an 1.20 m auger. Soil colors

were noted according to the "Revised Standord Color Charts" (Japan). pH was measured; if not otherwise indicated, pH values always refer to the upper, mostly humic soil layer at about 10 cm depth. They were measured by Mieke Cleef--van Rens using an electrometric equipment Metrohm. pH records of water are marked are marked an asterisk *). About 1-20 cc soil sample was left in suspension in distilled water, up to 50 cc, during approximately 24 hours and measured after stirring. The suspensions were measured after 48, 72 and 96 hours. Samples mostly showed a slight decrease of acidity with time. The measurements, also applied in soil samples from the Buritaca transect in the Sierra Nevada de S. Marta, seem to be reliable as they agree well with measurements according to international standards by the Laboratory of Physical Geography and Soil Science of the University of Amsterdam carried out 1-2 months later. Only occasionally pH values were determined along the whole soil profile. A sample of the upper soil layer (0-20 cm) of each relevé is in store and will be used for determination of grain size, organic content and probably some of the bio-elements. These data will contribute to a characterization of the pedological properties of the different páramo plant communities.
Further field data taken concern locality, altitude, physiography, inclination, size of the relevé area, exposition, shadow, drainage, phreatic level, macroscopic (soil) fauna, influence of fauna, fire and man. Mostly also a photo or colorside was taken from the relevés. Vareschi (1980) determined the minimal area for some zonal and azonal phytocoenoses inhabited by Espletiinae in the Venezuelan Andes. Minimal areas applied by me in páramo grassland (25-35 m^2) and in tall shrub (up to 50 m^2) of the study area, agree well with those of Vareschi.

A few zonal and azonal shrub and dwarfforest stands are only briefly treated here, because they will be described elsewhere in more detail. Omitted were all epiphytic and epilithic communities, as well as the plantcover of deep páramo lake bottoms. A number of plants collected in these habitats, however, may give a first glance on the floristic composition of these communities.

Laboratory methods and synthesis

First of all the rich botanical collections exceeding more than 10.000 numbers had to be named. A good number of vascular plants was yet identified by colleagues and the author in the Herbario Nacional Colombiana (COL) at the Instituto de Ciencias Naturales of the Universidad Nacional in Bogotá, which was our base in Colombia. Back at the Utrecht Institute of Systematic Botany numberous unidentified collections were forwarded to specialists in various countries, because floras do not exist for the study area. Determination activities took some years and are still not yet completed. With regard to liverworts and lichens all support towards their identification was given by respectively Dr. S.R. Gradstein and Mr. H.J.M. Sipman. Dr. D. Griffin, III (Gainesville) supported by a visitor's grant of WOTRO, took over general determinations of the mosses from the late Dr. P.A. Florschütz. All colleagues and friends, which gave a consistent support towards identification of the páramo plant collections are alphabetically listed below. Their help is most gratefully acknowledged here. Some 100 new taxa were found; most of them have been published by now.

Ando, H.	HIRO (Hiroshima, Japan)	*Hypnum, Pleurozium*
Balslev, H.	NY/AAU (New York, USA/ Aarhus, Denmark)	Juncaceae
Bell, B.G.	ACHE (Penicuik, Great Brittain)	*Grimmia*
Bicudo, R.M.T.	SP (Sao Paulo, Brazil)	*Nitella*
Buck, W.R.	NY (New York, USA)	Polytrichaceae
Camargo, L.	COL (Bogotá, Colombia)	*Berberis*
Cuatrecasas, J.	US (Washington, USA)	Compositae

Campbell, E.O.	MPN (Palmerston North, New Zealand)	*Marchantia*
Díaz-Piedrahita, S.	COL (Bogotá, Colombia)	Compositae
Dunn, D.B.	UMO (Colombia, USA)	*Lupinus*
Fernandez-Pérez, A.	COL (Bogotá, Colombia)	Orchidaceae, Lentibulariaceae
Florschütz, P.A.	U (Utrecht, Netherlands)	general identification of mosses
Frahm, J.-P.	Frahm (Duisburg, Federal Republic of Germany)	*Campylopus, Chorisodontium, Pilopogon*
Fuchs-Eckert, H.P.	- (Trin-Vitg, Switzerland)	*Isoetes*
Fulford, M.	CINC (Cincinnati, USA)	*Leptoscyphus*
Görts-van Rijn, A.R.A.	U (Utrecht, Netherlands)	*Peperomia, Polygala*
Gradstein, S.R.	U (Utrecht, Netherlands)	general identification of liverworts
Griffin III, D.	FLAS (Gainesville, USA)	general identification of mosses, esp. *Prionodon, Sphagnum*, Bartramiaceae, watermosses
Grolle, R.	JE (Jena, German Democratic Republic)	*Tylimanthus, Cheilolejeunea Neesioscyphus*
Gronde, K. van der	U (Utrecht, Netherlands)	*Jensenia, Symphyogyna*
Haarbrink, J.	U (Utrecht, Netherlands)	*Frullania* subg. *Chonanthelia*
Hale, M.E.	US (Washington D.C., USA)	Parmeliaceae
Harley, R.M.	K (Kew, Great Britain)	Labiatae
't Hart, H.	U (Utrecht, Netherlands)	*Tillaea*
Hawksworth, D.	CMI (Kew, Great Britain)	*Alectoria*
Hofstede, J.W.	U (Utrecht, Netherlands)	*Parietaria*
Holm-Nielsen, L.B.	AAU (Aarhus, Denmark)	*Potamogeton, Lilaea*
Inoue, H.	TNS (Tokyo, Japan)	*Plagiochila, Syzygiella*
Jaramillo Mejía, R.	COL (Bogotá, Colombia)	general identification of Compositae,
Jeppesen, S.	AAU (Aarhus, Denmark)	*Centropogon, Lobelia*
Jermy, A.C. & J.A. Crabbe	BM (London, Great Britain)	*Isoetes*
Jovet-Ast, S.	P (Paris, France)	*Colura*
Kärnefelt, J.	LD (Lund, Sweden)	*Cetraria*
Kastelein, W.J.	U (Utrecht, Netherlands)	*Drymaria*
Kieft, E.G.B.	U (Utrecht, Netherlands)	*Lachemilla*
Kirkbride Jr., J.H.	UB (Brasilia, Brazil)	Rubiaceae
Koyama, T.	NY (New York, USA)	Cyperaceae
Koponen, T. & A.	H (Helsinki, Finland)	*Plagiomnium*, Splachnaceae
Kramer, K.U.	ZSS (Zürich, Switzerland)	Polypodiaceae
Krapovickas, A.	CTES (Corrientes, Argentina)	*Acaulimalva* (in study)
Kuwahara, Y.	- (Fukuoka, Japan)	*Metzgeria*
Kuyt, J.	LEA (Lethbridge, Canada)	Loranthaceae
Leeuwenberg, A.J.M.	WAG (Wageningen, Netherlands)	*Desfontainea*
Lellinger, D.	US (Washington, USA)	*Selaginella*
Loon, J.C. van	U (Utrecht, Netherlands)	*Geranium*
Lourteig, A.	P (Paris, France)	*Ranunculus, Oxalis Limosella; Montia* (in study)
Lowy, B.	- (Bouton Rouge, USA)	*Auricularia, Tremella*
Maas, P.J.M.	U (Utrecht, Netherlands)	*Burmannia, Tofieldia, Orthrosanthus*

Mathias, M.E. & L.E. Constance	UC (Berkeley, USA)	Umbelliferae
Meenks, J.	U (Utrecht, Netherlands	*Riccardia*
Mickel, J.T. & L. Atehortúa	NY (New York, USA)	*Elaphoglossum*
Molau, U.	GB (Göteborg, Sweden)	*Calceolaria*
Moldenke, H.N.	FMH (Plainfield, USA)	*Lantana*, Eriocaulaceae
Mora Oseja, L.E.	COL (Bogotá, Colombia)	*Lilaea*, Cyperaceae, Haloragaceae
Möschl, W.	GZU (Graz, Austria)	*Cerastium*
Murillo, M.T.	COL (Bogotá, Colombia)	Polypodiaceae, *Equisetum*
Ochi, H.	Ochi(Tottori, Japan)	Bryoideae
Øllgaard, B.	AAU (Aarhus, Denmark)	*Lycopodium*
Pinto Escobar, P.	COL (Bogotá, Colombia)	Gramineae
Pócs, T.	EGR (Vácrátót, Hungary)	*Lepidozia*
Ponce de Leon, P.P.	F (Chicago, USA)	*Lycoperdon*
Pringle, J.	HAM (Hamilton, Canada)	*Gentiana, Halenia* (in study)
Punt, W.	U (Utrecht, Netherlands)	Euphorbiaceae
Rahn, K.	C (Copenhagen, Denmark)	*Plantago*
Raven, P.	MO (Saint Louis, USA)	Onagraceae
Ravenna, P.	SGO (Santiago, Chile)	*Sisyrinchium*
Read, R.H.	WIS (Madison, USA)	*Elagine*
Reenen, G.B.A. van	U (Utrecht, Netherlands)	*Herbertus*
Robinson, H.	US (Washington DC, USA)	Eupatorioideae
Robson, N.K.B.	BM (London, Great Britain)	*Hypericum*
Romero-C., R.	COL (Bogotá, Colombia)	*Aragoa*
Simpson, B.B.	TEX (Austin, USA)	*Polylepis*
Sipman, H.J.M.	U (Utrecht, Netherlands)	general identification of lichens, esp. *Cladonia*, Parmeliaceae
Slageren, M. van	U (Utrecht, Netherlands)	*Brachiolejeunea*
Sleumer, H.	L (Leiden, Netherlands)	*Escallonia, Clethra,* Ericaceae
Smith, L.B.	US (Washington DC, USA)	*Xyris, Begonia,* Bromeliaceae (esp. *Puya*)
Soderstrom, T.R.	US (Washington DC, USA)	Gramineae
Takaki, N.	Hb. Takaki (Nagoya, Japan)	*Aongstroemia*
Taylor, P.	K (Kew, Great Britain)	*Utricularia*
Tryon, A.F.	GH (Cambridge, USA)	*Jamesonia*
Turner, B.L.	TEX (Austin, USA)	*Aphanactus*
Uribe U., L.	COL (Bogotá, Colombia)	Melastomataceae
Vána, J.	PRC (Praha, Czechoslovakia)	*Anastrophyllum, Marsupella, Cephalozia, Gymnomitrion, Jungermannia*
Vitikainen, O.	H (Helsinki, Finland)	*Peltigera*
Wasshausen, D.C.	US (Washington DC, USA)	Acanthaceae
Weber, W.A.	COLO (Boulder, USA)	*Carex peucophila*
Westra, L.Y.	U (Utrecht, Netherlands)	Orchidaceae
Wurdack, J.	US (Washington, DC, USA)	Melastomataceae, *Monnina*
Zander, R.H.	BUF (Buffalo, USA)	Pottiaceae

In an early stage a first attempt was made to divide all (about 600) relevés in groups which share similarities in physiognomy, floristics and ecology. The relevé data were worked up as outlined in some technical descriptions of the Zürich-Montpellier approach of vegetation science cited before. Almost all available relevés were included, only few were left out for reasons of obvious heterogeneity. The syntaxonomical part of the present study is based upon about 270 relevés of mainly azonal vegetation. The other relevés, which are grouped in as yet unfinished tables of the vegetation, serve for the description of the zonal "communities" of the páramo vegetation. Formal syntaxonomical accounts and tables will be published in the future.

In the hierarchic system provided here for most of the azonal páramo vegetation the association differs from other associations by the presence of (proper) character species. Subassociations are mainly characterized by two, but usually more differential species. Variants are based on at least one differential species, which in extreme environmental conditions may attain a high cover. If two or sometimes more differential species are reported, they may have low presence and low cover. Units of lower rank are not recognized. Characterspecies are provisionally ranked in this study as exclusive, selective or preferential. The provisional status in the present study is applied because 1) no definite constancy tables are yet published, and 2) it is unknown in which other phytocoenoses character species occur at other latitudes and/or elevations. Diagnostic taxa include character and differential species or taxa. Also constant companions may have diagnostic significance, e.g. *Elatine* cf. *chilensis* in the *Elatino-Juncetum ecuadoriensis* (table 9). As a rule most diagnostic taxa are only (locally or) regionally relevant and identified as such on the basis of the few vegetation studies available from other parts of the Andes. Based on these studies also a few alliance, order and class character species could be identified. Especially with regard to azonal aquatic and boggy communities, which are wide tropical Andean in distribution, it was felt as a disadvantage that the high Andes south of Colombia was not surveyed by the author.
As far as possible the azonal páramo vegetation of the Cordillera Oriental is syntaxonomically ranked on the basis of the relevés available. Excepted are the *Sphagnum* bogs, which here are described as different communities on the basis of raw tables of the vegetation. They are omitted for the moment, because of the fact that the transition of azonal *Sphagnum* bog to zonal bamboo páramo is gradual. Both páramo *Sphagnum* bogs and zonal vegetation will be syntaxonomically treated in forthcoming studies, which will also include presence/constancy tables. Other azonal vegetation units, which were not finally classified, are also described here as "communities", though part of them undoubtedly belong to higher syntaxa described here. Few records, local presence, uncertain (syn-)taxonomical status, or optimal development elsewhere at other elevations or latitudes are some of the different reasons for not classifying them definitely in this paper. It should be emphasized that the term "characteristic species" mentioned under "communities" does not mean the same as "character species". Though, it is believed that most characteristic taxa will prove to be diagnostic taxa when the syntaxonomical classification is completed.
A syntaxon is given a provisional status ("prov.") when

1) its description is based on a single relevé or on
2) uncomplete record(s), or when
3) the identity of (some of) the diagnostic taxa is insufficiently known, or when
4) vegetation studies from other regions of the high tropical Andes might cause a future change in name or delimitation of a given syntaxon (e.g. *Gentiano-Oritrophion* prov., *Wernerietea* prov.).

As regards nomenclature, Barkman et al. (1976) has been followed. These authors do not deal with syntaxa under the rank of subassociation. In this study, however, also a nomenclatural type was assigned to the variant level. In the author's opinion this is a logical consequence of the type method adopted by the Nomenclature Commission of the International Society of Vegetation Science. Nomenclatural types are indicated in the table by symbols:

✱✱✱ type of the class
✱✱ type of the order
✱ type of the alliance
▲ type of the association
○ type of the subassociation
◡ type of the variant

The symbols for the association and subassociation were proposed by Daniëls (1980).

The application of the terms *typicum* and *inops* for subassociations and variants follows Westhoff & Van der Maarel (1973).
Apparently no previous syntaxonomical studies on the Colombian páramos were published. The only ones dealing with páramo vegetation are those of Vareschi (1953, 1955) from Venezuela. Names of páramo syntaxa recently published by the same author (Vareschi 1980) are not valid according to Barkman et al. (1976).
Other syntaxonomical studies in tropical high Andean vegetation include those of Ruthsatz (1977) for the NW Argentinan puna and those of Gutte (1980) on Peruvian vascular cushion bogs and high Andean lakes.
For various countries most useful chorological and ecological information was supplied by the following authors:
Chile: Roivainen (1954), Schmitthüsen (1956), Oberdorfer (1960), Ricardi & Marticorena (1966) and Villagrán (1980);
Argentina: Hunziker (1952), Cabrera (1958), Böcher et al. (1972), Werner (1974) and Ruthsatz (1977);
Bolivia: Herzog (1923) and Collot (1980);
Peru: Weberbauer (1911), Rauh & Falk (1959), Koepcke (1961), Tovar Serpa (1973), Mueller & Mueller (1974), Gutte & Gutte (1976) and Gutte (1980);
Ecuador: Acosta-Solis (1958), Diels (1937), Harling (1979) and Øllgaard & Balslev (1979);
Colombia: Cuatrecasas (1934, 1958 and in litt.), Lozano & Schnetter (1976), Aguirre & Rangel (1976), Fosberg (1944), Sturm (1978) and Rangel et al. (1976);
Venezuela: Aristeguieto & Ramia (1952), Azócar & Monasterio (1979), Farinas (1979), Monasterio (1979), and Vareschi (1953, 1955, 1956, 1958, 1980); and
Costa Rica: Weber (1958).
In addition other useful information was obtained from Beaman (1956), Beaman & Andresen (1966), and Villapanda (1968) on the Mexican high mountains and from Komarková (1979) on the high Colorado Rocky Mountains.

In the tables relevant ecological information is summarized in the heads of these tables. For soil texture the following abbreviations are used: "c" for clay, "s" for sand, "si" for silt, "g" for gravel, "p" for peat and "y" for gyttja. In the descriptions of the communities the word "soil" has been used in a rather wide sense, including proper soils (in the pedological sense), but also the upper layer of the substrate (of the lake sediment or peat) of in lakes, in mires and in bogs, where the plants usually are rooted.
According to the literature pH level of aquatic samples (indicated with an asterisk *) is slightly higher as compared with top soil samples. A relevé marked with an asterisk (*) means, that the survey generally was based on a quick, not complete inventory, usually without botanical collecting. The total number of species refers to the total number of cormophyte species distinguished up till January 1981, when final tables were constructed. Further data given include: date, locality, pH, collection numbers, soil depth (cm), exposition, slope, etc. Most of them are summarized in Appendix 3 or appear in the tables. Páramo plant species are usually cited without the authorities and without the corresponding family. Only for the native vascular species of the study area mentioned in this study, they are provided in a list (Appendix 2); whereas for mosses, liverworts and (macro)lichens reference is made to the recent checklists (Florschütz-de Waard & Florschütz 1979; Gradstein & Hekking 1979 and Sipman & Hekking, in prep.) and their supplements in preparation. Unknown species are listed with the author's collection number.
In the general community and habitat description for slope angle and acidity Daniëls (1980) was followed:

slope	$0-2^o$	flat/level	pH	3.5-4.5	strongly acid
	2^o-4^o	slightly sloping		4.5-5.5	moderately acid
	4^o-8^o	sloping		5.5-6.5	weakly acid
	8^o-15^o	moderately steep		6.5-7.5	neutral
	15^o-30^o	steep			
	30^o	and more very steep			

Boundaries between different pH levels run about parallel to the subdivision of e.g. Ratcliffe (1964). Thus, the upper pH level in oligotrophic environment is at 5.0 (5.5 in aquatic medium), in mesotrophic environment at 6.0 (6.5 in aquatic medium) and in eutrophic conditions from 6.0 onwards.

II. ALTITUDINAL ZONATION AND OUTLINE OF THE ZONAL PARAMO VEGETATION

ALTITUDINAL ZONATION*)

Altitudinal zones of the north Andean páramo vegetation have been described by Cuatrecasas (1934, 1958, 1968), Fosberg (1944) and Cleef (1978, 1979[a]) for Colombia; by Vareschi (1970) and Monasterio (1979) for Venezuela and by Diels (1937), Acosta-Solís (1968), Harling (1979) and Lauer (1979[a,b]) for Ecuador.

The altitudinal sequence of the zones of the zonal páramo vegetation on the atmospherically dry and humid sides of the Colombian Cordillera Oriental will be discussed. The subdivision is mainly based on differences in physiognomy and floristics. Whether the subdivision can be generally applied to the north Andean páramos remains to be determined. In the parque Los Nevados in the Colombian Cordillera Central, a proper subpáramo zone cannot be distinguished (Cleef et al., in press).

Apart from differences in edaphical conditions, the climate is the determining factor for spatial distribution, physiognomy and floristics (at least of the dominant plants) in the altitudinal zones of the recent páramo belt. Accordingly, the slopes facing dry inter andean-valleys or interjacent high plains are atmospherically dry. Slopes above the Amazonian Hylaea, the Orinoco savannes and the deep Magdalena river valley are atmospherically humid. Distinct differences in composition and structure of the Colombian páramo vegetation undoubtedly reflect different macro-climates. For example, "pajonales" dominated by tussocks or bunchgrasses (mainly *Calamagrostis effusa*) are characteristic for the dry side of the mountains. "Chuscales", open bamboo vegetation types (mainly *Swallenochloa* spp.), are predominant on the atmospherically humid slopes. Thus, a b u n c h g r a s s p á r a m o is found on the atmospherically dry side of the Cordillera and a b a m b o o p á r a m o on the atmospherically humid side.

On the basis of physiognomical and floristical criteria, Cuatrecasas (1954, 1958, 1968) subdivided the páramo into 3 altitudinal belts: 1) the subpáramo, 2) the páramo proper ("páramo propiamente dicho") and 3) the superpáramo. His division proved to be useful and has also been applied here. On the basis of our results and with the use of similar criteria a lower and an upper zone could be recognized in each altitudinal belt of the zonal páramo vegetation. These zones will be described for each side of the Cordillera in the order of increasing altitude (Fig. 8).

Atmospherically dry páramo slopes

The l o w e r s u b p á r a m o or s h r u b p á r a m o near the upper forestline carries bushes of Ericaceae, Compositae and Melastomataceae. Common and characteristic genera are: *Befaria, Cavandishia, Macleanea,*

*) An adapted version of this part of the chapter on the altitudinal zones of the páramo vegetation will be published by Van der Hammen & Cleef (in press).

Eupatorium (Ageratina), *Senecio*, *Baccharis* and *Diplostephium*, *Miconia*, *Bucquetia* and *Brachyotum*. *Solanum bogotense*, *Sericotheca argentea*, *Stevia lucida* and *Coriaria ruscifolia* ssp. *microphylla* are common in the transitional zone between forest and pâramo; just as scattered small trees of *Buddleia lindenii*, *Hesperomeles*, *Gynoxys*, *Monnina* and *Rapanea dependens*. Dense thickets of *Myrica parvifolia* are locally frequent.

At higher elevations the vegetation in the u p p e r s u b p â r a m o or d w a r f s h r u b p â r a m o is mainly dominated by rubiaceous dwarfshrubs of *Arcytophyllum nitidum*, accompanied by *Calamagrostis effusa* and other plants from the open grass pâramo. *Gaylussacia buxifolia*, a characteristic ericaeous dwarfshrub, and *Chaetolepis microphylla* are common. Terrestric orchids, e.g. the beautiful salmon-pink flowering *Spiranthes vaginata*, *Altensteinia leucantha*, *A. fimbriata*, as well as *Eupatorium* (= *Lourteigia*) *microphyllum*, *Miconia parvifolia*, *Paepalanthus paramensis* and *Verbesina baccharidea* seem to be restricted to this zone. The last mentioned species grows in rocky places with a thin soil and is associated with small, dense tussocks of *Sporobolus lasiophyllus*.

In the l o w e r zone of the p â r a m o p r o p e r – the l o w e r b u n c h g r a s s p â r a m o – dwarfshrubs generally disappear and are replaced by tussocks or bunches of *Calamagrostis effusa*, which become dominant with increasing altitude. Typical light-requiring plants of the open pâramo, which are also present in the upper subpâramo, are abundant, e.g. *Acaena cylindristachya*, *Azorella* aff. *cuatrecasasii*, *Castratella piloselloides*, *Lobelia tenera*, *Luzula* cf. *racemosa*, *Oreobolus obtusangulus* ssp. *rubrovaginatus* and *Rhynchospora paramorum*. Endemic species of the stemcomposites *Espeletia* and *Espeletiopsis* are undoubtedly the most characteristic components of the grass pâramo.

More or less closed stands of *Calamagrostis effusa* bunches make up the zonal plant cover in the u p p e r zone of the p â r a m o p r o p e r, the so-called u p p e r b u n c h g r a s s p â r a m o. Towards the upper part of this zone the grass cover is less and only few tussocks are found at the superpâramo border. Conspicuous in this zone are species of the Espeletiinae and *Hypericum selaginoides*, *Jamesonia bogotensis*, *Paepalanthus lodiculoides* var. *floccosus*, *Stephaniella paraphyllina* (Hepat.) and lichen species of *Diploschistes* and *Lecidea*.

Calamagrostis recta tussocks, dominant in the zonal grass pâramos of the Cordillera Central, are only known from the highest parts of the Cordillera Oriental; these parts are covered with grass pâramo vegetation. On the Cuchilla Puentepiedra, the watershed between the Pâramo Cóncavo and Alto Valle de Lagunillas, on the climatologically dry side of the Sierra Nevada de Cocuy, a continuous (upper) bunchgrass pâramo, with e.g. *Calamagrostis recta* and Espeletiinae, was observed up to at least 4450 m. The special edaphic conditions there are discussed by Van der Hammen et al. (1981).

In the superpâramo the plant cover is sparse; generally, vegetation is found in patches. Low temperatures are prevailing, and diurnal freezing and thawing causes various kinds of tropical solifluction phenomena, described by Troll (1958). Here, the number of plant species is smaller than in pâramo vegetation in lower areas, but the percentage of endemics is high, especially in the vascular flora of the Sierra Nevada del Cocuy.(Van der Hammen & Cleef, in press).

In the l o w e r s u p e r p â r a m o a narrow belt of the remarkable composite dwarfshrub *Loricaria complanata* fringes the upper grass pâramo line.

Dense composite thickets, mainly consisting of *Senecio vaccinioides* associated with *S. andicola*, *Diplostephium rhomboidale* and *D. alveolatum*, are found locally on young terminal moraines along the grass pâramo-superpâramo border (4300-4400 m) on the atmospherically drier W slope of the Sierra Nevada del Cocuy. Stems and branches of these interesting bushes are covered with a thick layer of the moss *Zygodon pichinchensis*, especially in sheltered stands.

Lower superpáramo vegetation on dry moraines is sparse and consists mainly of vascular plants. A creeping ericaceous dwarfshrub, *Pernettya prostrata* var. *prostrata*, is locally dominant. Common species are: *Agrostis boyacensis, A. haenkeana, Bartsia* sp., *Diplostephium colombianum, Draba litamo, Jamesonia goudotii, Lachemilla tanacetifolia, Luzula* cf. *racemosa, Lycopodium crassum, Orithrophium cocuyense, Senecio guicanensis, Poa* spp., *Bryum genucaule, Córa pavonia* (Lich.), *Polytrichum juniperinum* (Musci), etc. All the species mentioned are also present on the atmospherically humid slopes of the superpáramo and most of them locally also in the upper grass páramo.

In the uppermost zone, the u p p e r s u p e r p á r a m o, the biomass and the number of species are considerably reduced. Only a few scattered, often poorly developed species remain, e.g. *Agrostis boyacensis, Calamagrostis* sp. (5806), *Luzula* cf. *racemosa, Pernettya prostrata* var. *prostrata, Poa* sp., *Senecio guicanensis, S. cocuyanus, S. supremus, Andreaea rupestris, Bryum argenteum, Ditrichum gracile, Polytrichum juniperinum, Racomitrium crispulum, Stereocaulon vesuvianum* var. *nodulosum*.
The upper superpáramo in the Colombian Cordillera Oriental is restricted to the Sierra Nevada der Cocuy, where at present the permanent snowcap is withdrawn to about 4800 m, whereas glaciers reach about to 4400 m.

Atmospherically humid páramo slopes

Bamboos are an important component of the páramo vegetation on the humid side of the Cordillera, from the forest line up to the lower boundary of the superpáramo. *Swallenochloa* is the most common genus; *Swallenochloa tesselata* is widely distributed in the atmospherically humid páramos of the Cordillera Oriental. Some other bamboo species, e.g. *Chusquea scandens, Neurolepis aristata* and *Aulonemia trianae*, belong to the timberline vegetation and locally reach into the subpáramo.

The climatologically humid side of the Cordillera contains an altitudinal sequence of zonal páramo vegetation, comparable to that on the dry side, but the main difference is the predominance of bamboos in the lower part of the páramo belt. The presence of *Swallenochloa* might be explained by the high annual precipitation (Gradstein, et al. 1977, Cleef 1978) as well as by the permanent atmospherical humidity that causes a limited diurnal range of prevailing low temperatures.

A prominent formation, mainly consisting of Compositae, is found in the l o w e r s u b p á r a m o or s h r u b p á r a m o. Thickets of *Eupatorium (Ageratina) tinifolium* are conspicuous. In addition to many bryophytes, commonly associated vascular taxa are e.g. *Aragoa lycopodioides, Baccharis* spp., *Centropogon ferrugineus, Diplostephium* spp., *Escallonia myrtilloides* var. *myrtilloides, Gaiadendron punctatum, Gaultheria ramosissima, Hypericum* spp., *Oreopanax* spp., *Purpurella grossa, Miconia* sect. *Cremanium, Rapanea dependens, Symplocos* spp., *Ternstroemia meridionalis*. The bamboo *Neurolepis aristata* is locally found in large groves.

In the u p p e r s u b p á r a m o or (b a m b o o -) d w a r f s h r u b p á r a m o the aspect of the zonal vegetation is determined by a layer of dwarfshrub and bamboos.
Just as on the dry mountain side, *Arcytophyllum nitidum* is present but with a markedly lesser cover. This species is found on rocky slopes and associated with *Swallenochloa* and several species of bryophytes, e.g. the mosses *Rhacocarpus purpurascens, Campylopus cucullatifolius* and the liverworts

Jamesoniella rubricaulis and *Lepidozia* sp. Locally present are *Sphagnum magellanicum*, *S. sancto-josephense* and an unknown species of *S.* sect. *Malacosphagnum* (9910).

In general, various ericaceous dwarfshrubs, *Swallenochloa tesselata*, composites and the abundance bryophytes are typical for this zone. The ericaceous species *Disterigma empetrifolium* plays an important rôle in zonal vegetation, and is accompanied by other dwarfshrubs, é.g. *Befaria tachirensis*, *Vaccinium floribundum* and *Plutarchia* spp; further species of *Clethra*, *Ilex*, *Symplocos* and, *Ugni myricoides*, *Hypericum pimeoloides*, *H. papillosum*, *H. sabiniforme*, *Eupatorium (Ageratina) vacciniaefolium*, *Diplostephium huertasii*, *D.* spp., *Senecio* spp., and species of *Blechnum* subg. *Lomaria* with real trunks. Tiny whitish lilies of *Tofieldia falcata*, locally *Spiranthes coccinea* (= *S. vaginata)*, and the rare monotypic *Nephopteris maxonii* are characteristic endemic species for the atmospherically humid zonal subpáramo vegetation and seem to be restricted to this zone.

In the lower bamboo páramo, which is almost entirely dominated by *Swallenochloa tesselata*, some scattered dwarfshrubs can be observed In the driest localities *Calamagrostis effusa* is present but with a lower cover. Small rosettes of *Castratella piloselloides* (and locally *C. rosea*) are common in this belt, but were also observed in lower parts of the dwarfshrub páramo. They are generally associated with *Rhynchospora paramorum*, *Oreobolus obtusangulus* ssp. *rubrovaginatus*, *Oritrophium peruvianum* ssp., *Pinguicula elongata*, *Xyris acutifolia* and the moss *Rhacocarpus purpurascens*; *Lysipomia muscoides* ssp. *simulans*, *Sisyrinchium pusillum*, *Paepalanthus pilosus* and *P. lodiculoides* are commonly present. In the lower belt these species are associated with *Arcytophyllum nitidum*. Humid, flat or gently sloping areas contain dense *Swallenochloa* - *Sphagnum* bogs, with as most common *Sphagnum* species *S. magellanicum*, *S. oxyphyllum*, *S. cuspidatum* and *S. sancto-josephense*. These bogs have a particularly rich bryophyte flora, the most important elements of which are the mosses *Breutelia chrysea*, *B. allionii*, *Campylopus cavifolius*, *C. cucullatifolius*, *Chorisodontium speciosum* and *Leptodontium wallisii*; the liverworts *Adelanthus lindenbergianus*, *Anastrophyllum* spp., *Cephalozia dussii*, *Herbertus subdentatus*, *Isotachus multiceps*, *Kurzia verrucosa*, *Lepidozia* spp., *Leptoscyphus cleefii*, *Riccardia* spp., and *Telaranea nematodes* (Gradstein et al. 1977); and the lichens *Cladonia colombiana*, *C. furcata* and *C. polia* (Sipman & Cleef 1979).

An upper bamboo-bunchgrass páramo is different from the previous zone by a higher cover of *Calamagrostis effusa* and a lower one of *Swallenochloa*. The upper limit of the *Swallenochloa* dwarfbamboos is at 4100-4200 m (extending along streams up to nearly 4250-4300 m) and seems to be determined by frost damage and drought. Precipitation diminishes with altitude in the higher páramos. This is confirmed by the composition of the plant cover . Thus, the general vegetation in the upper part of this zone resembles that of the atmospherically dry slopes and is classified as upper bunchgrass páramo. It consists of an open sward of *Calamagrostis effusa* bunches with species of *Espeletia*, *Cerastium* and *Anastrophyllum*; *Jamesonia bogotensis* however, is nearly absent.

Along the lower boundery of the superpáramo, a narrow belt of low *Loricaria complanata* bushes is found again, especially on stony, shallow but stable soils. As a result of the nearly constant and high atmospherical humudity on this side of the Cordillera *Jamesonia goudotii*, *Lachemilla nivalis*, *Oritrophium peruvianum* ssp. *peruvianum* and *Valeriana plantaginea* are intermixed here with the *Loricaria* bush, and many species of bryophytes, e.g. *Rhacocarpus purpurascens*, *Racomitrium crispulum*, *Campylopus pittieri*, *Anastrophyllum nigrescens*, *Gymnomitrion atrofilum*, *Herbertus subdentatus*, *Jensenia florschützii*.

Conspicuous lichens are *Cora pavonia*, *Cladonia* subg. *Cenomyce*, *Peltigera* spp., *Siphula* spp. and *Sphaerophorus melanocarpus*.

In general, the more humid climate seems to be advantageous to a larger number of plant species (resulting in a less discontinuous vegetation in areas with more or less permanent fog) in the humid l o w e r s u p e r p á r a m o, as compared with that on the opposite dry side of the Cordillera. *Senecio niveoaureus* is the most conspicuous and characteristic plant in the open zonal communities covering the morainic slopes locally with loamy matrix. Other characteristic plants are *Erigeron chionophilus*, *E. ecuadoriensis*, *Senecio* spp., *Diplostephium rupestre*, *Valeriana plantaginea*, *Draba* spp. (e.g. section *Chamaegongyle)*, *Montia meridensis*, *Ourisia muscosa*, *Hymenophyllum trichophyllum*, *Arenaria venezuelensis* and *Cerastium* spp. Some species of the Espeletiinae penetrate into the lower part of this zone.Typical bryophytes are *Breutelia integrifolia*, *Blindia acuta*, *Erytrophyllopsis andina*, *Kingiobryum paramicola*, *Distichium cappillaceum*, *Zygodon* spp. (Musci) and *Cheilolejeunea* (subg. *Strepsilejeunea)* sp. and *Anastrophyllum austro-americanum* (Hepaticae). *Azorella multifida*, *Bartramia augustifolia*, *Aongstroemia julacea*, *Herbertus subdentatus*, *Plagiochila dependula*, *Rhacocarpus purpurascens* and *Sphaerophorus melanocarpus* apparently need a nearly continuous atmospherical humidity. For ecological and floristical data on the humid lower superpáramo in the Sierra Nevada del Cocuy, I refer to Cuatrecasas & Cleef (1978).

Apart from conspicuous Caryophyllaceae and *Draba* spp. (e.g.*Draba hammenii*), the floristic composition and physiognomy of the u p p e r s u p e r p á r a m o appear to be more or less similar to that on the opposite dry side of the Sierra Nevada del Cocuy. Botanical fieldwork was carried out here only occasionally.

Páramo vegetation zonation, upper forest line, altitude and climate

The altitude of the various páramo vegetation zones in the Colombian Cordillera Oriental has been studied in detail in the Páramo Cóncavo (dry side) and in the headwaters of the Rio Casanare (humid side), both located in the Sierra Nevada del Cocuy (Fig. 9). The vegetational differences on the dry side and the humid side of the mountains are prominent in the Cocuy region, which may serve as a model for páramo zonation. Fig. 9 shows that the páramo vegetation zones in the Sierra Nevada del Cocuy are arranged asymmetrically.

On the dry side of these mountains, continuous strong isolation and the resulting warm air rising from the inter-andean deep and dry Río Chicamocha valley is a daily event, that causes a distinct upward shifting of the local zones of the high Andean vegetation. A lower bunchgrass zone is rare to absent. The high watershed in this area nearly completely prevents the movement of humid air from the Casanare slopes towards the dry mountain side.

On the humid side of the Sierra Nevada del Cocuy, the timberline forest mainly consists of *Weinmannia rollottii* Killip (Cunon.), a simple-leaved species, heavily loaded with epiphytes, e.g. *Herbertus juniperoideus*, *Hymenophyllum* spp., Ericaceae, etc.; trees of *Brunellia colombiana* Cuatr. (Brunell.), *Clusia* sp. (Guttif.) and *Hedyosmum* sp. (Chloranth.) are also present, with an underlayer of the broad leaved bamboo *Neurolepis aperta* (Munro) Pilger.

On the dry side of the Sierra Nevada del Cocuy, however, forestline woods mainly consist of Compositae (e.g. *Diplostephium* spp., *Gynoxys* spp.), and Rosaceae (e.g. *Hesperomeles* cf. *goudotii*, *Polylepis quadrijuga*) and *Buddleia lindenii*, while trees of pinnate-leaved *Weinmannia* occur, but are rare. Sheltered places, evidently offering favourable environmental conditions, contain patches of *Hesperomeles* cf. *goudotiana* forest up to 3800 m and dwarfforests of *Polylepis quadrijuga* and *Gynoxys* spp. up to 4100 m.

Small patches of dwarfed trees of *Diplostephium rhomboidale* and *Valeriana arborea* are present here, even up to 4400 m.

On the humid slopes, dwarfed groves of *Gynoxys albivestita* and *Valeriana arborea* are found up to 4250 m, and one consisting of *Senecio flos-fragrans* var. *frigidophilus* up to 4300 m.

Although the floristical composition of the upper forests on either side of the Sierra Nevada del Cocuy is quite different. The two types are continuous, closed, well-developed, thick-stemmed timberline forests. Thus, a comparison of their higher parts is relevant for determining the actual upper forest line in the Sierra Nevada del Cocuy. Our timberline obeservations there largely agree with those of Cuatrecasas (1958) in other locations on the dry side of the Cocuy range.

Environmental conditions in the other, lower pâramos in the Cordillera Oriental are quite different. Consequently, on atmospherically dry slopes there the upper forest line is generally lower and running at (3000) 3200 - 3300 m. These timberline forests mainly consist of pinnate-leaved *Weinmannia* spp.,especially *W. tomentosa* L.f., mixed with composites and Melastomataceae, and occasionally Rosaceae (*Polylepis quadrijuga, Hesperomeles* sp.). In the dry upper Chicamocha valley the timberline forests are mainlv *Quercus* sp. (W side) or pinnate-leaved *Weinmannia fagaroides* HBK (E side) according to Van der Hammen,et al. (1981) and pers. comm. Unfortunately few original mountain forests without human interference remain.

On the atmospherically humid slopes the upper forest line is generally slightly higher and situated at 3300 - 3500 m. Timberline forests there consist mainly of *Weinmannia* (pinnate and simple-leaved species), with frequent (co-) dominance of Compositae (*Diplostephium* spp.) and Melastomataceae (*Miconia* spp.) and occasionally with either *Polylepis quadrijuga* or *Escallonia myrtilloides* var. *myrtilloides*. The atmospherically humid Magdalena valley slopes forests reaching up to the timberline at 3400 m in the Pâramo de Guantiva (Santander). The zonal upper subpâramo dominated by *Arcytophyllum nitidum* generally reaches up to 3500 m on the atmospherically dry and humid slopes.

Thus, the upper forest line in the Colombian Cordillera Oriental appears to be mainly determined by thermal conditions. On the atmospherically dry side of the mountains, minimum night temperatures are considerably lower than at the same height on the opposite humid side, where the upper forest line generally reaches slightly higher. Daily temperature amplitudes thus are largest on the dry side of the mountains. On the humid slopes, rain clouds and frequent fog cause oligothermic conditions, viz. low temperatures and a minor diurnal temperature range.

The vertical distance between the upper forest line and the lower pâramo vegetation zone on either side of the Cordillera is probably greatest in the Sierra Nevada del Cocuy. It is not quite clear why the pâramo belt on the humid SE slopes there reaches so far down. Extreme humidity causing boggy substrate, might have a lowering effect on the upper forest line. For further discussion I refer to Van der Hammen et al. (1981) and Van der Hammen & Cleef (in press).

The duration of the total period of high atmospherical humidity (including periods of precipitation and fog) in relation to the total annual precipitation apperently determines the bamboo cover in the lower pâramos (Fig.80). In the upper superpâramo, humidity conditions appear to be nearly similar on both sides of the Sierra Nevada del Cocuy.

The special floristic composition and the larger cover of the vegetation at the grass pâramo-superpâramo border, especially on the humid side of the Cordillera, may explain the presence of a marked upper condensation zone at

4000 - 4200 m. Gradstein et al. (1977) and Cleef (1978) reported on the rich vegetation of the condensation zone of 4000 m on the Nevado de Sumapaz. This interesting locality still remains as the best example of its kind in the Colombian and Venezuelan Andes. Weischet (1969) published an outstanding climatological study of the Colombian Andes, and he was probably the first to demonstrate such condensation levels at lower altitudes. Guhl (1974) reported three vertically arranged cloud belts, the upper one in the high pâramo. Lauer & Frankenberg (1978) and Lauer (1979) described condensation zones from lower levels in the Mexican Mountains and the Ecuadorian Andes. According to these authors, condensation zones are defined as vertically restricted zones. Regarding the pâramo belt, they locate the maximum precipitation and duration of fog. Clearly, these zones are of great biological and ecological importance.

SHORT SURVEY OF THE ZONAL COMMUNITIES

Introduction

Ahead of a future final tabular arrangement of the relevés according to the Zürich-Montpellier method, a synopsis of the zonal pâramo vegetation may be presented in order to complete the general picture of the vegetation of the study area. This outline is based upon preliminary tables (of *Swallenochloa* communities) and from not yet completed "differentiating tables", in which the relevés are arranged in "vegetation units" or communities on basis of their floristic, and - to some extent - their physiognomic and ecologic similarities, but without establishing their synsystematic rank (Mueller Dombois & Ellenberg 1974). The communities have been numbered consecutively.

A limited number of species is found in all altitudinal zones of the pâramo, e.g. *Bartsia* sp(p.), *Grammitis moniliformis, Hypochoeris sessiliflora, Luzula* cf. *racemosa, Pernettya prostrata, Senecio vaccinioides;* the bryophytes: *Andreaea rupestris, Bryum argenteum, Polytrichum juniperinum, Racomitrium crispulum, Anastrophyllum leucostomum, Stephaniella paraphyllina* and the lichens *Cladia aggregata, Cladonia andesita, C. chlorophaea* and *Cora pavonia.* The bryophytes are widely distributed species with pioneer character: "colonists" and "annual shuttle species" (During 1979). *Cora pavonia* and *Bryum argenteum* continue downslope into the warm tropical belt.

The lower part of the pâramo belt comprises both the subpâramo and the grass pâramo. It contains characteristic endemic vascular genera belonging to the pâramo element (Cleef 1979[a]): e.g. *Bucquetia, Aragoa, Castratella, Espeletia, Libanothamnus, Plutarchia, Purpurella* and *Swallenochloa.*

The stemrosettes of *Espeletia* and *Espeletiopsis* are most common and represented by a large number of endemic species. Recently Cuatrecasas (1979) reported 17 species of *Espeletiopsis* and 34 species of *Espeletia* for the Colombian Cordillera Oriental. Species of *Espeletiopsis* generally abound in the driest habitats, most of them on sandy soil, in the zonal pâramo. These species are nearly absent in the bamboo pâramos. Species of *Espeletia,* however, grow on dry to humid sandy, clayey and peaty soils and are only absent in deep and wet bogs, located e.g. on former lakes.

Calamagrostis effusa is abundant in the zonal pâramo, except in the superpâramo, in the dense shrub pâramo and in the wettest *Swallenochloa* stands. This species is the most important tussock of the pâramos of the Colombian Cordillera Oriental, forming the "pâjonales" on the dry side of the mountains. This bunchgrass species is also found in other north-andean pâramos from

Venezuela to Central Ecuador, but is probably absent in the Costa Rican páramos (Dr. J. Cuatrecasas, in litt.)

As pointed out earlier (Cleef 1978) *Swallenochloa tesselata* is only found in zonal páramo vegetation on the humid side of the mountains with the wettest climate. Towards higher altitude (upper grass páramo) or in less humid climatological conditions *Swallenochloa* gradually becomes restricted to always humid or wet valley floors or to bogs on slopes and in depressions.
Finally *Swallenochloa* is restricted to humid valley floor bogs with vegetation belonging to the azonal communities (Fig. 79).
The climatologically most humid páramos have been studied on the outer slopes above the cloudforest line, e.g. on the SE side of the Sierra Nevada del Cocuy in the headwaters of Río Casanare, in the páramos of the Pena de Arnical about 5 km N of Vado Honda (Sogamoso-Pajarito road), in the lower part of the Chuza valley between the Páramo de Palacio and the Páramo of Chingaza, and on the eastern slopes of the Nevado de Sumapaz and its surroundings.

The zonal communities will be treated below in sequence of altitude from the subpáramo up to the superpáramo, indicating whether they are found in dry or humid páramo climates. Only the communities, observed by the author, are treated, though references will be made to information in literature.
Numerous relevés were made in páramo vegetation, with noticeable human activities. Such vegetation contains a number of species from the next higher páramo zone, or it may be more or less completely temporarily replaced by a type of vegetation similar to the zonal vegetation of the next higher belt. In the latter case, the physiognomy and floristics of the replaced vegetation will be discussed under the higher páramo zone.

The following zonal communities (1 - 28) have been recognized. Most of them correspond probably closely to syntaxa, which will be described in the near future. Most characteristic taxa in the following descriptions are expected to become diagnostic taxa then. Two syntaxa, however, the *Acaeno-Plantaginetum sericeae* (18) and the *Loricarietum complanatae* (21) could already be named and described formally.

THE SUBPARAMO

Shrub páramo (or lower subpáramo)

The shrub páramo is dominated by Ericacae, Compositae Melastomataceae. Its floristic composition varies considerably according to geographic position and altitude, humidity, land form, soil factors, and human activity. A number of shrub communities can be recognized.
In the study area *Bucquetia* is the most characteristic genus for the shrub páramo and is mostly found as a shrub or dwarf tree. *Bucquetia vernicosa* is found from the eastern side of the Sierra Nevada del Cocuy northward; *Bucquetia glutinosa* is the common species in the southern part of the Colombian Cordillera Oriental (Fig. 10[a]). In general, more genera and species of Melastomaceae with a higher cover seem to be present in shrub páramos on the most humid side of the mountains, than on the drier slopes. Other characteristic shrub species are: *Purpurella grossa, Eupatorium (Ageratina) tinifolium, Aragoa lycopodioides, Gaultheria ramosissima, Symplocos theiformis, Ugni myricoides* and a number of shrub species of *Hypericum*, e.g. *H. lycopodioides, H. papillosum, H. magniflorum*.

The lower pâramos appear to be most strongly affected by human activities. The shrub pâramo suffers most from clearing for pasture, growing potatoes, and cutting for fuel. Only the most inaccesible areas remain more or less intact. In comparison to the higher pâramo zones, little is known of the vegetation of the shrub pâramo. Previous phytosociological studies dealing with the shrub pâramo of the Colombian Cordillera Oriental include those of Cuatrecasas (1934), Van der Hammen & Gonzâlez (1960[a], 1963), Van der Hammen et al. (1981), Van der Hammen & Jaramillo, (in prep.), Lozano & Schnetter (1976) and Rangel (1976). As the open pâramo vegetation was the main purpose of our studies, only a few relevês were sampled in the shrub pâramo.

1. Shrub pâramo with *Espeletiopsis*
Fig. 11

This is a rather open low shrub and dwarfshrub vegetation up to 2.5 m high and is extremely rich in leptophyllous species. *Espeletiopsis* species, e.g. *E. corymbosa, E. garciae, E. pleiochasia, E. muiska, E. jimenez-quesadae,* are geographical vicariants and they cover from 10 to 40% of the area. Common species are: *Bucquetia glutinosa, Brachyotum strigosum, Clethra fimbriata, Bulbostylis tropicalis, Gaultheria rigida, Castilleja integrifolia, Lycopodium complanatum* var. *tropicalis, Befaria* spp.*, Macleanea rupestris.*
The community occurs on steep (20°-35°) slopes, with 20-100 cm thick brownish clayey-sandy or sandy, moderately acid soil (pH 4.5-4.9).
Floristic composition is rather diverse, and it is expected that more vegetation units can be distinguished when more data become available. *Espeletiopsis* formations were studied between 2850 and 3790 m (generally between 3000 - 3400 m) on the dry side of the mountains, where they occupy rather small, mostly convex, well-drained areas, frequently near sandstone outcrops. The greatest floristic affinity is with *Macleanea rupestris* shrub, also reported (Lozano & Schnetter 1976) from ridges and other well-drained areas covered with thin soil.
The position of the *Espeletiopsis* shrub community is intermediate between the dense shrub pâramo vegetation and the *Arcytophyllum nitidum* dwarfshrub communities.

2. *Senecio vaccinioides* subpâramo shrub
Fig. 12

This type of zonal leptophyllous subpâramo shrub has only been studied in the Sierra Nevada del Cocuy and its southern extension in the Pâramo de Chita and Pisva. Although present on the dry side as well as on the humid side of this range, a larger area seems to be covered on the dry side, especially on the Alto de la Cueva and in the high valley of Lagunillas (3750-4000 m). *Senecio vaccinioides* shrub there is up to 2.5 m high, and generally present on the steep, well-drained slopes of valleys and on moraines. The dark brownish sandy and stony soils are thin (10-25 cm), with one measured pH of 5.3.
Lower *Senecio vacciniôides* shrub (1.5 m high) at 3530 m in the humid Pâramo de Pisva was also found on steep slopes on more humic, thicker, clayey soil (pH 4.7 in the upper layer). Thickets were observed between 3400 and 3550 (3750) m and may be associated with *Swallenochloa* The main floristic difference between both stands is found in the ground layer. Bryophytes cover half or more of the surface. Hygrophytic mosses, e.g. *Pleurozium schreberi,*

Chorisodontium sp., *Campylopus jamesonii* and *Leptodontium wallisii*, which abound on the humid slope, are replaced by the clearly less hygrophytic *Hypnum amabile* and *Thuidium peruvianum* in the composite thickets on the dry side of the mountains.
Senecio vaccinioides is found from Central Ecuador up to the Costa Rican páramos, and was also noticed as a patchy dwarfforest formation in the Parque Los Nevados, Colombian Cordillera Central (Cuatrecasas 1934; Cleef et al., in press).
Under nr. 81 and 96 other *Senecio vaccinioides* communities in the study area are discussed.

3. *Eupatorium (Ageratina) tinifolium* shrub
   Fig. 13
   photo: Gradstein et al. 1977: plate 2, A;
   lit.: Van der Hammen et al. 1981

Well-developed stands of the mesophyllous *Ageratinetum (= Eupatorietum) tinifoliae* (ined.) were studied in 1967 by Van der Hammen & Jaramillo (in prep.) in the headwaters of the Rio Casanare (Páramo de Pisva) between 3300 and 3700 m. Rangel (1976) reported a community of *Eupatorium tinifolium* and *Gynoxys* cf. *pendula* from the Páramo de Pisva at 3400 m. The present author visited the above mentioned stands and noted as associated species *Baccharis prunifolia, Escallonia myrtilloides, Hypericum lycopodioides, H. laricifolium, Gynoxys* sp., *Ribes* sp., *Vallea stipularis, Oreopanax* sp., *Miconia salicifolia* and shrubby species of *Senecio. Miconia* sect. *Cremanium, Cestrum* and *Bucquetia* are frequent in the vicinity of the wet cloud forest line. *Eupatorium tinifolium* thickets were also locally reported from the valley of Q. El Playón, Sierra Nevada del Cocuy, between 3400 and 3675 m; from the humid northern side of the Páramo del Almorzadero between 3400 and 3700 m; from the humid shrub páramo E of Bucaramanga, from the Páramo de Palacio, and from the Río Nevado and the Q. Sitiales valley in the Páramo de Sumapaz between 3300 and 3450 m. These thickets were also observed near the upper forestline in the Cordillera Central of Colombia (Cleef et al., in press). Judging from herbarium data, *Eupatorium tinifolium* must be present in the Colombian Andes between 2400 and 3800 m.
In general terms *Eupatorium tinifolium* groves are characteristic for the humid side of the mountains above the upper forestline.

4. Shrub and dwarfforest of the "*Vaccinion floribundi*" Cuatrecasas 1934
   photo: Cuatrecasas 1934: plate XIX; 3 photographs in Van der Hammen & González (1960[a], 1963)

Cuatrecasas (1934) first mentioned this alliance for the combined humid ecotonic nanophyllous and sclerophyllous shrub and dwarfforest, distributed in patches above the forestline in the Páramo de Guasca (3200-3550 m) in the Cordillera Oriental and on the Nevado del Tolima (3500-3800 m) in the Colombian Cordillera Central. Characteristic are *Vaccinium floribundum, Miconia ligustrina, Miconia salicifolia, Rapanea dependens, Escallonia myrtilloides, Senecio vaccinioides* and *Brachyotum strigosum*.
Van der Hammen & Gonzalez (1960[a], 1963), in association with J. Hernández-Camacho, reported similair communities in small protected valleys between 3500 and 3600 m in the Páramo de Palacio. Lozano & Schnetter (1976) published three relevés from residual humid dwarfforest in the Páramo de Cruz Verde, E of Bogotá at 3400 m. These stands on sloping ground are rather mixed as

regards their floristic composition. Dwarftrees up to 3 m high of *Gaultheria anastomosans* and *Hypericum goyanesii* shrub were noticed among the dominant species. In the ground layer, *Plagiochila* spp. and *Pleurozium schreberi* are dominant.
Own observations in a similar shrubby stand (2-3 m high) on thick humic peaty to clayey, slightly sloping soil (pH 4.3 in the upper layer) at 3370 m in the atmospherically humid Pãramo de Palacio (rel. 136) revealed that in the upper shrublayer *Swallenchloa* is dominant and *Vaccinium floribundum*, *Hypericum lycopodioides* and *Bucquetia glutinosa* are subdominant (cover 15 to 25 %). Low trunks of *Blechnum loxense* in the dwarfshrub layer cover about 30 %. *Plagiochila* sp. (5139) as dominant and *Hypnum amabile* together with *Hydrocotyle gunnerifolia* were subdominant in the ground layer (cover resp. 40, 30 and 20 %). There are many hygrophytic species, some of which belong to the upper Andean forest element.

In summary, this type of shrub pāramo of ecotonic dwarfforest seems most common on the humid side of the Colombian Oriental between 3200 and 3600 m. This vegetation type has been studied only in the southern pāramos (Guasca to Sumapaz). The community is rich in bryophyte species, both terrestric and epiphytic, and patches of *Sphagnum magellanicum* peat may be developed here.

Arcytophyllum nitidum dwarfshrub páramo

The zonal vegetation of the upper subpāramo is best characterized by bryophyllous rubiaceous dwarfshrub of *Arcytophyllum nitidum*. The vegetation is mostly three-layered: 1) a dwarfshrub layer, 2) a herb-graminoid layer, and 3) a ground layer of bryophytes and some low herbs. The herbaceous-graminoid layer is better developed in open dwarfshrub and mainly consists of photophytic species, e.g. *Castratella* spp., *Rhynchospora paramorum*, *Oreobolus obtusangulus* ssp. *rubrovaginatus*, which occur in open pāramo on shallow soil, just as: *Bartsia* spp., *Hypochoeris sessiliflora*, grasses, *Rhynchospora macrochaeta* and *Hypericum strictum*. Mosses dominate the reduced bryophyte layer (1-10 % cover) on the dry side, but mosses and/or hepatics attain almost 100 % cover on the humid side of the mountains.

Lycopodium contiguum and species of *Gaultheria* with glandular hairs are the most common and characteristic accompanying species. *Geranium multiceps* is frequent too, this conspicuous species is also found in boggy *Swallenochloa tesselata* pāramo with *Puya goudotiana* and species of *Sphagnum* at the same altitude. Other characteristic vascular species, reaching more or less their optimum in this dwarfshrub zone, are: *Lourteigia (Eupatorium) microphylla, Sporobolus lasiophyllus, Diplostephium phylicoides, Masdevallia coriacea, Baccharis rupicola, Spiranthes vaginata, S. coccinea, Tofieldia falcata, Diplostephium huertasii, Lycopodium complanatum* var. *tropicum, Achyrocline lehmannii, Gaultheria anastomosans, Gaylussacia buxifolia, Epidendrum chioneum, Odontoglossum lindenii, Paepalanthus alpinus, P. andicola* var. *villosus, P. paramensis, Pernettya hirta, Verbesina baccharidea, Miconia parvifolia, Brachyotum strigosum*. Noteworthy is that several of these species have the same distribution from the southern end of the Pāramo de Guantira to the northern Sumapaz, e.g. *Diplostephium phylicoides* (Fig. .. . . *Verbesina baccharidea, Miconia parvifolia*. The characteristic vascular genera mainly belong to the neo-tropical Andean element (Cleef 1979[b]).

The shallow soils are clayey to sandy and moderately to strongly acid (pH 5.2-4.1). Most of the stands are found on steep, well-drained slopes. *Arcytophyllum nitidum* vegetation is common and attains a considerably higher cover on the dry side of the mountains. This rubiaceous species occurs throughout the páramos of the Colombian Cordillera Oriental from 2800 to 4080 m. It is also known fròm Venezuelan páramos. Phytosociological data on *Arcytophyllum nitidum* vegetation were published earlier by Cuatrecasas (1934), Lozano & Schnetter (1976) and Sturm (1978).

5. Dense *Arcytophyllum nitidum* dwarfshrub
   Fig. 14

Dense *Arcytophyllum nitidum* dwarfshrub vegetation, if undisturbed, is up to 1.20 m high and covers about 60 to 80 % of the surface. Dominant *Arcytophyllum nitidum* shrub largely determines the aspect of the upper subpáramo. *Bryum* cf. *grandifolium* and *Lycopodium contiguum* are present and reach high cover valued under the nearly closed dwarfshrub layer. Because of the shrubby character of the stands, less photophytic species are found than in other more open *Arcytophyllum* communities (6, 7, 8). In comparison with other *Arcytophyllum nitidum* communities, this one is the poorest in species. Mosses and lichens cover about 5-12 %.
This dwarfshrub community is mainly present on moderately steep slopes (15°-20°) with black-brownish sandy soils not thicker than about half a meter. The pH of the upper brown sandy or black sandy clayey soil layer is 4.4 to 5.0.
This dense rubiaceous dwarfshrub vegetation is mainly found on the dry side throughout the study area between 3100 an 3600 m. In the Páramo Cóncavo in the Sierra Nevada del Cocuy this kind of dwarfshrub vegetation is well developed between 3750 and 3900 m. *Masdevallia coriacea* and an unknown species of *Scaphosepalum* (10019) are associated orchid species.

6. Dwarfshrub of *Arcytophyllum nitidum* with *Sporobolus lasiophyllus*, and *Achyrocline lehmannii*
   Fig. 15
   lit.: Lozano & Schnetter 1976.

The *Arcytophyllum nitidum* cover is about 30 % in this open dwarfshrub vegetation. Locally other woody species may contribute to the dwarfshrub layer, e.g. *Gaylussacia buxifolia* *Hypericum juniperinum* and *Valeriana triphylla*. *Sporobolus lasiophyllus* (cover up to 35 %) and to a lesser degree *Achyrocline lehmannii*, *Gaultheria rigida*, *Lobelia tenera*, *Diploschistes* sp. and *Verbesina baccharidea* reflect more xeric conditions
Paepalanthus paramensis is another cushionplant, which is most frequent in this vegetation (on both sides of the mountains). *Castratella piloselloides* is generally present, in some places associated with *Rhynchospora paramorum*
Soils are thin (10-30 cm), brownish, coarse sandy, and in many places stony (pH 4.6-5.2). The open dwarfshrub is found on well-drained and exposed steep slopes (5-44°; mean 25-30°), also on stony ridges and in summit areas.
This type apparently is present throughout the subpáramos of the Cordillera Oriental and was studied from 2925 to 3630 m. The stands in the humid subpáramos are found on the edaphically driest, steep places, where bamboos are absent.

7. Dwarfshrub of *Arcytophyllum nitidum* with *Diplostephium phylicoides*
Fig. 16, 10^b (also 52)
lit.: Lozano & Schnetter 1976

This dwarfshrub vegetation covers at least half of the area or more *Arcytophyllum nitidum* covers 30 to 70 %. *Diplostephium phylicoides* (Fig. 10^b), which is absent in the other *Arcytophyllum nitidum* communities, may contribute up to 30% of the dwarfshrub layer. *Gentianella corymbosa* and lichens, e.g. species of *Cladonia* subg. *Cladina*, are conspicuous. *Blechnum loxense* and *Oreobolus obtusangulus* ssp. *rubrovaginatus* indicate less xeric environmental conditions. *Swallenochloa*, however, is almost absent, *Castratella piloselloides* is common; *Rhychospora paramorum* occurs in most of the relevés. The soils are thick, humic, black sandy to clayey, 50 to more than 120 cm thick. The pH of the strongly acid toplayer is 4.1 to 4.7. The community is found on sloping to moderately steep ground.
This type of subpáramo dwarfshrub has only been found near Bogotá between 3275 and 3550 m, in climatologically dry as well as in more humid subpáramos. Some more relevés (belonging to this type) were mentioned by Lozano & Schnetter (1976) and Sturm (1978). This community is floristically heterogeneous, and probably will be subdivided in several syntaxa when more data become available.

8. Communities of *Arcytophyllum nitidum* in bamboo-dwarfshrub páramos
Fig. 17

Arcytophyllum nitidum dwarfshrub, of which unfortunately a few relevés only are available, is least represented on the (per)humid side of the mountains The different communities will be briefly characterized.
Swallenochloa tesselata and *Xyris acutifolia* are scarce or absent in zonal vegetation on the dry side of the mountains, but they are well represented here. Species characteristic for the dry side of the mountains are almost absent, and their cover decreases towards the (per)humid páramos: e.g. *Polytrichum juniperinum, Castilleja fissifolia, Altensteinia fimbriata, Baccharis tricuneata, Hieracium avilae* and species of *Lourteigia* and *Espeletiopsis*. The bryophyte layer is well developed and the cover of mosses and liverworts increases up to 100 % towards the upper perhumid cloudforest line.
In closed stands of *Arcytophyllum nitidum*, which are relatively rare on the wet side, *Swallenochloa* is dominant in the dense bamboo dwarfshrub fieldlayer, and this dwarfshrub is found on protected sites near the cloudforest border. Floristically, the open *Arcytophyllum nitidum - Swallenochloa* - vegetation is characterized by *Sphagnum* spp., *Spiranthes coccinea, Diplostephium huertasii, Tofieldia falcata, Rhacocarpus purpurascens, Campylopus cucullatifolius, Oritropium peruvianum, Pinguicula elongata, Kurzia verrucosa,* etc.,which are nearly absent in other *Arcytophyllum nitidum* communities. *Castratella* spp., *Rhynchospora paramorum* and *Oreobolus obtusangulus* ssp. *rubrovaginatus* are elements of the open lower part of the páramo belt, and they are opulent in the moderately humid páramos.
In open *Arcytophyllum nitidum* dwarfshrub (5-35 % cover) in the bamboo páramo, at least two different types may be distinguished. In one the (aero-) hygrophytic moss *Rhacocarpus purpurascens* is most common, while in the other more boggy one *Sphagnum* species are prominent. This last mentioned type has only been studied in the headwaters of Río Casanare just above the uppers forestline. The type with *Rhacocarpus* is present both in humid and in perhumid páramos (2900-3650 m). *Rhynchospora paramorum* (Fig. 10^c) is a conspicuous

constituent (30-75% cover) in the humid páramo where it is replaced by a rather low "grassy" zonal vegetation. *Disterigma empetrifolium*, *Tofieldia falcata* and locally *Castratella rosea* and *Nephopteris maxonii* are characteristic species also. *Sphagnum* spp., e.g. *S.* sect. *Malacosphagnum* (9910), and other commonly associated bryophytes are present with a lesser cover.
Stands in the páramos near Bogotá (Cruz Verde - Sumapaz) contain *Diplostephium phylicoides* as an associated species.

9. *Gaultheria ramosissima* and *Disterigma empetrifolium* dwarfshrub with *Arcytophyllum caracasanum*

This presumably zonal dwarfshrub community has only been noticed in the headwaters of the Casanare river, in the San Luis valley of the upper Playón stream at 3500 m. Dwarfshrub and low shrub dominated by Ericaceae and liverworts are found on stony moraines with steep slopes and shallow humic sandy soil of 10-15 cm with a pH of 4.6-5.0. The height of the stratum is only about 40 cm, but a number of low shrubs native to the shrub páramo (e.g. *Gaultheria ramosissima, Aragoa lycopodioides, Rapanea dependens, Hypericum lycopodioides)* indicate more favourable temperature conditions on these moraines than in the surrounding open *Sphagnum* bogs. Without grazing and trampling by cattle and human activities this community may develop into a shrub páramo. The presence of some cloudforest liverworts: e.g. *Leptoscyphus porphyrius* and *Omphalanthus filiformis* (Gradstein et al. 1977) is conspicuous. *Disterigma empetrifolium* (20 -30 % cover) and *Arcytophyllum caracasanum* (up to 35 % cover) are found on shallow stony steep soils predominantly in the humid páramos of the Colombian Cordillera Oriental. Other characteristic vascular species in the bamboo dwarfshrub páramo include: *Elaphoglossum* spp., *Ugni myricoides, Gaultheria anastomosans, G.* sp. nov. (9120^B), *Epidendrum chioneum*, and *Eupatorium (Ageratina) vaccinioides*. *Calamagrostis effusa* is not conspicuous; *Swallenochloa tesselata* patches may cover up to 35 %. A thick mass of terrestric and epiphytic liverworts associated with *Oropogon* sp. (9131) covering about 75 % reflects permanently humid climatological conditions *(Frullania* sp. (9143)). *Everniastrum cirrhatum* is the most common epiphyte. *Lepidozia alstonii*, a rare liverwort species, has been collected in this area only.

THE GRASS PARAMO

The grass páramo of the Colombian Cordillera Oriental contains the zonal graminoid communities associated with species of the *Espeletiinae*. These communities are found in a zone, limited below by the dwarfshrub-dominated subpáramo and above by the lower limit of the superpáramo.
Calamagrostis effusa is the most prominent páramo bunchgrass. In the climatologically humid páramos this species may be partly or entirely replaced by dwarfed *Swallenochloa tesselata* bamboo (Fig. 6, 8). The dominant grasses *Calamagrostis effusa* and *Swallenochloa tesselata* are endemic species of the northern Andean páramos; at the generic level they belong resp. to the wide temperate and the páramo element . *Calamagrostis effusa* is assigned to the section *Deyeuxia* of *Calamagrostis*, which is mainly distributed in the cool southern hemisphere and on tropical high mountains.

Numerous taxa are present in the grass pāramos. The most important are e.g. *Calamagrostis effusa, Espeletia, Espeletiopsis, Halenia, Bartsia, Pernettya prostrata, Vaccinium floribundum* var. *ramosissimum, Calamagrostis bogotensis, Oreobolus obtusangulus* ssp. *rubrovaginatus, Cladonia isabellina, Cladia aggregata, Gongylanthus liebmannianus, Stephaniella paraphyllina, Anastrophyllum leucostomum, Campylopus* spp. (e.g. *C. chrismarii* var. *suboblongus, C. cleefii).*
The number of species in the grass pāramo increases considerably towards lower parts. For example: the open *Calamagrostis effusa - Espeletiopsis colombiana* bunchgrass pāramo at 4400 m on the dry side of the Sierra Nevada del Cocuy contains 18 species (rel. 455). In the lower parts of the upper bunchgrass-dominated pāramo near 4100 m about 25 species were recorded on both sides of the Cocuy range. On the average about twice as many species are present in the lower bunchgrass pāramo and three times as many in the lower bamboo pāramo, compared to the upper bunchgrass pāramo at 4100 m. The closed bunchgrass pāramo is rather poor in species. A special, permanently humid microhabitat is found here between the tussocks in the shade of the bunches. Burning of the bunchgrass-dominated pāramos has a strong effect. The grass cover is considerably reduced and photophytic taxa become predominant in the newly open and drier habitat. Previously, these were unobtrusive as small rachitic or as viable seeds in the deep shade under the bunches. After burning they develop rapidly and soon reach their reproductive cycle, from flowering to fruiting, often several times per year. For example, brightly reddish flowering *Castilleja integrifolia* may determine the aspect a few weeks after the burning. *Paepalanthus karstenii, Arcytophyllum muticum, Eryngium humile, Castratella, Bartsia, Carex tristicha* e.g. become more conspicuous later on. Hygroshytic bryophytes disappear or may survive close to the tussocks. Xerophytic and/or photophytic liverworts, e.g. *Stephaniella paraphyllina, Gongylanthus liebmannianus* and *Isotachis multiceps* are then common on the bare mineral soil.

Bamboo páramo

As indicated before, relevés from the bamboo pāramos have not been analysed as much in detail as those from the bunchgrass pāramo, and the main communities can be treated summarily only. Most relevés were sampled in the lower bamboo pāramo and only some of them are from the upper bamboo-bunchgrass pāramo. Therefore, no distinction was made below between lower and upper parts of the bamboo pāramo, as most communities belong to the lower one. Zonal high-altitude bunchgrass-bamboo pāramo communities are described under 12 and 13[a].

The bamboo pāramo as defined in a zonal sense comprises all open zonal graminoid vegetations with *Swallenochloa*. Bunches of *Calamagrostis*, sometimes of *Festuca* cf. *dolichophylla* or *Cortaderia sericantha* are usually associated. The high degree of humidity is well reflected by the proportions of the cover of *Calamagrostis* and *Swallenochloa*. Bamboo is generally predominant, but with less humid environmental conditions *Calamagrostis effusa* becomes predominant (Cleef 1978). In perhumid lower bamboo pāramos, *Swallenochloa tesselata* is dominating in the zonal vegetation, even in the driest places on top of well-drained ridges and crests (Fig.79). Bunchgrasses, e.g. *Calamagrostis effusa* and *Festuca* cf. *dolichophylla* were found with a lesser cover in nearly all relevés. Localities on the wet slope with these atmospherically extreme humid pāramos were mentioned before. Bamboos are common on the slopes, but do not reach the highest parts or the driest places in a less humid climate. Thus, *Swallenochloa tesselata* may only be found in azonal boggy valley floor communities in the bunchgrass páramo. There is a gradual transition between bamboo and bunchgrass páramos, and it is rather difficult to distinguish floristically and ecologically pure bunchgrass páramo from grassland with some clumps of *Swallenochloa tesselata*. *Swallenochloa tesselata* in zonal vegetations reaches up to 4150 m. In most places a belt of about 100 m vertically with pure *Calamagrostis effusa* sward is found above the *Swallenochloa* páramo (see 20).

Characteristic and common taxa of the bamboo páramo proper are: *Swallenochloa tesselata*, *Calamagrostis effusa*, *Espeletia* spp., *Bartsia* spp., *Oreobolus obtusangulus* spp. *rubrovaginatus*, *Oritrophium peruvianum*, *Halenia* spp., *Rhynchospora macrochaeta*, *Carex pichinchensis*, *Hypericum lancioides*, *(H. garciae)*, *Pernettya prostrata* var. *purpurea*, *Arcytophyllum muticum*, *Nertera granadensis*, *Breutelia* spp., *Riccardia* spp., *Lepidozia* spp. (e.g. *Lepidozia auriculata)*, *Cladia aggregata*, *Rhacocarpus purpurascens*, *Adelanthus lindenbergianus*, *Anastrophyllum* spp., *Campylopus* spp., *Cladonia andesita* and *Cladonia* subg. *Cladina*.

10. Community of *Swallenochloa* with *Sphagnum* and/or *Breutelia*
Fig. 18 (also Fig. 10 and 51)
photo: Gradstein et al. 1977, plate 1D

Peat moss - bamboo vegetation on boggy and sloping valley floors and distributed on the humid slopes tends to be zonal. This actually azonal vegetation is common in the most humid páramos. Under less humid conditions, it is found in slight depressions on the slopes, and in many places it grades into well-drained (bamboo-) tussock grassland.

In general, *Breutelia* cover is larger in higher places, while that of *Sphagnum* is proportionally less. The floristic differences between slope and valley floor communities are not conspicuous. *Sphagnum magellanicum* and *S. cuspidatum* for example prefer level habitats on deep bogs; *Oreobolus obtusangulus* is mostly found on slope bogs on peaty mineral soil. *Festuca* cf. *dolichophylla* is a common tussock here. Characteristic bryophyte species include: *Gongylanthus granatensis*, *G. innovans*, *Adelanthus lindenbergianus*, *Anastrophyllum* spp., *Telaranea nematodes*, *Blepharostoma trichophyllum*, *Breutelia allionii*, *B. chrysea*, *Leptoscyphus cleefii*, *Sphagnum magellanicum*, *S. sancto-josephense*, *S. oxyphyllum*, *S. cuspidatum*, *S. cyclophyllum* and some small herbs as *Niphogeton lingula*, *Eriocaulon microcephalum*, *Senecio subruncinnatus*. *Glossidium aversum*, *Cladonia furcata*, and *Cladonia* (subg. *Cladina) confusa* are common lichens. Vicariating species of *Espeletia* are e.g. *E. summapacis*, *E. grandiflora* var., *E. lopezii* var. *major*, *E. incana* and *E. murilloi*.

In the upper reaches at 4000 m, e.g. in the Páramo de Sumapaz, a number of species of the upper condensation zone may be found in boggy, dense *Swallenochloa-Breutelia* slope vegetation with *Espeletia summapacis*, e.g. *Lachemilla nivalis*, *Luzula gigantea*, *Montia* cf. *meridensis*, *Valeriana plantaginea*, *Bartramia angustifolia*, *Herbertus subdentatus*, and composite shrub of *Senecio vernicosus* and *Diplostephium alveolatum*.

Peat growth started here about 5000 years B.P. (COL 266-GRN 8457 - 5090 B.P. ± 25); this date is based on radiocarbon dating of the base of the peat on the Rabona watershed at 4000 m. In view of similar and other ages for páramo peat, most of these bogs must have originated about 5000 years ago, or some 3000 years ago at the bounderies of Andean pollenzones VII an VIII when the climate became colder and more humid (Van der Hammen & Gonzalez, 1960b; Van der Hammen, pers. comm.).

Bamboo communities with *Sphagnum* and/or *Breutelia* prefer moderately acid (pH 4.6-5.4), humid, thick peaty soils. They are common to all humid páramos of the Colombian Cordillera Oriental between c. 3425 and 4000 m. As stated before, these communities are in fact azonal but are discussed here for their large distribution on the humid side of the mountains.
The area of zonal vegetation proper is proportionally smaller on the cloudy and wet side of the Cordillera.

11. Community of *Swallenochloa* with *Eryngium humile* and *Jensenia erythropus*
Fig. 19 (also Fig. 75)
photo: Cleef 1978, photo 165; Breure 1976, Fig. 25

This type of zonal bamboo-bunchgrass páramo occurs usually with stem rosettes on sloping ground and on moderately to very steep slopes. *Calamagrostis effusa* or *Swallenochloa tesselata* each may cover up to about 70 %. Vicariant species of *Espeletia* are e.g. *E. grandiflora* (div. var.), *E. annemariana*, *E. curialensis*, *E. cleefii*, *E. discoidea* var. *brevis* and *E. incana*. The presence of *Rhynchospora ruiziana*, *Eryngium humile*, *Gentiana sedifolia*, *Jensenia erythropus* is differential against other communities. Scarce or absent are: *Oreobolus obtusangulus* ssp. *rubrovaginatus*, *Grammitis moniliformis*, *Sphagnum* spp., *Cladia aggregata*, Eriocaulaceae, *Cladonia andesita* and *Arcytophyllum muticum*.

The humic black clayey soils are about 1 m thick. The upper peaty soillayer is moderately acid with a pH of 4.6 to 5.5.

The vegetation can easily be burned in the dry season. On the burnt sides there is a remarkable increase of herbaceous rosette species, e.g. *Eryngium humile*, *Lysipomia sphagnophila* ssp. *minor* var. *minor*, *Rhizocephalum candollei*, *Castilleja fissifolia*. Hygrophytic and skiophytic elements in the bryophyte layer become less common. This type of bamboo-grassland is apparently common throughout the humid páramos of the Colombian Cordillera Oriental between 3450 and 3850 m. A major part of the Páramo de Sumapaz is covered with this kind of bamboo-bunchgrass vegetation with *Espeletia* stemrosettes, reaching up to 4000 m.

12. Community of *Swallenochloa* with *Rhynchospora paramorum*/*Castratella piloselloides* and *Oreobolus obtusangulus* ssp. *rubrovaginatus*
Fig. 20, 10c

This community is mostly found on the well-drained or driest places in the lower bamboo páramos throughout the Colombian Cordillera Oriental between c. 3270 and 3875 m. Generally *Calamagrostis effusa* dominates over *Swallenochloa tesselata*. Characteristic and frequent species are *Hypericum strictum*, *Bartsia* sp., *Rhynchospora macrochaeta*, *Rhynchospora paramorum*, *Oreobolus obtusangulus* ssp. *rubro-vaginatus*, *Oritrophium peruvianum*, *Vaccinium floribundum* var. *ramosissimum*, *Pernettya prostrata* (mostly var. *purpurea*), *Cladia aggregata* and *Halenia* spp. Less common are *Calamagrostis bogotensis*, *Azorella cuatrecasasii*, *Arcytophyllum muticum* and *Paepalanthus andicola* var. *villosus*.

This vegetation type may be subdivided in 1) slope vegetation, with *Castratella piloselloides*, *Rhacocarpus purpurascens* and *Sisyrinchium pusillum*, and 2) boggy stands, with *Sphagnum* spp. (e.g. *S. compactum*, *S.* sect. *Malacosphagnum*).

The slope vegetation may be further subdivided in vegetation at intermediate altitudes (c. 3550 - 3875 m) with *Castilleja integrifolia* and *Aragoa cupressina*, and in vegetation at lower levels (3270-3320 m) with such characteristic species as *Lysipomia muscoides* ssp. *simulans*, *Xyris* spp., and *Paepalanthus pilosus* and *P. lodiculoides* var. *lodiculoides*. The main bamboo cover here is larger than in higher parts. Vicariant associated species are e.g. *Espeletia congestiflora*, *E. grandiflora*, *E. lopezii* var. *major* and *E. annemariana*. *Rhacocarpus* - *Swallenochloa* slope vegetation is found in humid páramos on brownish to black humic, thin (10-40 cm) sandy to clayey soils, moderately acid (pH 4.7-4.8) in the top layer. Slopes are up to 30°. The bryophyte layer is well developed and may cover up to 75%. This kind of *Swallenochloa* slope vegetation is common in all lower bamboo páramos of the Colombian Cordillera Oriental. Its lowermost stands with *Lysipomia muscoides* and *Paepalanthus pilosus* have only been studied in the perhumid bamboo páramos near the Pena de Arnical, NE of Lake Tota (Boyacá).

The boggy vegetation with *Sphagnum* spp., *Paepalanthus lodiculoides* and *Cladonia* spp. is also found on slightly sloping ground. *Castratella piloselloides* *Xyris* spp. and *Rhacocarpus purpurascens* are less common with a cover of less than 3%. The community is found on thicker, moderately acid (pH 4.6-5.3) humic sandy or sandy to clayey soil. The relevés are from the lower humid páramos (3300-3380 m) N and NE of Lake Tota.

13. Community of *Swallenochloa* with *Oreobolus obtusangulus* ssp. *rubrovaginatus*
Fig. 21 (also Fig. 28, 69 & 70)

This zonal humid bamboo - bunchgrass páramo differs from the previous *Swallenochloa* communities by the presence of *Oreobolus obtusangulus* ssp. *rubrovaginatus* in combination with the absence of *Sphagnum* spp., *Castratella* spp., *Rhynchospora paramorum*, *Xyris acutifolia*, *Eryngium humile*, *Gentiana sedifolia* and *Jensenia erythropus*.
In this unit can be recognized the following types: a) *Oreobolus* - *Swallenochloa* páramo with *Rhacocarpus purpurascens* *Oritrophium peruvianum* and Eriocaulaceae (*Paepalanthus karstenii*, *Eriocaulon microcephalum*). This kind of bamboo páramo vegetation is common throughout the study area between 3300 and 4150 m. It dominates especially bamboo-bunchgrass páramo (4000-4150 m).
The humic black clayey soils are about 30 cm thick or less. The pH of the moderately acid topsoil is 4.6-4.9 and the community is found on gentle as well as on steep slopes.
b) *Oreobolus* - *Swallenochloa* - bamboo-dwarfshrub páramo with *Hypericum laricifolium* ssp. *laricifolium* and *Blechnum loxense* as common associated species. This low shrubby bamboo vegetation is generally rich in species and is only locally noted in the lower páramos between 3300 and 3600 m.

Bunchgrass páramo

This páramo grassland is in the Cordillera Oriental of Colombia dominated by tussocks or bunches of *Calamagrostis effusa* with stemrosettes of *Espeletia* or *Espeletiopsis*. Some species of the Espeletiinae are nearly restricted to the bunchgrass páramo; e.g. *Espeletia barclayana*, *E. brachyaxiantha*, *E. jaramilloi*; and *Espeletiopsis corymbosa*, *E. guacharaco*, *E. muiska*, *E. colombiana*. Species of *Espeletiopsis* are practically absent in the bamboo páramo. Only a few species of *Espeletia* are common to both, the bunchgrass and the bamboo páramo where they occur in the same physiographic setting such as

Espeletia congestiflora, or in different habitats such as *E. grandiflora*. Other species common throughout the bunchgrass páramo are *Gongylanthus liebmannianus*, *Stephaniella paraphyllina*, *Gnaphalium antennarioides*, *Hypericum strictum*, *Castilleja integrifolia*, *Bartsia* sp., *Hieracium avilae*, *Hypochaeris sessiliflora*, *Vaccinium floribundum* var. *ramosissimum*, *Pernettya prostrata*, *Cladia aggregata*, *Cladonia isabellina*, *C. capitata*, *Siphula* sp., *Diploschistes* sp., *Halenia* sp., *Sisyrinchium pusillum*, *Polytrichum juniperinum*, etc.

Soils are 10 to 70 cm thick and consist of dark-brownish to black humic (sandy) clay in the lower parts or of thin brownish coarse sand in the upper grass páramo. The toplayer is moderately acid with a pH of about 4.8 (3.9 - 5.3). The zonal vegetation is found on moderately to very steep slopes.

Lower bunchgrass páramo

Bunchgrass vegetation with many species in the lowermost part of the grass páramo on the dry side of the Colombian Cordillera Oriental belongs to this zone of the páramo vegetation.
The communities of the lower bunchgrass páramo are mostly present on sloping to very steep parts. The toplayer of the brownish to black sandy an clayey soils is moderately acid.

14. Lower *Calamagrostis effusa* bunchgrass páramo with *Espeletiopsis*
Fig. 22 (also Fig. 78)

This type of tussock grassland is easily recognized by the presence of geographically vicariant species of *Espeletiopsis* (e.g. *E. corymbosa*, *E. guacharaco*, *E. muiska*) with their characteristic brittle, coriaceous leaves Stemrosettes of this genus have not been found in other communities of the lower bunchgrass páramo. Bamboos are absent in this vegetation, but may be present in adjacent flat areas.

This open grassland dominated by *Calamagrostis effusa* (65 - 95% cover) contains some scattered constituents of the dry dwarfshrub páramo: e.g. *Arcytophyllum nitidum* (1 - 15% cover), *Brachyotum strigosum*, *Siphocampylus columnae*, *Bucquetia glutinosa* and low *Gaultheria* species with glandular hairs such as: *G. cordifolia*, *G. hapalotricha*, *G. regia*, *G. rigida*. Other characteristic species are *Achyrocline lehmannii*, *Acaena cylindristachya*, *Geranium sibbaldioides*, *Luzula* cf. *racemosa*, *Polytrichum juniperinum*, *Lobelia tenera*, *Hypericum mexicanum*, and *H. caracasanum* ssp. *cardonae*.

The community is common on moderately to very steep slopes. The well-aerated soils consist of brownish-black sand or sandy clay and are 20-70 cm thick. The pH of the toplayer is about 4.8 (4.5 - 5.3). This type of *Espeletiopsis*- bunchgrass páramo was mainly studied between 3500 and 3750 m (range 2935 - 3760 m) in dry páramos surrounding the Sabana de Bogotá (e.g. Neusa) and extending towards the Páramo de Guantiva. It may be common throughout the dry páramos of the Colombian Cordillera Oriental.

15. Lower *Calamagrostis effusa* bunchgrass páramo with *Espeletia*, *Oreobolus obtusangulus* and *Castratella*
Fig. 23 (also Fig. 51, 71, 75 and 78)
photo: Cleef 1978, photo 164, 166
Gradstein et al. 1977, plate 2B

This open páramo bunchgrass vegetation or meadow is dominated either by *Calamagrostis effusa* (occasionally *Cortaderia sericantha*) or by Cyperaceae (*Rhynchospora paramorum*, *Oreobolus obtusangulus* ssp. *rubrovaginatus*). Characteristic are a number of sessile rosette and tufted species, which are nearly absent in the previous community: e.g. *Castratella piloselloides*, *C. rosea*, *Rhynchospora paramorum*, *Oreobolus obtusangulus* ssp. *rubrovaginatus*, *Oritrophium peruvianum*, *Azorella cuatrecasasii*, *Rhynchospora macrochaete*, *Gnaphalium antennarioides* and *Altensteinia leucantha*. Stem rosettes belong to geographically vicariant species of *Espeletia*, e.g. *E. congestiflora*, *E. barclayana*, *E. grandiflora*. *Arcytophyllum nitidum* has a low cover (1 - 5%); *Swallenochloa* is virtually absent.

The unit may be subdivided into:
a) a *Calamagrostis effusa* dominated grassland in the dry páramos (3450-3750 m), and
b) low cyperaceous meadows with few *Calamagrostis* bunches (cover up to 35%) in atmospherically humid páramos (3070-3700 m). *Rhynchospora paramorum* may cover up to 75% and *Oreobolus obtusangulus* ssp. *rubrovaginatus* up to about 50% of those meadows, which are floristically also different by the presence of *Xyris acutifolia* (or *X. subulata*) and of *Tofieldia falcata*, *Rhacocarpus purpurascens*, *Sphagnum compactum* and *Pilopogon laevis*. This cyperaceous humid páramo meadow has ecologically an intermediate position between the preceeding type *Calamagrostis effusa* dominated páramo (15^{a}) and the *Swallenochloa* - *Calamagrostis effusa* vegetation (12) in the grass paramos.

These both types of the lower bunchgrass páramo with *Castratella* are generally found on moderately steep slopes (8 - 15°).
Most of the soils are humic black sandy clay, 40 to 85 cm thick. The pH of the toplayer is slightly lower than in the *Espeletiopsis* lower bunchgrass páramo, 4.5 - 4.9 (range 4.0 - 5.1). This zonal community of lower bunchgrass páramo with *Castratella* spp. and/or *Rhynchospora paramorum* was observed in the entire study area, mainly between 3500 and 3750 m (range 3070 - 3760) both on the dry and on the humid side of the Cordillera. It is nearly absent in the most arid páramos, e.g. the west side of the Sierra Nevada del Cocuy, where a lower grass páramo zone is not present. In view of the wide distribution of the characteristic species, the unit is likely to occur throughout the Colombian Cordillera Oriental. *Castratella piloselloides* is found up to 3800 m, *Rhynchospora paramorum* up to 3950 m.
I believe, most relevés of open bunchgrass-dominated lower páramo vegetation published by Lozano & Schnetter (1976) from the Páramo de Cruz Verde belong to this community. The same applies to such relevés of the adjoining Páramo de Monserrate above Bogotá, presented by Sturm (1978).

16. Lower *Calamagrostis effusa* bunchgrass pâramo with *Oreobolus obtusangulus* ssp. *rubrovaginatus*
Fig. 24 (also Fig. 50)

The open *Calamagrostis effusa* dominated vegetation is characterized by tufts or low cushions of *Oreobolus obtusangulus*, the cover of which is 1 - 10% (40%). Frequently associated species are *Rhynchospora macrochaete*, *Oritrophium peruvianum*, *Gentianella corymbosa*, *Sisyrinchium pusillum*, and *Cladia aggregata*. *Rhynchospora paramorum* is infrequent; *Swallenochloa* and *Castratella* are absent.

Two types of vegetation can be recognized in this community.

a) The first one is zonal and covers dry slopes (5 - 35°) between 3600 and 3900 m. In the humid grass pâramos it is found adjacent to bamboo communities.
Geographically vicariant species of *Espeletia* are: *E. conglomerata*, *E. brachyaxiantha*, *E. discoidea* var. *brevis* (transgr.), *E. barclayana*, *E. grandiflora*.
The soils are 25 to 75 cm thick and consist of silty darkbrown to black clay. The pH of the humic top layer is about 4.8.

b) The second type is a more or less open *Calamagrostis effusa* grassland with azonal tendencies (Fig. 71). This vegetation is found on gently slopes (2 - 6°) and is transitional towards *Sphagnum* bogs. It is marked by a number of additional more or less hygrophytic species, e.g. *Carex pichinchensis*, *Blechnum loxense*, *Xyris acutifolia*, *Sphagnum compactum*, *S. cyclophyllum*, *S. magellanicum*, *Kurzia verrucosa*, *Lepidozia* sp., *Cladonia* subg. *Cladina*, *Siphula* sp., *Rhacocarpus purpurascens*. Cyperaceae and *Sphagnum* spp. may cover up to 35%. Both the subspecies *rubrovaginatus* and the ssp. *obtusangulus* of *Oreobolus* are found, the latter often associated with low hummocks of *Valeriana stenophylla*. *Espeletia chocontana* was noticed only in this vegetation type. In addition *Espeletia grandiflora* var., *E. miradorensis* and *E. killipii* var. *chisacana* are recorded as vicarious species. Soils are humic black clay, about 80 to more than 120 cm thick. The pH of the peaty top soil layer is 4.4 to 5.5. This azonal peaty bunchgrass vegetation has been studied in dry pâramos in the southern part of the Colombian Cordillera Oriental (Neusa to Sumapaz) between 3450 and 3700 m.

17. Lower *Calamagrostis effusa* bunchgrass páramo with *Espeletia argentea* or *E. boyacensis*
Fig. 25 (also Fig. 70)

This dry *Calamagrostis effusa* bunchgrass páramo is readily recognized by the almost sessile rosettes of both geographically vicarious species of *Espeletia* sect. *Argentina* Cuatr. (ined.): *E. argentea* and *E. boyacensis* with numerous long and small, white to silvery leaves. The tussocks cover 30 to 90%. Characteristic species are *Acaena cylindristachya*, *Geranium sibbaldioides*, *Luzula* cf. *racemosa*, *Arcytophyllum muticum* and *Polytrichum juniperinum*. Dwarfshrubs (e.g. *Arcytophyllum nitidum*, *Brachyotum strigosum*) attain 25 - 30% cover in stands near the dwarfshrub páramo zone. *Swallenochloa tesselata* is nearly absent, just as other characteristic species as *Castratella piloselloides*, *Rhynchospora paramorum*, *Oreobolus obtusangulus* and *Oritrophium pervianum*, characteristic of other lower grass páramo communities in the Colombian Cordillera (see 3.1). The greatest floristic affinity is with the *Espeletiopsis* - lower bunchgrass páramo vegetation (see 4.1), with many characteristic species in common.
The *Espeletia* - *Calamagrostis effusa* páramo described here is mainly found on black humic sandy or silty clay or on black sandy soil, 25 to 100 cm thick. The well-aerated, frequently stony top soil has a pH of 4.1 to 4.8 (5.2). The community may be found in flat areas, but is mainly present on moderately to very steep slopes in the southern part of the Cordillera Oriental (Guantiva to Sumapaz), between 3600 and 3800 m (range 3450 - 3865 m).
The "*Espeletietum argentea-Calamagrosti effusum*", described by Cuatrecasas (1934) from the Páramo de Guasca, is largely identical with this community, its *Espeletia grandiflora* patches, however, to the *Castratella*-bunchgrass páramo.

18. *Acaeno cylindristachyae - Plantaginetum sericeae* ass. nov.
type rel. 568; table 1. Fig. 26 (also Fig. 10^d, 13, 18)

Physiognomy: The dry and open low herbaceous páramo vegetation is dominated by small ground rosettes (cover 20-80%) with white-silvery leaves. The dominant foliage has the characteristics of xeromorphy: the shiny small leaves are covered with a sericeous dense indumentum of appressed silvery hairs.

Composition & syntaxonomy: *Plantago sericea* ssp. *argyrophylla* is a selective character species. Dr. K. Rahn (in prep.) recognized seven subspecies of *Plantago sericea*, widely distributed in the tropical high Andes from northern Argentina and Chile to Colombia and Venezuela, with some representatives in the Mexican mountains. *Acaena cylindristachya* is a preferential character species. Common species are *Stephaniella paraphyllina*, *Gongylanthus liebmannianus*, *Siphula* spp. (e.g. *S. fastigiata*), *Polytrichum juniperinum*, *Aciachne pulvinata*, *Luzula* cf. *racemosa*, and crustose lichens of *Diploschistes* and/or *Lecidea*. Locally associated are *Racomitrium lanuginosum* on foggy crests, *Pilopogon laevis* and *Stereocaulon atlanticum* in atmospherically humid habitats in the lower páramo, and the tiny *Funaria lindigii*. The average number of species is about 16 (12 - 19 in 5 relevés).
The new association has the greatest affinity with the *Aciachnetum pulvinatae* (see 107) and with zonal *Calamagrostis effusa* - Espeletiinae communities with *Acaena cylindristachya* and *Luzula racemosa* (see 10, 12 & 14).

Table 1. *Acaeno cylindristachyae - Plantaginetum sericeae* ass. nov.

rel.nr.	x564	x568	159	102	x407A	553x
relevé area m^2	4	4	4	1	1	2
slope (degree)	14	9	30	30	10	15
cover % grasses	3	3	1	-	3	2
dicots	72	81	27	45	10	75
soil	s/g	s/g	s	c	g	s/g
pH top soil	-	-	5.1	5.3	-	-
approx. number of species	19	17	15	18	12	7
alt. m	3825	3890	4065	3500	3880	3425
locality	Alm	Alm	Coc	Pi	Gua	Alm
cover %		▲				
c & d taxa and companions						
c *Plantago sericea* ssp. *argyrophylla*	60	80	25	45	10	70
Acaena cylindristachya	2	1	1+	<1	<1	5
Aciachne pulvinata	2	1	<1			2
Luzula cf. *racemosa*		<1+	<1+	1+	5	
Siphula sp.	<1	<1		1+	<1	
Lecidea/Diploschistes	<1+		1?	1/<1		1
Gongylanthus liebmannianus	10	10	50	20		
Stephaniella sp (p.)	5	<1	<1	<1		
Polytrichum juniperinum	1	<1	10	1		
Pernettya prostrata var. *prostrata*	10		<1		<1	
Oxalis sp.	<1	<1+	<1+			
Stereocaulon sp. *(S. atlanticum)*	<1	<1		<1		
Campylopus sp.	<1+	2		2		
Hypericum caracasanum ssp. *cardonae*	<1	<1				
Agrostis trichodes	1		<1			
Cladia aggregata	<1			1+		
Bryum sp. (fruct.)	<1		<1+			
Agrostis breviculmis		2			3	
Agrostis haenkeana			<1			<1
Racomitrium crispulum/R. lanuginosum				2	70	
Castilleja sp.	<1					<1
Leptodontium pungens	<1+				5	
Paepalanthus karstenii	<1					
Lachemilla sp.		<1+				
Funaria lindigii		5				
Cora pavonia		<1				
Parmeliaceae		<1				
Hypericum selaginoides			1			
Bartramia sp.			<1			
Pilopogon laevis				35		
Baeomyces imbricatus				<1+		
Gentianella corymbosa				<1		
Aphanactus piloselloides				<1		
Cladonia boliviana				<1+		
Cladonia andesita				<1		
Carex aff. conferto-spicata					1	
Thamnolia vermicularis					1	
Hypochoeris sessiliflora					<1	
Danthonia secundiflora						<1

Localities: Alm Almorzadero, El Tutal
Coc Cocuy, Lagunillas
Pi Pisva, El Cadillal
Gua NW of Belén, Laguna Larga

Synecology: This groundrosette community is present on level or in places sloping up to about 30°. The shallow gravelly brown clayey soil is 5 - 10 cm thick. pH of the toplayer is 5.1 and 5.3 in sandstone areas; pH data from the calcareous bedrock are not available. The wide distribution of this community on the dry side of the Páramo del Almorzadero may be attributed to intensive grazing of cattle in combination with a shallow soil, which is dry due to high porosity of the calcareous bedrock. The natural habitats of this xerophytic community are most probably places near crests and ridges with only a thin topsoil.

Distribution: The *Acaeno - Plantaginetum sericeae* is optimally developed on the dry southern slopes of the Páramo del Almorzadero between 3700 and 3900 m on calcareous rock. This zonal dicot association is found in the northern páramos of the study area and has been recorded in the páramos of Guantiva, Pisva, Cocuy and Almorzadero between 3425 and 4070 m. According to Dr. K. Rahn (in prep.) the subspecies *argyrophylla* of *Plantago sericea* occurs as far as the páramos of the Sierra Nevada de Mérida (Fig. 10^{d}). It is unknown whether or not this association is also present in the Venezuelan Andes.

Upper bunchgrass páramo

The highest located bunchgrass páramos extend from about 3900-4000 m up to the lower limit of the superpáramo (4250-4400 m). Spaced bunches of *Calamagrostis effusa* with up to 50% cover make up the main vegetation, and are usually associated with stemrosettes of the Espeletiinae, e.g. *Espeletiopsis colombiana, E. guacharaco, E. santanderensis,* and *Espeletia lopezii* var. *alticola* , *E. cleefii* and *E. azucarina*. Common species in the gravelly spaces between the tussocks are: *Stephaniella paraphyllina, Gongylanthus liebmannianus, Luzula* cf. *racemosa, Polytrichum juniperinum, Pernettya prostrata* var. *prostrata, Cladia aggregata, Cora pavonia, Bartsia* spp., *Castilleja* spp., *Hypochoeris sessiliflora, Siphula* sp., *Agrostis boyacensis, Campylopus* spp., *Grammitis moniliformis* and *Zygodon pichinchensis*. Dwarfshrubs of *Lachemilla polylepis, Diplostephum colombianum* and *Loricaria complanata* are locally common. Open gravelly stretches may contain superpáramo species, e.g. *Senecio cocuyanus, S. adglacialis, S. cleefii, Lycopodium crassum, Draba litamo, Loricaria complanata*. Frost heaving acts almost every night in open barren places. In contrast to the lower grasspáramo scarced or absent species are *Gentianella corymbosa, Azorella cuatrecasasii, Calamagrostis boyacensis, Geranium sibbaldioides, Rhynchospora macrochaeta, Rhynchospora paramorum* and *Arcytophyllum muticum*.
Upper bunchgrass páramo is well developed in the Sierra Nevada del Cocuy (3900-4500 m) and has been studied in the summit areas (4000-4200 m) of the Páramo de Guantiva and the Páramo del Almorzadero. The dry crests and watershed areas at 4000 m in the Páramo de Sumapaz carry an open sward of a similar nature. It seems appropriate to include the upper bunchgrass fringe on the clouded side of the mountains, although some floristic differences may be noticed.

19. Upper *Calamagrostis effusa* bunchgrass páramo with *Espeletiopsis*
Fig. 27 (also Fig. 34)

This bunchgrass community has its greatest distribution on the dry side of the Sierra Nevada del Cocuy, where *Jamesonia bogotensis* is characteristic. The lowermost stands between 3900 and 4100 m have a number of species in common

with the lower bunchgrass páramo, e.g. *Acaena cylindristachya, Gnaphalium antennarioides, Diploschistes* sp., *Lecidea* sp., *Castilleja fissifolia, C. integrifolia, Baccharis tricuneata, Carex* sp. *(C. pygmaea* type*), Geranium subnudicaule* or *(G. multiceps), Lycopodium spurium, Arcytophyllum nitidum* and occasionally *Plantago sericea* ssp. *argyrophylla.*
This open grassland is locally found up to 4500 m in nunatak-like places, which became free of snow and ice many thousands of years ago and were not covered by ice during the recent Neoglacial (Van der Hammen et al., 1981).
Calamagrostis recta, another major bunchgrass species, is characteristic, and may be (co)dominant with *Calamagrostis effusa. Calamagrostis recta* is the most common bunchgrass in the páramos of the Colombian Cordillera Central (Cleef et al., in press) and in the Ecuadorian páramos. This species is rare in the study area and could only be collected in the upper reaches of the Páramo de Guantiva and on the nunatak-like divide between the high valley of Lagunillas and the Páramo Cóncavo on the SW-side of the Sierra Nevada del Cocuy. The grasscover on such nunatak-like high crests is generally limited and does not exceed 40%. *Espeletia lopezii* var. *alticola* and *Poa* cf. *pauciflora* (5661) are frequently associated. The proportion of the superpáramo taxa is conspicuously high, as may be expected at this altitude.
Geographically vicariating species of *Espeletiopsis* are *E. santanderensis* in the Páramo del Almorzadero and Santurbán, *E. guacharaco* in the Páramo de la Rusia and Guantiva and *E. colombiana* in the Sierra Nevada del Cocuy.

Soils under the *Espeletiopsis - Calamagrostis effusa* vegetation in the Sierra Nevada del Cocuy are thin (to 20 cm), and they consist mainly of very dark gray or brown, coarse sand with a pH of 5.1 (range 4.9 - 5.3). The upper bunchgrass páramo is covering valley slopes as steep as 40° and moraines. According to van der Hammen et al. (1981) most of these moraines (in the Sierra Nevada del Cocuy) belong to Drift 5, and were formed during the Bocatoma stade between 12,000 and 7.500 B.P.

20. Upper *Calamagrostis effusa* bunchgrass páramo with *Espeletia*
Fig. 28

This open bunchgrass community is common on the clouded and misty side of the mountains, where it fringes the upper limit of the zonal páramo. Floristically, this community differs from that on the opposite and dry side of the Cordillera by the presence of species of *Espeletia, Cerastium, Halenia* and *Poa*. Other hygrophytic species, which are absent in the dry and highly located bunchgrass páramos, gradually appear towards the humid side, e.g. *Rhacocarpus purpurascens, Carex pichinchensis, Oreobolus obtusangulus* ssp. *rubrovaginatus,* and *Elaphoglossum* spp. The cover of *Anastrophyllum leucostomum* becomes larger, whereas that of the xerophytic *Stephaniella paraphyllina* diminishes in the bottom layer. Geographically vicariating *Espeletia* species are e.g. *E. conglomerata* (Almorzadero), *E. cleefii* (Cocuy), *E. azucarina* (Guantiva) and *E. grandiflora* (Sumapaz). This open grassland gradually passes into bamboo-bunchgrass vegetation with the appearance of the first clumps of dwarfed *Swallenochloa tesseleta*. Locally, along the upper bunchgrass limit (4260-4320 m), tussocks of *Lorenzochloa erectifolia* replace *Calamagrostis effusa* on fine sandy soils.

Soils, covered with the upper *Espeletia - Calamagrostis effusa* community, consist of brownish to black coarse sand with a pH of about 4.8. In the upper *Lorenzochloa* tussock stands, pH values of 5.4 and 5.5 have been measured, however, and this agrees better with the values in the lower superpáramo.

Calamagrostis recta vegetation on high nunatak-like watershed areas on the opposite dry side has species of *Espeletia*, *Poa*, *Halenia*, and *Cerastium* in common with the *Espeletia*-bunchgrass páramo. Frequent fog may be one of the causes of this floristic similarity between the two *Espeletia*-bunchgrass communities.

THE SUPERPÁRAMO

The superpáramo is the highest vegetation belt in the tropical northern Andes, located between the upper bunchgrass line and the lower limit of the nival belt. Ice-free places (nunataks), with vegetation in the nival belt belong to the upper superpáramo. Due to the high elevation and the tropical diurnal climate, nightfrosts occur daily throughout the year. As a result, the plant cover is scanty, and sessile rosette plants and dwarfshrub are most prominent in the zonal vegetation. Acrocarpous mosses are conspicuous, but they are replaced by liverworts and pleurocarpous mosses in the zonal superpáramo located in the upper condensation zone (Gradstein et al. 1977). Soils are generally stony and thin without a distinct profile. The brownish or grayish toplayer is less acid than in the grass páramo (pH 5.1-5.6).

At present, superpáramos are isolated in the highest parts of the Colombian Cordillera Oriental. During certain intervals in times of Pleistocene glaciation they were larger and they may have reached down to about 3500-3000 m (e.g. on moraines). During the coldest periods the superpáramo areas of the Sumapaz and Cocuy were much closer to each other but never adjoining; those of the Cocuy and Almorzadero, however, may have been united (Van der Hammen et al. 1981; Van der Hammen & Cleef, in press).

A number of vascular endemics are characteristic for the superpáramo. *Senecio niveo-aureus* is endemic for the Colombian Cordillera Oriental and is replaced by the vicariating closely related *Senecio latiflorus*, endemic in the high páramos of the Colombian Cordillera Central. Endemism is best examplified by species belonging to different sections of *Senecio* occuring at high altitudes, and species of *Draba*. Several endemic *Senecio* species are restricted to one summit or one range; e.g. *Senecio santanderensis*, is only known from the Páramo del Almorzadero and the Páramo de Santurbán, and its close ally *S. cocuyanus* to the Sierra Nevada del Cocuy. According to the theoretical model developed by Mc Arthur & Wilson (1967) for oceanic islands and applied by Vuilleumier (1979) to the páramo and puna avifauna, the highest rate of speciation for the páramos of the Colombian Cordillera Oriental is to be expected in the Sierra Nevada del Cocuy. This Sierra contains the highest range of the Cordillera Oriental and the largest recent extension of the superpáramo zone. Most of the endemic species of *Senecio* are actually found here, and they include the herbaceous *Senecio cocuyanus*, *S. adglacialis*, *S. supremus*, and *S. pasqui-andinus* and the shrubby species *S. guicanensis* and *S. cleefii*. *Draba litamo* and *D. hammenii* are endemic also, just as some new, undescribed species of *Draba* (8882, 8883, 8989, 8991, 10182). This region has at least one of these, a cushion species (8990, 9014), in common with the superpáramo of the Páramo del Almorzadero.

The superpáramo of the Nevado de Sumapaz (4250 m) probably contains at least one endemic large rosette species of *Draba* (1116, 7668), apparently not yet described. The limited size (less than 1 km^2) and the comparatively low altitude (4250-4300 m) of the Nevado de Sumapaz may account for the smaller number of endemic vascular species. *Senecio canescens*, *S. niveo-aureus*, *S. formosus* and *S. flos-fragrans* are species common to this region and the superpáramo of the Sierra Nevada del Cocuy. *Senecio vernicosus* and *S. summus* of the Sumapaz are the only species in common with the high páramos of the Colombian Cordillera Central; the latter species is also present in Ecuadorian páramos. The large number of species with their main distribútion in Central Colombian and Ecuadorian páramos is noteworthy in the high Páramo de Sumapaz. The following species belong to this southern páramo flora: *Senecio repens, S. vernicosus, S. summus, Ourisia muscosa, Werneria humilis, Valeriana plantaginea, Diplostephium rupestris, Baccharis caespitosa* var. *alpina, Geranium multipartitum, Cerastium imbricatum, Rumex tolimensis, Potamogeton asplundii*. A few of them are present also in the Sierra Nevada del Cocuy, e.g. *Valeriana plantaginea, Ourisia muscosa* and *Cerastium imbricatum*. On the other hand, the superpáramo of the Sierra Nevada del Cocuy have also a few species in common with the Colombian Cordillera Central, which have not yet been recorded from the Páramo de Sumapaz, e.g. *Distichia muscoides, Floscaldasia hypsophila, Werneria crassa*. Proportions of various phytogeographic elements in the vascular floras of the Cocuy and Sumapaz superpáramos are reported in Van der Hammen & Cleef (in press).

In the zonal superpáramo vegetation the absence can be noticed of *Calamagrostis effusa* tussocks and other associated upper grass páramo species as *Acaena cylindristachya, Achyrocline lehmannii, Gnaphalium antennarioides, Castilleja fissifolia, Siphula* spp. and *Hieracium avilae*. White and yellow flowering sessile rosettes with large penroots of *Hypochoeris sessiliflora* s.l. are common to all superpáramos. Species of *Senecio, Draba, Bartsia, Lucilia, Luzula* cf. *racemosa* and *Racomitrium crispulum* are frequent also. The last species, however, has the highest cover in the humid superpáramo, especially in the upper condensation zone where it is associated with many characteristic bryophytes, e.g. *Bartramia angustifolia, Breutelia integrifolia* and *B. lorentzii, Rhacocarpus purpurascens, H. acanthelius, Herbertus subdentatus, Metzgeria metaensis, Plagiochila dependula, Radula sonsonensis* and *Riccardia squarrosa*. The moss *Zygodon pichinchensis* attains its highest cover near the boundary between the superpáramo and grass páramo, especially in the Sierra Nevada del Cocuy. *Pernettya prostrata* is most common in the superpáramos on the dry side of the mountains, whereas *Senecio niveo-aureus, Erigeron chionophilus* and *Valeriana plantaginea* are characteristic for the humid páramos on the opposiste cloudy side. Espeletiinae may penetrate the lowermost part of the superpáramo on the humid side of the mountains and may be found as high as about 4650 m on nunatak-like divides, e.g. the Cóncavo-Bocatoma divide in the Sierra Nevado del Cocuy.

