STUDIES ON COLOMBIAN CRYPTOGAMS

IIA. HEPATICAE – OIL BODY STRUCTURE AND ECOLOGICAL DISTRIBUTION OF SELECTED SPECIES OF TROPICAL ANDEAN JUNGERMANNIALES

BY

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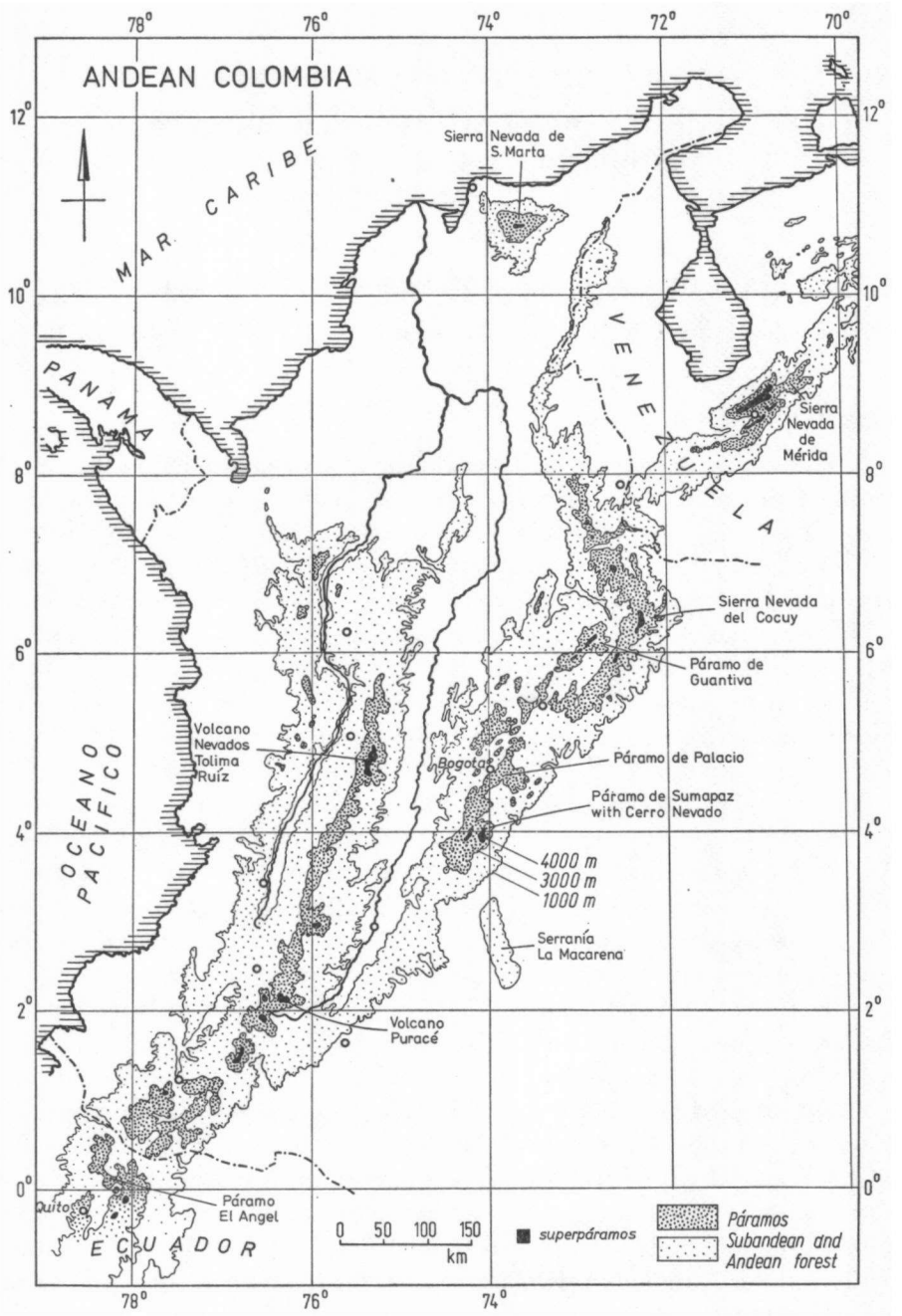
INTRODUCTION

This paper is the second (Florschütz & Florschütz-de Waard 1974) in the series of reports on cryptogams of Colombia, especially the high Andean bryophytes and lichens, in the framework of recent phytosociological and ecological studies in the area by A. M. Cleef and T. van der Hammen (Amsterdam) and his collaborators. The aim of these studies is to prepare comprehensive descriptions of the various Andean biota of Colombia as a basis for an evaluation of the biological diversity of the Andean environment of Colombia. This paper deals with the Hepaticae or liverworts and focuses on the structure of the oil bodies in the liverwort cell and the geographical and ecological distribution of the species.

There are few papers on tropical Andean liverworts. The classical work by Spruce (1884–85) included liverworts of the Ecuadorian and Peruvian Andes. A large number of Andean taxa are treated in Fulford's Manual of the leafy liverworts of Latin America (Fulford 1963, 1966, 1968, 1976) and the latter has been our main source of data on distribution of species. Some ecological notes on tropical Andean taxa are found in the works of Herzog (1934, 1955), Robinson (1967) and Winkler (1976), who for the first time presented a synthesis of liverwort species distribution in relation to Andean vegetation typology in a limited area in Northern Colombia.

The data presented here, especially those on species distribution, are based on identification of over 1500 collections from Colombia. The bulk of this material is from the páramos, where it was gathered by Cleef and his co-workers in 1971–73, in the area shown in map 1. In addition, we have seen several hundreds of specimens from Colombian cloud forests, collected by T. van der Hammen & R. Jaramillo in 1967, 1974 and 1975 and some collections gathered by P. A. Florschütz in 1975 and R. A. J. Grabandt & J. M. Idrobo in 1974, mainly from the Department of Cundinamarca. Material for the study of oil bodies was sent fresh by air mail to Utrecht for microscopic observation in the laboratory. Since these observations yielded many new data, additional investigations, for comparison, were



Map 1. Andean Colombia, showing the distribution of the Subandean and Andean forests and the Páramos.

made with fresh material from other neotropical areas, e.g. from the Ecuadorian Andes and the Galapagos Islands (collected by S. R. Gradstein et al. 1976), from Costa Rica (collected by A. M. Cleef & L. A. Fournier 1973), and from Brazil (collected by D. M. Vital since 1971). Some of these data have also been included in this paper.

The identification of the material was a tedious task for which we received help from several specialists: Dr. R. Grolle (*Gongylanthus, Neesioscyphus, Tylimanthus*), Dr. H. Inoue (*Plagiochila, Syzygiella*), Dr. S. Jovet-Ast (*Colura*) and Dr. J. Vaňa (*Anastrophyllum, Gymnomitriaceae, Jungermannia*). Their generous assistance is gratefully acknowledged. Thanks are also due to Miss E. M. Hupkens van der Elst and Mr. H. Rypkema (drawings), and Mr. A. Kuiper (photographs) for technical assistance; Dr. T. van der Hammen, Mrs. R. A. J. Grabandt and Dr. D. M. Vital (Sao Paulo) for providing fresh collections and photographs; the curator of the bryophyte herbarium of Geneva and Dr. S. Winkler (Ulm) for the loan of type specimens; the staff of the Instituto de Ciencias Naturales (Bogotá) and the Estación Biológica Charles Darwin (Galápagos) for fieldwork assistance; and to the Netherlands Foundation for the advancement of Tropical Research for financial support.

