

A molecular phylogeny of the *Lecanora varia* group, including a new species from western North America

Sergio Pérez-Ortega · Toby Spribille · Zdeněk Palice ·
John A. Elix · Christian Printzen

Received: 22 March 2009 / Revised: 25 January 2010 / Accepted: 27 January 2010
© German Mycological Society and Springer 2010

Abstract The phylogeny of the *Lecanora varia* group is inferred from ITS sequences using Bayesian and ML phylogenetic analysis methods. According to our data, usnic acid-containing, corticolous *Lecanora* species do not form a monophyletic group but occur in three major clades together with other groups of *Lecanora* and *Protoparmeliopsis*. The new combination *Lecanora filamentosa* (Stirt.) Elix & Palice is proposed. The new species *Lecanora schizochromatica* is described from northwestern North America. It produces atranorin as a major substance and is closely related to the morphologically and chemically similar *L. filamentosa*. The American *Biatora pullula* Tuck. is synonymised with *Lecanora anopta* Nyl., which is hereby reported for continental North America for the first time. The phylogenetic relationships between the major clades of *Lecanora* are still largely unresolved and require more intensive taxon and character sampling.

Keywords ITS · Phylogeny · *Lecanora varia* group · Lecanoraceae · Morphology

Introduction

Lecanora Ach. is a large, crustose lichen genus traditionally characterised by colourless, non-septate ascospores in eight-spored asci, green-algal photobionts and a lecanorine margin. Since the middle of the twentieth century, *Lecanora* has received considerable attention from systematists (e.g. Brodo 1984; Brodo et al. 1994; Dickhäuser et al. 1995; Eigler 1969; Eigler and Poelt 1965; Fröberg 1997; Grube et al. 2004; Guderley 1999; Laundon 2003a, 2003b; Leuckert and Poelt 1989; Lumbsch 1994; Lumbsch and Elix 2004; Lumbsch et al. 1997; Miyawaki 1988; Motyka 1995, 1996a, b; Poelt 1952, 1958, 1966; Poelt et al. 1995; Printzen 2001; Ryan 1989a, b, 1998; Ryan and Nash 1997; Ryan et al. 2004; Šliwa and Wetmore 2000; Šliwa 2007;

S. Pérez-Ortega · C. Printzen
Abt. Botanik und Molekulare Evolutionsforschung,
Forschungsinstitut Senckenberg,
60325 Frankfurt am Main, Germany

T. Spribille
Albrecht-von-Haller-Institut für Pflanzenwissenschaften,
Universität Göttingen,
Untere Karspüle 2,
37073 Göttingen, Germany

Z. Palice
Institute of Botany, Czech Academy of Sciences,
252 43 Průhonice, Czech Republic

Z. Palice
Department of Botany, Faculty of Natural Sciences,
Charles University,
Benátská 2,
128 01 Praha, Czech Republic

J. A. Elix
Research School of Chemistry, Building 33,
Australian National University,
Canberra, ACT 0200, Australia

Present Address:
S. Pérez-Ortega (✉)
Centro de Ciencias Medioambientales (CSIC),
c/Serrano 115 dpdo,
E-28006 Madrid, Spain
e-mail: sperezortega@ccma.csic.es

Present Address:
T. Spribille
Institute of Plant Sciences, University of Graz,
Holteigasse 6,
8010 Graz, Austria

van den Boom and Brand 2008) and is probably one of the best studied crustose lichen genera. *Lecanora*, in its traditional circumscription (Zahlbruckner 1926), has been recognized to be an artificial assemblage of species, and several genera have been split off over the years (Choisy 1929, 1949; Hafellner and Türk 2001; Kalb 1991; Motyka 1995, 1996a; Poelt 1983). Although the notion has prevailed that the remainder of *Lecanora* is still heterogeneous, few authors have attempted to split the rest of the genus into more natural units. Zahlbruckner (1926) distinguished several sections within *Lecanora*, and Poelt (1958) published an elaborate infrageneric classification of the lobate species. Eigler (1969) accepted deviating groups, such as *Aspicilia* A. Massal., *Haematomma* A. Massal., and *Harpidium* Körb., which had originally been described in the nineteenth century as separate genera, and split most of these, including *Lecanora* s.str. into “groups”. The last comprehensive attempt at a subgeneric classification of *Lecanora* was published by Motyka (1995, 1996a, b) who split several new or resurrected genera from *Lecanora* and divided the remainder of the genus into 14 sections.

Thallus morphology and secondary metabolites have traditionally been the most important characters for the separation of groups within *Lecanora*. However, based on chemical data, Brodo and Elix (1993) argued against a formal taxonomic recognition of species groups within *Lecanora*. Although the phylogenetic relationships among species groups are still largely unresolved, recent molecular studies indeed largely confirmed the notion that some are heterogeneous. Arup and Grube (1998) found the lobate subgenus *Placodium* paraphyletic and intermingled with species of the *L. varia* (Hoffm.) Ach., *L. dispersa* (Pers.) Sommerf. and *L. polytropa* (Hoffm.) Rabenh. groups and the genus *Arctopeltis* Poelt. The same authors demonstrated that *Rhizoplaca* Zopf is not monophyletic (Arup and Grube 2000) and concluded that thallus morphology does not reflect the phylogenetic relationships within the genus.

One of the species groups that has been treated by several authors in recent years is the ‘*Lecanora varia* group’. Choisy (1929) assigned *L. varia* to a new genus *Straminella* M. Choisy because of its yellow thallus colour (caused by usnic acid). Based mainly on pycnospore characters, Choisy (1949) assigned the members of the *Lecanora saligna* group to yet another new genus, *Lecanoropsis*, a name which was almost never subsequently used (except by, e.g., Weber and Wittmann 1992). Eigler (1969) accepted *Straminella* and assigned a number of other species with usnic acid, such as *L. conizaeoides* Nyl. ex Crombie, *L. expallens* Ach., *L. polytropa* (Hoffm.) Rabenh., *L. saligna* (Schrab.) Zahlbr., *L. subintricata* (Nyl.) Th. Fr. and *L. symmicta* (Ach.) Ach., to the genus, while Motyka (1996a, 1996b) distributed these species over several genera and sections. Recently, this “*Lecanora varia* group” has been studied by several authors.

