Studies on Colombian cryptogams

V. Taxonomy, distribution and ecology of macrolichens of the Colombian Paramos:

1. *Cladonia* subgenus *Cladina*

by H. J. M. Sipman and A. M. Cleef

Institute of Systematic Botany, University of Utrecht
Heidelberglaan 2, 3584 CS Utrecht

Communicated by Prof. F. A. Stafleu at the meeting of September 30, 1978

ABSTRACT

Morphology, chemistry, distribution and ecology of 6 species of *Cladonia* subgenus *Cladina* (Lichenes) from the Colombian páramos are described: *C. arcuata* Ahti, *C. boliviana* Ahti, *C. confusa* Sant., *C. polia* Sant., *C. rangiferina* (L.) Wigg. var. *abbayesii* Ahti, and *C. colombiana* spec. nov. *C. bicolor* (Müll. Arg.) Ahti is reduced to synonymy under *C. polia*.

RESUMEN

Se describe la morfología, la química, la distribución espacial y la ecología de las 6 especies siguientes de *Cladonia* subgénero *Cladina* (Líquenes) de los páramos colombianos: *C. arcuata* Ahti, *C. boliviana* Ahti, *C. confusa* Sant., *C. polia* Sant., *C. rangiferina* (L.) Wigg. var. *abbayesii* Ahti, and *C. colombiana* spec. nov. *C. bicolor* (Müll. Arg.) Ahti se ha reducido bajo el sinónimo de *C. polia*.

INTRODUCTION

This publication is part of a 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 T. van der Hammen (Amsterdam), his collaborators, and by the second author. This paper is the first dealing with lichens. It is part of a revision of macrolichens of the Colombian páramos based on numerous new collections.

The most complete study dealing with the macrolichens of the Colombian páramos is by Nylander (1863), who mentioned all lichen species known

Reprinted from: Proc. Kon. Ned. Akad. v. Wetensch. Series C, Vol. **82** *(2): June 1979*

from Colombia and described many new ones. Apart from a paper by Müller Arg. (1879) little has since been published on Colombian lichens. However, knowledge of lichen systematics, especially for macrolichens, has increased a great deal since then, and Nylander's enumeration is largely outdated now. More recent data on Colombian lichens are available only in scattered taxonomic revisions mainly in the families *Cladoniaceae*, *Parmeliaceae*, *Physciaceae* and *Umbilicariaceae*. For these revisions only scarce material from Colombia was available. Consequently examination of the numerous collections now available is likely to increase knowledge of the Colombian macrolichens substantially. *Cladonia* subgenus *Cladina* has been chosen as the first group to be treated, because it is well represented among the new collections and a good recent revision is available (Ahti 1961).

The study is based on about 180 specimens, mainly collected by the second author and his co-workers during phytosociological work in the páramos of the Colombian Cordillera Oriental in 1971–1973 and 1977. Complete sets of these collections are deposited in COL and U. Supplementary material was studied from the following herbaria: COL, K (in BM), L, S, TUR and UPS.

MORPHOLOGY

Cladonia species show great morphological variation. Due to their slow growth, the habitus of these plants can be modified not only by their age and the local environment, but also by changes in the environment during the years when the thallus develops. This concerns especially the podetia, the secondary, erect part of the thallus. Some peculiar modifications of subg. *Cladina* are the following:

1. In many species forms occur with podetia consisting of strongly inflated main stems and strongly reduced branchlets, which, at the apex, are often arranged in whirls. This polychotomic branching is an exception to the branching pattern referred to in the descriptions. Perhaps these forms depend on the age of the individual.
2. *Cladina* species grow at the apex while dying off at base. The length of the plants depends on the rate of both processes. Under less favorable circumstances the dying off goes so fast that only the apical portion is present, whereas the main stem, which appears somewhat below the apex, is absent. A comparable effect has trampling, by which the podetia are turned flat and regenerate from their sides. Development of new main stems takes considerable time, and is not achieved when trampling occurs repeatedly.
3. The cortical structure, often useful for the identification of the species may become obscure by bad preservation of the specimens.

To facilitate identification, one should pay special attention to the morphological variation of the species in the field before collecting them.

Collecting a range of forms of each species will make the characteristic features easier to recognize.

Though pycnidia are frequent in several species, the pydnicial jelly, whose colour provides an important character, is observed only rarely in dried specimens.

CHEMISTRY

Chemical analysis of the material has been carried out in most cases by thin layer chromatography (T.L.C.), with solvent system A (Culberson 1972). In *Cladonia arcuata*, *C. colombiana* and *C. rangiferina* part of the material has been tested by the micro-crystal test (M.C.T.) using GAoT (Thomson 1968), to identify atranorin.

The following substances have been found:

ATRANORIN. Found in *C. rangiferina* var. *abbayesii* and in a few specimens of *C. arcuata* and *C. colombiana*. Identified by TLC or MCT.

FUMARPROTOCETRARIC ACID. Found in all specimens of *C. arcuata*, *C. colombiana* and *C. rangiferina*, and in part of *C. boliviana*. Because the difference between this acid and protocetraric acid is not very pronounced in the TLC-method used, it might have been overlooked. However it has never been reported for *Cladonia*.

PERLATOLIC ACID. Found in all specimens of *C. polia* and in part of *C. confusa*. Identified only by TLC.

In addition to the main spot on the chromatograms up to 5 weak accessory spots have often been found above it and one just below. These spots were of the same bluish colour after sulphuric acid treatment as the margin of the main spot. They represent thermal decomposition products, as could be demonstrated by storing a fragment of *Cladonia polia* for 2 hours at 110° C. TLC of this fragment showed only these accessory spots, while an untreated part showed only the perlatolic acid-spot. The spots were found without the original perlatolic acid-spot, namely in a single *C. confusa*-sample dried together with phanerogams (Venezuela, Caracas, Cleef 10299 (U)). This could lead to the same confusion found in *Hypotrachyna* species by Culberson et al. (1977).

STICTIC ACID. Found in a few collections of *C. boliviana* only. In TLC several spots have been found with Rf 1 to 3 (cf. code of Culberson 1972). Usually three spots together are recognizable after treatment with sulphuric acid: the upper spot is brown, the central one weakly brownish and the lower one reddish brown and often double. They may include constictic acid.

USNIC ACID. Found in *C. boliviana* and *C. confusa*. Presence easily recognizable by the pale yellow colour of the specimens. Checked by TLC. In *C. confusa* the content appears to be variable, and sometimes nearly absent. Several times unidentifiable spots have been observed in TLC

which do not produce clear colours after sulphuric acid or bromcresolgreen treatment. They are apparently accessory spots.