Partly edaphically determined pioneer vegetation, similar to zonal superpáramo vegetation, occurs on young (Neoglacial) moraines, down to several hundreds of meters below the climatic zonal boundary of upper grass páramo and lower superpáramo.

Superpáramo vegetation in the Colombian Cordillera Oriental has been studied on 1) the Nevado de Sumapaz (4100-4250 m) and the adjacent high peaks of Sitiales (4040 m) and S. Mateo (estimated at 4100 m) in the Páramo de Sumapaz; 2) the Pan de Azucar (4220-4270 m) and Morro Verde, the highest peaks of the Páramo de Guantiva near Belén (Boyacá); 3) the southern part of the Sierra Nevada del Cocuy ((4250) 4400-4800 m) and 4) the Páramo del Almorzadero (4250-4375 m).
Not studied was the superpáramo vegetation on the Morro Nevado (c. 4300 m) in the Páramo Romeral about 20 km W of Pamplona, and on the highest ridges of the Páramo de Santurbán (c. 4100 m), about 3 km SW of Vetas (Santander - Santander de Norte). According to Dr. J. Cuatrecasas (in litt.) the last summit areas are heavily grazed and dry.

For comparison relevés were made in the superpáramo of the Colombian Cordillera Central in the Parque Los Nevados (Cleef et al., in press), on the volcano Puracé, and in the Páramo de Piedras Blancas, Sierra Nevada de Mérida, Venezuela.

L o w e r s u p e r p á r a m o

Most relevés were made in the lower superpáramos, which reach up to 4500 m. The climatologically dry and the humid zonal lower superpáramos are floristically basically different from each other, and they are found on all summit areas with superpáramo vegetation mentioned before.
Vegetation of *Luzula racemosa* and *Pernettya prostrata* is characteristic for the moraines on the dry side of the Cordillera, whereas communities with *Agrostis breviculmis, Senecio niveo-aureus, Erigeron chionophilus* and *Valeriana plantaginea* are found on gravelly screes and on outcrops in the superpáramo on the opposite humid side. Calcareous rocks were locally present in all investigated superpáramos.
In general the humid lowermost superpáramos support a more luxuriant vegetation which is richer in species. The bryophyte layer is well developed and has a larger cover than on the dry side of the Cordillera, where bryophytes are scarce or absent.

21. *Loricarietum complanatae* ass. nov.
type: rel. 468; table 2. Fig. 28, 29, 30.

Physiognomy: The community typically is a high-altitude páramo dwarfshrub vegetation of 3 layers:
1) an open dwarfshrub layer consisting of compositae of about 1-1.5 m high (cover 30-60%);
2) a herbaceous layer up to 35 cm high (20-25%);
3) a poor open or well-developed nearly closed bryophytic ground-layer.

Xeromorphic leaves are common. Thus, the most prominent species *(Loricaria complanata, Jamesonia goudotii, Lachemilla nivalis)* have a more or less imbricate leptophyllous foliage, often with indumentum or hairs of another nature. The coriaceous leaves of the shrubs are revolute and brownish.

Composition & syntaxonomy: Character species are *Loricaria complanata* (exclusive), and *Jamesonia goudotii* and *Lachemilla nivalis* (both preferential). Other common taxa are *Hypochoeris sessiliflora, Bartsia* spp., *Oritrophium peruvianum, Cladia aggregata, Cladonia* subg. *Cenomyce* and *Campylopus pittieri,* etc.
The number of taxa is about 25 in the driest páramos (rel. 460) and is about twice as high in the wettest páramos (rel. 270). *Loricaria,* a peculiar woody composite genus, is found in the high tropical Andes from northern Bolivia to Colombia (Cuatrecasas 1954). All three sections of the genus are found in southern Peru. *Loricaria complánata* (sect. *Thuyopsis*) is known from northern Ecuador, the Colombian Cordillera Oriental and Occidental and the Sierra Nevada de S. Marta. Its subspecies *occidentalis* Cuatr. is present only in the southern part of the Cordillera Occidental (3500-3700 m). *Jamesonia goudotii* and *Lachemilla nivalis* are widely distributed from southern Peru to northern Colombia (Tryon 1962; E.G.B. Kieft, pers. comm.). At the generic level, the most prominent vascular taxa of this association belong to the neotropical Andean element.

Table 2. *Loricarietum complanatae* ass. nov.

	460	412	331	270	468
relevé nr.	460	412	331	270	468
relevé area m^2	20	12	20	18	20
slope (degree)	15	20	10	20	5
cover % erect dwarfshrub	55	30	25	35	60
prostrata dwarfshrub	10	-	70	1	-
grasses (bamboos)	2	20	-	10	-
mosses	18	5	-	65	65
liverworts	1	-	-	35	3
soil	g	g	g	g	g
pH top soil	-	5.2	-	5.2	-
approximate number of species	20	14	18	46	19
alt. m	4380	4220	4330	4015	4200
locality	Coc	Gua	Coc	Sum	Coc
cover %	○			○	▲
c & d and other taxa					
Loricarietum complanatae					
c *Loricaria complanata*	50	30	25	35	60
c *Jamesonia goudotii*	15	1	1	1+	5
c *Lachemilla nivalis*	<1	<1+		4	3
d *Oritrophium peruvianum*		3		1	10
Grammitis moniliformis	<1			1	<1
Bartsia sp(p).- greenish fl. (reddish fl.)	<1+	1	<1	<1+	
Cladia aggregata	<1+	<1	<1	<1+	2
Hypochoeris sessiliflora (yellow ray fl.)		<1	<1	2	
Hypericum lancioides			<1	<1	
Oropogon loxensis			1	<1+	
Cladonia subg. *Cenomyce*		<1	<1		1
Jamesoniella rubricaulis	<1			3	
Zygodon pichinchensis	15				<1
Anastrophyllum leucostomum	1				2
Stereocaulon tomentosum			1		
Stereocaulon sp.					1
Agrostis cf. *haenkeana*	<1+				
Peltigera sp(p.)					2
Cora pavonia					1
d & o taxa *pernettyetosum prostratae*					
d *Pernettya prostrata* var. *prostrata*	10		70		
d *Calamagrostis effusa*	1	20			
Campylopus pittieri	2	5			
Carex pichinchensis	<1		15		
Senecio vaccinioides	3		<1		
Lycopodium crassum		1	1		
Senecio cocuyanus			<1		
Sisyrinchium trinerve			<1		
Elaphoglossum mathewsii			<1		
Acaena cylindristachya			<1		
Thamnolia vermicularis			<1		
Puya trianae		1			
Paepalanthus lodiculoides var. *floccosus*		1			
Halenia nivalis		1			
Diplostephium rhomboidale	5				
Diploschistes sp./*Lecidea* sp.	1+				
Gentianella corymbosa	<1+				
Lophonia incisa	<1				

		(460)	(270)	(468)
	d & o taxa *racomitrietosum*			
d	*Racomitrium crispulum*	1	1	25
d	*Rhacocarpus purpurascens*		45	30
d	*Valeriana plantaginea*		<1	2
d	*Riccardia* sp. (*R. wallisii*)		1	<1+
d	*Campylopus richardii*		1	1
d	*Siphula* spp.		1+	1
	Campylopus sp.			10
	Swallenochloa cf. *tesselata*		10	
	Anastrophyllum nigrescens		25	
	Leptodontium wallisii		8	
	Breutelia allionii		5	
	Breutelia chrysea'		3	
	Herbertus subdentatus		5	
	Campylopus sp. (7744)		3	
	Werneria humilis var. *angustifolia*		2	
	Aciachne pulvinata		<1	
	Vaccinium floribundum var. *ramosissimum*		1	
	Sphaerophorus melanocarpus		1	
	Syzygiella sp.		<1	
	Radula sonsonensis		<1	
	Jensenia florschützii (type sp.)		1+	
	Adelanthus lindenbergianus		1	
	Isotachis multiceps		<1	
	Cephalozia dussii		<1	
	Gymnomitrion atrofilum (type sp.)		<1	
	Stephaniella sp.		<1	
	Lepidozia macrocolea		1	
	Bartramia sp. (7753)		1	
	Physcomitrium sp. (7742)		1+	
	Leptolejeunea sp.		<1	
	Cladonia subg. *Cenomyce*		1	
	Lycopodium cf. *rufescens* (7735)		1	
	Rhizocephalum candollei		<1	
	Calamagrostis cf. *coarctata*		<1	
	Carex cf. *pygmaea*		<1	
	Carex aff. *conferto-spicata*		<1	

Locality: Coc = Cocuy: Páramo Cóncavo (Boyacá)
(rel. 331A, 460)
: Patio Bolos (Arauca)
(rel. 468)

Gua: Guantiva: Pan de Azucar
Sum: Nevado de Sumapaz

Syntaxonomically the association is well defined by its exclusive character-species *Loricaria complanata* that also determines its low shrubby aspect; it is closely related to the *Lachemilla nivalis* vegetation (see 28[a]) and to the *Valeriana plantaginea* - *Racomitrium* superpáramo community (see 27). The present description is made on the basis of the conditions in the Colombian Cordillera Oriental, where the subspecies *complanata* occurs. The association is subdivided into two subassociations, which reflect different conditions of humidity (21[a] and 21[b]).

Synecology: The new described association prefers well-drained stony thin soil near or on outcrops of bedrock, usually along the upper boundary of the bunchgrass zone proper with the superpâramo. Parent rock may be sandstone, quartzite or limestone. A distinct increase in the number of woody species at this height is noteworthy, and may be attributed to special cònditions in these places. They must have been covered with ice about 400 years ago during the Corralitos stade (Van der Hammen et al. 1981). The habitat of the *Loricarietum complanatae* on terminal moraines and outcrops was probably icefree at that time (the Neoglacial or Little Ice Age). It is supposed that present thermal conditions would allow for the development of a zonal upper bunchgrass pâramo Edaphic factors, immature soils and rockiness, however, seem to prevent this. The thin soils cosist of brownish or grayish clay or sand, and they are moderately to weakly acid (pH 5.0-5.7) according to elevation. The area slopes up to 20° or more.
Loricaria complanata has often been observed in lower places, in superpâramo-like habitats (bare soil) along swiftrunning rivulets and in crevices of roche-moutonnée.

Distribution: The *Loricarietum complanatae* is present throughout the high pâramos of the Colombian Cordillera Oriental from 4000 (3800) to 4400 m. Cuatrecasas (1954) reported *Loricaria complanata* also from the pâramos of the Cordillera Occidental, the Sierra Nevada de S. Marta and northern Ecuador; the *Loricarietum complanata* is supposed to be present here, but in the Venezuelan Andes it is virtually absent.

21a. Subass. *pernettyetosum prostratae* subass. nov. (prov.)
type: rel. 460; table 2. Fig. 30

Physiognomy: The physiognomy is similair to that of the association. The presence of a strongly reduced bryophyte layer (1-20% cover) accounts for the main physiognomical difference with the *racomitrietosum* (21b).

Composition & syntaxonomy: Differential against the *racomitrietosum* are e.g. *Calamagrostis effusa, Pernettya prostrata* var. *prostrata, Senecio vaccinioides, Lycopodium crassum, Diploschistes* sp. These differential species also noticed though less frequent and with reduced cover - in the zonal lower superpâramo on the cloudy side of the mountains. Presence of *Pernettya prostrata* and *Calamagrostis effusa* with a considerably cover in combination with the absence of hygrophytic bryophytes and vascular plants are the differential characters of this subassociation. The number of species is generally lower than in the *racomitrietosum*.

Synecology: The *pernettyetosum* fringes the upper bunchgrass pâramo and is adjacent to zonal superpâramo communities on the dry side of the mountains. The associated species are distinctly less hygrophytic than in the *racomitrietosum* .

Distribution: This subassociation is found in the Colombian Cordillera Oriental, on the dry side of the mountains from 4200 to 4400 m.

21b. Subass. *racomitrietosum crispuli* subass. nov. (prov.)
type: rel. 270; table 2. Fig. 29 (also Fig. 28)

Physiognomy: The physiognomy is similar to that of the association, but in addition there is a nearly closed bryophyte layer of 3-10 cm thickness.

Composition & syntaxonomy: This syntaxon is rich in hygrophytic species, mainly bryophytes, e.g.*Racomitrium crispulum, Rhacocarpus purpurascens, Breutelia* spp., *Lepidozia macrocolea, Campylopus richardii, Herbertus subdentatus, Anastrophyllum* spp., *Jensenia florschützii, Jamesoniella rubricaulis, Adelanthus lindenbergianus, Riccardia wallisii, Gymnomitrion atrofilum, Radula sonsonensis*. The last three liverwort species are only known from the upper condensation belt in the Colombian Andes (J. Meenks, comm.pers., Vana 1976, Jans 1979). *Oropogon loxensis, Siphula* spp., and *Sphaerophorus melanocarpus* are associated lichens, flourishing on damp soil or litter. *Valeriana plantaginea, Lycopodium* cf. *rufescens* and *Werneria humilis* var. *augustifolia* (the latter only in the Páramo de Sumapaz) are, as most of the mentioned species, characteristic for and restricted to the upper condensation zone.
Most hygrophytic species mentioned above are differential against the *pernettyetosum*. More relevés are required to decide whether the present rank is at subassociation or at the association level.

Synecology: This association was only found on soils derived from calcareous rock. Bamboos are generally absent in the *racomitrietosum*, but on the Nevada de Sumapaz, where the lower limit of the superpáramo is located between 4000 and 4100 m, the *racomitrietosum* is just reached by the uppermost thickets of *Swallenochloa*. *Rhacocarpus purpurascens* is predominant in stands on a soaking-wet soil; *Racomitrium crispulum* is common in less humid environment.
Silvilagus forages on sedges, *Hypochoeris sessiliflora*, and small grasses in rel 270.

Distribution: The *racomitrietosum crispuli* is characteristic for the zonal lowermost humid-superpáramo vegetation in the upper condensation zone from 4000 to 4250 m on the humid side of the Cordillera Oriental of Colombia.

22. Shrub of *Senecio vaccinioides* and *Diplostephium rhomboidale*
Fig. 30

These shrubs of Compositae were only noticed on terminal moraines along the grass páramo and superpáramo in the Páramo Cóncavo, Sierra Nevada del Cocuy (dry sidé) from 4300 to 4400 m. The *Senecio vaccinioides* shrub or the dwarfed trees of *Diplostephium rhomboidale* are 2.00-2.5 (4) m high and cover about 75%. Other characteristic and common associated species are *Espeletia lopezii* fma. *alticola, Senecio andicola, Lachemilla tanacetifolia, Jamesonia goudotii, Luzula racemosa, Senecio formosus, Zygodon pichinchensis, Bryum capillare, Campylopus jugorum* and *Lophozia incisa*. Most of these have not been found in the zonal *Senecio vaccinioides* subpáramo shrub (see 2). However, the two shrubby communities are physiognomically and floristically similar, as species *Senecio vaccinioides, Lachemilla* cf. *hispidula, Aciachne pulvinata, Pernettya prostrata, Cerastium subspicatum, Agrostis boyacensis, Thuidium peruvianum, Tortula andicola, Polytrichum juniperinum*. In an undisturbed stand at 4400 m a thick layer of the acrocarpous moss *Zygodon pichinchensis* is common on boulders and covers branches and thrunks.
Cetrariastrum dubitans and *C. equadoriense* are epiphytic lichens restricted to shrubby Compositae *(Loricaria, Senecio, Diplostephium)*or *Polylepis* dwarf forest vegetation (Sipman 1980).
The shallow soils are clayey to silty and a single pH of 5.0 was measured in the 10 cm thick blackish toplayer .

23. Community of *Pernettya prostrata* and *Luzula racemosa*
Fig. 31 (also Fig. 28, 30, 33, 35, 54, and 55)
photo: Gradstein et al. 1977, plate 2C; Gonzalez et al. 1965, photo 5; Van der Hammen et al. 1981, fig. 7 & 9.

This unit was only studied on young moraines and morainic sediments in the Páramo Cóncavo and in the high Bocatoma valley on the dry western slope of the Sierra Nevada del Cocuy between 4250 an 4500 m. According to Van der Hammen et al. (1981) these moraines belong to the most recent drift, which became icefree after the Corralitos of the "Little Ice Age", which may have lasted from 1500-1850 A.D. This means that this superpáramo community and the upper bunchgrass páramo in that area are only slightly more than a century in their present-day position. The upper bunchgrass-sward apparently was replaced by *Luzula* - *Pernettya* superpáramo vegetation during the Corralitos stade. Fresh Drift 6 sediments are still being uncovered by the receeding icecap, as demonstrated by photographs of the Páramo Cóncavo (Van der Hammen et al., 1981). Characteristic for the low superpáramo on moraines is the abundance and high cover of *Luzula* cf. *racemosa* (up to 10%) and the dwarfshrub *Pernettya prostrata* var. *prostrata* (up to 15%). *Lycopodium crassum* and poor specimens of *Grammitis moniliformis*, *Cora pavonia* and *Campylopus* cf. *chrismarii* var. *suboblongus* are common. Patches with many *Pernettya prostrata* are found on the lowermost moraines of the superpáramo.
The stony soil is about 20-30 cm thick, and consists of coarse sandy material, varying from brownish to gray and lightgray colors in the highest places.
The pH of the toplayer is 5.2 (5.1-6.1).
Young moraines in the headwaters of the El Playón river (between Lake La Plaza and Patio Bolos) on the opposite cloudy side of the Sierra are covered with a similar vegetation.

24. Community of Espeletiinae with *Geranium sibbaldioides*
Fig. 28

Dense populations of *Espeletiopsis colombiana* or *Espeletia cleefii* are locally found in the humid lower superpáramo of the Sierra Nevada del Cocuy near Patio Bolos (4250-4300 m). *Geranium sibbaldioides* (cover 5-8%), *Bartsia* sp., *Gnaphalium antennarioides*, *Castilleja fissifolia* ssp. *pygmaea*, *Hypericum selaginoides*, *Aphanactus ligulata*, *Erigeron ecuadoriensis*, *Cerastium subspicatum* and *Agrostis breviculmis* are conspicuous and commonly associated species. This stemrosette vegetation is floristically intermediate between the *Senecio niveo-aureus* gravelly scree community (26), the *Acaulimalva* - *Agrostis breviculmis* meadow (25) and the *Espeletia* upper bunchgrass páramo (20).
The pH of the gravelly soils, which show a high degree of solifluction, is about 5.0. Gravel deposits at the base of steep slopes, lower temperatures and frost action prevent *Espeletia cleefii* to reach higher locations. The same is observed in the much drier Páramo de Piedras Blancas in Venezuela. Espeletiinae reach up to about 4600 m. Monasterio (1979) described different superpáramo communities for this area, dominated e.g. by
1) *Espeletia lutescens* (Cuatr. & Arist) Cuatr. and *Coespeletia timotensis* (Cuatr.) Cuatr.;
2) *Espeletia moritziana* (Sch. Bip. ex Wedd.) Cuatr., and
3) *Coespeletia spicata* (Sch. Bip. ex Wedd.) Cuatr.

25. Community of *Agrostis breviculmis* with *Acaulimalva purdiei*
Fig. 32 & 58

Characteristic patches of closed, short meadow-like vegetation are found on stabilized screes (surrounded by communities 26 and 27) in the lower part of the superpáramo. Small, low, tufted *Agrostis breviculmis* is prominent and covers 20 to 60%. Sessile rosettes of *Hypochoeris sessiliflora, Acaulimalva purdiei* and *Calandrinia acaulis*, firmly rooted in the gravelly soil, are characteristic and may cover up to 25%. Other common species are *Oreomyrrhis andicola, Luzula* cf. *racemosa, Lachemilla pinnata, Aongstroemia julacea* and *Gongylanthus* sp. (9043[a]) and species of *Aphanactus* and *Halenia*.
The sandy-gravelly soil is not thicker than 10 cm and the pH of the top soil layer is estimated at 5.3. Frost heaving and deposition of gravel are the main factors that determine the size, pattern and cover of the stands.
This community has been studied on the Arauca slope of the Sierra Nevada del Cocuy (4250-4350 m) and in the summit area of the Páramo del Almorzadero (4100-4300 m). A similar community was also observed in the Páramo de Piedras Blancas at 4280 m in the Venezuelan Andes.

26. Community of *Senecio niveo-aureus*
Fig. 32 & 58 (also Fig. 28)
photo: Cleef 1978, photo 172

This high Andean community of whitish large rosettes with silvery indumented leaves is found on unstable gravelly screes, which are common in the humid superpáramo with high frost action. Daily the gravel is moving by freezing and thawing of the wet brownish clayey matrix. Soils are weakly acid (pH 5.4-5.8). In stands with giant *Lupinus alopecuroides*, a pH of 6.7 was measured in the topsoil layer.
Senecio niveo-aureus is the most characteristic rosette species, covering 1 to 15%. Other common and characteristic species are *Hypochoeris sessiliflora, Luzula* cf. *racemosa. Lachemilla tanacetifolia, Aongstroemia julacea, Zygodon pichinchensis, Tortula andicola, Bryum argenteum* and *Leprocaulon albicans*. Pioneer communities with a few rosettes of *Senecio niveo-aureus* are found on moderately steep (12-20^{o}) and extremely unstable, gravelly slopes. Patches of *Senecio cocuyensis* occur near outcrops of bedrock. On less sloping and more stable screes the vegetation cover is higher with more associated species as *Lupinus alopecuroides, Arenaria* sp., *Senecio formosus, Oreomyrrhis andicola, Erigeron ecuadoriensis, Erigeron chionophilus, Cerastium subspicatum, C. imbricatum* and *Lucilia* spp. (8956, 8979).
Frost action almost prevents seedling establishment in this habitat. Most companion species grow near the rosettes of *Senecio niveo-aureus* in more stable soil. Unattached mosses and lichens are common and adapted to these "mobilideserta" (Troll 1944) or areas of active solifluction, which are also known from other regions with an extremely cold and humid climate. Hedberg (1964) mentioned similar cryptogamic plantgrowth for the Afro-alpine zone and refered to relevant literature. Errant cryptogamic species in the humid superpáramo of the study area are: *Thamnolia vermicularis, Racomitrium crispulum, Bryum argenteum, Grimmia* sp., *Stereocaulon vesuvianum* var. *nodulosum*. Except *Thamnolia*, these species are almost absent in the dry superpáramos on the opposite side of the Cordillera.
In contrast to the earlier mentioned *Acaulimalva - Agrostis breviculmis* meadow (25), the *Senecio niveo-aureus* community is widely distributed between 4250 and 4350 m in superpáramos on the humid side of the Cordillera, e.g. in

the Sierra Nevada del Cocuy (Arauca-slope) and in the Páramo del Almorzadero (Santander). Small stands were observed on the Nevado del Sumapaz (4100-4230 m). The *Senecio niveo-aureus* cover decreases rapidly with height and only a few specimens were collected from 4350 to 4600 m. Patches of *Senecio niveo-aureus* on bare brownish-black soil with frost-heaving are also found in the bunchgrass páramo rockshelters on both sides of the Nevada del Cocuy. In the lower páramos the species grows in boggy valleys in *Calamagrostis ligulata* mire, representing the coldest spots at this height (see *Calamagrostion ligulatae)*. *Senecio latiflorus* is a close allied vicariant species endemic to high páramos of the Colombian Cordillera Central.

note:
The population *Senecio niveo-aureus* in the upper condensation zone of the Nevado de Sumapaz is associated with *Valeriana plantaginea*. Here the *Senecio niveo-aureus* rosettes are morphologically different from those of the Sierra Nevada del Cocuy populations by 1) slender lax plants with lower stature; 2) smaller and narrower lanceolate acuminate leaves, leaving the stem visible, and 3) loose panicles with less flowers (10-20) in comparison with the elongated contracted compact raceme containing more flowers (20-30).
The Cocuy population is morphologically rather similar to that of the Almórzadero. The morphological differences between the distinct superpáramo populations of the Colombian Cordillera Oriental perfectly reflect their isolatión. The greatest differences can be noticed between the Cocuy and Sumapaz populations, which at present and during the entire Pleistocene always were separated (Van der Hammen 1974; Van der Hammen & Cleef, in press).

27. Community of *Valeriana plantaginea* with *Racomitrium crispulum*
Fig. 32 & 58; lit.: Zander & Cleef, in press.

This rosette-bryophyte community is common on rocky slopes and outcrops with a humid thin (less than 10 cm), discontinuous, brownish, stony soil in the humid superpáramo of the upper condensation zone. Large *Valeriana plantaginea* rosettes with dark greenish, fleshy leaves and white to lilac flowers are characteristic and the species is generally associated with *Racomitrium crispulum, Erigeron chionophilus, Polystichum* sp., *Altensteinia paludosa, Montia meridensis* and with rosettes of *Senecio niveo-aureus* and *Draba* spp.
In superhumid upper condensation zone environment, as prevailing on the Nevado de Sumapaz, brownish mosses (e.g. *Rhacocarpus purpurascens, Racomitrium crispulum)* and reddish liverworts *(Herbertus subdentatus, H. acanthelius)* are predominant, covering up to 60%. The bryophyte layer is rich in species, e.g. *Plagiochila dependula, Kingiobryum paramicola, Radula sonsonensis, Riccardia wallisii, Gymnomitrion truncato-apiculatum, Anastrophyllum leucostomum, Blinda acuta,* and *Breutelia integrifolia.* Most of these are known also from other high areas reaching into the upper condensation zone. Studies in this zone in the Colombian Cordillera Central showed that *Racomitrium crispulum* dominates zonal rocky vegetation, whereas *Rhacocarpus purpurascens* was only noticed in azonal wet patches (Cleef et al., in press). *Rhacocarpus purpurascens* is dominant on zonal rocky soil in the lowermost part of the distinctly more humid lower superpáramo of the Nevado de Sumapaz (4000-4100 m), where *Racomitrium crispulum* is subdominant.
Towards higher parts (4200-4250 m) *Herbertus acanthelius* takes over together with *H. subdentatus,* which is more common on rocky soil. This last species forms a ring-like pattern on humid clayey soils. Frost-heaving is daily event in the humid, bare soils. *Valeriana planaginea* - superpáramo has a curious

purple-reddish colour at this height.
The thin soils are silty or gravelly and in the study area, they are derived from calcareous rocks. The pH of the brownish-black to darkgray lithosol is 5.4 to 6.0. At 4200 m still the presence of earthworms was noted.
The *Valeriana plantaginea - Racomitrium crispulum* community has been studied between 4050 and 4250 m on the Nevado de Sumapaz and near Patio Bolos in the Sierra Nevada del Cocuy. Communities without *Valeriana plantaginea* were studied in the upper reaches of the Páramo del Almorzadero at 4250 m. The community was also noticed on the high volcanoes of the Colombian Cordillera Central from 4250 to 4400 m (Cleef et al., in press), and it is supposed to be present also in Ecuadorian high and humid páramos.

28. Other zonal lower superpáramo communities

Both following superpáramo communities were observed locally, and only few phytosociological data have been collected.

a. *Lachemilla nivalis* vegetation is optimally developed at 4100 m on the Nevado de Sumapaz, where it is in contact with the *Loricarietum complanatae racomitrietosum* (Fig. 29). Grayey *Lachemilla nivalis* rosettes, which are woody at their base, apparently replace *Loricaria* shrub on flat ridges with thicker (about 30 cm) soils. Prostrate runners of *Arcytophyllum nuticum* cover the open spaces between the *Lachemilla nivalis* rosettes, while *Cladonia isabellina* is common under these rosettes. *Radula wallisii* is abundant here on decaying *Lachemilla nivalis*. The pH of the upper sandy to calyey black soil layer is 4.9. In the lower superpáramo of the northern Andes, *Lachemilla nivalis* is quite common and forms locally characteristic stands, which, when more relevés will be available, perhaps may be described as a proper syntaxon.

b. *Niphogeton josei* dwarfshrub vegetation (up to 25 cm high) was ocaasionally observed between 4270 and 4340 m in the sandy and gravelly zonal lower superpáramo in the Sierra Nevada del Cocuy, e.g. near Patio Bolos, and commonly on the Alto Nievecitas. In the latter locality, the endemic *Niphogeton josei* covers about 25% and is associated with *Senecio cleefii*, another low shrubby species that partly replaces *Pernettya prostrata* var. *prostrata* on the cloudy side of the Cocuy range.

Note: The *Drabetum pamplonensis* Vareschi 1953 is apparently a zonal superpáramo community of the Sierra Nevada de Mérida, Venezuela, which has not yet been found in Colombian páramos; though *Draba pamplonensis* was originally described from the Colombian Cordillera Oriental.

Upper superpáramo

In the Colombian Cordillera Oriental an upper superpáramo zone is only present in the highest areas of the Sierra Nevada del Cocuy, from 4500 to 4800 m. There are no floristic differences with the lower superpáramos, except the number and cover of species, which are distinctly decreasing near the snowline. A few vascular plants may grow in protected places, e.g. *Cerastium* sp., *Luzula* cf. *racemosa*, *Senecio niveo-aureus*. Poor specimens of *Stereocaulon vesuvianum* var. *nodulosum*, and some bryophytes (*Racomitrium crispulum*, Dicranaceae and Bryaceae) are present closest to the snowline. Depending on substrate and physiography, the plantcover is related to the various zonal communities of the lower superpáramo (e.g. 23, 26 & 27)

Table 3. Aquatic communities

A.M. Cleef 1981: The vegetation of the páramos of the Colombian Cordillera Oriental
Diss. Bot. 61, Vaduz

ALLIANCE	DITRICHO - ISOETION							TILLAEION PALUDOSAE**		POTAMETO-MYRIOPHYLLION			JUNCO-ELEOCHARITION		
association	29* Isoetetum karstenii		30	31 Isoetetum sociae	32	33	34 Isoetetum palmeri	36* Tillaeetum paludosae		39 a	39 b	40*	41* Eleocharitetum m.		42 Elatino-Juncetum
subassociation	29a typicum	29b ditrichetosum						36a isoetetosum	36b typicum				41a	41b tillaeetosum	
variant							34aa 34ab								
relevé nr.	449 461 323 448	461 189 271 1	161 484	456 168 457 338 330 424 477 1	292	358 301 248 304	327 501 264 416 190 200 200 97 395	476 485 416 264 264 500	161 223 442 298 81 380 41 405 358 389	294	297	266 153	10 11 300 300	300 498 184 404 195	193 197 190 204 67 498 495
relevé area (m²)	12 12 2 8	4 4 4 4	4 4	2 4 2 4 2 2 4 1	3	4 4 4 4	49 4 4 25 4 4 2 2 4	2 1 4 2 2 1	4 4 2 1 1 2 1 4 1 4	4	4	4 4	8 2 16 16	16 16 4 4 4	4 4 2 4 2 25 4
total cover vegetation (%)	20 5 65 80	85 60 95 70	100 100	60 60 90 90 50 95 100 100	100	100 100 100 100	60 100 100 100 100 95 90 100 100	100 100 75 80 98 100	100 97 100 100 100 50 100 100 80 80	100	100	100 100	100 99 80 100	90 100 100 80 75	100 100 100 80 100 100 100
total cover bryophytes (%)	- - - -	40 35 1 7	- 50	- - - 1 - 20 35 1	-	25 60 5 100	55 25 10 - 80 80 25 90 25	- - - - - -	- <1 - 1 - - - - <1 -	75	3	- <1	80 <1 - -	- - 1 60 -	4 75 80 <1 <1 - -
height of stand (cm)	10 15 20 10	25 10 10 12	20 40	3 5 3 3 1 2 10 3	25	25 60 40 25	25 25 20 15 25 30 40 30 30	25 15 30 20 5 10	40 10 15 5 1 1 35 20 15 5	30	35	3 10	50 45 45 45	40 40 45 40 40	25 20 30 30 30 30 15
soil	c/s c/s si c/s	c/s c/g c/s s/g	c g/s	si g si c/si si/g c/si si c/si	s/g	c c s c	c c/s s/g s/si c c/g c/g c/p c	cp c s/g s/st c/si cs	c c c cp c cp c c c c	c/g	s/g	c c	cp cp c cp	cp c c c cp	c/p c/p c cp csi c c
pH (* water)	- - 5.2	- - 6.1 -	- -	- 5.9 - 5.7 - 4.8 - -	-	5.7 5.6 5.1 5.7	5.2 - 6.4 6.1 4.6 4.8 - 4.7 5.2	- - 6.1 6.4 6.4 -	5.4 4.5 - 6.6 5.2 - 4.9 6.2 - 5.1	6.6	7.2	- 7.3	6.3 6.6 7.4 7.4	7.4 - - 6.0 4.9	5.0 - - 4.7 5.0 - -
depth water body (cm)	150 150 30 50	25 30 50 15	120 70	5 40 - - - - 25 -	-	60 60 40 100	35 15 65 80 50 100 50 30 70	10 10 15 20 5 (10)	20 - 15 - - - - 30 - -	40	35	3 15	1 30 25 10	1 1 30 20 35	30 15 30 30 10 - 10
number of taxa (algae excepted)	1 1 1 1	2 3 2 3	1 3	1 1 1 2 1 2 4 3	5	4 3 6 5	3 5 14 2 5 10 15 7 6	6 3 5 4 4 3	5 5 5 9 1 1 3 5 4 5	6	9	4 8	6 5 2 3	7 6 12 11 8	6 6 4 5 3 5 4
altitude (m)	4425 4350 4410 4425	4350 4270 4000 3750	4060 3875	4400 4390 4380 4380 4250 4065 4065 3700	3620	4150 3815 3745 3845	4435 3640 3510 3425 3700 3700 3700 3580 3550	3915 3895 3425 3510 3570 3640	4060 3565 3510 3425 3660 3375 3860 3725 4215 3330	3425	3410	3535 3640	3465 3465 3425 3425	3425 3870 3915 3710 3695	3685 3650 3700 3695 3460 3820 3820
locality	Coc Coc Coc Coc	Coc Coc Sum Sum	Coc Coc	Coc Coc Coc Coc Coc Coc Coc Sum	Sum	Coc Sum Rus Sum	Coc Sum Sum Pi LV LV LV Pal Tota	Coc Coc Pi Sum Sum Sum	Coc Rus Coc Sum Sum Tota Gua Gua Coc Tota	Sum	Sum	Sum Pal	Sum Sum Sum Sum	Sum Coc Coc Gua LV	LV LV LV LV CV Coc Coc
cover %	○	▲ ○	▲	▲	▲	▲	▲ ○ ▽	○	▲ ○ ▽			▲		▲ ○	▲
c taxa Isoetetum karstenii															
Isoetes karstenii	10 5 65 80	70 25 95 70			1										
Blindia magellanica		1													
c taxon Isoetetum glacialis															
Isoetes glacialis			100 90				1	25 15		10	3		<1	<1?	2?
c taxon Isoetetum sociae															
Isoetes socia				60 60 90 80 25 75 75 100					3 2 15 30					<1	1 50
c taxon Isoetetum andicolae															
Isoetes andicola					100		1 1								
c taxon Isoetetum cleefii															
Isoetes cleefii						80 100 60 1									
c taxon Isoetetum palmeri															
Isoetes palmeri							10 100 90 100 25 35 45 20 70	20 5 1	3					5	30
c taxa DITRICHO SUBMERSI - ISOETION															
Ditrichum submersum		40 33 5	50	1 20 3 1		25 10	1 25 5 5 30 <1		<1						
Isotachis serrulata s.l.		2 2		<1+		<1 5	55 2 3								
c taxon Tillaeetum p. & TILLAEION P.															
Tillaea paludosa					<1	10 1	5 1 15 <1 1	75 85 50 70 98 100	100 85 95 90 100 50 99 80 35 50		<1			15 5 20 2 1	
taxa comm. Scorpidium s. - Potamogeton															
Potamogeton illinoiensis										90					
Potamogeton asplundii							1		<1+		45		1		
Lilaeopsis schaffneriana									5 30 2	<1+	10			<1 5 <1	
Scorpidium scorpidioides							2 1			75	3	<1		<1	
c/d taxon Hydrocotylo r. - Myriophylletum e.															
Hydrocotyle ranunculoides							1 1 <1					20 5			
c & d taxa POTAMETO - MYRIOPHYLLION E.															
c Myriophyllum elatinoides							1			5	75	95 80	5 40 25 30	10	
Eleocharis acicularis							1 5 1		3	5	1	5 1			
c & d taxa Eleocharitetum macrostachyae & JUNCO E. - ELEOCHARITION M.															
c Eleocharis macrostachya													35 80 65 75	90 100 60 50 20	
Calliergonella cuspidata									1				80 <1	<1 <1+	
c & d taxa Elatino c. - Juncetum ecuadoriensis															
c Juncus ecuadoriensis									5			<1		30 1 15	5 45 25 80 80 2+ 5
Sphagnum cuspidatum							<1 30 25								1 40 3 <1 <1
c/d taxa order & classes; companions															
Elatine cf. chilensis				70	<1	10	1 1 <1 <1 10 <1	15 1 5 1 1	1+ 2 <1 <1		<1+	5 15		5 70+ 25 3	65 10 <1 1 80 80+ 40
Ranunculus limoselloides							15	5 5 5	10 3 2				80	1 <1 15 30 <1	10 30 2 5 10
Callitriche spp.			<1		<1	15	3 <1 20 2	<1 1	4 1					<1 2 1 15	
Drepanocladus exannulatus						90	75 75 10		<1		<1+	<1		<1	3 30 80
Eleocharis stenocarpa							<1	<1 2?	5 5					2	
Pilularia cf. mandoni								≤1	≤1						
c Limosella australis									10 30						
Alopecurus aequalis								10 30							
Riccardia paramorum							1 1 1								
Cardamine bonariensis									10				<1		
Potamogeton berteroanus							1					1			
Cryptochila grandiflora						1 1									
Calypogeia andicola						60 1									
Clasmatocolea vermicularis							10 2								
Fissidens rigidulus							3								
Radula episcia							<1								
Jensenia erythropus							<1 25								
Sphagnum cyclophyllum						<1	1						5		5
Spagnum pylaesii							5								
Fontinalis bogotensis							<1								
Herbertus oblongifolius				35											
Drepanocladus aduncus													1		
Drepanocladus revolvens														60	
Utricularia obtusa															
Gratiola peruviana								1							
ALGAE (x present, low cover)	10 x 10 80	40 15 1 1	x x	10 10 8 20 70 x x x	x	100 x 70 15	1 x x x 70 x 30 x x	15 x x 15 x x	x x x x 75 x x 10 10 x	100	x	x x	x x x x	x x x x x	x x x 90 100 x 60
Batrachospermum sp.							<1+ <1+								
Microcoleus sociatus						100									
Desmidiaceae				10											
Mougeotia sp.						15									
Zygnema sp.							20								
Spirogyra sp.							<1								
cf. Microspora sp.							50 1								90 100 60
Nitella acuminata											5				
Nitella clavata														<1	
Cyanophyta								15							

Addendum: rel. 298 Cotula minuta (1%)
338 Andreaea sp. (10%)
10 Agrostis sp. (3%)

The order TILLAEETALIA comprises only the alliance TILLAEION PALUDOSAE in the study area.

Localities:
Coc Sierra Nevada del Cocuy
CV Páramo de Cruz Verde
Gua Páramo de Guantiva
LV Páramos NW of Neusa, Laguna Verde
Pal Páramo de Palacio
Pi Páramo de Pisva
Rus Páramo de la Rusia
Sum Páramo de Sumapaz
Tota Páramos near Laguna Tota

c character taxon
d differential taxon

** type of the order
* type of the alliance
▲ type of the association
○ type of the subassociation
▽ type of the variant

III. THE AZONAL PARAMO VEGETATION

AQUATIC COMMUNITIES

Ditricho submersi - Isoetion all. nov.
type: *Isoetetum karstenii* (this study); table: 3

Physiognomy & synecology: This alliance comprises mainly submerged bryophytic-isoetid communities in pãramo lakes. Only in the highest and in the shallowest lakes bryophytes may be absent. The species of *Isoetes* vary in height from 2-3 cm *(Isoetes socia)* to about 60 cm *(I. cleefii)*. Species abundance and organic content of the topsoil increase from superpãramo lakes towards lower altitudes. The substrate shows all kinds of texture, varying from stones and gravel to clay and gyttja (Fig. 90).

Composition & syntaxonomy: Exclusive and selective character species are *Isoetes karstenii, I. glacialis, I. socia, I. andicola, I. cleefii, I. palmeri,* all species of the section *Laeves* Fuchs; further *Ditrichum submersum, Blindia magellanica* (rare), *Herbertus oblongifolius* (rare), *Isotachis serrulata, I. lacustris*. Preferential character species are *Fissidens rigidulus, Sphagnum pylaesii, Fontinalis bogotensis, Riccardia paramorum* and *Batrachospermum* sp. There are 1-2 species in the communities at the highest altitudes and about 7 in the *Isoetetum palmeri*.

On the basis of floristics and ecology this alliance can be subdivided into several associations and one unranked community. Presence, type and nature of bryophytes determine additional subdivisions, Identifications of the collected *Isoetes* specimens by Dr. H.P. Fuchs provided the floristic basis for the associations and communities within the *Ditricho-Isoetion*. The *Isoetetum lechleri* Gutte 1980 is likely to belong to this new alliance. The syntaxonomic position of this quillwort vegetation, however, will remain uncertain until the specimens of the species have been identified by a specialist.

Distribution: The alliance has been studied in the pãramos of the Cordillera Oriental between 3350 and 4450 m. Judging from plant collections and field observations, the *Ditricho-Isoetion* must be present all over the northern Andean pãramos from Venezuela to Ecuador, extending south to Bolivia *(Isoetetum glacialis)* and Peru *(Isoetetum sociae, Isoetetum andicolae)*.

<u>Phytogeographical comments and early evolution of aquatic pãramo biota</u>

All *Isoetes* species representing proper associations or communities in the *Ditricho-Isoetion* belong, according to Fuchs (in press), to the section *Laeves*, which apparently evolved in the Neo-tropics. The section *Laeves* of *Isoetes* seems to be almost endemic to the high tropical Andes, and the highest differentation and speciation is found in the northern Andean pãramos (Fuchs, in press). Van der Hammen et al. (1973) recorded the first *Isoetes* microspores in old Pleistocene sediments ("Guasca 2") of the Colombian Cordillera Oriental, which were dated at about 3.6 (± 0.67) millions of years. They are assumed to have belonged to early members of the section *Laeves* of *Isoetes*. *Potamogeton berteroanus* (Dr. L.B. Holm-Nielsen, in litt.), *Hydrocotyle ranunculoides*, *Myriophyllum elatinoides* and *Elatine chilensis* (?) are of austral origin. Austral-antarctic elements prominent among the bryophytes*) are e.g. *Isotachis* sect. *Subaequifolia*, *Blindia magellanica*, *Cryptochila grandiflora*, *Clasmatocolea vermicularis*, *Fissidens rigidulus* and *Jensenia erythropus*. The general occurence of members of this section of *Isoetes* in páramo lakes, together with a high proportion of other austral-antarctic aquatic plant taxa (Cleef 1978, 1979[b]), support the assumption that páramo lakes were mainly colonized by temperate plant taxa after the early Pleistocene.

29. *Isoetetum karstenii* ass. nov.
type: rel. 461; table 3; Fig. 33
lit.: Cleef et al., in press.

Physiognomy: The open to more or less closed layer of clumps of *Isoetes karstenii*, 10 to 20 cm high, are associated with high bryophytes, except in the highest superpáramo lakes. The water in these lakes is generally translucent. *Isoetes karstenii* has long roots, which prevent the plants to be removed by mechanical forces such as wave action, strong currents, etc.

Composition & syntaxonomy: *Isoetes karstenii* is present in all relevés. In lower areas a few species of bryophytes were found, e.g. *Ditrichum submersum*, *Isotachis serrulata* and *Blindia magellanica*. The last-mentioned species has only been recorded as far south as the type locality in southernmost S. America. Filamentous algae may cover up to 80%. In 8 relevés the average number of species is low, i.e. 1 in the highest lakes to 2 (1-3) in the lowermost.

Exclusive character species are *Isoetes karstenii* and *Blindia magellanica*. The association can be divided into subassociations, differing in presence of aquatic bryophytes.

Synecology: The *Isoetetum karstenii* grows mainly in deep, cold lakes in the upper part of the páramo belt. Most mineral soils are silty, but some clayey and stony substrate have been observed near the shores. Gravelly sediments are common in places with wind and wave action. As a result of its low organic content, the water is rather transparent in these lakes. The few pH data vary from 5.2 (lakewater at 4400 m) to 6.1 (calcareous sediment at 4100 m). With increasing depth or elevation, *Isoetes karstenii* decreases in height and cover.
The cover of *Ditrichum submersum* increases with a better protection against wind and wave action and with increasingly favourable temperatures.

Distribution: The *Isoetetum karstenii* is described from the páramos of the Colombian Cordillera Oriental (Cocuy, Sumapaz), from the grasspáramo at (3500-)3700 m up to the superpáramo at 4425 m. This association has also been studied in the Sierra Nevada de Mérida (Venezuela) at 4250 m and at 4300 m on the volcano S. Isabel, Colombian Cordillera Central. According to Fuchs (in press and in litt.) *Isoetes karstenii* is known from Venezuela (2500-4250 m) and Colombia (3200-4425 m).

*) For further phytogeographical analysis of the aquatic bryoflora of the *Ditricho-Isoetion*, see under the *Isoetetum palmeri* (34).

29^{a}. Subass. *typicum* subass. nov.
type: rel. 449; table 3; Fig. 33

Physiognomy: This submerged community consists of a more or less open isoetid fieldlayer up to 25 cm high, depending on waterdept and altitude.

Composition & Syntaxonomy: *Isoetes karstenii* is the only vascular plant, and has a cover of 5-80%. Filamentous green (and blue ?) algae generally cover the *Isoetes karstenii* clumps. Mosses are absent.

This new described subassociation is characterized by the character species *Isoetes karstenii* and by the absence of other cormophytes. The subassociation *typicum* has its closest affinities to the *Isoetetum karstenii ditrichetosum*, which is common in deep lakes in the lower páramos. The subassociation *typicum* is delimited here as a syntaxon for the superpáramo and in fact represents a pioneer community preceeding (in time and space) the *Isoetetum karstenii ditrichetosum*.

Synecology: This high altitude isoetid community occurs submerged in deep superpáramo lakes from the shore to at least 150 cm depth. *Isoetes karstenii* cover is much lower in the deepest parts. Throughout the year water temperature remains low in these cold polymictic lakes. They are never frozen, except near the shores. In more shallow water, the cover of *Isoetes karstenii* increases in some places up to 80%, apparently due to more protection (Fig. 33). The blue-grayish clayey to silty and sandy lake sediments are thick (at least 100 cm). Wind and waves often cause turbulences with fine soil particles. Strong wave action and quicksands may bury the *Isoetes karstenii*. The roots of *Isoetes karstenii* are longer than the large, stiff dark-greenish leaves (20-25 cm). Wind and wave action, and thus turbulence become stronger in higher areas with deep glacier lakes near the snowline. Unstable soils and low temperatures combined with high altitude, turbulance and depth of the lake represent limiting factors for the development of the *Isoetetum karstenii typicum*. A single pH for lake water is 5.2 (rel. 323). Lakes containing this syntaxon or the *Isoetetum sociae* probably yield the lowest primary production of all lentic waters of the páramos. Consequently, aquatic fauna is scarce in this subassociation. Near rel. 323, *Gammarus* sp. has been observed and small sanderlings foraging on these small crustaceans.

Distribution : The subassociation *typicum* is only known from (deep) superpáramo lakes in the Sierra Nevada del Cocuy (Boyacá) between 4350 and 4425 m, and from the volcano S. Isabel (4300 m) in the Colombian Cordillera Central.

29^{b}. Subass. *ditrichetosum* subass. nov.
type: rel. 461; table 3; Fig. 33

Physiognomy: This submerged vegetation is more or less closed, and consists of a 10-25 cm high isoetid-bryophytic layer. Erect bryophytes may be dense between the *Isoetes* foliage.The *Isoetes* herb layer is maximally closed in protected stands. The habit of the rare *Blindia magellanica* (in rel. 271) is similar to that of *Ditrichum submersum*.

Composition & syntaxonomy: *Isoetes karstenii* is the only prominent vascular species, as a rule accompanied by *Ditrichum submersum*, *Isotachis serrulata* and in some places by *Blindia magellanica*. The two last species are representatives of the austral-antarctic element. These bryophyte species are differential against the *Isoetetum karstenii typicum*.

Synecology: This subassociation is characteristic on mineral bottoms (e.g. clayey-silty and sandy-stony substrates) of deep high páramo lakes. These grayish sediments are poor in organic cóntent, but become brownish and richer in organic matter at lower heights. Erosion by wave action or currents of the original clayey deposits overlying the gravelly floor is common (e.g. rel. 1^B). The pH of 6.1 in a calcareous sediment in rel. 271 on the Nevado de Sumapaz is probably not representative for other stands in the Sierra Nevada del Cocuy on non-calcareous substrate, which is about 5.5 - 6.0. *Gammarus* and small black leeches are common in the habitat of the *Isoetetum karstenii ditrichetosum*. Many Copepodawere collected in rel. 271 at 4100 m.

Distribution: The *Isoetetum karstenii ditrichetosum* is described from deep lakes in the high páramos of the Sierra Nevada del Cocuy and the Páramo de Sumapaz. It is distributed from the grass páramo at 3750 m up to the superpáramo at 4350 m. A few specimens of *Isoetes karstenii* have been collected as low as 3200 m in the Páramo de Sumapaz (Fuchs, in litt.)

30. *Isoetetum glacialis* ass. nov. (prov.)
type rel. 161^A; table 3; Fig. 34

Physiognomy: The closed, dark green-brown isoetid layer, up to 40 cm high, is found on deep lake bottoms. The root system is very dense and at least 30 cm deep.

Composition & syntaxonomy: In both relevés *Isoetes glacialis*, the only character species, is dominant (cover 90-100%) and associated with *Callitriche* sp. near the shores. The number of species is low (1-3) in 2 relevés.

Synecology: This submerged association covers thick gyttja deposits, mainly in grass páramo lakes. The dense *Isoetes glacialis* vegetation hardly leaves enough space for other plants and only *Ditrichum submersum* is regularly associated. This community extends up to the low-water line for the dry season The *Isoetetum glacialis* in the Laguna Cuadrada (Sierra Nevada del Cocuy) became temporarily visible towards the end of the extremely dry season in March 1973. It remains unknown, however, whether the *Isoetetum glacialis* or *Nitella* (Characeae) communities occur in the deepest part of this lake. The pH of the sediment in the shallow margin (*Tillaeetum*, rel. 161) was 5.4. A pollendiagram for this lake (VL III, plate 3) was published by Gonzalez et al. (1965).

Distribution: The association is described from glacial lakes in the high valley of Lagunillas in the Sierra Nevada del Cocuy between 3900 and 4000 m. *Isoetes glacialis* has also been collected in the shallow near-short part of the deep lakes near the Nevado de Sumapaz at 3425 m. scarce isolated clumps of *Isoetes glacialis* are found in the *Isoetetum palmeri*, the *Potamogeton - Myriophyllum elatinoides* community and in the *Eleocharitetum macrostachyae*. The *Isoetetum glacialis* is believed to be present also in the deeper parts of the lakes. The association is probably also present in other tropical Andean lakes, for *Isoetes glacialis* was described as a new taxon from the Bolivian Andes (Prov. Murillo near La Cumbre) at 4700 m.

31. *Isoetetum sociae* ass. nov.
type rel. 338; table 3; Fig. 35
lit.: Weberbauer 1911

Physiognomy: The open isoetid layer consisting of tiny plants of

Isoetes socia is found in shallow lakes and ponds in the high páramo.

Composition & syntaxonomy: The dominant and nearly only vascular species is *Isoetes socia*. *Elatine* cf. *chilensis* and *Ditrichum submersum* may be present; the first one in ponds in the grass páramo, the last two in slightly deeper lakelets that do not fall dry through evaporation. Green and blue algae may be floating in the shallow, clear water, e.g. *Mougeotia* sp. (5703) and desmids. The average number of species is 2 (range 1-4) in 8 relevés.

Isoetes socia is the only character species of this high altitude syntaxon. There are no other vascular species in the superpáramo stands, but in the lowermost relevé *Elatine* cf. *chilensis* is found together with *Isoetes socia*. In the lower páramos the *Isoetetum sociae* is replaced by the *Tillaeetum* which ecologically shows a number of similarities with the *Isoetetum sociae* (Fig. 91A).

The *Isoetetum sociae* is ranked under the *Ditricho-Isoetion* because of the floristic composition (*Isoetes, Ditrichum submersum*) and the predominantly isoetid lifeforms in the association.

Synecology: The *Isoetetum sociae* is found in the high páramo on the bottom of small, shallow lakes and ponds, which may fall dry in the dry season. Then a crust of algae covers the *Isoetes socia* plants and part of the bare mineral bottom. The tiny *Isoetes socia* plants thus survive this dry period by this kind of protection and by their corms being buried in 1-2 cm deep, still humid soil. During most of the year, however, the *Isoetetum sociae* is submerged in 50 (-100) cm . The substrates are mostly less than 50 cm thick. The thin tóplayer is clayey to silty, in other places coarse-sandy. The pH of the top layer is 4.8-5.7, in superpáramo sediments slightly above 5.0. The temperature of the water in these shallow lakes and ponds increases on sunny days and may main high in the early hours of the evening, but in the early morning, the water may be frozen however. At 5.30 p.m. on September 30, 1972 the temperature of the water in a shallow lake (rel. 168) and the atmospherical temperature at 4400 m on the Cuchilla Puentepiedra in the Sierra Nevada del Cocuy were resp. 13° and 5°C. Thus, environmental conditions in these shallow high páramo lakes with the *Isoetetum sociae* are much more fluctuating than in the deeper páramo lakes with the *Isoetetum karstenii*. The *Isoetetum sociae* is subjected to 1) dry periods, 2) irregular sedimentation, 3) a wide diurnal temperature range, and 4) foraging animals. (*Sylvilagus* may eat fresh *Isoetes socia* foliage, when the plants are above water). Desiccation by evaporation apparently is the most extreme environmental factor. *Isoetes socia* is a specialized species well adapted to this harsh environment. It is the only amphibious vascular plant forming communities near the snowline (Fig. 91A).

Distribution: The association is described from the high páramos (upper grass páramo & superpáramo) in the Sierra Nevada del Cocuy between 4000 and 4400 m, and from the Páramo de Sumapaz (Chisacá) at 3700 m. *Isoetes socia* was originally described from the Mérida Andes, Venezuela. The *Isoetetum sociae* may thús be expected in other high parts of the tropical Andes; Weberbauer (1911) reported *Isoetes socia, Crassula bonariensis* and *Ranunculus mandonianus* from 4400 m in the Peruvian Andes (Ancash) without indicating the cover. It remains to be ascertained whether the *Isoetetum sociae*, the *Isoetetum karstenii* or the *Tillaeetum paludosae* is present in this region.

32. *Isoetetum andicolae* ass. nov.
type: rel. 292 A; table 3 & 4; Gutte 1980: table 5
Fig. 36 (this study); Rauh & Falk 1959 : Fig. 6 (p. 17)
photo: Rauh & Falk 1959 : some excellent photographs
lit.: Rauh & Falk 1959, Rauh 1978, Gutte 1980

Physiognomy: *Isoetes andicola* forms distinct long, boggy hummocks, up to 80 cm thick, along the mineral shores of tropical high Andean lakes. Hundreds of stiff-leaved specimens with dichotomous stems grow close together in firm cushions, on which one can walk, at least in the dry season.

Composition & syntaxonomy: *Isoetes andicola* is the main vascular plant and the character species. In lakes of the grass páramo *Isoetes karstenii*, *Callitriche* sp., *Tillaea paludosa* and *Elatine* cf. *chilensis* may be companion species. On the basis of the floristic composition the *Isoetetum andicolae* must be assigned to the *Ditricho-Isoetion*.

Table 4

Isoetetum andicolae ass. nov.

author	Cleef	Rauh & Falk	Gutte 1980	Gutte 1980
& rel. no.	292A	1959 (s.n.)	table 5, rel.4	table 5, rel.5
locality	a	b	c	c
alt. m	3620	4750	4700	4700
rel.				
area (m^2)	3	?	10	5
pH	-+)	4.8 (lakewater 5.5-5.8)	-	-
thickness bog (cm)	20-60	-80	?	?
cover %	▲			
c & o taxa				
Isoetetum andicolae:				
Isoetes andicola	100	100	(5)++)	(5)
Isoetes karstenii	1	.	.	.
Callitriche sp.	1	.	.	.
Tillaea paludosa	1	.	.	.
Elatine cf. *chilensis*	1	.	.	.
Lachemilla diplophylla	.	.	(1)	.
Plantago rigida	.	.	.	(+)
Oritrophium limnophilum	.	.	.	(+)

a Páramo de Sumapaz; Laguna del Medio
b Peru: Casapalca (Cord. Occ.) Laguna Caprichosa
c Peru: Yauli, Morococha, Base Puypuy

+) pH of the lake water near the stand in the neighbouring Laguna La Primavera was determined at 6.4
++) cover according to Braun-Blanquet scale

Synecology: The peat on lake sediment under the *Isoetes andicola* cushions consists of remnants of this remarkable quillwort species and thick layers of whitish macrospores. It forms a considerable contribution to the lake sediments. The Peruvian stands were found in water-loaded hollows in hydroseral *Distichia muscoides* bogs (Rauh & Falk 1959, Gutte 1980). *Isoetes andicola* peat has been reported by Rauh & Falk (l.c.). Apparently no other associated species were found. Rauh & Falk (l.c.) also provided pertinent data on ecological conditions, and published a line transect through hydroseral communities at 4750 m altitude in a Peruvian lake. The pH of the lakewater is 5.5-5.8 in the Peruvian Laguna Caprichosa at 4750 m, and 6.4 in the Colombian Laguna La Primavera at 3500 m. *Isoetes andicola* peat in the Peruvian type locality showed a pH of 4.8.

Distribution: *Isoetes andicola* is known from several localities in the Peruvian Andes (prov. Lima, Junín, Puno) between 3800 and 4780 m. In the Colombian Páramo de Sumapaz (dept. Meta), *Isoetes andicola* was collected (Cleef 7555[a] & 8247) in the Laguna La Primavera and Laguna del Medio in the lower grass páramo of the upper Sitiales valley,NW of Cerro Nevado between 3500 and 3620 m. The *Isoetetum andicolae* may eventually be found in the Ecuadorian páramos and in the páramos of the Colombian Cordillera Central.

Note: *Isoetes andicola* was described from the Peruvian high Andes. Rauh & Falk (1959) presented a detailed morphological and systematical study on *Stylites* E. Amstutz em. W. Rauh. The present author prefers to follow Dr. M.T. Murillo, Bogotá (pers. comm.), and Fuchs (1981[a], 1981[b]), who consider the genus *Stylites* as congeneric with *Isoetes: Isoetes andicola* (E. Amstutz) H.P. Fuchs, belonging to the section *Laeves* H.P. Fuchs. *Stylites gemmifera* W. Rauh is regarded to belong to the morphological range of *Isoetes andicola* The presence of *Isoetes andicola* in the Laguna del Medio and the Laguna La Primavera in the Páramo de Sumapaz is of considerable phytogeographical interest. The species represents the first record of this species in the páramos of the northern Andes and is new to Colombia.

33. *Isoetetum cleefii* ass. nov.
type: rel. 301; table 3; Fig. 37

Physiognomy: The high (20-60 cm) dense isoetid communities are found on clayey (to gyttja) - sandy bottoms of grass páramo lakes.

Composition & syntaxonomy: *Isoetes cleefii* is the character species (exclusive), only known from the páramos in the study area (Fuchs, 1981[b]). The taxon is closely related to *Isoetes palmeri*, but is different by its broader leaves and rhizomes, and by its triangular velum completely covering the sporangium, which is twice as large as in *I. palmeri*. *Cryptochila grandiflora* and *Calypogeia andicola* are diagnostic species. According to Gradstein et al. (1977) this is the first record of submerged *Calypogeia andicola*. The number of species is 4-5 (3-6 in 4 relevés). The low number of species is differential against the *Isoetetum palmeri* (34).

Synecology: The association may be found in clear lakes in the high grass páramo mainly surrounded by mineral shores. The pH values of the water are 5.1-5.7. Bryophytes are common on the clayey organic sediment between the *Isoetes* clumps and also between filamentous algae. *Sylvilagus* and/or *Cavia* forage on the emergent layer of *Isoetes* herbs in the dry season.

Distribution: According to Fuchs (1981[b]) this taxon, and thus also this isoetid community, is present between 3750 and 4250 m in the Colombian Cordillera Oriental (Sumapaz - Rusia - Cocuy).

Note: A pollendiagram of the Laguna Gobernador (type rel. 301, 304) in the páramo de Sumapaz has been prepared by Mr. Guido B.A. van Reenen and will be published in the near future. It covers the Late Glacial and the Holocene.

34. *Isoetetum palmeri* ass. nov.
type rel. 190; table 3; Fig. 38

Physiognomy: The association consists of a submerged, mostly closed aquatic bryophytic-isoetid layer. Elodeids and amphiphytes may be present with low cover.

Composition & syntaxonomy: The most prominent species is *Isoetes palmeri*. Other species with low cover values may be present too. Several accompanying herbaceous amphiphytes are characteristic, at least in near-shore localities, e.g. *Callitriche* cf. *nubigena*, *Tillaea paludosa* and *Elatine* cf. *chilensis*. Other conspicuous species are *Potamogeton berteroanus*, *Eleocharis acicularis* and *Hydrocotyle ranunculoides*. Attached and/or floating bryophytes are common, e.g. *Ditrichum submersum* and *Isotachis serrulata*. A number of characteristic aquatic bryophytes have low frequencies. Many of these belong tó the austral-antarctic flora element (see under *Ditricho-Isoetion*). *Sphagnum cyclophyllum* and the rare *S. pylaesii* represent the holarctic element. According to Florschütz-de Waard & Florschütz (1979), this is the first record of the common *Sphagnum cyclophyllum* in Colombia. *Ditrichum submersum*, *Fontinalis bogotensis*, *Riccardia paramorum*, *Radula episcia* (Jans 1979) are tropical Andean species and *Drepanocladus exannulatus*, *Scorpidium scorpiodes* (including *S. turfaceum* Herzog) and *Sphagnum cuspidatum* are cool temperate in distribution. *Drepanocladus exannulatus* and *Sphagnum cuspidatum* are locally abundant. Filamentous algae are common also. Most characteristic is *Batrachospermum* sp. (Rhodophyta). In addition, several species of *Zygnema*, *Spirogyra*, and cf. *Microspora* have been identified by Dr. A.J. Dop. With an average of 7 (2-15) different taxa in 9 relevés the *Isoetetum palmeri* represents the páramo community dominated by *Isoetes* richest in species.

The common character species is *Isoetes palmeri*. Rare character species are *Sphagnum pylaesii* (excl.), *Riccardia paramorum*, *Fissidens rigidulus* (pref.), and *Batrachospermum* sp. (sel.). The remaining bryophyte species may be considered as differential against the other aquatic páramo communities in this area. *Callitriche* sp.(p.),*Elatine* cf. *chilensis* and *Tillaea paludosa* are differential against most other syntaxa of the *Ditricho-Isoetion*. The low cover of *Tillaea* is also differential against the *Tillaeion*. In the *Isoetetum palmeri*, two mossy variants can be recognized, by the high cover either of *Drepanocladus exannulatus* or of *Sphagnum cuspidatum*.

Synecology: The *Isoetetum palmeri* is restricted to clayey and peaty sediments in páramo lakes (partly) surrounded by bogs or to boggy areas. This association occurs in peat-bottomed lakes and lakes with peaty lake sediments, in the lower part of the páramo belt.Lake floors are covered by the *Isoetetum palmeri* almost up to the low-water line in the dry season, when the tops of the *Isoetes* leaves may be visible above water. The presence of this association depends on water depth rather than on size of the waterbody. Maximum water

depth for the *Isoetetum palmeri* is unknown, but is at least 2.5 m, judging from (personal) observations.
Sediments are clayey or peaty; peat tends to form a dark gyttja. The organic content of most lakes in boggy páramo causes the relatively low pH from 4.6 to 6.4 and generally about 5.0. *Drepanocladus exannulatus* or *Sphagnum cuspidatum* may be prominent in the field layer of the *Isoetetum palmeri* in lakes next to *Sphagnum* bogs.

In most relevés up to 4435 m, species of *Gammarus* (Amphipoda, Crustaceae) and small black and brown leeches (Hirudinae) were noticed, and Coleoptera, worms and other waterinsects are common. Rel. 264 (3550 m) contained tiny whitish shells of freshwater bivalves, *Sphaerium lauricochae* Philippi.

Distribution: The *Isoetetum palmeri* is described from the subpáramo and grass páramo of the Colombian Cordillera Oriental. Most stands were studied between 3350 and 3850 m. Rel. 327 was made in a small superpáramo lake at 4435 m, surrounded by marshy ground with dense bunches of *Calamagrostis* sp. (8652). According to Fuchs (1981[a]), *Isoetes palmeri* is a true páramo species, geographically restricted to Venezuela, Colombia and Ecuador. Its vertical distribution is from forest line at 3200 m to the superpáramo at 4400 m (Cocuy, Chimborazo). The *Isoetetum palmeri* is probably native to the northern Andean páramos from Ecuador to Venezuela.

34[aa]. Variant of *Drepanocladus exannulatus*
type: rel. 200; table 3; Fig. 38, 39 (also Fig. 34)

Differential species is *Drepanocladus exannulatus*, which is mostly dominant (submerged or floating), and lowers the cover of *Isoetes palmeri*. The lakewater is oligotrophic and the variant has been recorded only near the shore of peat-bottomed lakes surrounded by *Sphagnum* bogs.
Relevés are located in the *Calamagrostis effusa* bunchgrass páramos at 3700 m in the southern part of the area.

34[ab]. Variant of *Sphagnum cuspidatum*
type: rel. 97; table 3

Sphagnum cuspidatum is a differential species , and thalloid aquatic hepatics may be common. This variant has been recorded for small lakes on *Sphagnum* bogs. The trophic level (pH 4.7-5.2) of the lake water presumably is relatively low.
The *Sphagnum cuspidatum* variant is common in the peaty bamboo páramos between 3350 and 3600 m on the humid side of the Colombian Cordillera Oriental.

35. Community of *Isoetes boyacensis*
table 5

Although *Isoetes boyacensis* was a common dominant in several ponds in El Tutal between 3800 and 3900 m on the southern calcareous slope of the Páramo del Almorzadero (Santander), only a single relevé has been sampled on November 20, 1978.

Table 5

Community of *Isoetes boyacensis*

rel. no.	575
size	2 m^2
soil	c
depth	10 cm
alt.	3825 m
loc.	Almorzadero; El Tutal
cover %	
Isoetes boyacensis	100
Ranunculus limoselloides	10

According to Dr. H.P. Fuchs (in litt.), the dominant *Isoetes* species (Aguirre C & Cleef 1050A) is new and yet to be described. It is unknown whether *Isoetes boyacensis* (sect. *Terrestres*) is restricted to ponds in the Páramo del Almorzadero, or whether this species is common in other shallow waterbodies in the northern páramos of the Colombian Cordillera Oriental. This relevé is provisionally classified within the *Ditricho-Isoetion* though *Ranunculus limoselloides* is more common in the other alliances of aquatic habitats (see table 3).

TILLAEETALIA order nov. (*L I M O S E L L E T E A* cl. nov. prov.)
type: *Tillaeion paludosae* (present study)

The order *Tillaeetalia* is erected to comprise all *Tillaea**)-dominated communities characteristic for pond and lake-shore habitats at sea level in cool-temperate southern latitudes and at high elevation in tropical mountains. These aquatic crassulaceous *Tillaea* communities are dominated e.g. by *Crassula granvikei* Mildbr. (Hedberg 1964, Coe 1967), *Crassula natans* Thunb. (Van Zinderen Bakker & Werger 1974), *Tillaea moschata* DC. (Huntley 1971; Gremmen 1981), *Crassula moschata* Forst. f. (Reiche 1907), *Crassula erecta*, Berger (Oberdorfer 1960) and *Tillaea paludosa* (this paper), all of which are character species for associations in this new order. Noteworthy is the presence of vicariant species of *Ranunculus* with floating leaves: e.g. *Ranunculus volkensii* Engl. (Kilimanjaro), *R. biternatus* Sm. in Rees (Subantarctic Zone), *R. mandonianus* Wedd. (Peru, Bolivia), *R. limoselloides* (Peru - Venezuela) and *R. spaniophyllus* (Colombia - Venezuela). The same seems to apply also to some species of *Callitriche*. As a rule, these amphiphytic communities are poor in species. The *Crassuletum natantis* Van Zinderen Bakker & Werger 1974 contained on average 4.1 species (range 3-5) in 8 relevés and the *Tillaeetum paludosae* (this paper) 4.3 species (range 1-9) in 10 relevés. Gremmen (1981) reported an average of about 5.0 species (range 2-11) in 32 relevés from the halophytic *Cotulo-Crassuletum moschatae* Gremmen 1981 of the islands Marion and Prince Edward. According to Oberdorfer (1960) the *Crassula erecta* communities on rocks along Lake Villarica in Chile contain no other phanerogamic species; according to Reiche (1907), halophytic *Crassula moschata* communities on rocks along the Pacific beaches were associated either with *Colobanthus quitensis* or with *Asplenium obtusatum* Forst. In conclusion, all these Chilean communities are extremely poor in species.

*) All herbaceous aquatic species of *Crassula* belong in the author's opinion to *Tillaea* L.

Substrates consist of a more or less clayey ooze with silty or peaty components. Most associations/communities occur in fresh water. The pH of the water varies considerably: e.g. from 7.9 to 8.6 in the Lesotho bogs (Van Zinderen Bakker & Werger 1974), and from 5.9. to 6.4 in the pāramos of the Colombian Cordillera Oriental. The pH in the rootzone of *Tillaea* was 5.2 in the Lesotho bogs, from 4.5 to 5.7 on Marion Island (Gremmen 1981) and varied from 4.5 to 6.6 for the *Tillaeetum* of the Colombian pāramos. Relevés are not available from other parts of the tropical Andes and from equatorial Africa. *Tillaea*- or *Limosella*- dominated communities, however, seem absent on the New Guinean high mountains (Dr. J.M.B. Smith & Dr. J.F. Veldkamp, pers. comm.).

The *Tillaeetalia* should be comprised into the *Limoselletea* (classis nov. prov.), which includes the *Tillaeetalia* (type) and other related communities, characterized by the presence of amphibian *Limosella* spp.: e.g. *L. americana* Glück, *L. australis* R. Br., *L. lineata* Glück, *L. aquatica* L., *L. capensis* Thunb. and *L. africana* Glück. *Limosella australis*, for instance, was found dominating pond vegetation on the high Colombian volcanoes (Cleef et al., in press) and on Marion Island (Gremmen 1981). The *Limoselletea* as provisionally outlined here represents a tropical high mountain and austral-antarctic vicariant against the *Litorelletea* Br.-Bl. & R.Tx. 1943 em. Den Hartog & Segal 1964 described from the northern hemisphere. The genus *Litorella* (Plantag.) is not completely absent in southern latitudes, however; *Litorella australis* Griseb. is reported from various localities in the southern hemisphere. The *Litorelletea australis* (prov.) Oberdorfer 1960 apparently comprises local sandy beach communities in temperate South America. In the author's opinion the *Scirpo-Limoselletum* Oberdorfer 1960 from temperate Chile fits better in the *Limoselletea* prov. as here defined, than in the *Nanojuncetea australis* prov. Oberdorfer 1960, which according to Barkman et al. 1976, is not a valid name.

TILLAEION PALUDOSAE all.nov.
type: *Tillaeetum paludosae* (present study); table 3

Physiognomy: These basically amphibian communities are dominated by a low mat of herbs. Characteristic is a layer of small floating leaves, mostly belonging to geographically vicariant, amphibian species of *Ranunculus*.

Composition & syntaxonomy: This alliance comprises all tropical high Andean pond and lake-shore communities in which *Tillaea palludosa* plays a major role. Character species include *Limosella australis* (pref.), *Pilularia* cf. *manconi* (excl.), and *Tillaea paludosa* (sel.). *Tillaea venezuelensis* Stmk. must be a synonym of *Tillaea paludosa*. This conclusion is based on the examination of the type of *T. venezuelensis*. Differential species are *Alopecurus aequalis* Sobol, and to a certain extent also *Ranunculus limoselloides*, and other geographically vicariant species: *R. spaniophyllus* , *R. mandonianus* Wedd. The high cover of the (dominant) *Tillaea paludosa* is also differential against all other aquatic communities in the study area. Amphibian *Ranunculus* species and species of *Isoetes* sect. *Laeves* generally have a low cover.
The number of species varies from 1 to 5 (range 1-9) in 24 relevés.

Synecology: The allicance is generally found in shallow water of small pāramo lakes and ponds, or along the shores of large and deep pāramo lakes. The *Tillaeion* is restricted to mineral (clayey and silty) soils, the pH of

which varies from 4.8 to 6.6 in the upper root zone. The pH of the water is 4.7 to 6.4. Small waterbodies in the grass páramo tend to have oligotrophic conditions, whereas those in higher areas (superpáramo) are mesotrophic. The stands along the shores of the large páramo lakes clearly reflect more eutrophic conditions.
Due to the shallowness of the water and the characteristics of the páramo climate, water temperature fluctuate during a 24 hours period.
Smith (1975 b) described the characteristic *Ranunculus* species with floating leaves as perfectly adapted to the amphibian environment. He found that *Ranunculus sphaniophyllus* rapidly produced long-petioled leaves in an artificially flooded stand at 3600 m in the Venezuelan Andes. This alliance contains sensitive and delicate species, which cannot endure grazing by cattle See further under community 37.

Distribution: The alliance is known at present from the high Andes from Venezuela to Peru. Relevés were made in the Colombian páramos of the Cordillera Oriental (3330-4250 m) and in the Cordillera Central in the Parque Los Nevados (3700-4200 m). Our observations and herbarium data indicate that the *Tillaeion paludosae* occurs in the Venezuelan Andes between 3600 and 4250 m. Øllgaard & Balslev (1979) reported a stand at 3350 m in a small pond near the Laguna Papallacta in the Ecuadorian Cordillera Oriental. A community with *Crassula bonariensis (= Tillaea paludosa ?)*, *Isoetes socia* and *Ranunculus mandonianus*, mentioned by Weberbauer (1911) from the Cordillera Negra near Caraz in the Peruvian Andes at 4400 m might also belong to the *Tillaeion paludosae*. Herbarium collections (Liogier 21572, Mandon 1460, NY) indicate that a *Tillaea aquatica* L. (= *T. paludosa* in the author's opinion)- dominated community may be present at 2200 m in Valle Nuevo on Hispaniola, and in the Bolivian Andes.

36. *Tillaeetum paludosae* ass. nov.
type: rel. 41; table 3; Fig. 39, 40 & 41
lit.: Weberbauer 1911; Ruthsatz 1977

Physiognomy: This basically amphibian herbaceous association is characterized by a practically closed (about 1-10 cm high) dense bright green layer of *Tillaea paludosa*. Other vascular plants may root in the *Tillaea* layer. Shallow waterbodies may contain a layer of floating leaves of mainly *Ranunculus limoselloides*, *Alopecurus aequalis* and sometimes *Callitriche* sp. (up to 40 cm). *Lilaeopsis schaffneriana* and *Juncus ecuadoriensis* may be present with part of their foliage and inflorescenses exposed.
Flowering in this association only shows whitish to greenish petals. Apparently, most dicots are autogamic. The cleistogamic *Tillaea paludosa* and *Elatine chilensis* are only flowering and fruiting when they emerge in the dry season. Physiognomically a strong resemblance can be seen with African high mountain vegetation: e.g. with the *Crassula granvikii* zonation in tarns on Mt. Kenya (Coe 1967) and Ruwenzori (Hedberg 1964). Hedberg (1964) described similar amphibious communities with *Subularia monticola* A. Br. ex Schweinf. (Cruc.), *Crassula granvikii* Mildbr., *Limosella africana* Glück, *Callitriche stagnalis* Scop. and *Ranunculus volkensii* Engl. (only Kilimanjaro) from the afro-alpine belt of several East African mountains. Van Zinderen Bakker & Werger (1974) described a *Crassuletum natantis* from pools in the Lesotho mountains at 3200 m, which is strikingly similar to the *Tillaeetum paludosae* as regards vascular generic composition, richness in species, synecology, structure, life and growth forms.

Composition & syntaxonomy: *Tillaea paludosa*, the crassulaceous, aquatic, selective character species is dominant. Its cover varies from 35 to 100% with an average of about 80%. Other character species are *Limosella australis* (sel.) and *Pilularia* cf. *mandoni* (excl.). *Alopecurus aequalis* is considered a differential species.*Isoetes* spp. (e.g. *I. palmeri, I. glacialis)* may be present with varying cover (1-25%), just as some other aquatic herbs, e.g. *Elatine chilensis* (especially in the *isoetetosum*) *Ranunculus limoselloides, Callitriche* sp(p)., *Eleocharis stenocarpa* and *Lilaeopsis schaffneriana* (especially in the subass. *typicum*). Incidentally present are *Cardamine* sp., *Juncus ecuadoriensis, Eleocharis acicularis* and *Potamogeton asplundii*. Mosses are sparse and liverworts nearly absent. Filamentous green algae are common in shallow waterbodies, sometimes covering much as 75%. The number of species averages about 4 (range 1-9) in 16 relevés.

The *Tillaeetum* can be divided into two subassociations: the *isoetetosum* and the *typicum*. The *isoetetosum* is characterized by the presence of *Isoetes* species penetrating from adjacent deep lake bottoms; it also contains *Elatine chilensis*, which is more frequent and has a higher cover. The *typicum* is characterized by the presence (with low cover) of *Limosella australis, Pilularia* cf. *mandoni* and/or *Isoetes socia*.

Synecology: The *Tillaeetum* is restricted to shallow and submerged habitats on mineral, mostly clayey soils. It occurs 1) along shores of deep páramo lakes *(isoetetosum)*, and 2) in ponds or on flat ledges bordering the shore of deep páramo lakes (subassociation *typicum*). Maximum water depth is about 40 cm. The pH of the upper layer of the substrate varied from 4.5 to 6.6. In ponds the pH is about 5, which is considerably lower than in lakes. As may be expected, the watertemperature rises considerably in daytime by insolation.In rel. 161 (Laguna Cuadrada, dry side of the Sierra Nevada del Cocuy at 4050 m), at 4.30 p.m. a temperature of 18°C was recorded for the water containing the subass. *typicum*, whereas the atmospherical temperature was about 8°C. Copulating páramo frogs (*Hyla* sp.) were observed in the *Tillaeetum* habitat. Mollusca, e.g. *Sphaerium lauricochae* Philippi and Gastropoda are common in lake border habitats, which are also rich in aquatic arthropods.

Distribution: The *Tillaeetum paludosae* is found from the upper subpáramo at 3330 m up to the lower limit of the superpáramo at 4250 m in the Cordillera Oriental of Colombia. This association and the *Isoetetum sociae* are altitudinally vicariant communities in the study area (Fig. 91). In lower areas, *Tillaea paludosa* was also recorded (as "*Elatine triandra*") in *Scirpus californicus* reedswamp of the Laguna de Tota (Boyacá) at 3000 m (Aguirre & Rangel 1976). *Tillaea paludosa* was never observed in the superpáramo, but *Elatine chilensis* only once at 4400 m near the sandy shore of a superpáramo lake (rel. 323). In the Colombian Cordillera Central the *Tillaeetum paludosae* has recently been studied from 4150 to 4250 m in the bunchgrass páramo on the Nevado S.Isabel (Cleef et al., in press). In the Venezuelan páramos of the Sierra Nevada de Mérida, the *Tillaeetum paludosae* has been observed from 3600 and 4250 m. From the Ecuadorian páramos Øllgaard & Balslev (1979) reported a *Crassula*-dominated pond vegetation with *Isoetes* sp. at 3350 m near the Laguna Papallacta (prov. Napo). Weberbauer (1911) describes a rather similar (or identical) community from a small lake at 4400 m in the Cordillera Negra near Caraz in Peru, where *Crassula bonariensis, Isoetes socia* and *Ranunculus mandonianus* (floating leaves) are associated. Ruthsatz (1977) referred to *Crassula paludosa* (with low cover) associated e.g. with *Limosella lineata* and *Eleocharis acicularis* from a dry shallow pond at 3600 m in the Tucumán Andes, Argentina.
Thus, this association appears to be well-represented at least in the northern

Andean páramos of Ecuador, Venezuela and Colombia, and possibly extends further south.

36[a]. Subass. *isoetetosum* subass. nov.
type rel. 485; table 3; Fig. 39

Physiognomy: The bright-greenish (up to 10 cm high) closed amphibious herblayer of mainly *Tillaea paludosa* is associated with isoetids, e.g., *Isoetes* species (up to 25 cm tall) and the inconspicuous *Elatine chilensis* (1-2 cm high). A layer of floating leaves, e.g. of *Ranunculus limoselloides* and *Alopecurus aequalis*, may be present also.

Composition & syntaxonomy: Dominant species is *Tillaea paludosa* (50-100% cover), with *Elatine chilensis*, a tiny aquatic herb with prostrate stems, as a constant companion (1-15% cover). *Isoetes palmeri*, or *I. glacialis* (1-25% cover) are differential species. *Callitriche* sp.(p.), *Eleocharis stenocarpa*, *Alopecurus aequalis* and *Ranunculus limoselloides* have a low frequency. The number of species averages about 4 (range 3-6) in 6 relevés.

The *isoetetosum* of the *Tillaeetum* can be easily recognized by the differential *Isoetes* species and the higher presence and cover of *Elatine chilensis*. The *isoetetosum* has the greatest affinity to the subass. *typicum* of the *Tillaeetum*, but has also floristic and ecologic properties in common with the *Isoetetum palmeri*; it may be considered intermediate or transitional between these aquatic syntaxa.

Synecology: This subassociation only occurs on gently sloping bottoms in shallow water on the shores of deep páramo lakes. At 30-50 cm depth, a transition is found to the *Ditricho-Isoetion*. At 3900 m and near rel. 476 a dense *Nitella* vegetation associated with *Lilaea subulata*, *Eleocharis acicularis*, *Callitriche* sp. was intermixed with the *Tillaeetum isoetetosum* and the *Ditricho-Isoetion*. The *isoetetosum* is generally submerged, but at the end of a long-lasting dry season this community may be partly or completely above water. Substrates vary from sandy-stony to clayey (silty) and peaty; the pH of the water at the lake is 6.1 to 6.4.

Distribution: The *isoetetosum* is restricted to the upper subpáramo and grass páramo in the Colombian Cordillera Oriental between 3400 and 3900 m. On the Nevado S. Isabel in the Colombian Cordillera Central, this subassociation was studied near the 4150 m level. In the Sierra Nevada de Mérida (Venezuela) this vegetation type (impoverished) was found in a lake at the transition from grass páramo into superpáramo at 4250 m (rel. 552; Páramo Piedras Blancas).

36[b]. Subass. *typicum* subass. nov.
type: rel. 41; table 3; Fig. 40

Physiognomy: Most conspicuous is the closed, bright-greenish *Tillaea paludosa*-herb layer up to about 10 cm high (waterlogged soil or submerged). The ground layer also contains other isoetids, e.g. *Isoetes socia*, *Elatine chilensis*, *Limosella australis*, *Eleocharis stenocarpa*. A floating layer of leaves of *Ranunculus limoselloides* and some of *Alopecurus aequalis* and *Callitriche* sp. is common.

Composition & syntaxonomy: *Tillaea paludosa* is dominant; *Limosella australis* and *Pilularia* cf. *mandoni* are character species of the order, and

Alopecurus aequalis and *Isoetes socia* are differential species with low cover (up to 30%); the last-mentioned species only in stands which are transitional to the *Isoetetum sociae*. *Limosella australis* is rather rare but if present it covers 10 - 30%. The same is true for *Alopecurus aequalis*. *Pilularia* cf. *mandoni* is rather inconspicuous, and may be easily overlooked. The number of species averages about 4 (range 1-9) in 10 relevés.

The subassociation *typicum* of the *Tillaeetum paludosae* is mainly negatively characterized against the *isoetetosum* by the absence of *Isoetes* species native to deep páramo lakes. Differential against the *isoetetosum* is *Lilaeopsis schaffneriana*, *Tillaea paludosa* is a differential species against the *Isoetetum sociae*. Some grass páramos ponds with *Isoetes socia* may represent a variant.

Note: Only few records of *Pilularia* are available from the Colombian páramos. Lozano et al. (1976) mentioned apparently the same species from the Páramo de Cruz Verde near Bogotá. *Pilularia* cf. *mandoni* is here reported from 3330 to 4060 m in the Boyacá páramos. This inconspicuous species may prove to be more common if this kind of habitat of the *Tillaeetum* is carefully examined throughout th Colombian páramos. The taxonomical position of this *Pilularia* species remains uncertain.

Synecology: The subass. *typicum* of the *Tillaeetum* is found in ponds and shallow small lakes, and as a separate zone on the flat submerged near-shore parts of deeper páramo lakes. In general this vegetation was found on thin mineral (silty-clayey) up to 65 cm thickness. Organic matter is rather scarce in these soils. Only in lake-shore habitats the soils are thicker (more than 120 cm) and consist of clayey peat and gyttja. In lower regions ooze is commonly present on the *Tillaea* mat. The pH of the upper soil layer varies from 4.5 to 6.6, depending on the kind of habitat. Pond soils are more acid (4.9 to 5.2) whereas the pH of lake sediments varies from 5.4 to 6.6. The water is not deeper than 30 cm; in comparison with the *isoetetosum* the habitat of the subass. *typicum* is more often dried out by evaporation. Near the beginning of the wet season the only more or less vital species found is the amphibious *Tillaea paludosa*. In some places it is accompanied by small *Isoetes socia* corms which are buried in the top soillayer (rel. 81 & 380 A). Other herbaceous species are supposed to survive as seeds, or as vegetative diaspores from elsewhere.

Distribution: This herbaceous amphibian (and amphiphytic) community is common to all páramos of the Colombian Cordillera Oriental from the upper subpáramo at 3300 m up to the superpáramo border at 4250 m. *Tillaea paludosa*-dominated communities are probably restricted to the humid tropical Andean páramos.

37. Communities of *Callitriche* and *Ranunculus* spp.

table 5[a]

The floristic composition and plant cover of the *Tillaeion* seems to change drastically, when the habitat is intensively grazed, trampled and manured by cattle. The tiny, delicate species disappear, e.g. *Tillaea paludosa* and (to a lesser extent) *Elatine* cf. *chilensis*. Generally the cover of *Callitriche* sp.(p.) and the floating leaves of *Ranunculus* spp. increases considerably, and so does a dense mass of filamentous green algae. *Alopecurus aequalis*, a nitrophytic (indicator)plant with floating leaves, may be present as well.

Relevés of such communities that are more or less affected by cattle have been listed in table 5[a].

table 5 [a]

Callitriche-Ranunculus spp. communities

rel.	616	536A	532	560
alt. m	4100	3650	3700	3815
size m^2	3	4	3	4
soil	c	cp	cp	c
depth cm	50?	25	10-30	10
d.d.	febr.'80	aug.'77	aug.'77	nov.'78
locality	Isabel Cord. Central	Chubdulá S.Marta	Cumbre S.Marta	Almorz. Cord. Oriental
cover %:				
Callitriche sp(p.)	1	.	10	50
Ranunculus limoselloides	90	x+)	2+)	35
Elocharis stenocarpa	.	x	<1	40
Lilaeopsis schaffneriana	.	.	.	1+
Alopecurus aequalis	.	.	.	<1
Isoetes sp.	.	x	.	.
Ditrichum submersum	65	.	.	.
Tillaea paludosa	35	.	.	.
filamentous algae	x	x	x	x

+) or *R. spaniophyllus*

Localities relevé
relevé 560: Santander; Páramo del Almorzadero, El Tutal
532: Magdalena; Sierra Nevada de S. Marta, Alto la Cumbre
536A: Magdalena; Sierra Nevada de S. Marta, Laguna Chubdulá
616: Caldas; Volcán S. Isabel, W slope, El Portál

Relevé 616 is situated at a small lake with the *Ditricho-Isoetion*, and is regularly trampled by cattle.

38. Communities with *Limosella australis*
table 6

In several páramos (Sumapaz, Guantiva, Cocuy, Almorzadero) small (up to 1 m^2) local *Limosella australis*-dominated patches in shallow stagnant water were found between 3600 and 4250 m. Rel. 560A & B from a small shallow pond at 3800 m in the Páramo del Almorzadero (El Tutal) offer examples of *Limosella australis* vegetation:

Table 6

Limosella australis community

rel. no.	560A	560B
alt. m	3800	3800
depth cm	5	3
soil	clayey	clayey
height cm	3	5
size m^2	1	0.5
loc.	Almorzadero	Almorzadero
colorslide Cleef	3943	3942
Limosella australis	35	12
Callitriche sp.	1	<1
Tillaea paludosa	3	5
Ranunculus limoselloides	5	<1

A *Limosella australis* community apparently also occurs submerged in swiftly running water of a small páramo stream surrounded by *Montia fontinalis* vegetation near a mire at 3800 m in the Parque Los Nevados, Colombian Cordillera Central (rel. 628). *Limosella australis*-dominated pond vegetation was observed at about 4150 m in the Parque Los Nevados (Cleef et al., in press) and it is perhaps to newly describe a *Limoselletum australis* (prov.) on basis of these data.
According to Lourteig (1956) *Limosella australis* is mainly distributed in the subantarctic zone. Gremmen (1981) mentioned a *Limosella australis* sociation from the Marian & Prince Edward islands. Recently, however, the Colombian *Limosella* material collected by the author was recognized by Dr. A. Lourteig as belonging to *Limosella australis*. Possibly after revision a number of S. American *Limosella* specimens will prove to belong to this species.

POTAMETO - MYRIOPHYLLION ELATINOIDES all. nov. (prov.)
type: *Hydrocotylo ranunculoides - Myriophylletum elatinoides;* table 3

Physiognomy: This aquatic syntaxon predominantly consists of myriophyllids an elodeids. Amphiphytes and isoetids may also be present with low cover. The vegetation mass is denser when the lake is more shallow.

Composition & syntaxonomy: Character species are *Myriophyllum elationoides* (select., transgr.), *Potamogeton asplundii* (excl.), *Hydrocotyle ranunculoides* (select/pref.), *Potamogeton illinoiensis* (pref.) *Eleocharis acicularis* (pref.) and *Scorpidium scorpioides* (pref.). The number of species is about 7 (4 to 9) in 4 relevés. For plantgeographical comments, see under associations, and Cleef (1978). *Elodea* species (Potamogetonac.) were never reported for Colombian páramo lakes, but Øllgaard & Balslev (1979) mentioned the genus for an Ecuadorian páramo lake (laguna Micacolha) at 4000 m. Collot (1980) reports *Elodea potamogeton* up to 4700 m in the Bolivian Andes.
The *Potameto-Myriophyllion* has affinities to both the *Eleocharitetum macrostachyae (Myriophyllum elatinoides* transgr.) and the *Isoetetum palmeri*. The *Potameto-Myriophyllion*, however, can be readily distinguished by the high cover of *Potampgeton asplundii* or *Myriophyllum elatinoides*. At present the alliance includes one association and two unranked communities, distinguished by the presence either of *Scorpidium scorpioides*, *Potamogeton asplundii*,

P. illinoiensis, Lilaeopsis schaffneriana, Isoetes glacialis and *Nitella acuminata* (both *Potamogeton* communities), or of *Hydrocotyle ranunculoides* (*Hydrocotylo-Myriophylletum*). More relevés are reguired to confirm this subdivision.
The *Myriophyllio-Potamion illinoiensis* Rangel & Aguirre (in press) from the Lake Tota at 3000 m in the Andean forest belt is an altitudinal vicariant of the *Potameto-Myriophyllion* of the páramo belt. Both alliances apparently belong to the *Potametea* (Tx. & Pr. 1942) Den Hartog & Segal 1964 em. Westhoff 1968, which is widely distributed in the Holarctic.

Synecology: The *Potameto-Myriophyllion* is found on shallow lake bottoms (at least to a depth of 3 m) with stagnant water and clayey gyttja-like sediments (*Hydrocotylo-Myriophylletum*) or nearly stagnant, slow to swift running water on peaty-clayey to stony substrates (*Scorpidium-Potamogeton* communities). The pH values of the water (6.6-7.3) indicate mesotrophic to eutrophic conditions. The habitat probably never becomes dry. The *Hydrocotylo-Myriophylletum* plays a major role in the submerged part of the hydroseral succession on clayey to peaty sediments. Collot (1980) mentions a depth of 1.50-2.50 m for a maximal development of *Myriophyllum elatinoides* in Lake Titicaca. Flowers of this species were only observed under these conditions.

Distribution: The *Potameto-Myriophyllion elatinoides* is presently known from the subpáramos and the bamboo páramos proper between 3450 and 3700 m in the southern part of the Colombian Cordillera Oriental. The alliance seems to be present also in páramo lakes of the Cordillera Central from 3300 m up to 4200 m. The *Potameto-Myriophyllion elatinoides* is probably widely distributed above the upper forestline in the tropical Andes. According to (Collot, 1980) related communities with *Potamogeton strictus* and *Myriophyllum elatinoides* were noticed also in Lake Titicaca at 3800 m.

39. Communities of *Potamogeton* spp. and *Scorpidium scorpioides*

characteristic relevés: 294 Community of *Potamogeton illinoiensis*
297 Community of *Potamogeton asplundii*
table 3; Figs. 41 (also Figs. 43, 50, 51)

Physiognomically, two herb layers can be recognized in these elodeid-dominated communities:
1) an isoetid layer of *Isoetes glacialis* and *Eleocharis acicularis*; and
2) a sligthly stratified uppper layer of elodeids (*Potamogeton, Myriophyllum*) and bryophytes (*Scorpidium*) reaching the surface of the water.

Communities with *Scorpidium* and *Potamogeton* were only studied in the Laguna La Guitarra (Meta), at 3425 m and 6 km NW of the Nevado de Sumapaz. Along its marshy shores are stands with *Potamogeton asplundii*. The swiftly running water of the outlet of this lake contains *Potamogeton illinoiensis*. According to Dr. L.B. Holm-Nielsen (in litt.) *Potamogeton illinoiensis* is widely distributed in tropical America from the southern United States to South Brazil; the as yet undescribed *Potamogeton asplundii* is only known from Ecuadorian and Colombian páramos. The presence of different *Potamogeton* species is the main floristical difference between the two elodeid communities, which have many species in common,e.g. *Scorpidium scorpioides, Myriophyllum elatinoides, Isoetes glacialis, Lilaeopsis schaffneriana* and *Eleocharis acicularis*. *Nitella acuminata* and *Isoetes glacialis* are invading from the deeper lake bottom, whereas amphibian species, e.g. *Tillaea paludosa* and

Elatine chilensis, are found closer to the shore. Fewer species are present in rel. 194 with *Potamogeton illinoiensis*, probably as a result of the strong current.

Note: *Scorpidium scorpioides* is considered as the only *Scorpidium* species in the cool aquatic habitats of the tropical high Andes. Specimens (5943, 5946), almost similar to those described by Herzog (1916) as *Scorpidium turfaceum*, were collected during the field work in the Colombian páramos (det. Dr. P.A. Florschütz). The differences with the holarctic *Scorpidium scorpidioides* are too weak, however, to consider the tropical Andean material as a separate species (Dr. D. Griffin III, pers. comm.).

The habitat of the two *Potamogeton* communities is quite different. *Potamogeton illinoiensis* vegetation covers the solid sandy to gravelly shallow bottom near the outlet of this moraine-damned lake. *Potamogeton asplundii* is predominantly found on clayey to peaty substrates and on gyttja. The pH values 6.6 and 7.2 by the water indicate eutrophic conditions. Leeches (Hirudinae) have been commonly observed.

Data on the distribution of the two *Potamogeton* species in the Colombian Andes are mainly based on our plant specimens identified by Dr. L.B. Holm-Nielsen (AAU). Both *Potamogeton* communities might be expected at least in the corresponding páramos and extending in the high Andes of Ecuador and other parts of the tropical Andes.
Potamogeton illinoiensis is known from lakes in the Colombian Cordillera Oriental, from the high plain of Bogotá (2600 m) up to the grass páramo (3800 m): Laguna de Fúquene, Laguna de Tota, Laguna La Guitarra (Páramo de Sumapaz) and Laguna El Alcohol (Páramo de Guantiva).
In Colombia, *Potamogeton asplundii* was only collected from 3300 to 3800 m from the upper forest line to the bamboo páramos of the Cordillera Central (Puracé) and the Cordillera Oriental (Sumapaz, Cuantiva).
Because of the small number of relevés no syntaxonomical rank was given to these *Potamogeton* -communities. *Scorpidium scorpidoides*, *Isoetes glacialis* and *Liliaeopsis schaffneriana* are not present in the *Hydrocotylo-Myriophylletum*.

40. *Hydrocotylo ranunculoides - Myriophylletum elatinoides* ass. nov.
type: rel. 266; table 3; Fig. 42 (also Fig. 49)

Physiognomy: Te weaky stratified herb layer mainly consists of dense *Myriophyllum elationoides*, which may be partly emergent. The foliage of *Hydrocotyle ranunculoides* is morphologically different when submerged or emerged. *Elatine chilensis* is found in a distinct ground layer partly covering thepeaty and muddy substrate.

Composition & syntaxonomy: The dominant and selective character species (transgr.) is *Myriophyllum elatinoides*, as a rule accompanied by some other vascular species, as *Hydrocotyle ranunculoides* (pref.), *Elatine chilensis* (the higher cover (5-15%) is differential against the communities with *Scorpidium* and *Potamogeton* species) and *Eleocharis acicularis*. Mosses are practically absent.
The number of species in 2 relevés is 4 and 8 respectively.
The *Hydrocotylo-Myriophylletum* is strongest related to the *Scorpidium-Potamogeton* communities and locally to the *Isoetetum palmeri* in the páramo belt.

Synecology: The association is reported from thick muddy and peaty substrates in stagnant water in páramo lakes, where the *Hydrocotylo-Myriophylletum* is the first truely aquatic vegetation near the shores. Water depths vary from shallow to about 50 cm. The pH of the water is 6.5-7.3. *Myriophyllum* stems are rather long and it is believed that the habitat of the *Hydrocotylo-Myriophylletum* experiences considerable changes in water level, but apparently it is never completely above the water-line. Leeches and frogs were noticed. Migrating aquatic birds (e.g. ducks) must have a strong influence on this vegetation by foraging and manuring, and are regarded as the principal agens responsible for the present wide distribution of the composing vascular taxa.

Distribution: The *Hydrocotylo-Myriophylletum elatinoides* is only known from the mainly bamboo-dominated upper subpáramo and the lower grass páramo in the southern part of the Cordillera Oriental. The association is reported from the Laguna La Primavera (3550 m.) near the Nevado de Sumapaz and from the Laguna Seca (3650 m) in the upper Río Chuza valley, East of Bogotá. This syntaxon may perhaps be found up to about 4000 m.
This association is supposed to be widely distributed in the Andes, as both *Myriophyllum elatinoides* and *Hydrocotyle ranunculoides* are common in the moutains of Latin America. *Myriophyllum elatinoides* is also known from the Islas Malvinas and Australia - Tasmania. The highest known Andean locations are the Laguna Aguascocha and the L. Caprichosa at 4750 m in Peru. In the Colombian Andes, this species is found from 2700 m to 4000 m.
In the Colombian Andes *Hydrocotyle ranunculoides* is present in the subandean forest belt up to 4000 m.

JUNCO ECUADORIENSIS - ELEOCHARITION MACROSTACHYAE all. nov.
type: Eleocharitetum macrostachyae; table 3

Physiognomy: The alliance consists of hydroseral reedswamp communities are structured in three layers:
1) an open isoetid ground layer (consisting of *Elatine chilensis*, *Tillaea paludosa* and *Isoetes* spp.),
2) an aquatic moss-herb layer reaching up to the water surface and consisting of *Sphagnum* spp., *Drepanocladus* spp., *Myriophyllum elatinoides*, *Callitriche* sp. and occasionally dense filamentous algae; floating foliage of *Ranunculus limoselloides*, and
3) a 50 cm high fieldlayer of the helophytes *Eleocharis macrostachya* and *Juncus ecuadoreinsis*.

Composition & syntaxonomy: Exclusive character species are *Eleocharis macrostachya* and *Juncus ecuadoriensis*, and also the purplish algae cf. *Microspora* sp. and/or *Zygnema* sp. probably are selective character species. *Ranunculus limselloides*, *Elatine chilensis*, *Tillaea paludosa*, *Myriophyllum elatinoides*, *Drepanocladus exannulatus* (and to a lesser extent, *Sphagnum cuspidatum* and *Calliergonella cuspidata)* are differential by presence or their higher cover.
The average number of species is 5 - 6 in 9 relevés.
Physiognomically and ecologically, the *Junco-Eleocharition macrostachyae* has the greatest affinity with the *Phragmitetea* R. Tx. & Pr. 1942. On the basis of the predominant species in the field layer, the alliance can be subdivided into two associations:the *Eleocharitetum macrostachyae* (41) and the *Elatino-Juncetum ecuadoriensis* (42).

Synecology: The *Junco-Eleocharition* occurs in shallow hydroseral habitats on silty to clayey and peaty soil:

1) along shores of deep páramo lakes *(Eleocharitetum macrostachyae myriophylletosum)*,
2) in ponds (mostly *Eleocharitetum macrostachyae tillaeetosum*), and
3) in pools *(Elatino-Juncetum ecuadoriensis)*.

The pH values vary from 6.3-7.4 in eutrophic large páramo lakes in acid pools. Just as discussed for the *Tillaeion*, the water temperatures may rise in day-time by insolation. The depth of the water is 50 cm or slightly more.

Distribution: The *Junco-Eleocharition macrostachyae* is widely distributed in the lower part of the páramo belt of the Colombian Cordillera Oriental from 3400 m to 3900 m. The alliance, especially the *Eleocharitetum macrostachyae*, seems to extend into the Andean forest belt to a height of 2700 m. Since both predominant and exclusive character species are common in the páramos of the Colombian Cordillera Central of Ecuador, the *Junco-Eleocharition* may be expected in most of the northern Andean páramos.

41. *Eleocharitetum macrostachyae* ass. nov.
type: rel. 300; table 3; Fig. 43 & 44

Physiognomy: The *Eleocharitetum macrostachyae* is a by sometimes helophytes dominated, cyperaceous reed swamp, sometimes falling dry in the dry season. This association is stratified in:

1) an open ground layer, which may consist of scarce specimens of *Isoetes* sect. *Laeves*, *Elatine chilensis*, *Tillaea paludosa* and *Eleocharis stenocarpa;*
2) a herb-moss layer up to the water surface of *Myriophyllum elatinoides*, *Callitriche* sp., aquatic mosses and occasionally *Utricularia obtusa* with at or just above the waterlevel *Ranunculus limoselloides* and *Lilaeopsis schaffneriana;* and
3) a field layer (about 40-50 cm high) with a conspicuous reddish-orange hue of *Eleocharis macrostachya* -stems, locally with *Juncus ecuadoriensis*.

Composition & syntaxonomy: An exclusive character species is *Eleocharis macrostachya*, a differential species is the moss *Calliergonella cuspidata*. *Myriophyllum elatinoides* is differential for the *myriophylletosum* and *Tillaea paludosa*, *Callitriche* sp., *Elatine chilensis* and *Ranunculus limoselloides* are differential for the *tillaeetosum*. Differential against the *Elatino-Juncetum ecuadoriensis* are *Tillaea paludosa* (up to 20%), *Callitriche* sp(p.) (up to 15%), *Myriophyllum elatinoides* (up to 40%) and *Calliergonella cuspidata* (up to 80%). Differential against the *Potameto-Myriophyllion* prov. are *Tillaea paludosa*, *Callitriche* sp., *Ranunculus limoselloides* and *Calliergonella cuspidata*. The *tillaeetosum* mainly differs from the *Tillaeetum paludosae* (36) by the presence of *Eleocharis macrostachya* and *Juncus ecuadoriensis* the *Tillaea* cover is low (up to 15%) compared to the predominance in the *Tillaeetum paludosae*.
The average number of species is 6 (2-11) in 9 relevés.

Synecology: This association of shallow water is locally present as a reedswamp along the shores of páramo lakes. Larger patches of the *Eleocharitetum macrostachyae* may indicate a transition of open water vegetation to land vegetation, e.g. communities of the *Marchantio-Epilobietalia*. *Eleocharis macrostachya* vegetation also may cover small lakes or ponds with practically stagnant water. This species is generally found on organic clayey lake sediments. Colonization begins on soft mud; towards the shore the *Eleocharis* rhizomes grow in a dense mat, thus contributing to soil

solidity. In zones with a stable water supply peat formation is uninterrupted and simultaneously, clayey particles are trapped. The pH of the substrate is 6.3-6.5, that of the lake water 4.9-7.4.
The *tillaeetosum* in smaller shallow lakes with stagnant water is richer in vascular species than the *myriophylletosum*, which forms a reedswamp zone in larger and deeper pâramo lakes. Towards open water, wave action, increasing depth and lesser light intensity are limiting factors for the *myriophylletosum*. During the dry season (part of) the *Eleocharitetum macrostachyae* is exposed. In the smaller lakes with the *tillaeetosum* the water evaporates more rapidly than in deeper lakes, and the *tillaeetosum* is emerged for a longer period of the year. This explains the higher frequency and cover of helophytes and amphiphytes. True hydrophytes (e.g. *Myriophyllum elatinoides)* are practically absent. In the transitional zone from the open water to the marshy shore, the *myriophylletosum* is replaced by the *tillaeetosum* of the *Eleocharitetum macrostachyae* (for example, see rel. 300).

The shallow water of the *Eleocharitetum macrostachyae*, especially the *tillaeetosum*, contains a rich fauna of small aquatic insects, leeches and Gastropoda (cf. *Planorbis*), and pâramo frogs have been noticed. If the water level falls considerably, the *Eleochariteum macrostachyae* becomes accessible for foraging *Cavia porcellus*.

Distribution: The *Eleocharitetum macrostachyae* is distributed in the pâramos of the Colombian Cordillera Oriental from the upper subpâramo at 3300 m up to the lower grass pâramo at 3900 m on the dry W side of the Sierra Nevada del Cocuy.
The *Eleocharitetum macrostachyae* might extend as far down as 2700 m, where similar reedswamp was observed in a small lake in the Andean *Quercus* forest near S. Cayetano (Cundinamarca). According to data from floras and herbaria, *Eleocharis macrostachya* is distributed from the southern Unites States to Argentina.

Note: Rel. 184 and later 498A were made at the location of the palynological section "VL VII", Sierra Nevada del Cocuy, published and illustrated (photo 3)by Gonzalez et al. (1965). Relevé 498A represents the strongh reduced plant cover near the end of the extremely long dry season in the beginning of 1977.

41^{a}. Subass. *myriophylletosum elatinoides* subass. nov.
type: rel. 11; table 3; Fig. 43

Physiognomy: See the association. The groundlayer, however, is dominated by *Myriophyllum elationoides*.

Composition & syntaxonomy: This subassociation is characterized by the presence of *Myriophyllum elatinoides* (cover up to 40%). The average number of species is 4 (2 to 6) in 4 relevés. In general, the number of species is less than in the *tillaeetosum*. The presence of *Myriophyllum elatinoides* and the absence of *Tillaea paludosa, Elatine chilensis, Callitriche* sp., *Lilaeopsis schaffneriana* and *Ranunculus limoselloides* are differential against the *tillaeetosum*. Some records of a higher cover (80%) of both *Ranunculus limoselloides* and *Calliergonella cuspidata* mark the transition from open water to mossy marsh and might be ranked at the variant level.

Synecology: See also under association. In the eutrophic pâramo lakes the pH of the toplayer of the substrate ranges from 6.3 to 6.5; the pH of the lake water is 7.4. High cover of *Calliergonella cuspidata* apparently causes a lesser cover of *Eleocharis macrostachya* and finally this moss species dominates. The nutrient content must be high in the *myriophylletosum*, as suggested by the high pH (and the abundance of young trouts).

Distribution: This subassociation was only observed in the Laguna La Guitarra at 3425 m near the Nevado de Sumapaz.

41^{b}. Subass. *tillaeetosum paludosae* subass. nov.
type: rel. 184; table 3; Fig. 43 & 44

Physiognomy: In contrast to the *myriophylletosum* amphiphytes *(Elatine chilensis, Tillaea paludosa, Ranunculus limoselloides)* dominate in the ground layer. The helophyte *Juncus ecuadoriensis* is found together with *Eleocharis macrostachya* in the upper stratum.

Composition & syntaxonomy: The *tillaeetosum* contains about twice as many vascular species as the *myriophylletosum*, with *Tillaea paludosa. Ranunculus limoselloides, Elatine chilensis, Lilaeopsis schaffneriana, Callitriche* sp(p.) and *Juncus ecuadoriensis*. For differential species, see also the association and the *myriophylletosum*. The *tillaeetosum* is differentiated from the *Elatino-Juncetum* by the presence of *Tillaea paludosa* and *Eleocharis macrostachya*. There are numerous mosaic-like patterns in the transition to the *Elatino-Juncetum ecuadoriensis* and to the *myriophylletosum* (of this association), which is reflected in some not fully homogeneous relevés.
The average number of species is 8 (range 6-11) in 5 relevés. *Utricularia obtusa* and *Drepanocladus revolvens* are occasionally present with a high cover.