Śliwa and Wetmore (2000) and Printzen (2001) treated all or a subset of the North American species, Laundon (2003a) discussed a set of 13 species and finally Martínez and Aragón (2004) revised the species occurring in the Iberian Peninsula. In the first two works, new, slightly deviating subgroups were proposed for the species putatively related to *L. varia*. Printzen (2001) doubted that the group is monophyletic and instead proposed four species groups mainly based on amphithecial characters: (1) *Lecanora brucei* (as *L. spec.* 1) and *L. symmicta* with a biatorine exciple, (2) *L. americana* (de Lesd.) Printzen, *L. confusa* Almb., *L. perconfusa* Printzen, *L. strobilina* (Spreng.) Kieffer and *L. substrobilina* with an ecorticate, lecanorine amphithecium, (3) *L. albellula* Nyl., *L. latens* Printzen, *L. mughicola* Nyl., *L. polytropa*, *L. saligna* and *L. subintricata* with an amphithecial cortex of more or less equal thickness, and (4) *L. coniferarum* Printzen, *L. densa* (Śliwa & Wetmore) Printzen, *L. laxa* (Śliwa & Wetmore) Printzen and *L. varia* with a basally thickened amphithecial cortex. The results of Arup and Grube (1998) already indicated that *L. symmicta*, *L. conizaeoides* and *L. varia* do not belong in the same clade within *Lecanora* but their study focused on lobate species of *Lecanora* and did not include more species of the group. In this study, we present a phylogenetic analysis of an extended sample of taxa from the “*L. varia* group” based on ITS sequences. Our main objective was to see whether *L. burgaziae* I. Martínez & Aragón, *L. densa*, *L. laxa* and *L. varia* are closely related species and form a monophyletic group. For this purpose, we have extended the available sequence data for *Lecanora* species with a focus on usnic acid-containing species. In order not to bias our taxon sampling towards the well-sampled groups within *Lecanora*, we left out some of the species that were included in the analyses of Arup and Grube (1998, 2000) and Grube et al. (2004). Our second intention was to see whether molecular data supported the species groups suggested by Printzen (2001). This objective was, however, somewhat impeded because we were unable to obtain fresh material or readable sequences from many of the relevant species. In the course of our work, two more species of the group from western North America came to our attention. One of them, *L. anopta*, had not been reported from continental North America, and a second, *L. schizochromatica*, is here formally described as new to science. The phylogenetic positions of both taxa were also analysed.

Materials and methods

Morphology and anatomy

Characteristics of the apothecia and thallus were investigated by light microscopy on hand-cut sections mounted in

water and 10% KOH, and stained with I Lugol (Merck 1.09261) or lactophenol cotton blue (LCB; Merck 1.13741). Photos were taken with a Zeiss Axioskop digital camera. Microscopic measurements were made at $\times 1,000$ magnification in water and are given as (smallest single measurement)–smallest mean–largest mean–(largest single measurement). The small and large means are based on ≥ 10 measurements on individual specimens. Nomenclature of non-soluble pigments follows Meyer and Printzen (2000). Thin layer chromatography was carried out according to Culberson (1972) and Culberson and Johnson (1982), and high performance liquid chromatography according to Elix et al. (2003).

Molecular analysis: DNA-isolation, PCR-amplification and sequencing

Specimens used for DNA extraction and sequencing are kept in FR (Herbarium Senckenbergianum), unless otherwise noted. DNA extraction was extracted from 1 or 2 apothecia per specimen. Apothecia were cut from the thallus with the help of a razor blade, moistened in a sterile water drop on a microscope slide and examined under the dissecting microscope in order to remove all possible contaminations such as detritus or epiphytic fungal hyphae. Samples were placed in 1.5-ml microcentrifuge tubes and DNA was extracted using either DNEasy Plant Mini Kit[®] (Qiagen) or NucleoSpin[®] Plant II (Macherey-Nagel) following the manufacturer's protocols with minor modifications. Sequences of the nuclear ribosomal ITS region were obtained using the primers ITS1F (Gardes and Bruns 1993) and ITS4 (White et al. 1990). PCR reactions were prepared for a final volume of 25 μ l, containing 2 μ l of each primer, 2 μ l of dNTPs (10 μ M), 2.5 μ l of Herculase[®] reaction buffer, 1.25 U of Herculase[®] enhanced polymerase (Stratagene), and 14.25 μ l of distilled water.

PCR amplifications were set up under the following conditions: one initial denaturing step at 94°C for 4 min followed by 6 touchdown cycles of 1 min at 94°C, 1 min at 62°C and 1 min 45 s at 72°C, decreasing the annealing temperature 1°C each cycle; 34 cycles of 30 s at 94°C, 30 s at 56°C and 1 min 45 s at 72°C; ending with an extension step of 10 min at 72°C, after which the samples were kept at 4°C. PCR products were extracted from the agarose gel and purified using either peqGOLD MicroSpin Gel Extraction Kit (Peqlab, Biotechnologie) or QIAquick[®] PCR purification Kit (QIAGEN 28106) following the manufacturer's instructions. PCR products were labelled using the Quick Start Kit (Beckman Coulter) and run on a CEQ[™] 8800 Genetic Analysis System (Beckman Coulter).

Sequence alignment and phylogenetic analysis

Sequence fragments obtained were checked, assembled and manually adjusted in SeqManII v.5.07[®] (DNASTAR). A

total of 29 newly obtained sequences were aligned together with 24 sequences retrieved from GenBank (Table 1). Sequence alignment was performed with Muscle v3.6 (Edgar 2004). Ambiguously aligned regions were removed from the alignment using Gblocks 0.91b (Castresana 2000), in which all parameters were set to fit minimal restrictions, yielding a final alignment of 441 bp. The species of the *L. subfusca* group were chosen as outgroup based on previous phylogenetic studies (Arup and Grube 1998, 2000).

Phylogenetic analyses were carried out using Metropolis coupled Bayesian Markov Chain Monte Carlo (MC)³ and Maximum Likelihood approaches, implemented in the software MrBayes v.3.1.2 (Huelsenbeck and Ronquist 2003) and PHYML v 2.4.4 (Guindon and Gascuel 2003), respectively. Separate nucleotide substitution models for each part of the nrITS region (ITS1, 5.8S, ITS2) were selected with the help of MrModelTest v2 (Nylander 2004) using the AIC as optimality criterion. The following substitution models were selected: GTR+ Γ for ITS1 and ITS2 and K80 for 5.8S.

