

SYSTEMATICS OF SOME REINDEER LICHENS (*CLADONIA* SUBG. *CLADINA*) IN THE SOUTHERN HEMISPHERE

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Abstract: *Cladonia arbuscula* subsp. *squarrosa* (Wallr.) Ruoss and *C. stygia* (Fr.) Ruoss are reported for the first time from the Southern Hemisphere. Populations of *C. arbuscula* in New Zealand and Australia are recognized as subsp. *stictica* Ruoss, subsp. nov., usually containing stictic acid, norstictic acid (first report in subg. *Cladina*), and sometimes also the fumarprotocetraric acid complex. *C. laevigata* (Vainio) Gyelnik is reinstated in *Cladonia* subg. *Cladina* sect. *Tenuis*, while *C. stygia* is considered to belong to sect. *Crustaceae* rather than to sect. *Tenuis*. *C. confusa* R. Sant. is morphologically highly variable, although chemically uniform, usually containing usnic acid and perlatolic acid. An usnic acid-deficient chemodeme is reported as new to New Zealand.

Introduction

During investigations on reindeer lichens (*Cladonia* subg. *Cladina*), especially the *Cladonia arbuscula* group (Ruoss & Ahti 1985, Ruoss 1987a,b) in Europe, some specimens of *C. mitis* Sandst. from the Southern Hemisphere were analysed chemically; other critical specimens from the Southern Hemisphere were also studied. As our field studies in the Southern Hemisphere were very limited, results presented in this paper are based primarily on herbarium material. The taxonomic concept of this paper is proposed by E. Ruoss and differs in several points from that of T. Ahti; it is based on results of investigations performed by E. Ruoss at the Botanical Institute of Helsinki.

Reindeer lichens of the Southern Hemisphere have been studied by several authors: e.g. by Vainio (1887), des Abbayes (1939), Santesson (1942), Martin (1960), Ahti (1961) and Ahti & Kashiwadani (1984). Of the holarctic reindeer lichens, only *C. mitis* and *C. rangiferina* (L.) Weber ex Wigg. have been reported from the Southern Hemisphere (Ahti 1961, 1984). *Cladonia laevigata* (Vainio) Gyelnik from Chile was thought to be closely related to *C. arbuscula* (Ahti & Kashiwadani 1984; Ahti 1984) and its status is reconsidered here in connection with the revision of the *C. arbuscula* group.

Cladonia arbuscula (Wallr.) Flot. and *C. stygia* (Fr.) Ruoss, two species with wide holarctic distributions, have not previously been recorded from the Southern Hemisphere (Ahti 1984). *Cladonia* 'sylvatica' was reported by des Abbayes (1939) for Bolivia and Brazil, but Ahti (1961) did not include these reports in his concept of *C. arbuscula*.

No Northern Hemisphere species of arctic to temperate reindeer lichens are known from the African continent. Some morphologically variable specimens

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of *C. confusa* R. Sant., agg. (Ahti 1984) from East and South Africa have been analysed chemically in order to clarify the chemical homogeneity of African material, formerly included in *C. alpestroides* des Abb. and *C. leptoclada* des Abb.

Cladonia mitis is the only recently recognized holarctic species from New Zealand and Australia. Of the seven species recorded at various times from New Zealand, four were accepted by Martin (1960), and two by Ahti (1984) and Galloway (1985). Ahti (1961) included reports of *C. impexa* Harm. and *C. alpestris* (L.) Rabenh., recognized by Martin, in *C. leptoclada* and later *C. confusa* (Ahti 1984). Since Ahti (1984) reported the presence of the stictic acid complex in *C. mitis* in Tasmania, and also because of problems in the separation of *C. mitis* and *C. arbuscula* (Ruoss 1987a,b), the status of the species in Australasia has been re-examined. Chemodemes containing stictic acid have been studied in connection with revised nomenclatural concepts of the *C. arbuscula* group.

Subgenus versus genus *Cladina*

In this study the generic and species concepts of the *C. arbuscula* group follow Ruoss (1985, 1987b), although Ahti (1984, 1986) favours recognition of the reindeer lichens as a distinct genus, *Cladina* (Nyl.) Nyl. The following discussion on the status of *Cladina* is based mainly on recent studies on *Cladina* by Ahti (1961, 1984, 1986), Ahti *et al.* (1987), Huovinen & Ahti (1986a) and Ruoss (1985, 1987b, and unpublished data), on sect. *Unciales* (Delise) Oxner ex Ahti by Ahti (1973) and Huovinen & Ahti (1986b), *C. gigantea* group by Ahti (1977) and chemical investigations by Huovinen (1986) and Huovinen & Ahti (1982).

The separation of *Cladina* from *Cladonia* as a genus was first proposed by Nylander (1866) (for a detailed discussion see Ahti 1961, 1984), and later revived without discussion by Hale & Culberson (1970). Ahti (1984) noted that lichenologists in North America and the Soviet Union now use *Cladina* at generic level, contrary to most European authors. The aim of Ahti's synopsis (1984: 25) was to discuss the characteristics of *Cladina* and 'to publish nomenclatural combinations for use by those who would like to recognize *Cladina* as a genus'. To Ahti, the most important diagnostic characteristics of *Cladina* are the crustose primary thallus, the ecorticate and ascyphous podetia, the regular branching ('but not highly regular') and the frequent occurrence of usnic and perlatolic acids.

Evidence against the generic segregation of *Cladina*

Morphology

Besides the subg. *Cladina*, there are numerous species with an intricately branching and/or ecorticate or only 'corticoid' thallus surface in the sect. *Unciales*, and in the *C. furcata*, *C. gigantea* or *C. gracilis* groups.

Reindeer lichens have no podetial squamules, but there are also several members of sect. *Unciales* (c. 50%) and *C. gigantea* group which have no or very rare squamules (e.g. *C. pachyclados* (Vainio) Ahti, *C. crassiuscula* Ahti, *C. spinea* Ahti, *C. steyermarkii* Ahti, *C. vareschii* Ahti, *C. gigantea* (Bory) H. Olivier, *C. glaucopallida* Vainio, *C. usambarensis* Ahti & Krog, *C. papuana* Stenroos).

The primary thallus is rarely visible and poorly known in members of the subg. *Cladina* and also in many other *Cladonia* species (only in c. 10% of *C. gigantea* group, c. 30% of *Cladina* and c. 30% of *Unciales*). Therefore further investigations are necessary to establish the importance of the absence and structure of the primary thallus as a possible generic character.

Statistical studies (Ruoss 1987*b*, present paper and unpublished data) do not support the regular branching patterns within the taxa which were presented by des Abbayes (1939) and Ahti (1961) in their branching models. Furthermore some species of sect. *Unciales* (e.g. *C. delavayi* des Abb., *C. medusina* (Bory) Nyl., *C. usambarensis* (Ahti *et al.* 1987), *C. perrieri* des Abb., *C. substellata* Vain., *C. spinea* Ahti, *C. pachyclados*, *C. siamea* des Abb. and *C. bangii* Ahti), and also *C. signata* (Eschw.) Vainio have comparable ramification systems.