Synecology: The pH range of the water is 4.9 to 7.4. This subassociation occupies a specific kind of habitat: 1) near the shores of large mesotrophic to eutrophic páramo lakes,and 2) in small lakes with mainly mineral bottoms with oligotrophic to mesotrophic conditions. Environmental conditions seem to be favourable for insect life (see assoc.). Water temperatures are high in daytime: e.g. 17° at noon on May 3, 1973, in rel. 404 at 3700 m. Such high temperatures of the lakes may explain why the *tillaeetosum* is found at greater heights than the *myriophylletosum*.
For further details, see association.

Distribution: The *tillaeetosum paludosae* is found throughout the Cordillera Oriental from the upper subpáramo at 3450 m to the grass páramo proper at 3900 m on the dry side of the Sierra Nevada del Cocuy.

42. *Elatino chilensis - Juncetum ecuadoriensis* ass. nov.
type: rel. 67; table 3; Fig. 71

Physiognomy: This association can be easily distinguished as patches of green to brown-reddish reed swamp. The structure of the *Elatino-Juncetum ecuadoriensis* is more or less similar to that of the *Eleocharitetum macrostachyae*. The submerged open ground layer contains *Isoetes* spp., *Elatine chilensis*, and rosettes of *Ranunculus limoselloides*. *Sphagnum cuspidatum* and *Drepanocladus exannulatus* may be floating. The characteristic small ellipsoid leaves of *Ranunculus limoselloides* are spread out on the water surface between the upper open stratum of the 20-30 cm high leaves, flowers and fruiting parts of the helophytic *Juncus ecuadoriensis*.

Composition & syntaxonomy: In the *Elatino-Juncetum ecuadoriensis*, either *Juncus ecuadoriensis* or *Elatine chilensis* may be dominant, each covering up to 80%. *Ranunculus limoselloides* is usually present (cover up to 30%) and completely submerged *Sphagnum cuspidatum* may be common, generally with low cover. Depending on size and depth of the waterbody, *Isoetes palmeri* and *I.* cf. *socia* may be present. *Drepanocladus exannulatus* locally attains a cover of up to 80%. Dense masses of characteristic violet-purple filamentous Chlorophyta (e.g. *Microspora* spp., *Zygnema* spp.) replace *Drepanocladus exannulatus*.
The average number of species is 4-5 (4-6 species in 7 relevés).

Juncus ecuadoriensis is a transgrediant selective character species; *Elatine chilensis* and *Ranunculus limoselloides* are preferential character species. The *Elatino-Juncetum ecuadoriensis* shows close affinities to the other associations of the *Junco-Eleocharition macrostachyae*, and to the two variants of the *Isoetetum palmeri* with *Sphagnum cuspidatum* (34^{ab}) and *Drepanocladus exannulatus* (34^{aa}). Differential against the *Eleocharitetum macrostachyae* are *Sphagnum cuspidatum* and *Drepanocladus exannulatus* and, with a higher cover, *Juncus ecuadoriensis* and *Elatine chilensis*. Differential is also the absence of *Eleocharis macrostachya*. *Drepanocladus exannulatus* and filamentous algae, e.g. *Microspora* and *Zygnema* spp. may be present in the *Elatino-Juncetum*, but absent are such species as *Tillaea paludosa, Callitriche* sp., *Sphagnum cyclophyllum, Drepanocladus revolvens* and other species belonging to the *Wernerietea*. In the *Elatino-Juncetum, Sphagnum cuspidatum* never becomes dominant, as in the floating *Sphagnum cuspidatum* community with *Juncus*. The *Elatino-Juncetum ecuadoriensis* is provisionally subdivided into two variants, one with *Drepanocladus exannulatus*, and the other with purplish algae *(Microspora/Zygnema)*. Additional relevés and observations in other páramos are required to confirm this subdivision.

Synecology: The *Elatino-Juncetum* is mainly found in pools in the large *Sphagnum* bogs or as a zone in larger páramo lakes, which are partly filled up with peat *(Sphagnum cuspidatum)*. Both relevés containing *Isoetes* cf. *socia* originate from ponds with clayey-silty bottom. In general, this sediment is thin, whereas the peat layer below may be much thicker (at least 2-4 m). The pH of the water in these oligotrophic pools is 4.6 to 5.0.

In rel. 67 the pH of the soil is 4.8 to 5.2. The water is not deeper than 50 cm. *Juncus ecuadoriensis* was often found to be rooting in the dense floating mass of either *Drepanocladus exannulatus* or filamentous algae. Such a floating carpet of algae causes poor, photosynthetic conditions for mosses and vascular plants, unless they have their leaves on top or above the algae mat. *Drepanocladus exannulatus* is absent and the cover of *Sphagnum cuspidatum* and *Ranunculus limoselloides* is low. The thick coherent mass of algae prevents the floating leaves and flowers of *Ranunculus limoselloides* to reach the surface. On the other hand, the helophyte *Juncus ecuadoriensis* reaches its highest cover (80%) in stands with a well-developed layer of algae. This species sticks it leaves through it. The pond vegetation with *Isoetes* cf. *socia* has been studied at the end of the extremely long dry season of 1977. The stand was completely dried out, and *Elatine chilensis* was dying or decaying. *Sphagnum cuspidatum* and *Drepanocladus exannulatus* were not present in this stand.

Distribution: The *Elatino-Juncetum ecuadoriensis* is known from the lower páramos in the Colombian Cordillera Oriental; from the upper subpáramo at 3450 m up to the grass páramo at nearly 3900 m (on the dry side of the Sierra Nevada del Cocuy). As the predominant species have a much wider distribution, at least in the tropical Andes, this association may be expected in other areas, e.g. in the Ecuadorian páramos, from where *Juncus* has been described.

RHEOPHYTIC COMMUNITIES

The type of submerged plant community in cold running páramo waters largely depends on the altitude and on the substrate. The *Philonoto-Isotachidetum serrulatae* is found on gravelly and stony streambeds between 3700 and 4350 m. In lower areas this liverwort community is replaced by the moss community *Dendrocryphaeo-Platyhypnidietum*. At present, both these rheophytic, bryophyllous associations have only been studied in the northern high páramos of the study area and in the Colombian Cordillera Central (Cleef et al., in press). The *Dendrocryphaeo-Platyhypnidietum* and related communities extend far down into the Andean forest belt to about 2000 m.

In about 1 m deep running water on sandy to loamy soil in the Río Lagunillas at 3900 m in the Sierra Nevada del Cocuy, a distinct isoetid community was observed, consisting only of *Isoetes novo-granadensis* (sect. *Terrestres*) and covering less than 10%. The same community was observed in a similar habitat at 3800 m in the headwaters of the Q. Minas, NW of Belén (Boyacá). According to Fuchs (1981[c]) the species is only known from the northern Andean páramos (Venezuela to Ecuador). In the Cordillera Oriental and Central of Colombia this species is reported from the subpáramo and grass páramo from 3300 to 3900 m in various aquatic habitats, e.g. streams, lake shores, *Werneria pygmaea* flush, and half emerged in mires. Submerged pure stands of *Myriophyllum elatinoides* are present in páramo streams with sandy to gravelly beds, 30 to 150 cm deep, at 3900 m.

In a small stream draining a steep moraine slope at 4250 m in the Bocatoma valley (Sierra Nevada del Cocuy), the rare semi-aquatic moss *Andreaea nitida* was collected by Dr. P.A. Florschütz. The same species was collected by us at 3700 m in the Filo Sitiales, Páramo de Sumapaz, and in the superpáramo of the volcano Ruíz (Colombian Cordillera Central) at 4250 m. The species was found in the dry bed of a streamlet, together with *Racomitrium dichelymoides*. The last species then was only known from its type locality in an Andean forest stream above Bogotá at 2800 m; and was recently collected also from a stream at 3150 m in the Páramo de Guasca (Dr. S.R. Gradstein, pers. comm.). Small páramo streams often partly hidden in bogs and alluvial sediments mainly have peaty to clayey beds. At heights from 3300 to 3700 m, a distinct community was observed of *Potamogeton drepanocladoides* and *Fontinalis bogotensis*. Other species are: *Lilaea subulata, Lilaeopsis schaffneriana, Isoetes bischlerae, I. killipii* (occasionally) and *Drepanocladus revolvens* *Isoetes bischlerae* was collected in the upper subpáramo (3300-3600 m).
Fontinalis bogotensis was first described from an Andean forest stream near Bogotá, an is present only known from streams and a páramo lake at 3700 m in the Colombian Cordillera Oriental. *Potamogeton drepanocladoides* is only known from páramo streams in northern Peru, Ecuador and Colombia (Dr. L. Holm-Nielsen, in litt.)

43. *Philonoto - Isotachidetum serrulatae* ass. nov.
type: rel. 454; table 7; Fig. 45 & 55

Physiognomy: This submerged rheophytic bryophyllous community consist of a dense mat of conspicuous reddish liverworts up to 5 cm high, with a cover from 60 to 100%.

Table 7 *Philonoto - Isotachidetum serrulatae* ass. nov.

rel.nr.	451	454	462	475	493	487	488	477c
alt.m.	4335	4315	4350	4085	3865	3875	3875	4070
water depth cm	30	5-35	10	10-40	3-5	20	-	40
		▲						
Isotachis serrulata	75	75	60	90	85	60	100	80
Chlorophyceae	1+	5	.	.	.	.	.	.
Callitriche	.	.	.	1	.	.	.	.
Philonotis andina	.	.	.	.	10	.	.	.

Composition & syntaxonomy: The dominant species is the liverwort *Isotachis serrulata*. Gradstein et al. (1977) discussed the taxonomic position, morphology, distribution and ecology of this polymorphic tropical Andean species. In one place *Philonotis andina* has been found associated with a species of *Callitriche*. Filamentous algae may locally be common. Stands of the rare *Isotachis lacustris* were present in the Parque Los Nevados in the Colombian Cordillera Central (Dr. S.R. Gradstein, pers. comm.); the species is expected in this association in the study area. The mean number of species is 1-2 in 8 relevés.
Isotachis serrulata is a selective character species and *I. lacustris*, and *Philonotis andina* are preferential character species. The *Philonoto-Isotachidetum serrulatae* has a contain affinity to the *Ditricho-Isoetion* in the high páramo lakes, and also to the high altitude *Carici peucophilae-Wernerietum crassae* in the large and wet or boggy glacial depressions between lower superpáramo moraines in the Páramo Cóncave, Sierra Nevada del Cocuy. This association is altitudinally vicariant with the *Dendrocryphaeo-Platyhypnidietum riparioides*.

Synecology: The *Philonoto-Isotachidetum* is found in shallow, cold and clear streams rich in oxygen, and mainly in swiftly running water. The submerged *Isotachis serrulata* mats usually grow on large stones (Fig. 45), but they also occur on top of clayey-silty to coarse sandy sediments. The pH of the water in streams on the high Cocuy páramos is 5.0 to 5.5. The water of the small stream in rel. 454 at 4315 m was frozen in the early mornings (February 26-28, 1973) after temperatures of -5°C at night.
In relevé 451 at 4335 m, many small black leeches (Hirudiinae) were present on the clayey and stony soil between the *Isotachis* stems.

Distribution: The *Philonoto-Isotachidetum serrulatae* is distributed in the Colombian Cordillera Oriental from 3850 to 4350 m, from the upper grass páramo up into the superpáramo. This association is known from the upper reaches of the Sierra Nevada del Cocuy (Arauca, Boyacá); it is also reported for the Parque Los Nevados (Cordillera Central) and is likely to be found in other high mountains of tropical America. Submerged plants of *Isotachis serrulata* have been collected in a small stream at 3850 m on the southern slope of the Páramo del Almorzadero (Santander), at 3730 m in the Páramo de la Rusia, and at 4000 m in the Parque Los Nevados, Colombian Cordillera Central.

44. *Dendrocryphaeo latifoliae - Platyhypnidietum riparioides*
type: rel. 1A; table 8 Cleef & Gradstein ass. nov.

Physiognomy & synecology: The single low pleurocarpous ground layer of this rheophytic community covers submerged stones in shallow river beds; stands are common in rapidly moving water, rich in oxygen.
The *Dendrocryphaeo-Platyhypnidietum* is apparently altitudinally vicariant with the *Philonoto-Isotachidetum serrulatae*, known from similar habitats in running water on the higher páramo.

Composition & syntxonomy: Dominant, almost single and exclusive character species is the moss *Platyhypnidium riparioides*, a wide temperate species. *Riccardia* sp. (1032), *Racomitrium* sp. (Gradstein & Aguirre 3665a), *Grimmia alpicola* var. *rivularis* and a new species of the austral-antarctic genus *Dendrocryphaea (D. latifolia)* have been observed once each.

table 8 *Dendrocryphaeo latifoliae - Platyhypnidietum riparioides* Cleef & Gradstein ass. nov.

rel. nr.	1A	13A	17A	6A	300A	607	638
rel. area: 1-4 m^2							
alt. m	3400	3500	3635	3450	3300	3675	3320
Platyhypnidium riparioides	▲ 60	35	25	40	75	80	80
algae	x	x	x	x	x	1	x
Dendrocryphaea latifolia	5	.	.	.	.	.	.
Riccardia sp.	.	5	x	.	.	.	.
Grimmia alpicola var. *rivularis*	1	.	.	.	.	.	.
Racomitrium sp. (Gradstein 3665a)	1	.	.	.	.	.	.

Localities & botanical collections:
1A Páramo de Sumapaz: Chisacá,Quebrada S. Rosa. in *Polylepis quadrijuga* forest (Cleef 220: Gradstein 3664, 3665, 3665[a], 3665[b]); 13A Páramo de Sumapaz: Q. Sitiales. (Cleef 1032, 1033); 17A Páramo de Sumapaz: C. Nevado. (Cleef 1228); 6A Páramo de Sumapaz: Laguna La Guitarra, stream ending in the lake. (Cleef 874); 300A Páramo de Sumapaz: Río Nevado. (Cleef 8302); 607 Volcán Otún (Cord. Central): Q. La Sierra; 638 Río Totarito (Cord. Central).

Distribution: *Platyhypnidium riparioides* is reported for tropical America from the Andes, Brazil and Costa Rica. In Costa Rica and the northern Andes its lowermost habitat is 2000 m (D. Griffin, pers. comm.). In the Colombian Cordillera Oriental and Cordillera Central, this moss community was studied from 3700 m in the lower páramos down to the Andean forest belt at 3000 m, especially the Páramo de Sumapaz and the páramos of Risaralda and Tolima.

Other aquatic communities

45. Community of *Eleocharis acicularis*
table 9; Fig. 46; lit. Ruthsatz 1977

Physiognomy: This community hardly shows any stratification and consists of an open submerged *Eleocharis* layer. Characteristically, the long rows of *Eleocharis* stolons grow in an irregular criss-cross pattern. Mosses and algae are floating.

Composition & syntaxonomy: The only vascular species is *Eleocharis acicularis*; it is accompanied by *Drepanocladus* sp. or *Sphagnum cuspidatum*, and by violet-greenish filamentous algae (mostly *Mougeotia* spp.)
No syntaxonomical rank has been assigned to this community.On basis of the available data it cannot be properly differentiated against other (holarctic) communities with *Eleocharis acicularis*.

Note: Apparently, this is the first mention of *Eleocharis acicularis* for the Colombian Andes. The species has been collected in many places by the present author between 3400 and 3850 m in the Cordillera Oriental.

table 9 Community of *Eleocharis acicularis*

rel. nr.	240	145	143A	194
rel. area m^2	4	1	1	1
water depth cm	30	35	25	20
substrate	gyttja	gyttja	gyttja	gyttja
depth cm	>120	>120	>120	>120
pH (*water)	5.8	4.7	-	4.8*
alt. m	3845	3550	3625	3690
locality	Rusia	Chisacá	Chisacá	Neusa
Eleocharis acicularis	20	20	5	30
Algae (*Mougeotia* sp.)	1	3	5	1
Drepanocladus sp.	.	60	.	.
Sphagnum cuspidatum	.	.	3	2

Synecology: Small shallow (20-35 cm), slowly drained pools in *Sphagnum* bogs of the grass páramo. The bottom of the pools consists of decayed peat of some meters thick. Probably, sites at which this community is found, never become dry. Stagnant water is always present in the habitat. The pH of the water is 4.7-5.8.

Distribution: The *Eleocharis acicularis* community is sparsely distributed in the lower bunchgrass and bamboo páramo proper of the Cordillera Oriental between 3550 and 3850 m. Its upper limit is probably correlated with that of *Sphagnum* bogs. Below 3550 m *Eleocharis acicularis* might be expected in pools in open *Sphagnum* bogs. This community is probably also present in other open *Sphagnum* bogs high in the tropical Andes. Ruthsatz (1977) reported the presence of *Eleocharis acicularis* from the northern Andes in Argentina between 3500 and 3800 m. The species was observed in the deepest part of shallow puna lakes, and was associated with *Marsilia punae* De la Sota, *Kardamoglyphos nana* Schldl. (Cruc.), *Plagiobotrys congestus* (Wedd.) I.M. Johnston (Borag.), *Distichlis humilis* Phil. (Gram.) and *Bouteloua simplex* Lach. (Gram.).

46. Community of *Equisetum bogotense*
table 10; Fig. 64

Physiognomy: The open herb layer dominated by *Equisetum bogotense* is about 25 cm high. The community in the Río Lagunillas(Sierra Nevada del Cocuy) was rheophytic and practically submerged with the *Equisetum* stems bending with the current.

Composition & syntaxonomy: *Equitesum bogotense* is the only vascular plant in the two páramo relevés.
This community has not been ranked phytosociologically, because of the low record of relevés and observations.

table 10 Community of *Equisetum bogotense*

rel. nr.	148	486
rel. area m^2	1	2
total size stand m^2	250	8
water depth cm	20	1-50
soil	gyttja	stony-clayey
pH substrate (root zone)	5.8	-
water current	-	+
alt. m	3730	3890
locality	Chuza	Cocuy
Equisetum bogotense	35	75
filamentous green algae	-	10
cf. *Microspora* sp.	x	x

Synecology: *Equisetum bogotense*-dominated stands are apparently present in different habitats: on lake gyttja in pools and in stony stream beds. In the former the species is surrounded by *Plantago rigida* and *Oreobolus* cushion bog. At 3450 m, near the Nevado de Sumapaz, an *Equisetum bogotense* stand was observed on a calcareous mire. Near Inza (Cauca), at 2700 m in the Andean forest belt of the Colombian Cordillera Central, an *Equisetum bogotense* community was examined on wet rocks; apart from *E. bogotense* it contained *Marchantia plicata, Anomobryum filiforme, Philonotis sphaerocarpa* and *Cora pavonia*. *Equisetum bogotense* apparently is an euryoicous species, locally dominant in wet roadside trenches in the upper andean forest as well as in the lower páramo.

Distribution: Herbarium data and additional observations indicate that *Equisetum bogotense* is widely distributed between 1500 and 4000 m in the tropical Andes and on the Galapagos Islands (Vareschi 1970)

47. *Lemno - Azolletum filiculoides* (Br.Bl. 1952 p.p.) Segal 1965
lit.: Cleef et al., in press; Aguirre & Rangel 1976.

The present distribution of this pleustophytic wide-temperate community in our area is between 2000 m (Laguna Pedro Palo) and 3700 m (Lagunas de Chisacá). The communities floating on grass páramo lakes contain few associated species, and merely consist of a low, dark reddish layer of *Azolla* plants. *Lemna minor* was found as an associated species up to 3300 m.
The *Lemno - Azolletum* is also present up to 3900 m in the grass páramo of the Colombian Cordillera Central (Cleef et al., in press.) and was reported by Øllgaard & Balslev (1979) from the volcano Antisana, Ecuador, at 4000-4150 m. Aguirre & Rangel (1976) provided phytosociological data on the *Lemno - Azolletum* from Lake Tota at 3000 m. *Lemna minor, Wolffia columbiana* Karst. and *Ricciocarpus natans* were reported as common associates.
Finally, *Azolla filiculoides* is present also in other pleustophytic communities in warm tropical lowland fresh water bodies (Cleef & Idrobo, in prep.)

REEDSWAMPS & MIRES

Marchantio - Epilobietalia order nov.
type:*Calamagrostion ligulatae* (this study); table 11

Physiognomy: The cyperaceous reedswamps and grass mires of the páramo generally show two layers:
1) a high cyperoid of graminoid field layer; and
2) a low herbaceous or bryophytic ground layer.
A third shrubby upper layer is locally developed (e.g. *Senecionetum reissiani*, *Ludwigia peruviana - Carex acutata* community.

Composition & syntaxonomy: Character species are *Marchantia plicata* (excl.), *Epilobium denticulatum* and *E. meridense* (excl.), *Ranunculus flagelliformis* (select.?), *Senecio subruncinnatus* (select.), *Cardamine africana* (pref.?),*Cardamine bonariensis* (sel.), *Lachemilla fulvescens* (excl.), *Eleocharis stenocarpa* (pref.?) and *Breutelia inclinata* (select.) in combination with the character species of the alliances and lower ranked syntaxa, as *Senecio reissianus*, *Carex pichinchensis*, *Valeriana plantaginea*, *Carex acutata*, *Carex jamesonii*, *Cyperus rivularis*, *Galium trianae*, *Gratiola peruviana*, *Symphyogyna sinuata*, *Mimulus glabratus*, *Lupinus alopecuroides*, *Calceolaria mexicana*, *Lupinus* cf.*verjonensis*, *Draba* sp. (white petals), *Stachys elliptica* *Geranium confertum*, *Bryum laevigatum*,*Drepanocladus aduncus*, *Calamagrostis ligulata*, *Cerastium imbricatum*, *Montia fontana*, *Montia* aff. *meridensis* and *Plantago australis* ssp. *oreades*.
The *Marchantio-Epilobietalia* contain a number of conspicuous vascular superpáramo elements, which grow in the cold and wet páramo reedswamps, mires and bogs and are morphologically different from the (presently,also isolated) superpáramo population. Taxa to be mentioned in this respect are *Valeriana plantaginea*, *Senecio canescens*, *Lupinus alopecuroides*, *Draba* sp. (264[a] - white petals), *Senecio niveo-aureus*, *Montia* cf. *meridensis* and *Cerastium imbricatum*. Specific comments on these species are given in following descriptions of the páramo swamp and mire vegetation.
The order comprises nearly all *Carex* and *Cyperus* reedswamps and *Calamagrostis ligulata* mire communities from the páramos studied.

Synecology: The reedswamps and grass mires are found on 1) sloping wet areas , 2) flat, marshy valley floors, including former lake floors and 3) lake shore marshes. Similar phytocoenoses of limited size also occur in the superpáramo, in springs and along páramo streams, in lake shore habitats regularly inundated and experiencing wave action, in the contact zone with *Sphagnum* bogs and calcareous mire. Depending on the kind of habitat and adjacent vegetation, conditions may be mesotrophic or eutrophic . Consequently, the pH in the rootzone varies from 4.5 to 7.5 in 34 relevés. The waterlogged clayey-peaty subsoil is permanently in a state of reduction.

Distribution: Most communities of the *Marchantio-Epilobietalia* occur in the upper superpáramo and lower grass páramo of the Colombian Cordillera Oriental. Superpáramo stands were studied up to 4450 m in the Cordillera Central and Oriental. The lowermost stand probably concern the cyperaceous reedswamps (except *Scirpus californicus)* on the Sabana de Bogotá (about 2600 m) and in other high plains of the Cordillera Oriental in the departments of Cundinamarca and Boyacá and is the lowest located vegetation. The *Marchantio-Epilobietalia* is probably restricted to the páramos and open marshes in the upper part of the forest belt of the northern Andes from Venezuela to northern Peru.

GALIO TRIANAE - GRATIOLION PERUVIANAE all. nov.
type: *Caricetum pichinchensis* (this study); table 11

Physiognomy: The alliance comprises cyperaceous reedswamps with a conspicuous fieldlayer of 40-80 cm high, covering 60-100% and a herbaceous-bryophytic ground layer. Occasionally shrubby composites may develop into a higher third layer (cover about 70%). Flowers are mainly white to lilac.

Composition & syntaxonomy: Cyperaceous reedswamp communities are dominated either by a distinct *Carex* species (*C. pichinchensis*, *C. acutata*, *C. jamesonii* or by *Cyperus rivularis* ssp. *lagunetto*). *Senecio reissanus* shrubs are locally dominant and are considered as climax vegetation, which belongs to a distinct assocation.
Character species are those reported under associations (and communities), which are mainly hummock species and dominant in the fieldlayers and apart from those *Galium trianae*(excl.),*Gratiola peruviana* (select.) and *Symphyogyna sinuata* (select.), which are mainly less conspicuous hollow species.
Differential species are *Philonotis andina*, *Bryum grandifolium* (both weak) and *Lachemilla mandoniana*. The *Galio-Gratiolion* may be considered as a cool neotropical vicariant of the holarctic *Magnocaricion* W. Koch 1926 (*Phragmitetea*).
The herb *Gratiola peruviana* is widely distributed in temperate South America.In the Colombian Andes this species grows on muddy and moist soil, in the open marshy parts at 2600 m in the Andean forest belt up to 3700 m in the grass páramo. *Gratiola bogotensis* Cortés is considered as a synonym of *Gratiola peruviana* L. by the present author. *Galium trianae* is restricted to the Colombian Andes and bridges a vertical range of the same height. *Symphyogyna sinuata* is a tropical Andean liverwort; from Colombia it is reported for wet habitats in cloud forest and bamboo páramo between 2150 m and 3700 m. *Lachemilla mandoniana* is present along the humid high Andes from Bolivia to Venezuela. This tiny, extremely variable, prostrate species occurs throughout the Colombian páramos up to 4450 m.
Note: *Carex acutata*, *C. fecunda*, *C. jamesonii* and *C. pichinchensis* may easily be confused.
The number of species of the *Galio-Gratiolion* is 8-12 under pioneer conditions and 25-38 in stable closed communities.

Synecology: The *Galio-Gratiolion* is present in humid and wet páramo habitats, including glacial valley floors, on former lakes, in hydroseral marsh and calcareous mire, in wet depressions and on sloping valley bogs. Most of the stands are in shallow water. A hummock-hollow relief is characteristic for this alliance except for the *Carex acutata* lake-shore community. This relief is common in páramo vegetation and in other humid to wet communities, e.g. boggy *Swallenochloa tesselata*-moss (*Sphagnum*, *Breutelia*) vegetation, *Agrostis foliata* community, hummock-like superpáramo stands with *Calamagrostis ligulata*, *Sphagnum* bogs and vascular cushion bogs. In the locations of these páramo vegetations the water-table shows seasonal changes. Frost action in the hollows is most common in the higher páramos, and prevents the establishment of seedlings. The open and moist hollows suffer more frost damage than the thick compact plantcover of the hummocks. Rill erosion is prominent after abundant rains. The *Galio-Gratiolion* is common on thick, clayey peat or gyttja (pH of the rootzone is 4.5-6.6).

The *Galio-Gratiolion* is probably the main habitat for *Cavia porcellus*, which especially feeds on Cyperaceae. Populations of these animals live in these páramo reedswamps, where they maintain a pathway system through the sheltered hollows. These also serve as an excellent refuge in case of danger.

Sylvilagus brasiliensis meridensis also feeds on cyperaceous foliage.

Distribution: The alliance is known from the subpáramo and grass páramo of the Colombian Cordillera Oriental from 3300 to 3800 m. The sedge communities have only been studied in the southern páramos, the *Cyperetum rivularis* was recorded in the northern Boyacá páramos (3300-3500 m). *Carex* sp. and *Cyperus* sp. reedswamps have been recorded by the author in the páramo of the Colombian Cordillera Central. This alliance can be expected in other neotropical páramos, and in lower regions of the Andean forest belt.

CARICENION PICHINCHENSIS suball. nov.
type: *Caricetum pichinchensis* (this study); table 11

Physiognomy: For a description of the different layers, see the associations and community. Most of the dicot herb species of this suballiance have white to lilac flowers.

Composition & syntaxonomy: This suballiance comprises all marshy sedge swamps in the herbaceous fieldlayer dominated by *Carex pichinchensis* (selective character species). Exclusive character species are *Senecio reissianus* and slender rosettes of *Valeriana plantaginea*. Differential against other communities of the *Marchantio-Epilobietalia* are *Lophocolea coadunata, Gentianella corymbosa, Polytrichum commune, Thuidium peruvianum, Peltigera* spp., *Senecio canescens* (a low altitude species) and an unknown species of *Selaginella* (5200). The high cover of *Carex pichinchensis* is also differential against other phytocoenoses, except for local *Sphagnum* bogs in the grass páramo, where a similar high cover of this sedge species had been recorded. Together with some other páramo swamps dominated by tall Cyperaceae, this suballiance is ranked under the *Galio-Gratiolion*.

Synecology: The *Caricenion pichinchensis* occurs on clayey peat or (calcareous) gyttja (topsoil pH 4.5-6.6), with optimal development on marshy glacial valley floors; a few stand were sampled in (lake) hydroseral marsh and wet depressions. The hummock-hollow relief (described under the *Caricetum pichinchensis*) is characteristic.

Distribution: The available relevés indicate that the *Caricenion pichinchensis* is found in the subpáramo and grass páramo between 3350 and 3800 m, mainly in the Páramo de Sumapaz. The *Senecionetum reissiani* is endemic, whereas the *Caricetum pichinchensis* may be present in other humid Andean páramos also.

Note: *Valeriana plantaginea* is mainly native to the atmospherical humid lower superpáramo. The páramos contain two populations of *Valeriana plantaginea* at different altitudes, in different habitats and characteristic for different communities:
1) the widely distributed (lower) superpáramo population of ground rosettes with firm fleshy broad leaves and purple-violet corollas on wet rocks and on gravelly to coarse sandy soils (see 27);
2) the population of the grass páramo and subpáramo with slender plants, smaller leaves and whitish flowers, only in marshy places and especially in the *Caricenion pichinchensis*.
Specimens of the two populations are morphologically different at the infra-specific level, probably at subspecies.

48. *Senecionetum reissiani* ass. nov.
type: rel. 139; table 11; Fig. 47

Physiognomy: The vegetation structure of this microphyllous shrubby association is well defined:

1) a grayish-leaved shrub layer (1-2 m) covering about 70%; the flowering aspect is yellowish.
2) a cyperaceous layer, 40-50 cm high, covering 60-80%.
3) a prominent bryophytic layer (cover up to 80%) with low herbs and some shrub species (e.g. *Hypericum prostratum, Arcytophyllum muticum, Pernettya prostata).*

Composition & syntaxonomy: The dominant shrub *Senecio reissianus* is an exclusive character species; it is accompanied by the hydrophytic *Hypericum laricifolium* ssp. *laricoides* (differential species) and the conspicuous stemrosettes of the endemic *Rumex tolimensis*. *Carex pichinchensis* is dominant in the cyperaceous understorey,generally accompanied by *Valeriana plantaginea* and *Gratiola peruviana*. Ground rosette species as *Senecio canescens* and in the shadow *Greigia* cf. *mulfordii* (Brom.) are associated also. Common taxa in the bryophytic layer are *Symphyogyna sinuata* and *Sphagnum sancto-josephense* or species of *Breutelia*.
The number of species is about 30 (range 25-38) in 2 relevés. This is slightly higher than in other associations of the *Galio-Gratiolion*,possibly because of the extra (shrub) layer. *Geranium confertum* and *Escallonia myrtilloides* may be present in this association.
Differential against other communities within the *Galio-Gratiolion* is *Breutelia chrysea*, and against those within the *Marchantio-Epilobietalia* are *Hypericum laricifolium* ssp. *laricoides, Hypnum mirabile* and *Cyclodictyon* sp. Lichens are rare and restricted to the driest places. Common small, low herbs are *Nertera granadensis, Selaginella* sp.(5200), *Lachemilla mandoniana, Muhlenbergia* sp.
This association is well defined and easily recognized by its exclusive character species *Senecio reissianus*. The association belongs to the *Galio-Gratiolion* and has the closest floristic and ecological affinities with the *Caricetum pichinchensis*, and also has a number of species in common with the hydrophytic *Hypericetum laricifolii* (see 74).

Synecology: The *Senecionetum reissiani* is found on marshy and peaty, gently sloping (0-5°) glacial valley floors or seepage areas with a more or less regular supply of water (pH 5.3 in rel. 139). The pH of the eutrophic clayey peat in the topsoil is 6.5. The Aoo layer is 3-5 cm thick. The subsoil (measured every 25 cm down to 125 cm) in rel. 139, proved to be more acid downward: pH 5.0-5.3. In the deeper part of the profile a rapid transition was noticed into blue-grayish sandy and clayey, increasingly gravelly deposits. Iron concretions around the roots indicate oxydation-reduction processes; oxydation was noticeable down to 50 cm. This might correspond to the lowest phreatic level in the dry season.
The *Senecionetum reissiani* possibly is successional to the *Caricetum pichinchensis* and apparently represents a more stabilized, slightly drier phase, characterized by structure, biomass and higher organic (peaty) content of the soil. The *Caricetum pichinchensis*, however, may also develop into *Diplostephietum revoluti*, and on more acid peat into *Carex-Sphagnum* bog (see other *Sphagnum* communities)

Distribution: *Senecio reissianus* is endemic for the southern pāramos of the Cordillera Oriental and especially common for the Pāramo de Sumapaz. This species has been collected there in the subpāramo and grass pāramo between

3400 and 3900 m. In marshy páramo near the Laguna Verde, about 60 km N of Bogotá, the author collected one specimen only.

49. *Caricetum pichinchensis* ass. nov.
type: rel. 138; table 11; Fig. 48 & 49 (also Fig. 41, 50, 51)

Physiognomy: This cyperaceous swamp vegetation consists of two strata:
1) a more or less solid 40-60 cm high fieldlayer, dominated by the sedge *Carex pichinchensis* (60-100% cover), and generally poor in species. *Valeriana plantaginea* inflorescences are conspicuous;
2) a low herb-bryophyte layer, 1-10 cm high, rich in species, in the shade of the overhanging sedges. The bryophyte cover is 2-3 cm thick.

Composition & syntaxonomy: *Carex pichinchensis* is dominant and a selective character species. In the study area it is accompanied by *Valeriana plantaginea* (preferential character species). Frequent are *Gratiola peruviana, Symphyogyna sinuata, Lachemilla mandoniana, Ranunculus flagelliformis, Nertera granadensis,* and *Senecio subruncinnatus.*
The *Caricetum pichinchensis* partly shows pioneer character. The number of species is low, 12 in rel. 277 and 18 in rel. 292. The average number of species in the stable valley floor communities of the 3 other relevés is 28 (23-35).

Synecology: The *Caricetum pichinchensis* is found in the subpáramo and grass páramo on peaty soils in very wet habitats, with a regular supply of water. Large stands are present on glacial valley floors, limited communities in groundwater-wet areas around lakes and in muddy old moraine depressions in the lower páramos. The darkish-brown to almost black peaty clayey soils (including gyttja) are thick (>120 cm) and the pH in the rootzone is 5.0-6.0. In the pioneer community of rel. 277, on a calcareous mire the pH of the top layer of the substrate was 6.6. Iron concretions on the roots indicate oxydation-reduction conditions in the topsoil. The sedge rhizomes may form a dense mat in the topsoil. A common feature of the *Caricetum pichinchensis* is a kind of hummock-hollow relief. Four to five hummocks per square meter with a diameter of 10-15 cm and a height of 5-20 cm are usual. The highest hummocks are found in habitats with the greatest fluctuation in phreatic level. Common *Carex pichinchensis* hummock species are *Valeriana plantaginea, Thuidium peruviana, Nertera granadensis* and Dicranaceae. The muddy hollows contain *Lachemilla mandoniana, Ranunculus flagelliformis, Philonotis andina, Scutellinia* sp.(p); *Calliergonella cuspidata, Gratiola peruviana, Selaginella* sp. (8257), *Sphagnum subsecundum* and *Gentianella corymbosa* mark the transition from hummocks to hollows.
Shepherds sometimes set fire to the sedge meadows, which in the dry seaso are grazed by cattle. Rodents, e.g. *Sylvilagus brasiliensis* and especially *Cavia porcellus*, forage on young *Carex* leaves. The last animal probably lives in the dense *Carex* meadows.

Distribution: The *Caricetum pichinchensis* is only known from the humid southern páramos of the Colombian Cordillera Oriental, and is common in the Páramo de Sumapaz. The association is present in the subpáramo and grass páramo between 3400 and 3800 m. The highest located stand was observed near the Laguna Gobernador (Sumapaz).
Judging from herbarium specimens (NY, L, K), *Carex pichinchensis* must be widely distributed in the tropical Andes from Bolivia to Colombia. In Colombia this sedge species was collected from 2600 m (Sabana de Bogotá) up to 4500 m

in the superpâramo of the Cordillera Central and Oriental and in the Sierra Nevada de S. Marta. *Valeriana plantaginea* is only known from atmospherical humid Colombian and Ecuadorian pâramos between 3400 and 4400 m. In the northern pâramos of the Colombian Cordillera Oriental and in the Sierra Nevada de S. Marta, *Valeriana plantaginea* is rather scarce.
The *Caricetum pichinchensis* is probably present in pâramos of the Colombian Cordillera Central and the Ecuadorian Cordillera Oriental.
Notes:
Small patches dominated by a bluish *Carex* sp. (probably *C. pichinchensis)* have been studied on the volcanoes Puracé (3300 m) and S. Isabel (4170 m) and in the Sierra Nevada del Cocuy (3950 m). These communities do not contain *Valeriana plantaginea* and may represent another syntaxon.
According to Dr. T. Koyama (NY) another large *Carex* species, *C. fecunda*, is locally found together with *Carex pichinchensis*.

50. Community of *Carex pichinchensis* and *Polytrichum commune*
table 11

Physiognomy: This type of sedge swamps is characterized by a musci layer of 10-20 cm.

Composition & syntaxonomy: *Polytrichum commune* is the most characteristic species, which furthermore only has been recorded in pâramo *Sphagnum* bogs. *Sphagnum magellanicum* is common in rel. 80 and apparently develops into *Sphagnum* bog. *Arcytophyllum muticum, Hypericum prostratum, Geranium sibbaldioides, Calamagrostis bogotensis* and *Paspalum bonplandianum* mark the transition towards the surrounding dry grass pâramo. *Polytrichum commune, Arcytophyllum muticum, Geranium sibbaldioides, Leptoscyphus cleefii* and *Hypericum prostratum* are not present in other reedswamp communities.

Synecology: This community of sedges and mosses is found along pâramo streams on thick humid (rel. 144) and wet ground (rel 80) and is flooded in the wet season. The dark reddish-brown to gray silty to clayey soil layers in rel. 144 are stream deposits, the gyttja in rel. 80 is a lake sediment, now deeply incised by the adjacent stream.
Rootzone soils are acid: pH 4.5-4.7. In rel. 144, at a depth of 70 cm, the soil consists of a 15 cm thick compact layer of plant remains, charcoal and fragments of gravel. Oxydation colours can be noticed above this layer. *Polytrichum commune* is common, and the layer is 15-20 cm thick. *Sphagnum magellanicum* cushions (up to 10 cm) grow on litter. Rel. 80 has a dense cover of the hydrophytic *Calamagrostis* cf. *planifolia*.

Distribution: This sedge community, studied in the Pâramo de Chisacâ (3600-3700 m), was also observed at 3520 m on the Nevado de Sumapaz and can be expected elsewhere in the Pâramo de Sumapaz.

Other cyperaceous communities

51. Community of *Carex acutata*
characteristic rel.: 265; table 11; Fig. 50, 51

Physiognomy, composition & syntaxonomy: These two-layered pâramo reed swamps contain *Carex acutata* dominant in the field layer. The bryophyte layer is dominated by *Symphyogyna sinuata* (3-4 cm high) in well-developed stands. This type of sedge vegetation is poor in species; the average number is 10

(8-11 in 2 relevés). This is probably to be attributed to the pioneer character of this sedge community along lake shores.
Carex acutata reedswamps have their optimal development in the Andean forestbelt.

Synecology: The páramo *Carex acutata* community is part of a reed belt in lake hydroseral zonation between the *Potameto-Myriophyllion* of the open water and the *Sphagnum-Calamagrostis ligulata* marhs directly near the lake water (Fig. 50, 51).
The substrate is eutrophic peat (rootzone pH 6.3), always wet or humid, also in the dry season. In rel. 265 the peat and lake sediments are at least 8.25 m thick as shown in the pollen section La Primavera (Fig. 7). A hummock-hollow pattern is absent. This reedswamp is rather a hollow- than a hummock vegetation, represented by the neighbouring boggy *Sphagnum-Calamagrostis ligulata* vegetation. Rel. 267A is less typical and grades into this vegetation (rel. 267).

Table 12 *Ludwigia peruviana* shrub

rel. nr.	423B
alt.	2800 m
cover shrub layer	90%
cover herb layer	95%
number of species	4
cover %	
Ludwigia peruviana var. *peruviana*	90
Carex acutata	80
Polygonum sp. (10.034)	2
Hydrocotyle ranunculoides	10

Distribution: The páramo *Carex acutata* community is only known from the marshy NW shores of the Laguna La Primavera at 3525 m in the Páramo de Sumapaz (Meta). *Carex acutata* is widely distributed in the tropical Andes between 2400 and 4000 m. This sedge species is more common in the lower reaches of the Andean forest belt. In the Laguna La Herrera on the Sabana de Bogotá (2560 m) there is a *Carex acutata* reedswamp (1 m high). Another community with *Carex acutata* has been studied at 2800 m in the Sierra Nevada del Cocuy in a small lake (El Claval), some km SW of Guicán (Boyacá), with a dense shrub (2 m high) of the widely distributed, yellow flowering, onagraceous *Ludwigia (Jussiaea) peruviana* var. *peruviana*. Rel. 423 B was made in this location (see table 12).
This stand probably represents an undescribed association (*Ludwigietum peruvianae* prov.) On the water under the *Ludwigia* shrubs floated the *Lemno-Azolletum filiculoides* (nr. 47) with *Azolla filiculoides* (50%) and *Lemna minor* (10%).

52. Community of *Carex jamesonii*
characteristic rel.: 309; table 11; Fig. 14

Physiognomy: The reedswamp of this community consists of two layers; *Carex jamesonii* is dominant in the field layer (30-40 cm).

Composition & syntaxonomy: *Carex jamesonii* grows on top of the 10-15 cm high hummocks with *Lachemilla mandoniana*, in some places together with

tussocky *Calamagrostis effusa*. Dwarf shrubs of *Pernettya prostrata* var. *purpurea* and *Blechnum loxense* are found in the transition to the humid hollows covered with a herb-bryophyte layer mainly consisting of *Callitriche* sp. and cf. *Odontoschisma* sp. (8420). *Symphyogyna* cf. *sinuata* is rare. *Carex pichinchensis* is present in the lowermost waterlogged area of this bog. The number of species is 20.
Rel. 309 represents a *Carex jamesonii* subpáramo community belonging to the *Galio-Gratiolion*. The diagnosis is only based on the single relevé available. *Cyperus* sp., *Sibthorpia repens* and *Blechnum loxense* are also characteristic for swamps and bogs in the lowermost páramo belt. It is possible that the reported *Carex jamesonii* community is altitudinally vicariant with the *Caricetum pichinchensis* in the Páramo de Sumapaz.

Synecology: As shown in Fig. 14 the *Carex jamesonii* stand occupies a convex bog site on sloping ground (9°) in a small subpáramo valley. The pH of the clayey peat in the rootzone is 5.8. About 8 months before our visit this stand had been burnt, and this explains the presence of the rather open cyperaceous fieldlayer (cover 75%). Whether dominance of cf. *Odontoschisma* (versus *Symphyogyna*) in the bryophyte layer is due to the burning is not known. *Scirpus inundatus* and *Juncus* species with low cover are species indicating manuring by cows. Shrub of *Diplostephium revolutum* occurs in the *Carex jamesonii* meadow and is probably succesional to this sedge community.
Cavia porcellus forages on *Carex jamesonii* foliage.

Distribution: The stand with *Carex jamesonii* is from 3560 m (upper subpáramo) near the cloud forest line on the Magdalena slope in the Páramo de Sumapaz. *Carex jamesonii* is a widely distributed and common sedge species on boggy ground in moist woods and subpáramos in the northern Andes (Venezuela to Ecuador) between 2000 and 3600 m. Habitats recorded from herbarium collections are: dry *Sphagnum* bog (colonies), *Sphagnum* meadows, moist cliffs, ditches, seepage areas, etc.

53. *Cyperetum rivularis* ass. nov.
type: rel. 234; table 11; Fig. 52

Physiognomy: Like all other herbaceous communities of the *Galio-Gratiolion*, this association consists of
1) an impressive, dense fieldlayer dominated by Cyperaceae ((50-) 70-80 (-100) cm), developed above
2) a generally shaded (low) herb-bryophyte layer. The moss layer may be 5-15 cm thick. Characteristic are the compact inflorescenses of giant *Puya* sp. reaching 1-2 m above the fieldlayer.

Composition & syntaxonomy: *Cyperus rivularis* ssp. *lagunetto* is the prominent species in the fieldlayer. Common species are *Sibthorpia repens*, *Lachemilla mandoniana*, and *Nertera depressa*. One tall *Cortaderia* sp. (probably *C. nitida*) was seen codominantly (rel. 409). Characteristic are species of *Puya*, e.g. *Puya bicolor*, *Puya santosii*. Mosses, e.g. *Brachythecium* sp. and *Sphagnum recurvum*, may be dominant in the bryophyte layer and cover up to 80-90%.
The number of species is 9 (rel. 235) to 23 (average of the other 3 relevés). The *Cyperetum rivularis* is well defined by its character species *Cyperus rivularis* ssp. *lagunetto* (excl. ?), *Sibthorpia repens* (pref.) and a small unknown species of *Scirpus* subg. *Isolepis*. *Puya santosii* is a differential

species. The *Cyperetum rivularis* is an altitudinal vicariant with *Caricetum pichinchensis* though both associations of the *Galio-Gratiolion* are described for different parts of the study area. The low and creeping, *Sibthorpia repens* is a selective character species of the *Hypericetum laricifolii* (74) a páramo shrub community on humid ground, which has also some other understorey species in common with the *Cyperetum rivularis*. Relevé 387 contains taxa from adjacent vegetation *(Eleocharitetum macrostachyae, Oritrophio-Wernerietalia)*.

Synecology: The *Cyperetum rivularis* is restricted to wet subpáramo habitats on peaty poorly-drained glacial valley floors, especially in former lakes. The thick waterlogged profiles consist of clayey peat or gyttja. Rootzone pH is 5.3-6.4. In rel. 235, a compact probably cyperaceous peatlayer was observed at a depth of 80 cm. A hummock-hollow relief similar to that described for the *Caricetum pichinchensis* is generally present.
The hummocks are best developed in rel. 409, where they have a diameter of 30-50 cm and a height of about 25 cm, probably caused by fluctuations of the phreatic level. In the wet season the hollows become inundated. A distinct pleustophytic community *(Lemno-Azolletum)* consisting of *Azolla filiculoides* and *Lemna minor* may be floating in the hollows. The hummocks mainly carry *Cyperus rivularis* and *Cortaderia* sp. The hollows are poor in species. Recorded are *Elatine* cf. *chilensis, Callitriche* sp., *Ranunculus flagelliformis, Philonotis andina, sphagnum recurvum, Drepanocladus fluitans* and *D. lycopodioides*. *Gratiola peruviana* is an excellent colonizer on barren mud. This species is absent, when *Sphagnum* and *Barchythecium* species colonize *Cyperus* litter effectively.
Large *Cortaderia* tussocks replace the *Cyperetum* in deeper parts of the swamp, where the vertical fluctuation of the phreatic level is higher (Páramos de la Rusia & Guina).
Rel. 234 contains many seedlings of *Escallonia myrtilloides* var. *myrtilloides*. As frequently observed in the lower páramos, this species locally develops into small dwarfforests on swampy ground along streams. Hirts sometimes set fire to the *Cyperetum rivularis*.
Mainly *Cavia porcellus*, but also *Sylvilagus brasiliensis* forage on *Cyperus* foliage. Frogs are common.

Distribution: The *Cyperetum rivularis* is only known from the lower páramos (lower grass páramo, subpáramo) between 3300 and 3500 m in the Department of Boyacá. In the Colombian Cordillera Central a reedswamp dominated by *Cyperus* sp. (probably the same species) was seen at 3900 m near the forest line in the Romeral valley, W slope of the volcano S. Rosa. *Azorella multifida* and slender rosettes of *Valeriana plantaginea* were associated.

CALAMAGROSTION LIGULATAE all. nov.
type: *Geranio confertae - Calamagrostietum ligulatae* (this study)

Physiognomy: The closed vegetation of this alliance is stratified into two layers:
1) a predominantly graminoid fieldlayer, up to 50 cm high, and
2) a ground layer of mosses or low matted herbs.

Composition & syntaxonomy: Character species are *Calamagrostis ligulata* (select.), *Cerastium imbricatum* (select.), *Montia fontana* (select.) and *Plantago australis* ssp. *oreades* (excl.). *Scorpidium scorpioides* is differential against the *Galio-Gratiolion*. *Drepanocladus aduncus* is hardly

present outside this alliance.
The average number of species varies from 13 (7-26) in the pioneer communities up to 23 (14-36) in the more stable *Bryo-Caricenion bonplandii*.

The *Calamagrostionligulatae* comprises various kinds of páramo vegetation with *Calamagrostis ligulata* (including communities with uncertain status). An exception is the *Carici-Wernerietum crassae (Oritrophio-Wernerietalia)*, with *Calamagrostis ligulata* as a weak differential species. Cuatrecasas (1934) reported *Calamagrostis ligulata* from the bunchgrass and lower superpáramo (3800-4430 m) of the Nevado de Tolima, in small groups with limited cover. Recent relevés in the same area (volcanoes S. Isabel - S. Rosa) indicated the presence of this grass species in the azonal páramo vegetation (Cleef et al., in press).

Synecology: The páramo mires of the *Calamagrostion ligulatae* are found in various environments: on sloping ground with accumulations of water, on marshy valley floors, on former lake floors, in lake-shore hydroseral zonation, in streams, in swamps, and on calcareous mires in dolines. The mesotrophic to eutrophic clayey to peaty substrates are generally thick with a rootzone pH varying from 5.1 in boggy conditions to 7.5 in the most eutrophic habitat in calcareous mire.

Distribution: The alliance is mainly based on relevés from the subpáramo and grass páramo of the Colombian Cordillera Oriental between 3400 and 4000 m. The highest communities (4430 m) have been recorded in the superpáramo. The *Calamagrostion ligulatae* is also present in the páramos of the Colombian Cordillera Central and probably also in those of the Sierra Nevada de Mérida in Venezuela (Vareschi 1970) and in Ecuador.

Calamagrostis chrysantha mainly forms grass mires in the Peruvian puna between 4500 and 4750 m, according to Rauh & Falk (1959) and Gutte (1980). The latter described the *Calamagrostietum nitidulo-chrysanthae* Gutte, which apparently belongs to another undescribed, but geographically vicariant alliance of the *Calamagrostion ligulatae*.

BRYO-CARICENION BONPLANDII suball. nov.
type: *Geranio confertae - Calamagrostietum ligulatae* (this study); table 11

Physiognomy: See alliance.

Composition & syntaxonomy: Character species are: *Bryum laevigatum* (almost excl.), and another still unnamed *Bryum* sp. (e.g. *B.* cf. *ellipsifolium)*, *Stachys elliptica* (sel.) and *Senecio niveo-aureus* (pref.). Differential species are *Carex bonplandii*, *Muhlenbergia* sp(p) _ *Juncus cyperoides*, *Scirpus inundatus* and *Leptodontium longicaule* var. *microruncinnatum*.
The average number of species is higher than in the other communities of the alliance, and is 23 in 13 relevés (14-36). Most of them are vascular plants and mosses. The *Bryo-Caricenion bonplandii* comprises all stable species-rich *Calamagrostis ligulata* páramo mire vegetations in the Colombian Cordillera Oriental, which are without extreme environmental factors.

Synecology: This suballiance comprises wel-developed stable páramo mire communities on sloping (up to 12°) peaty ground, in valley floor swamps and bogs, and in hydroseral sequence on swampy lake-shores. The *Calamagrostis ligulata* cover is higher (about 45%) in comparison to the other communities in more extreme habitats. The depths of the peaty substrates and sediments vary considerably, from 1 m to 8 m or more. Rootzone pH is 5.1-7.1 and clearly reflects mesotrophic and eutrophic habitats.

Distribution: This suballiance occurs from the subpáramo up into the superpáramo, from 3400 to 4150 m, in the Colombian Cordillera Oriental. The highest record is of the community with *Senecio niveo-aureus* and *Breutelia* (55^c) in the upper condensation zone on the Nevado de Sumapaz.

Note: Whitish, broad-leaved, giant rosettes of *Senecio niveo-aureus* with lax inflorescences are restricted to these cold azonal páramo mires. The *Senecio niveo-aureus* populations mainly represent zonal superpáramo communities (26) on the climatologically humid side of the mountains.

54. *Lupino alopecuroides - Mimuletum glabratae* ass. nov.
type: rel. 101; table 11; Fig. 13

Physiognomy: This rather closed herbaceous vegetation is stratified in:
1) a high herb-tussock grass layer of 50-100 (150) cm, covering about 75-100%, and
2) a low herbaceous - bryophyte mat, covering 30 to nearly 100% of the surface. The cover of bryophytes, mainly pleurocarpous mosses and some thallose liverworts, is 5-30%. *Lupinus alopecuroides, Senecio niveo-aureus, S.* sp. nov. (5736; rel. 169) and *Calamagrostis ligulata* are mainly present in the upper layer, whereas *Mimulus glabratus, Ranunculus flagelliformis, Brachythecium* sp. (4230) and *Bryum* sp. (4228, 4231) belong to the ground layer.

Composition & syntaxonomy: This association is rich in hydrophytic herbaceous species. Character species are *Lupinus alopecuroides* (excl.) *Mimulus glabratus* (select.); *Calceolaria mexicana* (select.), and probably *Anomobryum plicatum*.This last moss species is in the Colombian Andes only known from the Páramo de Pisva(3480-3600m).*Bartsia* sp. (reddish flowers) and *Sisyrinchium tinctorium* are differential species. *Brachythecium* sp. (e.g. *B. flexiventrosum)* are prominent in shady places. The number of species ranges from 22 to 36 in the two relevés available and is highest at lower altitude. The closest affinity is shown to the *Geranio- Calamagrostietum drabetosum* (55^a).

Synecology: The *Lupino-Mimuletum* is found in eutrophic wet flush on slopes (7-12°). The continuously perculating water is enriched by minerals from the surrounding páramo. The pH is 6.1-6.3 (flush water) and 7.1 (filty-humic rootzone). Thickness of the clayey to peaty substrate varies from 30 cm (rel. 169) to 100 cm (rel. 101). A sandy or clayey layer containing angular gravel is present at the base of the peat. Presence of *Lupinus alopecuroides* contributes to the high content of nitrogen in this habitat.
Frogs, insect larvae and bivalves of *Sphaerium lauricochae* were observed in the *Lupino-Mimuletum*. Trampling by cattle and foraging activity of *Sylvilagus brasiliensis* are common.

Distribution: This association is described from the Sierra Nevada del Cocuy (4000 m) and the adjacent Páramo de Pisva (3480 m), but stands close to the cloud forest line have also been observed in the Páramo de Palacio (Cundinamarca) and in the Páramo de Sumapaz (Meta). The *Lupino-Mimuletum* is most common in the atmospherically humid subpáramo on the E side of the Colombian Cordillera Oriental. It is present in the subpáramo and the lower grass páramo. *Mimulus glabratus* is a widely distributed species in the temperate and cool mountains of tropical America. *Lupinus alopecuroides* is only known from the Colombian and Ecuadorian páramos. Thus, the *Lupino-Mimuletum* is likely to occur in the latter area, probably mainly in subpáramo stands under humid conditions,as e.g. on the Orinoco and Amazonian side of the Colombian and Ecuadorian Cordillera Oriental.

Note: In the author's opinion the Ecuadorian and Colombian páramos contain two populations of *Lupinus alopecuroides*, which are morphologically different at infraspecific level:
1) a superpáramo population (high páramo up to 4700 m) with large, compact, columnar inflorescences and densely tomented leaves, and
2) a lower páramo population (3000-4000 m), dull greenish, with more loose and slender inflorescences, on wet ground, bog and peat.

Lupinus alopecuroides of the *Lupino-Mimuletum* belongs to the latter population. It is assumed that Pleistocene glaciations caused spatial isolation, resulting in morphological and ecological differences. The same applies to *Senecio niveo-aureus* (see *Bryo-Caricenion bonplandii* and *Valeriana plantiginea* (see *Caricenion pichinchensis)*.

55. *Geranio confertae - Calamagrostietum ligulatae* ass. nov.
type: rel. 109; table 11; Fig. 42, 51, 53.

Physiognomy: The association is characterized by:
1) a graminoid fieldlayer, covering as much as 80%;
2) a groundlayer, dominated by low herbs or mosses.

Composition & syntaxonomy: The character species *Calamagrostis ligulata* (transgr.) is prominent. *Geranium confertum* is a selective character species. Other character species are *Montia meridensis* fma. , *Draba* sp. (264[a]; white petals) and *Lupinus* cf. *verjonensis*. The identity of the two last species has not yet been determined. *Halenia* sp(p.), *Hypericum lancioides*, *Breutelia allionii* and *B. chrysea* are differential species. Mosses in stable stands cover about half of the surface, with as representatives *Breutelia allionii*, *B. chrysea*, *Campylopus cavifolius* and *Bryum laevigatum*.
The average number of species is 20 (14-32) in 10 relevés. In addition to its character and differential species, the *Geranio-Calamagrostietum ligulatae* is differential against other communities in extreme páramo environments by its abundance in (moss) species, and higher grass cover (average 40% versus 12%). *Geranium confertum* has not yet been noticed in *Calamagrostis ligulata* mires in the Colombian Cordillera Central, but on the basis of herbarium data this species occurs also in Ecuadorian páramos; it is characteristic for the *Hyperico-Plantaginetum rigidae breutelietosum* (65[b]).

Synecology: The *Geranio-Calamagrostietum ligulatae* is a community of páramo mires on former lake *(drabetosum)*, on marshy lake-shores and on flat or gently sloping valley floors (predominantly *breutelietosum*). It is found in mosaics together with reedswamps *(Galio-Gratiolion peruvianae)* or bogs dominated by *Sphagnum* and vascular cushion plants. The anaerobic clayey to peaty substrate is mesotrophic to eutrophic, with a rootzone pH of 6 (5.5-6.5). Sites surrounded by *Sphagnum* bogs are usually more acid in the toplayer. In most places the peat is thicker than 1 m, and sometimes more than 8 m (former lakes). Dense moss carpets are common on the climatologically humid side of the mountains. Type, nature and dominance of the almost continuous moss stratum are controlled by edaphic conditions. Generally, *Calamagrostis ligulata* tussocks are the first to colonize on mire, followed by a closing of the moss carpet.
There is mainly foraging by *Sylvilagus*, *Cavia* and cattle. Snails of *Plekocheilus succinoides cleeforum* were collected in rel. 127.

Distribution: The association is restricted to subpáramo and grass páramo mires of the Colombian Cordillera Oriental where is was studied between 3400 and 3900 m. In the author's opinion the stand in relevé 286 at 4120 m in the lower superpáramo of the Nevado de Sumapaz may represent an undescribed association restricted to the upper condensation zone (see 55[c]).

Note: *Montia* cf. *meridensis* is a common lax plant, the leaves of which bear two conspicuous teeth; it has white, orange and pink flowers in *Calamagrostis ligulata* mires. For the moment these specimens (e.g. 275, 1022, 1030) are considered as low altitude members of the superpáramo population. The superpáramo population of *Montia meridensis* in the Colombian Cordillera Oriental is morphologically characterized by:
1) a compact cushion-like appearance
2) white flowers with a faint yellowish hue
3) two smaller apices per leaf

55[a]. Subass. *drabetosum* subass. nov. (prov.)
type: rel. 127; table 11; Fig. 53

Physiognomy: Stratification is in two layers:
1) a ground layer, consisting of a dense cushion-like mat of low herbs, tiny grasses and mosses, and
2) an open tussock grass layer (15-50 cm high) with whitish rosettes of *Senecio niveo-aureus*.

The herbaceous matted groundlayer is often covering in an undulating way the underlaying clayey peat, thus causing a relief of hummocks and hollows (Fig. 53).

Composition & syntaxonomy: Differential species are herbs in low mats or low cushions: *Draba* sp. (264[a], 5261) and *Lupinus* cf. *verjonensis* (2609, 5262). In some places, *Festuca* sp. (5259) tussocks replace most of the *Calamagrostis ligulata* clumps. *Cyclodictyon* sp. (4820, 5264) and *Brachythecium* spp. (4819, 5270) are differential moss species against other communities of the *Calamagrostion ligulatae*.
More relevés are required to confirm the present rank of this subassociation *Festuca* sp. bunches are only locally present in the azonal communities (especially in *Sphagnum* bogs) of the páramos in the Colombian Cordillera Oriental. The taxonomic status of this grass species and of the species *Lupinus* and *Draba* still remains uncertain.

Synecology: This vegetation type is restricted to boggy mire covering former lake bottoms and also occurs locally on wet slopes. The pH of the clayey peat immediately under the low herbaceous mat is 5.2 and 6.2 in the two relevés. *Muhlenbergia* sp., *Draba* sp., *Cerastium imbricatum*, *Brachythecium* sp., *Bryum ellipsifolium* and *Bryum* sp. (4818) preferably grow on the cavernous hummocks of about 10 cm high, whereas the hollow habitats contain *Marchantia berteroana*, *Cyclodictyon* sp., *Bryum candicans*, *Reboulia hemispherica*, *Callitriche* sp., *Nerteria granadensis*, *Lupinus* cf. *verjonensis* and *Spirogyra* sp.

Distribution: This vegetation type has only been studied in the Páramo de Sumapaz between 3600 and 3900 m.

Note: The *Draba* species is probably identical with the not yet indentified *Draba* species with white petals (e.g. 1310, 1312), which abound in the superpáramo in the upper reaches of the Nevado de Sumapaz. If this proves to be correct, the *Draba* specimens (2611[a], 5261) in both relevés are an example of a superpáramo species in a cool grass páramo mire habitat.

55^{b}. Subass. *breutelietosum* subass. nov.
type: rel. 109; table 11; Fig. 42 (see also Fig. 51)

Physiognomy: Just as in the association, two layers can be distinguished.
1) a graminoid fieldlayer, 30-60 cm high, covering about half of the area.
2) a nearly closed 10-15 cm thick moss carpet.
Vascular plants are locally prominent.

Composition & syntaxonomy: *Breutelia allionii* and/or *B. chrysea* are differential as regards presence and higher cover (25-75%). In most relevés the cover of *Calamagrostis ligulata* is 60% or more.
The *breutelietosum* can be readily distinguished by its conspicuous moss cover; the number of species is differential against other moss-dominated communities of the *Calamagrostion ligulatae*.

Synecology: The *breutelietosum* occurs in 2 habitats:
1) in hydroseral lake-shore mires,
2) on boggy slopes surrounded by Sphagnum bog or by cushion bog of the *Hyperico-Plantaginetum rigidae*.
Origin and nature of the water in these páramo mires reflect in the values of the clayey or peaty rootzone. In eurotrophic lake-shore mires the pH is 6.0-6.6*, and in mesotrophic habitats in contact with *Sphagnum* bog 5.1-5.8.

Distribution: This mossy subassociation is common in the subpáramo and grass páramo (3400-3875 m) on the humid side of the Colombian Cordillera Oriental, and was also observed between 3800 an 4100 m on former lake floors on the SE side of the Nevado S. Isabel, Colombian Cordillera Central.

55^{ba} Variant of *Campylopus cavifolius*
type: rel. 295; table 11; Fig. 42

Physiognomy & composition: *Campylopus cavifolius* is dominant in the moss layer, in association with other bog elements, e.g. *Pernettya prostrata* var. *purpurea*, *Riccardia* spp., and locally with *Anastrophyllum leucocephalum* and *Lepidozia macrocolea*.
Campylopus cavifolius may be absolute dominant and then forms a conspicuous flat compact turf.

Synecology: With a less regular drainage and aeration, a thick compact *Campylopus cavifolius* turf develops in the *breutelietosum*, which may become absolutely dominant under bog conditions. The green to light-brownish *Campylopus cavifolius* is about 10-15 cm high. At the base of the moss layer is a thin blackish stratum (pH 5.1-6.6*), which deeper passes into a grayish peat.
The upper part of the *Campylopus cavifolius* peat contains many caterpillars.

Distribution: The variant has only been studied in the southern páramos (Sumapaz, Palacio) of the Cordillera Oriental between 3400 and 3650 m. It may be expected in other páramos of the Cordillera Oriental. The variant was also observed at 3800 m on the SE side of the Nevado S. Isabel, Colombian Cordillera Central.

55^c. *Calamagrostis ligulata* community with *Breutelia allionii, Senecio niveo-aureus* and *Luzula gigantea*
characteristic rel.: 286; table 11

Physiognomy: The vegetation structure is similar to that mentioned for the *breutelietosum* of the *Geranio-Calamagrostietum ligulatae*.

Composition & syntaxonomy: Several species are differential against all other communities of the *Calamagrostion ligulatae*. Part of these are superpáramo taxa:e.g. *Poa* cf. *pauciflora, Draba* sp. with yellow petals (8108), *Draba* sp. with white petals (1310, 1312), *Lachemilla tanacetifolia*. Nearly all species are hygrophytic and most of them skiophytic, generally found under páramo shrub and thickets in lower locations, e.g. *Luzula gigantea* and *Thuidium peruvianaum*. in shady habitats and *Rhacocarpus purpurascens* and *Breutelia allionii* in the open high páramo. This superpáramo community fits best in the *Geranio-Calamagrostietum ligulatae*.*Geranium confertum* was found associated, but is absent in rel. 286.

Synecology & distribution: This community was only observed in humid depressions on the slopes of the lower superpáramo in the summit area of the Nevado de Sumapaz between 4100 and 4200 m. The thin dark-brownish clayey soils are overlying limestone rocks. The pH of the rootzone was 6.2. Floristic composition and plantcover of this stand reflect the presence of an upper condensation zone. The clouds which most of the time cover the peak bring about an open hygrophytic and skiophytic vegetation of these heights. *Sylvilagus* forages on *Luzula gigantea*. Cattle sometimes grazes in higher areas.

Other *Calamagrostis ligulata* communities

56. Community of *Calamagrostis ligulata* with *Montia fontana*
characteristic rel.: 296; table 11; Fig. 49

Physiognomy, composition & syntaxonomy: This páramo spring vegetation is dominated by herbs in contrast to holarctic spring vegetations, which are generally rich in bryophytes (e.g. De Molenaar 1976). The spring community here described stands out by its higher cover of photophytic herbs: e.g. *Montia fontana* (20-80%) and *Epilobium meridense* (5-8%), while bryophyte species are scarce.
The number of species is 14 (13-15) in the two relevés.
Most conspicuous is the low herb layer with some pleurocarpous mosses and *Marchantia plicata*; this layer is slowly percolated by water rich in oxygen. This spring community fits well in the *Calamagrostion ligulatae*. It may represent a proper association .

Note: A herbfield is often developed on marshy banks of páramo streams, and may be dominated by one of the following species: *Mimulus glabratus, Cardamine africana* or *Montia fontana*. These communities have close floristic affinities with the here described páramo spring vegetation.

Synecology: *Ranunculus flagelliformis* and *Eleocharis stenocarpa* have much higher cover values in lake-shore habitats. The pH of the clayey to peaty rootzone was 6.6 and 6.7 in the two relevés. Black leeches and frogs are common.

Distribution: The studied stands are located in the Laguna La Guitarra marshes at 3425 m in the upper subpáramo of the Páramo de Sumapaz. The community was also observed in mires on the valley floor of Lagunillas, Sierra Nevada del Cocuy and can be expected in the páramos of the Cordillera Oriental. Further, it is also known from the Nevado de S. Isabel at 3800 m in the Cordillera Central. Relevé 629 in that place has been used for the present diagnosis.

57. Community of *Calamagrostis ligulata* with *Sphagnum sancto-josephense*
characteristic rel.:267; table 11; Fig. 50, 51

Physiognomy: The community is structured in two layers:
1) a closed *Sphagnum* peat layer, in which small vascular plants may attain a high cover, and
2) an open field layer, mainly 30-50 cm high mire grass clumps with a cover of 15%.

Composition & syntaxonomy: The lake-shore mires are dominated by peat mosses, e.g. *Sphagnum sancto-josephense, S. magellanicum* with *Pleurozium schreberi*, and the rare *Lophozia* cf. *patagonica* (see taxonomical comments of Dr. R. Grolle in Gradstein & Hekking 1979). Rel. 400 in the Páramo de Palacio near Bogotá is the northernmost location of this tiny cool-temperate austral liverwort species. *Eleocharis stenocarpa* has a higher cover within the reaches of the lake water (rel.400) and a lower cover in peat bog (rel. 267), 16 resp. 13 species were recorded in the two relevés.
Peat bog species are differential against other communities of the *Calamagrostion ligulatae*. This community is somewhat intermediate between the *Calamagrostion ligulatae* and the (páramo) *Sphagnum* bogs,

Synecology: This is a peat bog community in the hydroseral zonation in páramo lakes. The stand may be in direct contact with open water in lakes surrounded by *Sphagnum* bog (rel. 400) or separated there from the *Carex acutata* community (rel. 267[a]) in the transition from open water towards *Swallenochloa-Sphagnum* bog or *Diplostephietum revoluti* (Fig. 50, 51).
At least the upper part of the substrate consists of *Sphagnum* peat. The pH* in the top layer of rel. 400 was 5.3. A floating or emerging moss community, consisting of *Drepanocladus exannulatus* (60% cover) and *Sphagnum cuspidatum* (40% cover), is locally found along the shores of the lakes with *Sphagnum* bog (rel. 399; pH* 4.8).

Distribution: The community is known from the southern lower grass páramos in the Cordillera Oriental, at a height of 3350 m. The community must be present elsewhere in lacustric hydroseres in the lower páramos of the Colombian Andes.

58. Community of *Calamagrostis ligulata* with *Drepanocladus aduncus* and *Calliergonella cuspidata*
characteristic rel.: 279; table 11

Physiognomy: This community is composed of two distinct layers:
1) a more or less open ground layer, mainly of hydrophytic mosses,
2) an open graminoid field layer, about 30 cm high covering about 25% of the surface.

Composition & syntaxonomy: This mire community is rather poor in species (7-10 in 2 relevés), and dominated by pleurocarpous mosses (either *Drepanocladus aduncus* or *Calliergonella cuspidata*). High tussocks of *Calamagrostis ligulata, Scorpidium scorpioides, Campylium* sp., *Elatine* cf. *chilensis, Cardamine bonariensis*, and small brownish mushrooms (Agaricales) are generally associated species.

This community probably represents a rare, distinct calciphytic association within the *Calamagrostion ligulatae*. It is also to be expected in other páramos with calcareous rocks, e.g. the Páramo del Almorzadero. Furthermore this community seems geographically vicariant with holarctic calcareous mire communities, e.g. with *Calamagrostis neglecta* stands *(Scheuchzerio-Caricetea)* described from Greenland (Böcher 1933, De Molenaar 1976, Daniels 1980).

Synecology & distribution: This rare basiphytic community has only been found on calcareous mire in a deep doline at 3480 m, on the NW slope of the Nevado de Sumapaz and quite close to the northeastern shore of the Laguna El Nevado. The unstable mineral or clayey-organic soils are in a permanent state of reduction; the phreatic level is at the surface or slightly higher (in january 1973). The community represents the early pioneer stage,with *Drepanocladus aduncus* (rel. 279) on the bare, waterlogged mineral soil (pH of the top layer 7.5) and a more stable and closed cover of the *Calliergonella-Calamagrostis ligulata* community (rel. 278) on clayey organic soil (pH rootzone 6.5).
Part of the *Drepanocladus aduncus* mat apparently dies off during the low water period in the dry season. This causes mosaic-like mossy patches. A core drilled to a depth of 8 m showed alternating organic moss turf and mineral sediment with scarce pollen.
In the same doline, also the *Caricetum pichinchensis* (rel. 277) is found on more stable calcareous substrate.
Cavia and *Sylvilagus* frequently visit the locality.

59. Community of *Calamagrostis ligulata* with *Isolepis* sp. (5603) and *Calliergonella cuspidata*
characteristic rel.: 162; table 11

Physiognomy: The community is structured in two layers:
1) a predominant 5 cm thick moss layer with small and low herbs covering the surface.
2) an open graminoid field layer up to 35 cm high, covering up to 30%.

Composition & syntaxonomy: This mire community is rich in species (26 in rel. 162) and is dominated by *Isolepis* sp. (5603) and *Calliergonella cuspidata*. Many species are characteristic of the *Oritrophio-Wernerietalia:* e.g. *Luzula vulcanica, Altensteinia paludosa, Gentiana sedifolia, Plantago rigida,* and *Vesicarex collumanthus*. *Isolepis* sp. (5603) grows closely associated with *Clasmatocolea vermicularis* and *Breutelia chrysea*.
On the basis of ecological and floristical characteristics, this community belongs to the *Calamagrostion ligulatae*, but with a clear affinity to the *Oritrophio-Wernerietalia*.

Synecology & distribution: The stand is a local feature on the marshy, sloping thin (120 cm) valley floor (3960 m) of the Lagunillas river in the Sierra Nevada del Cocuy. The hummocky patches are surrounded by flush vegetation of the *Oritrophio-Wernerietum cotuletosum* (62^b).

60. Superpáramo vegetation with *Calamagrostis ligulata*
Fig.: 55

Our collections and herbarium specimens indicate that *Calamagrostis ligulata* also is present in the superpáramos of the Colombian Andes up to 4450 m.

Homogeneous superpáramo stands of this grass are scarce and poor in species. In the Sierra Nevada del Cocuy, huge hummocks of *Calamagrostis ligulata* occur along sandy lake shores between 4280 and 4430 m, generally associated with *Ditrichum gracile* and *Agrostis foliata* (see 109) and in some places with *Calamagrostis* aff. *pisinna* (8653).
On the Nevado Ruíz (Central Cordillera), at 4400 m, a *Calamagrostis ligulata* stand with an almost closed carpet of *Bryum* sp. was observed in a small depression draining moraines (Cleef et al., in press). These data may indicate other associations of the *Calamagrostion ligulatae* which have not yet been described.
In the upper condensation zone of the lower superpáramo of the Nevado de Sumapaz a *Calamagrostis ligulata* community rich in species is present; it will be treated separately under the *Bryo-Caricenion bonplandii* (see 55c).
Calamagrostis ligulata with low cover is found as a differential species in the *Carici-Wernerietum crassae (Oritrophio-Wernerietalia)* in the superpáramo of the Sierra Nevada del Cocuy between 4280 and 4430 m. Cuatrecasas (1934) reported *Calamagrostis ligulata* from the lower part (4320-4400 m) of the superpáramo on the volcano Nevado de Tolima, Cordillera Central.

In conclusion is is evident that the Colombian superpáramos contain at least three other syntaxa of the *Calamagrostion ligulatae* as yet remaining undescribed.

FLUSH VEGETATION AND CUSHION BOGS

WERNERIETEA cl. nov. (prov.)
syn. *Plantaginetea* Gutte 1980 (invalid name)
type: *Oritrophio - Wernerietalia* (this study); table 13
lit.: Ruthsatz 1977; Cleef 1978, Gutte 1980; Cleef et al., in press (cited authors provide a survey of the pertinent literature).

Physiogomy & synecology: The flush and cushion bog vegetation of this class is dominated by geophytes, and low cushion chamaephytes. It comprises:
1) hollow communities: e.g. flush vegetation, hollows at the edge of the firm hummocky bogs and between the vascualr cushions; and
2) hummock communities of low matted or cushion-forming vascular plants and mosses.

The fieldlayer may contain small tufted grasses an dwarfshrubs, mainly at lower elevations. Vascular plants cover 10-100% and bryophytes, mainly mosses, may cover 100% aquatic habitats and up to 75% on decaying cushions.
The pH values of the rootzone are 5.0-6.0; most of the cushion bogs are acid and the halophytic puna communities (Ruthsatz 1977) and waterlogged flush vegetation in the lower páramos are eutrophic. Soils are sandy and shallow in the highest areas and become clayey to peaty and thick in lower places. Slopes vary from 10^o-20^o.

Composition & syntaxonomy: Exclusive character species are *Werneria pygmaea, Altensteinia paludosa, Plantago rigida, Distichia muscoides* and *Castilleja fissifolia* ssp. *pygmaea* (ssp. nom. herb.; in ed.?). These small forms of *Castilleja fissifolia* - Weddell (1857) referred to the name "pumila" - are considered by the present author as a subspecies of *Castilleja fissifolia* (if not a distinct species), Other character species for the *Wernerietea* were listed by Ruthsatz (1977) and they include the species reported by her for the "*Wernerion pygmaeae* (prov.)", except *Lachemilla pinnata*. Gabrera (1958) mentioned *Oxychloe andina* (Junc.) from Argentinan high puna bogs, and

Weberbauer (1911) and Tovar Serpa (1973) listed *Lachemilla diplophylla* for the Peruvian, Ricardi & Marticorena (1966) for the northern Chilean *Distichia* cushion bogs. Finally all character species of the *Oritrophio-Wernerietalia* and of its alliances and associations reported in the present study, are characteristic of this class.
Oreobolus obtusangulus cushion bogs also occur in southern Chile. Oberdorfer (1960) ranked them under the *Myrteola-Sphagnetea* Oberd. The pāramo cushions of *Oreobolus* (Cleef 1978) apparently belong to the same species and might be different from magellanic *Oreobolus obtusangulus* at the infraspecific level.
The mean number of species is about 10-15 in 120 relevés. The lowest averages have been found in the Argentinan puna stands and in the north Andean *Wernerion crassae-pygmaeae*, the highest averages in the cushion bogs of the *Gentiano-Oritrophion* in the bamboo pāramos.
Phytogeographically, the newly described class shows distinct austral-antarctic affinities which were earlier noted (Cleef 1978). Details are provided below.
The *Wernerietea* is floristically and ecologically well-defined and contains a good number of regional an local character species and comprises flush vegetation and various successional stages towards vascular cushion bogs and their phases of decay.
The present diagnosis of the *Wernerietea* is somewhat tentative due to insufficient pertinent phytosociological data from the Ecuadorian, Peruvian. Bolivian and Chilean Andes, and from cusion bogs with *Oxychloe andina* and *Patosia clandestina* in the southern high tropical Andes.

Distribution: The *Wernerietea* communities occur along the high tropical Andes from Argentina and Chile to Colombia and Venezuela. Their distribution area corresponds roughly to that of *Werneria pygmaea* and includes also that of some small endemic tropical Andean juncaceous genera: *Patosia, Oxychloe* and *Distichia*. Its southern-most limit is the province of Mendoza in the Argentinan Andes, and the northern most limit is the Colombian Sierra Nevada de S. Marta. In the Colombian and Venezuelan pāramos this class is found between 3400 and 4500 m, though at some locations up to 4700 m and 5200 m, resp. in the Ecuadorian and Bolivian Andes. Cabrera (1958), Hunziker (1952) and Ruthsatz (1977) reported similar communities from 3500 to 5000 m in the norhern Andes of Argentina.

ORITROPHIO - WERNERIETALIA order nov.
type: *Wernerion crassae-pygmaeae* (this study); table 13

Physiognomy: Low matted herbs, predominantly geophytes and cushion chamaephytes, and/or mosses are most prominent. Liverworts have a rather limited cover. The ground layer contains vascular plants and/or mosses depending on edaphical conditions and altitude. The field layer is rather inconspicuous and covers only 10-25% or less. It consists of rale grasses, sedges and herbs. Dwarfshrubs may be common on cushion bogs with less vital cushions of vascular plants.

Composition & syntaxonomy: Character species are *Werneria pygmaea* (select.) and *Oritrophium limnophilum* (select.). Nearly exclusive character species of restricted geographical distribution in the north-andean pāramos are e.g. *Vesicarex collumanthus, Erigeron paramensis, Werneria crassa, Floscaldasia hypsophila. Distichia muscoides* and *Plantago rigido* are selective character species.

Table 11. Reedswamps and mires; MARCHANTIO - EPILOBIETALIA

A.M. Cleef 1981: The vegetation of the páramos of the Colombian Cordillera Oriental
Diss. Bot. 61, Vaduz

ALLIANCE	GALIO-GRATIOLION						CALAMAGROSTION LIGULATAE **							
association	48	50	49*	51	52	53	54	55* Geranio-Calamagrostietum			56	59	57	58
subassociation								55a	55c	55b breutelietosum				
variant										55ba				
relevé nr.	5 139	144 80	138 24 292 63 277	267 265	309	387 235 234 409	101 169	127 142	286	154 295 1 137 109 9 219 483	293 296	162	400 267	278 279 561
relevé area (m²)	25 16	16 9	9 9 25 16 16	9 9	16	16 36 25 36	16 16	9 16	15	4 16 4 4 4 9 4 6	4 4	3	18 6	16 12 3
slope (degree)	5 –	6 –	1 4 2 – –	– <1	9	– – – –	7 12	8 –	25	2 2 10 9 6 3 10 –	– 8	5	– –	– – –
cover % (dwarf) shrub	75 65	8 –	– – – – –	– –	30	– – 2 –	– –	– –	–	<1+ – <1 <1 – – <1 –	– –	–	3 –	– – –
Cyperaceae	60 90	80 70	100 95 65 100 65	20 90	65	98 95 95 70	5 1	<1 –	–	6 <1 – 5 40 – <1 1	65 5	80	85 –	<1 3 –
grasses	– –	10 65	– <1 – <1 <1	5 –	25	<1 – – 5	20 85	25 60	7	<1 65 4 35 60 60 <1 80	3 25	30	10 15	25 5 70
mosses	45 30	100 70	10 5 6 5 15	6 <1	1	70 90 3 <1	30 5	35 7	88	80 90 80 70 85 85 95 15	1 15	97	76 90	80 45 2
liverworts	40 5	5 5	<1 2 10 <1 –	3 80	40	8 – 2 1	<1 <1	<1 3	2	<1 2 70 30 – <1 5 1	1 15	<1	76 1	– – –
soil	P/k P/c	c/p y	c P/c P P P/c	P P	P	P P P P/y	P C	P P	C	P P P C P P C P/c	P P	C	P P	P P P
pH top soil (* water)	6.5 6.5	4.7 4.5	6.0 5.6 5.4 5.0 6.6	– 6.3	5.8	5.6 5.3 6.4 6.4	6.3* 7.1	6.2 5.5	6.2	6.6* 6.2 5.1 5.8 6.4* 6.0 5.3* –	6.6 6.7	6.4	5.3* –	6.5 7.5 –
approximate number of species	29 44	30 25	26 35 17 23 12	10 8	22	27 9 26 19	38 22	24 18	24	35 20 14 23 21 19 27 17	13 17	26	16 13	10 7 8
altitude (m)	3425 3680	3620 3700	3660 3715 3390 3350 3460	3535 3525	3560	3300 3605 3515 3290	3480 4005	3845 3625	4120	3640 3400 3580 3400 3580 3465 3660 3845	3415 3405	3960	3350 3535	3770 3485 3815
locality	Sum Sum	Sum Sum	Sum Sum Sum CV Sum	Sum Sum	Sum	Tota Cus Rus Gua	Pi Coc	Sum Sum	Sum	Chuz Sum Pal Pal Pi Sum Neu Coc	Sum Sum	Coc	Pal Sum	Sum Sum Alm
cover %	▲		▲			▲	▲	O		▽ ▲ O				
c & d taxa Senecionetum reissiani														
c Senecio reissianus	75 65	<1												
Hypericum laricifolium ssp. laricoides	1 <1+		<1							<1				
Hypnum amabile	<1 2		<1											
Cyclodictyon sp.	<1 <1							<1+ <1						
Rumex tolimensis	1													
Greigia mulfordii	<1													1
c & d taxa Caricetum p. & CARICENION P.														
c Carex pinchinchensis	60 75	75 70	90 95 65 100 65				1			<1				<1 3
c Valeriana plantaginea var. paludosa	2 5	1 2	20 10 20 <1					1		1+ <1+				
Lophocolea coadunata	<1+	3 <1	<1 <1+				<1	<1	<1					
Gentianella corymbosa	<1	<1	<1 <1							<1		<1		
Thuidium peruvianum	5		<1+ <1+						5	<1				
Peltigera spp.	<1	1+	<1						<1					
Senecio canescens	1	5												
Selaginella sp. (5200)	<1		<1											
Carex fecunda			3											
Conyza uliginosa			<1 <1		<1									
Scutellinia spp. (Pezizales)			<1 <1+ <1						<1					
characteristic taxa comm. Polytrichum c.														
Polytrichum commune		85 5				<1 <1								
Arcytophyllum muticum	3	25 <1											20	
Geranium sibbaldioides		<1 <1	<1?			<1	<1							
Leptoscyphus cleefii		<1+ <1	<1+											
Hypericum prostratum	<1	8												
Sphagnum magellanicum		40											1	
characteristic taxon comm. Carex acutata														
Carex acutata				20 90										
characteristic taxon comm. Carex jamesonii														
Carex jamesonii					65									
c & d taxa Cyperetum rivularis														
c Cyperus rivularis ssp. lagunetto					<1	95 95 95 50								
Sibthorpia repens	<1		<1?		<1+	5 2 2								
Puya santosii				<1	<1	5 1 1								
Isolepis sp.						<1 1	<1			<1		80		
c/d/o taxa GALIO TRIANAE - GRATIOLION P.														
c Galium trianae	<1	<1+	<1+ <1+		2	3 <1		<1+		<1				
c Gratiola peruviana	3 <1		<1 20 <1			5 5								
c Symphyogyna sp(p.) (mainly S. sinuata)	40 <1+		<1 1 5	3 80	<1	<1+ 1				<1 5				
Lachemilla mandoniana	5		3 15 <1	3	10	1 <1 1 1				<1 <1+				
Bryum grandifolium	<1+		<1+			<1 <1								
Philonotis andina			<1 1			<1+		<1?						
Blechnum loxense	<1		<1		3									
Isoetes sp. / I. cf. boyacensis	<1		1			<1				<1				
Callitriche sp.	1				25	<1	<1	<1						
c & d taxa Lupino a. - Mimuletum glabratae														
c Mimulus glabratus						<1	80 15				<1			
c Lupinus alopecuroides							50 60							
c Calceolaria mexicana							<1			<1				
Sisyrinchium tinctorium							<1 <1+							
Bartsia sp. (corolla reddish)							<1 <1							1+
Brachythecium sp. / B. flexiventrosum						70	15 5	1 2	<1					
c & d taxa Geranio c. - Calamagrostietum l.														
c Geranium confertum								<1		2 <1 1 40				
Halenia sp(p.)	<1	<1					<1+	<1+		3 10 <1 <1				
Hypericum lancioides								<1		<1				
Calamagrostis planifolia														
Montia meridensis fina								<1		1				
d taxa drabetosum														
d Lupinus cf. verjonensis (2609)								50 40		30				
d Draba sp. (5260 - white petals)								5 15	1					
characteristic taxa superpáramo comm. with Senecio niveo-aureus, Draba spp. & Lachemilla tanacetifolia														
Draba sp. (8108 - yellow petals)									1					
Poa cf. pauciflora									1	<1+				
Lachemilla tanacetifolia									<1					
Metzgeria metaensis									2	1				
d taxa breutelietosum														
d Breutelia chrysea	<1 5							<1 1		30 25 40 35 75 25 2				
d Breutelia allionii	1								80	20 35				
d taxon var. Campylopus cavifolius														
Campylopus cavifolius	1		<1					1	<1	50 65 50 1 1			1	
c/d/o taxa BRYO - CARICENION BONPLANDII														
c Carex bonplandii	1		5			<1 30	3 <1	<1		5 <1 5 40 <1 1				
c Bryum laevigatum / B. ellipsifolium							10	35 2		10 <1				
c Senecio niveo-aureus							35	15	55	25				
c Stachys elliptica							<1	<1+		<1				
d Juncus cyperoideus			1				<1	<1		<1+				
Leptodontium longicaule var. microruncinnatus							4			10 10				
Muhlenbergia fastigata	<1+						3	10		<1 <1				
Scirpus inundatus						<1?	2			1+				
characteristic taxon comm. Drep. aduncus - Calamagr. ligulata														
Drepanocladus aduncus														<1 45
c/d/o taxa CALAMAGROSTION LIGULATAE														
c Calamagrostis ligulata			<1	5		2	15 75	15 50	5	<1 65 4 35 60 60 <1+ 80	3 15	3	10 15	25 5 70
c Cerastium imbricatum							5	5 10	15	10 5 <1 3	5		<1+	
c Montia fontana						1	2			<1+	60 25	<1		
Scorpidium scorpidioides	<1						<1			<1 10	1			1 <1
c Plantago australis ssp. oreades							<1			1	1			
c/d/o taxa MARCHANTIO -EPILOBIETALIA														
c/d Nertera granadensis	<1	3	1 <1+ <1			<1 <1 5	<1+ 1	5		2 <1 1 <1 <1 <1+		<1	<1	
c/d Riccardia sp(p.)	<1 2	<1 <1+	<1		<1	5 <1		<1 <1+	<1	<1 <1+ 60 30		<1+	1	
c Marchantia plicata	<1		<1 5	<1 2		<1 1	<1 <1			1 <1 <1 1+ <1	1 15			
c Ranunculus flagelliformis		<1	1 5 25 <1+		<1	<1 <1	1 1	<1		<1 10	90 1			
c Epilobium meridense / E. denticulatum			<1 10	<1+		10 1	<1	<1	1	<1+ <1 1 1	1 8			
c Cardamine bonariensis / C. africana			<1 <1	<1+			<1	<1	<1	1+ <1 <1 3	1			1 1 <1?
c Senecio subruncinnatus		1	<1+ 1			3 1		2 1		<1 1	2		5 <1	2
d Caliergonella cuspidata	<1		15	2		<1	5			<1 <1 <1 2	25	95		75 <1
c/d Eleocharis stenocarpa	<1				<1	5 <1	<1			<1 85 <1	65 5		85 2	
Elatine cf. chilensis	<1	<1	<1 5			<1	<1 <1				<1		<1 <1	1 <1
Drepanocladus exannulatus	<1		<1 1	2 <1				1 <1		<1 2		<1	<1	
Sphagnum sancto-josephense	45 5	2		1		90 3				1 <1			75 85	
Cotula minuta			5			1 <1	<1 1			2 <1 3	5			
Agaricales		<1 <1		<1		<1		<1		<1			<1	<1
Breutelia sp. / B. subarcuata		<1 1	1 3		<1+					<1				
Calamagrostis planifolia		60				3 1				<1 <1		25		
Pernettya prostrata var. purpurea / elliptica	2		<1		30					<1	1+		<1	
Breutelia inclinata	2		4		<1								2	1?
Bryum argenteum		<1						1		<1 <1		1		
Festuca cf. dolichophylla		5					1	10		<1	10			
Arenaria spp.			<1			<1				<1+	<1			
Lysipomia sphagnophila ssp. minor	<1						<1				5		5	
Lilaeopsis schaffneriana						30				2	3	<1		
Luzula gigantea		<1							3	<1			<1	
Fossombronia sp.	1					3				<1	<1?			
Calamagrostis coarctata						<1+				1 <1				
Pleurozium schreberi		1								30			5	
Hydrocotyle ranunculoides				<1		<1							<1	
Tillaea paludosa			<1	5		1								
Lachemilla fulvescens			<1											
Altensteinia paludosa							<1			<1		3		
Eriocaulon microcephalum	<1												1	
Reboulia hemispherica						<1		<1						
Laestadia muscoides							3				<1			
Luzula vulcanica										<1				
Senecio guacensis										10				
Marchantia berteroana								2						
Sphagnum recurvum						90								
Senecio sp. nov.							20							
Hydrocotyle bonplandii										35				

Localities: Alm Páramo del Almorzadero; Chuz Río Chuza drainage basin; Coc Sierra Nevada del Cocuy; CV Páramo de Cruz Verde; Gua Páramo de Guantiva; Neu Páramos NW of Neusa; Pal Páramo de Palacio; Pi Páramo de Pisva; Rus Páramo de la Rusia; Sum Páramo de Sumapaz; Tota Páramos near Laguna Tota

c character taxa
d differential taxa
o other taxa

** type of the order
* type of the alliance
▲ type of the association
O type of the subassociation
▽ type of the variant

Table 13. Flush vegetation and cushion bogs; WERNERIETEA (prov.)

A.M. Cleef 1981: The vegetation of the páramos of the Colombian Cordillera Oriental
Diss. Bot. 61, Vaduz

ORITROPHIO - WERNERIETALIA ✱✱	61a	61b	62a	62b	63	64	65a	65b	66a	66b
ALLIANCE	WERNERION CRASSAE - PYGMAEAE ✱						GENTIANO - ORITROPHION (prov.)			
association	61 Carici p. - Wernerietum c.		62 Oritrophio l. - Wernerietum p. ✱		63	64	65 ✱ Hyperico l. - Plantaginetum r.		66 Oritrophio p. - Oreoboletum o.	
subassociation	61a wernerietosum c.	61b caricetosum p.	62a typicum	62b cotuletosum m.			65a gentianelletosum	65b breutelietosum	66a typicum	66b
variant	61aa	61bb	62aa, ab, 62ac, 62ad, 62ae					65bb	66aa	
relevé nr.	382 381 464 180 319 321 320 316 335	473 326 314 317 447 321	450 348 466 289 39 265 506 509 508 471 563 346 491	257 105 257 186 185 110 40 571	318 355 466 562	332 333 334	505 410 263 254 513 572 490	55 261 111 502 282 274 275	504 147 152 95 496 171 445 465 461 183	253 424 134
relevé area (m2)	9 16 1 12 4 6 4 2.5 4	2 16 4 6 2 9	1 1 1 2 4 1 2 2 2 1 1.5 9 1	4 1 1 4 4 1 3 2.5	60 80 4 4	16 100 36	25 21 24 16 4 4 4	9 9 4 9 16 16 15	9 4 2 6 4 6 2 4 9 9	2 2 4
slope (degree)	<1 2 1 10 5 – 10 1 4	2 – 5 1 3 12	1 1 3 – 7 – – – – 5 – 4 2	1 – 1 2 – 1 3 ?	– 7 3 –	3 2 1	– 3 8 4 – 2 3	5 3 1 3 <1 10 10	3 1 1 4 – 5 4 2 2 7	2 5 15
cover % vascular plants	95 70 50 100 17 20 10 53 95	75 40 88 100 80 99	40 100 75 15 60 15 50 60 20 90 25 99 65	80 95 100 95 95 100 99 95	95 100 97 99	55 50 55	100 86 100 97 100 100 75	95 60 95 100 92 50 80	95 90 55 80 50 70 75 70 60 65	80 85 90
monocots	1 15 5 10 2 1 1 5 70	– 40 6 30 75 40	– 10 – <1 6 – – – 5 – 1 10 3	7 30 5 35 55 100 10 –	80 90 96 96	50 30 25	7 5 30 3 2 3 3	5 15 25 <1 2 2 1	70 70 55 55 45 50 60 60 55 20	44 80 85
bryophytes	25 47 100 7 <1 <1 <1+ 1 –	50 7 100 30 40 75	– – – 85 40 95 100 100 100 75 95 35 25	– 15 – – 20 40 45 60	9 8 3 4	45 55 25	7 17 10 4 2 <1 25	7 35 15 5 9 50 70	15 11 40 75 30 3 17 12 14 3	20 15 10
liverworts	8 5 – 3 <1 – – 1 –	– <1 100 10 5 4	– – – <1 – – – – – – 5 1 –	– – – – – – <1 –	<1 <1 – –	2 15 15	<1 <1 1 <1 <1 – <1	1 <1 1 1 1 28 1	– 1 1 1 1 1 6 – 2 –	– – –
soil	C Cp Cp Cp S Cs S S C	Si C/s C/P S/Cp Pc Pc	? C/S C/S C C C P P P C Cp C C	Cp Cp C Cp Cp Pc Cp Cp	Pc Pc Pc Cp	Pc Pc Pc	Cp Cp Cp Cp Cp Cp Cp	Cp Cp Cp Cp P/c C C/S	Pc P/c Pc Cp Pc Cp Cp Pc Pc S	Pc Cp C
soil depth (cm)	>120 >120 ? 60 10 100 5 25 ?	20 50 100 105 >40 35	? ? – >120 40 ? >120 >120 ? ? ? >120 ?	>120 120 >120 50 >120 120 >120 –	>120 >120 ? ?	>120 >120 >120	? 85 >120 >120 – ? –	>120 >120 >120 – 75 25 10	– 100 >120 80 – >120 – – – 30	? 30 60
pH top soil (*water)	5.1* 5.0 – 5.2* 5.6 5.1 5.4 5.5* 6.4	– 5.5 5.5* 5.4* – 7.0	– – – 5.0 6.3 – – – – – – 6.6 –	7.2* 6.1* – 6.5* 6.4* 5.8* 6.3 –	5.1 6.3 – –	5.3 5.1* 5.1*	– 5.4 6.3 6.4 5.1 – –	4.4 – 5.2 – 5.3 5.1 6.2	– 4.8 4.8 4.9 – 6.0* – – – 5.1	– 5.0 4.8
approximate number of species	28 31 4 16 14 11 5 9 5	11 10 11 8 15 22	1 3* 1 13 9 3* 6 6 6 4 7 9 5	15 10 4 9 15 8 13 5	38 29 13 8	20 20 10	18* 23 36 38 23* 19* 16*	26 17* 25 22* 26 34 34	35* 19 10 36 16* 22 22* 9* 14* 18	13 11 23
altitude (m)	3905 3390 4355 4280 4085 4465 4390 4355 4125	4260 4430 4315 4335 4475 4410	4125 4190 4220 4170 3180 3920 3720 3710 3985 4275 3815 4260 3890	3775 3805 3775 3925 3920 3580 3610 3890	4190 4085 4260 3815	4100 4110 4120	3720 3805 3810 3720 3610 3900 3870	3685 3925 3580 4000 4055 4130 4100	4000 3730 3790 3575 3870 3980 4305 4126 4150 4205	3745 3150 3600
locality	Tota Tota Coc Coc Coc Coc Coc Coc Coc	Coc Coc Coc Coc Coc Coc	Coc Coc Coc Sum Gua Sum Sum Sum Sum Coc Alm Coc Coc	Rus Pi Rus Coc Coc Pi Pi Alm	Coc Coc Coc Alm	Coc Coc Coc	Sum Gua Rus Rus LV Alm Coc	Chis Sum Pi Sum Sum Sum Sum	Sum Pal Pal Pal Coc Coc Coc Coc Coc Coc	Rus Coc Chis
cover %	▽ ▲ O	O ▽	▽ ▲ ▽ ▽ O ▽	O	▲		▲ O	O ▽	▲ ▽ O	O
c/d taxa Carici p. - Wernerietum crassae										
c Werneria crassa ssp. orientalis	50 5 45 90 10 5 20 35								5 4	
c Carex peucophila	5 60	3 10 65 30 30 90					<1		1+? 3 1	
c Calamagrostis planifolia	1 <1 <1+ 1 1	<1 1 1	1?			1				
c Lucilia sp(p.)	<1 1	3 <1 1 1+ 1	<1+					8	15	
Isotachis serrulata	3 <1	<1 100 5 2 1			<1	10 5 <1				
Calamagrostis ligulata	10? 1 <1 <1+	10 1							<1	
Ditrichum gracile	3 <1 <1+	5 5	1							
d taxon wernerietosum crassae										
Pilopogon sp. nov. (5881, 8598)	1 <1 <1+							<1+		
d/o taxa caricetosum p. & var. Campylopus cf. incertus										
d Campylopus cf. incertus		35 70								
Conostomum pentastichum	<1+	<1 1								
Fossombronia sp(p.)		1+ 1								
d/o taxa Oritrophio l. - Wernerietum pygmaeae										
d taxon var. Breutelia lorentzii										
Breutelia lorentzii			40							
d taxon var. Sphagnum cyclophyllum										
Sphagnum cyclophyllum	1 1	20	40 95	40						20 5
d taxon var. Drepanocladus revolvens										
Drepanocladus revolvens	1 5		100 100				3 2	<1+		
d taxon var. Scorpidium scorpidioides										
Scorpidium scorpidioides			100 70 95 35 25	<1 20					5	
d/o taxa cotuletosum minutae										
d Cotula minuta				<1+ 90 75 75 60 90 35 10			<1	<1		
d Carex cf. grandiflora			3	75 30 5 5 5				10		
d Scirpus inundatus			1	<1 2 10						
Ranunculus flagelliformis				70 80						
Eleocharis stenocarpa	<1			1 30 2 80				<1		
Ranunculus nubigena				5 5						
c/d/o taxa Floscaldasio h. - Distichietum m.										
c Distichia muscoides	6				75 85 95 96	30 25 20				
c Floscaldasia hypsophila		5 1+ <1			<1+ <1	<1 <1+			2 25	
d Philonotis sp. (8915)					<1 <1				<1+	
Senecio flos-fragrans var. frigidophilus	1 1				<1	3 15 <1				
Lycopodium crassum s.l.		<1			<1	<1 <1		<1	2	
d Campylopus fulvus						<1+ 2 2				
c/d/o taxa Hyperico l. - Plantaginetum rigidae										
c Plantago rigida	3 30		<1	2 1	<1		97 80 70 90 98 90 75	90 35 75 95 85 40 50	15 10 1	30
d Hypochoeris sessiliflora	2 1 1	1+	<1		<1		<1 1 1+ 1 1 1	1 3 1+ <1 <1	<1+ <1	<1+
d Carex spp. (small) / C. tristicha							1 <1 <1+ <1? <1	3 <1+ <1 <1	<1+	
Eryngium humile	<1						<1+ <1 <1 3	<1		
d/o taxa gentianelletosum nevad.										
d Gentianella nevadensis	1		1 1				<1 1 <1 1+			
d Gentianella corymbosa	1+						1 <1		1+	
d Bidens triplinervia							<1 <1 <1			
d/o Baccharis tricuneata							<1 <1			
Breutelia chrysea							1+ 1			
d/o taxa breutelietosum										
d Chorisodontium speciosum / C. wallisii								15 <1 <1 2 3		
d Geranium confertum					<1+			<1 <1 <1	<1+	
Lysipomia sphagnophila ssp. minor	<1+ 1		<1+		<1+		<1 1+	<1 <1+ <1 <1+ <1 <1+	<1 1 1+	
Herbertus subdentatus			<1					<1 <1+ 25	<1+	
Rhacocarpus purpurascens	25 <1	25	45				<1	1 4 50 15	3 5 1 40 <1	10 5
Werneria humilis var. angustifolia			1				<1+	1? 2 5	1 2 5 <1	
d Oropogon loxensis								1 <1		
d taxa var. Valeriana plantaginea										
Valeriana plantaginea								2 3		
Diplostephium rupestre								<1 1		
Lachemilla nivalis		<1				1		4 <1		
c taxa Oritrophio p. - Oreoboletum obt.										
Oreobolus obtusangulus	10					10 <1	<1	5	70 70 55 35 45 25 50 60 30 10	40 60 40
Oritrophium peruvianum									<1+ 1 20 20 5 <1+ 25	1
d taxa xyridetosum acutifoliae										
d Xyris acutifolia										1 3
d Rhynchospora paramorum										20 20
d Pinguicula elongata										2 1
d Castratella piloselloides										2 <1
d Campylopus richardii										5 3
c/d/o taxa GENTIANO - ORITROPHION										
c Gentiana sedifolia	<1	1+	<1	<1	<1+ <1 <1		<1+ <1+ <1 <1+ <1+ <1+	1 <1+ <1+ <1 1+	<1+ <1+	
c Hypericum lancioides	2 10					1 1	<1 <1 <1 1	1 <1	3 <1 1 2 3 <1 1	<1
d Breutelia allionii	3 35				3 4 3 2		<1+ 1	5 15 12 <1+ <1+ 2	<1 <1 <1 5	1
d Campylopus cavifolius		<1 3		<1		1+ 10 6	2 <1 3 <1	2 <1 1	<1 4 <1 20 2 10	
d Bartsia sp(p.)	<1 <1		1	<1	<1	1 <1	<1+ <1	<1+ <1 <1	<1+ <1 <1 <1 <1	
c Castilleja fissifolia ssp. pygmaea	<1		5	<1	<1 <1 <1		1+ <1+ 2	4	<1+ 1+	<1+
d Pernettya prostrata var. purpurea	<1 5 <1				<1		<1 <1 <1	1 <1+ <1	2 2 <1	
d Calamagrostis effusa	<1				1	10 1 5	1 2		<1+ <1 10 <1	
d Cortaderia sericantha						4 1	2 <1 2		10 3 10	
d Nertera granadensis					<1+		<1 <1 <1+	1 <1+	<1 <1	
Cladia aggregata					<1			1 <1 <1 <1	<1 <1 <1+ <1	1+
c Altensteinia paludosa					1		<1+		<1 <1 10	
c Luzula vulcanica					<1 2			<1+	<1	
c Lycopodium cruentum-complex							3 1		4 1+ <1	
Halenia sp(p.)							<1+ <1+		<1 <1+	<1 <1
Sphagnum cuspidatum							2 <1+ <1		35 1 20	
Pohlia wahlenbergii					<1+					
c taxa order & class										
Werneria pygmaea	1 25	70 10 75 <1	40 90 75 15 25 15 40 1 10 90 25 80 60	1 35 10 85 30 60 95 85	10 15 5 3		1 2 1+	<1 1 <1 1+	<1 3	
Oritrophium limnophilum ssp. mutisianum	2 <1 3 2 10 <1	5 1 1+ 10	5 10 10 60	2	1 3 1+ <1		<1+ <1+ <1 1 <1	<1 <1 <1 <1+	<1+ 10 1 <1	1+
Vesicarex collumanthus			5 5 10		1		2 3	<1+ <1+	<1+	
Calamagrostis coarctata	1		3	<1 10			<1	1+	1+	1
Lachemilla mandoniana		? 30	<1 2 1	<1 1	1 1+ 1		<1 <1+	<1+		
Erigeron paramensis		<1+			1		<1 1			
d/o taxa										
Riccardia spp.	4 <1+ 90 <1 <1 1	<1 5 2 2	1			1 5 12	<1+ 1 <1 <1+	1 <1+ <1+ 3 <1	1+ <1+ <1 1 1 2	
Agrostis breviculmis		20 1 45 <1	10 <1 <1		1 5 1+ 1		3 1 <1 <1	<1 <1+		
Lachemilla spp.	1 1 3 <1	5 1 20 <1			1 <1		<1 <1+ 2	<1 <1 <1 10	1	
Anastrophyllum sp. / A. nigrescens	<1?	20 <1+ <1	5		<1			<1 <1+ <1+	<1 5	
Drepanocladus exannulatus		<1		<1 <1	2 <1		<1			
Peltigera spp.		<1+	<1		1 1		<1 <1+	<1	<1+	
Elatine cf. chilensis			<1 5	<1 <1						
Juncus cyperoides				2 <1 <1 <1			<1 <1 <1	<1		
Calliergonella cuspidata				15 <1			<1+ <1 25 <1			
Muhlenbergia fastigiata	<1			<1		1	<1		1	
Barbula sp. (aquatic blackish sp.)			<1	60			<1			
Fontinalis bogotensis				45						
ALGAE (x present)	70 x 45 10 x x x 100 70	20 x x 70 x x	25 x <1+ <1+ x x x x x 2	3		10	x x <1+	x x 5	<1	40

Alm Páramo del Almorzadero
Chis Páramo de Chisacá
Coc Sierra Nevada del Cocuy
Gua Páramo de Guantiva
LV Páramos NW of Neusa, Laguna Verde

Pal Páramo de Palacio
Pi Páramo de Pisva
Rus Páramo de la Rusia
Sum Páramo de Sumapaz
Tota Páramos near Laguna Tota

c character taxa
d differential taxa
o other taxa

✱✱✱ type of the class
✱✱ type of the order
✱ type of the alliance
▲ type of the association
O type of the subassociation
▽ type of the variant

The average number of species is 15 (1-38) in 66 relevés; the lowest averages occur in the flush communities of the *Wernerion crassae-pygmaeae*, and the highest in the vascular cushion bogs of the *Gentiana-Oritrophion*.

The *Oritrophion-Wernerietalia* comprises all Andean páramo vegetation in flushes and vascular cushion bogs. The "*Wernerion pygmaeae* (prov.)" described by Ruthsatz (1977) from the NW Argentinan Andes must be considered as a geographical vicariant in the southern puna of the Central and north-Andean *Oritrophio-Wernerietalia*.

Synecology: This order concerns flush or seepage areas and cushion bogs of vascular plants in the northern Andean páramos. The communities occur in:

1) small, steep valleys
2) boggy glacial valley floors including former lake floors.

The substrates are sandy-silty to clayey and peaty. The watertable may be higher than 10 cm, level with, or, especially in the dry season, lower than the surface. The pH of the rootzone is 4.4 in cushion bogs and 7.2* in flush vegetation. Mesotrophic conditions (pH 5-6) are common. The thickness of the soil varies from 5 cm to more than 120 cm; on former lake floors (e.g. in rel. 506, 507) more than 5 m has been measured. Generally, hollow communities of the *Wernerion crassae-pygmaeae* preceed in time and space the cushion bogs of the *Gentiano-Oritrophion*. Mosses are important in the formation of cushions, and again when the vitality of the vascular cushions decreases (see *Gentiano-Oritrophion*).

