
Studies on Colombian Cryptogams. X

The genus *Everniastrum* Hale and related taxa (Lichenes)

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ABSTRACT

The Colombian representatives of the lichen family Parmeliaceae with linear lobes and marginal cilia have been revised. A key is given and morphology, chemistry and distribution are treated of 12 species in three genera: *Cetrariastrum* Sipm. gen. nov, with *C. andense* (Kärnef.) Sipm. comb. nov., *C. dubitans* Sipm. spec. nov. and *C. equadoriense* (Sant.) Sipm. comb. nov., *Everniastrum* with *E. catawbiense* (Degel.) Hale, *E. cirrhatum* (Fr.) Hale, *E. columbiense* (Zahlbr.) Hale, *E. fragile* Sipm. spec. nov., *E. planum* Sipm. spec. nov., *E. sorocheilum* (Vain.) Hale and *E. vexans* (Zahlbr.) Hale, and *Parmelina cleefii* Sipm. spec. nov. and *P. swinscowii* (Hale) Hale.

This paper deals with foliose lichens possessing linear lobes with frequent marginal cilia and few or no rhizines. Lichens of this habit type are found in several genera of the family Parmeliaceae and in the genus *Heterodermia* (Physciaceae). Most species of this type belong to the genus *Everniastrum* Hale, a recent segregate of the large genus *Parmelia* Ach. *Everniastrum* is most closely related to the *Parmelia* segregates *Parmelina* Hale and *Parmotrema* Massal. by the presence of marginal cilia, a pored epicortex and the shape of the apothecia. The ciliate, linear lobes of *Everniastrum* are so characteristic that already long ago lichen authors were familiar with them. Initially only one species of this type was recognized, *E. cirrhatum*, which has been confused with *Parmelia camtschadalis* (Ach.) Eschw., a *Xanthoparmelia* species (cf. Du Rietz, 1924). Wainio (1899) added several new species based on asexual morphs, whereas recently Hale & Wirth (1971) described a number of new species by using chemical characteristics. Hale (1976) subsequently placed them in the new genus *Everniastrum* and produced the first synopsis of this genus.

The literature on Colombian *Everniastrum* reflects this historical development. Nylander (1863) recorded only *Parmelia camtschadalis* var. *americana* (= *E. vexans*) in his classical catalogue of the lichens of Colombia and surrounding areas. Wainio (1899) distinguished five species: *Parmelia propagulifera* Vain. (= *Hypotrachyna microblasta* (Vain.) Hale, fide determination slip of M. Hale, 1963), *P. vermicularis* Vain. (= *E. cirrhata*), *P. americana* (Mey. et Flot.) Mont. (= *E. vexans*), *P. granulosa* Vain. (= *E. columbiense*) and *P. sorocheila* Vain. (= *E. sorocheilum*).

In this paper seven Colombian species of *Everniastrum* are described, two of which are new (*E. fragile* Sipman spec. nov. and *E. planum* Sipman spec. nov.). In addition five species from other genera are dealt with which also possess linear, ciliate lobes and might therefore be confused with *Everniastrum*. Two of them belong to the genus *Parmelina* whereas the others are considered to constitute a new genus for which the name *Cetrariastrum* is proposed.

All species are usually found among thick bryophyte cushions in humid sites where fog and rain prevail during most of the year. In Colombia such sites are frequent in the upper Andean forests and paramos. One might consider the characteristic thallus shape to constitute an adaptive feature of these taxa by assuming that the narrow, ciliate lobes enhance evaporation – thus permitting the lichen to dry out periodically – while the reduction of rhizines could be looked upon as an impediment for the uptake of water from the substrate, serving the same purpose.

The present study is based mainly on material collected by A.M. Cleef and collaborators in the Colombian paramos during phytosociological fieldwork in 1971–73. Additional specimens are from Colombian collections made mainly by T. van der Hammen, R. Grabandt and the author. All collections are deposited in the herbaria of the Instituto de Ciencias Naturales in Bogota (COL) and the Institute of Systematic Botany in Utrecht (U). For comparison a few authorised specimens were borrowed from BM, S and US.

The chemistry of most of the specimens was studied by thinlayer chromatography using the Culberson method (with solvent A) and cochromatography of known lichens. Anatomical investigations were by light microscopy. Cortex structure and the structure of propagules were studied by scanning electron microscopy in all species except *Everniastrum cirrhatum*. Habitat data were obtained from field notes of A.M. Cleef and the author's personal observations.

KEY TO FOLIOSE LICHENS WITH LINEAR LOBES AND MARGINAL CILIA IN COLOMBIA

- 1a Thallus lobes linear, dorsiventral, with marginal cilia; lower surface corticate, brown to black 2
- b As above, but lower side ecorticate, pure white or with yellowish or reddish pigments 2
Heterodermia spp. (not treated further)
- 2a Isidia present 3
- b Soralia present 5
- c Isidia and soralia absent 11

3a	Medulla K + yellow → red, or C + red; thallus usually over 4 cm long; branching regularly dichotomic		4
b	Medulla K -, C -, KC -; thallus 2-4 cm long; branching irregular	2. <i>C. dubitans</i>	
4a	Isidia laminal	10. <i>E. vexans</i>	
b	Isidia terminal or marginal	7. <i>E. fragile</i>	
5a	Soralia pustular; internodes of thallus lobes short and wide, ca 2-3 cm long, 2 mm wide	8. <i>E. planum</i>	
b	Soralia sorediate; internodes of thallus lobes long and narrow, ca 2-5 mm long, 1-1.5 mm wide		6
6a	Soralia terminal		7
b	Soralia laminal		8
7a	Medulla K + yellow → red, C -	9. <i>E. sorocheilum</i>	
b	Medulla K -, C + red	4. <i>E. catawbiense</i>	
8a	Medulla K + yellow → red		9
b	Medulla K -		10
9a	Thallus lobes subfruticose; usually epiphytic	6. <i>E. columbiense</i>	
b	Thallus lobes loosely appressed; strictly epilithic	12. <i>P. swinscowii</i>	
10a	Medulla C + red; soralia clearly delimited	4. <i>E. catawbiense</i>	
b	Medulla C -; soralia ± diffuse	2. <i>C. dubitans</i>	
11a	Medulla K + yellow → red		12
b	Medulla K -, C + red or C -		13
12a	Thallus lobes loosely applanate	11. <i>P. cleefii</i>	
b	Thallus lobes subfruticose	5. <i>E. cirrhatum</i>	
13a	Thallus lobes branching regularly dichotomic; cilia 1-3 mm long	5. <i>E. cirrhatum</i>	
b	Thallus lobes branching irregular; cilia 3-5 mm long		14
14a	Thallus lobes 0.5-1 mm wide	1. <i>C. andense</i>	
b	Thallus lobes 1-2 mm wide	3. <i>C. equadoriense</i>	

Cetrariastrum Sipman gen. nov.

Type species: *C. equadoriense* (Sant.) Sipman

Thallus dorsiventralis, fruticosus, 1-7 cm diametro. Laciniae lineares, 0.5-2 mm latae, irregulariter dichotome ramosae, leviter convolutae. Latus superior convexum, cinereum fuscumve, aut nudum aut isidiis vel soraliiis instructum. Latus inferior concavum, costis irregularibus ± transversalibus instructum, fuscum nigrumve, raro pallidum, rhizinis nullis vel singulis raris instructum. Cilia marginalia 3-5 mm longa, dichotome ramosa, saepe ramulis perpendicularibus in partibus basalibus instructa. Cortex e paraplectenchyma pachydermatica compositus. Algae rotundae, 7-18 μm diametro, pariete crasso. Apothecia plana vel convexa, laminalia, disco fusco et margine cinereo fuscove, pedicello breve solido instructa. Hymenium 30-45 μm crassum. Excipulum cupulare, 40-55 μm crassum, e paraplectenchyma pachydermatica compositum. Asci clavati, ca 25-36 × 10-15 μm, camera oculare magna. Sporae unicellulares, incolores, 8-nae, 5-9 × 3.5-5 μm, pariete ca. 0.7 μm crasso. Pycnidia laminalia, immersa, ostiolis nigris, ca 0.15 mm lato, conidio-phoris endobasialibus. Pycnosporae bacilliformes, ca 5 × 1 μm. Materia chimica: atranorinum, acidum protolichesteranicum et substantiae ignotae A-E.