II. VEGETATION AND LIVERWORTS OF THE COLOMBIAN ANDES, WITH SPECIAL REFERENCE TO PÁRAMOS

Following Cuatrecasas (1958), four main altitudinal vegetation belts are distinguished in the Colombian Andes: 1. the warm tropical lowlands at the base of the Cordillera (c. 0–1000 m), 2. the Subandean forest (c. 1000–2300 m), 3. the Andean forest (c. 2200–3500 m) and 4. the páramos (c. 3000–4700 m). A useful figure of a schematic transsection of the Colombian Eastern Cordillera, showing these belts, was given by Van der Hammen (1974: 5, fig. 2). Although the borders between these belts generally are not sharp, each belt is readily distinguished by means of floristic and physiognomic characteristics. Since our paper focuses mainly on liverwort species from the high Andes, we will describe the lower reaches only superficially and pay more attention to the higher zones, especially the páramos.

1. In the warm tropical lowlands the rainforest is the most important biome for liverworts, which are mostly epiphytic and epipetric here. Most species belong to the family Lejeuneaceae and many of them grow on leaves. A short list of species was published by Winkler (1976) as part of a study on the occurrence of liverworts in the various altitudinal belts of the isolated Sierra Nevada de Santa Marta in northern Colombia.

2. The Subandean forest (plate 1A) is characterized by the lowermost occurrence of "cold" floristic elements, especially species belonging to the genus *Weinmannia* and *Quercus*, which become dominant as *Weinmannia* forests and *Quercus* forests. Other forest types of different floristic composition also occur.

3. Basically the same forest types occur in the higher Andean forest (plate 1B–C), which differs from the Subandean forest mainly by the disappearance of warm-tropical elements, particularly trees of the genus *Cecropia*, and by the occurrence of numerous cold elements, e.g. *Drimys*, *Oreopanax*, *Vallea*, *Viburnum*, *Bocconia*, *Clethra*, *Hesperomeles*, *Alnus jorullensis* and arborescent Compositae such as *Paragynoxys*, *Verbesina*, *Polymnia pyramidalis* and *Oyedaea*. Although *Quercus* and *Weinmannia* forests are the most common Andean forests, locally forest types dominated by *Alnus jorullensis*, *Hesperomeles* spp., *Hedyosmum* spp., *Clethra* spp. and *Styrax* spp. may occur (Cuatrecasas 1934, Van der Hammen, pers. comm.). Near the upper forest line (3000–3500 m), the floristic composition of the forest usually changes and either Compositae (*Diplostephium*, *Gynoxys*, *Senecio*) together with *Miconia* spp., or *Polylepis* spp. and *Buddleia* spp. are dominant or codominant.

The bryophyte cover in the Andean forest is most luxuriant and is both epiphytic and terrestric, especially in the upper, very humid *Weinmannia* cloud forests. Due to the presence of a condensation zone at about 3000 m these forests have continuous fog and rain throughout the year, which creates an optimal habitat for liverworts. In the literature these forests have often been called "mossy forests", which is incorrect because liverworts prevail, e.g. *Lepicolea pruinosa*, *Riccardia fucoides* and *Scapania portoricensis*, species of *Bazzania*, *Frullania* (especially pendulous species of the section *Meteoriopsis*), *Herbertus*, *Lepidozia* (e.g. *L. wallisiana*), *Lophocolea*, *Metzgeria*, *Radula* and numerous species of Plagiochilaceae and Lejeuneaceae. This richness of liverworts in this belt is indeed immense but little is known of its great diversity. Since adequate taxonomic literature is still lacking for many groups of Andean liverworts, analysis of the liverwort flora of the Andean forests is a very difficult, time-consuming task, on which we are making progress only very slowly.

4. The uppermost open vegetation belt (above 3000 m) in the Colombian Andes is called the páramo. Three páramo belts are distinguished by

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PLATE 1

A Subandean forest at c. 1500 m near Las Llanadas, Río Casanare valley, Colombian Cordillera Oriental (photograph T. van der Hammen).

B. Humid Andean cloud forest of *Weinmannia rollotii* with luxuriant epiphytic liverwort vegetation (e.g. *Plagiochila* spp.) at 3130 m, upper Río Casanare valley, Colombian Cordillera Oriental (photograph T. van der Hammen).

C Andean cloud forest of *Quercus humboldtii* at 2800 m on slopes West of the Sabana de Bogotá, Colombian Cordillera Oriental (photograph T. van der Hammen).

D. Humid bamboo páramo of *Swallenochloa* sp. and *Sphagnum oxyphyllum* at 3600 m, Páramo de Palacio, Colombian Cordillera Oriental. Vegetation with isolated *Espeletia grandiflora* and patches of *Werneria humilis* var. *angustifolia* (photograph A. M. Cleef).

S. R. GRADSTEIN, A. M. CLEEF and M. H. FULFORD: *Studies on Colombian cryptogams II. Hepaticae – oil body structure and ecological distribution of selected species of tropical Andean Jungermanniales.*