In the descriptions the usual colour reactions for rapid indication of the lichen substances are also given: P, K, C, KC. For an explanation of these abbreviations see Thomson (1968).

For the species studied 4 new chemical strains have been observed: in *C. arcuata* a strain without atranorin; in *C. boliviana* a strain without fumarprotocetraric acid and one with stictic acid instead of fumarprotocetraric acid; in *C. confusa* a strain without perlatolic acid.

DISTRIBUTION

Cladonia subgenus *Cladina* species generally occur in cool, humid climates (Ahti 1961). Consequently most species occur mainly in the high mountains, in the páramo belt at about 3200–4100 m alt. They sometimes occur at lower altitudes, depending probably on a locally cool and humid climate. Few species are found in lowland savannas, in Colombia only *C. rotundata*. One more species, *C. arcuata*, appears to have its main distribution below 3000 m, but not lower than 2500 m. The other species, *C. boliviana*, *C. colombiana*, *C. confusa*, *C. polia* and *C. rangiferina* var. *abbayesii*, are mostly found in the páramos. Except for *C. colombiana*, they are occasionally found at lower altitudes, down to about 1300 m.

The *Cladina* species known from Colombia are usually found on all high mountains in tropical America, e.g. in the northern parts of the Andes range, the Costa Rican highlands and the Coastal Cordillera of Venezuela. A few species, *C. confusa* and *C. rangiferina* var. *abbayesii*, extend into Mexico, the Caribbean Islands and even into Uruguay (Ahti 1961). *C. colombiana* is so far known only from Colombia.

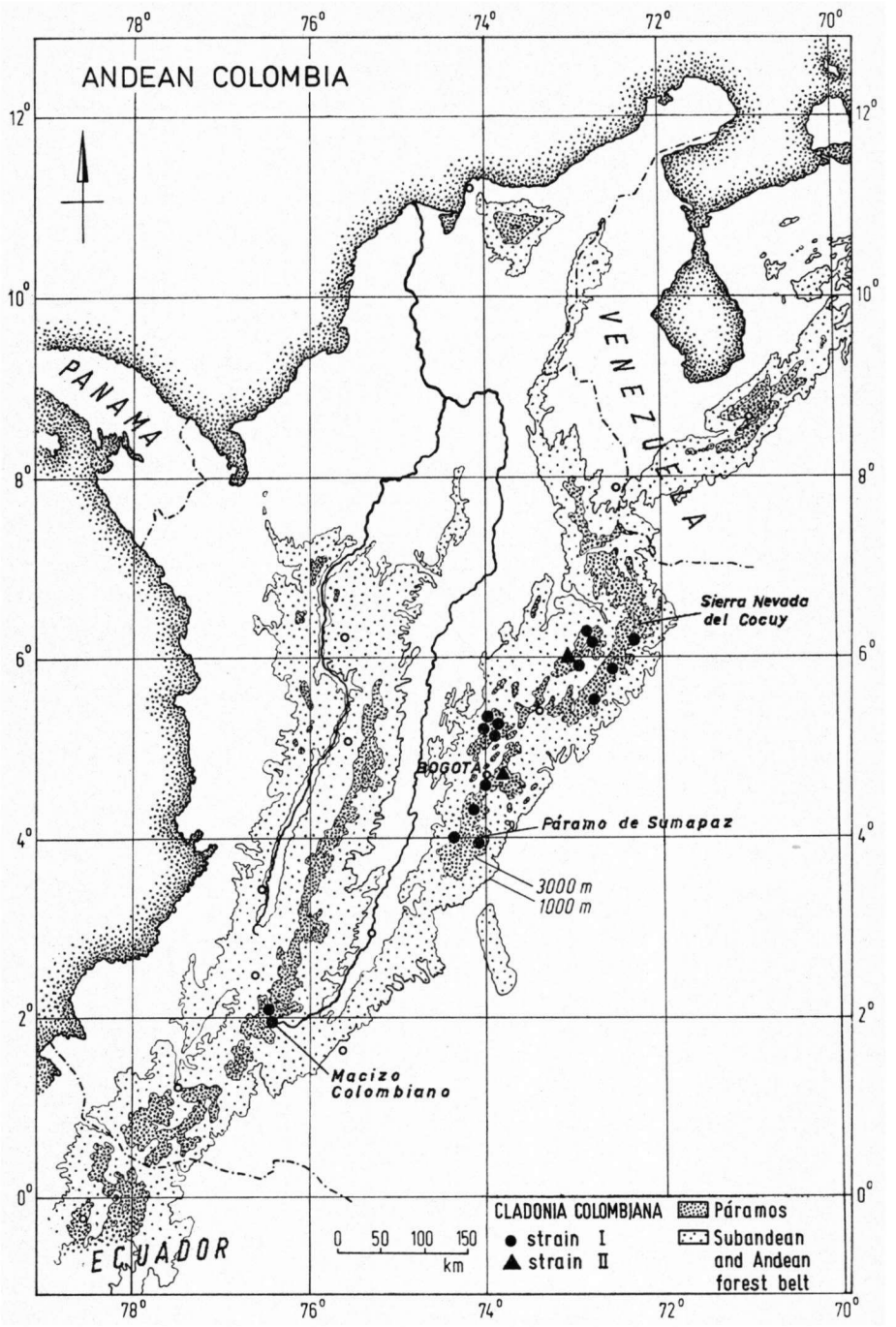
The geographical distribution within Colombia is still incompletely known. Most of the newly collected material comes from the Eastern Cordillera; the other Cordilleras are underrepresented.

The following range extensions, as compared with the data given by Ahti (1961), have been found: *C. boliviana*, new to the Eastern Cordillera and the Macizo Colombiano; *C. confusa* and *C. polia*, new to the Western Cordillera. The Colombian record of *C. rotundata* is the first outside Peru. An example of the usual distribution pattern is given by the map of *C. colombiana* (map 1).

ECOLOGY

The species of *Cladonia* subgenus *Cladina* nearly always grow in open vegetations; they are apparently strongly photophilous. A detailed account of their general ecology was provided by Ahti (1961).

In the Andean forest belt of Colombia they occur terrestrically in dry *Quercus* forests (e.g. *C. arcuata*, *C. confusa* strain I), on screes (*C. polia*) and under bushes in arid regions (*C. confusa* strain I, *C. rangiferina* var. *abbayesii*).



