DISSERTATIONES BIOLOGICAE UNIVERSITATIS TARTUENSIS
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EVOLUTIONARY RELATIONSHIPS IN SOME CETRARIOID GENERA (LICHENIZED ASCOMYCOTA)

ANDRES SAAG

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PRESS

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LIST OF ORIGINAL PUBLICATIONS

This thesis is based on the following publications, which are referred to in the text by their Roman numerals.

I Saag, A. & Randlane, T. 1995. Phylogenetic affinities of cetrarioid lichens. — Cryptogamic Botany 5(2): 128–136.

II Randlane, T. & Saag, A. 1989. Chemical variation and geographical distribution of *Asahinea chrysantha* (Tuck.) Culb. & C. Culb. — Lichenologist 21: 303–311.

III Randlane, T. & Saag, A. 1991. Chemical and morphological variation in the genus *Cetrelia* in the Soviet Union. — Lichenologist 23: 113–126.

IV Randlane, T., Thell, A., & Saag, A. 1995. New data about the genera *Cetrariopsis*, *Cetreliopsis* and *Nephromopsis* (Fam. Parmeliaceae, lichenized Ascomycotina). — Cryptogamie, Bryologie-Lichénologie 16: 35–60.

V Randlane, T. & Saag, A. Synopsis of the genus *Nephromopsis* (Fam. Parmeliaceae, lichenized Ascomycota). — Cryptogamie, Bryologie-Lichénologie. (Accepted for publication.)

VI Randlane, T., Saag, A., Thell, A. & Kärnefelt, I. 1994. The lichen genus *Tuckneraria* Randlane & Thell — a new segregate in the Parmeliaceae. — Acta Botanica Fennica 150: 143–151.

VII Thell, A., Randlane, T., Kärnefelt, T., Gao, X.-Q. & Saag, A. 1995. The lichen genus *Allocetraria* (Ascomycotina, Parmeliaceae). — In: Daniels, F. J., Schulz, M. & Peine, J. (eds.). Flechten Follmann. Contributions to lichenology in honour of Gerhard Follmann. University of Cologne, Germany, 353 – 370.

VIII Thell, A., Goward, T., Randlane, T., Kärnefelt, E. I. & Saag, A. 1995. A revision of the North American Lichen genus *Ahtiana* (Parmeliaceae). — Bryologist 98(4): 596–605.

IX Saag, A., Randlane, T. & Thell, A. Phylogenetic analysis of cetrarioid lichens with globose ascospores. (Submitted.)

List of other relevant publications

Randlane, T. & Saag, A. 1991a. Chemical variation and geographical distribution of *Asahinea chrysantha*. — In: N. S. Golubkova (ed.), The problems of experimental lichenology in the USSR. Leningrad, 58–65 (in Russian).

Randlane, T. & Saag, A. 1991b. Some chemosystematical data about the lichen genus *Nephromopsis* in the USSR. — Folia Cryptogamica Estonica 28: 26–30.

Randlane, T. & Saag, A. 1992a. Additional data about the genus *Nephromopsis* (Lichens, Parmeliaceae). — Mycotaxon 44(2): 485–489.

Randlane, T. & Saag, A. 1992b. New combinations of some cetrarioid lichens (Parmeliaceae). — Mycotaxon 44(2): 491–493.

Randlane, T. & Saag, A. 1992c. Genus *Cetrelia* Culb. et Culb. in URSS. — Novitates Systematicae Plantarum non vascularium 28: 118–133 (in Russian).

Randlane, T. & Saag, A. 1992d. *Tuckermannopsis americana* contra *Cetraria ciliaris* in Russia. — Folia Cryptog. Estonica 29: 33–36.

Randlane, T., Saag, A. & Kondratyuk, S. 1992. Genus *Cetrelia* Culb. et Culb. in the Ukraine. — Ukrainian Botanical Journal 48(1): 4–44 (in Ukrainian).

Randlane, T. & Saag, A. 1993. World list of cetrarioid lichens. — Mycotaxon 47: 395–403.

Kondratyuk, S., Randlane, T., Saag, A. & Oxner, A. 1993. Genus *Cetrelia* W. Culb. et C. Culb. — In: A. Oxner, Flora of the Lichens of Ukraine 2. Kiev, Naukova Dumka, 214–221 (in Ukrainian).

Kärnefelt, I., Thell, A., Randlane, T. & Saag, A. 1994. The genus *Flavocetraria* Kärnefelt & Thell (Parmeliaceae, Ascomycotina) and its affinities. — Acta Botanica Fennica 150: 79–86.

Randlane, T., Saag, A. & Thell, A. 1997. A second updated world list of cetrarioid lichens. — Bryologist 100(1): 109–122.

Randlane, T. & Saag, A. Changes in systematics of cetrarioid lichens. — Sauteria. (Submitted.)

ABSTRACT

The group of cetrarioid lichens (fam. *Parmeliaceae*, lichenized Ascomycota) comprises 131 species in 22 genera. Phylogenetic relationships within some of the cetrarioid genera — *Ahtiana, Allocetraria, Asahinea, Cetrelia, Cetreliopsis, Dactylina, Esslingeriana, Nephromopsis, Tuckneraria,* and *Tuckermannopsis* — are treated in more detail in this thesis.

Three chemotypes have been recognized in *Asahinea chrysantha*, one of them is supposed to represent the primitive chemistry of the genus. Chemosystematical and geographical studies reveal that a possible centre of speciation of *Asahinea* is in the Russian Far East or Japan.

Treatment of chemo- and morphotypes in genus *Cetrelia* is presented; a table is composed where vacant squares mark the species that are theoretically possible in the genus. The role of "primary" and "secondary" species in *Cetrelia* according to the "species-pairs" theory is discussed.

Species from the genera *Cetreliopsis, Nephromopsis,* and *Cetrariopsis* are thoroughly characterized and compared. Both species of *Cetrariopsis* are transferred to the genus *Nephromopsis,* as no difference in the morphology, anatomy, and chemistry of these two genera (except for their dissimilar positions of apothecia) could be detected.

The group of cetrarioid lichens, characterized by subglobose to globose ascospores in narrowly clavate asci, is cladistically analyzed. The present state of taxonomy in the whole heterogenous group of cetrarioid lichens is discussed. One new genus — *Tuckneraria* Randlane & Thell — is presented; four new species are described: *Cetrelia orientalis* Randlane & Saag, *C. pseudocollata* Randlane & Saag, *Tuckneraria ahtii* Randlane & Saag, *Cetreliopsis papuae* Randlane & Saag. A number of new combinations have also been proposed.

INTRODUCTION

The family Parmeliaceae, which consists of c. 60 genera and about 1000 species, has been colloquially divided into three simple but rather ill-defined morphological categories: alectorioid, parmelioid and cetrarioid. Alectorioid lichens are beard-like or truly fruticose, pendant or caespitose. Parmelioid lichens are clearly foliose, possessing laminal apothecia and pycnidia, and are usually more or less closely adnate to the substrate. Cetrarioid lichens, on the other hand, form quite a vague and undelimited group between these two, having a strap-shaped, subfruticose or ascending foliose thallus, possessing mainly marginal apothecia and pycnidia. However, this arrangement is based mainly on morphology and, as most morphological characters, often displays a large degree of variability. Evidently, these familiar categories (alectorioid, cetrarioid and parmelioid) have little to do with phylogeny. It was convincingly shown already at the beginning of the nineties (Kärnefelt *et al.* 1992) that there is no doubt about the cetrarioid group of lichens being polyphyletic. Therefore, all these species cannot be placed in one or two genera as it was done, for instance, by the Russian lichenologist Ksenya Rassadina (1950) or by the Finnish scientist Veli Räsänen (1952). Today we can count more than 130 cetrarioid lichen species which are divided between 22 genera.

The aim of the present thesis is to investigate evolutionary relationships of species in some cetrarioid genera (*Ahtiana*, *Allocetraria*, *Asahinea*, *Cetrelia*, *Cetreliopsis*, *Nephromopsis*, *Tuckneraria*) and to contribute to the arranging of their taxonomy according to the phylogeny. The critical revision of all the species in the above-listed genera was carried out to this purpose.

The thesis is based on nine original papers prepared by a team of authors. Twelve more papers, written mainly by the author and his supervisor, are also closely related to the subject under investigation.

Studies on the systematics of cetrarioid lichens in the University of Tartu were initiated in the late eighties by the author and his supervisor Tiina Randlane. At first our work focussed on some genera only (*Asahinea, Cetrelia*), with a special emphasis on chemical and geographical data. In 1992 we met with Arne Thell and Dr. Ingvar Kärnefelt, lichenologists from the Department of Systematic Botany, University of Lund (Sweden), who were carrying out similar studies on the same group of species paying extra attention to the anatomical characters. By that time it was evident that the so-called cetrarioid lichens form a heterogenous and informal assemblage which was in urgent need of more thorough investigation. During the following years several papers were published by the working team consisting of Arne Thell, Tiina Randlane, and the author. Working tasks were divided among the members of the team as

follows: identification and investigation of the morphological characters in all studied taxa — T. Randlane; the anatomical characters — A. Thell; the chemical characters — the author. The author of the thesis is also responsible for the ideas concerning the evolution and phylogenetic affinities of the species. The present dissertation is based on the papers that introduce numerous original data on morphology, anatomy, and chemistry of cetrarioid lichens; still, the main purpose of all these studies has been the revision of systematic arrangement based on evolutionary relationships.

Historical background

Already the early taxonomical history of cetrarioid lichen species reveals numerous confusions connected with these taxa. Carl Linné, who recognized only one genus among lichens (*Lichen*) in his classical "Species Plantarum" (1753), presented five species (*L. fahluensis, L. islandicus, L. nivalis, L. juniperinus,* and *L. glaucus*) that were later included in the group called cetrarioid lichens. The genus *Cetraria* was originally described by Eric Acharius in his "Methodus Lichenum" (1803), where he comprised eight taxa: *C. islandica, C. cucullata, C. nivalis, C. lacunosa, C. fallax, C. glauca, C. sepincola,* and *C. juniperina*, four of them already mentioned by Linné. The fifth species described by Linné (*L. fahluensis*) was incorporated in *Cetraria* only by Tuckerman almost eighty years later (1882). Two names mentioned by Acharius — *C. fallax* and *C. glauca* — later turned out to be synonyms. One more *Cetraria* species — *C. ciliaris* — was additionally introduced by Acharius some years after describing the genus (1810). Today only one of these early taxa — the type species *C. islandica* — has remained in the genus *Cetraria* according to the modern taxonomy.

William Nylander was the first lichenologist who started to split the genus *Cetraria.* He recognized five species in *Cetraria,* 25 species in the newly described *Platisma* ("*Platysma*"), and one species in *Dactylina* (both in 1860). Some other close genera were segregated during the following years (*Nephromopsis* in 1891 by Müller Argoviensis; *Tuckermannopsis* in 1933 by Gyelnik), but most of the specialists still recognized one big *Cetraria.* The genus was considered the largest by Ksenya Rassadina (1950), who incorporated 76 species in it.

The modern process of dissecting the polymorphic genus *Cetraria* was initiated by Dr-s William and Chicita Culbersons, who presented three new genera — *Asahinea, Cetrelia,* and *Platismatia* — in the 1960-ies (Culberson & Culberson 1965, 1968). These genera, as well as *Masonhalea* (Kärnefelt 1977), *Parmelaria* (Awasthi 1987), *Ahtiana* (Goward 1985) etc., are now accepted by everybody

without a doubt. We are quite sure that the same will happen to most of the new cetrarioid genera, which are predominantly described on the complex of different characters with special emphasis on the anatomical characters.

Four years ago 14 genera of cetrarioid lichens could be listed (Randlane & Saag 1993); at present there are 131 species divided between 22 genera (Randlane *et al.* 1997); in addition, four former *Cetraria* species have been transferred to *Melanelia* (Thell 1995). The list of separating all these cetrarioid genera in chronological order is presented in Table 1.

Table 1. Describing of cetrarioid genera in chronological order.

Year of description	Name of the genus and the author(s)	Number of species today
1794	*Cornicularia* Hoffm.	1
1803	*Cetraria* Ach.	33 (16 "true" Cetrarias + 17 uncertain species)
1860	*Dactylina* Nyl.	2
1891	*Nephromopsis* Müll. Arg.	11
1933	*Tuckermannopsis* Gyeln.	11
1965	*Asahinea* W. L. Culb. & C. F. Culb.	2
1968	*Cetrelia* W. L. Culb. & C. F. Culb.	17
1968	*Platismatia* W. L. Culb. & C. F. Culb.	10
1977	*Masonhalea* Kärnefelt	1
1981	*Cetreliopsis* M. J. Lai	5
1981	*Esslingeriana* Hale & M. J. Lai	1
1985	*Ahtiana* Goward	3
1987	*Parmelaria* D. D. Awasthi	2
1991	*Allocetraria* Kurok. & M. J. Lai	10
1991	*Coelopogon* Brusse & Kärnefelt	2
1993	*Arctocetraria* Kärnefelt & Thell	2
1993	*Cetrariella* Kärnefelt & Thell	2
1993	*Nimisia* Kärnefelt & Thell	1
1993	*Vulpicida* J.-E. Mattsson & M. J. Lai	6
1994	*Flavocetraria* Kärnefelt & Thell	2
1994	*Tuckneraria* Randlane & Thell	5
1996	*Kaernefeltia* Thell & Goward	2

MATERIAL AND METHODS

Herbarium material from B, BM, CANB, DUKE, COLO, E, FH, G, GZU, H, KW, LD, LE, M, MB, PC, S, TAIM, TBA, TNM, TNS, TU, UPS, US, WU, and private herbaria of A. Aptroot, D. D. Awasthi, J. A. Elix, and M. J. Lai has been used for this study.

Anatomical studies of cortical and reproductive structures were carried out by Dr. Arne Thell in the University of Lund (Sweden) using methods decribed in publication VII. The morphology was studied by T. Randlane and partly by the author using a stereomicroscope Technival 2. Chemical data are based on both "spot tests" and thin layer chromatographic analyses (TLC and HPTLC). The "spot tests" were made with 10% KOH, p-phenylendiamine in ethanol and sodium hypochlorite. The TLC and HPTLC analyses were carried out by the author, mainly according to the standardized TLC methods described by Culberson & Kristinsson (1970), Culberson (1972, 1974), and White & James (1985). The acetone extracts were run in solvent systems A, B, C and G (Culberson *et al.* 1981). The plates were developed with 10% H_2SO_4 either in H_2O or in C_2H_5OH. The major secondary compounds were identified in most specimens, the minor constituents were identified only when the spots were sufficiently well developed (mainly in the species of *Cetrelia*).

The cladistical analyses presented in publication I were carried out using the program PAUP version 3.0s (Swofford 1991) on a Macintosh IIci personal computer. The following option settings were used: character-state optimization — DELTRAN; MULPARS; MAXTREE = 1000, 3900; heuristic search; trees rooted using outgroup method; for functional outgroup rooting a monophyletic sister group used; addition sequence — simple; 3 trees held at each step during stepwise addition; tree-bisection-reconnection (TBR) branch-swapping performed; characters reweighted by maximum value of rescaled consistency indices. Strict consensus trees of both original data based cladograms and after characters reweighted were retained.

Computer programs for phylogenetic analysis PAUP 3.1.1 (Swofford 1993) and MacClade 3.04 (Maddison & Maddison 1992) were used in the cladistical analyses presented in publication IX. Both programs were run on a Macintosh Color Classic. Using the program PAUP 3.1.1, the follwing heuristic search settings were applied: character-state optimization - ACCTRAN; MULPARS; MAXTREE = 1000, 3000, 6000; addition sequence — simple; 1 tree held at each step during stepwise addition; tree-bisection-recollection (TBR) branch-swapping performed; multi-state taxa interpreted as uncertainty; characters weighted equally. The same settings were used in the successive approximations character weighting method. Tree support was investigated using Bremer support and bootstrap in PAUP 3.1.1 and by using the program Parsimony Jackknifer 4.22 (Farris 1995).

RESULTS AND DISCUSSION

Phylogenetic affinities in the whole group of cetrarioid lichens (I)

The group of cetrarioid lichens has always been an artificial conglomerate of species arranged in some heterogenous genera (e.g. *Cetraria, Nephromopsis, Parmelia, Tuckermannopsis*). To delimit the objects of the present study, a world list of cetrarioid lichens was compiled at first (Randlane & Saag 1993). This was the first attempt after 40 years (Rassadina 1950; Räsänen 1952) to sum up all the species closely related to the genus *Cetraria* Ach. The generic location and valid epithet of that time was indicated for each of the 120 species. It became evident that the generic location of 27 species was not acceptable and information available about nine species was unsufficient.

The list served as a starting point for the following studies. It was evident that the group under discussion was not monophyletic. The first review about the phylogeny of the group of cetrarioid lichens was presented by Kärnefelt *et al.* (1992), where cladistic analyses were carried out on 50 species as terminal taxa. This analysis was based mainly on the anatomical characters that had been originally revised. Morphological characters, as well as chemical characters, were represented comparatively poorly. In addition, the list of chemical characters was compiled in such a way, that the weight of some of them was clearly overrated. As a result, the analysed taxa were grouped in three separate aggregates described by important anatomical characters: taxa with an "apical ring structure"; taxa with "uniseriate asci"; taxa with "broadly clavate asci" (Fig. 1).

At about the same time (in 1991–92) the cladistic analyses on the same group of lichens were independently carried out also by us. The results were presented in IAL 2 symposium in 1992 but, unfortunately, were published only three years later (I). Of about 120 known cetrarioid lichen species, 83 were chosen for the analysis to evaluate the systematic arrangement of the taxa. 42 morphological, anatomical, and chemical characters, traditionally in wide use, were used altogether. Still, some of the common characters applied usually in handbooks of macrolichens (e.g. colour of the thallus, shape and arrangement of lobes etc.) were not used here because of difficulties in defining them properly. Morphological and chemical characters (character states) were identified or verified originally, while descriptions of anatomical characters were based mainly on literature data. The characters were grouped as follows: I thallus structures (9 characters), II apothecia and ascospores (8 characters), III conidiomata and pycnospores (6 characters), IV secondary chemical compounds (19 characters). In the selection of characters we kept to the idea that the taxa should not be described by the data of reproductive structures only but using also the thalline and especially the chemical characters. The possibly special role of secondary metabolites in the evolution of lichens has been referred to by J. Poelt

in his species-pairs theory (Poelt 1970, 1972). It seems plausible that the formation of biochemical pathways producing lichen substances has taken place earlier, during sexual stages, rather than through mutations in asexual "secondary taxa" (Bowler & Rundel 1975). The genus *Cetrelia* was selected as the outgroup for the present cladistic analysis; more detailed survey about *Cetrelia* species is presented in the next chapter.

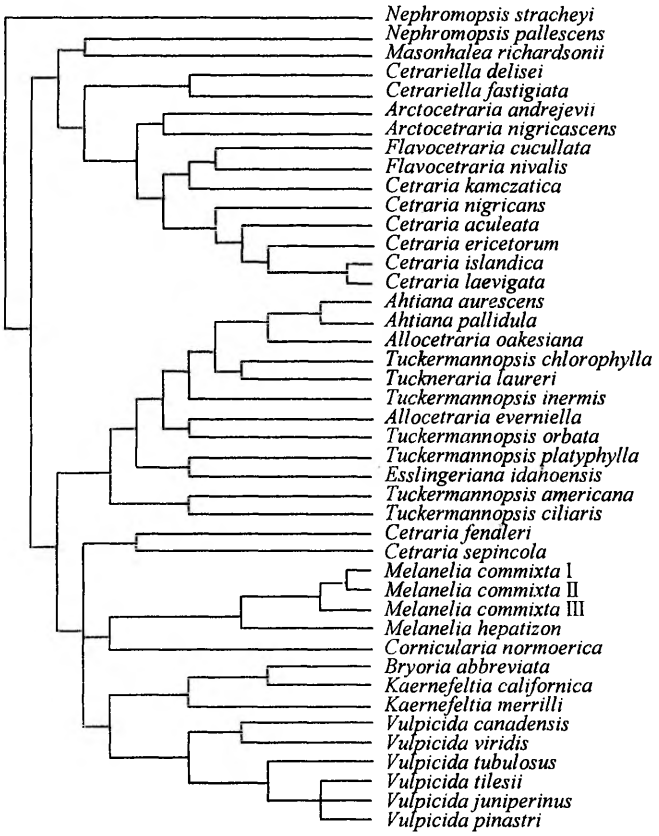

Fig. 1. One of 16 equally parsimonous cladograms. Length 192, consistency index 0.32, retention index 0.68 (Kärnefelt *et al.* 1992, names of terminal taxa according to the modern taxonomy).

Three separate analyses were carried out using the same data basis, which was arranged differently for each analysis. In the first analysis, major secondary metabolites were treated as separate characters, totally independent from each other. Evolutionary affinities shown in this analysis should be especially critically evaluated. One of the most important characters of higher taxonomical units — biochemical connections between different lichen compounds — is completely ignored here. That problem is avoided in the second and third

analyses, where the lichen substances were not represented as independent characters but grouped into biochemically related sets according to their chemical structure and possible biochemical pathways. The disadvantage of this method is the inability to determine affinities within subclades (several polytomies in cladograms) due to lack of detailed chemical data. In addition, in the third analysis, some characters treated as binary at first were coded as multistate. Methodically, the third analysis should be evaluated as the most correct.

The strict consensus tree of the third analysis (Fig. 2) was constructed of 3900 equally parsimonous cladograms (after reweighting the characters). Evolution for considerable number of species (from genera *Nephromopsis, Cetreliopsis, Cetrelia*) is unresolved (showing several polytomies in the respective part of the consensus tree). These are just the taxa that were not included in the cladistic analyses by Kärnefelt *et al.* (1992). The rest of the species are grouped in such a way, which shows considerable similarity with the main three assemblages pointed out in the analysis by our Swedish colleagues.

The most clearly separated clade in our analysis (Fig. 2) includes 14 species from the genera *Ahtiana, Allocetraria, Esslingeriana,* and *Tuckermannopsis*. This clade completely corresponds to the group described by Kärnefelt *et al.* (1992) as "taxa with uniseriate asci including mainly *Tuckermannopsis* and related entities".

Three further neighbouring clades in our analysis consist of species of *Kaernefeltia*; *Platismatia* and *Vulpicida; Melanelia* and *Cetraria fendleri* group. Two genera, *Platismatia* and *Vulpicida*, form separate subclades while species of *Melanelia* and *Cetraria fendleri* group are united in one subclade. The whole assemblage is referred to in the Swedish analysis as "taxa with broadly clavate asci". Membership of *Vulpicida, Melanelia* and *Kaernefeltia* species in this group was pointed out by Kärnefelt *et al.* (1992), while *Platismatia* was added according to our results.

One more clade shows good separation of several species. The clade comprises the *Cetraria islandica* group, species of *Flavocetraria, Arctocetraria, Masonhalea* and some other small genera. This grouping is called "taxa with an apical ring structure including mainly the *Cetraria islandica* group" in the Swedish survey and consists in general of the same species as in our consensus tree.

Resuming the results of two cladistic analyses carried out independantly in Lund and in Tartu, three separate groupings could be defined in both of them. Similar results are particularly remarkable because of the fact that the two analyses were based on different data matrices, with emphasis on anatomical characters in Swedish study, and morphological and chemical characters in our analysis. Still, during the preparation of data matrix it became evident that the descriptions of several cetrarioid species were unsufficient or even erronous, especially with regard to anatomy. This is probably the reason why several rare and poorly investigated species from genera *Nephromopsis,*

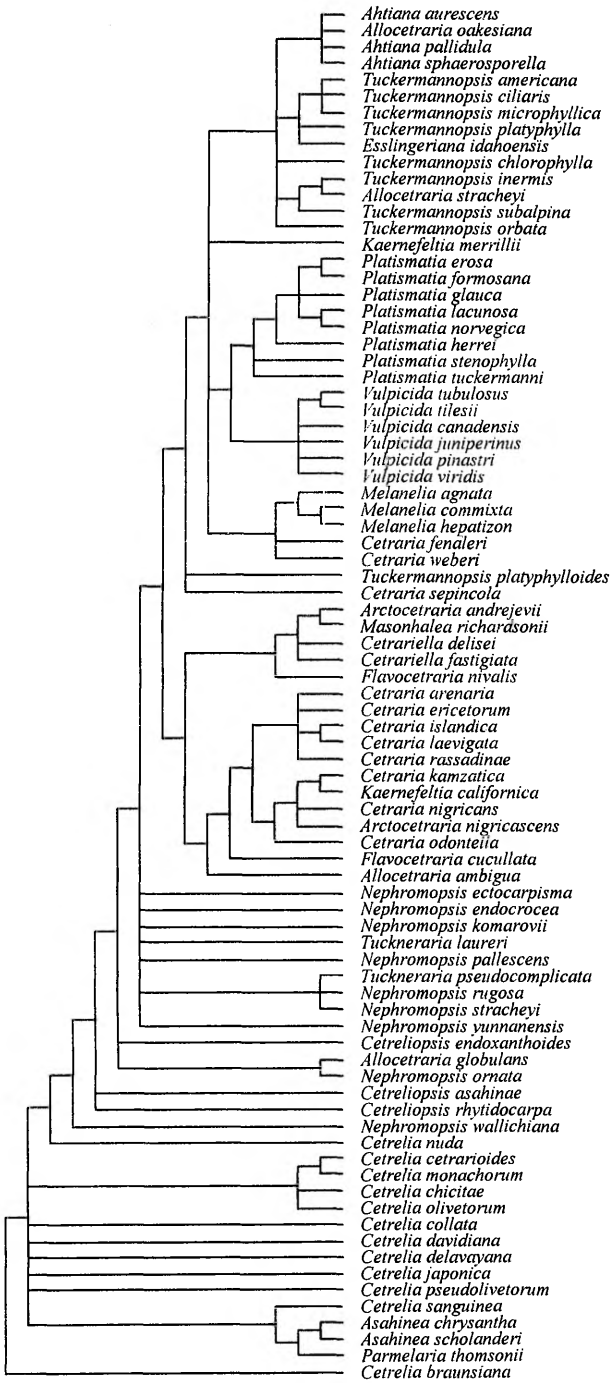

Fig. 2. Strict consensus tree constructed from 3900 equally parsimonous cladograms. Secondary compounds as representatives of biochemical groupings. Length of shortest trees 39307, consistency index 0.576, retention index = 0.863. (I, names of terminal taxa according to the modern taxonomy).

Cetreliopsis etc. remained unresolved in our cladistic analysis. Both analyses carried out six years ago on a great number of cetrarioid lichens demonstrated clearly the necessity of additional original studies on this group. The authors of both papers agreed that the results presented were introductory only and the taxonomical changes, although inevitable in many cases, could be done after further studies.

Today the polyphyletic origin of cetrarioid lichens is generally acknowledged. Three evolutionary lines referred to above, based mainly on reproductive structures and structural characters, have been recognized for the group. Two of the three lines are presumed to be monophyletic (Thell 1996). The first line includes species from seven genera: *Arctocetraria, Cetraria* s. str., *Cetreliopsis, Coelopogon, Flavocetraria, Masonhalea,* and *Nephromopsis*. They are all characterized by the ellipsoid ascospores in narrowly clavate asci with a small axial body. An amyloid ring structure in tholus is a significant character that is present in *Cetraria, Flavocetraria* and occasionally in *Nephromopsis*.

The second evolutionary line comprises six genera: *Ahtiana, Allocetraria, Dactylina, Esslingeriana, Tuckneraria,* and *Tuckermannopsis*. These species are anatomically characterized by subglobose to globose ascospores in narrowly clavate asci (earlier called "uniseriate asci"). This evolutionary line is also presumably monophyletic (Thell 1996). More detailed survey about the phylogenetic affinities inside the group is presented in the last part of this chapter (p. 29).

The third line is represented by several genera and informal groups: *Asahinea, Cetraria fendleri* group, *Cetrariella, Cetrelia, Cornicularia, Kaernefeltia, Melanelia commixta* group, *Nimisia, Parmelaria, Platismatia,* and *Vulpicida*. Ellipsoid ascospores in broadly clavate asci with a broad axial body are characteristic to these species. This heterogenous grouping is evidently paraphyletic in the previous treatments of cetrarioid taxa. A number of parmelioid lichens probably also belong here.

The present systematic arrangement of cetrarioid lichens is introduced in the second updated world list (Randlane *et al.* 1997). The list includes 131 cetrarioid lichen species placed into 22 genera. Six new genera (*Arctocetraria* Kärnefelt & Thell, *Cetrariella* Kärnefelt & Thell, *Flavocetraria* Kärnefelt & Thell, *Kaernefeltia* Thell & Goward, *Nimisia* Kärnefelt & Thell, and *Tuckneraria* Randlane & Thell) have been separated since 1993, when the first world list of cetrarioid lichens was published (Randlane & Saag 1993). Splitting of big genera and describing of several new small genera has been the obvious tendency in systematics of lichens during the last decade. In cetrarioid group of lichens this tendency is caused mainly by recent detailed studies of thallus structures and, especially, of ascomatal anatomy, accompanied by the revisionary work of morphological and chemical characters. Separation of most

of the new cetrarioid genera has been based on the complex of various characters with the certain emphasis on the anatomical characters (Randlane & Saag, in press). Nowadays the anatomical features especially of the inner structures of reproductive organs are considered more conservative and, therefore, suitable for delimitation at higher taxonomic levels (Hafellner 1984, Kärnefelt & Thell 1992). Still, the process of presenting several new genera has caused countless misunderstandings when using the nomenclature of cetrarioid lichens, and also objections in principle. We support the opinion that the main disagreement in this debate is not the grouping of taxa but their ranking (Elix 1993), although in some cases the separation of new genera has not been quite sufficiently founded (e.g. *Cetrariopsis*). In some cases lower taxonomic rank might be more suitable (e.g. subgenus for *Arctocetraria* and *Flavocetraria* inside the genus *Cetraria*). The description of many small genera is rather the first stage in the contemporary process of arrangement of systematics. In the group of cetrarioid lichens, this stage is mainly finished by now. The following stage will probably include proposals to join some closely related genera. The incorporating *Coelocaulon* species into *Cetraria* (Kärnefelt *et al.* 1993) and *Cetrariopsis* species into *Nephromopsis* (Randlane *et al.* 1997) are examples of this tendency already. This is accompanied by proposing numerous new combinations to establish a more convenient position for the species earlier included in big and ill-defined genera such as *Cetraria, Nephromopsis, Tuckermannopsis*. As a result, a number of cetrarioid genera that had originally been described deficiently, as monotypic or including a few species only, are now thoroughly characterized and comprise several taxa clearly related to each other. This is the case with *Ahtiana* (described as monotypic in 1985, now including 3 species), *Allocetraria* (described in 1990 with 3 species, now 10 species), *Cetreliopsis* (described as monotypic in 1981, now 5 species).

During the preparation of this thesis, the following new taxa have been described: *Cetrelia orientalis* Randlane & Saag (III), *Cetrelia pseudocollata* Randlane & Saag (III), *Tuckneraria ahtii* Randlane & Saag (VI), *Cetreliopsis papuae* Randlane & Saag (IV). A number of new combinations have also been proposed (only valid combinations are listed here): *Nephromopsis isidioidea* (Räsänen) Randlane & Saag (Randlane & Saag 1992a), *Nephromopsis yunnanensis* (Nyl.) Randlane & Saag (Randlane & Saag 1992a), *Tuckneraria pseudocomplicata* (Asahina) Randlane & Saag (VI), *Cetreliopsis endoxanthoides* (D. D. Awasthi) Randlane & Saag (IV), *Cetreliopsis laeteflava* (Zahlbr.) Randlane & Saag (IV), *Nephromopsis laii* (Thell & Randlane) Saag & Thell (Randlane *et al.* 1997).

The present state of taxonomy in the heterogenous group of cetrarioid lichens is far from being final. There are ten species described in *Cetraria* that we have not seen or for which the available material is sterile and too poor to decide on generic location. These species are: *C. albopunctata, C. annae,*

C. antarctica, C. dermatoidea, C. hypotrachyna, C. kurokawae, C. microphylla, C. nova-zelandiae, C. subscutata, and *C. zisangensis*. Furthermore, the present generic location of seven species from the genus *Cetraria (C. coralligera, C. fendleri, C. leucostigma, C. melaloma, C. sepincola, C. subfendleri, C. weberi*) is not acceptable in our opinion, but it is not clear where they belong (Randlane *et al.* 1997). Although the systematics in this group has changed considerably during the last decades, it is not truly phylogenetic yet. The contribution of cladistic analyses of the whole cetrarioid conglomerate to the taxonomy of this group has been limited primarily because of the difficulties in defining the monophyletic entities.

Evolutionary relationships in the genera *Asahinea* and *Cetrelia* (II, III)

Both genera — *Asahinea* W. L. Culb. & C. F. Culb. and *Cetrelia* W. L. Culb. & C. F. Culb. — represent the third, heterogenous evolutionary line of cetrarioid lichens characterized by ellipsoid ascospores in broadly clavate asci. The description of these genera (in addition to *Platismatia* W. L. Culb. & C. F. Culb.) in the 60-ies (Culberson & Culberson 1965, 1968) acted as a starting point to the modern splitting of the big genus *Cetraria.*

Segregation of *Asahinea* from the so-called "parmelioid Cetrariae" (*Cetrelia* and *Platismatia* according to the present taxonomy), as well as from *Cetraria* s. str., was based on the complex of different characters: prosoplectenchymatous upper cortex, absence of rhizines, laminal up to marginal position of apothecia and pycnidia, imperforation of the disc, contents of four aromatic compounds in the medulla and arctic-montane pattern of distribution (Culberson & Culberson 1965). Today the interpretation of the structure of the cortex has changed considerably. In earlier papers the terms "prosoplectenchyma" and "paraplectenchyma" referred to the form of cell lumina but since studies of thallus structures were carried out by Hale (1976), these terms are usually applied to indicate the hyphal orientation in the cortex. Thus, according to Culberson & Culberson (1965, 1968) the upper cortex of *Asahinea, Cetrelia,* and *Platismatia* was classified as prosoplectenchymatous, although not characterized by parallel periclinal orientation of the hyphae. According to the present terminology, all these genera have a pachydermatous paraplectenchymatic cortex with randomly oriented cells (IV).

Originally three species were included in *Asahinea* — *A. chrysantha* (Tuck.) W. L. Culb. & C. F. Culb., *A. scholanderi* (Llano) W. L. Culb. & C. F. Culb., and *A. kurodakensis* (Asahina) W. L. Culb. & C. F. Culb. *A. chrysantha* is easily distinguished from other members of the genus by its yellow upper cortex and absence of isidia. The range of it is more or less circumpolar. *A. scholanderi* was desribed as a *Cetraria* by Llano (1951) from Alaska. Later, Oxner & Rassadina (1960) described a new species from Asia, *Cetraria saviczii.* On the

basis of the diagnosis Krog (1962) supposed that *C. saviczii* might be identical with *C. scholanderi*, a view now widely accepted. *A. kurodakensis* was the least widely distributed of the three, supposedly endemic to Japan (Asahina 1953). The morphological and chemical similarity of *A. kurodakensis* and *A. scholanderi* was pointed out for the first time in our paper (II) on the basis of original descriptions; unfortunately we had not seen the type materials at that time. The careful comparison of the isotype of *A. scholanderi* from Alaska with the lectotype of *A. kurodakensis* from Japan some years later drew to the conclusion that these taxa are conspecific (Gao 1991).

Comparative studies on chemistry, morphology, and geographical distribution of *Asahinea chrysantha* and *A. scholanderi* were carried out by us to discuss the phylogenetic affinities of these taxa (II, Randlane & Saag 1991a). Composition of secondary metabolites in this genus is of special importance. It was generally believed that atranorin and usnic acid occur in the upper cortex and alectoronic acid in the medulla of *A. chrysantha* as constant metabolites, although usnic acid is sometimes lacking from Japanese material (Yoshimura 1979). A fourth compound, α-collatolic acid, was reported as constant for the Japanese specimens. Some other substances (e.g. β-alectoronic and β-collatolic acids) have also been announced in the material from the Russian Far East (Krivoschchekova *et al.* 1983). These results indicate that chemically interesting populations of *A. chrysantha* occur in Japan and in the Far East of Russia.

Sixty-two samples of *A. chrysantha* from the territory of the former Soviet Union were studied chemically by the author. Atranorin (in the cortex) and alectoronic acid (in the medulla) are the only compunds identified by us as occuring in all samples. Usnic and α-collatolic acids occur in the species in three combinations: I. α-collatolic acid alone; II. α-collatolic acid with usnic acid; III. usnic acid alone. Thus there are three distinct chemotypes of *A. chrysantha* in the former Soviet Union, each with its own particular geographical distribution. The presence or absence of α-collatolic acid does not seem to correlate with any morphological characters (colour of upper and lower cortices, width of brown edges on the lower surface, size of pseudocyphellae, degree of surface reticulation). The yellow colour of the upper surface depends on the quantity of usnic acid deposited in the cortex. Samples without usnic acid (chemotype I, segregated also as *Asahinea culbersoniorum* Trass) are uniformly grey. Such specimens, and samples containing usnic acid in small amounts (chemotypes II and III partly) are distinguished only with difficulty. Chemotypes II and III are very variable in the colour of the upper cortex. Treatment of a single chemotype on the level of independent species (Trass 1992) has not been generally accepted.

The geographical distribution of chemotypes of *A. chrysantha* is of special interest. The least numerous of the three is chemotype I which is known from Sikhote-Alin (Primorje region, Russian Far East), Badzhal (Khabarovsk region, Russian Far East) and Japan. Its chemistry (atranorin,

alectoronic and α-collatolic acids) is the same as that of *A. scholanderi*. Chemotype I of *A. chrysantha* is supposed — upon biogenetic relationships of lichen products — to represent the basic, primitive chemistry of *Asahinea* (II). In chemotype II, usnic acid is added to the original complex of substances. The distributional area of chemotype II shows a disjunction being found in Taimyr, Siberia, the Far East, Japan and North America, not however, in Tschukotka or Kamschatka. The lack of a-collatolic acid in chemotype III represents a second qualitative change in the chemical composition of *A. chrysantha*. Chemotype III is the most widely distributed ranging from Scandinavia and Kola over Tschukotka to North America. The different chemotypes of *A. chrysantha* and their relative distributions are shown schematically in Fig. 3. Combining the distributional patterns of the three chemotypes and assumptions about an original or primitive suite of secondary metabolites in *Asahinea*, we suggest that a possible centre of speciation of the genus was in Russian Primorye or Japan. This is the only region where chemotypes I and II of *A. chrysantha* coexist and where *A. scholanderi* also occurs, while chemotype III — the most derived chemotype in the genus — is absent.

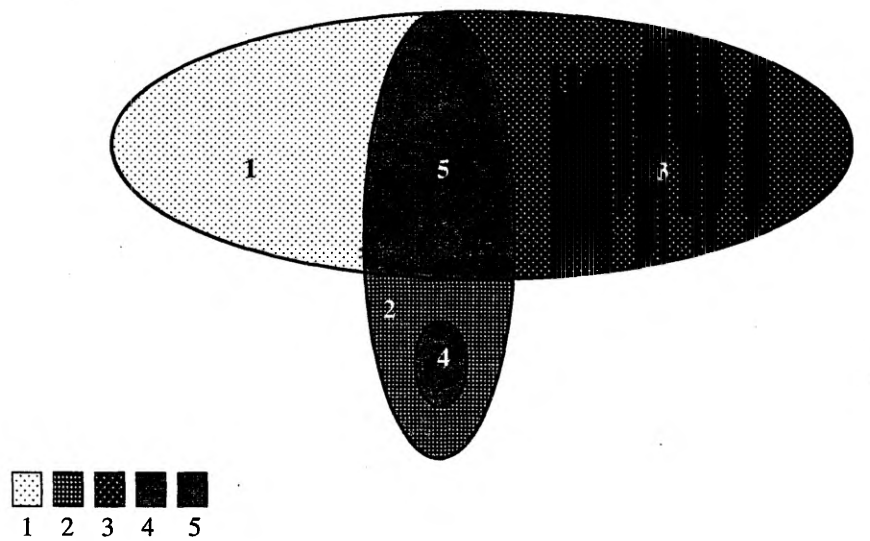

Fig. 3. Relative range of *Asahinea scholanderi* and chemotypes of *A.chrysantha* in Russia. 1 = chemotype III; 2 = chemotype II & *A. scholanderi*; 3 = chemotype III & *A. scholanderi*; 4 = chemotypes I & II & *A. scholanderi* (proposed centre of speciation of the genus); 5 = chemotypes II & III & *A. scholanderi*.

The genus *Cetrelia* was separated from the genera *Cetraria* and *Parmelia* on the complex of characters where the medullary compounds had a special importance — all the *Cetrelia* species produce aromatic substances (orcinol depsides and depsidones) only, and never contain aliphatic fatty acids which

occur in all taxa of the close genus *Platismatia* (Culberson & Culberson 1968). The so-called chemosyndromic variation was demonstrated analysing the medullary chemistry of *Cetrelia* species. Instead of accumulating only one or two medullary constituents, as previously believed, the species of *Cetrelia* syntesize lichen substances in characteristic biogenetically related sets called chemosyndromes. In each chemosyndrome one or two compounds are regularly the major components, and the minor constituents of one chemosyndrome may become major constituents of other chemosyndromes (Culberson & Culberson 1976).

15 species were originally included in the genus, of which the majority are distributed in eastern and south-eastern Asia. Several species had so far been found also on the territory of the former Soviet Union but no special chemical or distributional studies of this material had been carried out. Altogether 244 specimens all over the world (including 203 samples from the Soviet Union) were analysed chemically by the author (III, Randlane & Saag 1992c). These studies led to the specification of the species treatment in the genus *Cetrelia.*

A type of chemical species consept has traditionally been accepted within this group of lichens. Different species with similar or even totally identical morphology may differ from each other only by the medullary constituents (Culberson & Culberson 1976). We have proposed to call the morphological groups separated by the Culbersons "morphotypes". The terms "morphotype" and "chemotype" have been given precise meanings and they are applied to populations of undetermined taxonomic rank or of no taxonomic value (Hawskworth 1974). Although these terms are usually used for marking infraspecific variations, they can sometimes also be applied to supraspecific groupings, as the concept of species in different lichen genera varies considerably. Generally, each species in the genus *Cetrelia* belongs to one morphotype and to one chemotype. Thus the combination of morpho- and chemotypes makes it possible to characterize concisely all the species known (Table 2). This makes it possible to use the table as an identification guide to the species. Besides its practical use, this table has also some theoretical value. Vacant squares in the table mark the species that are theoretically possible in the genus. This suggestion is confirmed by the fact that there were two specimens found in our analyses that did not belong to any species hitherto described, but still fitted the vacant places in the table. Since we think that material showing new combinations of known morpho- and chemotypes deserves the rank of species, the two new species, *Cetrelia orientalis* Randlane & Saag and *Cetrelia pseudocollata* Randlane & Saag, were described (III).

In *Cetrelia* the highest number of combinations of morpho- and chemotypes (i.e. species) are represented in eastern and south-eastern Asia. From among five morphotypes, only one (*cetrarioides*) is widely distributed in the world, whereas the areas of non-sorediate morphotypes (*isidiata, sinensis, collata,* and *davidiana*)

Table 2. Morpho- and chemotypes of *Cetrelia* (new species are in bold italics).

Morphotypes and their diagnostic characters	Chemotypes and their major components					
	I Alectoronic and α-collatolic a-s	II Microphyllinic a.	III Olivetoric a.	IV Anziaic a.	V Perlatolic a.	VI Imbricaric a.
Cetrarioides Thallus sorediose	*C. chicitae*		*C. olivetorum*		*C. cetrarioides*	*C. monachorum*
Isidiata Thallus isidiate	*C. braunsiana*			*C. isidiata*		
Sinensis Thallus with lobules	***C. orientalis***	*C. japonica*	*C. pseudolivetorum*			*C. sinensis*
Collata Thallus without vegetative propagules; large pseudocyphellae	*C. nuda*	***C. pseudocollata***				*C. collata*
Davidiana Thallus without vegetative propagules; small pseudocyphellae			*C. davidiana*	*C. sanguinea*	*C. delavayana*	*C. alaskana*

fall only into East and Southeast Asia. Lichens that have developed soredia can expand and effectively enlarge their area of distribution contrary to species that use only ascospores. The complicated process of resynthesis of a lichen thallus from a germinated ascospore and a free-living photobiont first depends upon the distribution area of algae (Tehler 1982). The other forms of vegetative propagules should theoretically also have the ability to colonize habitats in which the photobiont cannot thrive in its free-living form. In the genus *Cetrelia*, isidia and lobules still appear to be almost as ineffective in colonizing new territories as the spores. Thus only four sorediate species are found also in Europe and North America, in addition to Asia. The centre of speciation in the genus is presumably located in eastern and southern Asia as can be seen from the vast majority of the combinations of chemo- and morphotypes.

The first scheme dealing with the connections between species of *Cetrelia* was proposed by Poelt (1970, 1972) and related to his discussion on "species-pairs". Our scheme includes all the combinations of chemo- and morphotypes known in the genus up to now (Fig.4). The horizontal axis on the scheme shows the direction of chemical evolution and the vertical axis represents the variety of reproductive propagules. We presume that the formation and evolution of biochemical pathways producing the complex of lichen substances has taken place during sexual stages in the evolution of lichens, rather than through mutations in asexual stages (Bowler & Rundel 1975). The genus *Cetrelia* fits into the theory of development of "species-pairs" rather well, since every chemosyndrome is represented not only by the "secondary" but also by the "primary" species. This avoids the necessity of referring to some hypothetical ancestral taxa. All "primary" species with sexual reproduction appear to be quite rare with a very restricted distribution. However, not only pairs of species but also triplets or even tetrades of species can be observed in the genus *Cetrelia* (III). A similar pattern has been reported only in a few other cases, for example in *Parmelia* and *Physcia* (Hawksworth & Hill 1984).

The taxonomic treatment proposed by Tehler (1982), to recognize fertile and sterile counterparts as infraspecific taxa with the rank of forma, could be acceptable theoretically but not in practice. "Primary" species differ from the "secondary" species essentially in their morphology, and the "secondary" species of one column differ from each other as well. The morphological similarity between the taxa of the same morphotype is certainly great, but they all have presumably quite a different origin and cannot belong to one species. Otherwise we would be "back to the traditional typological species concept adamantly blind to everything but morphology" (Culberson 1986).

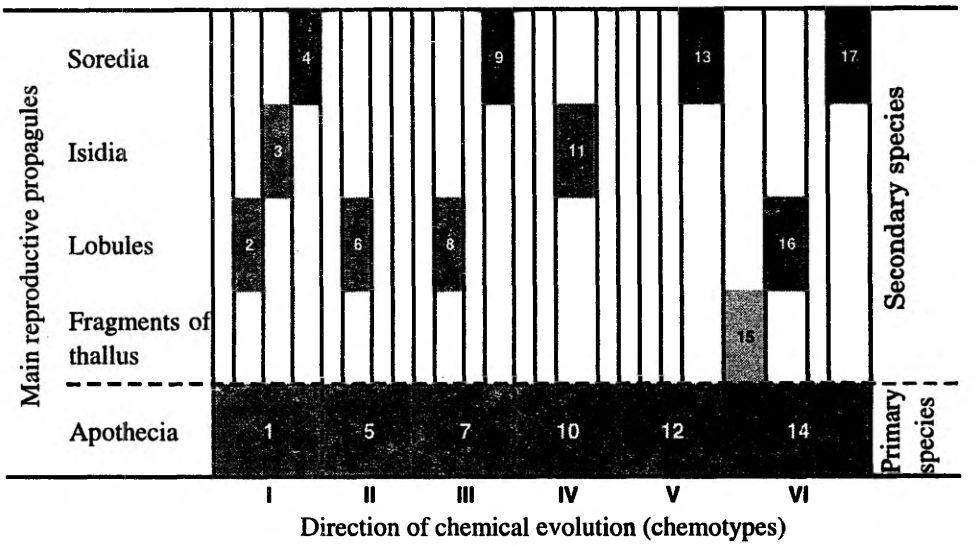

Fig. 4. Evolutionary relationships between *Cetrelia* species. Restricted to eastern and southeastern Asia (■), limited distribution outside eastern and southeastern Asia (▩), wide distribution both in- and outside eastern and southeastern Asia (■). 1 = *C. nuda*; 2 = *C. orientalis*; 3 = *C. braunsiana*; 4 = *C. chicitae*; 5 = *C. pseudocollata*; 6 = *C. japonica*; 7 = *C. davidiana*; 8 = *C. pseudolivetorum*; 9 = *C. olivetorum*; 10 = *C. sanguinea*; 11 = *C. isidiata*; 12 = *C. delavayana*; 13 = *C. cetrarioides*; *14* = *C. collata*; 15 = *C. alaskana*; 16 = *C. sinensis*; 17 = *C. monachorum*

The frequency and distribution of the examined species in the genus *Cetrelia*, serve, in our opinion, as good examples of some of the theoretical assumptions discussed above. All the sorediate species, although common and widely distributed, may be considered "evolutionary blind alleys". The organism loses its genetic flexibility by having an asexual propagation system superior to the sexual process (Tehler 1982). On the other hand, the sexual species, although occasionally less successful in dispersing, have retained their ability for further speciation by the process of gene recombination.

Evolutionary relationships in the genera *Cetreliopsis* and *Nephromopsis* (IV, V)

These genera — *Cetreliopsis* M. J. Lai and *Nephromopsis* Müll. Arg. — represent the first evolutionary line of cetrariod lichens characterized by the ellipsoid ascospores in narrowly clavate asci with a small axial body.

The genus *Nephromopsis* was described already in 1891 by Müller Argoviensis to accomodate *N. stracheyi* which was said to have a thallus similar

to *Cetraria* but the position of apothecia like in *Nephroma.* In contemporary lichenology the genus was not generally recognized until 1981, when Lai resurrected the treatment of the species with cetrarioid thallus, nephromoid apothecia, and pseudocyphellae on the lower surface in a separate genus under the name *Nephromopsis*. Still, the evaluation of important characters on the genus level has changed considerably. Today, as was remarked above, the anatomical features of the thallus and especially of the inner structures of ascomata are considered more conservative and, consequently, suitable for delimitation at generic level. Mainly on these grounds, the genus *Tuckneraria*) was separated from *Nephromopsis* (VI), and some taxa were transferred from *Nephromopsis* to *Allocetraria* (VII) or *Cetreliopsis* (IV).

The monotypic genus *Cetrariopsis* was separated from *Cetraria* s. lat. by Kurokawa in December 1980 (Kurokawa 1980). Less than a month later Lai (1981) proposed the genus *Ahtia* to accomodate the same species — *Cetraria wallichiana* (Taylor) Müll. Arg. Two essential characters were pointed out by both authors to describe the new genus — the numerous, small, laminal apothecia and the prosoplectenchymatic upper cortex. The structure of the cortex, however, was a misinterpretation by Kurokawa and Lai (see the discussion on p.19). According to the contemporary knowledge and terminology, the species of *Cetrariopsis* have a pachydermatous paraplectenchymatic cortex with randomly oriented cells like *Asahinea, Cetrelia,* and *Platismatia.* Still, *Cetrariopsis* is probably not closely related to those entities as it has been supposed earlier (Kurokawa 1980, Kärnefelt *et al.* 1992, Elix 1993).

The position of apothecia on the lower side of the thallus has been one of the most attractive and significant characters in defining the genus *Nephromopsis* since Müller Argoviensis, while the laminal position of apothecia over the upper surface remains the only true feature for the genus *Cetrariopsis* (Kurokawa 1980). The position of the apothecia is indeed a striking character, but a more thorough examination shows that specimens with clearly laminal apothecia usually have fruiting bodies along the margins as well. Furthermore, on many specimens with mostly marginal apothecia both submarginal or even truly laminal ascomata also occur. Our studies have shown that there is not much difference in the morphology, anatomy, and chemistry of these two genera except for their dissimilar positions of apothecia (IV). Therefore we have proposed transferring the two species of *Cetrariopsis* (*C. pallescens* and *C. laii*) to the genus *Nephromopsis* (Randlane *et al.* 1997).

The genus *Nephromopsis* is defined today by the following characters: a large foliose thallus; apothecia marginal on the lower surface of the thallus, or submarginal and laminal on the upper surface; presence of pseudocyphellae only on the lower surface; exciple usually three-layered but sometimes the

middle layer is not distinctly developed and is seen as two-layered in a few species; narrowly clavate asci and oblong ascospores; bifusiform pycnoconidia; usnic acid in the cortex; various fatty acids and/or some orcinol depsides-depsidones in the medulla. According to our present knowledge (V) the genus includes eleven species:

N. endocrocea Asahina
N. isidioidea (Räsänen) Randlane & Saag
N. komarovii (Elenkin) J. C. Wei
N. laii (Thell & Randlane) Saag & Thell
N. morrisonicola M. J. Lai
N. nephromoides (Nyl.) Ahti & Randlane,
N. ornata (Müll. Arg.) Hue
N. pallescens (Schaer.) Park
N. rugosa Asahina
N. stracheyi (Bab.) Müll. Arg.
N. yunnanensis (Nyl.) Randlane & Saag.

The genus *Cetreliopsis* was described by Lai (1981) in his paper on cetrarioid lichens in East Asia to settle the *Cetraria rhytidocarpa*-complex as he called it. The group included *Cetraria rhytidocarpa* Mont. & Bosch from Java, *Cetraria straminea* Vain. from the Philippines, and *Cetraria laeteflava* Zahlbr. from Taiwan. Lai synonymized all the three species on morphological and chemical grounds. He also pointed out the affinities of *Cetrelia* with *Nephromopsis* combining the names of these genera for the new taxon.

Our studies on *Cetreliopsis* have shown that this genus is well limited and clearly separated from other cetrarioid lichens. The identifying characters of the genus *Cetreliopsis* are: large foliose or subfruticose thallus; marginal or submarginal apothecia; presence of pseudocyphellae on both surfaces of the thallus; large, ellipsoid ascospores in rather broadly clavate asci and a two-layered exciple; content of fumarprotocetraric and protocetraric acids as major compounds in the medulla (PD+ red) and usnic acid in the cortex. We cannot agree with Lumbsch (Eriksson & Hawksworth 1988) who proposed to include *C. rhytidocarpa* in *Cetrelia* as a separate subgenus. He recognized mainly chemical differences between *Cetrelia* and *Cetreliopsis* and considered their morphology very similar. We find not only essential chemical differences but also morphological and anatomical differences between these two entities (IV: 47). The genus *Cetreliopsis* is probably more closely connected to *Nephromopsis* than to *Cetrelia*.

According to our present knowledge the genus cannot be treated as monotypic. Three new combinations have been proposed; furthermore, one new species and one new subspecies have been described (IV). We do not support in all parts the wide species treatment of *Cetreliopsis rhytidocarpa* proposed by

Lai (1981) and prefer to keep the sorediate Taiwan material as a separate species (*C. laeteflava*). The following five species are included in *Cetreliopsis:*

C. asahinae (Sato) Randlane & Thell
C. endoxanthoides (D. D. Awasthi) Randlane & Saag
C. laeteflava (Zahlbr.) Randlane & Saag
C. papuae Randlane & Saag
C. rhytidocarpa (Mont. & Bosch) M. J. Lai.

In our opinion these two genera — *Nephromopsis* (incl. *Cetrariopsis*) and *Cetreliopsis* — form a group of closely related taxa inside the first evolutionary line of cetrarioid lichens. Comparison of characters (Table 3) shows considerable similarity in general habit and anatomy of the thallus, inner structures of the ascocarps, conidial characters and cortical substances. All the 16 species of this generic complex are distributed in the mountainous forests of eastern and southeastern Asia only. Still, *Cetreliopsis* differs from *Nephromopsis* in some special morphological (pseudocyphellae on both surfaces), anatomical (asci rather broadly clavate, ascospores ellipsoid), and medullary chemical characters (absence of orcinol depsides and depsidones, and presence of ß-orcinol depsidones — fumarprotocetraric acid and related substances in all species), and is therefore maintained as a separate genus (V).

