

STUDIES ON COLOMBIAN CRYPTOGAMS XVIII THE GENUS *STEREOCAULON* (SCHREBER) HOFFMANN (LICHENES)

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ABSTRACT. Nineteen species of *Stereocaulon* are treated from the northern Andes, mainly from Colombia. Descriptions and keys are given, with notes on the north-Andean distribution and ecology. Seven species are new for the Colombian flora, viz. *St. atlanticum*, *St. claviceps*, *St. corticatum* (chem. strain with atranorin and perlatolic acid), *St. delisei*, *St. microcarpum*, *St. pachycephalum* and *St. pomiferum*. *St. crambidiocephalum* is reported for the first time from Costa Rica, as is *St. didymicum* from Venezuela, and *St. delisei* is reported for the first time from the New World (Colombia and Costa Rica). *St. cornutum* Müll. Arg. is reduced to synonymy under *St. pityrizans* Nyl.

INTRODUCTION

The present work deals with the lichen genus *Stereocaulon* from the northern Andes, mainly from Colombia, but observations on additional material from neighbouring countries (Costa Rica, Ecuador and Venezuela) have also been included. Most of the collections on which our study was based were made by A. M. Cleef during the years 1972–1974, mainly in the Colombian Eastern Cordillera. Additional collections were gathered in Colombia by H. J. M. Sipman & H. Valencia-Z. in 1979, and by the author in 1980 during fieldwork in the framework of the "ECOANDES" research project. These collections are kept at the Instituto de Ciencias Naturales in Bogotá (COL) and at the Institute of Systematic Botany in Utrecht (U). Literature on Colombian lichens is rather scarce and dates back to Nylander (1863) and Müller Arg. (1879). Some more recent information is available a.o. in Lindau (1912) and, for *Stereocaulon*, Dodge (1929). The most recent work on *Stereocaulon*, dealing with this genus on a world-wide scale, is by Lamb (1977), which forms the taxonomic base of the present work.

Up to now 11 species and 8 infraspecific taxa of *Stereocaulon* have been reported from Colombia: *St. crambidiocephalum*, *St. glareosum*, *St. meyeri* (Lamb 1977), *St. myriocarpum* (Nylander 1863), *St. novogranatense*, *St. pityrizans* (Lamb 1977), *St. ramulosum* (Nylander 1863), *St. ramulosum* fo. *elegans*, *St. ramulosum* var. *tomentosulum* (Lamb 1977), *St. strictum*, *St. strictum* var. *compressum* (Nylander 1863), *St. tomentosum* (Lamb 1977), *St. verruciferum*, *St. vesuvianum* (Dodge 1929), *St. vesuvianum* var. *efflorescens* (Müll. Arg. 1879), *St. vesuvianum* var. *nodulosum*, *St. vesuvianum* var. *nodulosum* fo. *depressum* and fo. *umbonatum* (Lamb 1977). In the present study the following species are recorded for the first time from Colombia: *St. atlanticum*, *St. claviceps*, *St. corticatum*, *St. delisei*, *St. microcarpum*, *St. pachycephalum* and *St. pomiferum*. In addition *St. crambidiocephalum* is reported for the first time from Costa Rica and *St. didymicum* is reported new to Venezuela. *St. delisei* is recorded for the first time from the New World (Colombia, Costa Rica).

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MORPHOLOGY

The genus *Stereocaulon* is characterized by a primary thallus, consisting of structures similar to the phyllocladia, and a fruticose secondary thallus consisting of erect to creeping pseudopodetia. These bear phyllocladia, cephalodia and apothecia.

According to Lamb (1951) the pseudopodetia may develop holostelidially, through elongation of the entire primary thallus-squamule, or enteropodially, through elongation of the medullary tissue only. The ramification of the pseudopodetia is sometimes helpful to characterize species. The following ramification types are distinguished here:

1. simple with cornute apices, sometimes dichotomously branched, rarely with short branchlets (e.g. *St. obesum* and *St. pityrizans*).
2. irregularly branched (e.g. *St. corticatulum*, *St. verruciferum* and *St. vesuvianum*).
3. at base simple or with long erect branches, towards the apex more or less dichotomously branched (e.g. *St. atlanticum*, *St. crambidiocephalum* and *St. strictum*).
4. at base simple or with long erect branches, towards the apex with short patent branchlets (e.g. *St. novogranatense*, *St. pachycephalum*, *St. ramulosum* and *St. tomentosum*).

The following types of phyllocladia can be distinguished (Magnusson 1926):

1. coralloid, cylindrical and furcate.
2. papillose, short and apically tapering.
3. verrucose, wart-like.
4. granular, grain-like.
5. squamuliform, flattened, attached with one side, frequently incised.
6. peltate, umbilicate with convex to concave surface.

Phyllocladia can be unicolorous or bicolorous, the latter especially within the granular and peltate types. According to Lamb (1951) the coralloid phyllocladia are in fact pseudopodetial branchlets (= phyllocladial branchlets).

Within the specimens seen two main types of cephalodia are present (classification according to Johnson 1938):

1. spherical; these are sessile or nearly so, sometimes partly immersed, often inconspicuous, up to 1.7 (2.5) mm in diameter. Spherical cephalodia appear in aggregates or irregular rounded, grey to brown or greenish masses. *St. glareosum* has cephalodia which belong to this type, but they are nearly globose and have some resemblance with the next type. The cortex consists of loosely tangentially interwoven hyphae.
2. scrobiculate (sacculate according to Lamb 1951); these are usually stalked at maturity, globular to more or less clavate, pitted and furrowed with fine convolutions, more or less concolorous with the pseudopodetium to greyish, large and numerous, 1–7 mm in diameter. The cortex consists in most cases of strongly gelatinized perpendicular hyphae. In *St. didymicum*, however, they are less gelatinized and in *St. corticatulum*, *St. delisei* (Lamb 1976, 1977) and also in *St. novogranatense* the cephalodial cortex has a dimorphic appearance containing both gelatinized perpendicular hyphae and ribs of non-gelatinized hyphae. Macroscopically the cephalodia of *St. didymicum* are recognizable by a pruinose surface and those of the latter three species by a glabrous surface with distinct white pruinose ribs.

As is also mentioned by Lamb (1976) the cephalodia of *St. corticatulum* and *St. delisei* frequently consist of distinct rounded lobes. Those of *St. novogranatense* should be characterized by flattened lobes (Lamb 1977), globose cephalodia have also been found in that species. According to Lamb (a.o. 1968) the scrobiculate type can be divided into two subtypes based on their medullary constitution:

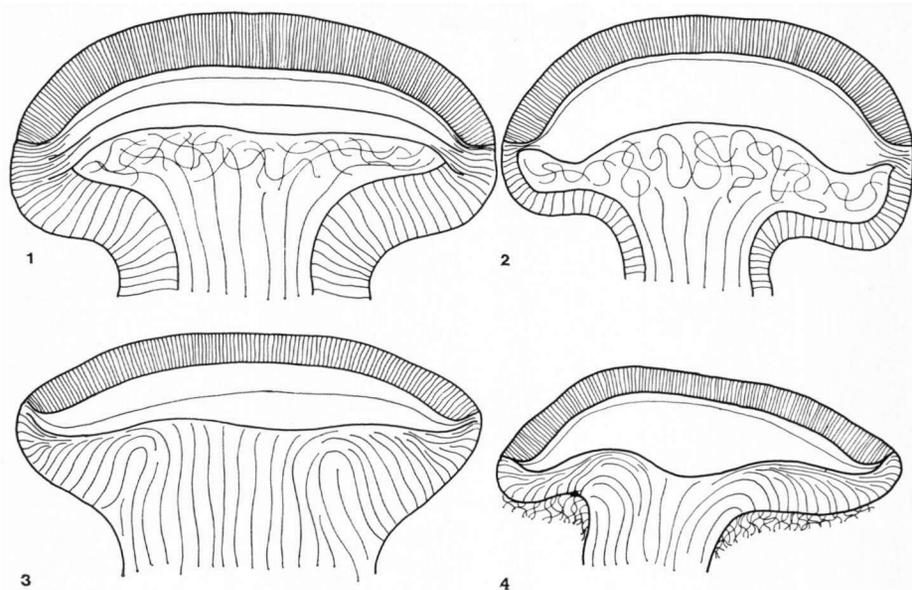


FIG. 1-4. Transverse sections of some apothecia; 1. *St. pomiferum*. 2. *St. ramulosum*. 3. *St. pityrizans*. 4. *St. vesuvianum*.

1. sacculate, internal tissue loose; 2. protosacculate, internal tissue solid and gelatinized. Observation on the cephalodia of *St. strictum* var. *strictum* and var. *compressum* proved, however, the presence of some loose hyphae just under the cephalodium cortex, the greater part is gelatinized. The second type is macroscopically recognizable by a peculiar bluish-grey waxy tinge. A specialization is the dactylaeform cephalodium, which has distinctly rounded digitiform lobes.

Three types of apothecia can be distinguished (fig. 1-4):

1. vesuvianum type, with a low hymenium (45-100 μm), an inconspicuous hypothecium, which passes into the pseudoexcipulum, and short ascospores (18-45 \times 2.0-4.4 μm). It is mostly of lecideine appearance (except in *St. pityrizans*). Examples are *St. glareosum*, *St. tomentosum*, *St. verruciferum* and *St. vesuvianum*.
2. ramulosum type, with a rather high hymenium (40-140 μm), a conspicuous hypothecium which is frequently yellowish-brown pigmented, a sharply delimited pseudoexcipulum and medium-sized ascospores (25-100 \times 2.0-4.7 μm). Of lecanorine appearance. Examples are *St. didymicum*, *St. microcarpum* and *St. ramulosum*.
3. pomiferum type. This type differs from the preceding types by the development of juvenile apothecia into clavate structures (clavulae). It has a high hymenium (100-220 μm), a distinct hypothecium and pseudoexcipulum, and long ascospores (100-220 \times 3.5-4.5 μm according to Lamb 1977). Examples are *St. claviceps* and *St. pomiferum*.

The ascospores show little morphological variation. They are elongated, slightly curved with one end attenuated and the other rounded. Size and number of septa are of taxonomic value (Lamb 1951).

Soralia do provide specific characters, both by their position and by their morphology. In some species they occur apically (e.g. *St. crambidiocephalum*, *St. delisei* and *St. strictum* var. *compressum*) and in others they occur both apically and laterally

(e.g. *St. atlanticum*, *St. claviceps*). In *St. crambidiocephalum* and *St. delisei* soralia develop on small branchlets.

St. microcarpum, *St. pachycephalum*, *St. didymicum* and rarely *St. atlanticum* produce coarse, white-granular, pseudosoredial granules, which seem characteristic for these species. Probably they are similar to the soredia as described in *St. mamillosum* Duvign. (= *St. pomiferum* Duvign., fide Lamb 1977) by Duvigneau (1955).

Pycnidia are uniform in *Stereocaulon* and do not provide infrageneric characters. They are lacking in the sorediose species. When present, they are always immersed in the subapical part of the pseudopodetia, globose and with internal surface-enlargements. The conidia are short, filiform and slightly curved, $4.5-11.5 \times 0.5-1.2 \mu\text{m}$.

CHEMISTRY

In many species of *Stereocaulon* colour reactions are not very reliable, even when carried out precisely on the phyllocladia or soralia. For that reason most of the collections have been investigated by thin-layer chromatography according to the method of Culberson (1972). The chemistry of many species is complex.

Atranorin has been observed in all studied specimens.

Perlatolic acid has been demonstrated in *St. atlanticum*, *St. corticatulum*, *St. crambidiocephalum*, *St. meyeri*, *St. novogranatense*, *St. ramulosum* and *St. strictum* var. *compressum*. These species seem to lack the stictic acid group (except *St. atlanticum*).

