Cladistics 18, 237–278 (2002)
doi:10.1006/clad.2002.0202

Phylogeny of the Genus *Cladonia* s.lat. (Cladoniaceae, Ascomycetes) Inferred from Molecular, Morphological, and Chemical Data

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Accepted February 11, 2002

Phylogenetic relationships within the genus *Cladonia*, including *Cladina* (Cladoniaceae, Lecanoromycetes), were reconstructed based upon simultaneous analyses of DNA sequences and morphological and chemical data. We used sequences from the internal transcribed spacer 1 (ITS1), the 5.8 rDNA gene, and the internal transcribed spacer 2 (ITS2) of the nuclear rDNA gene cluster, and partial sequences from the protein-coding β-tubulin gene. The analyses included 235 specimens of 168 taxa representing all currently recognized sections of *Cladonia* and *Cladina* and the outgroup genera *Cladia*, *Pycnothelia*, and *Ramalea*. Analyses were performed using optimization alignment with three different parameter values. The results of all analyses support the inclusion of *Cladina* in *Cladonia*. The current sectional division of *Cladonia* was not supported, and a new provisional classification for the genus is proposed.

With about 500 currently recognized species, the family Cladoniaceae of the Lecanoromycetes is among the largest and most diverse groups of lichen-forming fungi. Slightly more than 400 species are assigned to the genus *Cladonia*, while the remainder are distributed among a number of smaller genera that have been segregated from *Cladonia* (Ahti, 1993, 2000). The number of species recognized today is fourfold that of Vainio's (1887, 1894, 1897) monographic treatment. This increase is a result of numerous taxonomic revisions and regional surveys published over the century. However, only a handful of attempts have been made with contemporary methods to understand the infrageneric classification of the genus *Cladonia* s.lat. Indeed, there is no generally supported classification, although the existing schemes basically represent variations of a grouping proposed by Vainio (1894); see Mattick (1938, 1940), Dahl (1952), Huovinen and Ahti (1982), and Ahti (2000).

Concepts about the status of *Cladina* have been controversial. In the Americas, Asia, Australasia, and Russia, *Cladina* is widely accepted as a genus, whereas in most of Europe a subgeneric status under *Cladonia* is preferred (see summaries in Ruoss and Ahti, 1989; Stenroos *et al.*, 1997). Even more problematic is the infrageneric division of *Cladonia* s.str. In his recent survey, Ahti (2000) applied a division of *Cladonia* into

0748-3007/02 $35.00

seven groups ranked as sections (*Ascyphiferae*, *Cladonia*, *Cocciferae*, *Helopodium*, *Perviae*, *Strepsiles*, and *Unciales*) and *Cladina* into three sections (*Cladina*, *Impexae*, and *Tenues*). This division is essentially based on shared characters of gross morphology and/or secondary chemistry. Such characters are red apothecia, lack of cortex, perforated branch axils, branch topology, and the structure of the primary thallus, among others.

Vainio (1880, 1894), Choisy (1928), Mattick (1938), and Galløe (1954) discussed the phylogeny of *Cladonia* and constructed phylogenetic diagrams. Culberson (1986) presented a cladistic analysis based on secondary chemistry for the *Cladonia chlorophaea* group. The first molecular studies on Cladoniaceae were those by Blum and Kashevarov (1992) and Kashevarov (1992), who studied the generic status of *Cladina* using nucleotide sequence homologies of the DNA among four species of *Cladina* and six of *Cladonia*. Their surveys supported distinguishing the two groups at the generic level, but they did not present any proper phylogenetic analyses. Molecular studies by DePriest (1994) and Beard and DePriest (1996) concentrated on the *Cladonia chlorophaea* group and *Cladina subtenuis*, respectively, and those by Bulat and Dudoreva (1993) on infraspecific variability of *Cladonia cenotea*. The first serious attempt to examine the evolution of *Cladonia* was a cladistic analysis published by Stenroos *et al.* (1997). This survey, based on morphological and chemical characters, comprised 44 species of *Cladonia* (including *Cladina*), with 1 species of *Pycnothelia* and 2 of *Cladia* as outgroup taxa. The results did not support *Cladina* at the genus level or the current sectional division. The most recent surveys are those by Stenroos and DePriest (1998) and Wedin *et al.* (2000), who studied the placement of Cladoniaceae among the Lecanorales, and those by Kärkkäinen (1999), DePriest *et al.* (1999, 2000a, 2000b), Oksanen (1999), and Oksanen *et al.* (2000), who presented preliminary phylogenetic analyses on *Cladonia* based on molecular data.

All previous analyses have been based either on taxonomically restricted groups or on a limited number of species, and only morphological/chemical or molecular data have been used. The major complications in using morphological data are difficulties in defining homologies and, particularly in structurally simple organisms like fungi, the sheer lack of suitable characters. Chemical data are burdened with the same problems. As to molecular data, complications may be caused by ambiguous alignments, especially with sequences exhibiting considerable length variation. In some cases, the phylogeny obtained from a single gene or gene region might also reflect the evolution of that particular area, which may be different from the species evolution (Hillis, 1987; Doyle, 1992).

Our primary goal was to investigate the phylogenetic relationships of *Cladonia* (including *Cladina*) using simultaneous analyses (Nixon and Carpenter, 1996; total evidence, Kluge, 1989) of DNA sequences and morphological and chemical data. We anticipated that the existing schemes of the infrageneric classification of *Cladonia* s.lat. would not be supported as such. We further anticipated support for our current concept of including *Cladina* in *Cladonia*. This paper is an effort to unambiguously resolve the phylogeny of *Cladonia* as a step toward establishing taxonomy for the group, and the study is based on analyses of all available data. These results will be used as a basic guideline for the forthcoming treatment World Monograph of Cladoniaceae (Stenroos and Ahti, in preperation).

MATERIALS AND METHODS

Taxon Sampling

To construct a comprehensive phylogenetic data set, we sampled the morphological diversity shown by the species as thoroughly as possible. In addition, the sampled taxa were to represent all currently recognized sections of genera *Cladonia* and *Cladina* (sensu Ahti, 2000), and they also include representatives of type species of each section. By including any sample other than the actual type specimen of type species, we implicitly assume our species to be monophyletic. This assumption has its flaws. However, in most cases, original material is not usable simply because of its age. Special emphasis was also placed on selecting taxa from a variety of geographical regions in order to include as much of the potential genetic variation as possible. For most taxa, one specimen was chosen, again assuming that the species are monophyletic. In a few cases (*Cladonia arbuscula* and *C. uncialis*, in particular), multiple specimens were included to test this assumption. Altogether 235 representative samples of 168 taxa were selected for analyses. These samples represent *Cladonia* sections *Cladonia* (50 samples/41 taxa), *Cocciferae* (58/39), *Unciales* (38/22), *Perviae* (27/18), *Ascyphiferae* (16/10), *Helopodium* (15/15), and *Strepsiles* (3/2) and from *Cladina* sections *Cladina* (9/6), *Tenues* (7/6) and *Impexae* (8/6). Outgroup taxa were selected from genera *Pycnothelia* (1/1), *Cladia* (2/2), and *Ramalea* (*R. cochleata*; type species *R. tribulosa* not available)(1/1). The outgroup selection was based on preliminary analyses, which indicate that *Cladia*, *Pycnothelia*, and *Ramalea* are members of cladoniaceae but are placed outside *Cladonia.* (Stenroos *et al.*, 2002). Voucher specimens are listed in Appendix 1. In the case of duplicated specimens, we cited only the herbaria where the actual voucher duplicates used are deposited.

Character Data

Morphological and chemical data partition. Characters used were essentially those of gross morphology. Prothallus, i.e., the early, exclusively fungal stage of the developing lichen, was omitted because only preliminary studies are available describing its development and variability (see, e.g., Hammer, 1996). Similarly, horizontal primary thallus does not offer much because its squamules are simple in form and their size and shape are significantly affected by habitat. Unlike many other fungal groups, the hymenial characters of the Cladoniaceae are essentially uniform (Ahti, 2000) and therefore were not screened for this study. However, at least the spores may eventually prove to be more variable than expected when screened with proper methods (S. Huhtinen, personal communication). Most of the characters used here are shown by the vertical thallus segments (podetia or pseudopodetia). At maturity, these segments are hollow, terete, and unbranched to richly branched, and their apices exhibit particular shapes. Several species are entirely corticate, but many others produce various kinds of vegetatively dispersing propagules on their thallus surface (e.g., Ahti, 2000).

The majority of the chemical substances used in *Cladonia* taxonomy are phenolic secondary compounds. Of more than 600 compounds identified from lichen-forming fungi, some 60 are known from Cladoniaceae (Huneck and Yoshimura, 1996). Approximately 30 compounds have proved to be taxonomically significant in Cladoniaceae, whereas the rest are minor or less known satellites. The compounds can be grouped into higher aliphatic acids (fatty acids), depsides (ester-linked polyphenolics), depsidones (ester- and ether-linked polyphenolics), dibenzofurans (plus derivatives), anthraquinones, and triterpenoids (Huovinen and Ahti, 1982). Many of the aliphatic acids and triterpenoids are unidentified or inadequately recorded and therefore often unusable as character data.

The species morphology was used as a basis when building the morphological data set. However, each specimen used in the DNA analysis was screened for the presence of the expected characters and for possible supplementary characters. For chemical characters, each specimen used in the DNA analysis was tested with the standardized thin-layer chromatographic method in two solvent systems (Culberson, 1972, solvent A; White and James, 1985, solvent B). Many species are known to appear in several chemical strains, but using all these to form a single hypothetical species chemistry would be misleading (see, e.g., Mishler, 1994; Yeates, 1995). We allowed the following exceptions in our coding concept. The specimens of *Cladonia solitaria* and *C. perforata* were not available for a final and thorough morphological "cross-check" or for a chemical analysis, but because these species are not notoriously variable morphologically or chemically, we used their species characteristics in the data set. In addition, for all species, the color of hymenia and the color of slime in conidiomata were coded according to known species characteristics (if based on considerable background information), even when these characters could not be observed in the actual specimen. The data matrix containing morphological and chemical characters is shown in Appendix 2.

Morphological and chemical characters. We included as many morphological characters as possible. Many potentially useful characters had to be excluded because of interpretational problems. Surface structures of thalli, in particular, are difficult to define. Judging whether the surface is smooth, uneven, verrucose, rugulose, areolate, or more or less so, creates severe problems because virtually all conditions vary from thallus to thallus. We eventually came up with 30 morphological and 23 chemical characters, all of them binary. Among chemical characters, not only end products were used but compounds were also arranged according to biosynthetic groups (Huovinen and Ahti, 1982); thus, compounds in each group are biogenetically related. In cases where a biosynthetic group was represented by only a single compound, or the compound was present in only one taxon, we used the group and not the actual compound (characters 35, 41, and 47).

All character states were coded with (0) and (1). These codes do not designate *a priori* which of the states is plesiomorphic or apomorphic.

Morphological and chemical characters and character states are listed in Appendix 3.

DNA data partitions. We used sequences from the internal transcribed spacer 1 (ITS1), the 5.8 rDNA gene, and the internal transcribed spacer 2 (ITS2) of the nuclear rDNA gene cluster, as well as partial sequence from the protein-coding β-tubulin. The combined length of the sequences obtained from ITS1, 5.8S, and ITS2 was ca. 600 nucleotides, and that from β-tubulin was ca. 800 nucleotides.

Although the same gene or sequence region may show significant differences in variation at comparable taxonomic hierarchies in different organisms, ITS regions have generally been utilized in studies ranging from species up to the genus level (Cantrell and Hanlin, 1997; Goffinet and Bayer, 1997; Kuhls *et al.*, 1997; Lutzoni, 1997; Lohtander *et al.*, 1998, 2000; Thell, 1998; Myllys *et al.*, 1999a, 1999c, 2000b; Thomas *et al.*, 2000) or even higher (Berbee *et al.*, 1995; Lutzoni, 1997). However, the application of ITS at higher taxonomic levels has been assumed to cause problems (Friedlander *et al.*, 1994) because multiple hits are presumed to be more probable and nucleotide sites to be "saturated" (Mindell and Thacker, 1996) and, therefore, misleading as to phylogeny. Whether this poses a problem for phylogeny reconstruction has recently been challenged by Källersjö *et al.* (1999). They showed that most of the phylogenetic signal in a large analysis of protein-coding *rbc*L gene sequences of plants was in third position despite these positions being "saturated," i.e., showing a high degree of homoplasy. One should therefore avoid ignoring part of the data *a priori* based on untested assumptions about behavior of characters.

In general, single-gene analyses have proved to be inferior to the simultaneous analyses of many matrices representing different genes, morphology, chemistry, etc. (Tehler, 1995; Chase and Cox, 1998; Hyvönen *et al.*, 1998). Giribet (personal communication) in his study of centipede phylogeny has shown single-gene analyses to lead to very unexpected and novel groupings that were absent in the results obtained with simultaneous analyses. However, very few genetic markers complementing ITS have thus far proved to be usable at and around species level in lichen-forming fungi. Parts of the nuclear LSU rDNA have typically been used at slightly higher taxonomic levels (Platt and Spatafora, 2000; Wedin *et al.*, 2000). The Group I introns, numerous particularly in the nuclear SSU rDNA (e.g., Gargas *et al.*, 1995), have been used at population (Bhattachrya *et al.*, 1996; Myllys *et al.*, 1999b) and species levels (Myllys *et al.*, 2000b). However, Group I introns are mobile genetic elements and were in our samples absent from many of the taxa studied. In addition, both ITS and Group I introns reside in the ribosomal DNA gene cluster and may therefore be regarded as single-gene elements.

We chose β-tubulin to supplement our ITS data. Many reports have demonstrated the utility of β-tubulin sequences at the species level in fungi (Schardl *et al.*, 1994; Tsai *et al.*, 1994; Geiser *et al.*, 1998; O'Donnell *et al.*, 1998; Articus *et al.*, 2000). Myllys *et al.* (2000b) have shown that particularly the intron regions of the gene, as well as the third-codon positions in exon regions, give phylogenetic information even below the species level. In their study, β-tubulin offered more resolution than either ITS or Group I introns.

We obtained β-tubulin sequence data from 103 of the 235 specimens analyzed. In contrast to the ITS, the β-tubulin PCR products varied notably in DNA quantity. Despite serial trials and optimization efforts, many samples yielded too little or no product at all for further sequencing. In general, β-tubulin PCR produced much less DNA per reaction than ITS.

Sequences used in the present survey are unpublished and were produced at the Molecular Laboratory of Lichen Taxonomy at the Herbarium, University of Turku, Finland, and at the laboratory of Molecular Ecology and Systematics, University of Helsinki, Finland. As exceptions, extracted DNA of *Cladonia perforata* was donated to the senior author by R. Yahr (Duke University), and the ITS sequence for *C. solitaria* was produced by the senior author at the Smithsonian Institution (Washington, DC). For GenBank accession numbers for all sequences, see Appendix 1.

DNA extraction. Either fresh or herbarium material was used for extracting total DNA. Material no older than 2 years was preferred when available. Thallus fragments of 2–15 mg were used for the extraction, which was performed according to the manufacturer's protocol enclosed in the DNEasy Plant Mini Kit (Qiagen). The extracted DNA was eluted in 40–150 μl of elution buffer delivered with the kit and further diluted in water for PCR, or used as such. In addition to the Plant Mini Kit (suitable for "plant cells and tissues, or fungi" according to the manufacturer's guide), we also tried the QIAamp DNA Mini Kit (suitable for "genomic, mitochondrial, bacterial, parasite or viral DNA" according to the manufacturer's guide). Both of the commercial kits worked equally well and produced high-quality, clean DNA. They were clearly more efficient than the conventional protocols that we also tested, e.g., TES protocol described by Möller *et al.* (1992) and the fungal miniprep protocols described by Taylor and Swann (1993) and Grube *et al.* (1995).

Amplification and purification. The ITS regions and the 5.8S gene of the nuclear rDNA, as well as the partial β-tubulin gene, were amplified using a Perkin–Elmer Gene Amp PCR System 9700 thermal cycler. Ready-To-Go PCR beads in 0.2-ml (or 0.5-ml) tubes (Pharmacia Biotech Inc.) were used in amplification. We used the primers ITS1F and ITS4 for amplifying the ITS regions and Bt3 and Bt 10 for amplifying partial β-tubulin (Table 1). A solution containing 11.8 μl of distilled water, 0.35 μl each of the primers at 16 pmol concentration, and 12.5 μl of DNA was added to the PCR beads (reaction size ca. 25 μl for 0.2-ml tubes). Following an initial 2-min template denaturing at 95°C, a 30-cycle schedule was performed. The following cycling profile was used: denaturation at 95°C for 1 min, annealing at 60°C for 1 min, and extension at 72°C for 1 min.

In addition to the Ready-To-Go beads, we tried a PCR cocktail using AmpliTaq Gold DNA Polymerase (Perkin–Elmer). The beads were more reliable and produced high-quality, clean PCR products (see also Martín and Winka, 2000).

The PCR products were cleaned with QIAquick PCR purification kit (Qiagen) and diluted in 30–40 μl of elution buffer provided in the kit.

Sequencing. The sequencing reactions were prepared according to the protocol provided in the BigDye Terminator Cycle Sequencing Ready Reaction Kit (PE Biosystems). In a 10-μl reaction, 4 μl of BigDye, 2 μl of the primers at 5 pmol concentration, 1–4 μl of the purified PCR product, and 0–3 μl of distilled water were mixed. Two alternative schedules were utilized depending on the routines of the two sequencing laboratories used. These included a 25/29 cycle schedule and the following cycling profile: denaturation at 96°C for 10/30 s, annealing at 50°C for 5/15 s, and extension at 60°C for 4 min.

Both strands were sequenced, and alternative primer pairs were tested. For ITS and 5.8S regions, ITS1F, ITS1LM, or ITS5 at the 5′ end was used. These primers were combined with either ITS2KL or ITS4 (Table 1). All primer combinations worked equally well. However, for samples containing an intron at the 3′ end of SSU, the 5′ primer ITS1LM is recommended because it is located in the ITS region. Due to the high quality of the sequences, the internal primers attaching to 5.8S were not needed. For sequencing partial β-tubulin, we used *Cladonia*-specific primers, Bt13 and BT14, designed by L. Myllys (Table 1).

Sequencing was performed with an ABI Prism 377

TABLE 1

Internal Transcribed Spacers and β-Tubulin Primers Used in PCR and Sequence Analysis

Primer[a]	Sequence 5′ → 3′	Reference
ITS1F	CTTGGTCATTTAGAGGAAGTAA	Gardes and Bruns (1993)
ITS5	GGAAGTAAAAGTCGTAACAAGG	White *et al.* (1990)
ITS1LM	GAACCTGCGGAAGGATCATT	Myllys *et al.* (1999a)
ITS2KL	ATGCTTAAGTTCAGCGGGTA	Lohtander *et al.* (1998)
ITS4	TCCTCCGCTTATTGATATGC	White *et al.* (1990)
Bt3LM	GAACGTCTACTTCAACGAG	Myllys *et al.* (2000b)
Bt10LM	TCGGAAGCAGCCATCATGTTCTT	Myllys *et al.* (2000b)
Bt13LM[b]	GCATCCTCTGATAAATATGTTCC	Present paper
Bt14LM[b]	CATCTGCTGTGTCAATTCTGG	Present paper

[a] The odd numbers are 5′ primers and even numbers are 3′ primers.

[b] Used only as sequencing primers.

automatic sequencer (PE Biosystems). Nucleotide ambiguities in the obtained sequences were coded using IUPAC ambiguity codes.

Alignments and parsimony analyses. The β-tubulin sequences, being from protein-coding genes, showed no length variation (except for a one-base variation observed in the intron) in the taxa studied and were aligned manually without difficulties. The preliminary alignment of the continuous ITS1–5.8S–ITS2 region was made with Clustal X (Jeanmougin *et al.*, 1998) and adjusted manually. Six areas within this region were uniform in all sequences to such an extent that it enabled us to split the region into seven pieces for the analyses. This was done in order to save CPU time in these analyses. The noncoding ITS regions exhibit considerable length variation, which causes problems in their alignment. The split sequences were therefore aligned during the tree search (direct optimization, optimization alignment; Wheeler, 1996) using the program POY (Gladstein and Wheeler, 1997–2000). We first performed POY analysis with the DOS version 2.61 on a computer equipped with a 600-MHz Intel Celeron processor. To determine whether the optimization alignment was a viable alternative with the available computer resources, we started with test analyses using 40 taxa and subsequently increased the number of taxa to 88, 103, 125, and finally to 235. The final analysis was undertaken in two steps following Giribet and Ribera (2000). To restrict the time used for the last search, we first made a constraint tree by performing parsimony jackknifing (Farris *et al.*, 1996). A constraint tree based on the results of the first search was constructed using JACK2HEN, a complementary program available with POY.

In both analyses, transitions and transversions were given equal weight and a default value of 2 was used as a cost for gaps. The first part of the analysis (jackboot) lasted 2,721,801 s (approximately 1 month), and the constrained search based on these results lasted 118,370 s. It should be noted, however, that despite the long time used, we employed a shortcut in this analysis. Parsimony jackbooting is a strategy that cannot be recommended for general use when access to parallel computing facilities (and especially CPU time!) is readily available. It is a restricted search and how well it performs compared to more extensive strategies in POY has not, as yet, been explored.

More thorough analyses of the material were performed by Ward Wheeler, with the Unix beta-version of the POY run on a parallel computer cluster of the American Museum of Natural History, with 128 dual 500-MHz PIII processors (for a total of 256 CPUs) over a 100-Mb switched network and with each machine equipped with 512 Mb RAM. As can be seen already from the hardware used, this second analysis is immensely different from our first analysis. Over 100 processors connected in parallel allow possibilities to use algorithms to such extent that is not available (within reasonable time) when the analysis is performed on a single Celeron laptop. In addition, this version of POY included the new efficient algorithms that have been developed specifically for the analyses of large data sets (Goloboff, 1999).