PLATE 1

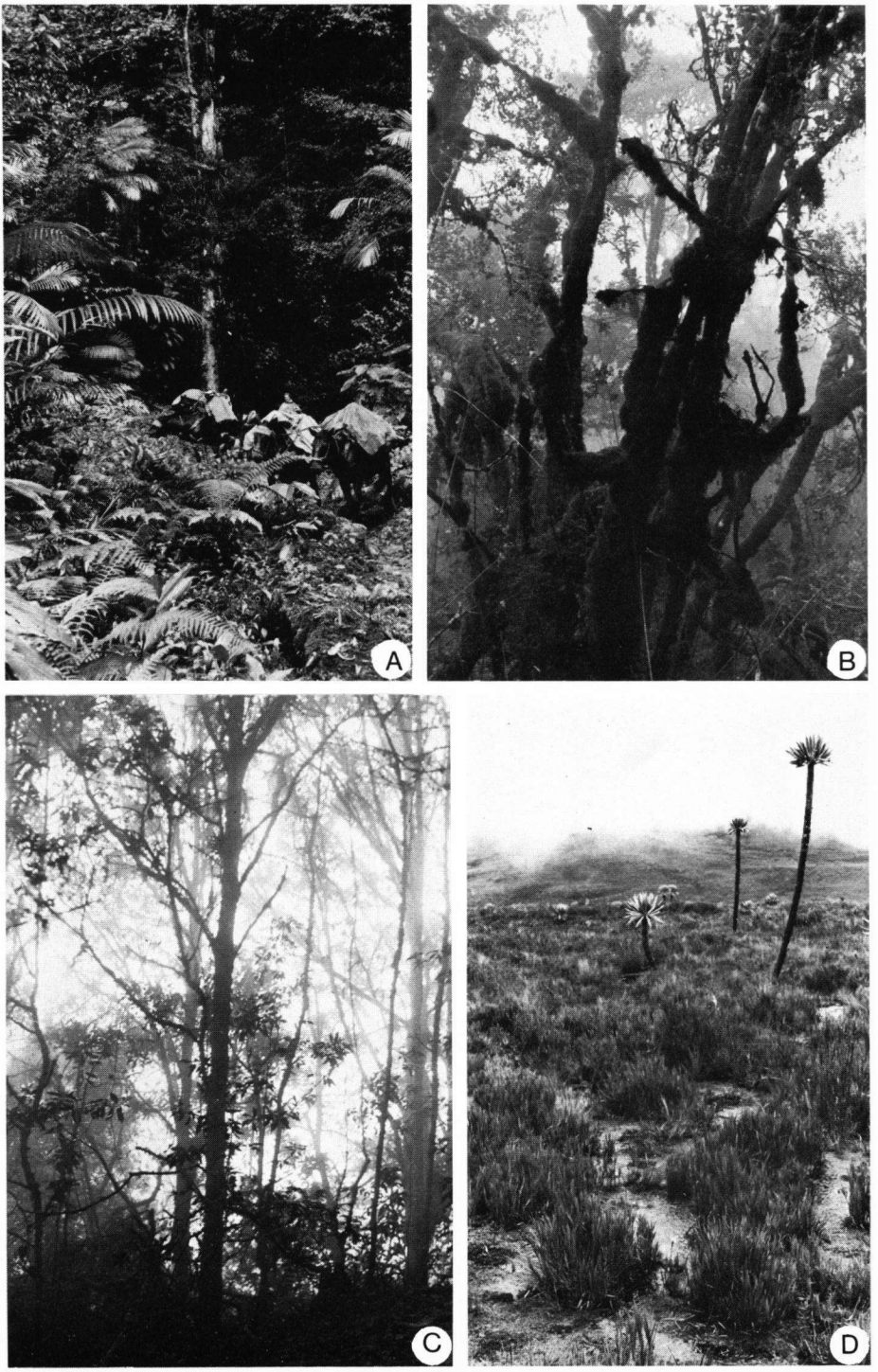
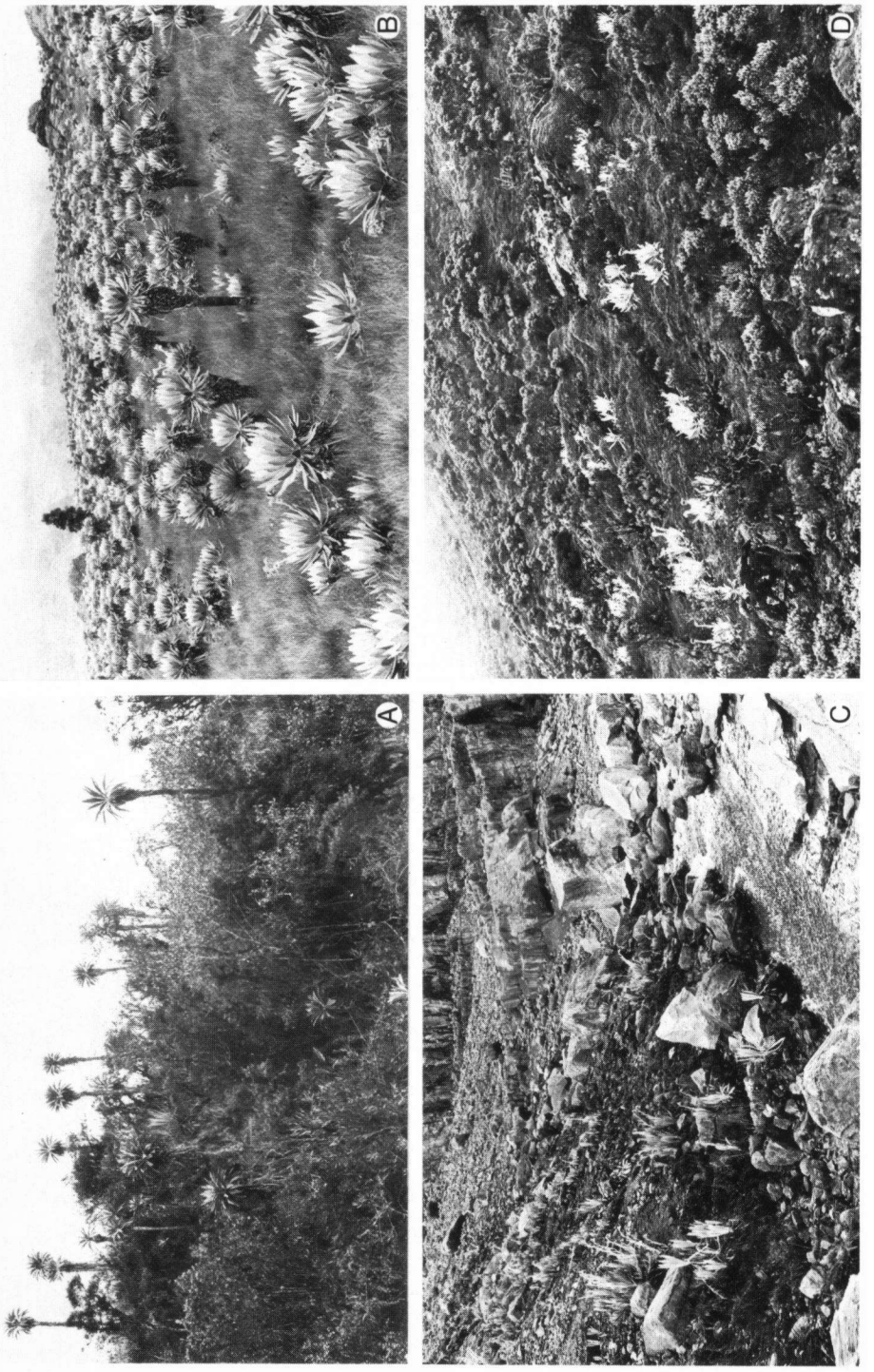


PLATE 2



Cuatrecasas ((1934, 1958; see also Cleef 1977, and in press): the subpáramo, near the timber line, 2) the grass-páramo, or "páramo propiamente dicho" above it and 3) the superpáramo, which reaches up to the snowcap at c. 4700 m.

The (lower) subpáramo of the rather dry slopes is characterised by tall shrub vegetation, consisting mainly of Ericaceae, Melastomataceae, *Hypericum*, *Aragoa* and various woody Compositae, such as *Senecio*, *Diplostephium*, *Baccharis* and, above all, species of the characteristic Espeletiinae. On humid slopes (plate 2A) this vegetation is sometimes replaced by bush of *Ageratina tinifolia* and patches of *Neurolepis aristata*, a tall bamboo endemic to páramos. The upper zone of the subpáramo is dominated by dwarf shrub of *Arcythophyllum nitidum*.

At higher elevations the *Arcythophyllum* vegetation is replaced by the grass-páramo: a bunch-grass-páramo of *Calamagrostis effusa* (plate 2B) on the drier slopes, and a bamboo-páramo of *Swallenochloa* spp. (plate 1D) on the humid slopes. Thus, the geographical distribution of the two types of grass-páramo, both common at least all along the Central and Eastern Cordillera of Colombia, reflects the spatial distribution of the annual precipitation in the páramo belt, which ranges from c. 700 mm to over 3000 mm (Cleef 1977). Bryophytes are most conspicuous in the bamboo-páramo.

Endemic species of Espeletiinae are important elements of the páramo landscape, from the timberline up to the lower superpáramo. These may occur as dense stands in protected sites on boggy soils, accompanied by many species of bryophytes, herbs and vascular cushionplants. Protected sites may also harbour "tree islands": dwarf forests made up of *Polylepis* spp. or various woody Compositae, which are particularly rich in epiphytic bryophytes. The upper grass-páramo is generally drier, the bamboo *Swallenochloa* disappears and the vegetation cover becomes discontinuous.