Chemistry

The chemical characteristics, the 'conservative' chemistry and the different biosequential patterns of the secondary compounds, were the main subject of the investigations by Huovinen (1986). The main distinction is the absence of β -orcinol depsides (except atranorin) with their biosequential pathways in *Cladina* (Ahti 1984). In the *C. gigantea* group all specimens contain β -orcinol depsides, but in sect. *Unciales* 16 of 43 members (37%) do not contain it. Very common chemical compounds in subg. *Cladina* (in 74%) are the β -orcinol depsidones, which are only present in seven species of sect. *Unciales* (14%) and totally absent in the *C. gigantea* group.

Nourish & Oliver (1974) pointed to the conservative character of the chemistry of subg. *Cladina*, but proposed retaining *Cladina* as a subgenus until more data on the chemistry of intermediates were available. However, Huovinen (1986) concluded that precursors and biosequential patterns of the main chemical groups, although somewhat different, were unreliable for the separation of two genera without specifying morphological and anatomical characteristics.

Anatomy

The anatomy of the genus *Cladonia* is not well known and therefore a separation of distinct genera according to anatomical characteristics is not possible. Anatomical investigations show few differences in hymenial characteristics. Apothecia are rare in some groups, and poor development of apothecia and spores is typical. No essential differences in spores are known within the genus *Cladonia*. The ascus structure of the genus *Cladonia* (*Lecanora*-type) is homogeneous within the groups studied (unpublished data, conf. Dr J. Hafellner). Furthermore the ontogenetic development of members of subg. *Cladina* is identical with that of some other groups of subg. *Cladonia* (e.g. *C. uncialis* or *C. furcata*) (Jahns & Beltman 1973). However, further phylogenetic, genetic and anatomical studies are necessary to obtain a clearer idea of the relationships within the genus *Cladonia*.

To establish new genera, either clear differences in anatomical characteristics or other significant morphological and chemical criteria (Culbertson & Culbertson 1968) are needed (discussed by Hawksworth 1976). As there are no definite anatomical distinctions, and only tendencies towards vague morphological and

chemical differences, segregation of a genus *Cladina* remains artificial. Numerous species of the *C. gigantea* group and sect. *Unciales* are apparently more closely related to subg. *Cladina* than to other groups of *Cladonia*.

The main differences of the closely related groups are:

- (1) *C. gigantea* group: β -orcinol depsides are the main secondary products, which are absent in subg. *Cladina* (except atranorin). Rarity of squamules, which are absent in subg. *Cladina*, is a minor characteristic.
- (2) sect. *Unciales*: chemical and morphological tendencies such as absence (with exceptions) of β -orcinol depsidones, which are often present in subg. *Cladina*; presence of a cortex (with some exceptions including transitional, 'corticoid' forms), and squamules (with exceptions).

As there are a high number of transitional species between subg. *Cladina* and subg. *Cladonia*, these taxa are kept within one genus, at least until a more reasonable segregation is supported by hymenial characteristics in accordance with new trends in the taxonomy of fungi and lichenized fungi (e.g., Hawksworth *et al.* 1983, Hafellner 1984). Due to the absence of clear generic characters, several authors have continued to use the subgeneric system in their recent publications, e.g. Cannon *et al.* (1985), Clauzade & Roux (1985), Hawksworth *et al.* (1983), Thomson (1984) and Wirth (1988).

Material and Methods

Specimens from the following herbaria were studied by E. Ruoss: BERN, BM, CHR, GZU, H, NY, S, STR, STU, TUR, UPS. Two-hundred-and-four samples were analysed chemically by thin-layer chromatography (TLC) according to the methods of Culberson & Ammann (1979), Culberson & Johnson (1982) and White & James (1985). Departures from these methods are discussed in Ruoss & Ahti (1985). Morphological methods are described in Ruoss (1987b); measurements were performed on dried specimens.

Results and Discussion

Key to *Cladonia* subg. *Cladina* taxa examined

- 1 Podetia anisotomous, perlatolic acid absent 2
Podetia isotomous, perlatolic acid present 5. ***C. confusa*** (p. 42)
- 2(1) Podetia yellow-green, K—, usnic acid present 3
Podetia grey, K+ yellow, usnic acid absent 6
- 3(2) Branching chiefly dichotomous 4. ***C. laevigata*** (p. 40)
Branching chiefly trichotomous: 1. ***C. arbuscula*** 4
- 4(3) Rangiformic acid present, sometimes fumarprotocetraric acid present;
South America 1.2. **subsp. mitis** (p. 35)
Rangiformic acid absent 5
- 5(4) Fumarprotocetraric acid present; South America
. 1.1. **subsp. squarrosa** (p. 34)
Stictic, norstictic and sometimes fumarprotocetraric acids present;
Australasia 1.3. **subsp. stictica** (p. 37)
- 6(3) Necrotic basal tissue coal-black, extending up to 2/3 of the podetia, red
slime in the conidiomata 2. ***C. stygia*** (p. 39)
Necrotic basal tissue brown, at the very base sometimes slightly black,
slime hyaline 3. ***C. rangiferina*** (p. 40)

Chemistry

The following substances and chemical complexes were found in the reindeer lichens of the Southern Hemisphere [chemistry follows Huovinen & Ahti (1982)]:

Usnic acids—Usnic acid complex: Usnic and isousnic acids. (*C. arbuscula*, *C. confusa*, *C. laevigata*)

Depsides —Perlatolic acid complex: Perlatolic acid, unidentified substances. (*C. confusa*) —Atranorin. (*C. rangiferina*, *C. stygia*)

Depsidones —Fumarprotocetraric acid complex: Fumarprotocetraric, protocetraric acids, Cph-2, unidentified substances (see Ruoss 1987b). (*C. arbuscula*, *C. laevigata*, *C. rangiferina*, *C. stygia*) —Stictic acid complex (with O-methylation at A-ring): Stictic, cryptostictic, constictic acids. —Norstictic acid complex (no O-methylation): norstictic, connorstictic acids. (*C. arbuscula* subsp. *stictica*)

Fatty acids—Rangiformic acid complex: Rangiformic and norrangiformic acids. (*C. arbuscula* subsp. *mitis*)

Cladonia Hill ex Browne subgenus *Cladina* (Nyl.) Leighton

Section Crustaceae Rabenh.

1. *Cladonia arbuscula* (Wallr.) Flotow

in Wendt, *Thermen Warmbrunn*: 94 (1839).—*Patellaria foliacea* var. *arbuscula* Wallr., *Naturg. Säulchen-Flechten*: 169 (1829).—*Patellaria arbuscula* (Wallr.) Wallr., *Fl. Crypt. Germ.* 1: 425 (1831).