The main difference between POY and the more conventional programs with the possibility of pairwise and multiple alignment is the treatment of the gaps (dynamic vs static). Traditionally, gaps have been treated either as missing data or as a fifth character state, but in direct optimization they are treated as events connecting the observed length-variable sequences of the organisms under study. With the algorithms of the program, one does not even try to find positional homology among all the different nucleotides simultaneously present in each sequence, and no alignment in its traditional sense exists (Wheeler, 1996). In our analyses we used three different parameter sets following Giribet and Ribera (2000). The parameter sets used were 2:1:1 (default), 4:2:1, and 4:1:1, implying costs for gap, transversion, and transition, respectively. This naturally represents only a small fraction of all possible cost functions that can be applied. The CPU time used for these searches with the 256 processor cluster was approximately 120 h each, but the time varied because of other jobs performed at the same time. Command lines (plus brief explanation of the commands) for all the POY analyses are presented in Appendix 4.

SPECIES DESCRIPTIONS AND NOMENCLATURAL NOTES

In our analysis, we used three species that have not yet been named. These species are described below.

In addition, a new nomenclatural combination is presented.

Cladonia fleigiae Ahti & S. Stenroos, sp. nova

Podetia erecta, albido-viridia, 3–6 cm alta, 0.8–1.5 mm crassa, mediocriter ramosa, ramulis curtis, axillis perforatis, superficie tomentosa et ad apices versus pruinosa; cortex et stereoma distincti, canalis centralis flocculosus; conidiomata terminales vel subterminales, gelatino purpureo. Hymenia rufa. Acidum thamnolicum continens.

Type. Brazil. Minas Gerais: Parque Natural de Caraça, near Gruta de Lourdes, 1997 *T. Ahti, S. Stenroos & M. Fleig 55604* (SP, holotype; H, TUR, isotypes).

Etymology of the epithet: Named to honor Dr. Mariana Fleig, Pôrto Alegre, RS, a distinguished student of Brazilian lichens, who together with us detected the species.

Primary thallus not seen. Podetia erect, forming 10- to 15-cm-wide cushions, whitish-green, not blackening at base, brown at the extreme tips, 3–6 cm tall, 0.8–1.5 mm thick, somewhat branched but branches short, branching type dichotomous, trichotomous, or tetrachotomous anisotomy, axils perforated, margins of perforations incurved. Surface of podetia matte, minutely tomentose, white-pruinose toward the tips, maculate, smooth, with scattered nonaxillary perforations. Podetial wall 150–250 μm thick; central canal with abundant, white, flocculose hyphae, appearing felty. Conidiomata at apical tips and frequently also laterally on podetia near tips, stalked, conical, containing red jelly. Hymenial disks at apical branch tips, brown, not seen in mature state. Chemistry: K+ yellow, PD+ yellow; contains thamnolic acid and probably traces of decarboxythamnolic acid.

Habitat. On constantly wet seepage slopes. As scattered colonies among abundant mosses, such as *Sphagnum*. In timberline scrub at about 1400 m.

Distribution. Minas Gerais, Brazil. Two localities at Caraça, not seen on other mountains in Minas Gerais. A member of the Napaean element (Ahti, 2000) in South America.

Additional specimens examined: BRAZIL. Minas Gerais: Parque Natural de Caraça, 1995 *R. C. Harris 35022* (NY), *S. Stenroos 5052a* (SP, TUR).

Cladonia fleigiae is fairly conspicuous since it forms whitish, rather large cushions. It may be most similar to *C. obscurata* Ahti (Ahti, 2000), which is darker in appearance due to blackening bases and brownish apical parts. Furthermore, *C. obscurata* has a more felty podetial wall because the cortex and stereome are weakly developed.

Cladonia furfuraceoides Ahti & Sipman, sp. nova

A *Cladonia furfuracea* differt podetiis brevioribus crassioribusque, non longe subulatis et squamulis latioribus, non isidioideis. Acidum fumarprotocetraricum continens.

Type. Guyana. Potaro-Siparuni Region: Kaieteur Falls National Park, near Kaieteur Guesthouse, 400 m, 1996 *T. Ahti 53102* (BRG, holotype; B, H, NY, US, isotypes).

Etymology of the epithet: Resembling *C. furfuracea.*

Primary thallus persistent or evanescent, consisting of incized, imbricate, 1.5- to 3-mm-wide squamules, lobes 0.5 mm wide, rounded. Podetia 1–3(4) cm tall, 0.5–2 mm thick, whitish-gray, hardly browned, clearly melanotic at base; unbranched to sparsely branched by dichotomy, axils closed, tips usually forming narrow scyphi, sometimes subulate, scyphi shallow, 0.7–1.5 mm wide, usually single per podetium. Surface of podetia largely decorticate, slightly arachnoid, with verruculae containing algal glomerules, loosely to densely squamulose, squamules elongate, ca. 1.0(–2.0) × 0.5 mm, deflexed with incurved tips, fragile and easily dehiscent; upper surface flat to convex. Podetial wall 130–260 μm, rather soft; cortex present only on verruculae; central canal smooth. Conidiomata common on scyphal margins, occasionally also on podetial squamules and laterally near tips of podetia, sessile to stalked, spherical to pyriform, strongly constricted at base, containing hyaline jelly. Hymenial disks frequent, dark brown, shortly stalked, forming agglomerations. Chemistry: K−, PD+ red; contains fumarprotocetraric, protocetraric, confumarprotocetraric, and often also convirensic acids; additional atranorin found in *Boom & Gopaul 7248* (NY).

Habitat. On sandy, open places in scrub savanna, being a colonizer of disturbed places in white sand areas and on sandstone tablelands.

Distribution. Brazil (Amazonas, Roraima), Colombia (Amazonas), Guyana, Venezuela (Amazonas, Bolívar). A member of the Guianan Shield subendemic elements, extending to Amazonia.

Representative specimens examined: BRAZIL. Amazonas: cemetery Tapereira along Rio Negro, 1979 *W.R. Buck 2200* (H, NY). Roraima: Mun. Boa Vista, Tepequem, 1800–2100 m, 1987 *E. Sette 982* (H). COLOMBIA. Amazonas: Araracuara, 350 m, *H. Sipman & J. Duivenvoorden 27887* (B, COL, H). GUYANA. Upper Mazaruni Dist.: Mt. Latipu, 1000 m, 1985 *H. Sipman & A. Aptroot 19141* (B). VENEZUELA. Amazonas: Cerro Pavón, 120 m, 1958 *K. Mägdefrau 294* (M). Bolívar: Cerro Guaiquinima, 800 m, 1991 *H. Sipman 27079* (B).

Cladonia furfuraceoides was included in *C. furfuracea* by Ahti (2000) with the suggestion that the Guianan material possibly represents a distinct species. This is now confirmed after additional field work in Guyana. The distribution map of *C. furfuracea* s. lat. published by Ahti (2000, Fig. 63) also indicates that the Guianan range is very distinct from the east Brazilian coastal range of *C. furfuracea* s. str. While both species have reflexed squamules on podetia, in *C. furfuraceoides* they are not isidioid but wide and flat. The dying bases of *C. furfuraceoides* have a strongly blackening medulla, and the podetia are short and stout rather than tall and slender as in *C. furfuracea*.

Cladonia hypomelaena (Vain.) S. Stenroos, comb. nova

Basionym: *Cladonia miniata* f. *hypomelaena* Vain., Acta Soc. Fauna Fl. Fenn. 4: 68. 1887. Type: Brazil. Minas Gerais: Caraça, *E.A. Vainio s.n.* (TUR-V 14193, lectotype selected by Stenroos, 1989c).

Representative specimens examined: BRAZIL. Minas Gerais: Parque Natural de Caraça, 1997 *T. Ahti 55407, 55605* (H, SP), *S. Stenroos 5041, 5068a* (SP, TUR).

Cladonia hypomelaena was included in *C. secundana* Nyl. by Stenroos (1989c) and Ahti (2000), but our field studies in Brazil have confirmed that it is a distinct species. *C. hypomelaena* was well described by Vainio (1887) in Latin, under *C. miniata* G. Meyer, although he thought that the observed character differences of the recognized "formae" were not constant. We observed well-developed colonies which appeared distinct from the other species of this group. Recent herbarium studies have supported its reclassification. The major diagnostic characters of *C. hypomelaena* include the presence of fairly large (3–11 mm long), thick primary squamules which have a dark brown to orange underside. The medulla is constantly white, however. Podetia, usually present and situated along the margins of the squamules, attain a maximum height of 10 mm. The major secondary metabolites are didymic acid and (in hymenia) rhodocladonic acid, but condidymic and subdidymic acids and the unknown substance M1 (Stenroos, 1989c) are also produced. The species is known only from Minas Gerais, S.E. Brazil.

Cladonia stenroosiae Ahti, sp. nova

Cladoniae substellari similis sed podetiis tenuissinis, magis dense ramosis, adpressis, flexuosis, apice curvatis, superficie rugulosis, intus solidis vel subsolidis; ramulis ultimis crystalla glaucescentia dense mox in herbario producentibus. Acidum usnicum et vulgo acidum sticticum continens. Vulgo rupicola.

Type. Brazil. Minas Gerais. Municipio Lima Duarte: Parque Estadual de Ibitipoca, Morro do Cruzeiro, altitude 1500 m, hanging on quartzitic cliff wall in treeless capetinga vegetation near mountain summit, 21° 42′ S, 43° 53′ W, 1993 *M.P. Marcelli, T. Ahti, O. Yano, M. Brügger & C.H. Ribeiro 27966a* (SP, holotype; CESJ, H, NY, isotypes).

Etymology of epithet: Named to honor Dr. Soili Stenroos, a distinguished student of Brazilian *Cladonia* flora and curator of E. A. Vainio's lichen herbarium, University of Turku, Turku, Finland.

Primary thallus unknown. Podetia growing strongly appressed on the substrate but forming wide, 1-cm-thick colonies, yellow-green, not blackening at base, extreme tips brown; very thin, thickest axes 0.2–0.5 mm wide, fairly densely branched, branching type irregular anisotomic dichotomy, extreme tips curved, all axes flexuose. Surface of podetia rugulose throughout, matte or slightly shiny. Podetial wall 100–150 μm, cortex absent, but an indistinct corticoid layer may be distinguishable, stereome softish, fibrose; central canal mostly absent but present in thicker branches, very narrow, surface furrowed. Conidiomata at tips of podetia, dark brown, cylindrical, not constricted at base. Hymenial disks rare, at tips of markedly thickened, erect podetia, brown. Chemistry: K−; PD+ yellow or PD−. Contains usnic acid and stictic acid as major compounds, constictic and occasionally also cryptostictic, norstictic, and connorstictic acids as minor compounds. The concentrations are low so that color may not always be obtained with color reagents. In addition, fine bluish-white crystals are produced in abundance at the podetial tips in the herbarium (probably a steroid; also present in *C. substellata* and its relatives).

Habitat. *Cladonia stenroosiae* characteristically grows on bare surfaces of siliceous rocks, forming large patches, even on vertical cliffs. This is unusual for *Cladonia* species, but in Brazil the brilliantly pink *C. salmonea* S. Stenroos also colonizes such habitats. However, *C. stenroosiae* also inhabits a thin layer of bare soil over rock outcrops.

Distribution. Minas Gerais, Brazil. *C. stenroosiae* seems to be another member of the many S.E. Brazilian Minas Gerais endemics discussed under the Napaean element by Ahti (2000, p. 25). So far it is known only from the Ibitipoca and Caraça Ranges, at 1200–1600 m, and is uncommon in these areas.

Representative specimens examined: BRAZIL. Minas Gerais: Parque Natural de Caraça, 1977 *Schindler 7331* (H), 1988 *Eliasaro 8344* (H), 1989 *Stenroos, Ahti & Marcelli 3822* (H, SP, TUR), 1997 *Ahti 55359* (H, SP), *55621* (H, SP), 1997 *Stenroos 5013* (SP, TUR); Parque Estadual de Ibitipoca (see type).

Cladonia stenroosiae was erroneously included in *C. substellata* Vain. by Ahti (2000), because its distinctness was not yet clear at the time that work was submitted. However, during the meeting "Recollecting Vainio," arranged in Parque Natural de Caraça in 1997, these two species were observed along the Cascatinha Trail in the park. The major differences lie in their habitat preferences as well as in the structures of their podetia. *C. substellata* grows on soil, while *C. stenroosiae* prefers bare rock surfaces; occasionally, they can be found immixed. *C. substellata* has more robust, often erect, smooth, shiny, and hollow podetia (Ahti, 1973, Fig. 8), whereas *C. stenroosiae* has thin, rugulose, mostly solid podetia growing in flattened mats. Chemically, the two species are similar, but *C. substellata* may lack the stictic acid complex (see Ahti, 2000). *C. substellata* is widespread in tropical South America (map in Ahti, 2000: Fig. 212); *C. stenroosiae* seems to be restricted to interior S.E. Brazil.

RESULTS

Preliminary analysis with optimization alignment using POY resulted in two equally parsimonious trees with the length of 6206 steps (not shown). It is, however, far from the optimal solution found with a more extensive search using the parallel version of POY. It is obvious that the new algorithms (tree fusing and tree drifting; Goloboff, 1999) are essential in finding the optimal solutions for a matrix with over 200 taxa. These algorithms are designed to avoid local optima by analyzing parts of the trees separately (Goloboff, 1999). In the more extensive analysis, the search with the same settings for gap:transversion:transition costs (default, 2:1:1) as in the previous analysis resulted in 20 (preset maximum for the number of trees saved for all searches) trees with the length of 6188 steps. The strict consensus of these trees is presented in Fig. 1. Different cost functions altered results, the one with 4:1:1 only slightly, but distinguishing transversions from transitions led to greater differences. A strict consensus of all 60 trees obtained from the three analyses with different settings is presented in Fig. 2 and three different topologies based on different parameters (211, 411, 421) are illustrated in Fig. 3.

DISCUSSION

Aligning and Analyzing

Both ITS and β-tubulin seem to be useful at the infrageneric level and in comparing closely related genera in Cladoniaceae. At higher levels, ITS becomes impossible to align if conventional aligning methods are used. At the infraspecific level, both ITS and β-tubulin generally provide only a few or no informative characters; in some cases, different populations of a species share entirely identical sequences.

Manual alignments have been criticized, and they may not be recommended for molecular data that are not readily alignable due to considerable length variation in the sequences. Criticism is based on manual alignments being subjective and thus not repeatable. If they are done (e.g., because of limited computational facilities), deposition of the final matrices for free retrieval in electronic repositories is essential (e.g., TreeBASE; Sanderson *et al.*, 1993). Another obvious defect in manual alignments is that gap costs are not explicit (Wheeler, 1995; Giribet and Wheeler, 1999) and that alternative, possibly better alignments are not explored. Programs such as Clustal X (Jeanmougin *et*

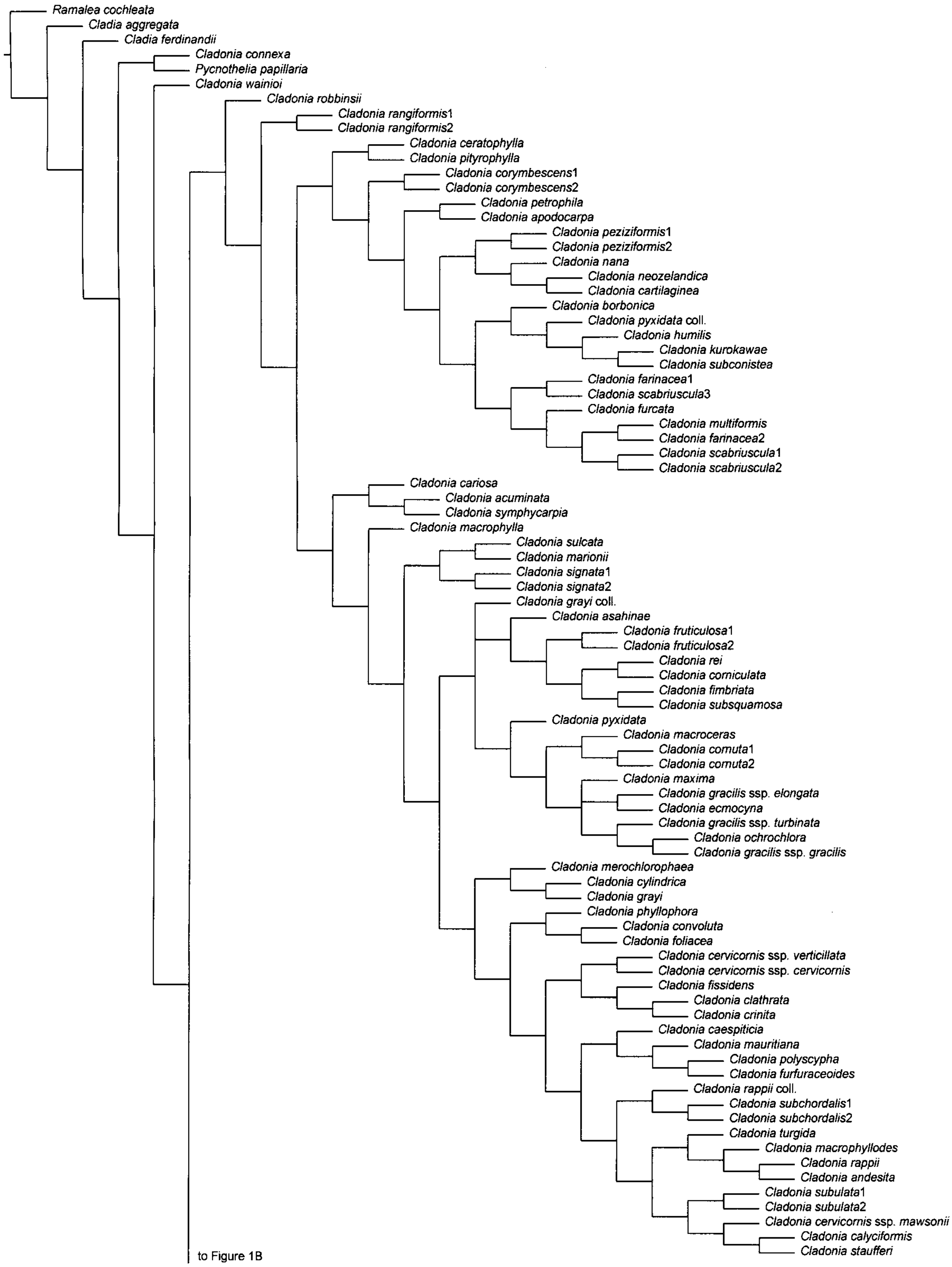

FIG. 1. Strict consensus tree of 20 trees based on a POY analysis of the combined data set with the default parameter set (2:1:1) for the gap, transversion, and transition costs used for direct optimization of the sequence data.