Map 1. Distribution of *Cladonia colombiana* spec. nov. (based on the collections studied).

In the páramo belt these species are best developed in *Sphagnum* bogs: *C. boliviana* strain I, *C. colombiana* strain I, *C. confusa*, *C. polia*. Other, more or less humid habitats are: dense *Espeletia* stands, with *C. colombiana* strain I and *C. confusa*; *Diplostephium revolutum* dwarf forests, with *C. confusa* strain I and *C. polia*; and *Swallenochloa* bamboo páramos, with *C. boliviana*, *C. confusa* strain I and *C. polia*. In the dry zonal *Calamagrostis effusa* páramos *Cladonia confusa* is the most frequent species, sometimes *C. polia*. The shelter of low subpáramo bush is another common habitat for several species: e.g. *C. boliviana*, *C. confusa* strain I, *C. rangiferina* var. *abbayesii*, *C. colombiana* strain I and *C. arcuata*. The occurrence of these lichens in the driest páramos is apparently limited by the frequency of fire and trampling of cattle. Nearly all taxa of *Cladonia* subgenus *Cladina* treated here may also grow on exposed rocks in the páramo belt, except for *C. confusa* and *C. arcuata*. *C. confusa* is probably the most common species in the páramos, growing in nearly all kinds of habitats.

The ecological notes provided here are based on vegetation relevées and field notes taken by the second author. For a general description of the vegetation belts of the Colombian Andes reference is made to Cuatrecasas (1934, 1958), Van der Hammen (1974) and Gradstein, Cleef and Fulford (1977). Special ecological information regarding Colombian páramos is given by Cuatrecasas (1968) and Cleef (1978). The altitudinal subdivision of the páramo belt is treated in detail by Cleef (in press).

Cladonia Wigg. subgenus **Cladina** (Nyl.) Leight. em. Vain. Important litt.: Ahti, Ann. Bot. Soc. "Vanamo" 32 (1). 1961.

Primary thallus absent (observed rarely, crustose); podetia without true outer cortex, soredia or squamules, strongly branched.

1a Main stems clearly distinct from base to near apex; tips of the podetia often "combed": tips deflexed in one direction; P+ red, rarely P−, but then podetia clearly combed 2
b Main stems indistinct or absent; tips not "combed"; P− . . . 5

2a Colour yellowish grey – greenish grey; usnic acid present; KC+ yellow, K− or K+ yellow-orange . . . . . **1. C. boliviana**
b Colour whitish grey; usnic acid absent; KC−, K− or K+ pale yellow 3

3a Tips strongly "combed"; atranorin mostly absent . . . . . **5. C. colombiana**
b Tips hardly "combed"; atranorin present 4

4a Main stems coarse, usually over 1.2 mm diam.; branchlets short and thick; pycnidial jelly colourless . . . . . **4. C. rangiferina v. abbayesii**
b Main stems slender, under 1.2 mm diam.; branchlets long and slender; pycnidial jelly red . . . . . **6. C. arcuata**

5a Colour pale grey, often with brown stains; usnic acid absent; KC− . . . . . **3. C. polia**

b Colour pale yellow – greenish grey, sometimes with brown stains; usnic acid present; KC+ yellow 6

6a Main stems rather coarse, usually about 1 mm thick; trichotomy frequent; plants of cool mountain areas . . . . . **2. C. confusa**

b Mains stems very thin, usually about 0.5 mm thick; dichotomy only; lowland plant . . . . . **7. C. rotundata**

1. Cladonia boliviana Ahti, Ann. Bot. Soc. "Vanamo" 32 (1): 131. 1961 – Type: Bolivia, La Paz; 10.000 ft., 1889 *M. Bang* 20 (UPS). Plate 2, fig. D.

Thallus yellowish- or greenish-grey, without brown stains.

Ramifications mainly dichotomic with a considerable amount of tetrachotomy; also sometimes trichotomy. Strong anisotomy; main stems well developed and easily discernible from base to near apex. Main stems and branches coarse; stem diameter (1–)1.5(–2) mm. Not forming round heads. Branches more or less unilaterally deflexed.

Cortex surface smooth. Pycnidia always present, with colourless jelly.

Chemistry. Strain I: usnic and fumarprotocetraric acid; colour reactions P+ red, K−, C−, KC+ yellow. Strain II: usnic acid only; colour reactions P−, K−, C−, KC+ yellow. Strain III: usnic and stictic acid; colour reactions P+ yellow-orange, K+ yellow-orange, C−, KC+ yellow.

OBSERVATIONS

C. boliviana resembles the boreal *C. arbuscula* (Wallr.) Rabenh. The exact degree of relationship should be further investigated.

The chemical strains recognized do not seem to be correlated with any morphological difference. The most distinct is strain III, represented by only 6 specimens, all of which are fairly small and slender.

Cladonia confusa strain II has the same chemical contents as *C. boliviana* strain II. It may be distinguished from forms of *C. boliviana* with frequent trichotomies by the absence of lateral deflexions, the rarity of pycnidia or by the different cortex structure, which is smooth in *C. boliviana* and somewhat felty in *C. confusa*.

DISTRIBUTION

Humid, high parts of the tropical Andes mountains, in Bolivia, Peru, Ecuador and Colombia (Ahti 1961).

In Colombia the species has been recorded from depts. Antióquia, Arauca, Boyacá, Cauca, Cundinamarca and Meta, mainly between 2900 and 4000 m alt. It was collected only once between 1500 and 2000 m. The collections of strain I (27) are located on both sides of the Eastern Cordillera from Cocuy to Sumapaz, and in the Central Cordillera; the

collections of strain II (13) are from the same part of the Eastern Cordillera, but mainly on the W-side; the collections of strain III (6) are from the Páramo de Guantiva and the Páramo de la Rusia in the Eastern Cordillera and from the northern Central Cordillera (alt. 1500–2000 m).

Additional material has been studied from Bolivia (Bang 1849, (UPS)).

ECOLOGY

Strain I occurs most frequently in subpáramo *Sphagnum* bogs with giant *Puya* spp., *Espeletiinae* and *Xyris acutifolia*, associated with *Cladonia colombiana*, *C. confusa* and *C. polia*. In the zonal páramo it is common in humid communities of *Swallenochloa*, and in drier open dwarf shrub of *Arcytophyllum nitidum*, *Disterigma empetrifolium*, *Hypericum* spp. and *Senecio* spp. Some specimens were collected on humid windswept rocks frequently enveloped by fog, at about 3700 m.