A total of 88 specimens of this species from the Southern Hemisphere were analysed by TLC. The main differences between the subspecies are in their secondary compounds. The morphology of Southern Hemisphere specimens is variable, and therefore it was not possible to distinguish subspecies by morphological characteristics. There are only tendencies towards differences in morphological characteristics and local geography, as discussed by Ruoss (1987b) for European material, but they are less clear in Southern Hemisphere populations than in Europe. The presence of secondary compounds with different precursors and biosequential patterns, and chorological differences are considered to be the most important criteria in the definition of infraspecific taxa in *C. arbuscula*, a conclusion also reached in connection with results of investigations of the *C. arbuscula* group from the Northern Hemisphere (Ruoss 1987a,b). The main difference between subsp. *squarrosa* and subsp. *mitis* is the absence or presence of rangiformic acid, since subsp. *mitis* often also contains fumarprotocetraric acid and subsp. *squarrosa* may be lacking fumarprotocetraric acid (in the Northern Hemisphere). According to a proposal by Hawksworth (1976), these two taxa should have the status of varieties rather than subspecies. However, there are dozens of old names at the variety level based on material which is difficult to locate and thus to lectotypify. Therefore Ruoss (1987b) decided to keep the cited names and to recognize them as subspecies.

Cladonia arbuscula subsp. *arbuscula* (with psoromic acid) and subsp. *stictica*

(with stictic and norstictic acid) contain both biosequentially different secondary compounds (see Huovinen & Ahti 1982) and clear geographical differences and are therefore distinguished at the subspecies level. Subsp. *arbuscula* is not treated here as it is not known from the Southern Hemisphere.

1.1. *C. arbuscula* subsp. *squarrosa* (Wallr.) Ruoss

(Fig. 1)

in Bot. Helv. 97: 260 (1987).—*Patellaria coccinea* var. *squarrosa* Wallr., Naturg. Säulchen-Flechten: 191 (1829).—*Cladonia squarrosa* (Wallr.) Flotow, Jber. Schles. Ges. vaterl. Cult. 27: 43 (1849).

Chemistry: Usnic acid, isousnic acid, fumarprotocetraric acid, protocetraric acid and Cph-2 present, sometimes unidentified substances in B/C: 5/5–6, unidentified fatty acids in A: 4 and 2–3/1–2/1–2.

Thallus: The specimens studied exhibit considerable morphological variation from slender, to very robust, with or without combed heads. Thallus colour varies from yellow-white to grey-green, with brown tips and brownish dying bases. Podetia 45–60 mm high, with 12–17 nodes, branching predominantly trichotomous (32–58%), (dichotomy (16–47%) and tetrachotomy (3–28%) less common). Crowns 10–16 mm wide, with 5–9 nodes, the base sometimes becoming slightly granulose. Conidiomatal slime hyaline. Photobiont layer commonly as thick as inner medulla, but may often be up to twice as thick. Branches combed to one side, or to all sides.

Specimens of *C. arbuscula* from southern South America have usually been included in *C. mitis*. Morphodemes are similar to the European subsp. *squarrosa* containing fumarprotocetraric acid. Furthermore specimens from Tierra del Fuego (Fig. 1) are very similar to specimens of subsp. *mitis* from the same area (Fig. 2). Subspecies *squarrosa* is reported here as new to the Southern Hemisphere, viz. from Chile and Argentina. More material of subsp. *squarrosa* was recently collected in Tierra del Fuego by Lic. Phil. S. Stenroos (Helsinki), although only one specimen is cited below.

Specimens of *C. laevigata* often resemble slender *C. arbuscula*, but the extremely thin photobiont layer and the highly dominant dichotomous branching pattern are the most important characteristics differentiating those two species. The specimen from Prov. Malleco, Chile, cited by Ahti & Kashiwadani (1984), Ahti (1984) and by Huovinen & Ahti (1986a) as *C. laevigata*, is *C. arbuscula* subsp. *squarrosa*.

Allied taxa in Latin America include *C. boliviana* Ahti, *C. imshaugii* Ahti, and *C. incurva* Ahti. Most probably they can all be considered as belonging to *C. arbuscula* s.lat., but the group is extremely variable, both chemically and morphologically, and needs extensive chemotaxonomical investigation (cf. Sipman & Cleef 1979, Huovinen & Ahti 1986a). *Cladonia imshaugii* is known only from the Dominican Republic; it looks very similar to densely branched subsp. *squarrosa*, and contains the same lichen substances. In any case, *C. incurva* is not a synonym of *C. confusa*, as proposed by Ahti (1984). A re-examination of its holotype revealed a close relationship to subsp. *squarrosa*, although it lacks fumarprotocetraric acid. *Cladonia incurva* is common at high elevations on Mt Itatiaya and Serra dos Orgaos, S.E. Brazil, and abundant material was recently collected there by T. Ahti (H, SP).

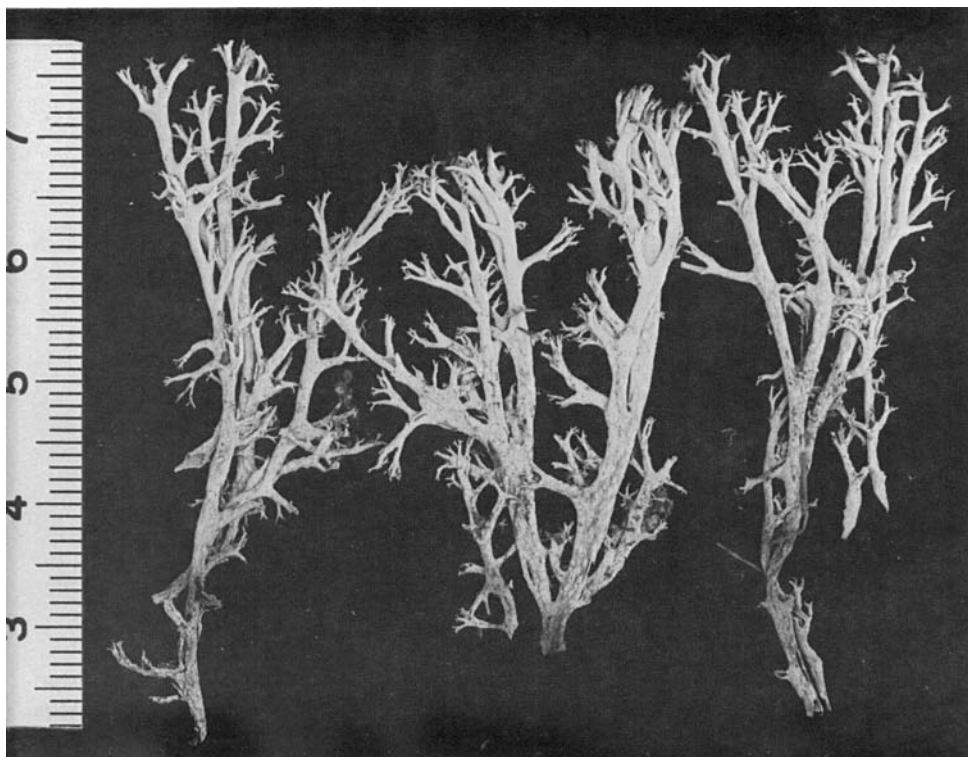


FIG. 1. *Cladonia arbuscula* subsp. *squarrosa* from Tierra del Fuego (Roivainen 487, H), scale in cm.