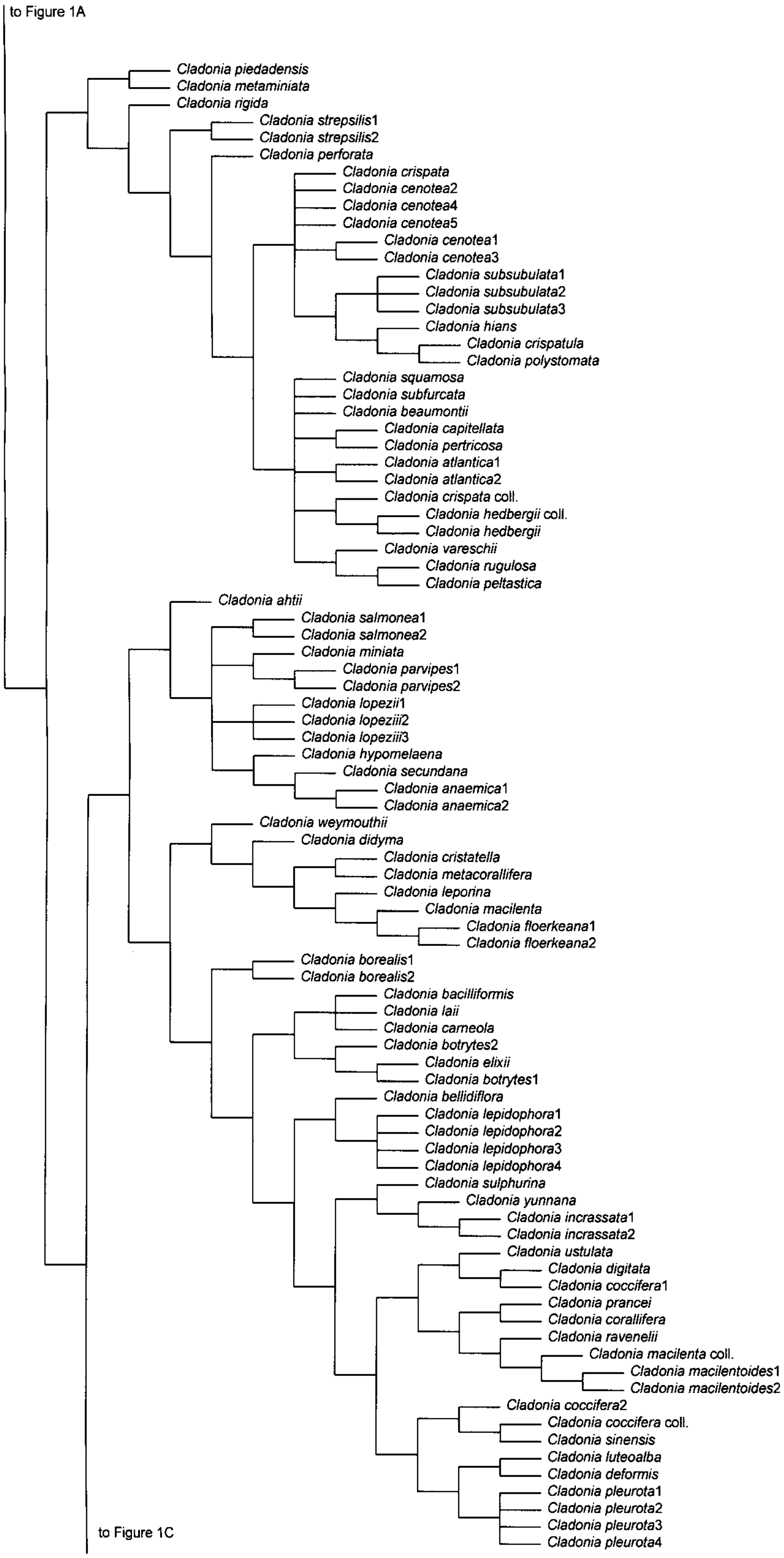

FIG. 1—*Continued*

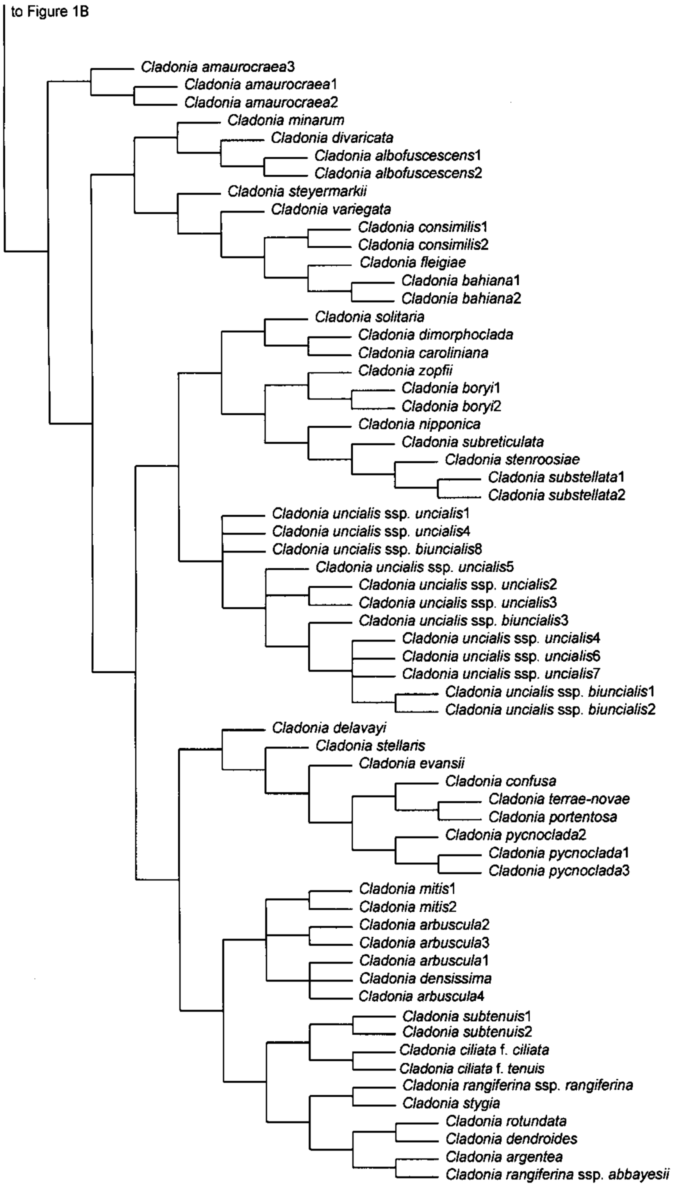

FIG. 1—*Continued*

al., 1998) or similar simple, straightforward aligning programs are often used as an alternative. In most cases, the resulting alignments are then adjusted manually. These adjustments are obviously needed because Clustal may align fully identical sequences in various ways, depending on the order of the sequences in the data set. Leaving the obvious mistakes (identical sequences aligned in different ways) uncorrected is not warranted. The requirement to leave preliminary homology assumptions uncorrected would be absurd if applied to morphological data; instead reciprocal illumination has been adopted as a strategy to further check, correct, and recheck preliminary homology statements (Hennig, 1966). We feel that manual adjustment of preliminary aligned sequences is comparable to some extent with the reciprocal illumination approach used for morphological data, although certain differences are present. While repeated analyses of morphological characters can lead us to find some genuine mistakes in primary homology hypotheses, this

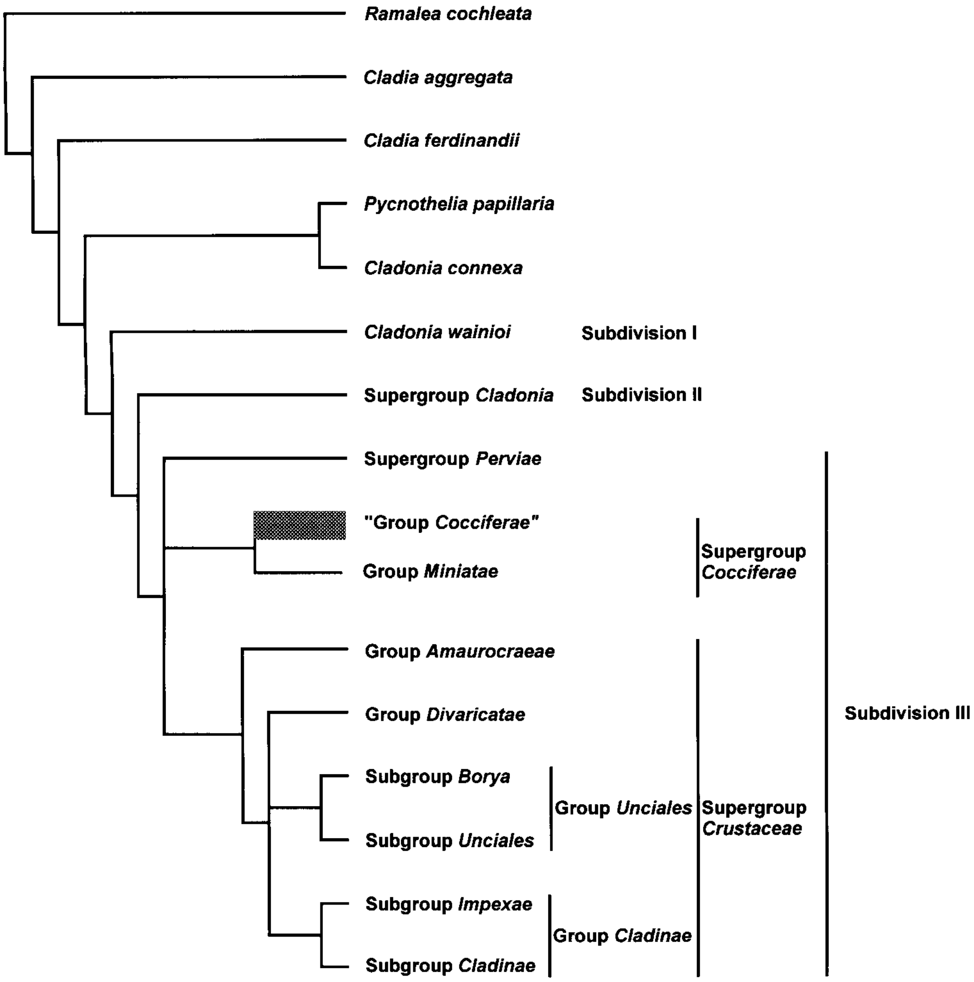

FIG. 2. Strict consensus tree of 60 (3 × 20) trees based on POY analyses of the combined data set with different parameter sets (2:1:1, 4:1:1, 4:2:1) for the gap, transversion, and transition costs used for direct optimization of the sequence data. Group *Cocciferae* is not monophyletic with the parameters 4:2:1 and therefore this group is indicated with a stippled bar.

is not possible for sequence-level data. Only four types of nucleotides exist, and there is no possibility of discerning the evolutionary history of any particular character or character state from this information. And while corrections of preliminary homology statements of morphological characters are based on phylogenetic hypotheses, this is normally not the case for manual adjustment of preliminary sequence alignments. The main reason for continuing to use programs such as Clustal despite their obvious shortcomings is their speed, which results from alternative alignments not being evaluated; the programs are simply algorithmic. These are, in many cases, however, the only alternative. More sophisticated programs, such as MALIGN (Wheeler and Gladstein, 1992) or POY (Gladstein and Wheeler, 1997–2000), might not be viable options if only limited computer resources are available.

The POY analyses performed represent the most comprehensive alignment of our data at the moment. No better way is available for the time being to test homology than with parsimony (Patterson, 1982), and only an alignment procedure congruent with the basic tenets of cladistics can rigorously test alternative homology assumptions (Wheeler and Gladstein, 1992). All the major groupings remain essentially unchanged throughout all analyses. However, instability was observed in the status of *Unciales* until the matrix was expanded to include 125 taxa. Increasing the amount

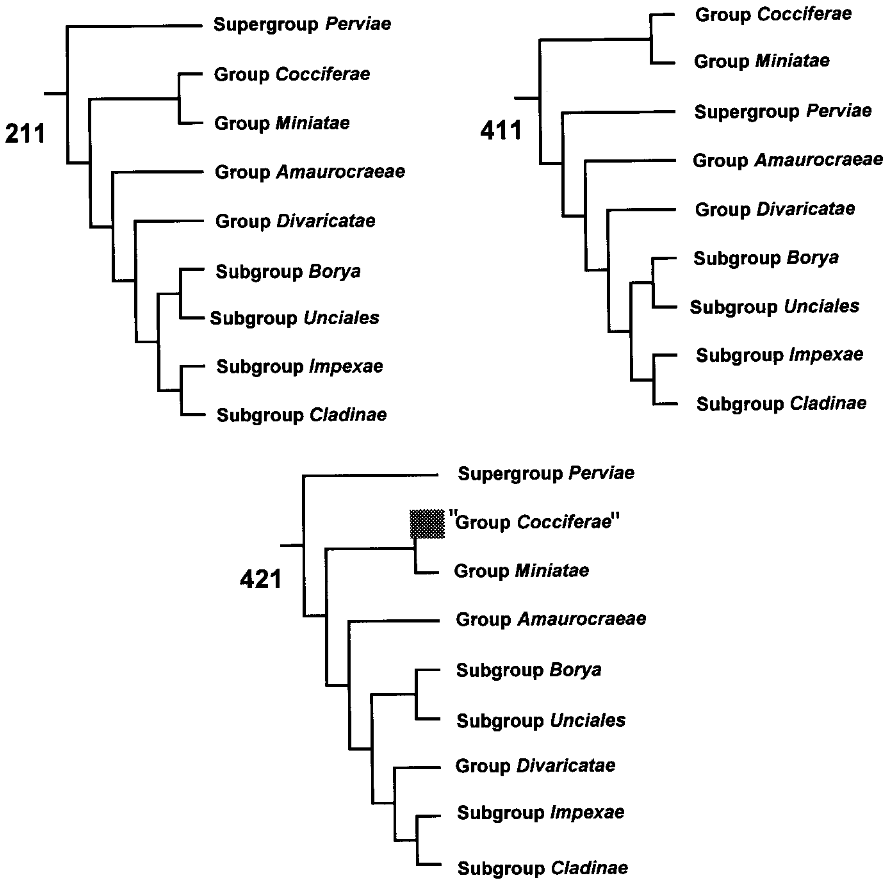

FIG. 3. Three different topologies for the Subdivision III of the tree illustrated in Fig. 2 based on different parameters used and indicated accordingly (211, 411, 421).

of taxa from 125 to 235 did not alter the groups except at the very terminal branches of the tree.

What Is Cladonia?

Our analyses support the monophyly of the genus *Cladonia* (including *Cladina*), except for *Cladonia connexa*, which remains outside and joins with *Pycnothelia papillaria* in a sister-group. Representatives of the genus *Cladia* and *Ramalea* are more distantly related to *Cladonia*. Wedin *et al.* (2000) showed that a clade, including *Cladia, Pilophorus,* and *Heterodea,* is a sister to *Cladonia,* and *Stereocaulon* is outside of both. These findings concur with analyses done by Stenroos and DePriest (1998) and Tehler *et al.* (2000). The poorly known *Ramalea cochleata* was tested out of curiosity; its relatedness to *Cladonia* has been uncertain. However, recent SSU rDNA analyses show that it should probably be included in the Cladoniaceae (Stenroos *et al.*, 2002). The delimitation of Cladoniaceae is not yet settled (Wedin *et al.*, 2000), but the family is likely to encompass at least *Pycnothelia, Cladonia connexa,* and *Metus,* in addition to the core *Cladonia.* The possible inclusion of the *Cladia–Pilophorus–Heterodea* clade in Cladoniaceae will be discussed elsewhere.

The exclusion of *Cladonia connexa* was not initially expected, although it has been difficult to classify in any section of *Cladonia* solely by morphology or chemistry. Even Vainio (1887, p. 289) noted under *C. connexa* that "Haec species ab omnibus aliis *Cladoniis* bene differt." Ahti (2000) grouped *C. connexa* in the section *Ascyphiferae,* although some of the diagnostic features did not support this placement. According to our analyses, the new placement of *C. connexa* would require nomenclatural changes, which we are reluctant to make at this point (but see Stenroos *et al.*, 2002).

Major Groups of Cladonia

We distinguished three informal subdivisions within the genus *Cladonia*. Within these subdivisions four supergroups and, further, seven groups and two subgroups were distinguished. The subgroups essentially correspond to the formerly used sections, with some modifications (Table 2, Fig 2).

In our analysis, *C. wainioi* appears basal to the rest of *Cladoniae*. We tentatively place it in its own group, Subdivision I. Although considered to be a member of *Ascyphiferae*, *C. wainioi* is rather distinct in its cladinoid branching and its production of merochlorophaeic acid.

The remainder of *Cladonia* forms two principal lineages, named here as Subdivisions II and III. Subdivision II includes species representing the *Cladonia* sections *Ascyphiferae*, *Helopodium*, and *Cladonia* (sensu Ahti). Subdivision III includes groups corresponding to the *Cladonia* sections *Cocciferae*, *Perviae*, and *Unciales* and the *Cladina* sections *Cladina*, *Impexae*, and *Tenues* (sensu Ahti).

Vainio (1894) presented a phylogenetic diagram in his world monograph, recognizing two major groups based on hymenial color (red-fruited as "Ser. A. *Cocciferae*" and brown-fruited as "Ser. B. *Ochrophaeae*"). Dahl

TABLE 2
A New Preliminary Classification of the Genus *Cladonia*

Proposed taxonomic entities (nomenclature provisional)	Provisional type species	Nomenclature sensu Ahti (2000)	Type species of current sections
Subdivision I	*Cladonia wainioi*	*Cladonia* section *Ascyphiferae* (p.min.p.)	
Subdivision II			
Supergroup *Cladonia*	*Cladonia subulata*	*Cladonia* section *Cladonia* (p.maj.p.)	*C. subulata*
		+*Cladonia* section *Ascyphiferae* (p.maj.p.)	*Cladonia furcata*
		+*Cladonia* section *Helopodium*	*Cladonia cariosa*
		+*Cladonia* section *Strepsiles* (p.p.)	
		+*Cladonia* section *Unciales* (p.min.p.)	
Subgroup *Graciles*	*Cladonia gracilis*	*Cladonia* section *Cladonia* (p.p.)	
Subdivision III			
Supergroup *Perviae*	*Cladonia cenotea*	*Cladonia* section *Perviae* (p.maj.p.)	*C. cenotea*
		+*Cladonia* section *Strepsiles* (p.p.)	*Cladonia strepsilis*
		+*Cladonia* section *Cocciferae* (p.min.p.)	
		+*Cladonia* section *Unciales* (p.min.p.)	
Supergroup *Cocciferae*	*Cladonia coccifera*		
[Group *Cocciferae*]	*C. coccifera*	*Cladonia* section *Cocciferae* (p.maj.p.)	*C. coccifera*
Group *Miniatae*[a]	*Cladonia miniata*	*Cladonia* section *Cocciferae* (p.p.)	
Supergroup *Crustaceae*[b]	*Cladonia rangiferina*		
Group *Amaurocraeae*[a]	*Cladonia amaurocraea*	*Cladonia* section *Unciales* (p.p.)	
Group *Divaricatae*[a]	*Cladonia divaricata*	*Cladonia* section *Unciales* (p.p.)	
		+*Cladonia* section *Perviae* (p.p.)	
		+*Cladonia* section *Cladonia* (p.min.p.)	
Group *Unciales*	*Cladonia uncialis*		*C. uncialis*
Subgroup *Unciales*	*C. uncialis*	*Cladonia* section *Unciales* (p.min.p.)	
Subgroup *Borya*[a]	*Cladonia boryi*	*Cladonia* section *Unciales* (p.p.)	
Group *Cladinae*	*Cladonia rangiferina*		
Subgroup *Cladinae*	*C. rangiferina*	*Cladina* section *Cladina*	*Cladina rangiferina*
		+*Cladina* section *Tenues*	*Cladina ciliata*
Subgroup *Impexae*	*Cladonia portentosa*	*Cladina* section *Impexae*	*Cladina portentosa*
		+*Cladonia* section *Unciales* (p.min.p.)	

Note. Taxon in brackets was not supported in all analyses.

[a] Names not formally used.

[b] Used as a section by Rabenhorst (1860; type species *Cladonia rangiferina*).

(1952) followed this division. Choisy (1928) partly followed Vainio's groupings, but his evolutionary scheme differed quite significantly. Choisy's two major lineages were defined by the size of the primary thallus, which was linked to the ontogeny of podetia and hymenial disks. Further divisions referred not only to the color of hymenia but also to the slime color of conidiomata. Mattick (1938, 1940) proposed another division, postulating that species with closed branch axils (section *Clausae*) and those with open axils (section *Perviae*) would represent two major lineages of *Cladonia*. This system was followed by Thomson (1968).

Our Subdivisions II and III are not in accord with any of the traditional schemes. Huovinen and Ahti (1982) presented a nonphylogenetic classification of *Cladonia* (including *Cladina*) based on morphology and particularly on the biosequential groups of the secondary products. They did not distinguish between two major groupings, but their groups (1) *Helopodium* and (2) *Cladonia* (including *Furcatae* = *Ascyphiferae*) concur with our Subdivision II, and their groups (3) *Cocciferae*, (4) *Squamosae* (= *Perviae*), (5) *Unciales*, (6) *Cladonia boryi* and allies, and (7) *Cladina* concur with our Subdivision III. Following the same scheme, Ahti (1982) emphasized two categories stating that the groups *Squamosae* (= *Perviae*), *Unciales*, and *Cocciferae* share p- and m-depsides, whereas the cortical p-depside atranorin is shared by the other groups. Stenroos *et al.* (1997), in their preliminary survey based on morphology and secondary chemistry alone, showed that *Cladonia* included two main clades, one encompassing representatives of *Ascyphiferae, Helopodium*, and *Cladonia*, and the other including mainly *Cladina, Unciales, Perviae*, and *Cocciferae*. The two major groupings in our present analysis also correspond to the preliminary results reported by DePriest *et al.* (2000b).

Subdivisions II and III are not defined by any nonhomoplastic morphological or chemical apomorphies. If anything, certain biosequential patterns of chemical compounds are more frequent in one or the other of the groups. Some characters, such as red pigment, centrally proliferating scyphi, and funnel-shaped branch axils, are present in only one of the subdivisions.

Subdivision II encompasses species that have brown hymenia and lack certain medullary chemical compounds such as the β-orcinol p-depsides barbatic (except for *Cladonia robbinsii*) and squamatic acids, the β-orcinol m-depside thamnolic acid, and dibenzofurans. On the other hand, β-orcinol depsinones are exceedingly common; in particular, fumarprotocetraric acid is often the only major compound produced. Red pigment (rhodocladonic acid) is entirely absent from hymenia and conidiomata. Of the cortical substances, usnic acid is rare in this group, present only in *C. subchordalis*, *C. robbinsii*, *C. convoluta*, and *C. foliacea*, while atranorin is commonly produced (see also Huovinen and Ahti, 1982).

Subdivision III includes species with red, pale ochraceous, or brown hymenia. Red pigment is common in conidiomata. The medullary β-orcinol p-depsides barbatic and squamatic acids, as well as the β-orcinol m-depside thamnolic acid and the cortical usnic acid, are very common, whereas orcinol depsidones are absent, and β-orcinoldepsidones are scattered over several clades.

Genus Cladina Is Included in Cladonia

The status of *Cladina* has been in dispute. *Cladina* has traditionally been treated as a subgenus of *Cladonia* (for its early history, see Ahti, 1961), but recently both generic (dating back to Nylander, 1866) and subgeneric statuses have been used. The *Dictionary of Fungi* (Hawksworth *et al.*, 1995) includes *Cladina* in the genus *Cladonia* without any statement of rank. The recognition of *Cladina* has typically been based on only a few diagnostic characters such as a crustose primary thallus (which is elusive and not observed in many species) and the lack of cortex. All *Cladina* are richly branched and are postulated to have a seasonal rhythm in branching. Ahti (1984) reviewed *Cladina* and accepted it, with some hesitation, at the genus level. Ruoss and Ahti (1989) summarized the pros and cons of the genus *Cladina*. Although mostly following the views of Ruoss, they strongly supported the subgeneric status.