For the (MC)³ analysis, the following settings were used. Substitution model parameters were unlinked across data partitions. Five parallel runs were started beginning with a random tree. Each run consisted of 6 incrementally heated chains using the default settings of MrBayes. Run length was preset to 6M generations sampling every 30th tree. To ensure that runs had converged, the average standard deviation of split frequencies for the five parallel runs was calculated every 100K generations discarding the first 25% of the tree sample as burn-in. Runs were stopped after 2M generations, when the standard deviation had dropped below the threshold of 0.01. A 50% majority-rule consensus tree with branch lengths, including all compatible groups with PP<0.5 was obtained from the 50K post-burn-in trees. The ML analysis was run with 1,000 bootstrap resamples using the GTR+ Γ +I substitution model (the closest approximation to the three models inferred for the three partitions of the ITS). The likelihood parameter scores were obtained in TRACER v1.4 (Rambaut and Drummond 2007). Phylogenetic trees were drawn with the program TreeView (Page 1996).

Results and discussion

We produced 29 new ITS sequences. The final alignment contained 53 sequences, with a total of 441 unambiguously aligned characters. The likelihood parameters of the Bayesian analysis are available upon request. The majority-rule consensus tree based on 50,000 trees from the (MC)³ sample is shown in Fig. 1. The ML analysis yielded a similar topology; branch support values for the (MC)³ (PP \geq 0.95) and the ML bootstrap analysis (BP \geq 70) are indicated above the branches. Bold branches have both

Table 1 Species of *Lecanora*, their origins, collectors, herbarium and accession numbers

Species	Country/State, Province	Collector, Herbarium	Accession number
<i>Lecanora achariana</i>	Germany, Hessen	<i>Ch. Printzen</i> s.n. (FR)	GU480092
<i>Lecanora aitema</i>	U.S.A., Arizona	<i>T.H. Nash 43991</i> (ASU)	GU480103
<i>Lecanora allophana</i>			AF070019
<i>Lecanora anopta</i> 1			AF159939
<i>Lecanora anopta</i> 2	Czech Republic	<i>Z. Palice</i> s.n. (hb. Palice)	GU480114
<i>Lecanora anopta</i> 3	Canada, British Columbia	<i>T. Spribille 16580</i> (FR)	GU480115
<i>Lecanora austrocalifornica</i>	Canada, Yukon Territory	<i>T. Spribille 25131</i> (hb. Spribille)	GU480116
<i>Lecanora burgaziae</i> 1	Spain, Cáceres	<i>S. Pérez-Ortega LB46</i> (FR)	GU480117
<i>Lecanora burgaziae</i> 2	Spain, Toledo	<i>S. Pérez-Ortega LB61</i> (FR)	GU480118
<i>Lecanora campestris</i>			AF159930
<i>Lecanora cf. fulvastra</i>	Cuba, Pinar del Río	<i>S. Pérez-Ortega 1159</i> (FR)	GU480119
<i>Lecanora concolor</i>			AF070037
<i>Lecanora confusa</i> 1	U.K., Scotland	<i>B.J. & A.M. Coppins</i> s.n. (E)	GU480120
<i>Lecanora confusa</i> 2	U.S.A., Montana	<i>S. Pérez-Ortega 1158 & T. Spribille</i> (FR)	GU480093
<i>Lecanora conizaeoides</i>			AF189717
<i>Lecanora densa</i> 1	U.S.A., Colorado	<i>S. Pérez-Ortega LD221</i> (FR)	GU480094
<i>Lecanora densa</i> 2	U.S.A., New Mexico	<i>S. Pérez-Ortega LD185</i> (FR)	GU480095
<i>Lecanora densa</i> 3	U.S.A., Arizona	<i>S. Pérez-Ortega LD171</i> (FR)	GU480096
<i>Lecanora densa</i> 4	U.S.A., Montana	<i>S. Pérez-Ortega LD128 & T. Spribille</i> (FR)	GU480097
<i>Lecanora dispersoareolata</i>			AF070016
<i>Lecanora epibryon</i>			DQ534469
<i>Lecanora</i> aff. <i>expallens</i>	Denmark, Hovedstaden	<i>S. Pérez-Ortega 1170 & U. Sochting</i> (FR)	GU480098
<i>Lecanora filamentosa</i> 1	Germany, Niedersachsen	<i>R. Cezanne & M. Eichler 6761</i> (FR, as <i>Lecidea hercynica</i> , topotype)	GU480099
<i>Lecanora filamentosa</i> 2	Czech Republic, W. Bohemia	<i>Ch. Printzen</i> s.n. (FR)	GU480100
<i>Lecanora flavoleprosa</i>	Poland	<i>P. Czarnota</i> s.n. (GPN)	GU480101
<i>Lecanora garovaglii</i>			AF070034
<i>Lecanora intricata</i>			AF189718
<i>Lecanora laxa</i> 1			AY398703
<i>Lecanora laxa</i> 2	U.S.A., Colorado	<i>S. Pérez-Ortega LL34</i> (FR)	GU480102
<i>Lecanora laxa</i> 3	U.S.A., Colorado	<i>S. Pérez-Ortega LL35</i> (FR)	GU480104
<i>Lecanora laxa</i> 4	U.S.A., Colorado	<i>S. Pérez-Ortega LL36</i> (FR)	GU480105
<i>Lecanora laxa</i> 5	U.S.A., Colorado	<i>S. Pérez-Ortega LL2</i> (FR)	GU480106
<i>Lecanora muralis</i>	U.S.A., Colorado	<i>S. Pérez-Ortega LL4</i> (FR)	GU480107
<i>Lecanora novomexicana</i>			AF159922
<i>Lecanora opiniconensis</i>			AF159923
<i>Lecanora orosthea</i>			AF159928
<i>Lecanora perpruinosa</i>			AY398701
<i>Lecanora polytropa</i> 1			AF070025
<i>Lecanora polytropa</i> 2			DQ534470
<i>Lecanora pruinosa</i>			AF070017
<i>Lecanora saligna</i> 1			AF070018
<i>Lecanora saligna</i> 2	U.S.A., New Mexico	<i>S. Pérez-Ortega 1161</i> (FR)	GU480108
<i>Lecanora semipallida</i> (sub <i>L. flotowiana</i>)			AF189716
<i>Lecanora schizochromatica</i> 1	Canada, British Columbia	<i>T. Spribille 17016</i> (hb. Spribille)	GU480109
<i>Lecanora schizochromatica</i> 2	Canada, British Columbia	<i>T. Spribille 16850-A</i> (hb. Spribille)	GU480110
<i>Lecanora subintricata</i> 1	U.S.A., Arizona	<i>S. Pérez-Ortega 1162</i> (FR)	GU480111
<i>Lecanora subintricata</i> 2	Canada, Alberta	<i>T. Spribille 10287</i> s.n. (hb. Spribille)	GU480112
<i>Lecanora sulphurea</i>			AF070030

Table 1 (continued)

Species	Country/State, Province	Collector, Herbarium	Accession number
<i>Lecanora symmicta</i> 1	Germany, Hessen	Ch. Printzen s.n. (FR)	GU480113
<i>Lecanora symmicta</i> 2			AF070024
<i>Lecanora varia</i> 1			AF070028
<i>Lecanora varia</i> 2			AF070027
<i>Lecanora varia</i> 3			AF070021

PP and BP values above these thresholds and are considered to be well supported.