This is the beginning of the superpáramo (plate 2C), where vegetation is scarce. Structure soils prevail, reflecting the diurnal climate of the cold

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PLATE 2

A Humid subpáramo with bush vegetation of *Ageratina tinifolia* associated with bamboos and tall *Espeletia curialensis*, at 3400 m in the headwaters of the Río Casanare, Colombian Cordillera Oriental (photograph A. M. Cleef).

B Dry grass-páramo of *Calamagrostis effusa* and *Espeletia barclayana* at 3600 m near the Laguna Verde, between Neusa and San Cayetano, c. 65 km North of Bogotá (photograph A. M. Cleef).

C Superpáramo with moraine vegetation of *Senecio cocuyanus*, *Agrostis* sp. and few mosses and lichens at 4330 m in the Bocatoma valley, Sierra Nevada del Cocuy, Colombian Cordillera Oriental (photograph A. M. Cleef).

D. Condensation zone at 4100 m in the lower subpáramo of the summit area of the Nevado de Sumapaz, Colombian Cordillera Oriental. Dense vegetation cover of *Azorella multifida* and bryophytes, e.g. *Breutelia* sp., *Racocarpus purpurascens* and *Herbertus subdentatus*. Also shown are low shrubs of *Senecio vernicosus* and white rosettes of *Senecio canescens* and *Draba* spp. (photograph A. M. Cleef).

tropics characterised by low night temperatures (mostly below 0°C). Relatively few plant species are adapted to these extreme climatic conditions, the greatest species diversification of the superpáramo being found in the lower reaches, where bushes of the morphologically remarkable Composite *Loricaria*, endemic to the tropical Andes, are common. Superpáramos have an island like distribution pattern along the tropical Andean chain and a large portion of their vascular flora is endemic including many species of *Senecio* and *Draba*. Near the snowcap only a few plants are found: among cryptogams *Stereocaulon* sp., *Anastrophyllum* sp., *Racomitrium crispulum* and various species of Bryaceae are the more common ones.

There are many special páramo habitats rich in liverworts, e.g. bogs, lakes and streamlets, and the microhabitats of the 4000 m condensation zone. The humid páramos have an abundance of bogs and lakes; their vegetation shows a marked altitudinal zonation. At lower elevations, from the upper Andean forest to the lower grass-páramo, bog vegetation is usually dominated by *Sphagnum* spp. (*S. magellanicum*, *S. oxyphyllum*, *S. sancto-josephense*, etc.) accompanied by some vascular plants (*Espeletia*, *Puya*, *Blechnum loxense*, etc.) and many bryophytes and lichens: species of *Cladonia*, *Campylopus*, *Breutelia* and *Riccardia* in particular. These bogs are rich in leafy liverworts, the most typical being *Kurzia verrucosa*, *Cephalozia dussii*, *Leptoscyphus cleefii* and *Isotachis multiceps*. At higher elevations cushion bogs of vascular plants of subantarctic origin, e.g. *Plantago rigida* and *Distichia* spp., occur (Cleef 1977). The liverwort flora of these cushion bogs is somewhat similar to that of the *Sphagnum* bogs.

Lakes of the lower páramos have a submerged (!) vegetation, consisting of *Isoetes brasiliensis* (dominant) and many hygrophytic bryophytes, e.g. *Sphagnum spp.*, *Ditrichum submersum*, *Drepanocladus* spp. and some liverworts: *Riccardia sp.*, *Calypogeia andicola*, *Cryptochila grandiflora*, *Radula* sp., *Isotachis lacustris* and *I. serrulata*. At higher elevations lakes have a much poorer vegetation, but *Isotachis serrulata* is mostly present. This liverwort also occurs in pure mats submerged in streamlets up to 4450 m.

The presence of a marked condensation zone at c. 4000 m on the humid side of the Cordillera is of special interest, because it allows for an abundance of bryophytes and enables many species from lower altitudes to penetrate the superpáramo. This phenomenon is particularly clear in the summit area of the Nevado de Sumapaz (4300 m), south of Bogotá, which is usually enveloped by clouds (plate 2D). At 4000-4300 m this steep peak has an extremely humid vegetation dominated by bryophytes, e.g. *Racocarpus purpurascens*, *Breutelia* spp. and *Herbertus subdentatus*. In rock-shelters many rare liverwort species abound, e.g. the Andean endemic *Plagiochila dependula* (= *Jamesoniella dependula*) and the tiny, filamentous *Arachniopsis diacantha*, a species previously only known from the humid Andean forest.

The liverwort flora of the Colombian páramo is a very rich one, with both endemic and wide spread species. The genera include *Adelanthus*,

Anastrophyllum, Aneura, Anoplolejeunea, Anthoceros, Arachniopsis, Bazzania, Blepharostoma, Brachiolejeunea, Calypogeia, Cephalozia, Cephaloziella, Cheilolejeunea s.l., Clasmatocolea, Colura, Cryptochila, Drepanolejeunea, Fossombronia, Frullania, Gongylanthus, Gymnomitrion, Harpalejeunea, Herbertus, Heteroscyphus, Isotachis, Jamesoniella, Jensenia, Jungermannia, Kurzia, Lejeunea, Lepicolea, Lepidozia, Leptolejeunea, Leptoscyphus, Lethocolea, Leucosarmentum, Lophocolea, Lophozia, Marchantia, Marsupella, Metzgeria, Microlejeunea, Neesioscyphus, Noteroclada, Odontoschisma, Omphalanthus, Pallavicinia, Plagiochila, Pseudocephalozia, Radula, Riccardia, Riccia, Stephaniella, Stephaniellidium, Symphyogyna, Syzygiella, Targionia, Taxilejeunea, Telaranea, Triandrophyllum, Trichocolea, Tylimanthus.

Among the species characteristic of the páramo are *Adelanthus lindenbergianus, Anastrophyllum leucostomum, Anastrophyllum leucocephalum, Gongylanthus liebmannianus, Herbertus spp., Isotachis multiceps, Isotachis serrulata, Jensenia erythropes, Jamesoniella rubricaulis, Lepidozia macrocolea, Kurzia verrucosa, Leptoscyphus cleefii, Neesioscyphus n.sp., Riccardia* spp. (many!), *Stephaniella paraphyllina, Triandrophyllum subtrifidum.*

III. THE OIL BODIES

Oil bodies are a characteristic feature of the cells of Hepaticae, especially the Jungermanniaceae (orders Metzgeriales and Jungermanniales). Through the light microscope they are seen as colourless, or rarely brownish or blueish bodies in the cytoplasma. Oil bodies are usually present in all green cells of fresh material[1], and show great variation in shape, size, segmentation, number, and chemical composition. It is only in the last decades that the taxonomic significance of this variation be recognised.

The classical paper is that by Müller (1939), who described oil bodies in over 200 liverwort species, mainly from Europe. More recently, oil bodies have been studied in North American liverworts by Schuster (e.g. 1966, 1969, en 1974) and in Japanese liverworts by Hattori (1951, 1953) and Inoue (1974, 1976).

Scattered data are available on oil bodies in species from southern temperate regions: Australasia (e.g. Schuster 1963, 1968, Inoue & Schuster 1971), South Africa (Arnell 1963) and southern South America (e.g. Hässel de Menendez & Solari 1975; Schuster & Engel 1974).