Distribution: This order is present in all Andean páramos from Venezuela to Bolivia, and the area of distribution corresponds to that of *Oritrophium limnophilum*, which is represented by some geographically vicariating subspecies. In the Colombian Cordillera Oriental the *Oritrophio-Wernerietalia* is found from the upper forest line to the superpáramo between 3400 and 4430 m. This vegetation was also observed in the Colombian Cordillera Central between 3300 and 4500 m, in the Sierra Nevada de S. Marta between 3750 m and 4500 m and in the Sierra Nevada de Mérida, Venezuela, between 3500 and 4400 m (Vareschi 1980, Cleef unpubl.). Communities belonging to this order were reported from Ecuadorian páramos between 3700 and 4700 m (Diels 1934, Benoist 1935, Øllgaard & Balslev 1979) and from the Peruvian Andes (Weberbauer 1911, Tovar Serpa 1973, Gutte 1980)

Phytogeographic comments:
Character species of the *Oritrophio-Wernerietalia* show local and regional endism at the generic, specific and infraspecific levels. According to Cuatrecasas (1969 and in litt.) the morphologically variable *Oritrophium limnophilum* is present with the ssp. *nevadensis* in the Venezuelan Sierra Nevada de Mérida and in the Colombian Sierra Nevada de S. Marta. Subspecies *mutisianum* is found in the other Colombian and in the Ecuadorian páramos extending south into norhern Peru. From northern Peru to northern Bolivia the ssp. *limnophilum* and the ssp. *punae* (only Peru) are present.
Plantago rigida probably has about the same distribution as the last species and is also found in puna bogs (Tovar Serpa 1973, Gutte 1980).
Distichia muscoides does not reach Venezuelan páramos; its NE limit is the Tamá depression between the Sierra Nevada de Mérida and the Colombian Cordillera Oriental.
Vesicarex collumanthus occurs in the Colombian and Venezuelan high páramos.
Floscaldasia hypsophila, according to Cuatrecasas (1979) is only known from the Cordillera Central (Quindio, S. Rosa, Ruíz) and the Cordillera Oriental (Sierra Nevada del Cocuy) of Colombia.

Werneria crassa is found with ssp. *crassa* in the Colombian Cordillera Central and in Ecuadorian páramos, and with ssp. *orientalis* in the Cordillera Oriental of Colombia (Quatrecasas 1980).
Erigeron paramensis is endemic to the northern páramos of the Colombian Cordillera Oriental and in the Venezuelan Sierra Nevada de Mérida.
Gentiana sedifolia according to Pringle (1979), is found from Costa Rica and Colombia towards southern Peru.
Hypochoeris sessiliflora is known from the northern Andes from Venezuela to Peru and from Costa Rica.
Hypsela reniformis (Campan.) is characteristic for the southern communities of this order.

WERNERION CRASSAE-PYGMAEAE all. nov.
type: *Oritrophio limnophili-Wernerietum pygmaeae* (this study); table 13

Physiognomy: This alliance concerns mainly low herbaceous-bryophytic flush vegetation. Small, about 5-40 cm high sedged and grasses participate in forming an open low field layer. Superpáramo flush may locally lead to a bryophytic-sedge peat, up to 50 cm thick.

Composition & syntaxonomy: Character species are *Werneria crassa* ssp. *orientalis* (excl.), *Carex peucophila* (pref.?), *Calamagrostis planifolia* (sel.), *Lucilia pusilla* (pref.), *Cotula minuta* (sel.), *Werneria pygmaea* (transgr.) and *Oritrophium limnophilum* (transgr.) Aquatic bryophytes may be-dominant, such as *Isotachis serrulata, Riccardia* sp., *Drepanocladus revolvens, Scorpidium scorpioides, Sphagnum cyclophyllum.*
The average number of species is 8 (1-31) in 36 relevés.
The abundance and higher cover of *Werneria pygmaea* (transgr. character species) in the *Wernerion crassae-pygmaeae* are differential against the *Gentiano-Oritrophion.* In addition, the low average number of species (8 in 36 relevés) of the *Wernerion crassae-pygmaeae* contrasts with the higher average (22 in 31 relevés) in the *Gentiano-Oritrophion. Werneria crassa* ssp. *orientalis* and *Carex peucophila* are character species at high altitudes. The endemic *Werneria crassa* spp. *orientalis* replaces *Werneria pygmaeae* on barren mineral soil in the superpáramo flush of the Sierra Nevada del Cocuy. *Oritrophium limnophilum* has a higher cover in these communities than in the cushion bogs *(Gentiano-Oritrophion)*.

Synecology: The alliance concerns minerotrafent páramo flush vegetation with a pioneer character in moist valleys with continuously flowing water. Habitats on damp soil and in hollows of vascular cushion bogs in valley floors and on former lake floors.
Different kinds of substrates are present, depending on elevation and habitat, e.g. sand, silt, clay and peat. Peat or gyttja occur in lacustric cushion bogs. The thickness of the substrate is 5 cm in superpáramo habitats and more than 120 cm in peat. Rootzone pH is 5.0-6.6 (7.0-7.2 of the water). This causes a mesotrafent to eutrafent páramo flush vegetation. Most superpáramo habitats are mesotrophic, those in the lower páramos are eutrophic. Succession towards cushion bogs of the *Gentiano-Oritrophion* may begin with flush vegetation of the *Wernerion crassae-pygmaeae*.
The grass páramo stands belonging to the last alliance may be fringed with bluish cushion grass meadows of *Muhlenbergia* spp., covering damp soil in the transition towards a dry vegetation (see 108). In the highest located flush, at about 4400 m, a sedge-moss turf may locally be developed.

Distribution: The *Wernerion crassae-pygmaeae* is found in the páramos of the Colombian Cordillera Oriental from the upper forest line at 3400 m up to the superpáramo at 4425 m. The alliance was also studied in the páramos of the Sierra Nevada de Mérida, Venezuela, the Sierra Nevada de S. Marta, and the Colombian Cordillera Central. Details are listed under associations and subassociations. *Werneria crassa* is restricted to Ecuadorian and Colombian paramos.

61. *Carici peucophilae-Wernerietum crassae* ass. nov. (prov.)
type: rel. 319; table 13; Fig. 54, 55 & 59

Physiognomy: The *Carici-Wernerietum crassae* concerns mainly superpáramo flush vegetation; swamps of small low sedges and thin peat of sedges and mosses, which are successional to flush vegetation. The following strata can be distinguished:
1) an open graminoid field layer with 10% cover,
2) a low sedge layer up to 10-15 cm high, covering up to 90%, and
3) a low open geophytic or bryophytic peat layer, up to 40 cm thick.

Composition & syntaxonomy: Exclusive character species are *Werneria crassa* ssp. *orientalis* and *Carex peucophila* (syn. *C. pinetorum* Willd.; Dr. W.M. Weber, in litt.).
Werneria crassa is a compact geophytic composite, endemic to the high North Andean páramos of Colombia and Ecuador. Its subspecies *crassa* in the Colombian Cordillera Central forms genuine cushion bogs (Cleef et al. in press). The population in the Colombian Estern Cordillera Oriental were recently distinguished by Cuatrecasas (1980) as the subspecies *orientalis*, which is fairly common in the high páramos of the Sierra Nevada del Cocuy (4000-4400 m). Populations were also found in lower area, in bogs and marshes in the Páramo del Almorzadero at 3850 m and at 3400 m in the Páramo de La Sarna, north of Lake Tota.
Carex peucophila, on the other hand, is a polymorphic species previously known from high locations in Mexico and Guatamala (Hermann 1974).
The average number of species in this association is 14 (4-31) in 15 relevés. The *Carici-Wernerietum crassae* is distinguished from the *Oritrophio-Wernerietum pygnaeae* by the two character species (*Carex peucphila*, *Werneria crassa* ssp. *orientalis*) and some differential species: e.g. *Isotachis serrulata*, *Ditrichum gracile* and scarce *Calamagrostis ligulata*. *Wermeria crassa* ssp. *orientalis* mainly replaces *W. pygmaea* in superpáramo flush over mineral soil with an extremely low humus content. *Werneria pygmaea* is most prominent in the *caricetosum peucophilae*, which occurs on peat or peat-containing soil. The floristic subdivision into two subassociations reflects ecological as well as succesional differences.

Synecology: The stands occur in dry or marshy young moraine valleys in the superpáramo of the Sierra Nevada del Cocuy. The flush consists of a thin sheet of cold slowly flowing water containing filamentous algae and thallous liverworts. The compact rosettes of *Werneria crassa* ssp. *orientalis* with darkish-green leaves and with bright white rayflowers remain just above the waterlevel. Vascular plants and bryophytes may cover up to 100%. Near the upper vegetation line, the number of species and the cover are considerably less due to harsh environmental conditions.
The thickness of the clayey and sandy substrate under the flush vegetation varies from 5 to 100 cm. The slope may be as steep as 12°. Humus content of the upper soil layer, nearly absent in flush, becomes more prominent under the low sedge-vegetation, which is mostly developed op peaty clay or fine

sand. The dense moss layer gradually prevents a proper drainage. Together with the cushion bogs of the *Floscaldasio-Distichietum* this turf belongs to the highest located bogs in the Colombian páramos. The pH is 5.0-5.6.

Distribution: The association is described from the high areas on the SW side of the Sierra Nevada del Cocuy. Relevés are located in the upper grass páramo at 4125 m and the superpáramo up to 4425 m. *Werneria crassa* vegetation was studied locally in lower places (3400-3850 m) between Lake Tota and the Páramo del Almorzadero. The *Caraci-Wernerietum crassae* is re estricted to the Colombian Cordillera Oriental (depts. Boyacá, Arauca, Santander).

61[a]. Subass. *wernerietosum crassae* subass. nov. prov.
type: rel. 319; table 13; Fig. 59
lit.: Cleef 1978

Physiognomy: The superpáramo flush vegetation of this association is dominated by geophytes and hemicryptophytes. Thallous liverworts are predominant in the ground layer in aquatic habitats. Peat is hardly or not present.

Composition & syntaxonomy: *Werneria crassa* ssp. *orientalis*, *Pilopogon* sp. nov. (5881, 8598), *Senecio flos-fragrans* var. *frigidophilus* are differential species. *Riccardia* is predominant in aquatic stands; *Ditrichum gracile* on humid soil. *Oritrophium limnophilum* ssp. *mutisianum* is present with tall fleshy broad-leaved rosettes, which are typical of high altitudes in the Sierra Nevada del Cocuy.
The average number of species is 9 (4-16) in 7 superpáramo relevés; the lowermost stands contain 28-31 species. This subassociation comprises all superpáramo flush communities with *Werneria crossa* ssp. *orientalis*, including some isolated patches in lower places of the variant of *Lysipomia sphagnophila* ssp. *minor* (61[aa]). *Werneria crassa* ssp. *orientalis* is absent in rel. 320, but this stand is included here, as it has a similar floristic composition and occurs at a similar site. Rel. 316 and 335 might represent a variant of *Carex peucophila*.

Synecology: The superpáramo flush of the *wernerietosum crassae* occurs in wet or humid valleys in young moraine areas, which have been ice-free during the last 200 years (Van der Hammen et al. 1981). Soils are clayey or sandy; and about 100 cm thick. The pH is 5.1-5.6 in the upper rootzone.

Distribution: The *wernerietosum crassae* is restricted to the northern páramos of the Colombian Cordillera Oriental, where it is mainly found in the superpáramo of the Sierra Nevada del Cocuy between 4125 and 4415 m. Stands are scarce near the lower limit of the grass páramo (3400 m).

61[aa]. Variant of *Lysipomia sphagnophilla* ssp. *minor* var. nov.
type: rel. 382; table 13

Physiognomy: This type of flush vegetation of the lower páramo contains many low herbaceous species (cover 60-90%), including scarce bunchgrasses, the culms of which are 100 cm high. The moss layer is about 10 cm thick, and the cover is 25-50%.

Composition & syntaxonomy: The vegetation of this variant is rich in species. Differential taxa are *Sphagnum cyclophyllum*, *Drepanocladus revolvens*,

Calliergon stramineum, Lysipomia sphagnophila ssp. *minor (= L. obliqua Wimmer), Hypochoeris sessiflora* (white rayflowers), *Plantago rigida, Breutelia allionii, Hypericum lancioides, Festuca* cf. *dolichophylla, Xyris acutifolia, Diplostephium revolutum, Sphagnum sancto-josephense, Leptoscyphus cleefii* and a reddish species of *Odontoschisma*.
There is a strong floristic and ecologic affinity with *Sphagnum* bogs and cushion bogs *(Hyperico-Plantaginetum)*, which are in contact with each other at this altitude.

The presence of *Werneria crassa* ssp. *orientalis* in the lower pāramo is another example of a superpāramo taxon occuring in a lower zone in bogs, reedswamps, mires and flush vegetation. See also under the *Marchatio-Epilobietalia*.

Synecology: Slowly drained boggy valleys with peaty clay (pH about 5.0). The phreatic table is near surface.
Small frogs (e.g. *Atelopus ebenoides marinkellei*; det. Dr. P.M. Ruīz-C., Bogotā) and black leeches are common.

Distribution: Flush vegetation of this variant was studied in the Pāramo de la Sarna, N of Lake Tota in the subpāramo-grass pāramo border at 3400 m. Another stand was observed at 3900 m in the Pāramo del Almorzadero.

61^{b}. Subass. *caricetosum peucophilae* subass. nov. (prov.)
type: rel. 314; table 13; Fig. 54, 55

Physiognomy: This subassociation concerns peaty depressions in the superpāramo with a mat of liverworts or moss peat. Small low vascular species of a geophytic nature cover 40-100%. The graminoid field layer is inconspicuous

Composition & syntaxonomy: *Carex peucophila* and bryophytes, mainly *Isotachis serrulata* and *Campylopus* cf. *incertus* (8593), are prominent. The endemic *Floscaldasia hypsophila* (Comp.) is a common differential species.
The average numbers of species is 12 (8-22) in 6 relevés.
Differential against the *wernerietosum crassae* are the presence and high cover of *Carex peucophila* in combination with the absence of *Werneria crassa* ssp. *orientalis*. On peaty substrate the latter is replaced by *Werneria pygmaea*.

Synecology: The vegetation concerns peaty valleys in young superpāramo moraine areas, adjacent to *wernerietosum crassae*. In the upper part of the sloping flat valley floors,a local vegetation of low sedges and bryophytes is developed into a thickness up to 40 cm *Campylopus* peat on mineral soil; pH of the water perculating in the peat 5.4-7.0. The substrates are peaty sand and clay, in places covered with mossturf.

Distribution: The *caricetosum peucophilae* is only known from the superpāramo of the Sierra Nevada del Cocuy, between 4250 and 4425 m.

61^{bb}. Variant of *Campylopus* aff. *incertus* var. nov. (prov.)
type: rel. 321; table 13

Physiognomy: The vegetation of this variant concerns superpāramo moss turf with geophytes. Small sedges may cover up to 90% (see for comparison Vareschi 1980, Fig. 130).

Composition & syntaxonomy: Differential species are *Campylopus* aff. *incertus* (8593), *Fossombronia* sp. (8587) and Bartramiaceae viz. *Philonotis* sp., *Conostomum pentastichum*. *Floscaldasia hypsophila* and *Lachemilla mandoniana* are present in both relevés.
The number of species is 15 and 22 in the two relevés.
The variant can be easily recognized by the differential species and the presence of moss turf.

Synecology: Patches, up to 40 cm thick, of mossy peat on mineral soil in the upper end of moist superpáramo valleys. The pH of the water in rel. 320 was 7.0. This kind of peat, probably is palynologically most revealing for the last 100-200 years. Together with vascular cushions of *Distichia muscoides* the patches represent the highest located páramo bogs.

Distribution: This vegetation is only found at high altitude in the superpáramo of the Sierra Nevada del Cocuy, between 4400 and 4425 m in the Páramo Cóncavo. Bogs of similar nature and under similar ecological conditions, but with a different composition, were studied in the Venezuelan Sierra Nevada de Mérida at 4125 m and 4400 m (Vareschi 1980), in the Parque Los Nevados in the Colombian Cordillera Central at 4400 m (Cleef et al., in press).

62. *Oritrophio limnophilae-Wernerietum pygmaeae* ass. nov.
type: rel. 39; table 13;
Fig.: see under subassociations and variants

Physiognomy: This bryophytic and low herbaceous flush vegetation is characterized by weak stratification viz. in lowermost moss layer (5 cm thick) and a herbaceous upper layer up to 15 cm. Herb cover is generally more than 50% and is highest in the *cotuletosum*. Average moss cover in the last subassociation is only 20% but reaches 75% in the subassociation *typicum*.

Composition & syntaxonomy: The character species *Werneria pygmaea* (transgr.) is present in each relevé, and has high cover (average 45% in 20 relevés). This is differential against all other syntaxa of the class.
Several species of hydrophytic mosses are prominent, and one of the following aquatic species may be dominant: *Scorpidium scorpioides*, *Sphagnum cyclophyllum*, *Drepanocladus revolvens*, and in some places *Fontinalis bogotensis*. Liverworts are nearly absent. Tiny herbs are *Cotula minuta*, *Carex* cf. *grandiflora*, *Ranunculus flagelliformis*, *R. nubigenus*, *Lachemilla mandoniana*, *Elatine chilensis*, *Juncus cyperoides*, *Eleocharis stenocarpa*, *Scirpus (Isolepis) inundatus* and *Vesicarex collumanthus*. The average numver of species is 7 (1-15) an is slightly higher in the *cotuletosum* than in the subass. *typicum*. *Cotula minuta* is a differential species, and is found optimally in the *cotuletosum*. *Elatine* cf. *chilensis* and *Eleocharis stenocarpa* are companions in this association. The latter species may be locally replaced , e.g. by *Ranunculus fkagelliformis* (a local facies). The present subdivision of the association is based on the presence of *Cotula minuta* together with other small herbaceous species as *Carex* cf. *grandiflora*,*Ranunculus* spp., *Vesicarex collumanus*, *Agrostis breviculmus*, *Juncus cyperoides*, *Eleocharis stenocarpa*.

Synecology: The habitat of the *Oritrophio-Wernerietum pygmaeae* is found in boggy depressions, rills, hollows of vascular cushion bogs, drainage areas in páramo mire and bogs, and in small sloping valleys with stagnant or

almost permanently slowly running water.
Slopes are up to 7°. Substrates are clayey to peaty. The highest proportion of the peaty componentis generally found in lower areas in the flush habitats. The pH of the rootzone in 9 relevés indicates eutrophic conditions, with values from 6.1 to 6.6 (5.0-7.2). Soil thickness is 40 cm to more than 120 cm. Thick peat and gyttja are present on former lake floors (rel. 506, 507). Most of the soils are black (clayey to peaty) in the upper part, passing downward into a grayish clayey layer, with a gravelly base on (sandstone) bedrock or moraine sediments. Some small cushions of *Plantago rigida* were found in the *Oritrophio-Wernerietum pygmaeae*. They initiate the succession towards the vascular cushionbog of the *Hyperico-Plantaginetum rigidae*.
Hirudinae and *Gammarus* sp. are common. Some frogs have been observed.. *Sylvilagus*, *Cavia* and cattle are frequent in the stands in the lower páramos.

Distribution: In the Colombian Cordillera Oriental this association is found from the upper forestline up into the superpáramo at 4425 m. It is most common in the grass páramo and upper subpáramo. The *Oritrophio-Wernerietum pygmaeae* is widely distributed in the high tropical Andes. Unfortunately, very few data are available on its phytosociological characteristics in other regions.

62[a]. Subass. *typicum* subass. nov.
type: rel. 346; table 13; (Fig. 42; see also under variants)

Physiognomy: This low bryophytic and herbaceous vegetation is mostly found in shallow and slowly running water. Most herbs grow as helophytes, the mosses remain submerged.

Composition & syntaxonomy: The character species of the order, *Werneria pygmaea*, *Oritrophium limnophilum* ssp. *mutisii* and *Vesicarex collumanthus* are prominently present in this subassociation. Aquatic moss species are e.g. *Sphagnum cyclophyllum*, *Drepanocladus revolvens* and *Scorpidium scorpioides*.
The average number of species is 6 (1-9) in 13 relevés.
The subassociation *typicum* can be readily distinguished by the conspicuous (aquatic) moss cover, which is differential against the *cotuletosum*. In addition, the absence of *Cotula minuta* and the lower number of species, average 6 versus 10 in the *cotuletosum*, are differential. The subassociation is subdivided into 5 variants, which are based on the composition of the moss cover. This community is ranked at the variant level and not regarded as a local facies, since field observations revealed that it is a feature of general occurrence. On the strength of our observations and of herbarium data, a variant of *Drepanocladus exannulatus* is distinguished as a hollow community in the *Floscaldasio-Distichietum* between 3800 m (Puracé) and 4250 m (S. Nevada del Cocuy).

Synecology: Flush vegetation in the high páramo usually with runoff water. Four mossy variants can be distinguished on the basis of specific - mostly edaphic - habitat factors.
One of these is the hollow phase in cushion bogs of the *Hyperico-Plantaginetum rigidae* on former lake floors. Mosses are absent in superpáramo stands on silty to gravelly clay on the dry side of the mountains. The pH of the clayey to peaty upper part of the soil is 5.0-6.6. The slopes are up to 7°.

Distribution: The subassociation *typicum* of the *Oritrophio-Wernerietum pygmaeae* is common throughout the high páramos of the Colombian Cordillera Oriental between 3700 and 4425 m, and has also been studied in the Cordillera Central and the Sierra Nevada de S. Marta, where it is found at the same heights. Some relevés between 4050 and 4150 m from the Sierra Nevada de Mérida, Venezuela, contained a not yet described variant of cf. *Calliergonella cuspidata* (differential species), while *Vesicarex collumanthus* was found with a higher cover (up to 70%). The subassociation *typicum* is expected to be widely distributed in the high tropical Andes

62[aa]. Variant *typicum* var. nov. (prov.)
type: rel. 450; table 13; Fig. 54
photo: Cleef 1978, photo 173

Physiognomy: See subassociation *typicum*.

Composition & syntaxonomy: This type of flush community is poor in species (1-3 species in each relevé). *Werneria pygmaea* and fleshy broadleaved rosettes of *Oritrophium limnophilum* ssp. *mutisianum* (fma., e.g. 8582), are common. Algae may be present, but bryophytes are virtually absent.
This high altitude variant is characterized by the absence of differential species (against other communities of the *Oritrophio-Wernerietum pygmaeae)*.

Synecology: These superpáramo flush communities are found in young moraine valleys on a thin clayey to silty or sandy to gravelly substrate The habitat is rather unstable as a result of intermittent deposition of sediments. The stands are common at the edge and in hollows of the cushionbogs of the *Floscaldasio-Distichietum*.

Distribution: This vegetation type has only been studied in the Sierra Nevada del Cocuy, from the highest places in the upper grass páramo up into the superpáramo between 4200 and 4425 m. The variant was found also in the superpáramo of the Colombian Cordillera Central.

62[ab]. Variant of *Breutelia lorentzii* var. nov. (prov.)
type: rel. 289; table 13

The differential species *Breutelia lorentzii* and *Rhacocarpus purpurascens* cover almost entirely the surface. *Ourisia muscosa, Breutelia lorentzii* and *Brachiolejeunea securifolia* are common here and elsewhere in the upper condensation zone of the Nevado de Sumapaz. A sequence of clayey and sandy layers with a clayey top is present, covering a presumably former lake sediment. Small patches of this variant were only observed in the upper reaches of the Nevado de Sumapaz.

62[ac]. Var. of *Sphagnum cyclophyllum* var. nov.
type: rel. 39; table 13; Fig. 56 (also Fig. 75)

Physiognomy: Similar as the subass. *typicum*.

Composition & syntaxonomy: *Sphagnum cyclophyllum*, a holarctic species has a cover of 40-95%, and is differential against the other variants.
The shallow, slowly flowing water contains also *Isoetes novo-granadensis* and spherical blue algae.

Synecology: This type of grass páramo flush vegetation is found on thin clayey soils (pH 6.3 in rel. 39).

Distribution: This variant was studied in the highest areas of the bamboo páramos only in the Páramo de Guantiva and the Páramo de Sumapaz between 3800 and 3900 m.

62^{ad}. Variant of *Drepanocladus revolvens* var. nov.
type: rel. 506; table 13; Fig. 57

Physiogromy & syntaxonomy: *Werneria pygmaea* or dark greenish rosettes of *Oritrophium limnophilum* ssp. *mutisianum* are the most conspicuous vascular plants, covering about 50%. An almost continuous carpet of *Drepanocladus revolvens*, a moss species common in temperate bogs, is found under the rosettes. *Drepanocladus revolvens* is the differential species.

Synecology: The variant of *Drepanocladus revolvens* is found in hollows in vascular cushion bogs of the *Hyperico-Plantaginetum rigidae* covering former glacial lake floors. The soil is thick and consists of *Plantago rigida* peat, at least in the upper part.

Distribution: The variant is only known from former glacial lake floors on the Andabobos watershed at 3725 m, in the humid Páramo de Sumapaz.

62^{ae}. Variant of *Scorpidium scorpioides* var. nov.
type: rel. 346; tabel 13

Physiognomy & syntaxonomy: This variant concerns flush communities with a high cover of *Werneria pygmaea* and *Scorpidium scorpioides* (25-100%; average 65% in 5 relevés). *Scorpidium turfaceum* Herzog from the Bolivian high Andes is considered as a synonym of the cool, wide temperate *Scorpidium scorpioides*. *Vesicarex collumanthus* is a common associated species. For further physiognomical data, see the subassociation and association.
Differential against other syntaxa of the association is the conspicuous moss carpet of *Scorpidium scorpioides*. Flush vegetation (rel. 570), reported by Aguirre et al. (in press) from the Páramo del Almorzadero at 3900 m with *Eleocharis stenocarpa* (100% cover), *Scorpidium scorpioides* (80% cover) and lax plants of *Colobanthus quitensis* (less than 1% cover) probably also belong to this variant.

Synecology: The flush communities of this variant are present in wet high páramo valleys (slopes up to 5°). One pH of 6.6 was measured in the yellowish-brown clayey to peaty rootzone in rel. 346. In the dry period the stand may temporarily dry out. This variant is present also in the hollows of *Distichia* cushion bogs.

Distribution: The variant was recorded from all high grass páramos of the Colombian Cordillera Oriental between 3800 and 4275 m, and just reaches the lower limit of the superpáramo

62^{b}. Subass. *cotuletosum minutae* subass. nov.
type: rel. 186; table 13; Fig. 70 (also Fig. 12, 13)

Physiognomy: The páramo flush vegetation of the *cotuletosum*, is dominated by low herbaceous species, either rosette plants or sedges, up to 15 (25) cm high. The herbs have a cover of about (80) 95-100%, whereas the moss cover is generally less than 50%.

Composition , phytogeographical notes & syntaxonomy: *Cotula minuta* is a differential species in all relevés,together with *Isolepis inundatus*,*Carex* cf. *grandiflora* and *Juncus cyperoides*. *Eleocharis stenocarpa* and *Ranunculus flagelliformis* most likely represent differential facies,but this remains to be proved. *Cotula minuta* is widely distributed from Mexico, northern Argentina and Chile, and has been collected in Colombia between 2700 and 4000 m. It is a differential species for the *Marchantio-Epilobietalia* of which *Ranunculus flagelliformis* is a widely distributed character species in cool tropical America (Lourteig 1956).*Isolepis (Scirpus) inundatus* is a widely distributed temperate species. *Eleocharis stenocarpa* is restricted to the northern tropical Andes from Venezuela to Ecuador,from the warm tropical interandean valleys at 600 m up to 4000 m.*Juncus cyperoides* occurs from Central Chile to the Colombian Andes. (Balslev 1979),in the Páramo del Almorzadero reaching its northernmost location known at present.
The number of species is 10 (4-14) in 8 relevés.

Cotula minuta is locally replaced by *Carex* cf. *grandiflora* sp. (7365), which may be dominant. This small sedge species also occurs in the *Hyperico-Plantaginetum rigidae*. The local high cover of *Eleocharis stenocarpa* represents a facies.

Synecology: Peaty meadows of the *cotuletosum* are present on glacial valley floors with eutrophic flush on brownish-black clayey peat, mostly thicker than 1 m. At the base it passes into a blue-grayish clayey layer, generally overlaying the bedrock. The pH of the water is 5.8-6.5 (-7.2). The watertable is mostly near surface. The slopes are up to 3^{o}.

Distribution: The *cotuletosum* has only been studied and observed between 3500 and 3925 m in the lower grass páramo in the northern part of the Colombian Cordillera Oriental. The highest records are from the dry side of the mountains bordering the deep and dry inter-andean Rio Chicamocha valley.

GENTIANO - ORITROPHION all. nov. (prov.)
type: *Hyperico lancioides - Plantaginetum rigidae* (this study); tablé 13

Physiognomy: The páramo cushion bogs are mainly dominated by low chaemaephytes.Cushion plants are species of Juncaceae, Cyperaceae and Plantaginaceae Bryophytes may cover a considerable part of the cushion; ofther vascular elements (dwarfshrub, grasses and low herbs) have a moderate cover.

Composition & syntaxonomy: Character species are *Castilleja fissifolia* ssp. *pygmaea* (excl.), *Gentiana sedifolia* (sel.), *Altensteinia paludosa* (sel.), *Lycopodium "cruentum-attenuatum* complex" (sel.) *Calliergon sarmentosum* (sel.) and those of the corresponding associations. Differential against the *Wernerion crassae-pygmaeae* are *Breutelia allionii*, *Campylopus cavifolius*, *Hypericum lancioides*, *Bartsia* sp(p.), *Nertera granadensis*, *Pernettya prostata*, *Calamagrostis effusa* and *Cortaderia cf. sericantha*.
The average number of species is rather high, about 22 (8 - 38 in 31 relevés) against 8 (in 36 relevés) for the *Oritrophio-Wernerion*.

The alliance is well defined by several character and differential species. *Werneria pygmaea* and *Oritrophium limnophilum* have a low cover and are not abundant. The more stable *Gentiano-Oritrophion* has a higher average number of species than the more unstable *Wernerion crassae-pygmaeae* due to extreme environmental conditions. The differential species for this alliance also occur in the zonal páramo vegetation, most of them in the boggy *Swallenochloa tesselata* - bamboo páramo. Further subdivision is based on floristic differences and altitude.

Synecology: This alliance concerns moist valleys and former filled up glacial lakes that have been in the páramo belt. Some cushions also are floating on lakes, others are found on damp slopes, at the edge of bogs and swamps in the zone transitional with the zonal páramo vegetation, and in the upper condensation zone. Cushions are soligenous and ombrogenous, the latter occur in the highest places of deep bogs completely depending on atmospherical humudity (fog, precipitation).Substrates are thick clayey peat or gyttja, but cushions are also found on sloping clayey soils or on barren gravelly or coarse to sandy glacial deposits. Slopes are up to 8°. The páramo cushion bogs are generally mesotrophic (pH 5 - 6). The *Oritrophio-Oreoboletum* is typical for oligotrophic conditions (pH 4.8 - 5.1).

Distribution: The *Gentiano-Oritrophion* is found between the subpáramo (3150 m) and the lower superpáramo (4350 m) of the Colombian Cordillera Oriental. The alliance is also known from the Sierra Nevada de Mérida, Venezuela, and from the Colombian Cordillera Occidental (*Hyperico-Plantaginetum rigidae* only) and the Colombian Cordillera Central (*Floscaldasio-Distichietum*, *Hyperico-Plantaginetum rigidae*). Details are presented under associations. The alliance seems to be absent in the Costa Rican páramos. Its southernmost occurrence is in the Peruvian and the Bolivian Andes.

Phytogeographical and physiognomical relationship
As pointed out before (Cleef 1978), the páramo cushion bogs floristically and physiognomically have a distinct austral-antarctic affinity. The páramos of the Colombian Cordillera Oriental are the northernmost American mountain areas containing all three described associations. As stated by Balslev (1977, 1979), *Distichia tolimensis* is a synonym of *D. muscoides* and the main region of distribution of this genus is the Bolivian Andes, also containing the endemic *D. filamentosa*.
Plantago rigida according to Rahn (1978) belongs to the southern hemisphere section *Oliganthos* of *Plantago* subg. *Plantago*. From Ecuadorian páramos and southward there is another cushion-forming species of this section, *Plantago tubulosa* Dcne., in high Andean bogs and on damp soil; however, this species does not become predominant.
Oreobolus cushion bogs are widely distributed in the temperate southern hemisphere and in pacific tropical high mountains (Godley 1978). *Oreobolus obtusangulus* bogs were only reported from southern S. America, the Islas Malvinas and Masafuera, and the páramos of the Colombian and the Ecuadorian Cordillera Oriental.

63. *Floscaldasio - Distichietum muscoides* ass. nov.
type: rel. 355; table 13; Fig. 58 (also Fig. 28, 32, 55)
lit.: Cleef 1978, Gutte 1980
photo: Cleef 1978, photo 171-173; photo 172 shows the type locality

Physiognomy: The vegetation consists of high páramo juncaceous cushion bogs dominated by low chamaephytes. Most of the associated vascular plants are low herbaceous species; the pale graminoid fieldlayer is up to 10 cm high. Patches of mosses up to 30 cm thick may cover the greater part of the decaying *Distichia* cushions.

Composition & syntaxonomy: *Distichia muscoides* is a regional exclusive character species from Northern Argentina and Chile to Colombia. The endemic *Floscaldasia hypsophila* is a regional selective character species, as it is restricted to the high páramos of the Sierra Nevada del Cocuy and the high Ruiz-S. Isabel volcanoes in the Colombian Central. *Lachemilla mandoniana* is a characteristic constituent with high frequency in *Distichia* bogs. *Lachemilla* sp. and *L. nivalis* are locally common. The *Floscaldasio-Distichietum* is defined by both its character species mentioned above in combination with character species of the *Gentiano-Oritrophion* and the *Oritrophio-Wernerietalia*.
The number of species is considerably variable and is highest on the humid side of the mountains. Low values are generally recorded for 1) young and firm cushions, 2) stands on the dry side of the mountains and 3) near the uppermost location of the cushion bogs. The average number of species is 20 (8 - 38 in 4 relevés).
In stands in the atmospherically rather dry páramos of both the Cordillera Central and Oriental of Colombia the average number of species is about 10. The *Distichia* bogs at Patio Bolos, Sierra Nevada del Cocuy contain some species that are lacking in other kinds of cushion bogs, e.g. *Campylopus subjugorum, C. aerodictyon, C. heterostachyus* and *Philonotis sp.* (8915). Shrub of *Senecio flos-fragrans var. frigidophilus* is locally present on the decayed hummocks.

Synecology: The *Floscaldasio-Distichietum* comprises the highest located cushion bog of vascular plants in the Colombian páramos. The cushions occur in moist valleys and may cover former lake areas. Slopes are up to 7° and the peaty substrate under the uppermost cushions is thin to more than 300 cm. A cyclic sequence of peaty (mainly remains of *Distichia*) and clayey layers is common in the boggy superpáramo valleys. Gravelly deposits are overlain by clayey sediments passing into peat when the water falls. These phenomena may partly be correlated with major climatic changes. Peat in the *Floscaldasio-Distichietum* bogs is mesotrophic with a pH of 5.1 - 6.3 in the upper layer. The *Distichia* hummocks on the humid side of the mountains are sooner decaying than those on the dry side, as indicated by mosses. Additional synecological data were presented earlier (Cleef 1978).

Distribution: This association has been studied between 3800 and 4300 m in the upper grass páramo and lower superpáramo of the northern part of the Colombian Cordillera Oriental. *Distichia* cushions are common her in the high grass páramo and were reported from the Sierra Nevada del Cocuy and adjacent western and southwestern páramos, the Páramo del Almorzadero, and from the páramos de S. Urbán and Vegas about 7° N, which seems the northernmost location of *Distichia muscoides* cushion bog in America. During more than 3 months fieldwork in the northern and central part of the Páramo de Sumapaz *Distichia* cushions have not been observed. They are also absent in the páramos of the Sierra Nevada de S. Marta an the Sierra Nevada de Mérida, Venuzuela, and were never reported from the Colombian Cordillera Occidental and Costa Rica. In the Colombian Cordillera Central the *Floscaldasio-Distichietum* has been studied between 3800 and 4500 m (Cleef et al, in press). According to Balslev (1979), *Distichia muscoides* occurs in the Ecuadorian páramos between 3600 and 4700 m. The southern boundary of this páramo association coincides with that of a combination of different character species, which may extend as far as the Ecuadorian or the northern Peruvian high Andes.

64. Community of *Distichia muscoides* with *Cortaderia sericantha* and *Campylopus cf fulvus*.
table 13; Fig. 59, 60
photo: Cuatrecasas 1958: plate XXII-2; idem 1968: fig. 8.

Physiognomy: These are probably floating cushions of vascular plants on a partly filled-up glacial lake in the upper bunchgrass páramo. Characteristic large grass tussocks with a cover of 5 - 15%. The graminoid fieldlayer contains also sparse composite dwarfshrub (40-130 cm) with a cover of 15%. The bryophyte layer is about 3-5 cm thick and covers 10 - 25%.

Composition & syntaxonomy: The community contains some species, that are scarce to absent in the *Floscaldasio-Distichietum*, e.g. *Cortaderia sericantha*, *Isotachis serrulata*, *Campylopus cavifolius*, *Calamagrostis effusa*, *Pseudocephalozia quadriloba*, and the rare *Symphyogyna digitisquama* (Van der Gronde 1980).
The average number of species is 16 (10-20) in 3 relevés. The community has not yet been assigned to a syntaxonomical rank, because it was only observed in one locality and character species of the order and some of the alliance are absent, e.g. *Breutelia allionii*. This vegetation type is more or less intermediate between the *Hyperico-Plantaginetum rigidae* and the *Oritrophio-Oreoboletum*, but its position may also be close to the *Floscaldasio-Distichietum*.

Synecology: This community has only been studied in one former glacial lake, in a location lower than that of the *Floscaldasio-Distichietum*. The *Distichia* cushions may be in root-contact with the lake bottom gyttja. They are most conspicuous where the cushions are fused. When *Distichia* dies off, algae, *Riccardia* sp. (8745) and *Floscaldasia hypsophila* appear, later followed by *Bartsia* sp., *Hypericum lanciodes*, *Campylopus cavifolius*, *Senecio flos-fragrans* var. *frigidophilus* and species of *Cladonia* subg. *Cenomyce*. In open water *Werneria crassa* ssp. *orientalis* is found between the cushions together with purplish *cf. Microspora*, *Isotachis serrulata* and some *Ditrichum sumersum*. *Oreobolus obtusangulus* hummocks locally replace *Distichia* cushions and may have a cover of 25%. The moss *Calliergon trifarium* and the liverworts *Pseudocephalozia quadriloba* and *Cephalozia dussii* are common on the wet *Oreobolus* hummocks. The pH of the water is 5.1 - 5.4.

Distribution: This community is only known from the Bocatoma valley at 4100 m in the Sierra Nevada del Cocuy. It was studied there in a nearly filled--up former glacial lake between lateral moraines covered by open *Calamagrostis effusa* grassland characteristic for the upper bunchgrass páramo.
Note: González et al. 1965 published a pollendiagram for Lake Bocatoma (VL IX, plate 7).

65. *Hyperico lancioides - Plantaginetum rigidae* ass. nov.
type: rel. 410; table 13; Fig.: see under subassociations
photo: Cleef 1978, photo 167-170 (photo 167 shows the type locality)
lit.: Cleef 1978; Gutte 1980; Cleef et al., in press

Physiognomy: These are grass páramo bogs of firm, young cushions associated with only a few other species, e.g. *Isoetes andina*. Smalle geophytes are common, e.g. *Altensteinia paludosa, Hypochoeris sessiliflora, Werneria pygmaea, W. humilis* var. *angustifolia, Eryngium humile, Geranium confertum, Isoetes andina*. Many other herbaceous species including grasses are present as well. In addition, sparse dwarfshrubs, e.g. *Hypericum lancioides* (up to 30 cm high), bryophytes and lichens are present in greater numbers on older, less vital and decaying cushions.

Note: The *Plantago rigida* plants flower in the dry season, from november - march.

Composition & syntaxonomy: *Plantago rigida* is an exclusive character species. Regional character species at least for the Colombian Cordillera Oriental are *Gentianella nevadensis* (select.), *Lysipomia sphagnophila* (pref.) and *Isoetes andina* (pref.). Differential species are *Geranium confertum, Hypochoeris sessiliflora* (both with white and yellow ligulae), *Carex tristicha* with some other still unidentified tiny sedges (e.g. 2584, 7365), *Juncus cyperoides, Eryngium humile, Chorisodontium speciosum, C. wallisii, Bidens triplinervia, Baccharis tricuneata, Halenia* sp. (7505). *Luzula vulcanica, Lachemilla hispidula (?), Drepanocladus revolvens, Hookeriopsis* sp. (4414), *Campylium chrysophyllum* (rare) and *Breutelia tomentosa* may occur in the altitudinally lowermost stands.
The average number of species is 25 (18-38) in 14 relevés. Actually this will be slightly higher, because, in 6 relevés the cryptogamic inventory was incomplete.

This association is best characterized by presence and dominance of its only exclusive character species *Plantago rigida* This association is distributed throughout the large northern tropical Andean distribution area of its character species. In the páramos of the Colombian Cordillera Oriental, two subassociations can be distinguished, one of which mainly on the dry side of the mountains, this subassociation has also been studied in the Venezuelan páramos of the Sierra Nevada de Mérida. The other subassociation prefers the humid and wet side of the mountains and is supposed to extend far south as Chachapoyas, Norhern Peru, on the Amazonian side of the high Andes. This subdivision not only reflects differences in floristics, cover and even succession between both subassociations, but also climatological differences.
Cushion bogs of limited size with firm hummocks occur on the dry side of the mountains (*gentianelletosum*), more and larger stands of the *breutelietosum* on the humid side, where *Plantago* cushions were found varying from vital to decaying. The *Plantago rigida* cushions in the wet páramos are probably highly sensative to decay. The firm cushions of the *gentianelletosum* in the climatologically dry páramos seem to be very persistent. The process of decay is not yet known, but other vascular species may play there in.
Recent fieldwork in the páramos on the volcanoes S. Isabel and Ruiz in the Colombian Cordillera Central indicated the presence of another not yet described subassociation of the *Hyperico-Plantaginetum rigidae*, characterized by tall tufts of grasses (*Festuca* sp., *Agrostis* sp.) and by herbaceous species as *Niphogeton lingula, Lupinus* sp., *Gentianella dasyantha* etc. (Cleef et al. in press).

In the southern *Plantago rigida* cushion bogs in Peru and Bolivia, additional new syntaxa can be expected. Relevés from there, as recently published by Gutte (1980) may provide more information on the phytosociological position of the *Plantago rigida* cushion bogs and their ecology.

Synecology: In the visited páramos of the Cordillera Oriental cushion bogs of the *Hyperico-Plantaginetum rigidae* occur: 1) in small and sloping boggy valleys; 2) on the boggy floor of U-shaped glacial valleys; 3) in bogs on former lake-floors; 4) floating on deep glacial lakes, and 5) in the lower superpáramo, if the upper condensation zone is well developed.
The slopes are up to 10°, the thickness of the peaty to clayey or gyttja sediments under the *Plantago rigida* cushions is about 10 cm (in soligenous superpáramo stands and more than 5 m in former lake-floors. Reduction-oxydation colours are common in profiles of soligenous bogs. The pH immediately under the cushions is 4.4-6.4, indicating mesotrophic conditions. Exceptional eutrophic values (pH 6.2-6.4) were measured in a soligenous bog on coarse sandy to gravelly calcareous substrates on the Nevado de Sumapaz (rel. 275), and in the Páramo de la Rusia (rel. 254, 263). For additional synecological data see Cleef (1978).

Distribution: According to the authors listed by Cleef (1978), *Plantago rigida* cushion bogs occur in the tropical high Andes from Bolivia to the Sierra Nevada de Mérida, Venezuela, between 3000 and 5200 m. In the Colombian páramos they are found between 3400 and 4280 m, but optimally developed between 3800 m and 4100 m. From the Colombian Cordillera Occidental there is only one report of *Plantago rigida*. Pennell collected it (10.579-US) on Cerro Tatamá between 3400 m and 3700 m. *Plantago rigida* cushion bog seem to be scarce in the Sierra Nevada de S. Marta, where it seems to be replaced by an *Azorella crenata* cushion bog (rel. 531), at least on the humid NW. side of the mountain.

65[a]. Subass. *gentianelletosum nevadensis* subass. nov.
type: rel. 410; table 13; Fig. 61 (also Fig. 12, 72)
photo: Cleef 1978, photo 167 shows the type locality

Physiognomy: These are bunchgrass páramo cushion bogs. Low herb species are common, bryophytes rather scarce.

Composition & syntaxonomy: Differential species are *Gentianella nevadensis* and *G. corymbosa*, *Baccharis tricuneata* var., *Bidens triplinervia* var., *Breutelia chrysea*, *Halenia* sp.(9771, 7505) and *Cortaderia* cf. *sericantha*. As a rule there are more herbaceous species and less bryophytic and lichen species than in the *breutelietosum*; in addition, the average number of species is slightly lower.
Gentianella species are the most constant differential taxa. *G. nevadensis* is only known from the grass páramos N of Bogotá and from the Venezuelan Sierra Nevada de Mérida. *G. corymbosa* is widely distributed in the Colombian and Ecuadorian páramos. The presence of *Gentianella* spp. (and also of other differential species), the high cover of the compact *Plantago rigida* cushions, and the absence of hygrophytic bryophytes and of lichens are characteristics of this subassociation.
Rel. 505, and the rings of floating *Plantago rigida* cushions described from the Páramo de Sumapaz (Cleef 1978) are provisionally ranked under the *gentianelletosum*. More data are needed, but these stands may represent a new syntaxon within the *Hyperico-Plantaginetum rigidae*.

The cushion bog of rel. 263 was not homogenous, as it included some elements from adjacent humid zonal and azonal vegetations.

Synecology: This subassociation occurs in gently sloping (up to 8^{o}) boggy valleys or on former lake-floors, most in the bunchgrass páramo. The substrate is generally peaty clay, 80 cm thick in soligenous stands to more than 120 cm above lake sediments. The pH in the rootzone is 5.1-6.4. The peaty clay (pH 5.4) of the soligenous bog (rel. 410) overlies a 20 cm thick compact sandy layer (pH 5.8) with root (or stem) fragments on red sandstone. The young compact *Plantago rigida* hummocks hardly permit establishment of seedlings. It may take years before the cushions begin to decay. *Eryngium humile* indicates frequent grazing cattle.

Distribution: The *gentianelletosum nevadensis* was studied most intensively in the bunchgrass páramo on the dry side of the mountains between 3600 and 3900 m, mainly in the western part of the Colombian Cordillera Oriental. Up to nearly 4200 m, stands were observed in the headwaters of Rio Lagunillas (Boquerón de Chusque) in the Sierra Nevada del Cocuy. The subassociation is also present between 4050 and 4150 m in the Sierra Nevada de Mérida, Venezuela.

65^{b}. Subass. *breutelietosum* subass. nov.
type: rel. 282; table 13; Fig. 57, 62, 63 (also Fig. 42, 70)
photo: Cleef 1978, photo 168

Physiognomy: This subassociation comprises bamboo páramo cushion bogs with bryophytes (mosses become predominant).

Composition & syntaxonomy: Differential species are *Chorisodontium speciosum* (common), *C. wallisii* (rare), *Herbertus subdentatus* (large form), *Rhacocarpus purpurascens*, *Cladia aggregata* (with inflated podetia), *Oropogon loxensis*, *Breutelia allionii*, *Anastrophyllum nigrescens*, *A. leucostomum*, *Geranium confertum*, *Werneria humilis* ssp. *angustifolia*, and those reported under the variant with *Valeriana plantaginea*.
The average number of species is higher than in the *gentianelletosum*. subassociation contains twice as many cryptogamic species as the *gentianelletosum*. The *breutelietosum* is floristically well defined and differs from the *gentianelletosum* by numerous differential species. The lower cover of *Plantago rigida* and simultaneously the higher cover of bryophytes are diagnostic characteristics also. The average cover of *Plantago rigida* is about 65%.

Synecology: Cushion bogs of the *breutelietosum* carry a number of hygrophytic taxa that are sustained by permanent humidity and fog. Most of these are bryophytes listed under "composition". They start to grow on the *Plantago rigida* cushions, or on the interstices, e.g. *Breutelia allionii*. This moss species may partly or completely cover the decayed *Plantago rigida* cushions, as observed in several locations between 3800 and 4000 m in the Páramo de Sumapaz. As a result of diminishing vitality the *Plantago rigida* cushions in the upper bamboo-páramo may die-off within about 10 years. The substrates are clayey peat or gyttja, and vary from shallow soligenous peat (rel. 275) to thick gyttja on former lake-floors (rel. 55, 111, 263^{A}). The pH under the *Plantago* cushions is 5.1-5.5 (-6.2). Slopes are 5^{o}-10^{o}.

Distribution: The subassociation has only been found on the humid side of the mountains in the bamboo páramos between 3600 and 4150 m. Particularly well developed are the stands in the Páramo de Sumapaz. Locally this vegetation type reaches into the lower superpáramo of the Nevado de Sumapaz e.g. with the variant of *Valeriana plantáginea*.

65bb. variant of *Valeriana plantaginea* var. nov.
type: rel. 275; table 13

Physiognomy & synecology: *Plantago rigida* cushions in the high páramos with a cover of about 50%, are mainly thriving on atmosperical humidity and to a less or degree on édaphical water. Bryophytes are conspicuous just as the large rosettes of *Valeriana plantaginea, Senecio niveo-aureus* and *Lachemilla nivalis*, which are about 30 cm high and have a cover of less than 10%. Most of the associated vascular species are geophytes.
Soils on calcareous bedrock are thin and clayey or gravelly. Frost heaving and successive solifluction are common at these heights and strongly affect the vegetation.

Composition & syntaxonomy: Differential species are mainly hygrophytic high páramo and superpáramo taxa, most of them characteristic for the humid side of the Cordillera, e.g. *Valeriana plantaginea*. Plants of this species belong to the superpáramo populations and generally grow on outcrops and screes in the Colombian Cordillera Oriental. Other differential species are *Lycopodium crassum, Lysipomia sphagnophila* ssp. *minor* (var. *cocuyensis* var. in ed.), *Cetraria islandica* var. *pseudo-islandica, Thamnolia vermicularis, Senecio niveo-aureus, Draba* sp. (1310, white petals) , *Draba* sp. (1300, yellow petals), *Ourisia muscosa, Plagiochila cuatrecasasii*. In addition may be mentioned: *Oropogon loxensis, Anastrophyllum* spp., *Lophocolea* sp., *Metzgeria* sp., *Siphula* spp.,*Riccardia* sp., *Anaplolejeunea conferta, Werneria humilis* var. *angustifolia* and *Azorella multifida, Didymodon laevigatus, Morinia ehrenbergiana*.
The vegetation is to be considered as an upper condensation zone variant of the *Hyperico-Plantaginetum rigidae breuteliètosum*. It is floristically well defined by a dozen differential species, mainly hygrophytic taxa from the high páramo, including the superpáramo.

Distribution: This variant is only known from the summit area of the Nevado de Sumapaz, 4100-4150 m. It can, however, also be expected on the Amazonian slope of the high Andes between 4100 and 4300 m, in the Colombian Cordillera Central and in Ecuador.

Note: The lichen *Oropogon loxensis* is also a common bark epiphyte of the timberline forest, in páramo thickets and dwarfforests. In the Páramo de Sumapaz this lichen species is common on top of *Plantago rigida* cushions, and retains much water from fog.

66. *Oritrophio peruvianae - Oreoboletum obtusanguli* ass. nov.
type: rel. 147; table 13; Fig. 64
photo: Cleef 1978, photo 174-176; Photo 175 shows the type locality
lit.: Cleef 1978, Godley 1978, Oberdorfer 1960, Roivainen 1954, Villagrán M. 1980

Physiognomy: This association comprises cyperaceous páramo cushion bog. Mosses may cover more than half of the cushions, but are nearly absent on young hummocks. In wet stands on peat in lower areas, *Sphagnum cuspidatum* and algae are characteristic in water-loaded depressions. Conspicuous rosettes of *Oritrophium peruvianum* up to 15 cm may have a cover of 25%.

Composition & syntaxonomy:: *Oreobolus obtusangulus* forms the páramo *Oreobolus* cushion bogs reported earlier (Cleef 1978). It develops into compact hummocks. *Oritrophium peruvianum* is a selective character species, distributed in the páramos from Venezüela to northern Peru (Cuatrecasas 1969 and in litt.). The average number of species is 20 (9-36) in 12 relevés. The *Oritrophio-Oreboletum* mainly differs by its two character species *Oreobolus obtusangulus* and *Oritrophium peruvianum* from the other associations of the *Gentiano-Oritrophion*. Character species of order and class are poorly represented and are nearly absent in the *xyridetosum*. The paramo *Oreobolus* cushion bogs *(Oritrophio-Oreoboletum)* are ranked under the *Gentiano-Oritrophion*. Alliance character species are scarce, but differential species are well represented. Ecologically the *Oritrophio-Oreoboletum* belongs undoubtedly to the páramo cushion bog alliance. In addition, *Oreobolus obtusangulus* was observed in succession with the *Hyperico-Plantaginetum rigidae* and with the *Floscaldasio-Distichietum*. Magellanic *Oreobolus obtusangulus* cushion bogs studied in southern Chile by Oberdorfer (1960) were placed in the *Astelio-Oreobolion* Oberd. *(Myrteolo-Sohagnetea* Oberd.). The páramo cushion bogs of the *Oritrophio-Oreoboletum (Wernerietea)* are altitudinally vicariant with the páramo *Sphagnum* bogs (with *Myrteola oxycoccoides)* in lower locations, which belong to a not yet described class.

Synecology: Páramo cushion bogs in wet depressions, in moist valleys and also on small former lake-floors. Soligenous *Oreobolus* cushions frequently occur on the sides of small moist valleys containing *Sphagnum* bogs, cushion bogs *(Gentiano-Oritrophion)*, flush-communities *(Wernerion crassae-pygmaeae)*, dense *Espeletia* stands and grass mires *(Calamagrostion ligulatae)*. They also occur on washed-out humid glacial sand at the basis of terminal moraines between grass páramo and superpáramo (Cleef 1978; photo 174).
The thickness and nature of the soils vary considerably. They are humic clayey to coarse sandy, and consist of clayey peat in valley bogs or of gyttja in filled-up lakes. The pH in the rootzone under soligenous cushions is 4.9-5.1. The *Oritrophio-Oreoboletum* is oligotrafent to mesotrafent. The slopes are up to 7°, as an exception 15°.

Distribution: Phytosociological relevés of the *Oritrophio-Oreoboletum* have only been collected in the páramos of the Colombian Cordillera Oriental, where *Oreobolus obtusangulus* cushion bog occurs from the subpáramo at 3150 m up into the lowermost superpáramo, at 4400 m. The association has not been obeserved in other páramos, but herbarium vouchers (COL, US) indicate that compact rigid *Oreobolus obtusangulus* cushions must be present in the southern part of the Colombian Cordillera Central (Macizo Colombiano, Cumbal) and in Ecuadorian páramos. For the last areas this is supported by lists of collections and descriptions of sites of Ecuadorian páramo cushion bogs by Øllgaard & Balslev (1979) and Øllgaard (in litt.).

Note: The zonal lower páramos of the Colombian Cordillera Oriental also contain small, more lax tufts of *Oreobolus obtusangulus*, with conspicuous reddish sheets. These belong to the ssp. *rubrovaginatus* described by Koyama (1969) from the summit area of Serra Neblina (Brasil).

66^{a}. Subass. *typicum* subass. nov.
type: rel. 147; table 13; Fig. 64
photo: Cleef 1978, photo 174-176; photo 175 (bog in the background shows the type locality).

Physiognomy: Cyperaceous cushion bog dominated by low chamaephytes; low rosette plants, rale dwarfshrub and mosses may be present as well.

Composition: Different against the *xyridetosum* are mostly the species that together are also differential for the alliance. They include *Altensteinia paludosa*, *Breutelia* spp., *Campylopus cavifolius*, *Bartsia* sp., *Nertera granadensis*, *Pernettya prostrata*, *Sphagnum cuspidatum*, *Riccardia* sp. and *Cortaderia sericantha*. The richness in species is similar as in the association.
The réleves available do not justify a subdivision as made for the *Hyperico-Plantaginetum rigidae* (viz. in a unit poor in species representing firm cushions, and a mossy cushion vegetation rich in species). Presence of the variant of *Rhacocarpus purpurascens* is determined by this moss species and/or *Werneria humilis* var. *angustifolia* (var. ined.)

Synecology: See association.

Distribution: The subass. *typicum* is distributed throughout the Colombian Cordillera Oriéntal and was studied from the lower grass páramo at 3575 m up into the lower superpáramo at 4400 m. This vegetation type extends as far as the high páramos in the southern part of the Colombian Cordillera Central and the Ecuadorian Cordillera Oriental.

66^{aa}. Variant of *Rhacocarpus purpurascens* var. nov.
type: rel. 152; table 13; Fig. 64
photo: Cleef 1978, photo 176

Physiognomy: Cyperaceous cushion bogs (see under association).

Composition & syntaxonomy: Differential species are the endemic cushion chamaephyte *Werneria humilis* var. *angustifolia* (var. ined.) and the moss *Rhacocarpus purpurascens*, (both hygrophytic). *Werneria humilis* only grows in the southern páramos (Sumapaz, Cruz Verde, Palacio) of the Colombian Cordillera Oriental but the species extends as far as the Ecuadorian páramos. *Rhacocarpus purpurascens* has a (wide) tropical-high montane and subantactic distribution. The number of species varies from 10 to 36 in 4 relevés depending on the age of the cyperaceous cushions.

Synecology: The variant occurs on small former lake-floors, on the edge of *Sphagnum* bog and on gently sloping peaty ground with *Hyperico-Plantaginetum rigidae*. The pH in the upper peat layer is 4.8-4.9 reflecting rather oligotrophic conditions.

Distribution: The variant is only known from the southern bamboo páramos (3575-4000 m) of the Colombian Cordillera Oriéntal, but is expected to extend to other humid grass páramos of the northern Andes.

66b. Subass. *xyridetosum* subass. nov.
type: rel. 134; table 13

Physiognomy: These are cyperaceous cushion bogs with a number of low herbaceous rosette species and dark green-blackish mosses.

Composition & syntaxonomy: Differential species are *Castratella piloselloides, Campylopus richardii* and *Rhynchospora paramorum,* which are characteristic elements for zonal grass páramo vegetation; further also *Pinguicula elongata* and *Xyris acutifolia.* The number of species is 11 and 23 in the two relevés.
Differential species and differences in habitat distinguish the two subassociations of the *Oritrophio-Oreoboletum.* The *xyridetosum* is intermediate between the *Gentiano-Oritrophion* and the *Xyris* bog communities. Floristics and physiognomy, e.g. mainly the presence and the dominance of *Oreobolus* cushion bog, determine the present assignment to the *Gentiano-Oritrophion.*

Synecology: The vegetation forms small wet boggy patches in depressions in the zonal lower páramos. The peaty to clayey soils are rather acid (pH 4.8-5.0) in the top layer and have a gravelly base. The stands are found on slopes (3°-15°).

Distribution: This vegetation was only seen in the Páramo de Sumapaz and the Sierra Nevada del Cocuy between 3150 an 3630 m.

SPHAGNUM BOGS

Sphagnum bogs are common in the lower part of the pāramo belt and the upper part of the Andean forest belt. In the study area they are located between 2800 and 3800 m on the humid as well as on the dry side of the Cordillera (Fig. 86). Towards higher altitudes they are gradually replaced by cushion bogs, made up of vascular plants, e.g. the *Hyperico - Plantaginetum rigidae* (63), the *Oritrophio - Oreoboletum* (66) and the *Floscaldasio - Distichietum* (63), belonging to the *Gentiano - Oritrophion (Oritrophio - Wernerietalia)*. *Sphagnum* bogs are floristically distinctly different from vascular cushion bogs, and they belong to another class, treated in a forthcoming paper.

Sphagnum magellanicum and *S. sancto-josephense* are most common characteristic species, that make up the pāramo *Sphagnum* bogs. Other *Sphagnum* species are *S. cuspidatum, S. oxyphyllum, S. subsecundum, S. recurvum*, and *S. compactum*. *Sphagnum cyclophyllum*, however, is common in the *Oritrophio - Wernerietalia*. Characteristic bryophytes in the *Sphagnum* bogs include also *Riccardia* spp., *Campylopus cucullatifolius, Leptodontium wallisii, Breutelia* spp., *Lepidozia* spp. (e.g. *L. auriculata, L. macrocolea, L. wallisii), Kurzia verrucosa, Adelanthus lindenbergianus, Anastrophyllum leucostomum, A. nigrescens, Leptoscyphus cleefii* and *Cephalozia dussii*. *Cladia aggregata* and species of *Cladonia* subg. *Cladina* are common lichens. The taxonomy and ecology of rendeer mosses in the Colombian pāramos was treated by Sipman & Cleef (1979), who reported *Cladonia boliviana* (strain I), *C. colombiana* (strain I), *C. confusa* and *C. polia* as true *Sphagnum* bog species. Frequently associated plants, also common in zonal pāramo communities, are *Calamagrostis effusa, Swallenochloa tesselata, Pernettya prostrata, Vaccinium floribundum* var. *ramosissimum, Rhynchospora macrochaeta, Hypericum lancioides, Oreobolus obtusangulus, Xyris acutifolia, Carex pinchinchensis, Blechnum loxense* and *Halenia* spp. Rare are *Rhynchospora ruiziana, Hypericum graciliforme* and *Xyris subulata*. *Pernettya prostrata* is present with var. *purpurea; Festuca* cf. *dolichophylla* tussocks are less frequently associated species. *Blechum loxense* is a characteristic dwarf treefern and is one of the highest located species of the austral-antarctic section *Lomaria* This fern species is common on peaty soil in the lower boggy pāramos (3000-3700 m) from southern Ecuador to Venezuela and Costa Rica.

Pāramo *Sphagnum* bogs are generally about 1 to 4 m thick. The upper peatlayer is moderately acid (pH 4.6-5.3). A hummock-hollow relief described from other cool and temperate *Sphagnum* bogs is reported here for all types of bogs. Lozano & Schnetter (1976, Fig. 2) illustrated this for *Puya goudotiana - Sphagnum* bogs at 3400 m in the Pāramo de Cruz Verde near Bogotá. Some other examples are presented in this study.
All characteristic species are not always present in each phytocoenosis but from wet hollow to dry hummock the following species are respectively represented: *Sphagnum cuspidatum, S. sancto-josephense* and *S. magellanicum*. The last species also takes the same hummock position in the European *Oxycocco - Sphagnetea* Br.-Bl. et R.Tx. 1943 and the magellanic *Myrteolo - Sphagnetea* Oberd. 1960. In paramo *Sphagnum* bogs the presence or absence of *Swallenochloa* bamboo clumps is decisive for the type of hollow-hummock sequence. A number of typically *Swallenochloa*-associated bryophyte species determine the composition and shape of the hummocks in the bamboo-*Sphagnum* bogs (Fig. 67). *Swallenochloa* clumps are frequently associated with *Sphagnum magellanicum*, or in drier places with *Breutelia chrysea*. *Lepidozia auriculata* and/or *Leptodontium wallisii* are characteristic for well-developed bamboo hummocks, together with *Chorisodontium* spp. and *Sphaerophorus melanocarpus*. Other hummock taxa are *Campylopus pittieri, Atractylocarpus longisetus*, grasses (*Calamagrostis effusa, C. planifolia, Festuca* cf. *dolichophylla*), *Disterigma empetrifolium, Vaccinium floribundum* var. *ramosissimum* and species of *Cladonia* subg. *Cenomyce*. In the hollows occur

Sphagnum cuspidatum, *S. recurvum*, *S. sancto-josephense*, *Riccardia* spp. (e.g. 9396), *Carex pichinchensis*, *Anastrophyllum nigrescens*, *Isoetes boyacensis*, *Cladonia colombiana*, etc. Intermediate between hummock and hollow (at the edge of the hummocks), e.g. *Breutelia* sp., *Carex bonplandii*, *Xyris acutifolia*, *Glossodium aversum*, *Blechnum loxense*, *Gongylanthus innovans* and *Sphagnum oxyphyllum* are found.

About the succession in páramo *Sphagnum* bogs relatively little is known at present. In addition to pollendiagrams in a number of studies interpreted by Van der Hammen and coworkers, only Weber (1958) and Lozano & Schnetter (1976) deal with this subject. Weber (l.c.) reported from old, relatively dry hummocks of *Sphagnum* in Costa Rican páramo bogs *Gentiana sedifolia*, *Elaphoglossum latifolium* Sw., *Arcytophyllum lavarum* Schum. and *Rubus* cf. *eriocarpus* Liebm. Lozano & Schnetter (l.c.) described and illustrated four different stages, from *Puya goudotiana* - *Sphagnum* bog to a climax thicket with *Diplostephium revolutum*, from the Páramo de Cruz Verde at 3400 m near Bogotá. This sequence is as follows. A huge *Sphagnum magellanicum* hummock is first colonized by *Calamagrostis effusa*, *Carex bonplandii*, *Valeriana longifolia* and *Myrteola oxycoccoides*. In the meantime most *Sphagnum magellanicum* dies off, while *Myrteola oxycoccoides* covers the hummock. Next, a dwarfshrub of *Aragoa abietina*, *Eupatorium (Ageratina) gynoxoides* and *Diplostephium phylicoides* appears with *Geranium multiceps* in the herbaceous understorey. Another stage (which might be successional to the previous one) is the development of *Diplostephium revolutum* shrub on old dead *Sphagnum magellanicum* hummocks with the bamboo *Aulonemia trianae* and *Senecio garcia-barrigae*. The hollows contain, according to Lozano & Schnetter (l.c.), *Sphagnum capillaceum*, which probably might be identical with *S. sancto-josephense* or *S. cuspidatum*, which are frequent species of hollows in the bog vegetation of this páramo. *Blechnum loxense* was mostly found on young low reddish hummocks of *Sphagnum magellanicum*.
In addition to *Diplostephium revolutum* climax bush (71) other shrub communities are found on *Sphagnum* bogs: e.g. the *Aragoetum abietinae* (72) and, locally, *Senecio flos-fragrans* or *Baccharis revoluta* shrub. Also dense *Espeletia* stands are frequently found and they are dominated by one of the following geographically vicariant species: *Espeletia grandiflora*, *E. miradorensis*, *E. chocontana*, *E. arbalaezii*, *E. murilloi*, *E. incana*, *E. nemenkenii*, *E. lopezii* and *E. rositae* var. *monocephala*.
The *Aragoetum abietinae* develops in *Xyris acutifolia* - *Sphagnum* bogs in the páramos between Neusa and S. Cayetano (Cundinamarca). There, at 3660 m, decaying *Sphagnum magellanicum* appeared to be overgrown by *Riccardia* sp. (6226^a) and *Cephaloziella* cf. *fragillima* (6226) and to a lesser extent by *Lepidozia* sp. (6223). In a next stage, prostrate dwarfshrub of *Vaccinium floribundum* var. *ramosissimum* becomes settled and together with *Riccardia* it may have a cover of about 50%. The died off small trunks of *Blechnum loxense* are covered with *Cladonia andesita* and *C. hypoxantoides*. The succession terminates with the appearance of *Aragoa abietina* dwarfshrub containing *Pleurozium schreberi*, *Hypnum amabile*, *Bryum billardieri*, and *Geranium sibbaldioides*.

Apparently these *Sphagnum* bogs are mainly of two ages. Radiocarbon dating of several of them indicated about 2800-3000 yrs B.P. and about 5000 yrs B.P. for the various samples. These ages are corroborated by a number of pollendiagrams for the Páramo de Palacio (Van der Hammen & Gonzalez 1960), the Ciénaga del Visitador, Páramo de Guantiva (Van der Hammen & González 1965), the Sierra Nevada del Cocuy (González et al. 1965, Van der Hammen et al. 1981) and the Laguna Gobernador, Páramo de Sumapaz (G.B.A. van Reenen, in prep.).

In lower bamboo páramos the *Sphagnum* bog is also distributed on the hillsides, where they give way to slope bogs (Fig. 79). The gradual transition to zonal slope vegetation (e.g. comm. 10: community of *Swallenochloa* with *Sphagnum* and/or *Breutelia*) is basically not much different from the *Sphagnum* bogs. All páramo *Sphagnum* bog communities in the study area will be treated in a syntaxonomic study to be published in future. With the exception of shrubby climax vegetation, four main types of *Sphagnum* bogs (67-70) can be distinguished in the páramos of the Colombian Cordillera Oriental. *Sphagnum* spp. have an average cover of about 50% in the following communities, except in the first one.

67. *Sphagnum* bog with *Espeletia* and *Blechnum loxense*
68. *Sphagnum* bog with *Swallenochloa*
69. *Sphagnum* bog with giant *Puya*
70. *Xyris-Sphagnum* bog.

The *Aragoetum abietinae* and (part of the) *Diplostephietum revoluti* are shrubby climax communities, which may develop on *Sphagnum* bogs in the study area. They will be treated presently together with other azonal páramo shrub-communities.

67. *Sphagnum* bog with *Espeletia* and *Blechnum loxense*

Fig. 65; photo: Van der Hammen 1973, Fig. 2.

Small patches on gently sloping (1-5°) wet valley floors in the upper Andean forest or shrubpáramo carrying a dense, low (tree) fern brake with stemrosettes of *Espeletia*. *Blechnum loxense* grows in dense clumps up to 100 cm high and with a cover of 50-75%.

Espeletia killipii var. *killipii* and *E. nemenkenii* are common geographically vicariant species in this kind of habitat. Large eriocaulaceous rosettes are common also e.g. *Paepalanthus* cf. *crassicaulis* and *P. alpinus*. Dwarfshrub of *Baccharis revoluta*, *Hypericum graciliformis* and *Swallenochloa* clumps may cover most of the fieldlayer. The *Sphagnum* cover is much lower than in other types of *Sphagnum* bog, due to shade.

The black peaty to clayey soils are thick and waterlogged. The upper layer is moderately acid (pH 4.9-5.5). The Aoo-layer is well developed (up to 5 cm thick) and consists mainly of litter of Cyperaceae, Gramineae and *Blechnum loxense*. This bog type is becoming very rare, as a result of agricultural activities following drainage through ditches. The endemic *Espeletia nemenkenii* and *E. killipii* var. *killipii* must be considered as endangered species.

68. *Sphagnum* bog with *Swallenochloa*

Fig. 66 & 67; photo: Gradstein et al. 1977, plate 1D.

Dense bamboo - *Sphagnum* bogs are present in the upper part of the Andean cloud forest belt and go up to 3600 m in the lower grass páramo. The depressions filled with peat bog are rather deep and characterized by *Swallenochloa tesselata* and various species of *Sphagnum*, each of which with a cover of 30-90%. Also present are *Breutelia* spp. (cover up to 15%) and *Campylopus cucullatifolius* (cover up to 5%). The cover of species of *Espeletia* is usually low. Some taxa of other *Sphagnum* bogs are absent, e.g. species of *Rhynchospora*, *Hypericum*, *Xyris*, *Cladonia* subg. *Cladina*, *Oreobolus obtusangulus* and *Blechnum loxense*. The bogs, which were studied between the Sumapaz and the Cocuy, are mostly large and level, and are mainly located on the outer wet slopes of the Cordillera, on which bamboo páramos are found.

The upper part of the wet peat layer is moderately to weakly acid (pH 5.1-6.1).

69. *Sphagnum* bog with giant *Puya*

This kind of *Sphagnum* bog is easily recognized by the giant rosettes of *Puya goudotiana* or locally *P. aristiguietae* with large columnar inflorescences of about 3-5 m. The diameter of these prickly rosettes is 1-2 m and their height is up to 1-1.5 m. After flowering the rosettes die off but it takes a long time before they decay to litter (Fig. 68). The large rosettes provide shelter to frogs, e.g. *Hyla*. Small Anurae are common in páramo *Sphagnum* bogs and in the

boggy bamboo vegetation, but scarce to absent in vascular cushionbogs in higher areas.
Puya goudotiana, according to Smith & Downs (1974), is widely distributed in the humid lower pâramos of the Colombian Cordillera Oriental between 2800 and 3500 m. *Puya aristeguietae* is described from Venezuelan pâramos, but is now known to extend into Colombia, where its south-western limit was found on the dry side of the Sierra Nevada del Cocuy between 3500 and 3770 m. *Puya hamata* L.B. Smith, is the giant species characteristic in *Sphagnum* bogs in the pâramos of southern Columbia and northern Ecuador.
Geranium multiceps of *G. subnudicaule* with their characteristic leathery, microphyllous, crenate leaves are associated species but they are virtually absent in other *Sphagnum* bogs. Geographically vicariant species of *Espeletia* with stemrosettes, e.g. *Espeletia lopezii*, *E. oswaldiana* (forma), *E. murilloi* (? lev. 393) and *E. grandiflora* may be associated. Other common and characteristic species are *Rhynchospora macrochaeta*, *Hypericum lancioides*, *Oreobolus obtusangulus*, *Campylopus cucullatifolius*, *Breutelia* spp., *Blechnum loxense*, *Carex pichinchensis*, *Arcytophyllum muticum*, *Vaccinium floribundum* var. *ramosissimum*, *Pernettya prostrata*, *Cladonia boliviana* and *Disterigma empetrifolium*. Species of *Xyris* and *Halenia* are not common.

This type of bog is common in the bamboo pâramos between 2800 and 3770 m, where it covers wet valley floors, but also occurs on the gentle slopes of the surrounding hill-sides (up to 5°(-10°)).
The soil is a black clayey peat, in most places thicker than 120 cm. The top layer of the peat is strongly to moderately acid (pH 4.2-5.2 (5.7)).

69[a]. *Sphagnum* bog with *Swallenochloa* and *Puya goudotiana*

Fig. 68 (also Fig. 69)
photos: Cuatrecasas 1934, Lam. 32, fig. 1; Cuatrecasas 1958, plate 17; Lozano & Schnetter 1976, fig. 1 & 2.

Sphagnum bog with *Puya goudotiana* are common in the lower bamboo pâramos and in the upper Andean cloud forest in the Colombian Cordillera Oriental. In addition to the species mentioned above for giant *Puya sphagnum* bogs, these bogs contain the following species: *Swallenochloa tesselata*, *Senecio subruncinnatus*, *Bartsia* sp., *Breutelia allionii*, *Campylopus cucullatifolius*, *Lepidozia* sp., *Kurzia verrucosa*, *Cladonia andesita*, *Lycopodium cruentum* and *Cladonia boliviana*. Species of *Halenia* are absent. *Pseudocephalozia quadrifolia* (rel. 61), *Sphagnum recurvum* (rel. 365) and *S. subsecundum* (rel. 393) have been found associated in one place. The *Sphagnum* species have a cover of more than 50%.

Juvenile *Diplostephium revolutum* shrub is common in this type of bog and is considered by Lozano & Schnetter (1976) as successional to the climax with *Diplostephium revolutum* dwarfforest. Our data suggest a succession to the *Diplostephium revoluti* (70) from *Puya goudotiana* - *Sphagnum* bog as well as one from the *Hyperico* - *Plantaginetum rigidae* (65) and the *Caricetum pichinchensis* (49) to the *Diplostephietum revoluti*.

Puya goudotiana - *Sphagnum* bog is found throughout the humid lower pâramos of the Colombian Cordillera Oriental between 2800 and 3500 (3680) m.

Note: In the pâramos near Bogotâ (Cruz Verde, Chisacâ) low *Senecio flos-fragrans* shrub was locally notices associated with *Pleurozium schreberi*, *Hypnum amabile* and *Myrteola oxycoccoides* in *Sphagnum* bog (3500-3700 m). Mossy hummocks in the Pâramo de Cruz Verde may vary from 40 to 70 cm in height.

69[b]. *Sphagnum* bog with *Puya aristiguietae*

Puya aristiguietae is a geographically vicariant *Puya* species in Venezuelan subpâramo bogs of the Sierra Nevada de Mérida. On the dry side of the Sierra

Nevada del Cocuy this giant rosette species replaces *Puya goudotiana* in *Sphagnum* bogs between 3550 and 3770 m (Pāramo Cōncavo), and is associated with *Espeletia lopezii*, *Xyris subulata*, *Geranium subnudicaule*, *Carex bonplandii*, *Oritrophium peruvianum* and *Juncus echinocephalus*. *Sphagnum oxyphyllum* seems the main hummock species and *S. sancto-josephense* is characteristic for the hollows.

70. *Xyris-Sphagnum* bog

Pāramo bogs with *Xyris acutifolia* are common, mainly between 3300 and 3700 m in the upper subpāramo and lower grass pāramo of the Colombian Cordillera Oriental. *Xyris acutifolia* is the most characteristic species in the pāramos from Chachapoyas (N. Peru) to Venezuela between (2200) 2900 and 3750 m. In the study area *Xyris subulata* may locally replace *Xyris acutifolia*. Common characteristic species are *Hypericum lancioides* and other *Hypericum* species, *Blechnum loxense*, *Halenia* spp. and *Kurzia* sp. *Swallenochloa tesselata* and *Arcytophyllum muticum* are absent in *Xyris - Sphagnum* bogs.

The top layer of the clayey to peaty black soils is moderately acid (pH 4.6 - 5.3). The *Xyris* pāramo bogs apparently represent a clearly distinct syntaxon, which will be defined in the future. According to Weber (1958), *Sphagnum - Xyris* peatbog of a similar nature is found also in the Costa Rican pāramos.

70^{a}. *Espeletia - Xyris - Sphagnum* bog

In contrast to *Xyris acutifolia - Sphagnum* bog (70^{b}), the average cover of *Xyris* is rather low in this bog reaching not more than 25%. *Espeletia* spp. are frequent and may have a cover of about 50%. Other common species are *Breutelia*, *Lepidozia* and *Cladonia* subg. *Cladina* (Sipman & Cleef 1979), and also *Pernettya prostrata* and *Cladia aggregata*.

The black upper layer of the water-logged peat is moderately acid (pH 4.6 - 4.8). A more impermeable layer underlying the upper layer may be the cause of the present *Sphagnum* bog.

Espeletia - Xyris - Sphagnum bogs are common in the study area between 3300 and 3700 m. On the basis of mainly floristical properties these bogs can be subdivided into bogs with either *Campylopus cucullatifolius* or *Oreobolus obtusangulus*.

70^{aa}. *Espeletia - Xyris - Sphagnum* bog with *Campylopus cucullatifolius*
Fig. 78

These *Sphagnum* bogs are presently only known from the dry lower bunchgrass pāramos North of Bogotā (Neusa, San Cayetano) between 3600 and 3700 m. It is developed as large ombrotrophic peat bog near the Laguna Verde and in small *Sphagnum*-filled valleys. *Xyris acutifolia* has a cover of 20%. *Campylopus cucullatifolius* generally has a low cover. *Espeletia chocontana*, *Campylopus pittieri*, *Aragoa abietina* dwarfshrub, *Rhacocarpus purpurascens* and *Vaccinium floribundum* var. *ramosissimum* are frequently associated, and have a low cover. Rosettes of *Puya santosii* and *P. trianae* are present in all relevés with an average cover of about 10%.

This vegetation type apparently may lead to the rare *Aragoetum abietinae*, the climax vegetation in the pāramo bogs near Bogotā (see 72).

70^{ab}. *Espeletia - Xyris - Sphagnum* bog with *Oreobolus obtusangulus*
photo: Van der Hammen 1962, Fig. 1

This community is common in the study area between 3300 and 3600 m, generally on former filled-up lakes and in small valleys. The presence of *Oreobolus obtusangulus* against the absence of *Campylopus cucullatifolius* and *Aragoa abietina* is the main floristic difference with the previous community. The average cover of *Puya* species is about 1%, of *Xyris* species about 10%. Stemrosettes of *Espeletia* may be denser than in the previous community (average cover 15%; 0 - 55%). The principal geographically vicariant species are *Espeletia grandiflora, E. arbelaeziana, E. incana* and *E. murilloi*. *Hypericum* species may be present, e.g. *H. laricifolium* ssp. *laricoides, H. lancioides, H. strictum* and *H. graciliforme*. Low shrub of *Diplostephium revolutum* may also be present and indicates that this community is successional to the *Diplostephietum revoluti* (79) also.

The black peaty, clayey soils are about 2 m thick, with an underlying pale yellow or light brownish to gray clayey sand.

70^{b}. *Xyris acutifolia* bog
Fig. 38, 69

Characteristic for this bog type are small tufts of yellowish-orange flowering *Xyris acutifolia*, with a cover of 10 - 80% (average 50%), accompanied by *Rhacocarpus purpurascens, Halenia* sp(p.), *Riccardia* spp., *Blechnum loxense* and tufts of *Calamagrostis effusa* and *Cortaderia sericantha*. Scarce to absent are *Swallenochloa tesselata, Cladia aggragata, Pernettya prostrata (var. purpurea), Campylopus cucullatifolius* and *Lepidozia*. The average number of species is 22 (12 - 35) in 8 relevés. Most of the stands consist of a well--developed field layer and several rosette plants. *Hypericum lancioides* dwarfshrub has a low cover.

The substrate is peaty clay of more than 120 cm deep. The pH in the upper soil layer is 5.0 (4.8*)-5.5. Slopes are up to 15°.
The studied pure *Xyris* bogs occupy relatively small areas in the southern páramos of the Colombian Cordillera Oriental, e.g. Páramo de Palacio, Cruz Verde, Chisacá and between Neusa and S. Cayetano. They occur from the subpáramo at 3350 m up into the lower grass páramo at 3700 m.

Xyris acutifolia bog vegetations can be subdivided into:
1) moderately sloping (12 - 15°) soligenous bogs, which are present as small patches in zonal páramo vegetation. Floristic affinities with the zonal grass páramo is constituted here by e.g. *Rhynchospora macrochaeta, Castratella piloselloides* and *Campylopus richardii*. Characteristic are *Myrteola oxycoccoides* and a few solitary cushions of *Oreobolus obtusangulus*. *Sphagnum* species are absent. This type has a strong affinity to the *Oritrophio - Oreoboletum xyridetosum* (66^{b}).
2) the gently sloping (3 - 5°) *Xyris acutifolia - Sphagnum* bog areas contain *Aragoa abietina*, slender reddish clubmosses (*Lycopodium cruentum* complex) and *Kurzia verrucosa* as accompanying characteristic species. *Sphagnum cuspidatum, S. sancto-josephense* or *S. magellanicum* may be dominant. *Isoetes boyacensis* may be immersed in the wet *Sphagnum cuspidatum* layer in bamboo páramo bogs (e.g. Páramo de Palacio). *Espeletia chocontana* and *Vaccinium floribundum* var. *ramosissimum* are characteristic for stands in bunchgrass páramo bogs (e.g. páramos NW of Neusa).

Other *Sphagnum* communities

Wet patches of *Sphagnum* bog hollows contain e.g. *S. cuspidatum* (Fig. 46) and/or *S. sancto-josephense* and are locally distributed along peaty lake shores and in boggy glacial valleys between 3600 and 3850 m in the southern páramos of the study area. One of these *Sphagnum* species may be dominant and may be associated with sedges. In such a peaty hydrosere with small sedges (occasionally with *Carex bonplandii*), other associated species are *Lysipomia sphagnophila ssp. minor* (large flowers), *Bartsia* sp. and *Werneria humilis* var. *angustifolia*. Species of *Lepidozia, Breutelia and Riccardia* are common but with a low cover. *Carex pichinchensis* (cover 70-80%) is also a common associate. The ecological difference with the *Caricetum pichinchensis* (49) is the absence of mineral soil. The *Sphagnum* turf is slightly acid (pH 4.7-5.2). It cannot be ruled out that the original sedge marsh of the *Caricetum pichinchensis* preceeded the *Sphagnum* bog in the past. Stands were observed between 3650 and 3850 m in the southern páramos

An interesting aquatic growth of *Sphagnum* was earlier described from the Andabobos watershed at 3700-3750 m in the Páramo de Sumapaz (Cleef 1978), where a *Sphagnum cuspidatum* layer floats in open water of deep glacial lakes, which are also covered with floating cushions of *Plantago rigida*. The 15-25 cm thick *Sphagnum cuspidatum* layer supports different herbaceous species, e.g. *Callitriche* sp., *Elatine chilensis, Tillaea paludosa, Juncus* cf. *ecuadoriensis, Ranunculus limoselloides* and even tufts of *Calamagrostis coarctata* and rosettes of *Oritrophium limnophilum* ssp. *mutisianum* (Cleef 1978, photo 170).

Zonation from open water in the central part of the lake towards the shore is as follows:

1) Initially *Plantago rigida* rings float on open water while the *Sphagnum cuspidatum* carpet just starts to develop. Submerged masses of *Sphagnum cyclophyllum* and *Drepanocladus revolvens* may cover the interstices between the *Plantago* cushions, and several other character species of the *Oritrophio--Wernerietalia*, e.g. *Werneria pygmaea, Oritrophium limnophilum* ssp. *mutisianum* and *Calamagrostis coarctata*, are associated.
2) Next, the *Sphagnum cuspidatum* mat becomes predominant. *Callitriche* sp. and such amphibious species as *Elatine chilensis* and *Tillaea paludosa* become settled.
3) Towards the marshy shore, where the *Sphagnum cuspidatum* layer reaches the bottom, 1-2 m broad, lagg-like zone dominated by *Ranunculus limnoselloides* may fringe the lake.

The pH of the water (4.5-4.9) in the *Sphagnum cuspidatum* layer indicates slightly acid conditions. When the *Plantago rigida* cushions grow close together the lake's surface becomes filled up. Cushionbog of the *Hyperico-Plantaginetum rigidae* (65) then contains wet hollow-communities of the variant of *Drepanocladus revolvens* (62ad) of the *Oritrophio-Wernerietum pygmaeae*.
The described *Sphagnum cuspidatum* vegetation represents a truely neotropical vicariant community, which is closely related to other temperate communities with *S. cuspidatum*.

SHRUBS & DWARFFORESTS

The azonal shrub formations in the páramo belt of the Colombian Cordillera Oriental are generally dominated by one single species, which mainly belongs either to the Compositae (*Senecio, Diplostephium*) or to the Hypericaceae (*Hypericum* sect. *Brathys*). Species of Ericaceae and Melastomataceae are largely present or dominating in zonal forest line formations. They are only companions in the azonal shrubs and dwarfforests. Compositae, mainly species of *Gynoxys* and *Diplostephium* are also dominant in the canopies of dwarfforests of the páramo belt; though also rosaceous (mainly *Polylepis*) dwarfforests are common. With regard to the woody genera mentioned above, some noteworthy aspects of their evolution and speciation in the páramos are given below, except for *Polylepis*, which is recently discussed by Simpson (1979).

The *Compositae* are undoubtedly the main constituents of azonal thickets and dwarfforests in the study area. *Senecio* (Senecioneae) and *Diplostephium* (Astereae) are predominant in thickets; species of *Gynoxys* (Senecioneae) represent different types of dwarfforest in the páramo belt. A comprehensive systematic survey of tropical Andean Senecioneae is not yet available, and only preliminary notes are presented on evolution and distribution of the above three genera. Cuatrecasas (1969) treated *Diplostephium* for Colombia. He mentioned its austral-antarctic affinities. The most primitive features are the enrolled leaves in the species of the series *Denticulata* Cuatr, which are micro- to mesophyllous trees in the upper Andean forest. The most advanced members of *Diplostephium* are leptophyllous or nanophyllous dwarfshrub species of the high páramo. In the study area they are represented by *Diplostephium colombianum* and *D. glutinosum* (ser. *Lavandulifolia* Cuatr.), and *D. rupestre* (ser. *Rupestria* Cuatr.). The other *Diplostephium* species from intermediate altitudes in the study area belong to the ser. *Schultziana* Cuatr. (*D. juajibioyi, D. alveolatum, D. rhomboidale)* and the ser. *Rosmarinifolia* Cuatr. (e.g. *D. heterophylla, D. lacunosa, D. revolutum*). In spite of the numerious new *Diplostephium* species described from the Peruvian and Ecuadorian Andes, the Colombian Andes with 80 (-100) species must be considered as the recent centre of *Diplostephium*.

Carlquist (1974) described the "insular woodiness", i.e. originally herbaceous taxa that develop secundary xylem in isolated (sub)tropical habitats, as prevailing on oceanic islands and in summit areas on high mountains. He assumed that the temperate herbaceous taxa are more suited to develop woodiness than the tropical ones. This applies e.g. to Senecioneae including *Gynoxys* (Carlquist, 1974) and also to *Paragynoxys*, by the present author regarded as one of the possible precursors of tropical woody *Senecio*. According to Cuatrecasas (1951) the woody species of *Senecio* dominating the azonal páramo shrub belong to four sections of the genus:

1) Sect. *Ledifolium* Cuatr.: e.g. *Senecio ledifolius* and *S. cacaosensis* in dry resp. wet habitat.
2) Sect. *Vaccinioides* Cuatr.: e.g. *Senecio vaccinioides, S. pulchellus, S. quantivanus, S. pungens* and *S. flos-fragrans* in dry to wet habitats.
3) Sect. *Granata* Cuatr.: e.g. *Senecio nitidus, S. vernicosus, S. andicola* and *S. reissianus* in dry to humid (wet) habitats.
4) Sect. *Reflexus* Cuatr.: e.g. *S. guicanensis* in dry to slightly humid zonal habitats. This section also contains other endemic superpáramo species, e.g. *S. gelidus* (Parque Los Nevados).

Other examples of páramo species demonstrating "insular woodiness" are *Niphogeton fruticosa* (Umbelliferae), the rosaceous *Lachemilla polylepis*, which belongs to the monotypic section *Polylepides* (Perry) Rothm. of *Lachemilla*, and species of *Valeriana* sect. *Porteria* Killip. From the latter some endemic species are present in the study area: e.g. *Valeriana triphylla* and *Valeriana arborea*, but not in well-developed thickets as in adjacent páramos.

The woodiness of *Hypericum*, however, must be explained otherwise. The very ancestors of the neotropical section *Brathys* (Mutis ex L.f.) Choisy of *Hypericum* are closely related to woody species of the most primitive section *Campylosporus* (Spach) R. Keller of tropical Africa (Robson 1977), which today are found in similar habitats as the tropical Andean species of *Hypericum* on the high equatorial African mountains. According to Robson (1977, fig. 4) the most primitive species of the section *Brathys* are presently found in the northern Andes of Colombia and Venezuela, Roraima (1 species), adjacent Central America and Cuba. The páramos of the study area probably contain most of the species of this section in the northern Andes and may thus be considered as its major South American centre.

SHRUBBY COMMUNITIES

71. *Diplostephietum revoluti* ass. nov.
type: rel. 27; table 14; Fig. 70 (also Fig. 14, 50, 51)
lit.: Lozano & Schnetter 1976
photo: Cleef 1978, photo 163 (the *Diplostephium revolutum* stand represents rel. 116); Cuatrecasas 1954, plate 19.

Physiognomy: This nano- to microphyllous dark greenish shrub is best characterized by its conspicuous spherical umbrella-like canopies. The general structure of the stands is as follows:

1) shrub layer, 1 - 3 m high, mainly of dark greenish spherical canopies of *Diplostephium revolutum*, with a cover of 60 - 90%. The up to 2 m high bamboos have a cover of 10 - 45% and are part of the shrublayer;
2) an open herb and dwarfshrub layer, with a cover of about 30%; and
3) a conspicuous bryophyte layer, 1 - 5 (25 cm) thick, with some low herbs. Lichens are scarce.

Composition & syntaxonomy: The shrub *Diplostephium revolutum* is dominant; this endemic composite species is common in the páramos of the Colombian Cordillera Oriental (3200 - 4200 m) and less common in the Tolima - Ruiz massif in the Colombian Cordillera Central (Quatrecasas 1969, Cleef et al., in press). Other frequent or conspicuous species are *Swallenochloa tesselata, Blechnum loxense, Carex pichinchensis, Relbunium hypocarpium, Ophioglossum crotalophoroides, Pernettya prostrata* (especially var. *elliptica), Geranium sibbaldioides, Arcytophyllum muticum, Adelanthus lindenbergianus, Leptoscyphus cleefii, Bazzania robusta, Syzygiella liberata,* and species of *Hypericum, Plagiochila, Sphagnum, Riccardia* and *Lepidozia; Sphagnum* spp, and *Hypnum amabile* have high cover values.

Epiphytic cryptogams are abundant in the *Diplostephietum revoluti*. The most common are *Usnea* spp. (1694, 3057), *Frullania tetraptera, Frullania* spp. (1697[a], 4519), *Brachiolejeunea laxifolia, Sphaerophorus melanocarpus, Everniastrum* spp. (e.g. *E. cirrhatum, E. catawbiense), Oropogon loxensis, Zygodon goudotii, Zygodon reinwardtii, Metzgeria* spp. (e.g. 943, 1072, 4517) and *Lejeuneaceae* (e.g. 1697[b], 1700, 4518). Pleurocarpous mosses (4523, 4524) and *Lophocolea fragmentissima* have also been collected.
The average number of (terrestric) species is 42 (21-62 in 8 relevés).

Diplostephium revolutum is the only (excl.) character species; this eliminates confusion with other related bog communities, e.g. the *Aragoetum abietinae* (72), the *Senecionetum andicolae* (73) and the *Diplostephium alveolatum* community (88). Bamboos are mostly present in the *Diplostephietum revoluti* in the study area, but they are absent in the nearby Cordillera Central. Most stands show a strong relationship to páramo *Sphagnum* bogs, as indicated by a number of characteristic species (see "bog taxa", table 14). The "asociación de *Diplostephium revolutum*" of Lozano & Schnetter (1976) represents rather a distinct subpáramo syntaxon, which together with rel. 65 (present study) may be assigned to the subassociation level. Differential species include e.g. *Paepalanthus colombiensis* (?) or *P. alpinus* (det. Dr. H.N. Moldenke), *Aragoa abietina* (low cover), *Aulonemia trianae* and *Geranium multiceps*.

Synecology: Thickets or dwarfforest with *Diplostephium revolutum* are common on boggy, waterlogged ground in grasspáramos, e.g. in moist valleys and depressions, along lake-shores and filled-up former lakes. The association is most common in the bamboo páramos.

The *Diplostephietum revoluti* is a climax association that marks the end of the succession in several azonal boggy páramo communities. However, not each bog succession leads to the *Diplostephietum revoluti*; some may lead to other shrubby climax communities, e.g. *Senecionetum reissiani* (48), the *Senecionetum andicolae* (73), *Diplostephium alveolatum* shrub (88), the *Aragoetum abietinae* (72).

Succession to the *Diplostephietum revoluti* was observed in the *Caricetum pichinchensis* (49), *Carex jamesonii* community (52), *Sphagnum sancto-josephense - Calamagrostis ligulata* community (57), the *Hyperico - Plantaginetum rigidae* (65), and further in the giant *Puya - Sphagnum* bog (69), *Espeletia - Xyris - Sphagnum* bog with *Oreobolus obtusangulus* (70^{ab}) and in dense *Sphagnum - Breutelia - Swallenochloa* vegetation (10). Floristic elements of these communities are common in the understorey of the *Diplostephietum revoluti*. In the high páramos (3800 - 3900 m) of the Sumapaz, *Diplostephium revolutum* shrub was also noticed on a thick homogeneous mat of *Breutelia chrysea* and *B. allionii*. *Sphagnum cyclophyllum*, rather a species of the *Oritrophio - Wernerietalia*, may be associated also. Apparently the *Diplostephietum revoluti* in this case is developed on former *Hyperico - Plantaginetum rigidae breutelietosum*. Common is *Diplostephium alveolatum* shrub (88), which takes over the rôle of *Diplostephietum revoluti* in the highest located bogs on the crests of the Páramo de Sumapaz. Bamboos and species of *Sphagnum* are important with a cover of resp. about 40% and 65%. The presence of *Sphaerophorus melanocarpus* and of a number of hygrophytic liverworts reflect a rather steady and high atmospheric humidity. Epiphytic species are also common on dense *Swallenochloa* clumps and on other organic matter.

The peaty soils are thicker than 120 cm and consist of brownish to grayish clayey peat or gyttja with numerous roots. The upper part is moderately to weakly acid (pH 4.9-6.4). Schnetter et al. (1976) measured the pH in the upper soil layer for one year, but they did not find a correlation with climatic fluctuations. Biological activity in the upper soil layer is extremely low Schnetter & Cardozo (1976), as may be expected in waterlogged bogs. The stands are found in level or slightly sloping areas (1 - 5°).

Observed were foraging activities by *Sylvilagus* and *Cavia*. Cattle uses dwarfforests for shelter. The use for fuel endangers this páramo bush.

Distribution: The *Diplostephietum revoluti* is common in the páramos of the Colombian Cordillera Oriental on both sides of the mountains, between 3300 and almost 4000 m. Stands in higher locations can be expected on the west slope of the Sierra Nevada del Cocuy (Cuatrecasas 1969). The association was also reported as scarce from the Colombian Cordillera Central in the Tolima - Ruiz - massif between 3800 and 3900 m (Cuatracasas 1969, Cleef et al., in press).

72. *Aragoetum abietinae* ass. nov.
type: rel. 197; table 14; Fig. 71 & 78

Physiognomy: The dark greenish nano- to leptophyllous conifer-like shrubs are dotted with white flowers. Closed stands are structured in:

1) a shrublayer, 1 - 2 m high. Bamboos, if present, reach up to the canopy stratum.
2) a herbaceous - dwarfshrub layer up to 40 cm high, covering 1 to 15%.
3) a groundlayer mainly made up of *Sphagnum*, usually together with pleurocarpous mosses. The mosslayer covers 80 to nearly 100%, but in dense stands only 15 to 25%.

Composition & syntaxonomy: *Aragoa abietina* is the dominant shrub species which is restricted to the southern páramos of the Colombian Cordillera Oriental (Cleef 1979^{b}). *Sphagnum* bog taxa are common in the *Aragoetum abietini* and together they altain a considerable cover. Other frequent species include *Nertera depressa*, *Pernettya prostrata*, *Campylopus pittieri*, *Cladia aggregata* and *Metzgeria* sp. The number of species varies from 19 to 51 in 7 relevés and is lowest in *Sphagnum* bog (subass. *puyetosum*).
Common epiphytic cryptogams are *Macromitrium longifolium*, *Zygodon reinwardtii*, *Daltonia* sp. (6412^{c}), *Frullania lobulo-hastata*, *F.* sp. (5398), *Metzgeria dorsipara*, *Radula ramulina*, *Brachiolejeunea laxifolia*, *Usnea* sp. and *Oropogon loxensis*.

Dominance of the single (select.) character species *Aragoa abietina* distinguishes this association from related *Xyris* bog communities. The *Aragoetum abietinae* includes two subassociations, easily recognized by the presence or absence of e.g. bamboos.

Synecology: The *Aragoetum abietinae* is a rare shrub association on boggy slopes (up to 20° inclination) and on gently sloping or level *Sphagnum* bog. The habitat is moist and cool, and is present both in the bunchgrass and in the bamboo páramos
Soils are humic, clayey and 70 cm to more than 120 cm deep. The upper soil layer is strongly to moderately acid (pH 4.3 to 5.1 in 7 relevés).
Succession towards the *Aragoetum abietinae* starts with (*Xyris*-) *Sphagnum* bog and probably also with the *Sphagnum Breutelia* - *Swallenochloa* community (10). Future pollenanalyses of soil and peat bog sequences under stands of the *Aragoetum abietinae* may provide more information about the succession.
Cavia porcellus, Sylvilagus brasiliensis and frogs are the most common vertebrates observed in this vegetation type.

Distribution: The *Aragoetum abietinae* is only known from páramos near Bogotá between 3480 and 3700 m.

Phytogeographic comment: The woody scrophulariaceous genus *Aragoa* is endemic to the páramos of Colombia (except the Cordillera Central and the Venezuelan Sierra Nevada de Mérida. *Aragoa* is an old páramo genus, which was reported by Van der Hammen et al. (1973) for the oldest páramos in the area at the Pliocene-Pleistocene boundary. On the basis of its peculiar morphology, Pennell (1937) and Mennega (1974) consider as the nearest relatives members of the Veroniceae. The Colombian Cordillera Oriental and especially its southern páramos, where 4 of the 8 described species are found with the maximal subgeneric morphological diversity must be considered as the main centre of evolution of this interesting genus (Cleef 1979[b], Fig. 1).

note: Other *Aragoa* species also may dominate vegetation types in the study area. Thus, *Aragoa dugandii* also represents a proper bog community on the wet eastern slopes between Lake Tota and the Sierra Nevada del Cocuy (3030 - 3550 m). *Aragoa dugandii* is a rare endemic species, and hence this community is scarce also. *Aragoa perez-arbelaeziana* is a shrub or dwarf tree, attaining considerable cover in timberline bush or dwarfforest in the Páramo de Sumapaz (see 101). *Aragoa cupressina* is zonal in subpáramos near Bogotá and in grasspáramos in the Páramo de la Rusia and Páramo de Guantiva (2800 - 4000 m). *Aragoa lycopodioides* is zonal at wet timberlines, and is also found in zonal thickets in the bamboo páramo (3000 - 3900 m).

72[a]. Subass. *swallenochloetosum* subass. nov.
type: rel. 149; table 14.

Physiognomy: These scrophulariaceous thickets contain bamboos, about 2 m high. See also under the association.

Composition & syntaxonomy: *Swallenochloa tesselata, Lachemilla* spp. (5375[B], 5376, 5383), *Espeletia grandiflora, Berberis* sp. and *Bartsia* sp. e.g. are differential against the *puyetosum*. Several species from the surrounding zonal vegetation are present, and therefore the number of species (39 - 51 in 2 relevés) is higher than in the *puyetosum*. With more relevés available the lower bamboo páramo and the subpáramo stands may be expected to be distinguished as altitudinal variants of the *swallenochloetosum*.

Synecology: Patches of this unit may be present on wet sloping ground (12 - 20° inclination) in (slight) depressions. The phreatic level was found at about 15 cm below surface. The profiles are not deeper than 1 m and consist of humic black clay in the upper layer (pH 4.3 - 4.6). The dark grayish lower part contains more sand and pebbles.

Distribution: The *swallenochloetosum* is not common and only known from the bamboo páramos near Bogotá (Palacio, Chuza - Cruz Verde) between about 3480 and 3700 m. The lowermost stand (rel. 59) is in the subpáramo.

72^{b}. Subass. *puyetosum* subass. nov.
type: rel. 197; table 14; Fig. 71 & 78

Physiognomy: This climax scrophulariaceous shrub with a thick bryophyte layer is present on former *Sphagnum* bog or on peaty soil.

Composition & syntaxonomy: Presence and high cover (3 - 15%) of *Puya santosii*, *P. cryptantha* and probably also of *P. trianae* are, combined with the absence of bamboos, the main differential features. Other differential taxa are *Espeletia chocontana*, *Vaccinium floribundum* var. *ramosissimum*, *Campylopus tunariensis* and *Bryum billardieri*. Weak differential species are *Xyris acutifolia*, *Cladonia boliviana*, *Cladonia colombiana* and *Gongylanthus innovans*. The number of species is lower than in the *swallenochloetosum* and varies from 19 to 38 in 5 relevés.

Synecology: Rel. 197 with an abundance of *Pleurozium schreberi* and dwarfed Ericaceae (*Pernettya*, *Vaccinium*) marks the end of the succession beginning on *Xyris* - *Sphagnum* bogs. A drier, shady habitat is present near the trunks of *Aragoa* and contains *Pleurozium schreberi*, *Hypnum amabile*, *Metzgeria* sp., *Bryum billardieri*, *Gongylanthus innovans* and *Peltigera* sp. Most of these species cover the raw needle litter of *Aragoa abietina*. *Campylopus tunariensis* is frequent on organic remains, e.g. of *Puya*.
The succession from open *Xyris* - *Sphagnum* peat to the *Aragoetum abietinae puyetosum* is described under *Sphagnum* bogs. The *puyetosum* covers extensive areas on level peat bog, but also on sloping *Sphagnum* bog in small wet valleys and on boggy ground.
The black upper peat layer is moderately acid (pH 4.7 - 5.1) and the peaty to clayey substrates are about 1 m (mineral soil) to 4 m (*Sphagnum* bog) deep. *Cavia porcellus* is common; a pattern of trails is found on the *Sphagnum* peat.

Distribution: The *puyetosum* is only known from the (lower) bunchgrass páramos north of Bogotá between Neusa and S. Cayetano at about 3650 - 3680 m near the Laguna Verde, where *Aragoa abietina* thickets cover several hectares. The *Aragoetum abietinae* was also observed in the headwaters of Río Salto some km north of the Laguna Verde.

note: The páramos near the Laguna Verde between Neusa and S. Cayetano stand out by the presence of well-developed *Aragoa abietina* bush, which is scarce to absent in other páramos near Bogotá. The same applies to the *Senecionetum nitidae* (84) and the *Lorenzochloetum erectifoliae* (106). The *Calamagrostis effusa* - *Espeletia* (*E. barclayana*, *E. argentea*) vegetation is one of the best examples of the characteristic, well-developed, lower bunchgrass páramos in the Colombian Cordillera Oriental. It seems important to establish a small National Park in the páramos between Neusa and S. Cayetano including this vegetation. This would also protect the catchment areas of the Neusa barrier lake.