Specimens examined: **Chile:** Malleco: Depto. Angol, Parque Nac. de Nahuelbuta, Laguna de Las Totoras, 13 March 1971, *M. Mahu* 2342 (H).—**Argentina:** Tierra del Fuego: Paso Garibaldi, subalpine peat bog, 390 m, 29 September 1969, *H. Roivainen* 487 (H); Peninsula Mitre, between Puerto Donatia and Bahía Valentin, January 1987, *S. Stenroos* 2812 (H, Hb. Ruoss).

1.2. *Cladonia arbuscula* subsp. *mitis* (Sandst.) Ruoss

(Fig. 2)

in *Bot. Helv.* 97: 260 (1987).—*Cladonia mitis* Sandst., *Cladoniae* exs. no. 55 (1918).—*Cladonia arbuscula* var. *mitis* Sipman in Hennipman & Sipman, *Wetensch. Mededel. Koninkl. Nederl. Nat. hist. Ver.* 124: 43 (1977).

Chemistry: Usnic, isousnic, rangiformic and norrangiformic acids; unidentified substance in 2–3/1–2/1–2 present. One specimen without the rangiformic acid complex. Fumarprotocetraric acid complex sometimes present, mostly in low amounts.

Thallus: Colour yellow-white to yellow. Podetia mainly 20–60 mm tall, branching predominantly trichotomous (42–60%), but also often dichotomous (22–32%) or tetrachotomous (14–22%). Crowns 9–12 mm wide, with 7–8 nodes; tips brown. Terminal branches combed to all sides. Photobiont layer compact, and as thick as inner medulla. The base is brown and often granulose, the photobiont layer is loose and the inner medulla shines through.

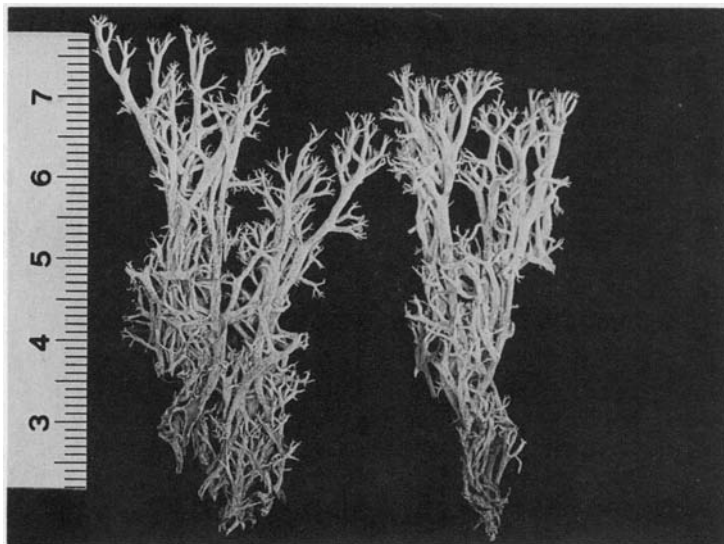


FIG. 2. *Cladonia arbuscula* subsp. *mitis* from Tierra del Fuego (Roivainen 1479, H), scale in cm.

Morphodemes of subsp. *mitis* essentially correspond to those of European material, and the more yellow-white colour is similar to that seen in specimens from subarctic and arctic regions. Specimens from the antarctic regions contain high amounts of rangiformic and norrangiformic acids. Subspecies *mitis* has already been reported from Chile, Argentina, South Georgia and the Antarctic e.g. by Ahti (1961), Lindsay (1974) and Ahti & Kashiwadani (1984). The record of *C. pycnoclada* containing rangiformic and (+)-usnic acids from South Georgia by Huneck *et al.* (1984) must belong to *C. arbuscula* subsp. *mitis*. Of the 120 specimens from New Zealand called *C. mitis* which were examined using TLC none contained fatty acids. This taxon is not presently known from New Zealand and Australia, though it has been reported from there by several authors (Ahti 1961, Galloway 1985). Part of the material examined belongs to subsp. *stricta*.

Representative specimens examined: **Chile:** Llanquihue: Parque Nac. V. P. Rosales, Cerro V. P. Rosales, 1400 m, March 1970, J. Redón 2182 (H). **Magallanes:** About 12 km south of Lago Parrillar, Peninsula de Brunswick, among mosses (*Sphagnum*) in *Nothofagus* forest, 3110 m, 12 December 1981, H. Kashiwadani 19269, Lich. rar. et crit. exs. 554 (BM, GZU, H); Sandy Point, September 1852, W. Lechler (BM, S); Punta Arenas. Cerro Canchas de Sky, 500 m, 31 December 1951, Pfister-Ricardi, Herb. Mahu 3604 (H); Club Andino, 15 March 1966, T. Yoshida (H); Isla Navarino, Lago Primero II, 18 January 1966, T. Yoshida (H). **Tierra del Fuego:** Rio Bueno, in palude, 10 December 1928, H. Roivainen 2173 (H, S); Estancia Cameron, Puesto Medio, 13 December 1928, H. Roivainen 1887 (H, S).—**Argentina:** Rio Negro: Parque Nac. Nahuel Huapi, Brazo del Viento, above the camp 'Los Cantaros', 1130 m, 16 May 1934, E. & A. Ljungner 1095 (S). **Tierra del Fuego:** Ushuaia, Montes Martiales, humous sandy soil in open *Nothofagelum pumilionis*, 320 m, 30 December 1969, H. Roivainen 1470 (H); Rancho Hambre, *Sphagnetum magellanici* in open peat bog, 250 m, 16 January 1970, H. Roivainen 1992 (H); Peninsula Mitre, between Puerto Donatia and Bahía Valentin, peatland, January 1987, S. Stenroos 2812 (H, Hb. Ruoss).

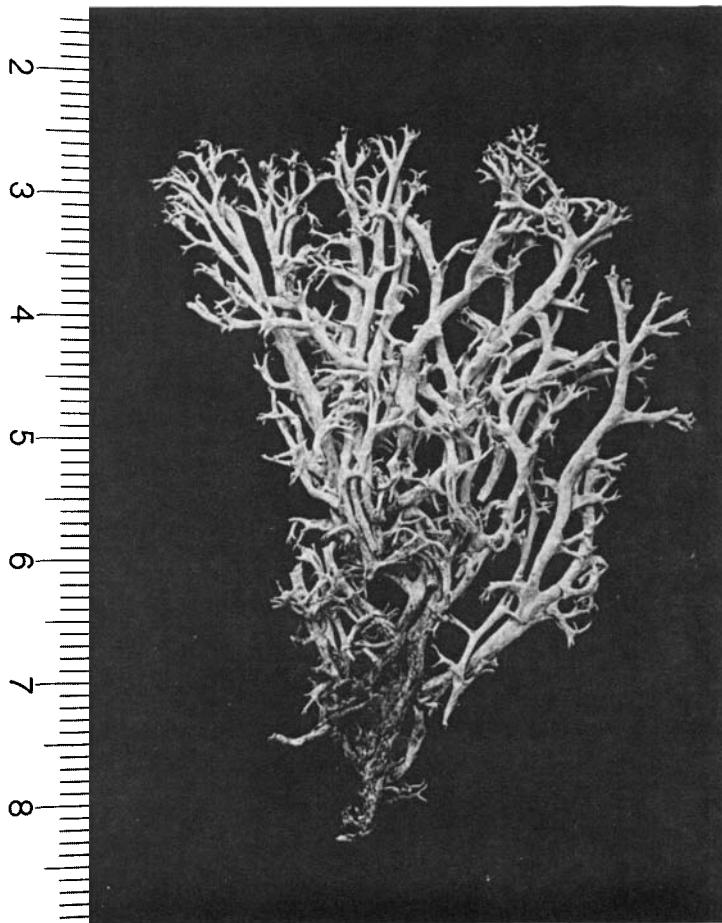


FIG. 3. *Cladonia arbuscula* subsp. *stictica* from New Zealand (1985, Johnson, CHR 417704), scale in cm.