Table 3. Comparison of characters in *Cetreliopsis* and *Nephromopsis.*

Character	*Cetreliopsis*	*Nephromopsis*
Thallus	foliose	foliose
Upper and lower cortex	1-layered, paraplectenchymatous	1-layered, paraplectenchymatous
Pseudocyphellae	on both surfaces	on lower surface
Soredia	may be present	absent
Marginal cilia	may be present	absent
Apothecia	marginal and submarginal on upper surface	marginal on lower surface, submarginal and laminal on upper surface
Exciple	2-layered	usually 3-layered, sometimes 2-layered

Ascus shape	rather broadly clavate	narrowly clavate
Ascospores	ellipsoid, 6–12 × 4–7 µm	oblong, 5–10 × 2,5–5 µm
Axial body	2,5–4 µm	0,5–4 µm
Ring structure	absent	present in two species
Pycnidia	laminal or marginal, immersed or on projections	laminal or marginal, immersed or on projections
Pycnoconidia	bifusiform, 5 × 1–2 µm	bifusiform, 4–5 × 1–1,5 µm
Cortical substances	usnic acid	usnic acid
Medullary substances: a) fatty acids	present	present
b) orcinol depsides & depsidones	–	alectoronic a., physodic a., olivetoric a.
c) β-orcinol depsidones	fumarprotocetraric a., protocetraric a., physodalic a., salazinic a., Cph-1	–
d) secalonic acids	–	endocrocin, secalonic acids A and C

Evolutionary relationships in the group of cetrarioid lichens with globose ascospores (VI, VII, VIII and IX)

The species belonging to the second evolutionary line of cetrarioid lichens are treated in more detail here. This evolutionary line, anatomically characterized by subglobose to globose ascospores in narrowly clavate asci, is considered monophyletic (Thell 1996). This assumption is supported by two earlier cladistic analyses on several various species of cetrarioid lichens, carried out independently in Lund (Kärnefelt *et al.* 1992) and in Tartu (I). In both analyses the clade including species with globose ascospores was clearly separated. The group comprised at first (Thell 1996) five genera — *Ahtiana, Allocetraria, Esslingeriana, Tuckneraria,* and *Tuckermanniopsis*; we also add the genus *Dactylina* here because of its obvious affinities to *Allocetraria.* Four genera of

the six, *Ahtiana, Allocetraria, Dactylina,* and *Tuckneraria*, have been thoroughly revised lately (VI, VII, VIII, Kärnefelt & Thell 1996). The sole species of the monotypic genus *Esslingeriana* was described completely by Esslinger (1971). *Tuckermannopsis* is the only taxon still in need of revision. Nevertheless, the data characterizing these taxa are scattered in many papers and evolutionary affinities between all the species included have not been evaluated yet.

Phylogenetic analysis of the group was carried out using cladistic parsimony methods.

Taxa analysed. 30 species from the six above-listed genera were applied as terminal taxa (IX).

For choosing the outgroup we had, in principle, two alternatives: a taxon either from the group close to *Cetraria* (the first evolutionary line of cetrarioid lichens) or from the group related to the so-called "parmelioid Cetrariae" (the third evolutionary line). The form of asci — narrowly clavate — is the same in the ingroup and in the group close to *Cetraria,* while the third group has typically broadly clavate asci. Therefore, the parmelioid and allied genera were discarded at first. Two genera of those seven included in the first evolutionary line — *Cetraria* s. str. and *Flavocetraria* — were seriously considered as possible outgroups. Ascocarps of *Flavocetraria* are characterized by ellipsoid ascospores, narrowly clavate asci with a small axial body, and presence of an amyloid ring structure. These characters are similar to *Cetraria* s. str. and differ from those of the ingroup. Still, the stucture of upper and lower cortices and secondary chemistry of *Flavocetraria* is more similar to the studied taxa. Finally, *Flavocetraria cucullata* was selected as outgroup for one series of analyses.

Later the species from the third evolutionary line were also evaluated as possible samples for outgroup. In earlier analyses (Kärnefelt *et al.* 1992, I) *Cetraria fendleri* appeared as one representative of the sister group to the assamblege which is treated as ingroup here. Anatomically, ascocarps of *C. fendleri* are characterized by ellipsoid ascospores, broadly clavate asci, a large axial body, and absence of an amyloid ring structure. The ingroup differs from the species under discussion in two former and is similar in two latter characters. Therefore, *C. fendleri* was additionally chosen as outgroup.

Both selected species — *Flavocetraria cucullata* and *Cetraria fendleri* — were used to root the trees in separate series of analyses.

Characters. All in all, 36 morphological, anatomical, and chemical characters were used for the analysis. Lichen substances were not treated independently from each other but grouped into biochemically related sets, as suggested in our previous study (I).

Character states were coded as 0, 1, 2, 3 and 4; all multistate characters were treated as unordered. The characters and character states were the following.

1. Form of thallus: adnate (0), ascending (1)
2. Symmetry of thallus: dorsiventral (0), radial-symmetrical (1)
3. Interior of thallus: of densely arranged hyphae (1), of loosely arranged hyphae (1), becoming hollow (3)
4. Form of lobes: length of lobes ~ width of lobes (0), lobes longer than wide (1)
5. Width of lobes: up to 3 mm (0), up to 6 mm (1), up to 12 mm (2)
6. Colour of upper surface: yellow (0), brown (1), grey (2)
7. Colour of lower surface: whitish (0), yellow (1), brown (2), black (3)
8. Pseudocyphellae on upper side: absent (0), present (1)
9. Pseudocyphellae on lower side: absent (0), present (1)
10. Form of pseudocyphellae on lower side: spots (0), lines (1)
11. Cilia: absent (0), present (1)
12. Rhizines: absent (0), present (1)
13. Soredia: absent (0), present (1)
14. Isidia: absent (0), present (1)
15. Structure of the cortex (orientation of hyphae): both corteces paraplectenchymatous, i.e. hyphae randomly oriented (0), upper cortex palisade plectenchymatous, i.e. hyphae anticlinally oriented (1), both corteces palisade (2), both corteces prosoplectenchymatous, i.e. hyphae parallel to cortex (3)
16. Cell wall thickness (compared to cell lumina): leptodermatous (0), pachydermatous (1)
17. Position of apothecia: marginal only (0), marginal to submarginal (1), laminal (2), terminal (3)
18. Ascus shape: broadly clavate (0), narrowly clavate (1)
19. Ascus form: melanelia type (0), tuckermannopsis type (1), cetraria type (2)
20. Tholus: small (0), large (1)
21. Axial body: medium [3–5 μm] (0), broad [>5 μm] (1), narrow [<3 μm] (2), very narrow [<1 μm] (3)
22. Shape of ascospores: globose to subglobose (0), broadly ellipsoid (1), ellipsoid (2)
23. Length or diameter of ascospores: short [6 μm] (0), long [>6 μm] (1)
24. Position of pycnidia: marginal only (0), marginal and laminal (1), laminal only (2)
25. Emergency of pycnidia: emergent (0), immersed (1)
26. Shape of pycnoconidia: bacillariform (0), oblong citriform (1), dumb-bell shaped incl. disc-bar shaped (2), filiform (3), sublageniform (4)
27. Length of pycnoconidia: short [<7 μm] (0), medium [7–10 μm] (1), long [>10 μm] (2)
28. Usnic acid: absent (0), present (1)
29. Atranorin: absent (0), present (1)
30. Fatty acids: absent (0), present (1)

31. Substance of fatty acids: lichesterinic-protolichesterinic type acids (0), caperatic acid (1), rangiformic acid (2), unidentified (3)

32. Secalonic acids: absent (0), present (1)

33. Orcinol depsides and depsidones: absent (0), present (1)

34. Substance of orcinol depsides and depsidones: alectoronic and collatolic acids (0), physodic acid (1), olivetoric acid (2), microphyllinic acid (3), gyrophoric acid (4)

35. β-orcinol depsidones: absent (0), present (1)

36. substance of β-orcinol depsidones: fumarprotocetraric acid (0), physodalic acid (1)

The data matrix and terminal taxa are presented in publication IX.

Results. Two series of separate analyses were carried out using different outgroups (*Cetraria fendleri* and *Flavocetraria cucullata*) (IX).

With *Cetraria fendleri* as outgroup, 36 equally parsimonous trees were obtained (heuristic search, all characters with equal weights, length of trees = 121 steps, Fig. 5). The strict consensus tree and the 50% majority-rule consensus of 36 trees were also retained. The successive approximations character weighting method produced 108 equally parsimonous trees and, after the second reweightening of characters, 81 equally parsimonous trees were

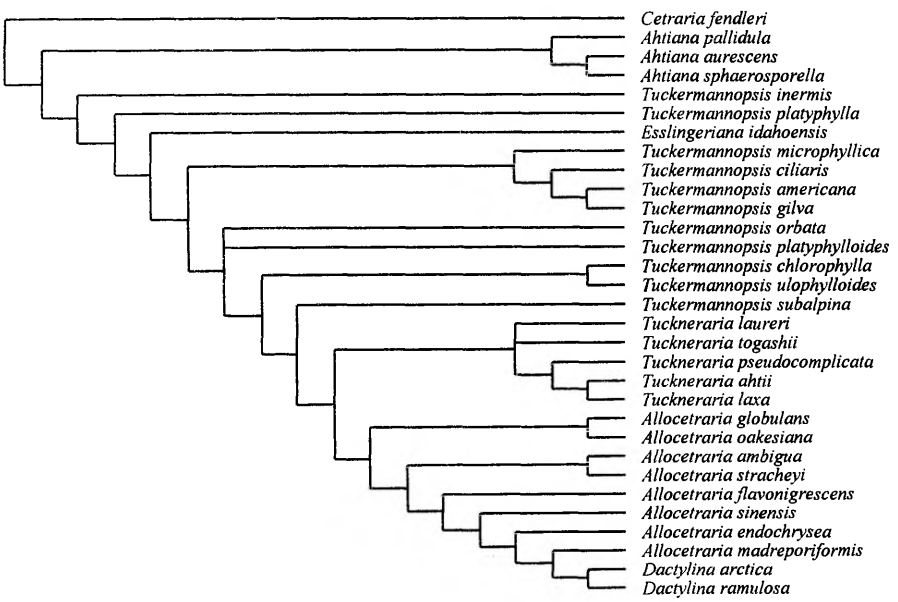

Fig. 5. One of 36 equally parsimonous cladograms (based on characters with equal weights; *Cetraria fendleri* used to root trees). Length 121, consistency index 0.405, retention index 0.654.

obtained (strict consensus tree on Fig. 6). Successive weighting is particularly useful when applied to data sets with much homoplasy (Tehler & Egea 1997). Character reweighting by maximum value of rescaled consistency indices generated remarkably low weights for some conspicuous morphological characters often used in key-books, such as presence of isidia and soredia. This is quite acceptable, in our opinion, as these asexual structures are certainly derived but they cannot be treated as shared characters. In other words, we suppose that sorediate and isidiate species did not share sorediate or isidiate ancestors but descended from sexual species instead. The most highly weighted characters are either connected with the anatomy of the thallus (characters 2, 3, 15), anatomy of the ascocarps (18, 19, 20) or medullary secondary compounds (31, 34, 36).

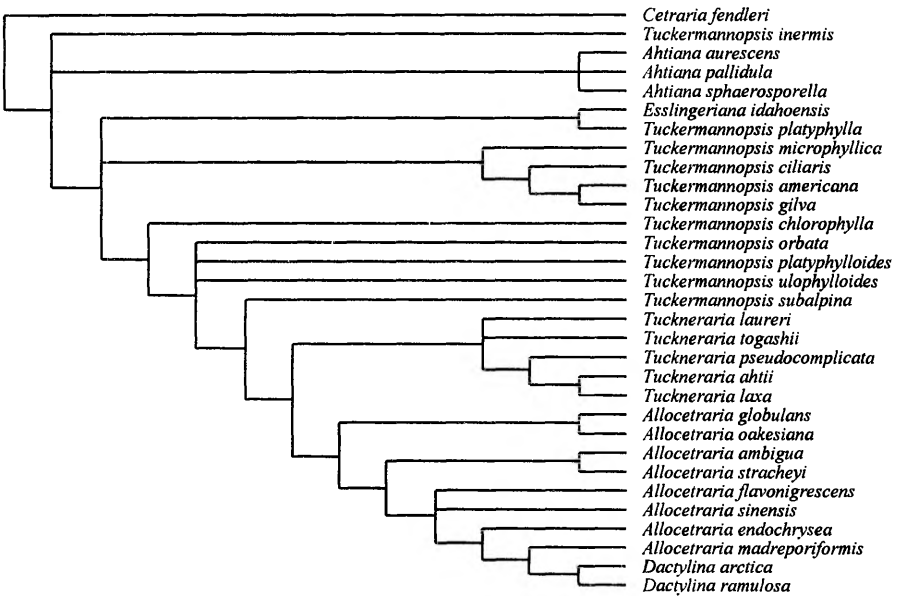

Fig. 6. Strict consensus tree constructed from 108 equally parsimonous cladograms (based on characters reweighted; *Cetraria fendleri* used to root trees). Length of shortest trees 35 723, consistency index 0.644, retention index 0.800.

Some clades, which are seen on one of the equally parsimonous cladograms of the initial analysis (Fig. 5), are distinct also in the following analyses (Fig. 6). The biggest clade consists of eight *Allocetraria* and two *Dactylina* species. Next clade includes five *Tuckneraria* species. Four species of *Tuckermannopsis* (the so-called *T. ciliaris* group) also form a separate clade, while the other members of that genus are solved differently in different analyses. The fourth clade, including three *Ahtiana* species, is supported by 92% of trees (characters with equal weights); trees produced by the successive approximations character weighting method always show the same *Ahtiana* clade.

The Bremer support test was carried out next. In this test all the trees are kept successively one step longer than the shortest tree, until all the groups are lost in consensus. Bremer's length difference has also been referred to as the decay test or decay index (Parmasto 1996, Tehler & Egea 1997). In our analysis, inclusion of trees one step longer than the shortest tree, causes the majority of the tree to collapse into a polytomy, and only the *Allocetraria–Dactylina* clade remains separately. The latter begins to decay by the Bremer support value of three.

With *Flavocetraria cucullata* as outgroup, 1557 equally parsimonous trees (heuristic search, all characters with equal weights, length of trees = 123 steps) were obtained. Both strict consensus tree and 50% majority-rule consensus (Fig. 7) were saved. The clade of *Ahtiana*, consisting of three species, is supported by 78% of trees. The clade of *Allocetraria* (including *Dactylina*), which was strongly supported in the first analysis, collapses into a polytomy. Still, two species of *Dactylina* form a separate clade with two *Allocetraria* species (*A. endochrysea* and *A. madreporiformis*) in the strict consensus tree. The clade including *Tuckneraria* species is not supported by this analysis either. One new clade, which consists of 11 species of *Tuckermannopsis* and one species of *Esslingeriana,* is composed in all cladograms. When characters were reweighted by maximum value of rescaled consistency indices, five equally parsimonous trees were obtained. Strict consensus tree (Fig. 8) of them is essentially different from that achieved by analysis, where characters were with equal weights (Fig. 7); besides, some groups similar to the clades mentioned in the first series of analysis (with *Cetraria fendleri* as an outgroup), are formed. These are: the clade of three species of *Ahtiana*; the clade of eight species of *Allocetraria* and two species of *Dactylina*; the clade of four species of *Tuckermannopsis* (*T. ciliaris* group). *Tuckneraria* species do not form a clade in this analysis.

In addition, analyses were carried out using the parsimony jackknifer programme Jac, to identify well-supported monophyletic groups. In Jac, the data are resampled with a jackknifing technique, i. e. in every replicate c. 66% of the characters are chosen at random, without replacement for parsimony analysis. The resampling procedure can be repeated up to 10 000 times, as it was also done in the present study. The objective of the jackknife method in Jac is the same as that of bootstrapping in PAUP (Tehler & Egea 1997), but considered much faster than other available techniques. The resulting tree (not presented) shows that all the clades described above are not supported by this very efficient procedure, except for a group consisting of two *Dactylina* species, and another group comprising *Allocetraria globulans* and *A. oakesiana.*

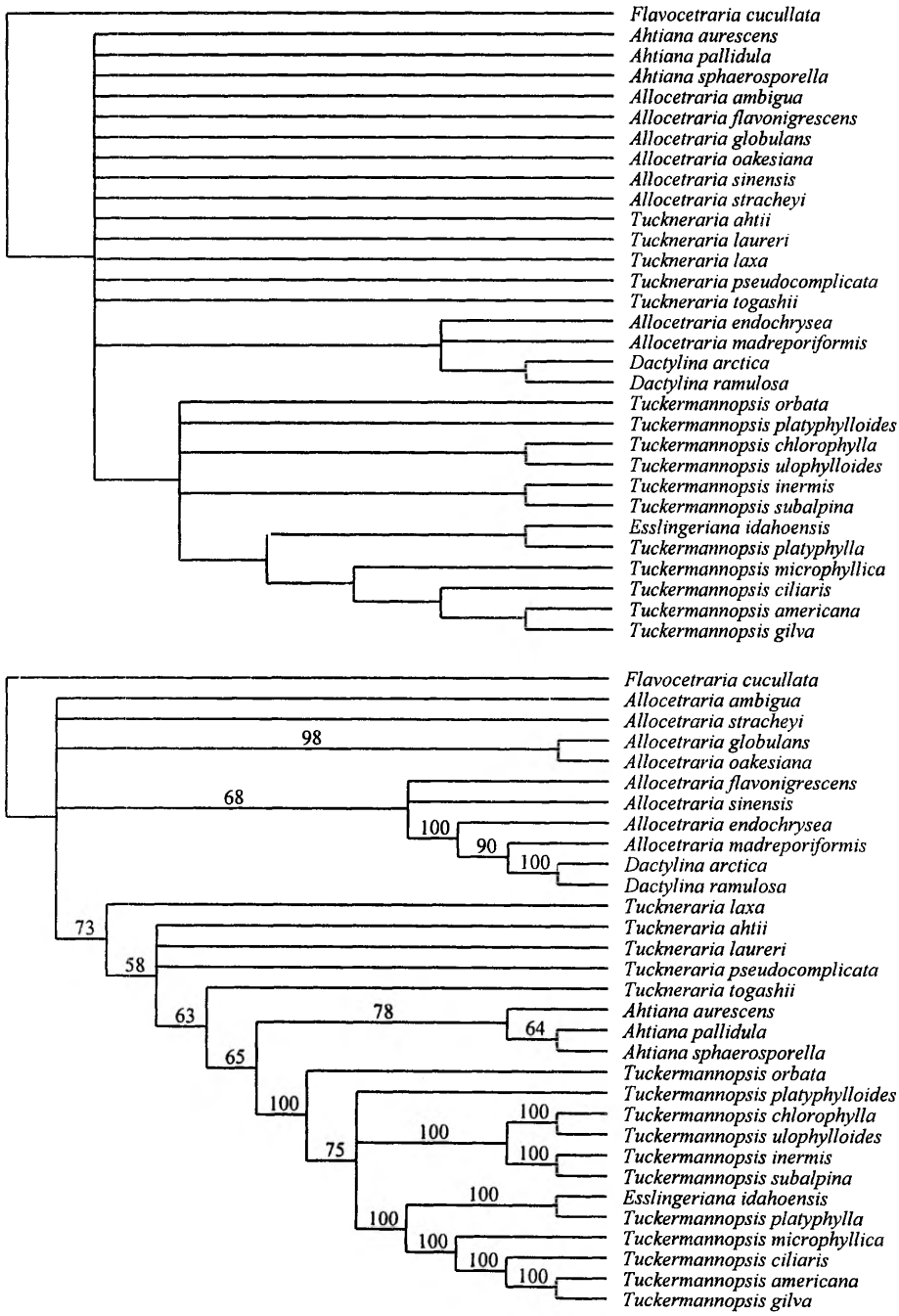

Fig. 7. Strict consensus tree and 50% majority-rule consensus tree constructed from 1557 equally parsimonous cladograms (based on characters with equal weights; *Flavocetraria cucullata* used to root trees). Length of shortest trees 123, consistency index 0.415, retention index 0.650.

Bootstrapping (500 replicates) was used as well — on the same purpose. Three small groups were supported by this method: *Allocetraria globulans – A. oakesiana*; *Tuckermannopsis americana – T. ciliaris – T. gilva*; *Allocetraria endochrysea – A. madreporiformis* together with the two Dactylinas as a subclade.

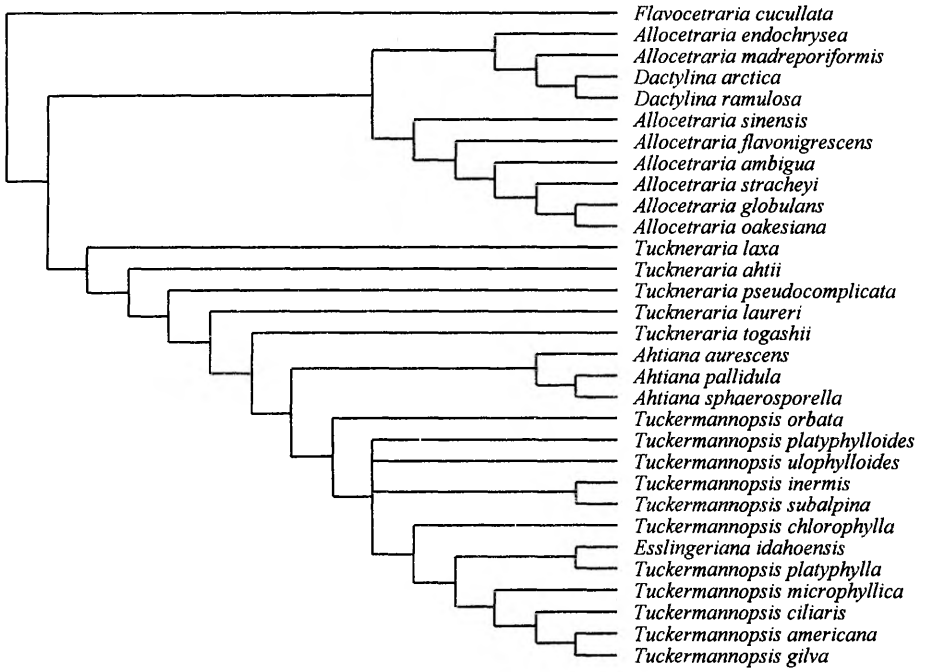

Fig. 8. Strict consensus tree constructed from 5 equally parsimonous cladograms (based on characters reweighted; *Flavocetraria cucullata* used to root trees). Length of shortest trees 43 164, consistency index 0.658, retention index 0.808.

Discussion. The aim of the present phylogenetic analysis was to search for the monophyletic groups inside the ingroup and check the correspondence of the present taxonomy to the probable evolution of taxa involved.

Originally monotypic genus *Ahtiana* was segregated from *Parmelia* s. lat. on the basis of emergent pycnidia, globose ascospores, leptodermatous cortex, and presence of medullary caperatic acid (Goward 1985). Despite its parmelioid habit with laminal apothecia and pycnidia, *Ahtiana sphaerosporella* was shown to be closely allied to *Cetraria pallidula*. Today the genus includes three species. In our present analysis, it appears as a separate clade in most of the cladograms of characters with equal weights and also in the successive weighting strict consensus trees of both series of analyses (with different outgroups). This fact supports the latest changes in the systematics of the genus — transferring *C. pallidula* and *C. aurescens* to the originally monotypic *Ahtiana* (VIII).

The genus *Allocetraria*, at first including only three species from high altitudes in south-east Asia, was introduced by Kurokawa & Lai (1991). It was separated from *Cetraria* because of the dichotomously branched lobes, the special appearance of pseudocyphellae, the palisade plectenchymatous cortex, and on the unique chemistry. The authors did not pay attention to ascomatal and pycnidial characters. Later studies of these structures confirmed the necessity of a separate genus (VII). Today, ten species are combined in the genus; eight of them were included in our analyses. We have not seen the herbarium material of two taxa (*A. denticulata* and *A. isidiigera*), and their descriptions (Hue 1899; Kurokawa & Lai 1991) are too poor to present them properly in the data matrix. The value of these taxa is rather uncertain — both species are known from the type localities only; in addition, they are sterile according to literature.

The paraphyletic nature of the genus with respect to two species of *Dactylina* is obvious. The closeness of these two genera was noticed only recently when two former Dactylinas — *A. madreporiformis* and *A. endochrysea* — were transferred to *Allocetraria* (Kärnefelt & Thell 1996). Presence of filiform pycnoconidia and asci with extremely broad axial body are the essential characters for separating *Allocetraria*. *Dactylina* is distinguished by the radialsymmetrical thallus becoming hollow, the terminal position of apothecia, and also the secondary chemistry. The palisade plectenchymatous arrangement of cortical hyphae, which is rather unusual in the group of cetrarioid lichens, is characteristic of both *Allocetraria* and *Dactylina*. The splitting of the species involved into two separate genera is not supported by our present study. At the same time, the analyses based on morphological, anatomical, and chemical characters only do not show enough confidence when using more severe methods, such as jackknifing or bootstrapping. We share the opinion recently approved by the symposium on taxonomy, evolution and classification of lichens and related fungi (January 9–11, 1998, London), that on such occasions quick changes in nomenclature are not advisable. At the present stage of lichenological studies, additional phylogenetic analyses using the modern molecular data should be carried out, before proposing extensive nomenclatural changes.

Tuckneraria includes five species. Most of them were transferred from *Nephromopsis* to the newly described genus because of important anatomical characters (globose ascospores, Tuckermannopsis-type asci, small axial body etc.) (VI). Today the genera *Nephromopsis* and *Tuckneraria* are even considered to represent different evolutionary lines (Thell 1996) of cetrarioid lichens. The idea of close affinities of *Tuckneraria* and *Ahtiana* has also been proposed (VIII). The monophyletic origin of the genus *Tuckneraria* is supported in one series of our analyses (*Cetraria fendleri* used to root trees). In the other series (*Flavocetraria cucullata* used to root trees) the species of *Tuckneraria* do not form a separate clade but are branched out successively.

Genus *Tuckermannopsis* was described by Gyelnik (1933) in a very short manner: "Affinis generi Nephromopsi sed thallus subtus pseudocyphellis

deficientibus". Today much more is known about the genus but the correct description is still not presented. According to different authors (Lai 1981, Hale in Egan 1987, Kurokawa 1991, Weber in Egan 1991) various species have been transferred to *Tuckermannopsis*; many of them have later been combined again into other genera (*Ahtiana, Allocetraria, Kaernefeltia, Melanelia, Vulpicida*). At present it is generally accepted that globose ascospores in narrowly clavate asci, large axial body, dumb-bell shaped pycnoconidia, and moderately small foliose brown to greenish thallus (absence of usnic acid in the cortex) are the important characters in delimiting the genus. Eleven species are now recognized in *Tuckermannopsis*. Our phylogenetic analyses reveal further problems within this taxon. Monophyletic origin can be declared only for the so-called *Tuckermannopsis ciliaris* group (*T. ciliaris* is also the type species of the genus). The clade consisting of four close species is strongly supported in all parsimonous trees. On the whole, the genus *Tuckermannopsis*, in its generally accepted treatment, should be considered paraphyletic. For instance, *E. idahoensis*, the sole species of the genus *Esslingeriana*, is predominately connected with *Tuckermannopsis platyphylla* and this pair of species always branches out next to *Tuckermannopsis ciliaris* group. Other members of the genus do not form a distinguished group. In our opinion, any further taxonomical rearrangements in this genus are not justified before additional — preferably molecular — research has been carried out.

CONCLUSIONS

1. The group of cetrarioid lichens (fam. *Parmeliaceae*, lichenized Ascomycota), comprising 131 species in 22 genera, is polyphyletic. Three evolutionary lines, based mainly on reproductive structures and anatomical characters, have been recognized for the group. Phylogenetic relationships within some cetrarioid genera representing different evolutionary lines have been treated in more detail.

2. Chemosystematical and geographical studies in genus *Asahinea* reveal that a possible centre of speciation of the genus is in the Russian Far East or Japan. Three chemotypes have been recognized in *Asahinea chrysantha*: I — atranorin, alectoronic acid, and a-collatolic acid; II — atranorin, alectoronic acid, a-collatolic acid, and usnic acid; III — atranorin, alectoronic acid, and usnic acid. Chemotype I of *A. chrysantha* is the same as that of *A. scholanderi*; this is supposed to represent the basic, primitive chemistry of the genus.

3. A type of chemical species concept has traditionally been accepted in genus *Cetrelia*. We propose to treat every species in this genus as a combination of morpho- and chemotypes, and present an appropriate table where vacant squares mark the species that are theoretically possible in the genus. As a result, two new species — *Cetrelia orientalis* Randlane & Saag and *C. pseudocollata* Randlane & Saag — are described. The role of "primary" and "secondary" species in the systematics of the genus according to the "species-pairs" theory is discussed.

4. Altogether 16 species from the genera *Cetreliopsis*, *Nephromopsis*, and *Cetrariopsis* are thoroughly characterized and compared. In our opinion two of these taxa — *Nephromopsis* and *Cetreliopsis* — are separate, although closely related units, while the species of *Cetrariopsis* are transferred to the genus *Nephromopsis*. One new species (*Cetreliopsis papuae* Randlane & Saag) is described.

5. The group of cetrarioid lichens comprising six genera (*Ahtiana, Allocetraria, Dactylina, Esslingeriana, Tuckneraria,* and *Tuckermannopsis*), characterized by subglobose to globose ascospores in narrowly clavate asci, is phylogenetically analysed. Genus *Tuckneraria* is originally described and two other genera — *Ahtiana* and *Allocetraria* — are thoroughly revised. Cladistic analyses refer to further necessary changes in the systematics of the group.

6. The present state of taxonomy in the heterogenous group of cetrarioid lichens is far from being final. Splitting of big genera and describing of several new small genera has been the obvious tendency in systematics of lichens during the last decade. This process has caused difficulties when using the nomenclature and also objections in principle. We support the opinion that the main disagreement in this debate is not the grouping of taxa but their ranking. At the present stage of lichenological studies, additional phylogenetic analyses using molecular data should be carried out, before proposing extensive nomenclatural changes.

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EVOLUTSIOONILISED SEOSED MÕNEDES TSETRARIOIDSETES PEREKONDADES (LIHHENISEERUNUD KOTTSEENED)

Kokkuvõte

Tsetrarioidsete samblike rühm (suguk. *Parmeliaceae*, lihheniseerunud kottseened), mis sisaldab praegu teadaolevatel andmetel 131 liiki 22 pere-konnast, on üldtunnustatult polüfüleetiline. Vaadeldavas rühmas on täheldatud kolme evolutsioonilist suunda, mille piiritlemine põhineb eelkõige samblike anatoomilistel tunnustel ja viljakehade siseehitusel. Käesolevasse doktoritöösse on koondatud uurimused, mis käsitlevad üksikasjalikumalt fülogeneetilisi seoseid järgmistes tsetrarioidsetes samblikuperekondades: *Ahtiana, Allocetraria, Asahinea, Cetrelia, Cetreliopsis, Dactylina, Esslingeriana, Nephromopsis, Tuckneraria* ja *Tuckermannopsis*.

Kemosüstemaatiline ja geograafiline analüüs võimaldab teha oletusi perekonna *Asahinea* liikide tõenäose tekkekeskme kohta. Liigis *A. chrysantha* on määratud kolm kemotüüpi: I kemotüüp sisaldab atranoriini, alektoroonhapet ja α-kollatoolhapet; II — atranoriini, alektoroonhapet, α-kollatoolhapet ja usniinhapet; III — atranoriini, alektoroonhapet ja usniinhapet. *A. chrysantha* I kemotüüp esindab sama samblikuainete komplekti, mis esineb ka liigis *A. scholanderi*. Lähtudes samblikuainete keemilisest koosseisust ja nende tekke biosünteesi radadest, võib väita, et see kemotüübi keemiline koostis on vaadeldavas perekonnas ürgseim. Võttes arvesse eri kemotüüpide levikut, tuleb perekonna *Asahinea* liigitekke tsentriks pidada Venemaa Kaug-Ida või Jaapanit.

Perekonna *Cetrelia* liikide puhul on samuti oluliseks tunnuseks samblikuainete koosseis. Käesolevas töös vaadeldakse *Cetrelia* liike kui kemo- ja morfotüüpide kombinatsioone ning esitatakse vastav tabel, mille tühjad ruudud viitavad teoreetiliselt võimalikele liikidele selles perekonnas. Tabelist lähtudes kirjeldataksegi kaks teadusele uut liiki. Käsitletakse ka liikide paaride teooriat ning selle rakendamise tulemusi perekonnas *Cetrelia*.

Esitatakse üksikasjalik ülevaade perekondade *Cetreliopsis, Nephromopsis* ja *Cetrariopsis* liikidest. Tunnuste võrdlemisel selgub, et pole olulisi erinevusi perekondade *Nephromopsis* ja *Cetrariopsis* vahel (v.a. apoteetsiumite erinev asend tallusel). Seetõttu ei peeta vajalikuks perekonna *Cetrariopsis* tunnustamist iseseisva taksonina. Perekondi *Cetreliopsis* ja *Nephromopsis* käsitletakse erinevate, kuid fülogeneetiliselt lähedaste rühmadena.

Morfoloogiliste, anatoomiliste ja keemiliste tunnuste alusel analüüsitakse kladistiliselt rühma, kuhu kuulub kuus perekonda (*Ahtiana, Allocetraria, Dactylina, Esslingeriana, Tuckneraria* ja *Tuckermannopsis*), et anda hinnang selle rühma praegusele taksonoomiale. Selgub, et vajalikud on süsteemi ja nomenklatuuri täiendavad muudatused, kuid neid ei peeta võimalikuks enne molekulaarseid uuringuid.

Seniste uurimuste käigus on kirjeldatud üks uus perekond: *Tuckneraria* Randlane & Thell, ning neli uut liiki: *Cetrelia orientalis* Randlane & Saag, *C. pseudocollata* Randlane & Saag, *Tuckneraria ahtii* Randlane & Saag, *Cetreliopsis papuae* Randlane & Saag. Samuti on esitatud mitu uut kombinatsiooni.

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PUBLICATIONS

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Cryptogamic Botany

Phylogenetic affinities of cetrarioid Lichens

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SUMMARY

Of about 120 known cetrarioid lichen species, 83 were chosen for cladistic analysis to evaluate the present systematic arrangement of these taxa. 42 classically accepted morphological, anatomical and chemical characters were examined using original and literature data. According to the analysis, several recently described cetrarioid genera (e.g. *Cetrelia, Platismatia, Masonhalea, Cetrariopsis, Vulpicida*) appear to be monophyletic and thus acceptable. Species of *Nephromopsis* are very closely related to the monospecific genus *Cetreliopsis*. Neither the brown fruticose *Cetraria* species group nor the genus *Tuckermannopsis* could be treated as monophyletic.

Introduction

The genus *Cetraria* has been since its description by E. Acharius in 1803 a heterogeneous assemblage of poorly related taxa. From eight species originally included in *Cetraria*, now only the type species – *C. islandica* – has been left in the genus. *C. cucullata* and *C. nivalis* are proposed to be included in *Allocetraria* [17]; *C. lacunosa, C. glauca* and *C. fallax* represent species of *Platismatia* [6]; *C. sepincola* belongs to the poorly defined genus *Tuckermannopsis* [7]; and *C. juniperina* is a member of the newly described *Vulpicida* [12]. In the contemporary taxonomy of lichenized fungi, about 120 species are known as cetrarioid [16], i.e. Cetraria-like. While the original delimitation of the genus *Cetraria* is insufficient, it is still more complicated to define the colloquial term "cetrarioid". The total list of cetrarioid lichens [18] presents all species that ever have been included in the genus *Cetraria*, and the allied taxa. The list serves as a starting point for the present paper. It is evident that the group of species under discussion is not monophyletic. 14 different genera have been newly described or resurrected to accommodate the species [18]. Still, the present systematic arrangement of these taxa is not convincing in all aspects. The objective of the present paper was to evaluate the traditional classification of this group on the basis of cladistic analysis and get new ideas for further studies.

Material and Methods

The data matrix for the cladistic analysis was compiled on the basis of both literature (mainly on anatomical and partly chemical characters) and original studies (morphological and chemical data). Although the reliability of the information in the literature may be doubtful in some cases, it was not practical to investigate all the characters of all species newly. Herbarium material has been examined from H, KW, LD, LE, TB, TU and UPS using microscope MBS-9. Chemical analyses were performed according to the standardized TLC methods [3, 4]. Cladistic analyses were carried out using the program PAUP version 3.0s [19] on a Macintosh IIci personal computer. The following option settings were used: character-state optimization – DELTRAN; MULPARS; MAXTREE = 1000, 3900; heuristic search; trees rooted using outgroup method; for functional outgroup rooting a monophyletic sister group used; addition sequence -simple; 3 trees held at each step during stepwise addition; tree-bisection-reconnection (TBR) branch-swapping performed; characters reweighted by maximum value of rescaled consistency indices. Strict consensus trees of both original data based cladograms and after characters reweighted were retained.

Three analyses were carried out independently on the same data basis which was arranged differently for each analysis. In the first analysis the major secondary compounds of lichens were treated as separate characters (characters 26, 32 and 39 excluded). In the second analysis the lichen substances were not represented as independent characters (characters 27–29, 33–38, 40–42 exluded) but grouped into bigger units (fatty acids, orcinol series products, β-orcinol series products) according to their

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Table 1. (1.) Data matrix and terminal taxa.

	00000000011111111112222222222333333333344 12345678901234567890123456789012345678901234567890123456789012
Ahtiana sphaerosporella	00000010010010101101000101100000000000000
Allocetraria ambigua	20100010001011000012???? 1010010000000000000
A. cucullata	20110010101011000011000101001100000000000
A. nivalis	20010010000101100001100010000000000000000
A. stracheyi	20100010101010101010001100001100000000000
Asahinea chrysantha	11000000011021011010010110000001001000000
A. scholanderi	10000100011C1101111001001000000100100000
Cetraria agnata	01000010011011011010000000000000000000000
C. andrejevii	20010000101021001011010001010000000000000
C. arenaria	20110000101011000010010001001000000000000
C. californica	31000001001011000011000000000000000000000
C. commixta	00100010101011011010000000000010010000000
C. delisei	20010000001011000011000000000010000100000
C. ericetorum	20100000101011000010010001001000000000000
C. fastigiata	20010000001011000011000000000010000100000
C. inermis	10100010001010101010010001001000000000000
C. islandica	20110000101021000010010001001000000000110 0
C. kamczatica	20000000001001000012?2000100100000000000
C. laevigata	20100000101011000010010001001000000000110 0
C. nigricans	20000001101011000010010001001000000000000
C. nigricascens	20000001101011000011000001010000000000000
C. odontella	20100001101001001011000001001000000000000
C. rassadinae	20110000101011000010010001001000000000000
C. subalpina	10000000101010101010010001001000000000000
C. weberi	00000110011011001111000000000001000100000
Cetrariopsis wallichiana	10010010010001010?????? 1010010010010000000
Cetrelia braunsiana	11000110010001012011000010000001001000000
C. cetrarioides	11011010010001012011000010000001100000000
C. chicitae	11011010010011012011000010000001001000000
C. collata	11010010010021012011000010000001100000000
C. davidiana	11010010010021012111000010000001000100000
C delavayana	11010010010011012011000010000001100000000
C. japonica	11010110010011012011000010000001000001000
C. monachorum	11011010010001012011000010000001100000000
C. nuda	11010010010021011111000010000001001000000
C. olivetorum	11011010010011012011000010000001000100000
C. pseudolivetorum	11010110010021012011000010000001000100000
C. sanguinea	11010010010021012010010010000001010000000
Cetreliopsis rhytidocarpa	11011010100111011012???? 1010010000000001100
Esslingeriana idahoensis	10000010011010101111000011000100000000000
Masonhalea richardsonii	20010000001011001010010000000010010000000
Nephromopsis asahinae	11010010100111011111???? 1000000000000001100
N. ectocarpisma	10010010000111000012???? 1010000000000000000
N. endocrocea	10010010100111000011000001000100000000000
N. endoxanthoides	11010010100111001012???? 0010011000000001100
N. globulans	10010010100111010102???? 1010011000000000000
N. komarovii	10010010100111000?????? 1010010000000001000
N. laureri	10011010000111000011000101001000000000000
N. ornata	10010010100120101012???? 1000001000000001100
N. pallescens	10010010000101000012???? 1010010000000000000
N. pseudocomplicata	10010010100121000012???? 1000000010010000000
N. rugosa	10010010100121000112???? 1000000010001000000
N. stracheyi	10010010000121000011000100000010101000000
N. yunnanensis	11010010100111000112???? 1010010000000000000
Parmelaria thomsonii	10000011010021022010010010000001001000000
Platismatia erosa	11010110001011000010100011100000000000000
P. formosana	10010010001011000010100011100000000000000
P. glauca	10001110001011100010100011100000000000000
P. herrei	10000110001011101010100011100000000000000
P. lacunosa	10000010001021000110100011100000000001100
P. norvegica	11000110001021000010100011100000000000000
P. stenophylla	10000010001011101010100011100000000000000

Table 1. (2.)

	00000000011111111112222222223333333333444 12345678901234567890123456789012345678901234567890123456789012
P. tuckermanni	10000010011011001101000111000000000000000
Tuckermannopsis americana	10000011101010101111000010000001001000000
T. aurescens	10000010001010101111????101100000000000000
T. chlorophylla	10001110001010101011000001001000000000000
T. ciliaris	10000011101010101111000010000001000100000
T. fendleri	00000010001011001011000001001000000000000
T. hepatizon	00100010111011011111000000000000000001011
T. merrillii	10000010011011001111000000000000000000000
T. microphyllica	10000011101010101001001000000100000100000
T. oakesiana	10001010001010101????101100100000000000000
T. orbata	10000011101010101111000001001000000000000
T. pallidula	10000010001010101????101100000000000000000
T. platyphylla	10000110001010101111000011001000000000000
T. platyphylloides	10000010101011000111000001001000000000000
T. sepincola	10000010001011000011000001001000000000000
Vulpicida canadensis	10000010011011001100100100000010000000000
V. juniperinus	10000310001011001110100100000010000000000
V. pinastri	00001010001011001010100100000010000000000
V. tilesii	20000010101011001010100100000010000000000
V. tubulosus	2,3000001010110011101001000001000000000
V. viridis	10000010011011001110100100000010000000000

chemical structure and possible biochemical pathways. Data matrix for these two analysis is presented in table 1. In the third analysis some characters treated as binary at first (2–3, 3–4, 10–12, 14–15, 18–19, 20–23) were coded now as multistate while the chemical characters were arranged as in the second analysis.

Taxa analysed

All the cetrarioid lichens, about 120 species, were taken into account at first. Then 10 species were excepted because of insufficient information. Also, 28 species which are sterile or for which reproductive structures have not been sufficiently studied were also excluded from the further work. Finally, the following 83 cetrarioid lichen species were included in the cladistic analysis as terminal taxa of the ingroup: *Ahtiana sphaerosporella, Allocetraria ambigua, A. cucullata, A. nivalis, A. stracheyi, Asahinea chrysantha, A. scholanderi, Cetraria agnata, C. andrejevii, C. arenaria, C. californica, C. commixta, C. delisei, C. ericetorum, C. fastigiata, C. inermis, C. islandica, C. kamczatica, C. laevigata, C. nigricans, C. nigricascens, C. odontella, C. rassadinae, C. subalpina, C. weberi, Cetrariopsis wallichiana, Cetrelia braunsiana, C. cetrarioides, C. chicitae, C. collata, C. davidiana, C. delavayana, C. japonica, C. monachorum, C. nuda, C. olivetorum, C. pseudolivetorum, C. sanguinea, Cetreliopsis rhytidocarpa, Esslingeriana idahoensis, Masonhalea richardsonii, Nephromopsis asahinae, N. ectocarpisma, N. endocrocea, N. endoxanthoides, N. globulans, N. komarovii, N. laureri, N. ornata, N. pallescens, N. pseudocomplicata, N. rugosa, N. stracheyi, N. yunnanensis, Parmelaria thomsonii, Platismatia erosa, P. formosana, P. glauca, P. herrei, P. lacunosa, P. norvegica, P. stenophylla, P. tuckermanni, Tuckermannopsis americana, T. aurescens, T. chlorophylla, T. ciliaris, T. fendleri, T. hepatizon, T. merrillii, T. microphyllica, T. oakesiana, T. orbata, T. pallidula, T. platyphylla, T. platyphylloides, T. sepincola, Vulpicida canadensis, V. juniperinus, V. pinastri, V. tilesii, V. tubulosus, V. viridis.*

Characters

In all, 42 morphological, anatomical and chemical characters, traditionally in wide use, were chosen for the analysis of cetrarioid lichens. Still, some of the common characters applied usually in handbooks of macrolichens (e.g. colour of the thallus, shape and arrangement of lobes etc.) were not used here because of difficulties of defining them properly.

Multistate characters were treated as unordered except the characters of numeral measurements (nos. 13, 16, 17) which were ordered.

I THALLUS STRUCTURES

1. Thallus habit
   a) foliose thallus closely adnate to the substrate (0)
   b) foliose thallus loosely adnate to the substrate (1)
   c) foliose erect thallus (2)
   d) fruticose thallus (3)
2. Pseudocyphellae on upper cortex (absent-0, present-1)
3. Pseudocyphellae marginal (absent-0, present-1)
4. Pseudocyphellae on lower cortex (absent-0, present-1)
   In the third analysis the characters 2–4 are coded as multistate characters pseudocyphellae on upper cortex (absent-0, laminal-1, marginal-2) and pseudocyphellae on lower cortex (absent-0, laminal-1, marginal-2).
5. Soredia (absent-0, present-1)
6. Isidia (absent-0, present-1)
7. Rhizines (absent-0, present-1)
8. Cilia (absent-0, present-1)
9. Marginal projections (absent-0, present-1)

II APOTHECIA AND ASCOSPORES

10. Apohtecia laminal on the upper surface (absent-0, present-1)
11. Apothecia marginal on the upper surface (absent-0, present-1)
12. Apothecia on the lower surface (absent-0, present-1)
    In the third analysis the characters 10–12 are connected to

one multistate character (apothecia laminal on the upper surface-0, apothecia marginal on the upper surface-1, apothecia on the lower surface-2).
13. Diameter of the apothecia
    a) d < 2 mm (0)
    b) 2 mm < d < 10 mm (1)
    c) d > 10 mm (2)
14. Spores ellipsoid (absent-0, present-1)
15. Spores globose (absent-0, present-1)
    In the third analysis the characters 14,15 are connected to one multistate character (spores ellipsoid-0, globose-1).
16. Medium length of the spores
    a) l < 8 um (0)
    b) 8 um < l < 20 um (1)
    c) l > 20 um (2)
17. Medium width of the spores
    a) w < 4,5 um (0)
    b) 4,5 um < w < 8 um (1)
    c) w > 8 um (2)

III CONIDIOMATA AND PYCNOSPORES (absent-0, present-1)
18. Pycnidia laminal
19. Pycnidia marginal
    In the third analysis characters 18, 19 are connected to one multistate character (pycnidia laminal-0, marginal-1).
20. Conidia bifusiform
21. Conidia sublageniform
22. Conidia bacillariform
23. Conidia filiform
    In the third analyis characters 20–23 are connected to one multistate character (conidia bifusiform-0, sublageniform-1, bacillariform-2, filiform-3).

IV SECONDARY CHEMICAL COMPOUNDS (absent-0, present-1)
24. Usnic acid
25. Atranorin
26. Fatty acids
27. Caperatic acid
28. Rangiformic and/or norrangiformic acids
29. Lichesterinic and/or protolichesterinic acids
30. Anthraquinones
31. Pulvinic acid derivates
32. Orcinol series products
33. Imbricaric and/or perlatolic acids
34. Anziaic acid
35. Alectoronic and/or collatolic acids
36. Olivetoric and/or physodic acids
37. Hiascic and/or gyrophoric acids
38. Microphyllinic acid
39. β-orcinol series products
40. Protocetraric and/or fumarprotocetraric acids
41. Norstictic and/or salazinic acids
42. Stictic acid

Outgroup

In the selection of characters we kept to the idea that the taxa should be described not by the data of reproductive structures only but equally also by the thalline and especially by chemical characters. The possible special role of secondary metabolites in the evolution of lichens has been referred by J. Poelt in his species-pairs theory. It seems plausible that the formation of biochemical pathways producing lichen substances has taken place earlier, during sexual stages rather than through mutations in asexual "secondary taxa" [2]. This concept has been applied in the dissection of evolution of the genus *Cetrelia* [14]. Structure of medullary secondary metabolites as well as morphological and anatomical characters of all *Cetrelia* species refer to the monophyletic origin of that group. The genus is probably related to other cetrarioid lichens and may represent the more primitive trend. This is why the genus *Cetrelia* (*C. braunsiana, C. cetrarioides, C. chicitae, C. collata, C. davidiana, C. delavayana, C. japonica, C. monachorum, C. nuda, C. olivetorum, C. pseudolivetorum* and *C. sanguinea*) was selected as the sister group (outgroup) for the present cladistic analysis.

Results

The strict consensus trees were constructed of 1000 (fig. 1 and 2) and 3900 (fig. 3) equally parsimonous cladograms after reweighting of characters. In the first analysis (secondary metabolites treated as separate characters) the unrooted trees could not be rooted such that specified ingroup was monophyletic. *Parmelaria thomsonii* together with *Asahinea chrysantha* and *A. scholanderi* shows close relations to outgroup (12 species of *Cetrelia*). Genus *Nephromopsis* together with *Cetreliopsis rhytidocarpa* and *Cetrariopsis wallichiana* form a clade supported by the presence of usnic acid. Another branch including all the rest of the species is supported by the thallus habit, lack of the pseudocyphellae on the lower cortex and the marginal position of apothecia on the upper surface. Two genera, *Platismatia* and newly described *Vulpicida* (the group of species with yellow medulla, containing pulvinic acid derivates) can be treated homogeneous. The subclade of *Allocetraria ambigua, A. cucullata* and *A. nivalis* is related to the group of brown "fruticose" *Cetraria* species. Genus *Tuckermannopsis* is clearly heterogeneous.

In the second analysis (fig. 2) lichen substances were grouped according to their chemical structure. *Parmelaria thomsonii, Cetrariopsis wallichiana, Asahinea chrysantha* together with *A. scholanderi* and *Masonhalea richardsonii* are the closest to the outgroup. The complex of brown "fruticose" *Cetraria* species is evidently not homogeneous. The affinities between *C. rassadinae, C. nigricans, C. islandica – C. laevigata, C. ericetorum, C. arenaria, C. andrejevii* and the rest of the group remain dissolved. Taking secondary metabolites of these species into account as additional information might be of use here. Three *Allocetraria* species (*A. ambigua, A. cucullata* and *A. nivalis*) form a separate subclade as well as genera *Platismatia* and *Vulpicida*. In the last polytomy three main entities can be noticed: genus *Nephromopsis* (13 species) together with *Cetreliopsis rhytidocarpa, Tuckermannopsis ciliaris* group together with *Esslingeriana idahoensis*, and a subclade consisting of species from quite different genera.

In the third analysis lichen substances were grouped according to their chemical structure and homologous character states as multistate characters. The unrooted trees could not be rooted such that specified ingroup was monophyletic. The affinities of the proposed ingroup and *Parmelaria thomsonii* together with *Asahinea chrysantha* and *A. scholanderi* remain dissolved. The species of genus *Platismatia* and genus *Vulpicida* form one clade consisting

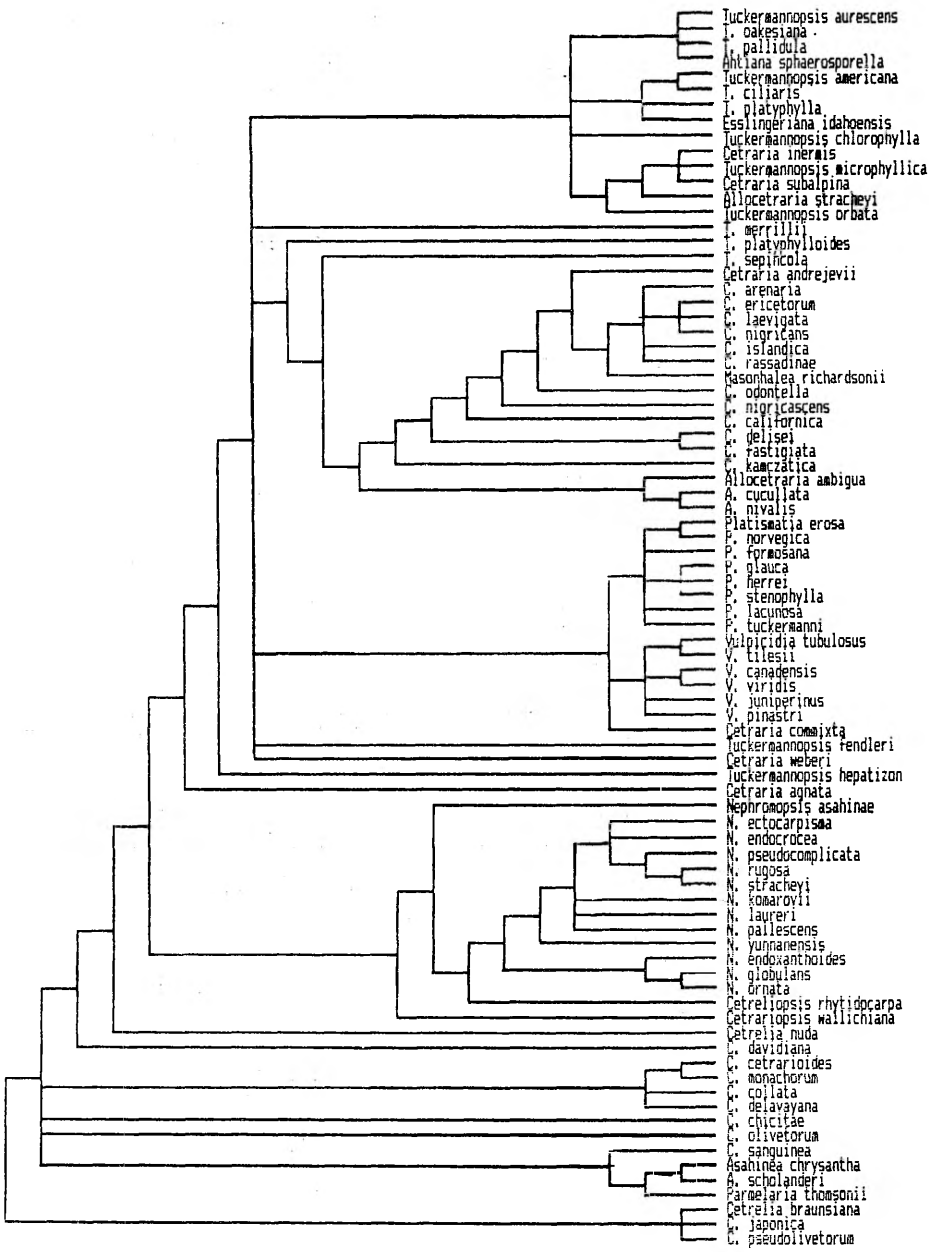

Fig. 1. Strict consensus tree constructed from 1000 equally parsimonous cladograms. Secondary compounds treated as separate characters. Length of shortest tree = 28544. Consistency index = 0.480. Retention index = 0.878.