The analyses by Hyvönen *et al.* (1995) as well as by Stenroos *et al.* (1997) gave no support for *Cladina* at the genus level, with the former survey indicating paraphyly of *Cladina* relative to *Cladonia* and the latter showing *Cladina* as monophyletic within *Cladonia*. *Cladina* was demonstrated to be paraphyletic by DePriest *et al.* (2000b; see also Ahti and DePriest, 2001), supporting the inclusion of *Cladina* into *Cladonia*. However, all of these surveys have failed to unambiguously solve the status of *Cladina*.

In addition to Hyvönen *et al.* (1995) and DePriest *et* *al.* (2000b), Choisy (1928), fairly radically for his time, treated *Cladina* as not monophyletic. He placed *Cladina* species as terminal in three separate lineages. In Choisy's work, *C. stellaris* was postulated to originate from ancestors such as *Cocciferae*, some members of *Perviae*, and *C. uncialis*, which produce red pigment in their hymenia or conidiomata. In most works, *Cladinae* were considered monophyletic, but their affinity to other groups was seldom discussed. In Mattick's (1938, 1940) system, which Galløe (1954) and Thomson (1968) adopted, *Cladina* was included in the section *Perviae*, together with *Unciales* and with the species traditionally placed in *Perviae* (including current members of *Ascyphiferae*). Later, *Cladinae* were anticipated to be closely grouped with members of *Unciales*, in particular (Ahti, 1984; Ruoss and Ahti, 1989).

Our analysis supports the monophyly of *Cladina*, but because it resides within *Cladonia*, it does not warrant a generic status. In our analyses, *Cladina* is referred to as Group *Cladinae* and is related to groups of current *Unciales* and more distantly related to *Perviae* and *Cocciferae*. *Cladina* and all groups of current *Unciales* form a clade tentatively referred to as Supergroup *Crustaceae*.

Ahti (1993; see also Huovinen and Ahti, 1986; Ahti, 2000) distinguished the three sections within the genus *Cladina* as *Cladina*, *Tenues*, and *Impexae*. Three additional sections, recognized in his earlier monograph (Ahti, 1961), were later included in *Impexae* (Ahti, 1984). The remaining sections, *Cladina*, *Tenues*, and *Impexae*, concur with those presented by des Abbayes (1939; ranked as series *Rangiferinae*, *Tenues*, and *Impexae*). These groups have particularly been defined by chemical characters, such as perlatolic acid (*Impexae*), or red pigment in the conidiomata (*Tenues*; Ahti, 1984; Huovinen and Ahti, 1986).

In our analyses, *Cladinae* includes two major clades. One of these clades encompasses members of the *Impexae* plus *Cladonia delavayi*, which earlier was placed in *Unciales* (with hesitation because of morphological similarity to *Cladina*). All these species produce usnic acid and orcinol depsides; in *C. delavayi*, the m-depside cryptochlorophaeic acid is formed, whereas the others produce the p-depside perlatolic acid. The sister clade to *Impexae* is composed of the species representing sections *Cladina* and *Tenues*. However, neither of the latter sections is monophyletic, as currently delimited, but instead their members are intermixed. *C. arbuscula*, together with *C. mitis* and C. densissima cluster together in a smaller clade, while the rest remain in a sister clade. Moreover, the type species of *Cladina* and *Tenues* (*Cladonia rangiferina* and *C. ciliata*, respectively) both reside in the latter clade. Even earlier authors have been unable to clearly distinguish between *Cladina* and *Tenues* because the differences are not consistent (Ahti, 2000). We propose that the section *Tenues* be reduced to synonymy with the section *Cladonia*, if formal section names are used.

It is apparent that the current data are not very helpful in solving relationships at the termini of the tree. However, we would like to point out that in our analyses it was not possible to differentiate between *Cladonia arbuscula* and *C. mitis* (see also Ruoss and Huovinen, 1989; Myllys *et al.*, 2000a). Furthermore, *C. densissima* was intermixed with *C. mitis–C. arbuscula*. Ahti (2000) noted that *C. arbuscula* consists of several geographic subspecies, and Ruoss (1987) brought forth evidence that *C. arbuscula* and *C. mitis* hybridize. In our analyses, *C. rangiferina* subsp. *abbayesii* appeared not to be very close to *C. rangiferina* itself, but more to *C. argentea*. Ahti (2000) distinguished the latter two by their branching systems, color of slime in conidiomata, as well as coloring of the apical branchlets. However, *C. rangiferina* is highly variable and therefore this species complex needs reexamination.

Sections Ascyphiferae, Helopodium, and Cladonia Mingling

The currently recognized sections *Ascyphiferae, Helopodium*, and *Cladonia* form the entire Subdivision II in our analyses. None of these sections, however, appear monophyletic even if we allow for subtle adjustments to their current contents. In general, Subdivision II is not very stable in its subgroupings, as judged from the different analyses performed.

Ascyphiferae was not really recognized before Dahl (1952). Its members were earlier included in *Perviae* or at least regarded as more closely related to *Perviae* than to *Cladonia* or *Helopodium* (e.g., Mattick, 1940; Dahl, 1952; Thomson, 1968; referred to as *Furcatae*). However, Huovinen *et al.* (1990) noted that the secondary chemistry of *Ascyphiferae* (as "group *Furcatae*") is very similar to that of section *Cladonia*, with atranorin and fumarprotocetraric acid complex dominating. Chemical similarity with the section *Helopodium* was also noted.

In our analyses, the core species of *Ascyphiferae*, viz.

Cladonia furcata (type of section), *C. farinacea, C. scabriuscula,* and *C. multiformis,* appear monophyletic in one of the three parallel POY analyses. Other species that are referred to the *Ascyphiferae,* such as *C. corymbescens, C. signata, C. rangiformis,* and *C. turgida,* appear more distantly placed. As to *C. signata* and *C. turgida,* their more distant position was predictable. The sectional position of the former has been in dispute, and its inclusion in *Ascyphiferae* was not well supported (its isotomically branching podetia form rounded heads, and it has no cortex, unlike *C. furcata,* for instance). The distinctiveness of *C. turgida* was recognized by Vainio (1897; see also Mattick, 1940, and Thomson, 1968), who placed it in the group *Megaphyllae* instead of *Microphyllae,* which contained, among others, the species corresponding to the current *Ascyphiferae.*

Dahl (1952; see also Vainio, 1897) used two categories for the current *Helopodium.* These categories, "ser. *Helopodium*" (containing, e.g., *C. apodocarpa, C. cariosa,* and *C. symphycarpia*) and "ser. *Macropus*" (*C. alpicola* = *C. macrophylla,* and *C. acuminata*), do not concur with our groupings. However, it is apparent that the current section *Helopodium* should be divided into at least five aggregates: (1) The psoromic acid-containing species *Cladonia macrophylla* remains solitary, and we do not expect any other species to join it; (2) *C. cariosa, C. acuminata,* and *C. symphycarpa* form a clade in two of the three analyses (these species produce atranorin and are calciphiles); (3) *C. sulcata* and *C. marionii*; (4) *C. caespiticia* is separate from any other *Helopodium* sampled, but a preliminary analysis with currently inadequate data suggests that *C. subcariosa* s.lat. may be closely related to it; (5) *C. peziziformis, C. nana, C. neozelandica,* and *C. cartilaginea* appear monophyletic in all analyses. Some further members of current *Helopodium,* such as *C. apodocarpa, C. ceratophylla,* and *C. pityrophylla,* appear distinct from the others, but their inclusion even in the current *Helopodium* has been doubtful.

Representatives of the section *Cladonia* are scattered over Subdivision II. Several informal groupings have generally been recognized. These include the groups around *C. verticillata, C. gracilis,* and *C. chlorophaea,* in particular. The so-called *C. verticillata* group, defined by centrally proliferating verticillate scyphi, is here represented by *C. andesita, C. calyciformis, C. cervicornis* subsp. *cervicornis, C. cervicornis* subsp. *mawsonii, C. cervicornis* subsp. *verticillata, C. clathrata, C. crinita, C. fissidens, C. macrophyllodes, C. rappii, C. rappii* coll., and *C. staufferi.* The *C. verticillata* group is not monophyletic in our analyses, but as the sequence variation is very low at this level, and the taxa do group rather close to each other, we wait for improved data before making any taxonomic conclusions. Some of the South American verticillate species may have strongly perforate or rimose scyphal plates; the three representatives in our analysis, *C. clathrata, C. fissidens,* and *C. crinita,* form a clade. We anticipate species, such as *C. imperialis,* which share this character to join the clade.

Somewhat surprisingly, the type species of *Cladonia, C. subulata,* is nested together with some of the verticillate species; this clade also includes some other members of the current section *Cladonia,* as well as *C. turgida* from *Ascyphiferae* and *C. caespiticia* from *Helopodium.*

The so-called *C. gracilis* group (Ahti, 1980), represented by *C. cornuta, C. ecmocyna, C. gracilis, C. macroceras,* and *C. maxima,* and supplemented by *C. ochrochlora,* was monophyletic in our analysis and referred to Subgroup *Graciles. C. ochroclora* joining this clade was not unexpected. However, we did not anticipate one of the representatives of *C. pyxidata* appearing here; we suspect a sequencing error that should be rechecked. The usnic acid-containing *C. subchordalis* has been placed close to *C. gracilis* and its postulated allies by Evans (1955), but it was later transferred into section *Unciales* by Ahti (1980). However, *C. subchordalis* certainly does not belong to the *Unciales,* which is in Subdivision III, nor does it appear close to *C. gracilis* or its postulated allies. *C. gracilis,* with its three subspecies, does not appear monophyletic in the present analyses.

The wide-scyphose species, which exhibit remarkably complex chemistries (Culberson *et al.*, 1985), do not form a monophyletic group. *C. pyxidata* from Mexico (fumarprotocetraric and homosekikaic acid), *C. kurokawae* (atranorin and fumarprotocetraric acid), *C. humilis* (fumarprotocetraric and bourgeanic acid), and *C. subconistea* (atranorin and psoromic acid) appear in a clade with *C. furcata* and its allies (*Ascyphiferae*). In our analyses, the members of the so-called *C. chlorophaea* group, or *C. grayi* group (Ahti, 1966; Holien and Tønsberg, 1985; DePriest, 1993, 1995; Ahti, 2000), namely, *C. grayi* (grayanic acid and fumarprotocetraric acid), *C. grayi* coll. (grayanic acid), *C. cylindrica* (grayanic and fumarprotocetraric acid), and *C. merochlorophaea* (merochlorophaeic acid), as well as *C. pyxidata* from Iceland (fumarprotocetraric acid) and *C. asahinae* (fumarprotocetraric and rangiformic acid), scatter over the other clades in Subdivision II without any obvious logical pattern. No morphological or chemical characters help in determining the positions of the wide-scyphose species, except for the currently vague pattern of atranorin-containing species being found in only one of the major clades. It is possible that the widespread *C. pyxidata* consists of more than one species, and the as yet unanalyzed *C. pocillum* probably further complicates the picture. We also lack *C. novochlorophaea, C. imbricarica, C. cryptochlorophaea*, and the widespread and problematic *C. chlorophaea* s.str. (fumarprotocetraric acid). Based on a preliminary survey, we anticipate that the latter will not cluster with *C. grayi* or its postulated allies but possibly with *C. subsquamosa* and *C. fimbriata*, both of which only contain fumarprotocetraric acid. The commonly used name *C. chlorophaea*-complex would in that case be misleading. All the wide-scyphose species are notoriously difficult to identify, and therefore, their chemical composition has been used to clarify their taxonomy. However, the final solution for treating these species seems to be more complex than that.

Some *Cladoniae* have been referred to as foliose, indicating that their primary thallus consists of exceptionally large squamules, and their podetia are usually poorly developed or absent. Only a few species have been assigned to this group, namely, *C. foliacea* and *C. strepsilis* (Vainio, 1897), later supplemented by *C. convoluta, C. firma, C. prostrata, C. pseudalcicornis*, and *C. robbinsii* (Dahl, 1952; Huovinen *et al.*, 1989a). The group has typically been ranked as subsection *Foliosae*, and it has been included in the larger group of closed-axil *Cladoniae* (Vainio, 1897; Mattick, 1940) near or within *Helopodium* (Choisy, 1928; Huovinen *et al.*, 1989a). Ahti (2000), with some hesitation, described a new section *Strepsiles* for those foliose species that contain the β-orcinol depsides (essentially barbatic and/or squamatic acid), including only *C. strepsilis* (type species) and *C. robbinsii*. The rest of the species typically produce the β-orcinol depsidone fumarprotocetraric acid and were therefore placed in section *Cladonia*, but without any subsectional rank. Our results show that *C. convoluta* and *C. foliacea* are in Subdivision II, and they form a clade together with *C. phyllophora. C. robbinsii* appears basal or next to basal of Subdivision II—surprisingly, as *C. robbinsii* is the only one with β-orcinol depsides in the whole Subdivision. *C. strepsilis* (defining section *Strepsiles*) is not related to any of the other "foliose" species treated here, but it belongs to Subdivision III (see below).

Our results show that Subdivision II includes all three sections, *Cladonia, Ascyphiferae*, and *Helopodium*. As currently delimited, these sections do not form monophyletic groups, and no other stable groupings around their type species (*C. subulata, C. furcata*, and *C. cariosa*, respectively) could be defined. In addition, much of Subdivision II remains unstable, as judged from varying positions of terminal taxa in different analyses. In these analyses, we have treated only some 80 taxa of the estimated 260 belonging to the three sections together (Ahti, 2000). However, it is evident that major changes are to be expected in the taxonomy of these groups. We postulate that, even by adding data, the sections *Ascyphiferae* and *Helopodium*, as currently delimited, will not appear monophyletic in the analyses. While waiting for further analyses, we prefer to include sections *Ascyphiferae* and *Helopodium* in a group currently referred to as section *Cladonia*.

Unciales Collapsing

Unciales have been defined by characters such as evanescent primary squamules (rarely observed in only a few species), absence of podetial squamules, presence of usnic acid (with some exceptions), and presence of β-orcinol depsides (typically barbatic, squamatic, and thamnolic acids). The overall similarity in the growth habit of *Unciales* and *Cladina* led Nylander (1866) to include both in his genus *Cladina*. Vainio (1897) classified *Unciales* (as unranked) under "Ser. B *Ochrophaeae*," in a parallel lineage with the other unranked groups *Chasmariae* (corresponding to *Perviae*) and *Clausae* (essentially corresponding to *Helopodium* and *Cladonia*). Mattick (1940), following his own scheme based on open and closed axils in podetia, placed *Unciales* as a subsection under the section *Perviae*, together with the other subsections *Chasmariae* (corresponding to the current *Perviae*) and *Cladinae*. Dahl's (1952) treatment essentially follows Vainio (1897) in placement of *Unciales*, but ranks it as a subsection. Aasamaa (1961) went further in ranking *Uncialis* as a distinct subgenus.

No recent treatment is available focusing on the taxonomy of *Unciales*, except for Ahti's (1973) review on a restricted group within the section. Even the present survey includes only 19 of the postulated 40 members of *Unciales*. In our analyses, *Unciales* appears paraphyletic relative to *Cladinae*. However, we obtained well-defined groupings incorporating the current *Unciales*, excluding only a few species (see below, and Tables 2 and 3).

Vainio (1897) attempted to make a preliminary subdivision of *Unciales*, based on 12 species. He had three major groupings; one was represented by *Cladonia divaricata* only and the third by *C. peltasta*. The second group encompassed the remaining 10 species, and subgroups were listed. *C. boryi* (as "*Cl. reticulata*"), *C. capitellata, C. substellata, C. uncialis*, and *C. amaurocraea* all appeared in different subgroups. Choisy (1928) also showed *C. uncialis* and *C. amaurocraea* to belong to entirely different lineages. Ahti (1973) designated a so-called *C. boryi* group. The defining characters included the production of needle crystals (not reliably codable relative to various crystals or other pruina that appear on some other *Cladoniae*) in the apical parts of the podetia and a fibrous skeletal tissue in the medulla. In this group, he included *C. boryi, C. caroliniana, C. dimorphoclada, C. kanewskii, C. nipponica, C. pachycladodes, C. subreticulata, C. substellata*, and *C. zopfii* and excluded the following species: *C. alaskana, C. obscurata* (as *C. boryi* var. *albida*), *C. amaurocraea* (incl. *C. hokkaidensis*), *C. southlandica, C. sublacunosa, C. subsetacea, C. uncialis, C. wainioi*, and implicitly also *C. albofuscescens* (see Ahti, 1973; under *C. boryi* var. *albida*).

In our analyses, the *C. boryi* group, referred to here as the informal Subgroup *Borya*, forms a clade. It includes essentially the same species as already accepted by Ahti (1973). However, we have not yet been able to analyze *C. kanewskii* or *C. pachycladodes*. We have added to the group a newly described species, *C. stenroosiae*, and the enigmatic Hawaiian endemic *C. solitaria*. As an exception for the group, *C. solitaria* lacks "steroid" crystals.

The tentative Subgroup *Unciales* includes *C. uncialis*. We examined several morphological variants of *C. uncialis* from different regions. One of the variants has been referred to as *C. uncialis* subsp. *biuncialis* because of dichotomic branching instead of the normal polytomies found in *C. uncialis* s.str. Representatives of *C. uncialis* form a clade, but the variants do not form any distinct subgroups that would warrant taxonomic recognition. Furthermore, it is possible that *C. uncialis* (the type species of the section *Uncialis*) will remain the sole member of the Subgroup *Unciales* group. There are some species, however, that may join this clade, but we have not been able to obtain material for analysis. At least *C. papuana* from Papua New Guinea, *C. sublacunosa* from Austria (perhaps extinct, as postulated by Huovinen and Ahti, 1986), and possibly *C. robusta* from Puerto Rico are among the candidates. Subgroups *Unciales* and *Borya* form a clade referred here to Group *Unciales*.

TABLE 3
Major Changes in Positions of Species

Species	New position	Earlier position and citation
Cladonia albofuscescens	Supergroup *Crustaceae*	Section *Cladonia* (Ahti, 2000)
Cladonia bahiana	Supergroup *Crustaceae*	Section *Perviae* (Ahti, 2000)
Cladonia capitellata	Supergroup *Perviae*	Section *Unciales* (Huovinen and Ahti, 1986)
Cladonia[a] *connexa*	Non *Cladonia*	Section *Ascyphiferae* (Ahti, 2000)
Cladonia consimilis	Supergroup *Crustaceae*	Section *Perviae* (Ahti, 2000)
Cladonia delavayi	Supergroup *Crustaceae* (Group *Cladinae*)	Section *Unciales* (Huovinen and Ahti, 1986)
Cladonia metaminiata	Supergroup *Perviae*	Section *Cocciferae* (Ahti, 2000)
Cladonia peltastica	Supergroup *Perviae*	Section *Unciales* (Ahti, 2000)
Cladonia perforata	Supergroup *Perviae*	Section *Unciales* (Thomson, 1968)
Cladonia piedadensis	Supergroup *Perviae*	Section *Cocciferae* (Ahti, 2000)
Cladonia robbinsii	Supergroup *Cladonia*	Section *Strepsiles* (Ahti 2000)
Cladonia strepsilis	Supergroup *Perviae*	Section *Strepsiles* (Ahti, 2000)
Cladonia subchordalis	Supergroup *Cladonia*	Section *Unciales* (Huovinen and Ahti, 1986)
Cladonia variegata	Supergroup *Crustaceae*	Section *Perviae* (Ahti, 2000)
Cladonia wainioi	Subdivision I	Section *Ascyphiferae* (Huovinen *et al.*, 1990)

[a] The status of *C. connexa* will be discussed in Stenroos *et al.*, 2002.

Group *Divaricatae* has members exhibiting a "spiny" appearance. These include *C. albofuscescens, C. consimilis, C. divaricata, C. fleigiae, C. minarum, C. steyermarkii, C. variegata*, and the enigmatic *C. bahiana*. Usnic acid is present or absent and does not define any smaller groups. Two different medullary components can be found in the species: a group with *C. minarum, C. divaricata*, and *C. albofuscescens* produce fumarprotocetraric acid, whereas all the others produce thamnolic acid. Vainio (1897) already noted the distinctiveness of *C. divaricata*, and later Ahti (2000) questioned the inclusion of *C. divaricata* in *Unciales. C. variegata, C. bahiana*, and *C. consimilis* were included by Ahti (2000) in *Perviae* and *C. albofuscescens* in *Cladonia*. Our preliminary results indicate that *C. spinea* (usnic, barbatic, and thamnolic acids) also belongs to this clade. We further anticipate that at least *C. bangii, C. crassiuscula, C. dilleniana, C. glabra, C. minarum*, and *C. sufflata* may belong here.

C. amaurocraea remains basal to all *Crustaceae*, forming its own tentative group. However, we anticipate that *C. nipponica* from Japan will join it.

As to the other members of the current section *Unciales, C. delavayi* (usnic, 4-*O*-methylcryptochlorophaeic, and cryptochlorophaeic acids) is now included in Group *Cladinae* (*Impexae*), close to *C. stellaris*. Moreover, *C. capitellata, C. peltastica*, and *C. perforata* (all with usnic and squamatic acids) clearly belong to *Perviae* (see below), and *C. subchordalis* (usnic acid) appears in *Cladonia* in Subdivision II (see above).

Open-Axiled Perviae

The section *Perviae* has traditionally been defined by its open podetial tips and axils. In some species, these openings become dilated and form superficially cup-like funnels. This has led some authors to treat these structures as open scyphi (versus closed scyphi, which are known from many other *Cladoniae*). Axil openings are not only confined to *Perviae* but are also found in species currently referred to as sections *Ascyphiferae* and *Unciales*. The major biogenetic pattern of the phenolic compounds in *Perviae* is clearly the β-orcinol depside pattern, and the major phenolic compounds are squamatic and thamnolic acids. From a biosynthetic point of view, *Perviae* forms a homogeneous group (Huovinen and Ahti, 1988).