1.3. *Cladonia arbuscula* subsp. *stictica* Ruoss subsp. nov.

(Fig. 3)

Cladoniae arbusculae subsp. *mitis* (Sandst.) Ruoss similis a qua imprimis differt chimice (acidum usnicum et vulgo gregem acidi stictici et norstictici continens).

Type: New Zealand, Otago, Mt Maungatua, summit bogs, 1935, *J. S. Thomson* 2146 (CHR—holotype; CHR, H, NMLU—iso-types). Contains usnic, stictic, norstictic, cryptostictic, connorstictic and constictic acids.

Chemistry: Usnic, stictic, norstictic, cryptostictic, connorstictic and constictic acids, rarely (six specimens) also fumarprotocetraric, protocetraric acids, Cph-2 and unidentified substances; five specimens do not show any substance other than usnic acid, or possibly contain supplementary substances only in

trace amounts. If a PD test gives a positive reaction, it seems due to fumarprotocetraric acid; specimens with stictic acid are mainly PD –. Norstictic and connorstictic acids are reported here for the first time in the subgenus *Cladina*. Fatty acids of the rangiformic acid complex are absent, in contrast to subsp. *mitis*.

Thallus: The material studied shows similarities to specimens of the ‘*mitis* morphodeme’ (Fig. 3) (cf. Ruoss 1987b). The apical branchlets are mostly erect, but often also slightly combed to all sides, or to one side. Colour green-white to yellow-green, tips brown. Podetia are 18–65 mm high, with 9–18 nodes. Branching predominantly trichotomous (39–79%), [dichotomy (10–59%) and tetrachotomy (2–41%) also common]. Basal parts of podetia granulose, the outer layer thin, inner medulla sometimes shining through. In upper parts, inner medulla and outer photobiont layer are nearly equal in thickness. On average, the main stem is about 1.2 mm (0.6–1.8 mm) thick, the wall 129 μ m (67–200 μ m), with an inner medulla of 70 μ m (34–120 μ m), and photobiont layer of 61 μ m (30–102 μ m). However, the range of variability of morphological characteristics is comparable to that of European specimens of *C. arbuscula* s.lat. (Ruoss 1987b). Apothecia are rarely present, spores poorly developed, simple, ovoid, 8–10 \times 2–4 μ m.

Cladonia arbuscula subsp. *stictica* appears to be restricted to Australasia (S.E. Australia, Tasmania and New Zealand). The most closely related species in S.E. Asia are *C. luzonensis* Ahti, and *C. papuana* Stenr. *Cladonia luzonensis* contains usnic and fumarprotocetraric acid complexes, and it has, in contrast to subsp. *stictica*, dichotomous branching (74–88%). *Cladonia papuana* has been considered by Stenroos (1986) to be a species of the subg. *Cladonia*, sect. *Unciales*. It contains usnic acid only and has anisotomic, dichotomic branching and appears somewhat different from the reindeer lichens. It is without a true cortex, and this, together with its chemistry, allies it with sect. *Crustaceae* (= *Cladina* sect. *Cladina*; Ahti 1984), as earlier stated by Huovinen & Ahti (1986b: 187). However, *C. luzonensis* and *C. papuana* have clearly different morphologies and are therefore considered to be separate species.

The biosequential pathways leading to the formation of stictic, norstictic acids and fumarprotocetraric acid complexes are different (Huovinen & Ahti 1982). Reindeer lichens containing the stictic acid group are also known from the northern Andes in South America and have been referred to *C. boliviana* s.lat. (Sipman & Cleef 1979, Huovinen & Ahti 1982, 1986a, Ahti 1984). It is uncertain whether the stictic acid chemodeme there belongs to *C. arbuscula* subsp. *stictica*. In comparison with Andean material, subsp. *stictica* is more slender, the photobiont layer is often thinner and the inner medulla shines through. Furthermore the crowns are more divaricately branched and rarely combed.

According to available habitat data, most specimens of subsp. *stictica* came from soil in grasslands, tundra vegetation, among tussocks, in herbfields, or among mosses in subalpine bogs. Most collections were from South Island, New Zealand, some from Tasmania, and one from New South Wales.

Selected specimens examined (66 analysed with TLC):

- (i) Usnic, stictic, norstictic, cryptostictic, connorstictic and constictic acids: **Australia:** *New South Wales*: Central Snowy Mts, Mt Northcote, in prostrate *Epacris* on exposed moraine, 1910 m,

January 1967, *D. McVean* 670 (H). *Tasmania*: Mt Wellington, summit plateau, 25 November 1980, 18 March 1981 and 6 January 1981, *D. A. Ratkovsky* (BM); Mt Mawson Plateau, occasional on peaty soil on exposed alpine moor, 1260 m, 26 March 1980, *G. Kantvilas* (H); Mt Barrow, 25 km NE of Launceston, 1400 m, 14 September 1982, *A. W. Archer* 1406A (H); Near Cradle Mtn, among grasses and shrubs, 120 m, February 1967 *D. McVean* 6754 (H); 130 km NW of Hobart, by side of track to Mt Rufus, at tree line, 1300 m, 3 December 1983, *A. W. Archer* 1540 (H); Mt Field West, in dwarf shrub heath on exposed shoulder, 1280 m, February 1967, *D. McVean* 6737 (H); Ben Lomond Natl Park, near Legges Tor, among grasses and shrubs, 400 m, February 1967, *D. McVean* 6768 (H).—**New Zealand: South Island**: Nelson: Lake Rotoiti, December 1959, *B. Kidson* (H). Marlborough: Raglan Range, on soil, 1525 m, 6 November 1980, *B. P. J. Molloy* (CHR 348205). Westland: near Otira, in grassland on summit of Kelly Range, *J. S. Thomson* (CHR 425274). Canterbury: Nina Valley, west of the Lewis River. 610–640 m, mountain beech forest with open boggy areas, *P. W. James* (BM); Arthur's Pass, 26 April 1964, *W. Martin* (CHR 425266); Cass, Woolshed Hill, May 1958, *W. R. Philipson* (CHR 425270); Nina Valley below Lucretia Stream Lewis Pass, 12 January 1979, *D. J. Galloway* (CHR 346660); Milford Sound, Key Summit, among shrubs and grasses, 150 m, May 1965, *D. McVean* 65150 (H); Lammerlaw Range, Teviot Swamp, in cushion bog, on raised drier parts, with *Phyllachne* and *Rhacomitrium*, 975 m, 16 January 1985, *P. N. Johnson* (CHR 417704); Blue Mountains, above Black Gully, on peaty soil of summit bog, 1005 m, 15 November 1970, *P. Child* (CHR 425309).