Stictic and constictic acids are present in *St. atlanticum*, *St. claviceps*, *St. didymicum*, *St. microcarpum*, *St. pomiferum*, *St. pityrizans*, *St. tomentosum*, *St. verruciferum* var. *sur-reptans* and *St. vesuvianum*.

Norstictic acid is mostly present as well in the species of this group, except in *St. atlanticum*, *St. didymicum* and *St. vesuvianum*.

Lobaric acid has been demonstrated in *St. glareosum* and in *St. obesum*.

No distinction has been made between fumarprotocetraric and protocetraric acids, which both have been recorded in this paper as (fumar) protocetraric acid. This seems to be a characteristic constituent of *St. didymicum*, *St. pachycephalum* and *St. novogranatense*.

Didymic acid has thus far been demonstrated only in *St. didymicum* (Lamb 1977).

Besides these constituents, most chromatograms contain unidentified U.V.-sensitive spots in several rf-classes. In rf-class 4 (just beneath perlatolic acid) red, grey and yellow spots occur. In rf-class 6-7 frequently blue spots occur and more rarely fluorescent, yellow or violet spots. Between rf-class 5 and 6 violet, brown or greyish spots occur. Finally, above atranorin a H_2SO_4 -sensitive (yellow-brown) spot occurs. Deficient strains seem to occur. The spots of atranorin, constictic, norstictic, perlatolic and stictic acids are also U.V.-sensitive (violet).

The following abbreviations are used: o=orange, r=red, y=yellow.

ECOLOGICAL NOTES

All *Stereocaulon* species appear to prefer open habitats (photo 1, 2). Most species are epilithic e.g. *St. microcarpum*, *St. pachycephalum* and *St. pomiferum*. A few species occur also on bare gravelly soil, e.g. *St. atlanticum*, *St. glareosum*, *St. ramulosum*, *St. strictum* var. *compressum* and *St. vesuvianum*. Most of the species

occur on several types of substrate: e.g. *St. pomiferum* on limestone debris and volcanic rocks, and *St. tomentosum* and *St. vesuvianum* on sandstone, quartzitic and volcanic rocks. *St. ramulosum* has the broadest amplitude and occurs on all mentioned types of substrate. Road banks are a characteristic habitat for most of the species. A comparison of the altitudinal distribution of the species shows the following differentiation: *St. didymicum*, *St. microcarpum*, *St. novogranatense*, *St. pachycephalum* and *St. strictum* var. *strictum* reach upwards into the subpáramo; *St. crambidiocephalum*, *St. obesum*, *St. pomiferum* and *St. pityrizans* have thus far been found only in the grasspáramo; *St. atlanticum*, *St. corticatulum*, *St. delisei*, *St. meyeri*, *St. ramulosum*, *St. strictum* var. *compressum*, *St. tomentosum* and *St. verruciferum* range from the upper forest belt into the superpáramo; *St. claviceps* is thus far only known from the lower superpáramo; *St. vesuvianum* is very abundant in the high superpáramo and *St. glareosum* seems limited to this zone.

NOTES ON GEOGRAPHY

Because Lamb (1951) stated different distributions for the subgenera *Stereocaulon* and *Holostelidium* and because the northern Andes seems to be a bottle-neck in species-dispersion, it seems worthwhile to focus on the geography of the north-Andean *Stereocaula*.

Recently Cleef (1979) distinguished eight phytogeographical elements for the indigenous vascular páramo flora of the Colombian Eastern Cordillera: 1. páramo element, 2. neotropical element, 3. wide tropical element, 4. austral-antarctic element, 5. holarctic element, 6. wide temperate element, 7. cosmopolitan element and 8. species with unknown affinity.

Basing on species-distribution data given by Lamb (1977), it appears that most of the north-Andean species of *Stereocaulon* belong to the neotropical flora element, e.g. *St. crambidiocephalum*, *St. didymicum*, *St. obesum*, *St. pachycephalum*, *St. pityrizans* and *St. strictum*. *St. verruciferum* ranges along the entire Andean chain.

Probably the following species could be regarded as belonging to the wide tropical flora element: *St. atlanticum*, *St. claviceps*, *St. meyeri*, *St. ramulosum* and *St. pomiferum*.

St. corticatulum seems an example of the austral-antarctic flora element and *St. glareosum* and *St. tomentosum* constitute the holarctic flora element.

St. delisei has a wide temperate distribution and *St. vesuvianum* is cosmopolitan.

St. novogranatense seems endemic to the volcano Puracé in the south of the Colombian Central Cordillera.

St. microcarpum occurs predominantly in Southern America, but is also reported from the U.S.A. and from the Pacific (Lamb 1977).

TAXONOMIC TREATMENT

Stereocaulon (Schreber) Hoffmann nom. conserv.

For full literature and synonymy of the following accepted species, see Lamb 1977.

KEY TO THE SPECIES

- 1a. *Cephalodia* spherical. *Phyllocladia* verrucose, papillose, granular, squamuliform or peltate. 2
- 1b. *Cephalodia* sacculate or protosacculate. *Phyllocladia* coralloid or sometimes hardly separable from the pseudopodetium branches. 7
- 2a. *Phyllocladia* unicolorous, verrucose or squamuliform. 3
- 2b. *Phyllocladia* bicolorous, with a dark centre, verrucose, granular or peltate 4
- 3a. *Cephalodia* nearly globose, with a smooth olive-green or brownish surface. *Phyllocladia* verrucose, papillose or even squaty coralloid. Apothecia terminal, large, up to 3.0 mm in diameter, often becoming divided. Pseudopodetia slightly tomentose, little branched, up to ca. 30 mm long. *St. glareosum* (Sav.) Magnusson
- 3b. *Cephalodia* with an irregularly greenish to brownish surface. *Phyllocladia* squamuliform or partly verrucose, sometimes partly coralloid. Apothecia predominantly on lateral branchlets, small, up to 1.5 mm in diameter. Pseudopodetia densely tomentose, strongly branched, up to 110 mm long. *St. tomentosum* Th. Fr.
- 4a. *Phyllocladia* peltate. *St. vesuvianum* Pers.
- 4b. *Phyllocladia* verrucose to granular. 5
- 5a. *Phyllocladia* granular and solitary (on lowermost part of the pseudopodetium tending to squamuliform type). Pseudopodetia slender, up to 3.0 mm broad (incl. *phyllocladia*), erect, not branched or with cornute apices, sometimes with small branchlets. 6
- 5b. *Phyllocladia* verrucose and aggregated in little lumps. Pseudopodetia coarse, ca 5.0 mm broad (incl. *phyllocladia*), creeping, irregularly branched. Containing atranorin, stictic and norstictic acid.
..... *St. verruciferum* Nyl. var. *surreptans* (Lamb) Lamb
- 6a. Apothecia of lecanorine appearance, with a conspicuous pale margin. Containing atranorin, stictic and norstictic acids. *St. pityrizans* Nyl.
- 6b. Apothecia of lecideine appearance. Containing atranorin and lobaric acid.
..... *St. obesum* Th. Fr.
- 7a. *Cephalodia* protosacculate (often recognizable by a bluish-grey waxy tinge). 8
- 7b. *Cephalodia* sacculate (without such a tinge).11
- 8a. *Cephalodia* dactylaeform. Apothecia not developing in clavulate structures. 9
- 8b. *Cephalodia* clavate to globose. Apothecia developing in clavulate structures.10
- 9a. Soralia absent. Apothecia small, black and of lecanorine appearance.
..... *St. strictum* Th. Fr.
- 9b. Soralia present on flattened apices of pseudopodetia. Apothecia mostly absent.
..... *St. strictum* var. *compressum* (Nyl.) Lamb
- 10a. Soralia present. *St. claviceps* Th. Fr.
- 10b. Soralia absent. *St. pomiferum* Duvign.
- 11a. *Cephalodial* cortex dimorph, macroscopically with white ribs. Hypothecium colourless.12
- 11b. *Cephalodial* cortex uniform, macroscopically unicolorous. Hypothecium brown. ...14
- 12a. *Phyllocladia* well developed, coralloid. Soralia absent. *Cephalodia* frequently with flattened lobes. (Fumar) protocetraric acid present, cortex P + yellow or red, medulla P + yellow → orange *St. novogranatense* Lamb
- 12b. *Phyllocladia* often hardly developed, flake-like. Soralia present. *Cephalodia* partly

- with rounded lobes. (Fumar) protocetraric acid absent, P + faint yellow.13
- 13a. Soralia effuse, without internal branchlets. *St. corticatum* Nyl.
- 13b. Soralia capitate, with internal branchlets.*St. delisei* Bory
- 14a. Soralia present.15
- 14b. Soralia absent.17
- 15a. Soralia globose, internally with fine branchlets. Pseudopodetia not or little branched at base. *St. crambidiocephalum* Lamb
- 15b. Soralia not globose, without fine branchlets. Pseudopodetia mostly branched at base.16
- 16a. Phyllocladia occurring only at the lowermost part of the pseudopodetium. Soralia terminal and lateral at the terminal part of the pseudopodetium, farinose. Atranorin, norstictic, perlatolic and stictic acids present. *St. atlanticum* (Lamb) Lamb
- 16b. Phyllocladia covering the whole pseudopodetium. Soralia terminal at the pseudopodetium and its subterminal branchlets, fine-granular. Atranorin and perlatolic acid present. *St. meyeri* Stein
- 17a. Pseudosoredial granules absent. Pseudopodetia for the greater part decorticated. Atranorin and perlatolic acid present. *St. ramulosum* (Sw.) Rausch.
- 17b. Pseudosoredial granules present. Pseudopodetia for the greater part corticated. Chemistry more complex, (fumar)-protocetraric, norstictic and stictic acids and/or didymic acid present.18
- 18a. Cephalodial cortex not gelatinized, pruinose. Didymic acid present.
..... *St. didymicum* Lamb
- 18b. Cephalodial cortex gelatinized, glabrous. Didymic acid absent.19
- 19a. Spores under 50 μm long, 3 septate, Hymenium 70–115 μm high. K + yellow, orange, red, P + yellow. *St. microcarpum* Müll. Arg.
- 19b. Spores over 45 μm long, 4–11 septate. Hymenium 100–160 μm high. K + yellow, P + yellow-orange, orange, red. *St. pachycephalum* Vainio

Subgen. *Stereocaulon* sect. *Stereocaulon*

Stereocaulon glareosum (Sav.) Magn.

Illustration: photo 4.

Primary thallus squamules similar to phyllocladia. Pseudopodetia erect, coarse, nearly unbranched to moderately branched, decorticated, covered by a white tomentum, creamy white, except at base which is ochraceous, to about 30 mm high and at base to about 3.5 mm thick. Phyllocladia abundant and crowded in the upper part of the pseudopodetium, more scattered towards base, papillose to squaty coralloid, glossy greyish-green, frequently with a brownish apex. Cephalodia semiglobose or rarely somewhat expanded becoming crowdedly verrucose, concolorous with the pseudopodetium to olive-green, pruinose or slightly tomentose, to about 1.5 mm in diameter; cortex about 20–25 μm thick, consisting of pachydermatous yellow-brown hyphae; internal tissue hyaline, gelatinized; phycobiont nostocoid or stigonemoid. Apothecia, if present, large, terminal on the pseudopodetium or on apical branchlets, to 3.0 mm in diameter; disc irregular, convex, sometimes breaking up, brown-black; margin somewhat tomentose; hymenium 50–55 μm thick; hypothecium 45–60 μm thick, hyaline or somewhat brownish, internally bounded by the central cone, which consists of hyaline gelatinized pachydermatous hyphae; pseudoexcipulum consisting of yellow-brown hyphae which are perpendicular to the outer surface. Ascospores 26–31 \times 2.6–3.0 μm , 3–4-

septate. Pycnidia not observed.