Earlier, *Ascyphiferae* was sometimes placed in *Perviae* (Vainio, 1897; Dahl, 1952). Mattick (1940) emended *Perviae* to also include *Unciales* and *Cladina*. Huovinen and Ahti (1982) were the first to recognize *Perviae* basically in its present form (as "*Squamosae*"). They also stated that *Perviae* and *Ascyphiferae* (as "*Furcatae*") are not closely related. Huovinen and Ahti (1988) noted that within *Cladonia, Unciales* are most closely related to *Perviae*.

Perviae, as currently delimited, is essentially recognized as such in our analyses, with only a few additional species, *C. piedadensis, C. metaminiata*, and *C. perforata*, now included in the traditional group and a couple of species, *C. variegata* and *C. bahiana*, excluded. We tentatively refer to this group as the Supergroup *Perviae*.

In our analysis, the clade including the core *Perviae* is a sister-group to *Cladonia piedadensis* and *C. metaminiata*. Both species were erroneously placed in *Cocciferae*, although some features did not support that decision (Ahti *et al.*, 1995; Ahti, 2000). *C. piedadensis* contains the dibenzofuran didymic acid, which is characteristic of *Cocciferae*, but on the other hand, the slime in its conidiomata is hyaline, and hymenial disks have not been observed to confirm their color. *C. metaminiata* was given its name because of its superficial resemblance to *C. miniata* and allies. *C. metaminiata* does contain didymic acid, typical to *Cocciferae* (see below), but has dark brown hymenial disks. Our analyses support the inclusion of *C. piedadensis* and *C. metaminiata* in *Perviae* or the distinction of a separate Supergroup for the two species. Following the rule of minimal nomenclatural change, we have chosen the former option for now.

Representatives of *C. cenotea*, sampled from different regions, do not cluster together (see below). The austral *C. subsubulata* (sampled from Tierra del Fuego and the Falkland Islands) form a clade, as do the Neotropical *C. polystomata, C. crispatula*, and *C. hians*.

C. strepsilis, the type species of the newly described section *Strepsiles* (Ahti, 2000), appears alone within *Perviae*. Our samples of *C. strepsilis* specimens contain β-orcinol p-depsides (baeomycesic and squamatic acids) similar to typical *Perviae*. Its diagnostic compound strepsilin is a dibenzofuran; other dibenzofurans are common in *Cocciferae*, but are also present in *C. piedadensis* and *C. metaminiata*. Huovinen *et al.* (1989b) predicted that *C. strepsilis* may ultimately be relocated to *Cocciferae*. The recognition of *Strepsiles* would force

Perviae to be nonmonophyletic. We propose *Strepsiles* be included in *Perviae*.

All Cocciferae Are Not Red-Fruited

The members of the section *Cocciferae* are among the most conspicuous *Cladoniae* with their bright red hymenial disks. The red color is caused by a naphthoquinone pigment(s), known as rhodocladonic acid.

Cocciferae has been recognized at various infrageneric ranks (see Duby, 1830; Vainio, 1897; Asahina, 1939; Mattick, 1940), but it has always been considered a monophyletic entity. Evans (1930) was the first to recognize *Cocciferae* at the sectional level. *Cocciferae* was initially solely defined by its red hymenial disks, but later, some other diagnostic chemical characteristic, such as dibenzofurans and β-orcinol depsides, were shown to characterize the group (Evans, 1944; Huovinen *et al.*, 1989b). These compounds are also found in *Perviae*, but in somewhat different combinations. Compound combinations, such as thamnolic and barbatic acid, or squamatic and barbatic acid, are typical in *Perviae*, whereas all these compounds commonly occur together with usnic or didymic acid in *Cocciferae*. These chemical characteristics are not, however, possible to define precisely.

Vainio (1897), Mattick (1940), and Dahl (1952) used group names *Subglaucescentes* and *Straminoflavidae* to distinguish between grayish-green (no usnic acid) and yellowish (with usnic acid) species, respectively. These groups were later abandoned (Thomson, 1968; Huovinen *et al.*, 1989b; Stenroos, 1989b) and were not supported in our analyses, either.

We placed special emphasis on a small group of peculiar Neotropical *Cladoniae* referred to as the *C. miniata* group (Stenroos, 1989c). The bright orange-red color of the medulla and the flattened vertical thalli were the "classic" features distinguishing *C. miniata* s.lat. from other species (Martius, 1828; Eschweiler, 1833), although most of the current species are white-medullate and their overall thallus morphology varies. Until recently, only two species were recognized, namely, *C. miniata* and *C. erythromelaena* (Vainio, 1887). Stenroos (1989c) thoroughly screened the group and described six new species. Ahti (2000) added a species by raising *C. anaemica* from a varietal level, as we did for *C. hypomelaena* in the present paper. We sampled the majority of the species recognized in the *C. miniata* group, namely, *C. ahtii*, *C. anaemica*, *C. hypomelaena*, *C. lopezii*, *C. miniata*, *C. parvipes*, *C. salmonea*, and *C. secundana*. All our analyses show a monophyletic group, which we tentatively refer to as the Group *Miniatae*. The red-medullate species *C. miniata*, *C. parvipes*, and *C. salmonea* are not monophyletic, and the palmate vertical thallus shown by *C. lopezii*, *C. miniata*, and *C. salmonea* does not define any grouping.

The pale-fruited *Cladoniae*, referred to as *Ochroleuceae* (e.g., Vainio, 1897), were transferred to *Cocciferae* by Dahl (1952). *Ochroleuceae* are chemically similar to other *Cocciferae*, except that they lack the red pigment. Later authors (Mattick, 1940; Thomson, 1968; Huovinen *et al.*, 1989b; Stenroos, 1989b; Ahti, 2000) unanimously followed Dahl's scheme. In one of the three analyses, *Ochroleucae*, including *C. bacilliformis*, *C. laii*, *C. carneola*, *C. elixii*, and *C. botrytes*, forms a clade. However, all these species belong to *Cocciferae*.

Section *Cocciferae*, as currently delimited, appears to be a good monophyletic group, and it is recognized here as the Supergroup *Cocciferae*. Within *Cocciferae*, we distinguished the Group *Miniatae*, while the rest of the species, forming a sister clade to *Miniatae* in two of the three analyses, are not referred to any group for the time being.

Morphological and Chemical Characters in the Analyses

Both morphological and chemical characters show ample homoplasy. Only very few characters appeared to have nonhomoplastic synapomorphies. Character 1(1) defines, as anticipated, the core Cladoniaceae (including genus *Cladonia*, *C. connexa*, and *Pycnothelia*), character 5(1) defines the Group *Miniatae*, character 7(0) defines the Group *Cladina*, and character 28(1) defines the Group *Cocciferae*.

Indeed, surprisingly few characters have been used as a basis even for earlier classifications. Red hymenia have traditionally defined *Cocciferae*, as they do now. Perforated branch axils have been used to define *Perviae*. In our analyses, this character could not unambiguously be optimized to a particular clade. It is possible that the axil openings observed in different groups are not homologous but precede different ontogenies. Fissured podetia have characterized *Helopodium*, but this character is homoplastic and the group itself nonexistent. The section *Cladonia* has traditionally not been characterized by any particular morphological or chemical character, nor was it in our analyses. All the commonly used morphological and chemical characters in the genus, such as the presence of soredia, scyphi, stereome, cortex, usnic acid, and atranorin, have been known to be homoplastic and to define only small groups of species or even a single species. This was also shown in our analyses.

The groups now formed were essentially or entirely defined by DNA sequence characters. However, it is likely that we still miss many conventional characters that could prove powerful. Furthermore, some of the characters are perhaps currently misinterpreted. Many of the groups that we obtained are, in essence, congruent with the conventional groups that were largely formed by intuition, on the basis of overall similarity and dissimilarity. Similarity must implicitly comprise various morphological, anatomical, and ontogenetic characters, which are currently unknown or are difficult to define. It may well be that the lack of synapomorphies in the conventional characters does not indicate that they truly are absent but that *Cladoniae* has to date been insufficiently screened.

Species Delimitation

We used multiple samples, when available, in order to see if our terminal taxa (mostly species) appear as monophyletic entities in our analyses. We did not expect any problems with species, which show a rather restricted distribution and which are both morphologically and chemically uniform throughout their range. Examples of these include *C. anaemica, C. lepidophora, C. lopezii, C. subchordalis, C. bahiana, C. pycnoclada,* and *C. boryi*. Species with a wider range and which are also morphologically and chemically uniform are represented by *C. amaurocraea, C. cornuta, C. incrassata,* and *C. subulata*. All of these appear monophyletic in our study, although we have thus far only included a few samples of each.

We did expect problems with many of the widespread species such as *C. pleurota, C. pyxidata,* and *C. coccifera*, as well as the *C. furcata*-complex. *C. pleurota* samples included were from Australia, Mexico, Canada, and the United States. These samples were chemically identical but showed subtle morphological variation. However, they did form a clade. *C. pyxidata*, collected from Iceland and Mexico, was morphologically uniform but represented different chemotypes (see above). Although the tree may not be stable at its termini, it can hardly be expected that *C. pyxidata*, as currently delimited, is a single species. Also problematic was *C. coccifera*, although it is chemically and largely also morphologically uniform throughout its range. *C. furcata* and its supposed relatives *C. farinacea* and *C. scabriuscula* present yet another problem. They differ in their surface structure by being smoothly corticate, sorediate, or granulose-microsquamulose, respectively. However, it is quite often difficult to tell them apart and many intermediate types can be found. It is clear that a worldwide study sampling sequence-level characters is needed to resolve their phylogeny.

The representatives of *C. cenotea* did not group together. The samples, collected from Chile, Finland, and Newfoundland, all contain squamatic acid and are morphologically rather uniform. Bulat and Dudoreva (1993), reporting a high molecular variation of *C. cenotea* in the Murmansk Region, Russia, suspected that several species might be included. As to other species, *C. botrytes* did not group together although the samples were collected practically in the same locality. *C. uncialis* and *C. arbuscula* have already been discussed above.

Some *Cladonia* species are notoriously variable in their chemistry. *C. peltastica*, for instance, exhibits 15 different chemotypes (Ahti, 2000). It has been common practice to distinguish this kind of variation as informal chemotypes, particularly if insufficient material is available for thorough comparisons. Even notable morphological differences, correlating with chemistries, may have been overlooked. This was observed in the *C. miniata* complex, for instance (Stenroos, 1989c). Although our sampling is far from satisfactory in volume, and keeping in mind that the gene regions used are not powerful at low taxonomic levels, our results indicate that some currently delimited species of *Cladonia* might turn out to be more complex than currently recognized. Particularly species with wide ranges and complex chemistries should be studied further.

Conclusions

ITS and β-tubulin proved useful in resolving phylogeny, particularly in the basal parts of the tree. However, these gene regions appear less influential in resolving relationships between closely related species or within species in the terminal parts of the tree.

We agree with Wiley (1979; see also Benton, 2000; Nixon and Carpenter, 2000) in that we should incorporate cladistic information in existing classifications with as little disturbance to the current nomenclature as possible, not only to avoid violating monophyly but also to maintain maximal stability. To date we have screened no more than 35% of all species referred to the genus *Cladonia*. We therefore hesitate to make major formal changes in the classification of the genus. We are tentatively proposing a new classification for *Cladonia*, but by using informal names for the groups (Table 3).

Supported entities from the current classification (sensu Ahti, 2000) include section *Cladonia* (here Supergroup *Cladonia*, emended to encompass *Ascyphiferae* and *Helopodium*), genus *Cladina* (here Group *Cladinae*, including Subgroups *Cladinae* and *Impexae*), and sections *Perviae* and *Cocciferae* (here Supergroups *Perviae* and *Cocciferae*, the latter including Group *Miniatae*; Table 3). Rejected entities (sensu Ahti, 2000) are sections *Ascyphiferae, Helopodium, Tenues, Unciales*, and *Strepsiles*. Furthermore, we have established the Supergroup *Crustaceae* to incorporate species referred to sections *Cladina* and *Unciales*. *Crustaceae* includes four groups, viz. *Amaurocraeae*, *Divaricatae*, *Unciales*, and *Cladinae*. Finally, *Cladonia connexa* is excluded from *Cladonia*, but its renaming will be done elsewhere. *C. wainioi* appears distinct from other species and is here included in its own category, Subdivision I. Major changes in the taxonomic positions of species are listed in Table 4.

The names used are applied such that they maintain the highest correspondence possible with earlier taxa and diagnosis usage (Nixon and Carpenter, 2000). In formal use, the rank "Subdivision" would preferably refer to a Subgenus, "Supergroup" to a Section, "Group" to a Subsection, and "Subgroup" to a Series. The names *Amaurocraeae, Divaricatae, Borya*, and *Miniatae* have not been formally used, which must be noted if formal ranks are to be applied.

It is evident that matrices for phylogeny reconstruction keep growing exponentially, and the need for analyses to be made with the most powerful algorithms is obvious. Our analyses also illustrated the need for powerful computing capacity in order to take full advantage of these algorithms. Moreover, analyses with the "conventional" methods, i.e., with programs providing only simple branch-swapping algorithms, are clearly no longer a viable alternative for large matrices.

In our future study, we will concentrate on adding taxa and characters, with special emphasis on *Unciales* and *Cladina*. The best test for the current hypotheses is not the indices, but the next added character and taxon (Kluge, 1997). We have a number of nucleotides and some 300 more species to go.

APPENDIX 1: LIST OF TAXA AND SOURCE MATERIAL

Taxon name[a]	Current classification[b]	Collection	GenBank No.[c]	
			ITS	Bt
Cladia aggregata (Sw.) Nyl.		New Zealand, 1993 *Stenroos 4506* (H)	AF453268	—
Cladia ferdinandii (Müll. Arg.) Filson		Australia, Western Australia, 1990 *W.L. & C.F Culberson 21285* in Vězda Lich. Sel. Exs. 2495 (H)	AF453269	—
Pycnothelia papillaria Dufour		Canada, Nova Scotia, 1999 *Ahti 57167* (H)	AF453271	AF458484
Ramalea cochleata Müll. Arg.		New Caledonia, 1999 *Dennetière 53* (TUR)	AF453267	AF458483
Cladonia acuminata (Ach.) Norrl.	*Helopodium*	Finland, 1999 *Puolasmaa s.n.* (TUR)	AF455231	—
Cladonia ahtii S. Stenroos	*Cocciferae*	Brazil, Paraná, 1999 *Ahti & Eliasaro 57582* (H)	AF453275	AF458486
Cladonia albofuscescens Vain. [1]	*Cladonia*	Brazil, Minas Gerais, 1997 *Stenroos 4946* (TUR)	AF455241	AF458548
C. albofuscescens Vain. [2]	*Cladonia*	Brazil, Minas Gerais, 1997 *Stenroos 5019* (TUR)	AF455242	—
Cladonia amaurocraea (Flörke) Schaer. [1]	*Unciales*	Finland, 1999 *Stenroos 5159* (TUR)	AF455244	—
C. amaurocraea (Flörke) Schaer. [2]	*Unciales*	Finland, 1999 *Stenroos 5172* (TUR)	AF455245	AF458549
C. amaurocraea (Flörke) Schaer. [3]	*Unciales*	Bhutan, 1998 *Søchting 9147* (H)	AF455246	—
Cladonia anaemica (Nyl.) Ahti [1]	*Cocciferae*	Brazil, Minas Gerais, 1997 *Stenroos 4994a* (TUR)	AF453276	—
C. anaemica (Nyl.) Ahti [2]	*Cocciferae*	Brazil, Minas Gerais, 1997 *Stenroos 4959a* (TUR)	AF453277	AF458487

APPENDIX 1—*Continued*

Taxon name[a]	Current classification[b]	Collection	GenBank No.[c]	
			ITS	Bt
Cladonia andesita Vain.	*Cladonia*	Kenya, 1997 *Chuah-Petiot 947* (TUR)	AF453844	—
Cladonia apodocarpa Robbins	*Helopodium*	USA, North Carolina, 1998 *Ahti 60198* (H)	AF455237	AF458546
Cladonia arbuscula (Wallr.) Flot. [1]	*Cladina: Cladina*	Sweden, 1997 *Stenroos 5122* (TUR)	AF458292	AF458577
C. arbuscula (Wallr.) Flot. [2]	*Cladina: Cladina*	Canada, Nova Scotia, 1999 *Ahti 57095* (H)	AF458291	AF458576
C. arbuscula (Wallr.) Flot. [3]	*Cladina: Cladina*	Finland, 1999 *Stenroos 5203* (TUR)	AF458293	AF458578
C. arbuscula (Wallr.) Flot. [4]	*Cladina: Cladina*	Chile, Prov. Valdivia, 1999 *Feuerer 60333* (TUR)	AF458309	AF458585
Cladonia argentea (Ahti) Ahti & DePriest	*Cladina: Cladina*	Guyana, 1997 *Stenroos 4918* (TUR)	AF458305	—
Cladonia asahinae J. W. Thomson	*Cladonia*	Iceland, 1999 *Baldursdottir & Jonsdottir s.n* (H)	AF455229	—
Cladonia atlantica A. Evans [1]	*Perviae*	USA, Massachusetts, 1998 *Ahti 56853* (H)	AF457884	AF458561
C. atlantica A. Evans [2]	*Perviae*	Canada, Newfoundland, 1999 *Ahti 56944* (H)	AF457887	—
Cladonia bacilliformis (Nyl.) Glück	*Cocciferae*	Finland, 1999 *Stenroos 5158* (TUR)	AF454450	—
Cladonia bahiana Ahti [1]	*Perviae*	Brazil, Bahia, 1994 *Stocker s.n.* (H)	AF456402	—
C. bahiana Ahti [2]	*Perviae*	Brazil, Minas Gerais, 1995 *Splett 968* (H)	AF456403	—
Cladonia beaumontii (Tuck.) Vain.	*Perviae*	USA, Georgia, 1999 *Ahti 58268* (TUR)	AF457895	AF458566
Cladonia bellidiflora (Ach.) Schaer.	*Cocciferae*	Finland, 1999 *Stenroos 5152* (TUR)	AF453700	AF458497
Cladonia borbonica Nyl.	*Cladonia*	New Caledonia, 1998 *Dennetière 109* (H)	AF455214	—
Cladonia borealis S. Stenroos [1]	*Cocciferae*	Finland, 1999 *Stenroos 5157* (TUR)	AF454434	AF458504
C. borealis S. Stenroos [2]	*Cocciferae*	Iceland, 1997 *Ahti 54928* (H)	AF454435	—
Cladonia boryi Tuck. [1]	*Unciales*	Canada, Nova Scotia, 1999 *Ahti 57176* (H)	AF457906	—
C. boryi Tuck. [2]	*Unciales*	Canada, Newfoundland, 1999 *Ahti & Scott 56962* (H)	AF457907	—
Cladonia botrytes (K. G. Hagen) Willd. [1]	*Cocciferae*	Finland, 1999 *Stenroos 5165* (TUR)	AF455163	AF458515
C. botrytes (K. G. Hagen) Willd. [2]	*Cocciferae*	Finland, 1999 *Stenroos 5162* (TUR)	AF455164	AF458516
Cladonia caespiticia (Pers.) Flörke	*Helopodium*	Canada, Nova Scotia, 1999 *Ahti 57084* (H)	AF455205	AF458532
Cladonia calyciformis Nuno	*Cladonia*	Australia, 1999 *Wall s.n.* (TUR)	AF455176	AF458525
Cladonia capitellata (Hook. f. & Taylor) C. Bab.	*Perviae*	Australia, New South Wales, 1998 *Hammer 7057* (H)	AF456399	—
Cladonia cariosa (Ach.) Spreng.	*Helopodium*	Finland, 1999 *Puolasmaa s.n.* (TUR)	AF455230	—
Cladonia carneola (Fr.) Fr.	*Cocciferae*	Finland, 1995 *Stenroos 5583* (TUR)	AF454452	—
Cladonia caroliniana Tuck.	*Unciales*	USA, South Carolina, 1999 *Ahti 58186* (H)	AF456408	AF458557
Cladonia cartilaginea Müll. Arg.	*Helopodium*	Brazil, Minas Gerais, 1997 *Stenroos 4926* (TUR)	AF455212	AF458535
Cladonia cenotea (Ach.) Schaer. [1]	*Perviae*	Chile, Prov. Magallanes, 1999 *Feuerer 60174* (TUR)	AF457899	—
C. cenotea (Ach.) Schaer. [2]	*Perviae*	Canada, Newfoundland, 1999 *Ahti 56950* (H)	AF457900	—
C. cenotea (Ach.) Schaer. [3]	*Perviae*	Argentina, Tierra del Fuego, 1999 *Stenroos 5453* (TUR)	AF457898	AF458569
C. cenotea (Ach.) Schaer. [4]	*Perviae*	Finland, 1999 *Myllys 213* (TUR)	AF457896	AF458567
C. cenotea (Ach.) Schaer. [5]	*Perviae*	Finland, 1999 *Myllys 214* (TUR)	AF457897	AF458568
Cladonia ceratophylla (Sw.) Spreng.	*Helopodium*	Brazil, Minas Gerais, 1997 *Stenroos 5081* (TUR)	AF455171	—
Cladonia cervicornis (Ach.) Flot. ssp. *cervicornis*	*Cladonia*	Corsica, 1999 *Gueidan s.n.* (TUR)	AF455187	AF458542
Cladonia cervicornis ssp. *mawsonii* (C. W. Dodge) S. Stenroos & Ahti	*Cladonia*	Kérguelen, 1999 *Poulsen RSP-1044* (TUR)	AF455178	—
Cladonia cervicornis ssp. *verticillata* (Hoffm.) Ahti	*Cladonia*	Canada, Newfoundland, 1999 *Ahti 56951* (H)	AF453845	—
Cladonia ciliata Stirt. f. *ciliata*	*Cladina: Tenues*	Ireland, 2000 *Rikkinen s.n.* (TUR)	AF458310	—
Cladonia ciliata f. *tenuis* (Flörke) Ahti	*Cladina: Tenues*	Portugal, 1997 *Ahti & Burgaz 55883* (H)	AF458311	—
Cladonia clathrata Ahti & L. Xavier	*Cladonia*	Brazil, Minas Gerais, 1997 *Stenroos 5085a* (TUR)	AF455185	AF458541
Cladonia coccifera (L.) Willd. [1]	*Cocciferae*	Canada, Newfoundland, 1999 *Ahti 56952* (H)	AF454437	AF458505
C. coccifera (L.) Willd. [2]	*Cocciferae*	Finland, 1999 *Stenroos 5155* (TUR)	AF454436	—
C. coccifera (L.) Willd., coll.	*Cocciferae*	Bhutan, 1998 *Søchting 9225* (H)	AF454444	AF458509
Cladonia confusa R. Sant.	*Cladina: Impexae*	Brazil, Minas Gerais, 1997 *Stenroos 5091* (TUR)	AF458296	—
Cladonia connexa Vain.	*Ascyphiferae*	Brazil, Minas Gerais, 1997 *Stenroos 5024* (TUR)	AF453270	—
Cladonia consimilis Vain. [1]	*Unciales*	Brazil, Minas Gerais, 1997 *Stenroos 5048* (TUR)	AF456400	—