Strain II generally grows in slightly humid, open, low shrub of e.g. *Aragoa abietina*, *Arcytophyllum caracasanum*, *A. nitidum*, *Ericaceae* etc., most frequently in the lower grass páramo. Single records are 1) from a rather dry habitat in a bog below *Aragoa abietina* thicket at about 3600 m; 2) from exposed humid rocks at 3800 m, associated with *Siphula pteruloides*, *Stereocaulon* spp., *Thamnolia vermicularis* and *Campylopus pittieri*; 3) on soil in the atmospherically humid bamboo páramo.

Strain III has been collected in slightly humid habitats in the upper subpáramo and grass páramo. Two specimens, gathered at about 3900 m came from *Arcytophyllum caracasanum* vegetation over humid sandstone outcrops, associated with *Rhacocarpus purpurascens* and *Racomitrium crispulum*.

2. **Cladonia confusa** Sant., Ark. Bot. 30A, 10: 13. 1942 – Type: Ecuador, Imbabura, Lake Cuicocha, Islote Chica, in a block field, 3150 m, 1939, *E. Asplund* L 107, Lich. austroamer. herb. Regnell. 351 (S) (seen). Plate 1, fig. B.

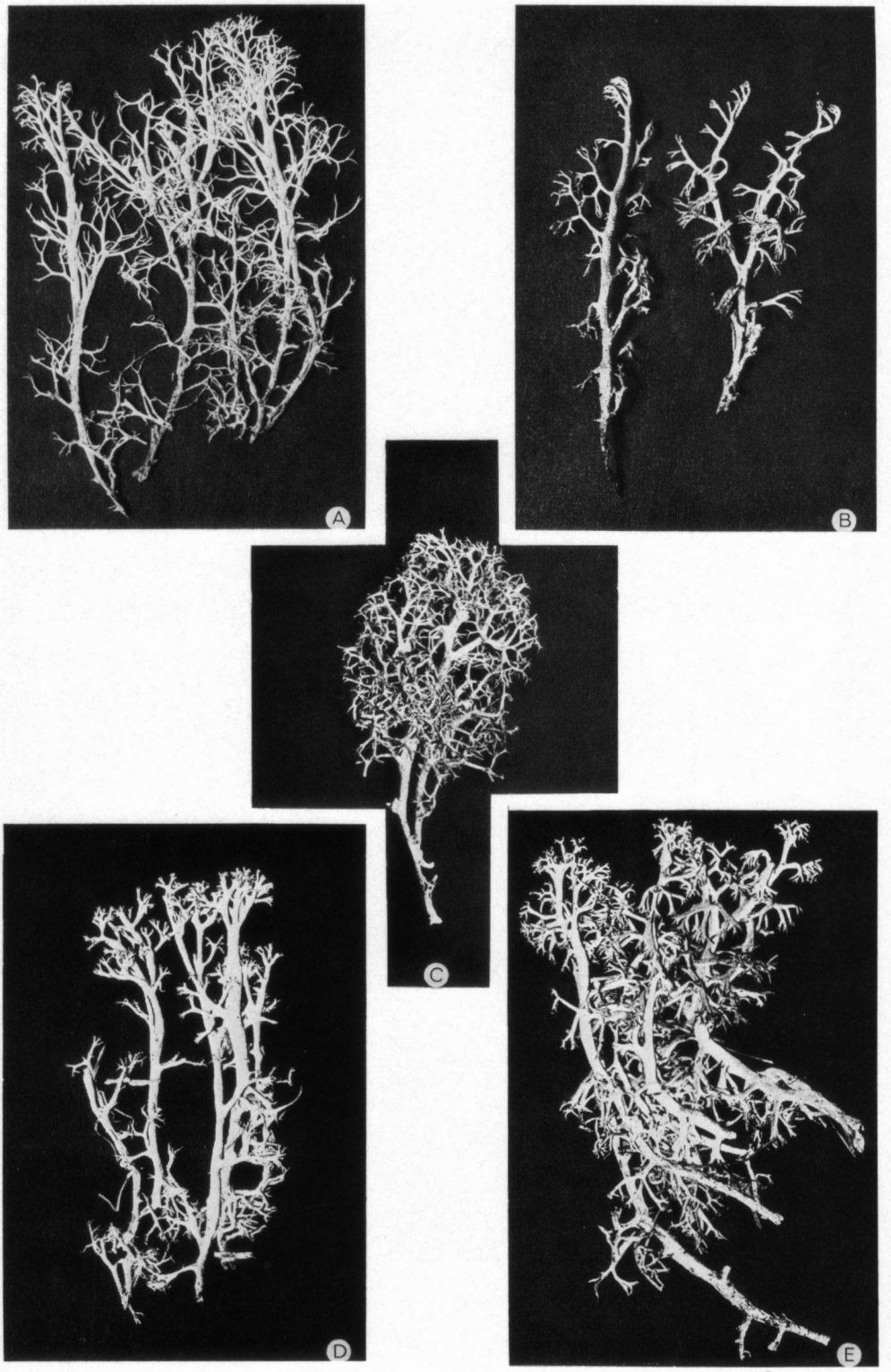
Thallus pale yellow-greenish grey, sometimes with brown or purplish-brown stains covering large portions of the thallus.

Ramifications usually distinctly trichotomic, but often dichotomy being dominant. Anisotomy little developed; main stems little developed and dichotomously branched, often not clearly recognizable. Main stems thin, 0.5–1(–1.5) mm diam. Often forming round heads. Branches not unilaterally deflexed.

Cortex surface usually felty. Pycnidia infrequent, with colourless jelly (according to Ahti 1961).

Chemistry. Strain I: usnic acid, perlatolic acid; colour reactions P—, K—, C—, KC+ yellow. Strain II: usnic acid only; colour reactions P—, K—, C—, KC+ yellow.

Plate 1A, *Cladonia colombiana* spec. nov. on soil in bamboo-páramo *Sphagnum* bog at 3600 m near the Lagunas de Buitrago, Páramo de Palacio near Bogotá, Colombia, Cordillera Oriental (colour-slide A. M. Cleef). **B,** *Cladonia confusa* Sant. (strain II; Cleef 5350) growing over organic litter in humid bamboo-páramo at 3650 m in the headwaters of Río Chuza near the Laguna Seca, about 30 km East of Bogotá, Colombian Cordillera Oriental (colour-slide A. M. Cleef).