[1]) According to Crandall-Stotler (1971) and Stotler (1976) the morphological and chemical constitution of the oil body may change when the plants are kept in total darkness for a period of days. Since many of our specimens were kept in plastic bags in darkness for several days before observations were made, our descriptions may not always correspond with conditions in nature. When working with exotic material it is difficult to avoid this. Understanding the different types of oil bodies and their specific patterns of disintegration, described in this paper, seems important when working with material that is not entirely fresh!

Very few data are available on oil bodies in taxa from tropical areas. Important papers are by Schuster & Hattori (1954) on Lejeuneaceae, and Inoue (1967) on Malayan liverworts. This is the first report of the oil bodies in species from tropical South America.

Morphologically, a distinction is to be made between homogeneous oil bodies and oil bodies that are segmented (made up of small globules). Different types of homogeneous and segmented oil bodies can be distinguished (Müller 1939, Schuster 1966). The four main types that we recognized are: the *Massula* type (Müller's "Schrotkorn" type), the *Bazzania* type, the *Jungermannia* type, and the *Calypogeia* type (Müller's "Trauben" type = Schuster's "grape-cluster" type). The names "*Massula* type", "*Calypogeia* type" and "*Jungermannia* type" as well as data on the process of disintegration of oil bodies are new.

1. *Massula* type (fig. 6, 7)

Oil bodies homogeneous or with 1–4 vague segments, small (2–6 μm long) and numerous, in median leaf cells more than 8 per cell. Upon degeneration the oil body first becomes finely transversally segmented and subsequently disintegrates into minute granules (Gradstein 1975:19). Consequently, degenerating oil bodies of the *Massula* type resemble the *Jungermannia* type (see below)! The *Massula* type was found in *Anoplolejeunea*, *Brachiolejeunea*, *Lophozia incisa* (belonging to *Lophozia* subgenus *Massula*) and *Porella*. Oil bodies of *Telaranea nematodes* are transitional between the *Massula* type and the *Jungermannia* type.

2. *Bazzania* type (fig. 4, 5)

Oil bodies homogeneous or with 1–4 vague segments, large (4–15 μm long) and up to 8 per cell. Disintegration has not been observed in Andean taxa but observations in material of *Nardia scalaris* from Europe indicate that the process is basically similar to that of the *Massula* type; first the oil body becomes transversally segmented into globules of variable size and number, and subsequently each globule disintegrates into minute granulae. Before disintegration the globules, when large, may become separate from each other, thus increasing the number of oil droplets per cell! In the Andean material the *Massula* type was only found in *Bazzania*. According to Schuster (1966) the *Bazzania* type is also found in the genus *Herbertus*, but oil bodies in *Herbertus* species studied by us are of the *Jungermannia* type.

3. *Jungermannia*-type (fig. 8, 14)

Oil bodies finely segmented, consisting of numerous minute, indistinct globules within a more or less discrete outer membrane. The oil body thus appears to be granulose and often, when globules protrude through the membrane, papillose. Size and number of oil bodies per cell vary. Upon degeneration the oil body first becomes almost homogeneous and "grayish" (fig. 1, 2, 3) and subsequently disintegrates. Consequently, *Jungermannia-*

type oil bodies may resemble *Massula*-type or *Bazzania*-type oil bodies in plants that are not fresh! Over 2/3 of the genera treated in this paper have *Jungermannia*-type oil bodies.

4. *Calypogeia*-type (fig. 9, 12)

Oil bodies coarsely segmented (like a grape-cluster), consisting of distinct globules. Size and number per cell vary. The oil body seems to lack a discrete outer membrane and upon degeneration usually falls apart into separate globules, which in turn disintegrate. The *Calypogeia* type occurs in *Blepharostoma*, *Microlejeunea*, *Omphalanthus*, *Pseudocephalozia* and some species of *Colura*, *Calypogeia*, *Frullania*, *Isotachis*, *Lepidozia* and *Lophocolea*.

In the above descriptions, emphasis has been laid upon the process of disintegration because it is a source of errors on the one hand, whereas on the other hand previous workers have totally neglected it. Since our data are based on a limited number of observations only, a more comprehensive study of the disintegration of oil bodies is called for.

In 62 species of Jungermanniales treated, oil bodies are described for the first time in 54 of them. Among there are 6 genera in which oil bodies were unknown previously: *Chaetocolea*, *Clasmatocolea* (?), *Lethocolea*, *Leucosarmentum*, *Neesioscyphus* and *Stephaniella*. Some new data on Lejeuneaceae resulting from this study, e.g. *Anoplolejeunea*, *Brachiolejeunea* and *Omphalanthus*, have been published earlier (Gradstein 1975).

The species treated in this paper in which oil bodies were already known, are widespread elements such as the holarctic *Blepharostoma trichophyllum*, *Jungermannia sphaerocarpa* and *Lophozia incisa* (all of them with few, scattered localities in the tropical Andes) and the pantropical *Lejeunea flava*. In the latter species oil bodies in Colombian plants described here differ from those in North American plants described by Schuster (1957). Deviating oil body characters were also found in the Colombian populations of the widespread *Triandrophyllum subtrifidum*, *Lophozia incisa* and *Telaranea nematodes*. Whether the observed variation has any geographic significance and may serve to delimit different geographic races (see e.g. Schuster 1966: 214) cannot yet be decided, since such conclusions are to be based on many more observations.

The oilbodies of the genera treated here agree with previously published generic descriptions except for *Calypogeia* (see sub *C. cyclostipa*) and *Colura* (see sub *C. patagonica.*).

IV. SPECIES DESCRIPTIONS

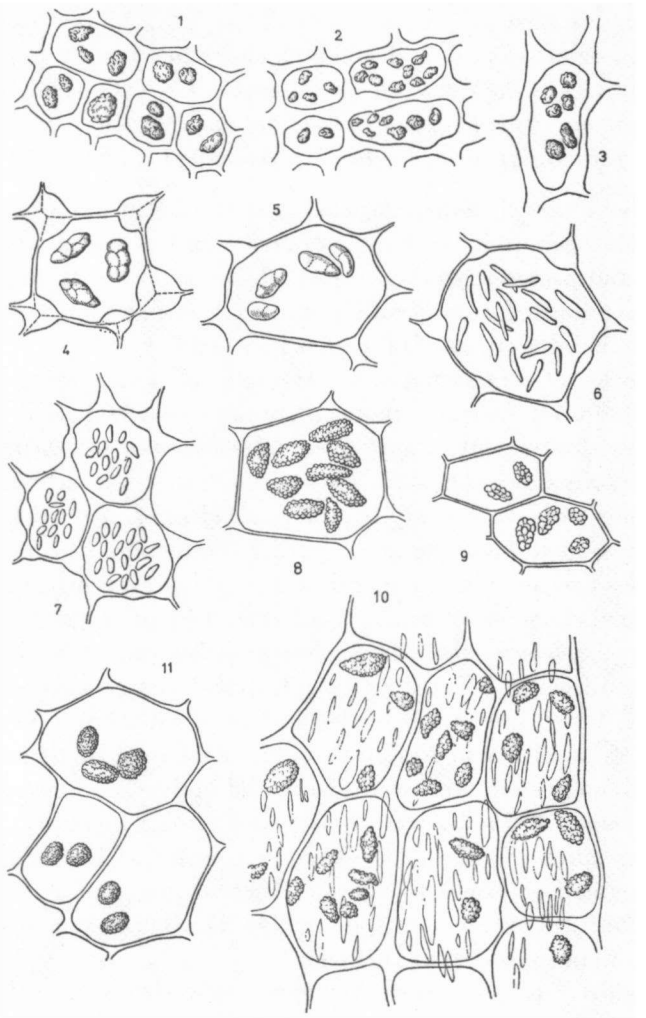
Adelanthus lindenbergianus (Lehm.) Mitt. (fig. 1)

Oil bodies in the leaves 1–3(–4) per cell except in elongated leaf-base cells, which have 4–8 oil bodies; globose to ellipsoid, sometimes rather angular (Cleef 307), 4–8 × 3–5 μm, when one per cell larger, up to 12 × 8 μm; colourless becoming grayish on age, finely granulose-papillose (Colombia, Cundinamarca, Cleef 287b, 307 & 3252).