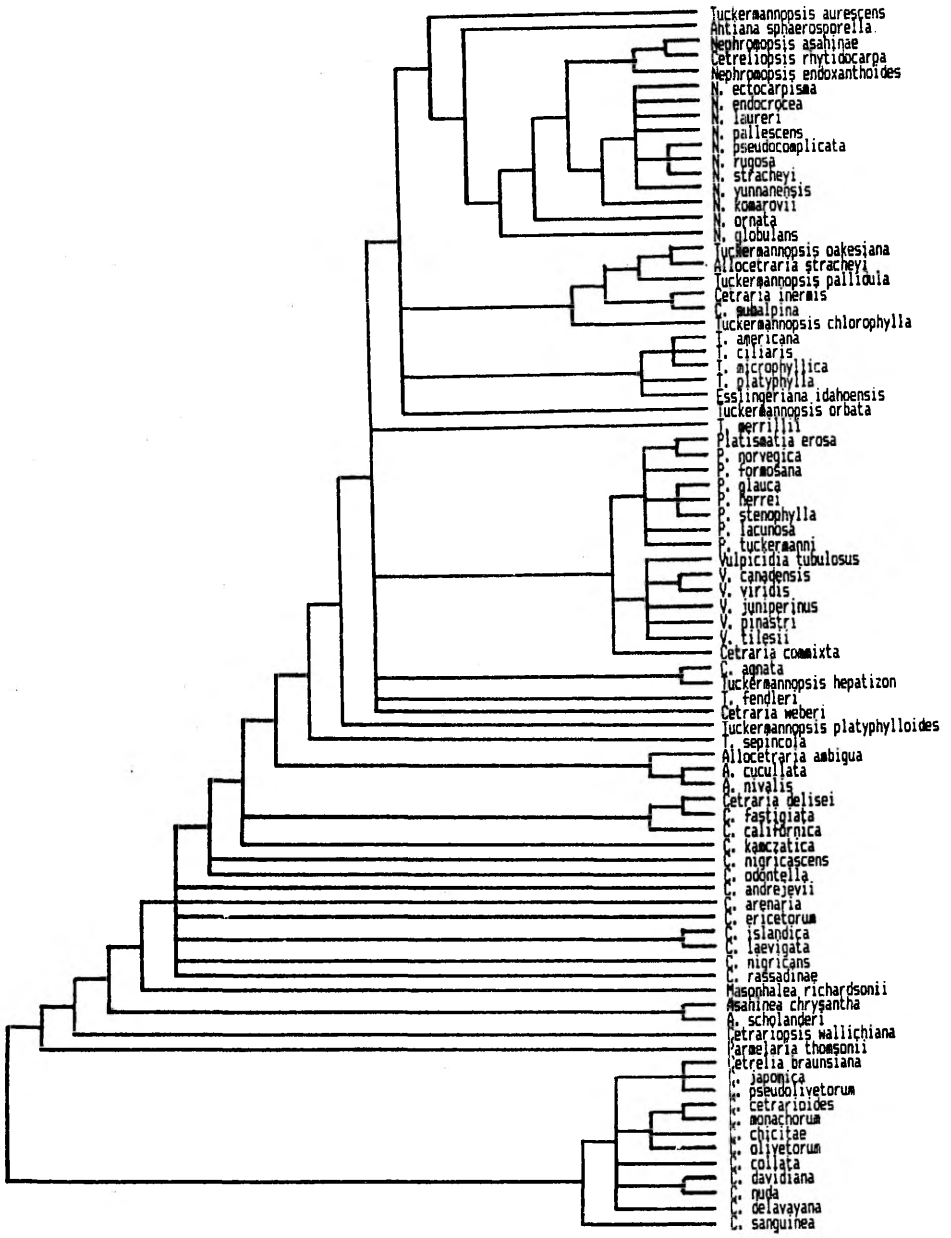

Fig. 2. Strict consensus tree constructed from 1000 equally parsimonous cladograms. Secondary compounds as representatives of biochemical groupings. Length of shortest tree found = 24660. Consistency index = 0.381. Retention index = 0.871.

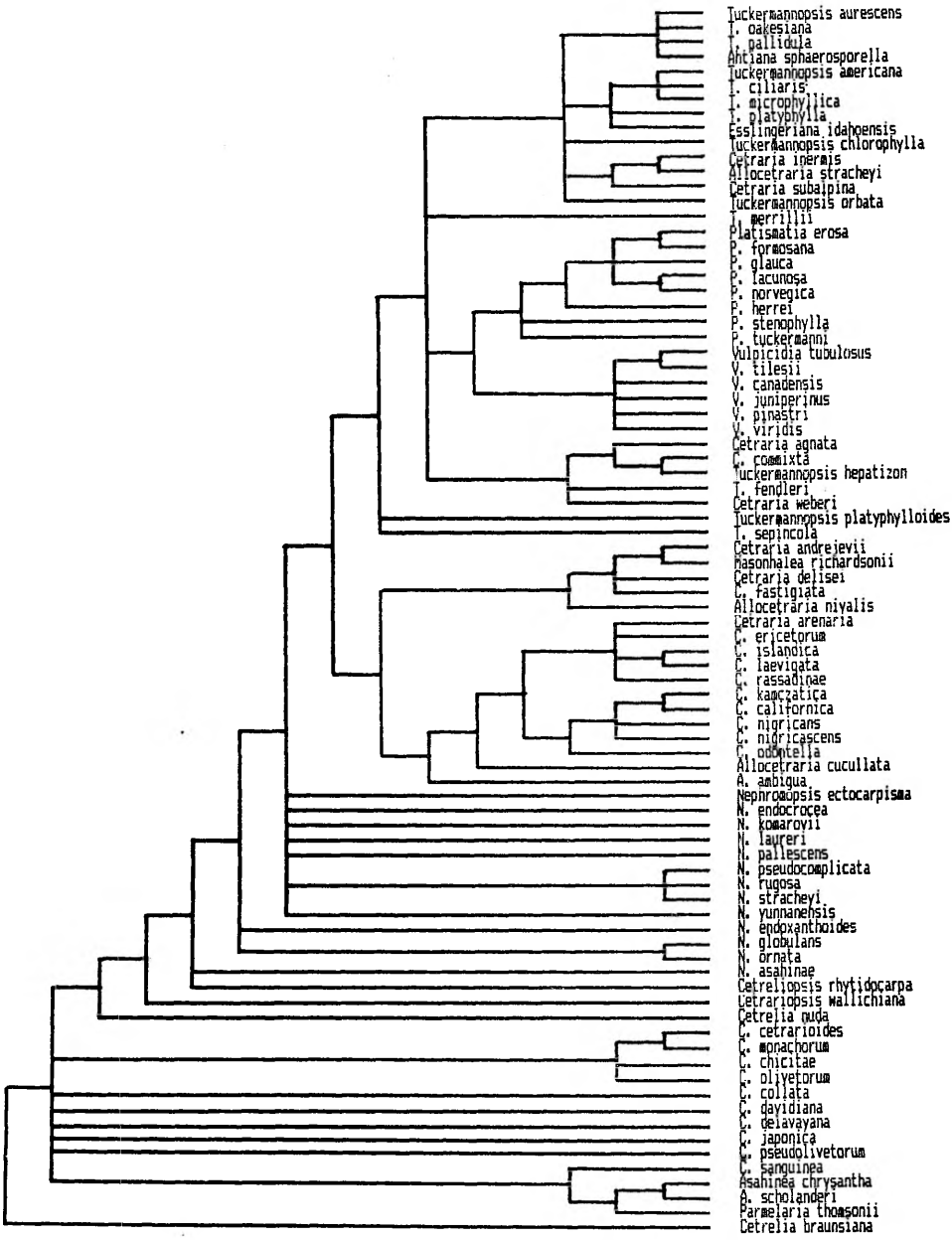

Fig. 3. Strict consensus tree constructed from 3900 equally parsimonous cladograms. Secondary compounds as representatives of biochemical groupings. Homologous character states are coded as multistate characters. Length of shortest tree = 39307. Consistency index = 0.576. Retention index = 0.863.

of two subclades. *Allocetraria ambigua, A. cucullata* and *A. nivalis* together with *Masonhalea richardsonii* are related to the group of brown "fruticose" *Cetraria* species. Genus *Tuckermannopsis* is clearly heterogeneous, the affinities between the species of genus *Nephromopsis* remain dissolved in this analysis.

Discussion

The question of monophyly or polyphyly seems to be essential in the interpretation of the results obtained. The monophyletic evolution of all cetrarioid taxa analysed here is not probable. Therefore, it would not be justified to make extensive rearrangements in the system on the basis of either of the present analyses only. Evolutionary affinities of separate entities shown in the first analysis (fig. 1), where the major secondary metabolites are treated totally independently from each other, should be evaluated especially critically. One of the most important characters of higher taxonomical units – biochemical connections between different lichen compounds – is completely ignored here. That problem is avoided in the second and third analysis (fig. 2 and 3) where the lichen substances are grouped into biochemically related sets. The inability to determine affinities within subclades (several polytomies on cladograms of the second analysis) due to the lack of detailed chemical data is the disadvantage of that method.

On all cladograms of the first and second analysis, all the 13 species of *Nephromopsis* form a monophyletic entity, closely related to *Cetreliopsis rhytidocarpa*. The latter is the species of a monotypic genus separated from other cetrarioid lichens by its complicated chemistry (usnic acid, fatty acids as well as derivatives of β-orcinol series) and some morphological characters (pseudocyphellae on both thallus surfaces). M. J. Lai, the author of the genus, says its relationships to *Cetrelia* and *Nephromopsis* are obvious [11]. We are inclined to consider the affinities with *Cetrelia* not to be tight and include the species into the genus *Nephromopsis* as done by Zahlbruckner in 1928. The species seems to be quite close to *N. asahinae* (both contain fumarprotocetraric acid, have pseudocyphellae also on the upper cortex, etc.). The problem of synonymity of *C. rhytidocarpa* with *Cetraria straminea* Vainio and *Cetraria laeteflava* Zahlbr. established by Lai, needs additional study. Our analyses surely support the recent inclusion of several species (*N. endoxanthoides* [15], *N. komarovii* [20] *N. laureri* [9], *N. pallescens* [13], *N. yunnanensis* [15]) into this genus.

Thus the separation of *Cetreliopsis rhytidocarpa* as an independent genus is not supported by the present cladistic study, but some other taxa such as *Parmelaria thomsonii, Cetrariopsis wallichiana* and *Masonhalea richardsonii* form clearly separate clades (fig. 2). This does not contradict the concept of treating them as monotypic genera as has been proposed for some time ago [1, 8, 10].

The genus *Platismatia* and the recently defined genus *Vulpicida* are both monophyletic entities according to the present analyses. This similarity is achieved due to the fact that all the members of these genera contain the same cortical and medullary substances (atranorin and caperatic acid in *Platismatia* species and usnic acid together with pinastric and vulpinic acids in the species of *Vulpicida*). Consequently there are no differences between our two analyses for these genera, and the consensus trees are practically identical for that part. Relationships inside the heterogeneous group of brown "fruticose" *Cetraria* species are better resolved in the first analysis where the detailed data of secondary metabolites enable the finding of some more mutual affinities between the species, and in the third analysis. *C. inermis* and *C. subalpina* cannot be included in this complex. The pair of *C. delisei – C. fastigiata* and *C. kamczatica* appear to be the most separated taxa from the group. The latter has also affinities to the genus of *Allocetraria* (*A. ambigua, A. cucullata* and *A. nivalis*). The position of *Allocetraria stracheyi* far from the other close species on all cladograms is the most incomprehensible result of the present study.

The heterogeneous nature of the genus *Tuckermannopsis* is certain even if the species with pulvinic acid derivates are excluded. Two main entities can be noticed. The group of *T. ciliaris*, the so-called "true" *Tuckermannopsis* consists of *T. americana, T. ciliaris, T. microphyllica, T. platyphylla* and somewhat surprisingly also of *Esslingeriana idahoensis*. Another entity in the genus includes the yellowish species with usnic acid in the cortex – *T. pallidula, T. oakesiana, T. aurescens* and perhaps also *Ahtiana sphaerosporella*. This group is well delimited on the cladograms of the first and third analysis and quite scattered on the second one showing affinities partly with such taxa as *Allocetraria stracheyi, Cetraria inermis – C. subalpina* and partly with the genus *Nephromopsis*. Several *Tuckermannopsis* species (*T. sepincola, T. platyphylloides, T. merrillii, T. fendleri* and *T. weberi*) are not closely related to any of the examined taxa, and consequently this genus is in urgent need of revision.

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Key words: Ascomycotina, Lecanorales, Parmeliaceae, cetrarioid lichen genera, phylogeny, cladistics.

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II

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Lichenologist 21(4): 303–311 (1989)

CHEMICAL VARIATION AND GEOGRAPHICAL DISTRIBUTION OF *ASAHINEA CHRYSANTHA* (TUCK.) CULB. & C.CULB.

T. RANDLANE* and A. SAAG*

Abstract: Sixty-two samples of *Asahinea chrysantha* from different localities in the Soviet Union were analysed by TLC. Three different chemotypes are recognised, each with a different geographical distribution. The most restricted of the three is an usnic acid deficient chemotype (I), with atranorin, alectoronic and α-collatolic acids, which is chemically the same as *A. scholanderi* and *A. kurodakensis*. Chemotype II contains usnic acid in addition to the basic chemistry, and chemotype III is α-collatolic acid deficient and has the widest geographical range. A centre of speciation of *Asahinea* in Soviet Primorje or Japan is proposed.

Introduction

Cetraria Ach. s.lat., is now divided into several more restricted genera, one of which is *Asahinea* Culb. & C.Culb. (Culberson & Culberson 1965) which comprises three species: *A. chrysantha* (Tuck.) Culb. & C.Culb., *A. scholanderi* (Llano) Culb. & C.Culb and *A. kurodakensis* (Asahina) Culb. & C.Culb. The principal morphological characteristics of the genus are: foliose, loosely appressed thallus; grey or yellow upper cortex and black lower cortex; and absence of rhizines. The genus shows an arctic-alpine distribution (Krog 1968). Characteristic secondary metabolites of *Asahinea* are atranorin and usnic acid as the main cortical substances, and the orcinol depsides alectoronic and also usually α-collatolic acids, as diagnostic medullary substances. Some purple, lavender or pink pigments have also been reported for all three species (Culberson 1969, 1970; Culberson *et al.* 1977). More precise characteristics of *Asahinea* and related genera in the Parmeliaceae are given in Goward (1985).

The Species

Morphology and distribution

Asahinea kurodakensis is the least widely distributed of the three and is supposedly endemic to Japan. It has been collected only three times in the high mountains on the islands of Hokkaido and Honshu (Asahina 1953, Culberson & Culberson 1965, Yoshimura 1979). According to both morphological and chemical characteristics, *A. kurodakensis* is closely allied to *A. scholanderi*. Both are tan to blackish (lacking usnic acid in the upper cortex), produce isidia, and their upper surface lacks pseudocyphellae. *Asahinea kurodakensis* and *A. scholanderi* contain atranorin, alectoronic and α-collatolic acids. Unfortunately

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we have not seen a sample of *A. kurodakensis*, and from the literature the difference between *A. kurodakensis* and *A. scholanderi* is unclear. It is significant that *A. scholanderi* has not been reported from Japan.

Asahinea scholanderi was described as a *Cetraria* by Llano (1951). Later, Oxner & Rassadina (1960) described a new species from Asia, *C. saviczii*. Krog (1962) supposed, on the basis of the diagnosis, that *C. saviczii* might be identical with *C. scholanderi*, a view now widely accepted. *Asahinea scholanderi* is an arctic-alpine amphi-Beringian species (Krog 1968), its recorded range extending from eastern Siberia to the Behring Straits and to northern and central Alaska (Culberson & Culberson 1965; Handbook of the lichens of the USSR 1971). However, its distribution is considerably wider and it occurs in the Soviet Union in the Urals (Rjabkova 1982), in Taimyr (Piin & Trass 1971), in Kamchatka (Mikulin 1987), in the Khabarovsk region, Badzhal (Randlane 1984), and in the Primorje region, Sikhote-Alin (herbarium specimens in TU). Thomson (1984) remarks that in North America its range extends eastward to Baker Lake and the mouth of the Black River.

Asahinea chrysantha is readily distinguished from other members of the genus by its yellow upper cortex, the presence of pseudocyphellae, and by the absence of isidia. It has a wide morphological variation. The size of the white pseudocyphellae on the upper surface varies as does the degree of reticulation of the thallus. The lower surface is black with brown margins, while the width and darkness of the margins is also variable. The upper surface of the thallus is usually bright to pale yellow but specimens with an almost grey or greenish grey upper cortex are also known; taxa such as *C. chrysantha* f. *cinerascens* Asahina, and f. *glaucescens* Oxner & Rassad. (Asahina 1934; Oxner & Rassadina 1960) represent these latter extremes.

The range of *A. chrysantha* is considerably broader than that of *A. scholanderi* which occurs within the arctic–alpine distribution area of *A. chrysantha*. Both species may grow together. In Eurasia, *A. chrysantha* is known from Norway, Sweden, and Finland, in the northern parts of the USSR (from Kola to Tschukotka and in the mountainous regions from the Urals to Sikhote-Alin), in Mongolia, Korea, and Japan. In North America it is recorded from the Aleutian Islands, Alaska, the Northwest Territory and the southern part of Baffin Island. The distribution of *A. chrysantha* is thus ± circumpolar, but it is most abundant in Siberia, the Far East and Alaska. Distribution maps are given by Oxner & Rassadina (1960), Culberson & Culberson (1965), Hakulinen & Ulvinen (1966) and Thomson (1984).

Chemistry

It is generally believed that atranorin and usnic acid occur in the upper cortex and alectoronic acid in the medulla of *A. chrysantha* as constant metabolites although usnic acid is sometimes lacking from Japanese material (Yoshimura 1979). A fourth compound, α-collatolic acid, is reported as constant for the Japanese specimens. Culberson & Culberson (1965) found this substance in only one non-Japanese sample tested (Siberia, the Tschita region). Subsequently, α-collatolic acid was mentioned as an accessory in material from Alaska (Krog 1968) and other North American localities (Thomson 1984). As

the Culbersons mention, the colour of the upper cortex does not depend on the presence or absence of α-collatolic acid for it is a colourless medullary substance, rather the intensity of the yellow colour of the upper cortex is determined by the amount of usnic acid deposited there.

In addition, several unidentified purple or lavender pigments are also known in *A. chrysantha* and in other species of the genus. These occasionally occur in the medulla, particularly near the lower cortex in older parts of the thallus (Culberson & Culberson 1965).

Collaborators of the Pacific Institute of Bio-organic Chemistry in Vladivostok working on specimens collected from the Soviet Far East have shown the following. Six purple and lavender coloured anthraquinone pigments were identified from *A. chrysantha* and their structures determined (Mischenko *et al.* 1980, Krivoshchekova *et al.* 1983*b*). Krivoshchekova *et al.* 1983*a* reported the presence of two new substances in *A. chrysantha* and *A. scholanderi*. β-Alectoronic acid was isolated and identified for the first time from plant material, although it was earlier detected by Asahina from alkaline hydrolysis of α-collatolic acid. A specimen of *A. chrysantha* from Magadan was reported to contain α- and β-alectoronic acids, usnic acid, atranorin and methyl-β-orcinol-carboxylate. The latter substance was previously known only from *Parmelia tinctorum* (Culberson 1969). A specimen of *Asahinea scholanderi* (also from Magadan) contained α- and β-alectoronic, α- and β-collatolic acids, usnic acid and atranorin. This finding of usnic acid in *A. scholanderi* is somewhat surprising.

Stepanenko *et al.* (1985) examined two morphologically different specimens of *A. chrysantha* (Table 1). Compounds 9–11 are anthraquinonoid pigments. Haematommic acid and methyl-β-orcinol-carboxylate are recorded for the first time for this species, in rather low concentrations. However, Sample I (with a yellow upper surface, from the Magadan region) did not contain α- or β-collatolic acids while Sample II (with a grey upper surface, from the Primorje

TABLE 1. *Chemical compounds isolated from* Asahinea chrysantha*

Number	Compound	Amount (% dry wt)	
		Sample I	Sample II
1.	Usnic acid	1·39	0·22
2.	Atranorin	0·09	0·25
3.	α-Alectoronic acid	0·25	—
4.	β-Alectoronic acid	0·31	—
5.	α-Collatolic acid	—	0·31
6.	β-Collatolic acid	—	0·23
7.	Methyl-β-orcinol-carboxylate	0·01	0·021
8.	Haematommic acid	—	0·003
9.	Islandicin	0·001	0·001
10.	Cynodontin	0·001	0·001
11.	Asahinin	0·001	0·001

*Data from Stepanenko *et al.* (1985).

region) lacked either α- or β-alectoronic acids; the first reported absence of alectoronic acid in the genus *Asahinea*.

These results indicate that chemically interesting populations of *A. chrysantha* occur in Japan and in the Far East.

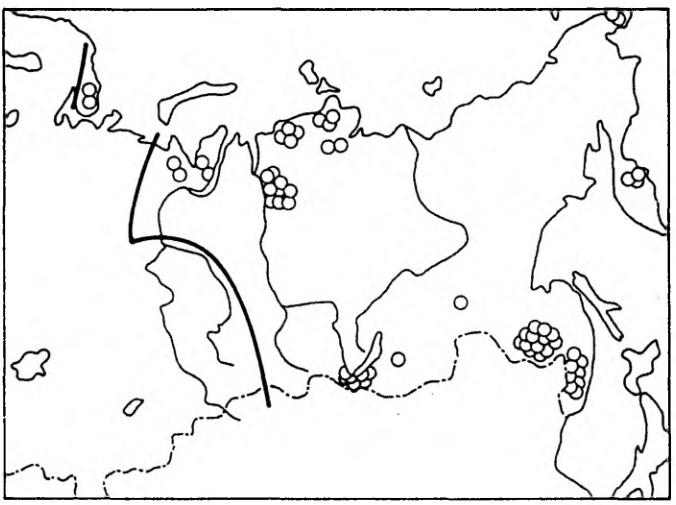

FIG. 1. Distribution of *Asahinea chrysantha* in the USSR (from Oxner & Rassadina 1960, Culberson & Culberson 1965). Dots (62) show localities of samples analysed by TLC. The line marks the limits of its distribution.

Materials and Methods

In the lichen herbaria of TU and TBA material of *A. chrysantha* is well represented from the whole of the Soviet Union. Sixty-two samples of *A. chrysantha* (localities shown in Fig. 1) were studied chemically between 1981 and 1987. For comparison, a specimen from North America (Yukon) was also analysed, as were specimens of *A. scholanderi*. Standard methods were used (Culberson & Kristinsson 1970, C. Culberson 1972, 1974, Culberson & Amman 1979, White & James 1985). Although SILUFOL UV 254 plates were used, controls were also run on MERCK Silica gel 60 F 254 TLC and HPTLC plates. Secondary metabolites were extracted with acetone rather than chloroform/hexane as used by Stepanenko *et al.* (1985). Atranorin, usnic, alectoronic and collatolic acids were positively identified. Anthraquinonoid pigments and some accessory compounds were noted but not determined further.

Results

Nine specimens of our material from the Primorje region, Sikhote-Alin, were analysed by TLC by Dr C. F. Culberson (Duke CFC no. 5703-07; 5717-20). Atranorin, alectoronic and α-collatolic acids, traces of physodic acid, and an unidentified substance were detected in all samples. Usnic acid was found in 8 specimens but no traces of it in one of the samples. This prompted us to investigate the main secondary metabolites of *A. chrysantha* in specimens from as many different localities in the Soviet Union as possible with special emphasis on Far Eastern material.

α-*Alectoronic acid and atranorin.* These substances occurred in all samples and thus are of no importance in separating different chemotypes of *A. chrysantha*.

Usnic acid was determined in the majority of our samples, but was not found in two specimens from the Primorje region, Sikhote-Alin and in one from the Khabarovsk region, Badzhal. Yoshimura (1979) also mentioned the occasional absence of usnic acid in Japanese material.

α-*Collatolic acid* was detected only in specimens from the eastern part of the Soviet Union (excluding the Kamchatka and Tschukotka Peninsulas) up to the Baikal region, and the Taimyr Peninsula. In material from the regions of Baikal and Taimyr there were specimens of both chemotypes, with and without α-collatolic acid. The three specimens without usnic acid mentioned above undoubtedly contain α-collatolic acid. The only North American sample (Yukon) did not contain this substance.

β-*Alectoronic and* β-*collatolic acids* were detected by chemists in Vladivostok. Working with pure samples of α- and β-alectoronic, and α- and β-collatolic acids (sent by colleagues at the Pacific Institute of Bio-organic Chemistry) we observed that both β-forms ran on chromatograms lower than the spots of the respective α-forms, while differences in Rf values of α- and β-collatolic are considerably greater than those of α- and β-alectoronic acids. Thus β-collatolic is situated only a little above α-alectoronic acid. All four spots have a similar colour.

In our herbarium collections we found β-collatolic acid in only a few cases, but never β-alectoronic acid. β-Collatolic acid was detected in a sample of *A. chrysantha* from the Baikal region and in a sample of *A. scholanderi* from the Magadan region. The latter specimen contained both forms of collatolic acid.

In vitro, β-alectoronic acid was obtained by treating pure α-alectoronic acid with alkaline solution. The same treatment of pure α-collatolic acid gave us β-collatolic acid and, somewhat suprisingly, both forms of alectoronic acid in trace amounts. All four forms of the acids were identified by TLC comparison with pure samples. The problem is whether the β-forms of alectoronic and collatolic acids occur in fresh material, and under what conditions the change from one into another might take place. In their treatment of *Parmelia* subgen. *Amphigymnia* in East Africa, Krog & Swinscow (1981: 150) record '. . . in old specimens with alectoronic and α-collatolic acids we obtained additional spots below those of the main substances on the TLC plates. . . We found no correlation between morphological characters and the presence or absence of such substances, and were inclined to regard them as artefacts'. We consider it possible that these unidentified substances are simply β-forms of alectoronic and collatolic acids.

Discussion

Atranorin and alectoronic acid are the only compounds identified by us as occurring in all samples of *Asahinea chrysantha*. Usnic and α-collatolic acids occur in the species in three combinations: (1) α-collatolic acid alone; (2) α-collatolic acid with usnic acid; (3) *usnic acid alone*. Thus there are three distinct chemotypes of *A. chrysantha* in the Soviet Union, each with its own particular geographical distribution (see Table 2 and Fig. 2).

TABLE 2. *Occurrence of chemotypes of* Asahinea chrysantha

Chemotype	Composition of major aromatic compounds	Occurrence in the Soviet Union
I	α-Collatolic acid (+ atranorin and α-alectoronic acid)	Primorje region, Sikhote-Alin (2)*; Khabarovsk region, Badzhal (1)
II	Usnic acid, α-collatolic acid (+ atranorin and α-alectoronic acid)	Primorje region, Sikhote-Alin (6); Khabarovsk region, Badzhal (12); Amur region (1); Tscita region (1); Baikal region (2); Taimyr (8)
III	Usnic acid (+ atranorin and α-alectoronic acid)	Tschukotka (2); Kamchatka (3); Jakutia (1); Baikal region (5); Taimyr (12); Jamal (2); the Urals (2); the Khibins (2)

*Number of analysed specimens.

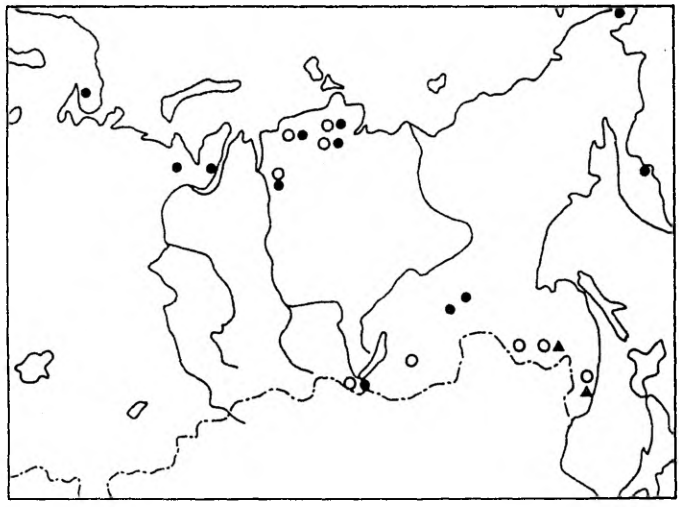

FIG. 2. Occurrence of chemotypes of *Asahinea chrysantha* in the USSR ▲ = chemotype I, ○ = chemotype II, ● = chemotype III.

The systematic rank of these three chemotypes is not treated in this account. The presence or absence of α-collatolic acid does not seem to correlate with any morphological characters (colour of upper and lower cortices, width of brown edges on the lower surface, size of pseudocyphellae, degree of surface reticulation). The yellow colour of the upper surface depends on the quantity of usnic acid deposited in the cortex. Samples without usnic acid are uniformly grey. Such specimens, and samples containing usnic acid in small amounts, are distinguished only with difficulty from chemotypes II and III. Chemotypes II and

III are very variable in the colour of their upper cortex, and there are specimens in our herbarium that are yellow in one part and almost grey in another part of the same thallus.

The geographical distributions of chemotypes of *A. chrysantha* is of special interest. The least numerous of the three is chemotype I (without usnic acid), which is known from Sikhote-Alin, Badzhal and Japan. Its chemistry (atranorin, alectoronic and α-collatolic acids) is the same as that of *A. scholanderi* and *A. kurodakensis*.

In a paper concerning biogenetic relationships of lichen products in the genus *Cetrelia*, Culberson & Culberson (1976) state that microphyllinic acid, an orcinol depside which combines two phenolic acid units with seven-carbon side chains, is the most primitive product of this genus. Chemosyndromic variation in *Cetrelia* may reflect a trend towards reduced side-chain length. Alectoronic and α-collatolic acids are orcinol depsidones, both having the greatest number (7+7) of carbons in the side-chains. It is known that depsidones are derived directly from depsides and hence the somewhat primitive character of alectoronic and α-collatolic acids in *Cetrelia* is also evident. Such considerations support the hypothesis of a possible origin of the genus *Cetrelia* from an *Amphigymnia*-like ancestor producing alectoronic and α-collatolic acids (Culberson & Culberson 1968). As in *Cetrelia*, all species of *Parmelia* subgen. *Amphigymnia* also produce atranorin in the upper cortex. It is significant that the other common cortical substance, usnic acid, also occurs in some species of subgen. *Amphigymnia* but never in those which produce alectoronic and α-collatolic acids. This indicates that *Asahinea* may also share a similar ancient chemical composition which includes atranorin in the cortex and alectoronic and α-collatolic acid in the medulla. Thus chemotype I of *A. chrysantha* is thought to represent the basic, primitive chemistry of *Asahinea*.

Chemotype II contains, in addition to atranorin, alectoronic and α-collatolic acids, usnic acid in the cortex. The distributional area of this chemotype shows a disjunction, being found in Taimyr, Siberia, the Far East, Japan and North America but not in Tschukotka or Kamtschatka. The lack of α-collatolic acid in chemotype III represents a second qualitative change in the chemical composition of *A. chrysantha*. Chemotype III is the most widely distributed, ranging from Scandinavia and Kola over Tschukotka to North America.

The different chemotypes of *A. chrysantha* and their relative distributions are shown schematically in Fig. 3. The distribution area of chemotype II is sympatric over most of its range with that of chemotype III. Thus two chemotypes (II and III) occur simultaneously in this territory and α-collatolic acid may be present or absent in specimens collected in this zone. Krog (1968: 114) considers α-collatolic acid as an accessory in Alaskan populations of *A. chrysantha* and Thomson (1984) in North American populations. We record the same for populations in the Taimyr Peninsula and the Baikal region. That part of the distribution area of chemotype II, where specimens of chemotype III do not occur, includes the known distribution of chemotype I.

Combining the distributional patterns of the three chemotypes of *A. chrysantha* (Fig. 3) and assumptions about an original or primitive suite of secondary metabolites in *Asahinea*, we suggest that a possible centre of speciation was in Soviet Primorje or Japan. This is the only region where chemotypes

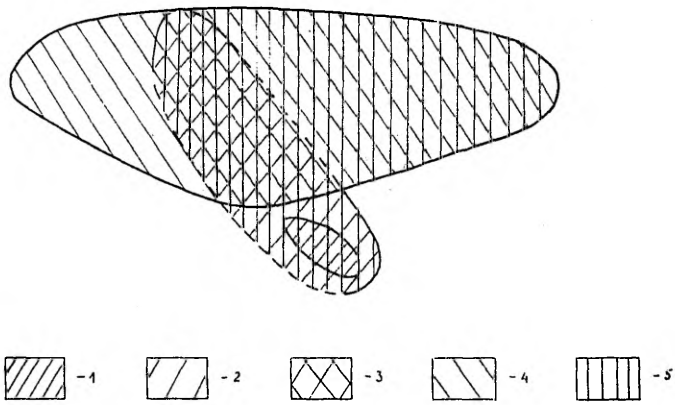

FIG. 3. Relative ranges of chemotypes of *Asahinea chrysantha* (1–4) and *A. scholanderi* (5) in the USSR 1 = Chemotypes I & II, 2 = chemotype II, 3 = chemotypes II & III, 4 = chemotype III.

I and II of *A. chrysantha* coexist, and where *A. scholanderi* and *A. kurodakensis* also occur. Chemotype III of *A. chrysantha* (the most derived chemotype in the genus) is absent from there. The present distribution of *A. chrysantha* has the limits of the ranges of chemotypes II and III, both containing usnic acid. The wider distribution of *A. chrysantha* compared with the known ranges of the other two species of the genus may be in part a reflection of antimicrobial properties of usnic acid, a cortical substance which is additional to the primitive assemblage of secondary metabolites characteristic for the genus

Thanks are due to Prof. Hans Trass for his encouragement and supervision of this study. We are very grateful to Taimi Piin from Tallinn Botanical Garden for performing some chemical analyses and for many critical and constructive remarks. We are also indebted to collaborators from the Pacific Institute of Bio-organic Chemistry in Vladivostok for pure samples of some lichen substances.

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III

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Lichenologist 23(2): 113–126 (1991)

CHEMICAL AND MORPHOLOGICAL VARIATION IN THE GENUS *CETRELIA* IN THE SOVIET UNION

T. RANDLANE* and A. SAAG*

Abstract: Two hundred and three specimens belonging to the genus *Cetrelia* from the Soviet Union and also 41 samples from other countries have been analysed by TLC. Eight species were determined in the Soviet Union. In addition two new species, *C. orientalis* and *C. pseudocollata* sp. nov. are described. Five morphotypes and six chemotypes have been recognized in the genus: their main characteristics are tabulated in a form that can be used for identification and a key is also included. Evolutionary relationships between the 'primary' and 'secondary' species related to 'species-pairs' are discussed.

Introduction

The genus *Cetrelia* was separated from the genera *Cetraria* and *Parmelia* by Culberson & Culberson (1968). It is mainly characterized by the foliose, loosely attached thallus; ashy white or tan upper cortex and black lower cortex; sparse rhizines; laminal pseudocyphellae; marginal pycnidia; ellipsoid ascospores; atranorin as the main cortical substance, and various orcinol depsides and depsidones as diagnostic medullary substances (see Goward 1985). Fifteen species were previously included in the genus, of which the majority are distributed in eastern and south-eastern Asia. In the Soviet Union eight species have so far been found, i.e. *C. braunsiana, C. cetrarioides, C. collata, C. chicitae* and *C. pseudolivetorum* (Kopaczevskaja *et al.* 1971), *C. alaskana* (Makarova 1980), *C. olivetorum* (Malysheva & Smirnov 1982) and *C. japonica* (Skirina 1987). However, no special chemical or distributional studies of the Soviet material had been carried out.

Materials and Methods

Two hundred and three specimens belonging to the genus, collected in the Soviet Union and kept in TU, LE and KW, were studied chemically in 1988–1989. For comparison, 41 specimens from Austria, Germany, Great Britain, Hungary, Italy, Norway, Poland, Portugal, Romania, Spain, Sweden and Switzerland; Canada and the USA; Japan, Mongolia, China and Tibet; the islands of Java, Sumatra and the Philippines and kept in TU, LE, LD and UPS were also analysed. The major medullary compounds were identified according to standardized methods (Culberson 1972, 1974). The minor constituents were identified only when the spots were sufficiently well developed. The acetone extracts were run in solvent system C only and the plates were later developed with 10% H_2SO_4 in ethanol. The plates were air dried after spraying with reagent and then heated at about 100–120°C for up to 15 min.

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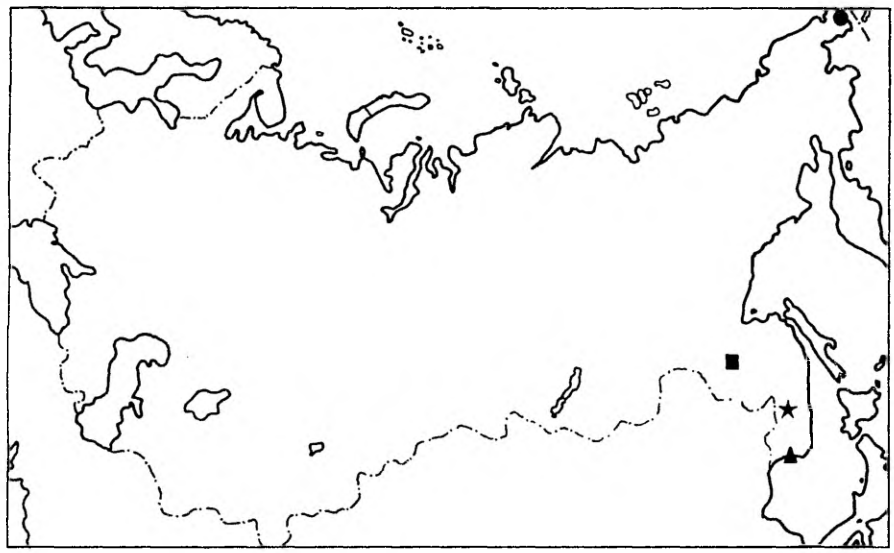


FIG. 1. Distribution of *Cetrelia alaskana* (●), *C. japonica* (★), *C. orientalis* (■) and *C. pseudolivetorum* (▲) in the Soviet Union.

Results

Species recorded in the Soviet Union

The following eight species with their respective major medullary compounds were determined in the USSR according to the previously accepted systematics (Culberson & Culberson 1976).

(1) *C. alaskana* (Culb. & C. Culb.) Culb. & C. Culb. Very rare in the Soviet Union, found only in Tschukotka (Fig. 1); three specimens analysed. The major medullary substance is imbricaric acid.

(2) *C. braunsiana* (Müll. Arg.) Culb. & C. Culb. Distributed in Khabarovsk and Primorje regions in the Far East (Fig. 2); 44 specimens examined. The major medullary substances are alectoronic and α-collatolic acids. Contrary to Culberson & Culberson (1976) we consider physodic and 4-O-methylphysodic acids to be minor compounds.

(3) *C. cetrarioides* (Del. ex Duby) Culb. & C. Culb. Found in the zone of mixed and deciduous forests throughout the Soviet Union (Fig. 3); 51 specimens examined. The major substance is perlatolic acid.

(4) *C. chicitae* (Culb.) Culb. & C. Culb. Quite common in the Far East but very rare in the western districts (Fig. 2). Of the 29 specimens examined 27 are from the Khabarovsk and Primorje regions, one from Siberia (Krasnoyarski region) and one from the European part (the Crimea Peninsula). The major substances are alectoronic and α-collatolic acids.

(5) *C. japonica* (Zahlbr.) Culb. & C. Culb. Found only in the Far East–Primorje region (Fig. 1); 14 specimens examined. The major substance is microphyllinic acid.

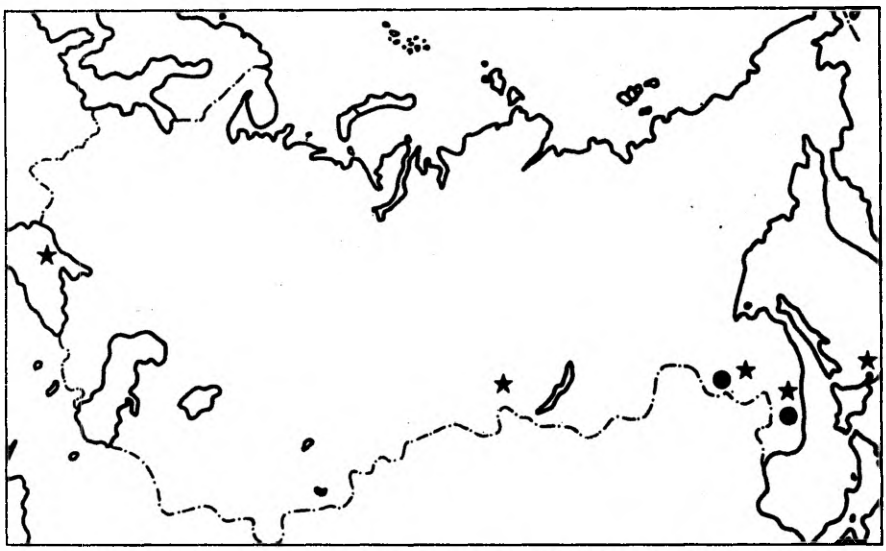


FIG. 2. Distribution of *Cetrelia braunsiana* (●) and *C. chicitae* (★) in the Soviet Union.

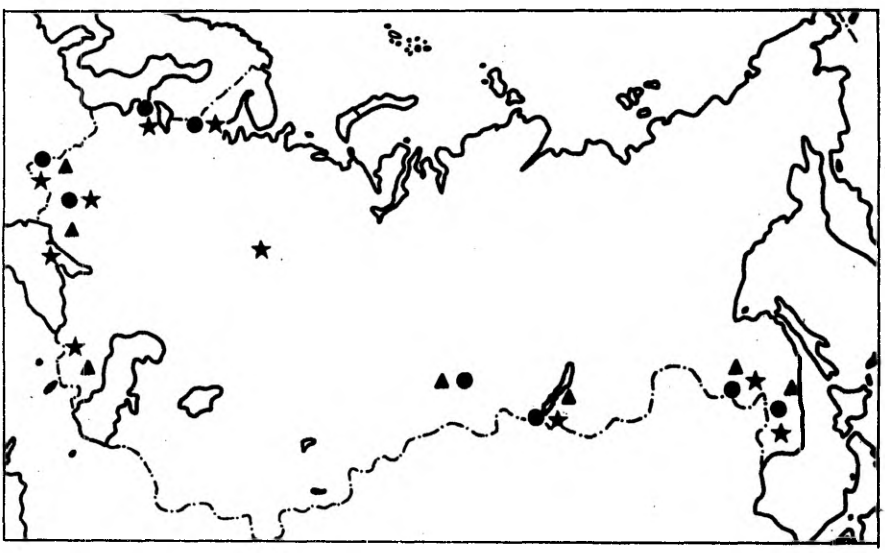


FIG. 3. Distribution of *Cetrelia cetrarioides* (●), *C. monachorum* (▲) and *C. olivetorum* (★) in the Soviet Union.

(6) *C. monachorum* (Zahlbr.) Culb & C. Culb. Distributed in the zone of mixed and deciduous forests on the whole territory of the Soviet Union (Fig. 3); 29 specimens examined. The major medullary substance is imbricaric acid.

(7) *C. olivetorum* (Nyl.) Culb & C. Culb. Distributed throughout the USSR (Fig. 3); 31 samples examined. The major substance is olivetoric acid.

(8) *C. pseudolivetorum* (Asah.) Culb & C. Culb. According to the literature it has been found only in the Far East (Kopaczevskaja *et al.* 1971, Knjazheva 1973) (Fig. 1). The only specimen tested was collected in the Primorje region. The major medullary compound is olivetoric acid.

New species

In addition to the species mentioned above there is one specimen from the Khabarovsk region in the Soviet Far East, with alectoronic and α-collatolic acids as major medullary substances, that does not seem to belong to any described species (Culberson & Culberson 1968). It is described here as *C. orientalis*.

Another specimen, collected by Dr J. C. Wei from China, distributed in *Lichenes Sinenses Exsiccati* no. 20 as *C. collata*, contains microphyllinic acid as the major medullary compound. It is described here as *C. pseudocollata*.

Furthermore, the species *C. collata* (Nyl.) Culb. & C. Culb., which had been reported from the Primorje region in the eastern part of the USSR (Kopaczevskaja *et al.* 1971, Skirina & Knjazheva 1985, Skirina 1987), must be excluded from the list of the lichens of the Soviet Union. *C. collata* is in fact a rare species occurring in China with imbricaric acid as major medullary substance but lacking soredia, isidia or lobules (Culberson 1965, Culberson & Culberson 1968). Not a single specimen examined from the USSR corresponds to these characteristics. This misunderstanding is probably due to a somewhat different circumscription of *Cetraria collata* in the Soviet lichenological literature. It mainly included various infraspecific taxa presently treated as synonyms of other species in *Cetrelia*, e.g., *Cetraria collata* f. *isidiata* Asah. = *Cetrelia braunsiana* Culb. & C. Culb and *Cetraria collata* f. *microphyllina* (Hue) Zahlbr. = *Cetrelia japonica* (Zahlbr.) Culb. & C. Culb.

Cetrelia orientalis Randl. & Saag sp. nov.

Thallus mediocris, 10–12 cm latus; laciniae 0·5–1·5 cm latae, marginibus dense intructae vel planta tota saepe cristata lobulis, vel expansis et foliosis. Superficies superior cana vel cinerea, levis, pseudocyphellata; pseudocyphellae punctatae vel nonnihil elongatae, parvae (tenus 0·5 mm latae). Superficies inferior nigra, marginibus castanea vel pallida, levis vel subrugosa, non punctata; rhizinae nigrae. Cortex superior 16–23 µm crassus, medulla 112–162 µm crassa, cortex inferior 20–23 µm crassus. Apothecia et pycnidia ignota. Atranorinum in cortice superiore, acidum alectoronicum et acidum α-collatolicum in magna summa et acidum physodicum et acidum 4-O-methylphysodicum in minima summa in medulla.

Typus: USSR, the Far East, Khabarovsk region, the Badzhal Mountains, the valley of the Urmi River, mixed forest, on a fallen trunk, 2 July 1981, *Randlane* 223 (TU—holotypus.)

(Figs 1, 4)

Morphology: Thallus medium, 10–12 cm broad; lobes 0·5–1·5 cm broad, the margins densely fringed with lobulae, quite broad and lobe-like so that the specimen may appear cristate. *Upper surface* light grey to ashy, smooth, pseudocyphellate, the pores punctiform or somewhat elongate, small (up to 0·5 mm broad). *Lower surface* black, marginal zone brown to pale, smooth or

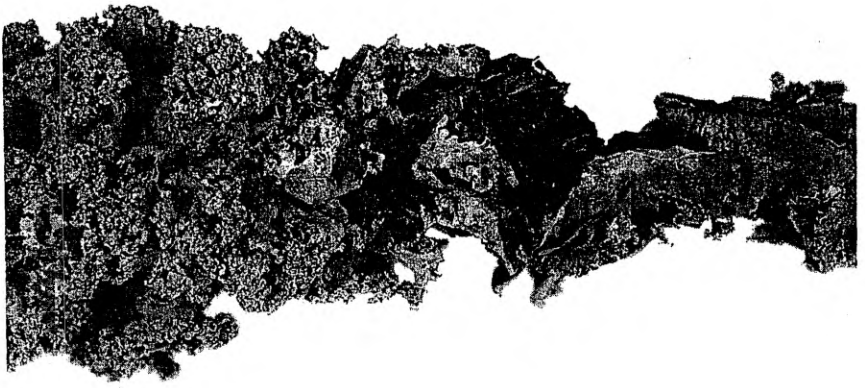


FIG. 4. *Cetrelia orientalis* (magnified × 1·5).

little wrinkled, not punctate; rhizines black. *Upper cortex* 16–23 μm thick, medulla 112–116 μm thick, lower cortex 20–23 μm thick. *Apothecia* and *pycnidia* not observed.

Chemistry: Atranorin in the upper cortex, alectoronic and α-collatolic acids in major amounts and physodic and 4-0-methylphysodic acids in minor amounts in the medulla.

This species is mainly characterized on its medullary chemistry and presence of abundant marginal lobules. It differs from *C. japonica* and *C. pseudolivetorum* distributed in the same region in the presence of alectoronic and α-collatolic acids in the medulla as the major compounds.

Cetrelia pseudocollata Randl. & Saag sp. nov.

Thallus mediocris; laciniae 0·7–2·0 cm latae. Superficies superior glauca vel cinerea, levis, pseudocyphellata; pseudocyphellae magnae, crebrae, saepe confluentes et ad 1 mm. Superficies inferior nigra, marginibus castanea, levis vel subrugosa, nonnihil nitidus, fere punctata; rhizinae nigrae. Cortex superior 11–20 μm crassus, medulla 70–112 μm crassa, cortex inferior 11–16 μm crassus. Apothecia ignota. Pycnidia numerosa, marginalia; conidia 5–6 × 1–1·5 μm recta, extremis nonnihil inflatis. Atranorinum in cortice superiore, acidum microphyllinicum in medulla.

Typus: China, Anhui, Mountain Huang Shan, Beihai, on the bark of *Quercus* sp., alt. 1720 m, 1980, *J. C. Wei* [*Lich. Sinenses Exs.* no. 20] (LD—holotypus).

(Fig. 5)

Morphology: Thallus medium; lobes 0·7–2·0 cm broad. *Upper surface* greenish grey to ashy, smooth pseudocyphellate, the pores large, numerous, often becoming confluent and exceeding 1 mm. *Lower surface* black, marginal zone brown, smooth or little wrinkled, somewhat glossy, with single pores; rhizines black. *Upper cortex* 11–20 μm thick, medulla 70–112 μm thick, lower cortex

FIG. 5. *Cetrelia pseudocollata* (magnified × 1·5)

11–16 µm thick. *Apothecia* not observed. *Pycnidia* numerous, marginal, unstalked; conidia bifusiform, the ends slightly inflated, 5–6 × 1–1·5 µm.

Chemistry: Atranorin in the upper cortex, microphyllinic acid in the medulla.

Cetrelia pseudocollata is mainly characterized by the medullary chemistry. It is structurally similar to *C. collata* and *C. nuda* Culb. & C. Culb. and differs from these entities in the presence of microphyllinic acid as medullary compound. Other taxa without vegetative propagules such as *C. davidiana* Culb. & C. Culb., *C. sanguinea* Culb. & C. Culb. and *C. delavayana* Culb. & C. Culb. have tiny punctiform pseudocyphellae in contrast to the large irregular pseudocyphellae of *C. pseudocollata*.

Key to the Species of Cetrelia

1 Terricolous, occurring on tundra soil. Thallus sterile, lacking propagules for asexual reproduction . . . . . **C. alaskana**
Corticolous or occurring on boulders in the zone of mixed or deciduous forest. Thallus usually sorediate, isidiate, with lobules or with apothecia 2

2(1) Thallus sorediate. Distributed in Europe, eastern North America and in E and SE Asia 3
Thallus not sorediate. Species restricted to E and SE Asia 6

3(2) Medulla C+ pink to reddish (olivetoric acid) . . . . . **C. olivetorum**
Medulla C− 4

4(3) Medulla KC+ red (alectoronic and α-collatolic acids) . . **C. chicitae**
Medulla KC− 5

5(4) Perlatolic acid as the major medullary component (TLC needed) . . . . . **C. cetrarioides**
Imbricaric acid as the major medullary component (TLC) . . . . . **C. monachorum**

6(2) Thallus with cylindrical and coralloid isidia or dorsiventral lobules, apothecia extremely rare 7
Thallus without isidia or lobules, often with apothecia 12

7(6) Medulla C+ pink to red 8
Medulla C− 9

8(7) Thallus with abundant marginal dorsiventral lobules, some small isidia-like structures may also be present. Olivetoric acid as the major medullary component . . . . . **C. pseudolivetorum**
Thallus with globose or coralloid isidia (may be poorly developed), dorsiventral lobules absent. Anziaic acid as the major medullary component . . . . . **C. isidiata** Culb. & C. Culb.

9(7) Medulla KC+ red 10
Medulla KC−. Imbricaric acid as the major medullary component . . . . . **C. sinensis** Culb. & C. Culb.

10(9) Thallus with laminal and marginal well developed isidia. Alectoronic and α-collatolic acids as the major medullary components . . . . . **C. braunsiana**
Thallus with mainly marginal, dorsiventral lobules 11

11(10) Microphyllinic acid as the major medullary component (TLC) . . . . . **C. japonica**
Alectoronic and α-collatolic acids as the major medullary components (TLC) . . . . . **C. orientalis**

12(6) Medulla C+ pink to red 13
Medulla C− 14

13(12) Olivetoric acid as the major medullary component (TLC) . . . . . **C. davidiana**
Anziaic acid as the major medullary component (TLC) **C. sanguinea**

14(12) Medulla KC+red 15
Medulla KC− 16

15(14) Alectoronic and α-collatolic acids as the major medullary components (TLC) . . . . . **C. nuda**
Microphyllinic acid as the major medullary component (TLC) . . . . . **C. pseudocollata**

16(14) Pseudocyphellae large, irregular and becoming confluent, some of them more than 1 mm diam. Imbricaric acid as the major medullary component . . . . . **C. collata**

Pseudocyphellae small, punctiform, less than 1 mm in diam. Perlatolic acid as the major medullary component . . . . . **C. delavayana**

Species Concept in the Genus *Cetrelia*

Traditionally a type of chemical species concept has been accepted within this group of lichens. Different species with similar or even totally identical morphology may differ from each other only by the medullary constituents (Culberson & Culberson 1976). We propose here to call the morphological groups separated by the Culbersons 'morphotypes'. The terms 'morphotype' and 'chemotype' have been given precise meanings and they are applied to populations of undetermined taxonomic rank or of no taxonomic value (Hawksworth 1974). If these terms are usually used for marking infraspecific variations, then sometimes they can also be applied to supraspecific groupings, as the concept of species in different lichen genera varies widely. Generally, recognized species in the genus *Cetrelia* are restricted within very narrow limits and do not contain essential morphological or chemical variation *per se*.

Generally, each species within the genus *Cetrelia* belongs to one morphotype and to one chemotype. Thus, the combination of the morpho- and chemotypes makes it possible to characterize concisely all 17 known species (Table 1). This enables the table to be used as an identification guide to the species. Besides its practical use, this table also has some theoretical value. Vacant squares in the table mark the species that are theoretically possible in the genus. This suggestion is confirmed by the fact that there were two specimens found in our analyses that did not belong to any hitherto described species but fitted the vacant places in the table. Since we consider that material showing new combinations of known morpho- and chemotypes deserves the rank of species the two new species *C. orientalis* and *C. pseudocollata* have been described above.

Some hints about one more specimen fitting another vacant space Table 1 have already been published. In the description of *C. sanguinea*, Culberson & Culberson (1968) noted a single Japanese collection lacking apothecia and possessing marginal lobules, somewhat reminiscent of *C. japonica*. Their chemical studies showed that it contained anziaic acid. For that reason we believe the sample could be assigned to the morphotype of *sinensis* and chemotype IV. This place in the table is unfilled. Unfortunately we have not seen the herbarium material and therefore cannot decide its proper taxonomic position.

Morphotypes

Morphological groups within *Cetrelia* as presented by Culberson & Culberson (1976) were designated by the Latin epithets of the most prominent species in the respective group. We have adopted the same terminology here. Five morphotypes can basically be recognized in the genus: *cetrarioides*, thallus with soredia; *isidiata*, thallus with isidia; *sinensis*, thallus with marginal dorsiventral lobules; *collata*, thallus without soredia, isidia or lobules, often with

TABLE 1. *Morpho- and chemotypes of* Cetrelia *(new species are in bold italics)*

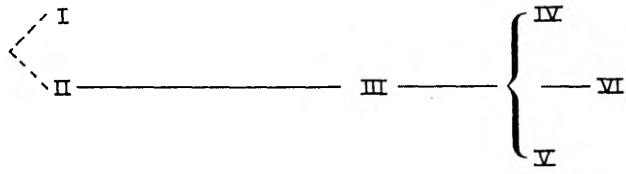
Morphotypes and their diagnostic characters	Chemotypes and their major components					
	I Alectoronic and α-collatolic	II Microphyllinic	III Olivetoric	IV Anziaic	V Perlatolic	VI Imbricaric
Cetrarioides						
Thallus sorediose	*C. chicitae*		*C. olivetorum*		*C. cetrarioides*	*C. monachorum*
Isidiata						
Thallus isidiate	*C. braunsiana*			*C. isidiata*		
Sinensis						
Thallus with lobules	***C. orientalis***	*C. japonica*	*C. pseudo-olivetorum*			*C. sinensis*
Collata						
Thallus without vegetative propagules; large pseudocyphellae	*C. nuda*	***C. pseudocollata***				*C. collata*
Davidiana						
Thallus without vegetative propagules; small pseudocyphellae			*C. davidiana*	*C. sanguinea*	*C. delavayana*	*C. alaskana*

apothecia and large pseudocyphellae; *davidiana*, thallus without vegetative propagules and frequently with apothecia, but pseudocyphellae small. The division of species into morphotypes is, however, somewhat conventional. For example we suggest that *C. alaskana* should be placed in the morphotype *davidiana*, although it differs externally from the other species of this morphotype (*C. davidiana, C. delavayana, C. sanguinea*) to some degree. This is probably due to the different habitat selection in *C. alaskana*, since it is the only terricolous species in the genus occurring on barren tundra soil. *Cetrelia sanguinea* belongs in its typical form to the same morphotype but occasionally marginal lobules can also be developed, which makes it fall into the variation type of *sinensis* as defined above. Retaining the division of *Cetrelia* species into morphotypes makes the survey of the genus simpler.