A
B
C
D
E

OBSERVATIONS

C. confusa resembles the boreal *C. portentosa* (Duf.) Zahlbr. (syn. *C. impexa* Harm., fide Ahti in Poelt & Vezda 1977) by the trichotomy, the felty cortex and the presence of perlatolic acid. It differs in the more isotomic branching and in the less regular presence of perlatolic acid.

The two chemical strains of *C. confusa* were not found to differ significantly in morphological respects. As the content of perlatolic acid seems to be somewhat variable, strain II may include specimens with perlatolic acid in undetectable amounts.

Some specimens have a curious bicoloured appearance: a large part of the thallus is stained with brown but the upper part is pale yellow. They resemble *C. polia* specimens described as *C. bicolor* but differ in the presence of usnic acid.

See the discussions under *C. boliviana* and *C. polia* for differences between these species.

DISTRIBUTION

Humid mountain areas throughout tropical America, from Mexico to the Dominican Republic, Uruguay and Bolivia (Ahti 1961).

This species seems to be widely distributed in the Colombian Andes. It has been found in dept. Antióquia, Arauca, Boyacá, Cauca, Cundinamarca, Meta, Santander, Tolima and Valle, between 2300 and 3950 m alt., mainly between 3200 and 3800 m. The specimens available of strain I (45) and of strain II (5) were found in the Eastern, Central and Western Cordillera.

Further material was studied from Costa Rica (Cleef 10209 (U)) and Ecuador (type, and Cotopaxi: Gradstein, Sipman & De Vries 91 (U)).

ECOLOGY

Strain I: Below the páramo belt this strain was found in dry *Quercus* and *Weinmannia* forests in the Andean forest belt, as well as in protected sites on stony slopes in semidesert vegetation at 2450 m.

In the páramo belt it is most common on the atmospherically dry side of the mountains up to 3950 m. Especially it is characteristic for the dry zonal upper subpáramo vegetation of *Arcytophyllum nitidum* and *Cala-*

Plate 2, (All figures approximately natural size). **A,** *Cladonia arcuata* Ahti. Colombia, dept. Boyacá. Near Arcabuco, alt. 2600 m. Andine oakwood (Cleef 7523b, U). **B,** *Cladonia colombiana* spec. nov. Colombia, dept. Cundinamarca. Páramo de Cruz Verde, alt. 3455 m. In bog (Cleef 3207, U). **C,** *Cladonia polia* Sant. Colombia, dept. Cundinamarca. Páramo de Palacio, alt. 3230 m. Dry open subpáramo bush (Cleef 3662b, U). **D,** *Cladonia boliviana* Ahti. Colombia, dept. Boyacá. Sierra Nevada del Cocuy: Páramo Cóncavo, alt. 3770 m. *Sphagnum* bog (Cleef 10012, U). **E,** *Cladonia rangiferina* (L.) Wigg. var. *abbayesii* Ahti. Colombia, dept. Boyacá. Páramo de la Sarna, East of Sogamoso, alt. 3570 m. In bog (Cleef 3570, U).

magrostis effusa associated with *Espeletiopsis spp.*, e.g. *E. corymbosa*, *E. garciae*, *E. glandulosa*, *E. guacharaca* and *E. pleiochasia*. In the grass páramo it occurs in several grassland communities, usually with *Calamagrostis* or *Swallenochloa*, associated with *Espeletia* spp. and bryophytes. Also it was gathered under low shrubs of *Aragoa spp.*, *Arcytophyllum caracasanum*, *Disterigma empetrifolium* and *Hypericum spp.* Common is its occurrence in *Sphagnum* bogs with *Espeletia* spp., giant *Puya spp.* and *Swallenochloa*. Other collections were made in the humid zones surrounding bogs and in humid dense *Espeletia* stands of e.g. *E. arbelaezii*, *E. barclayana*, *E. congestiflora*, *E. murilloi*. One specimen was collected on hummocks in marshy *Diplostephium revolutum* dwarf forest at 3800 m.

Strain II was mostly collected in páramos in various vegetation types but always at protected sites: e.g. in dense *Espeletia* stands and in humid vegetation surrounding páramo bogs.

3. **Cladonia polia** Sant., Ark. Bot. 30A, 10: 15. 1942. Type: Venezuela, Federal District, the Coastal Cordillera between Caracas and La Guaira, west of the Silla de Caracas, on the ground in rather low, open wood, 1600–1800 m, 1941, *R. Santesson* 6665 (S) (seen). – **C. bicolor** (Müll. Arg.) Ahti, Ann. Bot. Soc. 'Vanamo' 32 (1): 45. 1961. **Syn nov.** – Type: Colombia, prope Aganche, in alte valle flum. Cauca, inter saxa, in locis denudatis frequens, terricola, 1280 m, 1876, *Ed. André* 926 (K, isotype) (seen). Plate 2, fig. C.

Thallus gray-white, usually with brown or purplish-brown stains covering large portions of the thallus.

Ramifications usually dominantly trichotomic, but often dichotomy being dominant, and occasionally tetrachotomy occurs. Anisotomy generally little developed; main stems often little developed and dichotomously branched, but usually recognizable in well developed plants (over 3 cm high). Main stems thin, 0.5–1(–1.5) mm diam. Often forming round heads. Branches not unilaterally deflexed.

Cortex surface felty. Pycnidia infrequent, about as frequent as the apothecia, with colourless jelly.

Chemistry. Perlatolic acid only; colour reactions P –, K –, C –, KC –.

OBSERVATIONS

C. polia in many respects resembles *C. confusa*. It differs by: 1. absence of usnic acid; 2. constant presence of perlatolic acid; 3. absence of yellow colour (due to absence of usnic acid); 4. more frequent brown stains; 5. slightly more distinct main stems. Although the morphological differences are rather weak, the correlation with conspicuous chemical differences provides reason for maintaining *C. polia* as a species.

Cladonia bicolor is characterized according to Müller Arg. (1879, as forma) by the presence of brown apices. According to Ahti (1961) it differs from its nearest relatives as follows: from *C. confusa* mainly by

presence of brown staining, absence of usnic acid and less strongly developed globose heads; from *C. polia* mainly by the more chocolate-brown staining and shorter internodes. The morphological differences cited and the degree of brown staining proved to be so variable in our specimens that only *C. confusa* and *C. polia* could be accepted, while *C. bicolor* is reduced to synonymy under *C. polia*.

DISTRIBUTION

Humid zone of the high mountains in Central and South America: found in Costa Rica, Colombia, Peru, Venezuela (Ahti 1961).