Three species of the *L. subfusca* group were chosen as outgroup based on previous phylogenetic analyses (Arup and Grube 1998, 2000). These species (*L. epibryon*, *L. allophana* and *L. campestris*) form a monophyletic group (PP=1, BP=100). The rest of the species are distributed over three well supported clades but the relationships among these clades are unresolved (Fig. 1). The new species *L. schizochromatica* belongs to clade 1 (PP=1, BP=100), which also comprises *L. filamentosa* and *L. expallens*. The relationship between clade 1 and the *L. symmicta* group (clade 2) has no support.

Clade 2 (PP=1, BP=100) consists of the saxicolous species *L. orosthea* and *L. sulphurea*, as well as the epiphytic *L. aitema*, *L. confusa*, *L. flavoleprosa*, *L. symmicta* and a sister clade made up of the two epiphytic species *L. cf. fulvastra* collected in western Cuba and characterised by the presence of calycin, and *L. austrocalifornica* Lendemer & K. Knudsen. The third highly supported clade (PP=1, BP=94) combines the rest of the species, and falls into *Protoparmeliopsis* s. lat. and the *L. varia*, *L. dispersa*, *L. saligna*, *Placodium*, and *L. varia* groups.

Species belonging to the *dispersa* group (*L. semipallida*, *L. perpruinosa* and *L. pruinosa*) form a strongly supported clade (PP=1, BP=99) sister to *Protoparmeliopsis* (PP=1; BP=88), agreeing with results in Grube et al. (2004). *Protoparmeliopsis* is also well supported (PP=1; BP=96) and includes the lobate species *P. muralis*, *P. achariana* and *L. garovaglii*. The '*L. varia* clade' is also well supported (PP=1; BP=89), but the relationships of this group within clade 3 lacked statistical support. Previous studies (Arup and Grube 1998, 2000) also failed in assessing the natural relationship of this group to others within *Lecanora*.

None of the other groups receives statistical support, indicating that more genetic loci and perhaps a more comprehensive taxon sampling are necessary to resolve their relationships. Nevertheless, there is independent morphological evidence to support some of the groups. For example, the two lobate species, *L. novomexicana* and *L. opiniconensis* included in the subgenus *Placodium*, group together, as do two species of *L. saligna*, *L. anopta* and *L. saligna*, both

with isousnic acid. *Lecanora subintricata* also produces isousnic acid but it is unclear whether it belongs in the same group. In a preliminary analysis based on a slightly different taxon sample, it grouped with *L. anopta*, although also with low support.

Finally, two different clades can be distinguished in the '*L. varia* group'. The first of them (PP=1, BP=0.98) comprises four taxa closely related to *L. varia*. *Lecanora conizaeoides*, a species that is morphologically very similar to *L. varia* but distinguished among other things by containing fumarprotocetraric acid, is basal to the rest of the species within the clade. GenBank sequences of *Lecanora varia* appear paraphyletic with *L. densa* and two specimens of *L. burgaziae*, a recently described species from the Iberian Peninsula, intermixed. The second clade combines five collections of the epiphytic *L. laxa*.

Our results illustrate that the taxonomy and systematics of the *Lecanora varia* group are still in need of revision. This involves species delimitation as well as the distinction of phylogenetic groups. A number of recently described species (e.g. *L. burgaziae*) are probably synonymous with known species. The nomenclatural implications arising from our analysis will be treated in a separate contribution. However, there are not only new synonymies but also new species to science that have come to light recently, including *Lecanora schizochromatica*, described below, and *L. austrocalifornica* (Lendemer and Knudsen 2009).

The distinction of species groups within the large genus *Lecanora* is a long-standing problem, as the previous attempts by Eigler (1969) and Motyka (1995, 1996a, b) illustrate, and seems at least partly due to highly homoplasious morphological characters. Clades one and two of our analyses separate *L. symmicta* from the morphologically very similar *L. schizochromatica* and *L. filamentosa*. Because of their similar apothecial anatomy, *L. filamentosa* (as *L. ramulicola*) was regarded as a member of the *L. symmicta* group by Printzen and May (2002). However, it was noted that this species produced atranorin as major secondary compound and usnic acid only in trace amounts. Atranorin is also produced in *L. schizochromatica*, which indicates that secondary chemistry could be a good character to separate phylogenetically related groups within *Lecanora*. However, *L. expallens* which is sister to *L. filamentosa*

produces usnic acid as major compound. Further, the only species of the *Lecanora varia* group s. lat. that produce fumarprotocetraric acid, *L. conizaeoides* and *L. austrocalifornica*, belong to two different highly supported groups of species: *L. conizaeoides* is closely related to *L. varia* whereas *L. austrocalifornica* is sister to *L. cf. fulvastra* from Cuba. Then again, *L. varia*, *L. densa*, and *L. burgaziae*, the three species in our dataset that produce psoromic acid as major secondary compound, form a well-supported monophyletic group. The distinction between *L. burgaziae*, *L. densa* and *L. varia* will form part of a future study. In our analysis, *L. burgaziae* appears as sister to two sequences of *L. varia*, but a third GenBank sequence of *L. varia* appears basal to the clade formed by *L. burgaziae*, *L. densa* and *L. varia*. Finally, five sequences of *Lecanora laxa*, described as a subspecies of *L. varia*, form a well-supported clade outside *L. densa*, *L. varia* and *L. conizaeoides*, contradicting the statement in Laundon (2003a) that *L. laxa* is a psoromic acid-deficient chemomorph of *L. densa*, and hence it merits species rank. A closer relationship between *L. laxa* and *L. coniferarum* than between *L. laxa* and *L. varia* was previously anticipated by Printzen (2001). Unfortunately, *L. coniferarum* is lacking from our dataset.

To conclude, the species groups distinguished recently within the *Lecanora varia* group (Śliwa and Wetmore 2000, Printzen 2001) are in need of revision. As the backbone of clade three is still poorly supported, more gene loci should be included in future studies. Finally, taxon sampling may have to be improved to come to a stable systematic solution for the *Lecanora varia* group, as has been demonstrated in other taxonomic groups (Lumbsch et al. 2007). In order to achieve this, intense field work, even in the comparatively well-explored regions of Europe and western North America, will be necessary.