Grolle (1972) reported (2–)3–4(–5) oil bodies per cell in plants from Ireland.

Distribution and ecology:

According to Grolle (1972) this polymorphic species has a pluriregional distribution: Ireland, Mexico, Costa Rica, Venezuela, Colombia, Ecuador, Bolivia, Chile, Argentina, Tristan da Cunha, South Africa, Madagascar (?), Reunion, Zaire ? (Kivu), Kinshasa and Uganda.



(PLATE 3) Oil bodies in Andean Jungermanniales. – 1. *Adelanthus lindenbergianus* (Lehm.) Mitt., degenerating oil bodies, Cleef 307 (500×). 2. *Anastrophyllum leucocephalum* (Tayl.) Steph., degenerating oil bodies, in leaf base cells, Cleef 589 (500×). 3. *Anastrophyllum leucostomum* (Tayl.) Steph., degenerating oil bodies, Cleef 282a (500×). 4. *Bazzania hookeri* (Lindenb.) Trevis., Cleef 666b (500×). 5. *Bazzania longistipula* (Lindenb.) Trevis., Cleef 395b (500×). 6. *Brachiolejeunea laxifolia* (Tayl.) Schiffn., Cleef 398b (750×). 7. *Brachiolejeunea nitidiuscula* (Gott.) Schiffn., Gradstein et al. 100 (500×). 8. *Calypogeia cyclostipa* (Spruce) Steph., Cleef 666d (750×). 9. *Calypogeia peruviana* Nees & Mont., Cleef 3410e (500×). 10. *Chaetocolea palmata* Spruce, cells from base of leaf lobe, cuticle with striate papillae, van der Hammen 3381 (500×). 11. *Clasmatocolea vermicularis* (Lehm.) Grolle, Cleef 490b (500×).

In the Andes of Colombia *Adelanthus lindenbergianus* has been collected between 2600 and 4100 m in the Central and Eastern Cordillera and the Sierra Nevada de Santa Marta. It is apparently a common species in the humid upper Andean *Weinmannia* and *Quercus* cloud forest, as well as in isolated dwarf forests in the páramo belt consisting of e.g. *Gynoxys* spp. and *Diplostephium revolutum*.

The species reaches upwards into the lower zone of the atmospherically very humid superpáramo, e.g. at the Cerro Nevado de Sumapaz, where it was found in the *Loricaria complanata* scrub zone and in dwarfscrub of *Diplostephium rupestre*. *Adelanthus lindenbergianus*, however, is most common in the humid páramos, where it grows mainly terrestric in bogs with dwarf bamboos (*Swallenochloa* spp.), *Sphagnum* spp. and other hygrophytic bryophytes.

Anastrophyllum leucostomum (Tayl.) Steph. (fig. 3)

Oil bodies in leaves usually 4–9 per cell, in elongated cells of the leaf base up to 15 per cell; ± globose, more rarely subellipsoid, 4–5 × 3–4 μm; colourless, becoming grayish on age, finely granulose-papillose (Costa Rica, Cordillera de Talamanca, humid subpáramo with *Swallenochloa*, 3325 m, Cleef & Fournier 10197).

Distribution and ecology:

A common species of the mountainous regions of tropical America (J. Vaňa in litt.).

In Colombia known from the Central and Eastern Cordillera, including the Sierra Nevada de S. Marta, frequently occurring terrestric and epilitic in páramos. It ranges in altitude from the Subandean (*Weinmannia*) forest at about 2000 m up to the superpáramo. The highest record came from about 4500 m in the Sierra Nevada del Cocuy. *Anastrophyllum leucostomum* is a conspicuous and very common liverwort in the lower part of the superpáramo; here it often grows associated with shrubs of *Loricaria*. In the grass-páramo it occupies a lot of (humid) habitats: exposed wet boulders, dense *Espeletia* stands, humid *Diplostephium* dwarf forests, cushions of *Plantago rigida*, humid *Swallenochloa* páramo and shrubs of *Senecio* spp. In the subpáramo this species is very common in shrubs of *Disterigma empetrifolia* and *Gaultheria ramosissima* on boulders, associated with many other species of bryophytes.

Anastrophyllum nigrescens Steph.

Oil bodies in leaves 2–4(–5) per cell, in elongated cells of the leaf base up to 18 per cell; irregularly globose to subellipsoid, 3–5 × 2–4 μm; colourless, finely granulose, becoming almost homogeneous on age (Colombia, Cundinamarca, Cleef 287, det. teste J. Vaňa).

Distribution and ecology:

This species has a tropical Andean distribution, from Colombia to Bolivia, like *A. leucocephalum*. Herzog (1916) reported *A. nigrescens* from

the upper forest line near Tablas in Bolivia, here growing epiphytically.

In Colombia this liverwort has been found only terrestric at humid sites between about 2000 and 4320 m in the Andean forest belt and the páramos of the Central and Eastern Cordillera, as well as in the Sierra Nevada de Santa Marta.

In the páramos this darkish species commonly grows in bogs of *Sphagnum* and *Plantago rigida*, in humid bamboo vegetation and in swampy *Diplostephium revolutum* vegetation and occasionally on slightly humid slopes with *Calamagrostis effusa – Espeletia* vegetation. The highest records came from the lower superpáramo, e.g. from thickets of *Loricaria* and *Senecio* spp.

Anoplolejeunea conferta (Meissn.) Evans

Oil bodies (Gradstein 1975: 138) in leaves 25–50 per cell; ellipsoid, very small, 3–4 × 1,5–2 μm; colourless and glistening, homogeneous (Colombia, Cundinamarca, Florschütz 4464 & 4485a).

Distribution and ecology:

An exclusively epiphytic liverwort of the mountainous regions of tropical America.

Throughout Colombia this species is widely distributed between about 1400 and 3500 m in Subandean (*Weinmannia*) and Andean (*Weinmannia, Quercus, Alnus*) forests. The highest record came from the ecotonic *Weinmannia* forest and subpáramo at 3500 m, where *Anoplolejeunea conferta* was found growing together with *Brachiolejeunea laxifolia, Frullania* sp. and *Metzgeria* sp. on an isolated tree in the shelter of a ravine.

Bazzania hookeri (Lindenb.) Trevis. (fig. 4)

Oil bodies in leaves 2–5 per cell; bluntly ellipsoid, more rarely globose, large, (6–)10–15 × 5–7 μm; colourless, opaque, segmented and consisting of few large globules, upon degeneration splitting into smaller segments or becoming homogeneous (Colombia, Cauca, Cleef 666b).

Distribution and ecology:

A widespread and common liverwort in hilly and mountainous areas in tropical America, growing in humid forests "in deep tufts, on soil and on bases and trunks of trees" (Fulford, 1963) and also on rocks (Bischler 1962). The species occurs throughout Andean Colombia and has been collected at about 200 m in the Amazonian rainforest of Vaupés as well as at 3280 m in the humid subpáramo!