Thallus dorsiventral, fruticose, 1–7 cm diameter. Lobes 0.5–2 mm wide, linear, irregularly dichotomically branched, convoluted. Upper surface convex, grey to brown, bare or with laminal isidia or soralia. Lower surface concave with irregular, \pm transverse ridges, brown to black, rarely pale over a larger part, bare or sometimes with a few isolated rhizinae. Cilia present along the brown to black margins, very conspicuous, 3–5 mm long, branching dichotomously and often with perpendicular branchlets on lower parts. Upper and lower cortex of pachydermatic paraplectenchyma. Upper cortex of a palissade-like structure inside, ca 13–25 μm thick, with pored epicortex (cf. plate 1b). Lower cortex 14–18 μm thick. Algae *Trebouxia*-like, roundish, ca 7–18 μm diameter, with thick wall, frequently covered by coiling hyphae.

Apothecia (seen in *C. andense* and *C. equadoriense*) flat to convex, concave only when young, laminal, with brown disc and grey–brown margin, on solid stalk: lower cortex not approaching the exciple inside the stalk (cf. fig. 1). Hymenium 30–45 μm thick. Exciple cupular, 40–55 μm thick, of pachydermatic paraplectenchyma. Asci clavate, ca 25–36 \times 10–15 μm , with large ocular chambre (cf. fig. 2). Spores unicellular, colorless, 8/ascus, 5–9 \times 3.5–5 μm , with ca 0.7 μm thick wall.

Pycnidia (seen in *C. andense* and *C. equadoriense*) laminal, immersed, with black ostiole, ca 0.15 mm wide. Conidiophores of bajonet-type (endobasidial). Pycnospores rod-shaped, ca 5 \times 1 μm .

Lichen substances: atranorin present, sometimes in small quantities only; in addition protolichesterinic acid and unknown substances A–E (see below).

This genus closely resembles *Everniastrum* in habit, but is immediately recognized in the field by its more shrubby, erect growth and its irregular rather than regularly dichotomic branching. The cilia are longer and more conspicuous than in *Everniastrum*, and often have perpendicular branchlets. An important difference is the presence of flat apothecia on solid stalks, a character which seems to be unique in the *Parmelia* complex. The large ocular chamber, small and thick-walled spores and thick exciple provide additional characters to

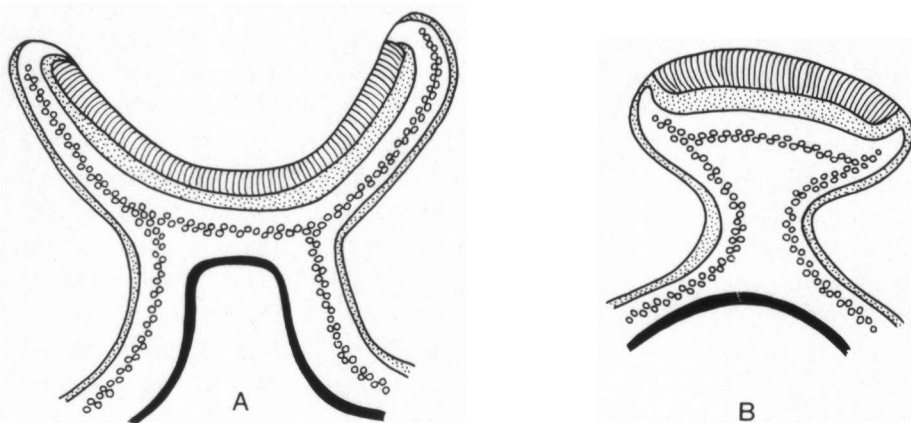


Figure 1. Transverse section of apothecium, schematically. A. *Everniastrum*; B. *Cetrariastrum*.

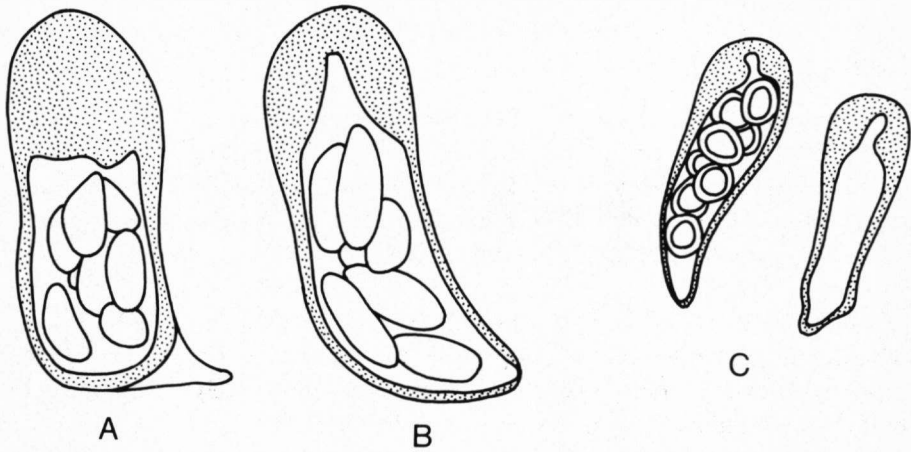


Figure 2. Ascus types. A. *Everniastrum cirrhatum* (Sipman & López 11275); B. *Everniastrum cirrhatum* (Cleef 250); C. *Cetrariastrum andense* (Sipman & López 11303).

separate *Cetrariastrum* from *Everniastrum*. The chemistry is also different, protolichesterinic acid being the only substance they have in common besides atranorin.

Probably the genus is related to *Cetraria*, which it resembles by its fruticose habit and the form of the apothecia. However, in *Cetrariastrum* the apothecia are laminal, not marginal, a pored epicortex is present and the cilia are rhizine-like as in *Everniastrum*.

The plants often cover whole branchlets of shrubs with swarms of small plants consisting of few lobes only. These may be parts of a single thallus of which the connecting parts have been decayed.

The genus is thus far only known from the northern Andes, where it is restricted to the paramo and superparamo belt at ca 3500–4400 m altitude. It seems to prefer branchlets in dwarfshrub vegetation. Because of its small size and its restriction to high altitudes, it has probably been overlooked.

The unidentified substances are characterized as follows (cf. fig. 3):

A. In *C. dubitans* as accessory. Rf class 3. Color after sulphuric acid treatment pale greyish brown. Visible in short-wave UV light, and with a pale fluorescence in long-wave UV light.

B. In *C. equadoriense*. Rf class 3, below A. Color after sulphuric acid treatment grey–black. Visible in short-wave UV-light, without fluorescence in long-wave UV light.

C. In *C. andense* as accessory. Rf class 3, on level of gyrophoric acid. Color after sulphuric acid treatment pale brown. Weak spot. Visible in short-wave UV light, without fluorescence in long-wave UV light.

D. In *C. dubitans* as accessory. Rf class 2, slightly below salazinic acid. Color after sulphuric acid treatment pale brown. Visible in short-wave UV light, and with a pale fluorescence in long-wave UV light.

E. In *C. andense*, one specimen. Rf class 2, below D. Color after sulphuric

acid treatment pale brown. Visible in short-wave UV light, and with a pale fluorescence in long-wave UV light.

1. *Cetrariastrum andense* (Kärnefelt) Sipman comb. nov.

Everniastrum andense Kärnefelt, Bot. Notiser 133: 387 (1980)

Type: Venezuela, Mérida, Sierra de Santo Domingo, Páramo de Muchuchies, near Laguna Negra, 3500–3750 m, on dead twigs of *Hypericum laricifolium*, 13.I.1979, Santesson 29418 (S holotype, seen)

Thallus ca 2 cm diameter. Lobes 0.5–0.8 (–1) mm wide, little branched, with internodes ca 8 mm long. Upper side convex, grey to brown. Lower side concave, brown to black. Cilia 4–5 mm long, moderately dichotomously branched, sometimes with a few perpendicular branchlets.