Taxonomy

Lecanora anopta Nyl., Flora 56: 292 (1873) (Fig. 2)

Syn. Biatora pullula Tuck., Synopsis North Amer. Lich. II: 129 (1888). **Type:** Washington Terry. [sic], 1882, *W.N. Suksdorf 200* (FH!, holotype). Isousnic acid was detected by HPLC.

Syn. Lecidea pullula (Tuck.) Zahlbr., Cat. Lich. Univ. 3: 814.

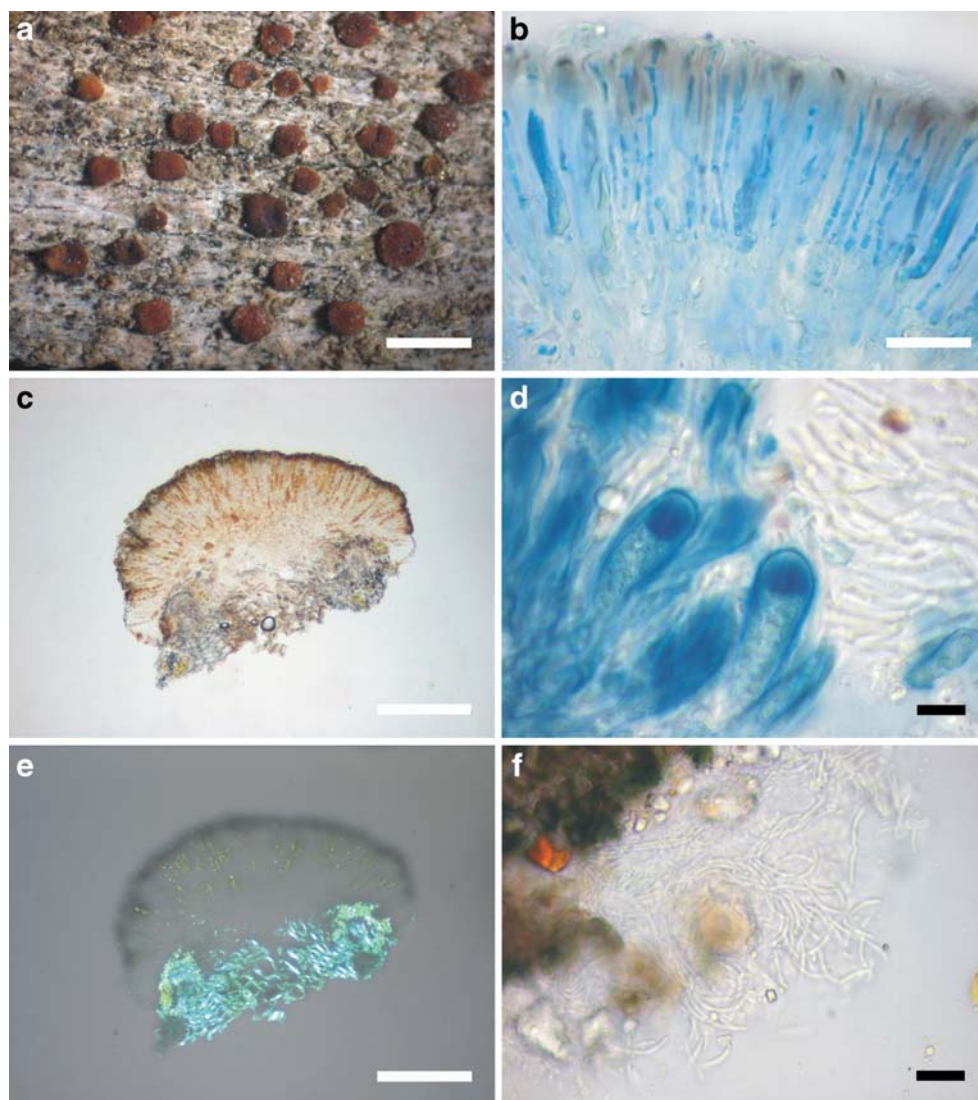
Description Thallus immersed, rarely superficial in small patches, then thin and creamish white, soredia and isidia absent; photobiont trebouxoid, (8.0–)10.7–12.5(–17.0) μm diam.; apothecia rounded, mostly single or in groups of 2–3, to 68–184 per cm^2 , broadly adnate, (0.38–)0.45–0.53 (–0.64) mm diam.; disc matt, epruinose to strongly pruinose, flat to strongly convex, pale to dark reddish

brown (Fig. 2a) to greyish/greenish black; thalline margin distinctly present only on young apothecia, in mature apothecia usually poorly developed, quickly receding but rarely preserved until maturity; proper margin inconspicuous when viewed from above, matt, creamish, receding in older apothecia; proper exciple in section (40–)45.5–59(–75) μm wide laterally, (27–)34–68(–190) μm measured at thickest point at base, strongly gelatinised, with POL+ interhyphal crystals that vary in quantity, sometimes only found at base of stipe (Fig. 2e), these dissolving in K; algae occasionally present in same area; exciple of thick-walled, branched, radiating hyphae with lumina 1.5–2.0 μm , terminal cell with lumen occasionally up to 5.0 μm , unpigmented or pale brownish to rarely dark greenish (HNO₃+ reddish *cinereorufa*-green pigment occasionally present), IKI-; hypothecium 50–130 μm tall, colourless; subhymenium consisting of thickened ascogenous hyphae, well differentiated, 20–37 μm tall, colourless; hymenium (40–)44–51(–55) μm tall, strongly interspersed with yellowish brown grana (guttulae sensu Hedlund 1892) apparently derived from lumina of old ascospores or ascogenous hyphae (Fig. 2c), sclerotised parts dissolving in K; hymenium also with brown to green-black pigment streaks in upper 1/3–1/5 and 5–12 μm of K+olivaceous, greyish-olivaceous pigments; granular epihymenium±present; paraphyses commonly branched, sometimes anastomosed, colourless or with faint brown to blue-green pigment in outer gel sheath at tips, to 2 μm , lumina ca. 0.5–1.5 μm wide, apically to 2.0 μm wide, lumina to 1.3–2.0 μm ; asci similar to *Micarea*-type, 30–41×10.0–12.2 μm (Fig. 2d); ascospores 8 per ascus, colourless, simple, ellipsoid, (7.0–)8.5–10.0(–12.0) × (3.0–)4.2–5.4 (–6.0) μm . Pycnidia infrequent, black, half immersed, globose to pyriform, 60–90 μm in diam., walls brown to dark greenish, HNO₃+ reddish/purplish (due to the presence of *cinereorufa* green pigment), more intensively coloured apically to almost colourless basally, paraplectenchymatous; conidia bacilliform, gently curved, 7–9 × 1 μm (Fig. 2f).