APPENDIX 1—*Continued*

Taxon name[a]	Current classification[b]	Collection	GenBank No.[c]	
			ITS	Bt
C. consimilis Vain. [2]	*Unciales*	Brazil, Minas Gerais, 1997 *Stenroos 5050* (TUR)	AF456405	—
Cladonia convoluta (Lam.) Anders	*Cladonia*	Sweden, 1997 *Stenroos 5119* (TUR)	AF455168	AF458520
Cladonia corallifera (Kunze) Nyl.	*Cocciferae*	Guyana, 1997 *Stenroos 7876* (TUR)	AF453706	AF458503
Cladonia corniculata Ahti & Kashiw.	*Cladonia*	China, Hunan, 1998 *Koponen et al. 55630* (H)	AF455201	—
Cladonia cornuta (L.) Hoffm. [1]	*Cladonia*	Chile, Prov. Magallanes, 1999 *Feuerer 60175a* (TUR)	AF455196	—
C. cornuta (L.) Hoffm. [2]	*Cladonia*	Estonia, 1999 *Jüriado s.n.* (TUR)	AF455197	—
Cladonia corymbescens Nyl. [1]	*Ascyphiferae*	Bhutan, 1998 *Søchting 9206* (H)	AF455239	AF458547
C. corymbescens Nyl. [2]	*Ascyphiferae*	New Caledonia, 1998 *Dennetière 0045* (TUR)	AF455235	—
Cladonia crinita (Delise ex Pers.) Ahti	*Cladonia*	Brazil, Minas Gerais, 1997 *Stenroos 4963* (TUR)	AF455186	—
Cladonia crispata (Ach.) Flot.	*Perviae*	Finland, 1999 *Stenroos 5214* (TUR)	AF457888	AF458563
C. crispata (Ach.) Flot., coll.	*Perviae*	Australia, New South Wales, 1998 *Hammer 7200* (H)	AF456397	—
Cladonia crispatula (Nyl.) Ahti	*Perviae*	Brazil, Minas Gerais, 1997 *Stenroos 5090* (TUR)	AF457891	—
Cladonia cristatella Tuck.	*Cocciferae*	Canada, Nova Scotia, 1999 *Ahti 57069* (H)	AF453693	AF458494
Cladonia cylindrica (A. Evans) A. Evans	*Cladonia*	USA, South Carolina, 1999 *Ahti 58196* (H)	AF455188	—
Cladonia deformis (L.) Hoffm.	*Cocciferae*	Finland, 1995 *Stenroos 5584* (TUR)	AF454448	—
Cladonia delavayi Abbayes	*Unciales*	Bhutan, 1998 *Søchting 8498* (H)	AF458304	AF458582
Cladonia dendroides (Abbayes) Ahti	*Cladina: Tenues*	Guyana, 1997 *Stenroos 4897* (TUR)	AF458295	—
Cladonia densissima (Ahti) Ahti & DePriest	*Cladina: Tenues*	Guyana, 1997 *Stenroos 4899* (TUR)	AF458294	—
Cladonia didyma (Fée) Vain.	*Cocciferae*	USA, North Carolina, 1998 *Ahti 56216* (H)	AF453703	AF458500
Cladonia digitata (L.) Hoffm.	*Cocciferae*	Finland, 1999 *Stenroos 5164* (TUR)	AF453701	AF458498
Cladonia dimorphoclada Robbins	*Unciales*	USA, South Carolina, 1999 *Ahti 58180* (TUR)	AF456407	AF458556
Cladonia divaricata Nyl.	*Unciales*	Brazil, Minas Gerais, 1997 *Stenroos 4999* (TUR)	AF457910	AF458572
Cladonia ecmocyna Leight.	*Cladonia*	Greenland, 1998 *Hansen*, Lich. Groenl. Exs. 747 (H)	AF455199	—
Cladonia elixii Ahti & V. Wirth	*Cocciferae*	New Zealand, 1995 *Wirth 28144* (H)	AF454453	—
Cladonia evansii Abbayes	*Cladina: Impexae*	USA, Georgia, 1999 *Ahti 58302* (H)	AF458303	—
Cladonia farinacea (Vain.) A. Evans [1]	*Ascyphiferae*	Chile, Prov. Magallanes, 1999 *Feuerer 60101* (TUR)	AF455215	AF458537
C. farinacea (Vain.) A. Evans [2]	*Ascyphiferae*	Canada, Nova Scotia, 1999 *Ahti 57238* (H)	AF455216	—
Cladonia fimbriata (L.) Fr.	*Cladonia*	Chile, Prov. Magallanes, 1999 *Feuerer 60132* (TUR)	AF455224	—
Cladonia fissidens Ahti & Marcelli	*Cladonia*	Brazil, Minas Gerais, 1997 *Stenroos 5045* (TUR)	AF455184	—
Cladonia fleigiae Ahti & S. Stenroos	*Unciales*	Brazil, Minas Gerais, 1997 *Stenroos 5052a* (TUR)	AF456401	AF458555
Cladonia floerkeana (Fr.) Flörke [1]	*Cocciferae*	Finland, 1995 *Stenroos 5582* (TUR)	AF453697	—
C. floerkeana (Fr.) Flörke [2]	*Cocciferae*	Taiwan, 1999 *Virtanen 17* (H)	AF453698	AF458495
Cladonia foliacea (Huds.) Willd.	*Cladonia*	Corsica, 1999 *Gueidan s.n.* (TUR)	AF455169	AF458521
Cladonia fruticulosa Kremp. [1]	*Cladonia*	Bhutan, 1998 *Søchting 8383* (H)	AF455189	AF458543
C. fruticulosa Kremp. [2]	*Cladonia*	New Caledonia, 1998 *Dennetière 170* (TUR)	AF455190	—
Cladonia furcata (Huds.) Schrad.	*Ascyphiferae*	USA, Georgia, 1999 *Ahti 58283* (TUR)	AF455220	AF458539
Cladonia furfuraceoides Ahti & Sipman	*Cladonia*	Guyana, 1997 *Stenroos 4794* (TUR)	AF455202	—
Cladonia gracilis ssp. *elongata* (Wulfen) Vain.	*Cladonia*	Chile, Prov. Valdivia, 1999 *Feuerer 60318* (TUR)	AF455198	—
Cladonia gracilis (L.) Willd. ssp. *gracilis*	*Cladonia*	Sweden, 1999 *Thell 9931* (TUR)	AF455194	—
Cladonia gracilis ssp. *turbinata* (Ach.) Ahti	*Cladonia*	Finland, 1999 *Stenroos 5171* (TUR)	AF455193	—
Cladonia grayi G. Merr. ex Sandst.	*Cladonia*	Finland, 1995 *Stenroos 5587* (TUR)	AF455226	—
C. grayi G. Merr. ex Sandst., coll.	*Cladonia*	Finland, 1999 *Stenroos 5169* (TUR)	AF455228	—
Cladonia hedbergii Ahti	*Perviae*	Kenya, 1997 *Chuah-Petiot 864* (TUR)	AF457882	—
C. hedbergii Ahti, coll.	*Perviae*	Zimbabwe, 1993 *Becker s.n.* (H)	AF457881	—
Cladonia hians Ahti	*Perviae*	Guyana, 1997 *Stenroos 4810* (TUR)	AF457893	—
Cladonia humilis (With.) J. R. Laundon	*Cladonia*	China, Hunan, 1998 *Koponen et al. 54045* (H)	AF455209	AF458534
Cladonia hypomelaena (Vain.) S. Stenroos	*Cocciferae*	Brazil, Minas Gerais, 1997 *Stenroos 5041* (TUR)	AF453278	AF458488

APPENDIX 1—*Continued*

			GenBank No.[c]	
Taxon name[a]	Current classification[b]	Collection	ITS	Bt
Cladonia incrassata Flörke [1]	*Cocciferae*	Canada, Nova Scotia, 1999 *Ahti 57126* (H)	AF453691	AF458493
C. incrassata Flörke [2]	*Cocciferae*	USA, Massachusetts, 1998 *Ahti 56841* (H)	AF453692	—
Cladonia kurokawae Ahti & S. Stenroos	*Cladonia*	China, Hunan, 1998 *Koponen et al. 55724* (H)	AF455207	AF458533
Cladonia laii S. Stenroos	*Cocciferae*	Bhutan, 1998 *Søchting 9080* (H)	AF454451	AF458514
Cladonia lepidophora Ahti & Kashiw. [1]	*Cocciferae*	Chile, Prov. Osorno, 1999 *Feuerer 60297* (TUR)	AF454440	AF458506
C. lepidophora Ahti & Kashiw. [2]	*Cocciferae*	Chile, Prov. Magallanes, 1999 *Feuerer 60175* (TUR)	AF454441	AF458507
C. lepidophora Ahti & Kashiw. [3]	*Cocciferae*	Chile, Prov. Valdivia, 1999 *Feuerer 60319* (TUR)	AF454439	—
C. lepidophora Ahti & Kashiw. [4]	*Cocciferae*	Chile, Prov. Valdivia, 1999 *Feuerer 60405* (TUR)	AF454438	—
Cladonia leporina Fr.	*Cocciferae*	USA, Georgia, 1999 *Ahti 58276* (H)	AF453687	AF458490
Cladonia lopezii S. Stenroos [1]	*Cocciferae*	Brazil, Minas Gerais, 1997 *Stenroos 5029* (TUR)	AF453279	—
C. lopezii S. Stenroos [2]	*Cocciferae*	Brazil, Minas Gerais, 1997 *Stenroos 5007* (TUR)	AF453280	—
C. lopezii S. Stenroos [3]	*Cocciferae*	Brazil, Minas Gerais, 1997 *Stenroos 5085b* (TUR)	AF453281	—
Cladonia luteoalba Wheldon & A. Wilson	*Cocciferae*	Iceland, 1997 *Ahti 54923* (H)	AF454447	AF458512
Cladonia macilenta Hoffm.	*Cocciferae*	Canada, Nova Scotia, 1999 *Ahti 57091* (H)	AF453696	—
C. macilenta Hoffm., coll.	*Cocciferae*	Chile, Prov. Magallanes, 1999 *Feuerer 60175b* (TUR)	AF453690	—
Cladonia macilentoides Ahti & Fleig [1]	*Cocciferae*	Brazil, Minas Gerais, 1997 *Stenroos 5095* (TUR)	AF453695	—
C. macilentoides Ahti & Fleig [2]	*Cocciferae*	Brazil, Minas Gerais, 1997 *Stenroos 4942* (TUR)	AF453694	—
Cladonia macroceras (Delise) Hav.	*Cladonia*	Iceland, 1997 *Ahti 54921* (H)	AF455200	—
Cladonia macrophylla (Schaer.) Stenh.	*Helopodium*	Finland, 1995 *Stenroos 5586* (TUR)	AF455243	—
Cladonia macrophyllodes Nyl.	*Cladonia*	Greenland, 1998 *Hansen*, Lich. Groenl. Exs. 683 (H)	AF455173	AF458523
Cladonia marionii S. Stenroos	*Helopodium*	Kérguelen, 1999 *Poulsen RSP-692* (TUR)	AF455232	—
Cladonia mauritiana Ahti & J.C. David	*Cladonia*	Seychelles, 1999 *Saaristo s.n.* (TUR)	AF453846	AF458530
Cladonia maxima (Asahina) Ahti	*Cladonia*	Canada, Nova Scotia, 1999 *Ahti 57109* (H)	AF455195	—
Cladonia merochlorophaea Asahina	*Cladonia*	Finland, 1999 *Stenroos 5168* (TUR)	AF455227	—
Cladonia metacorallifera Asahina	*Cocciferae*	Finland, 1999 *Stenroos 5156* (TUR)	AF453705	AF458502
Cladonia metaminiata S. Stenroos & Ahti	*Cocciferae*	Brazil, Minas Gerais, 1997 *Stenroos 5029a* (TUR)	AF453286	—
Cladonia minarum Ahti	*Unciales*	Brazil, Minas Gerais, 1997 *Stenroos 4961* (TUR)	AF457909	—
Cladonia miniata G. Meyer	*Cocciferae*	Brazil, Minas Gerais, 1997 *Stenroos 5035* (TUR)	AF453284	—
Cladonia mitis Sandst. [1]	*Cladina: Cladina*	Finland, 1999 *Stenroos 5209* (TUR)	AF457914	AF458574
C. mitis Sandst. [2]	*Cladina: Cladina*	Sweden, 1999 *Thell 9915* (TUR)	AF457915	AF458575
Cladonia multiformis G. Merr.	*Ascyphiferae*	USA, Nova Scotia, 1999 *Ahti 57065* (H)	AF455213	AF458536
Cladonia nana Vain.	*Helopodium*	Brazil, Minas Gerais, 1997 *Stenroos 4940* (TUR)	AF455211	—
Cladonia neozelandica Vain.	*Helopodium*	New Zealand, 1995 *Wirth 28180* (H)	AF455206	—
Cladonia nipponica Asahina	*Unciales*	USA, Alaska, 1997 *Neitlich & Hasselberg 2160d* (H)	AF456406	—
Cladonia ochrochlora Flörke	*Cladonia*	Sweden, 1997 *Stenroos 5118* (TUR)	AF455192	—
Cladonia parvipes (Vain.) S. Stenroos [1]	*Cocciferae*	Brazil, Minas Gerais, 1993 *Marcelli et al. 27931* (H)	AF453272	—
C. parvipes (Vain.) S. Stenroos [2]	*Cocciferae*	Brazil, Minas Gerais, 1997 *Stenroos 5047b* (TUR)	AF453273	—
Cladonia peltastica (Nyl.) Müll. Arg.	*Unciales*	Guyana, 1997 *Stenroos 4797b* (TUR)	AF457902	—
Cladonia perforata A. Evans	*Unciales*	USA, Florida, *Yahr 93/2* (US)	AF457903	AF458570
Cladonia pertricosa Kremp.	*Perviae*	Australia, New South Wales, 1998 *Hammer 7100* (H)	AF457885	—
Cladonia petrophila R. C. Harris	*Cladonia*	USA, North Carolina, 1998 *Ahti 56654* (H)	AF455222	AF458544
Cladonia peziziformis (With.) J. R. Laundon [1]	*Helopodium*	USA, North Carolina, 1998 *Ahti 56670* (H)	AF455182	—
C. peziziformis (With.) J. R. Laundon [2]	*Helopodium*	USA, District of Columbia, 1997 *Stenroos 5198* (TUR)	AF455221	AF458540
Cladonia phyllophora Hoffm.	*Cladonia*	Finland, 1999 *Stenroos 5161* (TUR)	AF455170	—
Cladonia piedadensis Ahti	*Cocciferae*	Brazil, Minas Gerais, 1997 *Stenroos 5000a* (TUR)	AF453285	AF458489
Cladonia pityrophylla Nyl.	*Helopodium*	Brazil, Minas Gerais, 1997 *Stenroos 5096* (TUR)	AF455238	—
Cladonia pleurota (Flörke) Schaer. [1]	*Cocciferae*	Canada, Nova Scotia, 1999 *Ahti 57075* (H)	AF454442	—
C. pleurota (Flörke) Schaer. [2]	*Cocciferae*	USA, Georgia, 1999 *Ahti 58282* (TUR)	AF454443	AF458508

APPENDIX 1—*Continued*

Taxon name[a]	Current classification[b]	Collection	GenBank No.[c]	
			ITS	Bt
C. pleurota (Flörke) Schaer. [3]	*Cocciferae*	Mexico, Veracruz, 1999 *Stenroos 5143* (TUR)	AF454445	AF458510
C. pleurota (Flörke) Schaer. [4]	*Cocciferae*	Australia, New South Wales, 1999 *Wall "AT705"* (TUR)	AF455165	AF458517
Cladonia polyscypha Ahti & L. Xavier	*Cladonia*	Guyana, 1997 *Stenroos 4789* (TUR)	AF453847	—
Cladonia polystomata Ahti & Sipman	*Perviae*	Guyana, 1997 *Stenroos 4799* (TUR)	AF457892	—
Cladonia portentosa (Dufour) Coem.	*Cladina: Impexae*	Germany, 1999 *Thell 9930* (TUR)	AF458302	AF458581
Cladonia prancei Ahti	*Cocciferae*	Peru, 1998 *Tuomisto & Gardenas 12927* (TUR)	AF453702	AF458499
Cladonia pycnoclada (Pers.) Nyl. [1]	*Cladina: Impexae*	Chile, Prov. Osorno, 1999 *Feuerer 60257* (TUR)	AF458297	AF458579
C. pycnoclada (Pers.) Nyl. [2]	*Cladina: Impexae*	Chile, Prov. Osorno, 1999 *Feuerer 60275* (TUR)	AF458298	—
C. pycnoclada (Pers.) Nyl. [3]	*Cladina: Impexae*	Chile, Prov. Osorno, 1999 *Feuerer 60296* (TUR)	AF458299	—
Cladonia pyxidata (L.) Hoffm.	*Cladonia*	Iceland, 1999 *Baldursdottir & Jonsdottir s.n.* (H)	AF455223	—
C. pyxidata (L.) Hoffm., coll.	*Cladonia*	Mexico, Veracruz, 1999 *Stenroos 5127* (TUR)	AF455208	—
Cladonia rangiferina (L.) F. H. Wigg. ssp. *rangiferina*	*Cladina: Cladina*	Finland, 1999 *Stenroos 5173* (TUR)	AF458306	AF458583
Cladonia rangiferina ssp. *abbayesii* (Ahti) Ahti & DePriest	*Cladina: Cladina*	Guyana, 1997 *Stenroos 4867* (TUR)	AF458307	—
Cladonia rangiformis Hoffm. [1]	*Ascyphiferae*	Sweden, 1997 *Stenroos 5125* (TUR)	AF455172	AF458522
C. rangiformis Hoffm. [2]	*Ascyphiferae*	Faeroe Islands, 1995 *Stenroos 4692* (H)	AF455234	—
Cladonia rappii A. Evans	*Cladonia*	Bhutan, 1998 *Søchting 8205* (H)	AF453843	AF458529
C. rappii A. Evans, coll.	*Cladonia*	Australia, New South Wales, 1999 *Wall s.n.* (TUR)	AF455177	AF458526
Cladonia ravenelii Tuck.	*Cocciferae*	USA, Georgia, 1999 *Ahti 57289* (H)	AF453688	AF458491
Cladonia rei Schaer.	*Cladonia*	Canada, Nova Scotia, 1999 *Ahti 57074* (H)	AF455191	—
Cladonia rigida (Hook. f. & Taylor) Hampe	*Perviae*	Australia, New South Wales, 1998 *Hammer 7021* (H)	AF455166	AF458518
Cladonia robbinsii A. Evans	*Strepsiles*	USA, North Carolina, 1998 *Ahti 56696* (H)	AF455167	AF458519
Cladonia rotundata Ahti	*Cladonia*	Guyana, 1997 *Stenroos 4854* (TUR)	AF457913	—
Cladonia rugulosa Ahti	*Perviae*	Guyana, 1997 *Stenroos 4831* (TUR)	AF457894	AF458565
Cladonica salmonea S. Stenroos [1]	*Cocciferae*	Brazil, Minas Gerais, 1997 *Stenroos 4950* (TUR)	AF453282	—
C. salmonea S. Stenroos [2]	*Cocciferae*	Brazil, Minas Gerais, 1997 *Stenroos 5083a* (TUR)	AF453283	—
Cladonia scabriuscula (Delise) Nyl. [1]	*Ascyphiferae*	Canada, Newfoundland, 1999 *Ahti 56969* (H)	AF455217	—
C. scabriuscula (Delise) Nyl. [2]	*Ascyphiferae*	China, Hunan, 1998 *Koponen et al. 54509* (H)	AF455218	—
C. scabriuscula (Delise) Nyl. [3]	*Ascyphiferae*	Chile, Prov. Magallanes, 1999 *Feuerer 60212* (TUR)	AF455219	AF458538
Cladonia secundana Nyl.	*Cocciferae*	Guyana, 1997 *Stenroos 4812b* (TUR)	AF453274	AF458485
Cladonia signata (Eschw.) Vain. [1]	*Ascyphiferae*	Brazil, Minas Gerais, 1997 *Stenroos 4955* (TUR)	AF455233	—
C. signata (Eschw.) Vain. [2]	*Ascyphiferae*	Guyana, 1997 *Stenroos 4876* (TUR)	AF457901	—
Cladonia sinensis S. Stenroos & J. B. Chen	*Cocciferae*	Bhutan, 1998 *Søchting 8402* (H)	AF454446	AF458511
Cladonia solitaria H. Magn.	*Unciales*	USA, Hawaii, 1996 *Palmer et al. 2677* (US)	AF457905	—
Cladonia squamosa Hoffm.	*Perviae*	Sweden, 1997 *Stenroos 5120* (TUR)	AF457886	AF458562
Cladonia staufferi Abbayes	*Cladonia*	Australia, New South Wales, 1998 *Hammer 7051* (H)	AF455179	AF458527
Cladonia stellaris (Opiz) Pouzar & Vězda	*Cladina: Impexae*	Finland, 1997 *Stenroos 5102* (TUR)	AF458301	—
Cladonia stenroosiae Ahti	*Unciales*	Brazil, Minas Gerais, 1997 *Stenroos 5013* (TUR)	AF456409	—
Cladonia steyermarkii Ahti	*Unciales*	Guyana, 1997 *Stenroos 4916* (TUR)	AF456404	—
Cladonia strepsilis (Ach.) Grognot [1]	*Strepsiles*	Canada, Nova Scotia, 1999 *Ahti 57244* (H)	AF457879	—
C. strepsilis (Ach.) Grognot [2]	*Strepsiles*	Finland, 1999 *Stenroos 5160* (TUR)	AF457880	AF458559
Cladonia stygia (Fr.) Ruoss	*Cladina: Cladina*	Finland, 1999 *Stenroos 5200* (TUR)	AF458308	AF458584
Cladonia subchordalis A. Evans [1]	*Unciales*	Chile, Prov. Osorno, 1999 *Feuerer 60406* (TUR)	AF455174	—
C. subchordalis A. Evans [2]	*Unciales*	Chile, Prov. Magallanes, 1999 *Feuerer 60166* (TUR)	AF455175	AF458524
Cladonia subconistea Asahina	*Cladonia*	China, Hunan, 1998 *Koponen et al. 55878* (H)	AF455210	—
Cladonia subfurcata (Nyl.) Arnold	*Perviae*	Finland, 1999 *Stenroos 5166* (TUR)	AF457890	AF458564
Cladonia subreticulata Ahti	*Unciales*	Brazil, Minas Gerais, 1997 *Stenroos 5078* (TUR)	AF457904	AF458571
Cladonia subsquamosa Kremp.	*Cladonia*	Guyana, 1997 *Stenroos 4802* (TUR)	AF455225	—
Cladonia substellata Vain. [1]	*Unciales*	Brazil, Minas Gerais, 1997 *Stenroos 5017* (TUR)	AF457876	—