Apothecia abundant, 1–3 mm diameter, with crenulate margins sometimes bearing a few cilia when old.

TLC: atranorin, protolichesterinic acid, additional substance C or E.

Differences with *C. equadoriense* are discussed under the latter species.

C. andense has not yet been found in Colombia, but it is to be expected because of its presence in Venezuela and Ecuador (Kärnefelt 1980). It is known from branchlets in dwarfshrub vegetation, mainly on *Hypericum laricifolium*, at 3500–4200 m altitude.

Specimens examined:

Venezuela, Mérida: López 14254, 16761 (MERF), López, Ahti & Jörgensen 17813 (MERF), López & Keogh 11766, 11769 (MERF), Sipman & López 11303 (U, MERF), Schulz 43 pr. p. (U)

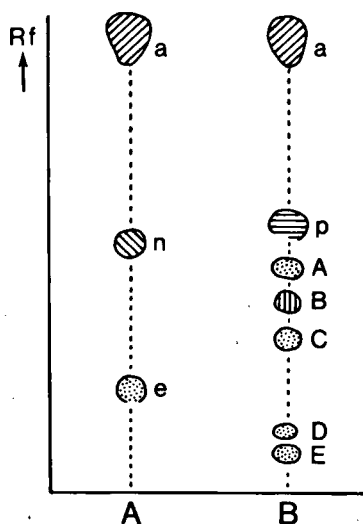


Figure 3. TLC-spots of *Cetrariastrum*, schematically. A. standard (*Cladonia symphylicarpa*), a: atranorin, n: norstictic acid, e: connorstictic acid. B. spots in *Cetrariastrum*, a: atranorin, p: protolichesterinic acid, A–E: unidentified spots.

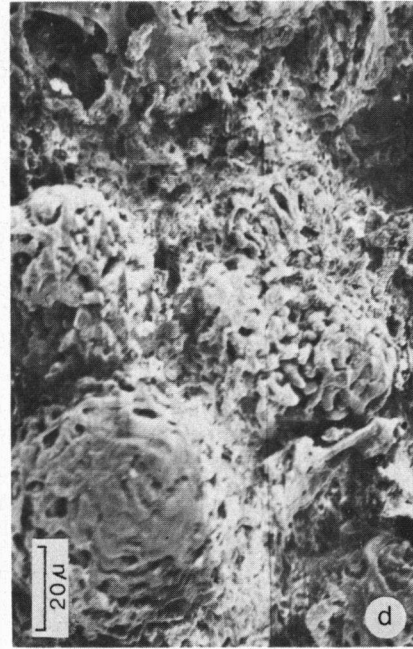
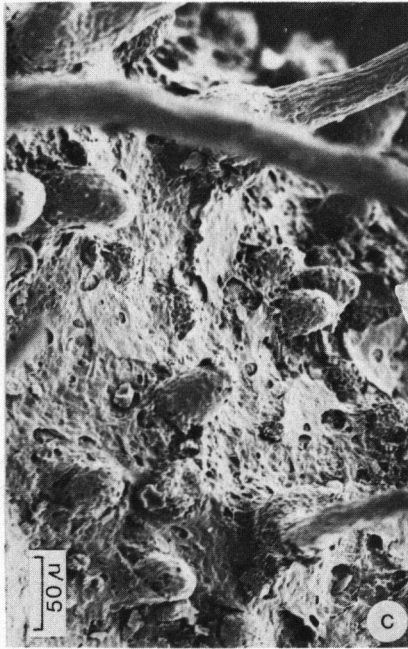
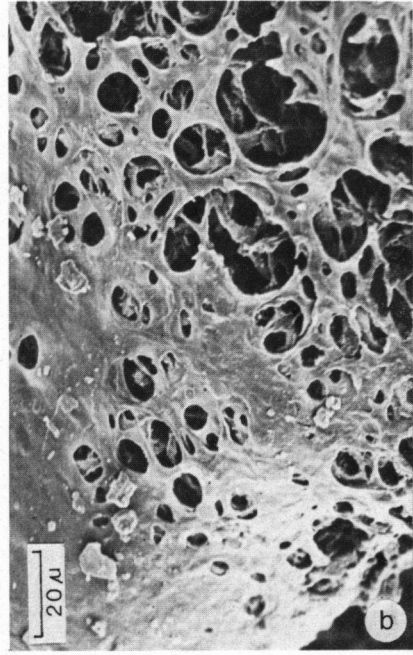
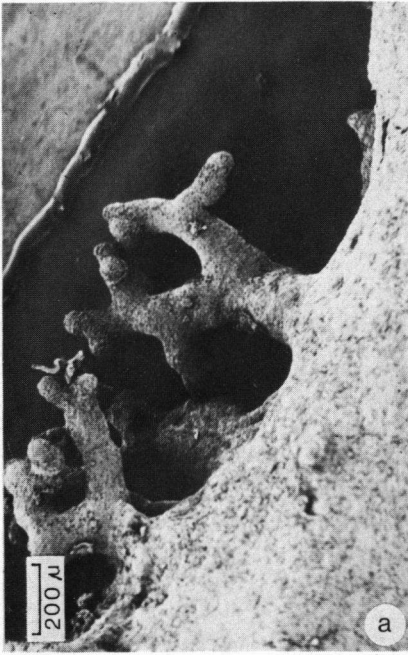


Plate 1. a. *Everniastrum fragile*, isidia (SEM) (Sipman & Valencia 10512); b. *Cetrariastrum dubitans*, epicortex (SEM) (Sipman & Valencia 10496b); c. *Cetrariastrum dubitans*, isidia (SEM) (Sipman & Valencia 10496); d. *Cetrariastrum dubitans*, soredia (SEM) (Sipman & Valencia 10496b).

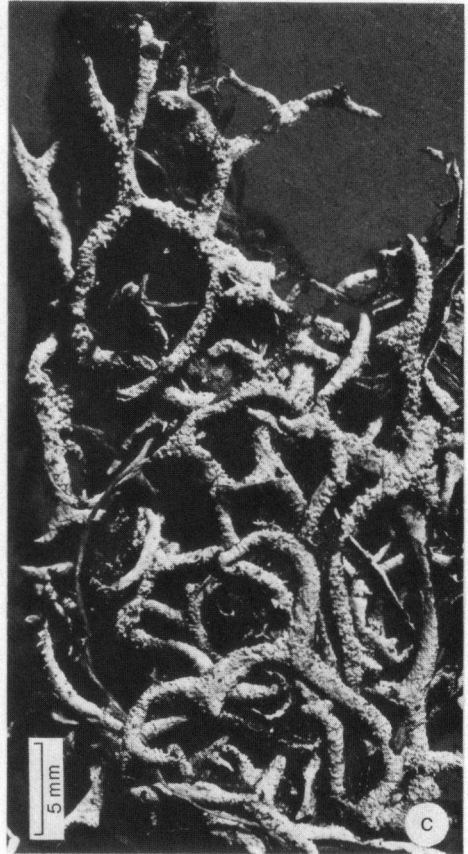
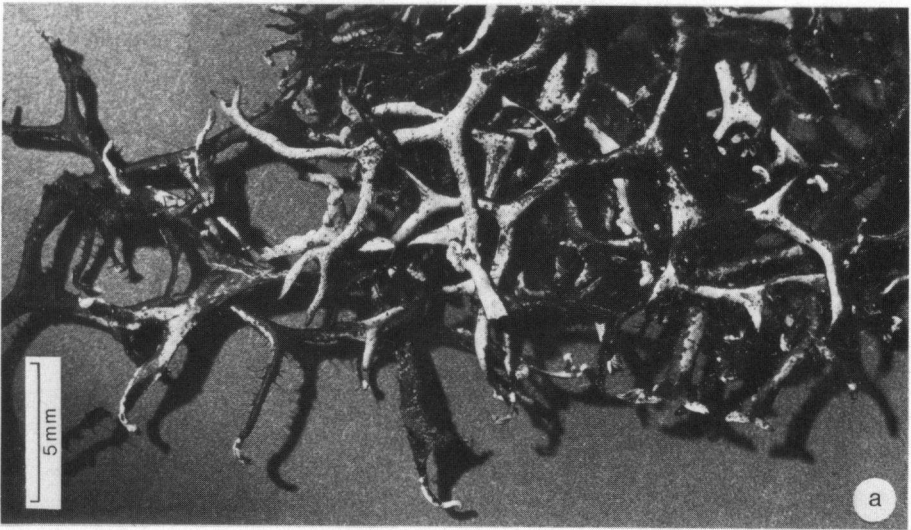