Chemistry: K + y, P – or faint y, on phyllocladia y – o, containing atranorin and lobaric acid.

Colombian distribution and ecology: Only known from high altitudes (4100–4530 m) in the Central and Eastern Cordillera (Nevados del Ruiz and St. Isabel, Nevado del Sumapaz and the Sierra Nevada del Cocuy). It occurs both epilithically and terrestrially on several types of substrate: limestone outcrops, quartzitic soil of bare moraines and volcanic soils and rocks.

Associated species on the Nevado del Sumapaz are: *Anastrophyllum leucostomum*, *Breutelia integrifolia*, *Campylopus pittieri*, *Distichium capillaceum*, *Erigeron chionophilum*, *Kingiobryum paramicola*, *Plagiochila* spec. and *Racomitrium crispulum*.

In the upper grasspáramo of the St. Isabel it grows among dense *Calamagrostis recta* bunches.

Specimens examined²: COLOMBIA, Boekhout 102, 141 (COL), 133, Cleef 8085', 8514 (COL, U), Sipman & Valencia-Z. 10433' (COL, U).

Notes: According to Lamb (1977) the cephalodia of this species are very characteristic: nearly globose, but sometimes also somewhat expanded when large. The colour of the cephalodia varies according to Lamb (1978) from brown to reddish-brown (rarely blue-greenish), but Magnusson (1926) describes them as pale brownish-violet or rose-whitish. In our material cephalodia are concolorous with the pseudopodetium to olive-green. According to Magnusson (1926) the phyllocladia are abundant at the base of the pseudopodetia and somewhat more scattered towards their apices, which does not agree with the Colombian specimens studied, in which the upper part of the pseudopodetia is densely covered by phyllocladia.

***Stereocaulon tomentosum* Th. Fr.**

Illustration: photo 3

KEY TO THE VARIETIES

- 1a. Phyllocladia squamuliform. var. *tomentosum*
 1b. Phyllocladia granular, only at the base of the pseudopodetium tending to squamuliform.
 var. *alpestre* Flot.

St. tomentosum* var. *tomentosum

Pseudopodetia forming creeping or erect growing tufts, at base strongly branched, without a distinct main axis, apically with short branchlets, covered by a well developed tomentum, which often erodes at base, whitish, grey or pale ochraceous, 15–110 mm long and 1.0–2.0 mm thick at base. Phyllocladia squamuliform, sometimes somewhat coralloid and towards apex more verrucose, margin mostly incised, concolorous with the pseudopodetium to greenish-grey. Cephalodia spherical, with an uneven greenish surface, inconspicuous while hidden by the tomentum, up to 1.7 mm in diameter, with nostocoid phycobiont. Apothecia both apical and lateral in the upper part of the pseudopodetium, sometimes absent, small, up to 1.5 mm in diameter; disc brown-black, at first applanate to convex with a light margin, which is frequently somewhat tomentose, later becoming strongly convex, so that the pseudoexcipulum becomes invisible; hymenium 45–60 μm thick; hypothecium brownish, 25–40 μm thick; central cone consisting of colourless pachydermatous hyphae, passing towards the margin into the pseudoexcipulum; this consists of somewhat yellowish perpen-

² chromatographed specimens are indicated with '.

dicular pachydermatous hyphae. Ascospores $20-30 \times 2.0-3.0 \mu\text{m}$, 1-3 septate. Pycnidia not observed.

Chemistry: K + y, P + faintly y, containing atranorin, constictic, norstictic and stictic acids, probably consalazinic acid is also present.

Colombian distribution and ecology: The Colombian specimens were collected between 3000 and 4400 m, both in the Central and Eastern Cordillera. It is found both epilithically and terrestrially on several types of substrate: quartzite, sandstone and volcanic material, and occurs usually associated with *St. ramulosum* and *St. strictum* var. *compressum*.

Specimens examined: COLOMBIA: Boekhout 54, 588, Boekhout & Valencia-Z. 850, Cleef 151', 215a, 1472', 4265', 4366, 8550', 8708', Cleef & Florschütz 5916, Cleef & Jaramillo-M. 3109, Cleef, Jaramillo-M. & García-B. 3568', Cleef & Uribe-U. 6732 (COL, u), Cuatrecasas 1447, 1586a (COL), Florschütz 4434', 4436, 4496 (COL, u), de Garganta Fábrega 1014, García-B. & Jaramillo-M. 206.17 (COL, u), Guzmán 9799, Mora 15 pp, Uribe-U. 6799 (COL). COSTA RICA: Cleef & Fournier 10210a, Sipman 11751, 11785 (u). ECUADOR: Gradstein, Sipman & de Vries 93 (u). VENEZUELA: Sipman & López-F. 11084, 11207, 11210, 11214, 11215 (MERF, u).

Stereocaulon tomentosum var. *alpestre* Flot.

Differs from the typical variety by its predominantly verrucose phyllocladia. Material was seen from the Colombian Eastern Cordillera (Dept. Cundinamarca; páramo de Sumapaz and páramo near Tausa) and the Colombian Central Cordillera (Dept. Tolima, along Rio Totarito).

Specimens examined: COLOMBIA: Boekhout 600, Guzmán 9140 (COL), Salamanca, Boekhout & van Reenen 930 (COL, u). ECUADOR: Gradstein, Sipman & de Vries 471 (u).

Notes: *St. myriocarpum* Th. Fr., recorded from the northern Andes by a.o. Lamb (1977), Nylander (1863), is a close relative of *St. tomentosum*. According to Lamb (1977) this species differs from *St. tomentosum* by its thinner tomentum and larger cephalodia. According to her key (Lamb 1978) it differs further by the presence of both lateral and terminal apothecia, while *St. tomentosum* should have lateral apothecia only. This, however, could not be confirmed by our investigations.

A collection from Costa Rica (Cleef & Fournier 10120a) has phyllocladia, which differ somewhat from those of *St. tomentosum* by their papillose to compact coralloid form, a character also found in the lectotype of *St. myriocarpum* Th. Fr. (UPS). Because only fragmentary material from *St. myriocarpum* was available for study, the status of this species remains unclear to the author.

Sect. *Denudata* Jatta subsect. *Denudata* Lamb

Stereocaulon obesum Th. Fr.

Illustration: photo 7

Pseudopodetia slender, erect, towards apex attenuate, unbranched to cornute, more or less tomentose, 15-50 mm long and about 1.0 mm thick at base. Phyllocladia verrucose, towards the apex of the pseudopodetium becoming sorediiform, in the lowermost part of the pseudopodetium more or less squamuliform with an incised lobed margin, bicolorous with a grey-greenish centre or unicolorous. Cephalodia rare, of the spherical type. Apothecia on and among the phyllocladia in the upper part, of lecideine appearance, small, up to 0.7 mm in diameter; disc appanate, dark brown; hymenium 45-70 μm high; hypothecium up to 90 μm thick, towards the margin becoming less thick, nearly colourless; central cone con-

sisting of pachydermatous gelatinized tissue, marginally forming a thin layer just beneath the hypothecium which forms the pseudoexcipulum; this consists of pachydermatous, somewhat creamy coloured hyphae. Ascospores $25-30(45) \times 2.3-3.7 \mu\text{m}$, 2-7 septate. Pycnidia not seen.

Chemistry: K + y, P - or faintly y, containing atranorin and lobaric acid. According to Lamb the isotype contains only atranorin (note on exsiccate).

Distribution and ecology: Not yet known from Colombia. Found in Ecuador (Cotopaxi National Park) at 3400 m in an open habitat, growing both epilithically and terrestrially.

Specimens examined: ECUADOR: Gradstein, Sipman & de Vries 119', 123' (U). COSTA RICA: Ørsted s. n. (UPS iso).

Notes: The two Ecuadorian specimens studied differ considerably in their gross morphology. 119 consists of solitary erect pseudopodetia while those of 123 form a compact, nearly crustaceous group. 119 grows terrestrially while 123 is epilithic. Because of their similar chemistry and phyllocladia the latter is considered to be an environmentally caused modification. *St. obesum* differs from *St. pityrizans* by its apothecia and chemistry. The species is already known from Venezuela (Vareschi 1973). *St. weberi* Lamb, described from the Galapagos Islands, differs only by its very small phyllocladia. In a collection seen from the Galapagos [Sipman L-53 (U)] the phyllocladia are polymorphous, partly peltate as in *St. vesuvianum* and partly granular, towards the apex of the pseudopodetium becoming sorediiform.

Stereocaulon pityrizans Nyl.

Ann. Sci. Nat. Bot. sér. 4, II: 209 (1859). Type: Peru, prov. Carabaya, leg. Weddell s.n., 1847 (H-Nyl, holotype !)

Synonym: *St. cornutum* Müll. Arg., Flora 69: 252 (1886). *Syn. nov.* Type: Jamaica, Gordontown, leg. Joshua s.n., 1885 (G, holotype !)

Illustration: photo 9, fig. 3

Pseudopodetia slender, erect, unbranched or at apex dichotomously branched, sometimes more irregularly branched, towards apex attenuate, decorticated, covered by a thin to well developed tomentum, dark grey, to about 80 mm long and about 1.5 mm thick at base. Phyllocladia at least in the upper part of the pseudopodetium verrucose, towards the base becoming more peltate to nearly squamuliform, bicolorous with a grey-green centre and a white margin, or unicolorous grey. Cephalodia of the spherical type, greyish-black. Apothecia on and among the phyllocladia in the upper part of the pseudopodetium or on short branchlets, up to 2.5 mm in diameter; disc of lecanorine appearance, black, convex with a brown to grey pruinose or slightly tomentose margin; hymenium 55-100 μm thick; hypothecium up to 90 μm thick, consisting of brown pigmented hyphae interwoven with hyaline hyphae, in the lowermost part with scattered lumps of yellow-brown pigment; central cone hyaline, gelatinized with scattered brown pigment, towards margin passing into the pseudoexcipulum, which is strongly pigmented just near the hymenium. Ascospores $25-43 \times 2.0-3.3 \mu\text{m}$. Pycnidia not observed.

Chemistry: K + y, P + y, containing atranorin, norstictic and stictic acids.

Colombian distribution and ecology: Material was seen from the Colombian Central and Eastern Cordillera (Nevado del Ruiz and páramos de las Papas and de Tamá respectively), ranging from 3400 to 3500 m. The species grows epilithically in open habitats.

Specimens examined: COLOMBIA: Bischler 837 (COL), Cuatrecasas et al. 12628 (COL, FH), Sipman

& Valencia-Z. 10560 (COL, U). JAMAICA: leg. Joshua s.n., 1885 (holotype *St. cornutum*, G), Hart s.n., in Lojka, Lichenotheca universalis n. 154 (G).

Notes: Both type-collections studied are similar in morphology and are characterized by slender, unbranched to dichotomously branched, attenuated pseudopodetia as well as by similar large apothecia of lecanorine appearance. They also agree in their chemistry. Because of these similarities it is concluded here that these types are conspecific. *St. vulcani* (Bory) Ach. seems most related, but it differs by its lecideine apothecia (Fries 1857) and according to Lamb (1978) by a persistent primary thallus. *St. pityrizans* (as *St. cornutum*) has already been found in Venezuela (Vareschi 1973) and Costa Rica (Lamb 1977).

Stereocaulon verruciferum Nyl. var. *surreptans* (Lamb) Lamb

Illustration: photo 6

Pseudopodetia coarse, loosely branched, creeping, not firmly attached to the substrate, tomentose, with a light grey to ashy upper side and dark grey underside, including phyllocladia 3.0–5.0 mm broad. Phyllocladia peltate to verrucose, aggregated in distinct lumps, towards the apex of the pseudopodetium nearly crustose but not confluent, unicolorous whitish to grey, sometimes tending to bicolorous. Cephalodia of the spherical type with an uneven, dark olive-brown surface, with stigonemoid phycobiont. Apothecia not numerous, small, up to 0.5 mm in diameter, of lecideine appearance; disc appanate, brown; hymenium about 50–57 μm thick; hypothecium about 35–40 μm thick, colourless, bounded by stratum which passes into the pseudoexcipulum; pseudoexcipulum 60–90 μm thick, consisting of pachydermatous yellow-brown hyphae. Ascospores 20–25 \times 2.1–2.3 μm , 2–4 septate. Pycnidia not seen.