(ii) Usnic, stictic, norstictic, cryptostictic, connorstictic, constictic, fumarprotocetraric, protocetraric acids, Cph-2 and unidentified substances: **New Zealand: South Island**: Otago: Old Man Range, Obelisk near Fruitlands, 1690 m, alpine *Celmisia-Raoulia* vegetation, siliceous rocks, 6 November 1981, *V. Wirth & C. Meurk* (STU 11298); Mt Pisgah, in moss, *J. S. Thomson* (CHR 425257); Pisa Range, 1910 m, summit Plateau, 5 January 1970, *J. Child* (CHR 384302); summit of Rock and Pillar Range, herbfield, 1340 m, 14 February 1971 *P. & J. Child* (CHR 425310, 425261, 388871).

(iii) Usnic acid only: **New Zealand: South Island**: Canterbury: Bealey Range, 120 m, on soil among snow tussock, 28 February 1976, *P. Child* (CHR 425172); St Arnaud Range, summit, grassland, 17 November 1977, *D. J. Galloway* (CHR 266621). Westland: Great Unknown Tarns, Barlow, river catchment, 1524 m, fellfield on weathered schist, 14 February 1978, *A. D. Campbell* (CHR 306855).

2. *Cladonia stygia* (Fr.) Ruoss

in *Bot. Helv.* **43**: 241 (1985).—*Cladonia rangiferina* f. *stygia* Fries, *Nov. sched. crit.* **3**: 22 (1826).

Chemistry: Atranorin, fumarprotocetraric, protocetraric acids, Cph-2 present, plus traces of unidentified substances.

Thallus: Major taxonomic characters distinguishing the recently separated species *C. stygia* (Ahti 1984, Ahti & Hyvönen 1985, Ruoss 1985) from *C. rangiferina* are the red slime in the conidiomata and the blackening necrotic inner medulla of podetia. This basal coal-black tissue may extend above the middle of the podetia, and is visible at the base under the loose, white surface layer. In addition, the olive-grey colour, and irregular, divaricating branching are characteristic of *C. stygia*. The branching of the podetia in Chilean material is predominantly tetrachotomous (54%), rarely trichotomous (13%) or dichotomous (8%). The epihymenium is brown and the spores are simple and hyaline (7–10 × 3–4 µm).

The two specimens of *C. stygia* from Tierra del Fuego reported below, are very poor and no slime could be found in the conidiomata. However, other characteristics correspond to those of samples from the Northern Hemisphere, and are clearly different from *C. rangiferina* from the same area. The lichens were from a bog and associated with *Sphagnum magellanicum* and *Polytrichum strictum*.

In spite of the red slime, *C. stygia* is considered to be closely related to *C. rangiferina*. Due to similar chemistry and morphology, *C. stygia* belongs to the section *Crustaceae* rather than to other sections, although Ahti (1984) placed it in the section *Tenues*.

Specimens examined: **Chile**: *Magallanes*: Tierra del Fuego, Rio Bueno, in palude, 8–10 December 1928, *H. Roivainen* 2128, 2139 p.p. (H).

3. *Cladonia rangiferina* (L.) Weber ex Wigg.

Fl. Holsatica: 90 (1780).—*Lichen rangiferinus* L., *Sp. pl.*: 1153 (1753).—*Cladonia vicaria* R. Sant., *Ark. Bot.* 30A(10): 11 (1942).

Chemistry: Atranorin, fumarprotocetraric and protocetraric acids, Cph-2 present, plus traces of unidentified substances. The secondary compounds correspond to those of *C. stygia*. No difference between samples from Northern and Southern Hemispheres could be found (see also Huovinen & Ahti 1986a).

Some specimens of *C. rangiferina* from Tierra del Fuego were analysed as controls for separation towards *C. stygia*. Populations of *C. rangiferina* in southern South America were recognized by Santesson (1942) as a distinct species, *C. vicaria* R. Sant. However, Ahti (1961) reduced this taxon to a variety and later included it without taxonomic status in *C. rangiferina* s.str. (Ahti 1984).

Selected specimens examined: **Chile**: *Magallanes*: Tierra del Fuego, Fjordo Finlandia, in *Nothofagus betuloides* forest, 28 February 1929, *H. Roivainen* (H).—**Argentina**: *Tierra del Fuego*: Ushuaia, Montes Martiales, hummock of peat bog, 300 m, 30 February 1969, *H. Roivainen* 1471 (H); Estancia Cameron, Puesto Medio, in parte marginali *Sphagneti magellanici*, 13 December 1928, *H. Roivainen* 1886 (H).

Section *Tenues* des Abb.

4. *Cladonia laevigata* (Vainio) Gyelnik

(Fig. 4)

Lichenotheca no. 148 (1937).—*C. sylvatica* var. *laevigata* Vainio in Hariot, *J. Bot. (Morot)* 1: 284 (1887—Nov.).

Chemistry: Usnic, isousnic, fumarprotocetraric and protocetraric acids, Cph-2 present.

Thallus: Podetia of the holotype are 9 cm high, yellow-white, branching irregular, predominantly dichotomous (80–84%), rarely trichotomous (c. 18%) or tetrachotomous. Tips brown, often combed to one side, the base brown and often verruculose, outer medulla thin and discontinuous, inner medulla shining through. Spores 9–12 × 3–4 µm.

Cladonia laevigata (Vainio) Gyelnik was considered by Ahti (1961) to be closely related to *C. ciliata* Stirton from N. Hemisphere. Ahti & Kashiwadani (1984) reported hyaline slime in the conidiomata of one specimen, supposedly indicating a closer relationship to *C. arbuscula*, and Ahti (1984) and Huovinen & Ahti (1986b) therefore included it in the section *Crustaceae*. The cited specimen (Mahu 2342; H) is here included in *C. arbuscula* subsp. *squarrosa*. However, *C. laevigata* (Fig. 4) is very similar to *C. ciliata*, and certainly belongs to

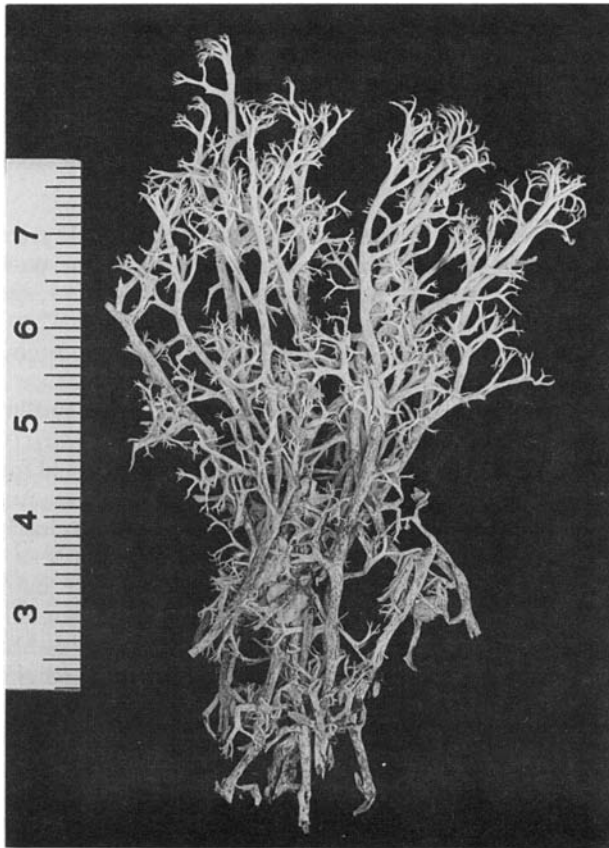


FIG. 4. *Cladonia laevigata* from Tierra del Fuego (Roivainen 2139, H), scale in cm.

sect. *Tenuis*, although until now the red slime in the conidiomata, characteristic of sect. *Tenuis*, has not been observed in *C. laevigata*.