Plate 2. Different types of soralia in *Everniastrum*. a. *E. sorocheilum*, terminal soralia, anchor-shaped lobe-tips (Cleef 444); b. *E. catawbiense*, laminal, subterminal soralia (Cleef 2276d); c. *E. columbiense*, laminal, punctiform soralia (Cleef 35b).

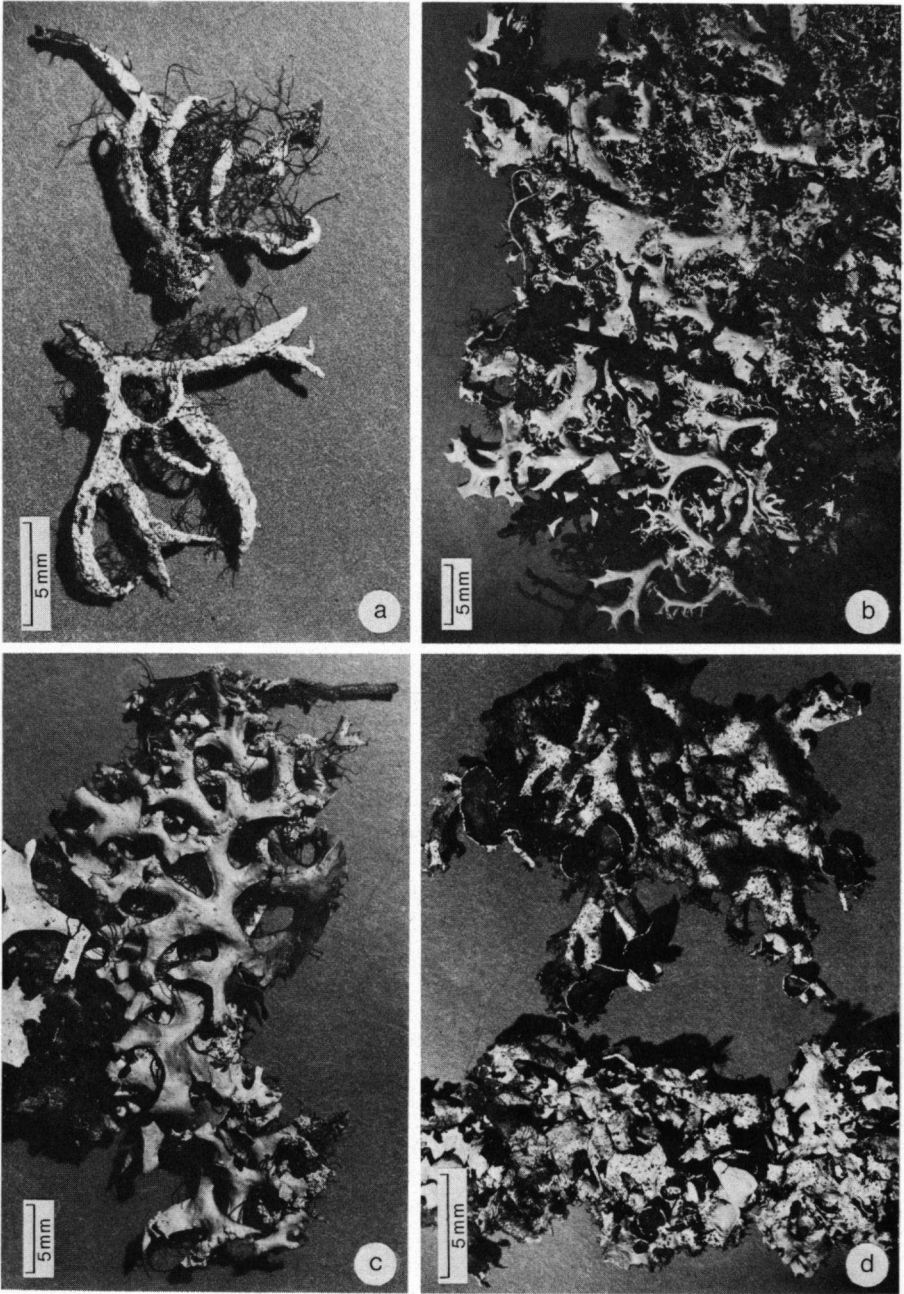


Plate 3. a. *Cetrariastrum dubitans*, habitus (Sipman & Valencia 10496b); b. *Everniastrum fragile*, habitus (Sipman & Valencia 10512); c. *Everniastrum planum*, habitus (Rangel & Cleef 864); d. *Parmelina cleefii*, habitus (Cleef 1997).

2. *Cetrariastrum dubitans* Sipman spec. nov.

Type: Colombia, Caldas, Nevado del Ruiz, NW-side in stunted *Polylepis* forest, 3900 m, 3.II.1979, H. Sipman & H. Valencia 10496b (COL holotype, U isotype)

Thallus 2–4 cm diametro, laciniis (0.5–) 0.7–1.5 mm latis, paulo ramosis, internodiis 3–20 mm longis. Cilia ramulis perpendicularibus infrequenter provisā, raro vel frequenter dichotome ramosa. Isidia vel soralia vel ambo presentes. Isidia dispersa, ca 50 μm diametro, subteretia, usque ad 0.1–0.15 mm longa. Soralia maculiformia, sorediis ca 30 μm diametro. Apothecia ignota. Materia chimica: stirps I, atranorino, acido protolichesterinico et substantia accessoria D; stirps II, atranorino, substantia ignota A et substantia accessoria D.

Thallus 2–4 cm diameter. Lobes (0.5–) 0.7–1.5 mm wide, little branched, with internodes 3–20 mm long. Upper surface weakly convex, grey to brown. Lower surface weakly concave, brown to black, occasionally white. Cilia 3–5 mm, long, little to richly dichotomously branched, with few or no perpendicular branchlets. Isidia and/or soralia present: isidia scattered over the surface, ca 50 μm diameter, irregularly cylindrical, to 0.1–0.15 mm long, frequently tipped by a cilium; soralia maculate, with soredia ca 30 μm diameter. The soralia are most concentrated near the lobe ends, and may occupy the whole width of the lobes (cf. plate 1b–d, 3a).

Apothecia not observed.

TLC: strain I, atranorin, protolichesterinic acid and accessory substance D; strain II, atranorin, unknown substance A and accessory substance D.

Because soralia and isidia are sometimes present on the same plant, sorediate and isidiate plants are united here into one species. SEM analysis reveals that both isidia and soredia arise from an interruption in the epicortex, through which a protuberance rises. This protuberance may produce an epicortex and become an isidium, or remain without and give rise to a soredium (plate 1, c and d).

C. dubitans has been included in *Cetrariastrum* and not in *Everniastrum* because of the presence of long cilia with occasional perpendicular branchlets, the irregular branching of the lobes, and the chemistry. In the field the more erect position of the lobes at once distinguishes it from *Everniastrum* species.

In the type collection the lower surface is almost entirely white whereas in other specimens this is pale brown to black.