In Colombia the species seems to be widely distributed along the Andes, between about 2300 and 4000 m alt., occasionally descending to ca 1280 m. Material was seen from depts. Antióquia, Arauca, Boyacá, Cauca, Cundinamarca and Meta. In addition records from Putumayo and Tolima are given by Ahti (1961). The known localities (43) are situated along both sides of the Eastern Cordillera from Cocuy to Sumapaz, in the Macizo Colombiano, the Western and the Central Cordillera.

Additional material was studied from Venezuela (type) and Peru (sub. nom. *C. bicolor*: Lechler, P. Peruv. 3129 (UPS); Pennell 1948 (UPS)).

ECOLOGY

Most specimens are from *Sphagnum* bogs in the subpáramo and grass páramo belt (3270–4020 m). Typical accompanying species here are: *Espeletia spp.*, *Puya goudotiana*, *Swallenochloa spp.*, *Xyris spp.*, *Breutelia spp.*, *Campylopus cucullatifolius*, *Sphagnum magellanicum*, *S. oxyphyllum*, *S. sancto-josephense*, *Cladonia boliviana*, *C. colombiana* and *C. confusa*. In addition the species is known from boggy *Diplostephium revolutum* dwarf forest between about 3500 and 3800 m and from the zonal open upper subpáramo vegetation.

C. polia usually grows on soil over organic material, although a few epilithic records are also known from exposed outcrops in atmospherically humid páramos (at 3600–3900 m). The lowermost record at 1280 m is from a scree.

4. Cladonia rangiferina (L.) Wigg. var. **abbayesii** Ahti, Ann. Bot. Soc. 'Vanamo' 32 (1): 94. 1961. – Type: Colombia ("Nova Granata"). Bogotá, alt. 3100 m, 1860–'70 *Lindig* 2513 (UPS) (seen). Plate 2, fig. E.

Thallus chalky white, sometimes with brown or purplish-brown stains covering a considerable part of the thallus.

Ramifications dichotomic with hardly any exceptions. Strong anisotomy; main stems well developed, easily discernible from the base to near the apex. Main stems and branches coarse; stem diameter 1–1.5(–2) mm. Not forming round heads. Branches spuriously unilaterally deflexed.

Cortex surface smooth but spuriously felty; cortex often thick. Pycnidia always present, with colourless jelly.

Chemistry. Atranorin and fumarprotocetraric acid; colour reactions P+ red, K+ pale yellow, C−, KC−.

OBSERVATIONS

Cladonia rangiferina var. *abbayesii* differs from the widespread boreal species *C. rangiferina* by the constant scarcity of unilateral deflexions and of tetrachotomy. The remaining Colombian specimens resembling *C. rangiferina* in the grey colour and the positive P-reaction are described below as *C. arcuata* and *C. colombiana*. They differ from it by the presence of red instead of colourless pycnidial jelly, and by the frequent absence of atranorin. Moreover *C. colombiana* differs from var. *abbayesii* by the presence of strong unilateral deflexions.

Some plants have very short and almost upright, reduced branches, e.g. Cleef 4043, 9413.

The characteristic thick cottony cortex is sometimes poorly developed, even on young branches.

Slender forms resemble *C. arcuata*, which differs by the absence of a thick cortex, the slender habitus and the presence of red pycnidial jelly (which, however, could not be observed in our Colombian material).

The exsiccate of *C. rangiferina* var. *abbayesii* in Hale, Lich. Am. Exs 178, actually belongs to *C. arcuata*.

DISTRIBUTION

Humid mountains in tropical America, from Colombia and Venezuela to Haïti and Mexico (Ahti 1961).

In Colombia it has been found in the depts. Antióquia, Boyacá, Cundinamarca and Santander, between 2450 and 4050 m alt. (Ahti 1961). The available collections (12) are from the Eastern Cordillera, between Bogotá and the Sierra Nevada del Cocuy, mainly from the drier side of the range.

ECOLOGY

The lowermost records in Colombia are from arid to semi-desertic areas. Several specimens were collected in the zonal dry upper subpáramo under shrubs on stony slopes. In the humid bamboo páramos at 3700–3800 m it is only found on rock outcrops, probably the driest habitat in this environment. Two records are from *Sphagnum* bog with *Espeletia murilloi* and *Xyris acutifolia*.

5. Cladonia colombiana Sipman, **spec. nov.** – Type: Colombia. Boyacá: Páramo de la Sarna entre Sogamoso y Vado Hondo. Turbera con *Sphagnum, Xyris* y *Espeletia murilloi*. Alt. 3375 m. 5.IV.1973. *A. M. Cleef* 9382 (COL, isotypes in U, US, H). Plate 1, fig. A; plate 2. fig. B.

Diagnosis. Podetia cinereo-albida, saepe late fuscescentia, dichotome inaequaliter ramosa, axibus principalibus apertis a basi usque ad vicinitatem apicis, ramis paulum latioribus, 0.7–1.2(–2) mm diametro, in summo

ramulis unilateraliter nutantibus, pulvillos rotundatos haud efficientia, superficie plana sed laeviter tomentosa. Pycnidia frequentissima, gelatinam coccineam continentia. Podetia acidum fumarprotocetraricum et nonnumquam atranorinam continentia.

Thallus ash-white, often with brown or purplish-brown stains covering most of the thallus.

Ramification dichotomic, with hardly any exceptions. Strong anisotomy; main stems well developed, easily discernible from the base to near the apex, but usually not much thicker than the branches. Main stems 0.7–1.2(–2) mm diam. Not forming round heads. Branches strongly unilaterally deflexed.

Cortex surface smooth but spuriously felty. Pycnidia mostly present, with red jelly.

Chemistry. Strain I: fumarprotocetraric acid only; colour reactions P+ red, K−, C−, KC−. Strain II: fumarprotocetraric acid and atranorin; colour reactions P+ red, K+ pale yellow, C−, KC−.

OBSERVATIONS

Cladonia colombiana forms part of the Colombian specimens of *Cladonia* subgenus *Cladina* which resemble *C. rangiferina* by their grey colour and positive P-reaction. These specimens can be arranged mostly into two groups, one with atranorin and with hardly deflexed apical branchlets, and the other without atranorin and basely deflexed apical branchlets. The first group can be classified as *C. rangiferina* var. *abbayesii* or *C. arcuata*. The second group (*C. colombiana*) resembles *C. arcuata* because of the slender podetia and red pycnidial jelly, but the strong unilateral deflexion of the branchlets makes a marked difference. Also it is found at higher altitudes, usually in the subpáramo and páramo belt, whereas *C. arcuata* in Colombia is found only in the Andean forest belt. Therefore I have described it as a new species. A few specimens with atranorin have been detected.