73. *Senecionetum andicolae* ass. nov. (prov.)
type: rel. 255; table 14; Fig. 72 (also Fig. 12)

Physiognomy: This microphyllous Compositae shrub possesses grayish foliage and yellow flowers. Stands are structured in:

1) a closed shrublayer in well-developed thickets up to 2.5 m high, with bamboo up to 130 cm high;

Table 14. Some selected páramo shrub associations

A.M. Cleef 1981: The vegetation of the páramos of the Colombian Cordillera Oriental
Diss. Bot. 61, Vaduz

association	71 Diplostephietum r.								72 Aragoetum a.							73	74				84	
subassociation									72a		72b puyetosum											
relevé nr.	482	253	65	291	13	8	116	27	59	149	197	213	207	206	207	255	262	262	51	236	189	99
relevé area (m^2)	35	50	36	36	64	100	16	100	16	20	16	36	8	16	8	24	40	35	45	36	49	36
slope (degree)	–	2	3	10	3	3	15	2	12	20	–	9	8	8	–	5	18	15	12	3	7	–
cover % (dwarf) shrub / dwarf trees	75	90	75	75	60	90	95	80	95	100	85	85	45	50	100	95	100	85	100	100	65	10
bamboos	45	10	15	40	15	30	15	10	30	3	–	–	–	–	–	25	1	3	–	–	–	–
mosses	70	100	45	40	80	60	50	60	13	75	95	55	20	95	70	95	95	95	50	25	18	95
liverworts	30	1	1	50	15	25	15	20	1	40	1	2	2	1	<1	–	–	–	<1	1	1	5
soil	P	PC	PC	PC	P	PC	PC	PC	Cp	Cp	P	Cp	Cp	C	–	P	Cs	Cp	C/s	Cp	C	C
soil depth (cm)	>120	>120	>120	110	>120	>120	100	>120	140	70	>120	120	95	>120	–	>120	45	80	>120	>120	60	85
pH top soil (*water)	–	6.4	4.9	5.2	6.0	6.0	5.8	4.9	4.3	4.6	4.9	4.7	5.1	4.7*	–	4.9	5.5	–	4.4	5.2	4.6	4.6
approximate number of species	23	34	35	55	48	42	62	45	39	51	31	38	19	22	19	36	36	28	43	29	23	35
altitude (m)	3520	3775	3355	3715	3550	3420	3620	3800	3460	3700	3655	3680	3675	3670	3645	3730	3800	3800	3760	3520	3685	3645
locality	Coc	Rus	CV	Sum	Sum	Sum	Pi	Sum	CV	Pal	LV	LV	LV	LV	LV	Rus	Rus	Rus	Gua	Rus	LS	Neu
cover %								▲		○	▲ ○					▲	▲				▲	
c/d/o taxa Diplostephietum revoluti																						
c Diplostephium revolutum	75	90	75	75	60	90	90	80														
Swallenochloa tesselata	45	10	10	40	15	30	15	10	10	3						25	1	3				
Eleocharis stenocarpa		1			<1	<1	<1												<1+			
Campylopus cucullatifolius			<1		<1		1	1+			<1											
Campylopus cavifolius		2			4		25							<1								
Gongylanthus liebmannianus						<1	<1	<1														
Lachemilla mandoniana	1+					<1	<1															
Leptodontium wallisii	3			1			3															
Oritrophium limnophilum ssp. mutisii	<1							<1														
Sphaerophorus melanocarpus	<1+				<1+	<1		<1														
Scirpus inundatus			<1				3+															
Hypericum lancioides		<1	<1				<1+									<1						
Herbertus subdentatus	1				15	1	1				1											
Drepanocladus exannulatus		<1				5		<1														
Breutelia chrysea	<1						1	<1									<1					
Chorisodontium speciosum / C. setaceum	1						<1															
Breutelia inclinata		15					<1															
Bazzania sp. / B. robusta	<1			2																		
Anlonemia trianae			5																			
Myrteola oxyccocoides	1+	1																				
Rhacocarpus purpurascens			<1	2	10								3									
Isoetes andina					<1+			<1														
Disterigma empetrifolium			<1	<1+	1	<1		<1														
Werneria humilis var. angustifolia				<1	<1+			5														
Sphagnum cyclophyllum					5			30					<1									
Anastrophyllum nigrescens				<1	3																	
Senecio pungens				1				3														
c/d/o taxa Aragoetum abietinae																						
c Aragoa abietina									95	100	80	85	45	50	100							
Puya santosii					5					<1	3	10	5	15	3							
Campylopus tunariensis											<1	<1+		<1+		<1						
Cladonia hypoxantha											<1	<1										
Vaccinium floribundum var. marginatum											30	40	1			<1						
Xyris acutifolia													75		2							
Bartsia sp.									<1													
Paepalanthus karstenii								<1+		<1+	1	<1										<1
Campylopus pittieri										1	3	50										5
Cephalozia sp.									<1		<1											
Radula ramulina									<1	<1	<1											
Siphula sp(p.)										<1		<1										
Bog taxa																						
Riccardia spp.		<1+	<1	4	12	25	<1	25		1	1	<1	<1	<1+						1		
Lepidozia spp. / L. auriculata	20	<1		20	<1			<1		30	<1+	<1		<1+								
Plagiochila spp.	10		<1	20	3		25	<1	<1	6		<1										
Sphagnum magellanicum	50	25	40	25	4					5	8			15								
Sphagnum sancto-josephense	15	45	2	5							10		15	80		15						
Blechnum loxense	<1		35		3	1			1		1						2					
Leptoscyphus cleefii	2	<1	<1	<1		<1				2				<1								
Cladonia subg. Cladina				<1	<1	<1		<1		<1	6				<1							
Cladonia andesita				<1	<1		<1	<1	<1		<1	1										
Metzgeria spp.				<1	<1		2			<1		1		<1								
Adelanthus lindenbergianus	10			<1+				<1		3		<1										
Sphagnum cuspidatum					60		15	40		25												
Anastrophyllum leucostomum							<1	<1			<1+	<1										
Gongylanthus innovans					<1								<1	<1	<1							
Isotachis multiceps		<1						<1	<1	2												
Lophocolea coadunata				<1				3		<1												
Kurzia cf. verrucosa				<1								<1	1									
Aneura sp.								<1					1	<1								
Eriocaulon microcephalum				1	<1+								<1+									
Baccharis tricuneata			<1							<1												
Niphogeton lingula							<1+			<1+												
Tylimanthus setaceus				1									<1									
c/d/o taxa Senicionetum andicolae																						
c Senecio andicola																95						
Carex pichinchensis		1	<1	<1	5	5	<1	5			<1	<1		3		5						1
Nertera granadensis	2	<1+	1			<1			20	<1	<1	<1	<1			<1+			<1			
c/d/o taxa Hypericetum laricifolii																						
c Hypericum laricifolium ssp. laricoides				<1	<1+	3		<1					<1			<1	100	80	100	100		
c Sibthorpia repens																<1	<1+	3	80	1+		
Orthrosanthus chimboracensis																	1	1		<1		
Oxylobus glanduliferus																	<1	5	<1			
Niphogeton dissecta																	1	1	<1			
Rubus sp.																	1	1	<1			
Stachys elliptica																	1		5			
Lepidopilum cf. muelleri									3								1+		3			
Miconia salicifolia										<1							1		<1			
Arenaria serpyllifolia							<1												<1	<1+		
Plagiothecium schraderi																	1+		3			
Leptodontium luteum							1		1								1	40		<1	<1	
Halenia gigantea																	1	25				
Azorella multifida																			60			
Plantago australis ssp. oreades																	<1+	1				
Hesperomeles pernettyoides																	<1+	2				
Cinna poaeformis																	2	2				
c/d/o taxa Senecionetum nitidi																						
Senecio nitidus																					65	10
Carex conferto-spicata																					10	
Lorenzochloa erectifolia																					5	<1
Calamagrostis effusa									10								<1				45	10
Poa cf. pauciflora																					15	<1
Paspalum bonplandii																15					<1+	30
Niphogeton glaucescens																<1					15	
Carex bonplandii							<1														<1	70
skiophytic & other taxa																						
Breutelia sp.	<1	<1	<1		6	10	3	<1	1		1	<1	2		70	5	1	10		7		
Pernettya prostrata / var. elliptica		1		1	4	<1	<1	<1		1	20	<1		1	15	<1	1		5	<1		
Geranium sibbaldioides		<1	<1			<1	5			2	1			<1		<1	1		2	<1		
Hypnum amabile		55				30		<1		2	2			<1		1	1	5	5	1	2	
Peltigera spp. (P. dolichorhiza/P. pulverulenta)					<1	<1	<1		<1	<1		<1				<1+	1	1	<1	<1+	2	
Thuidium peruvianum						3		25		35	<1					<1	3	40	40	1	1	
Cladia agregata					1		<1	<1	<1		1	20	1		5						<1	1
Arcytophyllum muticum		<1+		2	1		<1	<1		<1						2			10			60
Rhynchospora macrochaete			<1	1					5	<1	<1					10		5		1		
Pleurozium schreberi								<1			70					75	90	<1			10	85
Lachemilla sp.		<1			<1				1	1							<1	<1				<1+
Spagnum compactum				<1	<1				2						1						<1	<1
Halenia spp.		<1								<1		<1				<1					<1	1+
Brachythecium spp.							1				<1	<1				<1				10	<1	
Relbunium hypocarpium		<1	<1			<1	<1											<1	3			
Ribes cf. columbianum										<1						<1	<1+	2			1	
Bryum billardieri												1		<1	<1				<1	1		
Senecio vaccinioides							<1		<1							<1	<1		<1			
Valeriana longifolia		3								3	3						3	2				
Senecio formosus			<1							<1							<1			<1		
Ophioglossum crotalophoroides		<1		<1						<1+									<1			
Espeletia incana		1														2	2	3				
Oritrophium peruvianum			<1				<1															<1
Luzula gigantea																10			1			
Leptodontium longicaule var. microruncinnatum																<1			1			
Breutelia allionii																	1	10				
Rhynchostegium scariosum									1										<1			
Espeletia chocontana													1	<1								
Espeletia barclayana												3									1	
Espeletia lopezii							<1															
Espeletia grandiflora									2													

Coc Sierra Nevada del Cocuy
CV Páramo de Cruz Verde
Gua Páramo de Guantiva
LS Páramos NW of Neusa, Laguna Sec
LV Páramos NW of Neusa, Laguna Verde

Neu Páramos NW of Neusa
Pal Páramo de Palacio
Pi Páramo de Pisva
Rus Páramo de la Rusia
Sum Páramo de Sumapaz

c character taxa
d differential taxa
o other taxa
▲ type of the association
○ type of the subassociation

2) layer of Cyperaceae and Juncaceae, up to 70 cm high with a cover of 25%. a few grasses and dwarfshrubs are present;
3) a layer of mainly pleurocarpous mosses, 10-15 cm high.

Composition & syntaxonomy: *Senecio andicola* dominates the association. This woody species is distributed from northern Ecuador to Venezuela and Costa Rica between 3200 m, from the forest line up to 4400 m in the superpáramo. Other conspicuous taxa are *Swallenochloa tesselata, Carex pichinchensis, Sphagnum sancto-josephense, Rhynchospora macrochaeta, Luzula gigantea* and *Pleurozium schreberi*. (The approximate number of species in rel. 255 is 36).
The recognition of the *Senecionetum andicolae* as a distinct thicket association on boggy páramo ground is based on dominance of *Senecio andicola* which is a selective character species. The association is tentatively described as more relevés are needed. The *Senecionetum andicolae* has some species in common with *Sphagnum* bog communities, but it has the greatest affinity with the *Hypericetum laricifolii* (74), as indicated by the species *Sibthorpia repens, Luzula gigantea, Pleurozium schreberi* and (juvenile) *Hypericum laricifolium* (see table 14).

Synecology: *Senecio andicola* is a species with a wide ecological range. *Senecionetum andicolae* bush is locally common on sloping (5 - 10°) boggy ground along páramo streams. Pure *Senecio andicola* thickets are not common in the study area. Mostly, other woody composite species may be associated e.g. *Senecio vaccinioides, Diplostephium alveolatum, Espeletia incana* and *E. lopezii*. On the other hand, *Senecio andicola* is often present in other páramo shrub, for example in the *Diplostephietum revoluti* (71), *Hypericetum laricifolii* (74) and *Senecio vaccinioides*. Weber (1958) reported *Senecio andicola* from Costan Rican páramo thickets and together with *Senecio firmipes* Greenm., *Diplostephium costaricense* Blake (*D. alveolatum* is probably a synonym), *Hypericum silenoides* Juss., *Myrtus oerstedii* (Berg) Hemsl. and *Berberis nigricans* Kuntze.
The profile in rel. 255 consists of a peaty clay, moderately acid (pH 4.9) in the the top layer. In higher places, the soil is thinner.
Observed were foraging activities by *Cavia* (or *Sylvilagus*) indicated by grazed young bamboo and *Luzula gigantea*.

Distribution: The *Senecionetum andicolae* is only known from the páramos of Boyacá (Rusia, Pisva, Cocuy) between 3600 and 4000 m. The association may be expected in other páramos where the species is present.

Note: Low *Senecio andicola* shrub was also noticed in open bog vegetation with *Myrteola oxycoccoides* and dense mats of bryophytes (*Atractylocarpus* sp., *Sphagnum sancto-josephense, Ditrichum* cf. *capillare, Nardia succulenta, Pseudocephalozia quadriloba*) surrounding hot springs in the wet Andean cloudforest at 3280 m on the volcano Puracé in the Colombian Cordillera Central. *Senecio andicola* is dominant in the shrublayer in zonal *Gynoxys tolimensis* dwarfforest with *Neurolepis aristata* in the wet upper Andean forestline (3800-3900 m) on the W slope of the Parque Los Nevados located farther north in the same range (Cleef et al., in press).

shrub of *Hypericum* spp.

Species of the section *Brathys* (Mutis ex L.f.) Choisy determine the hypericaceous shrub in the study area.

74. *Hypericetum laricifolii* ass. nov.
type: rel. 262; table 14; Fig. 73 (also Fig. 26)

Physiognomy: Well-developed stands of this tall hypericaceous shrub with slender twigs, leptophyllous leaves and bright yellow flowers are structured in:
1) a shrub layer, up to 3-3.5 m. The cover of the canopies is about 100%;

2) an open high herb-dwarfshrub layer (up to 20% cover), possibly including few bamboos; and
3) a thick (3-25 cm) ground layer, consisting of low, creeping herbaceous species and/or mosses; this is the most conspicuous stratum under the shrub canopy.

Composition & syntaxonomy: *Hypericum laricifolium* ssp. *laricoides* is a dominant and selective character species. According to Dr. N.K.B. Robson (in litt.) *Hypericum laricifolium* is widely distributed in the high tropical Andes from Peru to Venezuela. The ssp. *laricoides* (previously *H. laricoides* Gleason) is restricted to the Venezuelan Sierra Nevada de Mérida and the Colombian Cordillera Oriental between 2900 and 4200 m. *Sibthorpia repens* is a preferential character species,optimumally developed here. The Andean distribution is about the same as that of *Hypericum laricifolium* (Hedberg 1955). Other common taxa are *Thuidium peruvianum, Hypnum amabile, Peltigera dolichorhiza, P. pulverulenta, Rubus* sp., *Niphogeton dissecta, Oxylobus glanduliferus, Leptodontium luteum, Orthrosanthus chimboracensis, Geranium sibbaldioides* and *Pernettya prostrata*. The average number of species is 40 (36-45 in 4 relevés).
Except in the densest and most shady stands (e.g. rel. 236), epiphytes are numerous. *Usnea* sp. (2275) and *Ramalina* sp. (2290) are abundant. Common are *Oropogon loxensis, Frullania* sp, (2286), *Metzgeria* sp. (2292) *Hypotrachyna caracacensis, Cora pavonia, Parmotrema arnoldii, Everniastrum catawbiense, Leptogium* sp., *Brachiolejeunea nitidiuscula, Holomitrium* sp. (2282) and *Colura patagonica*.

The closest relationship is shown to the *Senecionetum andicolae* (73) and it seems that edaphic factors, particularly the phreatic level, determine which of the two associations develops. The stand on peat (rel. 263, 263A) may represent a variant with presence of *Halenia gigantea, Cinna poaeformi, Valeriana* cf. *longifolia*, and *Swallenochloa tesselata* as main differential species. This variant is not described, because the two relevés comprise two parts of the same stand. More relevés from other localities are required for a further subdivision.

Synecology: The *Hypericetum laricifolii* is restricted to small humid valleys and depressions supplied with run-off water from a minor catchment area. The shrubs grow mostly on poorly drained humic sandy to clayey soils, which do not dry out in rainless periods. The shrubzone is only a few meters wide and develops downslope like strips along the small waterlogged valley floors. The slopes are 3 - 18°. On level wet peaty ground, *Senecio andicola* shrub may replace the *Hypericetum laricifolii*.
The black to brown sandy clayey soils, containing many roots, are 50 to more than 120 cm thick. The upper soil layer is moderately acid (pH 4.4-5.5) and is covered by an Aoo-layer of 2-3 cm thickness. In the dense shady stand of rel. 236 bare raw litter of *Hypericum laricifolium* covers about 60%
Rel. 51 contains a low herblayer dominated by *Azorella multifida* and *Sibthorpia repens*. Other conspicuous species in this layer are *Thuidium peruvianum, Arcytophyllum muticum* and *Stachys elliptica*. This stand provides shelter for cattle, the effects of which are shown by the presence of *Rumex acetosella* and *Acaena elongata*. Part of this stand was damaged by cutting for fuel. Near rel. 236, at about 3500 m in the Páramo de la Rusia, a vegetation succession was studied about one year after burning. Under the scorched stems of *Hypericum laricifolium* photophytic species have a cover of about 85%, against 3% in rel. 236. *Orthrosanthus chimboracensis* and *Eleocharis stenocarpa* were abundant, accompanied by *Senecio formosus, Rhynchospora macrochaeta* and *Valeriana vetasana*. Stand on wet peaty ground (rel. 263, 263A) contained e.g. *Swallenochloa tesselata, Cinna poaeformis, Halenia gigantea, Pleurozium schreberi, Blechnum loxense, Valeriana* cf. *longifolia* and *Juncus echinocephalus*.
Cavia porcellus is common in the *Hypericetum laricifolii* (hiding, foraging).

Distribution: The *Hypericetum laricifolii* is probably widely distributed in the Colombian Cordillera Oriental from the upper forestline up to 3800 m.

Relevés in the study area from the southern end of the Páramo de la Rusia. The association was further observed in the Páramo de Palacio and Sumapaz at 3700 m. The association may also be present in the Venezuelan Sierra Nevada de Mérida, as Dr. N.K.B. Robson (in litt.) reported the ssp. *laricoides* also from these high mountains.

75. Community of *Hypericum laricifolium* ssp. *laricifolium*

Hypericum laricifolium ssp. *laricifolium* is widely distributed in the high tropical Andes from Central Peru to Venezuela (Dr. N.K.B. Robson, in litt.). In the Colombian Andes this subspecies is present in zonal timberline shrub (Cuatrecasas 1934, Cleef et al., in press) or in páramo rockshelter bush between boulders.

In the Sumapaz páramo at 3580 m near the Laguna La Primavera, a stand in a rockshelter was studied (rel. 12). On a bouldery slope (up to 15°) *Hypericum* shrubs and small trees up to 6-7 m high have a cover of 70%. Other characteristic shrubs or dwarf trees common to upper Andean dwarf forest are *Miconia salicifolia, Berberis* sp. *Senecio andicola, Oreopanax mutisiana, Acnistus quitoensis, Eupatorium (Ageratina) glyptophlebium, Cestrum parvifolium* and *Gaultheria ramosissima*; also lianas, e.g. *Valeriana pavonii* and *Muhlenbeckia thamnifolia* are present. Herbaceous species include *Epidendrum erosum, Oxalis cornuta, Cerastium subspicatum, Myrrhidendron glaucescens, Peperomia hartwegii, Luzula gigantea, Greigia* cf. *mulforfii, Niphogeton ternata* var. *ternata*, and some Polypodiaceae. *Herbertus subdentatus* (large form) covers about half of the ground layer. Associated are *Plagiochila ovata, Bartramia angustifolia, Plagiochila pachyloma, Anastrophyllum nigrescens, Lepidozia squarrosa* and *Campylopus pittieri*. *Usnea* sp. (967) is the most common and conspicuous *Hypericum* stem epiphyte. Other common epiphytes are *Frullania* sp. (980), Parmeliaceae and *Radula ramulina* with its two varieties (Jans 1979). The open character of this *Hypericum* stand permits the growth of *Calamagrostis effusa* (cover 30%) between the boulders. In the site of rel. 12 at the base of the scree this hypericaceous shrub is gradually replaced by *Escallonia myrtilloides* dwarfforest.

Other hypericaceous communities

Several other communities, each of which dominated by a different woody species of *Hypericum*, were observed in the study area. Only brief descriptions will be presented with notes on physiognomy, composition, ecology and distribution.

76. Shrub of *Hypericum lycopodioides*

Thickets up to 2.5 m high of this leptophyllous species are apparently common in the subpáramos on the humid eastern side of the Colombian Cordillera Oriental. They were observed e.g. between 3250 and 3700 m in the headwaters of Río Casanare in zonal and azonal habitats. *Hypericum lycopodioides* was hardly collected in the past. Its habit resembles that of *H. laricifolium*, but the leaves are distinctly larger.

77. Shrub of *Hypericum magniflorum*

Patches of these nanophyllous shrubs (1.0-1.5 m) were observed in the headwaters of Río Casanare between 3000 and 3350 m. They are found on azonal boggy ground in the lower part of the bamboo páramos commonly associated with *Espeletia lopezii, Senecio cacaosensis* and *Swallenochloa*. *Hypericum magniflorum* is endemic to the northern portion of the Colombian Cordillera Oriental.

78. Shrub of *Hypericum goyanesii*

High leptophyllous thickets (2-3 m) of this species are only known from lower páramos near Bogotá (Cruz Verde, Guasca, Guerrero) between 2700 and 3500 m. Lozano & Schnetter (1976) reported pure stands of *Hypericum goyanesii* at 3400 m in the Páramo de Cruz Verde, which they consider as secundary vegetation; they observed that this species is very sensitive to damage by fire. The same authors observed a vegetative growth of broken twigs of *Hypericum goyanesii*. This can be confirmed by the present author. *Hypericum goyanesii*, however, is mainly found scattered in subpáramo shrub formations and dwarfforests (e.g. Lozano & Schnetter 1967, table 9).

79. Shrub of *Hypericum thuyoides*

High leptophyllous shrubs (1-3 m) of *Hypericum thuyoides* occur in the forest line and the lower part of the páramo belt (3000-3600 m). Pure stands of this species are locally present on boggy valley floors (e.g. in the headwaters of Río Guandoque). With its preference for humid peaty soil and in its habit this species resembles *Hypericum laricifolium* ssp. *laricoides*. *Hypericum thuyoides* shrub is an important element in shrubby communities and dwarfforests in the bamboo páramo with *Vaccinium floribundum* and *Bucquetia glutinosa*.

80. Shrub of *Hypericum humboldtianum*

Shrubby (subserial ?) vegetation of *Hypericum humboldtianum* (including *H. jussiaei*) is present in the subpáramo and open places of the upper Andean forest belt (2500-3200 m) near Bogotá. The collections by Dr. J. Cuatrecasas (nr. 25) and Dr. E. Killip (nr. 34178) were made in thickets and low shrub, according to the labels.

81. Shrub of *Hypericum trianae* and *Senecio vaccinioides*

Low *Hypericum trianae* - *Senecio vaccinioides* shrub is only known from the humid W side of the Páramo de Guantiva. One stand was analysed at 3870 m in the Q. Minas valley (rel. 32) in the same physiographical setting as described for the *Senecionetum nitidi* (84). The rale *Hypericum trianae* is only 30 cm high; while *Senecio vaccinioides* is 1-1.5 m high. *Leptodontium pungens* is dominant in the moss layer. The thin (40 cm) humic clayey soil is strongly acid (pH 4.1).

82. Dwarfshrub of *Hypericum juniperinum*

Hypericum juniperinum (previously *H. brathys*) is a common leptophyllous dwarfshrub in the northern Andean páramos (Ecuador, Colombia, Venezuela) between 2650 (2200) - 3700 m. *Hypericum juniperinum* dwarfshrub vegetation, apparently is a final stage in the secondary succession on former potatoe fields, e.g. in the northern part of the Páramo de Sumapaz. *Hypericum juniperinum* dwarfshrub is successional to the *Rumex acetosella* vegetation, which covers the bare field after harvest. Here in the Páramo de Chisacá at about 3600 m, a *Hypericum juniperinum* stand was found (rel. 132) in a small, slightly humid valley floor, where potatoes had been raised 7 years before according to residents. The *H. juniperinum* dwarfshrub was about 80 cm high and had a cover of about 65%. Scarce 50-100 cm high stemrosettes of *Espeletia grandiflora* and some tussocks of *Calamagrostis effusa* were already present also. Apart from herbs, prostrate *Arcytophyllum muticum* covered almost half of the ground layer. The moss layer of *Breutelia* spp. (4926, 4928) had a cover of only 8%.

The humic clayey soil containing numerous annelid worms was about 100 cm thick, and the pH in the top soil layer was 4.4.

83. Other hypericaceous shrub and dwarftree vegetation

Some more species of the section *Brathys* of *Hypericum* may form genuine hypericaceous communities: e.g. *Hypericum phellos*, which is a dwarftree and shrub in Andean forests and lower pâramos (2600-3800 m) in the northern part of the Colombian Cordillera Oriental; the same applies to *Hypericum cuatrecasasii*, a species very close to *H. goyanesii*, from the forest line near Arcabuco.
This and other hypericaceous vegetation types have not been studied in detail, since they are primarily part of the high Andean forest vegetation, which falls outside the scope of this study.

84. *Senecionetum nitidi* ass. nov.
type: rel. 189; table 14.

Physiognomy: Well-developed stands (e.g. rel. 189) of this nanophyllous composite shrub with dark-greenish brilliant, revolute foliage and yellowish inflorescences, are structure as follows:
1) a dwarfed shrublayer, 1-1.5 m, the cover of which may be as high as 70%;
2) a herbaceous layer, mainly of grasses, about 40 cm high; cover 90%; and
3) a predominantly pleurocarpous moss layer, with a cover of about 20%. When there is cattle grazing, (e.g. rel. 99), the cover of the shrub layer is about 10%. The cover of the pleurocarpous mosslayer is about 80%. Under grazing most of the tussocks are replaced by cyperaceous and graminoid tufts and prostrate dwarfshrubs.

Composition & syntaxonomy: *Senecio nitidus* is the dominant and exclusive character species. Other frequent (and partly diagnostic) species are *Calamagrostis effusa, Pleurozium schreberi, Carex* cf. *conferto-spicata* (6126A), *Lorenzochloa erectifolia, Poa* cf. *pauciflora* (6123, 4129A), *Paspalum bonplandianum, Niphogeton glaucescens, Carex bonplandii, Arcytophyllum muticum, Halenia* sp. (6127, 4134), *Sphagnum compactum, Cladia aggregata, Campylopus albidovirens, Campylopus pittieri* and *Anastrophyllum leucostomum*.
Epiphytic cryptogams are scarce: e.g. *Metzgeria dorsipara*, Parmeliaceae, *Usnea* sp., Lejeuneaceae, *Sticta* sp. (6139).
Lorenzochloa and *Poa* cf. *pauciflora* were not observed in other shrubby communities at this height. The greatest affinities are with the *Senecionetum andicolae* (73), the *Hypericetum laricifolii* (74) and the azonal *Senecio vaccinioides* shrub (81, 96).

Synecology: This type of composite shrub is found in moist to humid valleys in the lower bunchgrass pâramos, where water collects from the catchment areas. Slopes are up to 7°. The phreatic level is at a depth of 10-15 cm.
The humic black, clayey soil is 60-90 cm thick and its upper layer is (strongly to) moderately acid (pH 4.6). The Aoo-layer is up to 5 cm thick.

Distribution: *Senecio nitidus* occurs as a shrub or dwarftree only in pâramos near Bogotâ between 3000 and 3700 m. The association is rare and has only been described from the pâramos between Neusa and S. Cayetano (3600-3700 m).

85. *Senecionetum vernicosi* ass. nov.
type: rel. 281; table 15; Fig. 29.
photo: Gradstein et al. 1977, plate 2D
lit.: Cleef et al., in press.

Physiognomy: Well-developed stands of these green-grayish microphyllous composite shrub with pale yellowish flowers are structured into:
1) a shrub layer 1-2(3-5) m high, with a cover of 50-80%;
2) a herbaceous layer generally with a low cover. In upper grass-pâramo stands bunchgrasses may penetrate the *Senecionetum vernicosi* and have a cover of 50% (in the understorey); and
3) a thick bryophyte layer, dominated by mosses; the covers is 50-100%. Liverworts are prominent in the ground layer (up to 40% cover) under the permanently humid conditions of the upper condensation belt.

Composition & syntaxonomy: *Senecio vernicosus* is a selective character species, endemic to the pâramos of the Colombian Cordillera Central and the Pâramo de Sumapaz, between 3600 and 4350 m. Frequent and characteristic species are *Leptodontium wallisii, Lachemilla holosericea, Peltigera dolichorhiza, Azorella multifida, Geranium sibbaldioides, Cora pavonia, Bryum* sect. *Rhodobryum* (?), *Senecio formosus, Oreomyrrhis andicola, Campylopus cavifolius, C. pittieri,* and *Carex tristicha.* True superpâramo taxa are *Lachemilla tanacetifolia, Draba* sp. (1300, petals yellow), *Valeriana plantaginea, Lachemilla nivalis* and *Breutelia lorentzii.* Species of bryophytes are dominant in the groundlayer: e.g. *Campylopus* sp. (8093) and *Plagiochila triangulifolia* in the most humid stand on the Nevado de Sumapaz; *Leptodontium wallisii* resp. *Campylopus* sp. on the Nevado Ruíz (4130 m) and S. Rosa (4350 m) in the Colombian Cordillera Central. *Plagiochila cleefii*, a skiophytic species, is only known from the Nevado de Sumapaz. Only a few specimens of our *Plagiochila* collections have been identified, and this new species is likely to occur in other parts. Some epiphytic mosses may be present on *Senecio* stems.
For the present diagnosis of the *Senecionetum vernosi*, data (Cleef et al. in press and unpublished) from stands in the Cordillera Central) have been used.

Table 15 *Senecionetum vernicosi* ass. nov.

relevé nr.	281	*Oreomyrrhis andicola*	<1(x)
relevé area m^2	18	*Draba* sp. (1300, yellow petals)	1
slope (degree)	3	*Bartsia* sp.	<1
cover % shrub	70	*Geranium confertum*	<1+
herbs	12	*Geranium sibbaldioides*	<1(x)
mosses	55	*Cerastium* sp.	<1
liverworts	40	*Lachemilla nivalis*	<1(x)
approx. number of species	39	*Senecio formosus* (juv.)	<1+(x)
soil	si	*Azorella crenata*	<1
depth cm	>120	*Laestadia muscicola*	1
pH top soil	5.0	*Luzula gigantea*	<1
alt. m.	4050	*Pernettya prostrata*	<1
locality	Sum	*Grammitis moniliformis*	<1
cover %	▲	*Acidodontium* cf. *megalocarpum*	1(x)
c *Senecio vernicosus*	70(x)	*Thuidium peruvianum*	1
Plagiochila triangulifolia	35	*Riccardia squarrosa*	1
Campylopus	40(x)	*Breutelia lorentzii*	<1
c *Leptodontium wallisii*	5(x)	*Bartramia angustifolia*	<1
c *Plagiochila cleefii*	2	*Peltigera dolichorhiza*	<1(x)
Azorella multifida	10(x)	Bryoideae (8046)	<1
Breutelia chrysea	10	pleurocarpous moss (8049)	<1
Herbertus subdentatus	2	*Lophocolea* spp. (8037, 8044)	<1
Cora pavonia	2(x)	*Anastrophyllum* sp.	<1
Satureja nubigena	1	*Syzygiella* sp. (8045[a])	<1
Lachemilla holosericea	<1(x)	*Chiloscyphus* sp. (8045[b])	<1
Carex cf. *tristicha*	<1	*Lachemilla* sect. *Lachemilla* (8034b)	<1

(x) Species in common with stands in the Parque Los Nevados, Cordillera Central.

Synecology: The composite thickets of the *Senecionetum vernicosi* are present on humid soil in the upper bunchgrass páramo and lower superpáramo. The *Senecionetum vernicosi* is well developed in protected sites in small valleys and ravines along the grasspáramo-superpáramo boundary. Scattered *Senecio vernicosus* shrub is also present in the zonal upper bunchgrass páramo, especially on the high volcanoes in the Parque Los Nevados (Cleef et al., in press). The cover becomes higher towards the lower limit of the superpáramo. High *Senecio vernicosus* shrub occurs also on azonal boggy ground in the grass páramo of the Páramo de Sumapaz, where it is common in *Swallenochloa-Breutelia* bog (10) with cushions of *Oreobolus obtusangulus* and *Eriocaulon microcephalum*. These locations have many species in common with the type relevé. The studied sites were located in watershed areas at 3800 m on the Cuchilla Los Frailes, 3 km NE of Alto S. Agustin, and at 4000 m on the Cuchilla La Rabona (rel. 503).
The grayish-brown silty soil on calcareous bedrock is about 1 m thick, the upper layer is moderately acid (pH 5.0), and is rich in organic content. In other places, the *Senecionetum vernicosi* is found on sandstone and volcanic bedrock.

Distribution: The *Senecionetum vernicosi* is found at 4000-4100 m on the Nevado de Sumapaz in the Cordillera Oriental. Similar stands may be common between 3800-4100 m in all high watershed areas of this vast páramo. The *Senecionetum vernicosi* is also present in the Colombian Cordillera Central, e.g. between 4100 and 4350 m on the volcanoes in the Parque Los Nevados (Cleef et al., in press).

86. *Cortaderio sericanthae - Arcytophylletum caracasani* ass. nov.
type: rel. 407; table 16; Fig. 74 (also Fig. 75)
lit.: Vareschi 1980

Physiognomy: This rale, leptophyllous, dark olive-green, rubiaceous shrub with rounded dense canopies and conspicuously shiny yellowish-orange stipulae, white or faint-lilac flowers and twisted stems. Most of the rubiaceous shrubs or dwarftrees have twisted stems with seasonal rings (probably reflecting) dry periods with water stress. In well-developed stands the following layers can be recognized:

1) an open, rale shrub layer (0.5-2 m), whit a cover of about 50%;
2) a herb-dwarfshrub layer up to 50 cm, with a cover of 5-40%. Grasses are the main component;
3) a cryptogamic ground layer, with a cover of 10 to 40%, predominantly consisting of mosses and lichens.

Composition & syntaxonomy: *Arcytophyllum caracasanum* is a (selective?) character species, with a cover of 30% or more. In contrast to Steyermark (1971), the present author considers *A. caracasanum* (or: *A. nitidum* ssp. *caracasanum* var. *culmenicolum*) as a valid species that differs morphologically from *A. nitidum* (ssp. *nitidum*, sensu Steyermark 1971) as well as ecologically, at least in the Colombian Cordillera Oriental. *Acrytophyllum caracasanum* var. *culmenicolum* is found in the Colombian Cordillera Oriental between 2500 and 4050 m, as far as the Nevado de Huila 3000-3600 m and the Sierra Nevada de Mérida up to 4300 m (Steyermark 1971); together with the var. *caracasanum* it occurs on the highest peaks of the Cordillera de la Costa above Caracas (Steyermark & Huber 1979).
For other character species reference is made to table 16. Common taxa in our study area are *Oreobolus obtusangulus* ssp. *rubrovaginatus*, *Cortaderia sericantha*, *Carex* aff. *conferto-spicata*, *Gentianella corymbosa*, *Bartsia* sp. *Calamagrostis effusa*, *Rhacocarpus purpurascens*, *Campylopus richardii*, *Jamesoniella rubricaulis*, *Siphula* spp., *Cladia aggregata* and *Cladonia isabellina*,

Table 16. *Cortaderio-Arcytophylletum caracasani* ass. nov.

	subass. (prov.)	86[a]		86[b]		
	relevé nr.	247	261	407	239	383
	relevé area m^2	16	20	35	25	36
	slope (degree)	3	20	30	13	12
	cover % (dwarf)shrub	75	37	30	50	13
	grasses (bamboos present)	5	20	2	15	27
	mosses	8	8	33	17	10
	liverworts	<1	2	4	<1	5
	lichens	1	10	2	18	27
	soil depth cm (max.)	10	15	10	2	5
	soil	cSg	Sg	C/g	g/s	g/s
	pH top soil	5.0	4.9	5.0	4.7	5.1
	approximate number of species	33	42	53	43	35
	alt. m	3725	3820	3605	3935	3605
	locality	Rus	Rus	Min	Rus	Arn
	cover %			▲		
	c & d taxa *Arcytophylletum car.*					
c	*Arcytophyllum caracasanum*	10	30	30	15	5
c	*Cortaderia sericantha*	5	15	1	10	25
c	*Oreobolus obtusangulus* ssp. *rubro-vag.*	10	15	10	3	<1
c	*Carex* aff. *conferto-spicatae*	<1	<1+	1	1	1+
c	*Rhacocarpus purpurascens*	5	5	15	10	5
c	*Campylopus richardii*	2	3	7	1	2
	Jamesoniella rubricaulis	<1	2	1	<1	
	Cladonia isabellina	<1	<1	<1	<1	<1
	Bartsia sp.	<1	1+	<1		<1
	Calamagrostis effusa	<1+	1		1	2
	Siphula spp.		<1+	<1+	10	25
	Cladia aggregata	<1+	1		1	2
	Gentianella corymbosa	<1	<1		<1+	<1+
	Diploschistes sp.	<1	<1	?		<1
	Puya trianae	<1	1		<1	
c	*Diplostephium colombianum*	60			35	
	Racomitrium lanuginosum	1			1	
	Racomitrium crispulum	1		10		
	Andreaea rupestris		5		<1	<1
c	*Hypericum tetrastichum*	5	5			
	Aragoa cupressina	<1	<1			
	Toninia sp.	<1	<1			
	Geranium multiceps	<1	<1			
	Gnaphalium antennarioides	<1	<1			
	Castratella piloselloides	<1+	1			
	Rhynchospora paramorum	1	2			
	Pterichis galeata		<1			
	Paepalanthus paramensis	<1+				
	Xyris acutifolia	1				
	Espeletia congestiflora	1	35			
	Hypericum strictum		<1			
	Swallenochloa tesselata			<1	2	2
	Grammitis moniliformis			<1+	<1	<1
	Sisyrinchium pusillum			<1+	<1	
c	*Hypericum garciae*				20	8
	Leprocaulon albicans				<1+	<1

	(247)	(261)	(407)	(239)	(383)
Disterigma empetrifolium			<1+		<1
Halenia sp.(p)			<1		<1
Leptodontium pungens			<1	<1	
Alectoria ochroleuca			<1	<1	<1
Carex pichinchensis			2		3
Cora pavonia			<1+	<1	
Spiranthes vaginata			<1		
Espeletia grandiflora ssp. *boyacensis*			5		
Stereocaulon atlanticum			<1		
Cladonia boliviana			<1	<1	
Oritrophium peruvianum			<1+		
Herbertus acanthelius				<1	1
Other taxa:					
Lycopodium contiguum		<1		<1	
Pernettya prostrata	<1+	<1+		1	
Castilleja integrifolia		1+		<1	
Rhynchospora macrochaeta		1	1		
Lepidozia sp.(p)		<1			2
Vaccinium floribundum var. *ramosissimum*		<1	10	1	
Agrostis haenkeana		<1	1		
Riccardia sp.(p)	<1	<1+			<1
Anastrophyllum leucostomum	<1		1		
Herbertus subdentatus		<1	3		
Diplostephium phylicoides		<1			
Vaccinium floribundum var. *marginatum*	1				
Harpalejeunea sp.	<1+				
Hypericum laricifolium		2			
Bartramia angustifolia		<1+			
Gaultheria ramosissima				1	
Calamagrostis bogotensis				1	
Aongstroemia julacea			<1		
Thamnolia vermicularis				<1	
Campylopus pittieri				<1	
Cladonia miniata					<1
Cladonia polia			<1		
Cladonia confusa				<1	
Cladonia rangiferina var. *abbayesii*				2	
Cladonia colombiana				<1	
Hesperomeles pernettyoides					1
Lupinus sp.					<1+
Sphaerophorus melanocarpus				<1	

Cortaderia sericantha is widely distributed in open vegetation in the páramos from Ecuador to Colombia and Venezuela and in the study area on mineral soil and in sandstone crevices from the forest line up into the superpáramo at 4350 m. *Carex* (aff.) *conferto-spicata* (e.g. 6990) seems to be related to the low sedge species *C. tristicha* (Dr. T. Koyama, in litt.). *Carex tamana* Steyermark is probably synonymous. *Diplostephium columbianum* may be an associated endemic low shrub in the northern páramos of our area. Some endemic species of *Hypericum* also are associated, e.g. *H. tetrasticha* and *H. garciae*.

Synecology: In the study area, the *Cortaderio-Arcytophylletum caracasani* is found in bamboo páramos. The open shrubby *Arcytophyllum caracasanum* vegetation is found in crevices or patches with soil in areas with e.g. "lajas" and "roche moutonnée". Such high altitude species as *Diplostephium colombianum* and *Cortaderia sericantha* find their habitat in these places.
A number of taxa from the thin stony soils in grass páramos is present also: e.g. *Campylopus richardii*, *Jamesoniella rubricaulis*, *Herbertus acanthelius*,

Carex conferto-spicata, Siphula spp., *Diploschistes* sp., *Leprocaulon congestum, Puya trianae, Espeletia congestiflora, E. annemariana* var. *rupicola, Racomitrium lanuginosum, Racomitrium crispulum, Stereocaulon atlanticum* and *Oreobolus obtusangulus*. Most of these species have their optimum in the bamboo páramos. The lithosols are moderately acid (pH 4.7-5.1 in 6 relevés). The clayey to sandy dark brownish thin soil in the rock crevices retains the moisture for a longtime.
Species of *Dysdercus* are common.
Transpiration probably is reduced at these sites with shallow soil since the plants possess clear xeromorphic features such as imbricate leptophyllous leaves (*Arcytophyllum caracasanum*), cushion form (*Oreobolus*), and blackish colours in mosses, the leaves of which have a hyaline hairpoint (*Campylopus richardii* and *Racomitrium* spp.). Species as *Jamesoniella rubricaulis, Herbertus subdentatus, H. acanthelius* (all liverworts) and the lichen *Leprocaulon albicans* thrive because of the permanent fog and are excellent indicators for humid conditions. Apparently these species persist during short dry periods.

Distribution: In the study area the *Cortaderio-Arcytophylletum caracasani* is present in bamboo páramos from the forest line up to 4050 m. The relevés are from the central part of the Cordillera Oriental (Guantiva, Rusia, Tota) between 3600 and 3950 m. According to herbarium data *Arcytophyllum caracasanum* is present on the southern slopes of the Páramo de Sumapaz (Cordillera de Los Cruces) between about 3400 and 3650 m (Fosberg 20859, 20903 - US), in the northern páramos of the Cordillera Oriental (Santurbán, Romeral, Tamá) and in the Páramo de Guasca where Fosberg (21698 US) reported this species as a common shrub on ridges (3500-3600 m).
Vareschi (1970, 1980) reports *Arcytophyllum caracasanum* shrub from screes up to 4100 m in the Sierra Nevada de Mérida, Venezuela. Associated species are *Ottoa oenanthioides* HBK, *Gynoxys violaceae* Sch.Bip., *Aragoa* and *Vallea*; or with *Valeriana phylicoides* Briq., *Draba funckeana* Planch., *D. lindenii* Planch., *Hinterhubera columbica* Sch.Bip. and *Polystichum* sp. Because of different floristic composition, apparently this may represent another syntaxon.
Timberline forest with gnarled trees of *Arcytophyllum caracasanum* (4-6 m high) with codominance of *Senecio vaccinioides* and Espeletiinae, was studied by T. van der Hammen & R. Jaramillo Mejía (in prep.) at 3850 m on the west slope of the northern part of the Páramo de Guantiva near the Laguna La Jequera. Probably this type of humid timberline forest with *Neurolepis* may pass into the *Cortaderio-Arcytophylletum* at higher altitudes.

87. *Myricetum parvifoliae* Van der Hammen & Cleef ass. nov. (prov.)
type: T. van der Hammen & A.M. Cleef rel. 188; table 17

Physiognomy: The up to 2.5 m high microphyllous thickets have windpollinated flowers and a strongly aromatic foliage. The stand in rel. 188 is structured in:
1) a shrub layer (cover 95%);
2) a rale herb layer with a cover of about 5% and up to 40 cm high, and
3) a thick ground layer dominated by pleurocarpous mosses covering up to 80%.

Composition & syntaxonomy: *Myrica parvifolia* is the principal shrub and only selective character species. This gale species is also present (locally frequent) as small tree in the upper part of the Andean forest belt and subserial thickets. According to herbarium labels *Myrica parvifolia* is common between 2650 and 3400 m in the Colombian Cordillera Oriental, in the Venezuelan Sierra Nevada de Mérida, and in the Andes of northern Ecuador.
Myrica parvifolia stands can be easily recognized by dominance of this *Myrica* species. The floristic affinity is with the shrub associations of the *Senecionetum andicolae* (73) and the *Hypericetum laricifolii* (74).

Table 17.

Myricetum parvifoliae Van der Hammen & Cleef ass. nov. (prov.)

author rel. & ref. nr. T. van der Hammen & A.M. Cleef	▲ 188
relevé area	50 m^2
cover shrubs	95%
herbs	6%
cryptogams	80%
slope	20%
altitude m	3700 m
locality	Sierra Nevada del Cocuy; Salto Río Cóncavo

cover %

shrublayer:		groundlayer:	
Myrica parvifolia	60	*Relbunium hypocarpium*	<1
Rapanea dependens	15	*Peperomia microphylla*	2
Senecio andicola	5	*Hypnum amabile*	50
Berberis sp.	5	*Leptodontium luteum*	15
Eupatorium theaefolium	3	*Campylopus* sp.	10
Sericotheca argentea	2	Dicranaceae	2
Arcytophyllum nitidum	2	Parmeliaceae	1
Cestrum sp.	1	*Cladia aggregata*	<1
Miconia salicifolia	1	*Cladonia* spp.	
herblayer:		(subg. *Cenomyce*)	2
Orthrosanthus chimboracensis	1		
Polypodium murorum	1		
Polypodium sp.	1		
Acaena elongata	<1		
Acaena cylindristachya	<1		
Rubus sp.	<1		

note: *Symplocos theiformis*, and dwarftrees and shrubs of *Befaria* sp. are present in the same phytocoenosis.

Synecology & distribution: The association forms timberline thickets on slightly humid ground, where water accumulates from the zonal *Arcytophyllum nitidum* dwarfshrub paramo. The slope is about 20°. The *Myricetum parvifoliae* was only observed along the Rio Cóncavo in the Sierra Nevada del Cocuy (dry side) between 3680 and 3750 m. As discussed before in chapter II, subpáramo vegetation is present here higher altitudes due to different climatic factors on either side of the Cordillera. The *Myricetum parvifoliae* is scarce in the páramos of our area.

Note: In pollen diagrams from clayey to peaty deposits from the last glacial period in the high plain of Bogotá, local *Myrica*-dominated vegetation is reflected, accompanied by Compositae and sometimes *Symplocos* (Van der Hammen et al. 1980). This azonal vegetation on these soils was apparently widely distributed in the high plains. The corresponding plant community may have been closely related to the *Myricetum parvifoliae*.

88. Shrub of *Diplostephium alveolatum*

Microphyllous to nanophyllous *Diplostephium alveolatum* is probably an Andean subspecies of *Diplostephium costaricense* Blake (Cuatrecasas 1969). In the study area, morphological and ecological differences can be noticed between the populations of *Diplostephium alveolatum* in the Sierra Nevada del Cocuy and in the páramos near Bogotá.
Specimens of the Cocuy population are found in *Gynoxys albivestita* dwarf forest

and in zonal subpáramo thickets, together with *Senecio vaccinioides*, on the dry side of the Sierra up to 4060 m.
The Sumapaz population of *D. alveolatum* (3400-4020 m) probably represents another undescribed variety, that occurs along páramo streams, and constitutes a low shrub community in the highest *Swallenochloa-Espeletia* bogs with *Breutelia* along the crestline between 3800-4000 m. Stands of these shrubs were commonly observed from the Media Naranja and La Rabona to the Cuchilla Los Charcos and Chorreras watershed areas in the central part of the Páramo de Sumapaz.

Other dwarsshrub of Compositae

Apart from the five already treated shrubby composite communities, the area contains a number of patches of other Compositae. The vegetation of some of these patches may deserve a separate syntaxonomical description, if more representative relevés are available. The following (dwarf)shrub communities have been observed.

89. Dwarfshrub of *Diplostephium glutinosum*

Diplostephium glutinosum is a nanophyllous, dark greenish rale and low dwarfshrub with white ray flowers. This species is endemic to the northern páramos of the Colombian Cordillera Oriental. Patches of *Diplostephium glutinosum* ssp. *cocuyensis* grow on exposed rocks and ridges along the wet slopes of the Cordillera from the páramos NE of Lake Tota to Pisva and to the Sierra Nevada del Cocuy (3600-4000 m); the ssp. *glutinosum* was collected in the Páramo del Almorzadero, Santurbán, Romeral and Tamá (3950-4150 m). The present distinction in two subspecies, one of which is subdivided into three formas (Cuatrecasas 1969, 1975), reflects the spatial isolation of these small populations on the high mountains in the northern part of the area.

90. Dwarfshrub of *Diplostephium juajibioyi*

Open microphyllous cinereous shrub of *Diplostephium juajibioyi*, 1-1.5 m tall, with white rayflowers and a purple disc have only been noticed on bouldery screes on the humid side of the Cordillera. Common associates are *Centropogon ferrugineus*, *Gynoxys* sp., *Acnistus quitoensis*, *Miconia andina*, *M. mesmeana* var. *jabonensis*, *M. salicifolia*, *Polystichum* sp., *Ribes* sp., *Solanum bogotense*, *Echeveria* sp. (9186), *Herbertus subdentatus*, *Disterigma empetrifolium*, *Rhacocarpus purpurascens*, *Chorisodontium setaceum*, *Jamesoniella rubricaulis*, etc. The endemic dwarfshrub *Niphogeton fruticosa* may be present too. *Diplostephium juajibioyi* scree bush is only known from the northern páramos of the Colombian Cordillera Oriental, where it is present in the Páramo del Almorzadero, on the E slope of the Sierra Nevada del Cocuy (common), in the Páramo de Pisva and on the Peña de Arnical, NE of Lake Tota between 3550 and 3950 m. This applies to the ssp. *juajibioyi*, and the community might be a separate association when more representative relevés are available.
From the Páramo de Sumapaz a 2-4 m high shrub was recently described by Cuatrecasas (1975) as ssp. *leucopappum*. This subspecies is present in *Escallonia* dwarfforestpockets in the open grass páramo at 3500-3550 m.

91. Dwarfshrub of *Diplostephium columbianum*

Diplostephium columbianum is a heather-like leptophyllous dark-greenish dwarfshrub (30-100 cm high) with white to faintly lilac rayflowers. It is most common in the zonal transition from the upper bunchgrass páramo, including higher nunatak-like areas, to the lower superpáramo (4000-4500 m) in the Sierra Nevada del Cocuy. In lower places *Diplostephium colombianum* patches are found in crevices on roches moutonnées in the Páramo de la Rusia (3750-3950 m) and in the Páramo del Almorzadero (3850 m). In some places these patches are associated with open shrub of the *Cortaderio-Arcytophylletum caracasanae* (see 86).

92. Dwarfshrub of *Diplostephium rupestre*
Fig. 29

Diplostephium rupestre is a nano-to microphyllous dwarfshrub (up to 80 cm high) with cream-coloured to lilac rayflowers, hairy, green foliage, and a well-developed root system. This species is reported as new to the Colombian Cordillera Oriental, where it is presently only known from the summit area of the Nevado de Sumapaz between 4000 and 4250 m. *Diplostephium rupestre* was previously known from the high páramos in northern Ecuador and the Colombian Cordillera Central and Occidental (Cuatrecasas 1969). The high volcanoes of the Colombian Cordillera Central contain two other related species of the series *Rupestria* Blake: the widely distributed *Diplostephium eriophorum* Wedd. and *D. ritterbushii* Cuatr., which is endemic to the Nevado de Huila.
Diplostephium rupestre dwarfshrub vegetation is found on the Nevado de Sumapaz on humid clayey soil and on limestone screes (slope 10-22°) between 4100 and 4180 m. The pH of the very dark-brown upper soil layer is 5.1-5.3. Water is regularly perculating through the calcareous gravel and soil (up to 70 cm thick). Nect to *Diplostephium rupestre* which covers of 15-20%, species of the *Valeriana plantaginea-Racomitrium crispulum* community (27) are growing on the rocky slopes.
Characteristic species for *Diplostephium rupestre* dwarfshrub are *Bartsia* sp. (8146B, reddish corolla), *Poa* cf. *pauciflora* (8094), *Werneria humilis* var. *angustifolia, Lucilia pusilla, Bryoerythrophyllum jamesonii* (especially in wet places), *Zygodon squarrosus, Siphula* sp. (8099C), *Radula sonsonensis, Anastrophyllum* sp., *Leptolejeunea* sp. (1849), and *Cheilolejeunea* subg. *Strepsilejeunea* 1849C). The floristic composition and the number of species (about 35) indicates a permanent and high humidity.

93. Dwarfshrub of *Senecio guicanensis*

This yellowish to grayish nanophyllous shrub (up to 1.5 m high) dotted with light yellow flowering heads is endemic to the scattered superpáramo vegetation of the Sierra Nevada del Cocuy between 4200 and 4500 m. Though this species is mostly present in zonal superpáramo communities on moraines, denser stands were locally observed on humid sandy ground along streams, among rocks and in slight depressions on moraines (pH 5.1 in rel. 324)

94. Dwarfshrub of *Senecio cacaosensis*

Senecio cacaosensis is a rale grayish nanophyllous shrub with strongly revolute leaves covered with sericeous indumentum and whitish flowers, endemic in subpáramo *Sphagnum* bogs in the headwaters of Río Casanare and the Páramo de Pisva between 3080 and 3430 m. Common associates are *Espeletia lopezii* var. *major, Swallenochloa tesselata, Hypericum magniflorum, Diplostephium revolutum* and *Puya goudotiana*.

95. Dwarfshrub of *Senecio guantivanus*

This species forms microphyllous shrubs or dwarftrees in the subpáramo and (subserial) in the andean forest belt between 2200 and 3500 m, mainly in the department of Boyacá. Subserial dwarfshrub of *Senecio guantivanus* is distributed in the arid Páramo de Guîna near S. Rosa, where in many places the original shrub páramo is destroyed due to intensive grazing and burning.

96. Shrub of *Senecio vaccinioides*
photo: Cleef 1978, photo 167.

Azonal patches of *Senecio vaccinioides* are common on humid soil in the Páramo de Guantiva between 3800 and 3900 m. These dark-greenish nanophyllous thickets with yellowish flowers are present in depressions on slopes and in "pockets", or locally adjacent to humid meadows with *Lachemilla orbiculata*, the *Oritrophio-Wernerietum pygmaeae* (62) and the *Hyperico-Plantaginetum rigidae* (65). *Leptodontium wallisii* is dominant in the groundlayer. *Hypericum trianae* or/and *Swallenochloa tesselata* may be associated species on the western wet side of the Páramo de Guantiva (see 81). Soils are humic, sandy to clayey, and strongly acid (pH 4.1 in rel. 32) in the upper layer. *Senecio vaccinioides* shrub in the Páramo de Guantiva is geographically vicariant with the *Senecionetum nitidi* (84) in the dry bunchgrass páramos of Cundinamarca.

97. Other dwarfshrub communities

Other (dwarf)shrub species have not been found in proper communities in azonal patches.
Lachemilla polylepis, a woody species, is present up to 4450 m in the northern páramos of the Colombian Cordillera Oriental and also in the páramos of the Sierra Nevada de S. Marta, in the Venezuelan Sierra Nevada de Mérida, and in Costa Rica (E.G.B. Kieft, unpubl.). This species provides a good example of the evolution of an originally herbaceous species towards a woody species, as discussed by Carlquist (1974). *Lachemilla polylepis*-dominated shrub is common in screes in the Sierra Nevada de S. Marta between 3800 and 4100 m (Rangel et al., in prep.). As far as known, the study area contains only solitary dwarfshrubs of *Lachemilla polylepis*
The same applies to another rosaceous shrub, *Sericotheca argentea* (3400-4400 m), which is a common constituent of páramo thickets, mostly on the dry side of the mountains.

Valeriana triphylla (previously *V. mutisiana* (Wedd.) Hoeck.) is locally found in large clumps in the páramos of our area between 3300 and 4080 m. This rare white flowering endemic shrub (30-1.50 m high) may be locally abundant on thin soils near outcrops of or on moraines. *Valeriana triphylla* is known from the páramos near Bogotá, the Páramo de la Rusia and the Sierra Nevada del Cocuy (Arauca).

DWARFFORESTS

98. Dwarfforest of *Polylepis quadrijuga*
Fig. 75

A phytosociological study on *Polylepis quadrijuga* dwarfforests in the Colombian Cordillera Oriental is in preparation by T. van der Hammen, R. Jaramillo-Mejía and the present author, and only some general information will be presented here.
According to Simpson (1979) *Polylepis quadrijuga* is endemic to the Colombian Cordillera Oriental, and is closely related to *Polylepis reticulata* Hieron., *P. weberbaueri* Pilger and to *P. lanuginosa* HBK, all Ecuadorian species. *Polylepis* (Rosaceae, Sanguisorbeae) is endemic to the high tropical Andes, from northern Argentina and Chile to Colombia and Venezuela, between 1800 and 5200 m. Simpson (l.c.) considered *Polylepis* as the arborescent angiosperm genus with the highest natural occurrence in the world. Rosaceous parallel genera at lower altitudes in tropical Africa are *Hagenia* and *Leucosidea*. Simpson distinguished

15 species of *Polylepis* in her recent revision. The nanophyllous *Polylepis quadrijuga* (syn. *P. cocuyensis* Cuatr., *P. boyacensis* Cuatr.) with compound leaves occurs from the upper forestline at 2900 m up to the lower limit of the superpáramo at 4200 m (Cuatrecasas 1958). *Polylepis quadrijuga* dwarfforests are common on the western Magdalena slopes of the Cordillera Oriental and rather scarce on the eastern side. Especially the western sides of the Páramo de Sumapaz, the Páramo de Guantiva and the Sierra Nevada del Cocuy contain most stands. *Polylepis quadrijuga* dwarfforest is present as isolated patches in the grass páramo or is found as Andean timberline forest. Terrestric and epilithic bryophytes have a cover of 70-100%.

In the grass páramo isolated dwarfforests dominated by *Polylepis quadrijuga* were studied between 3735 and 4025 m in the páramos of Guantiva, Rusia and the Cocuy, where they grow on boulder screes or in rockshelters or on steep slopes. Height of the stunted dwarftrees is 5-10 m. Thermic conditions in the rockshelter habitats in Venezuelan páramos according to microclimatological data mentioned by Azócar & Monasterio (1979), are more favourable for the growth of arborescent species than the surrounding grass páramos. The average temperature is 2-3° C higher and the number of days without severe frosts is considerably less than in the surrounding zonal grass páramo. The ecology of *Polylepis* was discussed by Walter & Medina (1969), Ellenberg (1958 a,b), and A.P. Smith (1977), and their results were summarized by Simpson (1979).
Characteristic vascular species in isolated *Polylepis quadrijuga* stands in the grass páramo of the study area are: *Eupatorium (Ageratina] glyptophlebium, Echeveria* spp., *Stachys* cf. *elliptica, Luzula gigantea, Senecio formosus, Cerastium* sp., *Polystichum* sp., *Oxylobus glanduliferus, Gynoxys albivestita, Galium canescens, Eupatorium (Ageratina) theaefolium, Niphogeton ternata, Miconia andina.* The austral-antarctic element is represented by the rare *Dysopsis glechomoides,* an euphorbiaceous herbaceous species, found in temperate forests in Chile and Juan Fernandez, the moss *Lepyrodon tomentosus*, and species of *Chorisodontium.* Apart from the characteristic species *Polylepis quadrijuga* stands include the following common vascular species: *Monnina salicifolia, Gynoxys* spp., *Oxalis* spp., *Peperomia hartwegii, Miconia andina, Relbunium hypocarpium, Sibthorpia repens, Grammitis moniliforme,* and species of *Berberis* and *Ribes.*

T. van der Hammen and R. Jaramillo-Mejia studied timberline stand of *Polylepis quadrijuga* in the Páramo de Chisacá (3450 m) and the Páramo de Guantiva (3350-3750 m). The *Polylepis* trees generally grow together with other codominant species of the upper Andean forest and shrub páramo, e.g. *Weinmannia fagaroides, Escallonia myrtilloides, Gynoxys* spp., *Eupatorium (Ageratina) tinifolium, Hesperomeles* spp., *Brachyotum* sp., *Hypericum* sp., *Miconia* spp. (sect. *Cremanium* prob.). *Bucquetia glutinosa, Ilex kunthiana,* which are scarce to absent in *Polylepis*-dominated patches in the grass páramo. Van der Hammen & Gonzalez (1960[a], 1963) published an inventory of a "*Polylepietum*" from the Páramo de Guantiva at 3400 m. Timberline stands may be found on flat sandy valley floors and on steep slopes.

Palynological data from the Plio-Pleistocene sediments of the Sabana de Bogotá and surroundings (Van der Hammen et al. 1973) suggest that *Polylepis* pollen is already present (2.5-2.7 million years ago). According to Van Geel & Van der Hammen (1973) the area of Lake Fúquene (2650 m), N of Bogotá must have been covered with *Polylepis* woodlands during a warmer and drier interstadial complex of the Middle Pleniglacial about 30.000 - 40.000 years B.P.

99. Dwarfforest of *Hesperomeles* cf. *goudotiana*

Isolated stands dominated by the microphyllous rosaceous *Hesperomeles* cf. *goudotiana* were observed on the dry West side of the Sierra Nevada del Cocuy (Páramo Cóncavo) at 3800 m, and on the dry South side of the Páramo del Almorzadero from 3700 m to 3850 m.
The trunks with diameters of more than 1 m are the thickest observed in páramo dwarfforests; the canopies reach a height of about 8 m. The stands occur in sheltered sites facing the dry interandean Chicamocha valley. This semiarid habitat with high average temperatures at these heights is favourable for arborescents. The identity of this species of *Hesperomeles* is not yet certain (*H. lanuginosa?, H. goudotiana?*). Wet *Hesperomeles lanuginosa* forest with *Neurolepis aristata* is present as zonal Andean timberline forest at 3700-3750 m on the western Cauca slope of the old volcano ruins of S. Rosa and Otún in the Colombian Cordillera Central (Cleef et al., in press) and in the Páramo of Barragán (Cuatrecasas 1954). The *Hesperomeletum lanuginosae* Cuatr. 1958 (syn. *Hesperomeletum ferrugineae* Cuatr. 1934) was described by Cuatrecasas (1934, 1958) from the upper Andean forestbelt on the Nevado de Tolima.

100. Dwarfforest of *Escallonia myrtilloides*
table 18.

Escallonia myrtilloides is a nanophyllous dwarftree in high altitudes of the tropical Andes (Sleumer 1968). Sleumer (1968) recognized the variety *myrtilloides* (Colombia to northern Argentina) with smaller leaves and the var. *patens* Sleumer (Costa Rica to Venezuela and Bolivia) with larger leaves. According to Dr. H. Sleumer (L), our specimens belong to var. *myrtilloides*. In the Colombian Cordillera Oriental this taxon is found between 2650 m (Sabana de Bogotá) up to 3750 m in the open páramo belt.

Van der Hammen & González (1960) reported already on an "*Escallonietum*" from the Ciénaga del Visitador at 3300 m in the Páramo de Guantiva. *Escallonia myrtilloides* is dominant, and *Eupatorium fastigiatum* is codominant, next to 17 other vascular species. Similar stands of *Escallonia* were also observed along páramo streams elsewhere in the Páramo de Guantiva and in the Páramo de la Rusia at 3550 m, together with 3-4 m high shrubs of *Hypericum laricifolium* ssp. *laricoides*. Boggy stands with *Escallonia myrtilloides* are known in mires surrounding the Laguna la Guitarra at 3425 m, some km W of the Nevado de Sumapaz (Meta). Vareschi (1958) reported an *Escallonia tortuosa* HBK (= *E. myrtilloides*) dwarfforest on the marshy shores of the Laguna Coromoto at 3400 m in the Venezuelan Sierra Nevada de Mérida, where *Dryopteris paleacea* Christ. and *Sibthorpia repens* are abundant in the understorey.

Timberline dwarfforest with dominance of *E. myrtilloides* was studied by T. van der Hammen & R. Jaramillo-Mejia in the headwaters of Río S. Rosa at 3450 m in the Páramo de Chisacá, the northernmost part of the Páramo de Sumapaz. A phytosociological treatment of this type of *Escallonia* dwarfforest is in preparation. *Escallonia myrtilloides* stands on the cloud forest timberline have been observed elsewhere in the Páramo de Sumapaz, e.g. in the Río Nevado valley and its tributaries (Meta) between 3300 and 3550 m. *Eupatorium (Ageratina) tinifolium* is a common associate, just as *Miconia salicifolia, Gaultheria ramosissima, Monnina salicifolia, Chusquea scandens, Gynoxys* sp., *Berberis cretata, Oreopanax mutisii, Centropogon ferrugineus* and *Espeletia tapirophila*. An inventory follows of an *Escallonia myrtilloides*-dominated pocket surrounded by open bunchgrass - bamboo páramo at 3535 m above the SE shore of the Laguna El Nevado on the WSW slope of the Nevado de Sumapaz, surveyed in January 1973. Its floristics mainly reflect the vicinity of the wet timberline.

Table 18

Escallonia myrtilloides "pocket, 3535 m (Nevado de Sumapaz, Meta).

woody species:

Escallonia myrtilloides
Miconia latifolia
Senecio andicola
Diplostephium juajibioyi ssp. *leucopappum*
Miconia cleefii
Senecio flos-fragrans
Diplostephium sp.
Senecio vaccinioides
Senecio guadelupe
Berberis cf. *sumapazana*
Eupatorium tinifolium
Oreopanax mutisii
Gaultheria ramosissima
Cestrum parvifolia
Acnistus quitoensis
Gynoxys sp.
Diplostephium cf. *alveolatum*

herbaceous species:

Calceolaria penlandii
Peperomia sp. (8018)
Peperomia sp.
Swallenochloa tesselata
Rhynchospora sp.
Pteridium aquilinum
Grammitis spp.
Hydrocotyle sp.
Rumex tolimensis
Greigia sp.

lianas:

Valeriana pavonii

bryophytes (epiphytic):

Herbertus subdentatus (large form)
Bartramia angustifolia
Syzygiella sp. (8021)
Porotrichodendron robustum
Chorisodontium setaceum
Zygodon goudotii
Acrocarpous moss (8029)
Metzgeria decipiens
Lejeuneaceae (8030)

(terrestric):

Dicranaceae (8029)
Trichocolea sp. (8025)
Atractylocarpus longisetus

(epiphytic lichen)

Sphaerophorus melanocarpus

Other *Escallonia myrtilloides* stands at the wet cloudforestline were also observed in the headwaters of Río Casanare (Alto El Poleo, Quebrada Los Osos, Q. El Playón) between 2750 and 3100 m.
An open *Escallonia myrtilloides*-dominated dwarfforest was observed at 3750 m in the plain at the base of Páramo Cóncavo on the dry W side of the Sierra Nevada del Cocuy In the Colombian Cordillera Central *Escallonia myrtilloides* dwarfforest was recently studied in the Parque Los Nevados (Cleef et al., in press). Around Lake Otún *Escallonia myrtilloides* shrub and dwarfforest is present between 3900 and 4000 m. In well-developed stands *Escallonia myrtilloides* is the only dominant dwarftree species. Dominant species in the groundlayer are *Geranium sibbaldioides*, *Leptodontium* sp. *Zygodon pichinchensis* and *Agrostis* cf. *haenkeana*. Sleumer (1968) reported pure stands of *Escallonia myrtilloides* from the Ecuadorian Cordillera Occidental near Riobamba.

101. Dwarfforest of *Gaultheria ramosissima* and *Aragoa perez-arbelaeziana*

This type of ericaceous dwarfforest with *Aragoa perez-arbelaeziana* and Compositae shrubs was only seen and studied in the Chorreras valley on the W side of the Páramo de Sumapaz. A stand was found in a pocket at 3750 m on a steep, rocky slope surrounded by open *Calamagrostis effusa* - *Oreobolus obtusangulus* ssp. *rubrovaginatus* bunchgrass páramo, and facing NW towards the village of S. Juan.

The blackish clayey soil (pH 4.4) between the boulders was not thicker than 15 cm. A 10 cm thick felty, brownish Aoo layer was overgrown by bryophytes. Rel. 305 (see table 19) represents record of this stand. Other common species in this dwarfforest, but not recorded here, are *Gynoxys* sp. (grayish leaved species, also present in rockshelters near the Laguna Gobernador; see table 20), *Miconia salicifolia* and *Tristerix* sp.

Table 19

Gaultheria ramosissima - Aragoa perez-arbelaeziana dwarfforest.

rel. nr.	305
exp.	NW
slope (degree)	25°
sample plot area	100 m^2
cover trees	65% (height up to 6 m)
cover shrub	50% (" " " 5 m)
cover dwarfshrub	22% (" " " 1.5 m)
cover herbs	30% (" 30-100 cm)
cover bryophytes	100% (10-30 cm)
alt.	3780 m
locality	Páramo de Sumapaz, Alto de Chorreras

cover % dwarftree layer

40	*Gaultheria ramosissima*
15	*Aragoa perez-arbelaeziana*
5	*Diplostephium heterophyllum*
5	*Rapanea dependens*

cover % shrub layer

10	*Gaultheria ramosissima*
10	*Aragoa perez-arbelaeziana*
15	*Diplostephium heterophyllum*
10	*Berberis goudotii*
3	*Hesperomeles pernettyoides*
2	*Eupatorium (Ageratina) glyptophlebium*

cover % dwarfshrub layer

10	*Vaccinium floribundum* var. *marginatum*
1	*Vaccinium floribundum* var. *floribundum*
1	*Hypericum caracasanae* ssp. *cardonae*
5	*Disterigma empetrifolium*
5	*Senecio guadelupe*
1	*Blechnum* sp. (subg. *Lomaria*)
1	*Rubus* sp.

cover % herb layer

10	*Hydrocotyle gunnerifolia*
15	*Elaphoglossum* aff. *engelii* (8359)
2	*Elaphoglossum* sp. (8362)
1	*Hymenophyllum* sp. (8361)
2	*Oxalis medicaginea*
1	*Nertera depressa*
1	*Luzula gigantea*
1	Gramineae *(Calamagrostis* sp.?)
2	*Cortaderia* sp.
<1	*Relbunum hypocarpium*
<1	*Cerastium* sp.

cover % bryophytes

40	*Plagiochila* sp. (8377)
35	*Jamesoniella* cf. *undata* (8369)
15	*Herbertus subdentatus* (large form)
2	*Atractylocarpus* sp. (8384)
1	*Dicranum frigidum*
5	*Sphagnum magellanicum*
<1	*Riccardia* sp. (8381)
1	Jungermanniales (8371)
<1	" (8382)
<1	" (8383)
1	*Plagiochila* sp. (8375)
<1	*Lepidozia* sp. (8376, 8378)
1	*Radula ramulina*
1	*Metzgeria* sp. (8371)
<1	pleurocarous moss (8373)
<1	*Bartramia angustifolia*
<1	*Pleurozium schreberi*
<1	*Chorisodontium* sp.

cover % lichens

1	*Sphaerophorus melanocarpus*

The stand is extremely rich in epiphytes, mainly *Usnea* sp. (8386), *Frullania* sp. (8394), Parmeliaceae and mosses. Erect and pendulous polypodiaceous ferns (e.g. *Polypodium angustifolium, Grammitis flabelliformis, G. variabilis, G. meridensis)* are conspicuous among the vascular epiphytes. A thick mat of liverworts covers the litter on the ground completely. This indicates wet atmospherical conditions, mainly caused by fog from the timberline condensation zone. *Aragoa perez-arbelaeziana* dominates in more open dwarfforest. *Berberis goudotii*, *Sphagnum magellanicum*, and *Jamesoniella rubricaulis* attain a higher cover than in the shady stands dominated by *Gaultheria ramosissima*. The cover of the skiophytic *Plagiochila* sp. (8377) is strongly reduced under *Aragoa* dwarftrees and shrubs. The leptophyllous to bryophyllous dwarftrees of *Aragoa perez-arbelaeziana* are 5-9 m high and have pale yellow flowers. This species is the only tree species in the genus (Romero 1972, Mennega 1974). The pāramo genus *Aragoa* apparently has its main centre in the southern pāramos of the Colombian Cordillera Oriental.

Observation: The stand provides shelter to numerous raccoons (*Nasuella olivacea*).

102. Dwarfforest of *Gynoxys albivestita*

Gynoxys albivestita dwarfforest are found in the Sierra Nevada del Cocuy between 3900 and 4000 m in the high valley of Lagunillas. These grayish microphyllous Compositae trees are 5-8 m high and predominant on rocky slopes. *Diplostephium alveolatum*, *Senecio vaccinioides*, *Solanum bogotense* and *Sericotheca argentea* are associated species.
Gynoxys albivestita dwarfforest is also found on the opposite humid side of the Sierra Nevada del Cocuy between 3400 and 4250 m. *Valeriana arborea* is an associated species above the 4000 m level. It occurs commonly between boulders at 4100 m from the Paso de Ranchería to the Alto de Cusirí. Characteristic in bamboo pāramo stands in the Sierra Nevada del Cocuy are *Acnistus quitoensis*, *Miconia andina*, *Vaccinium floribundum*, *Miconia salicifolia*, *Centropogon ferrugineus*, *Ribes* sp. (9188), *Echeveria* sp. (9186) and in the lower areas also *Miconia mesmeana* var. *jabonensis*.
Gynoxys albivestita is common in *Polylepis quadrijuga* dwarfforest in our area, e.g. in the Pāramo de la Rusia and in the high valley of Lagunillas, Sierra Nevada del Cocuy (3700-4000 m). *Gynoxys albivestita* is endemic to the pāramos of Boyacā, Arauca and Santander.

103. Other dwarfforests of *Gynoxys*

A number of other *Gynoxys* species were described from the Colombian Cordillera Oriental, but a systematic treatment of this genus is not yet available. *Gynoxys* occurs in isolated more or less pure dwarfforest stands in open pāramo. Sometimes even two species may dominate. It also is an constituent of the upper Andean forest together with other species. At present about 10 species of Gynoxys can be recognized in the Colombian Cordillera Oriental. Some of these form communities in their own right, e.g. *Gynoxys hirsuta*, *G. paramuna*, *G. subcinerea*, *G. subhirsuta*, *G. trianae*.

Gynoxys-dominated dwarfforests were studied by Van der Hammen & Jaramillo M. (in prep.) on the Alto de Oseta in the pāramo E of Monguí near Lake Tota. There at 3715 m, the composite dwarfforest consists of two species of *Gynoxys* (one species dominant) associated with *Ageratina* sp. (Jaramillo-Mejía 4055) and *Miconia salicifolia*. About 15 km SE of this locality, a *Gynoxys-Acnistus* dwarfforest pocket has been observed at 3400 m in bamboo pāramo at the base of the Pena de Arnical. Associated species are *Hesperomeles* sp., *Eupatorium (Ageratina) tinifolium*, *Diplostephium schultzii*, *Berberis* sp., *Miconia* cf. *ligustrina*, *Purpurella grossa*, *Rapanea dependens*, *Hypericum* sp., *Symplocos* sp., *Senecio vaccinioides*, a solitary *Weinmannia* sp. (8 m), *Swallenochloa tesselata*, Caryophyllaceae (9490), *Nertera granadensis* (dominant), *Moritzia lindenii*, *Peperomia* sp. and bryophytes as *Campylopus chrismarii* var. *suboblongus*, *C. trichophorus*, *Catagonium politum*, *Oreoweisia* cf. *laxiretis*, *Prionodon* *fusco-lutescens*, *Porotrichodendrum superbum*, *Syzygiella* sp.

In bamboo páramos near Bogotá, some dwarfforests stands with *Gynoxys* have been sampled. Here *Acnistus quitoensis* was subdominant, and associated with *Gynoxys* dwarfforest in the lower part of the bamboo páramos, especially on the eastern side of the Cordillera. A pocket with *Acnistus-Gynoxys* dwarfforest surrounded by bamboo páramo was found in the Chuza valley E of Bogotá at 3550 m (rel. 403). Up to 10 m high trees of *Gynoxys* sp. loaden with epiphytes are dominant and *Acnistus quitoensis* is subdominant. The herbaceous layer is dominated by *Drymaria villosa* ssp. *paramorum* and *Salvia killipiana* and has a cover of about 100%. Terrestric bryophyte cover about 90%; *Plagiochila* sp. (9626) and *Metzgeria* sp. (9634) are prominent. Between 3600 and 3750 m, in the headwaters of the same valley, and farther north to the Páramo de Palacio small patches of a *Gynoxys* species with grayish leaves are common. *Sibthorpia repens*, *Moritzia lindenii* and *Thuidium peruvianum* are present in the groundlayer.
At 3850 m in the Páramo de Chisacá, a rale *Gynoxys subhirsuta* dwarfforest is present on boulders at the base of a steep wet cliff on the southern shore of the glacial lake Laguna Negra. Associated species are *Cestrum parvifolium*, *Hesperomeles* cf. *pernettyoides*, *Myrrhidendron glaucescens* and *Hydrocotyle hederaceae* Boggy ground between the boulders contains hummocks of *Sphagnum magellanicum* and *S. oxyphyllum*. Other cryptogams characteristic for wet conditions are *Leptodontium wallisii*, *Chorisodontium mittenii*, *Campylopus cavifolius*, *Anastrophyllum leucostomum* and *Sphaerophorus melanocarpus*.
Another inventory (table 20) was made 30-35 km SSW from this locality in *Gynoxys* dwarfforest on the W slope of the Páramo de Sumapaz. There, in a rockshelter at 3885 m near the Laguna Gobernador also a *Gynoxys* species was dominant, probably also *G. subhirsuta*.

Table 20

Gynoxys dwarfforest near the Laguna Gobernador (3885 m), Páramo de Sumapaz

dwarf trees and shrubs:	bryophytes:
Gynoxys sp. (dominant)	*Sphagnum magellanicum*
Miconia salicifolia	*Campylopus gertrudis*
Hypericum laricifolium ssp. *laricifolium*	*Atractylocarpus longisetus*
Diplostephium cf. *heterophyllum*	*Chorisodontium speciosum*
Hesperomeles sp.	*Dicranum frigidum*
Berberis sp.	*Omphalanthus filiformis*
Cestrum parvifolium	*Jamesoniella rubricaulis*
Diplostephium sp. (8332)	*Leptoscyphus porphyrius*
Ugni myricoides	
herbacous species:	
Swallenochloa tesselata	
Myrrhidendron glaucescens	
Hydrocotyle sp.	
Rumex tolimensis	
Elaphoglossum spp.	
Grammitis moniliformis	
Hymenophyllum karstenianum	

104. *Senecionetum flos-fragrantis* ass. nov. (prov.)
type: rel. 467; table 21

Physiognomy: This dark-green, nanophyllous dwarfforest, consists of 3 layers:
1) an upper stratum of gnarled *Senecio flos-fragrans* dwarf trees, up to 2.30 m high with a cover of 75%;

2) a rale open herbaceous fieldlayer, about 30 cm high, with a cover of about 12%, and
3) a groundlayer, with a cover of 80%, and consisting of a nearly closed mat of vascular plants with prostrate stems (*Lachemilla tanacetifolia, Geranium sibbaldioides, Lachemilla holosericea*), cushion-like herbs (*Cerastium* sp., *Montia meridensis*) and bryophytes.

Composition & syntaxonomy: Gnarled dwarf trees of *Senecio flos-fragans* var. *frigidophilus* are characteristic. *Senecio formosus, Montia meridensis, Lachemilla tanacetifolia, Jamesonia goudotii* and *Lycopodium crassum* are superpáramo taxa and reflect the high location of the stands. The relatively low number of species is also an indication (17 in rel. 467).

Table 21

Senecionetum flos-fragrantis ass. nov. (prov.)

rel. nr.	▲ 467
alt.	5160 m
loc.	Sierra Nevada del Cocuy Patio Bolos, S. Luis (Arauca)
relevé area	24 m^2
soil	sandy

dwarf tree layer:	cover %		
Senecio flos-fragrans var. *frigidophilus*	75	*Cerastium subspicatum* (cushions)	5
fieldlayer:		*Geranium sibbaldioides*	2
Senecio formosus	10	*Lachemilla holosericea*	1
Lorenzochloa erectifolia	1	*Montia meridensis*	<1+
Jamesonia goudotii	1	*Calandrinia acaulis*	1
Lycopodium crassum	1	*Breutelia* sp.	15
groundlayer:		*Leptodontium* sp.	15
Lachemilla tanacetifolia	30	*Campylopus pittieri*	5
		Peltigera sp.	1
		Cora pavonia	3
		Tayloria sp.	2

Floristically the greatest affinity is shown to high altitude thickets and dwarf forests of *Senecio vaccinioides* and *Diplostephium rhomboidale* fringing the grasspáramo-superpáramo moraines between 4300 and 4400 m in the Páramo Cóncavo at the western side of the Sierra Nevada del Cocuy.

Synecology: The dwarfforest is found on brown, humic, sandy probably fluvio-glacial deposits in protected sites at the grasspáramo-superpáramo transition. Patches of similar composition can be noticed on decayed soligenous *Distichia* bogs in the lower superpáramo.

Distribution: This type of dwarfforest was only observed at 4160 m near Patio Bolos, south of the Laguna La Plaza on the eastern slope of the Sierra Nevada del Cocuy (dept. of Arauca). Some patches may be present in the lower superpáramo in this area (4300 m).

Note: *Senecio flos-fragrans* var. *frigidophilus* has been collected in bogs in the upper subpáramo and the lower superpáramo between 3770 and 4525 m in the Cocuy area. The var. *flos-fragrans* occurs as a low shrub (0.5-2 m) in the southern páramos of the Cordillera Oriental (Cruz Verde to Sumapaz) on humid soils and in bogs between 3300 and 4000 m. The shrub *Senecio ramentosus* (= *S. flos-fragrans* var. *ramentosus* in the author's opinion is characteristic in the northern part (Almorzadero to Santurbán and Tamá) of the Cordillera Oriental.

105. Dwarfforest of *Diplostephium rhomboidale*

This grayish nanophyllous Compositae dwarfforest is distributed in patches in the dry upper bunchgrass pāramo on the dry side of the Sierra Nevade del Cocuy between 4100 and 4400 m, where it is restricted to boulders in protected areas. *Poa* cf. *pauciflora* is abundant in these patches at 4350 m on the Cōncavo - Bocatoma divide.
An incomplete survey of an open *Diplostephium rhomboidale* stand on the southern shore of the *Distichia* lake (of community 64) at 4100 m in the Bocatoma valley is given below (table 22). The stunted *Diplostephium rhomboidale* trees are about 3.5 m high.

Table 22

Diplostephium rhomboidale dwarfforest

rel. nr.	335[A]
slope	-
sample area	400 m^2
cover dwarftrees & shrubs	45%
dwarfshrub	10%
herbs	60%
bryophytes	7%
lichens	3%
boulders	60%
alt.	4110 m
locality	Bocatoma valley, Sierra Nevada del Cocuy (Boyacā)

cover %

dwarftrees & shrubs:
40 *Diplostephium rhomboidale*
<1 *Diplostephium lacunosum*
1 *Valeriana arborea*
3 *Senecio vaccinioides*
1 *Eupatorium (Ageratina) glyptophlebium*

dwarfshrubs & herbs
1 *Hypericum caracasanum* ssp. *cardonae*
10 *Pernettya prostrata*
<1 *Miconia chionophila*
60 *Calamagrostis effusa*
<1 *Jamesonia bogotensis*
2 *Castilleja* sp.
<1 *Peperomia* sp.
<1 *Cerastium* sp.
<1 *Senecio* cf. *formosoides* (8767)

terrestric bryophytes
1 *Breutelia*
<1 *Herbertus subdentatus*
5 *Campylopus pittieri*
1 *Brachythecium* cf. *pseudorutabulum*
<1 *Hypnum mirabile*
<1 *Peltigera* sp.
3 *Cladonia coccifera*

epiphytes
Usnea sp., *Peperomia hartwegii*

Diplostephium rhomboidale is generally associated with *Senecio vaccinioides* in the Sierra Nevada del Cocuy:
1) at the lower border of the superpāramo up to 4400 m (see 22), and
2) in subpāramo thickets, together with *D. alveolatum*, in lower locations up to the Andean forest line.
According to Cuatrecasas (1969) and our own observations, *Diplostephium rhomboidale* occurs in the Sierra Nevada del Cocuy, on the dry side of this mountain chain, between 3800 and 4400 m. Its rare var. *pauciflora* Cuatr. has been collected in pāramos near Bogotā (3450-3700 m) and in northern Ecuadro (3500-4000 m).

Note: *Diplostephium lacunosum* is a rare endemic shrub which was found by the author only in the Bocatoma valley (4050-4100), in the Sierra Nevada del Cocuy, where it grows in local small groves on moraines, often associated with scattered dwarftrees of *Valeriana arborea* and *Gynoxys albivestita*.

DRY AND HUMID MEADOWS

Various types of azonal meadows are present in the study area. They are subdivided into short grass meadows and low rosaceous herbfields.
The grassy meadows are dominated by Gramineae of low stature, e.g. cushion-like grasses *(Aciachne, Muhlenbergia)* and tufts or small tussocks (resp. *Agrostis foliata* and *Lorenzochloa erectifolia*). Low grasses are also present in the rosaceous herbfields, which are mainly made up of acaulescent rosette species of *Acaena* or *Lachemilla* (both Sanguisorbeae).

106. *Lorenzochloetum erectifoliae* ass. nov.
type: rel. 187; table 23; Fig. 76.

Table 23. *Lorenzochloetum erectifoliae* ass. nov.

	rel. nr.	514	515	100	187
	slope (degree)	4	5	8	10
	relevé area m^2	12	20	16	16
	cover vegetation %	100	100	100	100
	soil	c/s	c	c	c
	pH topsoil	-	-	4.6	4.7
	soil depth cm	-	-	110	100
	approximate number of species	15	21	32	20
	alt. m	3620	3550	3620	3640
	locality: Pāramos near Neusa	LS	LS	N	LS
	cover %				▲
	c & d and other taxa				
	Lorenzochloetum erectifoliae				
c	*Lorenzochloa erectifolia*	80	95	75	95
	Senecio nitidus	1	<1	<1	<1
	Polytrichum juniperinum	3	1+	<1	<1
	Cladia aggregata	1	<1+	<1	<1
	Cladonia isabellina	2		<1+	<1
	Arcytophyllum muticum	3		1	<1
	Valeriana longifolia	15			5
	Cladonia cf. *squamosa*	<1+		<1	<1+
	Cladonia subg. *Cenomyce*	<1+	<1+	<1+	<1+
	Geranium sibbaldioides		<1+		<1
	Lachemilla spp.		<1+	<1	
d	*Acaena cylindristachya*	2	8		
d	*Satureja nubigena*	1	1		
	Espeletia argentea	20	10		
	Cora pavonia	<1	<1		
	Lycopodium spurium	2			
	Orthrosanthus chimboracensis	5			
	cf. *Erythrodontium* sp.	2			
	Diploschistes sp.	<1			
	Cladonia capitata		<1		
	Breutelia sp.		10		
	Hypericum mexicanum		1		
	Peltigera sp.		<1+		
d	*Campylopus suboblongus*			3	10
d	*Lepidozia* sp(p). (4171, 6102)			<1	1
	Cladonia hypoxanthoides			<1	<1
d	*Isopterygium* sp. (4164, 6106)			<1	<1
	Paspalum bonplandianum			15	

Paepalanthus karstenii var. *corei*	10	
Poa cf. *pauciflora*	3	
Calamagrostis effusa	3	
Campylopus sp. (4163)	3	
Senecio formosus	1	
Laestadia muscicola	<1+	
Carex sp. (4156)	<1+	
Miconia chionophila	<1	
Calamagrostis bogotensis	<1	
Espeletia barclayama	<1	
Agrostis breviculmis	<1	
Pottiaceae (4169) or *Mielichoferia?*	<1	
Leptodontium pungens	<1	
Blechnum loxense	<1	
Rumex acetosella	<1	
Leptodontium cf. *luteum*		15
Ophioglossum crotalophoroides		<1
Werneria granadensis		<1
Marchantia berteroana		<1+
Sibthorpia repens		1
Hypericum thuyoides		1
Cladonia bacillaris		<1
C. cf. *fimbriata*		<1+

Locality: LS Laguna Seca
N Neusa, Telecomunicacion

Physiognomy: The *Lorenzochloetum* is an almost closed dry to slightly humid bunchgrass vegetation. The bunchgrass layer is most conspicuous and has a cover of 75-100%. The cover of the bryophyte layer is 3-25%, and this layer is dominated by acrocarpous mosses.

Composition & syntaxonomy: *Lorenzochloa erectifolia* is a selective characterspecies. Other characterspecies are absent. *Lorenzochloa* is a monotypic tropandean tussock grass closely related to the monotypic *Aciachne*. Both belong to the tribe Stipeae, and are also reported for Costa Rican páramos (Pohl 1980). As other taxa in the same tribe, *Lorenzochloa erectifolia* stands out by a number of xeromorphic features. This species was found between 3500 and 4350 m in the páramos of the Colombian Cordillera Oriental. Other common species are juvenile shrubs of *Senecio nitidus*, and *Arcytophyllum muticum*, *Espeletia argentea*, *Acaena cylindristachya*, *Polytrichum juniperinum*, *Campylopus argyrocaulon* (or *C.* cf. *suboblongus*), *Cladia aggregata* and *Cladonia isabellina*. The association is rich in species of *Cladonia* subg. *Cenomyce*. The number of species is about 20 (15-32 in 4 relevés). This association has affinities with the zonal *Espeletia argentea*-*Calamagrostis effusa* lower bunchgrass páramo (17). Though *Lorenzochloa erectifolia* clearly finds its optimum in the present community, it is a species with a wide ecological range, and has also been found:

1) locally with Espeletiinae along the upper bunch grass line (4250-4350 m) in the Sierra Nevada del Cocuy and Páramo de Guantiva (see 20);
2) adjacent to the *Aciachnetum pulvinatae* (3850-3900 m), together with *Senecio canescens*; and
3) locally on terrace sediments along páramo streams and associated with *Carex pichinchensis* and *Polytrichum commune* at c. 3600 m (see 50).

Synecology: This bunchgrass association is distributed in patches in the lower bunchgrass páramo with zonal *Espeletia* - *Calamagrostis effusa* swale. As a rule the *Lorenzochloetum* is found on concave slopes (4-10°), where the water is collected from the zonal *Calamagrostis effusa* páramo with *Espeletia argentea* or *E. barclayana*. At the base of the *Lorenzochloetum* the zonal humid shrub of the *Senecionetum nitidi* may be found and also boggy sloping valley floor communities. In dense stands an Aoo-layer (up to 3 cm thick) may be found in the dense shadow of the tussocks. The upper black clayey layer is about 70 cm thick. Below this layer to about 100 cm follows a dark gray or yellowish brown, sandy clayey layer. The topsoil layer is moderately acid (pH 4.6-4.7); in rel. 187, at a depth of 1 m and near the sandstone bedrock, the pH was 5.1.

Distribution: The *Lorenzochloetum* is only known from the dry lower buchgrass pãramos between Neusa and S. Cayetano (60 km north of Bogotá) between 3550 and 3650 m.

107. *Aciachnetum pulvinatae* Vareschi 1953 em. Cleef
type: rel. 328; table 24; Fig. 27 (also Smith 1972, fig. 4).
lit.: Vareschi 1953, 1970; Smith 1972, Cleef 1978.
In the last publication, reference is made to other authors dealing with *Aciachne pulvinata* growth, and additional data are provided on composition, ecology and distribution.
photo: Cleef 1978, photo 179; Vareschi 1953, fig. 8; Vareschi 1970, fig. 4c & b; Smith 1972, fig. 2b, fig. 3.

Physiognomy: The *Aciachnetum* forms low prickly cushion grass meadows. The grass hummocks are 10-25 cm high and ring-shaped due to decay of the older parts of the grass.

Table 24. *Aciachnetum pulvinatae* Vareschi 1953 em. Cleef

rel. nr.	31	156	328	336	452*	567*	PRESENCE TABLE		
slope (degree)	10	12	3	5	1	5	Study area (Cord. Or.)	Mérida (Venezuela)	Cordillera Central, C.
relevé area m^2	2	2	12	9	15	16			
cover % vegetation	100	95	85	95	90	90			
soil	C	Sc	S	C	Cs	C			
pH topsoil	3.9	4.6	5.2	5.0	-	-			
soil depth cm	70	35	20	35	?	?			
approximate number of species	10	8	15	7	18	16			
alt. m.	3845	3985	4045	3955	3735	3885			
locality	Gua	Coc	Coc	Coc	Coc	Alm	(6)	(3)	(3)
cover %			▲						
c & d and other taxa *Aciachnetum pulvinatae*									
c *Aciachne pulvinata*	98	90	85	95	85	80	x	x	x
c *Aciachne pulvinata* †	<1	5	15	5	10	10	x	x	x
c *Acaulimalva purdiei*	<1	2	<1	<1		1	x	x	
Calandrinia acaulis	<1+		<1+	<1	1+	1+	x	x	x
Geranium sibbaldioides	<1		<1+		1	1	x		x
Rumex acetosella	<1	1	<1+		<1+		x	x	
Agrostis breviculmis		<1		<1+	<1+	<1+	x	x	
Hypericum caracasanum ssp. *cardonae*			3	<1	3	2	x		
Lachemilla pinnata			1		1+	<1+	x		
Acaena cylindristachya			<1		<1+	1	x		
Arenaria sp.			<1			<1	x	x	
Agrostis trichodes			<1			<1+	x		
Sisyrinchium trinerve			<1+		<1+?		x		
Polytrichum juniperinum			<1		<1+		x		
Cladia aggregata			<1+		<1+		x		x
Carex sp. (C. peucophila?)				<1+		10	x		
Cerastium sp.	<1+						x		x
Leptodontium pungens					<1	3	x		x
Oreomyrrhis andicola		2					x		x
Lachemilla orbiculata					<1		x		x

Hypochoeris cf. sessiliflora	<1+	x	x	x
and 12 infrequent species				
main d/o taxa Sierra Nevade de Mérida				
Niphogeton dissectum			x	
Thamnolia vermicularis			x	
Leptodontium flexifolium			x	
Lobelia sp.			x	
main d/o taxa Nevado S. Isabel, Cord. Central				
Eryngium humile				x
Satureja nubigena				x
Agrostis haenkeana				x
Calamagrostis				x
Hypericum lancioides				x
Lupinus cf. *humifusus*				x
Bromus lanatus				x
Senecio repens				x
Gentianella dasyantha				x

+) number of relevés: ( )

Composition & syntaxonomy: Dominant and exclusive character species is *Aciachne pulvinata*, a small xerophytic cushion grass. It is closely related to *Lorenzochloa erectifolia*. *Acaulimalva purdiei* and *Calandrinia acaulis* are preferential characterspecies. Their sessile rosettes are opulent in patches of gravel in the atmospherically humid lowermost superpáramo (see 25), and they are also present in Venezuelan stands of this association. Other frequent species in the study area are *Geranium sibbaldioides*, *Rumex acetosella*, *Hypericum caracasanum* ssp. *cardonae*, *Agrostis breviculmis*, *Lachemilla pinnata*, *Acaena cylindristachya* and *Leptodontium pungens*. *Cetraria arenaria* and *C. islandica* ssp. *crispiformis* are common in cattle-free areas on top of the cushions of *Aciachne*. *Thamnolia vermicularis* is common in the Venezuelan meadows; *Cetraria* spp. in the meadows of the Colombian Cordillera Oriental. In the *Aciachnetum pulvinatae*, in the Parque Los Nevados in the Colombian Cordillera Central, the following taxa are absent: *Acaulimalva*, *Agrostis breviculmis*, *Hypericum caracasanum*, *Lachemilla pinnata* and *Acaena cylindristachya*. Common species are here *Eryngium humile*, *Satureja nubigena*, *Oreomyrrhis andicola*, *Agrostis* sp., *Lachemilla orbiculata*, *Hypericum lancioides* and *Lupinus* cf. *humifusus* (Cleef et al., in press). The *Aciachnetum* has strong floristic affinities to the *Acaeno-Plantaginetum sericeae* (see 18) as well as to the *Acaulimalva-Agrostis breviculmis* lower superpáramo vegetation on stable, gravelly slopes (see 25). *Aciachne*-dominated meadows seemto develop zonally in some places of the Peruvian puna, where according to Hitchcock (quoted by Chase 1924) *Aciachne* is "the dominant or even the only grass on whole hills". There might be a number of regional associations dominated by this monotypic genus throughout the tropical Andes, which may be combined into an *Aciachnion pulvinatae* (prov.).

Synecology: The *Aciachnetum* is found in all kinds of dry depressions, on dry valley floors, on gently sloping (up to 12°) dry ground, and on sandfilled former lakelets. Soils are clayey or sandy, and depending on bedrock and altitude, black to dark and light gray. Thickness is 20-70 cm. The pH of the toplayer is strongly to moderately acid (3.9-5.2). According to Smith (1972) *Aciachne pulvinata* retains the moisture from fog, the direction of which it originates, reflects the direction of growth. In slightly more humid flat ground the *Aciachnetum* is replaced by the *Agrostio-Lachemilletum orbiculatae* (111).
The *Aciachnetum* is grazed by horses and sheep. The manured soil carries *Rumex*

acetosella, Lachemilla orbiculata, Agrostis trichodes and *Paspalum bonplandianum*.

Distribution: Dry meadows with *Aciachne pulvinata* occur throughout the high tropical Andes from the puna of NW Argentina to the Colombian and Venezuelan páramos. In the study area the *Aciachnetum pulvinata* is present in the dry páramos of the northern part of the Cordillera Oriental (Boyacá, Santander) between 3700 and 4100 m. The association was also studied in the Venezuelan Sierra Nevada de Mérida between 3800 and 4150 m (Vareschi 1953, Smith 1972, Cleef, unpubl.) and in the Parque Los Nevados (3800-3900 m) in the Colombian Cordillera Central (Cleef et al., in press).

Other communities with *Aciachne pulvinata*: In areas between the *Aciachnetum pulvinatum* and the surrounding zonal and azonal vegetation some other azonal communities occur, the most common of which is equally dominated by an *Aciachne pulvinata* - *Agrostis breviculmis* - *Lachemilla pinnata* meadow (pH topsoil 5.5). Where about one third of the *Aciachne* hummocks have died, *Niphogeton josei* appears locally. Rosettes of *Plantago sericea* ssp. *argyrophylla* and the rare *Phyllactis rigida* may found together with *Aciachne* on bare sandy slopes.

108. *Muhlenbergietum fastigiatae* ass. nov.
type: rel. 106; table 25; fig. 27 (also fig. 75).

Physiognomy: The association forms graminoid, low hummocky, humid and wet meadows. Mosses, low herbs and sedges are often associated or may be codominant. If a moss layer is present, it is up to 8 cm thick and may have a cover of 80%. *Muhlenbergia* and mosses are intermingled. The graminoid layer with its characteristic bluish hue is about 20 cm thick and as a result of its ramifications it forms a dense cushion-like grass carpet.

Table 25. *Muhlenbergietum fastigiatae* ass. nov.

rel. nr.	106	415A	491	566	257B	160
slope (degree)	1	-	5	1	-	1
relevé area m²	1	1	4	6	1	4
cover % grasses	60	70	95	40	35	60
mosses	80	10	7	60	72	-
pH top soil	5.8	-	-	-	-	5.8
number of species (approx.)	11	4	6	3	4	8
alt. m	3535	3610	3870	3850	3775	4060
locality	Pi	Pi	Coc	Alm	Rus	Coc
cover %	▲					
c sp. *Muhlenbergietum fastigiatae*						
c *Muhlenbergia fastigiata*	60	70	95	40	35	40
other taxa						
Breutelia chrysea	80	10	<1			
Leptodontium luteum	<1+		2			
Carex pichinchensis		60		1		
Breutelia allionii				60		
Sphagnum cuspidatum					70	
Agrostis sp.					1	<1
Juncus cyperoides	10					1
Carex cf. *peucophila*	5					
Werneria pygmaea	5					
Galium trianae	50					
Montia fontana	<1+					
cf. *Drepanocladus*	2					
Calliergonella cuspidata	1					
Geranium confertum		5				
Campylopus cf. *cavifolius*			5			

	(566)	(257^b)	(160)
Jungermanniales	1		
Gentianella corymbosa	<1		
Pleurozium schreberi		2	
Agrostis breviculmis			20
Carex bonplandii			1
Callitriche sp.			<1
Eleocharis stenocarpa			<1

localities: Pi Páramo de Pisva
Coc Sierra Nevada del Cocuy: Alto Valle Lagunillas
Alm Páramo del Almorzadero: El Tutal
Rus Páramo de la Rusia: Pena Blanca

Composition & syntaxonomy: This association is dominated by the selective character species *Muhlenbergia fastigiata*. Like the grasses in the previously described associations, this tiny hummocky grass species with involute green-bluish blades belongs to the tribe Stipeae, and is widely distributed in the tropical Andes from northern Argentina and Chile to Colombia. In the subpáramos and grass páramos of the study area *Muhlenbergia fastigiata* is the most common species in such meadows, but according to herbarium data *Muhlenbergia ligularis* and *M. linearis* may be present also. Common associated species are *Breutelia chrysea*, *B. allionii*, *Sphagnum* cf. *cuspidatum* and *Carex pichinchensis*.
A number of occasional character and companion species of the *Oritrophio-Wernerietalia* and the *Marchantio-Epilobietalia* (especially the *Calamagrostion ligulatae*) indicate that syntaxonomically the association might occupy an intermediate position between these orders. The number of species and the composition largely depends on altitude and neighbouring communities. Mosses are common in peaty páramo stands of the *Muhlenbergietum fastigiatae*, but they seem absent in the communities described by Ruthsatz (1977) and Cabrera (1958) from the Argentinan puna, which are distinctly different from the described páramo association.

Synecology: The azonal graminoid cushion meadows of the *Muhlenbergietum* are characteristic and common on damp soil in the transitional zone between wet azonal communities and zonal páramo vegetation. This is an edaphically controlled association, common along wet flush, *Sphagnum* and cushionbogs (e.g. *Hyperico-Plantaginetum rigidae*) and a long the mineral shores of grasspáramo lakes and ponds on flat to slightly sloping (0-6°) ground. The width of the *Muhlenbergietum* zone, then depends on the slope. On steeper slopes the zone of the *Muhlenbergietum* becomes narrower. In some places along small streams or drainage rills, the *Muhlenbergietum* is temporarily flooded. Species of *Breutelia* and *Sphagnum* are almost
The darkbrown, peaty upper layer of the clayey soils is rich in organic material. The deeper sandy to clayey layers are grayish-brown to light yellowish-brown. The thickness of the soil is 50-120 cm. The upper top soil is slightly acid (pH 4.8).

Distribution: The *Muhlenbergietum fastigiatae* is found from the upper forestline at 3500 m up to the lowermost limit of the superpáramo at 4250 m throughout the Colombian Cordillera Oriental. In view of the wide distribution of *Muhlenbergia fastigiata*, the association must be present also in other Andean páramos and in the puna. Ruthsatz (1977) described *Muhlenbergia fastigiata Distichlis humilis* salt meadows from the northern Argentinan puna (3500-3680 m). She pointed out that *Muhlenbergia fastigiata* might be the character species of a distinct syntaxon.

109. *Agrostietum foliatae* ass. nov. (prov.)
type: rel. 179; table 26; Fig. 77
lit.: Cuatrecasas 1934; photo: Cuatrecasas 1958, plate 23-1

Physiognomy: The *Agrostietum foliatae* is an open, small tussock grass vegetation, with a cover of about 20%. The small tussocks have stiff erect blades and conspicuously purplish, contracted inflorescences, and are 25 cm high. The bryophytic layer consists mainly of acrocarpous mosses and is only present on the low sandy hummocks under the grass tufts. Minuscule blue algae (*Aphanocapsa gervillei*) are abundant in the humid, bare glacier sand, and cause a faint purplish hue.

Table 26. *Agrostietum foliatae* ass. nov. (prov.)

	rel. nr.	179	172
	relevê area m^2	9	9
	cover vegetation %	30	75
	soil	s	s
	pH topsoil	5.1	5.2
	number species	7	6
	alt. m	4280	4310
	locality	Coc	Coc
	cover %	▲	
	c/d/o taxa *Agrostietum foliatae*:		
c	*Agrostis foliata*	10	3
	Aphanocapsa gervillei	20	60
	Luzula cf. *racemosa*	<1	<1
	Polytrichum juniperinum	<1	<1
	Cora pavonia	<1	
	Ditrichum gracile	10	
	Calamagrostis ligulata		20
	companions:		
	Hypochoeris cf. *sessiliflora*	<1	
	Anastrophyllum sp.	1	
	Lucilia sp.		<1
	Aongstroemia julaceae		1+

Both relevés are from the Sierra Nevada del Cocuy; Bocatoma valley (Boyacá).

Composition & syntaxonomy: *Agrostis foliata* (previously *A. nigritella* Pilger) is an (exclusive) character species with a wide distribution in the high, northern Andean páramos from Peru to Venezuela between 3500 and 4700 m. *Luzula* cf. *racemosa*, *Ditrichum gracile*, *Polytrichum juniperinum* and *Lucilia* are common associates. In some places *Calamagrostis ligulata* tussocks are present also (see 60). Blue algae, mainly *Aphanocapsa gervillei* (Hass.) Rabenh. (det. Dr. G.H. Schwabe, Plön), are abundant in humid sand. According to Dr. G.H. Schwabe (in litt.) this is a pioneer species also known from the high Alps and Surtsey. As in all pioneer communities, the number of species is low (6-7 in 2 relevés).

The *Agrostietum foliatae* has affinities to the *Carici peucophilae-Wernerietum crassae* (61) and the *Calamagrostis ligulata* superpáramo communities (see 60). The association has been described provisionally. It is possible that at a later date also the pioneer community on volcanic ashes and pumice of the Colombian Cordillera Central has to be included in this association.

Synecology: This superpáramo pioneer grass community is characteristic for humid sandy and silty beaches of superpáramo lakes, for floodplains of braided streams. The subsoils there consist of varvae-like sequences of humic clay and coarse sand. Topsoil pH values are 5.1 and 5.2. Wind and water determine the size and shape of the low hummocks. These are formed by sand-loaded wind and may be carried away by water floods. Bryophytes (e.g. *Anastrophyllum* sp., *Ditrichum gracile)* are able to hold the low sandy hummocks. *Ditrichum gracile* occurs on the wind-exposed side; *Anastrophyllum* sp. is found on the leeward side of the *Agrostis foliata* hummock (Fig. 75). *Agrostis foliata* is a specialized pioneer species on humid sandy superpáramo beaches, but is also found as first vascular colonizer on ashes and pumice slopes on Colombian volcanoes (Cuatrecasas 1934, Cleef et al., in press). Some clumps of this grass species may be present in the grass páramos.

Distribution: Superpáramo beach vegetation of the *Agrostietum foliatae* is well developed in the Sierra Nevada del Cocuy between 4300 m (Bocatoma valley) and 4600 m (Ritacuva glacier). According to herbarium labels of collections made by Dr. J. Cuatrecasas such superpáramo vegetation also occurs in the Colombian Cordillera Central on the sandy shores of superpáramo lakes.

ROSACEOUS HERBFIELD

The herbaceous meadows are dominated by low rosettes with silvery-tomented blades and semi-woody stems and roots, belonging the Rosoideae, Rosaceae. Rosaceous herbfield must be considered as a degraded zonal or azonal vegetation due to intensive grazing by cattle (e.g. 110 & 111) and frequent burning (e.g. 112).

110. Community of *Agrostis breviculmis* and *Lachemilla pinnata*
characteristic rel.: 554; table 27

Table 27. *Agrostis breviculmis-Lachemilla pinnata* community

rel. no.	554	157
exp.	S	W
slope (degree)	15	7
relevé area m^2	25	2
alt. m	4100	3890
locality	Almorzadero	Cocuy
cover %		
Lachemilla pinnata	80	35
Agrostis breviculmis	40	25
Cerastium sp.	2	<1
Acaulimalva sp.	<1	15
Stachys elliptica	<1	<1
Bryum billardieri	<1	<1
Hypochoeris sessiliflora	25	
Aciachne pulvinata		30
Geranium sibbaldioides	5	
Aphanactus sp.	2	
Gentianella corymbosa	1	
Oreomyrrhis andicola	1+	
Erigeron sp.	<1	
Leptodontium cf. *pungens*	<1	
Bartramiaceae	<1	
Campylopus spp.		1
Lachemilla orbiculata		<1
Rumex acetosella		1
Veronica serpyllifolia		<1
Potentilla heterosepala		<1
Senecio niveo-aureus	5	

Physiognomy: This community forms a grassy herbfield of dense growing low rosettes (*Lachemilla, Hypochoeris, Aphanactus, Oreomyrrhis, Acaulimalva*), the height of which is not more than 10-15 cm. The cover of the bryophyte layer consisting of a few acrocarpous mosses is 1%.

Composition & syntaxonomy: Low rosette plants with silvery indumented pinnate leaves of *Lachemilla pinnata* are dominant; *Agrostis breviculmis* and *Hypochoeris sessiliflora* are subdominant. *Lachemilla pinnata* is a polymorphic species, widely distributed from the Argentinan puna to the north Andean pāramos of Colombia and Venezuela and the Mexican mountains.
The pāramo meadows with *Lachemilla pinnata* represent a separate well-defined syntaxon, which will be described when more relevēs become available.
Ruthsatz (1977) reported a *Lachemilla pinnata-Eleocharis albibracteata* association (prov.) from the Argentinan puna between 400 and 4300 m. This community fringes cushion bogs, and on the basis of its composition and ecology rather belongs to the *Wernerion pygmaeae* (prov.) Ruthsatz 1977, i.c. the *Wernerietea* (prov.). The *Agrostis breviculmis-Lachemilla pinnata* pāramo has a different syntaxonomical position. The greatest affinity is to the *Agrostio breviculmis-Lachemilletum orbicularis* (111), the *Aciachnetum pulvinatae* (107) and to other pāramo communities with *Agrostis breviculmis* (25).

Synecology: Xeromorphic rosette meadows on moderately sloping (7-15°) dry ground, where the *Aciachnetum* is absent. In the Pāramo del Almorzadero *Lachemilla pinnata* is dominant in depressions and gullies on calcareous slopes up to 4330 m, with occasional rain water. In the Sierra Nevada del Cocuy rosettes of *Lachemilla pinnata* were seen locally bordering the *Aciachnetum pulvinatae*.
The humic, brownish-black, sandy soils are stony and shallow. The upper soil layer in rel. 157 is weakly acid (pH 5.4-5.5).
Grazing and manuring by cattle is common, as indicated by the presence of *Rumex actosella* and *Veronica serpyllifolia*. *Lachemilla pinnata* has a wide ecological range and occurs on all kinds of substrate.

111. *Agrostio breviculmis-Lachemilletum orbiculatae* ass. nov.
type: rel. 624; table 28; Fig. 75
lit.: Cuatrecasas 1934, 1958; Oberdorfer 1960; Cleef et al, in press.

Table 28. *Agrostio breviculmis-Lachemilletum orbiculatae* ass. nov.

	rel. nr.	576	577	618	624
	rel. area m^2	4	4	1	4
	slope (degree)	3	-	5	1
	number of species	8	9	4	12
	alt. m	3740	4000	3920	3800
	locality	Alm	TPN	TPN	TPN
	cover %				▲
	c,d & o taxa *Agrostio-Lachemilletum*				
c	*Lachemilla orbiculata*	80	70	99	85
c	*Agrostis breviculmis*	10		1	5
	Leptodontium pungens	3	2		1+
	Veronica serpyllifolia	1			1
	Hypochoeris sessiliflora	1			1
	Agrostis cf. *haenkena*		35		
	Festuca breviaristata		1	1	2
	Rumex acetosella		1+	1+	
	Taraxacum sp.		1		1
	Lachemilla pinnata	10			
	Cerastium sp.	1			

	(576)	(577)	(624)
Arenaria sp.	1+		
Bromus lanatus		1	
Calandrinia acaulis		1	
Halenia sp.		1	
Ranunculus peruvianus			1+
Salvia sp.			1
Lupinus humifusus			5
Oreomyrrhis andicola			3
Senecio repens			1

Localities: Alm Páramo del Almorzadero
TPN Parque Los Nevados , Cordillera Central

Physiognomy: The *Agrostio-Lachemilletum orbiculatae* forms low herbaceous meadows on flat or slightly sloping ground, dominated by semi-woody, microphyllous, rosaceous ground rosettes; e.g. "cryptolignum" sensu Cuatrecasas (1934).