C. dubitans is so far only known from Colombia, at 3460–4400 m altitude in the paramo- and lower superparamo-belt of the Eastern Cordillera (Cocuy and Sumapaz areas) and the Central Cordillera (Ruiz). The lower localities are in or near *Polylepis* forest, where the species grows as epiphyte. The superparamo collections are from branchlets of dwarfshrubs, e.g. *Loricaria* sp.

Specimens examined:

Colombia, Arauca: Cleef 9098c (COL, U); *Boyacá*: Cleef 8698c (COL, U); *Caldas*: Sipman & Valencia 10437, 10496, 10496b (type collection); *Cundinamarca*: van der Hammen & Jaramillo 4383e (COL, U).

3. *Cetrariastrum equadoriense* (Sant.) Sipman **comb. nov.**

Parmelia equadoriensis Santesson, Bot. Notiser 1942: 328 (1942)

Everniastrum equadoriense (Sant.) Hale, Mycotaxon 3: 347 (1976)

Type: Ecuador, León, Cotopaxi, SW-slope of the volcano, on twigs of *Chuquiragua* sp., alt. 4300 m, 3.VII.1939, E. Asplund, Iter Regnell. quart. L 180 (Lichenes austroamerici ex Herb. Regnell. 356) (S holotype!).

Thallus 4–7 cm diameter. Lobes ascending, 1–2 mm wide, repeatedly branched, with internodes ca 4–10 mm long. Upper surface weakly convex, grey or in part brownish. Lower side weakly concave, brown to black. Cilia 3–5 mm long, little dichotomously branched, but with numerous perpendicular branchlets.

Apothecia as in genus.

TLC: strain I, atranorin and protolichesterinic acid; strain II, atranorin and substance B.

This species differs from *C. andense* by its larger size, its more branched and less flattened lobes, and the frequent occurrence of perpendicular branchlets on the cilia.

In the type description the position of the apothecia and pycnidia is erroneously stated as marginal.

The Colombian specimens have been collected in the Eastern Cordillera (Cocuy) and the Central Cordillera (Ruiz), at ca 4300 m altitude on the transition paramo – superparamo. Here it grows on branchlets of dwarfshrubs, e.g. *Loricaria* sp.

Specimens examined:

strain I:

Ecuador, León: Asplund, Iter Regnell. quart. L 180 (type collection)

strain II:

Colombia, Arauca: Cleef 9098b (COL, U); *Boyaca*: Cleef 8700d (COL, U); *Caldas*: Sipman & Valencia 10596 (COL, U).

Everniastrum Hale, Mycotaxon 3: 345 (1976)

Parmelia subg. *Everniiformes* (Hue) Hale & Wirth, Phytologia 22: 36 (1971)

Type species: *E. cirrhatum* (Fr.) Hale

Thallus dorsiventral, often fruticose, 5–10 (–30) cm diameter. Lobes 1–3 mm wide, linear, regularly dichotomously branched, usually convoluted or even subtubular. Upper surface convex, grey, sometimes with a brown tinge,

becoming blackened with age, sometimes grooved or maculate, bare or with isidia or soralia; adventitious young lobules sometimes present, resembling isidia but less numerous and soon becoming much larger and flattened, distinctly dorsiventral. Lower surface concave, brown to black, at the tips more pale, bare or sometimes with a few scattered rhizines on wider parts, rarely with more numerous rhizines (in some non-colombian species the lower surface is covered with nearly unbranched rhizines of very unequal length), often with irregular transverse ridges, often extending beyond the margin over the upper surface as a black rim. Cilia present along the brown – black margin (absent in some non-colombian species), usually conspicuous, 1 – 3 mm long, unbranched or more or less dichotomously, often strongly anisotomically, branched. Upper and lower cortex of pachydermatic paraplectenchyma. Upper cortex 20 – 30 μm thick, of a palissade-like structure inside, outside covered by a pored epicortex (Hale, 1973). Lower cortex 14 – 18 μm thick. Algae *Trebouxia*-like, roundish with thick walls, ca 5 – 9 μm diameter.

Apothecia cup-shaped with strongly concave disc, becoming flat only when over 0.5 cm wide, laminal, with brown disc and grey margin. Margin often maculate and ridged on underside. Apothecia on a hollow stalk: the lower cortex comes close to the exciple inside the stalk, and runs over some area parallel to it (cf. fig. 1). Hymenium ca 50 (40 – 60) μm high. Exciple cupular, 25 – 30 μm thick, of pachydermatic paraplectenchyma. Asci cylindrical, ca 36 – 40 \times 16 – 18 μm , mostly with compressed base (cf. fig. 2). Spores unicellular, ovate, colorless, 8/ascus, 10 – 16 \times 6 – 7 μm .

Pycnidia immersed, with black ostiole, in cross-section \pm triangular, rarely emersed and oval in cross-section, ca 150 μm wide. Conidiophores of bajonet-type (endobasidial). Pycnospores rod-shaped, ca 5 \times 0.5 μm .

In non-colombian species asci to 50 \times 20 μm , spores 19 – 21 \times 7 – 9 μm , pycnospores 6 – 7 \times 0.5 μm .

Lichen substances: atranorin and protolichesterinic acid always present (not repeated in the species descriptions); in addition gyrophoric or salazinic acid (in non-colombian species also protocetraric, norstictic, alectoronic or fumar-protocetraric acids).

For general description see also Hale (1976, p. 345). The descriptions of ascomycarp and pycnidium are based on specimens of *E. cirrhatum* and the non-colombian *E. neocirrhatum* and *E. nepalense*.

The genus *Everniastrum* is easily recognizable among the foliose lichens because of its linear, regularly dichotomously branching lobes with brown to black lower surface. For differences with *Cetrariastrum*, see the general description of that genus.

The general distribution of *Everniastrum* is in the tropical mountains. Some species are widely distributed in Asia, Africa and America, e.g. *E. cirrhatum*, *E. sorocheilum* and *E. vexans*. Many species are restricted to limited parts of the neotropical mountains, with apparent centers of diversity in Mexico and the Andes. A few are African. (From Hale, 1976). In Colombia, near the equator,

most species occur at 3000 to 3500 m altitude. At this level most chemical diversity is found, too. Away from the equator lower altitudes are occupied.

The characters of the only regular unknown substance are: F, present in part of the specimens with salazinic acid; Rf class 3, on the same level as stictic acid; color after sulphuric acid treatment a weak greyish brown; not visible in UV-light. Additional weak spots were occasionally found, but were too faint or too incidental to be of taxonomic use.

4. *Everniastrum catawbiense* (Degel.) Hale, Mycotaxon 3: 347 (1976)
Parmelia sorocheila var. *catawbiense* Degelius, Ark. f. Botanik 30A (3): 65 (1941)

Type: U.S.A., Tennessee, Mt. Le Conte, G. Degelius (hb. Degelius holotype, not seen)

Plants generally small, ca 2–5 cm diameter. Lobes clearly convoluted with internodes 3–6 × 0.7–1.5 (–2.5) mm. Applanate basal lobes not clearly developed. Soralia present, laminal or subterminal, maculiform or capitate. Soredia ca 35 (–50) μm diameter when full-grown. Rhizinae mostly absent. Cilia well developed (cf. plate 2b).

Apothecia and pycnidia rare, not examined.

TLC: with gyrophoric acid.

E. catawbiense differs from *E. sorocheilum* chemically by the presence of gyrophoric acid instead of salazinic acid, and morphologically by the laminal soralia and the absence of anchor-shaped sorediate lobe-ends. Among the other sorediate *Everniastrum* species in Colombia, *E. planum* differs by its much wider lobes and the presence of pustular soralia. *E. columbiense* differs by the presence of punctiform soralia on a warty thallus surface, and the possession of salazinic acid.

The available colombian specimens originate from the Eastern Cordillera (Cocuy to Sumapaz) and the Central Cordillera (Ruiz), but probably the species is widely distributed in all the high mountains. Its altitudinal range is from 2800 to 4100 m. This and the habitat do correspond with *E. sorocheilum*. However, all *E. catawbiense* collections were from hardly disturbed vegetations whereas *E. sorocheilum* is frequent in cultivated areas as well.