Bazzania longistipula (Lindenb.) Trevis. (fig. 5)

Oil bodies in leaves 2–6 per cell; bluntly and some what narrowly ellipsoid (globose when seen from the side!), 4–7 × 2–3 μm: colourless, opaque, faintly segmented into 2–3 large globules of unequal size (Colombia, Cundinamarca, Cleef 395b).

The oil bodies in this species differ from those in *B. hookeri* by their somewhat smaller size.

Distribution and ecology:

The general geographical distribution of this species is quite similar to that of *Bazzania hookeri:* the mountains of tropical America.

Though mainly an epiphytic liverwort, Fulford (1963) listed this species also from rocks and logs.

Bazzania longistipula is rather common in the Colombian Andes and was collected here between about 1500 and 3500 m, in the Subandean and Andean *Weinmannia* forests.

Blepharostoma trichophyllum (L.) Dum.

Oil bodies in median leaf cells 3–7 per cell; globose to subellipsoid, small, c. 2–5 × 2–3 μm; colourless, granulose (Colombia, Tolima, van der Hammen & Jaramillo 3374).

The oil bodies agree with descriptions of oil bodies in northern temperate material of *B. trichophyllum* by Müller (1954) and Schuster (1966).

The specimens from Colombia fit Schuster's diagnosis of *B. trichophyllum* ssp. *trichophyllum* (Schuster 1966: 750) except for the leaves, which are 3-fid on sterile stems and 3–4-fid on fertile stems. In this respect the plant approaches Schusters ssp. *australis* (nom.nud.), known from one Peruvian collection. Now that new South American material of the species has turned up, the taxonomic status of the ssp. *australis* as a separate South-American race of *Blepharostoma trichophyllum* needs to be reconsidered.

Distribution and ecology:

A widespread tiny liverwort, with holarctic distribution.

Recently the species has been reported from scattered localities in high tropical mountains between 2500 and about 4000 m, e.g. from East Africa, Java, New Guinea and the Peruvian Andes. *Blepharostoma trichophyllum* is reported here for the first time from Colombia as well as from Venezuela (Mérida: leg. Boerboom s.n.).

In Colombia the species is actually known from the humid upper Andean cloud forests (epiphytic?) with *Weinmannia* and *Alnus jorullensis* between 3100 and 3750 m on the south facing slopes of the volcano Nevado del Tolima in the Central Cordillera.

In the Eastern Cordillera Oriental, viz. the Páramo de Sumapaz, *B. trichophyllum* has been collected terrestric in boggy páramo with *Sphagnum* spp. and in swampy dwarf forest of *Diplostephium revolutum* between about 3550 and 3700 m.

Brachiolejeunea laxifolia (Tayl.) Schiffn. (fig. 6)

Oil bodies (Gradstein 1975: 144) in median leaf cells 15–25 per cell, narrowly ellipsoid-fusiform (appearing as roundish when seen from the side!), 5–6 × 1,5 μm, glistening and homogeneous; oil bodies much smaller and more numerous in stem cortex cells, c. 35–50 per cell (Colombia, Cundinamarca, Cleef 398b).

Distribution and ecology:

A common epiphytic liverwort, occurring throughout the tropical mountains of America from Mexico to Argentina.

In Colombia this species has been collected between about 2000 and 3800 m in the upper Andean *Weinmannia* and *Alnus jorullensis* forests, in the ecotonic dwarf forests and in subpáramos on shrubs.

Brachiolejeunea nitidiuscula (Gott.) Schiffn. (fig. 7)

Type: Colombia, Páramo Choachi, 3400 m, Lindig 1739, IX. 1860 (PC iso!)
Syn. nov.: *Brachiolejeunea hans-meyeri* Steph., Spec. Hep. 5: 118.1912.
Syntypes: Ecuador, Páramo El Altar, 4000 m, Hans Meyer 4220 & 4225, VII. 1903 (G!)

Oil bodies in median leaf cells 10–20 per cell; ellipsoid to subglobose, small, ± homogeneous, falling apart into minute droplets upon degeneration (Colombia, Boyacá, Cleef 1889; ibid., Meta, Cleef 7789; Ecuador, Páramo de Cotopaxi, Gradstein, Sipman & de Vries 100)

Brachiolejeunea nitidiuscula is a very distinct species, characterised by the strongly imbricated, ± convoluted, dark-brownish leaves, which are apiculate and have a 2-toothed lobule. The perianth, with 2 innovations, is rather short obovate, triangular in transverse section with three smooth, rather wide keels. It somewhat resembles the nutlet of *Carex*! In some respects the species has affinity to the genus *Dicranolejeunea*, from which it differs however by its smooth perianth keels, the rudimentarily winged female bracts and the apparently homogeneous oil bodies (but specimens not quite fresh upon examination!).

Distribution and ecology:

Brachiolejeunea nitidiuscula is one of the few species of Lejeuneaceae characteristic for neotropical páramos. We have seen collections from Bolivia, Peru, Ecuador and Colombia at altitudes between 3000 and 4000 m, and from Costa Rica, where it was collected in montane cloud forest at 2900 m (Griffin et al. 435 & 560, IX. 1973; FLAS, U).

In Colombia the species is only known from the Eastern Cordillera, between 3400 and 4085 m, where it was mostly found epiphytic, e.g. on stems of *Hypericum* shrub or *Aragoa abietina* shrub, but occasionally also terrestric and epilitic.

Calypogeia andicola Bischl.

Oil bodies present in all leaf cells, 4–8 per cell; ellipsoid to globose, 5–12 × 4–5 μm; colourless, rather finely granulose-papillose (Colombia, Cundinamarca, Cleef 380b).

The oil bodies in *C. andicola* resemble those of *Calypogeia sullivantii* Aust. (Schuster 1969: 118, fig. 106).

Distribution and ecology:

This liverwort is only known from the tropical Andes of Colombia,

Ecuador and Bolivia, occurring at about 2300–4100 m (Fulford 1968).

In Colombia the species is recorded from high Andean forests and especially from páramos in the Central and Eastern Cordillera, where it grows "on damp soil and rotten wood in shaded places" (Bischler 1962: 79), as well as on wet rocks, along streamlets, and even submerged with *Isoetes brasiliensis* in a cold páramo lake at 3800 m!

It is frequently found associated with *Noteroclada confluens*, *Isotachis serrulata*, *Isotachis madida*, *Anastrophyllum* spp., *Jungermannia sphaerocarpa* and *Philonotis* sp. Bischler (1962) considered *C. andicola* a typical representative of the páramo flora.

Calypogeia cyclostipa (Spruce) Steph. (fig. 8)

Oil bodies present in all leaf cells, 3–10 per cell: 3–5 in upper leaf cells and 5–10 in cells of the lower half of the leaf; broadly ellipsoid to bone-shaped or subglobose, rather large, 6–12 × 4–6 μm, somewhat smaller in leaf margin cells; colourless, finely granulose-papillose, becoming almost homogeneous on age (Colombia, Cauca, Cleef 666d; ibid., Cundinamarca, Cleef 3410c).

This is the first report of oilbodies in a species of *Calypogeia* subg. *Caracoma* Bischl. The oil bodies in *C. cyclostipa* resemble those of the genus *Metacalypogeia* and of *Calypogeia granulata* Inoue from Japan (Inoue 1968),! except for their colour (colourless in *C. cyclostipa*, not brownish). Most other species of the genus have coarsely segmented oil bodies of the "*Calypogeia*-type".