The specimens examined were mainly from peat bogs, associated with *Sphagnum magellanicum*, *Caltha appendiculata*, *Juncus scheuchzerioides* and *Rostkovia magellanica* or on humic sandy soil in open forests of *Nothofagus pumilio*.

Selected specimens examined: **Chile:** Llanquihue: Yervas Buenas, Escorial del Fundo de Hugo Kuchel, bosque de *Nothofagus dombeyi* y *Gevuina avellana*, en roca, 25 m, 15 January 1986, M. Mahu & S. Tapia 21758 (H). **Magallanes:** Isla Navarino, Lago Primero II, 18 January 1966, T. Yoshida (H); Punta Arenas, Cerro Canches, 500 m, 31 December 1951, Pfister-Ricardi CONC 11703, ex hb. Mahu 3604 (H); Punta Arenas, Club Andino, 15 March 1966, T. Yoshida (H); Tierra del Fuego, Estancia Cameron, Puesto Medio, 13 December 1928, H. Roivainen (H); Río Bueno, in palude, 10 December 1928, H. Roivainen 2139 (H).—**Argentina:** Tierra del Fuego: Lago Fagnano, in palude, 19 January 1929, H. Roivainen (H); Rancho Hambre, *Sphagnetum magellanicum* in open peat bog, 250 m, 16 January 1970, H. Roivainen 1992 (H); Ushuaia, Montes Martiales, humic sandy soil in open *Nothofagetum pumilionis*, south exposition, 320 m, 30 December 1969, H. Roivainen (H); Paso Garibaldi, border of subalpine peat bog, 390 m, 29 November 1969, H. Roivainen (H).

Section Impexae des Abb.

5. *Cladonia confusa* R. Sant.

in *Ark. Bot.* 30A(10): 13 (1942).

Chemistry: Usnic, perlatolic acids and sometimes ursolic acid; usnic acid rarely absent.

Thallus: Podetia mainly 2–9 mm high, yellow-green or pale green, branching isotomous, sometimes clearly anisotomous, forming dense cushions. Outer medulla thin (25 µm), especially at the base, sometimes absent, and then glossy brown stereome shining through. Podetial wall thick (200–220 µm), mainly composed of inner medulla (190–200 µm). Branching trichotomous (58–70%), but often also dichotomous (10–36%), rarely tetrachotomous.

Most of the specimens seen have a very dense branching system and a dense photobiont layer. Some specimens are very similar to *C. stellaris* (Opiz) Pouzar & Vězda from the Northern Hemisphere. As many transitional forms are present, these morphodemes are not separated from *C. confusa*. Another robust morphodeme occurring in Southern Africa is smaller and clearly anisotomic and the photobiont layer is rather thick. Morphologically it may closely resemble some thick 'mitis morphodemes' from extreme habitats, but all specimens contain perlatolic acid. Therefore it appears reasonable to keep the morphodemes together in the *C. confusa* agg., as suggested by Ahti (1984).

The taxonomy of *C. confusa* has been reconsidered in the light of chemical investigations. However, besides the typical chemodeme, only two specimens from New Zealand differed by lacking usnic acid. The name *Cladina confusa* f. *bicolor* (Müll. Arg.) Ahti was used for the latter chemodeme by Ahti (1984). Besides the grey colour (due to the absence of usnic acid), no other differences are evident and therefore it is treated here only as a chemodeme. Earlier records were from South America and Madagascar only (Ahti 1984).

Cladonia confusa has a wide distribution in Latin America (here reported as new to Paraguay), Africa and Australasia. In Southern and East Africa it is the only known reindeer lichen. In New Zealand it has often been misidentified as *C. stellaris* or *C. mitis*.

Selected specimens examined (85 analysed with TLC):

(i) Usnic and perlatolic acids: **Uruguay:** *Rocha:* Estancia Siete Cerros, ad rupes, 20 February 1935, C. C. Hosseus, Gyelnik: Lichenotheca no. 148, Hb. Frey 5612 (BERN).—**Paraguay:** Nova Germania, 'Parkmaterial', 1904 coll. unknown (STR).—**Columbia:** Monserrat near Bogotá, 3200 m, 1938, Hayoz, Hb. Frey 4403 (BERN).—**Brazil:** Bahia, Blanchet (STR).—**Tanzania:** Kilimanjaro, above Marangu in the *Philippia* region, in *Philippia* scrub below Peters hut, 3385 m, 21 June 1948, O. Hedberg (H, UPS).—**South Africa:** *Cape Province:* Cape Div., Table Mountain, 1962, L. Kofler (H); Oudtshoorn Div., Swartberg, December 1946, T. P. Stokoe 9341 (H); Paarl Div., summit of Wemmershoek Peak, on damp soil, 1737 m, 5 November 1950, E. Esterhuysen 17736 (H). *Natal:* Bergville Dist., Drakensberg, Cathedral Peak Area, summit plateau under bushes, July 1944, E. Esterhuysen 10264 (H).—**Madagascar:** *Antananarivo:* Manjakandriana, Lac Mantasoa, 1400 m, 22 September 1977, P. Tixier 10965 (H); sine loco, 1975, Boiteau 512 (H).—**Mauritius:** Petrin, on laterite, at base of *Philippia* and *Phyllica* bushes. 2 November 1967, D. M. Henderson (H).—**New Zealand:** Numerous specimens (CHR).

(ii) Perlatolic acid only: **New Zealand:** *South Island:* Otago: Dunedin, Mt Flagstaff, summit, in tussock grassland amongst large rocks, 650 m, 31 December 1956, W. Martin (CHR 425258). Southland: Stewart Island, Deceit Peaks, 550 m, 9 December 1969, D. J. Galloway (CHR).