DISTRIBUTION

Known from the high Andes of Colombia only, where it was collected in the depts. Boyacá, Cauca, Cundinamarca and Meta, between 2800 and 3950 m alt. The collections of strain I (25) are from both sides of the Eastern Cordillera and from the Macizo Colombiano. The collections of strain II (2) are from the Páramo de la Rusia and the Páramo de Palacio in the Eastern Cordillera (map 1).

ECOLOGY

Strain I of *Cladonia colombiana* was collected mostly in *Sphagnum* bogs and surrounding humid vegetation between 2900 and 3700 m in the lower part of the páramo belt. A frequent site was in marshy, dense *Espeletia* stands, associated with *Xyris spp.*, *Oreobolus sp.*, *Puya spp.*, *Pleurozium*

schreberi, *Breutelia spp.*, *Cladonia boliviana*, *C. confusa* and *C. polia*. In the more or less open, zonal vegetation of the lower páramos at about (2800–)3300–3800 m *C. colombiana* occurs commonly on protected sites with dwarfshrubs, e.g. *Aragoa abietina*, *Arcytophyllum nitidum*, *Gaylussacia buxifolia*, *Hypericum spp.*, *Senecio nitidus*, and with mosses. Occasionally it is found in *Calamagrostis effusa* páramos on open humid sites at 3500–3800 m, with *Espeletia spp.* and many bryophytes, terrestrial as well as on humid sandstone and limestone rocks.

Strain II was found on sandstone outcrops in atmospherically humid bamboo páramos at 3800 and 3825 m, associated with *Parmeliaceae*, *Alectoria sp.*, *Andreaea rupestris*, *Campylopus pittieri*, *C. richardii*, *Cladonia boliviana*, *Cora pavonia*, *Grimmia sp.*, *Jamesoniella rubricaulis*, *Racomitrium crispulum* and *Rhacocarpus purpurascens*.

6. Cladonia arcuata Ahti, Ann. Bot. Soc. 'Vanamo' 32 (1): 73. 1961. – Type: Bolivia, La Paz, prov. Yungas, inter San Felipe et El Chaco, 2500 m, 1920, *E. Asplund* 34 (S) (isotype from UPS seen). Plate 2, fig. A.

Thallus chalky white, without brown stains.

Ramifications dichotomic with hardly any exceptions. Clear but not very strong anisotomy; main stems and branches slender. Main stems 0.7–1.2 mm diam. Not forming round heads. Branches spuriously unilaterally deflexed.

Cortex surface smooth but spuriously felty. Pycnidia always present, with red jelly.

Chemistry. Strain I: fumarprotocetraric acid; colour reactions P+ red, K−, C−, KC−. Strain II: fumarprotocetraric acid and atranorin; colour reactions P+ red, K+ yellow, C−, KC−.

OBSERVATIONS

The isotype studied differs from the type description and the Colombian specimens by its lack of atranorin. The red pycnidial jelly has not been observed in the available material.

C. arcuata resembles *C. colombiana* by its slender form and the presence of red pycnidial jelly. It differs in the almost complete absence of unilaterally deflexed branchlets. Moreover it is a species of the Andean forest rather than the páramo belt.

For differences with *C. rangiferina* var. *abbayesii* see under this taxon.

Cladonia sandstedei des Abb., a related tropical lowland species with slender habitus and red jelly, differs by the isotomic branching.

DISTRIBUTION

High mountains of tropical South America: Bolivia, Colombia, Ecuador, Venezuela (Ahti 1961).

Our Colombian records (3), all belonging to strain II, are from depts. Boyacá and Santander (Eastern Cordillera), alt. 2600–2825 m. Ahti reports

collections from the Western Cordillera, depts. Antióquia, alt. 2100 m (Ahti 1961) and Chocó, alt. 2680 m (in litt.) and from the Central Cordillera, dept. Cauca, alt. 2700 m (in litt.).

An additional collection has been studied from Venezuela (Hale, Lich. Am. Exs. 178, sub nomine *C. rangiferina* var. *abbayesii*).

ECOLOGY

Our Colombian collections are from dry, open *Quercus* forest and dry, stony lower subpáramo with *Espeletiopsis*. Probably the species is common in open, ecotonic vegetation types in the Andean forest belt between about 2000 and 3000 m alt.

7. Cladonia rotundata Ahti

This species was present among the collections in COL, e.g. Garcia-Barriga 13743 (illustrated in Garcia-Barriga 1974, fig. 10; det. H. Sipman). It is not treated further because it is a lowland species.

EXCLUDED NAMES

Cladonia bicolor (Müll. Arg.) Ahti

This species is reduced to synonymy under *C. polia*.

Cladonia incurva Ahti

This species is recorded by Ahti (1961) with doubt. Its presence in Colombia could not be confirmed.

COLOMBIAN SPECIMENS SEEN (preserved in COL and U, unless otherwise stated)

Cladonia arcuata Ahti

BOYACA: Cleef 7523b; SANTANDER: Cleef, Garcia-B. & Jaramillo-M. 3499b; Fassett 25709 (UPS).

Cladonia boliviana Ahti, strain I.

ARAUCA: Cleef 9127; BOYACA: Cleef 4245, 4264, 4423, 4469, 4588b, 4631, 9268, 9331, 9349, 9369, 9388, 9388b, 9752b, 9866c, 9931, 9948, 10012; CAUCA: Cleef 2625; CUNDINAMARCA: Barclay & Juajibioy 6134 (COL); Cleef 6445b, 8318; Cleef & Jaramillo-M. 3087; META: Cleef 913c, 914, 8198b.

Cladonia boliviana Ahti, strain II.

BOYACA: Cleef 6995, 7161b; CUNDINAMARCA: Cleef 18, 162, 724, 3276, 3346b, 4022d, 5228d, 5350, 6215, 6381, 6418c.

Cladonia boliviana Ahti, strain III.

ANTIOQUIA: Archer 1217 (S); BOYACA: Cleef 6758, 6829b, 6858, 7005c, 9717a.

Cladonia colombiana Sipm. nov. sp., strain I.

BOYACA: Cleef 4588, 6757, 6857, 7161b, 9311, 9330, 9373, 9382, 9386, 9752d, 9866d; CAUCA: Bischler 788 (COL); CUNDINAMARCA: Cleef 104,

728, 3207, 3595c, 6148, 6187, 6378, 6418, 8321; Cleef & Jaramillo-M. 3083, 4145; META: Cleef 7617.