Chemistry: K + y, P + y, containing atranorin, constictic and stictic acids.

Colombian distribution and ecology: Dodge (1929) reported the typical variety from Colombia. In this paper only material from Ecuador is cited. Our material seen was collected in the Cotopaxi National Park, ranging in altitude from 3400–4700 m. It grows terrestrially on a gravelly plain with scattered scrubs.

Specimens examined: ECUADOR: Gradstein, Sipman & de Vries 118', A. Woudstra sO11 (U).

Notes: This variety is already known from Ecuador (Cotopaxi) (Lamb 1955, as *St. speciosum* var. *surreptans*). According to Lamb (1978) this variety differs from the typical form by its pseudopodetia, which lay loose on the ground and show a certain dorsiventrality.

Stereocaulon vesuvianum Pers.

Illustrations: photos 1, 2, 8, fig. 4

Pseudopodetia forming loose to dense tufts, sometimes nearly crustaceous, grey to dark grey, at apex often with a distinct purplish tinge, except when sorediose, little to strongly branched, including phyllocladia towards apex distinctly attenuated, whitish, decorticated, covered by a thin tomentum, up to 60 mm long and about 0.5–0.9 mm thick at base. Phyllocladia peltate, towards apex of the pseudopodetium becoming granular or even sorediiform, solitary or in little stalked lumps, sometimes somewhat confluent or foliose, bicolorous with a pale grey to olive-green centre (becoming brownish after a long time of conservation) and a whitish often somewhat inflated margin. Cephalodia of the spherical type, inconspicuous,

with an uneven brown to brown-black surface, with stigonemoid phycobiont. Soralia frequently present on the uppermost part of the pseudopodetium. Apothecia, if present, lateral among the phyllocladia in the upper part of the pseudopodetium, of lecideine appearance, small, up to 1.0 mm in diameter; disc at first concave, finally becoming planoconvex, brown-black; hymenium 40–80 μm thick; hypothecium colourless to brownish, up to 35–45 μm thick, towards the margin becoming less thick; central cone consists of gelatinized pachydermatous colourless hyphae, which passes into the pseudoexcipulum; this consists of pachydermatous pale yellow-brown hyphae. Ascospores 18–36 \times 2.0–4.4 μm , (1)2–3 septate. Pycnidia sometimes present; conidia filiform and slightly curved, 8.0–11.0 \times about 1.2 μm .

Chemistry: K + y, P + faintly y, containing atranorin, constictic and stictic acids.

Colombian distribution and ecology: This cosmopolitan species is widely distributed in the Colombian Central and Eastern Cordillera, ranging between 3350–4700 m. In the lower part of the páramo belt, where it is rather rare, it has been found on bare quartzitic, volcanic and sandstone rocks. It is most common in the superpáramo, where it is able to grow on bare stony soil just near the limit of snow and ice. Together with the mosses *Andreaea rupestris* and *Racomitrium crispulum* it is among the first pioneers of plant life near the melting snow. Especially in the superpáramos of the volcanos of the Central Cordillera extensive *St. vesuvianum* dominated zonal communities occur on bare, mobile soils (see Cuatrecasas 1934: Cuadro 26, sub nom. *St. denudatum* Frey). Most frequent associates are: *Bromus lanatus*, *Cerastium floccosum*, *Draba pachythyrsa*, *Gentianella dasyantha*, *Lupinus alopecuroides*, *Lysipomia muscoides* ssp. *muscoides* and *Racomitrium crispulum*.

Specimens examined: COLOMBIA: Barclay 5242, Barclay & Juajibioy 6368, 6447 (COL), Boekhout 59, 70, 80, 81, 938, 939a (COL, U), 102, 189, 211 (COL), Cleef 712, 2314c, 2324', 6962, 8507, 8619', 8657, 8946, 9717', 9717c (COL, U), Cleef & Fernandex-P. 494', Cleef & Hart 2408, 2416', 2417, 2453', 2536', 2546, 2555, 5631', 5991b (COL, U), Florschütz F 4003 (COL, U), Guzmán 5554, Pinto et al. 1825 (COL), Sipman & Valencia-Z. 10425, 10432, 10434, 10566 (COL, U), Valencia-Z. & Boekhout 78, 97 (COL, U). COSTA RICA: Rossbach 3127 (FH, U), Sipman, 11753 (U). VENEZUELA: Dennis 1798 (FH).

Notes: *Stereocaulon vesuvianum* is extremely variable, but in the author's opinion the variation concerns in all cases environmentally induced modifications. Distinct infraspecific taxa could not be distinguished. The species is best characterized by its peltate, bicolorous phyllocladia and its apothecia of lecideine appearance.

Subgen. *Holostelidium* Lamb Sect. *Holostelidium* Subsect. *Holostelidium*

Stereocaulon claviceps Th. Fr.

Pseudopodetia erect, slender, at base not or little branched, in the upper part more or less dichotomously branched, decorticated, up to 50 mm long. Phyllocladia coralloid, attenuated, sometimes with transverse furrows, in the upper part of the pseudopodetium sometimes partly granular sorediose, glossy greenish-grey. Cephalodia scattered on the pseudopodetium, protosacculate, bluish-grey to light grey, somewhat pruinose. Soralia on terminal branchlets or whole upper part granular sorediose. Apothecia (only seen in isotype) developing in clavulae, disc dark reddish-brown; margin reddish-brown; hymenium 230–280 μm thick; hypothecium 92–104 μm thick, compact, yellow-brown pigmented, pseudoexcipulum at some distance from the hymenium a palissadic plectenchyma; with central cone loosely hyphose with scattered yellow-brown pigment, becoming very compact in the axis. Ascospores according to Fries (1857) 76–102 \times 3.0–4.0 μm . Pycnidia not seen.

Chemistry: K + y, P + faintly y, containing atranorin, constictic, norstictic and stictic acids.

Colombian distribution and ecology: Only one Colombian collection was available, collected from

the Nevado del Ruiz (dept. Caldas) at 4300 m, where it was found growing in low vegetation sheltered by rocks.

Specimens examined: COLOMBIA: Sipman & Valencia-Z. 10595 (COL, U). MEXICO: Liebmann 71a (C, iso).

Note: This species is very closely related to *St. pomiferum* from which it differs by the presence of soralia.

***Stereocaulon pomiferum* Duvign.**

Illustration: photo 19, fig. 1

Pseudopodetia slender, not branched at base, more or less dichotomously branched in upper part, decorticated, glabrous or somewhat tomentose, towards the apex corticated, pale yellow-brown, 20–65 mm long and to about 1.3 mm thick at base. Phyllocladia scattered, coralloid with acute apices, towards apex of the pseudopodetium becoming verrucose, greyish-green to greyish-white, sometimes with a dark apex. Cephalodia not numerous, protosacculate, nearly globose or distinctly furrowed, dark grey, greenish-grey or greyish-beige, with surface sometimes somewhat pruinose (pruina in patches) and frequently with a waxy tinge, up to 1.0(1.8) mm in diameter; cortex two-layered, outer wall 30–90 μm thick, consisting of a palissadic plectenchyma, inner wall consisting of tangentially running hyphae; with nostocoid phycobiont. Apothecia developing in clavulae, up to 1.0 mm in diameter; disc at first convex, becoming applanate, dark brown to black; margin brownish to reddish-brown; hymenium 190–220 μm thick; subhymenium to 35 μm thick, colourless; hypothecium 160–300 μm thick, consisting of bundles of colourless to faintly brown hyphae; pseudoex-cipulum a palissadic plectenchyma. Ascospores in examined material not well developed; according to Lamb (1977) (100)140–180(220) \times 3.5–4.0(4.5) μm and 15–22(32) septate. Pycnidia subterminal; conidia 8.0–11.0 \times about 0.7 μm .

Chemistry: K + y, P + y, containing atranorin, norstictic and stictic acids [chem. str. I according to Lamb (1977)]. Collection Cleef & Rangel lacks norstictic acid.

Distribution and ecology: Four collections are thus far available from Colombia, from the Eastern Cordillera (dept. Cundinamarca), the Central Cordillera (depts. Antioquia and Risaralda) as well as from the Sierra Nevada de Santa Marta (dept. Magdalena).

It is strictly epilithical, growing on limestone and volcanic rocks. Probably it prefers humid conditions as three collections were gathered from the atmospherically humid sub- or grasspáramo. Altitudinally it ranges from 3300 to 3700 m.

Specimens examined: COLOMBIA: Boekhout 578, Cleef 3761', Rangel & Cleef 887' (COL, U), Daniel 3827 (COL). VENEZUELA: Sipman & López-F. 11208 (MERF, U).

Note: According to Duvigneau (1955) the subhymenium is brown, while in our material examined the subhymenium is colourless.

Subsect. *Dactyloideum* (Lamb) Lamb

***Stereocaulon strictum* Th. Fr.**

KEY TO THE VARIETIES

- 1a. Soralia absent. *St. strictum* var. *strictum*
 1b. Soralia present on flattened apices of pseudopodetia.
 *St. strictum* var. *compressum* (Nyl.) Lamb

Stereocaulon strictum* var. *strictum

Illustration: photo 15

Pseudopodetia slender, not or little branched at base, in the upper part dichotomously

branched, decorticated, covered by a thin tomentum, creamy white, 35–100 mm long and 1.0–2.0 mm thick at base. Phyllocladia scattered on the pseudopodetium, slender, coralloid, becoming shorter towards the apex of the pseudopodetium, pale yellow-green to greenish-white, sometimes with dark apices, in the upper part of the pseudopodetium sometimes with coarse white granules (as in *St. microcarpum*). Cephalodia dactylaeform, concolorous with the pseudopodetium, to about 1.5 mm in diameter; cortex 25–50 μm thick, strongly gelatinized with more or less isodiametric lumina, internal tissue gelatinized, but just under the cortex loose hyphae can occur. Apothecia terminal at the branches of the pseudopodetium, small, to about 1.5 mm in diameter; disc appanate to faintly convex, black; margin tomentose; hymenium 66–125 μm thick; hypothecium 70–125 μm thick, compact and brown pigmented, bounded by gelatinized central cone; pseudoexcipulum 120–140 μm thick, just near the hymenium composed of gelatinized yellowish white pachydermatous hyphae, elsewhere more loosely hyphose. Ascospores 60–63 \times 3.5–4.7 μm , 5–12 septate. Pycnidia subterminal; conidia 4.5–10.0 \times about 0.7 μm .

Chemistry: K + y, P –, containing atranorin only.

Distribution and ecology: Two Colombian collections were available, both from the Central Cordillera (dept. Cauca, east of páramo de Guanacas and dept. Tolima, along road from Murillo to Manizales). It grows epilithically in the humid andean forest belt between 2500 and 3200 m.

Specimens examined: COLOMBIA: Boekhout 1, Cleef & Fernandez-P. 671b' (COL, U). COSTA RICA: Sipman 12388 (U). MEXICO: Liebmann 7661 (C, isolectotype).

Notes: The reports on ascospore size differ considerably: in Dodge (1929) 50–55 \times 4.0–4.5 μm (as *St. lecanoreum* Nyl.), in Nylander (1858) 72–80 \times 5.0 μm (as *St. lecanoreum* Nyl.), in Fries (1857) 86–90 \times 3.5–4.0 μm .