Specimens examined:

Colombia, Boyacá: Cleef 2276d (COL); Caldas: Sipman & Valencia 10494 (COL, U); Cundinamarca: Cleef 1618, 1698c, 2812d (COL, U), 4212 (COL), 5230d (COL), Grabandt & Idrobo 151b (COL), Sipman, Reyes & Valencia 10623 (COL, U)

Ecuador, Cotopaxi area: Gradstein, Sipman & de Vries 126 (U)

Venezuela, Mérida: Sipman & López 11151, 11342 (MERF, U)

5. *Everniastrum cirrhatum* (Fr.) Hale, Mycotaxon 3: 347 (1976)

Parmelia cirrhata E. Fries, Syst. Orb. Veg. 1: 283 (1825)

Type: Nepal (UPS holotype, not seen, according to Du Rietz, 1924)

Parmelia camtschadalis var. *americana* (Mey. et Flot.) Nylander, Syn. Meth. 1: 387 (1860)

Parmelia vermicularis Vain., Hedwigia 38: (123) (1899)

Plants growing in cushions of up to several dm² in diameter. Lobes convoluted to subtubular, ascending, very long and narrow, with internodes ca (3 – 5 – 9 × 0.8 – 2 (– 3) mm. Short, applanate basal lobes not observed. Lower surface of the lobes often pale over a greater part of their length. Isidia or soredia absent. Adventitious lobules sometimes present on the thallus upper surface. Rhizines absent. Cilia rather richly branched.

Apothecia common, but often without asci, structure as in the general description.

Pycnidia very common but often degenerated, structure as in the general description.

TLC: strain I, with salazinic acid; strain II, with salazinic acid and unknown substance F; strain III, with gyrophoric acid; strain IV, without additional substance.

E. lipidiferum (Hale & Wirth) Hale may be conspecific with strain IV, judging from the original description of that species. *E. imitatum* (Hale & Wirth) Hale agrees chemically with strain III, but according to the original description it should be morphologically different, resembling *E. neocirrhatum* (Hale & Wirth) Hale.

The nomenclature of *E. cirrhatum* is rather complicated, cf. Du Rietz, 1924.

The Colombian specimens originate from the Eastern Cordillera (Cocuy to Sumapaz), the Central Cordillera (Ruiz and Tolima) and the Macizo de Colombia, at 2500–4200 m altitude. Probably the species is widespread all through the Andes of Colombia.

E. cirrhatum usually grows among thick bryophyte cushions on open places on soil and rock, but also frequently as epiphyte. At 3000 to 4000 m altitude *E. cirrhatum* can be found in a wide range of vegetation types.

Specimens examined:

Strain I: (*: tested only by color reaction)

Colombia, Arauca: Cleef 9128 (COL, U), 9165b (COL); Boyacá: Cleef 1786c (COL), 2301 (COL, U), 2306 (COL, U), 4217 (COL, U); Caldas: Sipman & Valencia 10460 (COL, U); Cauca: Cleef 2652b* (COL), Cleef & Fernandez 667b (COL); Cundinamarca: Cleef 1696 (COL, U), 3122L* (COL), Cleef & Jaramillo 250 (COL, U), van der Hammen & Jaramillo 4303 (COL, U), 4394 (COL, U); Magdalena: Rangel & Cleef 883b, 1066, 1082, 1086e (COL, U); Meta: Cleef 913d* (U), 7800 (COL, U), 8103 (COL, U); Tolima: van der Hammen & Jaramillo 3313 (COL)

Argentina, Ladesma: Ferraro 565 (U)

Costo Rica, Cartago: Sipman 11754 (U)

Ecuador, Cotopaxi area: Gradstein, Sipman & de Vries 130 (U)

Peru, Cajamarca: de Graaf P6–4, P7–4 (U)

Venezuela, Monagas: Hooft s.n. (U); Mérida: Sipman & López 11097, 11140, 11274, 11275, 11295 (MERF, U); Trujillo: López & Keogh 11286, 11368, 11379 (MERF), López & Ruiz 10983, 11059 (MERF)

Strain II:

Colombia, Cundinamarca: Sipman, Reyes & Valencia 10678 (COL, U); Magdalena: Rangel & Cleef 862 (COL, U)

strain III:

Colombia, Boyacá: Cleef 4686 (COL, U); Magdalena: Rangel & Cleef 1071b (COL, U)

strain IV:

Colombia, Arauca: Cleef 9128c (COL, U)

Costa Rica, Cartago: Sipman 11713 (U)

6. *Everniastrum columbiense* (Zahlbr.) Hale, Mycotaxon 3: 347 (1976)

Parmelia columbiensis Zahlbr., Catal. Lich. Univ. 6: 61 (1929)

Parmelia granulosa Vain., Hedwigia 38: (123) (1899) (non Ach.)

Type: Colombia, prope Bogota, J. Weir 47 pr. p. (BM holotype!)

Plants usually rather small, with appanate basal part and ascending lobes above it, ca 5–10 cm diameter. Longer lobes convoluted, with internodes ca 5–10 cm diameter, the ascending (sorediate) ones often with few branches at the ends; short basal lobes often well developed, less convoluted. Soralia present, laminal, developing from punctiform spots on a warty surface where the cortex bursts. The spots may fuse together to make the whole lobe surface becoming sorediate except for the tips by fusion of the soralia. Soredia 55–80 μm diameter when full-grown. Rhizinae mostly absent. Cilia rather scarce, especially on the basal parts (cf. plate 2c).

Apothecia and pycnidia rare, not examined.

TLC: with salazinic acid.

Aberrant specimens from Ecuador and northern Peru, tentatively identified as *E. columbiense* (see below), differ from the Colombian ones by the smaller soredia, 35–50 μm diameter, and the more regularly confluent soralia. Moreover the soralia frequently are (sub)terminal on shorter lobes, thus approaching *E. sorocheilum*. Perhaps these specimens belong to a different species.

In some Colombian specimens the coarse soredia tend to remain attached to each other, resulting in the development of tree-like soralia.

An Ecuadorian specimen (Gradstein, Sipman & de Vries 72) deviates by its well developed basal lobes, of which the widest and shortest lack cilia but possess numerous rhizinae.

The available Colombian specimens originate from a limited area in the Eastern Cordillera, between La Calera and Sumapaz, at 2700–3600 m altitude. But likely the species is more widespread. Apparently *E. columbiense* prefers slightly lower elevations than the other sorediate species of *Everniastrum* in Colombia. The plants usually grow on trees in open mossy forest, sometimes also on man-made substrates such as road banks and poles, and in plantations. The aberrant Ecuadorian and Peruvian specimens inhabit similar habitats.

Specimens examined:

Colombia, Cundinamarca: Cleef 35b, 3822b (COL, U), 5343c (COL), van der Hammen & Jaramillo 4388b (COL), Weir 47 pr. p. (type collection)

Venezuela, Mérida: Sipman & López 11082, 11340 (MERF, U)

aberrant specimens:

Ecuador, Cotopaxi area: Gradstein, Sipman & de Vries 72 (U); *Quito*: Sipman 7806 (U), Woudstra S009 (U)

Peru, Amazonas: de Graaf P 9–3, P 10–6 (U)

7. *Everniastrum fragile* Sipman spec. nov.

Type: Colombia, Caldas, Nevado del Ruiz, NW-side, near hotel Termales, alt. 3500 m, 4.II.1979, Sipman & Valencia 10512 (COL holotype, U, US isotype)

Thallus minor, 2–4 cm diametro vel nonnumquam maior, 5–20 cm diametro, laciniis paulo convolutis, modice applicatis, brevibus et latis, satis uniformibus, internodiis ca 2–5 × 1.5–4 mm. Isidia terminalia vel marginalia, teretia vel coralloideo-ramosa, 90–200 μm lata, 0.5–3 mm longa, fragilissima. Rhizinae absentes vel singulae raras. Cilia sparsa. Apothecia et pycnidia ignota. Materia chimica: stirps I, acido salazinic; stirps II, acido salazinic et substantia ignota F.