Chemistry Isousnic acid (major).

Additional specimens examined CANADA. Alberta. Kananaskis area, Rocky Creek, east of Hwy 40 (Kananaskis Trail Hwy.) and north of Peter Lougheed Provincial Park, 50°51'N, 115°10'W, calcareous cliffs along the creek in a lush *Pinus contorta*, *Picea glauca*, *Populus balsamifera*, *Shepherdia canadensis* forest, 18 Jun 1986, J.E. Marsh 1958 (CANL, filed under *Xylographa parallela*); British Columbia. Purcell Mountains, Toby Creek canyon, on wood of abandoned bridge, 20 Jul 2004, T. Spribille 15313 & T. Goward (CANL); East Kootenays, E of Canal Flats, Moscow Road, 50° 13.373'N, 115°28.556'W, on rotten log, 1,170 m, 27 Jul 2005, T. Spribille 16546 (UBC); *ibid.*, on wood of stump, T. Spribille 16580 (hb. Spribille); *ibid.*, Moscow Road fen, on lignum in fen, 27 Jul 2005, T. Spribille 16509 & C.R. Björk

Fig. 2 *Lecanora anopta*. **a** Habit (*Spribille 25131*), **b** hymenium in LCB (*Spribille 16580*). **c,e** section of apothecium in normal light (**c**) and polarised light (**e**) (both *Spribille 16580*), **d** asci, in Lugol's (*Spribille 16580*), **f** conidia, in water (*Spribille 25131*). Scale bars **a**, 1 mm, **b,d**, **f** 10 μ m, **c,e** 200 μ m



(CANL); Liard Plain, Dease River area, 5 mi N of Baking Powder Creek, 14 mi N of Boya Lake along Cassiar Hwy., 59°32.780'N, 129°14.067'W, on rotten log in open sandy *Pinus contorta* forest, 710 m, 9 Oct 2007, *T. Spribille 25131* (CANL, FR, PRA); Yukon. ALCAN Highway, S of Johnson's Landing near Teslin Lake, 60°28.641'N, 133°16.527'W, on decorticated *Picea glauca* branch, 719 m, 8 Oct 2007, *T. Spribille 27075* (CANL, FR, PRA); same locality and day, *T. Spribille 25077* (GZU). U.S.A. Montana. Lincoln Co., S of Trego, Brimstone Creek, on decorticated log, 2 Jun 2004, *T. Spribille 13828* (hb. Spribille).

Lecanora anopta was recently reported from Greenland (Hansen 2004), and is here reported as new to continental North America. It is a locally common species found on conifer wood in sub-continental forests of the Rocky Mountain Trench and the southern Yukon south to Washington (where it appears to be rare) and northwestern Montana. *Lecanora anopta* could easily be confused with a species of *Lecidea* s. lat., because it often lacks the thalline

margin normally associated with *Lecanora* species. It is similar to *Lecanora saligna* but likewise differs in the evanescent thalline margin. The ascus is also somewhat atypical of *Lecanora* (Fig. 2D). The species can be recognized most readily by the diagnostic presence of sclerotised grains (old spores) in the hymenium (only rarely absent) and the presence of isousnic acid. In habit it somewhat resembles *Lecanora cadubriae*, but that species can readily be distinguished by the presence of norstictic acid (K+ orange to red on the thallus, K+ red needles in section). Specimens with pruinose apothecia may be reminiscent of *Lecanora sarcopoidoides* (A. Massal.) A.L. Sm., a species thus far known only from Europe which, however, has narrower ascospores and contains pseudopla-codiolic acid as the major constituent (van den Boom and Brand 2008). Small specimens with reddish apothecia can resemble *Lecidea rubrocastanea* (Spribille and Printzen 2007), but differ in the longer, narrowly ellipsoid ascospores (8.5–10 μ m vs 6–8 μ m in *L. rubrocastanea*), the

nearly *Micarea*-like as opposed to *Lecidella*-type ascus, and the presence of isousnic acid.

Notes The description given above refers to examined North American material. In Fennoscandia and the Alps, *L. anopta* has been found to be a very variable species in terms of thallus development, pigmentation, and size of apothecia/ascospores as well as apothecial anatomy (both lecanorine and lecideine may occur) (Hedlund 1892). Well-developed European specimens issued in various exsiccata often contain cinereorufa-green pigment in apothecia and pycnidia. Large dark pycnidia are often present and contain characteristic shorter and slightly curved pycnosporangia (?mesoconidia), which have so far not been detected in material from North America. Also, the ascospores of European specimens may be slightly larger (see Hedlund 1892, but see also description of *Lecanora anopta* by Nylander 1873). Hedlund (1892) described several morphotypes, but North American specimens collected to date seem to display only part of the known variability of the species and might be referable to f. 1 sensu Hedlund (1892). However, our ITS sequence data indicate that samples from the two continents differ in only a few nucleotides. The nomenclatural status of *Lecanora anopta* is not yet resolved. Several names are applicable. *L. anopta* is the same as the species mentioned as '*Lecanora cadubrioides ined.*' by Spribille et al. (2008, in supplementary material).

Lecanora filamentosa (Stirt.) Elix & Palice comb. nov

Basionym

Lecidea filamentosa Stirt., Scottish Naturalist 5: 218 [“1879”] (1880).

Type

Scotland, Glen Lochay, Killin, 21 July 1879, *Stirton* (GLAM—NHB. 1927. 8.01010!—lectotype selected here—atranorin, usnic acid, paraensic acids C and D detected by HPLC; BM 731241!—isolectotype)

Lecidea filamentosa Stirt. appears to be the oldest valid name for *Lecanora ramulicola* (H. Magn.) Printzen & P.F. May (Printzen and May 2002), hence a new combination is introduced here.