Composition: *Lachemilla orbiculata* is a (selective) character species. This polymorphic species (E.G.B. Kieft, pers. comm.) is native to the high Andes from Peru to Venezuela. In páramo communities a number of meadow species is associated e.g. *Agrostis breviculmis, Leptodontium* cf. *pungens, Veronica serpyllifolia, Hypochoeris* sp., *Lachemilla pinnata, Arenaria* sp., *Gnaphalium antennarioides*.
The *Lachemilletum orbiculatae* was originally described by Cuatrecasas (1934, 1958) from clearings in the upper part of the Andean forests in the Nevado del Tolima (2600-3300 m) and near Bogotá (2700-2950 m). A number of vascular plants may be codominant or predominant and Cuatrecasas ranked such stands respectively at the subassociation or association level. The *Lachemillion orbiculatae* Cuatrecasas 1934 corr. Cuatrecasas 1958 was originally erected for the forestclearing communities of the *Lachemilletum orbiculatae* and the *Dactyletum glomeratae* Cuatrecasas 1934. This alliance may also include the páramo vegetation of the *Agrostio breviculmis-Lachemilletum orbiculatae*.
The forestclearing communities with *Lachemilla orbiculatae* apparently belong to several associations and they are distinctly different from the *Agrostio-Lachemilletum orbiculatae* by a number of species. Among the most common species are *Lachemilla aphanoides, Salvia* sp., *Spilanthes americana* (Mutis)Hieron. (Comp.), *Gnaphalium spicatum, Trifolium* spp., *Paspalum bonplandianum, Anthoxanthum odoratum L., Dactylis glomerata L., Holcus lanatus L., Hydrocotyle bonplandii* and *Agrostis perennans*. Alien species are prominent. Such communities commonly fringe roads and paths through the upper Andean forest and shrubpáramo. Oberdorfer (1960) reported a similar community at 2800 m above Quito, Ecuador.
As to the *Agrostio-Lachemilletum orbiculatae* it was observed that *Lachemilla pinnata* is associated in the dry páramos of the Sierra Nevada del Cocuy and the Páramo del Almorzadero. In páramo meadows in the Colombian Cordillera Central (Parque Los Nevados), tufted species of *Festuca* and *Taraxacum* sp. are characteristic (Cleef et al., in press). The greatest affinity is with the *Aciachnetum pulvinatae* and the *Agrostis breviculmis-Lachemilla pinnata* community.

Synecology: This community is characteric for intensively grazed and manured, (slightly) humid, level ground in the páramos, where it spreads easily in places where the tussocks disappear. Mats of *Azorella pedunculata* and *Plantago rigida* are associated in one place in the Páramo de Guantiva (rel. 40). Soils are humic clay or sand and moderately acid (pH 4.5-5.0).

Distribution: In the study area the *Agrostio breviculmis - Lachemilla orbiculatae* is distributed between 3700 and 4000 m (Cocuy - Almorzadero). This type of meadow is common in the neighbourhood of ranches. In the páramos of the Parque Los Nevados in the Colombian Cordillera Central the *Agrosto breviculmis - Lachemilletum orbiculatae* is present up to 4200 m (Cleef et al., in press).

112. Community of *Acaena cylindristachya*
Fig. : 13, 26
lit. : Van der Hammen & González 1960, Cleef 1978, Vareschi 1980

Acaena cylindristachya is a conspicuous low rosette plant of the zonal open dry bunchgrass páramo (see 14, 16, 17, 19). Locally, as mentioned by Van der Hammen & González (1960) and Cleef (1978), *Acaena cylindristachya* tends to be dominant, and patches are present in zonal grass páramo. In the study area these stands are mainly found in the northern páramos between 3450 m (Páramo de Guantiva and Pisva) and 4000 m (Sierra Nevada del Cocuy). The Páramo de Guasca contains a small patch of *Acaena cylindristachya* at 3350 m.
In the Sierra Nevada de S. Marta, *Acaena cylindristachya* herbfield is found on the Alto La Cumbre (3500-3700 m) and in the Donachui valley (4300 m) according to Van der Hammen & González (1960[a]), and Rangel et al. (in prep.). The *Acaena cylindristachya* rosettes have a cover of 40-90%; common associates are *Lachemilla* sp., *Polytrichum juniperinum*, *Hypericum* spp. *Hypochoeris sessiliflora*, *Gentianella corymbosa*, *Halenia* sp., *Agrostis trichodes*.
Acaena cylindristachya herbfield is supposed to develop where bunchgrasses disappear by intensive grazing and repeated burning. This view is supported by a fieldstudy on the Alto La Cumbre in the Sierra Nevada de S. Marta where transitions from bunchgrass to rosaceous herbfield have been observed. *Acaena cylindristachya* vegetation is well developed on concave slopes and may pass into another rosaceous herbfield, the *Agrostio-Lachemilletum orbiculatae* (111) on level humid ground, where water temporarily accumulates.
This vegetation has floristic affinities with the *Acaeno-Plantaginetum sericeae* (18), and also with the *Aciachnetum*, the *Lorenzochloetum* and zonal bunchgrass communities with *Acaena cylindristachya*. *Acaena cylindristachya* was not found in the páramos of the Colombia Cordillera Central.

SCREE AND OUTCROP VEGETATION

The exclusively epilithic vegetation, that is not depending on soil, has not been studied. Cryptogams restricted to such epilithic vegetation include species of crustose lichens, and *Usnea*, *Umbilicaria*, *Neuropogon*, Parmeliaceae, *Stereocaulon* (Boekhout, in prep.) *Grimmia*, *Andreaea rupestris*, *Rhizocarpon* cf. *geograficum* (rare).

113. Moss vegetation of *Rhacocarpus purpuracens* and *Racomitrium crispulum*

Bare, steep, rocky surfaces ("lajas") in the grass páramo and in the lower superpáramo within reach of the upper condensation zone, may support brownish moss vegetation of *Rhacocarpus purpurascens* and of *Racomitrium* species. Usually they grow together and one of them is predominant.
Rhacocarpus purpurascens mats dominate under permanently wet conditions, either atmospherically or edaphically by seepage. Wet *Rhacocarpus* mats on steep rocky slopes are brownish to strongly orange from a distance. They are common in the bamboo páramos (e.g. Andabobos, Q. Sitiales valley in the Páramo de Sumapaz) and in the lower superpáramo of the upper condensation zone (e.g. Nevado de Sumapaz, and to a lesser extent in the summit area of the Páramo del Almorzadero). *Racomitrium crispulum* takes over when the conditions are less humid, edaphically as well as atmospherically, or towards higher elevations.

In grass páramo watershed areas (3600-3900 m) the crests are normally covered by cloud banks coming from the wet side of the Cordillera. *Racomitrium crispulum* vegetation is abundant on those crests, mixed with whitish *Racomitrium lanuginosum*, previsously not known from the Colombian Andes.
In the less humid upper condensation zone on the NW side of the Nevado Ruíz and on other volcanoes in the Parque Los Nevados in the Colombian Cordillera Central, *Racomitrium crispulum* dominates on rocky surface. *Rhacocarpus purpurascens* only becomes prominent in seepage zones (Cleef et al., in press). This vegetation type was also seen on the volcano Puracé further to the south (Dr. T. van der Hammen, pers. comm.).

114. Community of *Thamnolia vermicularis* and *Alectoria* cf. *ochroleuca*

This vegetation type is extremely rich in lichen species. Phisiognomically and partly floristically it is reminiscent of arctic-alpine lichen communities. The stands are small and restricted to exposed tocky ridges, ledges and outcrops on the crest, expecially in watershed areas. This lichen community is characteristic for divides with wet bamboo páramos on one side. The habitat is permanently covered in fog and clouds. Lichens are thriving well under these conditions of high atmospheric humidity.
Stands on "lithosols" studied in the Páramo de Pisva and Páramo de Palacio (3700-3800 m) have in common:
1) a high cover (70-80%) of lichens, especially the fruticose forms;
2) a low cover (1-10%) and number of vascular species (not more than 5).
Vascular species common both areas are *Luzula racemosa*, *Grammitis moniliformis* and *Draba* sp. (4696A). Common lichens are *Thamnolia vermicularis*, *Alectoria* cf. *ochroleuca* (4576, 5235), *Oropogon loxensis*, *Leprocaulon albicans*, *Stereocaulon atlanticum*, *Cladia aggregata*, *Umbilicaria* sp. (4581), *Everniastrum catawbiense*, *Cora pavonia*, *Cladonia andesita*, *C. isabellina*, and species of *Siphula* and *Cladonia* subg. *Cladina:* e.g. *Cladonia colombiana*, *C. boliviana*. Common bryophytes are *Campylopus richardii*, *C. pittieri*, *Jamesoniella rubricaulis*, *Rhacocarpus purpurascens* and *Riccardia* sp. (4585). *Breutelia karsteniana*, rare in the study area, is found in the exposed windswept habitat, together with some taxa from higher altitudes (superpáramo): e.g. *Draba*, *Thamnolia*, *Luzula racemosa*, *Lachemilla nivalis*, *Jamesonia goudotii*.
The lithosols are overlying sandstone bedrock, and they are strongly (pH 4.2-4.4) to moderately acid (pH 4.9). The habitat is frequented by *Sylvilagus* and birds.

115. Community of *Senecio niveo-aureus* and *Erythrophyllopsis andina*

This rare high altitude moss community is dominated by the acrocarpous *Erythrophyllopsis andina* with a conspicuous red colour. According to Zander (1977) this species is widely distributed in the tropical Andes from Argentina to Colombia. In the study area *Erythrophyllopsis andina* vegetation was studied at 3950 m on the Alto de Torquitá in the Páramo de Sumapaz. A gregarious moss ball carpet of reddish to dark-brownish *Erythrophyllopsis andina* practically covers the humid gravelly or clayey soil, in which frost heaving is a common feature. This moss community was found in depressions in the upper grass páramo on level or gently sloping ground (up to 5^{o}). *Erythrophyllopsis andina* (dominant) is accompanied by *Senecio niveo-aureus*, and by *Draba* sp. (7750), *Lucilia* sp. (7548) and *Cladonia* sp. (7551), all with a cover of 1-5%). A similar community was also studied in the lower superpáramo in the calcareous summit zone of the Páramo del Almorzadero at 4300 m (rel. 558). *Erythrophyllopsis andina* is further known from humid epilithic habitats in rockshelters and caves in the páramos of the study area between 3700 and 4300 m.

Notes on bryophyte communities:

Moss-dominated communities are common in the open bamboo páramos of our area. *Sphagnum* bog is a striking example, but páramo mires contain also mossy communities. The *Calamagrostion ligulatae* comprises several syntaxa and communities dominated by resp. *Campylopus cavifolius, Sphagnum sancto-josephense, Drepanocladus aduncus and Calliergonella cuspidata.*
the *Wernerion crassae-pygmeae* also contains aquatic mosses with high cover: e.g. *Rhacocarpus purpurascens, Sphagnum cyclophyllum, Drepanocladus revolvens* and *Scorpidium scorpioides.* On decayed cushion bogs of the *Hyperico-Plantaginetum rigidae* a closed mat of *Breutelia chrysea* and *B. allionii* may be developed.
Rhacocarpus-Racomitrium ssp. communities cover rocky surfaces and humid exposed ridges in the grass páramo and in the wet upper condensation zone in the lowermost part of the superpáramo. The liverwort species *Herbertus subdentatus* and *H. acanthelius* determine the reddish aspect of the upper condensation belt vegetation in the summit area of the Nevado de Sumapaz.
Some communities are restricted to streams; here thrive the rheophytic *Dendrocryphaeo-Platyhypnidietum riparioides* and the *Philonoto-Isotachidetum serrulatae.* The latter association consists of liverworts. In the Colombian Cordillera Central another liverwort community of *Nardia succulenta* is present in warm water of sulphur-containing volcanic springs.

116. Community of *Senecio summus*

This community is only known in the study area in humid crevices in the calcareous rock of the summit area (4000-4200 m) on the Nevado de Sumapaz. The abundance of species and the high cover of liverworts, especially of *Metzgeria gigantea* and *Plagiochila dependula* and further *Porotrichum* sp. (8165), *Amphidium cyathicarpum, Bartramia angustifolia, Mohrinia ehrenbergiana, Radula* sp. (8156), *Plagiochila cuatrecasasii, Herbertus subdentatus,* etc. reflect a well-developed upper condensation zone. *Draba* sp. (yellow petals), *Valeriana plantaginea* and other species of the *Racomitrium-Valeriana plantaginea* community (27) are conspicuous also. *Senecio summus* is the most characteristic herbaceous species, reported here for the first time from the Colombian Cordillera Oriental. It was only known from the high páramos of Central and northern Ecuador and the Colombian Cordillera Central (Parque Los Nevados), where it is restricted to similar habitats between 4000 and 4400 m. *Senecio summus* belongs to the sect. *Culcitiopsis* Cuatr., which comprises high altitude species endemic to the tropical Andes from Peru to Colombia. The blackish clayey lithosol in the locality at 4170 m on the Nevado de Sumapaz is slightly acid (pH 5.7).

Contrasting with the rich community of *Senecio summus* is that of the endemic *S. pasqui-andinus (S.* sect *Hypsobates* Cuatr.), which is common between quartzite boulders in the lower part of the superpáramo, mainly on the humid side of the Sierra Nevada del Cocuy (4200-4300 m).

117. Rock shelter vegetation

lit.: Vareschi 1958

Dry and humid rockshelters are common in the páramos of the study area. In several of them between 3500 and 4350 m, a cursory inventory has been made when sheltering for heavy rain.
Some of the species that are restricted to this habitat are *Cystopteris diaphana, Asplenium triphyllum, Elaphoglossum lindenii,* Cruciferae (probably *Lepidium bipinnatifolium), Brachypodium mexicanum, Parietaria debilis, Urtica bellotaefolia, Tortula andicola, Anoectangium aestivum, Morinia ehrenberginana,*

Miconia chionophila, Kingiobryum paramicola.
Ferns are common in lower superpáramo rockshelters in the upper condensation belt at 4300-4350 m in the Sierra Nevada del Cocuy near Patio Bolos (Arauca). Among them are *Asplenium castaneum, A. triphyllum, Cystopteris diaphana* and *Polystichum polyphyllum. Poa* cf. *pauciflora* (8726) is prominent in the super páramo rockshelters, especially as humid scree vegetation at the base of steep wet cliffs. This was observed on the Nevado de Sumapaz, the Pan de Azucar (4270 m) in the Páramo de Guantiva, and in the Sierra Nevada del Cocuy and S. Marta (4100-4400 m).
Common vascular species in grass páramo rockshelter are *Salvia killipiana, Parietaria debilis, Urtica bellotaefolia, Cinna poaeformis, Bromus unioloides B.* cf. *lanatus, Brachypodium* cf. *mexicanum* (5369, 7371), Cruciferae (5367, 7370), *Nertera granadensis, Muhlenbeckia vulcanica, Stachys* sp. (7368, 7398), *Echeveria* sp., *Eriosorus hirsutulus, Elaphoglossum lindenii, Sibthorpia repens, Draba* spp., *Miconia chionophila, Arenaria* sp., *Bidens triplinervia, Eupatorium (Ageratina) gracile.* Among the numerous cryptogams the mosses *Anoectangium aestivum, Distichium capillaceum, Amphidium cyathicarpum, Bryum argenteum, Morinia ehrenbergiana, Breutelia integrifolia, Bartramia mathewsii, B. potosica, Kingiobryum paramicola, Philonotis* spp. and the liverworts *Herbertus acanthelius, Metzgeria* sp., *Pycnolejeunea* subg. *Strepsilejeunea,* and *Anastrophyllum trollii* are characteristic
The presence of various floristic elements from dwarfforest and upper forest line in páramo rockshelters reflect the favourable humid microclimate.
Superpáramo taxa may be present in lower areas such as species of *Draba* and *Erigeron chionophilus.*
Sheltering cattle and deer may have introduced the nitrophytic taxa as Cruciferae, *Parietaria, Urtica, Bidens, Rumex acetosella.*

OTHER COMMUNITIES

Some other communities, the syntaxonomical position of which could not be established with certainty, will be treated below.

118. *Azorelletum multifidae* ass. nov. (prov.)
type: rel. 276; table 29; Fig. 29
photo: Gradstein et al. 1977, plate 2D; Cleef 1978, photo 177, 178
lit.: Weberbauer 1945, Cleef 1978

Physiognomy: The association concerns cushion vegetation of vascular plants. The well-developed leptophyllous cushions are 30-40 cm high. The thick moss stratum (up to 20 cm) may cover the cushions for 80% or more, depending on age of the cushions.

Table 29 *Azorelletum multifidae* ass. nov. (prov.)

rel. nr.	276
relevé area	18 m^2
cover dwarfshrub	6%
vascular cushion plants	60%
bryophytes	35%
height cushions	40 cm
bryophyte layer	20 cm
slope (degree)	-
soil	c/s
pH top soil	5.4
1 m depth	5.9
approx. number of species	45
alt. locality	4100 m
locality	Nevado de Sumapaz (Meta)

	cover %	▲		
	c/d % o taxa *Azorelletum multifidae*			
c	*Azorella multifida*	60	*Valeriana plantaginea*	1
	Breutelia chrysea	25	*Senecio summus*	1
	Diplostephium rupestre	5	*Campylopus pittieri*	1
	Plantago rigida	5	*Anastrophyllum leucostomum*	1
	Draba sp. (cf. 1300-yellow petals)	3	*Tortula andicola*	1
	Senecio niveo-aureus	3	*Satureja nubigena*	<1+
	Herbertus subdentatus	5	*Oritrophium muscosa*	<1+
	Zygodon cf. *pichinchensis* (7982)	2	*Oreomyrrhis andicola*	<1+
	Senecio vernicosus	1	*Campylopus tunariensis*	<1+
	Draba sp. (cf. 1310-white petals)	1	*Cetraria* sp.	<1+

With a cover lesser than 1% *Hypochoeris sessiliflora* (yellow), *Senecio formosus*, *Gentiana sedifolia*, *Ophioglossum crotalophoroides*, *Carex* cf. *tristicha*, *Geranium confertum*, *G. sibbaldioides*, *Lysipomia sphagnophila* ssp. *minor*, *Cerastium imbricatum*, *Bryum ellipsifolium*, *Hypnum cupressiforme*, *Brachythecium* sp., *Racomitrium crispulum*, *Peltigera canina*, Parmeliaceae, *Leprocaulon albicans*, Jungermanniales (7977), *Oropogon loxense*, *Bryum argenteum*, *Bryum* sp., *Riccardia* sp., *Philonotis* cf. *revoluta*, *Fissidens* sp. (7978), *Calliergon* sp., *Barbula* sp., *Stereodon hamatus*.

Composition & syntaxonomy: *Azorella multifida* is a selective character species. *Breutelia chrysea* is conspicuous on decaying cushions of *Azorella*. *Bryum ellipsifolium* is only known from high areas on Kilimanjaro, and from Venezuela, Colombia, Bolivia and Tierra del Fuego (Ochi 1980).

Synecology: The *Azorelletum multifidae* constitutes the cushion vegetattion of in humid small valleys in the upper reaches of the Nevado de Sumapaz. The cushions are restricted to the upper condensation zone with a permanently high humidity. The pH of the brown to yellowish-brown deep colluvial clayey and sandy soil is 5.4 in the top layer, and 5.9 at a depth of 1 m. Succession after decay of the *Azorella multifida* cushions may lead here to the *Senecionetum verñicosi* (85). Further data on the synecology of the *Azorelletum multifidae* are given in Cleef (1978).

Distribution: Cushion vegetation of the *Azorelletum multifidae* is well developed between 4050 and 4200 m on the Nevado de Sumapaz; also in small patches on other high peaks and in watershed areas of the Páramo de Sumapaz above 3900 m that reach into the upper condensation zone. Solitary cushions of *Azorella* cf. *multifida* were seen on the high volcano Nevado de S. Isabel in the Colombian Cordillera Central; they are supposed to be present in the Ecuadorian cushion páramos (Øllgaard & Balslev 1979) and Peru (Weberbauer 1945).

119. Bamboo grove of *Neurolepis aristata*
characteristic rel.: 17; table 30

Physiognomy: This type of high altitude bamboo grove occurs near to patches of upper Andean dwarfforest. The dense bamboo layer is up to 3 m high an has a cover of 100%. A dwarfshrub layer and a low herbaceous layer are almost absent. The well-shaded ground layer consists almost entirely of hygrophytic bryophytes with a cover of about 50%.

Composition: The grove consists of the odd bamboo species *Neurolepis aristata*. *Trichocolea* sp. (1212) is dominant in the moss layer, which contains a number of hygrophytic taxa, e.g. *Metzgeria leptoneura*, *Riccardia* spp., *Fissidens* and *Chorisodontium setaceum*.

Table 30 *Neurolepis aristata* bamboo grove

rel. nr.	17
alt.	3635 m
loc.	Nevado de Sumapaz
incl.	20^o
relevé area m^2	8
soil	humic clay

cover %			
Neurolepis aristata	100	*Fissidens* sp. (1216)	5
Swallenochloa tesselata	5	*Riccardia* sp. (1215)	1
Baccharis macrantha ssp. *denticulata*	1	*Plagiochila* sp. (1217)	1
Ribes sp.	1	acrocarpous moss (1214)	1
Geranium sibbaldioides	1	*Chorisodontium setaceum*	1
Miconia cleefii	1	cf. *Plagiochila* sp. (1220)	1
Pereromia hispidula	1	hepaticae div. spp. (1211, 1221, 1227)	1
Trichocolea sp. (1212)	30	*Sphagnum magellanicum*	1
Metzgeria leptoneura	10	*Peltigera dolichorhiza*	1
Riccardia sp. (1218)	5	*Cladonia isabellina*	1

Synecology: Steeply sloping ground in small protected valleys near the upper cloud forest line. The upper soil layer consists of sandy, humic clay (pH 4.6). The bryophyte cover has strong floristic affinities to that of the superhumid upper part of the cloud forest, which contains taxa indicative of high humidity. The presence of *Sphagnum magellanicum* indicates boggy conditions. *Neurolepis aristata* is also a characteristic species of the upper Andean forest and high Andean dwarf forest in the Parque Los Nevados, Colombian Cordillera Central (Cleef et al., in press).

Distribution: *Neurolepis aristata,* according to Mc Clure (1973), is found throughout the border area of humid Andean forest and bamboo páramo from Chachapoyas in NE peru, to Colombia, between 2900 and 4000 (4500 ?) m, locally in large, almost impenetrable clumps. In the Colombian Cordillera Oriental this odd bamboo is found in some places on the humid side of the mountains between 3000 and 3750 m.

120. Dense *Espeletia* stemrosette communities
Fig. 78 (also Fig. 27, 52, 54, 55, 72)

Patches with dense *Espeletia* stemrosettes are common from the forestline up to the superpáramo. Such macróphyllous stemrosette community is found in protected places, mostly in depressions on humid or wet, boggy ground. Stemorosettes of *Espeletia,* also grow closely together along the humid sides of wet valleys. *Espeletia* has a cover of 35-80%. The higher cover of the stemrosettes causes the grass bunches to be largely replaced by low matted brownish- to dark-greenish skiophytic species. The floristic composition is variable and depends on drainage, substrate, shadow and altitude. Species of *Paepalanthus* (e.g. *P. karstenii*, *P.andicola* var. *villosus*) are characteristic in this type of stands on dry sloping soil, mainly in the subpáramo. Other frequent taxa are low shrubby species, e.g. *Baccharis tricuneata*, *Arcytophyllum muticum*, *Vaccinium floribundum* var. *ramosissimum* and *Disterigma empetrifolium*. *Oritrophium peruvianum* ssp. *peruvianum* fma. *intermedia*, *Carex pichinchensis*, *Rhacocarpus purpurascens*, *Breutelia allionii* are characteristic in dense *Espeletia lopezii* stands (3500-4250 m) on humid, clayey soil (pH 5.1-5.8 in the rootzone) in depressions and in the heads of wet valleys. These stands fringe such wet valleys downslope to the forest line. In rel. 117, *Campylópus paramoensis* dominates this habitat.
This species was previously only known from Costa Rican páramos.
Characteristic taxa in *Sphagnum* bogs may appear in dense *Espeletia* stands (e.g. *E. chocontana*, *E. murilloi*, *E. incana*) on wet peaty ground in the lower páramos. Such stands rather belong to the communities of the páramo *Sphagnum* bog formation.

121. Commity of *Orthrosanthus chimboracensis*

The iridaceous *Orthrosanthus chimboracensis* is endemic and restricted to the lower páramo.
On the dry side of the mountains where shrub páramo is replaced by low herbaceous mats after cutting timber, burning and grazing, large tufts of *Orthrosanthus chimboracensis* var. *chimboracensis* become predominant. This is seen in many places in degraded subpáramos facing the high plains of Bogotá, in other parts of Cundinamarca and Boyocá, and on the dry side of the Sierra Nevada del Cocuy and the Páramo del Almorzadero.

In sloping dry depressions and gullies from the bunchgrass pāramo towards the former forestline above Belēn (Boyocā), *Orthrosanthus chimboracensis*-dominated herbfield is common. The stands are developed on thick colluvial black sandy clay, slightly acid in the upper part (pH 5.4), and they are present between 3400 and 3650 m. Such an iridaceous herbfield (1 m high, 10° slope) at 3645 m contained the following herbaceous species:

Orthrosanthus chimboracensis (dominant)
Lachemilla spp.
Ranunculus peruvianus
Acaena cylindristachya (locally codominant)
Rhynchospora sp.
Calamagrostis sp.
Agrostis
Lupinus sp.
Oxalis sp.
Conyza sp.
Bidens triplinervia
Paspalum bonplandianum
Viola humilis
Noticatrum marginatum
Geranium sibbaldioides
Gnaphalium sp.
Bartsia sp.
Digitalis purpurea L.
Anthoxanthum odoratum L.
Holcus lanatus L.

IV. DISCUSSION AND CONCLUSIONS

GENERAL COMMENTS

The open pāramo belt contains a much larger number of plant communities than the Andean cloud forest belt, at least when there are no human activities. This is typical for the high mountains of tropical and temperate latitudes. For North America, Komārková (1979, fig. 73 & table 29) presented quantitative data for the Front Range, Colorado Rocky Mountains.
At lesser altitudes the vegetation from the Andean forest to the open pāramo shows the presence of an increasingly high number of different zonal and azonal plant communities. This is corroborated by the present study, and by ECOANDES studies in Andean forests and pāramos in the Cordillera Central (Cleef et al., in press), and the Buritaca transect in the Sierra Nevada de S. Marta (Rangel et al., in prep.). The formerly glaciated pāramo belt with numerous lakes in boggy valleys, separated by dry moraines, represents a diversified landscape with a large variety in habitats and vegetation. The diversity is expressed by the floristic composition of the vegetation as well as by its structural character (height, growth form). In the superpāramo, solifluction and other phenomena are responsible for the diversity in habitat and plant cover. In this respect, conditions in the pāramo and superpāramo belt are in contrast with those in the lower pāramo zones and forest belt.

Some general conclusions will presently be discussed on the relation of the pāramo vegetation and its growth forms and leaf sizes to temperature and humidity, and also on the phytogeography of the pāramo vegetation.

Vegetation in relation to temperature and humidity

The open vegetation in the equatorial high mountains is exposed to a diurnal climate, characterized by daily fluctuations in temperature, with the lowest values at night and the highest in daytime.Temperature is the main determining factor, with humidity as an additional agent; the two are interrelated to a certain extent.
The pāramo vegetation in the study area shifts in accordance with these two major factors. The factor temperature is mainly determined by the temperature with increasing altitude (the lapse rate is generally 0.6°C per 100 m). This is the most important gradient and it determines the shift from woody to graminoid and other herbaceous zonal pāramo vegetation from the forest line up to the nival belt (Fig. 6, 8). As a consequence of prevailing low temperatures, the uptake of water and nutrients by the roots of vascular plants becomes lower and transpiration by the leaves slows down. Species of tropical orgin apparently are less adapted to this environment; this may explain the predominance of temperate (wide temperate, holarctic, austral-antarctic) genera in the highest areas of the pāramo belt (Van der Hammen & Cleef, in press). Towards higher elevations atmospherical radiation increases, and plants seem to protect themselves against the high radiation by developing various kinds of leaf coatings or by changes in leaf colours. In areas with permanent high atmospherical humidity, however, radiation has distinctly less effect.

The factor moisture is mainly determinated by the gradient from low to high (atmospherical) humidity. High moisture conditions cause narrow temperature

Table 31

PARAMOS COLOMBIAN CORDILLERA ORIENTAL	number of months with high precipitation 1)			mean total annual precipitation (mm)
	100 mm	50 mm	water deficit 1)	
1 zonal bamboo páramo	9	12	-	2000
2 bamboo-bunchgrass páramo	6 - 9	10 - 11½	-	1100 - 2000
3 bunchgrass páramo	1½ - 6	6 - 10	0 - 1	1100

1) based on climatediagrams (Fig. 3)

amplitudes and low values of nightly radiation. Thus, oligothermic conditions are more pronounced on the humid side of the Cordillera, and this causes asymmetrical altitudinal vegetation belts (Lauer 1976, 1979; Cleef 1979b; Van der Hammen et al. 1981). This is most prominent in the so-called "condensation belts" near the upper forest line, and along the lower border of the superpáramo, especially on the wet side of the Cordillera (Fig. 6 & 8).
The condensation belts are botanically characterized by:
1) a high cover and abundance of terrestric and epiphytic bryophytes;
2) a conspicuous abundance of plant species;
3) presence of woodiness (due to favourable temperatures) in the upper condensation belt, as indicated by such specialized composites as species of *Loricaria*, *Senecio* and *Diplostephium*. Adjacent zonal vegetation is herbaceous, however;
4) relatively larger leafsizes of vascular plants and bryophytes than in the adjacent zones; and
5) presence and high cover of bamboos (usually belonging to two or three genera) in the forestline-condensation belt.

High atmospherical humidity is most prominent in the lower part of the páramo belt. Physiognomically, this can be concluded from the occurence of (dwarf) bamboos in zonal and azonal vegetation, and of numerous bogs (Fig. 6 & 8).

Thus, three main types of páramo grassland may be recognized (Fig. 79):
1) bunchgrass páramos, practically without bamboos (e.g. communities 14-20)
2) bamboo-bunchgrass páramos or bunchgrass páramos with bamboos, more or less restricted to boggy valley floors and slopes (e.g. communities 10-20), and
3) zonal bamboo páramos with a strongly lower cover of bunchgrasses (communities 10-13).

Zonal bamboo páramos are restricted to the lower part of the páramo belt. Atmospherical humidity generally decreases with altitude (Weischet 1969, Lauer 1979; this study Fig. 3 & 4), and thus zonal lower bamboo páramo passes into bunchgrass bamboo páramo. At greater heights, bamboos become more restricted to moist depressions and the bamboo grassland is gradually replaced by an (upper) bunchgrass páramo (community 20). Edaphic factors controlled by physiography act most strongly on the presence and distribution of dwarfed bamboo vegetation in grass páramos belonging to group 2, which probably covers the greater part of the study area. The presence and cover of bamboos in comparison to bunchgrasses has been discussed in relation to annual precipitation (Cleef 1978, 1979a). It is now evident that distribution, cover and height of the bamboo vegetation are determined also by other interrelated factors, e.g. humidity, physiography and temperature.
In order to prove the interrelation of these factors, pluviometric data have been collected from different altitudes in the páramo and the upper part of the Andean forest belt, where field work has carried out. Most of these pluviometric stations are located in the southern part of the study area in bunchgrass páramos where, depending on humidity and elevation, bamboos may be common also. In the most humid bunchgrass páramos the area of bamboo-covered valley and slope bogs is rather large.
A close correlation may be made with the duration of the humid period(s), calculated as the period during which the precipitation curve rises above the temperature line on the climatic diagram (Fig. 3), the mean annual precipitation and the altitude (Fig. 80; table 31). Lauer (1952) based his humid periods on the formula of De Martonne. Basically, not many differences can be noticed with the method used in the present study when both methods are applied to the lower part or the páramo belt of the upper Andean forest.

Mainly climatically determined boundaries could be provisionally recognized between the bunchgrass páramos, the bamboo-bunchgrass páramos and the bamboo páramos. In the bamboo-bunchgrass páramos the boundaries are spatially controlled by the physiography. These boundaries are still provisional, however, as they have to be confirmed by additional pluviometric data, especially from the atmospherically wettest and driest páramos.

In conclusion, the relation between altitude, climate and zonal páramo vegetation is depicted in Fig. 81. It is constructed in a similar way as the "ecograms" published by Ellenberg (1975, 1979) for the Ecuadorian and Peruvian Andes. From Fig. 81 it is apparent that, along a given altitudinal gradient in the grass páramo, the differences in humidity and temperature cause different types of páramo vegetation.

The climatic relations of páramo and puna vegetation have been dealt with by several authors. According to climate diagrams (Fig. 3 m, i) from the most arid páramos in the study area (Páramo de Berlín, 3230 m; El Hato, 3150 m), the period of water deficit lasts not much longer than one month. Ellenberg (1975, 1979), assigned páramos to "perhumid" and "euhumid" supraforest climates (humidity classified following Lauer 1952) in the Ecuadorian and Peruvian Andes, whereas moist puna is present under "subhumid" and semihumid" climatic conditions. Some climate diagrams published by Walter et al. (1975) from about equally high altitudes in the Peruvian and northern Bolivian Andes (e.g. Caillona 3960 m, Puno 3822 m) are indeed strikingly similar to páramo climate diagrams. Likewise, the climate diagram of the Venezuelan lower superpáramo of Pico de Aquila (Mucuchies) at 4118 m is surprisingly similar to that of Cerro de Pasco (4350 m) in Peru, but it should be noted that the snowline is situated much higher here than in the northern Andes (Troll 1968). The number of humid months was determined by Troll (1968) and Lauer (1979) as 10 - 12 for the páramos, 7 - 10 for the moist puna, 4½ - 7 for the dry puna, and 2 - 4½ for the thorn puna. In climate diagrams along an E - W transect in the southern Peruvian Andes or from NE to SW through the Peruvian uplands a similar relation can be noticed (Walter et al. 1975; Ellenberg 1979). The length of the deficit period increases in SW direction: e.g. Cuzco (3380 m - 3½ month), Jauja (3450 m - ca. 5 months), Galeras Pampa (4000 m - ca. 5 months, this paper).
Going from per- and euhumid conditions to subhumid and semihumid climates the floristic shift is not restricted to one from *Swallenochloa* - bamboo páramo to *Calamagrostis*-bunchgrass páramo. With lower humidity, xeromorphy increases too, and this is floristically expressed by the presence of bunches of *Festuca* and tufts of *Stipa, Dissanthelium* etc. In puna grassland, there are also more xeromorphic species of *Calamagrostis* sect. *Deyeuxia* (Tovar Serpa 1973; Gutte & Gutte 1976; Ruthsatz 1977).
Extremely dry páramo grassland with *Cortaderia nitida* and *Stipa* is described from the Páramo de Batallón in the Venezuelan Andes by Vareschi (1980), whereas Harling (1979) reported dry *Stipa* páramos from southern Ecuador. Van Geel & Van der Hammen (1973) even referred to arid páramos in the vicinity of the Lake Fúquene about 21,000-14,000 BP.
The vegetation with spaced grass bunches in the lowermost part of the páramo belt is frequently caused by intensive grazing of cattle and burning by man. The effect of human activities can be noticed in these dry páramos.
In the upper grass páramos, spacing of bunches is a natural feature, mainly caused by physiographical and edaphical factors. Soils are very thin, with stony patches, rocks and boulders. Indications of solifluction become more frequent towards the superpáramo. At the same time the amount of water available for the vegetation gradually diminishes.

Growth forms and leaf sizes

Growth forms of zonal and azonal communities are also related to elevation and climate. Fig. 6 shows in a schematic way the optimal development of prominent páramo growth forms for the dry and humid side of the Colombian Cordillera Oriental, as indicated by the various environmental conditions on both sides of the Sierra Nevada del Cocuy. As for the altitudinal belts, an asymmetrical distribution can be noticed for growth forms (bamboos, bunchgrasses, rosettes) in zonal páramo vegetation. This may be explained as response to different climatic conditions.

With regard to leaf sizes (Fig. 86), the zonal shrub páramo is determined by nanophyllous and microphyllous shrub. On the humid side of the mountains predominates a microphyllous shrub páramo. In the dwarfshrub páramo on the dry side of the Cordillera dominate bryophyllous rubiaceous species, whereas leptophyllous and/or nanophyllous dwarfshrubs are components of this zone in the wet bamboo páramos.

Tussocks with revolute microphyllous leaves are characteristic for the bunchgrass páramo, but they are largely replaced by dwarfed microphyllous bamboos in humid and wet páramos. In the upper grass páramo the revolute-leaved tussocks are also prominent, but the bunches are more widely spaced.

Zonal lower superpáramo bush (*Loricarietum complanatae*) is imbricate leptophyllous, or even bryophyllous. Nanophyllous and leptophyllous zonal superpáramo vegetation is found on the dry side of the mountains. Within the reaches of the upper condensation zone on the humid side of the Cordillera, leptophyllous *Loricaria* are found, as well as an abundant bryophyllous vegetation of Bryophyta together with many mesophyllous plant species, e.g. *Senecio canescens*, *Valeriana plantaginea*, *Lupinus alopecuroides*, *Espeletia cleefii* and *E. lopezii*. Microphyllous *Senecio niveo-aureus* is also prominent here. Most of these species are covered with a dense indumentum.

Phytogeography

As to the phytogeographical relationships of páramo vegetation the following general conclusions may be drawn, based on dominant or prominent genera and species. For a more comprehensive review, see Van der Hammen & Cleef, in press.

At the generic level, most of the associations and communities are made up of the wide temperate elements, especially in the upper part of the páramo belt. The neotropical (-Andean) element is mainly represented in the upper condensation belt (*Loricarietum complanatae*), in most short grass of herbaceous meadows and in the *Distichia* cushion bogs. The páramo element is common in the *Aragoetum abietinae*, which,unlike the communities of the *Swallenochloa* bamboo pāramo, has a limited distribution. Purely austral-antarctic (e.g. *Philonoto-Isotachidetum*) or holarctic (e.g. *Myricetum*) communities are rare. The wide-tropical element is only represented in the lower páramo, e.g. *Xyris* bog, *Cyperus* reedswamp. Most associations and communities are endemic to the páramos. Several of them are also present (or may be expected so) in the Puna of Peru and Bolivia, e.g. *Isoetetum andicolae*, *I. glacialis*, *I. socia* , *Tillaeetum paludosa*, *Potameto-Myriophyllion elatinoides*, *Philonoto-Isotachidetum serrulatae*, the *Oritrophio-Wernerietum pygmaeae*, the cushion bogs of the *Gentiano-Oritrophion* (prov.), *Hypericum laricifolium* shrub, *Escallonia myrtilloides* dwarfforest, the *Lorenzochloetum*, the *Aciachnion (prov)*, the *Muhlenbergietum fastigiatae*, the communities with *Lachemilla pinnata* and *Azorella multifida*, and probably zonal *Pernettya prostrata-Luzula racemosa* moraine vegetation.Wide-temperate communities are scarce and mainly aquatic, e.g. the *Dendrocryphaeo-Platyhypnidietum ripariodes*, the *Eleocharis acicularis* community and the *Lemno-Azolletum filiculoides*.

In general, it seems that páramo waterbodies were first colonized by southern immigrants, long before the Panamanian isthmus came into being possibly about 2.5. millions years B.P. according to Raven & Axelrod (1974).

ZONAL PARAMO VEGETATION

A number of factors determine the distribution and the floristic composition of zonal páramo plant communities in the study area. The general zonation of the páramo vegetation has different altitudinal sequences for the humid and the dry sides of the mountains (chapter II).

The climate is primarily responsible for differences in physiognomy and floristics. The temperature, principally the minima (and their frequency), controls the vertical distribution of the zonal communities (Fig. 82), which on the dry side of the Sierra Nevada del Cocuy (e.g. communities 2, 5, 19, 21ª, 22) have markedly shifted upslope compared to the situation elsewhere; this is to be attributed to ascending warm air from the adjacent inter-andean dry Chicamocha valley.

The concept of zonal vegetation according to Mueller Dombois & Ellenberg (1974), following Walter (1954), is taken in a rather wide sense. Consequently, zonal habitats may be controlled by various primary physiographic conditions. In addition, secondary factors, e.g. the shape of slopes (concave of convex), the thickness of the soil, the drainage conditions, affect the habitats (Figs. 79, 84). Similarly, on a dry slope, mesic habitats may be present at the lower part of the slope and grade into xeric habitats at the higher part (Figs. 79, 83) This type of gradient causes differences in floristic composition and vegetation structure, and thus different zonal plant communities.

Under a similar or comparable physiographic setting on slopes from the upper forest line up to the snowcap, a number of altitudinally vicariant zonal communities may be developed. On the other hand, climatologically vicariant communities may be found in the same setting at about equal altitudes, either on the dry or on the humid side of the mountains.

In this study the following example: different zonal communities can be seen to replace each other with increasing elevation in the most xeric settings on steep slopes on the dry side of the mountains:

- Shrub páramo with *Espeletiopsis* (1);
- Dwarfshrub of *Arcytophyllum nitidum* with *Sporobolus lasiophyllus* and *Achyrocline lehmanii* (6);
- *Espeletiopsis* - *Calamagrostis effusa* lower bunchgrass páramo (14), and
- *Espeletiopsis* - *Calamagrostis effusa* upper bunchgrass páramo (19).

In the superpáramo these dry habitats are occupied by the *Loricarietum complanatae pernettyetosum* (21ª) in the lower parts, and the *Luzula racemosa* - *Pernettya prostrata* community in the higher parts (23).

In these habitats the humid zonal soils are thin (Fig. 84) and the Ph ranges from 4.5 in the shrub páramo, to 5.3 in the upper bunchgrass páramo and to 5.8 near the upper vegetation line (Fig. 85). On the same eastern side of the Cordillera there are mesic parts which support with increasing altitude respectively:

- *Arcytophyllum nitidum* dwarfshrub with *Diplostephium phylicoides* (7) *Espeletia argentea/E. boyacensis* (17),
- *Oreobolus obtusangulus* ssp. *rubrovaginatus* - *Calamagrostis effusa* lower bunchgrass páramo (16ª), and probably
- *Espeletia* - *Calamagrostis effusa* upper bunchgrass páramo (20).

Here, the average thickness of humic zonal soil varies from about 10 cm in the upper bunchgrass páramo to about 50 cm (45 - 55 cm) in the lower páramo (Fig. 84); the pH of the topsoil is 4.1 - 4.8 (Fig. 85). The difference in pH range between the strongly acid mesic and the moderately acid xeric sequences may be explained by the effect of the bedrock, which is directly underlying the xeric sequences, whereas mesic sequences are found on accumulated material with a high organic content (Fig. 84).

Vicariant zonal páramo plant communities along a climatic gradient are for example the two subassociations of the *Loricarietum complanatae* (21), as well as the two upper bunchgrass communities (19, 20), and at about 3500 - 3700 m the *Calamagrostis effusa* lower bunchgrass páramo with *Oreobolus* and *Castratella* (15) and the *Rhynchospora paramorum* - *Oreobolus* - *Swallenochloa* páramo (12 p.p.). Vicariism of *Espeletia* and *Espeletiopsis* is expressed geographically, altitudinally and climatologically. It is expected that a large number of geographical races of associations may be described after a detailed synsystematical treatment of the zonal communities.
In an earlier paper (Cleef 1978, Fig. 4) the present author presented an example of the geographical, climatological and altitudinal distribution of 12 different species of *Espeletia* and *Espeletiopsis* in a 75 km cross-section through the study area near Duitama and Sogamoso. In that study major habitat conditions (wet, humid, dry) for each species were indicated. At the species level a distinct conspicuous vicariism of the Espeletiinae is found in the northern part of the study area. Particular altitudinal, climatic and ecological preferences of the different genera of this subtribe are shown in various figures of this study (e.g. Figs. 14, 27, 28, 75, 78).

Some general conclusions follow in regard to the phytogeographic position of the zonal páramo vegetation of the Colombian Cordillera Oriental.
Zonal ericaceous, melastomataceous and composite shrubs are characteristic for the lowermost part of the páramo belt, whereas zonal rubiaceous dwarfshrub (*Arcytophyllum nititum*) and dwarfed bamboo (*Swallenochloa*) vegetation of the páramo are unique for the neotropical high mountains.
Bunchgrass vegetation, similar to that described is characteristic for many tropical high mountains and other humid cool temperate regions of the southern hemisphere (Cleef 1978). Zonal bunchgrass vegetation is present as far north as the high Mexican volcanoes. Cyperaceae (e.g. *Kobresia* spp., *Carex* spp.), which may determine the composition and physiognomy of the zonal plant cover in the alpine belts of the Holarctic, are represented to a lesser degree in the zonal páramo vegetation, although *Rhynchospora paramorum* and *Oreobolus obtusangulus* ssp. *rubro-vaginatus* are important diagnostic cyperaceous species and some other cyperaceous species (of *Carex* and *Rhynchospora*) are common in the study area.
The zonal superpáramo of the study area is mainly determined by temperate elements, e.g. *Luzula, Draba, Valeriana, Senecio, Erigeron* and *Pernettya*. The local tropical element is scarce. *Valeriana* and *Erigeron* are definitely holarctic immigrants, and *Pernettya* represents the austral-antarctic element up to the nival belt.

AZONAL PÁRAMO VEGETATION

The altitudinal distribution and the pH range of the toplayer of the substrates of the various azonal páramo communities are given in Figs. 87 and 88.

The submerged communities in páramo lakes (Fig. 41) more or less fit in some of the phytosociological classes described from the Holarctic: e.g. *Isoetetea* Br. Bl. 1937 and *Potametea* R.Tx. & Preising 1942. *Charetea* Krausch 1964 are supposedly present in the deepest parts of the lakes, but no relevés have been made. The *Limoselletea*, provisionally described here from pond and lake shore habitats, is vicariant with the *Litorelletea* Br. Bl. & R. Tx. 1943 em. Den Hartog & Segal 1964, described from the northern hemisphere and the *Litorelletea australis* (prov.) Oberdorfer 1960 from Chile. Fig. 89 shows the altitudinal ranges of the submerged syntaxa in the study area and as a comparison in the

Bolivian Andes, as based on herbarium specimens and literature data (e.g. Collot 1980). The Bolivian communities reach to considerably higher elevations, because here the lower limit of the nival belt is located at 5400 m, whereas in our study area this limit lies at 4800 m. The vertical shift from predominance of the *Isoetetea* to predominance of the *Potametea*, noticed from high páramos towards lower areas, finds its parallel in the pollendiagram Laguna de Fúquene II (Van Geel & Van der Hammen 1973). This pollendiagram revealed, that during the Late Glacial between about 13,000 and 10,000 years B.P. the Fúquene lake area (about 2600 m) underwent a change from cold páramo conditions to the present-day cool conditions of the Andean forest belt, and that *Potamogeton* replaced *Myriophyllum* (*elatinoides*) and *Isoetes*.

The *Ditricho-Isoetion* includes the *Isoetetum karstenii* and the *Isoetetum sociae*, which are pioneer communities on gravelly and sandy substrates in superpáramo lakes.(Fig. 87) he syntaxa and communities of this alliance in the study area have been arranged according to altitude and substrate. The *Isoetetum lechleri* Gutte 1980 from Central Peru (4500-4900 m) is vicarious with the *Isoetetum palmeri* and the *Isoetetum cleefii*. The quillwort species,after which these associations are named, are closely related (Fuchs 1981a, b). The *Isoetetum cleefii* is thus far the only association of this alliance endemic to the study area. The *Isoetetum andicolae* is a unique isoetid cushionplant vegetation along the mineral clayey and sandy beaches of páramo and puna lakes. In the Peruvian puna this association is apparently transitional to cushion bogs of the *Isoeto andicolae-Distichietum muscoides* Gutte 1980 corr. Cleef. This sequential series of zonation has not yet been observed in the Colombian páramos, but it is quite possible, that it does occur there.

The *Limoselletea* are dominated by callitrichids and isoetids: e.g. *Tillaea paludosa* and/or *Limosella australis*. The *Isoetetum sociae* is a pioneer association, altitudinally vicariant with the *Tillaeetum paludosae* and the communities of *Limosella australis*. Fig. 91[a] shows the vertical distribution of these tiny amphibious communities and Fig. 91[b] their correlation with the various substrates in the area. *Limosella australis* dominated communities are rare in our area, but common at 4150 m in the Parque Los Nevados, Colombian Cordillera Central, from where a well-defined association may be described.

Prominent species in both alliances comprising the submerged and amphibious vegetation of páramo lakes and ponds, have strong austral-antarctic affinities, and they must have been present already in páramo water bodies shortly after these biota developed (Van der Hammen & Cleef, in press).

The *Potameto-Myriophyllion elatinoides* (prov.) as yet based on as few phytosociological records only, is the highest located alliance in the northern Andes, and mainly consists of elodeids and/or myriophyllids. Lower down it is replaced e.g. by the *Myriophyllo-Potamion illinoiensis* Rangel & Aguirre (in press) described from Lake Tota at about 3000 m (Boyacá). Elodeids are predominant there. *Myriophyllum elatinoides* and *M. brasiliensis* are diagnostic species, the latter with a low cover.
Pure stands of *Myriophyllum elatinoides* can be observed in lakes and streams reaching up almost to the lower superpáramo in the Colombian Andes and these myriophyllid phytocoena are supposed to represent a fragment of communities with *Myriophyllum* in the lower part of the páramo belt. The *Hydrocotylo-Myriophylletum elatinoides* is present along the unstable shores of peat-bottomed páramo lakes, where a hydroseral zonation can be noticed with mire communities of the *Calamagrostion ligulatae* (Fig. 42, 49, 51). Species of *Potamogeton* are apparently absent where the average annual temperature is lower than 5°C. *Potamogeton berteroanus* seems the highest located species up to 4000 m. Its distichous, lanceolate to linear (nanophyllous) leaves suggest a strongly specialized way of life. In lower places *Potamogeton asplundii* is common in bamboo páramo lakes and the euryoicous *P. illinoiensis* may locally be present

also. The latter two *Potamogeton* species are characteristic for the *Myriophyllo-Potamion illionoiensis* Rangel & Aguirre (in press) of lakes in the Andean forest belt. *Elodea* has not been observed in páramo lakes in the study area. More relevés on different substrates at various altitudes are needed, however, for a more solid phytosociological basis and a further subdivision of the *Potameto-Myriophyllion elatinoides*.

Eleocharis reedswamp communities are present from warm tropical lowland (J.W. Bristow, unpubl. list; Lindeman 1953) up to about 4000 m in the Colombian Andes, but are absent in the superpáramo. The *Eleocharitetum macrostachyae* and the *Elatino-Juncetum ecuadoriensis* have the same horizontal and vertical distribution in the study area, but they are markedly different in floristic composition and ecology (Fig. 87). *Eleocharis macrostachya* reedswamp borders eutrophic páramo lakes. *Juncus ecuadoriensis* is conspicuous in or along mesotrophic small lakes or pools with a peaty floor and partly or completely surrounded by *Sphagnum* bog. *Eleocharis macrostachya* is widely distributed in temperate America; *Juncus ecuadoriensis*, however, is restricted to the northern Andean páramos (Balslev 1979). The *Junco ecuadoriensis-Eleocharition macrostachyae* apparently belongs to a not yet described new tropical Andean order.

Reedswamp and mire vegetation together are comprised in the *Marchantio-Epilobietalia*. This order has floristic affinities with the *Scheuchzerio-Caricetea fuscae* Tx. 1937 and the *Montio -Cardaminetea* Br.Bl. & R.Tx. 1943 but most likely it belongs to an undescribed tropical Andean class. The tall sedge associations of the *Galio-Gratiolion* are generally supposed to occur throughout the north Andean páramos as well as in open azonal habitats in the adjacent Andean forest belt, but they seem to be absent in the superpáramo. Ecologically, they are in many respect reminiscent of the *Magnocaricion* W. Koch 1926 from the temperate northern hemisphere. The *Magnocaricion* belongs to the *Phragmitetea* R.Tx. & Pr.1942, but in the northern Andes this syntaxon does not occur. (*Phragmites australis* (Cav.) Trin. & Stend. seems almost absent in tropical S. America except for few stands described e.g. from Peru (Koepcke 1961; Müller & Müller 1974)).

Communities and associations of the *Galio-Gratiolion* mainly thrive on moderately to weakly acid clayey soils which are rich in organis matter (Fig. 87). Of its associations, the *Senecionetum reissiani* has a limited distribution and requires a more stable habitat; the *Caricetum pichinchensis* and the *Cyperetum lagunetto* grow on soils with widely different pH's. This is not surprising, since both species easily colonize azonal wet habitats. The same is true for the *Geranio-Calamagrostietum ligulatae*, found in *Sphagnum* bog as well as in lakeshore habitats. Grass mire vegetation is extremely rich in gradients, and as a result rapidly changes in floristic composition,forming a fine-grained mosaic of a fairly large number of communities recognized in this study. *Calamagrostis ligulata* is well represented in different types of open wet páramo habitats: e.g. beaches of superpáramo lakes, flooded flat depressions along streams, unstable turf in the páramo lake hydrosere. In contrast, the *Carex acutata* community roots only in compact turf along lake shores. *Calamagrostis ligulata* mire is optimally developed under slightly acid conditions, which implies a continuous influx of eutrophic water from adjacent higher areas or from lakes. In the hydroseral environment usually this grass mire forms a contact community with several other vegetationtypes due to the diversity in environmental gradients in this habitat: e.g. *Carex acutata* community, *Caricetum pichinchensis*, *Diplostephietum revoluti*, *Oritrophio-Wernerietum pygmaeae*, *(Swallenochloa-) Sphagnum* bog and towards open water the *Potameto-Myriophyllion elatinoides* (Fig. 42, 50, 51). With increasing acidity some *Calamagrostis ligulata* stands may develop into *Sphagnum* bog (Fig. 42, 50). Pioneer communities of the *Marchantio-Epilobietalia* in extreme habitats are poor in species: e.g. the *Carex acutata* community, the *Calamagrostis ligulata* superpáramo community, and the *Drepanocladus aduncus-Calamagrostis ligulata* community of calcareous mires.

Wet flush vegetation in the study area belong to the *Wernerietea*. Here, two associations are described, one of which, the *Carici-Wernerietum crassae*, is endemic, and mainly restricted to high locations in the Sierra Nevada del Cocuy. The other, the *Oritrophio-Wernerietum pygmaeae*, is widely distributed vertically and horizontally (Fig. 87). Rhizomatous creeping, chamaephytic composites (*Werneria, Senecioneae)* are in tropical Andean flush vegetation, so that these communities are floristically unique among the other flush communities of vascular plants in the world with e.g. Cruciferae, Cyperaceae, Rosaceae.
Werneria becomes less conspicuous on moss turf. The development may start with filamentous algae and/or liverworts (*Riccardia, sp., Isotachis serrulata)* growing in a dense submerged moss layer in the *Carici-Wernerietum crassae*. Emerged thick *Campylopus* cf. *incertus* turf or hummocks of the *Floscaldasio-Distichietum* mark the disappearance of the *Wernerion crassae-pygmaeae* at these heights. The *Oritrophio-Wernerietum pygmaeae* is often dominated by a single species of aquatic mosses, e.g. *Sphagnum cyclophyllum, Scorpidium scorpioides* or *Drepanocladus exannulatus* in the lower superpáramo and the (upper part of) the grass páramo in the study area. Low rosettes of composites or low sedges generally replace these aquatic mosses in the lower part of the páramo belt. These wet flush communities are generally surrounded by a small belt of the *Muhlenbergietum fastigiatae*, a syntaxon which occupies the gradient from wet to dry and which is characterized by its low, bluish, soft hummocks of graminoids. Floristically, this is an intermediate association between different syntaxa and communities: e.g. the *Calamagrostion ligulatae, Wernerietea, Spaghnum* bog communities, the *Aciachnetum* and the humid and dry zonal vegetation (Fig. 27, 75). Succession of the *Wernerion crassae-pygmaeae* leads to the mire of the *Calamagrostion ligulatae* and/or to hard hummock bogs of the *Gentiano-Oritrophion* (prov.), which are discussed below.

Bogs are common throughout the páramo belt and consist of peat mosses (*Sphagnum* spp.) in the lower páramos and cushions of vascular plants (dicots resp. monocots) in the higher páramos (Fig. 6, 87). Páramo bogs thus belong to two essentially different syntaxonomic groups: 1) *Wernerietea*, comprising the compact vascular cushion bogs, 2) *Sphagnum* bogs (*Sphagneta*), which include all *Sphagnum* bogs in the páramo.
At 3600-3700 m these bogs are in contact and frequently intermixed. The *Floscaldasio-Distichietum* is hardly or never a contact community of *Sphagnum* bog (Fig. 87). A hummock-hollow relief, known from bogs in other parts of the world, is characteristic for both types of páramo bogs.
The vascular cushion bogs in the study area are physiognomically and floristically tropical andean and austral-antarctic in distribution (Cleef 1978). *Sphagnum* bogs are basically wide-temperate, and occur in cool and humid climates throughout the world, although the páramo *Sphagnum* bogs are characterized by a number of local tropical elements.
It is remarkable that the (azonal) páramo bogs have their lower limit slightly below that of the corresponding zonal páramo vegetation. This may be explained by the colder environment of páramo bog compared to the prevailing environment on the surrounding slopes. The mean year isothermes that control the vertical distribution of zonal vegetation in the páramos are supposed to run through páramo bogs considerably farther downslope. In boggy depressions cold air collects at night, as was demonstrated in Ecuadorian and Venezuelan páramos by resp. Øllgaard & Balslev (1979) and Hedberg & Hedberg (1979), who showed that at 5 cm above ground the temperatures were fluctuating maximally. This temperature minimum is also reflected by the preponderance of low rosettes and leptophyllous species in this

habitat.

Floristics, phytogeography, distribution and ecology of cushion bogs of vascular plants in the Colombian pãramos were discussed before (Cleef 1978). It was demonstrated that they are austral-antarctic in origin, composition and physiognomy. They are present as soligenous bogs or floating at the surface of glacial lakes. *Oreobolus* cushion bogs were reported as new to the pãramo belt, where they occur together with the *Hyperico-Plantaginetum rigidae*. They were also found on decayed *Distichia* bog at 4350 m in the Sierra Nevada del Cocuy. The *Oreobolus* hummock bogs have a limited distribution in the study area and are supposed to be interrelated with certain phases in the succession towards the *Hyperico-Plantaginetum rigidae* and the *Floscaldasio-Distichietum*. Under similar climatical conditions these bogs probably return again to the original floristic composition, either or not via an *Oreobolus* phase. The pH records of the peaty top layer under the three types of pãramo cushion bogs show that the *Floscaldasio-Distichietum* prefers a moderately to weakly acid substrate, the *Hyperico-Plantaginetum rigidae* a moderately acid substrate and the pH of the substrate under the *Oritrophio-Oreoboletum* is intermediate (Fig. 87). Decay of the hummocks often begins with the establishment of "epiphytic" vascular plants, but in wet climates usually proceeds with that of mosses (e.g. *Breutelia allionii*, *Campylopus cavifolius*). Lichens (*Oropogon lozense*, *Cladonia spp.*) appear together with dwarfshrubs (*Hypericum lancioides*, *Pernettya prostrata*, *Disterigma empetrifolium*) towards the end of the succession.
The *Hyperico-Plantiginetum* and the *Floscaldasio-Distichietum* (Fig. 87) each have distinct vertical range. Near 4000-4200 m, they may occur together forming mosaics completely covering the valleys. This was also observed in the Parque Los Nevados (4000-4300 m) in the Colombian Cordillera Central (Cleef et al. in press), and according to Gutte (1980) this is common between 4200 and 4700 m in the high Central Peruvian Andes.
The vascular hummock bogs of the study area consist of leptophyllous, pulvinate chamaephytes, showing definite tendencies upslope towards xeromorphy. Comparing growthform and leaf characteristics of resp. *Plantago rigida*, *Oreobolus obtusangulus* and *Distichia muscoides* the following is noticed:
1) hummocks become more compact towards higher altitudes;
2) the small *Plantago* rosettes have indumented leaves parallel with the surface of the bog. The small blades of *Oreobolus* are set close to the stem under an angle of 30°) those of *Distichia* are almost imbricate and both are without indumentum;
3) Diminishing size of the leaves with height and together with increasing size of the sheats, which become gradually more amplexicaulous. Petioles are present in *Plantago rigida* but absent in the two other species;
4) Rounded or blunt leaftips of *Plantago rigida* contrast with pointed dark leaf tips of *Oreobolus* and *Distichia*;
5) Coriaceous leaves in *Plantago rigida* contrast with sclerophyllous leaves in the two other species.
6) Flat leaf surfaces of *Plantago rigida* differ from the slightly more plicate of *Oreobolus* to the completely plicate leaflets with a sharp keel of *Distichia*;
7) The symmetrical rosettes of *Plantago rigida* are replaced by bilateral compressed rosettes of *Distichia muscoides* at higher altitudes.

Weberbauer (1911) and Rauh (1939) provided excellent line-drawings of the species discussed.
For the time being the cushion bogs of the study area are provisionally assigned to the *Gentiano-Oritrophion* and the *Wernerietea*. It cannot be ruled out that future classifications, based on additional data, rank the hummock and hollow communities as separate classes, as in European *Sphagnum* bogs.

Pãramo *Sphagnum* bogs occur in the lower part of the pãramo belt. Owing to the relatively climate, *Sphagnum* bogs occupy a minor part of the pãramo landscape in the bunchgrass pãramo. Their trophic levels range from weakly a cid

(Espeletia-Blechnum community; *Swallenochloa-Sphagnum* community) to moderately acid (other *Sphagnum* communities)(Fig. 87). Their upper limit coincides with the lower limit of the cushion bogs. Some basically different *Sphagnum* communities were recognized which may be further subdivided. The *Swallenochloa-Breutelia-Sphagnum* slope bog also belongs to the *Sphagneta*; it is transitionel to zonal bamboo-(bunchgrass) páramo. This slope bog is floristically and ecologically closely related to the *Swallenochloa-Sphagnum* valley bog community and the giant *Puya-Sphagnum* community, and may be considered as a special type of"blanketbog"-vegetation restricted to the (continental) humid equatorial high mountains. The slope bogs, however, considered true blanketbogs in the sense of those described e.g. from oceanic Ireland, because they also depend on watersupply from neighbouring slopes. These bogs are absent in the drier bunchgrass páramos.
The *Aragoetum abietinae puyetosum* is a shrubby climax community on *Xyris-Sphagnum* bog and the *Diplostephietum revoluti* marks the end of the succession on *Sphagnum* bogs with *Xyris*, *Oreobolus* and *Gentianella cerymbosa* and giant *Puya-Sphagnum* bog. Most (dwarf) shrub species in páramo *Sphagnum* bogs are leptophyllous. Dense, usually tall *Espeletia* stands are also frequently noted successional to soligenous *Sphagnum* bogs covering small wet peaty ground along pāramo streams.
Probably only a small part of the *Sphagnum* bogs in the study area may represent true raised bogs, as ombrotrophic *Sphagnum* growth is restricted to the central part of the largest bogs, especially, the *Xyris-acutifolia-Campylopus cucullatifolius-Sphagnum*-bog (70[aa]) in the bunchgrass páramo. A lower precipitation causes a lesser runoff here. Most *Sphagnum* bogs are in direct contact with mineral soil or they are supplied with water from mineral soils. The latter explains the high pH values, e.g. in *Swallenochloa-Sphagnum* bogs. The runoff under humid páramo conditions is markedly higher than under dry conditions. Better drainage, enriched phreatic water and some decomposition apparently put a limit to the presence of ombrotrophic *Sphagnum* peat in the bamboo páramos, even though *Sphagnum* bogs are common.
Among the 15 *Sphagnum* species listed by Griffin (in press) for the Colombian and Venezuelan Andes, only *S. palustre* is absent from the páramo belt, whereas *S. meridense* just reaches this belt. *Sphagum cuspidatum*, *S. magellanicum*, *S. oxyphyllum* and *S. sancto-josephense* are the most common species in the *Sphagnum* bogs of our area. The first two species are wide temperate or sub-cosmopolitic in distribution; the last two are neotropical but may have originated from wide temperate ancestors (Crum & Crosby, 1974). *Sphagnum cyclophyllum* and *S. pylaesii* are holarctic immigrants. Their ecology is quite different from that of other peat-mosses. *S. cyclophyllum* is common in the *Wernerietea*, and *S. pylaesii* is a rare species in high located páramo lakes.
As to the phytogeographic composition of the *Sphagnum* bogs in the study area, it may be noted that presence and cover of (neo-)tropical genera increase towards lower areas, e.g. *Espeletia*, *Puya*, *Diplostephium*, *Swallenochloa*, *Aragoa*, *Arcytophyllum (muticum)*, *Xyris*. The austral-antarctic element is represented by *Oreobolus*, *Pernettya*, *Cladia*, *Myrteola*, *Rhacocarpus*. Originating from southern immigrant taxa are: *Laestadia*, *Diplostephium*, *Aragia*, *Breutelia*, *Blechnum loxense* and *Lepidozia/Kurzia*, *Oritrophium*, *Distachia* (Cuatrecasas 1969; Van der Hammen & Cleef, in press). From holarctic stock or origin are *Pleurozium schreberi*, *Telaranea nematodes*, *Geranium multiceps*, *Bartsia* spp., *Halenia* spp., *Gentiana sedifolia* and the *Sphagnum* species mentioned earlier.
Some species are restricted to cushion-bogs *(Gentiano-Oritrophion)*, e.g. *Hypericum lancioides*, *Bartsia* spp., *Nertera granadensis*, *Pernettya prostrata*, *Breutelia* spp., *Rhacocarpus purpurascens*, *Werneria humilis*, and *Gentiana sedifolia*. Species of *Lachemilla* are nearly absent in well-developed *Sphagnum* bogs.

In sum , cushion bogs and *Sphagnum* bogs are altitudinally vicariant, and floristically quite different. They have only got a few species in common. The hummock-hollow relief as known from other bogs in the world is well developed. Most bogs are soligenous, but they may cover open surfaces of former glacial lakes. The tropical element is conspicuous, and increasingly represented in *Sphagnum* bogs at lower elevations. The austral-antarctic element seems stronger represented here than the holarctic one. Species of *Breutelia* have a gradually higher cover towards higher altitudes, where they replace *Sphagnum*, which is almost absent in cushion bogs. Xeromorphy in cushionbogs increases with altitude.

The most striking aspect of the azonal shrub and dwarfforest vegetation in the study area is the large number of thicket communities dominated by one single species, generally of the Compositae or Hypericaceae. In a few communities, the following families may be dominant: Scrophulariaceae *(Aragoa)*, Rubiaceae *(Arcytophyllum)*, Myricaceae *(Myrica)*, Escalloniaceae *(Escallonia)* and Rosaceae *(Polylepis, Hesperomeles)*.Noteworthy is the absence of dominant Ericaceae and Melastomataceae in azonal thickets, but they are common or dominant in zonal communities of the subpáramo.

Woody formations of nanophyllous species of Compositae *(Diplostephium, Senecio, Gynoxys)* are most common. In more xeric habitats or at higher altitudes there is a tendency towards leptophyllous shrubs. Microphyllous, woody formations are mainly found on the humid side of the Cordillera.
Practically all páramo species of *Hypericum* are leptophyllous; some of them, native to the most hunid páramos, are nanophyllous. These are nearly absent in the superpáramo, except *Hypericum lancioides*, which may be present in *Distichia* bogs, and *H. selaginoides*, in the lowermost zonal superpáramo. Rosaceous thickets are rare in the study area, but rosaceous dwarfforests are still common, although they are endangered by human activities. The same is true for *Hesperomeles* cf. *goudotiana* dwarfforest, the groundlayers of which have largely been converted into meadows for cattle.
Polylepis quadrijuga is the only woody species in the páramo belt with compound leaves. In the Andean and Subandean forestbelt, mainly on the dry side of the mountains, woody species with compound leaves are often dominant: e.g. pinnate-leaved species of *Weinmannia* (Cunoniaceae) and *Brunellia* (Brunelliaceae), and further species of *Inga* (Caesalpiniaceae), all of which belong to the order Rosales. Members of the Rosales are in fact the main constituents of the canopies of the zonal high Andean forests, except the *Quercus* woodlands. In contrast, simple-leaved species of *Weinmannia* and *Brunellia* sect. *Simplicifolia* Cuatr. are dominant in the upper stratum of Andean forests on the opposite, humid side of the mountains. Even palms, e.g. *Geonoma weberbaueri*, Givnish (1978)referred especially to wet mountain forest when he concluded that compound leaves are more common in tropical lowland rain forest than in montane or elfin forest.

From the remaining thicket genera, *Aragoa, Escallonia* and *Polylepis* show austral-antarctic affinities beyond the genus level *Myrica* is a holarctic genus, and *Arcytophyllum* and *Hesperomeles* seem to be immigrants from the northern part of Central America.

All the mentioned woody species occur optimally in azonal habitats, and their (present) distribution is determined by a number of factors.
Humid to wet and boggy habitats contain the *Diplostephietum revoluti*, the *Aragoetum abietinae*, the *Senecionetum andicolae*, the *Senecionetum reissiani*, the *Hypericetum laricifolii*, and some dwarfforest and/or (dwarf) shrub communities with *Escallonia myrtilloides, Senecio cacaosensis*, and *Hypericum magniflorum*. Mesic habitats are occupied e.g. by the *Senecionetum nitidi*, *Senecionetum vernicosi*, *Hypericum* spp. shrub, the *Myricetum parvifoliae*,

the *Senecionetum flos-fragrantis* and *Senecio vaccinioides* shrub (in pockets in the Páramo de Guantiva). Well-drained habitats (rockshelters, screes, rocky exposed peaks and ridges) contain e.g. the *Cortaderio-Arcytophylletum caracasani*, dwarfforests of *Gynoxys albivestita*, *Polylepis quadrijuga*, and *Diplostephium rhomboidale*, and e.g. (dwarf) shrub of *Diplostephium glutinosum*, *D. colombianum*, *D. juajibioyi*.
The azonal dwarfforest and shrub communities apparently belong to several different not yet described syntaxa. Because of the constant and favourable humidity and shade conditions, some of these communities have species in common with the zonal upper Andean forest or with páramo bogs, especially species of the understorey (see table 14).
As to structural and textural characteristics, four different layers can be observed in páramo dwarfforests;

1) an almost closed groundlayer of bryophytes and low herbs,
2) an open or closed herb-dwarfshrub layer,
3) an open or closed shrub layer. Bamboos, if present, usually reach up into this layer, and
4) an open or closed dwarftree layer, generally not higher than 8 m, only in dwarfforests.

Most leaves are sclerophyllous, and some are coriaceous. The latter catagory is proportinally higher represented on the dry side of the mountains.
Most of the dominant woody species are nanophyllous, and smaller numbers are leptophyllous and microphyllous. Mesophyllous species are absent. This is in general agreement with Cuatrecasas (1934), who based his findings, however, on all woody species present in the páramo belt of the areas studied in the Cordillera Oriental and Central of Colombia. The azonal dwarfforests in the study area are dominated by nanophyllous and microphyllous species. Leptophyllous groves are practically absent. Wooded species on the humid side of the mountains generally tend to larger leaf surfaces. According to the revised Raunkiaer scale (see Werger & Ellenbroek 1978) all *Hypericum* shrub is leptophyllous and only a few of Raunkiaer's microphyllous species are (sub-)nanophyllous. If Barkman's category bryophyllous (previously also applied by Vareschi 1966) for the small leaf surfaces up to 4 mm^2 is applied, then the most hypericaceous and all rubiaceous (zonal & azonal *Arcytophyllum*) shrub belongs to this leaf-size class. The *Aragoetum abietinae*, with average leaf surfaces of about 5 mm^2, is somewhat intermediate between bryophyllous and leptophyllous. It thus appears, that the general trend for leaves of azonal páramo shrub is nanophyllous, followed by leptophyllous resp. microphyllous.

The azonal meadow communities of the páramo consist of short grasses of the xerophytic Stipeae or of low rosaceous herbs *(Lachemilla, Acaena)*. The *Lorenzochloetum* (Stipeae) and *Agrostietum foliatae* are the only communities with low bunches or stiff tufts. All the mentioned species become dominant in azonal habitats, which have in common a concave physiography, thick soils, and high soil humidity. *Lorenzochloa* is an euryoicous species present form the forest line up to the superpáramo line. This corresponds to data from the Venezuelan páramos (Farinas, 1979). The *Aciachnetum* is common in dry páramos in the northern part of the study area. The original description from Venezuela by Vareschi (1953) is emended here with floristic data from the Colombian Cordillera Oriental and Central.In view of its wide distribution along the tropical high Andes, it is supposed that a number of regional associations dominated by the monotypic *Aciachne* will be recognized that might be combined into an *Aciachnion pulvinatae* (prov.). The *Acaulimalva-Agrostis breviculmus* community (25) of higher altitudes (4000-4300 m) is a floristically and ecologically related community and its position amongst the zonal communities in this study is a provisional one. The *Muhlenbergietum* *fastigiatae* similarly has a wide tropical Andean distribution and is restricted to wet valley floors in the transition to the flush vegetation and/or vascular cushion bogs of the *Wernerietea.*

Rosaceous herb fields with widely distributed native species are considered as resulting from burning and/or intensive grazin by cattle. The *Agrostio-Lachemilletum orbiculatae* is found on flat valley floors; occasionally the roots are within reach of the phreatic level. The *Agrostis b reviculmis-Lachemilla pinnata* community replaces the *Aciachnetum pulvinatae* in the study area in moderately steep habitats, whereas the *Acaena cylindristachya* community replaces zonal *Calamagrostis effusa* pâramo, especially in the Sierra Nevada de S. Marta and according to Vareschi (1980) in the Venezuelan pâramos. As a result of intensive grazin and burning, tussocks dissapear, leaving a herbaceous mat, which locally may develop into a rosaceous herbfield. Weberbauer (1911, 1945), Rauh (1958) and Gutte & Gutte (1976) refered to such meadows in the Peruvian puna, where they may cover a larger area. Gutte & Gutte (1976) reported as characteristic meadow taxa from Central Peru at 3900-4800 m species of *Calamagrostis, Stipa, Dissanthelium, Poa, Muhlenbergia* (including *M. fastigiata), Aciachne* and *Bromus,* and herbs as *Oreomyrrhis andicola, Lachemilla pinnata, Tephrocactus* spp., *Acaulimalva engleriana.*

The non-shrubby vegetation of screes and outcrops in the study area is dominated by temperate elements, which include wide ranging taxa (e.g. *Cystopteris diaphana, Polystichum, Asplenium, Senecio, Montia, Draba, Poa, Thamnolia),* and taxa of originally holarctic (e.g. *Valeriana,* and austral-antarctic arrival (e.g. *Rhacocarpus purpurascens, Racomitrium crispulum, Neuropogon* spp.). Local tropical Andean genera are *Kingiobryum* (pâramo element) and *Erythrophyllopsis.* Among the most common vascular species restricted to rocks may be mentioned *Echeveria* spp., *Elaphoglossum mathewsii, Polystichum polyphyllum, Hymenophyllum trichophyllum,* and other polypodiaceous ferns. At present only a few records of epilithic communities in the Colombian Andes are available, and none for the floristically very rich non-vascular epiphytic communities and synusia.

Future research

The classification of the zonal vegetation, *Sphagnum* bogs and other still unranked communities remains a future target. Provisional tables are already available. Forthcoming studies should include synoptic tables and analyses of phytogeography, structure and texture of the pâramo vegetation. Mapping projects of some areas of pâramo vegetation are in progress (De Nies & Lebouille, unpubl.; Kloosterman & Salamanca, in prep.). Various vegetation types recognized in this paper occur in this mapped area. Soils analyses should also be dealt with in detail in future studies. The relation between modern pâramo vegetation and pollen influx in the study area is presently studied by Mrs. R.A.J. Grabandt (in prep.). The pollen diagrams mentioned in this study from the Pâramo de Sumapaz are to be published in a more defenite form in the framework of the current ECOANDES project, which is also focussed on this area (ECOANDES 1979). Preliminary notes have already been published (Van der Hammen 1979 ; Cleef, Carvajal et al., in press; Van der Hammen & Cleef, in press).

The overwhelming richness of the still incompletely known flora and vegetation of tbe pâramos of the Cordillera Oriental of Colombia made the present author realize the primary importance and necessity of taxonomic work. This applies also to bryophytes, lichens, algae and fungi, which are an important component of the pâramo ecosystem. Knowledge of cryptogams is indispensable for vegetation studies in the páramos and in general for humid high tropical mountains. Without intensive botanical collecting and the help of many specialists the present study would have been impossible.

As this study is only one of the first contributions towards a geobotanic inventory of the Colombian Cordillera Oriental, it should be realised that it is far from complete and that much work remains to be done. This type of geobotanic inventory of the recent and the study of the past neotropical plant communities and their environments, are however, the first step towards a better understanding of the present day neotropical ecosystems.

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APPENDIX 1

Figures

Fig. 1.

Approximate distribution of Neotropical páramos as defined by physiognomic and floristic criteria.
The distribution of the páramos in Peru and Bolivia is according to Troll (1968) and Ellenberg (1979). "Perhumid Alpine" in the sense of Ellenberg (1979) is considered as páramo. The northernmost Andean páramos are confined to altitudes above 3300-3800 m.

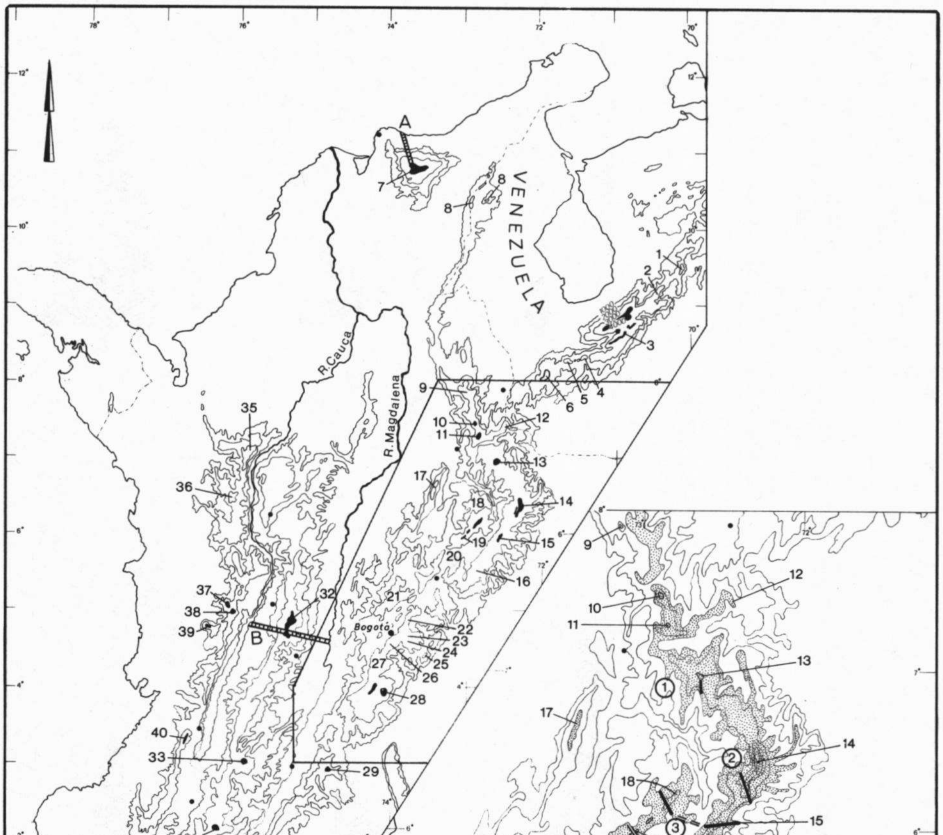

Zacatonal
Pico Duarte
3175 m
Pico de
Naiguatá 2750 m
&
Avila
2125 m
Sierra Nevada
de S. Marta
5775 m
Chirripó
3820 m
Chiriquí
3477 m
Study
area
PARAMO
Cerro
Neblina
3014 m
JALCA
Lake Titicaca
PUNA
Itatiaia
2797 m
Andean páramo s.l.
páramo-like vegetation
3000 m.
2000 m.
1000 m.
500 m.
200 m.
0 200 400 600 800 1000km
0 100 200 300 400 500 600 miles

Fig. 2.

Site locations of the northern Andean páramos (including those of the study area: 13-28).

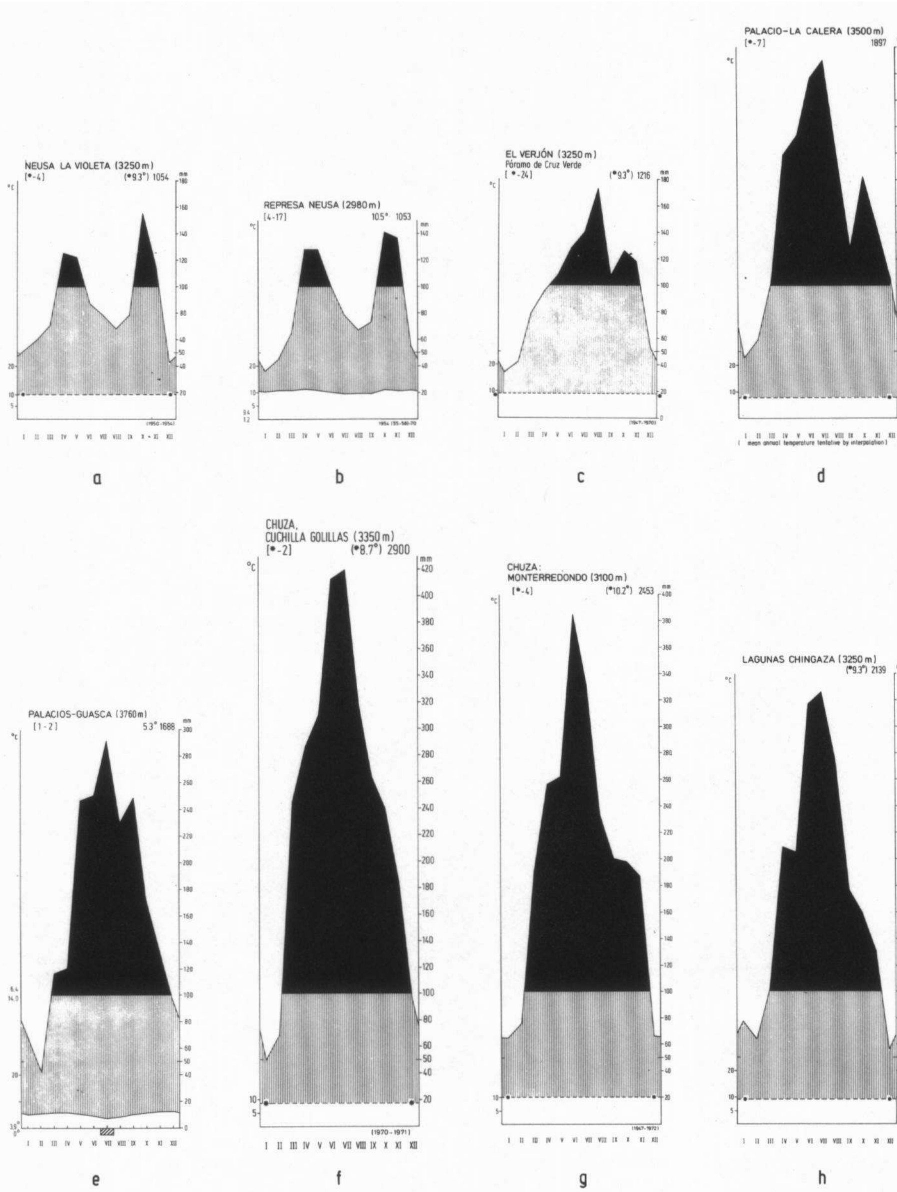
1. Cendé
2. Niquitao
3. Sierra Nevada de Mérida
4. La Negra
5. Batallón
6. Zumbador
7. Sierra Nevada de S. Marta
8. Perijá
9. Jurisdicciones/Oroque, Cáchira
10. Romeral
11. San Urbán
12. Tamá
13. Almorzadero
14. Sierra Nevada del Cocuy
15. Pisva-Chita
16. Tota-Vado Honda-Arnical
17. Cordillera de los Cobardes
18. Guantiva
19. Rusia
20. Tunja-Leiva-Arcabuco
21. Neusa-S. Cayetano
22. Guasca
23. Palacio
24. Chuza-Chingaza
25. Farallones de Medina
26. Cruz Verde-Chipaque
27. Chisacá
28. Páramo de Sumapaz with Nevado
29. Cordillera de los Picachos-C. Leiva
30. Cerro Punta
31. Picos de los Fragua
32. Parque Los Nevados (Ruíz, S. Isabel, S. Rosa, Tolima)
33. Nevado de Huila
34. Macizo Colombiano (Puracé)
35. Paramillo
36. Frontino
37. C. Tamaná
38. C. Tatamá
39. C. Torrá
40. Farallones de Cali
41. Doña Juana-C. Animas
42. Galeras
43. Cumbal
44. Chiles
45. Angel

1 to 8 : transects study area



VENEZUELA
ECUADOR
R. Cauca
R. Magdalena
Bogotá
ECOANDES TRANSECTS:
A Buritaca - La Cumbre 1977
B Parque Los Nevados (S. Isabel - S. Rosa) 1980
Colombian Cordillera Oriental
– study area –
0 50 100 150 km
0 50 100 km

Fig. 2


NEUSA LA VIOLETA (3250 m)
[•-4] (•9.3°) 1054
(1950-1954)
a
REPRESA NEUSA (2980 m)
[4-17] 10.5° 1053
b
EL VERJÓN (3250 m)
Páramo de Cruz Verde
[•-24] (•9.3°) 1216
(1947-1970)
c
PALACIO-LA CALERA (3500 m)
[•-7] 1897
(• mean annual temperature tentative by interpolation)
d
PALACIOS-GUASCA (3760 m)
[1-2] 5.3° 1688
e
CHUZA,
CUCHILLA GOLILLAS (3350 m)
[•-2] (•8.7°) 2900
(1970-1971)
f
CHUZA:
MONTERREDONDO (3100 m)
[•-4] (•10.2°) 2453
(1947-1972)
g
LAGUNAS CHINGAZA (3250 m)
(•9.3°) 2139
h

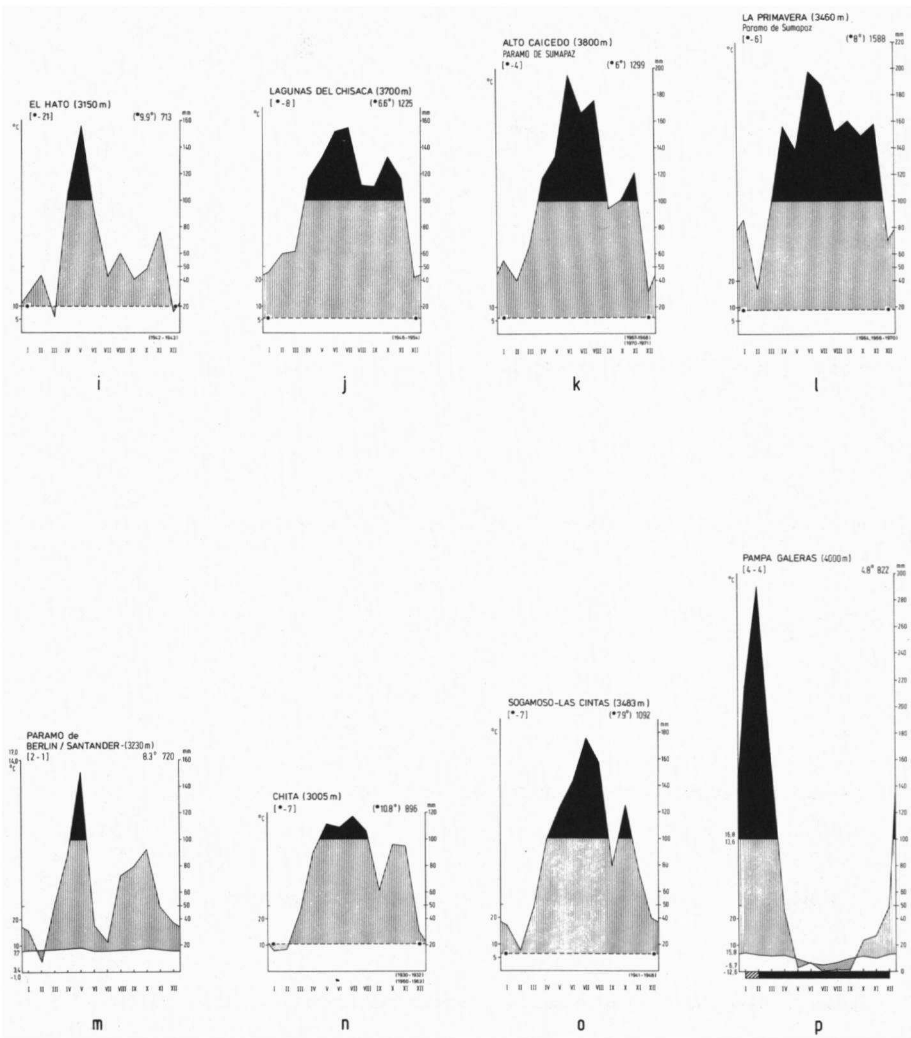


Fig. 3.

Climate diagrams of various stations in the páramo and upper Andean forest belt of the study area (a-o) and an example of the Peruvian bunchgrass puna (p). For a number of stations mean annual temperature values, when calculated, are marked with an asterisk.
Stations a-h are located from NW to SE in transect 5 and 6 (see Fig. 2); stations i-l are situated in transect 7 and 8 (Fig. 2) from NNW to SSW; and stations m-o are from the northern part of the study area.

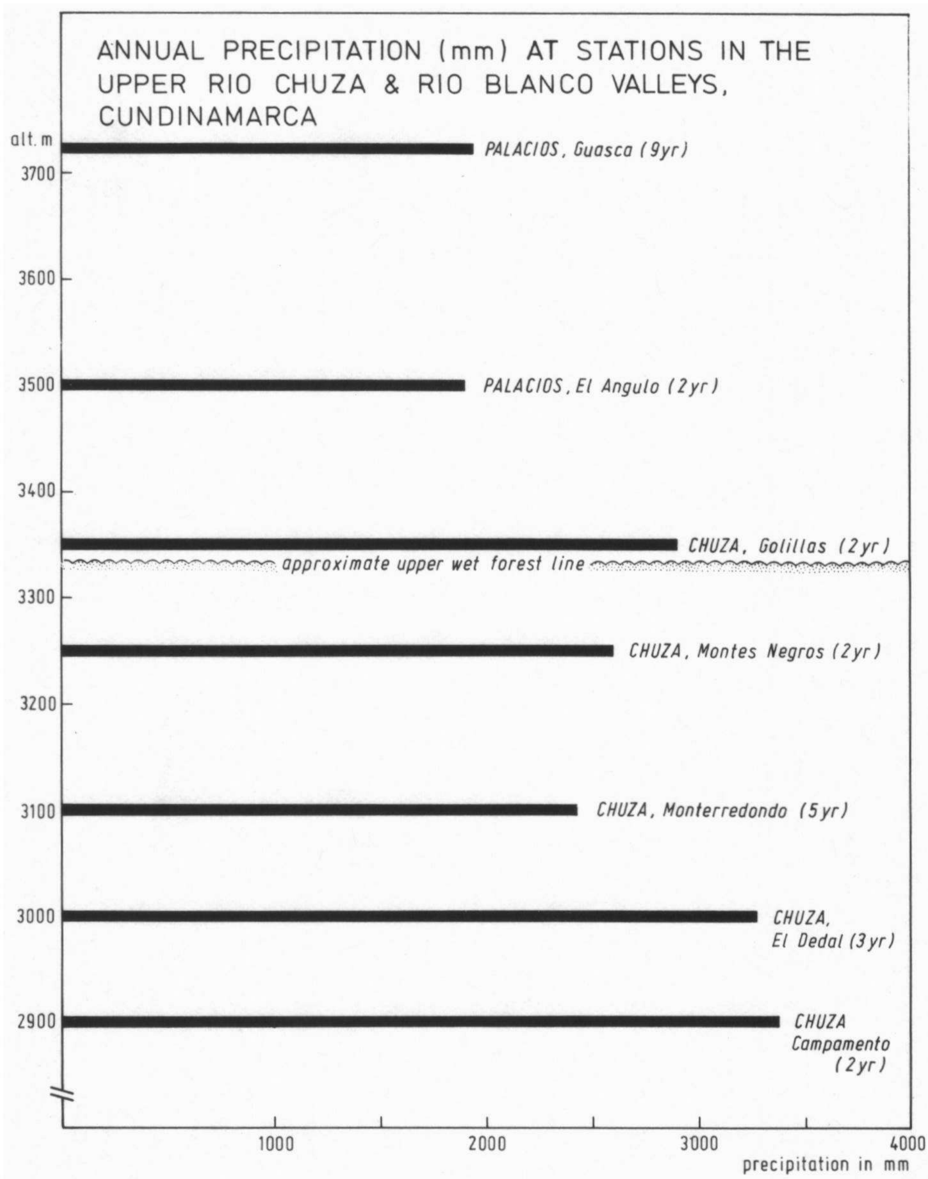


Fig. 4.

Mean annual precipitation at stations in the upper Andean forest and the lower part of the páramo belt at the humid side of the Cordillera E of Bogotá.

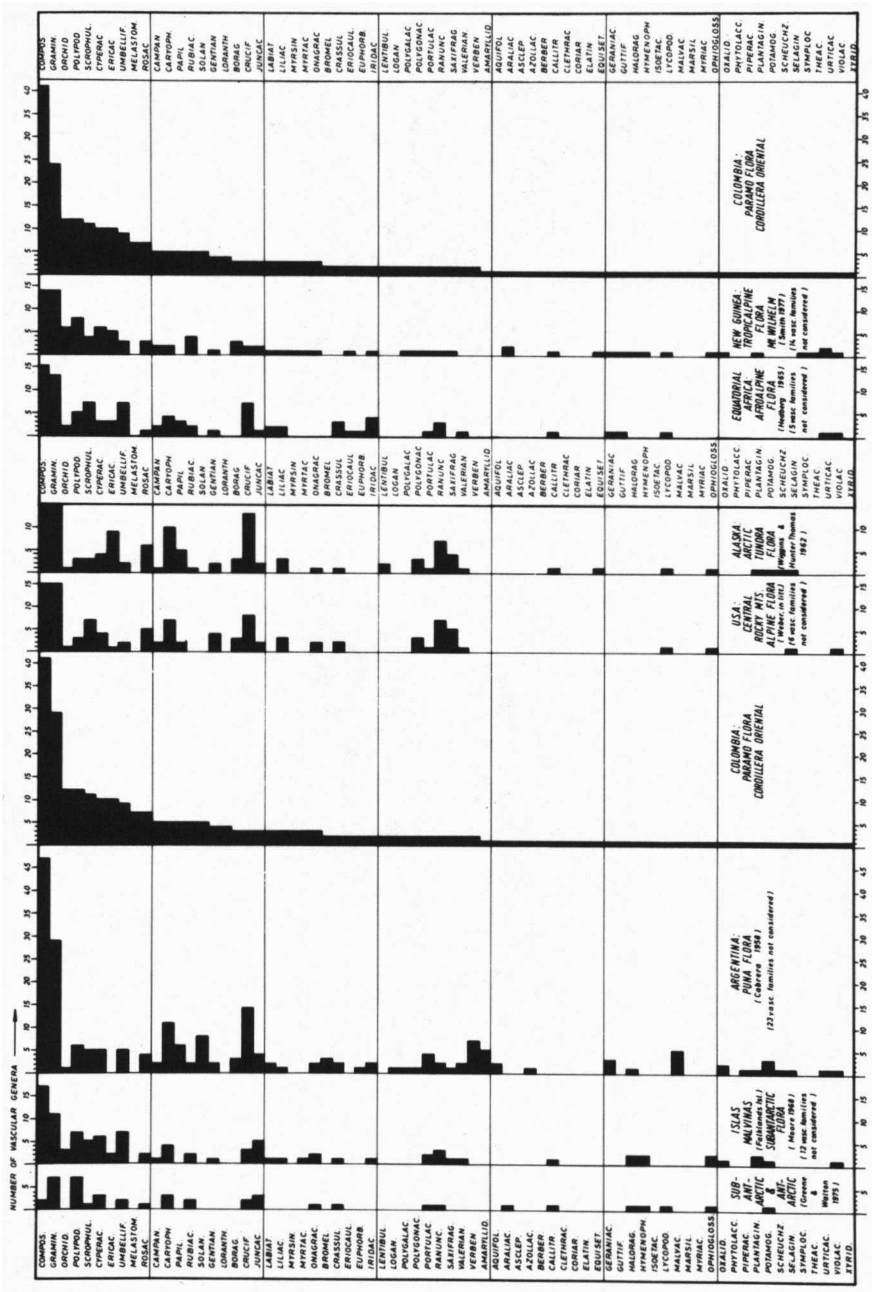


Fig. 5.

Composition of the vascular páramo flora of the Colombian Cordillera Oriental in comparison with that of some other selected cool-temperate vascular floras.

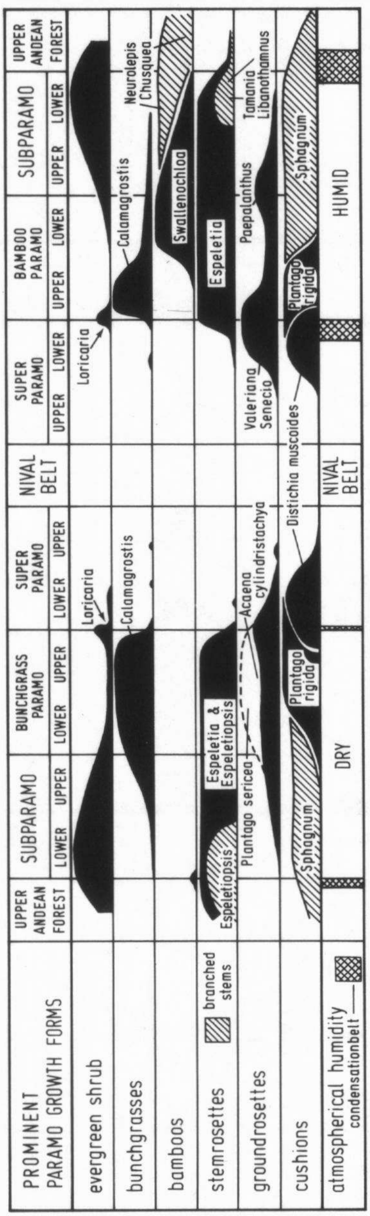


Fig. 6.

Prominent growth forms of the páramo vegetation of the study area in relation with altitudinal zones and climate, idealized for the dry and humid side of the mountains.

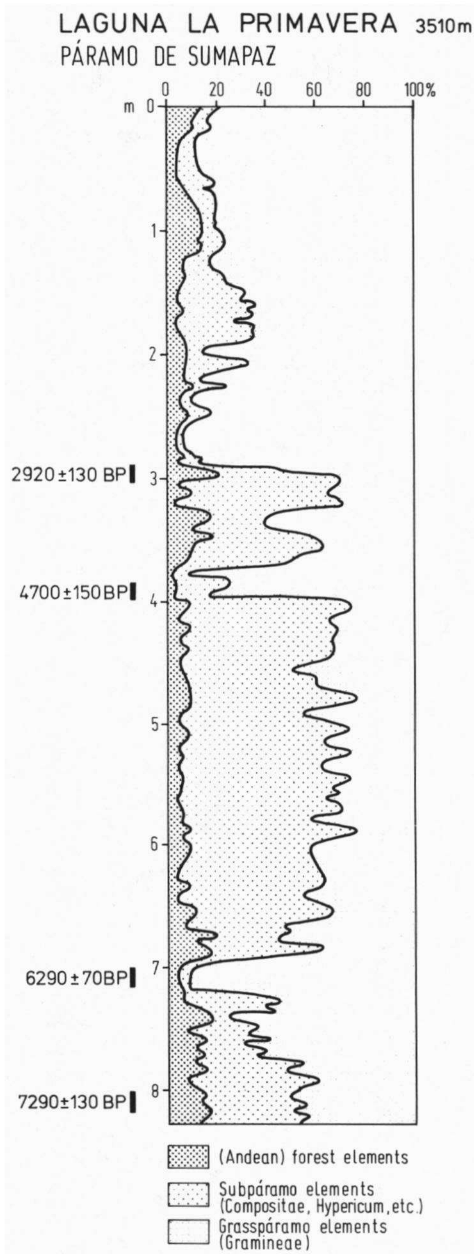


Fig. 7.

Simplified pollendiagram of the Laguna La Primavera (3510 m), Páramo de Sumapaz, covering the last 7500 years.

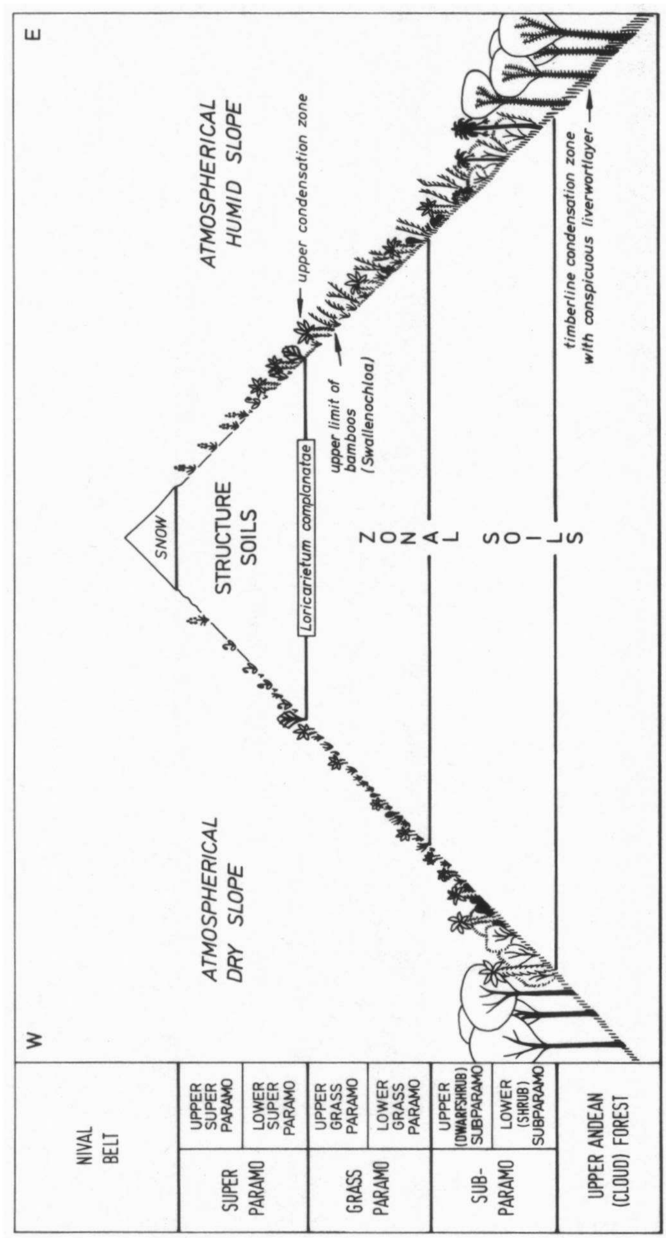


Fig. 8.

Physiognomical altitudinal zonation of the páramo vegetation in a achematic cross-section through the Colombian Cordillera Oriental.

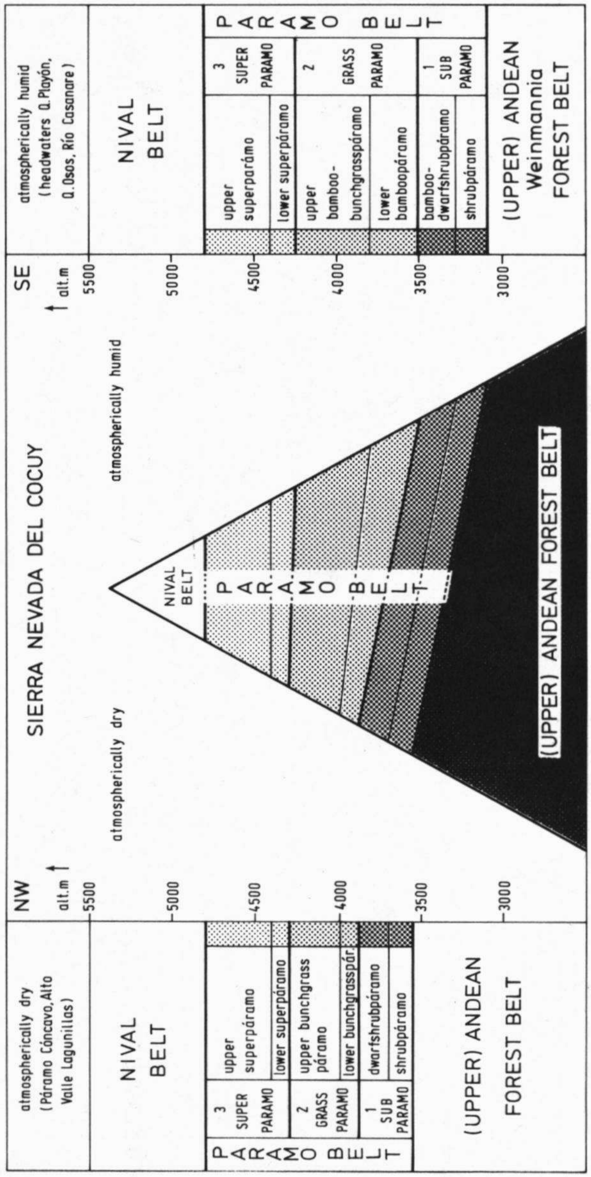


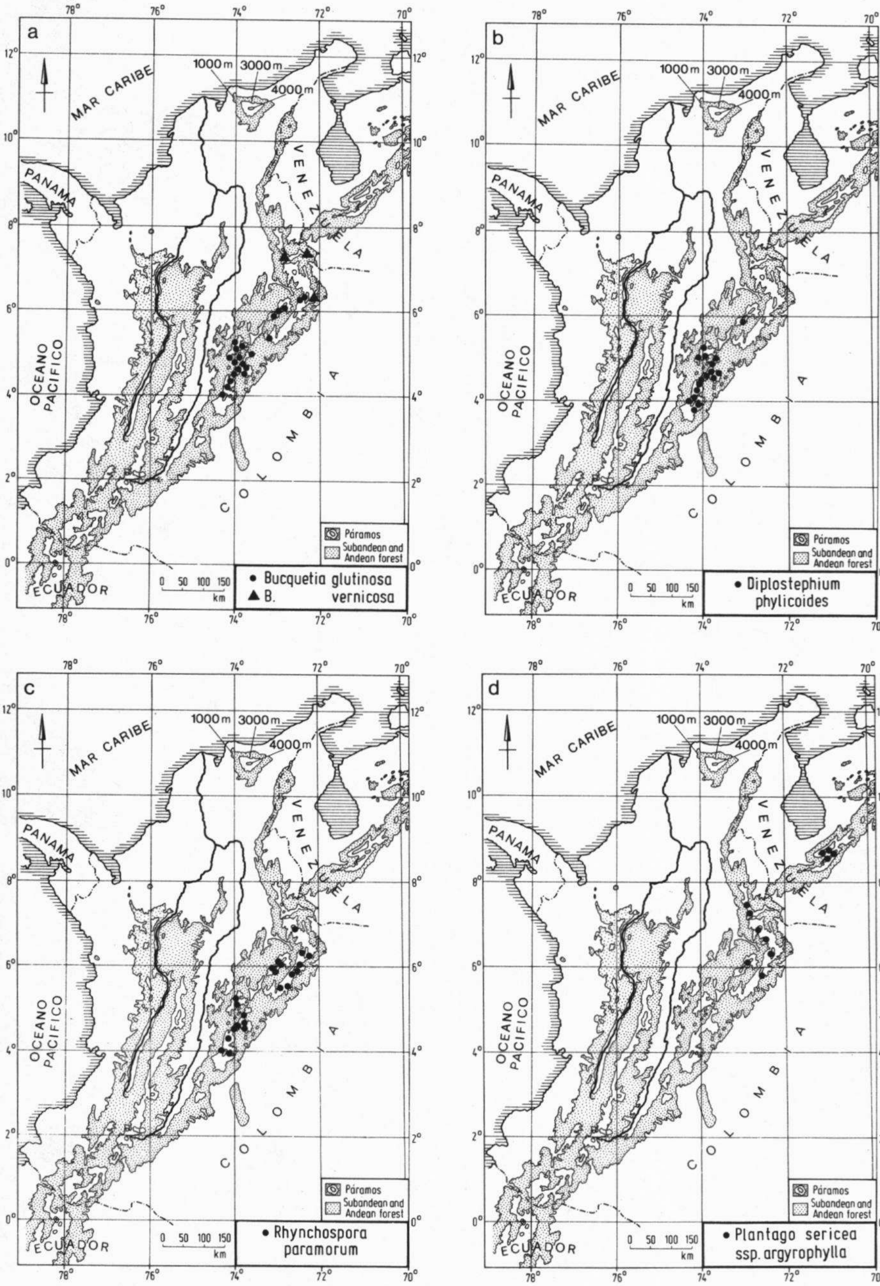
Fig. 9.

Average altitudes of the pāramo vegetation zones in a schematic NW-SE cross-section through the southern Sierra Nevada del Cocuy, Colombian Cordillera Oriental.

Fig. 10.