Plants usually only few cm in diameter, sometimes forming large rosettes of 5–20 cm diameter. Lobes weakly convoluted, especially the wider ones, rather appressed, short and wide, with internodes ca 2–5 × 1–1.5–4 mm, rather uniform. Isidia present, mainly on the lobe tips but sometimes also marginally, terete or coralloid-branched, 90–200 μm thick, 0.5–3 mm long, very fragile. Rhizinae absent or rarely an isolated one present. Cilia rather scarce (cf. plate 1a, 3b).

Apothecia and pycnidia not observed.

TLC: strain I, with salazinic acid; strain II, with salazinic acid and unknown substance F.

Linear, ascending lobes, characteristic for many species of this genus, are sometimes only poorly developed in *E. fragile*. Presumably the growth of isidia inhibits the extension of the lobes.

E. vexans, the only other isidiate species of the genus in Colombia, has much smaller, unbranched isidia which are laminal and frequently tipped by a cilium.

E. fragile has been found in Colombia so far in the Eastern Cordillera (Cocuy to Sumapaz) and the Central Cordillera (Ruiz), at 3200–3900 m altitude. A single found was at 4400 m. The species grows as epiphyte in open, mossy forest or shrub vegetation, and also in man-made habitats as an *Eucalyptus* plantation and a road bank.

Specimens examined:

Strain I:

Colombia, Boyacá: Cleef 1824b (COL, U); *Caldas*: Sipman & Valencia 10440 (COL, U), 10512 (type collection); *Cundinamarca*: van der Hammen & Jaramillo 4289a, 4430a (COL, U), Sipman, Reyes & Valencia 10621 (COL, U); *Tolima*: Sipman & Valencia 10414 (COL, U)

Ecuador, Quito: Sipman 7797b (U)

Strain II:

Colombia, Boyacá: Cleef 4524 (COL, U)

Venezuela, Mérida: Sipman & López 11343 (MERF, U)

8. *Everniastrum planum* Sipman spec. nov.

Type: Colombia, Magdalena, Sierra Nevada de Santa Marta, Alto Buritaca, alt. 3300 m, VIII.1977, Rangel & Cleef 864 (COL holotype, U isotype)

Thallus maior, ca 5–20 cm diametro, applanata, laciniis planis vel leviter convolutis, brevis et latis, internodiis ca 2–3 × 2 (–3) mm, laciniis basalibus apertis absentibus. Soralia laminalia vel subterminalia, primo pustulata. Pustulae 150–300 μm diametro, erodendae, soredia ca 60–80 μm diametro gerentes. Rhizinae absentes. Cilia bene evoluta. Apothecia et pycnidia ignota. Materia chimica: acido gyrophorico.

Plants rather large, ca 5–20 cm diameter, applanate. Lobes flat to somewhat convoluted, short and wide, with internodes ca 2–3 × 2 (–3) mm. Distinct basal lobes not observed. Soralia present, laminal or subterminal, starting as pustulate patches. Pustules 150–300 μm diameter, becoming eroded and producing coarse soredia ca 60–80 μm diameter. Rhizinae absent. Cilia well developed (cf. plate 3c).

Apothecia and pycnidia not observed.

TLC: with gyrophoric acid.

E. planum differs from the other sorediate *Everniastrum* species by the short and wide, flat or little convoluted lobes, and the pustulate soralia.

In the Colombian specimen the lobes are more convoluted than in the Costa Rican plant.

The Colombian specimen came from the Sierra Nevada de Santa Marta, at 3300 m, near the tree line. It was growing on a branch of *Diplostephium* sp. in dwarf forest. The Costa Rican plant was found at the same altitude, but on mossy rock on an exposed hill top.

Specimens examined:

Colombia, Magdalena: Rangel & Cleef 864 (type collection)

Costa Rica, Cartago: Sipman 11761 (U)

9. *Everniastrum sorocheilum* (Vain.) Hale, Mycotaxon 3: 349 (1976)

Parmelia sorocheila Vain., Hedwigia 38: (123) (1899)

Type: Colombia, prope Bogota, 8500' s.m., J. Weir 5 pr. p. (BM holotype!)

Plants generally small, ca 2–5 cm diameter. Lobes clearly convoluted, often rather short, with internodes 2.5–4 (–6) × 1–1.5 (–2.5) mm. Applanate basal lobes not clearly developed, all lobes rather short. Soralia present, terminal, capitate, often extending along the margins, sometimes with a few laminal ones near the lobe tips. Soredia ca 35 (–50) μm diameter when full-grown. Rhizinae mostly absent. Cilia well developed (cf. plate 2a).

Apothecia and pycnidia not observed.

TLC: strain I, with salazinic acid; strain II, with salazinic acid and unknown substance F; strain III, without additional substance.

E. sorocheilum can be distinguished easily from the other sorediate *Everniastrum* species in Colombia by the presence of anchor-shaped sorediate lobe tips. These consist of a bifurcation in which the two branchlets are much reduced in length and support terminal soralia, which are connected by extensions along the margin between the two tips. The branchlets are often curved outward (cf. plate 2a).

E. sorocheilum has been found in Colombia in the Eastern Cordillera (Cocuy to Sumapaz) and the Central Cordillera (Ruiz), at 3000 to 3900 m altitude. Probably it is common throughout the Andes range. It usually grows on rather thin, exposed branches of mossy shrubs. Many of the non-Colombian collections are from disturbed vegetations, e.g. *Eucalyptus* or *Pinus* plantations.

Specimens examined:

Strain I: (*: tested only by color reaction)

Colombia, Arauca: Cleef 9128* (COL); Caldas: Sipman & Valencia 10532 (COL, U); Cundinamarca: Cleef 35f (U), 444 (COL, U), 3916b* (COL), 6033b* (U), Grabandt & Idrobo 151a (COL), Weir 5 pr. p. (type collection)

Argentina, Tucumán: Colaris 1245 (U)

Costa Rica, Cartago: Sipman 11700, 12395 (U).

Ecuador, Cotopaxi area: Gradstein, Sipman & de Vries 51, 58 (U); Quito: Sipman 7793, 7798 (U)

Peru, Ancash: de Graaf P 17-3, P 19-3 (U)

Venezuela, Mérida: Sipman & López 11068 (MERF, U)

Strain II:

Ecuador, Quito: Sipman 7805 (U)

Strain III:

Venezuela, Mérida: Sipman & López 11263 (MERF, U)

10. *Everniastrum vexans* (Zahlbr.) Hale, Mycotaxon 3: 350 (1976)

Parmelia vexans Zahlbr., Fedde Repert. Sp. Nov. 33 : 55 (1934)

Parmelia americana in Vainio, Hedwigia 38: (123) (1899), non Mey. et Flot.

Type: Taiwan, Mt. Arison, Kainoodai, corticola, Asahina 79 (TNS holotype, not seen)

Plants growing in cushions up to several dm² in diameter. Lobes strongly convoluted to subtubular, ascending, very long and narrow, with internodes 5-10 × 0.7-1 (-2.5) mm. Shorter and appanate basal lobes occasionally present. Isidia present, laminal on central thallus parts, terete or coralloid-branched, ca 50-70 μm wide and 0.1-0.3 (-1) mm long, frequently tipped by a cilium, sometimes by a lobule. Rhizines mostly absent. Cilia always present, well developed but sometimes infrequent, usually unbranched.

Apothecia rare, not examined.

Pycnidia rare (examined in only one specimen), partly emersed and oval in cross section, otherwise as in the genus.

TLC: strain I, with salazinic acid; strain II, with salazinic acid and unknown substance F; strain III, with gyrophoric acid.

Hale (1976, p. 347) demonstrated the true nature of the species to which the epithet *americana* belongs. The name *E. vexans* has come into general use for this species since 1971 (Hale & Wirth).

Development of short and wide basal lobes is clearly seen in the specimen Cleef 444d.