Lecanora schizochromatica Pérez-Ortega, T.Sprib. & Printzen, sp. nov. (Fig. 3)

Mycobank accession number MB 513164

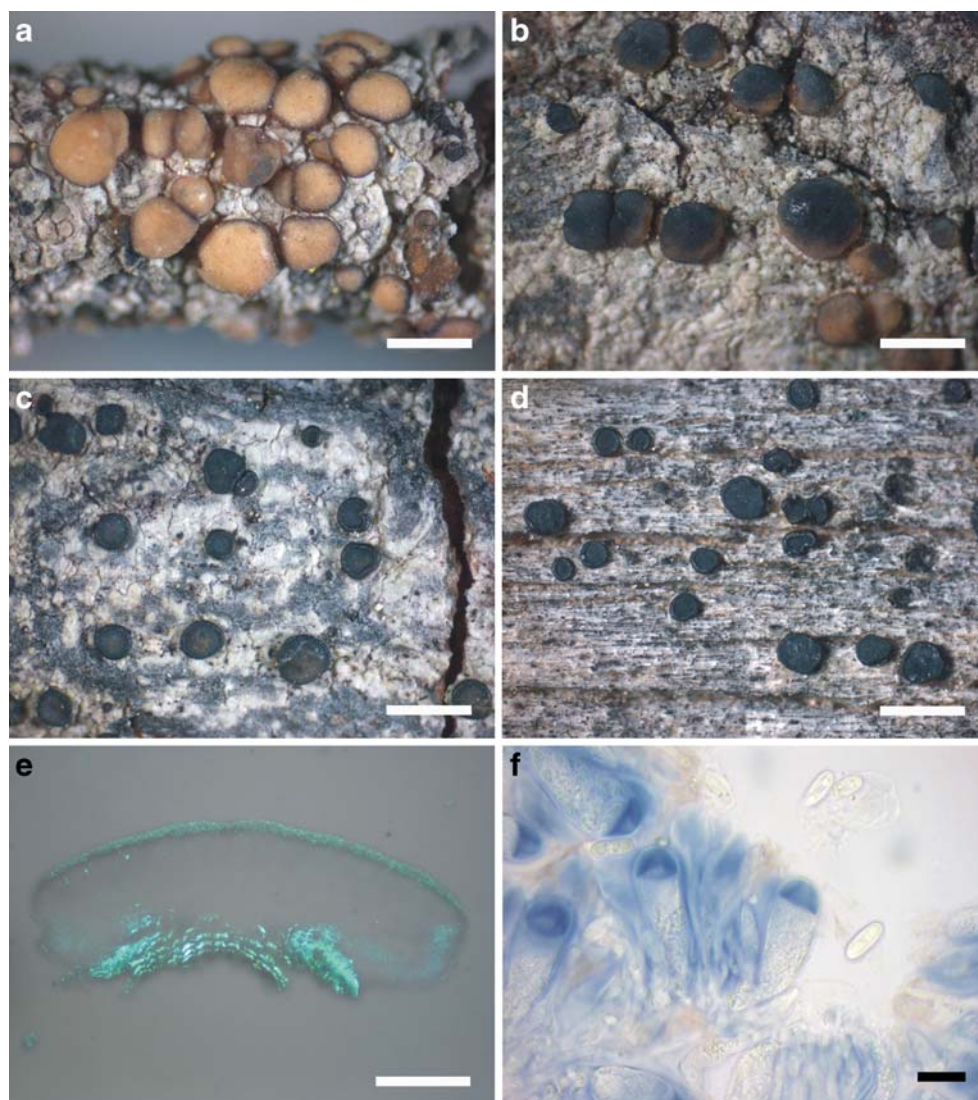
Diagnosis Species *Lecanorae filamentosae* similis sed ascosporis minoribus (9.7–11.1 × 3.5–4.1 μm). Margo

apotheciorum saepe nigrescens. A *L. symmicta* differt substantia major atranorinum continens.

Type Canada. British Columbia. Purcell Mountains, St. Mary's Alpine Provincial Park, trail to Mortar Lake, 49° 51.421'N, 116°24.433'W, corticolous on twigs and branches of *Picea engelmannii* and *Abies lasiocarpa* s.lat. in upper subalpine parkland, 2,380 m, 6 Jul 2006, T. Spribille 19965 & V. Wagner (CANL, holotype; FR, GZU, UBC, isotypes).

Description Thallus crustose, rimose to cracked-rimose or verrucose areolate, rarely immersed (on wood), soredia and isidia absent; areoles roundish, 0.14–0.2 mm diam., weakly to strongly convex, surface white or whitish grey or greenish white, roughened; hypothallus rarely present, if present then black; photobiont trebouxoid, (6.0–)10.1–14.0 (–17.0) μm diam.; apothecia rounded except when grouped, single or paired, less frequently aggregated in groups of 3–12, sessile with constricted base, (0.3–)0.5–0.9(–1.4) mm; disc matt, epruinose to finely pruinose, colour variable, from 'usnic yellow' to slate grey to bluish grey to greenish black to jet black or reddish brown (Fig. 3a–d), flat to concave in young apothecia, weakly to strongly convex in mature apothecia; proper margin prominent when young, translucent grey to jet black, shiny, receding when older or retained as a thin black line; proper exciple in section (40–)49–69(–90) μm wide laterally, (60–)68–119(–150) μm measured at thickest point at base, strongly gelatinised, of thick-walled, dichotomously branched and anastomosing hyphae with narrow, linear lumina ca. 1 μm wide, exciple filled with fine, less than 0.5 μm in diam, colourless, POL+ granular crystals (Fig. 3e), usually hazy brown within, with or without blue-green, HNO₃+ reddish pigment in outer parts, IKI-; algae present or absent around base of inner exciple; exciple externally sometimes with colourless, cutical-like coating to 25 μm thick; hypothecium 50–150 μm tall, colourless; subhymenium consisting of thickened ascogenous hyphae, well differentiated, (10–)30–80 μm tall, colourless, sometimes with small oily droplets; hymenium (37–)40–58 μm tall, colourless or with pale bluish-green, K+ greenish, HNO₃+ reddish mauve pigmentation in upper 1/4 or 1/5, occasionally hazy brownish; epihymenium 3–5(–7) μm thick, granular, POL+, rarely streaking into hymenium; paraphyses simple or weakly branched, colourless or with faint brown pigment in outer gel sheath at tips, lumina 0.8–1.0 μm wide, apically often unthickened or 2–3 μm wide, lumina to 1.5–2.0 μm wide; asci *Lecanora*-type, 32–41 × 9.3–12.0 μm (Fig. 3f); ascospores 8 per ascus, colourless, simple, narrowly ellipsoid, (8.0–)9.7–11.1(–12.0) × (3.0–)3.5–4.1(–5.0) μm. Pycnidia infrequent, black, immersed in part, pyriform, to 220 μm diam., walls brown, paraplectenchymatous; conidia filiform, straight or slightly curved, 10–16 × ca. 0.7 μm.