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REFERENCES

- Abbayes, des H. (1939) Révision monographique des *Cladonia* du sous-genre *Cladina* (Lichens). *Bulletin de la Société scientifique Bretagne* **16** (hors sér. 2): 1–154.
- Ahti, T. (1961) Taxonomic studies on reindeer lichens (*Cladonia* subg. *Cladina*). *Annales Botanici Societatis Zoologicae Botanicae Fennicae* “*Vanamo*” **32**: 1–60.
- Ahti, T. (1973) Taxonomic notes on some species of *Cladonia*, subsect. *Unciales*. *Annales Botanici Fennici* **10**: 163–184.
- Ahti, T. (1977) The *Cladonia gorgonina* group and *C. gigantea* in East Africa. *Lichenologist* **9**: 1–15.
- Ahti, T. (1984) The status of *Cladina* as a genus segregated from *Cladonia*. *Beiheft zur Nova Hedwigia* **79**: 25–61.
- Ahti, T. (1986) New species of reindeer lichens (*Cladina*). *Annales Botanici Fennici* **23**: 221–227.
- Ahti, T. & Hyvönen, S. (1985) *Cladina stygia*, a common, overlooked species of reindeer lichen. *Annales Botanici Fennici* **22**: 223–229.
- Ahti, T. & Kashiwadani, H. (1984) The lichen genera *Cladia*, *Cladina*, and *Cladonia* in Southern Chile. In *Studies on cryptogams in southern Chile* (H. Inoue, ed.): 125–151. Tokyo: Kenseisha.
- Ahti, T., Krog, H. & Swinscow, T. D. V. (1987) New or otherwise interesting *Cladonia* species in East Africa. *Annales Botanici Fennici* **24**: 85–94.
- Cannon, P. F., Hawksworth, D. L. & Sherwood-Pike, M. A. (1985) *The British Ascomycotina. An annotated checklist*. Kew: Commonwealth Mycological Institute.
- Clauzade, G. & Roux, C. (1985) Likenoj de Okcidenta Europo. *Bulletin de la Société Botanique du Centre-Ouest, n.s., numéro spéciale* **7**: 1–893.
- Culberson, C. F. & Ammann, K. (1979) Standardmethode zur Dünnschichtchromatographie von Flechtensubstanzen. *Herzogia* **5**: 1–24.
- Culberson, C. F. & Johnson, A. (1982) Substitution of methyl tert.-butyl ether for diethyl ether in the standardized thin-layer chromatographic method for lichen products. *Journal of Chromatography* **128**: 253–259.
- Culberson, W. L. & Culberson C. F. (1968) The lichen genera *Cetrelia* and *Platismatia* (Parmeliaceae). *Contributions U.S. National Herbarium* **34**: 449–558.
- Galloway, D. J. (1985) *Flora of New Zealand Lichens*. Wellington: P.D. Hasselberg, New Zealand Government Printer.
- Hafellner, J. (1984) Studien in Richtung einer natürlichen Gliederung der Sammelfamilien Lecanoraceae und Lecideaceae. *Beiheft zur Nova Hedwigia* **79**: 241–371.
- Hale, M. E. & Culberson, W. L. (1970) A fourth checklist of the lichens of the United States and Canada. *Bryologist* **73**: 499–543.
- Hawksworth, D. L. (1976) Lichen chemotaxonomy. In *Lichenology: Progress and Problems* (D. H. Brown, D. L. Hawksworth & R. H. Bailey, eds): 139–148. London: Academic Press.
- Hawksworth, D. L., Sutton, B. C. & Ainsworth, G. C. (1983) *Ainsworth & Bisby's Dictionary of the fungi*. 7th Edn. Kew: Commonwealth Mycological Institute.
- Huneck, S., Sainsbury, M., Richard, T. M. A. & Smith, R. I. L. (1984) Ecological and chemical investigations of lichens from South Georgia and the maritime Antarctic. *Journal of the Hattori Botanical Laboratory* **56**: 463–480.
- Huovinen, K. (1986) Chromatographic studies on the aromatic lichen substances in *Cladina* and *Cladonia* section *Unciales*. Helsinki: University of Helsinki.
- Huovinen, K. & Ahti, T. (1982) Biosequential patterns for the formation of depsides, depsidones and dibenzofurans in the genus *Cladonia* (lichen-forming ascomycetes). *Annales Botanici Fennici* **19**: 225–234.
- Huovinen, K. & Ahti, T. (1986a) The composition and contents of aromatic lichen substances in the genus *Cladina*. *Annales Botanici Fennici* **23**: 93–106.

- Huovinen, K. & Ahti, T. (1986b) The composition and contents of aromatic lichen substances in *Cladonia* section *Unciales*. *Annales Botanici Fennici* **23**: 173–188.
- Jahns, H. M. & Beltman, H. A. (1973) Variations in the ontogeny of fruiting bodies in the genus *Cladonia* and their taxonomic and phylogenetic significance. *Lichenologist* **5**: 349–367.
- Lindsay, D. C. (1974) The macrolichens of South Georgia. *British Antarctic Survey Scientific Reports* **89**: 1–91.
- Martin, W. (1960) The lichen genus *Cladonia*, subsection *Cladina*, in New Zealand. *Transactions of Royal Society of New Zealand* **88**: 169–175.
- Nourish, R. & Oliver, R. W. A. (1974) Chemotaxonomic studies on British lichens. 1. *Cladonia* subgenus *Cladina*. *Lichenologist* **6**: 73–95.
- Nylander, W. (1866) Adhuc circa characteres quosdam Lichenum. *Flora, Jena* **49**: 177–181.
- Ruoss, E. (1985) Die Rentierflechte *Cladonia stygia* in den Alpen. *Botanica Helvetica* **95**: 239–245.
- Ruoss, E. (1987a) Species differentiation in a group of reindeer lichens (*Cladonia* subg. *Cladina*). *Bibliotheca Lichenologica* **25**: 385–399.
- Ruoss, E. (1987b) Chemotaxonomische und morphologische Untersuchungen an den Rentierflechten *Cladonia arbuscula* und *C. mitis*. *Botanica Helvetica* **97**: 239–263.
- Ruoss, E. & Ahti, T. (1985) Die Rentierflechten (*Cladonia* subg. *Cladina*) im Herbarium Wallroth, Strassburg. *Nova Hedwigia* **41**: 147–158.
- Santesson, R. (1942) The South American *Cladinae*. *Arkiv för Botanik* **30A**(10): 1–27.
- Sipman, H. J. M. & Cleef, A. M. (1979) Studies on Colombian cryptogams. V. Taxonomy, distribution and ecology of macrolichens of the Colombian Paramos: 1. *Cladonia* subgenus *Cladina*. *Proceedings Koninklijke Nederlandse Akademie van Wetenschappen*, ser. C, **82**: 223–241.
- Stenroos, S. (1986) The family Cladoniaceae in Melanesia. 1. *Cladonia* sect. *Unciales*. *Annales Botanici Fennici* **23**: 161–164.
- Thomson, J. W. (1984) *American Arctic Lichens*. 1. The Macrolichens. New York: Columbia University Press.
- Vainio, E. A. (1887) Monographia Cladoniarum universalis. I. *Acta Societatis pro Fauna et Flora Fennica* **4**: 1–509.
- White, F. J. & James, P. W. (1985) A new guide to microchemical techniques for the identification of lichen substances. *British Lichen Society Bulletin* **57** (suppl.): 1–41.
- Wirth, V. (1988) *Die Flechten Baden-Württembergs*. Stuttgart: Ulmer.

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