Some Venezuelan specimens contain constictic acid in addition to the substances of strain I (pers. comm. M. Hale). This substance has not yet been demonstrated in Colombian plants.

E. vexans differs from the other isidiate species in Colombia, *E. fragile*, by the laminal position of the isidia and their smaller size.

The present Colombian specimens came from the Eastern Cordillera (Cocuy to Sumapaz), the Macizo de Colombia and the Western Cordillera, at 1900–3900 m altitude. Below 3000 m altitude it is the commonest member of its genus, and below 2500 m the only one. Probably the species is present throughout the mountains of Colombia. Strain II appears to prefer the lower altitudes, around 2000 m. The lowest record available (Galapagos Islands) was from 1000 m altitude.

Most of the available collections were epiphytic in mossy, not to dark forest. A number of collections are on mossy road banks, boulders or soil, often in connection with disturbance of the natural vegetation.

Specimens examined:

Strain I: (*: tested only by color reaction)

Colombia, Boyacá: Cleef 2260d* (COL), 9544b* (U); *Cundinamarca*: Cleef 226c* (COL), 444d (COL, U), 3656 (COL, U), 4846 (COL, U), 5230c* (U), 5254f (COL), 6051c* (COL), Grabandt & Idrobo 18a (COL, U), van der Hammen & Jaramillo 4431 (COL), Sipman, Reyes & Valencia 10677 (COL, U), Sipman & Valencia 10330 (COL, U), Weir 47 pr. p. (BM); *Huila*: Cleef & van der Hammen 5107 (COL, U); *Magdalena*: Rangel & Cleef 883 (COL, U)

Costa Rica, Cartago: Sipman 11701(U); *Puntarenas*: Sipman 11882 (U); *San José*: Sipman 11574 (U).

Ecuador, Galapagos Islands: Sipman L-77 (COLO, U); Weber & Lanier, Lich. Exs. 499 (COLO, U); *Quito*: Sipman 7797a* (U).

Venezuela, Mérida: López 12282 (MERF); *Trujillo*: López 13407, 13456 (MERF)

Strain II:

Colombia, Valle: Hartman 208 (U)

Mexico, Chiapas: den Held & van Rhijn Fl 18 (U)

Venezuela, Caracas: Sipman 10718, 10766 (MERF, U); *Mérida*: Sipman 10938 (MERF, U), Sipman & López 11098 (MERF, U); *Táchira*: Hale, Lich. Am. Exs. 182 (U)

Strain III:

Colombia, Cundinamarca: Cleef 125d (U)

Parmelina Hale, *Phytologia* 28: 481 (1974)

Type species: *P. tiliacea* (Hoffm.) Hale, *Phytologia* 28: 481 (1974)

This genus is not treated extensively here. Only two species are dealt with, *P. cleefii* and *P. swinscowii*, because they resemble *Everniastrum*. Usually *Parme-*

lina is very different because of its wider lobes, appanate thallus and abundant rhizinae. Krog & Swinscow (1979) discuss the delimitation of the genus *Parmelina*. They include some species, e.g. *P. swinscowii*, in *Hypotrachyna*, which they treat as a subgenus of *Parmelia*. Here the generic division of M. Hale is followed because it is based on a study of numerous neotropical collections.

Besides atranorin, protolichesterinic and salazinic acids have been found in many of the specimens studied here. Two substances could not be identified: unknown substance G, with Rf class 3, same level as gyrophoric acid, pale greyish after sulphuric acid treatment, and H, with Rf class 3, about the same level as hypoprotocetraric acid, pale grey after sulphuric acid treatment.

11. *Parmelina cleefii* Sipman, *spec. nov.*

Type: Colombia, Boyacá, Páramo NW de Belén, epilítico, 3820 m altit., 28.II.1972, Cleef 1997 (COL holotype, U and US isotype)

Thallus maior, rosulata, plurium dm diametro, laciniis modice applicatis, brevibus, uniformis, fere planis, internodiis 1.5–3 × 1–1.5 mm. Isidia soralique absentia. Rhizinae increbrae vel sparsae. Cilia breviora, ca 1 mm longa, frequentia vel rara. Apothecia frequentia, sporis 9 × 4 μm. Materia chimica: stirps I, acido salazinic; stirps II, acido salazinic et substantia ignota G.

Thallus growing in extensive rosettes often several dm in diameter. Lobes short, with internodes 1.5–3 × 1–1.5 mm, uniform, rather appanate, flat. Isidia and soredia absent. Rhizinae rather scarce. Cilia rather short, ca 1 mm long, sometimes numerous, sometimes scarce (cf. plate 3d).

Apothecia and pycnidia as in the general description of *Everniastrum*, see above. Apothecia frequent, with spores 9 × 4 μm.

TLC: strain I, with salazinic acid; strain II, with salazinic acid and unknown substance G.

This species appears to be the non-sorediate relative of *P. swinscowii*.

P. cleefii and *P. swinscowii* resemble *Everniastrum* by the presence of narrow lobes, sometimes by well developed cilia and poorly developed rhizinae, and by chemistry. They differ by the appressed thallus and the irregularly branching lobes.

The development of the rhizinae is very variable, and seems to alternate more or less with the presence of cilia. In lobes with few cilia the rhizinae are numerous, but even on the same specimen lobes may be present with many cilia and few rhizinae, e.g. Cleef & Florschütz 5554, Gradstein, Sipman & de Vries 159.

The Colombian specimens originate all from a limited area in the Eastern Cordillera, from Cocuy to Belén, and between 3800 and 4300 m altitude. The habitat is mossy boulders. Perhaps this species has, like the following, a preference for bird's perching stones.

Specimens examined:

Strain I:

Colombia, Arauca: Cleef 8839 (COL, U); *Boyacá*: Cleef 1997 (type collection)
Venezuela, Mérida: Hale & López 44592, 44652, 44678, 44685 (MERF, US), Hanselmann & Loveless 84 (US)

Strain II:

Colombia, Boyacá: Cleef & Florschütz 5554 (COL, U)

12. *Parmelina swinscowii* (Hale) Hale, *Phytologia* 28: 483 (1974)

Parmelia swinscowii Hale, *Phytologia* 27: 4 (1973)

Type: Kenya, Central Province, Mt. Kenya, above vertical bog near Naro Moru track, alt. 3500 m, I.1972, T.D.V. Swinscow K 31/33 (US isotype!)

Thallus growing in extensive rosettes, often several dm in diameter. Lobes short, with internodes $1.5 - 2 \times 0.5 - 1.5 (-2)$ mm, all uniform, rather appunate, flat. Soralia present, laminal, maculiform, mostly towards the lobe ends. Soredia 30–45 (–60) μm diameter when full-grown. Rhizinae present, but often scarce. Cilia short, ca 1 mm long, sometimes unfrequent.

Apothecia and pycnidia not observed.

TLC: strain I, with lobaric and salazinic acids; strain II, with salazinic and protolichesterinic acids; strain III, with salazinic acid and unknown substance G; strain IV, with salazinic acid and unknown substance H.

This species seems to be a sorediate relative of *P. cleefii*.

The Colombian specimens are identical to the type of *P. swinscowii* except for the absence of lobaric acid.

The specimens without protolichesterinic acid tend to have fewer cilia and more numerous rhizinae.

In Colombia the species has been found in the Eastern Cordillera, in the Cocuy and the Sumapaz areas, at 3400–4400 m altitude, on mossy boulders. It seems to prefer habitats rich in nitrates such as bird's perching stones.

Specimens examined:

Strain I:

Kenya, Central Province: Swinscow K 31/33 (isotype collection)

Strain II:

Colombia, Boyacá: Cleef 8698g (U); *Cundinamarca*: Cleef 170d (COL), 6454d (COL)

Venezuela, Mérida: Sipman & López 11286 (MERF, U)

Strain III:

Ecuador, Cotopaxi area: Gradstein, Sipman & de Vries 159, 160 (U)

Strain IV:

Chile, Santiago: Rundel 7243 (US)

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