Chemotypes

As with the morphotypes, the genus *Cetrelia* also contains a number of chemotypes related to the content of major medullary substances. Species of a certain chemotype always have the same (one or two) major constituents while the complex of minor substances may vary somewhat (in some species all the minor substances are possibly not yet characterized). Six chemotypes have so far been recognized in our examined material (Table 2) and also in the genus as a whole.

The numbering of the chemotypes corresponds to the trend of chemical evolution with reduced side-chain length in depsides and depsidones (Culberson & Culberson 1976). All the *Cetrelia* chemotypes are certainly related to each other, but the degree of connection between different chemotypes is unequal. We propose the following scheme of chemical relationships between the chemotypes observed in *Cetrelia*.



Chemotype I is presumably the most diverging type since it is the only chemotype which contains depsidones and no depsides. In addition it is the only chemotype where the detected compounds are not represented in the other chemotypes. Both major constituents of chemotype I have a great number of side-chain carbons (7–7). This is the reason why chemotype I is somewhat related to chemotype II. The major constituent of the latter, i.e. microphyllinic acid which combines two units of seven-carbon side chains, was considered to be the most primitive of the compounds occurring in *Cetrelia* (Culberson & Culberson 1976: 336). Chemotype III is a progression in the reduction of side chains of the major compound. Chemotypes IV and V, both characterized by major substances with 5 + 5 carbons in the side chain, could be interpreted as having reduced series of side chains. Chemotype VI can be

TABLE 2. *Contents of major* (M) *and minor* (m) *medullary substances in the chemotypes of genus* Cetrelia*

Chemotypes	Species	Medullary compounds: Depsidones: Alectoronic	α-Collatolic	Physodic	4-O-Methylphysodic	Depsides: 4-O-Demethylmicrophyllinic	Microphyllinic	Olivetoric	4-O-Methylolivetoric	Anziaic	Perlatolic	4-O-Demethylglomelliferic	Glomelliferic	4-O-Demethylimbricaric	Imbricaric	Loxodellic	Divaricatic
		Number of carbons in side-chain															
		7—7		7—5		7—7		7—5		5—5				5—3		3—3	
I	*C. chicitae*	M	M	m	m												
	C. braunsiana	M	M	m	m												
	C. orientalis	M	M	m	m												
	C. nuda	M	M	m	m												
II	*C. japonica*					m	M		m								
	C. pseudoeollata					m	M		m								
III	*C. olivetorum*					m		M		m							
	C. pseudolivetorum					m		M		m		m					
	C. davidiana					m		M		m							
IV	*C. isidiata*							m	m	M	m	m	m	m	m		
	C. sanguinea								m	M	m	m	m	m	m		
V	*C. cetrarioides*							m	m	m	M		m		m		
	C. delavayana								m	m	M		m		m		
VI	*C. monachorum*									m	m		m	m	M	m	m
	C. sinensis										m			m	M	m	m
	C. collata									m	M		m	m	M	m	m
	C. alaskana									m	m			m	M	m	m

*Data from Culberson & Culberson (1976) with some additions.

interpreted as the most advanced chemosyndrome characterized by several minor substances including divaricatic acid which represents the most advanced product in the genus with two units of three-carbon side chains. It is remarkable that the similarity of different chemotypes grows with numeration. Chemotypes IV, V and VI form a relatively uniform group regarding their chemosyndromes.

Discussion

In the genus *Cetrelia* the highest number of combinations of morpho- and chemotypes (i.e. species) are represented in eastern and south-eastern Asia

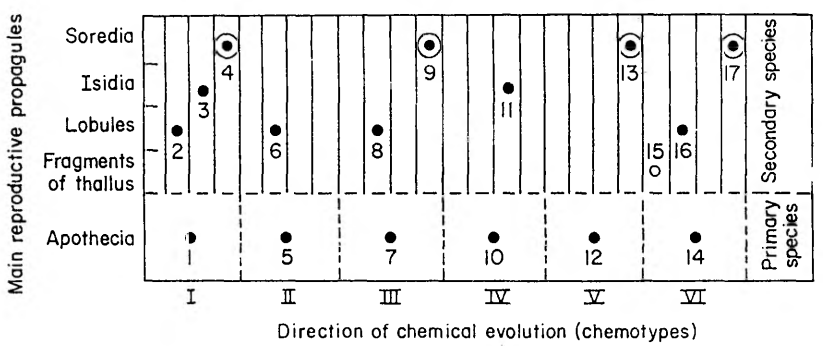


FIG. 6. Evolutionary relationships between the *Cetrelia* species. Restricted to eastern and southeastern Asia (●), limited distribution outside eastern and southeastern Asia (o), wide distribution outside eastern and southeastern Asia (○). 1, *C. nuda*; 2, *C. orientalis*; 3, *C. braunsiana*; 4, *C. chicitae*; 5, *C. pseudocollata*; 6, *C. japonica*; 7, *C. davidiana*; 8, *C. pseudolivetorum*; 9, *C. olivetorum*; 10, *C. sanguinea*; 11, *C. isidiata*; 12, *C. delavayana*; 13, *C. cetrarioides*; 14, *C. collata*; 15, *C. alaskana*; 16, *C. sinensis*; 17, *C. monachorum*.

(Culberson & Culberson 1968). From among five morphotypes, only one, namely *cetrarioides*, is widely distributed in the world, whereas the areas of non-sorediate morphotypes (*isidiata, sinensis, collata* and *davidiana*) fall only into East and Southeast Asia. Lichens that have developed soredia can expand and effectively enlarge their area of distribution in contrast to species that use only ascospores. The complicated process of the resynthesis of a lichen thallus from a germinated ascospore and a free-living photobiont first depends upon the distribution area of algae (Tehler 1982). The other forms of vegative propagules should theoretically also have the ability to colonize habitats in which the photobiont cannot thrive in its free-living form. In the genus *Cetrelia*, isidia and lobules still appear to be almost as ineffective in colonizing new territories as the spores. Thus, only four sorediate species (*C. cetrarioides, C. monachorum, C. olivetorum* and *C. chicitae*) are also found in Europe and North America. The centre of speciation in the genus is presumably located in eastern and southern Asia, as seen from the vast majority of the combinations of chemo- and morphotypes.

Evolutionary relationships

The first scheme dealing with the connections between species of *Cetrelia* was proposed by Poelt (1970, 1972) and related to his discussion on 'species-pairs'. Our scheme includes all the combinations of chemo- and morphotypes known up to now in the genus (Fig. 6). The horizontal axis on the scheme shows the direction of chemical evolution and the vertical axis represents the variety of reproductive propagules. We presume that the formation and evolution of biochemical pathways producing the complex of lichen substances has taken place during sexual stages in the evolution of lichens, rather than through mutations in asexual stages (Bowler & Rundel 1975). The genus *Cetrelia* fits rather well into the theory of development of species pairs since every chemo-syndrome is represented not only by the 'secondary' but also by the 'primary'

species. This avoids the necessity of referring to some hypothetical ancestral taxa. All 'primary' species with sexual reproduction appear to be quite rare with a very restricted distribution. However, we observe not only pairs of species but also triplets or even tetrads of species in the genus *Cetrelia*. A similar pattern has been reported only in a few other cases, for example in *Parmelia* and *Physcia* (Hawksworth & Hill 1984).

The taxonomic treatment proposed by Tehler (1982) to recognize fertile and sterile counterparts as infraspecific taxa with the rank of forma could theoretically be acceptable, but in practice it is not. 'Primary' species differ essentially from the 'secondary' species by their morphology as well as the 'secondary' species of one column from the other. It is difficult to imagine, for example, the treatment of *C. chicitae, C. braunsiana, C. orientalis* and *C. nuda* as one species. The morphological similarity is great between taxa such as *C. orientalis, C. japonica, C. pseudolivetorum* and *C. sinensis*, or *C. chicitae, C. olivetorum, C. cetrarioides* and *C. monachorum* but presumably they all have quite a different origin and cannot belong to one species. Otherwise we would be ' back to the traditional typological species concept adamantly blind to everything but morphology ' (Culberson, 1986).

One species, *C. alaskana*, with an isolated distribution, however, does not fit too well into the normal primary/secondary species relationship described above. This species is not an epiphyte, as are essentially all the other examined species, and furthermore neither soredia, isidia, lobulae nor any sexual reproductive structures have been observed. Presumably it reproduces through fragmentation as do many other macrolichens growing on tundra soil. Therefore, we suggest that *C. alaskana* can also be placed in the group of 'secondary' species.

The frequency and distribution of the examined species in the genus *Cetrelia*, in our opinion, serve as good examples of some of the theoretical assumptions discussed above. All the sorediate species, although common and widely distributed, may be considered 'evolutionary blind alleys'. The organism loses its genetic flexibility by having an asexual propagation system superior to the sexual process (Tehler 1982). On the other hand, the sexual species, although occasionally less successful in dispersing, have retained their ability for further speciation by the process of gene recombination.

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IV

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NEW DATA ABOUT THE GENERA *CETRARIOPSIS*, *CETRELIOPSIS* AND *NEPHROMOPSIS* (FAM. PARMELIACEAE, LICHENIZED ASCOMYCOTINA)

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ABSTRACT - New morphological, anatomical and chemical data about the lichen genera *Cetrariopsis, Cetreliopsis* and *Nephromopsis* are presented. Two new species, *Cetrariopsis laii* Thell & Randl., *Cetreliopsis papuae* Randl. & Saag, and one new subspecies *Cetreliopsis rhytidocarpa* subsp. *langtangi* Randl. & Tell, are described and the following new combinations proposed: *Cetrariopsis pallescens* (Schaerer) Randl. & Thell, *Cetrariopsis pallescens* var. *citrina* (Taylor) Thell & Randl., *Cetreliopsis asahinae* (Sato) Randl. & Thell, *Cetreliopsis endoxanthoides* (Awasthi) Randl. & Saag and *Cetreliopsis laeteflava* (Zahlbr.) Randl. & Saag. *Cetrariopsis* comprises now two, *Cetreliopsis* five and *Nephromopsis* nine species. All the three genera, distributed in East and Southeast Asia, are characterized by the dorsiventral foliose thallus, presence of pseudocyphellae on the lower surface, clavate asci usually with a rather large axial body in the tholus, oblong or ellipsoid ascospores and usnic acid as the cortical substance.

RÉSUMÉ - Des données morphologiques, anatomiques et chimiques nouvelles sont présentées, concernant les genres *Cetrariopsis, Cetreliopsis* et *Nephromopsis* (lichens). Deux nouvelles espèces, *Cetrariopsis laii* Thell & Randl., *Cetreliopsis papuae* Randl. & Saag. et une nouvelle sous-espèce *Cetreliopsis rhytidocarpa* subsp. *langtangi* Randl. & Thell sont décrites. Les combinaisons suivantes sont proposées: *Cetrariopsis pallescens* (Schaerer) Randl. & Thell, *Cetrariopsis pallescens* var. *citrina* (Taylor) Thell & Randl., *Cetreliopsis asahinae* (Sato) Randl. & Thell, *Cetreliopsis endoxanthoides* (Awasthi) Randl. & Saag et *Cetreliopsis laeteflava* (Zahlbr.) Randl. & Saag. *Cetrariopsis* comprend maintenant deux espèces, *Cetreliopsis*, cinq et *Nephromopsis*, neuf. Ces trois genres, distribués en Asie de l'Est et du Sud-Est, sont tous caractérisés par un thalle foliacé à symétrie dorsiventrale, la présence de pseudocyphelles à la face inférieure, des asques clavulés avec, dans le bouchon apical, un corps axial relativement grand, des ascospores oblongues et ellipsoïdales et de l'acide usnique dans le cortex supérieur.

KEY-WORDS - lichenized Ascomycotina, Parmeliaceae, *Cetrariopsis, Cetreliopsis, Nephromopsis*, anatomy of thallus and ascocarps.

INTRODUCTION

A general review of cetrarioid lichens (Kärnefelt *et al.* 1992, Randlane & Saag 1993) has clearly shown that besides the indistinctly limited genus *Tuckermannopsis*,

the complex *Cetrariopsis - Cetreliopsis - Nephromopsis* is another poorly studied group of taxa. In this paper we delimit these three genera, compare their various characters and identify the generic positions of the species involved. A new genus, *Tuckneraria*, was segregated from *Nephromopsis* in one of our previous papers (Randlane *et al.* 1994). As we consider *Tuckneraria* evolutionary allied rather to *Tuckermannopsis* than to *Nephromopsis*, the species included in that entity are not treated here.

MATERIAL AND METHODS

More than 300 herbarium specimens from BM, CAN, FH, G, GZU, H, KW, LD, LE, M, PC, S, TAIM, TNM, TU, UPS, US and private herbaria of A. Aptroot, D.D. Awasthi and J. A. Elix were examined.

Anatomical studies of cortical and reproductive structures were carried out on most of the specimens. Sections were made with a kryomat, Leitz freezing microtome and put in lactophenol cottonblue. After pretreatment with 10% KOH-solution, asci were squashed in a 0,3% Lugol's solution. The characters were studied with a Zeiss Axioscope light microscope, and the photos were made with a Zeiss M 35 W camera.

Chemical analyses were carried out according to the standardized TLC methods (Culberson & Kristinsson 1970, Culberson 1972) on about 200 specimens. The acetone extracts were run in solvent systems B, C and G (Culberson *et al.* 1981).

RESULTS AND DISCUSSION

1. The genus *Nephromopsis* Müll. Arg.

This genus was described already in 1891 by Müller Argoviensis to accomodate *N. stracheyi*, which was said to have a thallus similar to *Cetreria* but the position of apothecia like in *Nephroma*. In contemporary lichenology the genus was not generally recognized until 1980 when Lai resurrected the treatment of the species with cetrarioid thallus, nephromoid apothecia and pseudocyphellae on the lower surface, in a separate genus under the name *Nephromopsis*. Still, the marginal position of apothecia on the lower side of the thallus is a character that could be easily misidentified and also the anatomical differences had not been studied sufficiently in that time. In this paper we continue the revision of *Nephromopsis* (Randlane & Saag 1991, 1992) by presenting detailed anatomical data characterizing the whole genus, transferring some species (*N. asahinae, N. endoxanthoides, N. pallescens*) to other genera (*Cetreliopsis, Cetrariopsis*) and complementing the description of two rarely collected species (*N. morrisonicola, N. yunnanensis*).

The genus *Nephromopsis* is defined by the following characters: a large foliose thallus; marginal apothecia on the lower side of the thallus; presence of pseudocyophellae only on the lower surface; three-layered exciple; narrowly clavate asci and oblong ascospores; bifusiform pycnoconidia; usnic acid in the cortex; various fatty

acids and/or some orcinol depsides-depsidones in the medulla. The genus includes according to our present knowledge nine species:

N. ectocarpisma (Hue) Gyelnik
N. endocrocea Asahina
N. isidioidea (Räsänen) Randl. & Saag
N. komarovii (Elenkin) Wei
N. morrisonicola Lai
N. ornata (Müll. Arg.) Hue
N. rugosa Asahina
N. stracheyi (Bab.) Müll. Arg.
N. yunnanensis (Nyl.) Randl. & Saag

Several other species that have been treated as belonging to *Nephromopsis* do not correspond to these characters and were lately transferred to the other genera. Thus *N. laureri* (Kremp.) Kurok., *N. laxa* (Zahlbr.) Sato and *N. pseudocomplicata* (Asah.) Lai [including *N. nipponensis* (Asahina) Lai] differ in having marginal cilia, globose to subglobose ascospores, a two-layered exciple and were therefore removed to *Tuckneraria* (Randlane *et al.* 1994). *N. globulans* (Nyl. ex Hue) Lai shows clear affinities (globose to subglobose ascospores, filiform pycnoconidia, presence of secalonic acid in the medulla) with the genus *Allocetraria*. *N. asahinae* (Sato) Räsänen and *N. endoxanthoides* (Awasthi) Randl. & Saag are transferred here to *Cetreliopsis* (see below) due to the presence of pseudocyphellae also on the upper surface, two-layered exciple, rather broadly clavate asci and contents of fumarprotocetraric acid in the medulla. *N. pallescens* (Schaerer) Park has apothecia situated laminally on the upper surface and is included on these grounds in *Cetrariopsis* (see below).

NEPHROMOPSIS **Müll. Arg.,** ***Flora*** **74: 374 (1891).**

Type species: *Nephromopsis stracheyi* (Bab.) Müll. Arg. - (Fig. 15).

Thallus foliose, may be very large (up to 20 cm in diameter), often remarkably rugose or reticulated, greenish yellow on the upper and light to dark brown or even black on the lower surface. Isidia, soredia and true cilia absent but numerous black laminal and marginal emergent projections bearing pycnidia at their tops are present in many species. **Pseudocyphellae** occur over the lower surface either in the form of small white dots or larger regular patches, they may be plain, concave or convex, usually located on the ridges of the thallus or on the special plug-like outgrowths. **Rhizines** sparse or numerous, of the same colour as the lower surface. **Pycnidia** marginal and laminal, often on emergent black projections but may also be immersed in the thallus. **Cortical layers** paraplectenchymatous, either of the same type as in *Cetrariopsis* (see below) with larger cells near the medulla or with rather equal-sized, strongly gelatinized cells also characteristic for the genus *Flavocetraria* (Kärnefelt *et al.* 1994). **Apothecia** marginal, sometimes very large (to 32 mm in diameter), situated on the lower surface of the thallus but the disc often turns upwards which may confuse the true position of the ascocarps. Disc brown, rounded or reniform in outline, may

have a short stalk. **Exciple** usually distinctly three-layered, **asci** narrowly clavate, 30-70 x 8-14 µm, mainly with an axial body of medium size, 2-4 µm broad, but in some species with an amyloid apical ring structure and a very small axial body (0.5-1.2 µm broad) like in *Flavocetraria* (Kärnefelt *et al.* 1994). **Ascospores** 6-12 x 3-6 µm. Pycnoconidia bifusiform (dumb-bell shaped), 4-5 x 1-1.5 µm.

Chemical constituents: usnic acid (+/-) in the cortex; various fatty acids (lichesterinic, protolichesterinic, caperatic, nephrosteranic acids, etc.) and some orcinol depsides and depsidones (olivetoric, anziaic, physodic, conphysodic acids) in the medulla. A few species contain also substances related to the anthraquinonic pigments (endocrocin, secalonic acids A and C) colouring the medulla either orange or yellow.

Distribution and habitat: Eastern and Southeastern Asia. All the species within *Nephromopsis* with the exception of *N. komarovii* are corticolous on deciduous or coniferous trees in the montaneous forests. The latter grows on rocks and boulders or on the ground.

Two species of nine - *N. morrisonicola* and *N. yunnanensis* - have earlier been represented by a few specimens from very limited areas only (Taiwan, Mt Morrison and China, prov. Yunnan accordingly). The descriptions of these rare lichens are complemented here, since we have identified some additional specimens from other localities.

Nephromopsis morrisonicola Lai - (Fig. 10)

Quart. J. Taiwan Mus. 33: 223, 1980. - **Type**: Taiwan, Nanton Co., Mt. Morrison, alt. 3500-3900 m, *Lai*, 1978, *no. 10 438* (TAIM, holotype; seen).

Thallus foliose, up to 8 cm in diameter; upper surface yellow, smooth in the younger parts and somewhat rugose in the center; lower surface black with brown or even whitish margins; **pseudocyphellae** on the underside in the form of white conspicuous rounded spots, plain or slightly elevated. **Rhizines** sparse, black or brown, simple. **Pycnidia** marginal, located on the black emergent projections, may be absent on younger specimens. Both **cortical layers** c. 25 µm thick, composed of about three cell layers each, with the cells near the medulla somewhat larger. Lower cortex brownish pigmented. Medullary hyphae c. 5 µm in diameter. **Apothecia** marginal, up to 9 mm in diameter, disc brown, rounded or irregular, faced upwards. **Exciple** usually three-layered. The upper layer up to 50 µm thick and the middle layer, composed of cells with larger lumina, if present, 10-15 µm thick.The thickness of the lowest layer is also up to 50 µm. **Asci** 35-70 x 10-15 µm, axial body 2-4 µm, tholus may have an undistinct ring structure similar to that in *N. endocrocea* and *N. ornata*. **Ascospores** 7-12 x 3-6 µm. Pycnoconidia not seen.

Chemical constituents: usnic acid (+/-) in the cortex; lichesterinic, protolichesterinic acids and additionally some unidentified fatty acids (+/-) in the medulla.

Distribution and habitat: originally described as a Taiwanese endemic (Lai 1980). We have identified *N. morrisonicola* also from the Philippines, Java, Borneo and

the mainland of China. The lichen grows in comparatively high altitudes (about 2500 m and higher) on coniferous trees or shrubs.

N. morrisonicola (Fig. 10) is easily recognized due to its black lower surface. Black underside is present also in *N. ornata* and *N. endocrocea* but both of them have coloured medulla. Lai (1980) took notice of the morphological resemblance between *N. morrisonicola* and *Cetreliopsis asahinae*. Still, the latter has laminal pseudocyphellae also over the upper cortex and the fumarprotocetraric acid, characteristic to the genus *Cetreliopsis*, is easily identified with Pd positive reaction on the medulla.

Specimens examined. *Taiwan*. Nanton Co., Mt. Morrison, Maiyun Hostel to the peak, alt. 3500-3900 m, *Lai*, 1978, *no 10 438* (holotype), *no 10 459* (TAIM). *China*. Sikang, Kangting distr., Gülingkong, Gomba La, alt. 3700 m, *Smith*, 1934, *no 14 075* (UPS). *Indonesia*. Borneo, Mt. Kinabalu, Paka Cave to Lobang, *Strong Clemens*, 1915, *no. 10 760* (FH). Mt. Kinabalu, alt. 3600 m, *Samsudin*, 1984, (Herb. Elix). Java. Pangerango, *Schiffner*, 1894, *no 3004* (FH, TNM, US). Kamah Marwak, *Herman*, 1913 (FH). Mt. Gedah, *Seifriz*, 1920, *nos. 77, 1952* (US). Res. Pasoeroean, Goenoeng, Ardjoena, Lalidjiewa - Welirang track, *Du Rietz*, 1927, *no 61b:1* (UPS). *Philippines*. Luzon, Prov. Benquet, alt. 2400 m, *Curron, Zschokke, Merritt*, 1909 (H).

Nephromopsis yunnanensis (Nyl.) Randl. & Saag.

Mycotaxon 44: 488, 1992. **Basionym**: *Platysma yunnanense* Nyl., Lich. Novae Zelandiae: 252, 1888 - **Type**: China, Yunnan, alt. 1800 m, *Delavay, no. 1602* (H-NYL-36 134, lectotype; seen). - **Synonym**: *Cetraria yunnannensis* (Nyl.) Zahlbr., *Trudy Troitskos.-Kyakhtinsk. Otd. Priamursk. Otd. Imp. Russk. Geogr. Obshch.* 12: 89, 1911 (1909).

Thallus foliose, up to 7 cm in diameter; upper surface light greenish or yellowish, strongly rugose and reticulated in well developed specimens; lower surface white to light brown, conspicuously rugose, with numerous pseudocyphellae growing on the ridges of the underside or on the special outgrowths. **Rhizines** sparse, pale, simple. **Pycnidia** extremely numerous, situated laminally and marginally (and sometimes even laminally on the lower surface) on the emergent projections which are thallus coloured and black only at their tops. The projections may easily be broken away and leave white patches without cortical layer on the upper surface. Still, these patches can neither be considered true **pseudocyphellae** nor soredia as described by Hue (1899). Upper and lower **cortex** both c. 20 µm thick, composed of rather small, equal-sized, strongly gelatinized cells. Medullary hyphae 4-6 µm in diameter. **Apothecia** marginal, up to 13 mm in diameter, disc brown, rounded. **Exciple** two-layered, upper and lower layer c. 40 µm each. Occasionally, a thin, third middle-layer is present with larger lumina. **Asci** 40-45 x 12-14 µm, axial body 4 µm, **ascospores** 8-9 x 4-4.5 µm. **Pycnoconidia** 4 x 1 µm.

Chemical constituents: usnic acid in the cortex; lichesterinic and protolichesterinic acids in the medulla.

Distribution and habitat: China (prov. Yunnan); on deciduous and coniferous trees between 1800 and 2800 m altitudes.

The most characteristic feature of this species is the abundance of laminal pycnidia on pale emergent projections (all other species in *Nephromopsis* bear black pro-

jections, if they have them at all); pseudocyphellae on the lower surface are typically on the ridges and outgrowths of very rugose lowerside. The latter reminds somewhat of the lower surface of *Cetrariopsis pallescens* and is quite different from other species in *Nephromopsis*.

Specimens examined. *China*. Yunnan, *Delavay, no. 1602* (H, lectotype). Yunnan, An Ning Co., An Ning, alt. 1800 m, 24°55' N, 102°29' E, *Koponen*, 1981, *no 37 925* (H). Yunnan, Kon-toni, *Delavay*, 18.06.1888 (PC). Yunnan, Lijiang Co., Yulongshan, alt. 2600-2800 m, 27°11'N, 100°15' E, *Ahti et al.*, 1987, *no 46 370a* (H, TU). Yunnan, Lijiang Co., Yulongshan, Yufeng Temple, 26°58' N, 100°12' E, *Ahti*, 1987, *no. 46 303* (H). Yunnan, Ninglang Co., alt. 2700 m, *Wang Li-Song*, 1987, *no. 10 373* (H).

II. The genus *Cetrariopsis* Kurok.

The monotypic genus *Cetrariopsis* was separated from *Cetraria* s. lat. by Kurokawa in December 1980. Less than a month later Lai proposed the genus *Ahtia* to accomodate the same species - *Cetraria wallichiana* (Taylor) Müll. Arg. Two essential characters were pointed out by both authors to describe the new genus - the numerous, small, laminal apothecia (Fig. 4) and the prosoplectenchymatous upper cortex. The structure of the cortex, however, was a misinterpretation by Kurokawa and Lai. In earlier papers the terms «prosoplectenchyma» and «paraplectenchyma» referred to the form of the cell lumina, but since studies of thallus structures were carried out by Hale (1976), these terms are usually applied to indicate the hyphal orientation in the cortex. Thus, according to Culberson & Culberson (1965, 1968) the upper cortex of *Asahinea*, *Cetrelia* and *Platismatia* was classified as prosoplectenchymatous, although not characterized by a parallel periclinal orientation of the hyphae. All these genera as well as *Cetrariopsis* have a pachydermatous paraplectenchymatic cortex with randomly oriented cells. Still, *Cetrariopsis* is probably not closely related to those entities as supposed earlier (Kurokawa 1980, Kärnefelt *et al.* 1992, Elix 1993).

The characteristic features of the genus *Cetrariopsis* are: a large foliose thallus; comparatively small, marginal as well as laminal apothecia on the upper side of the thallus; presence of pseudocyphellae only on the lower surface; two-layered exciple; narrowly clavate asci and oblong ascospores; usnic acid in the cortex; fatty acids or alectoronic acid in the medulla.

This genus is considered to be a distinct taxon which is sometimes referred to as parmelioid. The laminal position of apothecia is really an easily recognized parmelioid character, while a nonpored epicortex (Elix 1993) and presence of pseudocyphellae on the lower surface remind of the cetrarioid genera. Our studies have shown that there is not much difference in anatomy of *Cetrariopsis* and *Nephromopsis*. Both genera are characterized by oblong ascospores and narrowly clavate asci with a medium sized axial body, 2-4 µm broad (Figs. 13, 15, 16). The exciple is two-layered in *Cetrariopsis* and three-layered in most species of *Nephromopsis* but sometimes the middle layer is not distinctly developed. The layer called upper excipular layer in this paper (Figs. 1, 12) is referred to by some authors as hypothecium.

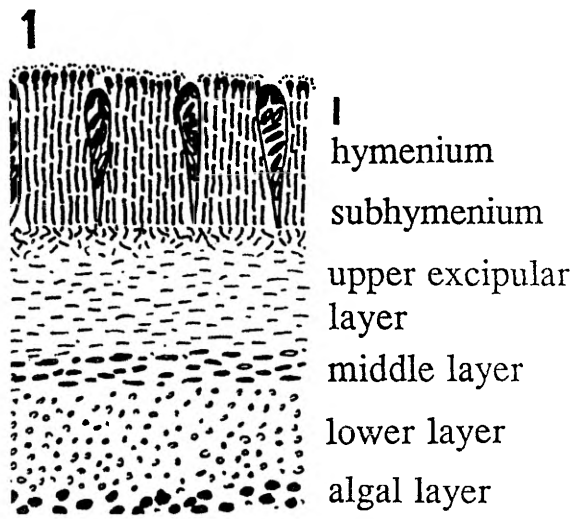

Fig. 1 - Schematic drawing of the hymenial and excipular layers of *Nephromopsis rugosa*. The upper excipular layer is by some authors called hypothecium. Bar = 10 µm.

The position of the apothecia is indeed a striking character but a more thorough examination shows that specimens with clearly laminal apothecia have usually fruiting bodies also along the margins. Furthermore, on many specimens with mostly marginal apothecia both submarginal or even truly laminal ones occur. Other morphological characters (reticulation of the thallus, presence of pseudocyphellae on the lower surface, absence of isidia, soredia and cilia) as well as cortical and medullary chemistry do not show essential differences. However, we still prefer to maintain the separation of the genera *Cetrariopsis* and *Nephromopsis* upon the position of the apothecia (*Cetrariopsis* with laminal and marginal apothecia; *Nephromopsis* with marginal apothecia only) until additional comparative studies have been carried out.

The genus *Cetrariopsis* includes two species: *C. pallescens* (Schaerer) Randl. & Thell and the newly described *C. lai* Thell & Randl.

***CETRARIOPSIS* Kurok., *Mem. Natl. Sci. Mus. (Tokyo)* 13: 140 (1980).**

Type species: *Cetrariopsis pallescens* (Schaerer) Randl. & Thell.

Thallus foliose, may be up to 16 cm in diameter but usually less than 10 cm, smooth to rugose, greenish yellow to yellow on the upper and white to yellow or brown on the lower surface. Isidia, soredia, cilia and emergent projections absent. **Pseudocyphellae** occur over the lower surface either in the form of small white dots or wider regular patches situated on the ridges of the thallus or on the special plug-like outgrowths. **Rhizines** sparse, white or brown. **Cortical layers** paraplectenchymatous, up to 30 µm thick, with larger cells near the medulla; medullary hyphae up to 6 µm thick. **Apothecia** 1-5 mm in diameter, laminal, submarginal or marginal but not situated on the lower surface of the thallus; disc brown, rounded or oblong and reniform,

may be surrounded by a thin thalline margin. **Exciple** two-layered, upper layer c. 20-30 µm and lower layer c. 30 µm thick. **Asci** narrowly clavate, 35-45 x 8-10 µm, axial body of medium size, 2.5-4 µm, **ascospores** oblong, 7-10 x 3-5 µm. **Pycnidia** and pycnoconidia not seen.

Chemical constituents: usnic acid (+/-) in the cortex; fatty acids (lichesterinic and protolichesterinic acids) and orcinol depsidones (alectoronic acid) in the medulla.

Distribution and habitat: Eastern and Southeastern Asia. Epiphytic on deciduous and coniferous trees in the montaneous forests.

Cetrariopsis pallescens (Schaerer) Randl. & Thell **comb. nov.** var. ***pallescens*** - (Fig. 4, 13)

Basionym: *Cetraria pallescens* Schaerer, in Moritzi, Syst. Verz.: 129, 1846. **Type**: Java, Mt. Pangerango, *Zollinger no. 449* (G, holotype; seen). - **Synonyms**: *Platysma pallescens* (Schaerer) Nyl., *Mém. Soc. Sci. Nat. Cherbourg* 5: 100, 1857. - *Nephromopsis pallescens* (Schaerer) Park, *Bryologist* 93: 122, 1990.

Sticta wallichiana Taylor in Hooker, *London J. Bot.* 6: 177, 1847, **syn. nov.** - **Type**: Nepal, *Wallich* (G, no. 2003/2 - lectotype, selected here; G, no. 2003/1, PC, isolectotypes; seen). - **Syn.**: *Parmelia wallichiana* (Taylor) Nyl., *Mém. Soc. Sci. Nat. Cherbourg* 5: 105, 1857. - *Platysma leucostigmeum* Nyl. var. *wallichianum* (Taylor) Nyl., Syn. Meth. Lich. I: 306, 1860. - *Platysma wallichianum* (Taylor) Nyl., *Flora* 52: 443, 1869. - *Cetraria wallichiana* (Taylor) Müll. Arg., *Flora* 71: 139, 1888. - *Cetrariopsis wallichiana* (Taylor) Lai, *Quart. J. Taiwan Mus.* 33: 220, 1980.

Cetraria sulphurea Mont. & v.d. Bosch, Mont., Syll. Gen. Sp. Crypt.: 322, 1856, invalidly published - **Type**: Java, *Junghuhn* (not seen).

Cetraria teysmanni Mont. & v.d. Bosch in Mont., Syll. Gen. Sp. Crypt.: 474, 322, 1856; in Miquel, Pl. Jungh. 4: 431,1857 - **Type**: Java, *Teismann* (not seen).- **Syn.**: *Platysma teysmanni* (Mont. & v.d. Bosch) Nyl., *Mém. Soc. Sci. Nat. Cherbourg* 5: 100, 1857.

Thallus foliose, up to 16 cm diameter but usually less than 10 cm; upper surface greenish yellow, lower surface white to yellow, slightly or strongly rugose. **Pseudocyphellae** present on the lower surface in the form of white small dots or white patches located on special plug-like outgrowths, sometimes surrounded by a light brown rim. **Rhizines** sparse, white or light brown. Soredia and cilia absent, pycnidia not observed. Upper and lower **cortex** 20-30 µm thick, with larger cells near the medulla, medullary hyphae up to 5 µm thick. **Apothecia** 1-2.5 mm in diameter, laminal, submarginal and marginal, at times extremely numerous and covering the whole thallus but sometimes located mainly in the marginal parts of the upper surface and only a few apothecia can be observed as really laminal. **Ascocarps** clearly appear to originate superficially since very tiny apothecia may usually be found not in the thallus margins but further to the center. Disc brown, flat or slightly convex, sometimes surrounded by a thin thalline margin. Hymenium c. 50 µm high, subhymenium c. 10 µm. **Exciple** two-layered, both layers c. 30 µm thick. **Asci** narrowly clavate, 35-40 x c. 10 µm, axial body 3-4 µm, ascospores oblong, 7-10 x 3-4 (5) µm.

Chemical constituents: usnic acid in the upper cortex; alectoronic and/or lichesterinic, protolichesterinic acids in the medulla. PD-, K-, KC+ or -.

Distribution and habitat: Nepal, India, China, Russian Far East (Primorye region), Taiwan, Java; Japan (Kurokawa 1980), South-Korea (Park 1990). Epiphytic on deciduous and coniferous trees in the montaneous forests.

Cetrariopsis pallescens was earlier known as *Cetrariopsis wallichiana* (Taylor) Kurokawa (type from Himalaya). *Cetraria pallescens* Schaerer being the oldest name, a new combination in *Cetrariopsis* must be presented here. This species is collected in Nepal, India, Java, South-Korea, China, Taiwan, Japan and Russian Far East (Awasthi 1982, Kurokawa 1980, Lai 1980, Park 1990, Rassadina 1971, Wei 1991). Lai (1980) drew attention to some other taxa in Southeast Asia which might belong to the same group, i.e. *Cetraria citrina* Taylor and *Cetraria teysmanni* Mont. & v.d. Bosch (both types from Java). Our studies of types and other herbarium material have shown that they represent the same species. Unfortunately, we did not succeed in finding type material of *C. teysmanni* (= *C. sulphurea* Mont. & v.d. Bosch, see below).

Cetraria sulphurea Mont. & v.d. Bosch (type also from Java) was described in 1856 (Montagne 1856: 322). A new name, *Cetraria teysmanni* Mont & v.d. Bosch, was presented for this taxon already in the same paper (Montagne 1856: 474) by the same authors: «Pag. 322, n°1189, loco: «Cetraria sulphurea», Legendum est: «Cetraria teysmanni M. et v.d. B.»». We think this a sufficient reason to consider the epithet *sulphurea* as invalid. Still, these authors presented a new description of *Cetraria teysmanni* once more a year after (Montagne & v.d. Bosch 1857: 431, Stafleu & Cowan 1981).

Cetrariopsis pallescens var. *pallescens* is distributed mainly in Nepal, China and Russia and the specimens are greenish yellow on the upper surface and white on the lower. They have numerous laminal apothecia and a strongly rugose lower side with large pseudocyphellae on special outgrowths on central parts of the thallus (Fig. 4). Younger pseudocyphellae in more marginal positions may still be quite small and plain. Most of the specimens from these regions contain alectoronic acid in the medulla (KC+) but also material with fatty acids (KC-) is known as well as specimens with both types of medullary substances. Also a few specimens from Java and Taiwan were identified as *C. pallescens* var. *pallescens*.

Some specimens from Nepal may differ considerably in their morphological features from most specimens collected in Java, usually called *Cetraria citrina*. The smoothness of the thallus, the colour of both cortices, the number and position of apothecia, and the form of pseudocyphellae, however show a continuous variation, and no strict limits can be drawn. As we cannot be sure whether the morphological variation described above is not due to the extreme ecological conditions only, and distribution of different variants is partly overlapping, we prefer to preserve *C. citrina* only as a variety.

Altogether 39 specimens were examined.

Selected specimens examined. *China.* Yunnan, Lopin-chan, Lan-Kong, alt. 3200 m, *Delavay*, 1888 (PC). Yunnan, Lijiang County, Yulongshan, alt. 2600-2800 m, 27°11' N, 100°15' E, *Ahti et al.*, 1978, *no. 46 370* (H, TU). *India.* Almora distr., Dhakuri ridge, alt. 9500 ft., *Awasthi*, 1950, *no. 641* (UPS ex Herb. Awasthi). *Indonesia.* Java. Pangerango, *Zollinger no. 449* (G - holotype of *Cetraria pallescens* Schaerer). Java. Gedeh, alt. 2400 m, *Kjellberg*, 1929, *no. 125L* (S). Java. Res. Pasoeroean, Goenoeng Ardjoens, Lalidjiwa - Welirang track, *Du Rietz*, 1927, *no. 54-1a* (UPS). *Nepal.* Langtang Area, slopes above Syarpagaon, alt. 2900 m, *Poelt*, 1986, *no. 86-L1010* (GZU). Langtang Area, Lambatis, alt. 2760 m, *G. & S. Miehe*, 1986, no. *15985a* (GZU). 15 km SSE Kathmandu, 2 km E Godawari, alt. 2760 m, 27°35' N, 85°20' E, *Thor*, 1979, *no. 1282* (S). *Russia.* Primorye region, Kedrovaya Padj, *Pärn*, 1961 (TU). *Taiwan.* Mt. Arisan, *Sato*, 1936 (S).

Cetrariopsis pallescens (Schaerer) Randl. & Thell **var. *citrina*** (Taylor) Thell & Randl., **comb. et stat. nov.**

Basionym: *Cetraria citrina* Taylor in Hook., *London J. Bot.* 6: 176, 1847. - **Type**: Java, *Hooker* (BM, lectotype, selected here). - **Syn.**: *Platysma citrinum* (Taylor) Nyl., *Mém. Soc. Sci. Nat. Cherbourg* 5: 100, 1857.

Thallus like *Cetrariopsis pallescens* but both surfaces uniformly light yellow, lower side more or less smooth (not rugose) and **pseudocyphellae** in the form of small, plain, white dots. **Apothecia** not numerous, mainly marginally and submarginally located although some laminal apothecia are also present. **Ascocarp** anatomy like in *C. pallescens* var. *pallescens*.

Chemical constituents: usnic acid in the cortex; lichesterinic, protolichesterinic acids (usually) or alectoronic acid (occasionally) in the medulla.

Distribution: Java, Taiwan.

This variety, known from southern regions (Taiwan and Java), is light or bright yellow in colour on both surfaces, the thallus is more or less smooth, the apothecia are not very numerous and situated mainly on the submarginal parts of the upper cortex while some truly laminal apothecia are usually present. The pseudocyphellae on the lower cortex mainly have the form of small white and plain dots but are larger sometimes and may be located on ridges or on almost outgrowth-like structures.

Both varieties of *Cetrariopsis pallescens* are present on Java. A majority of the specimens (including the type material of *C. pallescens* var. *citrina*) from there contain only fatty acids in the medulla but a few specimens represent the alectoronic acid chemotype. Thus, both varieties within *C. pallescens* are chemically variable and are represented by specimens with alectoronic as well as lichesterinic acid in the medulla. The distribution areas of these two varieties are also partly overlapping (in Java and Taiwan). In this case we consider variety as a suitable taxonomic level.

Altogether 30 specimens examined.

Selected specimens examined. *Indonesia.* Java. Pangerango, alt. 2820 m, *Schiffner*, 1894, *no. 2987a* (FH, M). Java. Preanger, Mt. Gedeh, alt. 2300 m, *Schiffner*, 1894, *no. 3387* (FH, M). Java. Kandang Badals, alt. 2600 m, *Yates*, 1927, *no. 2827* (US, LD). East Java, Andjasmora-complex, alt. 2100 m, *Groenhart*, 1937, *no. 2538* (Herb. Aptroot). Java. Res. Pasoeraean, Goenoeng Ardjoens, Tretes - Lalidjiwa track, *Du Rietz*, 1927, *no. 105-1b* (UPS). *Taiwan.* Mt. Arisan, *Asahina* (US).

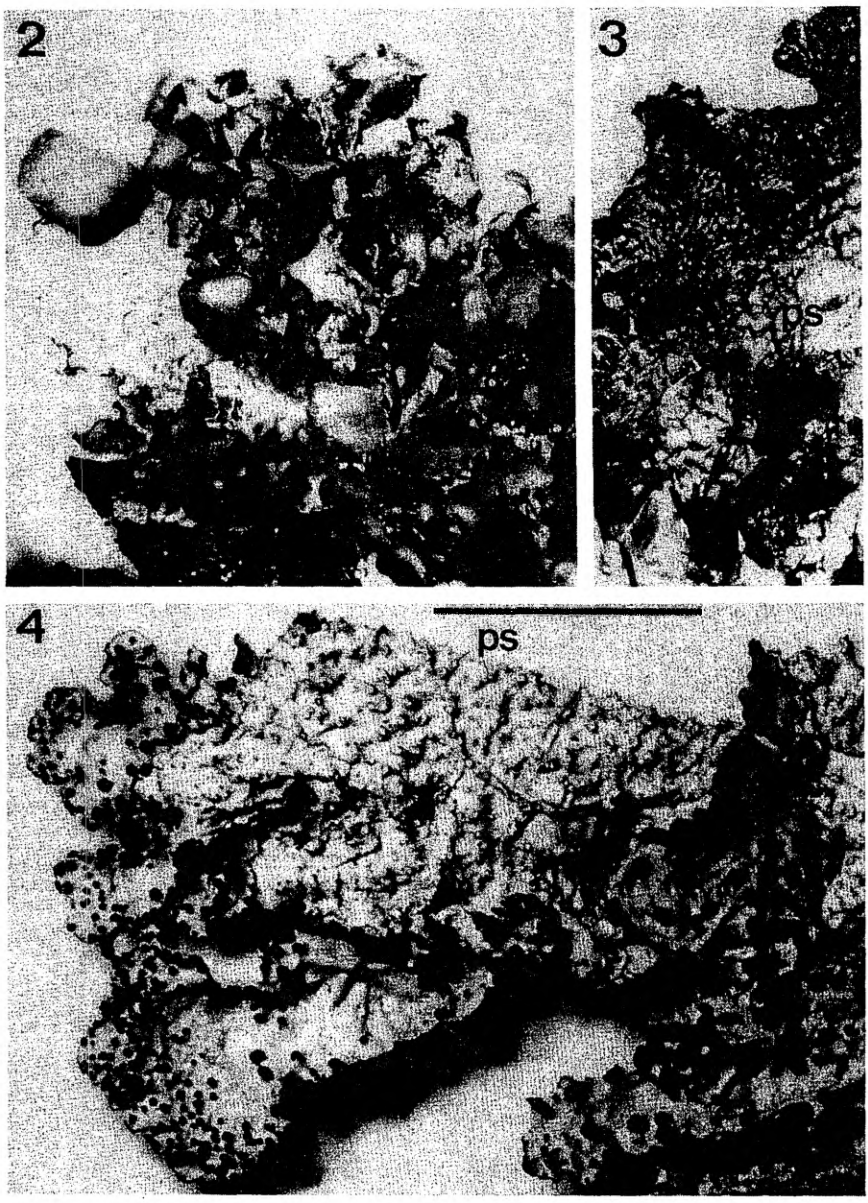

Fig. 2-4 - Morphology in *Cetrariopsis*. Fig. 2. *Cetrariopsis laii*, richly fertile part of upper surface, Russia, Primorye 17.09.1961, *S. Pärn* (TU). Fig. 3. Lower surface of the same specimen, showing the pseudocyphellae located on dark ridges. Fig. 4. *Cetrariopsis pallescens*, upper surface with numerous, small, laminal apothecia, and lower surface with characteristic pseudocyphellae on pale ridges, Nepal, Langtang, *Miehe 16139* (GZU). Bars in Figs. 2-4 = 1 cm, ps = pseudocephyllae.

Cetrariopsis laii Thell & Randl., **sp. nov.** - (Fig. 2, 3, 16)

Thallus foliaceus, ad 8 cm diametro, superficies superior virescens vel flavens, rugosa; subtus fusca ad pallide fusca, reticulosa et pseudocyphellata, rhizinata; pseudocyphellae praecipue in cristis. Soredia, cilia et spinulae marginales desunt, lobi lobulis marginalibus saepe ornati. Cortex superior paraplectenchymatus. Apothecia numerosa, marginalia, ad 5 mm lata; discus brunneus, oblongus. Excipulum 2-stratum. Asci clavati, 40-45 x 8-10 µm, ascosporae oblongae, 8 x 3 µm. Pycnidia et pycnoconidia non visa. Acidum usnicum in cortice superiore; acidum lichesterinicum et protolichesterinicum in medulla.

Typus: Russia, Primorye region, Kedrovaya Pedj Nature Reserve, on *Betula dahurica*, 17.09.1961 *S. Pärn* (TU - holotypus, LD - isotypus).

Thallus foliose, up to 8 cm in diameter, upper surface greenish yellow, moderately rugose; lower surface brown to light brown and whitish on the margins, densely reticulated and with white rounded or oval pseudocyphellae situated on the ridges, sometimes surrounded with a brown rim. Soredia, cilia and marginal projections absent. **Rhizines** on the lower surface brown and simple. Pycnidia not seen. Upper and lower **cortex** c. 20 µm thick, with larger cells near the medulla. Medullary hyphae 3-6 µm thick. **Apothecia** numerous, marginal, sometimes situated on the secondary marginal lobules, up to 5 mm in diameter; disc brown, usually oblong or reniform; in many specimens only juvenile apothecia in the form of marginal brown lines are present. **Exciple** two-layered, upper layer c. 20 µm, lower layer c. 30 µm. **Asci** 40-45 x 8-10 µm, axial body 2.5-3 µm, **ascospores** oblong, 8 x 3 µm.

Chemical constituents: usnic acid in the upper cortex; lichesterinic and protolichesterinic acids in the medulla.

Distribution and habitat: Russian Far East (Habarovsk and Primorye regions), Japan, Vietnam, Taiwan. Epiphytic on coniferous and deciduous trees in the zone of montaneous forests.

Cetrariopsis laii is named after our collegue, the Chinese lichenologist Mingjou Lai from Taiwan whose contribution to the knowledge of Asiatic cetrarioid lichens is significant.

This new *Cetrariopsis* species is not a rare lichen in the eastern Asia but it has been confused with other taxa, labelled usually in the herbaria as *Cetraria wallichiana* or *Cetraria pallescens* but occasionally also as *Nephromopsis ectocarpisma*. Two former names represent, as we know now, the same species - *Cetrariopsis pallescens*. In Russia where the new species is most widely distributed, it has been uncorrectly identified as *Cetraria pallescens* while the true *Cetrariopsis pallescens* with numerous laminal apothecia was named *Cetraria wallichiana*. Consequently these two lichens were practically separated but, because of the taxonomical disorder, the other of them has remained undescribed till now. Some specimens of *C. laii* may be quite similar to *C. pallescens* var. *pallescens* but the apothecia of the former are situated mainly marginally and submarginally, the disc is usually not rounded but reniform and sometimes only numerous juvenile apothecia are present. Other characteristic morphological featu-

res of *C. laii* that separate it from *C. pallescens* are as follow: strongly rugose upper and reticulated lower surface; darker (brown to light brown) colour of the lower side with pseudocyphellae located conspicuously on the ridges (Fig. 2, 3); presence of secondary marginal lobules as a fringe along the margins in many specimens.

Altogether 21 specimens from Russia, Japan, Vietnam and Taiwan were examined.

Selected specimens examined. *Japan.* Hokkaido, Mt. Daisetu, *Sato*, 1936 (FH). Gotenniwa, Mt. Huzi, *Asahina*, 1956 (*Lich. Jap. Exs.* 157, H). *Russia.* Primorye region, island Putyana, Mt. Startseva, *Chabanenko*, 1982 (LD). Primorye region, Lazo Nature Reserve, Mt. Tchornaya, alt. 1300 m, *Chabanenko*, 1982 (LD). Primorye region, Livadiski Range, Mt. Livadiskaya, alt. 1000 m, 43°8' N, 132°42' E, *Skirina*, 1980, *no. 7563* (LD). Primorye region, Sikhote-Alin Range, Mt. Eldorado, alt. 1300 m, 44°41' N, 135°20' E, *Skirina*, 1982, *no. 7564* (LD). Primorye region, Mt. Pryamaya, 43°20' N, 133°36' E, alt. 850 m, *Kärnefelt*, 1991, *no. 910 810* (LD). Habarovsk region, Badzhal Mt. Range, river Urmi, *Randlane*, 1981, *no. 167* (TU). *Taiwan.* Chiayi Co., Mt. Alishan, alt. 2275 m, *Lai*, 1978, *no. 10 198* (US). *Vietnam.* Zon Kin, Phan-si-Pau, Lao Kay, 2900 m, 1929, *no. 17 156* (PC).

III. The Genus *Cetreliopsis* Lai

This genus was described by Lai (1980) in his paper on cetrarioid lichens in East Asia to settle the *Cetraria rhytidocarpa*-complex, as Lai called it. The group included *Cetraria rhytidocarpa* Mont. & v.d. Bosch from Java, *Cetraria straminea* Vainio from the Philippines and *Cetraria laeteflava* Zahlbr. from Taiwan. Lai synonymized all the three species on morphological and chemical grounds. He also pointed out the affinities to *Cetrelia* and *Nephromopsis*, combining the names of these genera for the new taxon.

Our studies on *Cetreliopsis* have shown that this genus is well limited and clearly separated from other cetrarioid lichens. The identifying characters of the genus *Cetreliopsis* are: large foliose or subfruticose thallus; marginal or submarginal apothecia; presence of pseudocyphellae on both surfaces of the thallus; large, ellipsoid ascospores in rather broadly clavate asci and a two-layered exciple; content of fumarprotocetraric and protocetraric acids as major compounds in the medulla (PD + red) and usnic acid in the cortex (Figs. 5-7, 11, 14). We cannot agree with Lumbsch (in Eriksson & Hawksworth 1988) who proposed to include *C. rhytidocarpa* in *Cetrelia* as a separate subgenus. He recognized mainly chemical differences between *Cetrelia* and *Cetreliopsis* and considered their morphology very similar. We find not only essential chemical differences (atranorin and orcinol depsides in *Cetrelia*; usnic acid, β-orcinol depsidones and fatty acids in *Cetreliopsis*) but also morphological (ashy white or tan upper surface, perforate submarginal to laminal apothecia, lower cortex punctate or not in *Cetrelia*; yellow upper surface with frequent black-blotted areas, marginal and entire apothecia, lower cortex with distinct pseudocypellae in *Cetreliopsis*) and anatomical differences (large asci with a strongly amyloid tholus and large thick-walled ascospores - 11-24 x 6-12 µm - in *Cetrelia*; asci usually less amyloid and considerably smaller in *Cetreliopsis*, ascospores always smaller) between these two entities. The genus *Cetreliopsis* is probably more closely connected to *Nephromopsis* and *Cetrariopsis* than to *Cetrelia*.

The confusion within the *Cetraria rhytidocarpa*-complex has one more aspect. Asahina (1954) used the name *C. rhytidocarpa* for a Japanese lichen which is totally different from the complex treated here. Specimens of *Cetraria rhytidocarpa* f. *nipponensis* Asah. in Kurokawa's «Lichenes Rariores et Critici Exsiccati» and in all other collections from Japan belong to *Tuckneraria pseudocomplicata* (Randlane *et al.*, 1994). The latter is easily distinguished from the true *Cetraria rhytidocarpa* complex by the lack of pseudocyphellae on the upper side and the negative PD reaction in the medulla. Anatomy of ascocarps (globose to subglobose ascospores, asci with uniseriately arranged spores and broad axial body, two-layered exciple) refers to the affinities of this taxon rather to *Tuckermannopsis* than to *Nephromopsis* or *Cetreliopsis*.

According to our present knowledge *Cetreliopsis* cannot be treated as a monotypic genus. Three new combinations are proposed here; furthermore, one new species and one new subspecies is described. We do not support in all parts the wide species treatment of *Cetreliopsis rhytidocarpa* proposed by Lai (1980) and prefer to keep the sorediate Taiwan material as a separate species.

The following five species are included in *Cetreliopsis*:

C. asahinae (Sato) Randl. & Thell
C. endoxanthoides (Awasthi) Randl. & Saag
C. laeteflava (Zahlbr.) Randl. & Saag
C. papuae Randl. & Saag
C. rhytidocarpa (Mont. & v.d. Bosch) Lai.

***CETRELIOPSIS* Lai, *Quart. J. Taiwan Mus.* 33: 218 (1980).**

Type species: *Cetreliopsis rhytidocarpa* (Mont. & v.d. Bosch) Lai

Thallus dorsiventral, foliose or subfruticose, straw yellow or greenish yellow on the upper surface, often with black-blotted areas and conspicuous pseudocyphellae surrounded by a black rim or laminal emergent pycnidia. The lower surface is either totally black or black in central parts and brownish on margins, pseudocyphellae are present also on the lower side usually in the form of minute white dots. Black **rhizines** sparse or numerous. Cilia and soredia may be present on different species. The **pycnidia** are laminal and/or marginal, on emergent projections or immersed in the thallus. The cortical tissue is present beneath the pycnidium. The upper and lower **cortex** are composed of the same paraplectenchymatic type as in *Cetrariopsis*, with large cells near the medulla. **Apothecia** marginal or submarginal but not nephromoid (disc clearly faced upwards), to 14 mm in diameter; disc brown, surrounded by the thalline margin. **Exciple** two-layered, upper layer composed of longitudinally arranged hyphae. **Asci** rather broadly clavate, 35-60 x 11-20 µm; axial body 2.5-4 µm. **Ascospores** ellipsoid, 6-12 x 4-7 µm. **Pycnoconidia** bifusiform (dumb-bell shaped), 5 x 1-2 µm.