Cladonia colombiana Sipm. nov. sp., strain II.

BOYACA: Cleef 6994; CUNDINAMARCA: Cleef 5228e.

Cladonia confusa Sant., strain I.

ANTIOQUIA: Wallis s.n. (TUR); ARAUCA: Cleef 9127c; BOYACA: Cleef 2135, 6758c, 6810, 6840, 6931, 7161, 7522, 9268b, 9268c, 9354b, 9514, 9549a, 9752, 9866, 10012b; Cleef, Cuatrecasas & Jaramillo-M. 9227; Cleef, Garcia-B. & Jaramillo-M. 3473; CUNDINAMARCA: Cleef 20, 450, 708, 723, 1681, 2809, 2811, 3023, 3307, 3346, 3375, 3595b, 3662, 3670, 4876, 4948, 6291, 6369, 6405, 6468, 6503, 6522, 6655, 8320; META: Cleef 914; SANTANDER: Cleef, Garcia-B. & Jaramillo-M. 3499.

Cladonia confusa Sant., strain II.

ANTIOQUIA: Daniel 3404 (COL); BOYACA: Cleef 6397, 9369b; CUNDINAMARCA: Cleef 3818, 3953; VALLE: Cuatrecasas 20276 (COL).

Cladonia polia Sant.

ANTIOQUIA: Frère Vincente s.n. (L); Wallis s.n. (TUR: Vain. 13346 p.p.); ARAUCA: Cleef 9141, 10058, 10094; Cleef & Van der Hammen 10324; BOYACA: Cleef 4423b, 4631b, 6931b, 9354, 9390, 9514b, 9717b, 9933, 9947; CAUCA: André 926 (K in BM); Cleef 2625b; Cleef & Fernandez-P. 507; CUNDINAMARCA: Barkley, Garcia-B. & Vanegas 17c 789 (COL); Cleef 1606, 1682, 2983, 3208, 3324, 3381, 3595, 3662b, 3818b, 3953b, 5228, 5345, 6222, 6241, 6290, 6368, 6407, 6467, 8320b; Cleef & Florschütz 5474; Perez-Arbelaez 55 (COL); HUILA-CAUCA: Bischler 702 (COL); META: Cleef 1058, 8219.

Cladonia rangiferina (L.) Wigg. var. *abbayesii* Ahti

BOYACA: Cleef 7463, 7484, 7523, 9329, 9413, 9752c, 9869; Cleef, Garcia-B. & Jaramillo-M. 3474; CUNDINAMARCA: Cleef 10, 6458; Cleef & Jaramillo-M. 4043; Lindig 2513 (UPS).

ACKNOWLEDGEMENTS

Thanks are due to the staff of the Instituto de Ciencias Naturales – Museo de Historia Natural of the Universidad Nacional de Colombia in Bogotá for close colaboration during fieldwork, to Prof. Dr. T. Ahti (Helsinki), Dr. S. R. Gradstein (Utrecht) and Dr. M. E. Hale (Washington) for helpful criticism on the manuscript, Dr. Gradstein too for the correction of the English text and to the curators of the herbaria cited for generously providing specimens. Mr. A. Kuiper and Mr. H. Rypkema respectively took care of the photographs and the map. Financial fieldwork support to the second author by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO) is gratefully acknowledged.

REFERENCES

Ahti, T. – Taxonomic studies on Reindeer Lichens (Cladonia, subgenus Cladina). Ann. Bot. Soc. Zool. Bot. Fenn. "Vanamo" 32 (1), 1–160, pl. 1–44 (1961).

Cuatrecasas, J. – Observaciones geobotánicas en Colombia. Trab. Mus. Nac. Cienc. Nat. Ser. Bot. 27, 144 pp. (1934).

Cuatrecasas, J. – Aspectos de la vegetación natural de Colombia. Rev. Acad. Col. Cienc. E. F. Nat. 10, 40 (1958).

Cuatrecasas, J. – Páramo vegetation and its life forms. In: Geo-ecology of the mountainous regions of the tropical Americas. Coll. Geogr. 9, 163–186 (1968).

Cleef, A. M. – Characteristics of neotropical páramo vegetation and its subantarctic relations. Erdwiss. Forsch. 11, 365–390. Wiesbaden (1978).

Cleef, A. M. – Secuencia altitudinal de la vegetación de los páramos de la Cordillera Oriental, Colombia. Proc. 4. Int. Symp. Trop. Ecol., Panamá (in press).

Culberson, C. F. – Improved conditions and new data for the identification of lichen products by a standardized Thin-Layer Chromatographic method. J. Chromatography 72, 113–125 (1972).

Culberson, C. F., W. L. Culberson and A. Johnson – Thermally induced chemical artifacts in lichens. Phytochemistry 16, 127–130 (1977).

García-Barriga, H. – Flora Medicinal de Colombia I, 564 p. Bogotá, D. E. (1974).

Gradstein, S. R., A. M. Cleef and M. H. Fulford – Studies on Colombian cryptograms II, Hepaticae: Oil body structure and ecological distribution of selected species of Tropical Andean Jungermanniales. Proc. Kon. Ned. Ak. Wet. Ser. C 80 (5), 378–420 (1977).

Hale, M. F. Jr. and W. L. Culberson – A Fourth Checklist of the Lichens of the Continental United States and Canada. Bryologist 73, 499–543 (1970).

Hammen, T. van der – The Pleistocene changes of vegetation and climate in tropical South America. J. Biogeogr. 1, 3–26 (1974).

Müller, J. – Les Lichens neo-grenadiens et ecuatoriens récoltés par M. Ed. André. Rev. Mycol. 1879 (4), 160–171 (1879).

Nylander, W. – Lichenes I, in: J. Triana and J. E. Planchon, Prodromus Florae Novo-Granatensis. Ann. Sci. Nat. 4me série botanique, T. 19, 286–382 (1863).

Poelt, J. and A. Vězda – Bestimmungsschlüssel europäischer Flechten. Ergänzungsheft I. Biblioth. Lichenol. 9. J. Cramer, Vaduz, 258 pp. (1977).

Santesson, R. – The South American Cladinae. Ark. Botanik 30A (10), 1–27 (1942).

Thomson, J. W. – The Lichen Genus Cladonia in North America. Univ. Toronto Press, 172 pp. (1968).