Distribution of some selected endemic taxa of the zonal páramo vegetation.

a *Bucquetia glutinosa; B. vernicosa*
b *Diplostephium phylicoides*
c *Rhynchospora paramorum*
d *Plantago sericea* ssp. *argyrophylla*


a
MAR CARIBE
PANAMA
OCEANO PACIFICO
VENEZUELA
COLOMBIA
ECUADOR
1000 m
3000 m
4000 m
Páramos
Subandean and Andean forest
0 50 100 150 km
• Bucquetia glutinosa
▲ B. vernicosa
b
• Diplostephium phylicoides
c
• Rhynchospora paramorum
d
• Plantago sericea ssp. argyrophylla
78° 76° 74° 72° 70°
12° 10° 8° 6° 4° 2° 0°

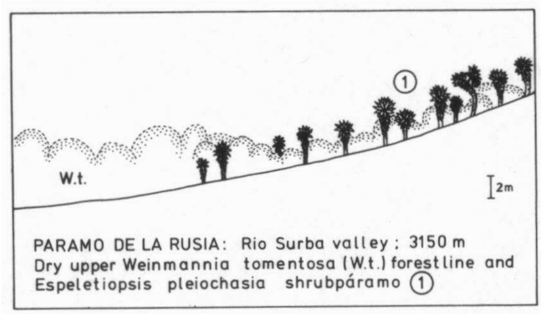


Fig. 11.

Shrub páramo with *Espeletiopsis pleiochasia* (1) at 3150 m on the dry eastern side of the Páramo de la Rusia.

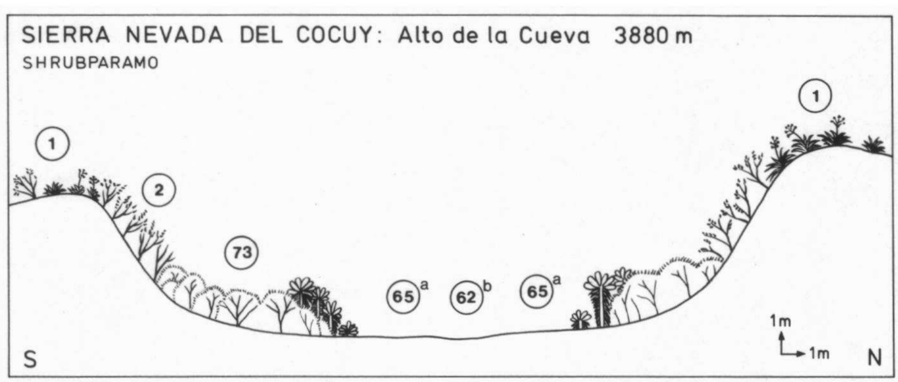


Fig. 12.

Shrub páramo vegetation profile across small moraine valley at 3880 m near the Alto de la Cueva, Sierra Nevada del Cocuy (Boyacá): zonal and azonal vegetation.

1 ***Espeletiopsis colombiana*-community (degraded shrub páramo)**
2 ***Senecio vaccinioides* shrub**
62b ***Oritrophio-Wernerietum pygmaeae cotuletosum***
65a ***Hyperico-Plantaginetum rigidae***
73 ***Senecio andicola*-shrub with *Espeletia lopezii* (rel. 421)**

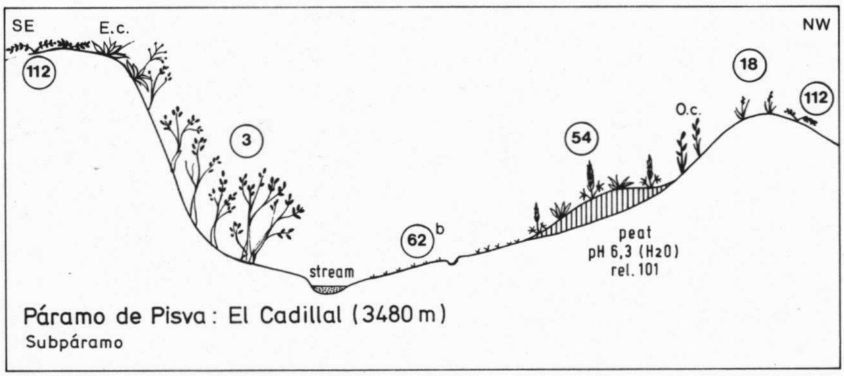


Fig. 13.

Vegetation profile from the borderline of the upper and lower subpāramo at 3480 m near El Cadillal, Pāramo de Pisva (Boyacā).

3 Shrubs of *Eupatorium (Ageratina) tinifolium*
18 *Acaeno cylindristachyae - Plantaginetum sericeae*
54 *Lupino alopecuroides - Mimuletum glabratae*
62b *Oritrophio limnophili - Wernerietum pygmaeae cotuletosum*
112 Community of *Acaena cylindristachya*
E.c. *Espeletiopsis colombiana*
O.c. *Orthrosanthus chimboracensis*

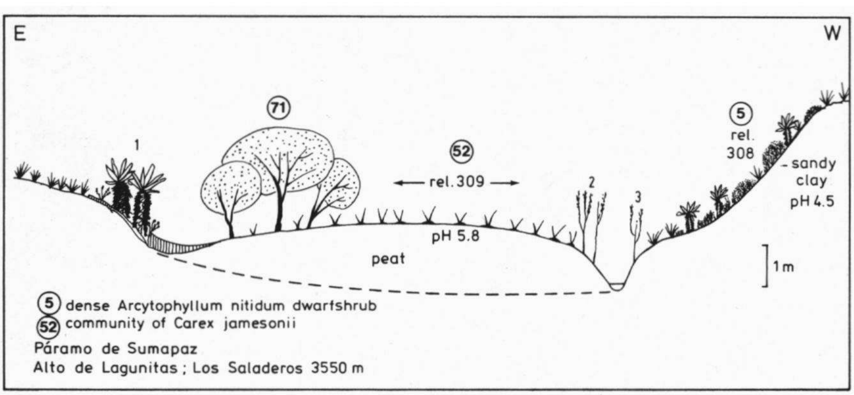


Fig. 14.

Zonal dense *Arcytophyllum nitidum* dwarfshrub pāramo (5) and azonal communities, e.g. community of *Carex jamesonii* (52), at 3550 m on the W side of the Pāramo de Sumapaz (Cundinamarca)

1 *Espeletia miradorensis* (type locality) with *Breutelia* sp. and *Xyris acutifolia*
2 *Baccharis revoluta*
71 *Diplostephietum revoluti*

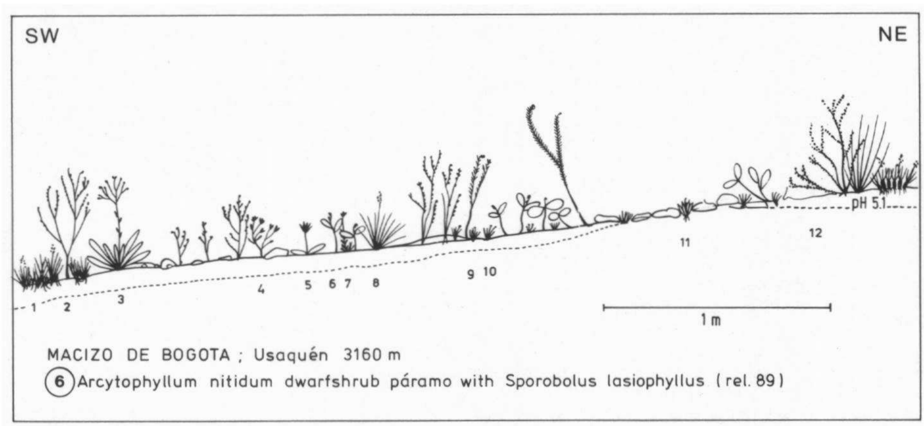


Fig. 15

Dwarfshrub of *Arcytophyllum nitidum* with *Sporobolus lasiophyllus* and *Achyrocline lehmannii* (6). Dry, stony subpáramo with *Espeletiopsis corymbosa* and *Gaultheria rigida* at 3160 m near Bogota.

1 *Sporobolus lasiophyllus*
2 *Arcytophyllum nitidum*
3 *Espeletiopsis corymbosa*
4 *Niphogeton glaucescens*
5 *Hypochoeris taraxacoides*
6 *Gaultheria rigida*
7 *Achyrocline lehmannii*
8 *Calamagrostis effusa*
9 *Hypericum strictum*
10 *Bulbostylis tropicalis*
11 *Paepalanthus paramensis*
12 *Baccharis tricuneata*

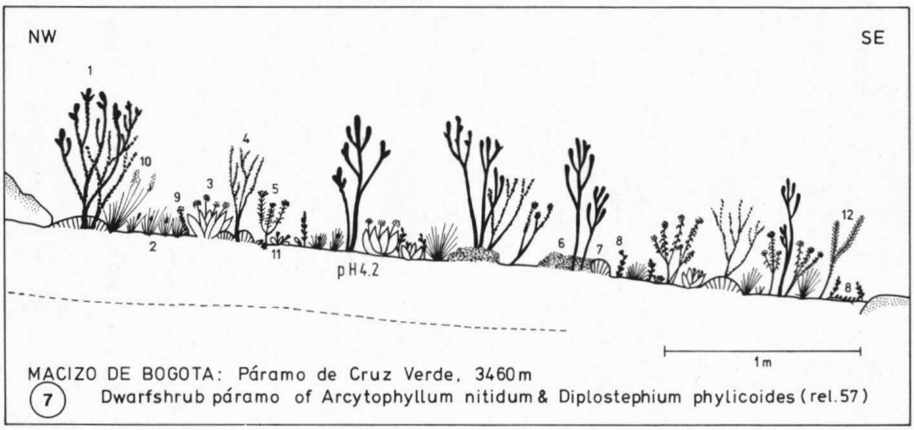


Fig. 16.

Dwarfshrub of *Arcytophyllum nitidum* with *Diplostephium phylicoides* (7) at 3460 m in the Páramo de Cruz Verde, E of Bogotá.

1 *Aragoa cupressina*
2 *Rhynchospora paramorum*
3 *Paepalanthus villosus* var. *andicola*
4 *Arcytophyllum nitidum*
5 *Diplostephium phylicoides*
6 *Cladonia confusa*
7 *Campylopus* sp. (2808)
8 *Vaccinium floribundum* var. *marginatum*
9 *Pernettya hirta*
10 *Calamagrostis effusa*
11 *Geranium multiceps*
12 *Hypericum strictum*

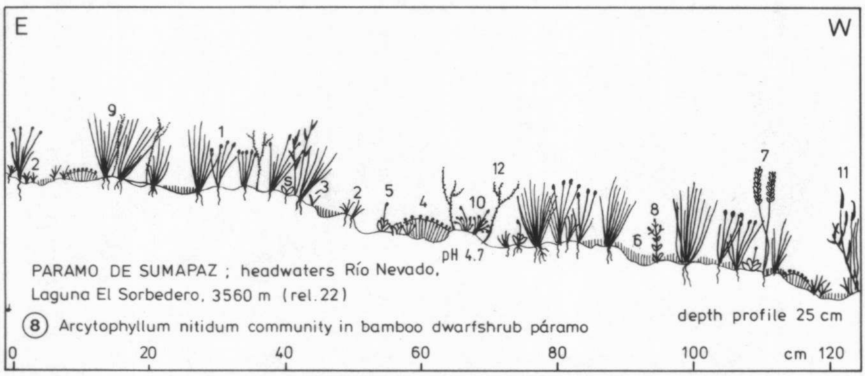


Fig. 17.

Arcytophyllum nitidum community with *Xyris acutifolia* (8) in bamboo-dwarfshrub páramo at 3560 m N of the Laguna El Sorbedero, Páramo de Sumapaz (Meta).

1 *Xyris acutifolia*
2 *Rhynchospera paramorum*.
3 *Carex* sp.
4 *Paepalanthus lodiculoides*
5 *Castratella piloselloides*
6 *Campylopus richardii*
7 *Hypericum strictum*
8 *Gentianella corymbosa*
9 *Calamagrostis effusa*
10 *Oreobolus obtusangulus* ssp. *rubrovaginatus*
11 *Swallenochloa* sp.
12 *Arcytophyllum nitidum*

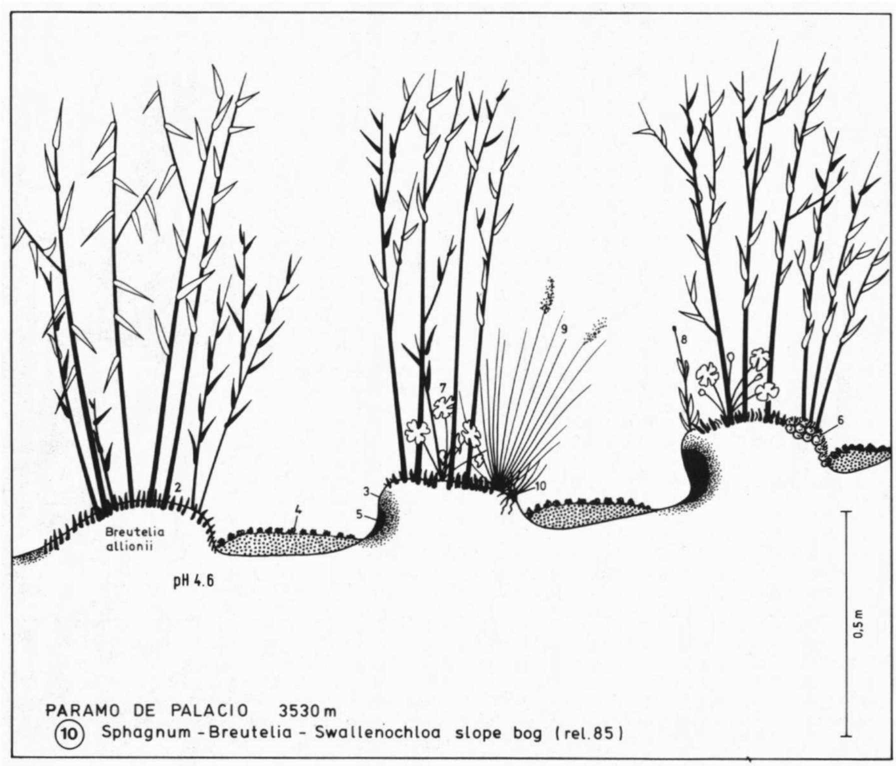


Fig. 18.

Azonal community of *Swallenochloa* with *Sphagnum* and *Breutelia* (10) on boggy slopes at 3530 m in the Páramo de Palacio, NE of Bogotá.

1 *Swallenochloa tesselata*
2 *Breutelia allionii*
3 *Riccardia* sp. and *Kurzia* sp. (3781) with *Cephalozia dussii*, *Blepharostoma trichophyllum*, *Anastrophyllum nigrescens*, *Lophocolea coadunata*, *Jungermannia sphaerocarpa*
4 *Sphagnum sancto-josephense*
5 *Gongylanthus innovans*
6 *Sphagnum magellanicum*
7 *Geranium multiceps*
8 *Senecio* sp. (juv.)
9 *Calamagrostis effusa*
10 *Isoetes* cf. *boyacensis*

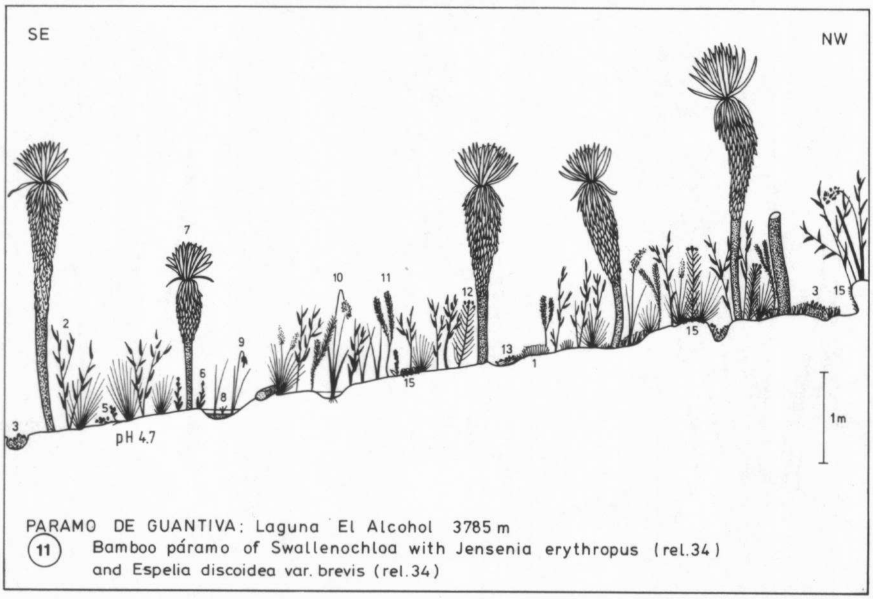


Fig. 19.

Bamboo páramo of *Swallenochloa* with *Eryngium humile* and *Jensenia erythropus* (11). Stemrosettes of *Espeletia discoidea* var. *brevis* are associated near the Laguna El Alcohol at 3785 m in the southern Páramo de Guantiva.

1 *Oreobolus obtusangulus* ssp. *rubrovaginatus*
2 *Swallenochloa* sp.
3 *Sphagnum cyclophyllum*
4 *Calamagrostis effusa*
5 *Vaccinium floribundum* var. *ramosissimum*/*Pernettya prostrata* var. *purpurea*
6 *Bartsia* sp.
7 *Espeletia discoidea* var. *brevis*
8 *Isoetes killipii*
9 *Carex pichinchensis*
10 *Rhynchospora macrochaete*
11 *Hypericum* sp.
12 *Senecio abietinus*
13 *Sphagnum cuspidatum*
14 *Breutelia* sp. (1892)
15 *Jensenia erythropus*

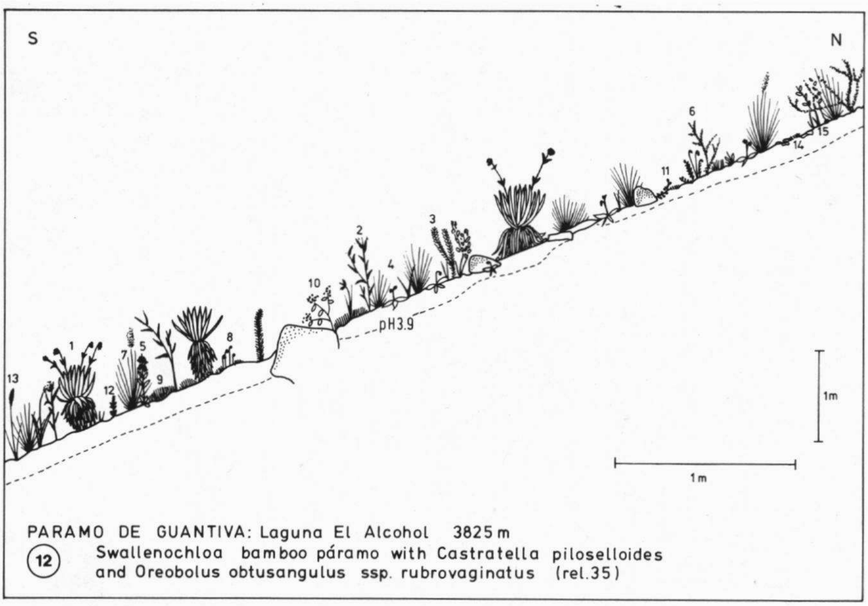


Fig. 20.

Swallenochloa bamboo páramo with *Castratella piloselloides* and *Oreobolus obtusangulus* ssp. *rubrovaginatus* (12). Stemrosettes of *Espeletia congestiflora* are associated at 3825 m in the southern Páramo de Guantiva.

1 *Espeletia congestiflora*
2 *Swallenochloa* sp.
3 *Hypericum strictum*
4 *Castratella piloselloides*
5 *Halenia* sp. (1834)
6 *Arcytophyllum nitidum*
7 *Calamagrostis effusa*
8 *Jamesonia bogotensis*
9 *Oreobolus obtusangulus* ssp. *rubrovaginatus*
10 *Gaultheria anastomosans*
11 *Vaccinium floribundum* var. *ramosissimum*, *Baccharis tricuneata*
12 *Gentianella corymbosa*
13 *Calamagrostis bogotensis*
14 *Campylopus cleefii*
15 *Carex* cf. *pichinchensis* (juv.)

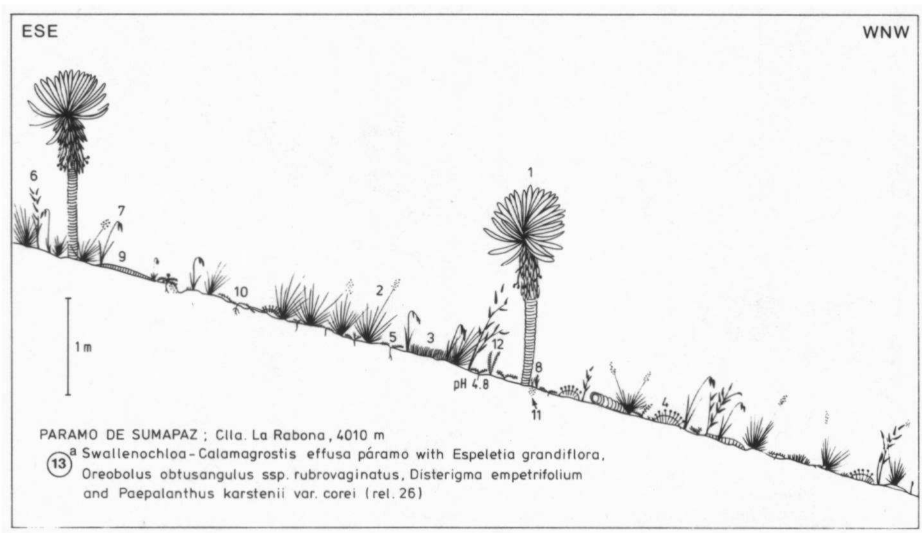


Fig. 21.

Community of *Swallenochloa* with *Oreobolus obtusangulus* ssp. *rubrovaginatus*, *Rhacocarpus purpurascens*, *Oritrophium peruvianum* and *Paepalanthus karstenii* var. *corei* (13a) at about 4000 m on the Cuchilla La Rabona, Páramo de Sumapaz (Cundinamarca).

1 *Espeletia grandiflora*
2 *Calamagrostis effusa*
3 *Oreobolus obtusangulus* ssp. *rubrovaginatus*
4 *Paepalanthus karstenii* var. *corei*
5 *Disterigma empetrifolium*
6 *Swallenochloa* cf. *tesselata*
7 *Carex pichinchensis*
8 *Carex* cf. *tristicha*
9 *Campylopus pittieri*
10 *Arcytophyllum muticum*
11 *Gymnomitriaceae*
12 *Grammitis (Ctenopteris) moniliformis*

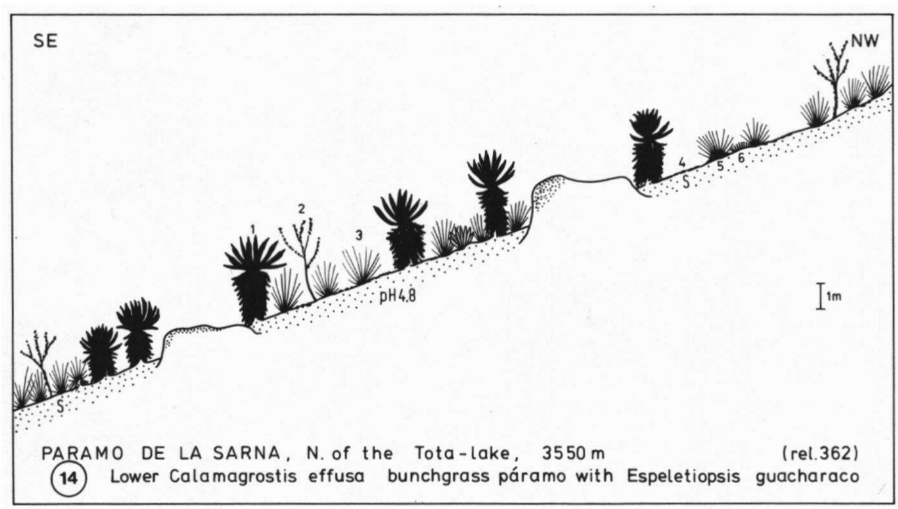


Fig. 22.

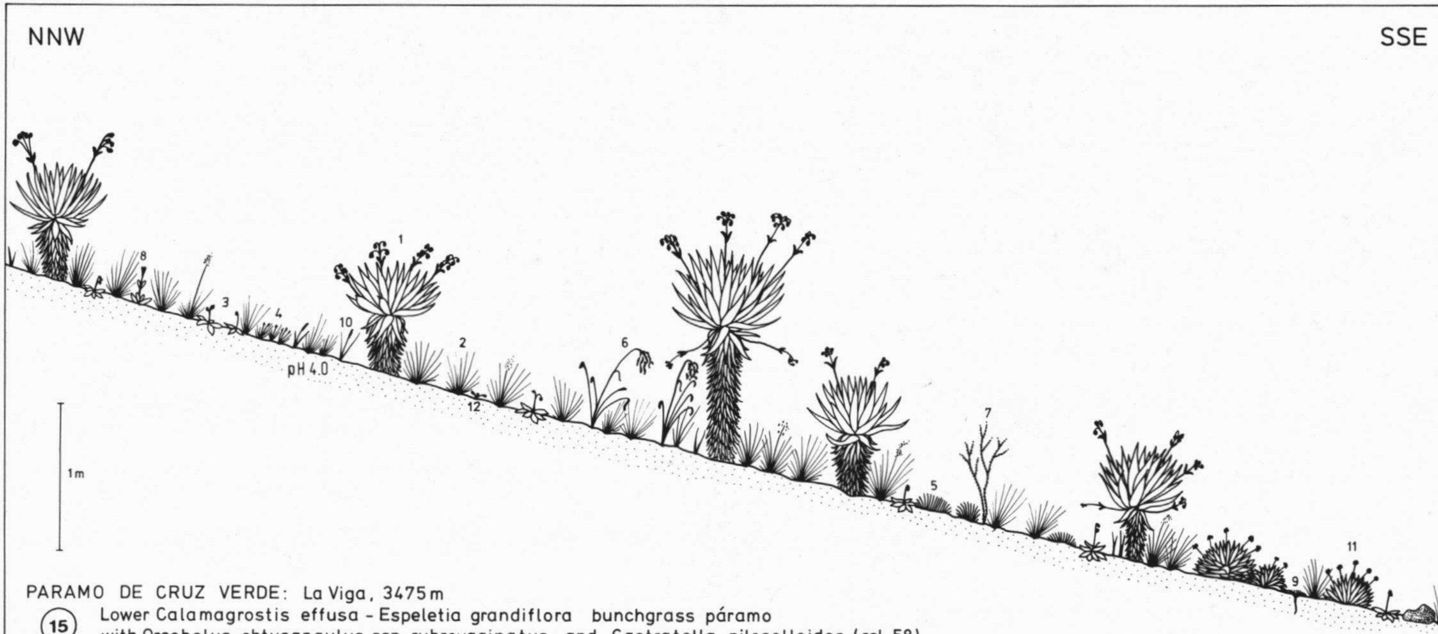
Lower *Calamagrostis effusa* bunchgrass páramo with *Espeletiopsis guacharaco* at 3550 m in the Páramo de la Sarna, N of the Lake Tota (Boyacá).

1 *Espeletiopsis guacharaco*
2 *Arcytophyllum nitidum*
3 *Calamagrostis effusa*
4 *Gongylanthus liebmannianus*, *Cladia aggregata*
5 *Campylopus pittieri*
6 *Leptodontium pungens*

Fig. 23.

Lower *Calamagrostis effusa* bunchgrass páramo with *Espeletia grandiflora*, *Oreobolus obtusangulus* ssp. *rubrovaginatus* and *Castratella piloselloides* (15) at 3475 m in the Páramo de Cruz Verde, E of Bogotá.

1 *Espeletia grandiflora*
2 *Calamagrostis effusa*
3 *Castratella piloselloides*
4 *Rhynchospora paramorum*
5 *Oreobolus obtusangulus* ssp. *rubrovaginatus*
6 *Rhynchospora macrochaete*
7 *Arcytophyllum nitidum*
8 *Gentionella corymbosa*
9 *Hypochoeris sessiliflora*
10 *Carex* sp.
11 *Paepalanthus andicola* var. *villosus*
12 *Azorella* aff. *cuatre-casasii*



PARAMO DE CRUZ VERDE: La Viga, 3475 m

15 Lower Calamagrostis effusa - Espeletia grandiflora bunchgrass páramo
with Oreobolus obtusangulus ssp. rubrovaginatus and Castratella piloselloides (rel. 58)

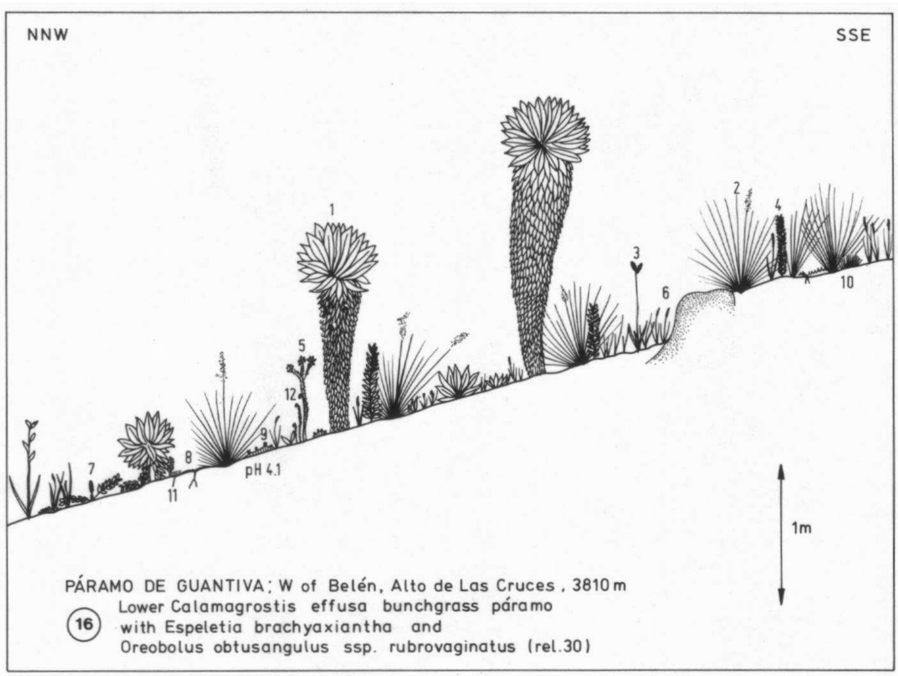


Fig. 24.

Lower *Calamagrostis effusa* bunchgrass páramo with *Oreobolus obtusangulus* ssp. *rubrovaginatus* (16). Stemrosettes of *Espeletia brachyxiantha* are associated in a stand at 3810 m near the Alto de las Cruces (Vereda S. José de la montana), W of Belén (Boyacá).

1 *Espeletia brachyaxiantha*
2 *Calamagrostis effusa*
3 *Orthrosanthus chimboracensis*
4 *Senecio vaccinioides*
5 *Senecio abietinus*
6 *Carex* cf. *conferto-spicata/C. tristicha*
7 *Acaena cylindristachya*
8 *Arcytophyllum muticum*
9 *Paepalanthus karstenii*
10 *Oreobolus obtusangulus* ssp. *rubrovaginatus*
11 *Polytrichum juniperinum*
12 *Jamesonia rotundifolia*

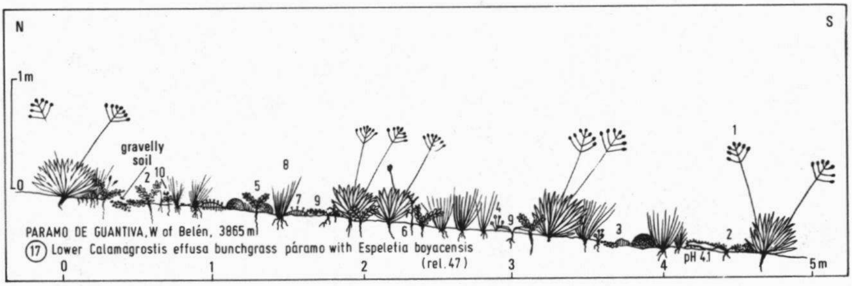


Fig. 25.

Lower *Calamagrostis effusa* bunchgrass páramo with *Espeletia boyacensis* (17) and *Acaena cylindristachya* at 3865 m in the southern Páramo de Guantiva near the Alto de La Cruces, W of Belén (Boyacá).

1 *Espeletia boyacensis*
2 *Vaccinium floribundum* var. *ramosissimum*
3 *Leptodontium pungens*
4 *Geranium sibbaldioides*
5 *Acaena cylindristachya*
6 *Paspalum bonplandianum*
7 *Paepalanthus karstenii* var. *corei*
8 *Calamagrostis effusa*
9 *Arcytophyllum muticum*
10 *Azorella* aff. *cuatrecasasii*

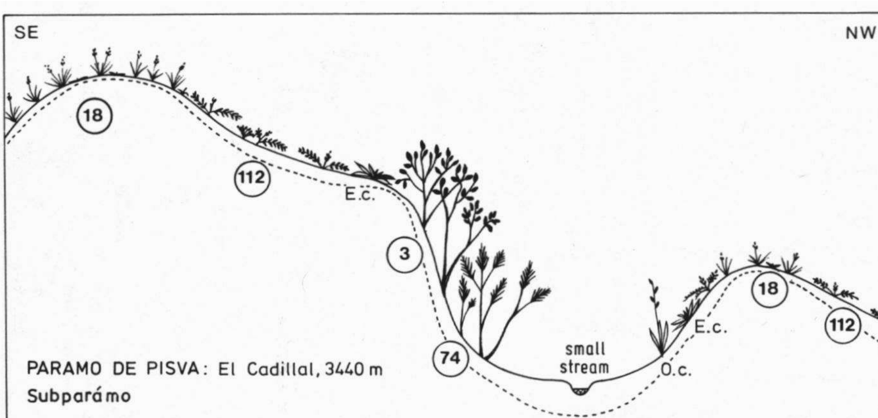


Fig. 26.

Vegetation profile in the borderline of the upper and lower subpáramo at 3440 m near El Cadillal, Parámo de Pisva (Boyacá).

3 Shrub of *Eupatorium (Ageratina) tinifolium*
18 *Acaena cylindristachya* - *Plantaginetum sericeae* (rel. 102)
74 *Hypericetum laricifolii* (probably)
112 Community of *Acaena cylindristachya* (rel. 103)
E.c *Espeletiopsis colombiana*
O.c *Orthrosanthus chimboracensis*

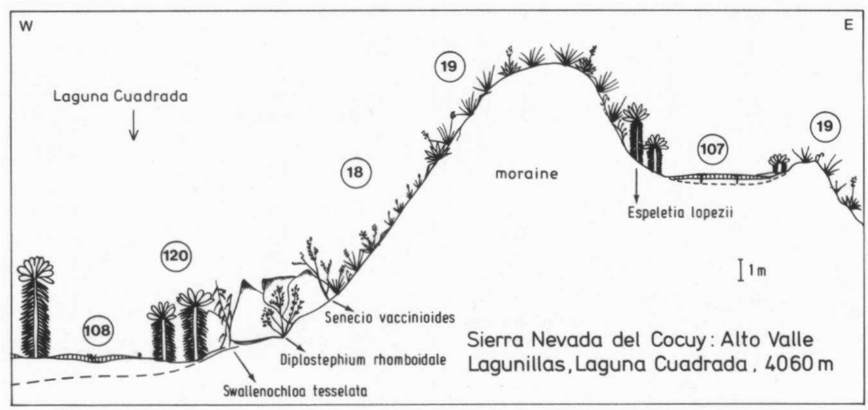


Fig. 27.

Schematic vegetation profile across moraine supporting zonal upper bunchgrass vegetation with *Espeletiopsis colombiana* (19) and locally *Acaeno-Plantaginetum sericeae* (18). Other azonal communities are the *Aciachnetum pulvinatae* (107) and dense *Espeletia lopezii* stands (120) which border the peatland with e.g. *Muhlenbergietum fastigiatae* (108) along the southern shore of the Laguna Cuadrada at ca 4060 m in the Sierra Nevada del Cocuy (Boyacá).

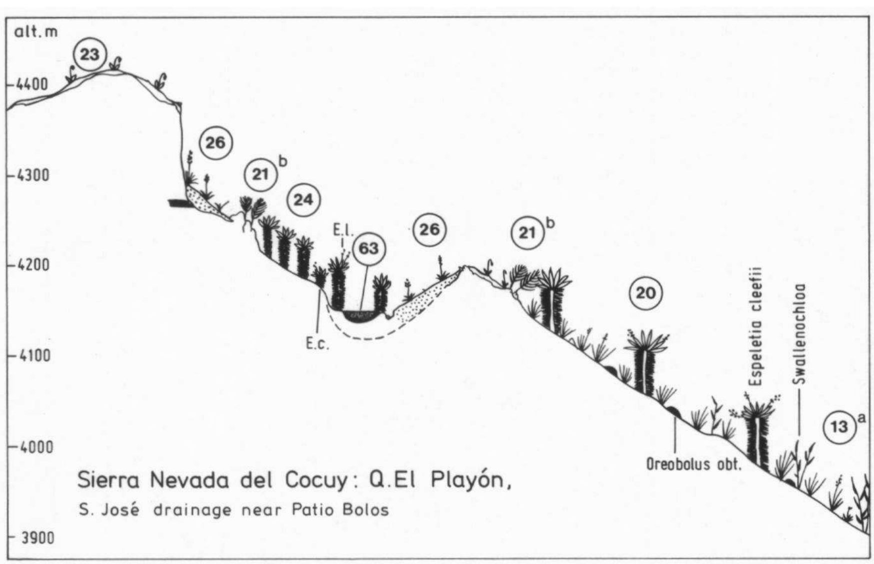


Fig. 28

Schematic vegetation profile across the eastern slope of the Sierra Nevada del Cocuy near Patio Bolos showing the position of various zonal high páramo communities:

13a *Swallenochloa* bamboo páramo with *Oreobolus obtusangulus* ssp. *rubrovaginatus*
20 Upper *Calamagrostis effusa* bunchgrass páramo with *Espeletia cleefii*
21b *Loricarietum complanatae racomitrietosum*
23 Community of *Pernettya prostrata* and *Luzula racemosa*
24 Community of *Espeletia cleefii* with *Geranium sibbaldioides*
26 Community of *Senecio niveo-aurens*
63 *Floscaldasio-Distichietum muscoides (azonal)*
E.c *Espeletiopsis colombiana*
E.1 *Espeletia lopezii*

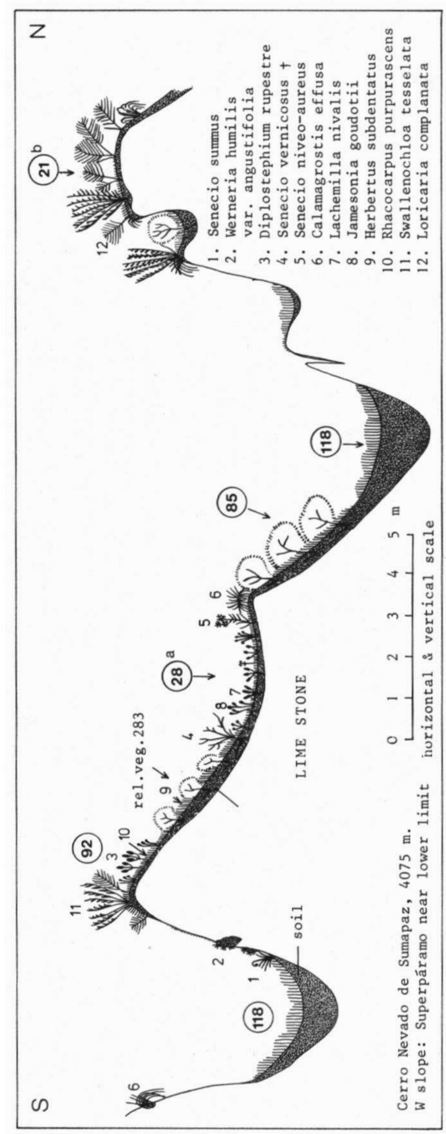


Fig. 29.

Zonal and azonal vegetation of the lowermost superpáramo at 4075 on the W slope of the Nevado de Sumapaz (Meta).

21b *Loricarietum complanatae racomitrietosum*
28a Community of *Lachemilla nivalis* with *Jamesonia goudotii*
85 *Senecionetum vernicosi*
92 Dwarfshrub of *Diplostephium rupestre*
118 *Azorelletum multifidae*

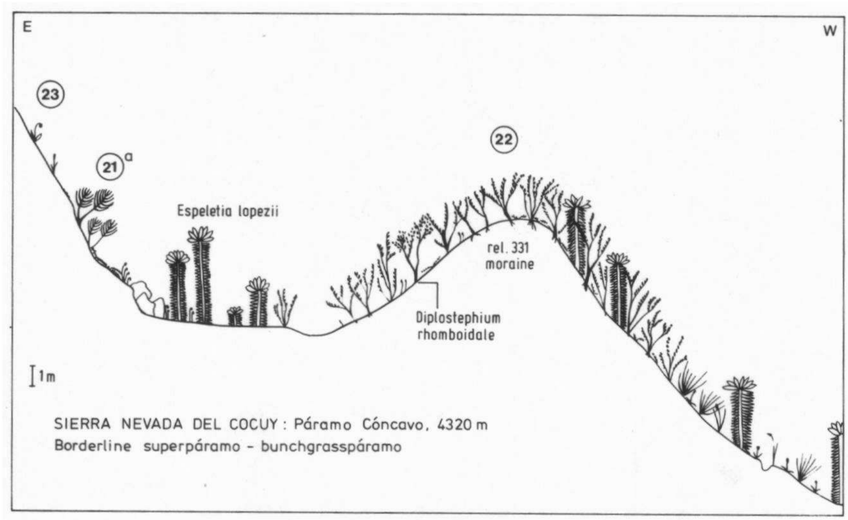


Fig. 30.

Shrub of *Senecio vaccinioides* and *Diplostephium rhomboidale* (22) in the boundary of the zonal upper grass páramo (19) and superpáramo (21a, 23) at 4320 m in the Páramo Cóncavo, Sierra Nevada del Cocuy (Boyacá).

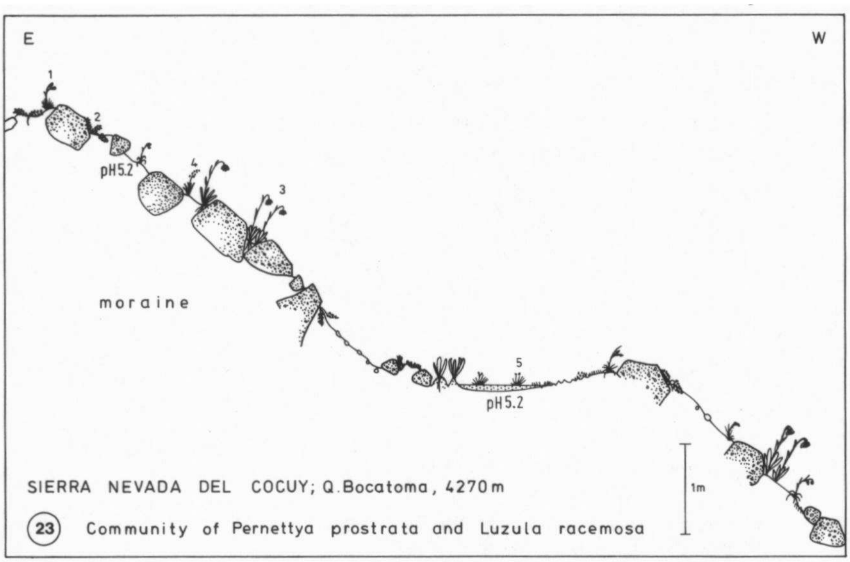


Fig. 31.

Lower superpáramo community of *Pernettya prostrata* and *Luzula racemosa* (23)

1 *Luzula racemosa*
2 *Pernettya prostrata* var. *prostrata*
3 *Senecio cocuyanus*
4 *Poa* sp.
5 *Agrostis breviculmis*

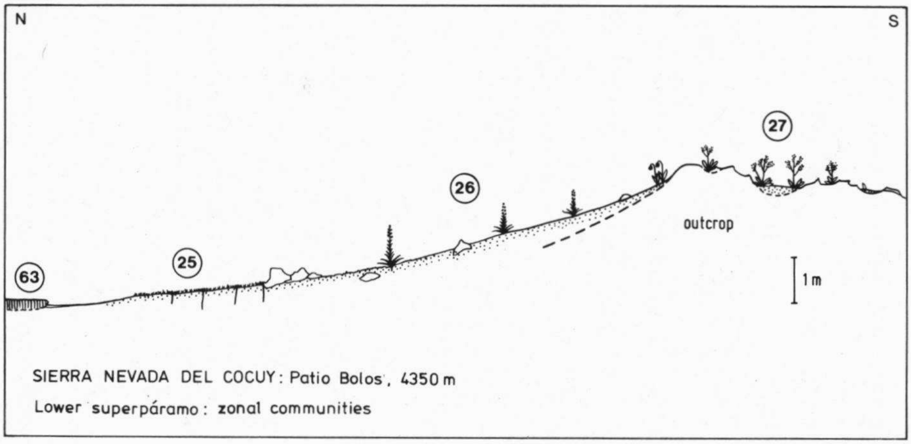


Fig. 32.

Zonal lower superpáramo communities on gravelly slopes and outcrops at Patio Bolos (4350 m): *Agrostis breviculmis* community with *Acaulimalva purdiei* (25), *Senecio niveo-aurens* community (26) and the *Valeriana plantaginea* community with *Racomitrium crispulum* (27). In the wet depression *Floscaldasio-Distichietum* cushionbog (63).

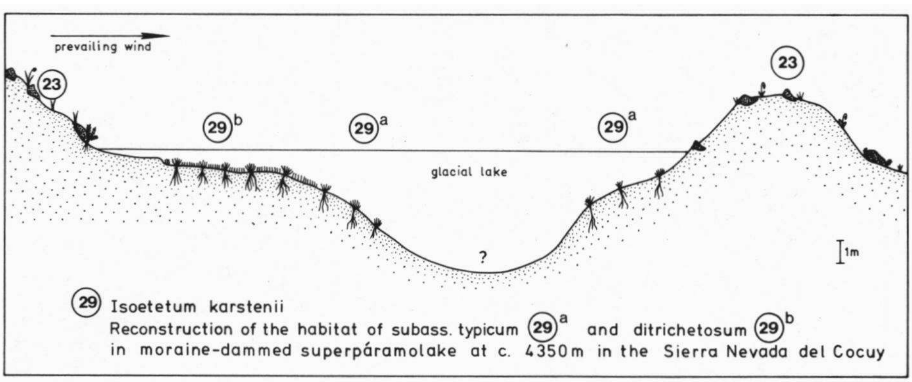


Fig. 33.

Isoetetum karstenii (29). Reconstruction of the habitat of the subass. *typicum* (29a) and the *ditrichetosum* (29b) in a moraine dammed superpáramo lake at c. 4350 m in the Sierra Nevada del Cocuy.

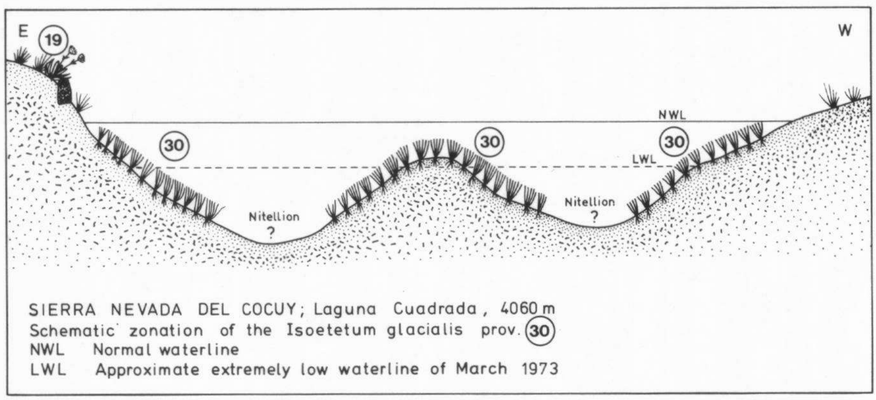


Fig. 34.

Isoetum glacialis prov. (30) in the Laguna Cuadrada at 4060 m in the Sierra Nevada del Cocuy (Boyacá), schematic zonation.

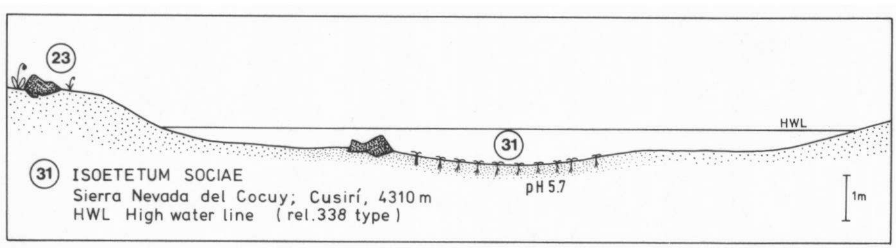


Fig. 35.

Isoetetum sociae (31) in a lower superpáramo pond at 4310 m on the Alto de Cusirí, Sierra Nevada del Cocuy (Boyacá)

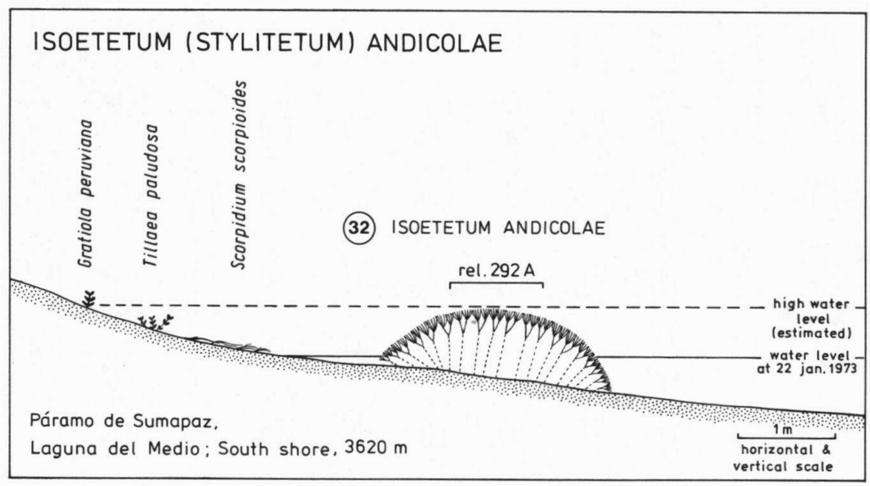


Fig. 36.

Isoetetum andicolae (32) at 3620 m along the southern shore of the Laguna del Medio, headwaters Q. Sitiales in the Páramo de Sumapaz (Meta).

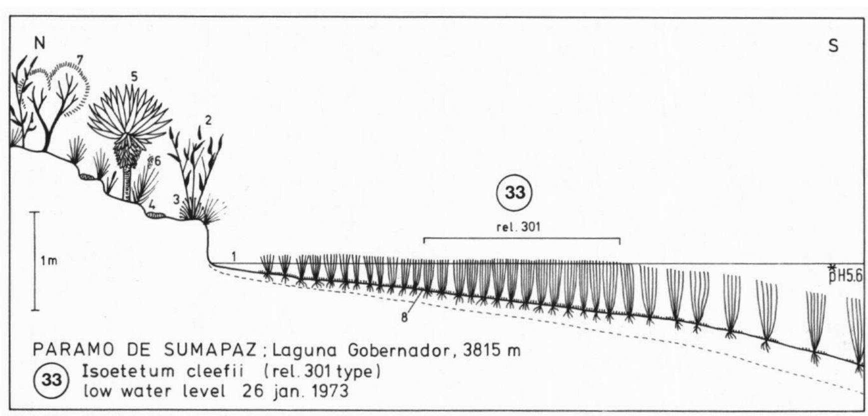


Fig. 37.

Isoetetum cleefii (33) along the northern shore of the Laguna Gobernador at c. 3815 m on the W side of the Páramo de Sumapaz.

1 *Chlorophyta*
2 *Swallenochloa* cf. *tesselata*
3 *Pleurozium schreberi*
4 *Sphagnum* cf. *cuspidatum*
5 *Espeletia* sp. (*E. grandiflora* complex)
6 *Calamagrostis effusa*
7 *Diplostephium revolutum*
8 *Calypogeia andicola*

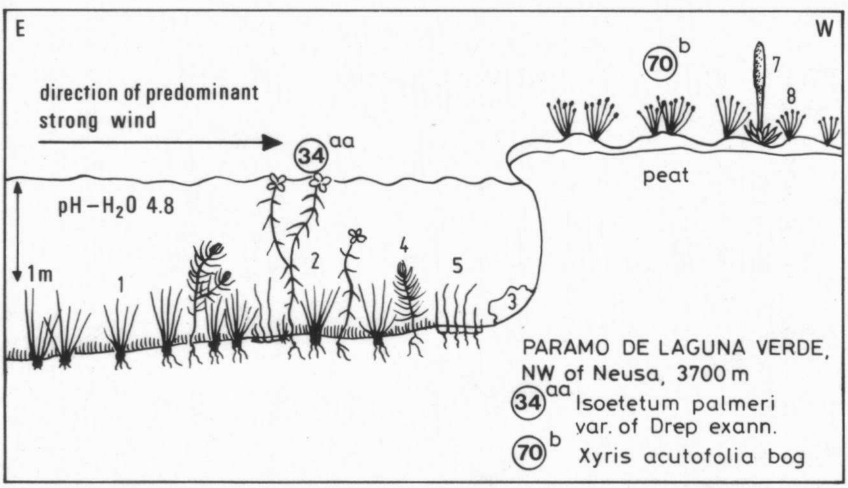


Fig. 38.

Isoetetum palmeri: variant of *Drepanocladus exannulatus* (34aa).

Lower bunchgrass páramo lake at 3700 m near the Laguna Verde, NW of Neusa. *Xyris acutifolia* bog (70b) is present on the western shore.

1 *Isoetes palmeri*
2 *Callitriche* sp. (6253)
3 *Batrachospermum* sp.
4 *Myriophyllum elatinoides*
5 *Eleocharis acicularis*
6 *Depranocladus exannulatus*
7 *Puya santosii*
8 *Xyris acutifolia*

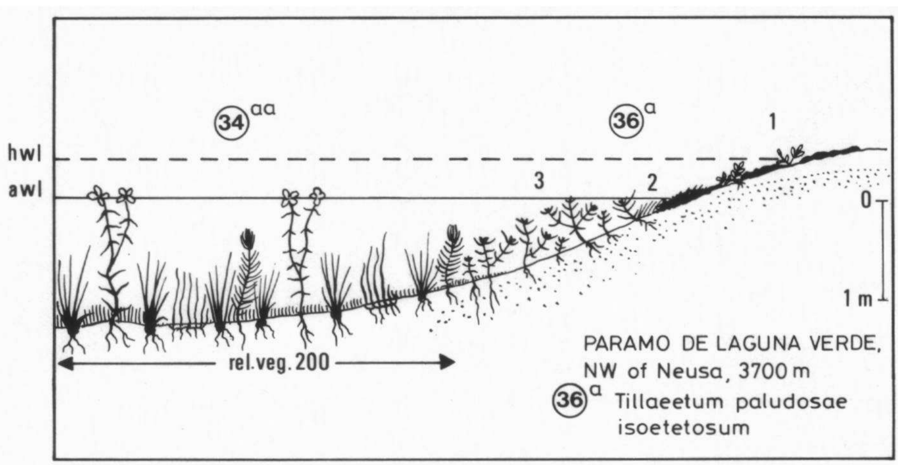


Fig. 39.

Zonation of the *Tillaeetum paludosae isoetetosum* (36a) and the *Isoetetum palmeri*, variant of *Drepanocladus exannulatus* (34aa) in a small lake at 3700 m in the lower bunchgrass páramo near the Laguna Verde, NW of Neusa.

1 *Sphagnum* sp., *Elatine chilensis*
2 floodmark of detritus of *Isoetes* and *Sphagnum*
3 *Tillaea paludosa*

hwl: high water level
awl: waterlevel on nov. 11, 1972

For other conventions see Fig. 38 (same lake).

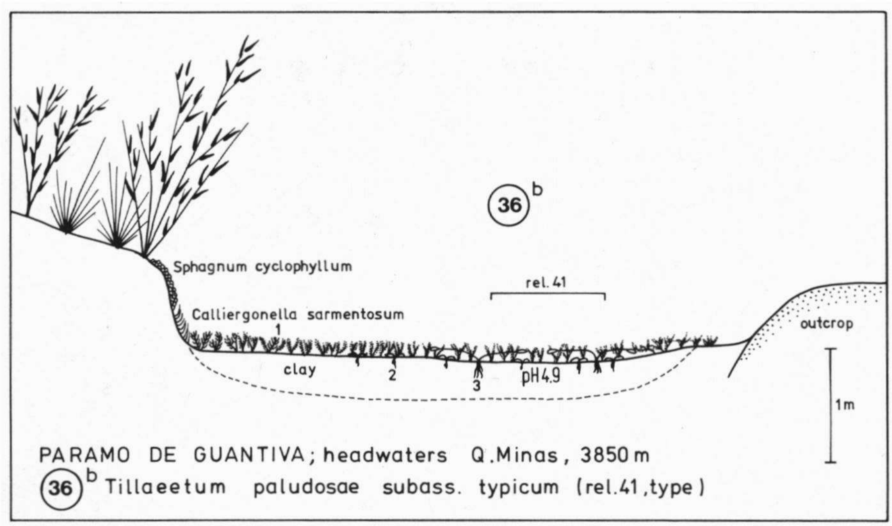


Fig. 40.

Tillaeetum paludosae (36). Amphibious vegetation of the subass. *typicum* (36a) in pond in bamboo-bunchgrass-páramo at 3850 m in the southern Páramo de Guantiva.

1 *Tillaea paludosa*
2 *Isoetes socia*
3 *Ranunculus limoselloides*

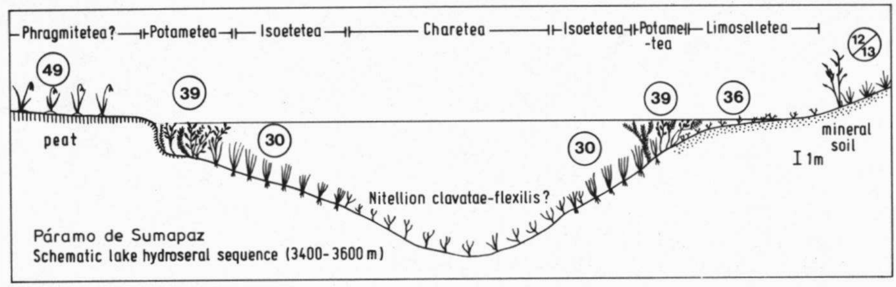


Fig. 41.

Schematic zonation of vegetation in a lake in the lower páramos of the Páramo de Sumapaz. The *Nitellion clavatae-flexilis* (Rangel & Aguirre, in press) is supposed to be present on the lake bottom in deep water.

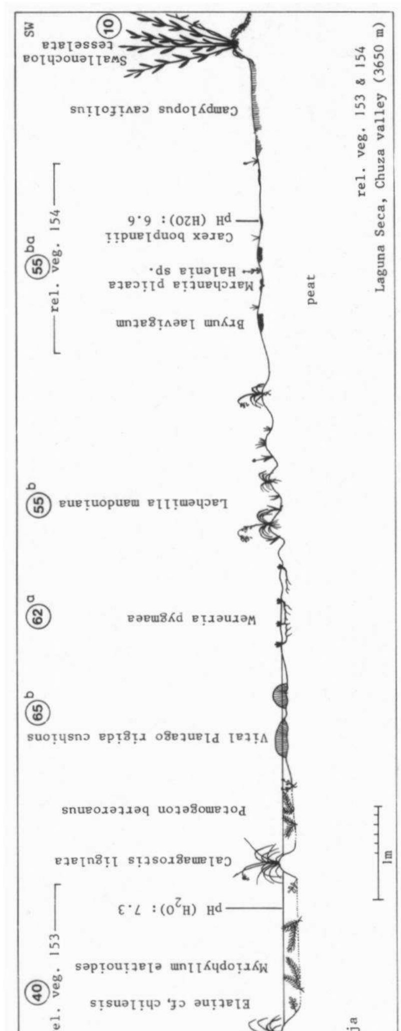


Fig. 42.

Vegetation zonation along the peaty shore of the Laguna Seca at about 3650 m in the headwaters of Río Chuza, NE of Bogotá.

Hydroseral sequence:

40	*Hydrocotylo ranunculoides - Myriophylletum elatinoides*
65b, 62a	*Oritrophio - Wernerietalia*
55b	*Geranio-confertae-Calamagrostietum ligulatae breutelietosum*
55ba	id. var. of *Campylopus cavifolius*
10	Community of *Swallenochloa* with *Sphagnum* and *Breutelia*

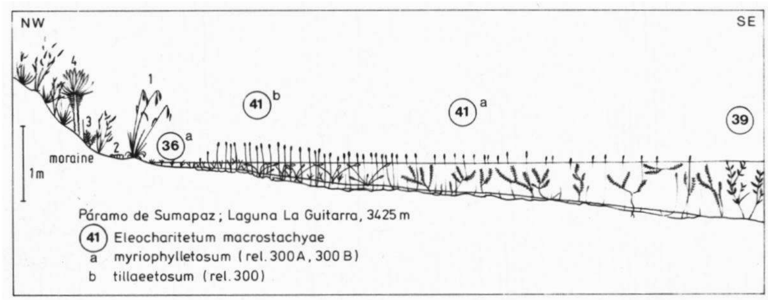


Fig. 43.

Eleocharitetum macrostachyae (41) in the Laguna La Guitarra (3425 m), Páramo de Sumapaz, showing the location of the *myriophylletosum* (41a) and the *tillaeetosum* (41b).

1 *Cortaderia nitida*
2 *Plantago rigida*
3 *Blechnum loxense*
4 *Potamogeton asplundii*

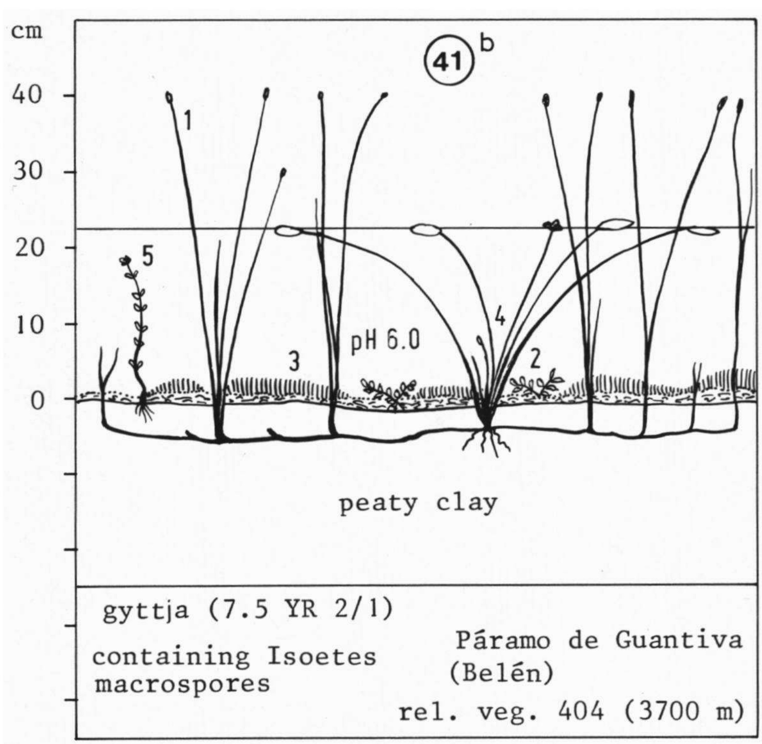


Fig. 44.

Eleocharitetum macrostachyae tillaeetosum (41b) at 3700 m in a small lake in the southern Páramo de Guantiva near the Alto de Las Cruces, W of Belén (Boyacá).

1 *Eleocharis macrostachya*
2 *Elatine chilensis*
3 *Drepanocladus revolvens*
4 *Ranunculus limoselloides*
5 *Callitriche* sp.

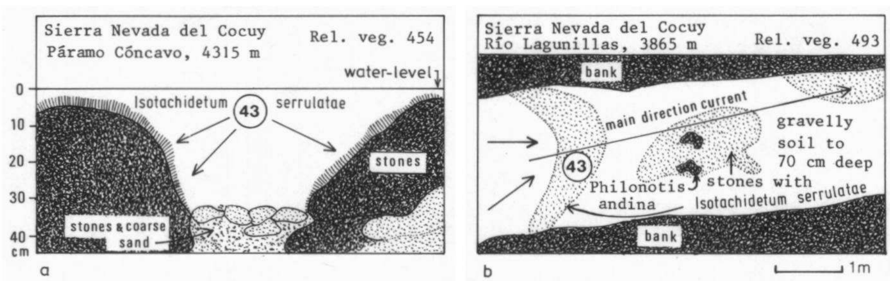


Fig. 45.

Philonoto-Isotachidetum serrulatae (43) in high páramo streams in the Sierra Nevada del Cocuy (Boyacá).

a crossection
b map

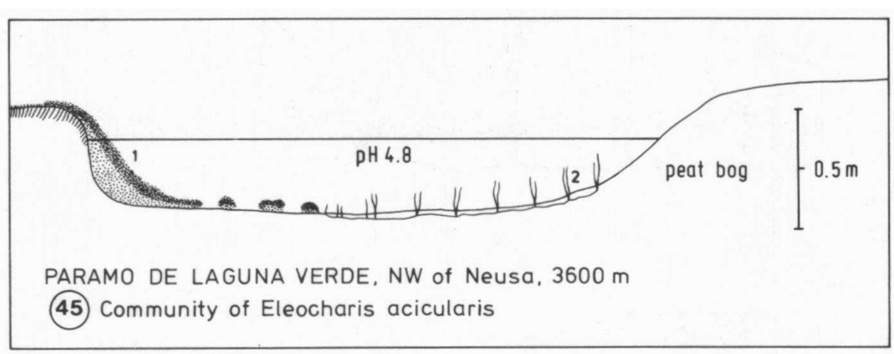


Fig. 46.

Community of *Eleocharis acicularis* (45) in *Sphagnum* bog at 3600 m in the lower bunchgrass páramos near the Laguna Verde, NW of Neusa.

1 *Sphagnum cuspidatum*
2 *Eleocharis acicularis*

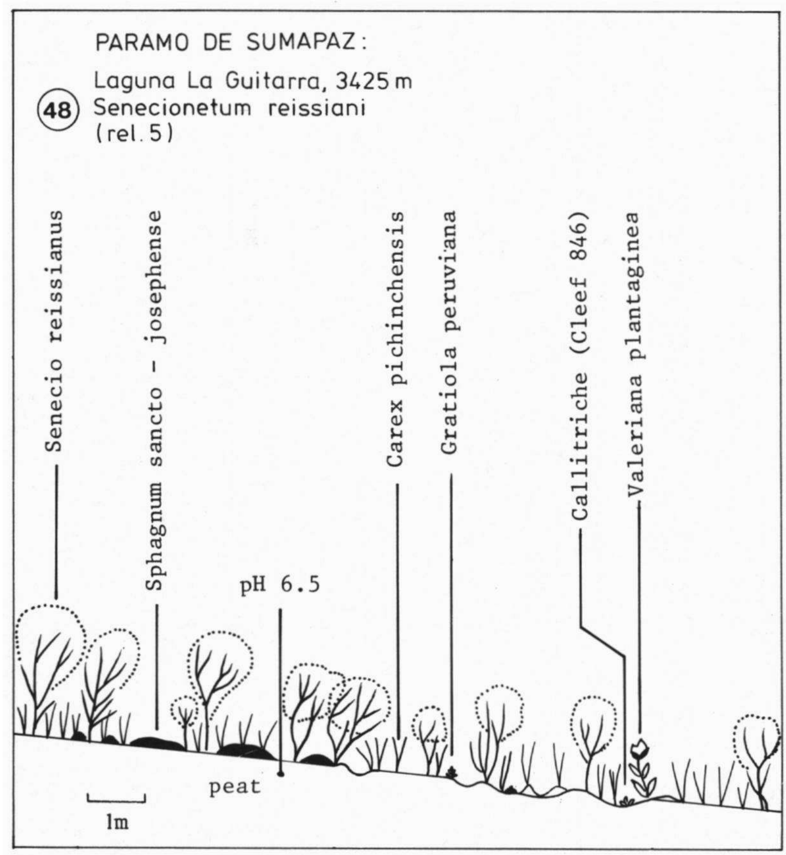


Fig. 47.

Senecionetum reissiani (48) at 3425 m near the marshy southern shore of the Laguna La Guitarra, Páramo de Sumapaz (Meta).

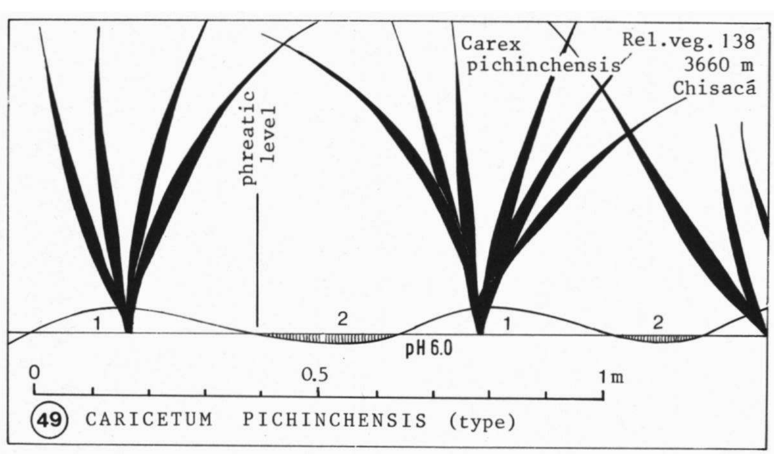


Fig. 48.

Caricetum pichinchensis (49). Schematic detail of hummock-hollow topography in stand at 3660 m in the headwaters of Río S. Rosita, Chisacá (Cundinamarca).

1 hummock: *Chorisodontium* sp. (5194)
Pernettya prostrata var. *elliptica*
Breutelia inclinata
Thuidium peruvianum

2 hollow: *Lachemilla mandoniana*
Cotula minuta
Breutelia inclinata
Symphyogyna sinuata

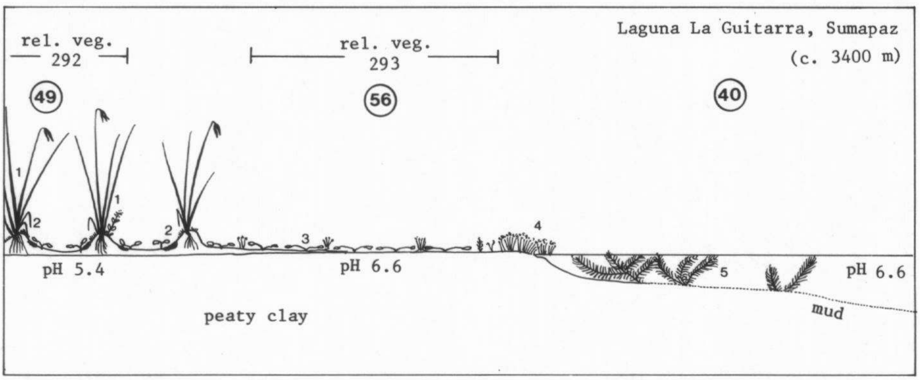


Fig. 49.

Vegetation zonation along the marshy SW shore of the Laguna La Guitarra at c. 3400 m (Páramo de Sumapaz, Meta) with a sequence of *Potameto-Myriophyllion* (40), *Calamagrostis ligulata* community with *Montia fontana* (56), and *Caricetum pichinchensis* (49).

1 hummock: *Carex pichinchensis*
Valeriana plantaginea var. *paludosa* (var. ined)
Stokesiella praelonga
Breutelia sp. (8258)

2 hollow: *Ranunculus flagelliformis*
Marchantia plicata

3 *Ranunculus flagelliformis*, *Eleocharis stenocarpa*, *Montia fontana*

4 *Eleocharis stenocarpa*

5 *Myriophyllum elatinoides*

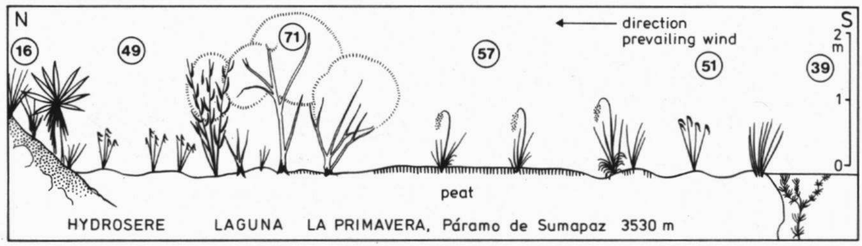


Fig. 50.

Vegetation zonation in the Laguna La Primavera at 3530 m in the Páramo de Sumapaz (Meta). See also fig. 51.

16 Lower *Calamagrostis effusa* páramo with *Espeletia grandiflora* and *Oreobolus obtusangulus* ssp. *rubrovaginatus*
39 *Potameto-Myrriophyllion elatinoides*
49 *Caricetum pichinchensis*
51 Community of *Carex acutata* (rel. 267A)
57 Community of *Calamagrostis ligulata* with *Sphagnum sancto-josephense* (rel. 267)
71 *Diplostephietum revoluti*

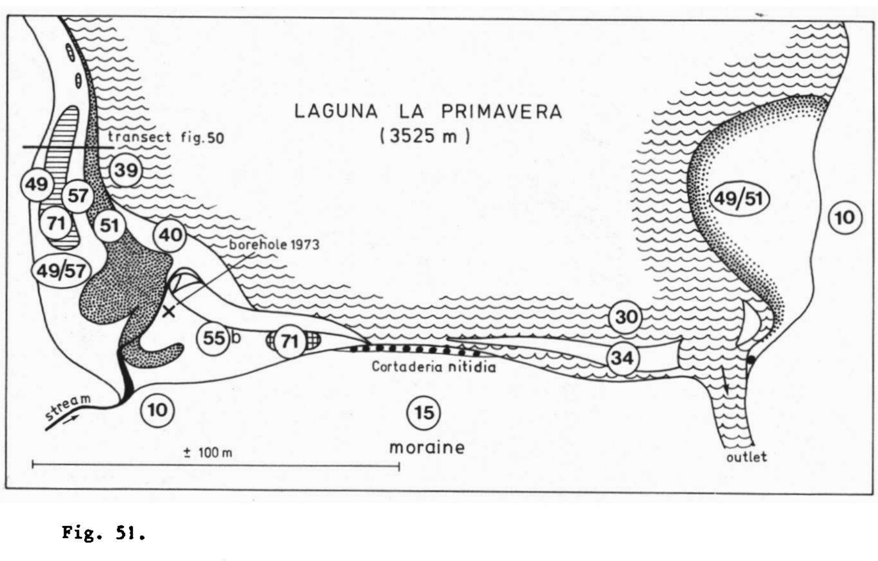


Fig. 51.

Sketch of the vegetation zonation in the western part of the Laguna La Primavera at 3525 m in the Páramo de Sumapaz (Meta).

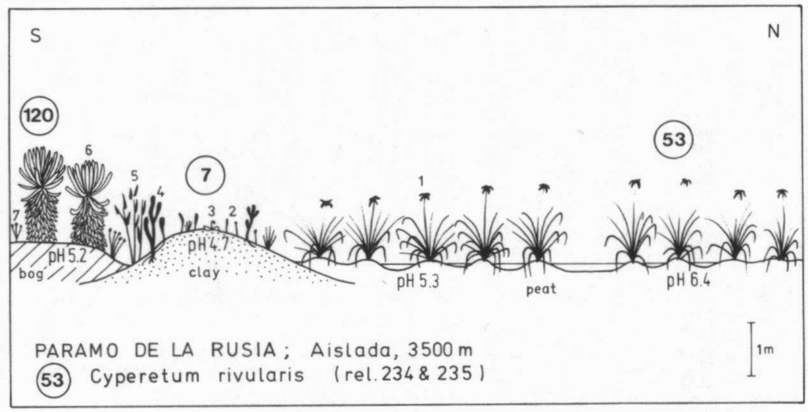


Fig. 52.

Cyperetum rivularis **(53)**

1 ***Cyperus rivularis*** **ssp.** ***lagunetto***
2 ***Lycopodium contignum***
3 ***Castratella piloselloides***
4 ***Aragoa cupressina***
5 ***Swallenochloa*** **sp.**
6 ***Espeletia murilloi***
7 ***Xyris subulata***

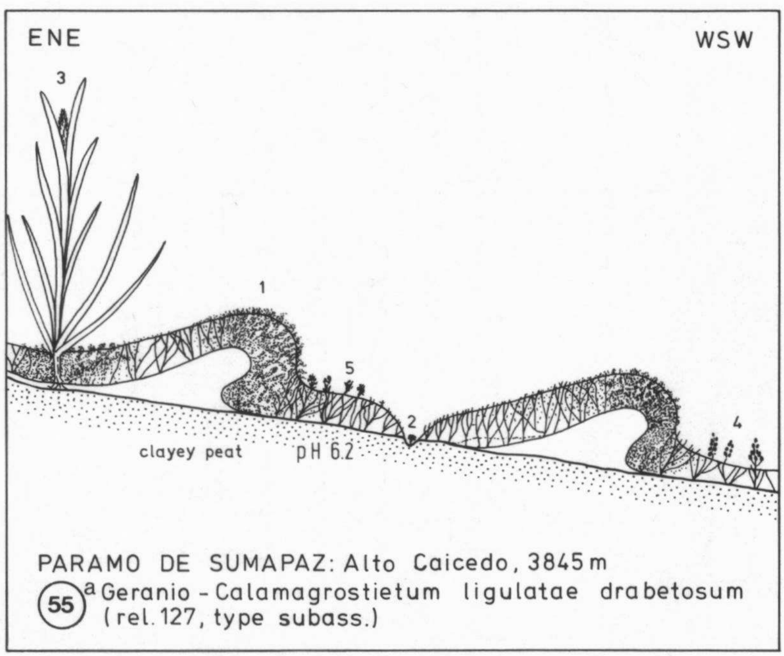
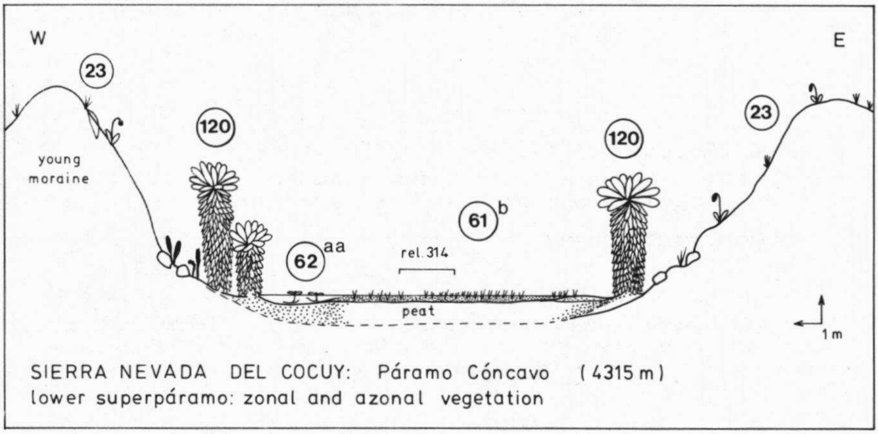


Fig. 53.

Hummock-hollow relief in the ***Geranio confertae-Calamagrostietum ligulatae drabetosum*** **(55a)**

1 ***Breutelia chrysea***
Cerastium imbricatum
Muhlenbergia **cf.** ***fastigiata***
Bryum **sp. (4818)**
Brachythecium **sp. (4819)**

2 ***Cyclodictyon*** **sp. (4820)**
Cardamine **sp.**
3 ***Senecio niveo-aureus***
4 ***Lupinus*** **cf.** ***verjonensis***
5 ***Draba*** **sp. (2611A/white petals)**



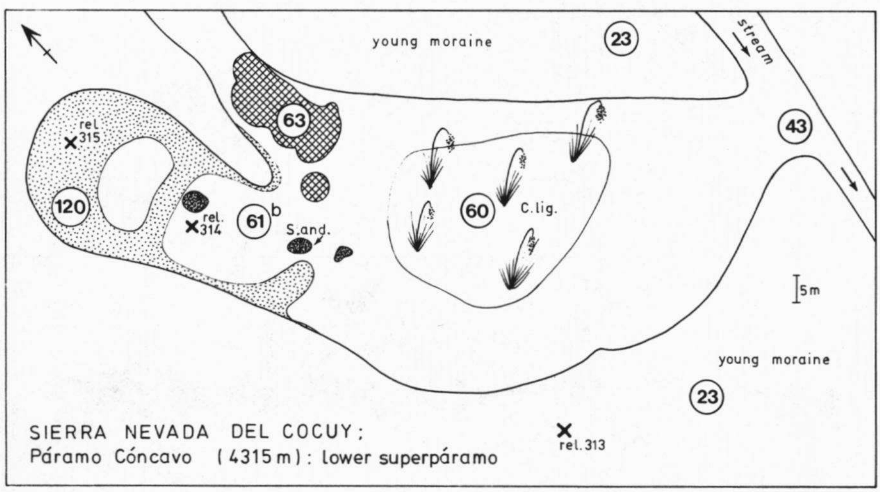


Fig. 54 & 55.

Vegetation profile and map of zonal and azonal lower superpáramo vegetation at 4300 m in the Páramo Cóncavo, Sierra Nevada del Cocuy (Boyacá).

23	Community of *Pernettya prostrata* and *Luzula racemosa*
43	*Philonoto-Isotachidetum serrulatae* (rel. 454)
61b	*Carici pencophilae-Wernerietum crassae caricetosum pencophilae*
62aa	Variant *typicum* of *Oritrophio-Wernerietum pygmaeae*
120	Dense *Espeletia lopezii* grove on peat
S. and.	*Senecio andicola*
C. lig.	*Calamagrostis ligulata*

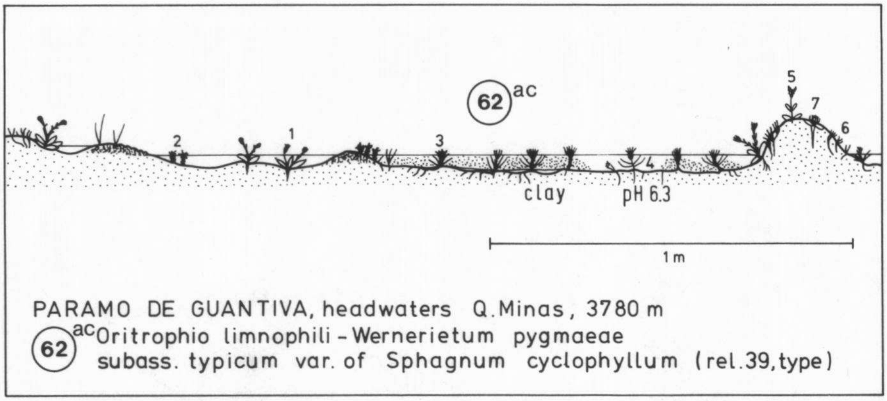


Fig. 56.

Oritrophio limnophili-Wernerietum pygmaeae (62). Detail of flush-vegetation of the variant of *Sphagnum cyclophyllum* (62ac) on wet glacial grass pāramo valley floor at 3780 m in the headwaters of Q. Minas, southern Páramo de Guantiva.

1 *Oritrophium limnophilum* ssp. *mutisianum*
2 *Plantago rigida*
3 *Werneria pygmaea*
4 *Sphagnum cyclophyllum*
5 *Gentianella nevadensis*
6 *Vesicarex collumanthus*
7 *Hypochoeris sessiliflora*

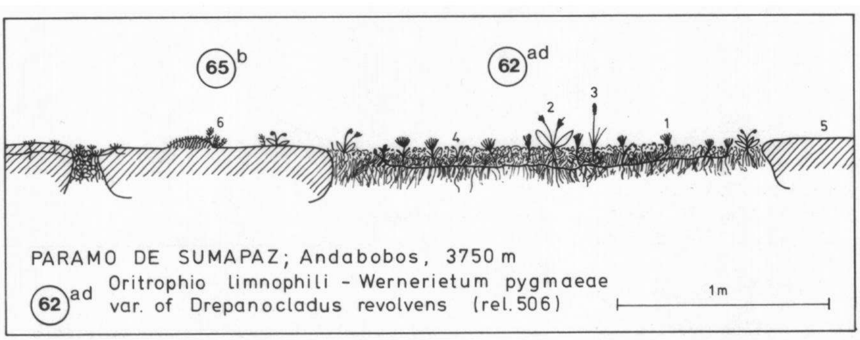


Fig. 57.

Oritrophio limnophili-Wernerietum pygmaeae (62)
Hollow vegetation of the variant of *Drepanocladus revolvens* (62ad) in cushion-bog of the *Hyperico-Plantaginetum rigidae breutelietosum* (65b)

1 *Werneria pygmaea*
2 *Oritrophium limnophilum* ssp. *mutisianum*
3 *Calamagrostis coarctata*
4 *Drepanocladus revolvens*
5 *Plantago rigida*
6 *Chorisodontium speciosum*

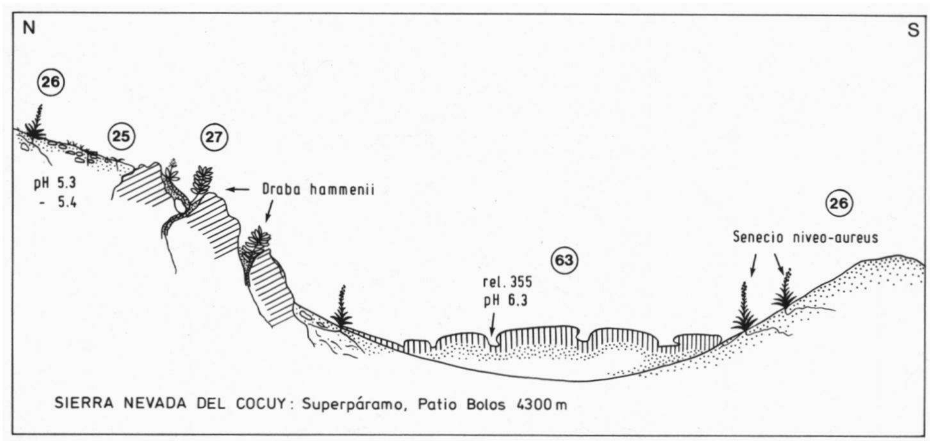


Fig. 58.

Floscaldasio-Distichietum muscoides (63) at 4300 m in the lower superpáramo near Patio Bolos, Sierra Nevada del Cocuy (Arauca). Adjacent are zonal communities of *Agrostis breviculmis* with *Acaulimalva purdiei* (25); of *Senecio niveo-aurens* (26) and of *Valeriana plantaginea* with *Racomitrium crispulum* (27).

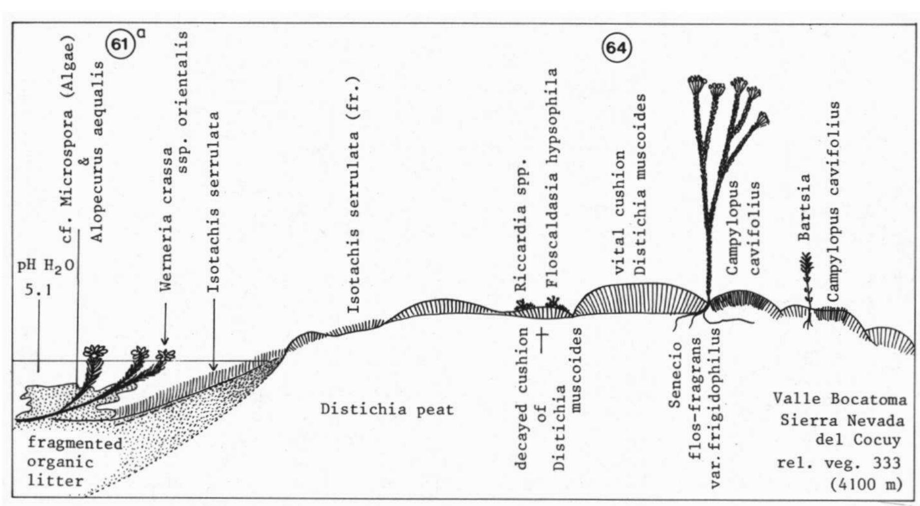


Fig. 59.

Community of *Distichia muscoides* with *Isotachis serrulata* and *Campylopus fulvus* (64) at 4100 m on a former glacial lake in the Bocatoma valley, Sierra Nevada del Cocuy (Boyacá).

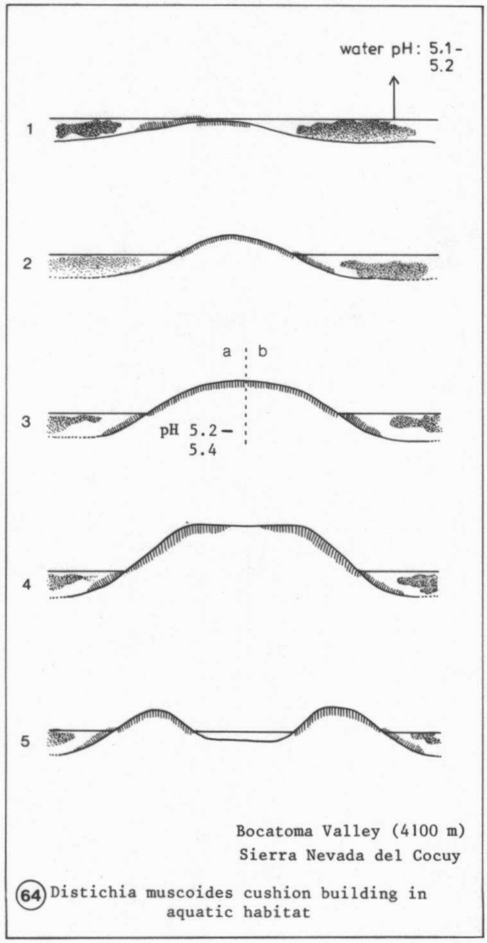


Fig. 60.

Possible development and decay of *Distichia muscoides* cushions in aquatic habitat as observed in the stand of Fig. 59.

1 vital *Distichia muscoides* with *Isotachis serrulata* and algae (cf. *Microspora*)
2 vital *Distichia muscoides* cushions
3 decaying *Distichia muscoides* cushion with *Oreobolus obtusangulus*, and *Riccardia* sp. colonizing first (a);
later follow grasses (*Cortaderia* sp., *Calamagrostis effusa*), algae (8758) and mosses (*Campylopus cavifolius*, *C. fulvus*)
4 decaying *Distichia muscoides* cushion with podetia of *Cladonia* subg. *Cenomyce* (8761) on top of the dry cushions.
Lycopodium sp., *Floscaldasia hypsophila*, *Pernettya prostrata* var. *purpurea*, *Hypericum lancioides*, *Bartsia* sp., *Senecio flos-fragrans* var. *frigidophilus*, *Lachemilla nivalis*, *Loricaria complanata*, and *Diplostephium rhomboidale* may arrive. *Pseudocephalozia quadriloba*, *Cephalozia dussii* and *Calliergon trifarium* grow over the *Oreobolus* cushions.
5 the ringlike pattern of the *Distichia* cushions is caused by final decay of the oldest central part of the cushions.

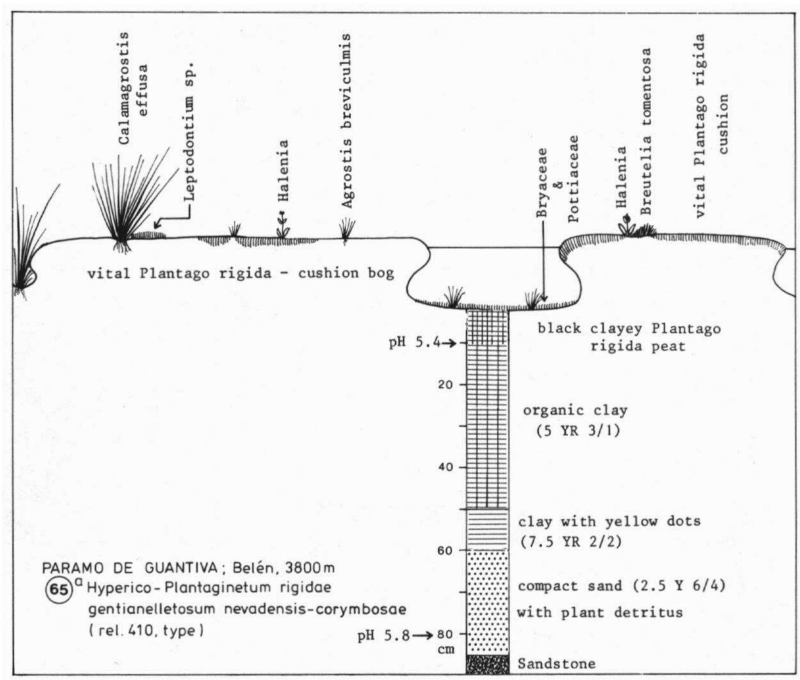


Fig. 61.

Hyperico lancioides-Plantaginetum rigidae gentianelletosum nevadensis (65a) at 3800 m in the Páramo de Guantiva, W of Belén (Boyacá).

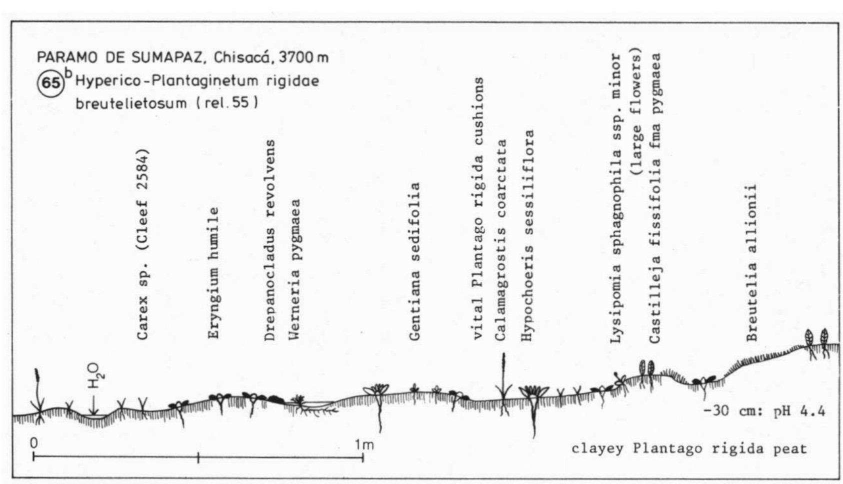


Fig. 62.

Hyperico lancioides-Plantaginetum rigidae breutelietosum (65b).
Grazed (Browsed) cushion bog at 3700 m near the Chisacá lakes (Cundinamarca).

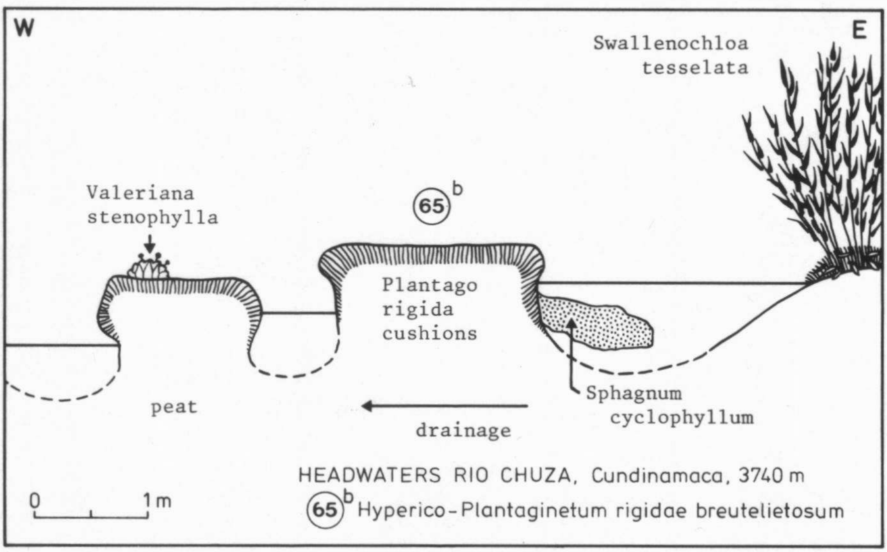


Fig. 63.

Detail of slope bog of the *Hyperico-Plantaginetum rigidae breutelietosum* (65b) at 3740 m in the headwaters of Río Chuza, NE of Bogotá.

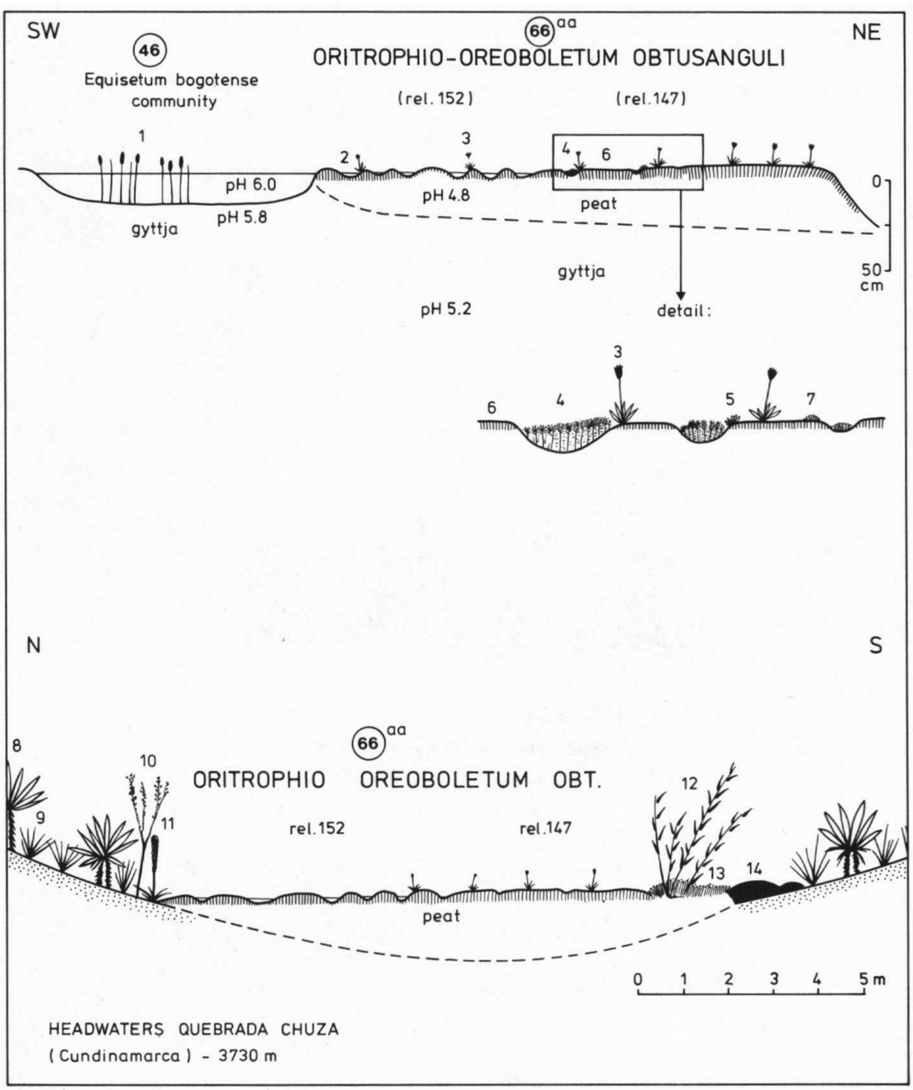


Fig. 64.

Oritrophio peruviani-Oreoboletum obtusanguli **(66aa) in grass páramo at 3730 m near the headwaters of Q. Chuza, ENE of Bogotá.**

1 *Equisetum bogotense*
2 *Sphagnum cuspidatum*
3 *Oritrophium peruvianum* ssp. *peruvianum* fma. *intermedia*
4 *Sphagnum sancto-josephense* & *Rhacocarpus purpurascens*
5 *Werneria humilis* var. *angustifolia*
6 *Oreobolus obtusangulus* and *Plantago rigida*
7 *Campylopus cavifolius*
8 *Espeletia grandiflora*
9 *Calamagrostis effusa*
10 *Senecio vaccinioides*
11 *Puya trianae*
12 *Swallenochloa tesselata*
13 *Rhacocarpus purpurascens* & *Campylopus* sp.
14 *Sphagnum compactum*

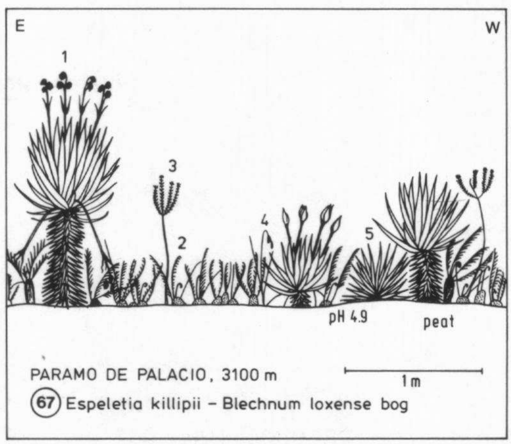


Fig. 65.

Sphagnum bog with *Espeletia killipii* and *Blechnum loxense*

1 *Espeletia killipii* var. *killipii*
2 *Blechnum loxense*
3 *Baccharis revolutum*
4 *Carex pichinchensis*
5 *Puya goudotiana*

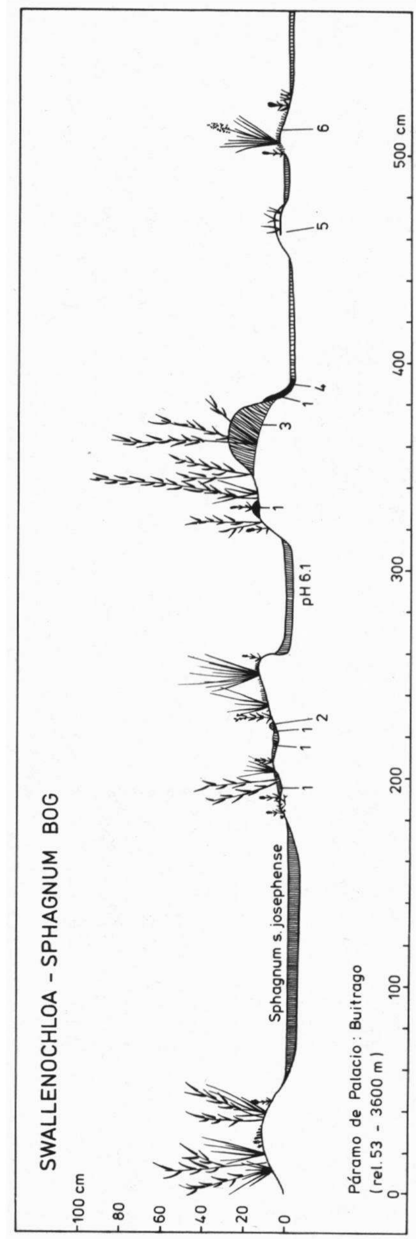


Fig. 66.

Sphagnum bog with *Swallenochloa* (68) at 3600 m near Buitrago, Páramo de Palacio.

1 *Campylopus* sp.
2 *Eriocaulon microcephalum*
3 *Sphagnum magellanicum*
4 *Anastrophyllum nigrescens*
5 *Campylopus pittieri*
6 *Breutelia chrysea*

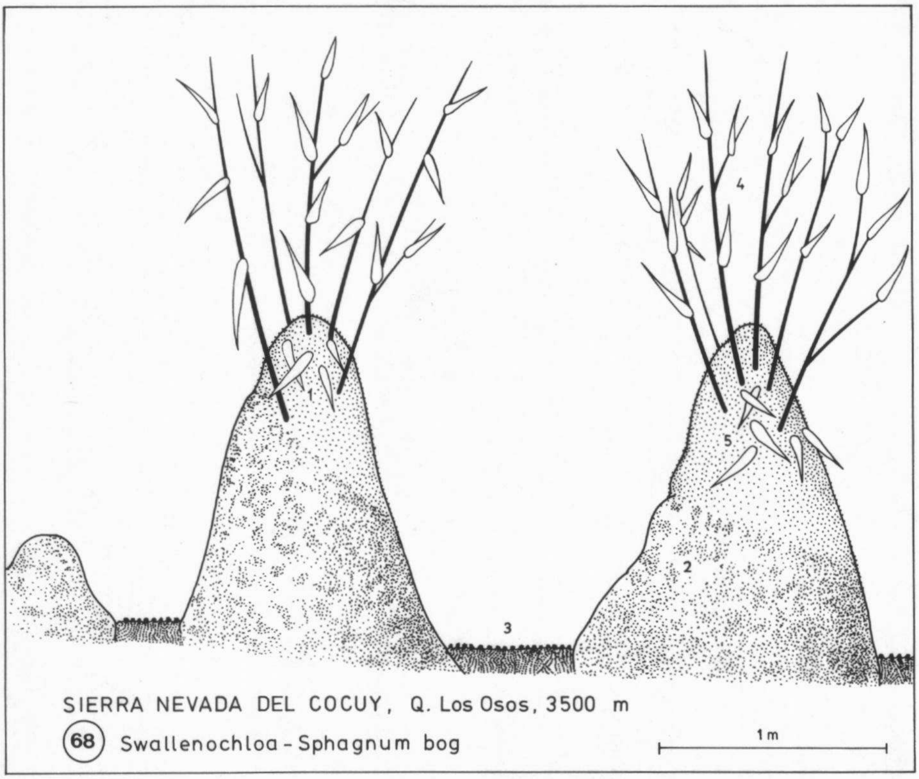


Fig. 67.

Swallenochloa-Sphagnum bog (68):
Detail of hummock-hollow relief. Upper valley of Q. Los Osos, Vado de Garbancillos at 3500 m in the bamboo páramo of the Sierra Nevada del Cocuy (Arauca).

1 *Lepidozia* sp.
2 *Sphagnum magellanicum*
3 *Sphagnum sancto-josephense*
4 *Swallenochloa* sp.
5 *Leptodontium wallisii*, *Sphaerophorus melanocarpus*
6 *Pernettya prostrata*

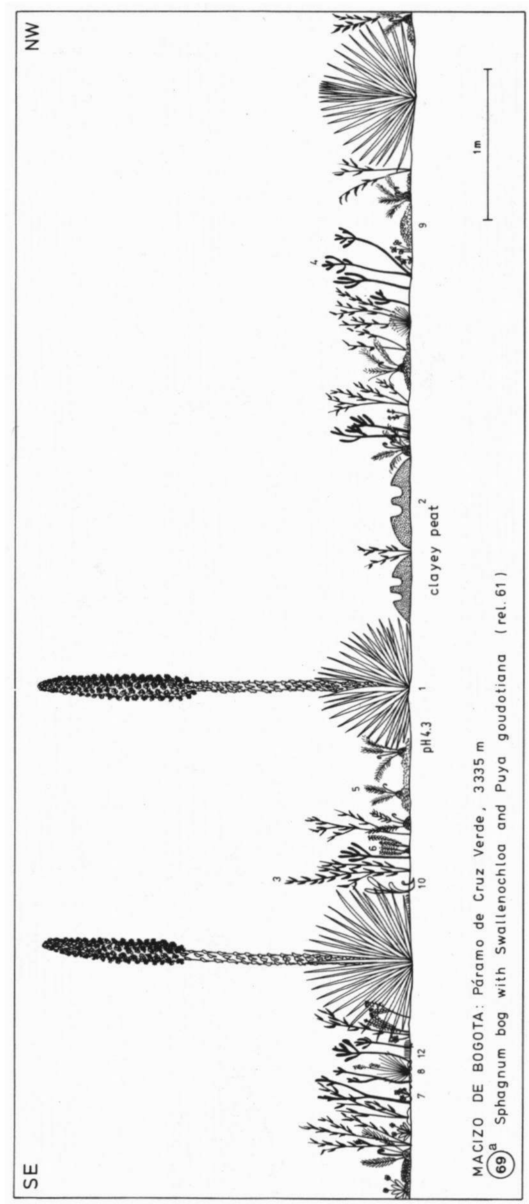


Fig. 68.