Chemical constituents: usnic acid (+/-) in the cortex; fumarprotocetraric acid and other closely related β-orcinol depsidones together with fatty acids in the medulla.

Distribution and habitat: Russian Far East, Japan, China, Vietnam, South-Korea, India, Nepal, Taiwan, the Philippines, Borneo, Java, New Guinea. Epiphytic on coniferous and deciduous trees.

Cetreliopsis asahinae (Sato) Randl. & Thell, **comb. nov.** - (Fig. 5, 6, 14)

Basionym: *Cetraria asahinae* Sato, *Saito Ho-on Kai Mus. Res. Bul.* 11: 12, 1936. - **Type**: Kuril Islands, Kunashiri, Tomarimura, *Yasuda* 16.08.1923 (not seen). - **Synonym**: *Nephromopsis asahinae* (Sato) Räsänen, *Kuopion Luonnon Ystäväin Yhdistyksen Julkaisuja* B 2(6): 50, 1952.

Thallus foliose, with ascending margins; upper surface yellowish green, lower surface black in central parts and with brown margins. **Pseudocyphellae** present on both surfaces, on upper surface surrounded with dark rim or black projections, on lower surface in the form of white patches located mainly on the thallus ridges. Soredia and cilia absent. **Pycnidia** laminal or marginal, on emergent projections. Upper **cortex** c. 15 µm, composed of three to four layers of cells, cells up to 5µm, the largest concentrated near the medulla; lower cortex similar to the upper but outer cells brownish pigmented; medullary hyphae c. 3 µm. **Apothecia** marginal or submarginal, to 14 mm in diameter, disc brown; hymenium c. 45 µm, subhymenium c. 10 µm, **exciple** usually two-layered, both layers 30-40 µm, sometimes with an undistinct third layer between with larger lumina, up to 10 µm thick; **asci** 35-40 x 12-17 µm, axial body 2.5 µm; **ascospores** 8-12 x 4-7 µm. **Pycnoconidia** c. 4 x1 µm.

Chemical constituents: usnic acid in the cortex (rarely absent); protocetraric (major), fumarprotocetraric acid and physodalic acid (+/-) in the medulla.

Distribution: Russian Far East (Primorye region, the Kuril Island), Japan, Vietnam; China (Wei 1991), South-Korea (Park 1990), India (*Cetraria rhytidocarpa* sensu Awasthi, in Awasthi 1982).

C. asahinae is a distinct entity and morphologically easily recognized by the pseudocyphellae on the upper cortex surrounded with a black rim and black emergent projections (Fig. 5-6). The medullary chemistry - presence of protocetraric acid as major compound - is also typical. *C. asahinae* has a wider distribution than other taxa in *Cetreliopsis*.

Altogether 20 specimens were examined.

Selected specimens examined. *Japan*. Mt. Akagi, Gunma, *Sato*, 1957 (H). Mt. Akagi, *Yasuda*, 1911, *no. 47* (LD). Hokkaido, Hidaka distr., Shizukai-cho, alt. 400 m, *Koponen*, 1970, *no. 14525* (H). *Russia*. Primorye region, Peter the Great Bay, Furughelm Island, 42°31' N, 130°55' E, *Skirina*, 1987, *no. 6251* (LD). Primorye region, Sikhote Alin Range, Abrek Urochische, 45°5 N, 136°40' E, *Skirina*, 1977, *no. 8932* (LD). Primorye region, Lazo Nature Reserve, Mt. Tumannaya, alt. 160 m, *Chabanenko*, 1983, *no. 23* (LD). Primorye region, Island Petrova, 42°45' N, 133°48' E, *Kärnefelt*, 1991, *no. 910 615* (LD). Primorye region, Kedrovaya Padj, *Vasineva*, 1954 (LE). Kuril Islands, Shikotan, Malokurilskoye, *Blum*, 1965 (KW). *Vietnam*. Zon Kiu, Phan-si-Pan, Lao Kay, alt. 2600 m, 1929, *no. 17 194* (PC).

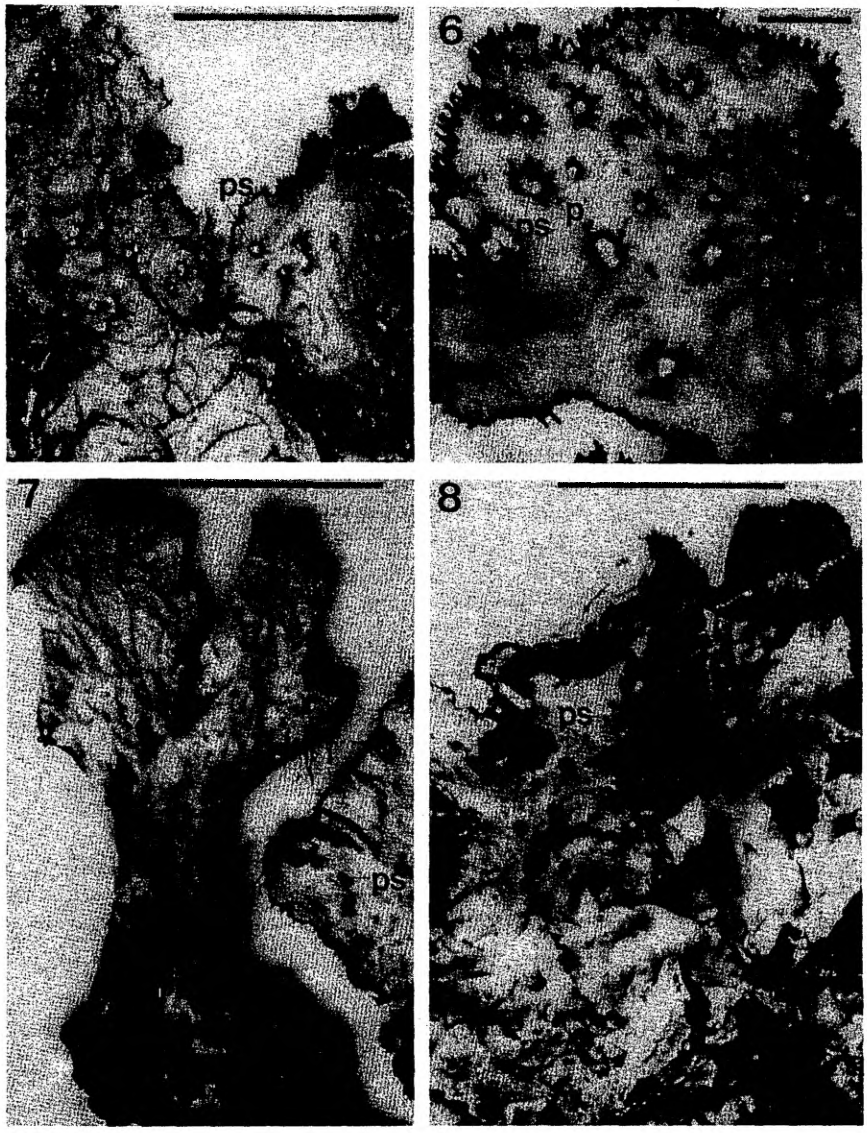

Fig. 5-8. Morphology in *Cetreliopsis*. Fig. 5. *Cetreliopsis asahinae*, upper surface, Russia, Primorye, *Guriljova* 1951 (TU). Fig. 6. Part of the same specimen showing the white pseudocyphellae surrounded by pycnidial projections. Fig. 7. *Cetreliopsis papuae*, habit, Papua-New Guinea, 05. 1975, *Hope, No. 483,* Univ. Col. Mus (US). Fig. 8. *Cetreliopsis rhytidocarpa* subsp. *langtangi*, upper surface with conspicuous pseudocyphellae surrounded with black rims, Nepal, Langtang, *Miehe 15 738 b*, holotype (GZU). Bars in Figs. 5, 7-8 = 1 cm, in Fig. 6 = 1 mm, p = pycnidia, ps = pseudocyphellae.

Cetreliopsis endoxanthoides (Awasthi) Randl. & Saag **comb. nov.**

Basionym: *Cetraria endoxanthoides* Awasthi, *Bull. Bot. Surv. India* 24: 9, 1982. - **Type**: E. Nepal, Mewakhola valley, alt. 2400-2700 m, *D.D. Awasthi*, 28.05.1953, *no. 2477* (Herb. Awasthi, holotype; not seen). - **Synonym**: *Nephromopsis endoxanthoides* (Awasthi) Randl. & Saag, *Mycotaxon* 44: 486, 1992.

Thallus foliose, greenish yellow on upper and black to dark brown on the lower side. **Pseudocyphellae** present on both surfaces, sparse on the upper cortex, coloured light orange and surrounded by a dark rim or black spinules; more numerous on the lower cortex, in the form of convex conspicuous white dots. **Rhizines** black, sparse. Cilia and soredia absent. Medulla pale orange. **Pycnidia** laminal and marginal, on emergent projections. Upper and lower **cortex** 20-25 µm, crystallized, composed of three to four layers of small, equal-sized, thick-walled cells, medullary hyphae 3-4 µm in diameter. **Apothecia** marginal, up to 6 mm in diameter, with dark brown disc, hymenium c. 50 µm, subhymenium to 10 µm, **exciple** two-layered, upper layer c. 10 µm, lower layer c. 30 µm; **asci** 50 x 15 µm, **ascospores** 9 x 5,5 µm. **Pycnoconidia** comparatively thick, 5-6 x 1.5-2 µm.

Chemical constituents: fumarprotocetraric acid (major), salazinic-like substance Cph-1 (major), protocetraric acid, salazinic acid, an unidentified fatty acid in the medulla.

Distribution and habitat: Nepal. Corticolous.

Awasthi (1982) mentions in the original description of the species the type collection only - E. Nepal, Mewakhola valley, alt. c. 2400-2700 m, 28.05.1953, *D.D. Awasthi no. 2477* (Herb. Awasthi). We have identified one more specimen from the same locality (no. 2227, collected 27.05.0953 and determined by Awasthi at first as *Cetraria asahinae* and in 1980 as *Cetraria rhytidocarpa*) on the grounds of orange coloured medulla, form of pseudocyphellae and complex of medullary substances. Earlier (Randlane & Saag 1992) this species was considered to have phylogenetic affinities with those taxa in *Nephromopsis* which medulla is similarly coloured (*N. endocrocea, N. ornata, N. globulans*). Although we were not able to identify exactly the pigment in it. Still, later studies have shown that the anthraquinones and secalonic acids occur in different genera of Parmeliaceae much more frequently than supposed and the colour of the medulla cannot be qualified as a genus character. Other medullary constituents as well as morphological and anatomical features of *C. endoxanthoides* undoubtedly unveil its close relations to *Cetreliopsis*.

Cetreliopsis laeteflava (Zahlbr.) Randl. & Saag **comb. nov.** - (Fig. 11)

Basionym: *Cetraria laeteflava* Zahlbr., Feddes, Repert. 33: 60, 1933. - **Type**: Taiwan, Mt. Arisan, Nimandaira, *Asahina* (H, US, isotype; seen). - **Synonyms**: *Cetraria straminea* Vainio var. *laeteflava* (Zahlbr.) Räsänen (nom. illeg., non *Cetraria straminea* Krempelh. ex Schwend., 1860), *Kuopion Luonnon Ystäväin Yhdistyksen Julkaisuja B* 2(6): 50, 1952.

Cetraria straminea Vainio var. *sorediata* Räsänen (nom. illeg.), *Suom. Elain-ja Kasvit. Seuran Van. Kasvit. Julk.* 3: 78, 1949 (1948).

Thallus foliose, to 12 cm in diameter, greenish yellow and occasionally black-blotted on the upper side; totally black on the lower side with brown marginal parts. Thallus margins partly sorediate; cilia absent. **Pseudocyphellae** present on both surfaces: in the form of small white and somewhat convex patches on the upper side, usually surrounded by a black rim and almost of the same size but plain dots on the lower side. **Pycnidia** rare, marginal, on emergent projections. Upper and lower **cortex** c. 30 µm thick, with the cells near the medulla clearly larger. **Apothecia** marginal, absent on many specimens, with disc faced upwards; hymenium including subhymenium 70-80 µm thick, **exciple** two-layered, both layers c. 30 µm. **Asci** 50-60 x 11-17 µm, axial body 3-4 µm, **ascospores** 8.5-9 x 5 µm. **Pycnoconidia** not observed.

Chemical constituents: usnic acid in the cortex (+/-); fumarprotocetraric acid (major), salazinic-like substance Cph-1 (major), protocetraric acid, salazinic acid, lichesterinic and protolichesterinic type fatty acids.

Distribution: Taiwan and the Philippines (Räsänen 1949). Corticolous in the montane districts.

C. laeteflava is morphologically recognized by the presence of marginal soredia and chemically by the occurrence of both fumarprotocetraric acid and Cph-1 as major substances in the medulla. It is the only sorediate species in the genus, evidently closely related to *C. rhytidocarpa*, the variety of which it has been treated by Räsänen (1952) and Lai (1980). The presence of soredia is usually considered a good character at the species level (Poelt 1973). As this distinctive quality is combined here with a small chemical differentiation (Cph-1 also as a major substance), we prefer to maintain the taxon on species level as it was originally described.

A taxonomical confusion with the name *Cetraria straminea* was caused by the fact that the epithet «*straminea*» has been used by two different authors, Schwendener (1860) and Vainio (1909), for two totally different lichens. *Cetraria straminea* Krempelh. ex Schwend., which has priority, has generally been forgotten; lately, with help from Prof. Rolf Santesson, we could make clear that this species is synonymous with *Tuckneraria laureri* (Randlane *et al.*, 1994). *Cetraria straminea* Vainio not valid is synonymous with *Cetreliopsis rhytidocarpa* (Mont. & v.d. Bosch) Lai.

Specimens examined. *Taiwan*. Nimandairana, Mt. Arisan, *Asahina*, 24.12.1925 (H, US, isotypes). Chiayi prov., Mt. Arisan, Sisters' Pond, alt. 2275 m, *Lai*, 1978 (H). Chiayi prov., Mt. Tsutson-san, Mt. Ali, alt. 2200-2600 m, *Kurokawa*, 1964, *no. 478* (H). Taitung prov., Mt. Lachiala-chiaerh, alt. 1800 m, *Kurokawa*, 1965, *no. 2473* (H, TAIM).

Cetreliopsis papuae Randl. & Saag **sp. nov.** - (Fig. 7)

Thallus foliaceus, lobi ad 12 mm lati et 45 mm longi; margo anthracina ciliata, cilia ad 2.5 mm longa; superficies superior sulfurea et nigra, pseudocyphellata; subtus nigra, pseudocyphellata, in margine sulfurea. Pseudocyphellae ambarum superficierum nigro cinctae. Rhizinae desunt. Cortex superior paraplectenchymatus, 20-25 µm; me-

dulla alba; cortex inferior c. 30 µm. Apothecia et pycnidia non visa. Acidum usnicum in cortice superiore; acidi fumarprotocetraricum, protocetraricum, substantia Cph-1 in medulla.

Typus: Papua New Guinea, Star Mountains, eastern side of Mt. Scorpion, elev. 3600 m, in an open herbfield of *Tetramolopium* and *Astelia*, May 1975, *G.S. Hope* (Lich. Exsic. distributed by the University of Colorado Museum, Boulder no. 483) (US - holotypus; isotypi in several herbaria, e.g. CAN, GZU).

Thallus foliose, 100-150 µm thick, consisting of separate oblong lobes with rounded margins to 45 mm long and 12 mm wide; upper surface sulphuric yellow with black patches here and there and wide **pseudocyphellae** often surrounded by a black rim; marginal cilia black, to 2.5 mm long; lower surface mainly black in the basal parts and sulphuric yellow black-blotted in the marginal portions; pseudocyphellae similar to those on the upper surface; **rhizines** absent. Upper **cortex** 20-25 µm, crystallized, composed of c. three layers of equal-sized cells, lower cortex c. 30 µm, less crystallized than the upper cortex, composed of c. four layers of equal-sized cells; algal cells usually in clusters, medulla white, medullary hyphae c. 4 µm in diameter. Pycnidia and apothecia not observed.

Chemical constituents: usnic acid in the medulla; fumarprotocetraric acid (major), protocetraric acid, salazinic-like substance Cph-1 and an unidentified fatty acid in the medulla.

Distribution and habitat: Papua New Guinea; grows in high mountains (more than 3000 m), evidently on the ground in open herbfields or shrublet communities.

Although the species lacks generative organs, there is no doubt about its generic position - presence of pseudocyphellae on both surfaces as well as the complex of medullary substances is typical for *Cetreliopsis*. Its morphology is different from the other representatives of the genus: the thallus is foliose, clearly dorsiventral, but the lobes are separated and probably growing on the ground partly upright why it could be difficult to identify on herbarium material which side is the upper (all other species in *Cetreliopsis* appear to be corticolous); true marginal cilia and not pycnidial projections as in other taxa are always present; relatively wide pseudocyphellae are similar on both sides of the thallus (Fig. 7). These conspicuous characters confirm the description of *C. papuae* as a separate species.

C. papuae is known from two localities in Papua New Guinea. Another studied specimen besides the type collection: Central distr., Tapini subdistr., Mt. Strong, summit area, elev. 3500 m, scattered component of low tussock-prostrate shrublet communities, 03.05.1971, *M.J.E. Coode, no. 3805* (Herb. Aptroot).

Cetreliopsis rhytidocarpa (Mont. & v.d. Bosch) **Lai subsp. *rhytidocarpa*** - (Fig. 9)

Basionym: *Cetraria rhytidocarpa* Mont. & v.d. Bosch, Miquel, Pl. Jungh. 4: 430, 1857. - **Type**: Java, *Junghuhn*, Herb. v.d. Bosch (PC, lectotype; seen). - **Synonym**: *Platysma rhytidocarpum* (Mont. & v.d. Bosch) Nyl., *Mém. Soc. Sci. Nat. Cherbourg* 5:

100, 1857. - *Nephromopsis rhytidocarpa* (Mont. & v.d. Bosch) Zahlbr., *Ann. Cryptog. Exot.* 1: 208, 1928.

Cetraria straminea Vainio, *Philipp. J. Sci. Bot.* 4: 657, 1909 (nom. illeg., non *Cetraria straminea* Krempelh. ex Schwend., 1860) - **Type**: Philippines, Luzon, Prov. Laguna, Mt. Banajao, *Curran & Merritt, no. 7988* (US, isotype; seen). - **Syn.**: *Nephromopsis straminea* (Vainio) Räsänen, *Kuopion Luonnon Ystäväin Yhdistyksen Julkaisuja B* 2(6): 50, 1952.

Thallus foliose, to 11 cm in diameter, upper surface greenish to sulphuric yellow, partly, especially in margins black-blotted, with small, regular and somewhat emergent **pseudocyphellae** with black rim; lower surface totally black, only occasionally with light brown or even whitish margins, pseudocyphellae usually in the form of small white plain punctae which sometimes may be quite large and even elevated. Soredia and cilia absent. **Pycnidia** marginal and laminal, on black emergent projections (in younger parts not always very emergent). **Rhizines** on the lower surface black and numerous. Upper **cortex** 20-25 µm thick, composed of about four layers of cells, usually somewhat larger near the medulla; lower cortex thin, 10-15 µm, composed of only one-two layers of cells, the outer layer brownish pigmented; medulla white, medullary hyphae c. 4 µm in diameter. **Apothecia** marginal or submarginal, up to 10 mm in diameter, disc brown, faced upwards; hymenium c. 55 µm, subhymenium c. 10 µm, **exciple** two-layered, sometimes with a thin, undistinct third layer, both upper and lower layers c. 20 µm. **Asci** 35-60 x 12-20 µm, axial body 3-4 µm, **ascospores** 6.5-11 x 4-6 µm. **Pycnoconidia** not seen.

Chemical constituents: usnic acid in the cortex; fumarprotocetraric acid (major), protocetraric acid, salazinic-like substance Cph-1, salazinic acid (+/-), and one or two lichesterinic-protolichesterinic type fatty acids (+/-) in the medulla.

Distribution and habitat: the Philippines, Java, Borneo; corticolous.

The material of *Cetreliopsis rhytidocarpa* from southern islands is typically yellowish on the upper and totally black on the lower surface while the pseudocyphellae are small and plain on upper as well as lower surface (Fig. 9). From the other species in the same genus, *C. rhytidocarpa* is morphologically distinguished by the white medulla (from *C. endoxanthoides*), absence of soredia (from *C. laeteflava*) and cilia (*C. papuae*) and lack of emergent projections around the pseudocyphellae (*C. asahinae*).

Specimens examined. *Indonesia.* Borneo. Mt. Kinabalu, Paka Cave to Lohang, *Strong Clemens*, 1945, *no. 10 755* (FH). Java. *Junghuhn*, Herb. v.d. Bosch (PC, lectotype). Pangerango, alt. 2500 m, *Schiffner*, 1894, *no. 3004* (TNM). *Philippines.* Luzon, Prov. Laguna, Mt. Banajao, *Curran & Merritt*, 1907, *no. 7988* (US, isotype of *Cetraria straminea* Vainio). Luzon, Mt. Banajao, alt. 1900 m, *Robinson*, 1909, *no. 6586* (H).

Cetreliopsis rhytidocarpa (Mont. & v.d. Bosch) Lai **subsp. *langtangi*** Randl. & Thell **subsp. nov.** - (Fig. 8)

Thallus foliaceus, ad 5 cm latus; superficies superior virescens vel straminea, pseudocyphellata; superficies inferior centro nigra, margine pallide fusca vel alba,

pseudocyphellata. Pseudocyphellae ambarum superficierum convexae rotundae vel irregulares, nigro cinctae. Apothecia marginalia, ad 10 mm lata, asci clavati, 45-60 x 14-20 µm; ascosporae ellipsoideae, 7.5-11 x 4-5.5 µm. Pycnidia laminalia et marginalia, parum emergentia.

Typus: Nepal, Central Himalaya, Langtang Area, below Dotsche, alt. 2880 m, *Quercus semicarpifolia* forest, on branches, 08.11.1986, *G. & S. Miehe, no. 15 738 b* (GZU - holotypus).

Thallus foliose, to 5 cm in diameter, greenish yellow on the upper surface, and from black on the central part of the lower surface to almost white on the margins. **Pseudocyphellae** present on both surfaces in the form of white rounded or irregular convex patches, usually with a black rim on the upper side and of the similar form or smaller on the lower side. Upper and lower **cortex** both 20-25 µm, composed of two layers of cells, those close to the medulla clearly larger. Medullary hyphae c. 4 µm thick. **Apothecia** marginal, hymenium c. 55 µm, subhymenium c. 10 µm, **exciple** two-layered, sometimes with a thin undistinct third layer, both upper and lower layers c. 20 µm. **Asci** 45-60 x 14-20 µm, **ascospores** 7.5-11 x 4-5.5 µm. **Pycnidia** marginal and laminal, slightly or more prominently emergent; pycnoconidia not seen.

Chemical constituents the same as in *C. rhytidocarpa* subsp. *rhytidocarpa.*

Distribution and habitat: Nepal and India (*Cetraria laeteflava* sensu Awasthi *in* Awasthi 1992). Epiphytic in the middle altitudes (2400-3300 m) of montane areas.

This subspecies, distributed in Nepal and according to the description by Awasthi (1982), also in India, incline to be more greenish on the upper side and black in the center to almost whitish in the marginal parts of the lower surface with large and emergent pseudocyphellae. Because of the well delimited distribution this material is described as a separate subspecies.

Specimens examined. *Nepal.* Central Himalaya, Langtang Area, below Dotsche, alt. 2880 m, *Miehe*, 1986, *no. 15 738b* (GZU, holotype). Langtang Area, SE of Schiabon Kedo, alt. 3300 m, *Miehe*, 1986, *no. 1185b* (GZU). Langtang Area, Upper Tadi Khola, alt. 2800 m, *Miehe*, 1986, *no. 15 822a* (GZU).

CONCLUSIONS

All the three genera treated here - *Cetrariopsis, Cetreliopsis* and *Nephremopsis* - form a group of related taxa. It is distinguished by large foliose thalli with rugose or reticulated central parts and ascending margins (Table 1). Apothecia develop in most species marginally. Pycnidia are immersed or situated on the marginal and/or laminal emergent projections. Presence of distinct pseudocyphellae on the lower surface is a good character for identifying this group from *Tuckermannopsis* in a strict sense. The yellowish colour of the thallus caused by the occurrence of usnic acid in the upper cortex makes differences from *Cetrelia* and *Platismatia.* The anatomy of the thallus of all studied species is clearly uniform showing pachydermatous paraplectenchymatic

Table 1. - Comparison of characters in *Cetrariopsis, Cetreliopsis* and *Nephromopsis*.

	Cetrariopsis	*Cetreliopsis*	*Nephromopsis*
Thallus	foliose	foliose	foliose
Upper and lower cortex	1-layered, paraplecten-chymatous	1-layered, paraplecten-chymatous	1-layered, paraplecten-chymatous
Pseudocyphellae	on lower surface	on both surfaces	on lower surface
Soredia	absent	may be present	absent
Marginal cilia	absent	may be present	absent
Apothecia	marginal and laminal on upper surface	marginal and sub-marginal on upper surface	marginal on lower surface
Exciple	2-layered	2-layered	3-layered
Ascus shape	narrowly clavate	rather broadly clavate	narrowly clavate
Ascospores	oblong, 7-10 x 3-5 µm	ellipsoid, 6-12 x 4-7 µm	oblong, 5-10 x 2.5-5µm
Axial body	2,5-4 µm	2,5-4 µm	0.5-4 µm
Ring structure	absent	absent	present in two species
Pycnidia	not seen	laminal or marginal, immersed or on projections	laminal or marginal, immersed or on projections
Pycnoconidia	not seen	bifusiform, 5 x 1-2 µm	bifusiform, 4-5 x 1-1.5 µm
Cortical substances	usnic acid	usnic acid	usnic acid
Medullary substances: **a) fatty acids**	present	present	present
b) orcinol depsides & depsidones	alectoronic a.	-	olivetoric a., physodic a.
c) β-orcinol depsidones	-	fumarprotocetraric a., protocetraric a., physodalic a., salazinic a., Cph-1	-
d) secalonic acids	-	-	endocrocin, secalonic a. A, secalonic a. C

cortices, usually with larger cells near the medulla. Anatomical characters of the ascocarps are also similar (clavate asci with a moderately large axial body in the tholus; oblong or ellipsoid ascospores) but not identical (two-layered exciple in *Cetrariopsis* and *Cetreliopsis* and usually three-layered in *Nephromopsis*; distinctly broader asci and ascospores in *Cetreliopsis* compared to those in *Cetrariopsis* and *Nephromopsis*). Still, the shape of ascospores and asci of investigated genera presents an essential difference from *Tuckermannopsis* and related groups including *Tuckneraria*. The latter is characterized by globose-subglobose ascospores which are arranged +/- uniseriately in asci with rather small tholus, very broad ocular chamber and broad axial body. The medul

Fig. 9-10 - Morphology in *Cetreliopsis* and *Nephromopsis*. Fig. 9. Upper surface of *Cetreliopsis rhytidocarpa* subsp. *rhytidocarpa*, Philippines, Luzon, 1909, *Robinson 6586* (H). Fig. 10. *Nephromopsis morrisonicola*, Philippines, Luzon, 1909, *Merrill et al. 16359* (H). Bars in Figs. 9-10 = 1 cm. ps = pseudocyphellae.

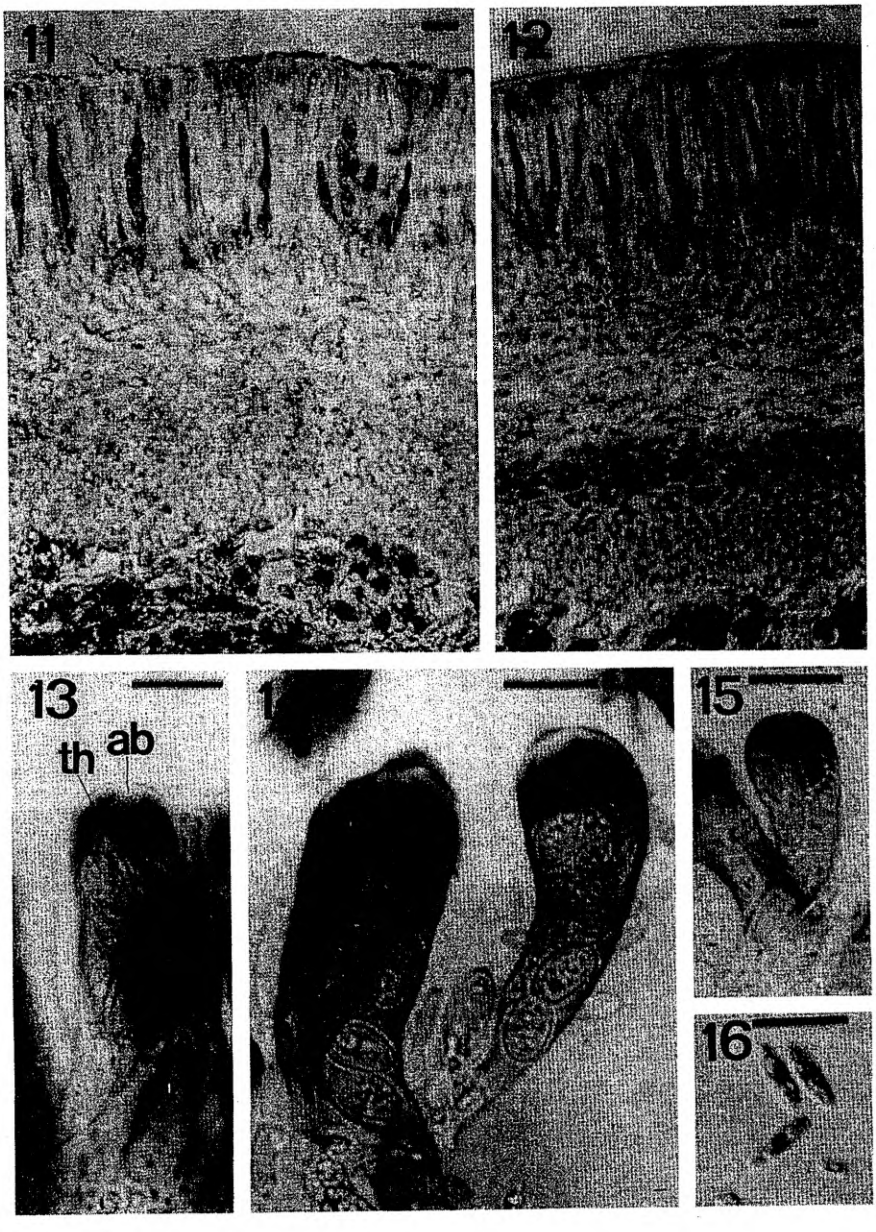
11
12
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Fig. 11-16 - Anatomy in *Cetrariopsis, Cetreliopsis* and *Nephromopsis*. Fig. 11. Cross section of an apothecium with a two-layered exciple of *Cetreliopsis laeteflava*, Taiwan, *Kurokawa* 205 (TAIM). Fig. 12. Cross section of an apothecium showing a three-layered exciple, typical for the genus *Nephromopsis*, *N. rugosa*, Russia, Primorye, *Skirina* 1982 (VLA). Fig. 13. Narrowly clavate ascus of *Cetrariopsis pallescens*, Nepal, Langtang, *Miehe 16139* (GZU). Fig. 14. Somewhat broader asci and ascospores of *Cetreliopsis asahinae*, Russia, Primorye, 1951, *Guriljova* (TU). Fig. 15. Ascus of *Nephromopsis stracheyi*, Himalaya, *Strachey & Winterbottom, 36138*, isotypus (H-NYL). Fig. 16. Oblong ellipsoid ascospores of *Cetrariopsis laii*, Russia, Primorye 17.9.1961, *S. Pärn* (TU). Bars in Figs. 11-16 = 10 μm, ab = axial body, th = tholus.

lary chemistry of *Cetrariopsis* - *Cetreliopsis* - *Nephromopsis* is determined mainly by the occurrence of fatty acids. Some orcinol depsides and depsidones may be present in *Cetrariopsis* and *Nephromopsis* while β-orcinol depsidones always occur in *Cetreliopsis*. All the 16 species of this generic complex are distributed in the montaneous forests of Eastern and Southeastern Asia only. So, we consider actually that the three genera - *Cetrariopsis*, *Cetreliopsis*, and *Nephromopsis* - form a group of phytogenetically related taxa.

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Randlane, T. & Saag, A. Synopsis of the genus *Nephromopsis* (Fam. Parmeliaceae, lichenized Ascomycota). — Cryptogamie, Bryologie-Lichénologie. (Accepted for publication.)

SYNOPSIS OF THE GENUS *NEPHROMOPSIS* (FAM. PARMELIACEAE, LICHENIZED ASCOMYCOTA)

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RÉSUMÉ - Un aperçu global du genre *Nephromopsis* Müll. Arg. (fam. Parmeliaceae) est presenté. La clé d'identification comprend les 11 espèces (*N. endocrocea, N. isidioidea, N. komarovii, N. laii, N. morrisonicola, N. nephromoides, N. ornata, N. pallescens, N. rugosa, N. stracheyi* et *N. yunnanensis*) reconnus dans ce genre; une description détaillée et la distribution mondiale de chacune d'entre elles sont présentées pour la première fois. Une nouvelle combination *N. nephromoides* (Nyl.) Ahti & Randlane est proposée.

ABSTRACT - The paper presents a global survey of the genus *Nephromopsis* Müll. Arg. (fam. Parmeliaceae). The identification key includes the 11 species now accepted in the genus (*N. endocrocea, N. isidioidea, N. komarovii, N. laii, N. morrisonicola, N. nephromoides, N. ornata, N. pallescens, N. rugosa, N. stracheyi* and *N. yunnanensis*); detailed descriptions and world distribution data of each taxa are presented for the first time. A new combination *N. nephromoides* (Nyl.) Ahti & Randlane is proposed.

KEY WORDS - lichenized Ascomycota, Parmeliaceae, *Cetrariopsis*, *Nephromopsis*, key for species, distribution maps.

INTRODUCTION

The genus *Nephromopsis* Müll. Arg., described in 1891, was again brought to light in 1981 when Lai resurrected it in a treatment of cetrarioid species with nephromoid apothecia and pseudocyphellae on the lower surface (Lai, 1981). Still, the evaluation of important characters on the genus level has changed considerably. Nowadays the anatomical features of the thallus and especially of the inner structures of ascomata are considered more conservative and therefore suitable for delimitation at generic level. Mainly on these grounds the genus *Tuckneraria* (Randlane *et al.*, 1994) was separated from *Nephromopsis* and some taxa were transferred from *Nephromopsis* to *Allocetraria* (Thell *et al.*, 1995b) or *Cetreliopsis* (Randlane *et al.*, 1995). The position of apothecia on the lower side of the thallus has been one of the most attractive and significant characters in defining the genus *Nephromopsis* since Müller Argoviensis (1891), while the laminal position of apothecia over the upper surface remains the only true feature for the genus *Cetrariopsis* (Kurokawa, 1980). Our studies have shown that there is not much difference in morphology, anatomy, and chemistry of these two genera except for their dissimilar positions of apothecia (Randlane *et al.*, 1995). Therefore we proposed transferring the two species of *Cetrariopsis* (*C. pallescens* and *C. laii*) to the genus *Nephromopsis* (Randlane *et al.*, 1997). The genus *Cetreliopsis*, also related to that group, differs considerably from *Nephromopsis* in morphological (pseudocyphellae on both surfaces), anatomical (asci rather broadly clavate, ascospores ellipsoid) and chemical (absence of orcinol depsides and depsidones and presence of ß-orcinol

depsidones - fumarprotocetraric acid and related substances in all species) characters, and is therefore maintained as a separate genus.

As a result, *Nephromopsis* includes now 11 species. The concise description of the genus has been published in an earlier paper (Randlane *et al.*, 1995); in this one, an identification key is presented as well as short descriptions and distribution data for these taxa that were not treated previously. Distribution maps are provided for all species.

MATERIAL AND METHODS

About 380 herbarium specimens from B, BM, CANB, C OLO, E, FH, G, GZU, H, KW, LD, LE, M, PC, S, TAIM, TNM, TU, UPS, US, WU and private herbaria of A. Aptroot, D. D. Awasthi and J. A. Elix were examined.

Anatomical studies of cortical and reproductive structures were carried out by Dr. Arne Thell in the University of Lund (Sweden) using methods described in Thell *et al.* (1995a). Chemical analyses were carried out according to the standardized TLC methods (Culberson & Kristinsson, 1970; Culberson, 1972). The acetone extracts were run in solvent systems B, C and G (Culberson *et al.*, 1981).

RESULTS

1. Identification key

1. Medulla coloured 2
- Medulla white 4
2. Lower side strongly rugose and reticulated, pseudocyphellae laminally developedon ridges and on special plug-like outgrowths. Rhizines absent. ..... *N. isidioidea*
- Lower side regularly reticulated, pseudocyphellae mainly developed in the marginal zone - on ridges or on the lower surface itself. Rhizines present..... 3
3. Medulla pale yellow, K+ yellow (secalonic acid). ..... *N. ornata*
- Medulla orange, K+ lilac (endocrocin). ..... *N. endocrocea*
4. Apothecia small and numerous, mainly laminal. ..... *N. pallescens* var. *pallescens*
- Apothecia of various size and number, mainly marginal. 5
5. Lower surface black, only margins brown to pale brown. . ..... *N. morrisonicola*
- Lower surface brown to whitish. 6
6. Epilithic; thallus strongly rugose, with concentric rings. ..... *N. komarovii*
- Epiphytic; thallus smooth or rugose but not in concentric rings. 7
7. Thallus light or bright yellow on both surfaces, more or less smooth; pseudocyphellae in the form of small flat white dots situated on the surface. ..... *N. pallescens* var. *citrina*
- Upper and lower surfaces of different colour, not uniformly yellow; thallus smooth to strongly rugose; pseudocyphellae different. 8
8. Medulla C+ red (olivetoric or anziaic acid). 9
- Medulla C - 10

9. Thallus regularly reticulated; pseudocyphellae small and flat developed mainly on ridges; pycnidia on emergent projections; olivetoric acid in medulla. ..... *N. rugosa*
- Thallus smooth or slightly wrinkled; pseudocyphellae medium to large, flat or concave, developed on the surface; pycnidia immersed; anziaic acid in medulla. ..... *N. stracheyi*

10. Medulla KC+ red (physodic acid). ..... *N. rugosa*
- Medulla KC - (lichesterinic and protolichesterinic acids). 11

11. Lower surface remarkably rugose, pseudocyphellae on ridges and plug-like outgrowths; pycnidia numerous on emergent projections, possible on both surfaces. ..... *N. yunnanensis*
- Lower surface smooth or moderately rugose, pseudocyphellae either on the surface or on ridges but not on special outgrowths; pycnidia absent or marginally immersed. 12

12. Thallus moderately rugose, often with secondary marginal lobules; pseudocyphellae small and flat, mainly developed on ridges. ..... *N. laii*
- Thallus smooth or slightly wrinkled, without secondary marginal lobules; pseudocyphellae medium to large, flat or concave, developed on the surface. ..... *N. nephromoides*

2. Taxonomical part

Nephromopsis Müll. Arg., Flora 74: 374, 1891.

Synonym: *Cetrariopsis* Kurok., Mem. Natl. Sci. Mus. Tokyo 13: 140, 1980.

Type species: *Nephromopsis stracheyi* (Bab.) Müll. Arg.

Decription of the genus was presented in a previous survey (Randlane *et al.*, 1995: 37-38). After transferring *Cetrariopsis pallescens* and *C. laii* to *Nephromopsis* (Randlane *et al.*, 1997) the description of that genus should be emended in the following way: **apothecia** marginal on the lower surface of the thallus, or submarginal and laminal on the upper surface, from small (1-2,5 mm) to very large (to 32 mm in diameter); **exiple** usually three-layered but sometimes the middle layer is not distinctly developed and is seen as two-layered in a few species.

Nephromopsis endocrocea Asahina, J. Jap. Bot. 11: 24, 1935.

Type: Japan, insula Nippon (Honshu), Nasuzan, *Faurie,* 30.07.1897, *no. 339* (KY, n. v.). **Synonyms**: *Cetraria endocrocea* (Asahina) M. Satô in Nakai & Honda, Nov. Fl. Jap. 5: 37, 1939.

Thallus foliose, up to 15 cm in diameter, with prolonged ascending lobes up to 8 mm wide; upper surface greenish or yellowish grey, smooth; medulla dark yellow or orange; lower surface light brown or dark brown to almost black, regularly reticulated; **pseudocyphellae** in the form of minute white dots, mainly developed marginally on the lower surface itself or on ridges. **Rhizines** numerous to sparse, slender. **Pycnidia** marginal and laminal, located on the black emergent projections, sometimes very numerous. **Pycnoconidia** bifusiform, 5 x 1,5 µm. **Apothecia** marginal on the lower side of the thallus, rounded or reniform, up to 12 mm in diameter, disc brown, faced upwards. Exciple three-layered. **Asci** 45 x 12 µm, axial body extremely small (0,5 µm), tholus with an amyloid ring structure, **ascospores** oblong, 9-10 x 4-5 µm.

Chemical constituents: usnic acid in the cortex; endocrocin and various fatty acids (e.g. lichesterinic and protolichesterinic acids) in the medulla. Medulla K+ lilac.

Distribution and habitat: Japan, Russian Far East; China (Wei, 1991) (Fig. 1); corticolous on coniferous (*Abies, Larix, Tsuga*) or deciduous (*Betula*) trees at lower and medium altitudes (up to 2500 m).

Morphologically quite similar to *N. ornata* except for the brighter colour of medulla and somewhat more delicate general habit.

Altogether 32 specimens examined.

Selected specimens examined. *Japan.* Prov. Shimotsuke, Karikomi-ko near Nikko, *C. & W. Culberson*, 1961, *no. 11076* , *11127* (M, US). Prov. Shinano, Yatsugatake, *Kurokawa*, 1951 (LD). Hokkaido, Mt. Tomurausi, alt. 1000 m, *Satô*, 31.07.1935 (UPS). *Russia.* Far East, Kuril Islands, Kunashir, Goryachi Plyazh, *Parmasto*, 20.09.1960 (TU). Far East, Primorye Reg., Sikhote Alin, Mt. Kitovoye Rebro, 44°33'N 136°80'E, alt. 600 m, *Skirina*, 1982, *no. 1661* (LD).

Nephromopsis isidioidea (Räsänen) Randlane & Saag, Mycotaxon 44: 487, 1992.

Basionym: *Cetraria wallichiana* var. *isidioidea* Räsänen, Arch. Soc. Zool. Bot. Fenn. Vanamo 5, 1: 25, 1950. **Type**: India, E. Himalayas (West Bengal), Darjeeling Distr., Rimbick to Sandakhpoo, alt. 9000 ft., *Awasthi*, June 1948, *no. 179* (H, holotype!). **Synonym**: *Cetraria isidioidea* (Räsänen) D. D. Awasthi, Bull. Bot. Surv. India 24: 10, 1982.

Thallus foliose, ca. 5,5 cm in diameter, with lobes 1-2 cm wide; upper surface yellowish grey, strongly rugose; medulla yellow to ochraceous; lower surface dark brown to black, strongly rugose and reticulated, with special plug-like outgrowths. **Rhizines** absent, possibly broken from the outgrowths. White small **pseudocyphellae** situated on ridges and outgrowths of the lower side. **Pycnidia** mainly laminal but also marginal, located on numerous black emergent projections. **Pycnoconidia** bifusiform, 5 x 1,5 µm. **Apothecia** not seen.

Chemical constituents: usnic acid in the cortex; secalonic acid C and fatty acids (lichesterinic and protolichesterinic acids) in the medulla. Medulla K+ reddish.

Distribution and habitat: known only from the type collection from India, East Himalaya, West Bengal (Fig. 1), at altitude of about 2700 m; on a dead tree stump.

The taxonomic status of *N. isidioidea* is not definitely clear, it is probably closely related to the other two species with coloured medulla, especially to *N. ornata* from which it differs in the more rugose and reticulated thallus, lack of rhizines and apothecia.

Nephromopsis komarovii (Elenkin) J. C. Wei, Enumer. Lich. China: 158, 1991.

Basionym: *Cetraria komarovii* Elenkin, Izv. Imp. S.-Peterburgsk. Bot. Sada 3: 51, 1903. **Type**: Russia, Irkutsk Region, in viciniis Nilova Pustyn, ad terram montis Chongoldoi montium Sajanensium, *Elenkin,* 1902, *no.155* (LE, holotype; FH, isotype!). **Synonym**: *Cetraria perstraminea* Zahlbr., Trudy Troitskos.-Kyakhtinsk. Otd. Priamursk. Otd. Imp. Russk. Geogr. Obshch. 12: 88, 1911 [1909]. Type: Russia, Transbaicalia, Chilgindin, *Mikhno* (n. v.).

Thallus foliose, up to 15 cm in diameter, with rounded lobes up to 2 cm wide; upper surface from bright yellow to yellowish green, strongly rugose in a somewhat concentric pattern; medulla white; lower surface brown, smooth or slightly rugose; **pseudocyphellae** in the form of regular flat white patches of various size, developed laminally on the lower surface. **Rhizines** numerous to sparse, short and slender, light

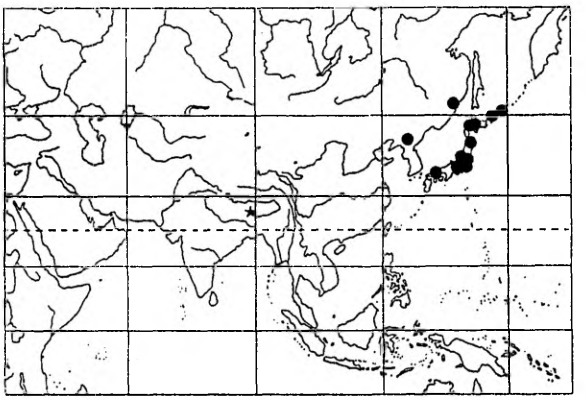

Fig. 1. World distribution of *N. endocrocea* (●) and *N. isidioidea* (★).

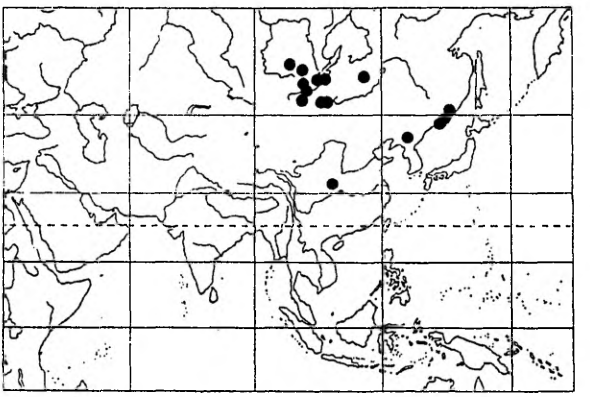

Fig. 2. World distribution of *N. komarovii.*

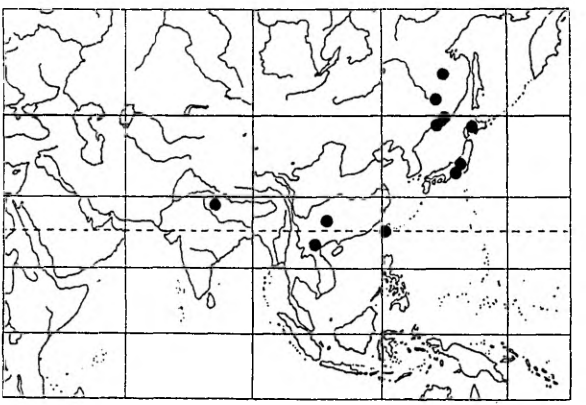

Fig. 3. World distribution of *N. laii.*

brown to whitish. **Pycnidia** not seen. **Apothecia** usually marginal, occasionally laminal, rounded or reniform, up to 15 mm in diameter, disc brown, faced upwards, often only juvenile apothecia present. Exciple three-layered. **Asci** 30 x 9 µm, axial body 3 µm, **ascospores** oblong, 6 x 3 µm.

Chemical constituents: usnic acid in the cortex; lichesterinic and protolichesterinic acids in the medulla; fumarprotocetraric acid (Huneck *et al.*, 1984) and stictic and constictic acids (personal comments by T. Ahti) have also been detected in some specimens.

Distribution and habitat: Russia (eastern Siberia and Far East), Mongolia, China (Fig. 2); the only epilithic representative of the genus, growing mainly over rocks and boulders in shaded localities, often together with mosses; in mountane forests at lower and medium altitudes (200-3000 m); prefers humid ecotypes, e.g. valleys of mountain rivulets.

Easily recognized by its characteristically rugosed upper surface which is usually intensively green up lemon yellow. Marginally situated juvenile apothecia are also frequent.

Altogether 36 specimens examined.

Selected specimens examined. *Russia.* Buryatia, eastern Sayans, Arshan, *Trass*, 1979 (TU). Baical Reg., Hamar-Daban, *Masing*, 1963 (TU). Far East, Primorye Terr., Sikhote Alin, Ternei, 44°20'N 136°35'E, *Skirina*, 1985, *no. 1661* (LD). *Mongolia.* Ulan-Bator, Bogd-uul in Zaisan, alt. 1600 m, *Huneck*, 1988, *no. 88-15* (B). Ara-Khangai Reg., Tevshrulek, river Khuh-Sumein-gol, *Biazrov*, 1970, *no. 7370* (LD). *China.* Yunnan, Setschwan Co., Hosö, alt. 2950 m, *Handel-Mazzetti*, 08.08.1915, *no. 1364* (WU). Chili Co., Hsiao-wu-tai-shan, *Smith*, 1921 (COLO).

Nephromopsis laii (Thell & Randlane) Saag & Thell, Bryologist 100: 111, 1997.

Basionym: *Cetrariopsis laii* Thell & Randlane, Crytog. Bryol. Lichénol. 16: 46, 1995. **Type**: Russia, Primorye region, Kedrovaya Padj Nature Reserve, *Pärn,* 17.09.1961 (TU, holotype!; LD, isotype!).

Description and discussion in Randlane *et al.* (1995: 46-47).

Distribution and habitat: Russia, China, Taiwan, Japan, India, Vietnam (Fig. 3); corticolous on coniferous (*Abies, Pinus*) and deciduous (*Betula, Quercus*) trees in mountainous forests between 600-3000 m elevation.

The species has usually been compared to *N. pallescens* (both taxa were earlier referred to *Cetrariopsis*); we now observe some similarities between *N. laii* and *N. nephromoides*, especially in the form, size and position of apothecia. The important characters to identify *N. laii* are the following: moderately rugose thallus with secondary lobules as a fringe along the margins; small and flat pseudocyphellae situated mainly on brown coloured ridges of the generally lighter lower surface.

Altogether 24 specimens examined.

Selected specimens examined. *Russia.* Far East, Primorye Reg., Sikhote Alin, Lazovsky Mt., alt. 950 m, 43°21' N, 133°50' E, *Skirina,* 1982, *no. 1448* (LD). Primorye Reg., Sikhote Alin, Mt. Kitovoye Rebro, alt. 600 m, 44°33' N, 136°80' E, *Skirina,* 1982, *no. 1445* (LD). Far East, Chabarovsk Terr., Obluchensk, Jadrino, *Pärn,* 08.08.1961 (TU). *China.* Yunnan, Lijiang Co., Mt. Yülung-schan, alt. 3500 m, *Handel-Mazzetti, no. 660* (WU). *Taiwan.* Chiayi Co., Mt. Alishan, alt. 2275 m, *Lai,* 1978, *no.10 198* (US). *Japan.* Nikko, *Miyoshi,* 1886 (FH). Goten-niwa, Mt. Huzi, *Asahina,* 1956, *Lich. Jap. Exs. no. 157* (H). *Vietnam.* Zon Kin, Phan-si-Pau, Lao Kay, alt. 2900 m, collector unknown, 1929, *no. 17 156* (PC).

Nephromopsis morrisonicola M. J. Lai, Quart. J. Taiwan Mus. 33: 223, 1981.

Type: Taiwan, Nanton Co., Mt. Morrison, alt. 3500-3900 m, *Lai,* 1978, *no. 10 438* (TAIM, holotype!).

Description in Randlane *et al.* (1995: 38-40).

Distribution and habitat: originally described as a Taiwanese endemic (Lai, 1981) - named after Mt. Morrison in Taiwan - but now known from a wide region in southeastern Asia: Taiwan, China, Nepal, Philippines, Indonesia (Java, Borneo, West Irian), Papua New Guinea (Fig. 4); grows as an epiphyte on coniferous (*Abies*) and deciduous (*Betula*) trees or shrubs (*Vaccinium*) at high altitudes (2400-4000 m).

The taxon is easily recognized by the black underside and white medulla (*N. endocrocea, N. isidioidea* and *N. ornata* also have a dark brown to almost black lower surface but the medulla is coloured in all these taxa).

Altogether 16 specimens examined.

Selected specimens examined. *China.* Muli Kingdom, Mts. of Kopati, Djago & Muli, alt. 3100 m, *Rock* (B). *Nepal.* Khumbu Himal, Ngotung La, alt. 3410 m, *Remus & Menzel*, 16.04.1981, *no. 239* (B). *Indonesia.* West Irian, Carstensz Mts., Lower Meren valley near Blue Lake, *Hope*, 30.12.1971, *no. CGE L43* (COLO). *Papua New Guinea.* Southern Highlands, Mt. Giluwe, alt. 11 000 ft., *McVean*, 1967, *no. 67142* (COLO).

Nephromopsis nephromoides (Nyl.) Ahti & Randlane **comb. nov.**

Basionym: *Platysma nephromoides* Nyl., Flora 52: 442, 443, 1869. **Type**: India, West Bengal, Darjeeling Distr., Tongloo, alt. 10,000 ft., *Hooker fil. & Thomson, no. 2080* (as *'2020'* in protologue) (H-NYL 36068, lectotype!; B, PC, UPS isolectotypes!). - **Synonyms:** *Nephromopsis stracheyi* var. *nephromoides* (Nyl.) Räsänen, Kuopion Luonnon Ystäväin Yhdistyksen Julkaisuja, ser. B 2, 6: 48, 1952. - *Cetraria nephromoides* (Nyl.) D. D. Awasthi, Bull. Bot. Surv. India 24: 11, 1982.

Nephromopsis stracheyi f. *ectocarpisma* Hue, Nouv. Arch. Mus. Hist. Nat., Sér. 4, 1: 218, 1899. Type: Japan, insula Yeso (Hokkaido), in sylvis Mombetsu, *Faurie,* 1891, *no. 3521* (PC, lectotype!, selected here). - *Nephromopsis ectocarpisma* (Hue) Gyeln., Ann. Cryptog. Exot. 4: 173, 1931.

Thallus foliose, up to 20 cm in diameter, with rounded wide lobes which may be convoluted; upper surface greenish grey, thick, smooth or slightly wrinkled; medulla white; lower surface light or yellowish brown, smooth or somewhat reticulated at the margins; **pseudocyphellae** conspicuous, oval or rounded, flat to concave, situated mainly on the surface, occasionally - in the marginal zone - also on ridges. **Rhizines** sparse, short and simple. **Pycnidia** rare, marginal, immersed. **Pycnoconidia** not seen. **Apothecia** usually numerous, marginal, comparatively small, up to 8 mm in diameter, disc brown, rounded or more often irregular, faced upwards. Exciple three-layered. **Asci** 35-40 x 10 µm, axial body small (3 µm), **ascospores** ellipsoid, 7-8 x 3 µm.

Chemical constituents: usnic acid in the cortex; lichesterinic and protolichesterinic acids and additionally some other fatty acids, e.g. caperatic acid (+/-) in the medulla.