APPENDIX 1—*Continued*

Taxon name[a]	Current classification[b]	Collection	GenBank No.[c]	
			ITS	Bt
C. substellata Vain. [2]	*Unciales*	Brazil, Minas Gerais, 1997 *Stenroos 4964* (TUR)	AF457877	AF458558
Cladonia subsubulata Nyl. [1]	*Perviae*	Argentina, Tierra del Fuego, 1999 *Stenroos 5472* (TUR)	AF457883	AF458560
C. subsubulata Nyl. [2]	*Perviae*	Falkland Islands, 1999 *Lewis-Smith 3* (AAS)	AF456398	AF458554
C. subsubulata Nyl. [3]	*Perviae*	Falkland Islands, 1999 *Lewis-Smith 8* (AAS)	AF457889	—
Cladonia subtenuis (Abbayes) Mattick [1]	*Cladina: Tenues*	Canada, Nova Scotia, 1999 *Ahti 57068* (H)	AF457911	AF458573
C. subtenuis (Abbayes) Mattick [2]	*Cladina: Tenues*	USA, Georgia, 1999 *Ahti 58277* (TUR)	AF457912	—
Cladonia subulata (L.) F. H. Wigg. [1]	*Cladonia*	Finland, 1997 *Stenroos 5106* (TUR)	AF455180	—
Cladonia subulata (L.) F. H. Wigg. [2]	*Cladonia*	Germany, 1999 *Thell 9932* (TUR)	AF455181	AF458528
Cladonia sulcata A. W. Archer	*Helopodium*	Australia, New South Wales, 1998 *Hammer 7101* (H)	AF455183	—
Cladonia sulphurina (Michx.) Fr.	*Cocciferae*	Greenland, 1998 *Hansen,* Lich. Groenl. Exs. 742 (H)	AF454449	AF458513
Cladonia symphycarpia (Flörke) Fr.	*Helopodium*	Canada, British Columbia, 1994 *Ahti 52303* (H)	AF455236	AF458545
Cladonia terrae-novae Ahti	*Cladina: Impexae*	Canada, Newfoundland, 1999 *Ahti & Scott 56942* (H)	AF458300	AF458580
Cladonia turgida Hoffm.	*Ascyphiferae*	Finland, 1999 *Jääskeläinen s.n.* (TUR)	AF455203	—
Cladonia uncialis (L.) F. H. Wigg. ssp. *uncialis* [1]	*Unciales*	Finland, 1999 *Stenroos 5163* (TUR)	AF455247	—
C. uncialis (L.) F. H. Wigg. ssp. *uncialis* [2]	*Unciales*	Canada, Nova Scotia, 1999 *Ahti 57167* (H)	AF455248	—
C. uncialis (L.) F. H. Wigg. ssp. *uncialis* [3]	*Unciales*	Canada, Nova Scotia, 1999 *Ahti 57066* (H)	AF455249	—
C. uncialis (L.) F. H. Wigg. ssp. *uncialis* [4]	*Unciales*	Sweden, 1997 *Stenroos 5116* (TUR)	AF455250	—
C. uncialis (L.) F. H. Wigg. ssp. *uncialis* [5]	*Unciales*	Finland, 1997 *Stenroos 5112* (TUR)	AF455251	—
C. uncialis (L.) F. H. Wigg. ssp. *uncialis* [6]	*Unciales*	Finland, 1999 *Stenroos 5170* (TUR)	AF456390	—
C. uncialis (L.) F. H. Wigg. ssp. *uncialis* [7]	*Unciales*	Finland, 1999 *Stenroos 5207* (TUR)	AF456391	AF458550
C. uncialis (L.) F. H. Wigg. ssp. *uncialis* [8]	*Unciales*	Canada, Newfoundland, 1999 *Ahti & Scott 56946* (H)	AF456392	AF458551
Cladonia uncialis ssp. *biuncialis* (Hoffm.) M. Choisy [1]	*Unciales*	Finland, 1997 *Stenroos 5099* (TUR)	AF456393	—
C. uncialis ssp. *biuncialis* (Hoffm.) M. Choisy [2]	*Unciales*	Finland, 1999 *Stenroos 5213* (TUR)	AF456394	AF458552
C. uncialis ssp. *biuncialis* (Hoffm.) M. Choisy [3]	*Unciales*	Finland, 1999 *Stenroos 5208* (TUR)	AF456395	AF458553
C. uncialis ssp. *biuncialis* (Hoffm.) M. Choisy [4]	*Unciales*	Iceland, 1997 *Ahti 54888* (H)	AF456396	—
Cladonia ustulata (Hook. f. & Taylor) Leight.	*Cocciferae*	Argentina, Tierra del Fuego, 1999 *Stenroos 5411* (TUR)	AF453699	AF458496
Cladonia vareschii Ahti	*Unciales*	Guyana, 1997 *Stenroos 4881* (TUR)	AF457878	—
Cladonia variegata Ahti	*Perviae*	Guyana, 1997 *Stenroos 4922* (TUR)	AF455240	—
Cladonia wainioi Savicz	*Ascyphiferae*	Canada, Newfoundland, 1999 *Ahti & Scott 56960* (H)	AF455204	AF458531
Cladonia weymouthii F. Wilson ex A. W. Archer	*Cocciferae*	New Caledonia, 1998 *Dennetière 10* (H)	AF453689	AF458492
Cladonia yunnana (Vain.) Abbayes ex J.C. Wei & Y.M. Jiang	*Cocciferae*	Bhutan, 1998 *Søchting 9080b* (H)	AF453704	AF458501
Cladonia zopfii Vain.	*Unciales*	Netherlands, 1997 *Aptroot 40545* (H)	AF457908	—

[a] Specimen number in brackets.
[b] Sectional classification sensu Ahti (2000).
[c] A dash indicates that no sequence is available.

APPENDIX 2

Data Matrix Containing Morphological and Chemical Characters[a]

Cladia aggregata	1000-----------------1011--00-0101111----11----11--11
Cladia ferdinandii	1000-----------------1011--00-0011111----11----11--01
Pycnothelia papillaria	01--1-1--------11---000111P00-0011111----11----11--11
Ramalea cochleata	0011-----------------1011--0--1-----1----01----11--01
Cladonia acuminata	01--001--------11---100010P00-0011110110111----11--11
Cladonia ahtii	01--011--------11---0-001101100101111----11----100111
Cladonia albofuscescens 1	01--0001---001011---011111110-1----10011111----11--11
C. albofuscescens 2	01--0001---001011---011111110-1----10011111----11--11
Cladonia amaurocraea 1	01--0001---01111010-000111100-0101111----11----11--01
C. amaurocraea 2	01--0001---01111010-000111100-0101111----11----11--01
C. amaurocraea 3	01--0001---01111010-000111100-0101111----11----11--01
Cladonia anaemica 1	01--011--------11---0-010101100101111----11----11--11
C. anaemica 2	01--011--------11---0-010101100101111----11----11--11
Cladonia andesita	01--0001---1---10011000110100-0011110011111----11--11
Cladonia apodocarpa	01--001--------11-----011-000-0011111----11----11--11
Cladonia arbuscula 1	01--1-00110---011---001111100-1----10011111----11--01
C. arbuscula 2	01--1-00110---011---001111100-1----10011111----11--01
C. arbuscula 3	01--1-00110---011---001111100-1----10011111----11--01
C. arbuscula 4	01--1-00010---111---0011111-0-1----10011111----11--01
Cladonia argentea	01--1-00010---111---001111110-0011110011111----11--11
Cladonia asahinae	01--001--------1000-000010100-1----10011111----11--11
Cladonia atlantica 1	01--0001---011001---000100110-0100011----11----11--11
C. atlantica 2	01--0001---011001---000100110-0100011----11----11--11
C. bacilliformis	01--001--------1010-00001010110101111----11----11--01
Cladonia bahiana 1	01--0001---011P11---011111110-1----01----11----11--11
C. bahiana 2	01--0001---011P11---011111110-1----01----11----11--11
Cladonia beaumontii	01--0001---011001---0001001-0-0100011----11----11--11
Cladonia bellidiflora	01--001--------1010-00010011100111011----11----11--01
Cladonia borbonica	01--001--------1000-000010P00-1----10011111----11--11
Cladonia borealis 1	01--001--------1000-00010011100101111----11----11--01
C. borealis 2	01--001--------1000-00010011100101111----11----11--01
Cladonia boryi 1	-1----01---011PP010-111111100-1----11----11----11--01
C. boryi 2	-1----01---011PP010-111111100-1----11----11----11--01
Cladonia botrytes 1	01--001--------11---00011-00110101111----11----11--01
C. botrytes 2	01--001--------11---00011-00110101111----11----11--01
Cladonia caespiticia	01--001--------11---00011-000-1----10011111----11--11
Cladonia calyciformis	01--0001---1---10011000110100-1----10011110101111--11
Cladonia capitellata	01--0001---001011---00011-110-0111011----11----11--01
Cladonia cariosa	01--001--------11---100110000-0011110011111----11--11
Cladonia carneola	01--001--------1000-00001010111---–11----11----11--00
Cladonia caroliniana	-1----01---011111---110111100-0111011----11----11--01
Cladonia cartilaginea	01--001--------11---00010-P00-1----10011011----11--11
Cladonia cenotea 1	01--0001---011001---000010100-0111011----11----11--11
C. cenotea 2	01--0001---011001---000010100-0111011----11----11--11

APPENDIX 2—*Continued*

C. cenotea 3	01--0001---011001---000010100-0111011----11----11--11
C. cenotea 4	01--0001---011001---000010100-0111011----11----11--11
C. cenotea 5	01--0001---011001---000010100-0111011----11----11--11
Cladonia ceratophylla	01--001--------101--000100000-0011110011111----11--11
Cladonia cervicornis ssp. *cervicornis*	01--0001---1---10011000110100-1----10011111----11--11
Cladonia cervicornis ssp. *mawsonii*	01--0001---1---10111000110100-1----10011111----11--11
Cladonia cervicornis ssp. *verticillata*	01--0001---1---10011000110100-1----10011111----11--11
Cladonia ciliata f. *ciliata*	01--1-00010---111---001111110-1----10011111----11--11
Cladonia ciliata f. *tenuis*	01--1-00010---111---001111110-1----10011111----11--01
Cladonia clathrata	01--0001---1---1001-000110100-1----10011111----11--11
Cladonia coccifera 1	01--001--------1000-00010011101----11----11----11--00
C. coccifera 2	01--001--------1000-00010011101----11----11----11--00
Cladonia coccifera coll.	01--001--------1000-00010011101----11----11----11--00
Cladonia confusa	01--1-00101---011---001111100-1----11----01----11--01
Cladonia connexa	-1----01---000011---001111100-0011111----11----11--11
Cladonia consimilis 1	-1----01---001111---001110110-1----01----11----11--11
C. consimilis 2	-1----01---001111---001110110-1----01----11----11--11
Cladonia convoluta	01--001--------1010-00011--00-1----10011111----11--01
Cladonia corallifera	01--001--------1000-00000011101----01----11----100101
Cladonia corniculata	01--001--------11---000010100-1----10011110101111--11
Cladonia cornuta 1	01--001--------101--000010100-1----10011111----11--11
C. cornuta 2	01--001--------101--000010100-1----10011111----11--11
Cladonia corymbescens 1	01--0001---001P11---000110000-0011110011111----11--11
C. corymbescens 2	01--0001---001P11---000110000-0011110011111----11--11
Cladonia crinita	01--0001---1---10010000110100-1----10011111----11--11
Cladonia crispata	01--0001---011001---000110110-0111011----11----11--11
Cladonia crispata coll.	01--0001---011011---0001101-0-0101101----11----11--11
Cladonia crispatula	01-0001---011P11---000110110-1----01-----11----11--11
Cladonia cristatella	01--001--------11---00011001100101111----11----11--01
Cladonia cylindrica	01--001--------1010-000010100-1----10011111----01--11
Cladonia deformis	01--001--------1000-00001011101----11----11----11--00
Cladonia delavayi	01--1-00010---111---001111100-1----11----10011111--01
Cladonia dendroides	01--1-00000---111---001111110-0011110011111----11--11
Cladonia densissima	01--1-00010---111---001111110-1----10011111----11--01
Cladonia didyma	01--001--------11---000100P1100101101----11----100111
Cladonia digitata	01--001--------1010-00001011101----01----11----11--11
Cladonia dimorphoclada	-1----01---011111---110111100-1----10101111----11--01
Cladonia divaricata	-1----01---011011---011111110-1----10011111----11--01
Cladonia ecmocyna	01--001--------1010-000110100-0011110011111----11--11
Cladonia elixii	01--001--------11---00011-00110101111----11----11--01
Cladonia evansii	01--1-00001---111---001111100-0011111----01----11--11
Cladonia farinacea 1	01--0001---001P11---000010100-1----10011111----11--11
C. farinacea 2	01--0001---001P11---000010100-0011110011111----11--11
Cladonia fimbriata	01--001--------1000-000010100-1----10011111----11--11
Cladonia fissidens	01--0001---1---10110000110100-1----10011111----11--11
Cladonia fleigiae	01--0001---011011---00011-1-0-1----01----11----11--11

APPENDIX 2—*Continued*

Cladonia floerkeana 1	01--001--------11---0001-001100101111----11----11--11
C. floerkeana 2	01--001--------11---0001-001100101111----11----11--11
Cladonia foliacea	01--001--------1010-00011--00-1----10011111----11--01
Cladonia fruticulosa 1	01--001--------1010-000010100-1----10101111----11--11
C. fruticulosa 2	01--001--------1010-000010100-1----10101111----11--11
Cladonia furcata	01--0001---001P11---000110100-1----10011111----11--11
Cladonia furfuraceoides	01--001--------1010-000100100-1----10011111----11--11
Cladonia gracilis ssp. *elongata*	01--001--------1010-000110100-0011110011111----11--11
Cladonia gracilis ssp. *gracilis*	01--001--------1010-000110100-1–---10011111----11--11
Cladonia gracilis ssp. *turbinata*	01--001--------1000-000110100-1----10011111----11--11
Cladonia grayi	01--001--------1000-000010100-1----10011111----01--11
Cladonia grayi coll.	01--001--------1000-000010100-1----11----11----01--11
Cladonia hedbergii	01--0001---011011---000110110-0101111----11----11--11
Cladonia hedbergii coll.	01--0001---011011---00011-1-0-1----01--–-11----11--11
Cladonia hians	01--0001---011001---000110100-1----01----11----11--11
Cladonia humilis	01--001--------1000-000010100-1----10011111----11--11
Cladonia hypomelaena	01--011--------11---0-011101101–---11----1-----100111
Cladonia incrassata 1	01--001--------11---00001001100111011----11–---11--01
C. incrassata 2	01--001--------11---00001001100111011----11–---11--01
Cladonia kurokawae	01--001--------1000-000100100-0011110011111----11--11
Cladonia laii	01--00---------1000-00001010110101111----11----11--01
Cladonia lepidophora 1	01--001--------1000-00010011100111011----11-–--11--01
C. lepidophora 2	01--001--------1000-00010011100111011----11-–--11--01
C. lepidophora 3	01--001--------1000-00010011100111011----11-–--11--01
C. lepidophora 4	01--001--------1000-00010011100111011----11-–--11--01
Cladonia leporina	01--00---------11---01011111100100011----11----11--01
Cladonia lopezii 1	01--011--------11---0-011101101----11----11----100111
C. lopezii 2	01--011--------11---0-011101101----11----11----100111
C. lopezii 3	01--011--------11---0-011101101----11----11----100111
Cladonia luteoalba	01--001--------11---00-010---------1----11----1---0-
Cladonia macilenta	01--001--------11---00001011100101111----11----11--11
Cladonia macilenta coll.	01--001--------11---00001011101----01-–--11----11--11
Cladonia macilentoides 1	01--001--------11---00001011101----01---–11----11--11
C. macilentoides 2	01--001--------11---00001011101----01----11----11--11
Cladonia macroceras	01--001--------1010-000110100-1----10011111----11--11
Cladonia macrophylla	01--001--------11---100110000-1–---10101111----11--11
Cladonia macrophyllodes	01--001--------10011000110100-0011110011111----11--11
Cladonia marionii	01--001--------1----000110100-1-–--10011011----11--11
Cladonia mauritiana	01--001--------1010-000110100-1----10011111----11--11
Cladonia maxima	01--001--------1010-000110100-1----10011111----11--11
Cladonia merochlorophaea	01--001--------1000-000100100-1----11----10110111--11
Cladonia metacorallifera	01--001--------1000-00010011100101011----11----11--01
Cladonia metaminiata	01--001--------11---01011-010-0101101----11----100111
Cladonia minarum	01--0001---001011---001111110-1----10011111----11--01
Cladonia miniata	01--011--------11---0-011101100101111----11----11--11
Cladonia mitis 1	01--1-00110---011---001111100-1----11----11----11--01

APPENDIX 2—*Continued*

C. mitis 2	01--1-00110---011---001111100-1----11----11----11--01
Cladonia multiformis	01--0001---011P1010-000110100-1----10011111----11--11
Cladonia nana	01--001--------11---100110000-1----10011111----11--11
Cladonia neozelandica	01--001--------11---000100-00-0011110110011----11--11
Cladonia nipponica	-1----01---011P1010-111111110-1----10101111----11--01
Cladonia ochrochlora	01--001--------1010-000010100-1----10011111----11--11
Cladonia parvipes 1	01--011--------11---0-011101100101111----11----11--11
C. parvipes 2	01--011--------11---0-011101100101111----11----11--11
Cladonia peltastica	01--0001---001P11-0-000110110-0111011----11----11--01
Cladonia perforata	-1----01---001P11---0101111-0-0111011----11----11--01
Cladonia pertricosa	01--0001---011P11---000110100-0101101----11----11--11
Cladonia petrophila	01--001--------11---10011-000-0011111----01----11--11
Cladonia peziziformis 1	01--001--------11---100110000-1----10011111----11--11
C. pezizformis 2	01--001--------11---100110000-1----10011111----11--11
Cladonia phyllophora	01--001--------1010-000110100-1----10011111----11--11
Cladonia piedadensis	01--001--------11---00011110--1----11----11----100111
Cladonia pityrophylla	01--001--------1010-000100000-1----10011111----11--11
Cladonia pleurota 1	01--001--------1000-00001011101----11----11----11--00
C. pleurota 2	01--001--------1000-00001011101----11----11----11--00
C. pleurota 3	01--001---------1000-000-011101----11----11----11--00
C. pleurota 4	01--001--------1000-00001011101----11----11----11--00
Cladonia polyscypha	01--001--------1000-000010100-1----10011111----11--11
Cladonia polystomata	01--0001---011001---000110100-1----01----11----11--11
Cladonia portentosa	01--1-00110---011---001111100-1----11----01----11--01
Cladonia prancei	01--001--------1010-00001011101----01----11----11--11
Cladonia pycnoclada 1	01--1-00000---111---001111100-1----10011101----11--01
C. pycnoclada 2	01--1-00000---111---001111100-1----10011101----11--01
C. pycnoclada 3	01--1-00000---111---001111100-1----10011101----11--01
Cladonia pyxidata	01--001--------1000-000100100-1----10011111----11--11
Cladonia pyxidata coll.	01--001--------1000-000100100-1----10011110101111--11
Cladonia rangiferina ssp. *rangiferina*	01--1-00110---011---001111100-0011110011111----11--11
Cladonia rangiferina ssp. *abbayesii*	01--1-00010---111---001111100-0011110011111----11--11
Cladonia rangiformis 1	01--0001---001P11---000110100-0011111----11----11--11
C. rangiformis 2	01--0001---001P11---000110100-0011111----11----11--11
Cladonia rappii	01--0001---1---10011000110100-1----10011111----11--11
Cladonia rapii coll.	01--00---------101--000110100-1----10011111----11--11
Cladonia ravenelii	01--001--------1010-00001001101----01----11----100111
Cladonia rei	01--001--------1010-000010100-1----10011111101111--11
Cladonia rigida	01--001--------11---000100-00-0101101----11----11--11
Cladonia robbinsii	01--001--------11---00011--00-0101111----11----11--01
Cladonia rotundata	01--1-00001---111---001111100-0011110011111----11--01
Cladonia rugulosa	01--0001---001111-0-000110100-0101101----11----11--11
Cladonia salmonea 1	01--011--------11---0-011101101----11----11----11--01
C. salmonea 2	01--011--------11---0-011101101----11----11----11--01
Clandonia scabriuscula 1	01--0001---001P11---000100100-1----10011111----11--11
C. scabriuscula 2	01--0001---001P11---000100100-1----10011111----11--11