As our measurements fall within the total range of these reports probably a range of 50–90 \times 3.5–4.7 μm approaches the real variability. According to Culberson (1970) this species contains also porphyrilic acid, which has, however, not been demonstrated in the Colombian specimen.

Stereocaulon strictum var. *compressum* (Nyl.) Lamb ex Vezda

Illustration: photo 12

Differs from the typical variety by the presence of farinose soralia on flattened apices of the pseudopodetia and its apical branchlets; pseudopodetia up to 130 mm long.

Chemistry: K + y, P + faintly y, containing atranorin and perlatolic acid (new chemical strain). The occurrence of perlatolic acid throughout the total range of *St. strictum* var. *compressum* deserves further study.

Distribution and ecology: This variety is very common in both the Colombian Central and Eastern Cordillera, ranging in altitude from 2200–3900(–4500) m. Open habitats are preferred in both the upper forest belt and the proper páramo. Occasionally it reaches the superpáramo where stunted forms occur. It is predominantly epilithic, but also terrestrial, and has been collected on limestone, sandstone and volcanic rocks.

Specimens examined: COLOMBIA: Alston 7462 (COL, U), Barclay & Juajibioy 6553 (COL), Boekhout 79, 599 (COL, U), 94 (COL), Cuatrecasas 18045, 19132 (COL), Cleef 207a', 761', 1460, 2303c, 3759', 5447, Cleef & Fernandez-P. 615, Cleef & Uribe-U. 6684, 6732e (COL, U), Grabandt 392, Grabandt & Idrobo 379' (U), Garcia-B. & Jaramillo-M. 19754, Guzmán 9083, 9152, 9771 (COL), v. d. Hammen 4140 (U), Jepes-A. 601 (COL), Hey c10 (U), Mora 623, 902, 990 (COL), Sipman & Valencia-Z. 10289, 10290, 10568 (COL, U), Soejarto 428 (COL). COSTA RICA: Sipman 11597, 11643, 11780, 11781 (U). VENEZUELA: Sipman & López-F. 11064 (MERF, U).

Subsect. *Aciculisporae* Du Rietz***Stereocaulon atlanticum* (Lamb) Lamb**

Illustration: photo 10

Pseudopodetia strongly branched at base, with long, erect branches, which are more or less dichotomously branched in the upper part, attenuated towards apex, corticated but at base decorticated, sometimes nearly completely decorticated, pale to greyish yellow-brown, 25–50 mm long and 0.9–1.3 mm thick at base. Phyllocladia present in the lower part of the pseudopodetium, coralloid to palmate, with transverse furrows, rarely with pseudosoredial granules. Cephalodia sacculate, grey to concolorous with the pseudopodetium, 1.0–3.3 mm in diameter. Soralia present, terminal and lateral on the upper part of the pseudopodetia, semiglobose and farinose. Pycnidia not seen.

Chemistry: K + y, P + faintly y, containing atranorin, constictic, norstictic, stictic and perlatolic acids.

Colombian distribution and ecology: The material studied was mainly collected in the Colombian Eastern Cordillera, but specimens from the Central Cordillera have also been seen. *St. atlanticum* ranges in altitude between 3350 and 4340 m. It has been found on sandstone and volcanic rock, and on thin soils both on the atmospherically dry and humid side of the mountains. In the Eastern Cordillera it occurs with such mosses as *Andreaea rupestris*, *Grimmia spec.* and *Racomitrium crispulum*, and, especially in the humid páramo, with *Rhacocarpus purpurascens*.

Specimens examined: COLOMBIA: Cleef 132', 2303', 2314', 4248', 5447c', 6985, 8947', 9720'. COSTA RICA: Sipman 11784' (U). VENEZUELA: Sipman & López-F. 11061, 11206 (MERF, U).

Notes: According to Lamb (1977) this species is closely related to *St. rugulosum* Lamb and *St. microcarpum* Müll. Arg. The former differs only by its chemistry and perhaps should better be regarded as a chemical strain. The latter, however, differs by the regular presence of apothecia. The rare occurrence of pseudosoredial granules in *St. atlanticum* probably indicates affinity to *St. microcarpum*. *St. crambidiocephalum* differs by the structure of its soralia and by its chemistry. According to Lamb (1977) the pseudopodetia of *St. atlanticum* are corticated, but in the studied specimens some were nearly completely decorticated. *St. atlanticum* is already known from Bolivia, Costa Rica, Ecuador and Venezuela (Lamb 1977).

***Stereocaulon corticatulum* Nyl.**

Illustration: photo 5

Pseudopodetia erect, strongly branched, forming low dense tufts, in upper part with small branchlets tending to dichotomy, coarse and often partly flattened, woody, at base and on under-side decorticated, partly with flaky remnants of cortex, towards the apex and the upper-side corticated, with surface uneven by furrows and warts, pale greyish-green, to about 25 mm long and at base to 3.5 mm thick. Phyllocladia variable, flaky, hardly distinguishable from the pseudopodetial cortex to short cylindrical, palmate or even short coralloid, forming a terminal whirl on the pseudopodetia, surface uneven by furrows. Cephalodia sacculate, when young globose, becoming crowdedly verrucose (descriptive term according to Lamb 1976) and finally with an irregular surface, pale grey, up to 5(8) mm in diameter; cortex 40–90 μm thick, composed of a palissadic plectenchyma. Soralia present in the upper part of the pseudopodetium, terminal on the phyllocladia and branchlets, capitate and fine granular. Apothecia not yet seen in the Colombian specimens, but present in the type of *St. corticatulum*, small; disc black and with a distinct margin. Pycnidia not observed.

Chemistry: K + y, P — or faintly y, containing atranorin and perlatolic acid.

Colombian distribution and ecology: The only Colombian collections known are from the Nevado del Ruiz (dept. Caldas), from an altitude of 4300 to 4500 m. It was found attached to volcanic rock in scarce superpáramo vegetation.

Specimens examined: COLOMBIA: Sipman & Valencia-Z. 10426', 10594 (COL, U). NEW ZEALAND: Colenso 5144 (H-Nyl. holotype).

Notes: The occurrence of a perlatolic acid-strain in *St. corticatulum* was first reported by Galloway (1980). After examination of the isotype of *St. wadei* (BM), he considered this to be a chemical strain of *St. corticatulum*. Thereby he ignores the mention of soredia born on minute corymbose branchlets in Lamb's (1977) description of *St. wadei*. Examination of the holotype of *St. wadei* (FH) revealed that it contains two different fragments. One piece agrees with *St. corticatulum* Nyl. by its granular effuse soralia at the apices of the pseudopodetia, and the other piece falls within the morphological range of *St. delisei* Bory bearing glomerule-like soralia on small branchlets. Examination by T.L.C. showed that both pieces contain atranorin and perlatolic acid as stated by Lamb (1977). It is necessary that more material of *St. wadei* becomes studied before a final conclusion can be made.

Stereocaulon crambidiocephalum Lamb

Illustration: photo 14

Primary thallus present, similar to the phyllocladia. Pseudopodetia erect, coarse, at base not or little branched, in upper part dichotomously branched, attenuated towards apex, decorticated, but partly with remnants of cortex, whitish grey, 30–70 mm long and 2.0–2.5 mm thick at base. Phyllocladia present only at lower part of the pseudopodetium, coralloid, with transverse furrows. Cephalodia sacculate, concolorous with the pseudopodetium to grey, to 3.5 mm in diameter. Soralia present, terminal at the pseudopodetia, capitate, up to 3.3 mm in diameter [according to Lamb (1977) up to 6.0 mm], consisting of small branchlets bearing the soredia. Pycnidia not seen.

Chemistry: K + y, P + faintly y, containing atranorin and perlatolic acid.

Colombian distribution and ecology: The Colombian specimens studied are from the Eastern Cordillera (páramo de Palacio), ranging in altitude from 3100 to 3680 m. Cleef 5547 was found on a sandstone outcrop in atmospherically humid grasspáramo where it was associated with *Andreaea spec.*, *Campylopus pittieri*, *C. richardii*, *Gymnomitrium setaceum*, *Herbertus subdentatus*, *Lysopomia muscoides* ssp. *simulans*, *Oreobolus obtusangulus* ssp. *rubrovaginatus*, *Rhacocarpus purpurascens*, *Stereocaulon atlanticum* and *St. strictum* var. *compressum*.

Specimens examined: COLOMBIA: Cleef 5547b' (COL, U), Mora 990 (COL). COSTA RICA: Sipman 11783' (U).

Stereocaulon delisei Bory ex Duby

Illustration: photo 11

Pseudopodetia erect, coarse, not or little branched, decorticated with flaky remnants of cortex and with corticated branchlets, to 25 mm long and 0.7–2.5 mm thick at base. Phyllocladia indistinct, verrucose to papillose or even palmate. Cephalodia sacculate, crowdedly verrucose, concolorous with the pseudopodetium, pruinose; cortex dimorphic, for the greater part gelatinized with isodiametric lumina, but partly not gelatinized, 45–50 μ m thick. Soralia terminal on the pseudopodetium, capitate, up to 6.0 mm in diameter, composed of small branchlets bearing the soredia. Pycnidia not seen.

Chemistry: K + y, P + y, containing atranorin, rangiformic acid and norrangiformic acid.

Colombian distribution and ecology: Only one small collection was available from the Colombian Central Cordillera (dept. Caldas), where it was found growing epilithically at 4300 m. Additional material was studied from Costa Rica (prov. Cartago), where the species was found growing at 3350 m on an exposed summit in a low vegetation.

Specimens examined: COLOMBIA: Boekhout 79a' (COL). COSTA RICA: Sipman 11752' (U). NEW ZEALAND: Wade s.n. (FH holotype *St. wadei* p.p.), Sipman 16274' (U).

Notes: The specimens studied belong to *St. delisei* Bory by their soralia born on small apical branchlets and the presence of rangiformic and norrangiformic acid. As presently known this species occurs in North Western Europe, Madeira, South Africa (Lamb 1977), Colombia, Costa Rica and New Zealand. This is the first record of the species from the New World and New Zealand.

Stereocaulon didymicum Lamb

Illustration: photo 18

Primary thallus similar to the phyllocladia. Pseudopodetia erect, little or more strongly branched, in upper part more or less dichotomously branched, corticated, except at base which is decorticated, with surface uneven by furrows and warts, grey, 25–35 mm long and to about 1.0 mm thick at base. Phyllocladia not numerous to abundant, coralloid, greyish-green, with surface uneven by furrows, frequently with coarse pseudosoredial granules. Cephalodia sacculate, globose when young, finally surface uneven by furrows, grey, distinctly pruinose, to 1.5 mm in diameter; cortex not gelatinized, more or less palissadic in structure, 37–67 μm thick. Apothecia terminal on the pseudopodetia and its terminal branchlets, to 2.7 mm in diameter; disc at first planoconvex, finally strongly convex, brown-black; margin reddish-brown; hymenium 85–105 μm thick; hypothecium 60–97 μm thick, consisting of bundles of yellow-brown pigmented hyphae; central cone more loosely hyphose, in upper part brown pigmented; pseudoexcipulum consisting of a palissadic plectenchyma of 50–60 μm thick. Ascospores 34–50 \times 2.3–3.5 μm , 3–6 septate. Pycnidia not observed.

Chemistry: K + y, P – , + y or + y \rightarrow o, containing atranorin, didymic and stictic acids.

Colombian distribution and ecology: Not yet known from Colombia. Material was studied from Costa Rica, Ecuador and Venezuela. The species ranges in altitude from 1500 to 3200 m, occurring both epilithically and terrestrially on loamy soil in the lower montane rainforest up to the subpáramo.

Specimens examined: COSTA RICA: Sipman 11550', 11558' (U); Lamb & Metzger s.n. (FH holotype). ECUADOR: Presscott An L-5 (FH). VENEZUELA: Sipman & López-F. 11212' (MERF, U).