Distribution and ecology:

This species occurs in tropical South America at altitudes of above 1000 m (Fulford 1968), preferably in humid mountain forests.

In Colombia this liverwort has been collected between about 1700 and 3600 m in the Eastern and Central Cordillera and in the Serranía de la Macarena. *Calypogeia cyclostipa* grows both epiphytic and terrestric. On wet gravelly soil it was found associated with *Herbertus* sp., *Lepidozia caespitosa*, *Bazzania hookeri*, *Odontoschisma longifolium*, *Calypogeia peruviana* and *Plagiochila* sp.

Calypogeia peruviana Nees & Mont. (fig. 9)

Oil bodies present in all leaf cells, 2–6 per cell; globose to ellipsoid, 4–11 × 4–7 μm; sepia (!), becoming brownish on age, rather coarsely granulose consisting of relatively large droplets (Colombia, Cundinamarca, Cleef 3410e; Galapagos Is., Santa Cruz, Media Luna, Gradstein, Lanier, & Weber (H120).

The brownish-purple ("blue") oil bodies of C. peruviana were observed previously by Schuster (1969) in North American material. This is the first report of oil bodies in South American material. Jones (1976) recently described *C. afrocoerulea*, an African species with "blue" oil bodies, which is doubtfully distinct from *C. peruviana*.

Distribution and ecology:

A common liverwort, widely distributed throughout tropical America (Fulford 1968), including the southeastern part of the USA (Schuster 1969), and occurring from the base of the mountains up to about 3200 m.

In Colombia, *Calypogeia peruviana* has a distribution similar to *Calypogeia cyclostipa*, ranging from 1700 to 3600 m; mainly in mountain forests. The highest record is from a grass-páramo bog with *Swallenochloa*, *Festuca* and *Sphagnum*.

Chaetocolea palmata Spruce (fig. 10)

Oil bodies present in all leaf cells, variable in number, c. 2–10 per cell; globose to ellipsoid with bluntish to rather sharply tapering points, 5–12 × 4–6 μm; colourless, finely granulose-papillose; cuticle striate-papillose (Colombia, Tolima, van der Hammen & Jaramillo 3381).

Chaetocolea palmata Spruce is the only representative known of the family Chaetocoleaceae Fulf. It is a rare Andean taxon, in which the sporophyte thus far remained unknown. Our materal is autoicous and has young sporophytes, with seta's which in cross section consist of about 20 outer cells and 15 inner cells. The seta thus fit's Douin's general type. The perianth, which is unistratose and bears ciliate-laciniate, leaf-like processes all over its surface, fits the description given by Schuster (1965).

Distribution and ecology:

Previously only known from the tropical Andes of Peru and Ecuador (Fulford 1963), the Colombian collection represents the third record of this peculiar monotypic Andean genus.

Its altitudinal range is between about 2500 and 3100 m. In Colombia this tiny hepatic was found epiphytically among other bryophytes in very humid *Alnus jorullensis* forest at 3100 m on the south facing slopes of the vulcano Nevado del Tolima in the Cordillera Central.

Clasmatocolea vermicularis (Lehm.) Grolle (fig. 11)

Oil bodies consistently 2–3 per cell in leaves, underleaves and stem cortex (!); ellipsoid to globose, 7–13 × 6–8 μm; colourless, very finely granulose-papillose (Colombia, Cauca, Volcán Puracé, Cleef & Fernandez 490b).

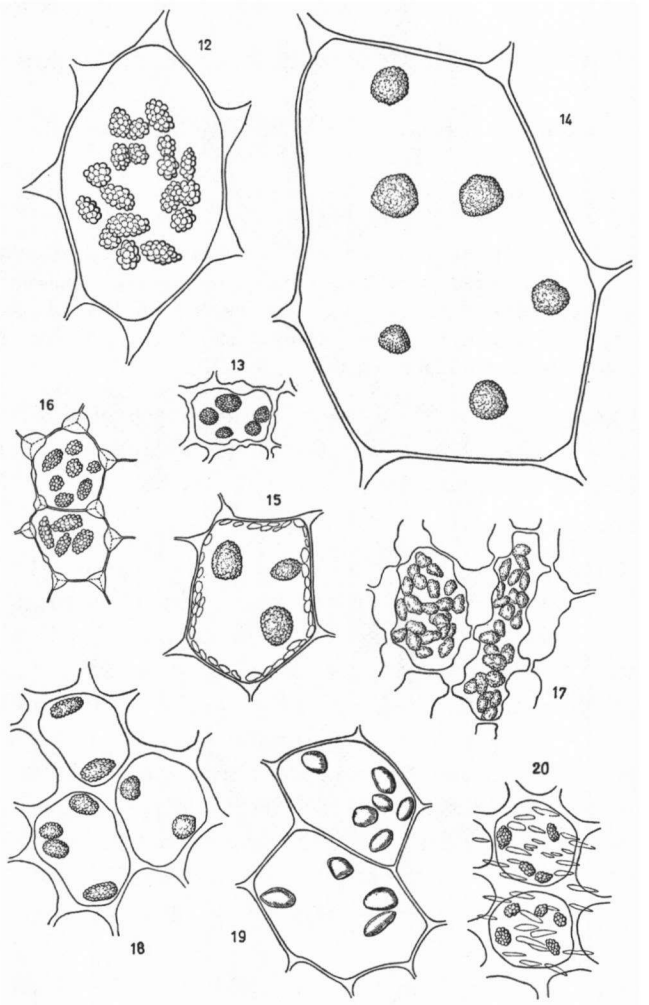
Distribution and ecology:

According to Grolle (1969) the area of distribution of this subantarctic-tropical-montane species comprises the southern Atlantic islands, southern Africa, South America and Central America (Costa Rica). Its altitudinal range in the tropical Andes is from about 1500 to 4500 m!

We have seen a few Colombian collections of this species, occurring on soil between 3470 and 4520 m, ranging from a clearing in the upper Andean *Weinmannia* forest belt up to the superpáramo of the Central and Eastern Cordillera.

In the Sierra Nevada del Cocuy this species was found in great quantity on a marshy valley floor at about 4000 m, growing between tiny plants of *Scirpus* sp.

In the superpáramo of the volcano Nevado de Ruiz, *Clasmatocolea vermicularis* grows on humid lava outcrops near the snowcap, together with *Triandrophyllum subtrifidum* which, like *C. vermicularis*, is supposedly from the southern extreme of South America.



(PLATE 4) Oil bodies in Andean Jungermanniales. – 12. *Colura patagonica* Jovet-Ast, leaf base cell, Cleef 2292c (750×). 13. *Drepanolejeunea navicularis* Steph., Cleef 550b (500×). 14. *Gongylanthus granatensis* (Gott.) Steph., van der Hammen 3324 (500×). 15. *Gongylanthus liebmannianus* (Lindenb. & Gott.) Steph., green cell with oil bodies and chlorophyll, Cleef 55c (500×). 16. *Harpalejeunea ancistrodes* (Spruce) Schiffn., Cleef 398c (500×). 17. *Herbertus limbatus* (Steph.) Herz., Cleef 666a (500×). 18. *Isotachis lindigiana* Gott., Cleef 490a (500×). 19. *Jungermannia sphaerocarpa* Hook., Cleef 380a (500×). 20. *Lepidozia caespitosa* Spruce, Cleef 666c (500×).