Sphagnum bog with *Swallenochloa* and *Puya goudotiana* (69a)

1 *Puya goudotiana*
2 *Puya goudotiana* (†)
3 *Swallenochloa* sp.
4 *Aragoa abietina*
5 *Blechnum loxense*
6 *Diplostephium phylicoides*
7 *Geranium sibbaldioides*
8 *Calamagrostis effusa*
9 *Sphagnum magellanicum*
10 *Elaphoglossum engelii*
11 *Paepalanthus andicola* var. *villosus*
12 *Polytrichum juniperinum*

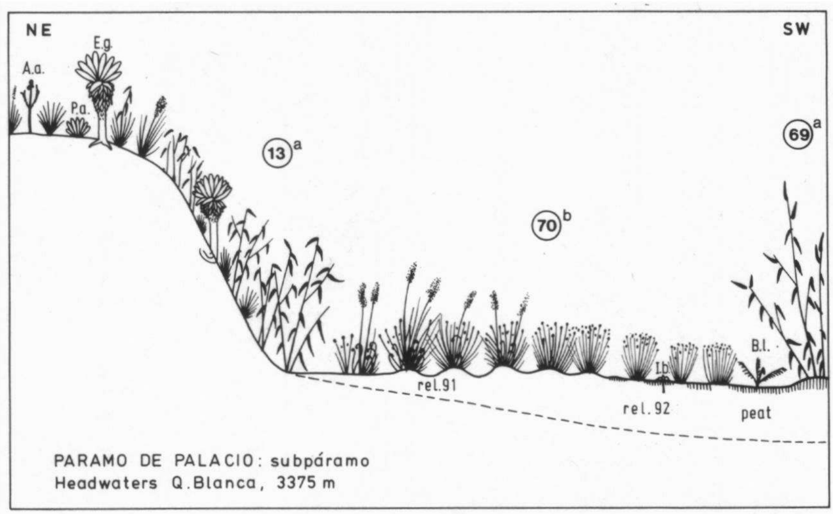


Fig. 69.

Xyris acutifolia-bog (70b) at 3375 m in the Páramo de Palacio, NE of Bogotá.
Adjacent communities are *Swallenochloa* páramo with *Oreobolus obtusangulus* ssp. *rubrovaginatus* (13a) and *Swallenochloa*-*Sphagnum* bog (68, 69a).

1 *Espeletia grandiflora*
2 *Blechnum loxense*
3 *Isoetes boyacensis*
4 *Aragoa abietina*
5 *Paepalanthus andicola* var. *villosus*
6 *Cortaderia nitida*

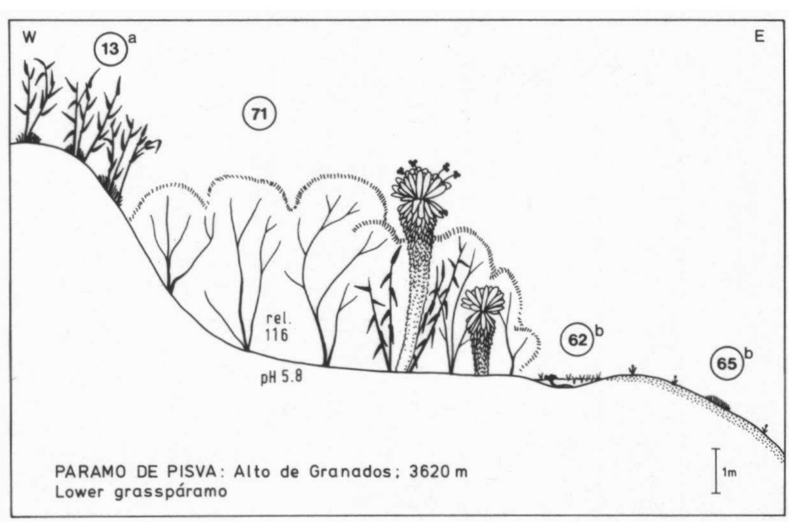


Fig. 70.

Diplostephietum revoluti (71) with *Espeletia lopezii* var. *major* at 3620 m in the Páramo de Pisva (Boyacá). Adjacent are *Swallenochloa* páramo with *Oreobolus obtusangulus* ssp. *rubrovaginatus* (13a), the *Oritrophio-Wernerietum pygmaeae cotuletosum* (62b) and *Hyperico-Plantaginetum rigidae breutelietosum* (65b).

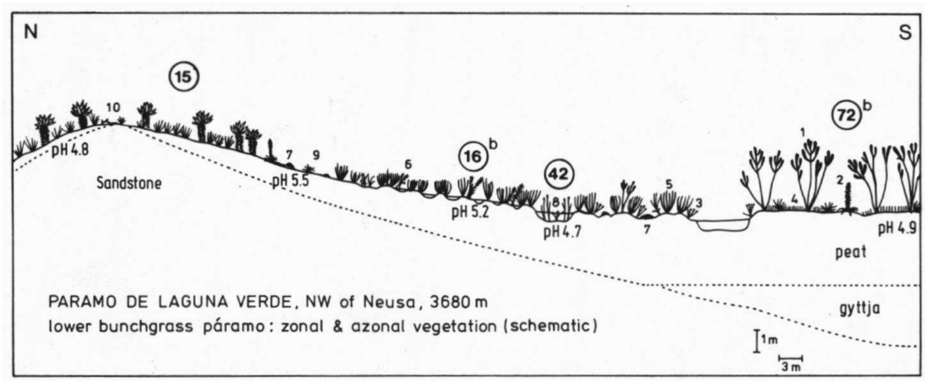


Fig. 71.

Transition from azonal *Aragoetum abietinae puyetosum* (72b) and the *Blechnum loxense-Espeletia chocontana* community (16b) towards zonal *Calamagrostis effusa* lower bunchgrass páramo with *Espeletia barclayana*, *Oreobolus obtusangulus* ssp. *rubrovaginatus* and *Castratella piloselloides*

1 *Aragoa abietina*
2 *Puya santosii*
3 *Xyris acutifolia*
4 *Sphagnum*-pleurocarpous moss layer
5 *Espeletia chocontana*
6 *Blechnum loxense*
7 *Valeriana stenophylla*
8 *Juncus ecuadoriensis*, *Ranunculus limoselloides*
9 *Rhacocarpas purpurascens* predominant
10 *Pernettya prostrata* predominant

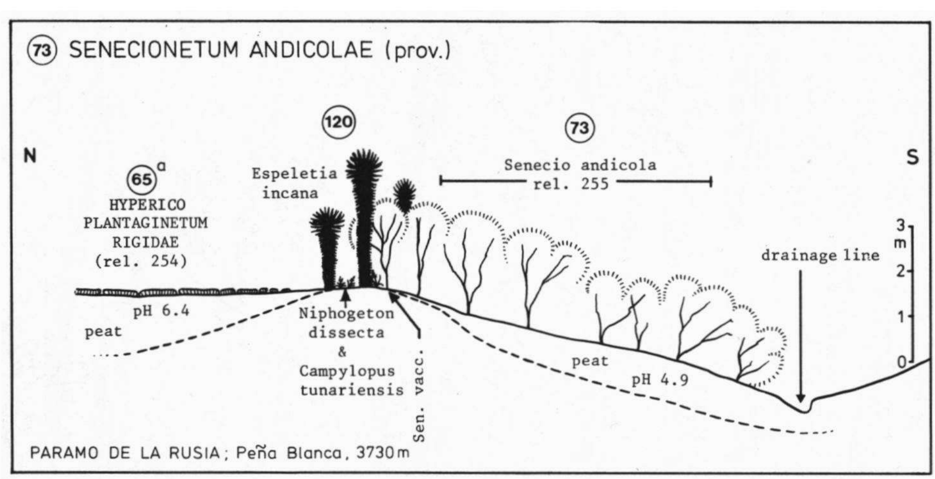


Fig. 72.

***Senecionetum andicolae* (73) and *Hyperico-Plantaginetum rigidae* (65a) at 3730 m near Peña Blanca in the Páramo de la Rusia (Boyacá).**

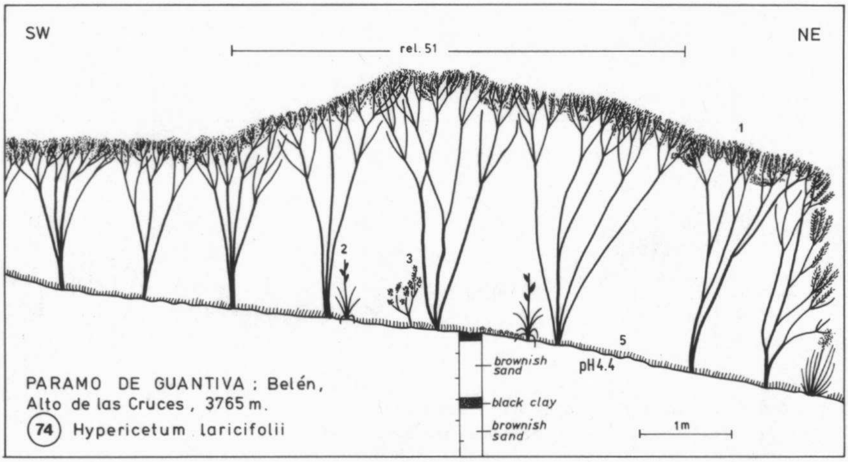


Fig. 73.

Hypericetum laricifolii (74) in humid protected valley in grass páramo at 3765 m near Alto de las Cruces, Vereda S. José de la montaña, W of Belén (Boyacá).

1 *Hypericum laricifolium* ssp. *laricoides*
2 *Orthrosanthus chimboracensis*
3 *Acaena elongata*
4 ericaceous dwarfshrub
5 low mat of *Sibthorpia repens*, *Azorella multifida* and *Thuidium peruvianum*

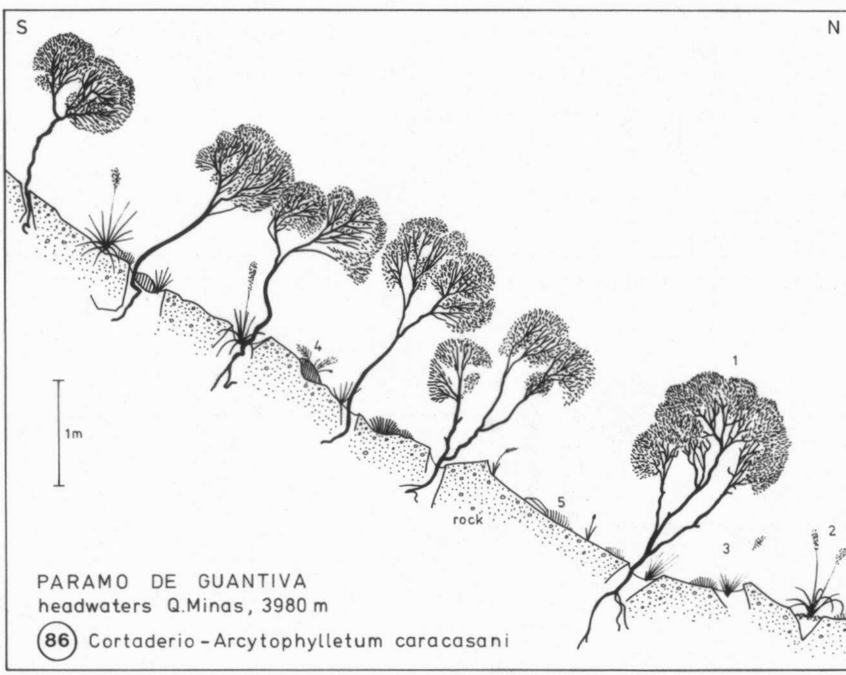


Fig. 74.

Cortaderio sericanthae-Arcytophylletum caracasani (86) on rocky slopes above *Polylepis quadrijuga* dwarfforest in the headwaters of Q. Minas, Páramo de Guantiva.

1 *Arcytophyllum caracasanum*
2 *Cortaderia sericantha*
3 *Calamagrostis effusa*
4 musci: *Rhacocarpus*, *Racomitrium*, *Campylopus richardii*
5 *Oreobolus obtusangulus* ssp. *rubrovaginatus*

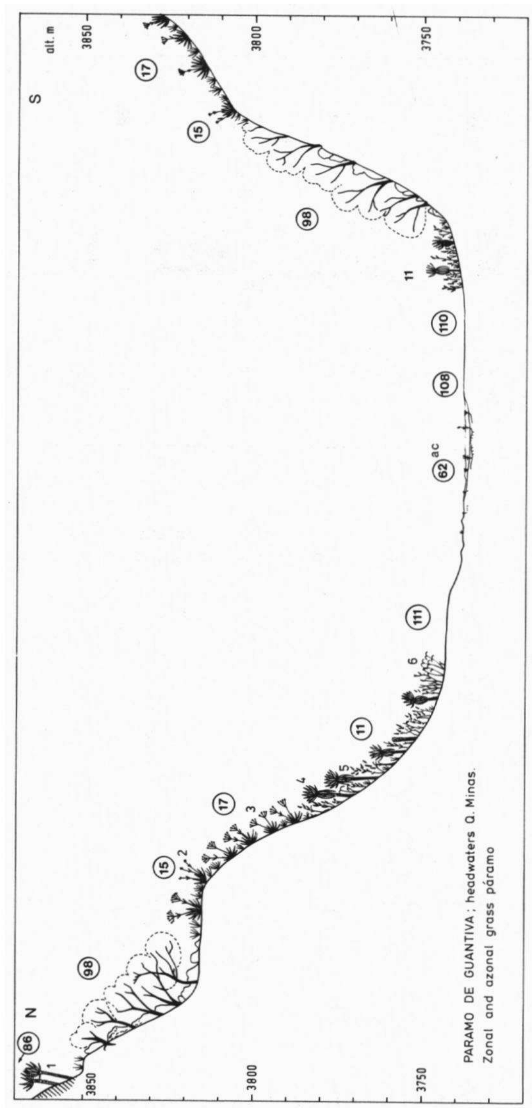


Fig. 75.

Patches of *Polylepis quadrijuga*-dwarfforest (98) in zonal grass páramo (11, 15, 17). Azonal meadows (108, 110) and flush vegetation (62ac) is present on the humid and wet valley floor.

1 *Espeletia grandiflora* ssp. *boyacensis*
2 *Espeletia congestiflora*
3 *Espeletia boyacensis*
4 *Espeletia discoidea* var. *brevis*
5 *Swallenochloa* sp.
6 *Hypericum trianae*
7 *Werneria pygmaea*

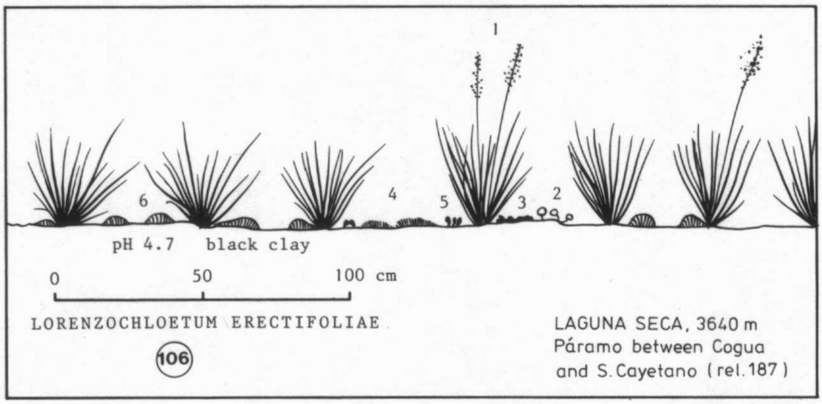


Fig. 76.

Lorenzochloetum erectifoliae **(76) in the lower bunchgrass páramo at 3640 m near the Laguna Seca between Cogua and S. Cayetano (Cundinamarca)**

1 *Lorenzochloa erectifolia*
2 *Sibthorpica repens*
3 *Marchantia berteroana*
4 *Campylopus* sp. (6101)
5 *Cladonia* cf. *fimbriata* (6103)
6 *Campylopus* cf. *pittieri*

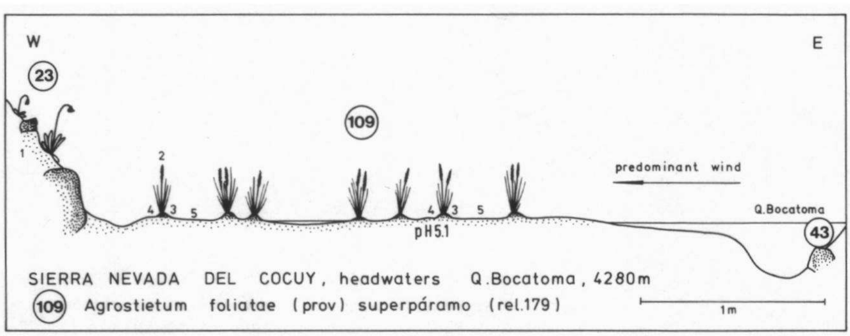


Fig. 77.

Agrostietum foliatae (109) on the sandy, frequently flooded shores of the braided Bocatoma stream at 4280 m in the superpáramo of the Sierra Nevada del Cocuy (Boyacá).

1 *Senecio cocuyanus* on moraine with zonal *Pernettya prostrata-Luzula racemosa* vegetation
2 *Agrostis foliata*
4 *Anastrophyllum* sp.
5 *Aphanocapsa gervillei*

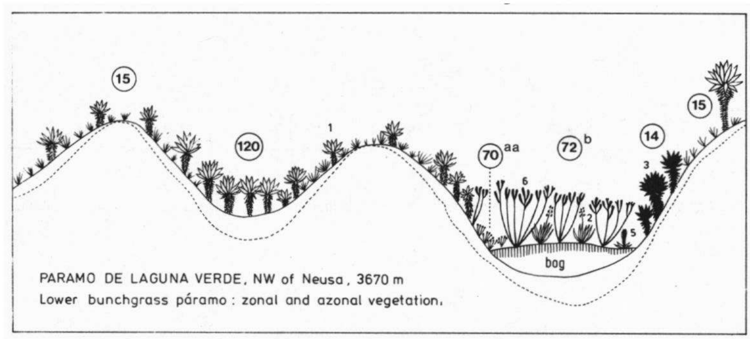


Fig. 78.

Zonal lower *Calamagrostis* bunchgrass páramo communities (14, 15) in contact with azonal dense *Espeletia barclayana* stemrosette community (120) and the *Aragoetum abietinae puyetosum* (72b) at 3670 m in the vicinity of the Laguna Verde, NW of Neusa (Cundinamarca).

1 *Espeletia barclayana*
2 *Espeletia chocontana*
3 *Espeletiopsis corymbosa*
4 *Xyris acutifolia*
5 *Puya* sp.
6 *Aragoa abietina*

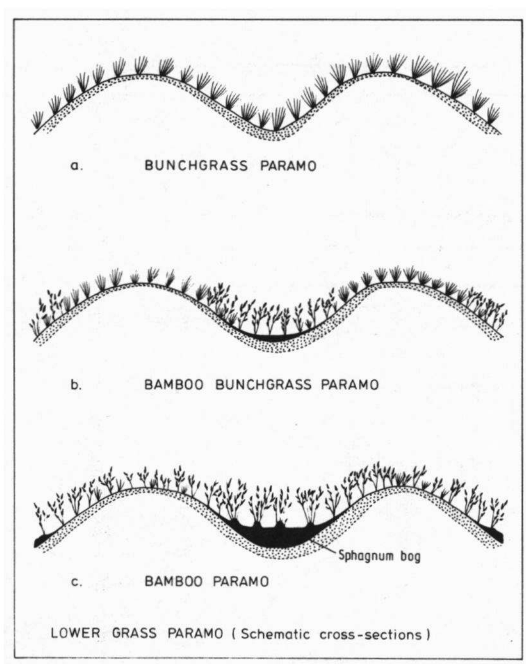


Fig. 79.

Schematic cross-sections through zonal vegetation in the lower grass páramo demonstrating a. bunchgrass páramo, b. bamboo-bunchgrass páramo and c. bamboo páramo. The *Sphagnum* bog (68/69) in bamboo páramo valleys are azonal and grade into azonal *Swallenochloa* communities with *Sphagnum* (10) and other bamboo communities (11, 12, 13). The cover of the bamboos versus bunchgrass depends on the degree of moisture. Only Gramineae are depicted.

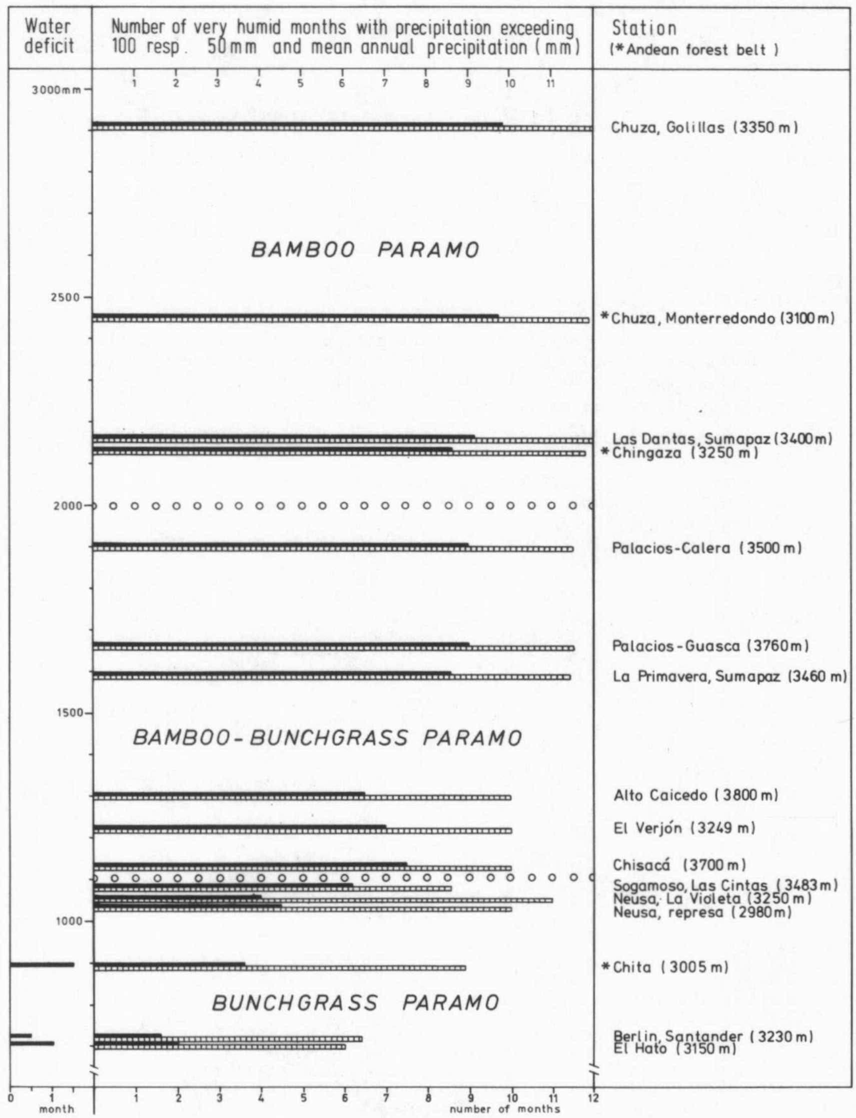


Fig. 80.

Relation between mean annual precipitation (in mm), number of humid months (> 50 mm - hatched bars) and very humid months (> 100 mm - black bars) and zonal páramo vegetation in the lower part of the páramo belt. Upper andean forests are marked with an asterisk.
For the puna climate diagram of Pampa Galeras (4000 m) of Fig. 3p mean annual precipitation is 822 mm and there are 4, resp. 3.2 months yearly with precipitation exceeding 50 resp. 100 mm. The duration of the waterdeficit is 4.5 month. The zonal puna grassland consists of spaced bunches of *Festuca* species mainly (Tovar-Serpa 1973).

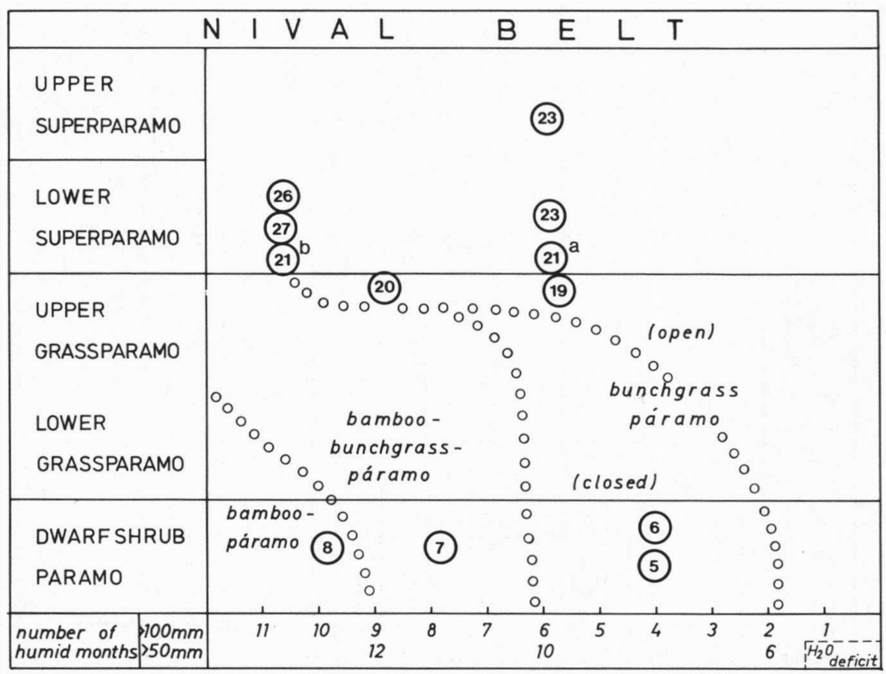


Fig. 81.

Tentative distribution of bamboo-, bamboo-bunchgrass- and bunchgrass páramos in the study area in relation to the number of humid and very humid months (as based on Fig. 3 and 79) and altitudinal zones. (bamboo páramo and bamboo-bunchgrass páramo: community 10-13; bunchgrass páramo: community 14-20)

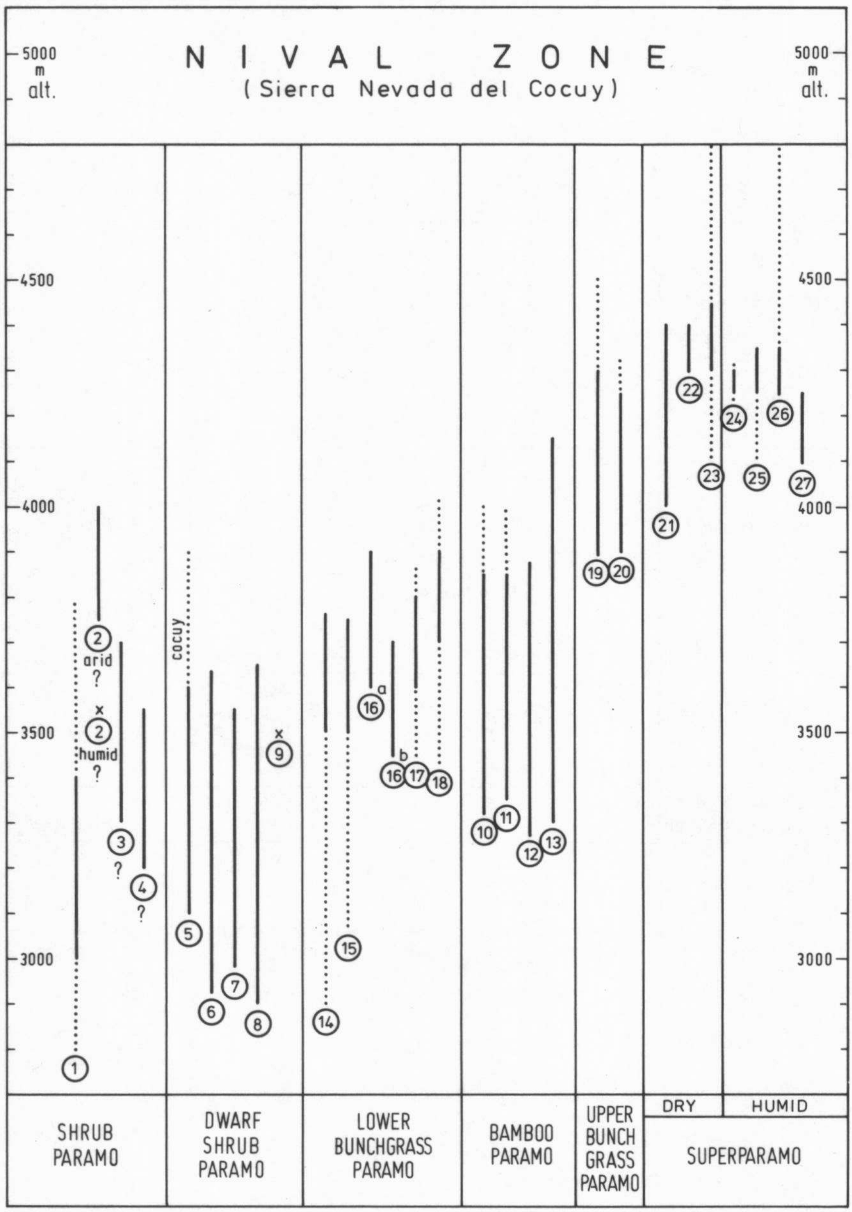


Fig. 82.

Altitudinal distribution of the zonal communities of the páramo vegetation in the Colombian Cordillera Oriental. The community numbers refer to those used in the present study.

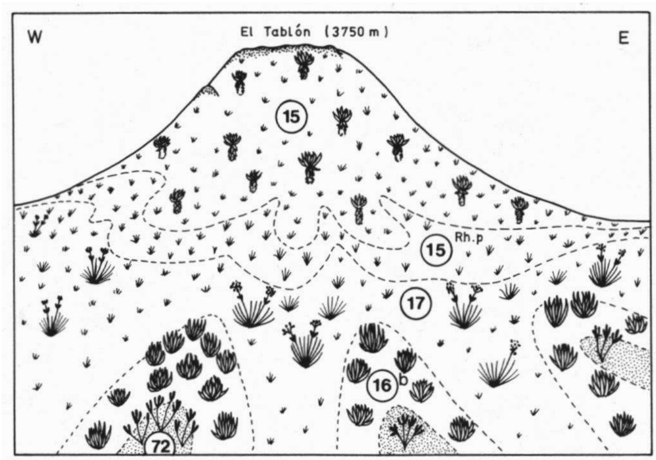


Fig. 83.

Schematic sketch of spatial distribution of zonal and azonal lower bunch grass páramo communities on El Tablón (c. 3750 m), north of the Laguna Verde, NW of Neusa.

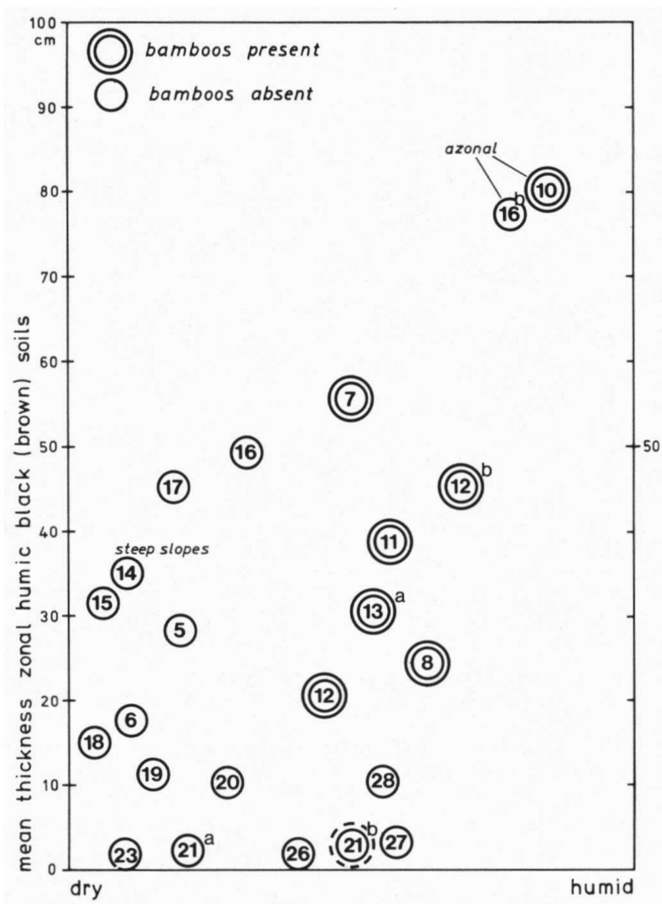


Fig. 84.

Mean thickness of zonal humic black soil in cm in sample plots of various zonal communities of the open páramo vegetation of the study area in relation to degree of moisture. Shallow soils are often brownish, or they lack humic content as do true superpáramo communities.

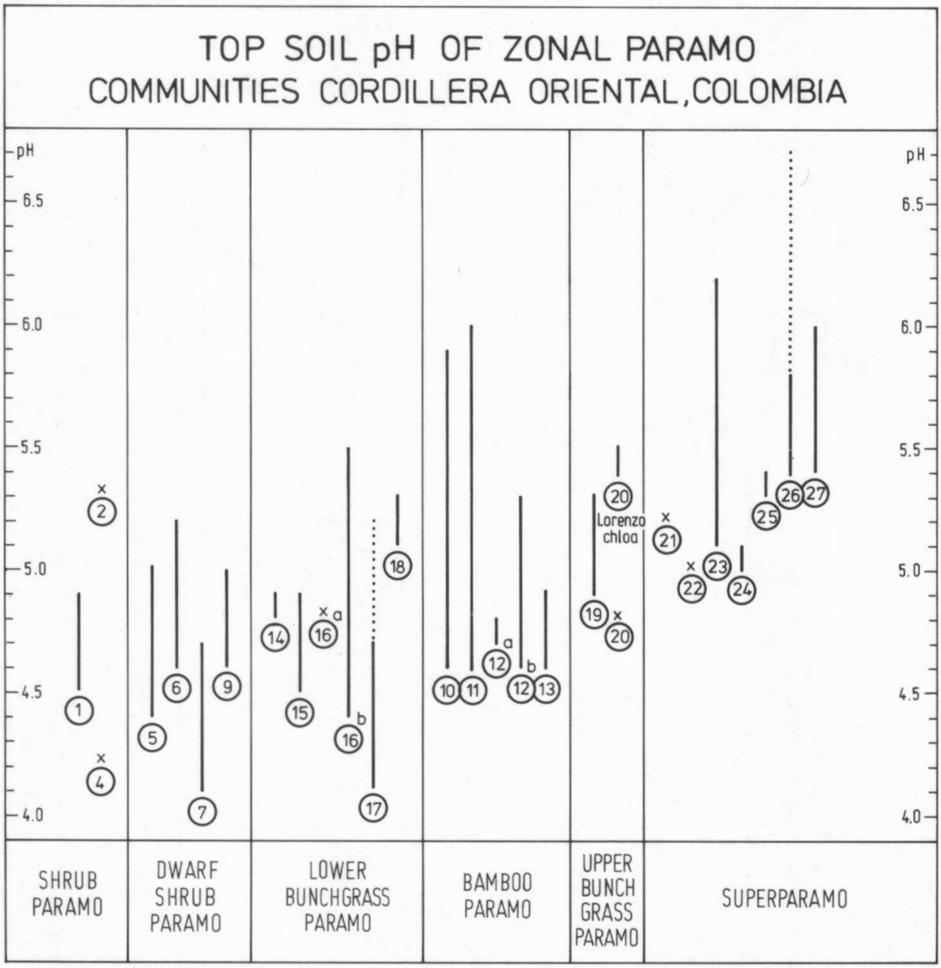
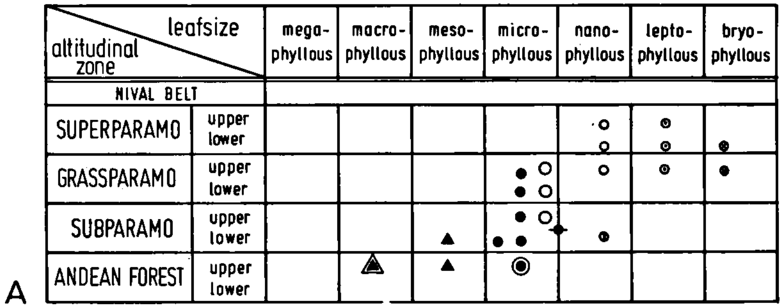


Fig. 85.

Top soil pH of the zonal communities of the páramo vegetation in the Colombian Cordillera Oriental. The community numbers refer to those used in the present study.



A

Zonal bamboo (black symbols)
and other grass species (open symbols)
Dominant species are underlined.

bamboo species:

- *Neurolepis aperta*
- *Neurolepis aristata*
- *Chusquea scandens*
- *Swallenochloa tesselata* and *Swallenochloa weberbaueri*
- *Aulonemia trianae*

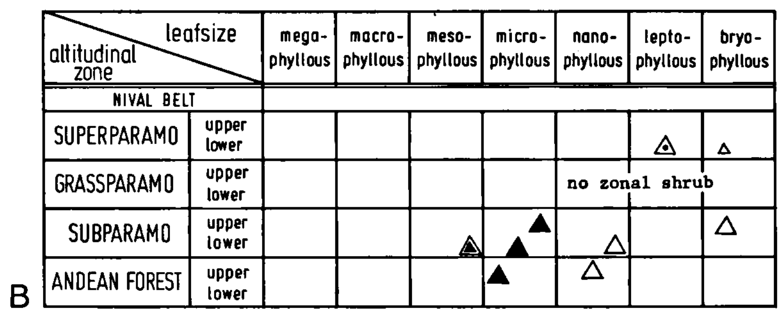
other grass species

revolutely leaved bunches: mainly

- *Calamagrostis effusa* (and *Festuca* cf. *dolichophylla*).

blades ± flat, strongly sheathing tufts:

- *Agrostis boyacensis* and *Agrostis haenkeana*
- *Agrostis brevicaulmis*
- *Sporobolus lasiophyllus*
- *Aciachne pulvinata* (bryophyllously leaved cushions)



B

Zonal shrub & dwarfshrub in
humid (black symbols) and
dry (open symbols) climates

- Predominant species of wet side of the mountains
- *Eupatorium (=Ageratina) tinifolium*
- Predominant species of dry side of the mountains
- *Loricaria complanata* (wet and dry side)
- *Pernettya prostrata* var. *prostrata*

Fig. 86.

Leaf-size characters of predominant graminoid (A) and woody species (B) of the zonal pâramo vegetation of the Cordillera Oriental, Colombia. Leaf-size classes are according to Raunkiaer (1916), except for the bryophyllous class, which is according to Barkman (1979). Herbaceous dicot species were not considered. The grass pâramo contains no zonal shrub except in (azonal) pockets. In the superpâramo there is no pronounced difference in woody species between wet and dry mountain sides. The climatic differences in this zone are more apparent in herbaceous species.

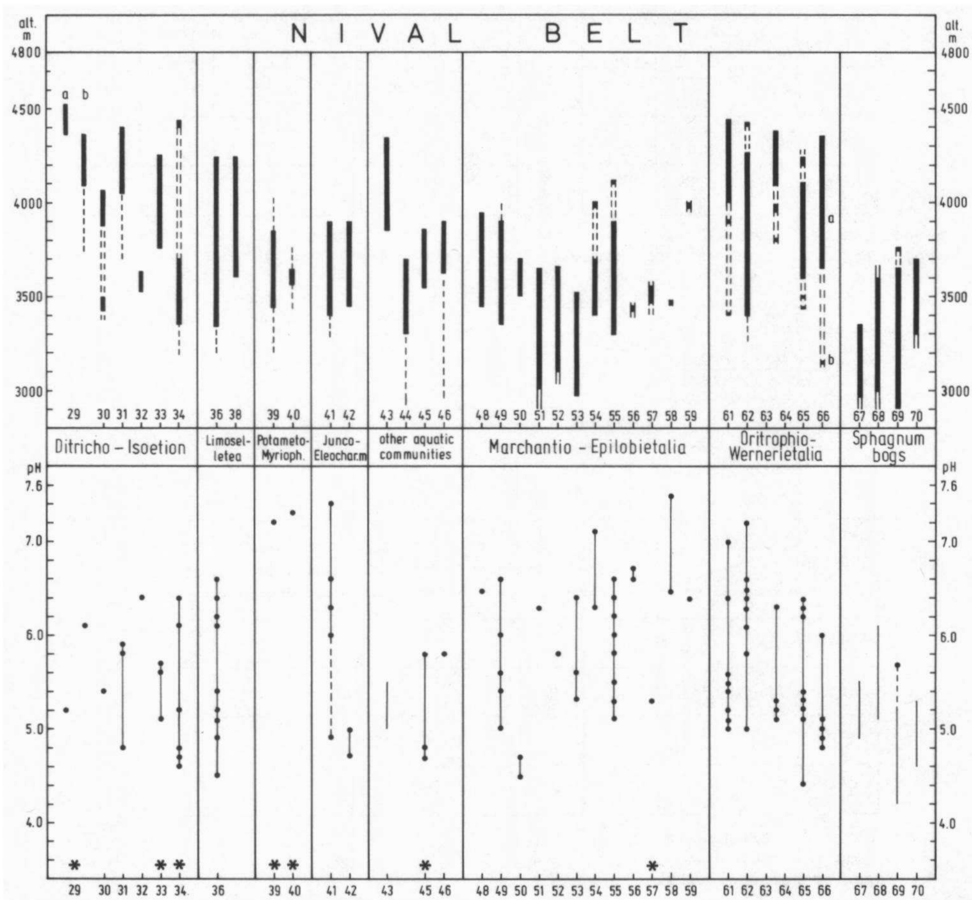


Fig. 87.

Altitudinal distribution and pH range (top soil/water *) of aquatic communities, reedswamp, mire and flush vegetation, cushionbog and *Sphagnum* bog in the páramos of the study area.

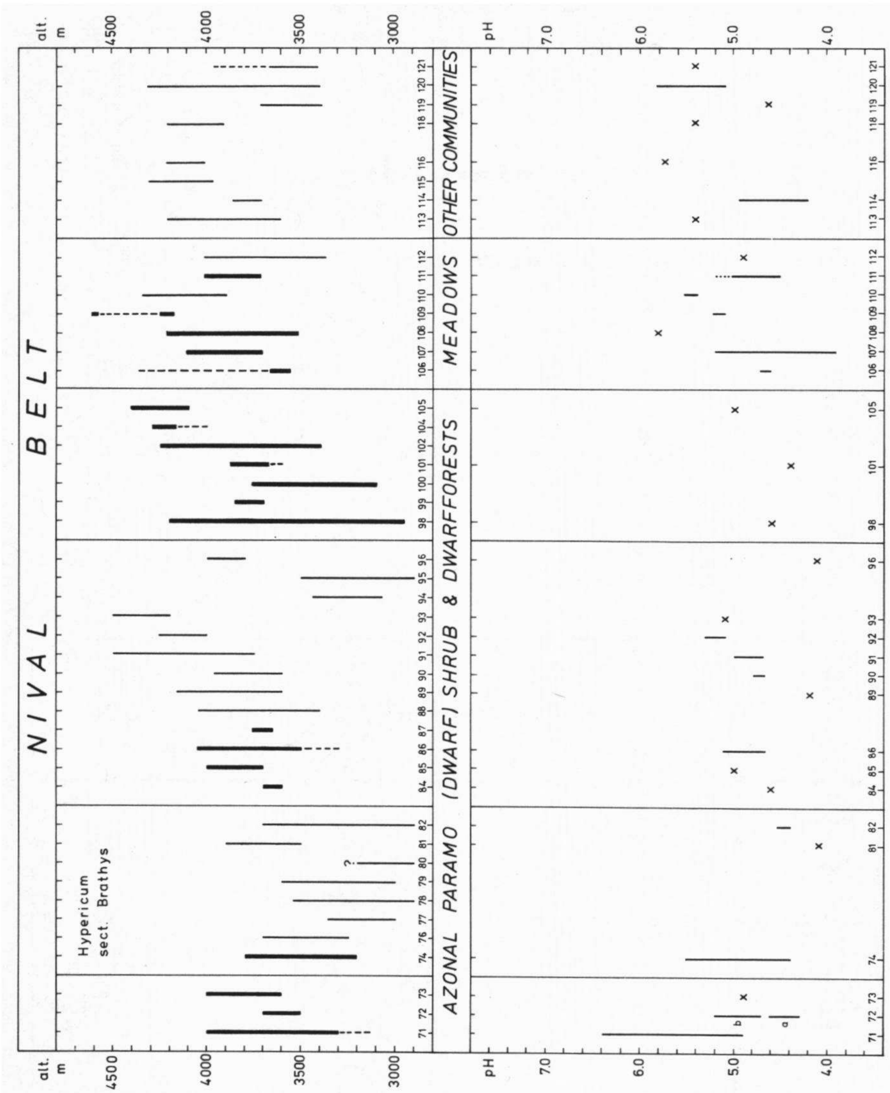


Fig. 88.

Altitudinal distribution and pH range of the topsoil in azonal păramo dwarfforests, meadows and other azonal communities of the study area.

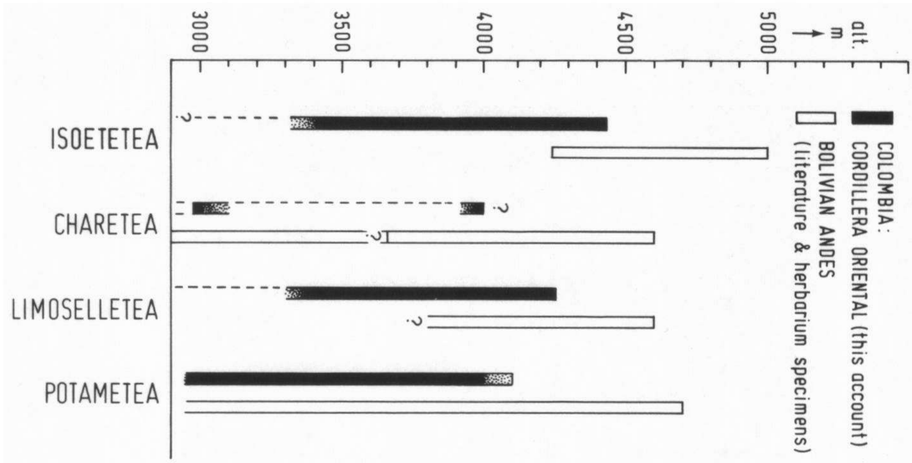


Fig. 89.

Altitudinal distribution of *Isoetetea*, *Charetea*, *Limoselletea* and *Potametea* in the Colombian Cordillera Oriental and in the Bolivian Andes.

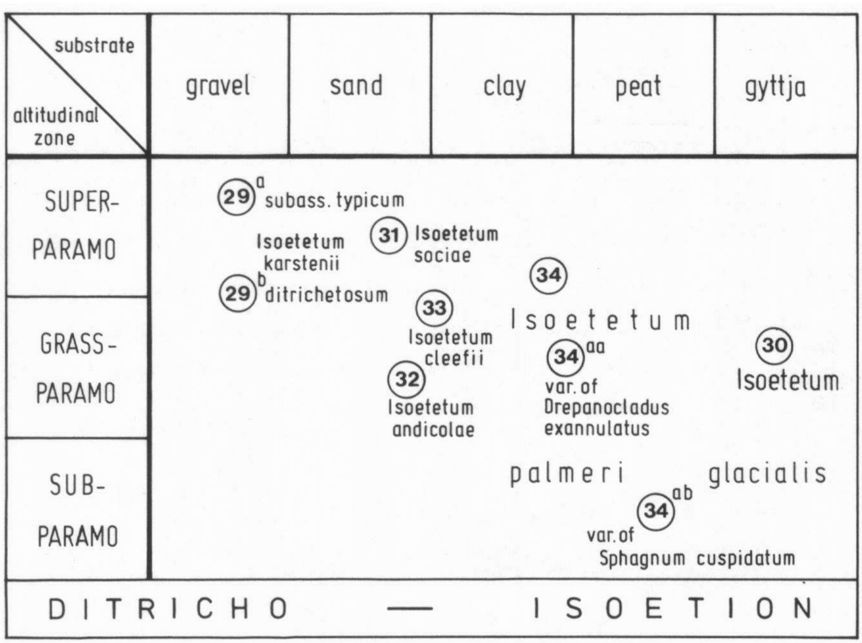


Fig. 90.

Distribution of syntaxa of the *Ditricho-Isoetion* in the study area in relation to altitude and substrate.

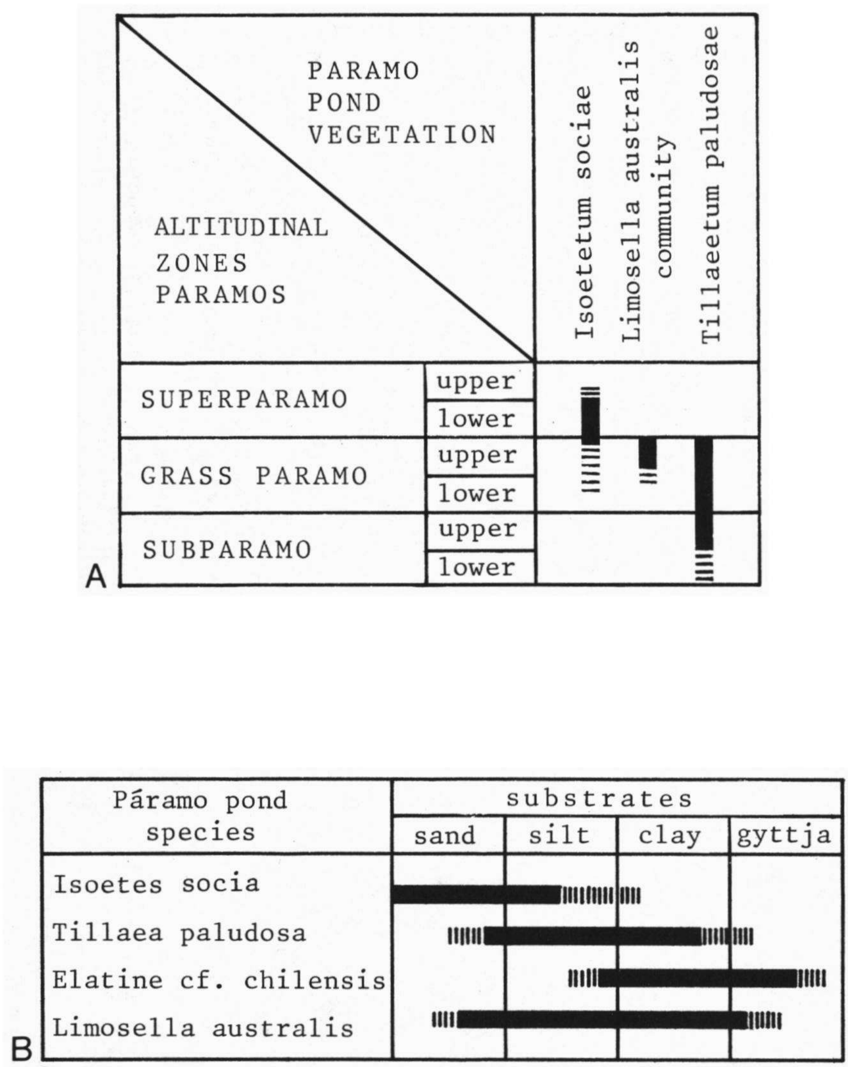


Fig. 91.

A. Altitudinal distribution of the *Isoetetum sociae* (31), the *Limosella australis* community (38) and the *Tillaeetum paludosae* (36) in the páramos of the Colombian Cordillera Oriental.

B. Distribution in relation to substrate of various amphibious vascular species in the páramos of the study area.

APPENDIX 2 +)

ALPHABETIC LIST OF THE REFERRED TROPICAL ANDEAN TAXA WITH THEIR AUTHORITIES

Acaena (Rosaceae)
- *A. cylindristachya* Ruíz Lopez et Pavõn
- *A. elongata* L.

Acaulimalva (Malvaceae)
- *A. purdiei* (A. Gray) Krapov.

Achyrocline (Compositae)
- *A. lehmannii* Hieron.

Aciachne (Gramineae)
- *A. pulvinata* Benth.

Acnistus (Solanaceae)
- *A. quitoensis* (Hook.) Hunz.

Ageratina fide *Eupatorium*

Agrostis (Gramineae)
- *A. boyacensis* Swallen
- *A. breviculmis* Hitchc.
- *A. foliata* Hook. f.
- *A. haenkeana* Hitchc.
- *A. trichodes* Roemer et Schultes

Altensteinia (Orchidaceae)
- *A. fimbriata* H.B.K.
- *A. leucantha* Reichb. f.
- *A. paludosa* Reichb. f.

Aphanactis (Compositae)
- *A. ligulata* Cuatrec.
- *A. piloselloides* Cuatrec.

Aragoa (Scrophulariaceae)
- *A. abietina* H.B.K.
- *A. cupressina* H.B.K.
- *A. dugandii* Romero
- *A. lycopodioides* Benth.
- *A. perez-arbelaeziana* Romero

Arcytophyllum (Rubiaceae)
- *A. caracasanum* (H.B.K.) Standley
- *A. muticum* (Wedd.) Standley
- *A. nitidum* (H.B.K.) Schldl.

Arenaria (Caryophyllaceae)
- *A. serpyllifolia* L.
- *A. venezuelana* Briq.

Asplenium (Polypodiaceae)
- *A. castaneum* Cham. et Schldl.
- *A. triphyllum* Presl

Aulonemia (Gramineae)
- *A. trianae* (Munro) McClure

Azolla (Azollaceae)
- *A. filiculoides* Lam.

Azorella (Umbelliferae)
- *A. crenata* (Ruíz Lopez et Pavõn) Pers.
- *A. cuatrecasasii* Mathias et Constance
- *A. multifida* (Ruíz Lopez et Pavõn) Pers.
- *A. pedunculata* (Sprengel) Mathias et Constance

Baccharis (Compositae)
- *B. caespitosa* (Ruíz Lopez et Pavõn) Pers.
  - var. *alpina* (H.B.K.) Cuatrec.
- *B. macrantha* H.B.K.
  - ssp. *denticulata* Cuatrec. (ssp. ined.)
- *B. prunifolia* H.B.K.
- *B. revoluta* H.B.K.
- *B. rupicola* H.B.K.
  - var. *orientalis* Cuatrec.
- *B. tricuneata* (L. f.) Pers.

+) Names marked "ined." are as yet not validly published.
They are not accepted by me for purposes of valid publication.

Befaria (Ericaceae)
  B. tachirensis Steyerm.
Berberis (Berberidaceae)
  B. cretata Camargo
  B. goudotii Triana et Planchon
  B. sumapazana Camargo
Bidens (Compositae)
  B. triplinervia H.B.K.
Blechnum (Blechnaceae)
  B. (Lomaria) loxense (H.B.K.) Hieron.
Brachyotum (Melastomataceae)
  B. strigosum Triana
Brachypodium (Gramineae)
  B. mexicanum Link
Bromus (Gramineae)
  B. lanatus H.B.K.
  B. unioloides H.B.K.
Bucquetia (Melastomataceae)
  B. glutinosa Gleason
Buddleia (Loganiaceae)
  B. lindenii Benth.
Bulbostylis (Cyperaceae)
  B. tropicales (Clarke) Britton

Calamagrostis (Gramineae)
  C. bogotensis (Pilger) Pilger
  C. boyacensis Swallen et Garc.-Barr.
  C. coarctata (H.B.K.) Steudel
  C. effusa (H.B.K.) Steudel
  C. ligulata (H.B.K.) Hitchc.
  C. planifolia (H.B.K.) Trin.
  C. recta (H.B.K.) Trin.
Calandrinia (Portulacaceae)
  C. acaulis H.B.K.
Calceolaria (Scrophulariaceae)
  C. mexicana Benth.
  C. penlandii Pennell

Callitriche (Callitrichaceae)
  C. nubigena Fassett
Cardamine (Cruciferae)
  C. africana L.
  C. bonariensis Juss. ex Pers.
    (= *C. flaccida* Cham. et Schldl.)
Carex (Cyperaceae)
  C. acutata Boott
  C. bonplandii Kunth
  C. conferto-spicata Boeckeler
  C. fecunda Steudel
  C. grandiflora (nom.herb., US)
  C. jamesonii Boott
  C. peucophila Holm
  C. pichinchensis H.B.K.
  C. pygmaea Boeckeler
  C. tristicha Spruce ex Boott
Castilleja (Scrophulariaceae)
  C. fissifolia L. f.
  C. integrifolia L. f.
Castratella (Melastomataceae)
  C. piloselloides (Bonpl.) Naudin
  C. rosea Gleason
Centropogon (Lobeliaceae)
  C. ferrugineus (L. f.) Gleason
Cerastium (Caryophyllaceae)
  C. imbricatum H.B.K.
  C. subspicatum Wedd.
Cestrum (Solanaceae)
  C. parvifolium Willd.
Chaetolepis (Melastomataceae)
  C. microphylla (Bonpl.) Miq.
Chusquea (Gramineae)
  C. scandens Kunth
Cinna (Gramineae)
  C. poaeformis (H.B.K.) Scribner et Merr.

Clethra (Clethraceae)
C. fimbriata H.B.K.
Colobanthus (Caryophyllaceae)
C. quitensis (Bartl.) H.B.K.
Conyza (Compositae)
C. uliginosa (Benth.) Cuatrec.
Coriaria (Coriariaceae)
C. ruscifolia L. ssp. *microphylla* (Poir.) L.Skog
Cortaderia (Gramineae)
C. nitida (H.B.K.) Pilger
C. sericantha (Steudel) Hitchc.
Cotula (Compositae)
C. minuta (L. f.) Sweet
Crassula (Crassulaceae)
C. bonariensis Cambess.
Cyperus (Cyperaceae)
C. rivularis var. *lagunetto* (Steudel) O'Neill
Cystopteris (Polypodiaceae)
C. fragilis (L.) Bernh.

Danthonia (Gramineae)
D. secundiflora Presl
Diplostephium (Compositae)
D. alveolatum Cuatrec.
D. colombianum (Cuatrec.) Cuatrec.
D. eriophorum Wedd.
D. glutinosum Blake
D. glutinosum var. *cocuyanum* Cuatrec.
D. heterophyllum Cuatrec.
D. huertasii Cuatrec.
D. juajibioyi Cuatrec.
D. lacunosum Cuatrec.
D. phylicoides (H.B.K.) Wedd.
D. revolutum Blake
D. rhomboidale Cuatrec.
D. ritterbushii Cuatrec.
D. rupestre (H.B.K.) Wedd.
D. schultzii Wedd.

Disterigma (Ericaceae)
D. empetrifolium (H.B.K.) Drude
Distichia (Juncaceae)
D. muscoides Nees et Meyen
(= *D. tolimensis* Benth. et Hook.)
Draba (Cruciferae)
D. hammenii Cuatrec. et Cleef
D. lindenii (Hook.) Planchon
D. litamo Uribe
D. pamplonensis Planchon et Linden
Drymaria (Caryophyllaceae)
D. villosa Cham. et Schldl.
ssp. *paramorum* (Blake) Duke
Dryopteris (Polypodiaceae)
D. paleacea Christ.
Dysopsis (Euphorbiaceae)
D. glechomoides Muell. Arg.

Elaphoglossum (Polypodiaceae)
E. engelii (Karsten) Christ.
E. lindenii (Bory ex Fée) Moore
Elatine (Elatinaceae)
E. chilensis Gay
Eleocharis (Cyperaceae)
E. acicularis (L.) Roemer et Schultes
E. macrostachya Britton
E. stenocarpa Svenson
Elodea (Hydrocharitaceae)
E. potamogeton Espin.
Epidendrum (Orchidaceae)
E. chioneum Lindley
E. erosum Ames et Schweinf.
Epilobium (Onagraceae)
E. denticulatum Ruíz Lopez et Pavón
E. meridense Hausskn.

Erigeron (Compositae)
E. chionophilus Wedd.
E. ecuadoriensis Hieron.
E. paramensis Aristeg. et Cuatrec.
Eriocaulon (Eriocaulaceae)
E. microcephalum H.B.K.
Eriosorus (Hemionitidaceae)
E. hirsutulus (Mett.) A. Tryon
Eryngium (Umbelliferae)
E. humboldtii F. Delaroche
E. humile Cav.
Escallonia (Escalloniaceae)
E. myrtilloides L. f.
var. *myrtilloides*
Espeletia (Compositae)
E. annemariana Cuatrec.
E. annemariana var. *rupicola* Cuatrec.
E. arbelaezii Cuatrec.
E. argentea Humb. et Bonpl.
E. azucarina Cuatrec.
E. barclayana Cuatrec.
E. boyacensis Cuatrec.
E. brachyaxiantha Díaz Piedr.
E. chocontana Cuatrec.
E. cleefii Cuatrec.
E. congestiflora Cuatrec.
E. conglomerata A.C. Smith
E. curialensis Cuatrec.
E. discoidea Cuatrec.
E. grandiflora Humb. et Bonpl.
ssp. *grandiflora*
E. grandiflora ssp. *boyacensis* Cuatrec.
E. incana Cuatrec.
E. jaramilloi Díaz Piedr.
E. killipii Cuatrec.
var. *killipii*
E. killipii var. *chisacana* Cuatrec.
E. lopezii Cuatrec.
E. lopezii var. *major* Cuatrec.
E. miradorensis Cuatrec.
E. murilloi Cuatrec.
E. nemenkenei Cuatrec.
E. oswaldiana Díaz Piedr.
E. rositae Cuatrec.
E. summapacis Cuatrec.
E. tapirophila Cuatrec.
Espeletiopsis (Compositae)
E. colombiana (Cuatrec.) Cuatrec.
E. corymbosa (Humb. et Bonpl.) Cuatrec.
E. garciae (Cuatrec.) Cuatrec.
E. guacharaca (Díaz Piedr.) Cuatrec.
E. jimenez-quesadae (Cuatrec.) Cuatrec.
E. muiska (Cuatrec.) Cuatrec.
E. pleiochasia (Cuatrec.) Cuatrec.
var. *socotana* Cuatrec.
Eupatorium (Compositae)
E. fastigiatum H.B.K.
E. glyptophlebium Robinson
E. gracile H.B.K.
E. gynoxoides Wedd.
E. theaefolium Benth.
Equisetum (Equisetaceae)
E. bogotense H.B.K.

Festuca (Gramineae)
F. breviaristata Pilger
F. dolichophylla Presl
Floscaldasia (Compositae)
F. hypsophila Cuatrec.

Gaiadendron (Loranthaceae)
G. punctatum (Ruíz Lopez et Pavón) G. Don
Galium (Rubiaceae)
G. canescens H.B.K.
G. trianae Wernham

Gaultheria (Ericaceae)
G. anastomosus (Mutis ex L. f.) H.B.K.
G. ramosissima Benth.
G. rigida H.B.K.
Gaylussacia (Ericaceae)
G. buxifolia H.B.K.
Gentiana (Gentianaceae)
G. sedifolia H.B.K.
Gentianella (Gentianaceae)
G. corymbosa (H.B.K.) Weaver et Rüdenb.
G. dasyantha (Gilg) Weaver et Rüdenb.
G. nevadensis (Gilg) Weaver et Rüdenb.
Geonoma (Palmae)
G. weberbaueri Dammer ex Burret
Geranium (Geraniaceae)
G. confertum Standley
G. multiceps Turcz.
G. sibbaldioides Benth.
var. *elongatum* R. Knuth
G. subnudicaule Turcz.
Gnaphalium (Compositae)
G. antennarioides DC.
G. meridanum Aristeg.
G. spicatum Lam.
Grammitis (Ctenopteris) (Polypodiaceae)
G. flabelliformis (Poir.) J. Smith
G. meridense (Kl.) Morton
G. moniliformis (Lag. & Sw.) J. Smith
G. variabilis (Mett.) Morton
Gratiola (Scrophulariaceae)
G. bogotensis Cortés
G. peruviana L.
Greigia (Bromeliaceae)
G. mulfordii L.B. Smith
Gynoxys (Compositae)
G. albivestita Cuatrec.
G. paramuna Cuatrec.
G. pendula Schultz-Bip. ex Wedd.
G. subcinera Cuatrec.
G. subhirsuta Cuatrec.
G. tolimensis Cuatrec.
G. trianae Hieron.

Halenia (Gentianaceae)
H. gigantea Allen
Hesperomeles (Rosaceae)
H. goudotiana Killip
H. lanuginosa Ruíz Lopez et Pavõn
Hieracium (Compositae)
H. avilae Zahn
Hinterhubera (Compositae)
H. columbica Schultz-Bip. ex Wedd.
Hydrocotyle (Umbelliferae)
H. bonplandii Richter
H. gunnerifolia Wedd.
H. hederacea Mathias
H. ranunculoides L. f.
Hymenophyllum (Hymenophyllaceae)
H. karstenianum Sturm
Hypericum (Hypericaceae)
H. caracasanum Willd.
ssp. *cardonae* (Cuatrec.) N. Robson
H. cuatrecasasii Gleason
H. garciae Pierce
H. goyanesii Cuatrec.
H. graciliforme N. Robson (ined.)
H. humboldtianum Steudel
H. juniperinum H.B.K.
H. jussiaei Planchon et Linden
(= *H. humboldtianum* Steudel)
H. lancifolium Gleason
H. laricifolium Juss.
ssp. *laricifolium*
H. laricifolium ssp. *laricoides* (Gleason)N.Robson(ined.)
H. lycopodioides Triana et Planchon
H. magniflorum Cuatrec.

H. mexicanum L. f.
H. papillosum N. Robson (ined.)
H. phellos Gleason
H. pimeloides Planchon et Linden ex Triana et Planchon
H. prostratum Gleason
H. sabiniforme Trev.
H. selaginoides N. Robson (ined.)
H. strictum Kunth
H. tetrastichum Cuatrec.
H. thuyoides Kunth
H. trianae N. Robson (ined.)
Hypochoeris (Compositae)
H. sessiliflora H.B.K.
Hypsela (Campanulaceae)
H. reniformis Presl

Ilex (Aquifoliaceae)
I. kunthiana Triana et Planchon
Isoetes (Isoetaceae)
I. andicola (Amstütz) H.P. Fuchs
I. andina Hook. ex Spruce
(= *I. triquetra* A. Braun)
I. bischlerae H.P. Fuchs (ined.)
I. boyacensis H.P. Fuchs (ined.)
I. cleefii H.P. Fuchs
I. glacialis Aspl.
I. karstenii A. Braun
I. killipii C. Morton
I. novo-granadensis H.P. Fuchs
I. palmeri H.P. Fuchs
I. socia A. Braun

Jaegeria (Compositae)
J. hirta (Lag.) Less.
Jamesonia (Polypodiaceae)
J. bogotensis Karsten
J. goudotii C. Chr.

Juncus (Juncaceae)
J. cyperoides Laharpe
J. echinocephalus Balslev
J. ecuadoriensis Balslev
J. microcephalus H.B.K.
J. stipulatus Nees et Meyen

Lachemilla (Rosaceae)
L. diplophylla (Diels) Rothm.
L. fulvescens (Perry) Rothm.
L. hispidula (Perry) Rothm.
L. holosericea (Perry) Rothm.
L. mandoniana (Wedd.) Rothm.
L. nivalis (H.B.K.) Rothm.
L. pinnata (Ruíz Lòpez et Pavón) Rothm.
L. polylepis (Wedd.) Rothm.
L. orbiculata (Ruíz Lopez et Pavón) Rydb.
L. tanacetifolia Rothm.
L. venusta Rydb.
Laestadia (Compositae)
L. muscicola Wedd.
Lemna (Lemnaceae)
L. minor L.
Lepidium (Cruciferae)
L. bipinnatifolium Desv.
Lilaea (Liliaceae)
L. subulata H.B.K.
Lilaeopsis (Umbelliferae)
L. schaffneriana (Schldl.) Coulter et Rose
Limosella (Scrophulariaceae)
L. australis R. Br.
L. lineata Glück
Lobelia (Lobeliaceae)
L. tenera H.B.K.
Lorenzochloa (Gramineae)
L. erectifolia (Swallen) J. et C. Reeder
Loricaria (Compositae)
L. complanata (Schultz-Bip.) Wedd.

Lourteigia (Compositae; Eupatorioideae)
L. microphyllum (L. f.) R. King et H. Robinson
Lucilia (Compositae)
L. pusilla (H.B.K.) Hieron.
Ludwigia (Onagraceae)
L. peruviana L.
var. *peruviana*
Lupinus (Papilionaceae)
L. alopecuroides Desr.
L. humifusus Benth.
L. verjonensis C.P. Smith
Luzula (Juncaceae)
L. gigantea Desv.
L. racemosa Desv.
L. vulcanica Liebm.
Lycopodium (Lycopodiaceae)
L. contiguum Kl.
L. crassum Humb. et Bonpl. ex Willd.
L. cruentum Spring
L. rufescens Hook.
L. spurium Willd.
L. thyoides H.B. Willd.
(= *L. complanatum* L. var. *tropicum* Spring)
Lysipomia (Campanulaceae)
L. muscoides Hook. f.
ssp. *simulans* McVaugh
L. sphagnophila Griseb. ex Wedd.
ssp. *minor* McVaugh
L. sphagnophila ssp. *minor*
var. *cocuyanus* Cleef (ined.)

Macleania (Ericaceae)
M. rupestris A.C. Smith
Masdevallia (Orchidaceae)
M. coriacea Lindley
Miconia (Melastomataceae)
M. andina Naudin
M. chionophila Naudin
M. cleefii Uribe
M. ligustrina Triana
M. mesmeana Gleason
var. *jabonensis* Wurdack
M. parvifolia Cogn.

M. salicifolia (Bonpl.) Naudin
Mimulus (Scrophulariaceae)
M. glabratus H.B.K.
Monnina (Polygalaceae)
M. salicifolia Ruíz Lopez et Pavón
Montia (Portulacaceae)
M. fontana L.
M. meridensis Friedrich
Moritzia (Boraginaceae)
M. lindenii (A. DC.) Benth. ex Gürke
Muehlenbeckia (Polygonaceae)
M. thamnifolia (H.B.K.) Meissner
M. vulcanica Endl.
Muehlenbergia (Gramineae)
M. fastigiata (Presl) Henrard
M. ligularis (Hackel) Hitchc.
M. linearis (nom. herb. ?)
Myrica (Myricaceae)
M. parvifolia Benth.
Myriophyllum (Haloragaceae)
M. brasiliense Cambess.
M. elatinoides Gaudich.
Myrrhidendron (Umbelliferae)
M. glaucescens (Benth.) Coulter et Rose
Myrteola (Myrtaceae)
M. oxycoccoides (Benth.) Berg

Nephopteris (Polypodiaceae)
N. maxonii Lellinger
Nertera (Rubiaceae)
N. granadensis (Mutis ex L. f.) Druce

Neurolepis (Gramineae)
N. aristata (Munro) Hitchc.
Niphogeton (Umbelliferae)
N. dissecta (Benth.) J.F. Macbr.
N. fruticosa Mathias et Constance
N. glaucescens (Kunth) J.F. Macbr.
N. josei Mathias et Constance
N. lingula (Wedd.) Mathias et Constance
N. ternata (Willd. ex Roemer et Schultes) Mathias et Constance var. *ternata*
Noticastrum (Compositae)
N. marginatum (H.B.K.) Cuatrec.

Odontoglossum (Orchidaceae)
O. lindenii Lindley
Ophioglossum (Ophioglossaceae)
O. crotalophoroides Walt.
Oreobolus (Cyperaceae)
O. obtusangulus Gaudich.
ssp. *rubro-vaginatus* (Kük.)T.Koyama
Oreomyrrhis (Umbelliferae)
O. andicola (Kunth) Hook. f.
Oreopanax (Araliaceae)
O. mutisianum (H.B.K.) Decne. et Planchon
Oritrophium (Compositae)
O. cocuyense (Cuatrec.) Cuatrec.
O. limnophilum (Schultz-Bip.) Cuatrec.
ssp. *mutisianum* (Cuatrec.) Cuatrec.
O. limnophilum ssp. *nevadanum* Cuatrec.
O. limnophilum ssp. *punae* Cuatrec.
O. peruvianum (Lam.) Cuatrec.
O. vahlii (Gaudich.) Cuatrec.
Orthrosanthus (Iridaceae)
O. chimboracensis (H.B.K.) Baker
var. *chimboracensis*
Ottoa (Piperaceae)
O. oenanthioides H.B.K.

Ourisia (Scrophulariaceae)
O. muscosa Benth.
Oxalis (Oxalidaceae)
O. cornuta L.
O. medicaginea H.B.K.
Oxylobus (Compositae)
O. glanduliferus (Schultz-Bip.) A. Gray

Paepalanthus (Eriocaulaceae)
P. alpinus Koern.
P. andicola Koern.
var. *villosus* Moldenke
P. columbiensis Ruhl.
P. crassicaulis Koern.
P. karstenii Ruhl.
P. lodiculoides Moldenke
var. *floccosus* Moldenke
P. paramensis Moldenke
P. pilosus (H.B.K.) Kunth
Parietaria (Urticaceae)
P. debilis Forster
Paspalum (Gramineae)
P. bonplandianum Fluegge
Peperomia (Piperaceae)
P. hartwegiana Miq.
P. hispidula (Sw.) A. Dietr.
P. microphylla H.B.K.
Pernettya (Ericaceae)
P. hirta (Willd.) Sleumer
P. prostrata (Cav.) DC.
var. *prostrata*
P. prostrata var. *purpurea* (Don) Sleumer
Phyllactis (Valerianaceae)
P. rigida Pers.
Pilularia (Marsileaceae)
P. mandoni A. Braun
Pinguicula (Lentibulariaceae)
P. elongata Benj.

Plagiocheilus (Compositae)
  P. *solivaeformis* DC.
    ssp. *multiflorus* Cuatrec.
Plantago (Plantaginaceae)
  P. *australis* Lam.
    ssp. *oreades* (Decne.) Rahn
  P. *rigida* H.B.K.
  P. *sericea* H.B.K.
    ssp. *argyrophylla* (Decne.) Rahn
  P. *tubulosa* Decne.
Poa (Gramineae)
  P. *pauciflora* Roemer et Schultes
Polylepis (Rosaceae)
  P. *quadrijuga* Bitter
Polypodium (Polypodiaceae)
  P. *angustifolium* Sw.
Polystichum (Polypodiaceae)
  P. *polyphyllum* (Presl) Presl
Potamogeton (Haloragaceae)
  P. *asplundii* Horn af Rantzien (ined.)
  P. *berteroanus* Phil.
  P. *drepanocladoides* Horn af Rantzien (ined.)
  P. *illinoensis* Morong
  P. *strictus* Phil.
Potentilla (Rosaceae)
  P. *heterosepala* Fritsch
Pterichis (Orchidaceae)
  P. *galeata* Lindley
Pteridium (Pteridiaceae)
  P. *aquilinum* (L.) Kuhn
Purpurella (Melastomataceae)
  P. *grossa* (L. f.) Cogn.
Puya (Bromeliaceae)
  P. *aristiguietae* Lyman B. Smith
  P. *bicolor* Mez
  P. *goudotiana* Mez
  P. *hamata* Lyman B. Smith
  P. *santosii* Cuatrec.
  P. *trianae* Baker

Ranunculus (Ranunculaceae)
  R. *flagelliformis* J.E. Smith
  R. *limoselloides* Turcz.
  R. *mandonianus* Wedd.
  R. *nubigenus* H.B.K. ex DC.
  R. *peruvianus* Pers.
  R. *spaniophyllus* Lourt.
Rapanea (Myrsinaceae)
  R. *dependens* (Ruíz Lopez et Pavón) Mez
Relbunium (Rubiaceae)
  R. *hypocarpium* (L.) Hemsley
Rhizocephalum (Campanulaceae)
  R. *candollei* Wedd.
Rhynchospora (Cyperaceae)
  R. *macrochaeta* Steudel
  R. *paramorum* Mora
  R. *ruiziana* (Boeckeler) Macbr.
Ribes (Saxifragaceae)
  R. *columbianum* Cuatrec.
Rubus (Rosaceae)
  R. *eriocarpus* Liebm.
Rumex (Polygonaceae)
  R. *acetosella* L.
  R. *tolimensis* Wedd.

Salvia (Labiatae)
  S. *killipiana* Epling
Satureja (Labiatae)
  S. *nubigena* (Kunth) Briq.
Scirpus (Cyperaceae)
  S. *californicus* Britton
  S. *inundatus* Sprengel
Senecio (Compositae)
  S. *adglacialis* Cuatrec.
  S. *andicola* Turcz.
  S. *cacaosensis* Cuatrec.
  S. *canescens* (Humb. et Bonpl.) Cuatrec.
  S. *canescens* var. *boyacensis* Cuatrec.
  S. *cleefii* Cuatrec.

S. cocuyanus (Cuatrec.) Cuatrec.
S. flos-fragans Cuatrec.
S. flos-fragans fma. *frigidophilus* Cuatrec.
S. formosus Wedd.
S. gelidus Wedd.
S. guadalupe Cuatrec.
S. guantivanus Cuatrec.
S. guicanensis Cuatrec.
S. latiflorus Cuatrec.
S. ledifolius (H.B.K.) DC.
S. nitidus (H.B.K.) DC.
S. niveo-aureus Cuatrec.
S. pascui-andinus Cuatrec.
S. pulchellus (H.B.K.) DC.
S. pungens (H.B.K.) DC.
fma. *pulchellus* Cuatrec.
S. ramentosus Cuatrec.
S. reissianus Hieron.
S. repens DC.
S. santanderensis Cuatrec.
S. subruncinnatus Greenman
S. summus Cuatrec.
S. supremus Cuatrec.
S. vaccinioides (H.B.K.) Schultz-Bip.
S. vernicosus Schultz-Bip. ex Wedd.
Sericotheca (Rosaceae)
S. argentea (Mutis) Raf.
Sibthorpia (Scrophulariaceae)
S. repens (Mutis ex L.) Kuntze
Sigesbeckia (Compositae)
S. orientalis L.
Siphocampylus (Campanulaceae)
S. columnae (L. f.) G. Don
Sisyrinchium (Iridaceae)
S. pusillum H.B.K.
S. tinctorum H.B.K.
S. trinerve Baker
Solanum (Solanaceae)
S. bogotense Dunal

Spiranthes (Orchidaceae)
S. coccinea Garray
S. vaginata (H.B.K.) Lindley ex B.D. Jacson
Sporobolus (Gramineae)
S. lasiophyllus Pilger
Stachys (Labiatae)
S. elliptica Benth.
Stellaria (Campanulaceae)
S. cuspidata Willd.
Stevia (Compositae)
S. lucida Lag.
var. *oaxana* (DC.) Grashoff
Swallenochloa (Gramineae)
S. tesselata (Munro) McClure
Symplocos (Simplocaceae)
S. theiformis (L. f.) Oken

Ternstroemia (Theaceae)
T. meridionalis Mutis
Tillaea (Crassulaceae)
T. paludosa Schldl.
Tofieldia (Liliaceae)
T. sessiliflora Hook.
(= *T. falcata* Pers.)

Ugni (Myrtaceae)
U. myricoides Berg
Urtica (Urticaceae)
U. ballotaefolia Wedd.
Utricularia (Lentibulariaceae)
U. obtusa Sw.

Vaccinium (Ericaceae)
V. floribundum H.B.K.
var. *marginatum* (Dunal) Sleumer
V. floribundum var. *ramosissimum* (Dunal) Sleumer
Valeriana (Valerianaceae)
V. arborea Killip et Cuatrec.
V. longifolia H.B.K.

V. pavonii Poeppig
V. plantaginea H.B.K.
V. stenophylla Killip
V. triphylla H.B.K.
(= *V. mutisiana* (Wedd.) Hoeck)
V. vetasana Killip
Vallea (Elaeocarpaceae)
V. stipularis Mutis ex L. f.
Verbesinea (Compositae)
V. baccharidea Blake
Veronica (Scrophulariaceae)
V. serpyllifolia L.
Vesicarex (Cyperaceae)
V. collumanthus Steyerm.
Vicia (Papilionaceae)
V. andicola H.B.K.
Viola (Violaceae)
V. humilis H.B.K.

Weinmannia (Cunoniaceae)
W. fagaroides H.B.K.
W. rollotii Killip
Werneria (Compositae)
W. crassa Blake
ssp. *orientalis* Cuatrec.
W. humilis H.B.K.
var. *angustifolia* Cuatrec. (var. ined.)
W. pygmaea Gillies

Xyris (Xyridaceae)
X. acutifolia (Heimerl) Malme
X. subulata Ruíz Lopez et Pavón

LOCALITY AND HABITAT DATA RELEVÈS

rel.nr.*)	date	Depto.	locality	alt.m	exp.	botan.coll.nr.*)
1	Dec.16 /71	Cund.	Pal.: Buitrago	3580	NW	274-286
1a	Dec.11 /71	"	Sum. : Chisacá	3700		153
1b	Dec.11 /71	"	" : "	3750		174
1c	Dec.14 /71	"	" : "	3400		220
5	Jan.22 /72	Meta	" : Lag. la Guitarra	3425	NNE	829-849
6a	Jan.22 /72	"	" : " " "	3450		874
8	Jan.24 /72	"	" : " " "	3420	S	916-944
9	Jan.24 /72	"	" : " " "	3465	S	945-956
10	Jan.24 /72	"	" : " " "	3465		957-959
11	Jan.24 /72	"	" : " " "	3465		
13	Jan.26 /72	"	" : Q. los Sitiales	3550	WSW	1041-1072
13a	Jan.26 /72	"	" : " " "	3500		1032-1033
17	Jan.29 /72	"	" : Nevado	3635	N	1211-1233
17a	Jan.28 /72	"	" : "	3635		1228
24	Febr.10 /72	Cund.	" : Andabobos	3715	NW	1557-1572/1577, 1578
27	Febr.12 /72	"	" : "	3800	S	1654-1678, 1686
31	Febr.24 /72	Boy	Belén: Alto de las Cruces	3845	SW	1776-1782
39	Febr.28 /72	"	" : Q. Minas	3780	SE	2027-2035
41	Febr.29 /72	"	" : " "	3850		2058-2060
51	March 7 /72	"	Gua : Belén, Alto de Cruces	3765	NE	2259-2271, 2273
55	March 23 /72	Cund.	Chisacá	3685	SW	2574-2585
59	April 12 /72	"	C.V. : La Viga	3480	S	2841-2871
63	April 22 /72	"	" :	3350		2993-3002
65	April 22 /72	"	" : " "	3355	NW	3032-3056
67	April 26 /72	"	"	3460		3152-3153
80	May 11 /72	"	Chisacá	3700		3605-3623
81	May 11 /72	"	"	3660	SW	3635-3637
95	May 25 /72	"	Pal.: Buitrago	3575	S	4084-4095
97	May 25 /72	"	" "	3580		4112-4117
99	May 26 /72	"	Neusa: La Guargua	3605		4129-4152
100	May 26 /72	"	"	3620	NW	4156-4172
101	June 8 /72	Boy	Pisva: El Cadillal	3480	SE	4218-4233
102	June 8 /72	"	" : " "	3500	SE	4234-4247
105	June 9 /72	"	" : " "	3535		4278-4282
106	June 9 /72	"	" " "	3535	S	4285-4289
109	June 11 /72	"	" : Calarcá	3580	NE	4390-4394
110	June 11 /72	"	" : "	3580	SE	4401-4406
111	June 11 /72	"	" : "	3580	SE	4409-4416

*) A.M.Cleef et al

116	June 14/72	Boy.	Pisva: Calarcá	3620	E	4493-4515
127	July 6 /72	Cund.	Sum.: Alto de las Sopas	3845	WSW	4818-4823
134	July 12 /72	"	Chisacá	3630	E	4939-4946
137	Aug.17 /72	"	Pal.: Q. Piedras Gordas	3400	SSE	5152-5162
138	Aug.22 /72	"	Chisacá	3660		5183-5196
139	Aug.22 /72	"	"	3680	S	5197-5214
142	Aug.25 /72	"	" : Valle Sta. Rosa	3625		5259-5272
143[a]	Aug.25 /72	"	" : " " "	3625		5286, 5217
144	Aug.25 /72	"	" : " " "	3620	SSE	5287-5299
145	Aug.25 /72	"	" : " " "	3650		5301-5303
147	Aug.30 /72	"	Pal.: Lag. Seca	3730	SW	5332-5338
148	Aug.30 /72	"	" : Chingaza	3730		5341
149	Sep.1 /72	"	" : Chuza	3700	NNW	5373-5396
152	Sep.19 /72	"	" : Chingaza	3740	WSW	5468-5472
153	Sep.19 /72	"	" : Lag. Seca	3640		5354-5360
154	Sep.19 /72	"	" : " "	3640	NE	5477-5491
156	Sep.25 /72	Boy.	Coc.: Lag. la Pintada	3985	W	5524-5526
157	Sep.25 /72	"	" : Lagunillas la Pintada	3890	W	5528-5532
159	Sep.26 /72	"	" : Alto Valle Lagunilla	4065	SW	5575-5576
160	Sep.26 /72	"	" : Lag. Cuadrada	4060	S	5578-5585
161	Sep.26 /72	"	" : " "	4060		5587-5589
161[a]	Sep.26 /72	"	" : " "	4060		5590
162	Sep.27 /72	"	" : Valle Lagunillas	3960	WNW	5596-5609
168	Sep.30 /72	"	" : " "	4390		5703-5704
169	Oct.2 /72	"	" : " "	4005	W	5723-5733
171	Oct.3 /72	"	" : Lag. Pintada	3980	NW	5778-5789
172	Oct.4 /72	"	" :	4310		5792-5796
179	Oct.5 /72	"	" : Valle Bocatoma	4280		5862-5867
180	Oct.5 /72	"	" : " "	4280	W	5868-5881
183	Oct.5 /72	"	" : " "	4205	W	5901-5911
184	Oct.7 /72	"	" : Valle Lagunillas	3915		5925-5934
185	Oct.7 /72	"	" : " "	3920		5939-5944
186	Oct.7 /72	"	" : " "	3925	N	5949-5950
187	Nov.9 /72	Cund.	Neusa: Lag. Seca	3640	SE	6100-6106
189	Nov.9 /72	"	" : " "	3685	NE	6122-6140
190	Nov.9 /72	"	" : " "	3700		6141-6142
190[a]	Nov.9 /72	"	" : " "	3700		
193	Nov.10 /72	"	" : Lag. Verde	3685		6177-6180
194	Nov.10 /72	"	" : " "	3690		6182
195	Nov.10 /72	"	" : " "	3695		6188-6190
197	Nov.11 /72	"	" : " "	3655		6201-6218

197a	Nov.12 /72	Cund.	Neusa: Lag. Verde	3650		
200	Nov.11 /72	"	" : " "	3700		6252-6256
200a	Aug.19 /72	"	" : " " Cogua	3625		
204	Nov.12 /72	"	" : " "	3695		6300-6301
206	Nov.13 /72	"	" : " "	3670	WNW	6314-6320
207	Nov.13 /72	"	" : " "	3675	SSW	6323-6329
207a	Nov.13 /72	"	" : " "	3675	SSW	6322
213	Nov.15 /72	"	" : " "	3680	S	6394-6419
219	Nov.17 /72	"	" : " Seca	3660	SE	6527-6540
223	Dec.6 /72	Boy.	Rusia: Aislada	3565		6740-6744
234	Dec.9 /72	"	" : "	3505		6875-6886
235	Dec.9 /72	"	" : "	3515		6887-6890
236	Dec.9 /72	"	" : La Aislada	3520	SE	6891-6906
239	Dec.10 /72	"	" : Lag. Agua Clara	3935	NNW	6988-7017
240	Dec.10 /72	"	" : " Negra	3845		6980
247	Dec.14 /72	"	" : " "	3725	ENE	7203-7219
248	Dec.14 /72	"	" : " "	3745		
253	Dec.15 /72	"	" : " "	3745	NW	7289-7301
253a	Dec.15 /72	"	" : " "	3745	NW	7308
254	Dec.16 /72	"	" : Pẽna Blanca	3720	S	7309-7327
255	Dec.16 /72	"	" : " "	3730	S	7331-7346
257	Dec.16 /72	"	" : " "	3775	WSW	7362-7365
257a	Dec.16 /72	"	" : " "	3775	WSW	
257b	Dec.16 /72	"	" : " "	3775	WSW	
261	Dec.18 /72	"	" : Lag. Negra/Pẽna Blanca	3820	NW	7467-7481
262	Dec.19 /72	"	" : Pẽna Negra	3800	SW	7485-7502
262a	Dec.19 /72	"	" : " "	3800	SW	
263	Dec.19 /72	"	" : " "	3810	W	7505-7516
263a	Jan.7 /73	Cund.	Sum. : Los Charcos	3925		7532
264	Jan.9 /73	Meta	" : Lag. Primavera	3510		7555-7562
264a	Jan.9 /73	"	" : " "	3510		
264b	Jan.9 /73	"	" : " "	3510		
265	Jan.9 /73	"	" : " "	3515		7564-7569
265d	Jan.9 /73	"	" : " "	3500		
266	Jan.9 /73	"	" : " "	3535		7572
267	Jan.9 /73	"	" : " "	3535		7573-7580
267a	Jan.9 /73	"	" : " "	3535		
270	Jan.13 /73	"	" : Nevado	4015	SW	7734-7761
271	Jan.13 /73	"	" : "	4090		7766-7767
274	Jan.16 /73	"	" : "	4130	NE	7922-7935

275	Jan.16 /73	Meta	Sum.	: Nevado	4100	NE	7945-7958
276	Jan.16 /73	"	"	: "	4100		7968-7983
277	Jan.17 /73	"	"	: " La Culebra	3460		7991-7995
278	Jan.17 /73	"	"	: " " "	3470		8003-8007
279	Jan.17 /73	"	"	: " " "	3485		8008-8009
281	Jan.18 /73	"	"	:	4050	NNW	8034-8953
282	Jan.18 /73	"	"	: "	4055	W	8055-8061
286	Jan.19 /73	"	"	: Boquerón Grande	4120	N	8104-8116
289	Jan.20 /73	"	"	: "	4170		8177-8178
291	Jan.21 /73			: Barranca del Palacio	3715	NNE	8196-8219
292	Jan.23 /73	"	"	: Lag. La Guitarra	3390		8256-8263
292[a]	Jan.22 /73	"	"	: " del Medio, Sitiales	3620		
293	Jan.23 /73	"	"	: " La Guitarra	3415	NNE	8264-8265
294	Jan.23 /73	"	"	: " " "	3425	N	8266-8271
295	Jan.24 /73	"	"	: " " "	3395	NNE	8277-8284
296	Jan.24 /73	"	"	: " " "	3405	ENE	8285-8290
297	Jan.24 /73	"	"	: " " "	3410		8291-8293
298	Jan.24 /73	"	"	: " " "	3425	N	8296-8297
300	Jan.24 /73	"	"	: " " "	3425		8299-8300
300[a]	Jan.24 /73	"	"	: " " "	3425		
300[b]	Jan.24 /73	"	"	: " " "	3425		
300[c]	Jan.24 /73	"	"	: " " "	3425		
301	Jan.26 /73	"	"	: Lag. Gobernador	3815		8308-8309
304	Jan.26 /73	"	"	: " "	3845	N	8345-8347
305	Jan.27 /73	"	"	: Alto de Chorreras	3780	NW	8350-8384
309	Jan.28 /73	"	"	: " Mirador	3560	NNW	8416-8420
314	Febr.26 /73	Boy.	Coc.	: Cóncavo	4315	SSW	8519-8523
316	Febr.26 /73	"	"	: "	4335	W	8552-8553
317	Febr.26 /73	"	"	: "	4335	WSW	8555-8558
319	Febr.27 /73	"	"	: "	4385	W	8576-8580
320	Febr.27 /73	"	"	: "	4390	W	8581
321	Febr.27 /73	"	"	: "	4410	W	8582-8594
322	Febr.27 /73	"	"	: "	4415		8596-8598
323	Febr.27 /73	"	"	: "	4410		8599
326	Febr.28 /73	"	"	: "	4430		8644-8646
327	Febr.28 /73	"	"	: "	4435		8647-8650
328	March 1 /73	"	"	: "	4045	WNW	8663-8664
330[a]	March 1 /73	"	"	: "	4250		
331[a]	March 1 /73	"	"	: "	4325	W	
332	March 3 /73	"	"	: Valle Bocatoma	4100	W	8730-8747
333	March 3 /73	"	"	: " "	4100	W	8749-8754

334	March 3 /73	Boy.	Coc.: Valle Bocatoma	4120	W	8756-8760
335	March 3 /73	"	" : " "	4125	NW	8762-8764
335[a]	March 3 /73	"	" : " "	4110		8765-8769
336	March 4 /73	"	" : Lagunillas	3955	W	8770
338	March 5 /73	"	" : Boquerón de Cusirí	4310		8785-8786
346	March 7 /73	Ar.	" : Patio Bolos	4260	SW	8873-8876
348	March 8 /73	"	" : " "	4190		8912-8926
348[a]	March 8 /73	"	" : " "	4190		
355	March 10 /73	"	" : " "	4285	W	9018-9030
358	March 11 /73	"	" : " "	4245		9088-9092
358[a]	March 11 /73	"	" : " "	4245		
380	April 5 /73	Boy.	Tota : Plan de la Sarna	3377		
381	April 5 /73	"	" : " " " "	3390		9399-9404
382	April 5 /73	"	" : " " " "	3405	S	9406-9412
383	April 6 /73	"	Vado Honda: Pẽna Arnical	3605	ENE	9440-9452
387	April 8 /73	"	Tota : Plan de Soriano	3300		9503-9509
389	April 8 /73	"	" : " " "	3330		9522
393	April 9 /73	"	" : Vado Honda	3015	S	9538-9541
400	April 37 /73	Cund.	Pal. : Buitrago	3550		9576-9585
404	May 3 /73	Boy.	Gua. : Alto de las Cruces	3710		9697
405	May 3 /73	"	" : " " " "	3725		9698-9699
407	May 4 /73	"	" : Q. Minas	3910	NNW	9713-9725
407[a]	May 4 /73	"	" : Belén, Alto de las Cruces	3880	E	
409	May 5 /73	"	Guina: Sta. Rosita	3290		9760-9766
410	May 6 /73	"	Belen: Boquerón	3805	E	9771-9773
412[a]	May 7 /73	"	Gua: Pan de Azucar	4220	NNE	
415	May 22 /73	"	Pisva: Alto de Granados	3610	W	9893-9894
415[a]	May 22 /73	"	" : Granados	3610	W	
416	May 22 /73	"	" : Lág. Colorado	3425		9897-9898
416[a]	May 22 /73	"	" : " "	3425		
423[b]	June 7 /73	"	Coc.: Guicán, el Claval	2800		
424[i]	June 11 /73	"	" : Lagunillas, Cuadrada	4065		
424[f]	June 10 /73	Ar.	" : El Playón	3150	NE	10134-10137
442	March 19 /77	Boy.	" : La Capilla	3510		Coll. R. Jaramillo-M. et al.
445	March 20 /77	"	" : Cóncavo	4305		
447	March 20 /77	"	" : "	4425		10356
448	March 20 /77	"	" : "	4425		
449	March 20 /77	"	" : "	4425		
450	March 20 /77	"	" : "	4425		
451	March 20 /77	"	" : "	4335	W	10355

452	March 21 /77	Boy.	Coc.:	Côncavo	3735		
454	March 21 /77	"	" :	"	4315		
456	March 21 /77	"	" :	"	4400		
457	March 21 /77	"	" :	"	4380		
460	March 21 /77	"	" :	"	4380	W	10361, 10362
461	March 21 /77	"	" :	"	4350		10363
461a	March 21 /77	"	" :	"	4350		
462	March 21 /77	"	" :	"	4350		10363
463	March 21 /77	"	" :	"	4355	NW	
464	March 21 /77	"	" :	"	4355	NW	
465	March 21 /77	"	" :	"	4350	W	
466	March 22 /77	Ar.	" :	Patio Bolos	4250	S	
466a	March 22 /77	"	" :	" "	4250		
467	March 22 /77	"	" :	" "	4160		
468	March 22 /77	"	" :	" "	4200	NW	10375-10378
473	March 22 /77	"	" :	" "	4250	NW	
474	March 22 /77	"	" :	" "	4275	N	10368
475	March 22 /77	"	" :	Vado Q. Calichal	4280		
476	March 23 /77	Boy.	" :	Lagunillas, Pintada	3915	E	
477	March 23 /77	Ar.	" :	Lag. El Amarillal	4065		10382-10384
477c	March 23 /77	"	" :	Q. Antiguas	4070		
482	March 25 /77	"	" :	Q. Los Osos	3500		
483	March 26 /77	Boy.	" :	Lagunillas Pintada	3875		
484	March 26 /77	"	" :	" "	3875		
486	March 26 /77	"	" :	" Q. Lagunillas	3890		
487	March 26 /77	"	" :	" " "	3875		
488	March 26 /77	"	" :	" " "	3875		
490	March 26 /77	"	" :	Lagunillas	3870	SW	
491	March 26 /77	"	" :	"	3870	SW	
493	March 26 /77	"	" :	"	3865		10385
494	March 26 /77	"	" :	"	3870		
495	March 26 /77	"	" :	"	3870		10386-10388
495a	March 26 /77	"	" :	"	3870		
496	March 26 /77	"	" :	"	3870		
498	March 26 /77	"	" :	"	3870		
500	April 2 /77	Cund.	Sum.:	Chisacá, Lag. Larga	3640		
501	April 2 /77	"	" :	" " "	3640		10396
502	April 2 /77	"	" :	La Rabona	4000	E	10393-10395; 10403-10404
503a	April 2 /77	"	" :	" "	3985		10390

504	April 2 /77	Cund.	Sum.: La Rabona	4000	W	10392
505	April 2 /77	"	" : Andabobos	3720		
506	April 2 /77	"	" : "	3720		10398-10399
507	April 2 /77	"	" : "	3710		
513	April 3 /77	"	Neusa: Lag. Seca	3610		Coll. S. Díaz-P.
514	April 3 /77	"	" : " "	3620		
515	April 3 /77	"	" : " "	3550		
553	Nov.19 /79	Sant.	:	3425		Coll. J. Aguirre-C. et al.
554	Nov.19 /79	"	" : El Tutal	4100		
560a	Nov.20 /79	"	" : " "	3800		
560b	Nov.20 /79	"	" : " "	3800		
561	Nov.20 /79	"	" : " "	3815		
562	Nov.20 /79	"	" : " "	3815		
563	Nov.20 /79	"	" : " "	3815		
564	Nov.20 /79	"	" : " "	3825	SSW	
566	Nov.20 /79	"	" : " "	3850	E	
567	Nov.20 /79	"	" : " "	3885	S	
568	Nov.20 /79	"	" : " "	3890	NW	
571	Nov.20 /79	"	" : " "	3890	SW	
572	Nov.20 /79	"	" : " "	3900		
575	Nov.21 /79	"	" : " "	3825		
576	Nov.21 /79	"	" : " "	3740		
577	Jan.15 /80	Ris.	Lag. Otún	3985		
607	Jan.24 /80	"	Volcano Otún: La Sierra	3680		
618	Febr.8 /80	"	Lag. Otún	3920		
624	Febr.9 /80	Tol.	Sta. Isabel: Q. Africa	3800		
638	Febr.12 /80	"	" " : Q. Totarito	3320		

Conventions:

Ar.	Arauca	Sum	Páramo de Sumapaz
Boy.	Boyacá	CV	Páramo de Cruz Verde
Cund.	Cundinamarca	Pal	Páramo de Palacio
Meta	Meta	Chuza	Río Chuza drainage basin
Ris.	Risaralda	Neusa	Páramos NW of Neusa
Sant.	Santander	Tota	Páramos near the Laguna de Tota
Tol.	Tolima	Arn.	Pena de Arnical, NE of Tota
Lag.	Lagunà (Lake)	Rusia	Páramo de la Rusia
Q.	Quebrada (Stream)	Gua	Páramo de Guantiva, southern part
		Pisva	Páramo de Pisva
		Coc	Sierra Nevada del Cocuy
		Alm	Páramo del Almorzadero

ABSTRACT

A phytosociological survey based on methods of the Zürich-Montpellier School was carried out in the páramo vegetation of the Cordillera Oriental, Colombia. The study area covers about 10,000 km^2 and comprises the páramo between the Nevado de Sumapaz (3°55'N, 4250 m), the Sierra Nevada del Cocuy (6°25'N, 5493 m) and the Páramo del Almorzadero (7°N, 4375 m). The páramo vegetation was studied along various altitudinal transects from the upper forest line (3000-3500 m) up to the lower limit of the snowcap (4800 m).

A general description of the study area includes data on geology, geomorphology, soils, climate, flora, phytogeography, morphological characters of the vegetation, fauna and landuse. The evolution and Quaternary history of páramo vegetation and climate is reviewed, incorporating the first data from the Lateglacial and Holocene of the Páramo de Sumapaz.

The general altitudinal zonation of the páramo vegetation was studied and is presented for both the dry and the humid side of the Cordillera. The zonal and azonal plant communities are described including their physiognomy, composition and syntaxonomy, habitat and distribution. Eighty five syntaxa from the rank of variant to that of the class are newly described, 17 of which are provisional. The vegetation is not ranked syntaxonomically yet, but described on the basis of preliminary tables. A number of azonal communities, part of them of lesser extent, are described in a similar way.

The páramo vegetation is primarily determined by the tropical diurnal high mountain climate. The diversity of the páramo vegetation is related to temperature (altitudinal gradient) and to humidity (dry and wet climate). The presence of zonal bunchgrass páramo, bamboo-bunchgrass páramo or bamboo páramo mainly depends on the complex interrelation between these factors. Finally a synthesis is provided on ecology, morphology and phytogeography of the páramo vegetation of the study area.

RESUMEN

Un estudio fitosociológico, basado en los métodos de la escuela Zürich-Montpellier, se llevó a cabo en la vegetación de los páramos de la Cordillera Oriental de Colombia. El area de investigación cubre aproximadamente 10.000 km^2 y comprende los páramos entre el Nevado de Sumapaz (3°55 N, 4250 m), la Sierra Nevada del Cocuy (6°25 N, 5493 m) y el Páramo del Almorzadero (7°N, 4375 m). La vegetación del páramo fue estudiada a lo largo de transectes altitudinales desdo al límite superior del bosque andine (3000-3500 m) hasta el límite inferior de la capa de nieve (4800 m).

La descripción general del area de investigacíon contiene datos sobre geología, geomorfología, suelos, clima, flora, fitogeografía, caracteres morfológicos de la vegetatión, fauna y sistemas de explotación del medio-ambiente La evolución y la historia de la vegetación y el clima del páramo, durente el Cuaternario, han sido resumidos incorporando los primeros datos del Tardiglacial y el Holoceno del Páramo de Sumapaz.

Se describe la zonación altitudinal de la vegetación del páramo para las vertientes húmedas y secas de la Cordillera. Las comunidades vegetales zonales y azonales han sido descritas incluyendo su fisionomía, composición florística y sintaxonomía, habitat y distribución. Ochenta y cinco sintaxa son descritos oficialmente por primera vez y su rango varia entre clase y variante ; diez y siete de ellos tienen un rango provisional. La vegetación zonal no está clasificado sintaxonómicamente, sino que está descrita en base a tablas preliminares. Gran parte de las comunidades vegetales han sido descritas en una forma similar.

La vegetación del páramo es determinada principalmente por el clima tropical de alta montaña con cambios de temperatura diarios extremos. La diversidad en la vegetación del páramo está relacionada a la temperatura (gradiente altitudinal) y la húmidad (clima seco y húmedo). La presencia de páramos zonales con pajonales, con chuscales o con una combinación de los dos, depende de la compleja interrelación de dichos factores. Además se presenta una síntesis de la ecología, morfología y fitogeografía de la vegetación del páramo de la Cordillera Oriental de Colombia.

SAMENVATTING

In deze studie wordt de vegetatie van de páramos van de Oost Cordillera van de Colombiaanse Andes beschreven. Páramos zijn de hoog gelegen open vegetaties in de vochtige tropische Andes. Het onderzochte gebied is ca. 10.000 km^2 groot en omvat de páramos tussen de Nevado de Sumapaz (3°55' NB, 4250 m), de Sierra Nevada del Cocuy (5493 m) en de Páramo del Almorzadero (7° NB, 4375 m). De páramo vegetatie werd bestudeerd volgens de Zürich-Montpellier methode in een aantal transecten van de Andiene bosgrens (3000-3500 m) tot de sneeuw (4800 m).

De inleiding omvat ondermeer algemene gegevens betreffende geologie, geomorfologie, bodems, klimaat, flora, plantengeografie, structuur en textuur van de vegetatie, fauna en land use, alsmede betreffende de evolutie en de geschiedenis van flora, vegetatie en klimaat gedurende het Kwartair. Aan de hand van de eerste pollendiagrammen van de Páramo de Sumapaz wordt een overzicht gegeven van de Laatglaciale en Holocene vegetatie- en klimaatsgeschiedenis van dit gebied.

De altitudinale zonering van de páramo vegetatie is beschreven voor de droge én voor de natte zijde van de Oost Cordillera. De zonale en azonale plantengezelschappen van de páramos zijn vervolgens beschreven met inbegrip van hun fysiognomie, floristische samenstelling en syntaxonomie, standplaats en verbreiding. 85 plantengezelschappen zijn officieel als nieuw beschreven en omvatten syntaxa van het niveau van variant tot en met dat van klasse. Hiervan hebben er 17 een voorlopige status. De zonale gezelschappen zijn grotendeels nog niet officieel beschreven, maar hun indeling berust wel op voorlopige tabellen van deze vegetaties. Er zijn een groot aantal azonale plantengezelschappen; een deel hiervan is slechts van een páramo bekend.

Páramo vegetaties worden in het algemeen bepaald door het tropische hooggebergte klimaat met de dagelijks terugkerende grote temperatuur fluctuaties. De diversiteit van de páramo vegetatie wordt bepaald door temperatuur (hoogte gradiënt) en vochtigheid (droog en nat klimaat). De aanwezigheid van horstgras-páramo, bamboe-horstgras-páramo of bamboe-páramo kan worden afgeleid van de complexe relatie tussen deze beide factoren. Tenslotte wordt een synthese gegeven van de oecologie, morfologie en plantengeografie van de páramo vegetaties van de Colombiaanse Oost Cordillera.

ERRATA

A.M. Cleef (1981): The vegetation of the pâramos of the Colombian Cordillera Oriental. Diss.Bot. 61. J. Cramer. Vaduz.

P. 21	line 18 from below: delete "proved";
P. 23	line 5: for "Holarctic" read "Holartic genera".
	line 12 and 13 from below: for "Chaetophora pisiformis" read "Chaetophora pisiformis (Roth) C.A. Agardh"
P. 24	line 4 from below: read " - wide temperate element comprises taxa, ..."
P. 26	line 18 from below: for "Cleef 1979b" read "Cleef 1979a"
P. 28	line 20 from below: for "pâramo in" read "pâramo life forms in.."
P. 30	line 4: read "flowering species of Bartsia pollinated by hummingbirds"
P. 38	line 9: for "Vareschi 1989" read "Vareschi 1980"
	line 19: for "rare" read "rale"
	line 21 from below: for "1" read "<1"
P. 49	line 8: delete "locally with loamy matrix"
P. 50	line 28: for "slopes" read "slopes contain"
P. 51	line 15 from below: for "Cleef 1979a" read "Cleef 1979b"
P. 58	line 17 from below: for "(9131) covering" read "(9131) and Frullaria sp. (9143) covering..."
P. 66	line 3: for "(also Fig. 70)" read "(also Fig. 75)"
	line 15: for "(see 3.1)" read "(see 15)"
	line 17: for "(see 4.1)" read "(see 14)"
P. 75	line 17 from below: for "species" read "species are"
P. 77	line 9: for "Corralitos of" read "Corralitos stade of"
	line 20: for "with many" read "of"
P. 83	line 23: delete "the"
P. 84	line 12 from below: for "near-short" read "near-shore"
P. 85	line 23 from below: for "main" read "maintain"
P. 89	line 21 from below: for "Fig. 34" read "Fig. 51"
P. 94	line 23: for "on" read "along"
P. 95	line 19 from below: for "or as" read "or arrive as"
	line 23: for "up" read "substrates up"
P. 100	line 24 from below: delete "are"
P. 101	line 5: for "lakes" read."lakes and from 4.6 - 5.2"
P. 106	line 25 from below: for "contain" read "certain"
P. 113	line 7 from below: for "by structure" read "by more structure"
P. 129	line 16 from below: for "endism" read "endemism"
P. 135	line 14 from below: for "This communty is" read "These communities are"
P. 147	line 7: for "Different" read "Differential"
P. 149	line 5: for "(Fig. 86)" read "(Fig. 6, 87)"
P. 159	line 12: for "Sphagnum" read "Sphagnum/ "
	line 20: for "Central" read "Central) "
P. 164	line 10: for "Schnetter 1967" read "Schnetter 1976"
P. 176	line 15: for "1954" read "1958"
P. 188	line 4 from below: for "fastigiata" read "fastigiata- "
P. 190	line 3: for "75" read "77"
P. 191	line 13: for "400" read "4000"
P. 201	line 16 from below: for "the temperature" read "the temperature fall"
P. 208	line 14: for "lakes....syntaxa" read "lakes (Fig. 87). The .."
P. 212	line 11 from below: delete "Aragia"
P. 213	line 16 from below: for "weberbaueri" read "weberbaueri are $\pm$ entire-leaved here".

ADDITIONAL REFERENCES

Carrera, E., J. Pichott & E.B. Alexander (1968): Estudio general de clasificacíon de los suelos de la cuenca alta del Río Bogotá para fines agrícoles. - Inst. Geogr. "Agustín Codazzi", Bogotá.

I.G.A.C. (1965): Suelos de Ubaté-Chiquinquirá. - Inst. Geogr. "Agustín Codazzi", Depto. de Agrología 1(1). Bogotá.

Smith, A.P. (1975a): Response of plants of an Andean páramo species to an artificial wet season. - Bull. Torrey Bot. Club 102(1): 28-30.

Smith, A.P. (1975b): Insect pollination and heliotropism in Oritrophium limnophilum (Compositae) of the Andean páramo. - Biotropica 7(4): 284-286.

Van der Hammen, T., J. Barelds, H. de Jong & A.A. de Veer (1981): Glacial sequence and environmental history in the Sierra Nevada del Cocuy (Colombia). - Palaeogeogr., Palaeochim., Palaeoecol. 32: 247-340.

A list of the infrequent species of table 11, 13, 14 and 24 is available on request.