Stereocaulon meyeri Stein

Illustration: photo 13

Pseudopodetia erect or creeping with ascending tips, not or little branched at base, towards apex attenuated or with short furcate to falcate branchlets, glabrous or tomentose, at base decorticated, sometimes more or less dorsiventral, with a decorticated underside and a corticated upper side, with surface irregular by furrows and flakes, pale ochraceous to greyish, to 75 mm long and to 3.0 mm thick at base. Phyllocladia present, sometimes only on the upperside of the pseudopodetium, coralloid or tending to palmate, becoming shorter towards the apex of the pseudopodetium, coarse, with an obtuse apex, greyish-green. Cephalodia sacculate, pale to ashy grey, up to 2.8 mm in diameter; cortex a gelatinized palissadic

plectenchyma. Soralia present, terminal on the pseudopodetia or terminal branches, fine granular. Pycnidia not seen.

Chemistry: K + y, P – or + faintly y, containing atranorin and perlatolic acid.

Colombian distribution and ecology: In Colombia *St. meyeri* is thus far known from the Eastern Cordillera (depts. Boyacá and Santander) and from the Central Cordillera (depts. Caldas and Tolima). The species ranges in altitude from 3910 to 4300 m, occurring epilithically on sandstone and volcanic rocks. Associates in the Eastern Cordillera are *Aongstroemia julacea*, *Campylopus richardii*, *Cladonia boliviana*, *C. polia*, *Oreobolus obtusangulus*, *Rhacocarpus purpurascens*, *Racomitrium crispulum*, *Siphula* spec. and *Stereocaulon atlanticum*.

Specimens examined: COLOMBIA: Aguirre 1021, Boekhout 590', Cleef 9720b', Florschütz F4003', Sipman & Valencia-Z. 10593 (COL, U). KENYA: v.d. Hammen 3419 (U).

Notes: According to Lamb (1977, 1978) *St. meyeri* has soralia only at the apex of the pseudopodetium. However, most of the Colombian specimens (Aguirre 1021, Boekhout 590, Sipman & Valencia-Z.10593) produce also soralia on terminal branchlets as in *St. soreidiferum* Hue, which otherwise differs by its chemistry (Lamb 1978). This, however, seems not contrary to Stein's description (1889), in which the pseudopodetia are described as simple or in the upper part furcate. As Lamb (1977) noted, *St. meyeri* is very closely related to *St. ramulosum*, and both species seem to be morphologically very variable.

Stereocaulon microcarpum Müll. Arg.

Pseudopodetia little to strongly branched, more or less dichotomous, corticated except at base which is decorticated, with surface uneven by transverse furrows and warts, greenish-grey, to 55 mm long and 1.0–2.5 mm thick at base. Phyllocladia palmate, with surface uneven by furrows, greenish-grey, frequently with a whitish tip and a pale underside, with coarse white pseudosoredial granules. Cephalodia sacculate, globose to surface becoming uneven by furrows, concolorous with the pseudopodetium to brownish, to 4.5 mm in diameter; cortex palissadic plectenchymatous, 35–70 μm thick. Apothecia terminal on the pseudopodetium, to 1.8 mm in diameter; disc planoconvex to convex, dark red-brown to black; margin reddish-brown; hymenium 70–115 μm thick; hypothecium 70–130 μm thick, compact, brown pigmented; central cone loosely hyphose, in upper part brown pigmented; pseudoexcipulum composed of a palissadic plectenchyma, 55–73 μm thick. Ascospores 28–46 \times 2.0–3.0 μm , 3 septate. Pycnidia subterminal, with conidia of 5.0–6.0 \times 0.5–0.9 μm .

Chemistry: K + y \rightarrow 0, P + y, containing atranorin, norstictic and stictic acids.

Colombian distribution and ecology: The Colombian specimens seen were collected in a semidesert vegetation near Villa de Leyva (dept. de Boyacá), where the species was found growing epilithically at an altitude of 2200 to 2450 m.

Specimens examined: COLOMBIA: Cleef 365', Cleef & Garcia-B. & Jaramillo-M. 3470' (COL, U). BRAZIL: Puiggari 151 (holo, G).

Notes: *St. microcarpum* is closely related to *St. didymicum* and *St. pachycephalum*. The first differs clearly by its not gelatinized cephalodial cortex and the presence of didymic acid, but the latter species is more difficult to separate. According to Lamb (1978) *St. microcarpum* differs from *St. pachycephalum* by the absence of fumarprotocetraric acid, a lower hymenium and shorter and less septate ascospores. In an earlier publication (1977), however, she mentions fumarprotocetraric acid as a constituent of *St. microcarpum*. The specimens studied differ from *St. pachycephalum*.

phalum by the absence of (fumar)protocetraric acid, the presence of stictic acid (and correlated colourreactions $K + y \rightarrow o, r$ and $P + y$ in *St. microcarpum* and $K + y, P + y \rightarrow o, o, r$ in *St. pachycephalum*), a less high hymenium and somewhat smaller, less septate ascospores. Thus it is appropriate to maintain *St. microcarpum* as a species. The close affinity between *St. microcarpum*, *St. pachycephalum* and *St. didymicum* is also demonstrated by the presence of pseudosoredial granules.

Stereocaulon novogranatense Lamb

Illustration: photo 16

Pseudopodetia at base not branched or with few erect branches, in the upper part with short branchlets, at base decorticated, medially in different stages of decortication and in the upper part corticated, slightly tomentose, at base ochraceous, otherwise yellow-beige or ashy-grey, to about 65 mm long and to 2.5 mm thick at base. Phyllocladia coralloid, becoming shorter towards the apex of the pseudopodetium, greyish. Cephalodia sacculate, frequently with flattened lobes and a strongly irregular surface, greyish, olivaceous or concolorous with the pseudopodetium, with distinct white ribs, to about 2.5 mm in diameter; cortex dimorphic, mainly composed of a 40–55 μm thick gelatinized palissadic plectenchyma, but on the ribs not gelatinized. Apothecia terminal on the pseudopodetia and its subapical branchlets, to 2.5 mm in diameter; disc convex, red-brown or black-brown; margin yellowish- or reddish-brown; hymenium 80–184 μm thick; hypothecium 90–214 μm thick, compact and colourless, internally bounded by a 80–115 μm thick brown pigmented stratum; central cone loose, brown pigmented; pseudoexcipulum consisting of a palissadic plectenchyma, 70–130 μm thick. Ascospores 42–100 \times 2.4–4.6 μm , (4)7–10 septate. Pycnidia subterminal; conidia 6.5–11.5 \times 0.6–0.8 μm .

Chemistry: $K +$ faintly y or $-$, P cortex $+ y$, medulla $+ y \rightarrow 0$, or $P + y \rightarrow r$, containing atranorin, perlatolic acid, (fumar)protocetraric acid and unknown brown spots in rf-class 2 and 4.

Colombian distribution and ecology: Up to now only known from the volcano Puracé in the southern Colombian Central Cordillera, where it was found epilithically in páramovegetation at 3300 m.

Specimens examined: COLOMBIA: Hey c10pp', c14' (u), Guzmán 5543 (FH, COL, type).

Notes: This species seems closely related to *St. implexum* Th. Fr. because of its dimorphic cephalodium cortex and its colourless hypothecium, but the latter differs by the absence of a pseudoexcipulum (Lamb 1978) and by its chemistry. *St. dusenii* Lamb, another relative, differs by its uniform cephalodium cortex, a less thick colourless hypothecium and a lower hymenium.

Despite the fact that Lamb (1977) describes the hypothecium as "dense fuscidulo-nubilatus", it was found that the greater part of the hypothecium is colourless. Also the cephalodial cortex proved to have a dimorphic structure, contrary to Lamb's description. The morphology of the cephalodia varies from sacculate to distinctly flattened (crystate). According to Lamb (1977) anziaic acid is also present.

Stereocaulon pachycephalum Vainio

Pseudopodetia not branched at base or with few erect branches, in upper part with short branchlets, sometimes dichotomously branched, when young corticated, finally at base decorticated, medially in different stages of decortication and in upper part corticated, with

surface uneven by furrows and warts, greenish-grey to dirty grey, to 57 mm long and to 2.2 mm thick at base. Phyllocladia coralloid or slightly palmate, with surface uneven by furrows, with pseudosoredial granules, greenish-grey, sometimes with pale underside. Cephalodia sacculate, clavate to globose, sometimes flattened, pale to dirty grey, to 3.0 mm in diameter; cortex composed of a palissadic plectenchyma, 40–60 μm thick. Apothecia terminal on the pseudopodetia and its subapical branchlets, to 3.1 mm in diameter; disc applanate to convex, dark red-brown to brownish; margin whitish to pale brown; hymenium 100–160 μm thick; subhymenium 23–50 μm thick, colourless; hypothecium 90–180 μm thick, brown pigmented, upper part less intense; with central cone loose, in upper part pigmented; pseudoexcipulum consisting of a palissadic plectenchyma, 57–120 μm thick. Ascospores 45–90 \times 2.1–4.6 μm , 4–11 septate. Pycnidia present, subterminal.

Chemistry: K + y, P + y \rightarrow o, r, containing atranorin, (fumar) protocetraric and perlatolic acids.

Colombian distribution and ecology: Up to now only known from the Colombian Central Cordillera (depts. de Caldas and Risaralda). It was found on rocks in grazed, secondary scrub and along a track between 3000 and 3500 m.

Specimens examined: COLOMBIA: Boekhout 518', Florschütz F4265', Sipman & Valencia-Z. 10561', 10567' (COL, U). MEXICO: Liebmann 176 (UPS, C iso).

Notes: *St. novogranatense* is related by its thalline and apothecial structure, but differs, however, by its dimorphic cephalodium cortex and a hyaline hypothecium.

Stereocaulon ramulosum (Sw.) Rausch.

Illustration: photo 17, fig. 2

Pseudopodetia branched at base with erect branches, in upper part with short branchlets, at base decorticated, medially in different stages of decortication with a woolly to fibrous surface and in the upper part corticated, sometimes dorsiventrally flattened, at base ochraceous but otherwise grey, yellowish-white, greenish-white or creamy-white, sometimes in upper part dirty grey or even purplish, 10–190 mm long and 1.0–4.0 mm thick at base. Phyllocladia coralloid, sometimes slightly palmate, obtuse, becoming shorter towards the apex of the pseudopodetium and concolorous with it. Cephalodia sacculate, with an irregular surface, scattered, grey (becoming concolorous with the pseudopodetium after a long time of conservation), to 2.5 mm in diameter; cortex a palissadic plectenchyma. Apothecia terminal on the pseudopodetium and its subterminal branchlets, to 4.0 mm in diameter; disc brown to brownblack, at first convex, becoming semiglobose; margin whitish to red-brown; hymenium 60–110 μm thick; hypothecium 70–160 μm thick, compact and yellowish-brown; central cone loosely hyphose and more pale; pseudoexcipulum composed of a palissadic plectenchyma, to 115 μm thick. Ascospores 23–60 \times 2.3–4.5 μm , 2–5(8) septate. Pycnidia present, subterminal; conidia 8.0–9.0 \times about 0.8 μm .

Chemistry: K + y, P + faintly y, containing atranorin and perlatolic acid.

Colombian distribution and ecology: This seems the commonest *Stereocaulon* species in Colombia. Material studied was collected in both the Central and Eastern Cordillera and in the Sierra Nevada de Santa Marta. *St. ramulosum* ranges in altitude between 2400 and 4500 m and is mostly found in the upper Andean forest belt and the páramos, but extends up into the superpáramo. It seems to prefer open habitats, growing either on volcanic, quartzitic, sandstone or limestone debris or rocks, or on stony soil.

On recently denudated roadside banks it is optimally developed, constituting a plant community of its own. Common associates are *Cora pavonia*, *Ditrichum gracile*, *Pilopogon laevis*, *Stereocaulon*

strictum var. *compressum* and *St. tomentosum*.