Distribution and habitat: Japan, China, Taiwan, Vietnam, India, Nepal (Fig. 5); corticolous on trees at the altitudes between 2400 and 3600 m.

The new combination *Nephromopsis nephromoides* has to be proposed for *N. ectocarpisma* because the name *Platysma nephromoides* Nyl. turned out not to be a nomen nudum as it was considered to be until recently (Randlane *et al.*, 1997). Some characters of that taxon are pointed out in the same paper where the species is mentioned for the first time (Nylander, 1869: 442), but under the description of quite another species (*Platysma stracheyi*) (Nylander, 1869: 443).

N. nephromoides is similar to *N. stracheyi* in general morphology (smoothness of the thallus, form of lobes and pseudocyphellae) but is slightly smaller and thinner, also the apothecia are considerably smaller and often more numerous; the secondary compounds (and thus the C reaction on medulla) are also quite different. Sometimes may resemble *N. laii* but the latter has typically marginal secondary lobes and different pseudocyphellae.

Altogether 50 specimens were examined.

Selected specimens examined. *Japan.* Prov. Aomori, Osorezan, *Faurie*, 1902, *no. 5341* (FH, PC); Prov. Nara, Yoshino, Mt. Odaigahara, *Nakanishi*, 1960 (US); Honshu, Prov. Tottori, Mt. Daisen, *Koponen*, 20.07.1971, *no. 21818* (H). *China.* Yunnan, Lijiang Co., alt. 3000 m, *L. S. Wang*, 06.08.1985, *no. 85-354* (H). *Taiwan.* Hwalien Co., Mt. Kilaishan, *Nakamura*, 30.12.1940, *no. 385* (US). *India.* West Bengal, Darjeeling, from Sandakhpoo to Phalut, alt. 3600 m, *Awasthi & Agarwal*, 16.06.1967, *no. 67442* (UPS). *Nepal.* Prov. Helambu-Langtang, Kutumsang, 27°57'N 85°29'E, alt. 2750 m, *Rettig*, 21.11.1988, *no. 6471a* (GZU). From Rakhshe to Ethung, alt. 9000 ft., *Awasthi*, 16.05.1953, *no. 2128* (UPS).

Nephromopsis ornata (Müll. Arg.) Hue, Nouv. Arch. Mus. Hist. Nat., Sér. 4, 2: 90, 1900.

Basionym: *Cetraria ornata* Müll. Arg., Nuovo Giorn. Bot. Ital. 23: 122, 1891. **Type**: Japan, Mt. Ontake, *no. 109* (n. v.). **Synonyms**: *Nephromopsis delavayi* Hue, Nouv. Arch. Mus. Hist. Nat., Sér. 4, 1: 219, 1899. - Type: China, Yunnan, Lopinchan, Lanhong, alt. 3200 m, *Delavay*, 31.07.1888 (DUKE, n. v.). - Syn.: *Cetraria delavayi* (Hue) M. Satô in Nakai & Honda, Nov. Fl. Jap. 5: 48, 1939.

Nephromopsis endoxantha Hue, Nouv. Arch. Mus. Hist. Nat., Sér. 4, 1: 220, 1899. - Type: Japan, Togakushi, *Faurie*, 17.09.1898, *no. 776* (KY, lectotype; DUKE, isolectotype; n. v.). - Syn.: *Tuckermannopsis endoxantha* (Hue) Gyeln., Acta Fauna Fl. Universali, Ser. 2, Bot. 1, 5/6: 6, 1933. - *Cetraria endoxantha* (Hue) D. D. Awasthi, Bull. Bot. Surv. India 24: 9, 1982.

Thallus foliose, up to 15 cm in diameter, with prolonged ascending lobes up to 1.5 cm wide; upper surface greenish or yellowish grey, smooth or somewhat wrinkled; medulla pale yellow; lower surface brown or dark brown to almost black, regularly reticulated; **pseudocyphellae** in the form of minute white dots, mainly developed marginally on the lower surface or on ridges. **Rhizines** sparse, slender. **Pycnidia** marginal and laminal, located on the black emergent projections, sometimes very numerous. **Pycnoconidia** bifusiform, 5 x 1 µm. **Apothecia** marginal on the lower side of the thallus, rounded or reniform, up to 20 mm in diameter, disc brown, faced upwards. Exciple three-layered. **Asci** 40-45 x 10 µm, axial body extremely small (0,5-1,2 µm), tholus with an amyloid ring stucture, **ascospores** oblong, 7-9 x 4-5 µm.

Chemical constituents: usnic acid in the cortex; secalonic acids A or C, traces of endocrocin and fumarprotocetraric acid (+/-), additionally some fatty acids (+/-) in the medulla. Medulla K+ deep yellow.

Distribution and habitat: Japan, Russian Far East; China (Wei, 1991), Taiwan (Lai, 1981), South Korea (Park, 1990) (Fig. 6); corticolous on coniferous (*Abies, Larix, Picea, Pinus, Taxus*) and deciduous trees (*Alnus, Betula, Padus, Phellodendron, Populus, Salix, Tilia*) or bushes (*Rhododendron*), occasionally also on boulders covered with mosses in various types of forests at lower and medium altitudes (up to 3200 m). The most common species among *Nephromopsis*.

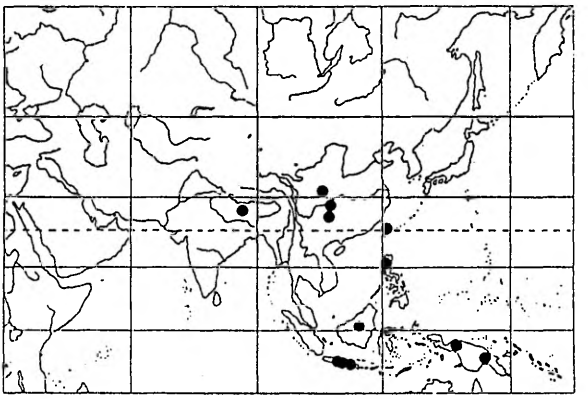

Fig. 4. World distribution of *N. morrisonicola.*

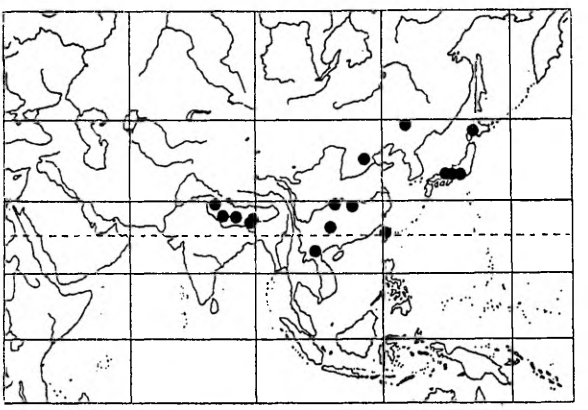

Fig. 5. World distribution of *N. nephromoides.*

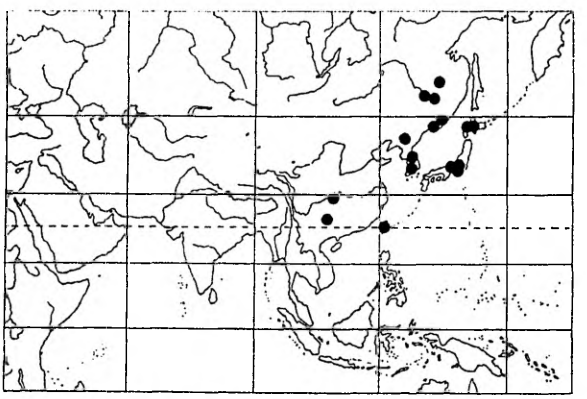

Fig. 6. World distribution of *N. ornata.*

N. ornata is a distinct taxon, easily recognized by its pale yellow medulla; systematically closely related and morphologically similar to *N. endocrocea* (see the differences on p. 3).

Altogether 78 specimens examined.

Selected specimens examined. *Japan.* Prov. Shinano, Mt. Kita-Yokodake, *Kurokawa*, 1958, *no. 58348* (M, US). Honshu, Prov. Kozuke, Sannoh Pass, alt. 1600 m, *Degelius*, 29.04.1964 (UPS). Mt. Fuji, alt. 1000-2400 m, *Hultén*, 05.10.1961 (S). *Russia.* Far East, Primorye Terr., Mt. Snezhnaya, *Randlane*, 17.09.1983 (TU). Primorye Terr., Sikhote Alin, Mt. Eldorado, 44°41'N 135°20'E, *Skirina*, 1984, *no. 8995* (LD). Khabarovsk Terr., Selihin, Kabansopka, *Pärn*, 18.08.61 (TU).

Nephromopsis pallescens (Schaer.) S. Y. Park **var. *pallescens***, Bryologist 93: 122, 1990.

Basionym: *Cetraria pallescens* Schaer., in Moritzi, Syst. Verzeichn.: 129, 1845-1846. **Type**: Java, Mt. Pangerango, *Zollinger, no. 449* (G, holotype!). **Synonyms**: *Platysma pallescens* (Schaer.) Nyl., Mém. Soc. Sci. Nat. Cherbourg 5: 100, 1858 [1857]. - *Cetrariopsis pallescens* (Schaer.) Randlane & Thell, Crytog. Bryol. Lichénol. 16: 42, 1995.

Sticta wallichiana Taylor, London J. Bot. 6: 177, 1847. - Type: Nepal, Wallich (FH, holotype, n. v.; G, no. 2003/2; G, no. 2003/1, PC, isotypes!). - Syn.: *Parmelia wallichiana* (Taylor) Nyl., Mém. Soc. Sci. Nat. Cherbourg 5: 105, 1858 [1857]. - *Platysma leucostigmeum* var. *wallichianum* (Taylor) Nyl., Syn. Meth. Lich. I: 306, 1860. - *Platysma wallichianum* (Taylor) Nyl., Flora 52: 443, 1869. - *Cetraria wallichiana* (Taylor) Müll. Arg., Flora 71: 139, 1888. - *Cetrariopsis wallichiana* (Taylor) Kurok., Mem. Natl. Sci. Mus. Tokyo 13: 140, 1980. - *Ahtia wallichiana* (Taylor) M. J. Lai, Quart. J. Taiwan Mus. 33: 220, 1981 (*nom. illeg.*).

Cetraria sulphurea Mont. & Bosch, in Montagne, Syll. Gen. Sp. Crypt.: 322, 1856 (not validly published). - Orig. coll.: Java, *Junghuhn* (n. v.).

Cetraria teijsmannii ("*Teysmanni*") Mont. & Bosch, in Montagne, Syll. Gen. Sp. Crypt.: 474, 1856. - Type: Java, *Teijsmann* (n. v.). - Synonym: *Platysma teijsmannii* ("*Teysmanni*") (Mont. & Bosch) Nyl., Mém. Soc. Sci. Nat. Cherbourg 5: 100, 1858 [1857].

Description and discussion in Randlane *et al.* (1995: 42-44).

Distribution and habitat: Nepal, India, China, Taiwan, Russian Far East, Indonesia (Java); Japan, Thailand (Kurokawa, 1980), South Korea (Park, 1990), Papua New Guinea (Streimann, 1986) (Fig. 7); epiphytic on coniferous (*Larix*, *Pinus*) and deciduous (*Carpinus*, *Quercus*) trees or shrubs (*Rhododendron*) in the mountainous forests at medium and high altitudes (1200-4000 m).

In its typical form, *N. pallescens* is very conspicuous and has always been easily recognized by numerous small apothecia laminally situated all over the thallus. In less typical cases the characteristic features of the lower side - strongly rugose and reticulated surface with pseudocyphellae on ridges and special plug-like outgrowths - are also of great help in identification.

Altogether 47 specimens examined.

Selected specimens examined. *Nepal.* Mewakhola valley, alt. 8000 ft., *Awasthi*, 27.05.1953, *no. 2237a* (UPS); Langtang Area, below Dotsche, alt. 2900 m, *G. & S. Miehe*, 1986, *no. 15 615* (GZU). *India.* Bhutan, Taba, Thimpu, 27°30'N 89°39'E, alt. 2500 m, *Grierson & Long*, 12.05.1979, *no. 972* (E). *China.* Yunnan, Lijiang Co., Mt. Tiejia Shan, 26°56'N 100°10'E, alt. 2750 m, *Moberg & Santesson*, 24.09.1987, *no. 8075* (UPS). Mt. Gibboh, alt. 4000 m, *Rock, no. 1630* (B). *Russia.* Far East, Primorye Terr., Kedrovaya Padj, *Ivaninnikova*, 1959 (TU).

Nephromopsis pallescens **var.** ***citrina*** (Taylor) Thell & Randlane, Bryologist 100: 110, 1997.

Basionym: *Cetraria citrina* Taylor, London J. Bot. 6: 176, 1847. **Type**: Java, *Hooker* (BM, lectotype!). **Synonyms**: *Platysma citrinum* (Taylor) Nyl., Mém. Soc. Sci. Nat. Cherbourg 5: 100, 1858 [1857]. - *Cetrariopsis pallescens* var. *citrina* (Taylor) Thell & Randlane, Crytog. Bryol. Lichénol. 16: 44, 1995.

Description and discussion in Randlane *et al.* (1995: 44).

Distribution and habitat: Indonesia (Java, West Irian) and Taiwan (Fig. 7); corticolous in mountainous forests (alt. 1300 - 3000 m).

This southern variety (with its main distribution area in Java) is recognized by its smooth and uniformly light or bright yellow thallus on both surfaces as well as minute flat pseudocyphellae on the lower side.

Altogether 59 specimens examined.

Selected specimens examined. *Indonesia.* Java. Pangerango, alt. 2820 m, *Schiffner,* 1894, *no. 2987a* (FH, M); Preanger, Mt. Gedeh, alt. 2300 m, *Schiffner,* 1894, *no.3387* (FH, M); Kandang Badals, alt. 2600 m, *Yates,* 1927, *no. 2827* (LD, US); East Java, Andjasmora-complex, alt. 2100 m, *Groenhart,* 1937, *no.2538* (Herb. Aptroot); Res. Pasoeroean, Goenoeng Ardjoena, Tretes - Lalidjiwa track, *Du Rietz,* 1927, *no. 105-1b* (UPS). *Taiwan.* Mt. Arisan, *Asahina* (US).

Nephromopsis rugosa Asahina, J. Jap. Bot. 11: 12, 1935.

Type: Japan, Prov. Musasi, Mt. Kobusi, *Asahina,* 22.07.1933 (DUKE, isotype). **Synonym**: *Cetraria rugosa* (Asahina) M. Satô, in Nakai & Honda, Nova Flora Japonica 5: 46, 1939.

Thallus foliose, up to 20 cm in diameter, with rounded lobes up to 2.5 cm wide; upper surface yellowish or glaucous olive, often with a significant green tinge, remarkably regularly reticulated; medulla white; lower surface light brown, yellowish or whitish, strongly reticulated; **pseudocyphellae** on the lower side in the form of minute flat white spots located mainly on ridges. **Rhizines** sparse. **Pycnidia** marginal and laminal, on the black emergent projections, which are often situated along the ridges of the upper surface. **Pycnoconidia** bifusiform, 5 x 1-1,5 µm. **Apothecia** marginal on the lower side of the thallus, rounded or reniform, up to 20 mm in diameter, disc brown, faced upwards. Exciple three-layered. **Asci** 35-40 x 10 µm, axial body 4 µm, **ascospores** oblong, 7-9 x 3-5 µm.

Chemical constituents: usnic acid in the cortex; two chemotypes: I - olivetoric acid; II - physodic and oxyphysodic acids, additionally fatty acids (+/-) in the medulla. Medulla C+ red in chemotyp I, C-, KC+ red in chemotype II.

Distribution and habitat: Russian Far East, Japan; Mongolia (Schubert & Klement, 1971) (Fig. 8); corticolous on coniferous (*Abies, Larix, Picea*) or deciduous trees (*Quercus*) in forests between 700-1700 m elevation..

N. rugosa can be morphologically recognized by its significantly reticulated thallus which often has a characteristic greenish tinge. Spot tests with C and KC are also of great help.

Altogether 21 specimens examined.

Selected specimens examined. *Russia.* Far East, Primorye Terr., Kedrovaya Padj, *Guriljova,* 1951 (TU; chemotype I). Primorye Terr., Sikhote Alin, Dzigitovka River valley, 44°50'N 136°10'E, *Skirina,* 1982, *no. 9280* (LD; chemotype II). Sikhote Alin, Kitovoye Rebro, alt. 800 m, 44°33'N 136°80'E, *Skirina,* 1982, *no. 1449* (LD;

chemotype II). *Japan.* Berg Buko, *Miyshi*, 1891 (UPS; chemotype I). Prov. Shinano, Mt. Mikuniyama, *Kurokawa*, 1958, *Lich. Jap. Exs. no. 254* (TAIM; chemotype II). Honshu, Prov. Musashi, Mikuni Pass., alt. 1750 m, *Shibuichi*, *Lich. Rar. et Critici Exs. no. 154* (B, LD, US; II chemotype).

Nephromopsis stracheyi (Bab.) Müll. Arg., Flora 74: 374, 1891.

Basionym: *Cetraria stracheyi* Bab., Hooker's J. Bot. Kew Gard. Misc. 4: 245, 1852. **Type**: Himalaya, Kathi, 7200 ft., *Strachey & Winterbottom* (BM, holotype; H-NYL 36138, isotype!). **Synonym**: *Platysma stracheyi* (Bab.) Nyl., Flora 52: 443, 1869.

Thallus foliose, thick, coriaceous, up to 20 cm in diameter, with rounded wide lobes up to 3 cm wide; upper surface greenish or yellowish grey, smooth or only slightly wrinkled; medulla white; lower surface light or yellowish brown, smooth or reticulated; **pseudocyphellae** conspicuous, medium to large, oval or rounded, flat to concave, situated directly on the surface. **Rhizines** sparse, short and simple. **Pycnidia** rare, marginal, immersed. **Pycnoconidia** bifusiform, 5 x 1.5 µm. **Apothecia** marginal on the lower side, sometimes extremely large (up to 20 mm in diameter), disc brown, rounded or somewhat irregular, faced upwards. Exciple three-layered. **Asci** 35 x 10 µm, axial body small (3 µm), **ascospores** ellipsoid, 7-8 x 2,5-3 µm.

Chemical constituents: usnic acid in the cortex; olivetoric (chemotype I) or anziaic acid (chemotype II) in the medulla. Medulla C+ red in both chemotypes.

Distribution and habitat: India, Nepal, Taiwan; China (Wei, 1991) (Fig. 9); corticolous on trees at low and medium altitudes (up to 2800 m).

N. stracheyi is mostly similar to *N. nephromoides* in general habit of the thallus and form of pseudocyphellae; differences can be easily noticed in the size of apothecia (much bigger in *N. stracheyi*) and spot test with C in medulla (positive in *N. stracheyi*).

Altogether 13 specimens examined.

Selected specimens examined. *India.* NW Himalayas, Almora Distr., Dhakuri, alt. 9500 ft., *D. Awasthi & A. Awasthi*, 1950, *no. 642* (UPS, US). *Nepal.* On ascent to Sandakhpoo, alt. 1100 ft., *Awasthi*, 1953, *no. 2470A* (FH, UPS). Langtang Area, Dunche, alt. 2800 m, *G. Miehe & S. Miehe*, 22.03.1986, *no. 346* (GZU). *Taiwan.* Miaoli Co., Nankonchi, alt. 2000 m, *Kao*, 1959, *no. 121* (US).

Nephromopsis yunnanensis (Nyl.) Randlane & Saag, Mycotaxon 44: 488, 1992.

Basionym: *Platysma yunnanense* ("*yunnense*") Nyl., Lich. Nov. Zeland.: 150, 1888. **Type**: China, Yunnan, alt. 1800 m, *Delavay, no. 1602* (H-NYL 36134, lectotype!). **Synonym**: *Cetraria yunnanensis* (Nyl.) Zahlbr., Trudy Troitskos.-Kyakhtinsk. Otd. Priamursk. Otd. Imp. Russk. Geogr. Obshch. 12: 89, 1911 [1909].

Description in Randlane *et al.* (1995: 39-40).

Distribution and habitat: endemic to China (prov. Yunnan) (Fig. 10); corticolous on coniferous (*Picea*) or deciduous trees (*Quercus*) in mountainous forests (alt. 1800-2800 m).

The most attractive character of *N. yunnanensis* is the abundance of laminal pycnidia on pale emergent projections (all the other *Nephromopsis* species bear black projections, if they have any); pseudocyphellae are typically developed on ridges and outgrowths of the very rugose lower surface.

Specimens examined in Randlane *et al.* (1995: 40).

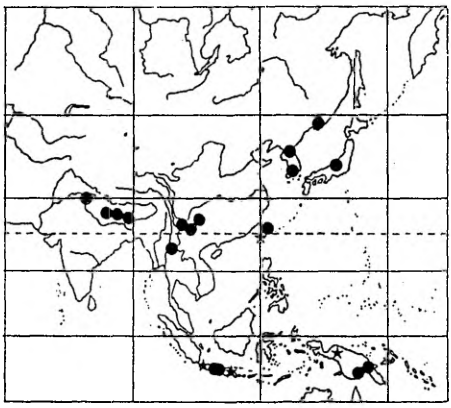

Fig. 7. World distribution of *N. pallescens* var. *pallescens* (●) and *N. p.* var. *citrina* (★).

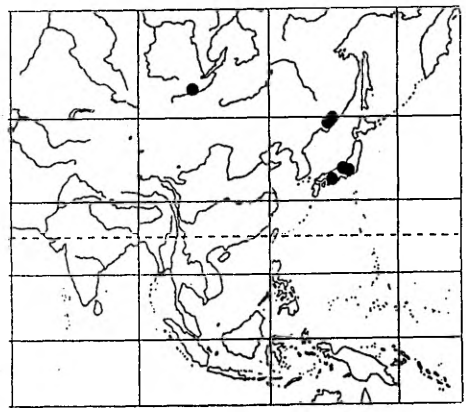

Fig. 8. World distribution of *N. rugosa.*

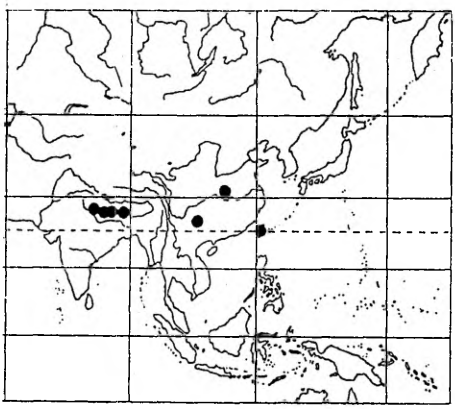

Fig. 9. World distribution of *N. stracheyi.*

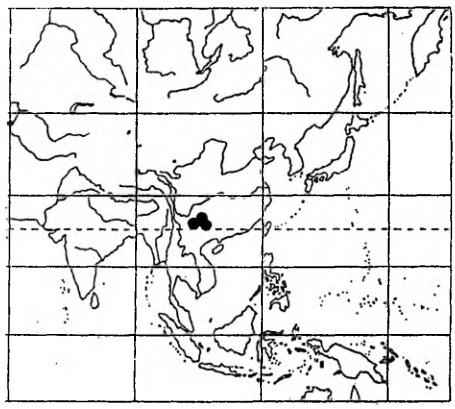

Fig. 10. World distribution of *N. yunnanensis.*

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The lichen genus Tuckneraria Randlane & Thell — a new segregate in the Parmeliaceae

TIINA RANDLANE, ANDRES SAAG, ARNE THELL and INGVAR KÄRNEFELT

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The new lichen genus *Tuckneraria* Randlane & Thell is described. The separation from *Nephromopsis* is based mainly on anatomical characters in the reproductive structures, such as shape and size of ascospores and structures of exciple and ascus, but also on morphological characters — thallus surface features and the presence of cilia. The genus *Tuckneraria* includes the three species *T. laureri* (Kremp.) Randlane & Thell, *T. laxa* (Zahlbr.) Randlane & Thell, *T. pseudocomplicata* (Asah.) Randlane & Saag and the newly described *T. ahtii* Randlane & Saag. *Nephromopsis nipponensis* (Asahina) M.J.Lai is considered synonymous with *Tuckneraria pseudocomplicata*.

Key words: lichenized Ascomycotina, *Nephromopsis*, Parmeliaceae, *Tuckermannopsis*, *Tuckneraria*

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INTRODUCTION

The generic complex comprising *Cetrariopsis–Cetreliopsis–Nephromopsis* (Ascomycotina, Parmeliaceae) has so far not been monographed on a worldwide basis. The species within these rare Asiatic genera are poorly known and have been referred to during the last few decades only in some local floristic studies (Rassadina 1971, Golubkova 1981, Awasthi 1982, Park 1990, Kurokawa 1991), with the exception of a significant paper on cetrarioid lichens of East Asia (Lai 1980). A team of reseachers is now carrying out a detailed study of this group and the present paper is the first report of the project.

Until recently, the genus *Nephromopsis* Müll.Arg. has been delimited mainly on the basis of morphological and chemical characters (Lai 1980, Randlane & Saag 1991, 1992) such as loosely attached foliose thallus; the tendency of marginal apothecia to be situated on the lower surface; the presence of laminal pseudocyphellae over the lower cortex; the occurrence of pycnidia, frequently on emergent projections, marginally and/or laminally; the complex of secondary compounds including usnic acid, fatty acids, orcinol depsides and depsidones and anthraquinones. However, anatomical studies of ascocarps clearly demonstrate that species

treated under this genus vary significantly in their shape of ascospores, ascus type and excipular structure. As the division of species into groups based on anatomical qualities is also correlated with morphological characters, the segregation of a new genus is fully justified.

MATERIAL AND METHODS

About 250 herbarium specimens from B, DUKE, FH, GZU, H, KW, LD, M, MB, S, TAIM, TNS, TU, UPS, US, the majority of them belonging to *T. laureri* (Kremp.) Randlane & Thell, were studied. Chemical analyses according to the standardized TLC methods (Culberson 1972, 1974) were carried out in Tartu University. The acetone extracts were run in solvent systems B, C and G (Culberson et al. 1981). After spraying with 10% sulphuric acid, the plates were air dried and then heated at about 100–120°C for up to 15 min.

Anatomy of ascocarps and conidiomata was examined at the University of Lund. Sections were made with a Kryomat, Leitz freezing microtome and stained in lactophenol cottonblue. After pretreatment with 10% KOH solution, asci were squashed in a 0.3% Lugol's solution. The characters were studied with a Zeiss Axioscope light microscope, and photomicrographs made with a Zeiss M 35 W camera.

TAXONOMY

Tuckneraria Randlane & Thell, *gen. nova*

Thallus foliaceus, mediocris (ad 7 cm latus), pallide flavescens, virescens vel glaucus; laciniae oblongae aut suborbiculares; partim ascendentes; marginibus interdum ciliatis; margine sorediata aut soredia desunt. Superficies inferior pallida, fusca vel nigra; pseudocyphellata; rhizinata. Apothecia marginalia, orbicularia vel reniformia, ad 10 mm lata; sporae 8-nae, subglobosae, 5–7 x 4–5 µm; asci 30–50 x 10–14 µm. Pycnidia marginalia, papillaria vel spinuliformia; conidia 4–5 x 1–1.5 µm, extremis nonnihil infiatis.

Type species: *Tuckneraria pseudocomplicata* (Asahina) Randlane & Saag

Thallus foliose, medium (to 7 cm broad), smooth or only slightly rugose; light yellow, yellowish-green or yellowish-grey, +/– loosely attached to the substratum; lobes elongate or rounded, with ascending margins and numerous or occasional marginal cilia; with or without marginal soredia; lower surface whitish, light to dark brown or black; white or light brown, usually small and plain pseudocyphellae situated on lower cortex; rhizines simple, at times long and numerous; both cortices paraplectenchymatous; cortical hyphae strongly gelatinized.

Apothecia marginal, disc brown, rounded or reniform, to 10 mm in diameter, facing up- or downwards; exciple 2-layered; ascospores simple, globose - subglobose, 5–7 x 4–5 µm, 8 per ascus; asci 30–50 x 10–14 µm, clavate, spores arranged +/– uniseriately; asci *Tuckermannopsis*-type (Kärnefelt et al. 1992) with rather small tholus, very broad ocular chamber and broad axial body (2.5–4 µm). Pycnidia on marginal (occasionally laminal on both surfaces) emergent projections; pycnoconidia bifusiform, 4–5 x 1–1.5 µm.

Chemical constituents: usnic acid +/– in the cortex; lichesterinic- and protolichesterinic-type fatty acids, caperatic acid and orcinol depsidones (physodic, conphysodic, alectoronic, collatolic acids) in the medulla.

The name for the new genus is compiled from the names of the related lichen genera *Tuckermannopsis* and *Nephromopsis*, com-bining them with *Cetraria*. The species within *Tuckneraria* are morphologically reminiscent of the species in *Nephromopsis* but in ascocarp anatomy more like *Tuckermannopsis*. These two genera are probably the most closely related entities to the new genus. Still, there are certain differences even in the morphological characters between *Nephromopsis* and *Tuckneraria* (Figs. 1–5): the thallus of the species within *Nephromopsis* is usually coriaceous, thick and often strongly

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Figs. 1–5. Morphology of the genus *Tuckneraria*. — 1: *T. ahtii*, part of the frequently ciliated thallus, China, Yunnan, *Handel-Mazetti 660* (US). — 2: *T. laureri*, showing the sorediate margin and the marginal apothecium, Austria, Stubaier Alpen, 1958 *Steiner* (LD). — 3: *T. pseudocomplicata*, part of the ciliated thallus; Japan, Shikoku, Awa, *Fujikawa 29560* (TNS). — 4: *T. laxa*, characterized by the same type of cilia; Taiwan, Miaoli Co., *Lai 7770* (TAIM). — 5: Lobes of the same specimen with marginal pycnidia and cilia. Scale in Figs. 1, 2, 4 = 1 cm, in Figs. 3, 5 = 1 mm. p = pycnidia, s = soredia.


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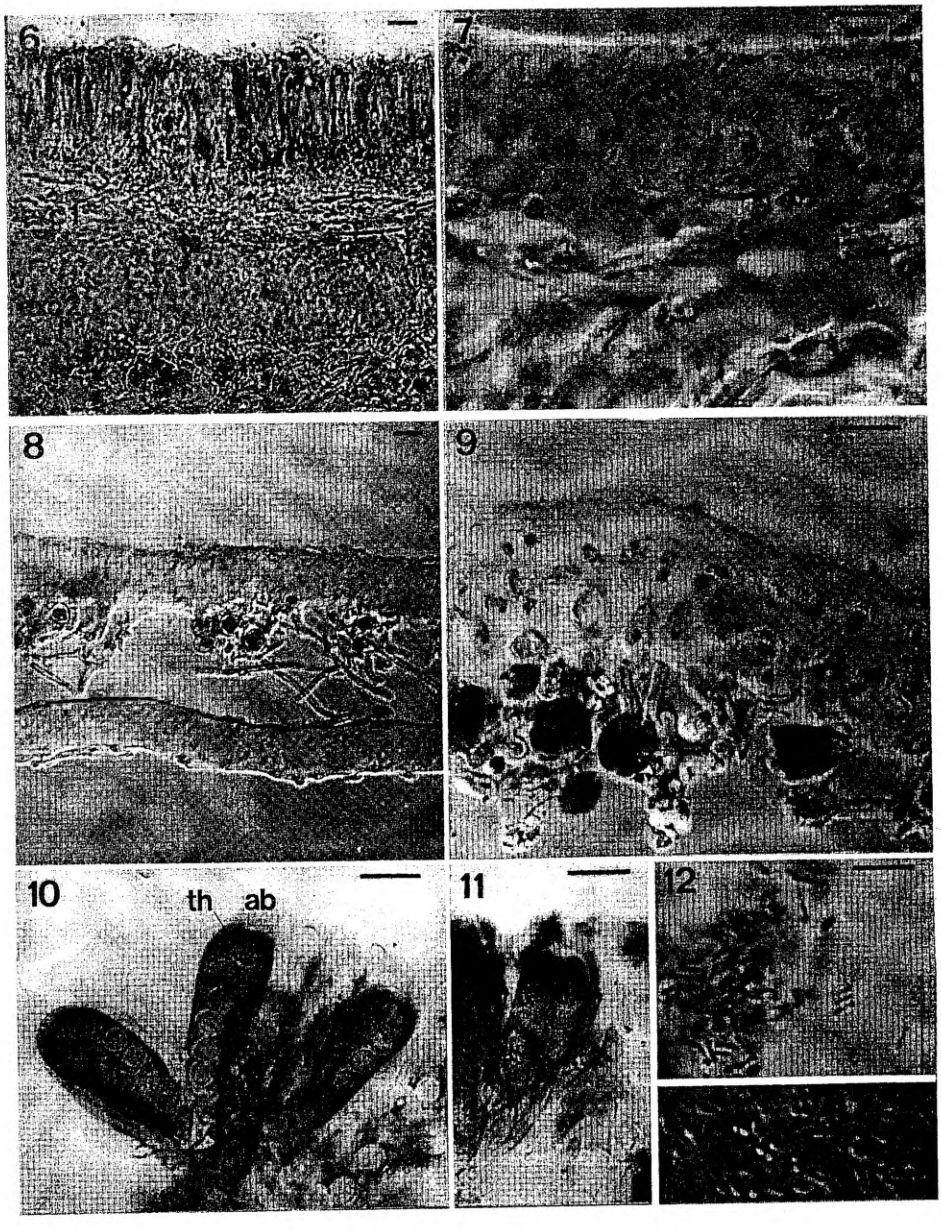
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reticulated or rugose; the lobes are usually rounded, not elongate; the marginal cilia are absent; pseudocyphellae on the lower surface are large, well delimited, either on special outgrowths or concave. In *Tuckneraria* cortical hyphae are always strongly gelatinized (Figs. 7–9). The ascospores of these two genera essentially differ, being ellipsoid in *Nephromopsis* and subglobose in *Tuckneraria*, while the anatomical characters of exciple (Fig. 8) and asci (Figs. 6, 10, 11) present similarities as well as differences (Table 1). Pycnoconidia are bifusiform (5 x 1–1.5 µm) in both genera (Figs. 12, 13). Secondary chemistry of *Nephromopsis* and *Tuckneraria* is similar: both have usnic acid in the cortex; both have lichesterinic- and protolichesterinic-type fatty acids and occasionally caperatic acid in the medulla together with the orcinol depsidones physodic and conphysodic acids; a few *Nephromopsis* species also contain orcinol de-pside olivetoric acid and the anthraquinone en-docrocin or secalonic acid, none of which are present in *Tuckneraria*.

The best characters for the separation of *Tuckneraria* from *Nephromopsis* are the general habit of the thallus and the ascospore shape. Species within *Tuckermannopsis* are easily separated from both genera by their lack of pseudocyphellae on the lower cortex.

The genus *Tuckneraria* includes 4 species growing on deciduous and coniferous trees mainly in eastern and south-eastern Asia.

Tuckneraria ahtii Randlane & Saag, *spec. nova*

Thallus foliaceus, laciniae 4–10 mm latae; marginibus interdum ciliatis; superficies superior virescens vel fuscesenti-flavens. Superficies inferior pallide fusca, in centro fere nigra, pseudocyphellata; rhizinae fuscae, ad 5 mm longae. Apothecia marginalia, ad 8 mm longa et 5 mm lata; ascosporae subglobosae, 5–7 x 4–5 µm; asci clavati, 30–50 x 10–14 µm. Pycnidia marginalia, papillaria vel spinuliformia; conidia 5 x 1–1.5 µm recta, extremis nonnihil inflatis. Acidum usnicum +/– in cortice superiore; acidum lichesterinicum et protolichesterinicum in medulla.

Type: China. Prov. Yunnan, Lijiang County, Mt. Yulongshan, lower central E slope, Ganheba, 3 200–3 300 m, 27°06′N, 100°14′E, on *Abies*, 23 April 1987, *Teuvo Ahti, Jian-Bin Chen & Li-Song Wang, 46 649* (H, holotype; TU, isotype).

Thallus foliose, upper surface pale glaucous or yellowish- brown, lower surface light to dark brown or almost black in central parts. Lobes rounded at the tips but usually elongate in ge-neral habit, 4 to 10 mm wide, bearing con-spicuous black marginal pycnidial projections and sometimes also numerous or occasional pale or brown cilia (Fig. 1). Pseudocyphellae on lower cortex plain, white or light brown, in-frequent on some specimens. Rhizines brown, simple, sometimes very long, to 5 mm, and numerous.

Apothecia marginal, with oblong or re-niform brown disc, to 8 x 5 mm; ascospores subglobose, 5–7 x 4–5 µm; asci 30–50 x 10–14 µm, narrowly clavate; axial body 2.5–4 µm. Pycnidia on emergent projections, usually marginal and numerous, some laminal pycnidial projections may be present on both surfaces (on the lower cortex growing out from rim of pseudocyphellae); pycnoconidia bifusiform, 5 x 1–1.5 µm (Fig. 12).

Chemistry: usnic acid present or absent in the cortex; lichesterinic- and protolichesterinic-

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Figs. 6–13. Anatomy of the genus *Tuckneraria*. — 6: Cross section of an apothecium of *T. pseudocomplicata*, showing the two layered exciple, Japan, Honshu, *Tagawa 319* (US).—7: Upper cortex of *T. laureri*; Austria, Tirolia, *Zahlbruckner 463* (LD). — 8: *T. laxa*, cross-section of thallus with strongly gelatinized hyphae; Taiwan, Miaoli Co., *Lai 7770* (TAIM). — 9: Upper cortex of *T. pseudocomplicata* with strongly gelatinized cortical hyphae; Japan, Honshu, *Tagawa 319* (US). — 10: Asci of *T. laureri*, with a small tholus and a rather broad axial body; *Zahlbruckner 463* (LD). — 11: Asci of *T. ahtii*; China, *Xizang, Zong Yu-chen & Liao Yin-shang 307* (LD). — 12: Pycnoconidia of *T. ahtii*; Nepal, Himalayas, *Miehe 11836* (GZU). — 13:. Pycnoconidia of *T. laureri*, Austria, Stubaier Alpen, *Steiner 1958* (LD). Scale = 10 µm.; exc 1 = upper excipular layer, exc 2 = lower excipular layer, th = tholus, ab = axial body.

Table 1. Comparison of characters of *Tuckneraria* with those of the related genera *Nephromopsis* and *Tuckermannopsis*.

	Nephromopsis	*Tuckneraria*	*Tuckermannopsis* s. str.
Thallus	foliose, coriaceous	foliose, paper thin	foliose, paper thin
Lobe shape	rounded	rounded to elongate	elongate
Lower surface	rugose or reticulated	+/– smooth	smooth
Marginal cilia	absent	present	present
Pseudocyphellae on lower surface	large, distinct	small, indistinct	absent
Exciple	3-layered	2-layered	2-layered
Asci	30–70 x 9–14 µm	30–50 x 10–14 µm	25–40 x 8–15 µm
Ascospores	ellipsoid, 5–10 x 2.5–5 µm	subglobose, 5–7 x 4–5 µm	globose, 3.5–5 x 3.5–5 µm
Axial body	2–4 µm	2.5–4 µm	3–4 µm
Cortical substances	usnic acid	usnic acid	atranorin
Medullary substances			
a) fatty acids	present	present	present
b) secalonic acids	present	absent	absent
c) orcinol depsides & depsidones	olivetoric or physodic acid	alectoronic, collatolic, physodic acid	alectoronic, collatolic, olivetoric or physodic acid

type fatty acids always present in medulla, while caperatic acid is an accessory substance.

Distribution: China, Nepal, Taiwan.

Specimens of this lichen species have usually been erroneously identified as *Nephromopsis delavayi* Hue, even though several characters do not correspond with the original description of *N. delavayi* (Hue 1899–1900). The most important character is the shape and size of the ascospores: *N. delavayi* has ellipsoid ascospores (7–11 x 4–5 µm) and therefore probably belongs to the genus *Nephromopsis*, while the ascospores of the species described here are subglobose (5–7 x 4–5 µm). Other characters such as the size and reticulation of the thallus, absence of cilia and the apothecial measurements highlight the essential differences between these two entities. According to Lai (1980), the type material of *N. delavayi* contains secalonic acid and is morphologically identical with *Nephromopsis ornata* (Müll.Arg.) Hue. We are in agreement about the synonymy of *N. delavayi* with *N. ornata* proposed by Lai but propound here a new species, *Tuckneraria ahtii*, to include the specimens that in many herbaria have been wrongly determined as *N. delavayi*. Teuvo Ahti collected wonderful material from China, Yunnan, and it was in the Helsinki herbarium in 1992 that we first began to speculate about the new species.

Specimens examined — China. Prov. Yunnan, Mt. Yulongshan near Lijiang, 3 450–3 500 m, *Handel-Mazzetti 3563* (US, FH), Lijiang County, Mt. Ndaza Ko, 4 000 m, *Rock (Zahlbruckner–Redinger:* Lich. Rar. Exs. 31 S); Lijiang County, Yangtze watershed, eastern slopes of Lijiang Snow Range, *Rock 11 773* (UPS); Prov. Xizang, 3 300 m, *Zong Yu-chen & Liao Yin-shang 307*. Nepal. Langtang area, Pamdang Karpo, 4 620 m, *Miehe 13 056f* (GZU), Langschisa Glacier, 4 090 m, 4 400 m, 4 480 m, 4 530 m *Miehe 11 725b, 13 846, 12 424, 11 835* (GZU), Dupku, Helambu, 4 090 m, *Miehe 7396e* (GZU), Pangtang, 4 300 m, *Miehe 2284* (GZU). Taiwan. Prov. Taichung, Mt. Armashan, *Lai 6860* (TAIM).

Tuckneraria laureri (Kremp.) Randlane & Thell, *comb. nova*

Cetraria laureri Kremp., Flora 34: 673. 1851. *Nephromopsis laureri* (Kremp.) Kurok., J. Jap. Bot. 66: 156. 1991.

Cetraria complicata Laurer in Fr., Lichenogr. Eur. Ref.: 459. 1831 (nomen nudum).

Cetraria straminea Kremp. ex Schwend. in Nägeli, Beitr. Wiss. Bot. 2: 154. 1860; syn. nov.

Thallus light yellow on upper surface, white to pale brown on lower surface. Lobes rounded, up to 5 mm broad, ascending in the margins, bearing marginal soredia (sometimes almost isidia- like structures) and scattered cilia (Fig. 2). Pseudocyphellae on lower cortex white, plain, rounded or irregular, often surrounded by a light brown line, at times absent from some specimens. Rhizines scattered.

Apothecia very rare, marginal, with brown disc and sorediose thalline margin; ascospores subglobose, 5–6 x 4–4.5 µm; asci clavate, 35–45 x 10–12 µm (Fig. 10); axial body 2.5 µm. Pycnidia on marginal emergent projections; pycnoconidia bifusiform, 5 x 1–1.5 µm (Fig. 13).

Chemistry: usnic acid in the cortex; lichesterinic- and protolichesterinic-type fatty acids in the medulla. Medulla Pd–, K–, C–, KC–.

Distribution: montane forests of Central Europe (the Alps, the Carpathians); Asia (Russia, China, Mongolia, Japan, Nepal); South-America (Venezuela, Colombia).

T. laureri is the only sorediate taxon within the *Cetrariopsis–Nephromopsis–Tuckneraria* complex, thus representing a 'secondary' species. In accordance with the 'species-pairs' theory (Poelt 1970), it is the most widely distributed of all other — 'primary' — species discussed here, growing widely in Eurasia and found also in the northern part of South America. Because of its superficial morphological similarity (yellowish thallus, marginal soredia) to the North American and European lichen *Tuckermannopsis oakesiana* (Tuck.) Hale, it has sometimes been confused with it. However, *Tuckneraria laureri* and *Tucknerrmannopsii oakesiana* cannot be phylogenetically closely related be-cause of essential differences in their repro-ductive structures and secondary chemistry. The present generic position of the former species is not satisfactory either, but this problem will be discussed in a future paper.

More than 170 specimens were examined from different parts of the whole distribution area.

Selected specimens examined — Austria. Steiermark, See-Eben, 1 400 m, *Poelt* (GZU); Tirol, Allgäu, 1 720 m, *Schauer* (M). Germany. Salzburg, Radstadt, 1 320 m, *Schauer* (M); Oberbayern, Garmisch, 1 280 m, *Schauer* (M). Italy. Tirol, Bolzano, *Hausmann* (Erbar. Crittog. Ital., 464; M, S). Yugoslavia. Alpes Julia, Pokljuka, Rudno Polje, 1 800 m, *Vězda,* Lich. Sel. Exs. 847 (LD, S). Romania. Hunedoara, Retezat Mts., 45°23′N 22° 49′E, 1 450–1 550 m, *Moberg 10 765* (UPS). Ukraine. Zakarpatska region, district Rahivska, Velikii Bichkiv, 800 m, *Makarevich 8261* (KW). China. Sikang, Kangting, Chungo Valley, Yara, 4 050 m, *Smith 14 011* (UPS). Japan. Honshu, Prov. Shinano, Mt. Takesbi-mine, 1 700 m, *Kashiwadani 15 043* (TNS). Mongolia. Ara-Khangai region, Zenkher district, Suvraga ridge, 2 200 m, *Biazrov 714* (LD). Nepal. Langtang area, Dubku Helambu, 4 090 m, *Miehe 7396e* (GZU). Russia. Irkutsk region, Hamar-Daban Mt. Range, Bolshaya Osinovka, *Trass 1031* (TU); Habarovsk region, Badzhal Mt. Range, Urmi, *Randlane 208* (TU). Colombia. Risaralda, volcano Santa Rosa, 4°49′N, 75°28′W, 4 130 m, *Wolf 1172* (B). Venezuela. Merida, Apartaderos, 8°45′N, 70°45′W, 3 500 m, *Kalb* (LD).

Tuckneraria laxa (Zahlbr.) Randlane & Thell, *comb. nova*

Nephromopsis ciliaris (Ach.) Hue var. *laxa* Zahlbr., Fedde, Repert. 33: 61. 1933. — *Nephromopsis laxa* (Zahlbr.) M.Sato, J. Jap. Bot. 14: 783. 1938. — *Cetraria laxa* (Zahlbr.) Sato, Parmeliales (I), in Nakai et Honda, Nova Flora Japonica 5: 51. 1939.

Cetraria daibuensis Räsänen, J. Jap. Bot. 16: 85 1940. — *Nephromopsis daibuensis* (Räsänen) Räsänen, Kuopion Luonnon Yst. Yhd. Julk. B 2(6): 47. 1952.

Thallus pale yellow on both surfaces, lobes elongate and narrow (up to 2 mm broad) with abundant marginal cilia, yellowish-brown or darker brown to black at the tips. Pseudocyphellae on lower cortex in the form of tiny, white, plain spots. Rhizines scattered, simple or occasionally branched.

Apothecia very rare, marginal, with a brown rounded disc; ascospores subglobose, 5 x 4 µm; asci clavate, 40–45 x 12–13 µm; axial body 3 µm. Pycnidia marginal, on +/– emergent projections. Pycnoconidia not seen.

Chemistry: usnic acid in the cortex; lichesterinic- and protolichesterinic-type fatty acids in the medulla. Medulla Pd–, K–, C–, KC–.

Distribution: endemic to Taiwan.

This species stands somewhat alone in the genus due to its highly characteristic morphology (uniformly pale colour of the thallus on both surfaces, narrow and elongate lobes, abundant marginal cilia, extremely small pseudocyphellae) (Figs. 4, 5). Evidently its distribution is restricted to the island of Taiwan. However, the presence of pseudocyphellae on the lower cortex and marginal position of apothecia in *T. laxa*, as well as the anatomical structures of the asci and thallus (Fig. 6), clearly place it in *Tuckneraria*.

Specimens examined — Taiwan. Nimandaira, Mt. Arisan, *Asahina*, (H). Miaoli County, Mt. Dapachienshan, *Lai 7770* (TAIM). Hua-lien County, Shyu-lin village, 2 700 m, *Koponen 18 024 (H).*

Tuckneraria pseudocomplicata (Asah.) Randlane & Saag, *comb. nova*

Cetraria pseudocomplicata Asahina, J. Jap. Bot. 12: 804. 1936. — *Nephromopsis pseudocomplicata* (Asahina)M.J. Lai, Quart. J. Taiwan Mus. 33: 224. 1980.

Cetraria rhytidocarpa Mont. & Bosch f. *nipponensis* Asah., J. Jap. Bot. 24: 228. 1954; syn. nov.

Nephromopsis nipponensis (Asahina) M.J.Lai, Quart. J. Taiwan Mus. 33: 223. 1980.

Thallus greenish on upper and white or light brown on lower surface. Lobes rounded, to 7 mm broad, bearing scattered marginal cilia (Fig.3). Pseudocyphellae on lower cortex not numerous; in the form of rounded or irregular white, small, plain patches, often with light brown margins. Rhizines pale, simple, long (to 3 mm). Apothecia marginal, rounded or reniform, to 6 mm in diameter, with reddish-brown disc; exciple 2-layered (Fig. 6); ascospores subglobose, 5–6 x 4–5 µm; asci clavate, 30–35 x 12–14 µm; axial body 3.5 µm. Pycnidia numerous, situated on marginal emergent projections; pycnoconidia bifusiform, 5 x 1–1.5 µm.

Chemistry: usnic acid present or absent in the cortex; as for the medullary compounds, two different chemotypes can be distinguished. The first chemotype, formerly *Nephromopsis pseudocomplicata*, contains alectoronic acids (α and ß forms) as the major, and α-collatolic acid as a minor substance in the medulla; lichesterinic- and protolichesterinic-type fatty acids may occur rarely. The second chemotype, formerly *Nephromopsis nipponensis*, contains equally constantly orcinol depsidones physodic and conphysodic acids as well as lichesterinic- and protolichesterinic-type fatty acids. Both chemo-types respond similarly to medullary colour tests: Pd–, K–, C–, KC+ red and no morpho-logical or anatomical differences.

Distribution: Eastern Asia (Sakhalin island, Japan, Taiwan).

T. pseudocomplicata is chosen to be the type species of the new genus because of its supposed central position in this group of taxa. It evidently has some affinities to all the species in *Tuckneraria*. Its chemical diversity can be interpreted in terms of evolutionary potential.

About 60 specimens were examined from Japan and Taiwan.

Selected specimens examined — The first chemotype with alectoronic acids. Japan. Prov. Suruga, Mt. Fuji, *Culberson & Culberson 10 805, 10 807* (US), Lake Saiko, *Culberson & Culberson 10 803* (M); Prov. Yamanashi, Adzumazawa, Mitomimura, 2 300 m, *Omura 395* (US); Prov. Shinano, Mt. Tadesina, *Kurokawa 51 747* (M), Mt. Yatsugatake, *Kurokawa 58 303* (TAIM); Honshu, Prov. Nara, Mt. Odaigakara, *Tagawa 319*, Komagatake, *Faurie 6759*. Taiwan. Taitung County, Yakou, 2 750 m, *Lai 9484* (US) — besides alectoronic acids also lichesterinic- and protolichesterinic-type fatty acids.

The second chemotype with physodic, conphysodic, lichesterinic and protolichesterinic acids. Japan. Prov. Kai, Mt. Yatsu-ga-take, *Asahina* (lectotype of *Cetraria rhytidocarpa* f. *nipponensis;* DUKE); Prov. Musashi, Mt. Kumatori, 1 900 m, *Shibuichi, 4533* (Kurokawa: Lich. Rar. Crit. Exs. 153; H, LD, M, TAIM, TU); Prov. Musashi, Titibu, Mt. Ryogami, *Kurokawa 55 0573-b* (M); Prov. Hida, Mt. Ontake, *Asahina*, Lich. Jap. Exs. 56, (H); Honshu, *Koponen* (H).

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THE LICHEN GENUS *ALLOCETRARIA* (ASCOMYCOTINA, PARMELIACEAE)

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Key Words

Cetrarioid lichens, *Allocetraria*, Parmeliaceae, axial body, filiform pycnoconidia

Abstract

The cetrarioid lichen genus *Allocetraria* (Parmeliaceae) includes eight species distinguished by a palisade plectenchymatous cortex, asci with a very broad axial body, globose or subglobose ascospores, and filiform pycnoconidia. Two new species, *A. flavonigrescens* THELL et RANDL. and *A. sinensis* GAO, are described, and the new combinations *A. denticulata* (HUE) THELL et RANDL., *A. globulans* (NYL.) THELL et RANDL., and *A. oakesiana* (TUCK.) RANDL. et THELL are proposed. *A. potaninii* (OXN.) RANDL. et SAAG is synonymized with *A. stracheyi* (BAB.) KUROK. et LAI. The anatomy of the genus is carefully described for the first time.

* Dedicated to Prof. Dr. GERHARD FOLLMANN on occasion of his 65th birthday and retirement from the University of Cologne, Germany, with respect to his appreciated pioneering lichenological works.

Introduction

The genus *Allocetraria*, originally including three species from high altitudes in South-east Asia, was introduced in the Parmeliaceae by KUROKAWA and LAI (1991). It was separated from *Cetraria* on the dichotomously or subdichotomously branched lobes, the special appearance of the pseudodyphellae, the palisade plectenchymatous cortex, and on the unique chemistry (fig. 7). Three species, *A. ambigua* (BAB.) KUROK. et LAI, *A. isidiigera* KUROK. et LAI, and *A. stracheyi* (BAB.) KUROK. et LAI were combined here. The authors did not pay attention to ascomatal and pycnidial characters consequently. However, our studies of these structures confirm the necessity of a separate genus for this species group also on the grounds of filiform pycnoconidia, *Lecanora* type of asci with an unusually broad axial body (THELL et al. 1994), and globose or subglobose ascospores (tab. 1). These are basic characters for the recognition of the genus *Allocetraria.*

Three more species have earlier also been combined in *Allocetraria* by RANDLANE and SAAG (1992). Two of them, however, *A. cucullata* (BELLARDI) RANDL. et SAAG and *A. nivalis* (L.) RANDL. et SAAG, have asci of the *Cetraria* type and bifusiform pycnoconidia and were recently separated into a new genus, *Flavocetraria* KÄRN. et THELL (KÄRNEFELT et al. 1994). After recent studies of the type material of *A. potaninii* (OXN.) RANDL. et SAAG it became clear that this species must be synonymized with *A. stracheyi* (BAB.) KUROK. et LAI. Three further species, however, *Nephromopsis globulans* (NYL.) LAI, *Tuckermannopsis oakesiana* (TUCK.) HALE, and *Cetraria denticulata* HUE, are transferred to *Allocetraria* in this paper. The two first entities were examined carefully and both show the characteristic features of the genus. No material was seen of *C. denticulata* but the Latin diagnosis clearly unveils its affinities to *Allocetraria.* Unfortunately, we did not succeed to get any material of the newly described *A. isidiigera*, but the species is obviously a good member of this well delimited genus.

Material and Methods

About 120 herbarium specimens from FH, GZU, H, KW, LD, LE, PC, S, TU, and UPS were examined. Methods used for anatomical studies have been described in detail by KÄRNEFELT et al. (1992). The secondary chemistry was investigated with standardized methods (CULBERSON 1972).

Taxonomy

Allocetraria KUROK. et LAI

Bull. nat. Sci. Mus. Tokyo, Ser. B, 17: 60; 1991. Type species: *Allocetraria stracheyi* (BAB.) KUROK. et LAI.

Thallus foliose or fruticose, suberect to erect; upper surface yellow to yellowish green or brown; lower surface of the same colour as upper or light tan or brown or black; lobes prostrate, unbranched or dichotomously branched, in most of the species quite narrow, elongated, and characteristically convex; soredia or isidia present on one species each; rhizines sparse; pseudocyphellae on the lower surface either punctiform and irregular or sublinear along the margins, absent in some species; cortical layers usually more or less palisade plectenchymatous; medulla white or coloured from light yellow to bright orange; medullary hyphae 3 - 6 µm in diameter; algae near the upper cortex.