APPENDIX 2—*Continued*

C. scabriuscula 3	01--0001---001P11---000100100-1----10011111----11--11
Cladonia secundana	01--011--------11---0-011101101----11----11----100111
Cladonia signata 1	01--000----000111---001111100-1----10011111----11--11
C. signata 2	01--000----000111---001111100-1----10011110101111--11
Cladonia sinensis	01--001--------1000-00010011101----11----11----11--00
Cladonia solitaria	-1----01---001111---0001111-0-1----11----11----11--01
Cladonia squamosa	01--0001---0110P1---000100110-0111011----11----11--11
Cladonia staufferi	01--0001---P---100P-000110100-1----10101111----11--11
Cladonia stellaris	01--1-00101---011---001111110-1----11----01----11--01
Cladonia stenroosiae	-1----01---001111---0--1111-0-1----10110011----11--01
Cladonia steyermarkii	-1----01---001P11---000111110-1----01----11----11--01
Cladonia strepsilis 1	01--001--------11---0-0110000-0110011----11----101011
C. strepsilis 2	01--001--------11---0-0110000-0110011----11----101011
Cladonia stygia	01--1-00110---011---001111110-0011110011111----11--11
Cladonia subchordalis 1	01--001-------11010-000110100-1----11----11----11--01
C. subchordalis 2	01--001-------11010-000110100-1----11----11----11--01
Cladonia subconistea	01--001--------1000-000010100-0011110101111----11--11
Cladonia subfucata	01--0001---011011---000110110-0101011----11----11--11
Cladonia subreticulata	-1----01---0110P010-111111100-1----10110011----11--01
Cladonia subsquamosa	01--001--------1000-000010100-1----10011111----11--11
Cladonia substellata 1	01--0001---001P11---0-1111100-1----10110011----11--01
C. substellata 2	01--0001---001P11---0-1111100-1----10110011----11--01
Cladonia subsubulata 1	01--0001---0110P1---000110110-1----01----11----11--11
C. subsubulata 2	01--0001---0010P1---000110110-1----01----11----11--11
C. subsubulata 3	01--0001---0110P1---000110110-1----01----11----11--11
Cladonia subtenuis 1	01--1-00010---111---001111110-1----10011111----11--01
C. subtenuis 2	01--1-00010---111---001111110-1----10011111----11--01
Cladonia subulata 1	01--001-------11010-000010100-1----10011111----11--11
C. subulata 2	01--001-------11010-000010100-1----10011111----11--11
Cladonia sulcata	01--001--------11---100110000-0011110110011----11--11
Cladonia sulphurina	01--001--------1010-00001011100111011----11----11--01
Cladonia symphycarpia	01--001--------11---100110000-0011111----11----11--11
Cladonia terrae-novae	01--1-00110---011---001111100-1----11----01----11--01
Cladonia turgida	01--00--------01010-000110P00-0011110011111----11--11
Cladonia uncialis ssp. *uncialis* 1	-1----01---011011---000111110-1----11----11----11--01
C. uncialis ssp. *uncialis* 2	-1----01---011011---000111110-0111011----11----11--01
C. uncialis ssp. *uncialis* 3	-1----01---011011---000111110-0111011----11----11--01
C. uncialis ssp. *uncialis* 4	-1----01---011011---000111110-0111011----11----11--01
C. uncialis ssp. *uncialis* 5	-1----01---011011---000111110-0111011----11----11--01
C. uncialis ssp. *uncialis* 6	-1----01---011011---000111110-0111011----11----11--01
C. uncialis ssp. *uncialis* 7	-1----01---011011---000111110-0111011----11----11--01
C. uncialis ssp. *uncialis* 8	-1----01---011011---000111110-1----11----11----11--01
Cladonia uncialis ssp. *biuncialis* 1	-1----01---001P11---000111110-0111011----11----11--01
C. uncialis ssp. *biuncialis* 2	-1----01---001P11---000111110-0111011----11----11--01
C. uncialis ssp. *biuncialis* 3	-1----01---001P11---000111110-0111011----11----11--01
C. uncialis ssp. *biuncialis* 4	-1----01---001P11---000111110-1----11----11----11--01

APPENDIX 2—*Continued*

Cladonia ustulata	01--001--------1010-00001011101----01----11----11--11
Cladonia vareschii	-1----01---011011---000110110-1----01----11----11--01
Cladonia variegata	01--0001---000P11---001111110-1----01----11----11--11
Cladonia wainioi	01--0001---011011---000111100-0011111----10110111--11
Cladonia weymouthii	01--001--------11---00001011100101101----11----11--11
Cladonia yunnana	01--001--------1000-00001011100111011----11----11--01
Cladonia zopfii	-1----01---001111---P--111100-1----11----11----11--01

[a] Polymorphism 0,1 marked with P.

APPENDIX 3

List of Morphological and Chemical Characters and Character States

0. Thallus dimorphic (0), not dimorphic (1). A *Cladonia* (and *Pycnothelia* and *Ramalea*) thallus is characterized by two distinct parts, a granulose or squamulose primary (horizontal) thallus and an erect secondary (vertical) thallus. In many species, the primary thallus persists throughout the life of the lichen, but even in cases where the primary thallus is evanescent, it exists at the early stages of development. In *Cladia*, although a granulose juvenile stage occurs in early development, its further development is different from that of dimorphic species (Filson, 1981).

1. Pseudopodetia (0), podetia (1). Both structures are erect and vary in their branching but are distinctly different in their ontogeny. Pseudopodetia in *Ramalea* and *Cladia* represent the vegetative thallus that bears apothecia (hymenial discs) while not being involved in their formation, whereas podetia in *Cladonia* and *Pycnothelia* include generative tissue and therefore belong to the apothecium itself (Jahns, 1970; Jahns and Beltman, 1973; Ahti, 1982).

2. Pseudopodetia dichotomously branched (0), irregular (1). *Cladia* species are repeatedly branched by regular dichotomy, whereas *Ramalea* species are simple or only slightly and irregularly divided in the upper parts.

3. Pseudopodetia solid (0), hollow (1).

4. In podetiate species, squamulose to foliose primary thallus present (0), absent (1). In some species, the primary thallus disappears in the early stages of development, but is, nevertheless, coded as present. It has not been possible to distinguish between genetically controlled primary thallus age and the influence of substrates such as bryophytes, which gradually overgrow the primary thallus and lower parts of the secondary thallus.

5. Podetia laminal on primary squamules (0), phyllopodial (1). In a regular laminal podetium, the growth starts from the upper surface of primary squamules, and three layers (cortical, medullary, and stereomal) are formed. In the phyllopodial type, the primary squamule lobes curve and become elongated to form a cylinder, but retain the original layers of the primary squamule (cortical, algal, medullary); a stereomal layer is not formed (see also Stenroos, 1989c).

6. Podetia repeatedly branched (0), unbranched or with occasional branches (1). The configurations of podetia are extremely variable. They range from simple to densely branched. However, these forms and their branching patterns are often difficult to interpret because of the variability due to age of the thallus and habitat factors. In our concept *Cladina* sensu Ahti show regular branching correlated with seasonal climates, i.e., they typically ramify once a year (des Abbayes, 1939; Ahti, 1984; Ruoss, 1989; Hammer, 1997). In *Cladonia* sensu Ahti branching is more irregular. We use the terms dichotomous, trichotomous, tetrachotomous, and polytomous for branching where two, three, or multiple branches are produced from the same point (des Abbayes, 1939; Thomson, 1968). Trichotomous and tetrachotomous branching is confined to certain species of *Cladina*, and polytomies are found in some *Cladonia* (excluding *Cladina*). In isotomous branching, the branches are more or less equal in length and thickness, whereas in anisotomous branching they are unequal. It should be noted that exceptions to these pat-

terns almost invariably occur even within a single podetium. For branching systems, see characters 7–13.

7. Repeated branching seasonally regular (0), irregular (1).

8. Repeated regular branching dichotomic (0), tricho-tetrachotomic (1).

9. Repeated regular branching isotomic (0), anisotomic (1).

10. Repeated regular branching with main stem (0), main stem absent (1).

11. Irregular branching by axil formation (0), scyphus formation (1). Branching by axil formation refers to dichotomy or polytomy. Species with centrally proliferating scyphi are here interpreted as branched because even if they form a single "stem" they produce many successive scyphi, each originating from the previous scyphal plate. If multiple "stems" are produced, two or three scyphi are formed on a single plate and all these continue to produce successive scyphi.

12. Irregular branching by axil formation dichotomic (0), dichotomic plus polytomic (1).

13. Irregular branching by axil formation isotomic (0), anisotomic (1).

14. Axils of podetia open (0), closed (1). Species that regularly form openings at branch axils are coded as open. However, most branched *Cladoniae* may form occasional holes at axils or elsewhere. This may cause misinterpretations, particularly if only one or a few specimens are examined.

15. Podetial tips and upper axils funnel-shaped (0), funnels absent (1). The term funnel has been established to describe the structure which formerly was referred to as an "open scyphus" (present in section *Perviae* sensu Ahti). However, funnels appear not to be homologous with scyphi. Rather, they probably develop from open branch axils, which become more or less dilated and trumpet-like.

16. Scyphi present (0), absent (1). Cup-formed structures referred to as scyphi are characteristic of some species of the genus *Cladonia*. Scyphi vary considerably in size and shape from species to species, but we have not been able to confirm whether these differences reflect actual characters. Clearly, some species are invariably scyphose, whereas others may or may not be scyphose (character 17). This seems to be correlated with the width of scyphi; invariably scyphose species usually have wider scyphi.

17. Scyphi obligatory (0), facultative (1).

18. Scyphi proliferating from margins (0), from the center (1). Centrally proliferating scyphi are shallow or almost flat disks and are often arranged in a succession of multiple tiers. They are here considered homologous to cup-shaped scyphi. However, the possibility that the two scyphus structures are nonhomologous cannot entirely be ruled out.

19. Centrally proliferating scyphal plates divided (0), not divided (1). Many South American species with centrally proliferating scyphi have deeply lacerated scyphal margins. These lacerations can be fairly flat or flagellate, and they can be simple or successively branched by dichotomy or trichotomy. In species that lack these lacerations, the scyphal margins are rarely entirely smooth either but are at least shallowly toothed (Ahti and Marcelli, 1995).

20. Podetial wall entirely uniform (0), longitudinally grooved to fibrose (1). Podetial wall grooved to fibrose has been viewed as a diagnostic character of *Cladonia* section *Helopodium* sensu Ahti, but similar wall structures can also be found in some *Unciales*. However, we anticipate that this character will eventually prove more complex than previously thought. The wall structure is apparently closely connected to the stereome structure (character 21).

21. Cylindrical stereome present (0), absent or very rudimentary (1). Stereome is the innermost layer in the vertical thallus (sometimes referred to as the inner medulla). It is cartilaginous and composed of longitudinally arranged hyphae. Its thickness and hardness vary (it is extremely hard in *Cladonia furcata*, for instance), and its surface can be variously grooved or papillose; these characters are, however, not well known.

22. Cortex present on podetia (0), absent (1). The ectal layer of the vertical thallus is referred to as corticate when it is compact and consists of short, pseudoparenchymatic cells. The term "corticoid" is sometimes used when the surface appears to be a thin, rather compact layer but without pseudoparenchymatic cells. In ecorticate species, the surface is arachnoid and the medulla is visible. The cortex is frequently discontinuous and may produce vegetative propagules. Nevertheless, only entirely ecorticate species were coded as character state (1).

23. Soredia present (0), absent (1). Soredia are produced on the surface of podetia and more rarely also on primary squamules. Soredia are typically produced

over the entire surface of the podetium (diffuse soralia), but are usually somewhat restricted to certain areas, most commonly near the apical parts. Soredia are always ecorticate. They vary from farinose to granulose, but cannot readily be placed in clear categories (however, see Stenroos, 1989a).

24. Corticate propagules present (0), absent (1). Corticate propagules include granules, microsquamules, and isidioid structures, which all easily detach from the thallus surface.

25. Podetial squamules present (0), absent (1). Podetial squamules (macrosquamules; Dahl, 1952) are commonly produced in varying quantities particularly at basal parts of the podetia. In contrast to much smaller microsquamules, they are clearly flat, dorsiventral, and firmly attached to the podetial surface.

26. Conidiomata and primordia basal on primary squamules (0), terminal (or lateral) on podetia (1). Conidiomata (pycnidia; Vobis, 1980) are typically associated with hymenial primordia (containing ascogonia), and they occur prior to the development of hymenial disks. The shape of conidiomata varies from cylindrical to globose, dolioliform, or pyriform, and their size varies considerably (Vainio, 1897; Stenroos, 1994, 1998). However, these characters could not be clearly defined. The placement of conidiomata either on primary squamules or on podetial tips undoubtedly correlates with the principal development of podetia (Jahns, 1970; Jahns and Beltman, 1973; Ahti, 1982; Jahns *et al.*, 1995). However, the developmental types or the conidiomata in general have not been thoroughly analyzed.

27. Slime in conidiomata hyaline (0), red (1).

28. Hymenial disks brown (0), other color (1).

29. Hymenial disks red, with rhodocladonic acid (0), ochraceous (1).

30. Beta-orcinol p-depsides present (0), absent (1). For final compounds of the group, see characters 31–34.

31. Atranorin present (0), absent (1).

32. Barbatic acid present (0), absent (1).

33. Baeomycesic acid present (0), absent (1).

34. Squamatic acid present (0), absent (1).

35. Beta-orcinol m-depsides (thamnolic acid) present (0), absent (1).

36. Beta-orcinol depsidones present (0), absent (1). For final compounds of the group, see characters 37–40.

37. Fumarprotocetraric acid present (0), absent (1).

38. Psoromic acid present (0), absent (1).

39. Norstictic acid present (0), absent (1).

40. Stictic acid present (0), absent (1).

41. Orcinol p-depsides (perlatolic acid, divaricatic acid) present (0), absent (1).

42. Orcinol m-depsides present (0), absent (1). For final compounds of the group, see characters 43–46.

43. Cryptochlorophaeic acid present (0), absent (1).

44. Homosekikaic acid present (0), absent (1).

45. Merochlorophaeic acid present (0), absent (1).

46. Sekikaic acid present (0), absent (1).

47. Orcinol depsidones (grayanic acid) present (0), absent (1).

48. Dibenzofurans present (0), absent (1). For final compounds of the group, see characters 49 and 50.

49. Didymic acid present (0), absent (1).

50. Strepsilin present (0), absent (1).

51. Usnic acid present (0), absent (1).

52. Zeorin present (0), absent (1).

APPENDIX 4

Command Lines and Brief Description of Commands Used in POY Analysis

Command line used for the initial analysis performed with a single processor:

```
poy -norandomizeoutgroup -noleading
-maxtrees 2 -jackboot -random 10 -seed -1
-nospr -notbr it1 it2 it3 it4 it5 it6 it7
-prealigned bet mor > jak235out
```

The commands result in the following operations (Janies and Wheeler, 2000):

-norandomizeoutgroup: prevents randomization of the outgroup

-noleading: leading and trailing gaps are ignored

-maxtrees 2: sets the maximum number of trees held in buffers

-jackboot: performs Farris'parsimony jackknifing

-random 10: specifies number of random addition searches performed

-seed -1: seed for pseudorandom number generation (-1, system time in seconds is used)

-nospr -notbr: spr and tbr branch swapping are prevented

-prealigned: the program does not optimize sequences specified with this command, i.e., homology statements are taken as is

(it1-7, bet and mor are the input file names, and jak235out the output file)

The final analysis was performed with the following command string:

```
poy -noleading -norandomizeoutgroup
-maxtrees 2 -random 10 -nospr -notbr
-ratchetpercent 50 - ratchetseverity 2
-ratchetspr 10 -ratchettbr 10
-ratchettrees 2 -seed -1 -slop 1
-prealigned mor bet -noprealigned it1 it2
it3 it4 it5 it6 it7 -constrain jak235.con
> jakout
```

-ratchetpercent 50: percentage of characters reweighted according to Nixon's (1999) ratchet procedure

-ratchetseverity 2: weight multiplier for reweighted characters

-ratchetspr 10 -ratchettbr 10: number of iterative rounds of ratcheting with spr and tbr branch swapping, respectively

-ratchettrees 2: number of trees saved during ratchet iterations

-slop 1: checks all cladograms within 0.1% of the obtained minimum value

(jak235.con is the constraint file based on the results of the jackknife analysis and jakout output file)

The command string used for the parallel analyses was:

```
poy -fuseafterreplicates
-repintermediate - fusemaxtrees 10
-jobspernode 2 -parallel -noleading
-norandomizeoutgroup -maxtrees 2
-holdmaxtrees 20 -fitchtrees -multibuild 32
-random 8 -multirandom -driftspr
-numdriftspr 10 -drifttbr -numdrifttbr 10
-treefuse -fuselimit 100 -seed 1 -slop 0
-checkslop 5 -molecularmatrix sg4t1.mat
-prealigned mor -noprealigned it1 it2 it3
it4it5 it6 it7 bet -controllers 8
-noapproxbuild -buildmaxtrees 2 >
clad411.tre 2> clad411.err.
```

-fuseafterreplicates: results of the random replicates are taken and treefusing is performed on them

-repintermediate: results of individual random replicates are printed

-fusemaxtrees 10: maximum number of trees held in buffers during treefusing

-jobspernode 2: specifies processes per node

-parallel: executes jobs in parallel using PVM

-holdmaxtrees 20: number of trees held during random replicates

-fitchtrees: trees kept in buffer are a random subset of trees that would have been retained if a larger tree buffer had been specified (algorithm developed by W. Fitch)

-multibuild 32: specifies number of random addition builds performed on slave nodes

-multirandom: individual random replicates are spawned to slave nodes

-driftspr -drifttbr: tree drifting based on spr and tbr branch swapping, respectively

-numdriftspr 10 -numdrifttbr 10: number of drift rounds

-treefuse: treefusion as described by Goloboff (1999)

-fuselimit 100: limits the number of treefusing pairs

-checkslop 5: checks cladogram lengths that are within 0.5% of the current minimum length by adding an extra tbr branch-swapping round

-molecularmatrix: reads in a cost matrix-specifying transition, transversion, and gap costs

-controllers 8: cluster is divided into eight subclusters in order to make parallellism more efficient

-noapproxbuild: heuristic tree calculation errors are corrected during the building process

-buildmaxtrees 2: specifies maximum number of trees held in buffers during the building process (clad411.tre and clad411.err are output files)

ACKNOWLEDGMENTS

We thank the following colleagues who kindly sent us fresh material; without their help, this work would not have been possible: A. Aptroot, S. Chuah-Petiot, B. Dennetière, T. Feuerer, C. Gueidan, I. Jüriado, K. Jääskeläinen, G. Kantvilas, T. Koponen, R. I. Lewis-Smith, R. Poulsen, A. Puolasmaa, J. Rikkinen, M. Saaristo, C. W. Smith, U. Søchting, H. Tuomisto, V. Virtanen, and S. Wall. We thank S. Koskinen for her skillful help with some of the DNA extractions. S.S. thanks R. Yahr for the extracted DNA of *C. perforata*, and P. T. DePriest for working facilities, excellent arrangements during research visits of the senior author to the Smithsonian Institution and a field trip to Guyana, and for help in sequencing *C. solitaria*. Special thanks are due to M. P. Marcelli for excellent organization of a field meeting to a *locus classicus*, Serra do Caraça, Brazil, where a great number of specimens were collected for the present work. S.S. thanks the best research group ever, for joining the effort. J. Muona and G.

Giribet are thanked for inspiring discussions and support. Last, but not least, we thank W. C. Wheeler. Without his generous advice and help, our analyses would have remained undone. C. A. Pelli revised the English of the manuscript. The study was funded partly by a University of Turku faculty grant to J. Hyvönen, who decided to spend it on lichenology instead of bryology. Partial support was obtained from the Academy of Finland (Grant 44079 to S.S.).

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