According to Huneck & Follmann (1967) this species is characteristic for the *Stereocaulum ramulosi* Follm., a pioneer association on volcanos in Chile.

Specimens examined: COLOMBIA: Bischler 723, 857 (COL), Boekhout 1, 60, 82, 84, 181, 939, Cleef 125, 151b', 667, 732, 738, 1239', 1261, 1440, 1445, 1471, 2303b', 2773b', 3470b, 3570b, 3761, 5451', 5916b, 6732b', 7874e, 9707b', 9918, 9958b (COL, u), Cuatrecasas 1586, 8787a, 25586, Garganta-F. 1015, Guzmán 5546, 5550, 5581, 9068, 9074, 9095, 9119, 9793 (COL), v. d. HAMMEN 3225', 3288a (COL, u), Hey c10, c14pp, Killip & Varela 34677 (u), Lozano-C. et al. 2572 (COL), Maas 635' (u), Mora 630, 990, Pinto 425, 434 (COL), Rangel & Cleef 1049, 1050, 1051, 1052, 1053 (COL, u), Sipman & Valencia-Z. 11063 (COL, u), Uribe-U. 218 (COL). COSTA RICA: Cleef & Fournier 10210' (u). VENEZUELA: Sipman & López-F. 11203, 11204, 11205, 11216, 11220 (MERF, u).

Notes: This species is extremely variable in many characters: besides the usual shrubby plants nearly crustose, low cushions occur. At high altitudes a dendroid-branched form occurs which has strongly reduced phyllocladia in the upper part of the pseudopodetium; the pseudopodetia vary from densely tomentose to glabrous, and the phyllocladia are coralloid (usually) to palmate. Distinct subtypes could not be separated, and the different forms are regarded here as environmentally induced.

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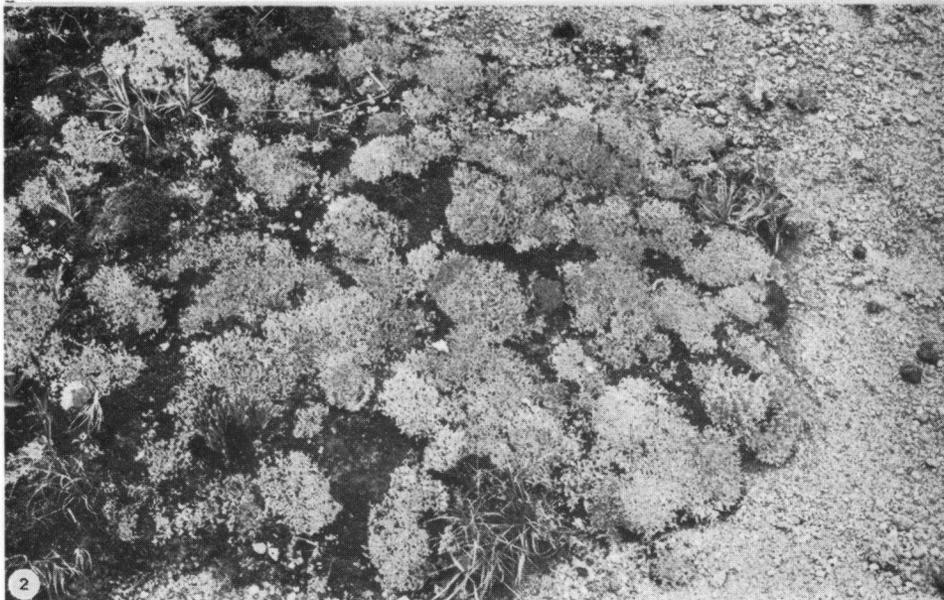
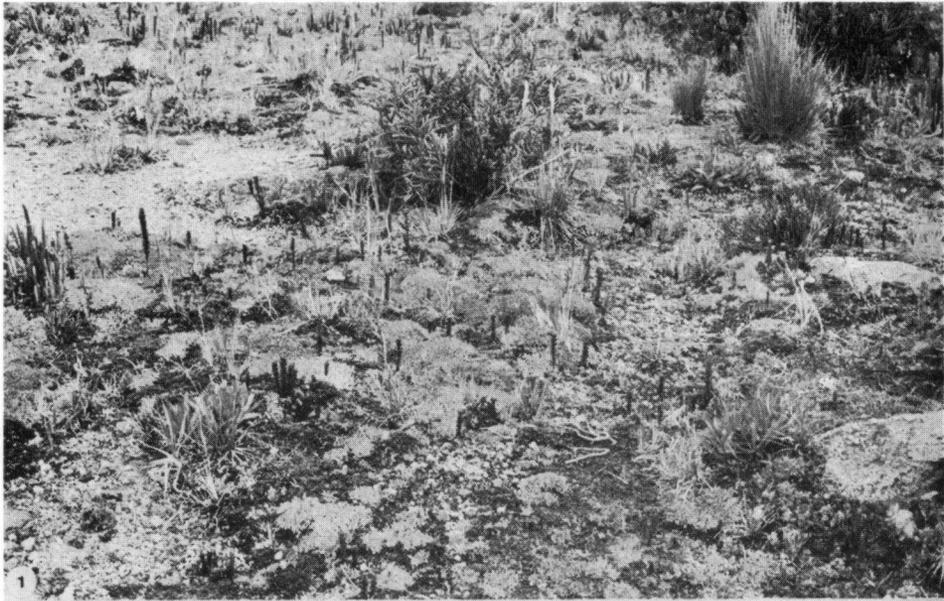


PHOTO 1 & 2. Lower superpáramo pioneer community dominated by *Stereocaulon vesuvianum* colonizing bare gravelly soil at about 4350 m on the NW-slope of the volcano Ruiz, Cordillera Central (Caldas), Colombia. Common associates are *Agrostis* spp., *Bromus lanatus*, *Festuca procera*, *Gentianella dasyantha*, *Lachemilla nivalis*, *Loricaria colombiana*, *Lycopodium carssum*, *Oreoweisia bogotensis*, *Racomitrium crispulum*, *Senecio gelidus* and *Valeriana plantaginea*. (photographs A. M. Cleef).

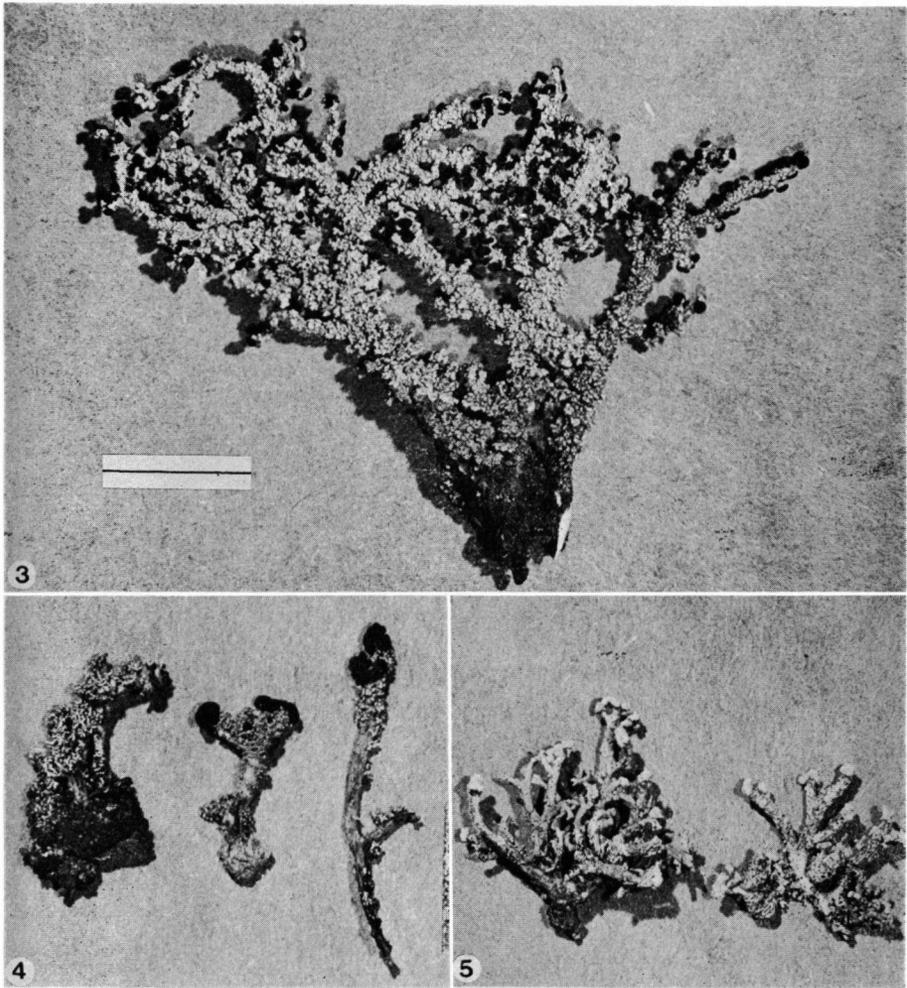


PHOTO 3-5. 3. *St. tomentosum*. 4. *St. glareosum*. 5. *St. corticatulum*. Bar indicates 1 cm.

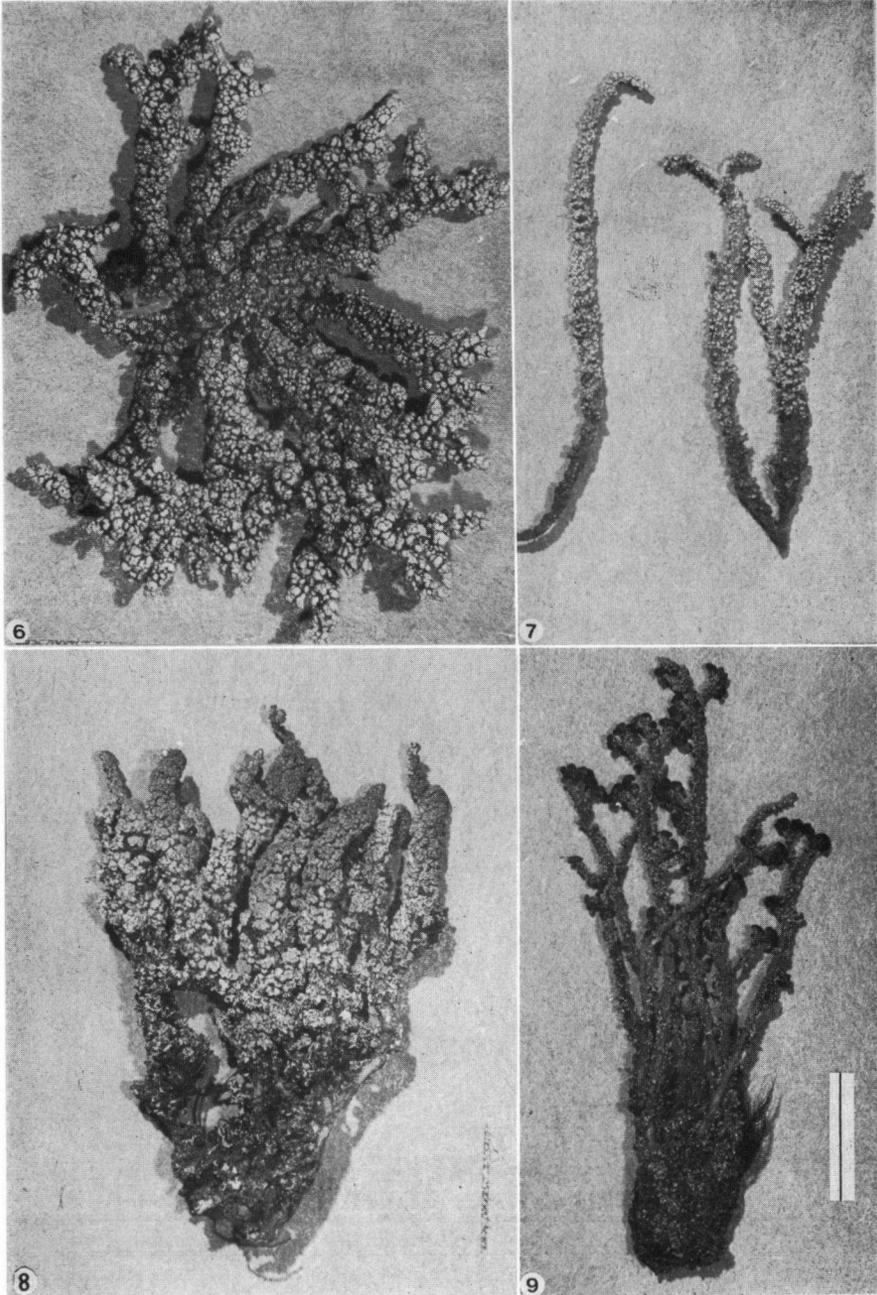


PHOTO 6-9. 6. *St. verruciferum* var. *surreptans*. 7. *St. obesum*. 8. *St. vesuvianum*. 9. *St. pityrizans*. Bar indicates 1 cm.