Apothecia lateral and marginal or submarginal to almost laminal, with brown disc and yellowish thalline margin, up to 7 - 8 mm in diameter; exciple 2-layered, 30 - 120 µm thick; asci usually rather narrowly clavate to cylindrical, 30 - 70 x 8 - 18 µm, tholus small, ocular chamber cylindrical and broad, axial body broad to very broad, 5 - 9 µm; ascospores globose to subglobose, rarely broadly ellipsoid, more or less uniseriately arranged, 5 - 10 x 5 - 8 µm; paraphyses usually straight, sparsely branched with swollen tips; pycnidia marginal to submarginal, rarely laminal, immersed or on emergent projections, dark pigmented; pycnoconidia filiform, usually slightly sublageniform, 10 - 19 x 0.5 - 2 µm.

Chemical substances: usnic acid in the cortex; different fatty acids (caperatic, lichesterinic, protolichesterinic) in the medulla together with secalonic acids and other related pigments. One species contains fumarprotocetraric acid.

The genus *Allocetraria*, including eight species mainly distributed in South-east Asia, is characterized on both structural characters, characters in the reproductive structures, and characters in the secondary chemistry. All species appear to be only rarely fertile and mature asci have been found only in *Allocetraria ambigua, A. globulans*, and *A. oakesiana*. Therefore much attention must be payed to the structure of the lobes when recognizing different species.

Of the structural characters is the palisade plectenchymatic arrangement of the cortical hyphal cells the most important. The asci are above all characterized by

an unusually large axial body in addition to globose or subglobose ascospores (tab. 1). The pycnidia furthermore produce a unique form of rather long, slightly sublageniform, filiform pycnoconidia. All species are also characterized by content of usnic acid in the cortex and several medually substances, lichesterinic-, protolichesterinic, and secalonic acids.

Tab. 1: *Allocetraria* compared with some other cetrarioid genera

Characters	*Allocetraria*	*Cetraria*	*Flavocetraria*	*Tuckermannopsis s. str.**	*Tuckneraria*
upper surface	yellow	brown	yellow	brown	yellow to greenish
upper and lower	1-layered, palisade plectenchymatous	usually 2-layered	1-layered, paraplectenchymatous	1-layered, paraplectenchymatous	1-layered, paraplectenchymatous
pseudocyphellae	usually present	present	present	absent	present
cilia	absent	present	absent	present	present
axial body	5 - 9 µm	0.8 - 1.6 µm	0.3 - 1.5 µm	3 - 4 µm	2.5 - 4 µm
conidial shape and size	filiform 10 - 19 x 0.5 - 2 µm	oblong citriform 5 - 7.5 x 1 - 1.5 µm	bifusiform c. 6 x 1 µm	bifusiform c. 5 x 1 µm	bifusiform 4 - 5 x 1 - 1.5 µm
cortical substances	usnic acid	—	usnic acid	atranorin	usnic acid
medullary substances except fatty acids	fumarprotocetraric and secalonic acid	fumarprotocetraric acid	endocrocin and parietin	alectoronic, collatolic, olivetoric, or physodic acid	alectoronic, collatolic, and physodic acid

* The genus *Tuckermannopsis* is still not clearly delimited; *T. americana, T. chlorophylla, T. ciliaris,* and *T. platyphylla* are studied here

The closest relatives are presumably to be looked for among the aggregate of cetrarioid genera which is presently recognized. Some characters, however, seem to be isolated such as the very broad axial body and the long filiform to slightly sublageniform pycnoconidia (tab. 1). Furthermore there is no ring structure in the tholus, which is otherwise characteristic of the genera *Arctocetraria, Cetraria, Flavocetraria,* and partly *Nephromopsis.* The fatty acids lichesterinic and protolichesterinic acids are in common with *Cetraria, Flavocetraria,* and *Nephromopsis.* In *Nephromopsis* in addition both usnic and secalonic acids occur

A majority of the species included in the genus occur at rather high altitudes, preferably above 3000 m, in mountainous areas in South-east Asia. They have been collected in India, Nepal, China, Mongolia, and Taiwan, but most frequently in the Himalayas. One species, however, *Allocetraria oakesiana* is distributed in montane forests in North America and Europe. The species can be both corticolous and terricolous.

Key to the Species

1a. Thallus sorediate or isidiate 2
1b. Thallus not sorediate or isidiatte 3
2a. Marginal soredia always present ..... *A. oakesiana*
2b. Sparse isidia present ..... *A. isidiigera*
3a. Lobes occasionally more or less radial symmetric..... *A. stracheyi*
3b. Lobes distinctly dorsiventral 4
4a. Lobes more or less convex on the upper side 5
4b. Lobes plane or concave on the upper side 7
5a. Lobes apically indented ..... *A. denticulata*
5b. Lobes not apically indented 7
6a. Lower surface pale yellow to brown, concave; medulla white or coloured, Pd- . .....*A. stracheyi*
6b. Lower surface dark brown to black, plane to slightly convex; medulla always white, Pd+ (orange) ..... *A. flavonigrescens*
7a. Epiphytic; upper surface from pale yellow to brown, lobes slightly concave; medulla white or coloured ..... *A. globulans*
7b. Always on soil; upper surface pale yellow, lobes plain or concave; medulla always white 8
8a. Lower surface brown, with marginal pseudocyphellae in the form of white lines ..... *A. sinensis*
8b. Lower surface pale yellow, without marginal white lines; lobes comparatively wide and distinctly concave ..... *A. ambigua*

1. *Allocetraria ambigua* (BAB.) KUROK. et LAI

Bull. nat. Sci. Mus. Tokyo, Ser. B, **17**: 60; 1991. Bas. *Cetraria ambigua* BAB., HOOKERS J. Bot. **4**: 244; 1852. Type: Bompras, Garhwal, Himalaya, on wood and mosses, alt. 16 000 ft., R. STRACHEY and E. WINTERBOTTOM 6 (lectotype, BM); seen. The type material of *Allocetraria ambigua* also contains a small branch of *Allocetraria stracheyi*.

Thallus suberect to erect foliose, forming 2 - 3 cm high tussocks, upper surface pale yellow, smooth, lower surface pale yellow, smooth or slightly rugose, with sparse concolorous rhizines; lobes comparatively wide (up to 3 mm), lobe margins and tips concave; pseudocyphellae marginal; upper and lower cortex ca.

30 µm, composed of 4 - 6 layers of cells, smaller near the surface; medulla always white, 120 - 160 µm. Apothecia rare, marginal, with brown disc, up to 5 mm in diameter; exciple 30 - 35 µm thick; ascospores broadly ellipsoid, 7 - 8 x ca. 5 µm; pycnidia marginal to submarginal, immersed or on emergent projections, dark pigmented; pycnoconidia 12 - 14 x 0.5 - 2 µm. Chemical substances: usnic acid (+/-) in the cortex; fatty acids (lichesterinic and protolichesterinic) in the medulla; secalonic acid A and/or C may also be present.

Allocetraria ambigua is easily recognized on the broad with rather narrow, concave apices (fig. 1). Morphologically it is sometimes very similar to *Flavocetraria nivalis*, and these two species sometimes also grow together. The species is endemic to the Himalaya.

Specimens examined: India. Bompras, Garhwal, Himalaya, alt. 16000 ft., STRACHEY and WINTERBOTTOM, no. 6 (BM, lectotype). China. South-eastern Kansu, Min Shan range, S from Bashi-Denga, Tebbu, HUMMEL, 1930, no. 14 190 (S). Prov. Shaanxi, Mt. Taibai, Baxiantai, alt. 3550 m, GAO, 13.07.1988, no. 3184 (LD). Qinghai, Central Tibet, North-central Tangula Shan, SE of Geladandong Glacier, 33° 27' N, 91° 13' E, alt. 5360 m, DICKORE, 31.08.1989, no. L-07 (GZU). Tibet, KOMARKOVA, no. 32, no. 369 (GZU). Nepal. Khumbakarna-Himal, Dhankuta, Barun Valley, alt. 5000 m, WRABER, 10.1972 (GZU).

Fig. 1: The typically concave thallus of *Allocetraria ambigua*, China, Shaanxi, Mt. Taibai, Baxiantai, on ground, 3650 m, GAO 13.07.1988 (LD). Bar = 1 mm

2. *Allocetraria denticulata* (HUE) THELL et RANDL. comb. nov.

Bas.: *Cetraria denticulata* HUE, Nouv. Arch. Mus. (Paris), **I, 4**: 85; 1899. Type: China, Yunnan, Yen-tze-hay, on ground, R. P. DELAVAY 08.08.1888 - not available at PC.

Thallus greenish-yellowish, foliose, erect, 2 - 3 cm long, flattened at the bases and caespitose; lobes 0.8 - 1.5 mm broad, apically indented and with marginal projections along the margins; marginal projections at their tops either whitish or bearing pycnidia or small spines; upper surface smooth, plane or somewhat convex; lower surface similar to the upper or slightly brownish and somewhat concave; upper cortex presumably palisade plectenchymatous, 25 - 60 µm, richly incrusted with crystals; lower cortex similar to the upper but more white, with fewer cells and crystals not as frequent; algal cells 5 - 6 µm broad, in clusters; medulla 25 - 60 µm thick with 3.5 - 5.5 µm broad hyphae. Apothecia unknown; pycnidia on marginal emergent projections, small, black; conidiophores 2 - 3 celled; pycnoconidia filiform of somewhat different appearances, 12 - 15 x 1 µm. Chemical compounds: unknown, but obviously usnic acid in the cortex.

The value of this taxon is still uncertain simply because it is known only from the type locality. *Cetraria denticulata* was described from China by HUE (1899) and probably forgotten later, mentioned again only by WEI (1991). Unfortunately, we have not been able to see any material of this taxon. However, according to the detailed Latin diagnosis HUEs species should definitely be included in the genus *Allocetraria*. The species is according to the description well separated from other taxa according to the indented lobe tips, the special appearance of the marginal projections and the thick upper cortex. We have asked for type material of *Cetrara denticulata* at PC, but without any result.

3. *Allocetraria flavonigrescens* THELL et RANDL. sp. nov.

Type: Nepal, Langtang, Pemdang Karpo, SW exposed rocks, on *Juniperus*, 29.09.1986. G. MIEHE and S. MIEHE 13 056 (GZU); selected here.

Thallus subfruticosus ad foliosus, suberectus ad prostratus, irregulariter ramosus, usque 4 cm longus, lobi concavi 1 - 3 mm lati, facies supera pallide lutea, infera fusca ad nigra valde rugosa, rhizinae et pseudocyphellae desunt; apothecia non visa; pycnidia marginalia ad laminalia immersa vel in prominentiis brevibus, pycnoconidia non visa.

Thallus subfruticose to foliose, suberect to prostrate, up to 4 cm, irregularly branched; lobes narrow, convex, 1 - 3 mm broad, thick; upper surface pale yellow with black spots, lower surface brown to black, strongly wrinkled; rhizines and pseudocyphellae absent; upper cortex ca. 30 µm, composed of 4 - 6 layers of cells, smaller near the surface; medulla white, 170 - 280 µm; lower cortex 15 - 20 µm, composed of 3 - 4 layers of equal sized cells, the outer cell-layer entirely black. Apothecia not seen; pycnidia marginal to laminal, immersed or on short projections, dark pigmented; pycnoconidia not seen. Chemical substances: usnic acid in the cortex, one unknown fatty acid and fumarprotocetraric acid in the medulla; an unknown violet pigment is also noticed.

Unfortunately we have not been able to detect either conidia nor ascospores in this species. However, the structural characters in the thallus and especially the cortical hyphal cells support that the new species should be accommodated here rather than in any other cetrarioid genus within the Parmeliaceae. The dark rugose lower surface and the black spotted upper side are the most characteristic and diagnostic features for *Allocetraria flavonigrescens* (fig. 2). *A. flavonigrescens* grows on the ground in the alpine tundra above 3000 m, occasionally at the base of shrubs. It is distributed in Nepal.

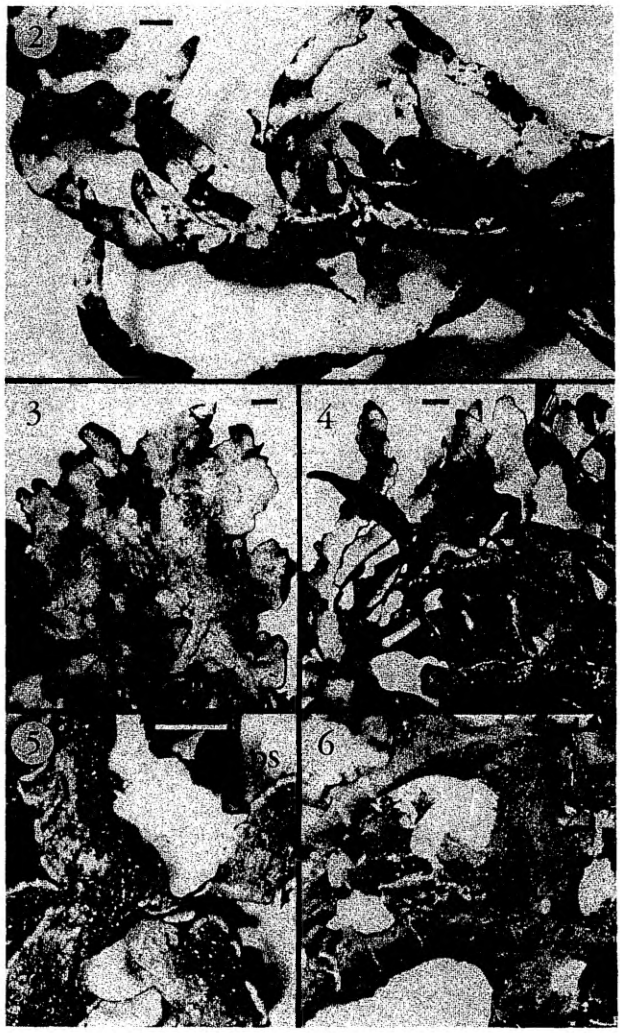
Specimens examined: Nepal. Langtang area, Pemdang Karpo, alt. 4620 m, G. MIEHE and S. MIEHE, 29.09.1986, no. 13 056 (GZU - holotype). Himalaya, Khombu Glacier, alt. 16000 ft. above tree line, IZZARD, 1954 (UPS).

4. *Allocetraria globulans* (NYL.) THELL et RANDL. comb. nov.

Bas.: *Platysma globulans* NYL., Flora (Regensburg) **70**: 134; 1887. Syn.: *Cetraria globulans* (NYL.) ZAHLBR., Trav. Sous-sect. Troitzkossawsk-Khiakta, Sect. Pays d'Amour Soc. Imp. russe Geogr. **12**: 89; 1911. *Nephromopsis globulans* (NYL.) LAI, Quart. J. Taiwan Mus. **13**: 222; 1980. Type: China, Yunnan, R. P. DELAVAY, 1885, no. 1570 (holotype, H-NYL 36 135); seen.

Thallus foliose; upper surface yellowish (from light yellow to almost brown), lower surface brown, with sparse concolorous rhizines; lobes plane to concave, prolonged, up to 8 mm wide, dichotomously branched, secondary lobes usually quite narrow, about 1 - 1.5 mm wide. Some pseudocyphellae-like structures may also be present on marginal warts. Upper cortex undistinctly palisade plectenchymatous, strongly crystallized, 15 - 30 µm, composed of 3 - 4 layers of equal-sized cells. Lower cortex similar to the upper but somewhat thinner and less crystal-

lized, the lower cells brown-pigmented. Medulla light yellow but specimens with white medulla also occur, and sometimes the yellowish layer is seen on the lower parts of the thallus only. Apothecia marginal and submarginal, up to 8 mm in diameter, with a brown disc. Exciple 40 - 120 µm thick, asci narrowly to rather



Figs. 2 - 6: Morphology in *Allocetraria*. (**2**) *A. flavonigrescens*, habit, showing the light, black spotted upper surface and the dark, strongly wrinkled lower surface, Nepal, Langtang, Pemdang Karpo, SW-exposed rocks, on *Juniperus*, 29.09.1986, G. MIEHE and S. MIEHE 13 056 (GZU). (**3**) Part of the type material of *A. globulans*, China, Yunnan, DELAVAY 1570, holotype (H-NYL 36 135). (**4**) *A. sinensis*, China, Shaanxi, Mt. Taibai, Baxiantai, on ground, 3650 m, 13.07.1988, GAO 3159 isotype (LD). (**5**) Detail structures of the same specimen showing the dark brown underside with pseudocyphellae (ps) along the margin. (**6**) *A. stracheyi* with typically convex lobes, India, Kumaon, Gori River, among mosses and dead leaves, alt. 4700 ft. (?), R. STRACHEY and J. E. WINTERBOTTOM, lectotype (H-NYL 36 055). Bar = 1 mm

broadly clavate, 45 - 70 x 15 - 20 µm, tholus small, axial body very broad, 5 - 9 µm, ascospores globose, 7 - 10 µm in diameter or subglobose, 6.5 - 9 x 5 - 6.5 µm; pycnidia numerous marginally and a few laminally, located on black and somewhat emergent projections which often grow out from special warts of the thallus; pycnoconidia 10 - 19 x 0.5 - 2 µm. Chemical constituents: usnic acid in the cortex; lichesterinic, protolichesterinic, and secalonic acids A and C (+/-) in the medulla.

Allocetraria globulans is sometimes difficult to separate from *A. stracheyi* but the upper surface of the latter is always pale yellow and the lobes more or less convex (fig. 6). Some specimens of *A. globulans* are rather broad-lobated (fig. 3). The structure of the ascus top and the pycnoconidial shape remove all doubts about the systematic position of the species (figs. 9 - 10). This epiphytic species is distributed in China (Yunnan County), Nepal (Langtang area and Topkegola). It grows on *Potentilla fruticosa, Rhododendron* sp., etc. in high altitudes, 3200 - 4700 m.

Specimen examined: China. Yunnan, Delavay, 1885, no. 1570 (H-NYL 36 135, holotype; H-NYL 36 136, H-NYL 36 137). Nepal. Langtang area, Chisedang Lekh, above Palpa, alt. 3700 - 3900 m, POELT, 07.09.1986, no. 86-1195 (GZU). Langtang area, above Langshisa Karka, Shalbachun Glacier, alt. 4500 m, POELT, 16.09.1986, no. 86-2342 (GZU). Langtang area, Dupka, alt. 4000 m, G. MIEHE and S. MIEHE, 30.07.1986, no. 7307a (GZU). Langtang area, Upper Langtang, Yala, alt. 4790 m, G. MIEHE and S. MIEHE, 10.07.1986, no. 5005 (GZU); alt. 4830 m, G. MIEHE and S. MIEHE, 02.07.1986, no. 4403 (GZU). Langtang area, Skidscha Kunda, alt. 4670 m, G. MIEHE and S. MIEHE, 11.08.1986, no. 8590 (GZU); alt. 4370 m, G. MIEHE and S. MIEHE, 11.08.1986, no. 8693 (GZU). Langtang area, Pemdang Karpo, alt. 4880 m, G. MIEHE and S. MIEHE, 05.10.1986, no. 13 482d (GZU). Eastern Nepal, Topkegola, between Rupa and Saju Pokhari, alt. 15000 ft., Awasthi, 30.05.1953, no. 2407 (UPS).

5. *Allocetraria isidiigera* KUROK. et LAI

Bull. nat. Sci. Mus. Tokyo, Ser. **B, 17**: 62; 1991. Type: China, Xisang (Tibet), Nylalam, on *Rhododendron* stem, alt. 3910 m, J.-C. WEI and J.-B. CHEN, no. 1857 (holotype HMAS, isotype TNS).

This species is distinguished from *Allocetraria stracheyi* by the presence of sparse isidia (KUROKAWA and LAI 1991). We have not been able to get any material of this rare lichen, known only from the type locality.

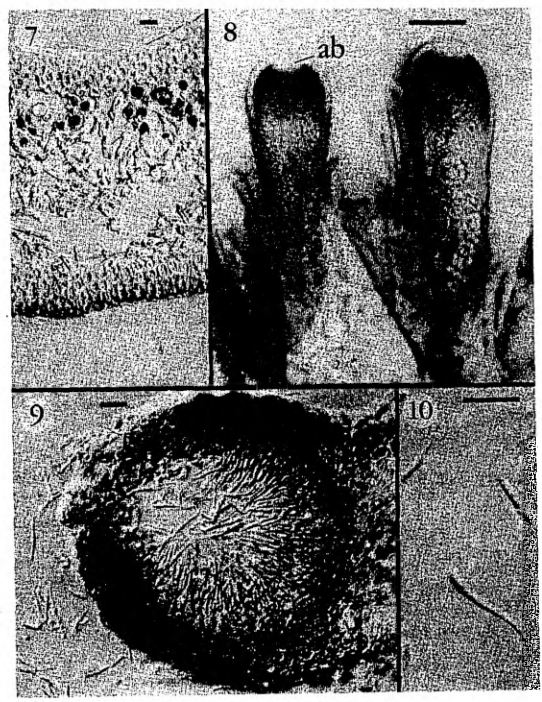
6. *Allocetraria oakesiana* (TUCK.) RANDL. et THELL comb. nov.

Bas.: *Cetraria oakesiana* TUCK., Boston J. nat. Hist. **3**: 445; 1841. Syn.: *Platysma oakesianum* (TUCK.) NYL., Mem. Soc. imp. Sci. nat. Cherbourg **3**: 172; 1855. *Tuckermannopsis oakesiana* (TUCK.) HALE in EGAN, Bryologist **90**: 164; 1987. Type: White Mountains, alpine regions, on small branches of dwarf firs, OAKES, 25.06.1839 (FH, lectotype); seen. *Cetraria oakesiana* TUCK. var. *spinulosa* MERRILL, Bryologist **13**: 25; 1910. *Cetraria bavarica* TUCK. KREMPELH., Flora **34**: 273; 1851. Type: Germany, Oberbayern, KREMPELHUBER, 06.1851 (isolectotype, UPS); seen.

Thallus foliose to subfoliose, upper surface greenish yellow, lower surface brown to light tan, somewhat wrinkled, with sparse rhizines; lobes concave, moderately broad, ca. 1 - 4 mm wide, weakly wrinkled, usually with abundant marginal soralia, soredia light yellow; rhizines and pseudocyphellae absent; upper and lower cortex paraplectenchymatous but the hyphae are sometimes anticlinally arranged. Both cortical layers ca. 20 µm, composed of ca. 3 rather gelatinized cell layers each; cells near the surface somewhat smaller than other cells. Medulla in many specimens yellowish in lower parts. Apothecia lateral, marginal to laminal, up to 6 mm in diameter, with brown disc and a thin thalline margin which may turn sorediate; exciple ca. 80 µm thick; asci narrowly clavate to cylindrical 30 - 40 x 7 - 12 µm, tholus small, ocular chamber cylindrical and broad, axial body broad, 6 - 7 µm, ascospores globose, ca. 5 x 5 µm; pycnidia marginal, immersed to raised (globose or spinulose; the latter type of variation has been described by MERRILL as var. *spinulosa*), pigmented or non-pigmented, sometimes with cortical tissue beneath, pycnoconidia 11 x 12 x ca. 1 µm. Chemical compounds: usnic acid in the cortex; caperatic, lichesterinic, protolichesterinic, and secalonic acids in the medulla. The two unidentified fatty acids reported by (DEY 1978) are obviously lichesterinic and protolichesterinic acids.

This species has since long been treated as a member of the genus *Cetraria*. However, detailed investigations of the reproductive structures clearly revealed that this species is better accommodated in the genus *Allocetraria*. Earlier *Allocetraria oakesiana* was usually also considered as a closely allied species to *Tuckneraria laureri*, due to the similar thallus colour and the sorediate margins. Later studies demonstrated that although the spores are subglobose in both taxa, the pycnoconidia are totally different, i. e., bifusiform in *T. laureri* and, in addition, there are several minor morophological and chemical differences (RANDLANE et al. 1994).

A relationship between *Allocetraria oakesiana* and *Tuckermannopsis chlorophylla* has also been presumed earlier by KÄRNEFELT et al. (1992). The investigations of the reproductive structures again clearly demonstrated that these two species are not closely allied. *A. oakesiana* differs in having a much broadar axial body (fig. 8), filiform conidia and presence of usnic acid, and seems in these important aspects to be a good member of *Allocetraria*. The cortex in *A. oakesiana* is not typically palisade plectenchymatous, like it is in most species within the genus. However, in many taxa the structure of the cortex seems to be variable and represents an uncertain character (KÄRNEFELT et al. 1992, 1993, RANDLANE and SAAG 1992, MATTSSON and LAI 1993, MATTSSON 1993). *Allocetraria oakesiana* differs from the other species included in the genus in being distributed also outside South-east Asia. It is present in China (WEI 1991), but also in North America (Canada, USA) and Europe (Austria, Germany, Italy, Slovakia, Russia, Ukraine). It grows on coniferous and deciduous trees in montane forests.



Figs. 7 - 10: Anatomy in *Allocetraria*. (**7**) Upper cortex of *A. sinensis*. Note the typically anticlinally arranged hyphae, most typical in the lower cortex (arrows indicating), Nepal, 02.07.1986, MIEHE 4403 (GZU). (**8**) Asci of *A. oakesiana*, showing very broad axial bodies (ab), USA, TUCKERMANN. (**9**) Pycnidium and pycnoconidia of *A. globulans*, Nepal, 02.07.1986, MIEHE 4403 (GZU). (**10**) Pycnoconidia of *A. globulans*, the same specimen

Selected specimens (74 specimens from Europae and North America examined): Austria. Steiermark, St. Radegrund, Graz, HOLZINGER, 1874 (LD). Untersteiermark, VRANG, 1986 (S). Salzburg, alt. 1040 - 1080 m, HERTEL, 17.07.1978, Lich. Alp. no. 317 (LD, S). Germany. Ostbayern, KREMPELHUBER, 06.1851 (UPS, isolectotype). Bavaria, Alpen, ARNOLD, 1893 (LD). Wendelstein, Nuremberg, JAMES, 07.06.1956 (LD). Ammergauer Alpen, Schwaben, Fleckenau, FÖRSTER and SCHRÖPPEL, 1960, Lich. Alp. no. 195 (LD, S). Italia. Südtirol, Predazzo, ARNOLD, 14.08.1879 (LD, S). Prov. d'Udine, Passo del Pura, alt. 1020 m, CLERC, 05.07.1982, no. 8608 - 8610 (UPS). Slovakia. Slovakia boreo-orient., Nizke Poloniny, Montis Hrubky, alt. 1180 m, PISUT, 06.09.1964, Lich. Slov. Exs. no. 68 (LD). Ukraine. Carpati Poloniny, Montis Pop Ivan, alt. 1300 - 1400 m, SUZA, 1928, Lich. Bohemoslovak. no. 87 (LD, S, TU). Canada. Algoma Distr., Lake Superior Provinical Park, 47° 40' N, 84° 50' W, BRODO, 07.09.1965, no. 7063 (LD). Ontario, Algoma Distr., MacGregor Lake, 47° 17' N, 84° 35' W, alt. 1000 ft., BRODO, 09.09.1969, Lich. Canad. Exs. no. 97 (LD, TU). USA. White Mountains, alpine regions, OAKES, 25.06.1839 (FH, lectotype). New York, St. Lawrence Co., Star Lake, KÄRNEFELT, 05.09.1981, no. 81-65-20 (LD). West Virginia, Randolph County, Cheat Bridge, HALE, 05.1956, Lich: Am. Exs. no. 64 (LD, S).

7. *Allocetraria sinensis* GAO sp. nov.

Type: China. Shaanxi, Mount Taibai, alt. 3400 m, on ground, GAO 3052 (holotype HMAS, isotypes UPS, LD).

Thallus erectus, foliosus, leviter adnatus, lobi concavi 1 - 3 mm lati, facies supera laevis nitidula viridi-lutea ad lutea, margine fusca ad nigra, facies infera fusca sat laevis et nitida, pseudocyphellae lineam secus marginem formantes; apothecia non visa; pycnidia marginalia, leviter prominentia, pycnoconidia filiformia, 12 - 16 µm longa.

Thallus erect, foliose, 2 - 3 cm high, loosely attached to the substrate, forming tussocks, more or less dichotomously branched; lobes concave, 1 - 3 mm broad; upper surface greenish yellow to yellow, brown to black on the margin, smooth, slightly shiny; lower surface brown, rather smooth and shiny; pseudocyphellae marginal, forming a white, continuous line; projections present, short; epicortex 3 - 4 µm, non-cellular; upper cortex 28 - 30 µm, composed of 1 - 2 layers of more dark-stained and small cells in outer part, 2 - 3 layers of less stained and large cells in inner part; lower cortex 17 - 23 µm, 2 - 3 layers of cells in inner part; not double-structured, lowermost part pigmented; medulla 85 - 100 µm. Apothecia not seen; pycnidia marginal, somewhat raised; pycnoconidia 12 - 16 µm long.

Chemical compounds: usnic acid in the cortex; lichesterinic, protolichesterinic, and an unidentified fatty acid in the medulla.

Allocetraria sinensis differs basically from *A. ambigua* and *A. stracheyi* by a dark brown underside with pseudecyphellae forming a white line along the margin (fig. 4 - 5). This species grows on the ground among mosses in the alpine tundra above 3000 m. It is found only in South-west China.

Specimens examined: China. Prov. Shaanxi, Mount Taibai, alt. 3400 m, GAO, no. 3052 (UPS, LD, isotypes); alt. 3550 m, GAO, 13.07.1988, no. 3184 (LD); alt. 3650 m, GAO, 13.07.1988, no. 3159 (LD). Nepal. Langtang area, above Yala, alt. 4830 m, G. MIEHE and S. MIEHE, 05.07.1986 (GZU).

8. *Allocetraria stracheyi* (BAB.) KUROK. et LAI

Bull. nat. Sci. Mus. Tokyo, Ser. B., **17**: 62 - 63; 1991. Bas.: *Evernia stracheyi* BAB., HOOKERS, J. Bot. **4**: 244; 1852. Type: India, Kumaon, Gori River, among mosses and dead leaves, alt. 4700 ft. (?), R. STRACHEY and J. E. WINTERBOTTOM (lectotype H-NYL 36 055, isolectotype BM); seen. *Platysma everniellum* NYL., Mem. Soc. Sci. nat. Cherbourg **5**: 100; 1857 (based on *Evernia stracheyi* BAB.). *Cetraria everniella* (NYL.) KREMPELH., Verhandl. zool.-bot. Ges. Wien **18**: 315; 1868. *Cetraria potaninii* OXN., J. Cycle Bot. Acad. Sci. Ukraine **7 - 8**: 168; 1933. Type: China, Tibet, Montes Kamenses, inter stats. Tasso et Penczamu, Tassaschanj, POTANIN, 31.05.1893 (KW, holotype); seen. *Allocetraria potaninii* (OXN.) RANDL. et SAAG, Mycotaxon **44**: 492; 1992.

Thallus prostrate to suberect foliose, up to 5 cm, upper surface pale yellow, smooth, lower surface pale yellow to brown, wrinkled, with sparse marginal rhizines; lobes convex, comparatively thick; upper and lower cortex ca. 30 µm, composed of 3 - 5 layers of cells, smaller cells near the surface; medulla white to orange, 200 - 230 µm thick. Apothecia rare, marginal, with brown disc, up to 5 mm in diameter, mature asci not found; pycnidia marginal, immersed or on emergent projections, dark pigmented; pycnoconidia 12 - 14 x 0.5 - 2 µm. Chemical substances: usnic acid in the cortex; fatty acids (lichesterinic and protolichesterinic) and secalonic acids (A and C) together with other related pigments (e. g., endocrocin) in the medulla.

This species has mainly been known under the name of *Cetraria everniella* (NYL.) KREMPELH. However, KUROKAWA and LAI (1991) cleared out the nomen-

clatural and consequently taxonomical misinterpretation of this name. The taxon was described originally as *Evernia stracheyi* by BABINGTON (1852) on the basis of material collected in the Himalayas. When it was transferred to *Platysma*, NYLANDER (1857) gave it a new name *Platysma everniellum*, because of an older homonym, *Platysma stracheyi* (BAB.) NYL. (= *Nephromopsis stracheyi* [BAB.] MUELL.-ARG.; see further discussion in KUROKAWA and LAI 1991).

Allocetraria stracheyi is similar to *A. ambigua* but differs in having more narrow, plane or convex lobes with a wrinkled lower surface (fig. 6). A further specific name described by OXNER (1933), *Cetraria potaninii*, was based on material from Tibet. He indicated that the type was preserved in Leningrad (LE). It was therefore feared that the type material was destroyed during World War II, but fortunately it was still present in Kiev (KW) and kindly sent to us. After having studied the material, we could only conclude this species being synonymous with *A. stracheyi* (BAB.) KUROK. et LAI. *A. stracheyi* has a rather wide distribution. It is terricolous in the alpine tundra (above 3000 m) in India, Nepal, China, Taiwan, and Mongolia.

Selected specimens (49 specimens examined): India. Himalaya, Gori River, Kumaon, alt. 4700 ft. (?), STRACHEY and WINTERBOTTOM (H-NYL 36 055, lectotype). Himalaya, Kumaon, Almora Distr., Phurkia-Pinderi Glacier, alt. 11500 ft., D. D. AWASTHI and A. M. AWASTHI, 23.05.1950, no. 781 (H, UPS). Nepal. Langtang area, from Kyangjin to Nubama Dhang, alt. 3750 - 3900 m, POELT, 11.09.1986, no. 86-1329 (GZU). Eastern Nepal. Topkegola, Thagalabhanjyang, alt. 14000 ft., D. D. AWASTHI, 29.05.1953, no. 2350 (UPS). Langtang area, Niang Tscha, alt. 4800 m, G. MIEHE and S. MIEHE, 12.10.1986, no. 13 962 (GZU). Langtang area, Yala, alt. 4830 m, G. MIEHE and S. MIEHE, 05.07.1986, no. 4603a (GZU). Langtang area, Donga, Tangsep, alt. 4730 m, G. MIEHE and S. MIEHE, 04.09.1986, no. 10 683 (GZU). Langtang area, above Pemdang Karpo, alt. 4640 m, G. MIEHE and S. MIEHE, 30.09.1986, no. 13 075 b. Upper Langtang, Kangsa, alt. 4300 m, G. MIEHE and S. MIEHE, 19.09.1986, no. 12 187 (GZU). Upper Langtang, Pemdang Karpo, alt. 4880 m, G. MIEHE and S. MIEHE, 26.09.1986, no. 12 901 (GZU). 33 km NW Pokhara, Machhapuchhare basecamp, 28° 30' N, 83° 52' E, alt. 3965 m, THOR, 27.11.1979, no. 1415 (S). China. Tibet, inter stat. Tasso et Penczamu, Tassa-schanj, POTANIN, 31.05.1893 (KW, holotype of *Cetraria potaninii*). Sikang, Taofu Distr., Taining (Ngata), alt. 4500 - 4600 m, SMITH, 07.09.1934, no. 14 032 (UPS). Mongolia. Bayan-Khongor region, Gurvan-Bulak Distr., Lake Khuh-nur, alt. 2600 m, BIAZROV, 18.08.1972, no. 700 (LD). Hangai, GOLUBKOVA (LE).

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VIII

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A Revision of the North American Lichen Genus *Ahtiana* (Parmeliaceae)

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Abstract. *The formerly monotypic genus* Ahtiana *(type species:* A. sphaerosporella *(Müll. Arg.) Goward is shown to include two additional species,* A. aurescens *(Tuck.) Thell & Randl. and* A. pallidula *(Riddle) Goward & Thell. All three species are endemic to North America, and are characterized by their greenish yellow upper surface, globose ascospores, and caperatic acid in the medulla. The habitat ecology of these lichens is very specialized.* Ahtiana *is presumably most closely related to* Tuckneraria *Randl. & Thell and other cetrarioid genera having globose ascospores.*

Goward (1985) originally segregated *Ahtiana sphaerosporella* from Parmelia s. lat. on the basis of the former's emergent pycnidia, globose ascospores, leptodermatous cortex, and presence of medullary caperatic acid. Despite its parmelioid habit with laminal apothecia and pycnidia, *Ahtiana sphaerosporella* was shown to be closely allied to *Cetraria pallidula* Riddle (Goward 1985). More recent studies on the morphology and anatomy of cetrarioid lichens, carried out in Lund and Tartu, clearly demonstrate that both *Cetraria pallidula* and *Cetraria aurescens* Tuck. should be placed in *Ahtiana.* The new combinations, *Ahtiana aurescens* (Tuck.) Thell & Randlane and *Ahtiana pallidula* (Riddle) Goward & Thell, are therefore presented here. As thus defined, *Ahtiana* is a morphologically well delimited group related to other cetrarioid genera having globose or subglobose ascospores, i.e., *Allocetraria* Kurok. & Lai, *Esslingeriana* Hale & Lai, *Tuckermannopsis* Gyelnik, and *Tuckneraria* Randlane & Thell (Table 1). Kärnefelt et al. (1992) showed by means of cladistic analysis that these five genera form a monophyletic group within the Parmeliaceae. *Esslingeriana, Tuckneraria,* and *Allocetraria* have already been examined by Esslinger (1971), Lai (1980), Randlane et al. (1994), Kurokawa and Lai (1991), and Thell et al. (1995*a,c*). However, the largest genus in the group, *Tuckermannopsis,* still requires critical examination (Kärnefelt et al. 1992, 1993).

MATERIAL AND METHODS

About 70 specimens have been consulted for this study from: ASU, B, BM, BRY, CANL, COLO, DUKE, FH, GZU, H, LD, MINN, NY, SFSU, UAC, UBC, UC, US, and WIS.

For anatomical observations, the lichens were sectioned with a Leica Cryostat 1800 Cryocut freezing microtome and stained in lactophenol cotton-blue. The asci were squashed in a 0.3% Lugol's solution after pretreatment with a 10% KOH solution. The secondary chemistry was investigated on HPTLC plates using standardized TLC methods (Culberson 1972).

RESULTS

AHTIANA Goward, THE BRYOLOGIST 88: 370. 1985.

TYPE SPECIES: *Ahtiana sphaerosporella* (Müll. Arg.) Goward

Thallus foliose, more or less closely appressed, up to 8 cm across; upper surface pale-yellow to pale yellow-green, wrinkled; lower surface usually light tan; pseudocyphellae absent; isidia and cilia present in one species; pycnidia laminal or marginal, black, conspicuous, usually abundant, up to 0.2 mm across; upper cortex paraplectenchymatous with crystals of usnic acid, 15–25 μm thick, composed of ca. 3 cell

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TABLE 1. Comparison of *Ahtiana* with other cetrarioid genera having globose or subglobose ascospores. The genus *Tuckermannopsis* is still not clearly delimited; results in this table are based on *T. americana, T. chlorophylla, T. ciliaris,* and *T. orbata.*

Species	*Ahtiana*	*Allocetraria*	*Esslingeriana*	*Tuckermannopsis*	*Tuckneraria*
Upper surface	yellow	yellow	grey	brown	yellow to greenish
Lower surface	tan or yellow	brown or yellow	black	light brown to blackish	whitish, light to dark brown or black
Pseudocyphellae	absent	present	absent	absent	present
Isidia	absent or sparse	absent	absent	absent	sparse
Cilia	absent or sparse	absent	absent	present or absent	present
Apothecial position	marginal to laminal	marginal	marginal to laminal	mostly marginal	marginal
Pycnidial position	laminal	marginal	mostly laminal	marginal	mostly marginal
Conidial shape and size	usually bifusiform, 5–7 × 1 μm	filiform, 10–19 × 0.5–2 μm	bifusiform, 5–7 × 1 μm	bifusiform, ca. 5 × 1 μm	bifusiform, 4–5 × 1–1.5 μm
Cortical substances	usnic acid	usnic acid	atranorin	atranorin	usnic acid
Medullary substances					
a) fatty acids	caperatic, lichesterinic, and protolichesterinic acids	lichesterinic and protolichesterinic acids	one unidentified fatty acid	lichesterinic and protolichesterinic acids	lichesterinic and protolichesterinic type fatty acids
b) anthraquinones	—	secalonic acid	endocrocin	—	—
c) orcinol & β-orcinol depsides & depsidones	— —	fumarprotocetraric acid in one species	— —	alectoronic, collatolic, olivetoric or physodic acids	alectoronic, collatolic and physodic acids
Distribution and ecology	corticolous in eastern or western North America	corticolous or terricolous mainly in Southeast Asia	corticolous in western North America	corticolous in northern Eurasia and North America	corticolous mainly in Southeast Asia

TABLE 2. Comparison of the three species included in *Ahtiana*. Lobe width measured on the widest part of fully developed lobes.

Species	*A. aurescens*	*A. pallidula*	*A. sphaerosporella*
Color of upper surface	light yellow to pale greenish yellow	light yellow to pale greenish yellow	pale yellowish green, in part olivaceous
Color of lower surface	pale to light tan	light yellow	whitish to pale tan, in part olivaceous
Lobe width	0.5–2.0 (3.0) mm	4–10 mm	2–3 (4) mm
Rhizinae	often abundant	often abundant	often abundant
Structure of the cortex	pachydermatous paraplectenchyma	pachydermatous paraplectenchyma	leptodermatous paraplectenchyma
Isidia	absent or sparse to rather frequent on central lobes	absent	absent
Cilia	absent or sparse, dark or black	absent	absent
Apothecia	common, marginal mostly restricted to thallus center	less common, marginal to submarginal	common, laminal, mostly restricted to thallus center
Disc color	usually dark brown	always light brown	always light brown
Thalline margin	wrinkled	wrinkled	smooth
Pycnidia	common, marginal or laminal, usually somewhat raised	common, marginal or laminal, immersed	common, mainly laminal, immersed to raised
Distribution	eastern N. America	western N. America	western N. America
Ecology	corticolous, most common on *Thuja*	corticolous, most common on *Larix* or *Pseudotsuga*	corticolous, most common on *Pinus albicaulis* or *Abies*

layers, lower cortex also paraplectenchymatous, 15–20 μm thick, composed of 2–3 layers of somewhat brownish cells; medulla white, medullary hyphae 3–4 μm thick; algal cells up to 10 μm. Apothecia frequent, laminal or marginal, up to 13 mm across, disc brown, entire; hymenium including subhymenium 50–60 μm high; exciple 2–layered, upper layer 10–30 μm thick, composed of periclinally arranged hyphae, lower layer 35–50 μm thick, paraplectenchymatous; asci clavate, 45–60 μm high, axial body 2–5 μm; ascospores globose or subglobose, more or less uniseriately arranged, 8 per ascus, 4–6 × 4–6 μm; paraphyses straight, somewhat branched, with thickened apices; pycnoconidia usually bifusiform or occasionally bacillariform, citriform or sublageniform, 5–7(–9) × ca. 1 μm.

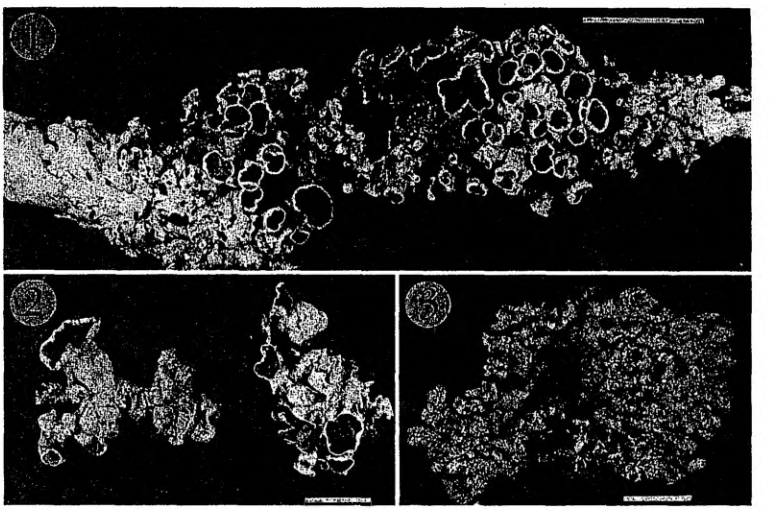
Chemical substances.—Usnic acid in the cortex; caperatic acid as major and lichesterinic-protolichesterinic type fatty acids as minor compounds in the medulla.

The three species included in *Ahtiana* are characterized mainly by their foliose habit, their more or less closely appressed, pale yellowish lobes, their lack of pseudocyphellae, and their narrowly clavate asci containing uniseriately arranged subglobose spores. The yellow-green colour of the lobes reflects the presence of usnic acid in the cortical layer. This substance also occurs in the related genera *Allocetraria* and *Tuckneraria,* in which the ascospores and ascus form are also similar. *Ahtiana*; however, differs from these and other cetrarioid genera in having caperatic acid instead of lichesterinic acid as a major medullary compound (Table 1), although it must be admitted that some species of *Allocetraria* and *Tuckneraria* contain caperatic acid as an accessory substance.

The genus *Allocetraria*; however, is easily distinguished from *Ahtiana* by the former's very broad axial body, filiform pycnoconidia, and palisade plectenchymatous cortex. Several cetrarioid species have recently been transferred to this genus, mainly distributed in eastern Asia (Thell et al. 1995*c*).

Presumably *Ahtiana* is most closely allied to *Tuckneraria,* also an essentially eastern Asian genus consisting of five corticolous species. However, in that genus pseudocyphellae are present on the lower surface (Randlane et al. 1994; Thell et al. 1995*a*), the lobe margins are frequently ciliate, and the apothecia are always marginal. Although these admittedly morphological points of distinction appear not to be supported by corresponding differences in apothecial structure or thallus chemistry, we prefer for the moment to maintain *Ahtiana* and *Tuckneraria* as separate genera; however, further studies are in progress. Points of separation with other related genera are summarized in Table 1.

The structure of the cortical hyphae is rather variable in *Ahtiana* (Table 2). All species have a paraplectenchymatous cortex, but the thickness of the walls in relation to the cell lumina differs between the species. In *A. pallidula* and especially *A. aures-*



FIGURES 1–3. Morphology of *Ahtiana.* — 1. *A. aurescens, Trana 8793* (MINN). — 2. *A. pallidula, Ryan 25308* (ASU). — 3. *A. sphaerosporella, Bird 14348* (WIS). (Bar in Figs. 1–3 = 1 cm).

cens, the walls are obviously thicker than the lumina, and may be termed pachydermatous (Frey 1936; Hale 1973). In *A. sphaerosporella,* by contrast the walls are thinner than the lumina, and may be referred to as leptodermatous (Goward 1985). An identical range of variation was observed in the lower excipular layer, with *A. aurescens* and *A. pallidula* having smaller lumina than *A. sphaerosporella.*

Ascus structures show almost no variation within *Ahtiana.* The asci are of the *Tuckermannopsis*-form, and are rather narrowly clavate with an amyloid tholus, a broad ocular chamber, and a broad axial body (Thell et al. 1995*b*). The ascus form also occurs in the related genera *Allocetraria, Esslingeriana, Tuckermannopsis,* and *Tuckneraria.* The ascospores are more or less uniseriately arranged in unsquashed asci. *Ahtiana* has typically dumbbell-shaped pycnoconidia, although slightly disc-bar-shaped ones, in which the ends are narrow and the thickenings subapical, are also present (Fig. 15). The range of variation is especially large in *A. pallidula* (see below). In *A. sphaerosporella,* the pycnoconidia may be as much as 9 μm long, although in the other species they are usually not longer than 7 μm. All species have a corticolous ecology and are apparently restricted to North America.

AHTIANA AURESCENS (Tuck.) Thell & Randlane *comb. nov.* (FIG. 1, 4–5)

Cetraria aurescens Tuck., Proc. Amer. Acad. Arts Sci. I: 208. 1847. TYPE: U.S.A., NEW HAMPSHIRE, White Mts., *Tuckerman,* 1848 (FH–Tuck)—Lectotype selected here.

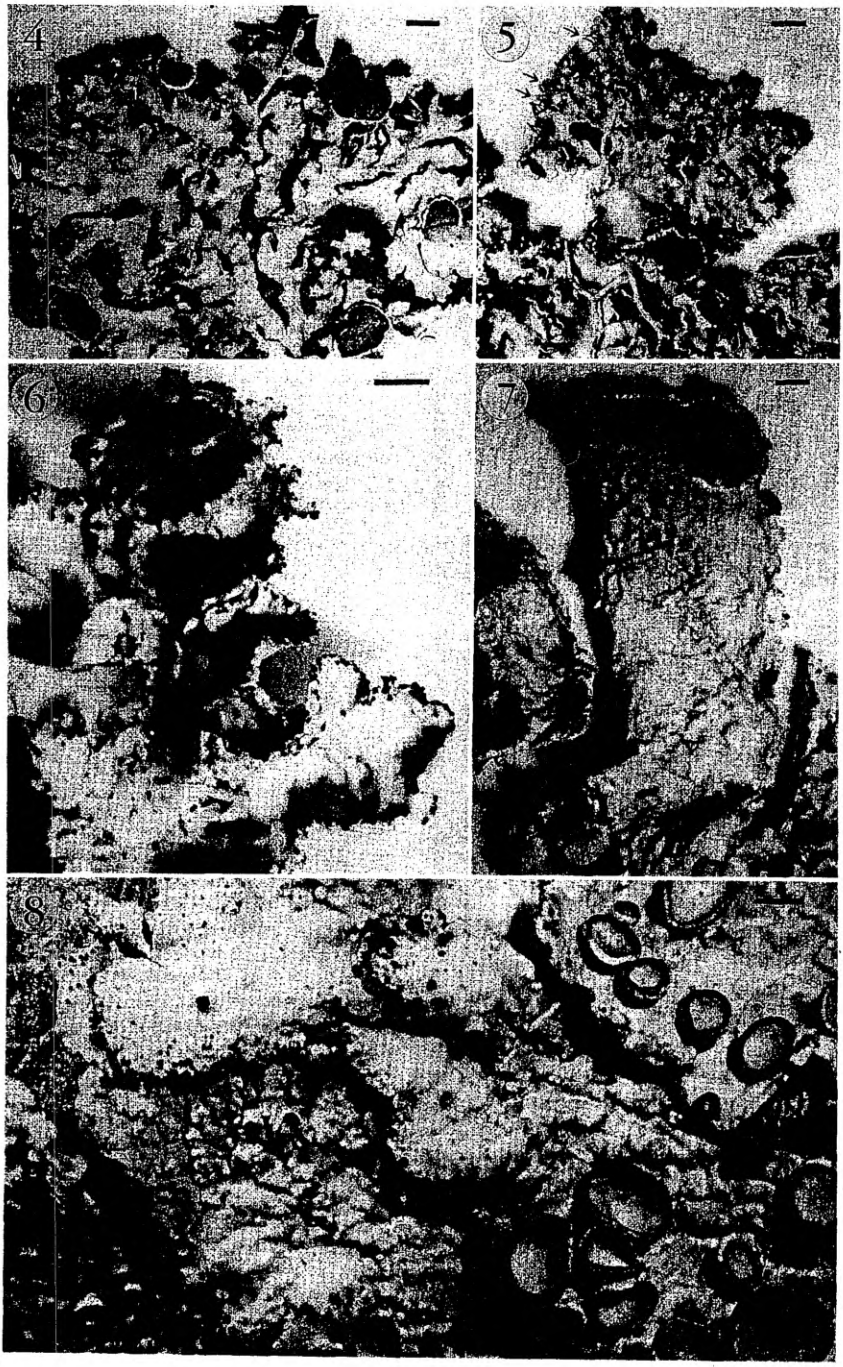
Platysma aurescens (Tuck.) Nyl., Synops. Lich. I: 313. 1860.

Tuckermannopsis aurescens (Tuck.) Hale, THE BRYOLOGIST 90: 164. 1987.

Thallus foliose, closely adnate, up to 6 cm across, surface smooth, lobes 0.5–2(–3) mm wide, often with somewhat indented but rounded tips, lobe margins slightly raised; upper surface pale yellow to pale greenish yellow, somewhat ridged; lower surface pale to light tan, strongly reticulate; isidia sparse to rather frequent in central parts of few specimens; cilia absent or sparse and black; rhizines abundant; pycnidia marginal or laminal, usually somewhat raised; upper and lower cortex composed of pachydermatous hyphae. Apothecia marginal, rarely submarginal, usually numerous, especially in central portions of thallus, up to 7 mm in diameter, thalline margin sometimes strongly wrinkled, disk usually dark brown; exciple 2-layered, upper layer composed of horizontally arranged hyphae, lower layer pachydermatous; asci narrowly clavate, 45–60 × 13–17 μm, axial body 2.0–3.5 μm; ascospores 4.0–5.5 × 4.0–5.5 μm in diameter; pycnoconidia bifusiform (dumbbell shaped), ca. 5 × 1 μm.

Chemical substances.—Usnic acid in the cortex; caperatic acid in the medulla. One unidentified fatty acid reported by Dey (1978) is, according to our investigations, allied to lichesterinic-protolichesterinic acids.

Ahtiana aurescens is easily distinguished from *A. pallidula* and *A. sphaerosporella* by its narrow lobes,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typically indented tips, and marginal apothecia (Fig. 1, 4–5). *A. aurescens* occurs at temperate latitudes in eastern North America, where it is restricted to the Appalachian Mountains and Great Lakes region between 34° and 48°N (Fig. 16). In some districts, it has been reported to be common (Degelius 1940; Dey 1978), although in at least the eastern and northern portions of its range it appears to be rather rare (Fink 1910; Wetmore 1981; Wong & Brodo 1992). *Ahtiana aurescens* has most frequently been reported on *Pinus* (Degelius 1942; Hale 1979), as well as on "old rails" (Fink 1935). In northern areas; however, it also colonizes *Thuja* and other conifers in swampy areas (Fink 1910, Harris 1977; S. Clayden, *pers. comm.*), whereas in the southern Appalachians it has been reported from "hardwood trees" (Dey 1978). Hale (1979) commented that this species is often associated with *Imshaugia placorodia.*

Selected specimens examined.—CANADA. ONTARIO. Lake Nipissing, *Macoun,* 1884 (FH-Tuck). Thunder Bay District, *Tibell 5290* (LD) 12 km S of Smooth Rock Falls, NW of Cochrane, *Wetmore 44037* (MINN). NEW BRUNSWICK. Carleton Co., *Clayden 77–132* (UBC).

U.S.A. ALABAMA. Franklin Co., *Harris 28482* (NY). ALABAMA/GEORGIA. Lookout Mts., *Calkins 354* (COLO). CONNECTICUT. New London Co., Norwich, *Setchell, 02.15.1882* (US). MASSACHUSETTS. Bristol Co., New Bedford, *Willey 12930* (B). MICHIGAN. Baraga Co., *Harris 8095* (MINN). Keweenaw Co., *Wetmore 49101* (MINN). MINNESOTA. Carlton Co., Kettle falls, *Fink 1423* (MINN). Cass Co., Snowball Lake, *Fink 869* (MINN). St. Louis Co., *Wetmore 28037* (MINN). NEW HAMPSHIRE. Grafton Co., North Woodstock, *Cummings,* 07.1884 (NY). White Mts., *Tuckerman,* 1848 (lectotype, FH-Tuck). NEW YORK. Essex Co., *Harris,* 1901 (MINN). NORTH CAROLINA. Jackson Co., *Trana 7949* (MINN). PENNSYLVANIA. Pike Co., *Wetmore 55833* (MINN). TENNESSEE. Greene Co., *Harris 27228* (NY). VIRGINIA. Bath Co., *Hale 12412* (COLO). VERMONT. Rutland Co., Brandon, *Dutton 2698* (MINN). VIRGINIA. Highland Co., *Anderson,* 09.06.1936 (NY). WISCONSIN. Vilas Co., *Newberry 2279* (WIS).

AHTIANA PALLIDULA (Riddle) Goward & Thell *comb. nov.* (FIG. 2, 6–7, 9, 11, 13–15)

Cetraria pallidula Riddle, THE BRYOLOGIST 18: 27. 1915. TYPE: U.S.A. Washington Territory, near Mt. Adams, 1881, *Pringle 218* (FH-Tuck, holotype).

Nephromopsis pallidula (Tuck.) Riddle, THE BRYOLOGIST 18: 27. 1915.–invalid publ.

Tuckermannopsis pallidula (Riddle) Hale, THE BRYOLOGIST 90: 164. 1987.