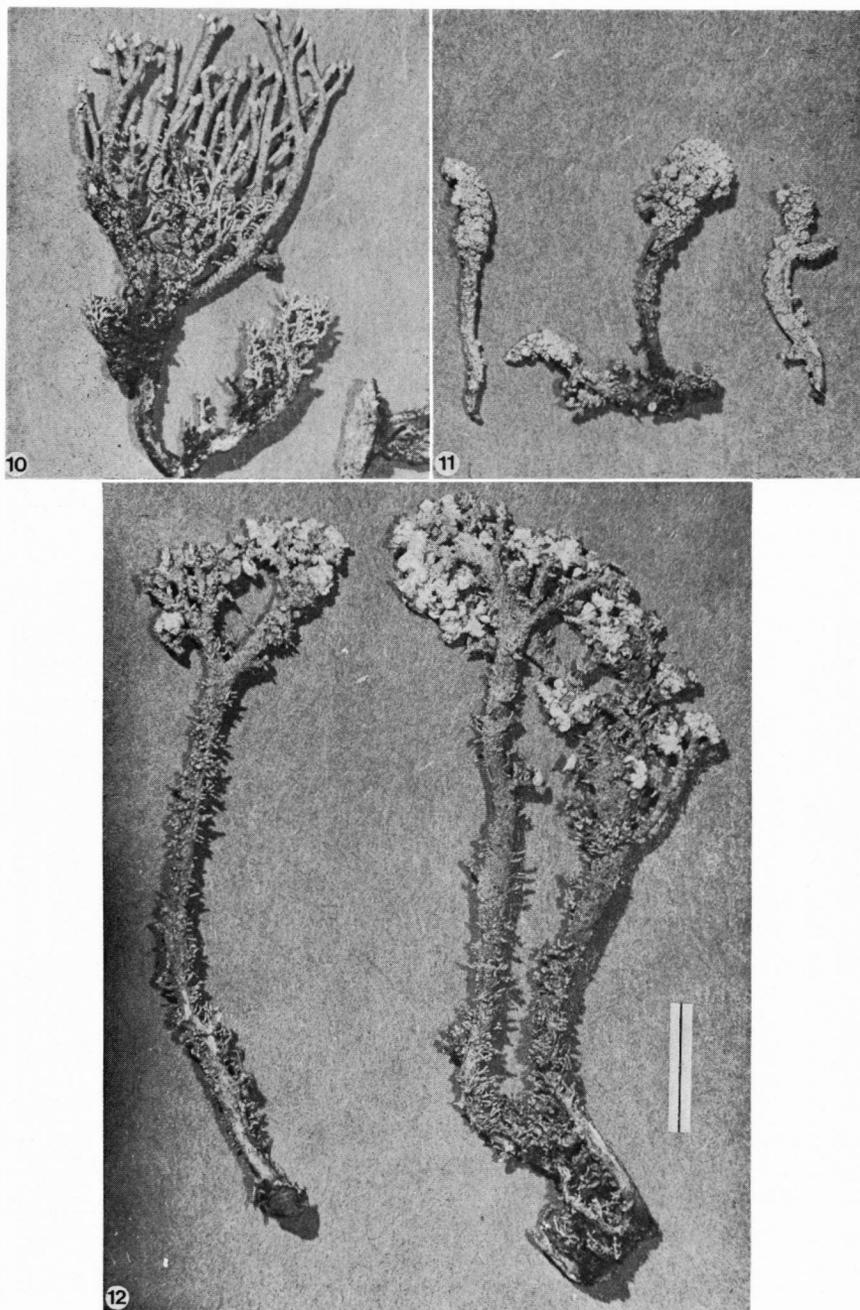
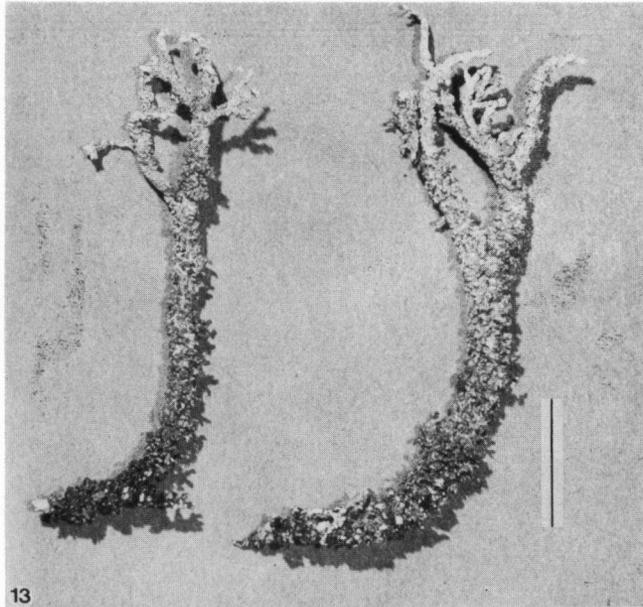
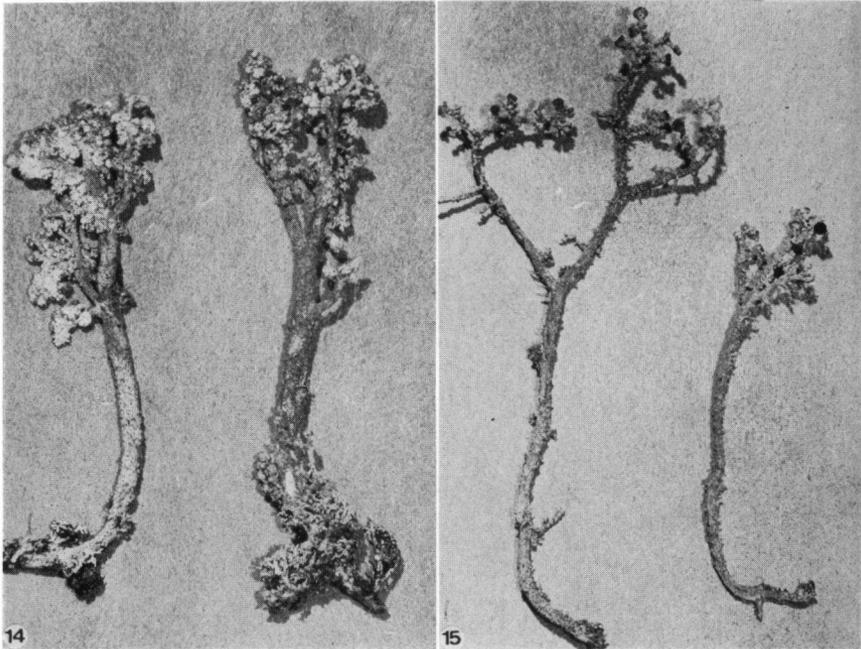


PHOTO 10-12. 10. *St. atlanticum*. 11. *St. delisei*. 12. *St. strictum* var. *compressum*.
Bar indicates 1 cm.



13



14

15

PHOTO 13-15. 13. *St. meyeri*. 14. *St. crambidiocephalum*. 15. *St. strictum*. Bar indicates 1 cm.

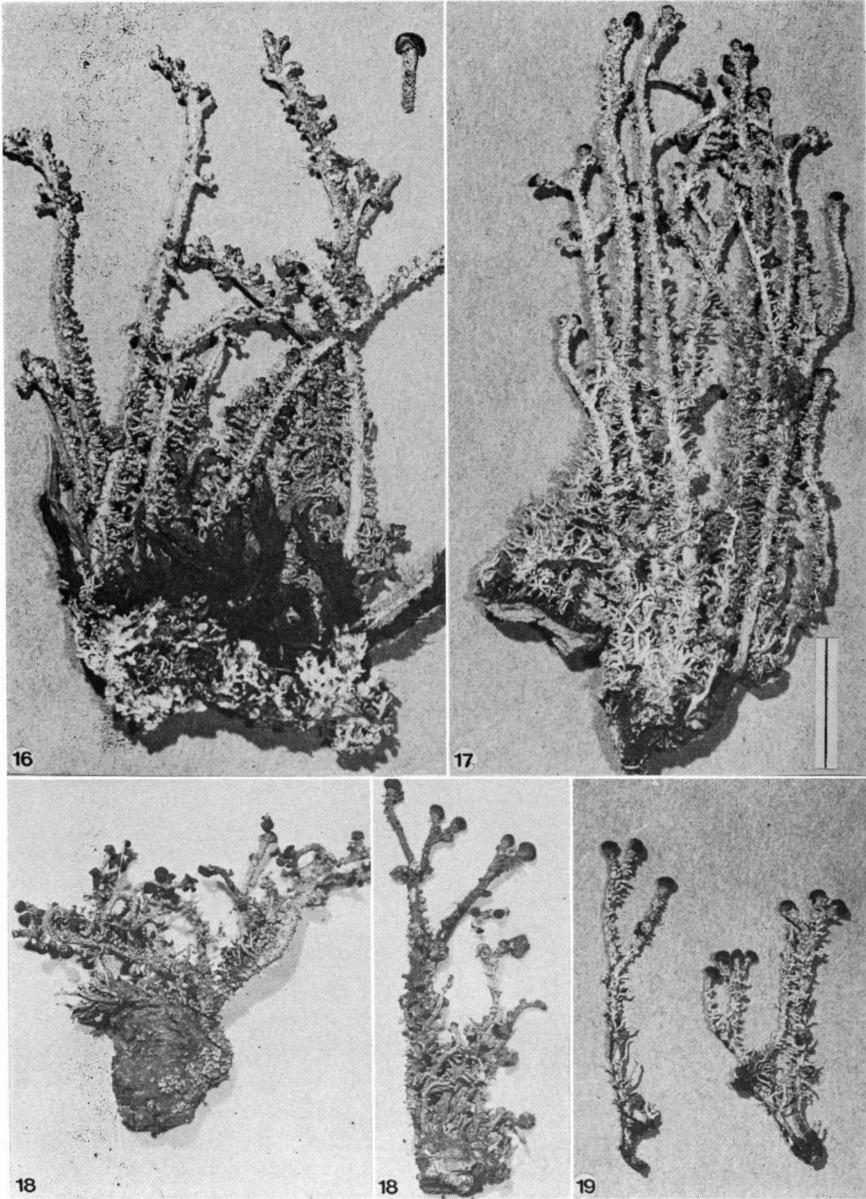


PHOTO 16-19. 16. *St. novogranatense* (iso COL). 17. *St. ramulosum*. 18. *St. didymicum* (holo FH). 19. *St. pomiferum*. Bar indicates 1 cm.