Thallus foliose with ascending lobes, rather loosely adnate; lobes 4–10 mm wide, more or less linear-elongate, apically rounded; upper surface pale yellow to pale greenish yellow, occasionally partly covered with a white pruina, strongly ridged; lower surface pale yellow, strikingly reticulate; cilia absent; rhizines often abundant; pycnidia common, marginal or laminal, immersed; upper and lower cortex composed of pachydermatous hyphae. Apothecia rather frequent, marginal to submarginal, situated on ascending lobes, thalline margin wrinkled, disc entire, predominantly pale brown; exciple 2-layered, upper layer composed of horizontally arranged hyphae, lower layer pachydermatous; asci narrowly clavate, 45–60 × 13–17 μm, axial body 3.0–4.5 μm broad; ascospores 4–6 × 4–6 μm; pycnoconidia usually bifusiform (dumbbell-shaped, rarely disc-bar-shaped) but several other pycnoconidial types (bacillariform, citriform, and sublageniform) are also found, 5–7 × ca. 1 μm.

Chemical substances.—Usnic acid in the cortex; caperatic acid as major and lichesterinic-protolichesterinic type fatty acids as minor compounds in the medulla.

The pycnoconidia of *A. pallidula* are highly variable, with bacillariform, bifusiform, citriform, and sublageniform pycnoconidia having all repeatedly been observed in a single pycnidium (Fig. 15). Such an astonishing array of pycnoconidial types has not previously been reported in the cetrarioid lichens. The pycnoconidia are invariably of the same length, measuring 5–7 μm. In conformity with *A. aurescens,* the apothecia and pycnidia have a marginal or submarginal position (Fig. 2, 6–7).

Ahtiana pallidula is endemic to western North America, where it occurs between about 37° and 59°N (Fig. 16). Throughout most of this latitudinal range it is restricted to the Coast Mountains and Cascades, but is absent from the outer coast. Between about 46° and 52°N, its range extends inland to the Columbia and Rocky Mountains—presumably in response to a corresponding inland extension of relatively oceanic climatic conditions (Goward & Ahti 1992; McCune 1984). In British Columbia, *A. pallidula* is generally confined to *Pseudotsuga menziesii* (Goward & Ahti 1992), though farther south it occurs also over *Pinus ponderosa* (Tucker 1973) and especially *Larix occidentalis* (R. Rosen-

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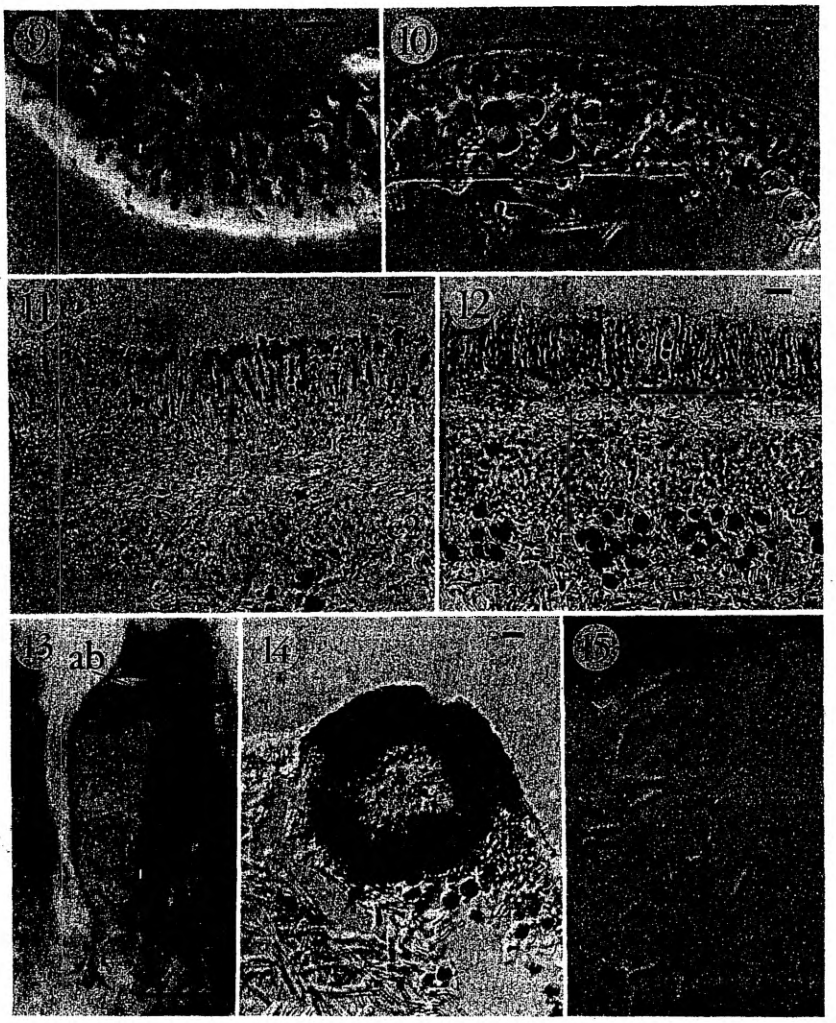
FIGURES 4–8. Morphology of *Ahtiana.* — 4. Close-up of the type material of *A. aurescens,* showing the narrow lobes with the typically indented tips (white arrow), *Tuckerman 1848* (lectotype, FH-Tuck). — 5. Ciliate portion (black arrows) of the same material. — 6. Close-up of *A. pallidula,* showing an apothecium and numerous, mostly marginal pycnidia, *Goward 91–663* (UBC). — 7. An ascending lobe and apothecium from the type collection of *A. pallidula, Pringle 218* (holotype, FH-Tuck). — 8. Close-up of *A. sphaerosporella* showing laminal apothecia and pycnidia. Note the smooth edge of the apothecia, *Imshaug 6037* (LD). (Bar in Figs. 4–8 = 1 mm).



FIGURES 9–15. Anatomy of *Ahtiana.* — 9. Pachydermatous lower cortex, *A. pallidula, Toren 2823* (SFSU). — 10. Leptodermatous upper cortex, *A. sphaerosporella, Imshaug 6037* (LD). — 11. Transverse section of an apothecium of *A. pallidula.* Note the strongly gelatinized paraplectenchymatous hyphae in the lower excipular layer (= e2), *Thiers 23274* (SFSU). — 12. Transverse section of an apothecium of *A. sphaerosporella* with rather large lumina in the lower excipular layer (= e2), *Imshaug 6037* (LD). — 13. Ascus of *A. pallidula* is typical of the genus, although the uniseriate arrangement has been lost here, due to the squash technique (ab = axial body), *Thiers 23274* (SFSU). — 14. Laminal pycnidium of *A. pallidula, Toren 2823* (SFSU). — 15. Pycnoconidia of different types present in the same pycnidium of *A. pallidula, Thoren 2823* (SFSU). (Bar in Figs. 9–15 = 10 μm.)

treter *pers. com.*). This species is most typical of lowland conifer forests, but in drier regions it is also found in middle elevation forests. *Ahtiana pallidula* seems to be of rather sparse, often localized, occurrence throughout its range.

Selected specimens examined.—CANADA. BRITISH COLUMBIA. Vancouver Isl.: *Goward 91–663* (UBC).

U.S.A. CALIFORNIA. Plumas Co., *Toren 2823* (SFSU); Shasta Co., *Hale 51865* (US); Siskiyou Co., Edge of Marble Mountain Wilderness, *Ryan 25308* (ASU); Tehama Co., *Thiers 39168* (SFSU). IDAHO. Latah Co., *Schroeder L568*

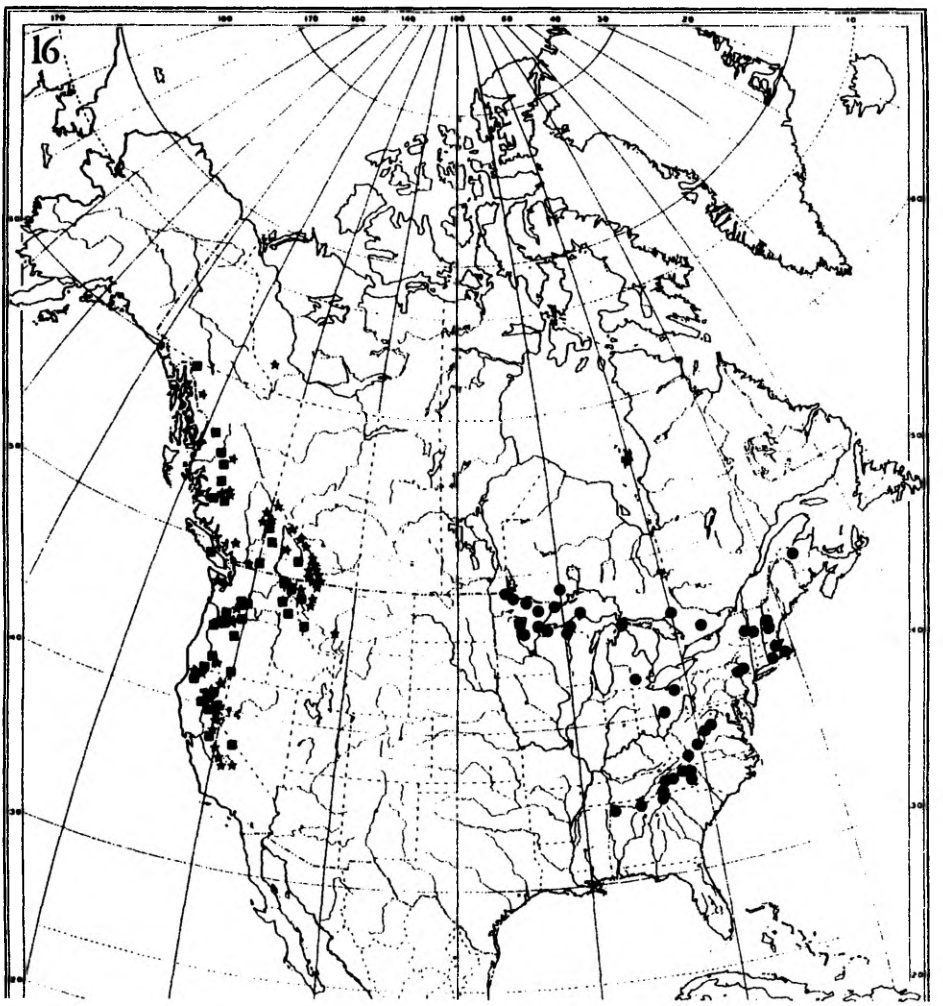


FIGURE 16. World distribution of the three *Ahtiana* species. ● *Ahtiana aurescens*; ■ *A. pallidula*; ★ *A. sphaerosporella*.

(WIS). OREGON. Bur Springs, *Toren 23274* (SFSU); Klamath Co., *Brown 848* (US). IDAHO. Bonner Co., *Thiers 17316* (SFSU). WASHINGTON. Klicktat Co., Goldendale, *Foster S12,325* (COLO). Mt. Adams, *Pringle 218* (FH-Tuck); Yakima Co., Lodge Pole Pine Camp., *Howard 3310* (COLO). Skamania Co., Ice Cave, *Suksdorf*, 09.26.1900 (NY).

AHTIANA SPHAEROSPORELLA (Müll. Arg.) Goward, THE BRYOLOGIST 88: 370. 1985.

(FIG. 3, 8, 10, 12)

Parmelia sphaerosporella Müll. Arg., Flora 74: 378. 1891. TYPE: Canada. British Columbia, Galton Mountains, *Lyall*, 1861 (BM, holotype)—verified by S. Clayden, 1985.

Thallus foliose, closely adnate; lobes 2–3(–4) mm wide, more or less linear-elongate, apically rounded; upper surface pale yellowish green (occasionally becoming dark olivaceous green), often with blackish margins, strongly wrinkled to more often becoming folded; lower surface whitish to pale tan or in part olivaceous, reticulate; cilia absent; rhizines often abundant; pycnidia common, laminal, immersed to emergent; upper and lower cortex composed of leptodermatous paraplectenchyma. Apothecia numerous, laminal, mostly restricted to thallus centre, thalline margin continuous, smooth, disc entire, light

brown; exciple 2-layered, upper layer composed of horizontally arranged hyphae, lower layer leptodermatous; asci rather broadly clavate, 40–50 × 13–18 μm; axial body 3–5 μm; ascospores 4–6 × 4–6 μm in diameter; pycnoconidia bifusiform (dumbbell shaped or slightly disc-bar shaped), 5–7(–9) × ca. 1 μm.

Chemical substances.—Usnic acid in the cortex; caperatic acid as major compound in the medulla together with other fatty acids of lichesterinic-protolichesterinic type as minor compounds.

Ahtiana sphaerosporella is endemic to western North America, where it occurs in open, well illuminated, conifer forests at temperate and boreal latitudes (Fig. 16). In the Canadian portion of its range, it is restricted primarily to *Pinus albicaulis*, on which it may often be abundant. However, it also occurs although usually as scraps, on *Abies lasiocarpa, Larix lyallii, Picea engelmannii, Pinus contorta, P. flexilis,* and *Pseudotsuga menziesii* (Goward 1985; Goward & Ahti 1992; Kalgutar & Bird 1969). As noted by Goward & Ahti (1992), the zonal distribution of *A. sphaerosporella* is determined largely by that of *Pinus albicaulis*, which is itself primarily confined to subalpine and alpine elevations. In the Canadian Rockies, for example, Bird and Marsh (1973) reported *A. sphaeroporella* over an elevational range from 1,300 m to 2,350 m, with a peak occurrence between 2,000 and 2,275 m. Outlying stands of *Pinus albicaulis* as low as 1,000 m have also been found to support healthy populations of this species (Goward 1985).

In the American portion of *A. sphaerosporella*'s range, *Pinus albicaulis* appears to be much less important as a host tree. Hale (1979), for example, reported this lichen to be "widespread on conifers, especially *Abies* and *Picea*, at higher elevations." In California, Hale and Cole (1988) stressed that it is "almost always" found over *Abies*. In the Pacific Northwest, *A. sphaerosporella* has been observed over *Abies lasiocarpa, A. concolor, Pinus monticola,* and *Pseudotsuga menziesii*. The phenomenon of substrate switches in relation to this species has already been briefly discussed by Goward (1985). *Ahtiana sphaerosporella* is easily separated from the two other species in the genus in having laminal apothecia with a smooth rim (Fig. 3, 8).

Selected specimens examined.—CANADA. ALBERTA. Livingstone Range, *Bird 14348* (WIS). Oldman River Watershed, *Bird & Lakusta 16164, 14823, 14921* (BRY, COLO, LD). BRITISH COLUMBIA. Bella Coola valley, *Ohlsson 2341* (WIS). Chilliwack, *Goward 78–1221* (UBC). Crowsnest Pass, *Goward 81–1710* (UBC). Mt. Robson Provincial Park, *Marsh 1112* (NY)

U.S.A. CALIFORNIA. Amador Co., *Weier 980* (UC); El Dorado Co., *Stone 1964* (DUKE). Fresno Co., *Thiers 13431* (ASU); Siskiyou Co., *Cooke 30039E* (US). Tulare Co., Sequoia National Park, *Wetmore 50453, 51065* (ASU, MINN). MONTANA. Columbia Falls, *Williams* 10.1895 (MINN, US). Glacier Co., Glacier National Park, *Imshaug 6037* (LD), OREGON. Hood River Co., Mt. Hood, *Shushan sl–2506* (BRY). WASHINGTON. Olympic National Park, *Sharpe 9933* (ASU).

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IX

Saag, A., Randlane, T. & Thell, A. Phylogenetic analysis of cetrarioid lichens with globose ascospores. (Submitted.)

PHYLOGENETIC ANALYSIS OF CETRARIOID LICHENS WITH GLOBOSE ASCOSPORES

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Abstract. The group of cetrarioid lichens with globose ascospores in narrowly clavate asci includes 30 species from six genera. Phylogenetic analyses were carried out, using programs PAUP 3.1.1, MacClade 3.04, and the Parsimony Jackknifer 4.22, to check the correspondence of the present taxonomy to the probable evolution of the taxa involved. A separate clade, comprising three *Ahtiana* species, is formed in most of the trees. The genus *Allocetraria* is paraphyletic with respect to *Dactylina*. The taxa belonging to the genera *Esslingeriana, Tuckneraria,* and *Tuckermannopsis* today, do not form separate groups and evidently need further studies.

Key words: cetrarioid lichens, *Parmeliaceae*, *Ahtiana, Allocetraria, Dactylina, Esslingeriana, Tuckneraria, Tuckermannopsis,* cladistic analysis.

Introduction

The group of cetrarioid lichens, comprising 22 genera and more than 130 species today (Randlane *et al.* 1997), is definitely polypheletic. Still, phylogenetic affinities between several cetrarioid genera are rather obscure. The first review about the phylogeny of the whole group of cetrarioid lichens was presented by Kärnefelt *et al.* (1992) where cladistic analyses were carried out on 50 species as terminal taxa. This analysis was based mainly on anatomical characters that had been originally revised. As a result, the analysed taxa were grouped in three separate aggregates, described by important anatomical characters: taxa with an "apical ring structure"; taxa with "uniseriate asci"; taxa with "broadly clavate asci". Independent cladistic analyses on the same group of lichens were also carried out by us (Saag & Randlane 1995). Of about 120 cetrarioid lichen species known at that time, 83 were chosen for the analysis to evaluate the systematic arrangement of the taxa. Morphological and chemical characters (character states) were identified or verified originally, while descriptions of anatomical characters were based mainly on literature data. Evolution for considerable number of species (from genera *Nephromopsis, Cetreliopsis, Cetrelia*) remained unresolved, showing several polytomies on the respective part of the consensus tree. The rest of the species were grouped in a way that shows considerable similarity with the main three assemblages pointed out by Kärnefelt *et al.* (1992). Similar results are particularly remarkable because of the fact that the two analyses were based on different data matrices, with emphasis on anatomical characters in the Swedish study and morphological and chemical characters in our analysis.

Today the polyphyletic origin of cetrarioid lichens is generally acknowledged. Three evolutionary lines referred to above, based on reproductive structures and structural

characters mainly, have been recognized for the group (Thell 1996). The first line, considered monophyletic, includes species from seven genera: *Arctocetraria, Cetraria* s. str., *Cetreliopsis, Coelopogon, Flavocetraria, Masonhalea,* and *Nephromopsis*. They are all characterized by the ellipsoid ascospores in narrowly clavate asci, with a small axial body. An amyloid ring structure in tholus is a significant character that is present in *Cetraria, Flavocetraria* and occasionally in *Nephromopsis*.

The second evolutionary line comprises six genera: *Ahtiana, Allocetraria, Dactylina, Esslingeriana, Tuckneraria,* and *Tuckermannopsis*. These species are anatomically characterized by subglobose to globose ascospores borne in narrowly clavate asci (earlier called "uniseriate asci"). Some other cetrarioid lichens, which also have almost subglobose ascospores but quite different type of asci (e.g. species of *Vulpicida* and *Platismatia*), are not included. The assumption about monophyletic origin of this line is supported by two earlier cladistic analyses of various species of cetrarioid lichens (Kärnefelt *et al.* 1992, Saag & Randlane 1995). In both analyses the clade comprising species with globose ascospores in narrowly clavate asci was clearly separated.

The third line is represented by several genera and informal groups: *Asahinea, Cetraria fendleri* group, *Cetrariella, Cetrelia, Cornicularia, Kaernefeltia, Melanelia commixta* group, *Nimisia, Parmelaria, Platismatia,* and *Vulpicida*. Ellipsoid ascospores in broadly clavate asci, with a broad axial body are characteristic to these species. This heterogenous gouping is evidently paraphyletic in the previous treatments of cetrarioid taxa. A number of parmelioid lichens probably also belong here.

The cetrarioid species of the second evolutionary line are treated here in more detail. Four genera of the six, *Ahtiana, Allocetraria, Dactylina* and *Tuckneraria*, have been thoroughly revised lately (Thell *et al.* 1995a, b, Kärnefelt & Thell 1996, Randlane *et al.* 1994). The sole species of the monotypic genus *Esslingeriana* was described completely by Esslinger (1971). *Tuckermannopsis* is the only entity that still needs to be revised. Nevertheless, the data characterizing these taxa are scattered in many papers and evolutionary affinities between all the species included have not been evaluated yet.

Material and methods

Herbarium material from B, DUKE, FH, GZU, H, KW, LD, LE, M, MB, PC, S, TAIM, TNS, TU, UPS, US has been used for this study. Morphological characters were examined using a stereomicroscope Technival 2; anatomical methods and equipment used are described in detail in Thell *et al.* (1995a); secondary chemistry was investigated according to the standardized methods of TLC (Culberson 1972, Culberson *et al.* 1981).

Computer programs for phylogenetic analysis PAUP 3.1.1 (Swofford 1993) and MacClade 3.04 (Maddison & Maddison 1992) were used. Cladistic analyses were carried out by the first author. Both programs were run on a Macintosh Color Classic. Using the program PAUP 3.1.1, the follwing heuristic search settings were applied: character-state optimization – ACCTRAN; MULPARS; MAXTREE = 1000, 3000, 6000; addition sequence – simple; 1 tree held at each step during stepwise addition; tree-bisection-recollection (TBR) branch-swapping performed; multi-state taxa interpreted as uncertainty; characters weighted equally. The same settings were used in the successive approximations character weighting method. Tree support was investigated using Bremer support and bootstrap in PAUP 3.1.1 and the program Parsimony Jackknifer 4.22 (Farris 1995).

Data

Taxa analysed. The following 30 cetrarioid species from the six above-listed genera were applied as terminal taxa of the ingroup: *Ahtiana aurescens* (Tuck.) Randlane & Thell, *A. pallidula* (Tuck. ex Riddle) Goward & Thell, *A. sphaerosporella* (Müll. Arg.) Goward, *Allocetraria ambigua* (Bab.) Kurok. & M. J. Lai, *A. endochrysea* (Lynge) Kärnefelt & Thell, *A. flavonigrescens* Thell & Randlane, *A. globulans* (Nyl.) Thell & Randlane, *A. madreporiformis* (Ach.) Kärnefelt & Thell, *A. oakesiana* (Tuck.) Randlane & Thell, *A. sinensis* X. Q. Gao, *A. stracheyii* (Bab.) Kurok. & M. J. Lai, *Dactylina arctica* (Richardson) Tuck., *D. ramulosa* (Hook.) Tuck., *Esslingeriana idahoensis* (Essl.) Hale & M. J. Lai, *Tuckermannopsis americana* (Spreng.) Hale, *T. chlorophylla* (Willd.) Hale, *T. ciliaris* (Ach.) Gyeln., *T. gilva* (Asahina) M. J. Lai, *T. inermis* (Nyl.) Kärnefelt, *T. microphyllica* (W. L. Culb. & C. F. Culb.) M. J. Lai, *T. orbata* (Nyl.) M. J. Lai, *T. platyphylla* (Tuck.) Hale, *T. platyphylloides* (Asahina) M. J. Lai, *T. subalpina* (Imshaug) Kärnefelt, *T. ulophylloides* (Asahina) M. J. Lai, *Tuckneraria ahtii* Randlane & Saag, *T. laureri* (Kremp.) Randlane & Thell, *T. laxa* (Zahlbr.) Randlane & Thell, *T. pseudocomplicata* (Asahina) Randlane & Saag and *T. togashii* (Asahina) Randlane & Thell.

For choosing the outgroup we had, in principle, two alternatives: a taxon either from the group close to *Cetraria* (the first evolutionary line of cetrarioid lichens) or from the group related to the so-called "parmelioid Cetrariae" (the third evolutionary line). The form of asci – narrowly clavate – is the same in the ingroup and in the group close to *Cetraria,* while the third group has typically broadly clavate asci. Therefore, the parmelioid and allied genera were discarded at first. Two genera of the seven included in the first evolutionary line – *Cetraria* s. str. and *Flavocetraria* – were seriously considered as possible outgroups. Ascocarps of *Flavocetraria* are characterized by ellipsoid ascospores, narrowly clavate asci with a small axial body, and presence of an amyloid ring structure. These characters are similar to *Cetraria* s. str. and differ from those of the ingroup. Still, the stucture of upper and lower cortices and secondary chemistry of *Flavocetraria* is more similar to the studied taxa. Finally, *Flavocetraria cucullata* (Bellardi) Kärnefelt & Thell was selected as outgroup for one series of analyses.

Later the species from the third evolutionary line were also evaluated as possible samples for outgroup. In earlier analyses (Kärnefelt *et al.* 1992, Saag & Randlane 1995) *C. fendleri* appeared as one representative of the sister group to the assemblage which is treated as ingroup here. Anatomically, ascocarps of *C. fendleri* are characterized by ellipsoid ascospores, broadly clavate asci, a large axial body, and absence of an amyloid ring structure. The ingroup differs from the species under discussion in two former and is similar in two latter characters. Therefore, *C. fendleri* was additionally chosen as outgroup.

Both selected species – *Flacocetraria cucullata* and *Cetraria fendleri* – were used to root the trees in separate series of analyses.

Characters. All in all, 36 morphological, anatomical, and chemical characters were used for the analysis. Lichen substances were not treated independently from each other but grouped into biochemically related sets, as suggested in our previous study (Saag & Randlane 1995).

Character states were coded as 0, 1, 2, 3 and 4; all multistate characters were treated as unordered. The characters and character states were the following.

1. Form of thallus: adnate (0), ascending (1)
2. Symmetry of thallus: dorsiventral (0), radial-symmetrical (1)
3. Interior of thallus: of densely arranged hyphae (1), of loosely arranged hyphae (1), becoming hollow (3)
4. Form of lobes: length of lobes ~ width of lobes (0), lobes longer than wide (1)
5. Width of lobes: up to 3 mm (0), up to 6 mm (1), up to 12 mm (2)
6. Colour of upper surface: yellow (0), brown (1), grey (2)
7. Colour of lower surface: whitish (0), yellow (1), brown (2), black (3)
8. Pseudocyphellae on upper side: absent (0), present (1)
9. Pseudocyphellae on lower side: absent (0), present (1)
10. Form of pseudocyphellae on lower side: spots (0), lines (1)
11. Cilia: absent (0), present (1)
12. Rhizines: absent (0), present (1)
13. Soredia: absent (0), present (1)
14. Isidia: absent (0), present (1)
15. Structure of the cortex (orientation of hyphae): both corteces paraplectenchymatous, i.e. hyphae randomly oriented (0), upper cortex palisade plectenchymatous, i.e. hyphae anticlinally oriented (1), both corteces palisade (2), both corteces prosoplectenchymatous, i.e. hyphae parallel to cortex (3)
16. Cell wall thickness (compared to cell lumina): leptodermatous (0), pachydermatous (1)
17. Position of apothecia: marginal only (0), marginal to submarginal (1), laminal (2), terminal (3)
18. Ascus shape: broadly clavate (0), narrowly clavate (1)
19. Ascus form: melanelia type (0), tuckermannopsis type (1), cetraria type (2)
20. Tholus: small (0), large (1)
21. Axial body: medium [3–5 μm] (0), broad [>5 μm] (1), narrow [<3 μm] (2), very narrow [<1 μm] (3)
22. Shape of ascospores: globose (0), subglobose (1), broadly ellipsoid (2), ellipsoid (3)
23. Length or diameter of ascospores: short [<6 μm] (0), long [>6 μm] (1)
24. Position of pycnidia: marginal only (0), marginal and laminal (1), laminal only (2)
25. Emergency of pycnidia: emergent (0), immersed (1)
26. Shape of pycnoconidia: bacillariform (0), oblong citriform (1), dumb-bell shaped incl. disc-bar shaped (2), filiform (3), sublageniform (4)
27. Length of pycnoconidia: short [<7 μm] (0), medium [7–10 μm] (1), long [>10 μm] (2)
28. Usnic acid: absent (0), present (1)
29. Atranorin: absent (0), present (1)
30. Fatty acids: absent (0), present (1)
31. Substance of fatty acids: lichesterinic-protolichesterinic type acids (0), caperatic acid (1), rangiformic acid (2), unidentified (3)
32. Secalonic acids: absent (0), present (1)
33. Orcinol depsides and depsidones: absent (0), present (1)
34. Substance of orcinol depsides and depsidones: alectoronic and collatolic acids (0), physodic acid (1), olivetoric acid (2), microphyllinic acid (3), gyrophoric acid (4)
35. β-orcinol depsidones: absent (0), present (1)
36. Substance of β-orcinol depsidones: fumarprotocetraric acid (0), physodalic acid (1)

The data matrix and terminal taxa are presented in Table 1.

Table 1. Data matrix and terminal taxa. Character numbers and coding of character states correspond to the text. & = and (polymorphism), / = or (uncertainty), – = gap, ? = character state unknown.

Names\Characters	0 0 1 2	0 0 0 0 3 4 5 6	0 7	0 0 1 1 1 1 1 8 9 0 1 2 3 4	1 5	1 1 6 7	1 1 2 2 8 9 0 1	2 2 2 2 2 3 4 5	2 2 6 7	2 2 3 3 8 9 0 1	3 3 3 2 3 4	3 3 5 6
Ahtiana aurescens	0 0	0 0 0 0	0	0 0 – 1 1 0 0&1	0	1 1	1 1 0 0/2	0 0 1 0	2 0	1 0 1 0&1	0 0 –	0 –
Ahtiana pallidula	1 0	0 0 2 0	1	0 0 – 0 1 0 0	0	1 1	1 1 0 0	0 0 1 1	2 0	1 0 1 0&1	0 0 –	0 –
Ahtiana sphaerosporella	0 0	0 0 0 0	0	0 0 – 0 1 0 0	0	0 2	1 1 0 0	0 0 1 0&1	2 0/1	1 0 1 0&1	0 0 –	0 –
Allocetraria ambigua	1 0	0 1 1 0	1	0 1 0 0 1 0 0	2	1 0	1 1 0 0	0 1 1 0&1	3 2	1 0 1 0	1 0 –	0 –
Allocetraria endochrysea	1 1	1 1 0 0	1	0 1 0 0 0 0 0	2	0 ?	? ? ? ?	? ? 2 1	3 2	1 0 1 0	1 0 –	0 –
Allocetraria flavonigrescens	1 0	0 1 0 0	2/3	0 0 – 0 0 0 0	2	0 ?	? ? ? ?	? ? 1 0&1	? ?	1 0 1 0&2	1 0 –	1 0
Allocetraria globulans	0 0	0 0 1 0/1	2	0 0 – 0 1 0 0	2	0 1	1 1 0 1	0 1 1 0	3 2	1 0 1 0	1 0 –	0 –
Allocetraria madreporiformis	1 0&1	1 1 0 0	1	0 0 – 0 0 0 0	2	0 3	1 1 0 0	1 1 2 1	3 2	1 0 1 0	0 0 –	0 –
Allocetraria oakesiana	0 0	0 0 1 0	2	0 0 – 0 1 1 0	0/2	0 1	1 1 0 1	0 0 0 0&1	3 2	1 0 1 0&1	1 0 –	0 –
Allocetraria sinensis	1 0	0 1 0 0	2	0 1 1 0 0 0 0	2	0 ?	? ? ? ?	? ? 0 0	3 2	1 0 1 0	0 0 –	0 –
Allocetraria stracheyi	1 0&1	0 1 1 0	1/2	0 1 0 0 1 0 0	2	1 0	1 1 0 1	0 0 0 0&1	3 2	1 0 1 0	1 0 –	0 –
Dactylina arctica	1 1	2 1 2 0/1	1/2	0 0 – 0 0 0 0	2	0 3	1 1 0 0	0 0 2 1	1 0	1 0 0 –	0 1 1&4	1 1
Dactylina ramulosa	1 1	2 1 0 1	1	0 0 – 0 0 0 0	2&3	1 3	1 1 0 0	0 0 2 1	1 0	1 0 0 –	0 1 1	1 1
Esslingeriana idahoensis	1 0	0 1 1 2	3	0 0 – 0 1 0 0	0	0 1	1 1 0 0	0 1 1 1	2 0	0 1 1 2	1 0 –	0 –
Tuckermannopsis americana	1 0	0 0 1 1	2	0 0 – 1 1 0 0	0	0 1	1 1 0 0	0 0 1 0	2 0	0 1 0 –	0 1 0	0 –
Tuckermannopsis chlorophylla	1 0	0 0 1 1	2	0 0 – 0 1 1 0	0	0 0	1 1 0 0	0 0 0 1	2 0	0 1 1 0	0 0 –	0 –
Tuckermannopsis ciliaris	1 0	0 0 1 1	2	0 0 – 1 1 0 0	0	0 1	1 1 0 0	0 0 1 0	2 0	0 1 0 –	0 1 1&2	0 –
Tuckermannopsis gilva	0 0	0 0 1 1	2	0 0 – 1 1 1 0	0	0 ?	? ? ? ?	? ? ? ?	? ?	0 1 0 –	0 1 0	0 –
Tuckermannopsis inermis	1 0	0 0 0 1	0	0 1 1 0 1 0 0	0	1 1	1 1 0 0	0 0 0 1	0 1	0 0 1 0	0 0 –	0 –
Tuckermannopsis microphyllica	1 0	0 0 1 1	2	0 0 – 0 1 0 0	0	1 1	1 1 0 ?	0 1 0 0	3 2	0 1 0 –	0 1 3	0 –
Tuckermannopsis orbata	0 0	0 0 1 1	2	0 0 – 1 1 0 0	0	0 0	1 1 0 0	0 0 1 0	2 0	0 0 1 0	0 0 –	0 –
Tuckermannopsis platyphylla	1 0	0 0 2 1	2	1 0 – 0 1 0 1	0	1 1	1 1 0 0	0 0 1 1	2 0	0 1 1 3	1 0 –	0 –
Tuckermannopsis platyphylloides	1 0	0 0 2 1	2	0 0 – 0 1 0 0	0	0 0	? ? ? ?	? ? 1 0	? 0	0 0 1 0	0 0 –	0 –
Tuckermannopsis subalpina	1 0	0 1 1 1	2	0 1 1 0 0 0 0	0	0 0	1 1 0 0	0 0 0 0	0 1	0 0 1 0	0 0 –	0 –
Tuckermannopsis ulophylloides	1 0	0 0 1 1	1/2	0 0 – 0 1 1 1	1	0 ?	? ? ? ?	? ? 0 0	? ?	0 0 1 0	0 0 –	0 –
Tuckneraria ahtii	1 0	0 1 2 0	2/3	0 1 0 1 1 0 0	0	1 0	1 1 0 0/2	0 0 1 0	2 0	1 0 1 0&1	0 0 –	0 –
Tuckneraria laureri	1 0	0 0 1 0	0/2	0 1 0 1 1 1 0	0	1 0	1 1 0 0	0 0 0 0	2 0	1 0 1 0	0 0 –	0 –
Tuckneraria laxa	1 0	0 1 0 0	1	0 1 0 1 1 0 0	0	1 0	1 1 0 0	0 0 0 0	? ?	1 0 1 0	0 0 –	0 –
Tuckneraria pseudocomplicata	1 0	0 0 2 0	0/2	0 1 0 1 1 0 0	0	1 0	1 1 0 0	0 0 0 0	2 0	1 0 1 0	0 1 0&1	0 –
Tuckneraria togashii	0 0	0 0 1 0	1/2	0 1 0 1 1 0 1	0	1 0	1 1 0 0	0 0 1 0	2 0	1 0 1 0&1	0 0 –	0 –
Flavocetraria cucullata	1 0	0 1 1 0	1	0 1 0 0 0 0 0	0/2	1 3	1 2 1 3	1 1 0 0	2 0	1 0 1 0	0 0 –	0 –
Cetraria fendleri	0 0	0 0 0 1	0	0 0 – 0 1 0 0	0	1 1&2	0 0 0 0	1 1 1 1	2 0	0 0 1 0	0 0 –	0 –

Results

Two series of separate analyses were carried out using different outgroups (*Cetraria fendleri* and *Flavocetraria cucullata*).

With *Cetraria fendleri* as outgroup, 36 equally parsimonous trees were obtained (heuristic search, all characters equally weighted, length of trees = 121 steps, Fig. 1). The strict consensus tree and the 50% majority-rule consensus of 36 trees were also retained (not shown). The successive approximations character weighting method produced 108 equally parsimonous trees and, after the second reweightening of characters, 81 equally parsimonous trees were obtained (strict consensus tree on Fig. 2). Successive weighting is particularly useful when applied to data sets with much homoplasy (Tehler & Egea 1997). Character reweighting by maximum value of rescaled consistency indices generated remarkably low weights to some conspicuous morphological characters often used in key-books, such as presence of isidia and soredia (Table 2). This is quite acceptable, in our opinion, as these asexual structures are certainly derived, but they cannot be treated as shared characters. In other words, we suppose that sorediate and isidiate species did not share sorediate or isidiate ancestors but came from sexual species instead. The most highly weighted characters are either connected with the anatomy of the thallus (characters 2, 3, 15) or medullary secondary compounds (31, 34). Anatomical characters of the ascocarps, presumably highly evaluated, are uninformative in this analysis as the ascus form is the same in the whole ingroup.

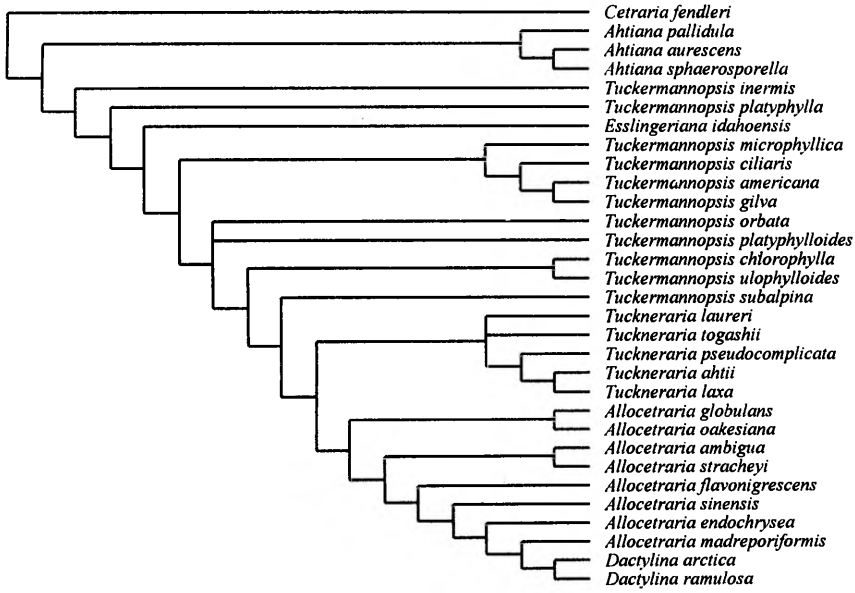

Fig. 1. One of 36 equally parsimonous cladograms (based on characters with equal weights; *Cetraria fendleri* used to root trees). Length 121, consistency index 0.405, retention index 0.654.

Table 2. Weights of all characters after the second reweighting according to maximum value of RC indices.

Character	Inform.	Weight	States
1. Form of thallus	Y	86	01
2. Symmetry of thallus	Y	**1000**	01
3. Interior of thallus	Y	**1000**	012
4. Form of lobes	Y	182	01
5. Width of lobes	Y	184	012
6. Colour of upper surface	Y	417	012
7. Colour of lower surface	Y	313	0123
8. Pseudocyphellae on upper side	N	1000	01
9. Pseudocyphellae on lower side	Y	120	01
10. Form of pseudocyphellae on lower side	Y	250	01
11. Cilia	Y	167	01
12. Rhizines	Y	417	01
13. Soredia	Y	63	01
14. Isidia	Y	0	01
15. Structure of cortex	Y	**1000**	0123
16. Cell wall thickness	Y	103	01
17. Position of apothecia	Y	688	0123
18. Ascus shape	N	1000	01
19. Ascus form	N	1000	01
20. Tholus	N	1000	0
21. Axial body	Y	250	012
22. Shape of ascospores	Y	0	01
23. Length (diameter) of ascospores	Y	0	01
24. Position of pycnidia	Y	103	012
25. Emergency of pycnidia	Y	167	01
26. Shape of pycnoconidia	Y	467	0123
27. Length of pycnoconidia	Y	250	012
28. Usnic acid	Y	458	01
29. Atranorin	Y	417	01
30. Fatty acids	Y	400	01
31. Substance of fatty acids	Y	**1000**	0123
32. Secalonic acids	Y	143	01
33. Orcinol depsides & depsidones	Y	222	01
34. Substance of orcinol depsides & depsidones	Y	**1000**	01234
35. β-orcinol depsidones	Y	250	01
36. Substance of β-orcinol depsidones	N	1000	01

Some clades, which can be seen on one of the equally parsimonous cladograms of the initial analysis (Fig. 1), are also distinct in all following analyses (Fig. 2). The biggest clade consists of eight *Allocetraria* and two *Dactylina* species. Next clade includes five *Tuckneraria* species. Four species of *Tuckermannopsis* (the so-called *T. ciliaris* group) also form a separate clade, while the other members of that genus are solved differently in different analyses. The fourth clade, including three *Ahtiana* species, is supported by 92% of trees (characters with equal weights); trees produced by the successive approximations character weighting method always show the same *Ahtiana* clade.

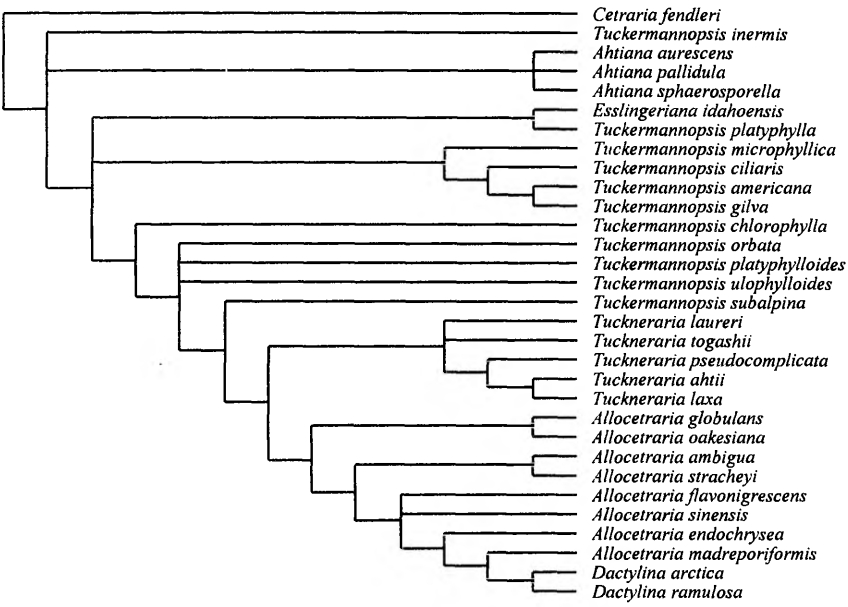

Fig. 2 Strict consensus tree of 108 equally parsimonous cladograms (based on characters reweighted; *Cetraria fendleri* used to root trees). Lenght of shortest trees 35 723, consistency index 0.644, retention index 0.800.

The Bremer support test was carried out next. In this test all the trees are kept successively one step longer than the shortest tree, until all the groups are lost in consensus. Bremer's length difference has also been referred to as the decay test or decay index (Parmasto 1996, Tehler & Egea 1997). In our analysis, inclusion of trees one step longer than the shortest tree, causes the majority of the tree to collapse into a polytomy, and only the *Allocetraria – Dactylina* clade remains separate. The latter begins to decay by the Bremer support value of three.

With *Flavocetraria cucullata* as outgroup, 1557 equally parsimonous trees (heuristic search, all characters equally weighted, length of trees = 123 steps) were obtained. Both strict consensus tree and 50% majority-rule consensus (Fig. 3) were saved. The clade of *Ahtiana*, consisting of three species, is supported by 78% of trees. The clade of *Allocetraria* (including *Dactylina*), which was strongly supported in the first analysis, collapses into a polytomy. Still, in the strict consensus tree, two species of *Dactylina* form a separate clade with two *Allocetraria* species (*A. endochrysea* and *A. madreporiformis*). The clade including *Tuckneraria* species is not supported by this analysis either. One new clade, which consists of 11 species of *Tuckermannopsis* and one species of *Esslingeriana,* is composed in all cladograms. When characters were reweighted by maximum value of rescaled consistency indices, five equally parsimonous trees were obtained. Strict consensus tree (Fig. 4) of them is essentially different from that achieved by the analysis where characters were with equal weights (Fig. 3); besides, some groups, similar to the clades mentioned in the first series of analysis (with *Cetraria fendleri* as an outgroup), are formed. These are: the clade of three species of *Ahtiana*; the clade of eight species of *Allocetraria* and two species of *Dactylina*; the clade of four species of *Tuckermannopsis* (*T. ciliaris* group). *Tuckneraria* species do not form a clade in this analysis.

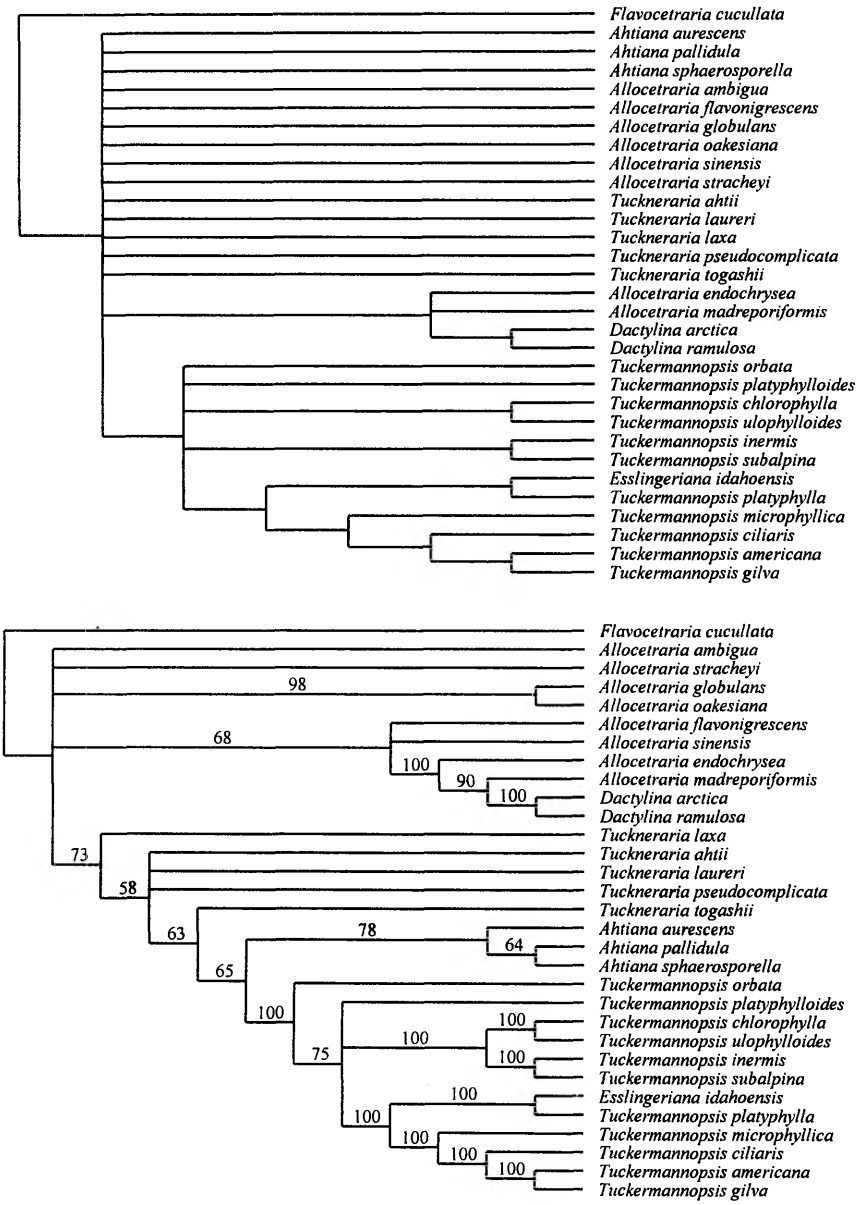

Fig. 3. Strict consensus tree and 50% majority rule consensus tree of 1557 equally parsimonous cladograms (based on characters with equal weights; *Flavocetraria cucullata* used to root trees). Length of shortest trees 123, consistency index 0.415, retention index 0.650.

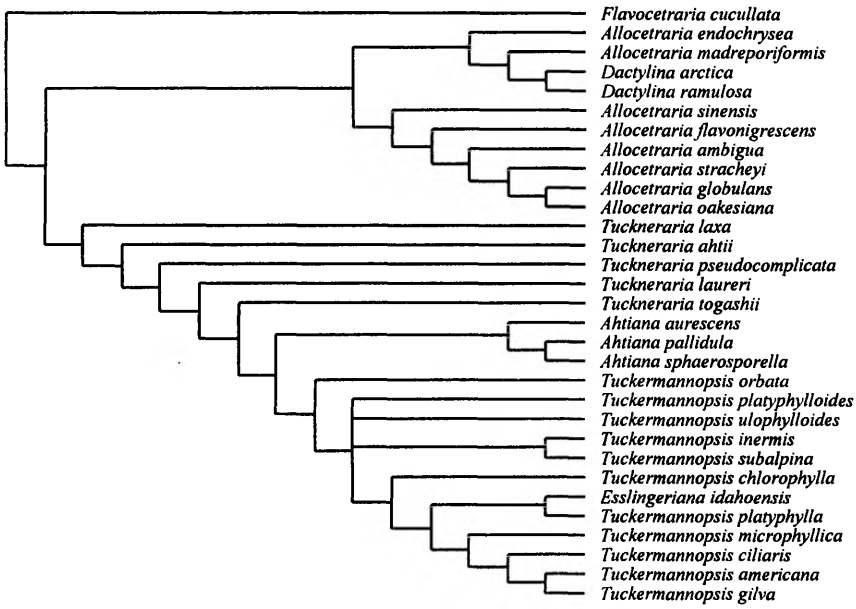

Fig. 4. Strict consensus tree of 5 equally parsimonous cladograms (based on characters reweighted; *Flavocetaria cucullata* used to root trees). Length of shortest trees 43 164, consistency index 0.658, retention index 0.808.

In addition, analyses with both outgroups were carried out using the parsimony jackknifer programme Jac (Farris 1995), to identify well-supported monophyletic groups. In Jac, the data are resampled with a jackknifing technique, i. e. in every replicate c. 66% of the characters are chosen at random, without replacement for parsimony analysis. The resampling procedure can be repeated up to 10 000 times, as it was done in the present study. The objective of the jackknife method in Jac is the same as that of bootstrapping in PAUP (Tehler & Egea 1997), but considered much faster than other available techniques. The resulting tree (not presented) shows that all the clades described above are not supported by this very efficient procedure, except for a group consisting of two *Dactylina* species, and another group comprising *Allocetraria globulans* and *A. oakesiana.*

Bootstrapping (500 replicates) was used as well – on the same purpose. Three small groups were supported by this method: *Allocetraria globulans – A. oakesiana*; *Tuckermannopsis americana – T. ciliaris – T. gilva*; *Allocetraria endochrysea – A. madreporiformis* together with the two Dactylinas as a subclade.

Discussion

The aim of the present phylogenetic analysis was to search for the monophyletic groups inside the ingroup and check the correspondence of the present taxonomy to the probable evolution of taxa involved.

Originally monotypic genus *Ahtiana* was segregated from *Parmelia* s. lat. on the basis of emergent pycnidia, globose ascospores, leptodermatous cortex, and presence of medullary caperatic acid (Goward 1985). Despite its parmelioid habit with laminal apothecia and pycnidia, *Ahtiana sphaerosporella* was shown to be closely allied to

Cetraria pallidula. Today the genus includes three species. In our present analysis it appears as a separate clade in most of the cladograms of equally weighted characters and also in the successive weighting strict consensus trees of both series of analyses (with different outgroups). This fact supports the latest changes in the systematics of the genus – transferring *C. pallidula* and *C. aurescens* to the originally monotypic *Ahtiana* (Thell *et al.* 1995a).

The genus *Allocetraria*, at first including only three species from high altitudes in south-east Asia, was introduced by Kurokawa & Lai (1991). It was separated from *Cetraria* because of the dichotomously branched lobes, the special appearance of pseudocyphellae, the palisade plectenchymatous cortex, and the unique chemistry. The authors did not pay attention to ascomatal and pycnidial characters. Later studies of these structures confirmed the necessity of a separate genus (Thell *et al.* 1995b). Today, ten species are combined in the genus; eight of them were included in our analyses. We have not seen the herbarium material of two taxa (*A. denticulata* and *A. isidiigera*), and their descriptions (Hue 1899; Kurokawa & Lai 1991) are too poor to present them properly in the data matrix. The value of these taxa is rather uncertain – both species are known from the type localities only; in addition, they are sterile according to literature.

The paraphyletic nature of the genus with respect to two species of *Dactylina* is obvious. The closeness of these two genera was noticed only recently, when two former Dactylinas – *A. madreporiformis* and *A. endochrysea* – were transferred to *Allocetraria* (Kärnefelt & Thell 1996). Presence of filiform pycnoconidia and asci with extremely broad axial body are the essential characters for separating *Allocetraria*. *Dactylina* is distinguished by the radialsymmetrical thallus becoming hollow, by the terminal position of apothecia, and also by the secondary chemistry. The palisade plectenchymatous arrangement of cortical hyphae, which is rather unusual in the group of cetrarioid lichens, is characteristic of both *Allocetraria* and *Dactylina*. The splitting of the species involved into two separate genera is not supported by our present study. At the same time, the analyses based on morphological, anatomical, and chemical characters only, do not show enough confidence when using more severe methods such as jackknifing or bootstrapping. We share the opinion recently approved by the symposium on taxonomy, evolution and classification of lichens and related fungi (January 9–11, 1998, London) that on such occasions quick changes in nomenclature are not advisable. At the present stage of lichenological studies, additional phylogenetic analyses using the modern molecular data should be carried out, before proposing extensive nomenclatural changes.

Tuckneraria includes five species. Most of them were transferred from *Nephromopsis* to the newly described genus because of important anatomical characters (globose ascospores, Tuckermannopsis-type asci, small axial body etc.) (Randlane *et al.* 1994). Today the genera *Nephromopsis* and *Tuckneraria* are considered even to represent different evolutionary lines (Thell 1996) of cetrarioid lichens. The idea of close affinities of *Tuckneraria* and *Ahtiana* has also been proposed (Thell *et al.* 1995a). The monophyletic origin of genus *Tuckneraria* is supported in one series of our analyses only (*Cetraria fendleri* used to root trees). In the other series (*Flavocetraria cucullata* used to root trees), the species of *Tuckneraria* do not form a separate clade but are branched out successively.

Genus *Tuckermannopsis* was described by Gyelnik (1933) in a very short manner: "Affinis generi Nephromopsi sed thallus subtus pseudocyphellis deficientibus". Today

much more is known about the genus but the correct description is still not presented. According to different authors (Lai 1981, Hale in Egan 1987, Kurokawa 1991, Weber in Egan 1991), various species have been transferred to *Tuckermannopsis*; many of them have later been combined again into other genera (*Ahtiana, Allocetraria, Melanelia, Vulpicida*). At present it is generally accepted that globose ascospores in narrowly clavate asci, large axial body, dumb-bell shaped pycnoconidia, and moderately small foliose brown to greenish thallus (absence of usnic acid in the cortex) are the important characters in delimiting the genus. Eleven species are now recognized in *Tuckermannopsis*. Our phylogenetic analyses reveal further problems with this taxon. Monophyletic origin can be declared only for the so-called *Tuckermannopsis ciliaris* group (*T. ciliaris* is also the type species of the genus). The clade consisting of four close species is strongly supported in all parsimonous trees. On the whole, the genus *Tuckermannopsis*, in its generally accepted treatment, should be considered paraphyletic. For instance, *E. idahoensis*, the sole species of the genus *Esslingeriana*, is predominately connected with *Tuckermannopsis platyphylla* and this pair of species always branches out next to *Tuckermannopsis ciliaris* group. Other members of the genus do not form a distinguished group. In our opinion, any further taxonomical rearrangements in this genus are not justified before additional – preferably molecular – research has been carried out.

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