Fig. 3 *Lecanora schizochromatica*. **a–d** Habit under different exposure conditions (**a** holotype, **b,c** *Spribille* 22575, **d** *Spribille* 15823), **e** section of apothecium in polarised light (*Spribille* 22575), **f** asci and ascospores in Lugol's solution (*Spribille* 13986). Scale bars **a–d** 1 mm, **e** 200 μ m, **f** 10 μ m



Chemistry Atranorin (major), usnic acid (major) and paraensic acids C and D (minor) (HPLC). (The last two substances of aliphatic character seem to be confined to apothecia and apparently form tiny droplets in exciple.)

Etymology The name makes a reference to the highly variable colour of the apothecial disc and proper exciple (Fig. 3a–d).

Additional specimens examined CANADA. British Columbia. East Kootenays, Moyie Lake SW of Cranbrook, corticolous on *Larix occidentalis*, 25 Aug 2003, *T. Spribille* 12760 & *C.R. Björk* (GZU); Central Interior, Upper Clearwater Valley, road to Phillips Creek, on fencepost, 6 Sep 2004, *T. Spribille* 15823 & *C.R. Björk* (CANL); Rocky Mountains, Albert River, 50°36.575'N, 115°33.229'W, corticolous on branches of *Betula*, 1,190 m, 30 Jul 2005, *T. Spribille* 16580-A (CANL); Skeena River valley, Keynton Lake, 55°12.332'N, 127°46.136'W, on *Pinus*

contorta twigs, 375 m, 26 Aug 2006, *T. Spribille* 22575 (CANL); East Kootenay region, near Yahk, on *Pseudotsuga menziesii* twigs, 12 Jun 2004, *T. Spribille* 13986 (CANL); Skookumchuck area, 49°57.826'N, 115°49.204'W, on *Pseudotsuga menziesii* twigs, 1,275 m, 02 Aug 2005, *T. Spribille* 17016 (UBC); Glacier National Park, Bald Mountain, 2,315 m, on branch of *Abies [lasiocarpa]*, *T. Goward* 05-526 (UBC); Shallow Lake, near Fraser border crossing, 59°43.478'N, 135°00.542'W, corticolous on *Abies lasiocarpa*, 835 m, 8 Oct 2007, *T. Spribille* 25019 (CANL); U.S.A. Alaska. Near Skagway, on bark of *Betula*, *T. Tønsberg* 32809 (BG); east side of White Pass, 59°36.754'N, 135°07.056'W, corticolous on *Abies lasiocarpa*, 966 m, 11 Sep 2008, *T. Spribille* 29396 (BG, hb. Klondike Gold Rush Natl Historic Park); Idaho. Bonner Co., on Gisborne Mtn., Priest River Experimental Forest, 48°21'N 116°46'W, bark of *Abies lasiocarpa*, 4,900 ft. 18 Jul 1969, *T.L. Esslinger* 1937 (ID); Montana. Flathead Co., Salish Mtns., near confluence of Lime and Magnesia

Creeks, Collins Ranch, 48°38.793'N, 114°53.180'W, on *Pinus ponderosa* twigs, 1010 m, 20 Jul 2006, *T. Spribille 20252* & *S. Pérez-Ortega* (to be issued in exsiccate *Dupla Graecensia Lichenum*); Lincoln Co., Fortine Creek, on *Betula glandulosa* twigs, 18 Aug 1997, *T. Spribille 7360* & *H.G. Stroh* (GZU); *ibid.*, Salish Mtns. near Mineral Mountain, 01 Jun 2004, *T. Spribille 13804* (GZU); Missoula Co., Jocko Falls, 47°13.876'N, 113°48.130'W, corticolous and lignicolous on *Pseudotsuga* twigs, 1,330 m, 25 Jul 2006, *T. Spribille 20621*, *S. Pérez-Ortega* & *T. Wheeler* (GZU); Ravalli Co., Bitterroot Range, S shore of Lake Como near W end, on *Pinus contorta* twigs, 1370 m, 20 Jul 1981, *B. McCune 11259* (hb. McCune); Oregon. Josephine Co., Siskiyou Mtns., Klamath Range, Grayback Creek near road crossing, 19 km E of Cave Junction, 42°09.22'N 123°24.15'W, on evergreen *Quercus* branch, 670 m, Jun 1996, *B. McCune 23085* (hb. McCune); Linn Co., Cascade Range, E ridge of Squaw Mt., 44°20' N, 122°09' W, on *Abies* trunk, 1,500 m, Sep 1996, *B. McCune 23210* (FR); Washington. Lewis Co., Chehalis, on Douglas-fir, *L. Berglund s.n.* OSC-86795; Skamania Co., Wind River Canopy Crane Research Facility, 45°49'N, 121°57'W, on bark, 355 m, 1996, *B. McCune 25137* (hb. McCune).

Notes Lecanora schizochromatica is one of the most common epiphytic lichen species in mesic forests of the inland Pacific Northwest of USA and adjacent southwestern Canada, known from around 41°N to over 60°N. It is also one of the most commonly misidentified lichens, having been labelled and reported as *Lecanora symmicta* (Noble 1982, pro parte), *Lecidea carnulenta* (Fink 1935), *Lecidea paddensis* (misapplied, in herb.), and *Ramboldia elabens* (syn. *Lecidea elabens*; e.g. McCune 1982, DeBolt and McCune 1993). *Ramboldia elabens* is only distantly related and, after review of hundreds of specimens, is still not known to occur in North America west of the Black Hills (Spribille, unpublished). More recently, *L. schizochromatica* has also been reported under the names *Lecanora spec. A* (Hauck and Spribille 2005), *Lecanora 'meliocarpella'* nom. nud. (Spribille 2006), *Lecanora sp. 1* (Houde et al. 2007) and *Lecanora ramulicola* s. lat. (Bunnell et al. 2008).

Amazingly, *L. schizochromatica* does not appear to have been assigned a name in the early days of Pacific Northwest lichen taxonomy. All the species described by Tuckerman (1888, i.a.) based on material collected by Wilhelm Suksdorf in the then Washington Territory have turned out to refer to other species of lecideoid lichens, including *Biatora pullula*, which is a later synonym of *Lecanora anoapta* (see that species). *Lecidea carnulenta*, described from New Hampshire (type: FH!) and widely applied based on its inclusion in the keys of Fink (1935), is possibly related to *L. symmictella* and is distinguished from *L. schizochromatica* amongst other things by its *Porpidia*-

type ascus s.lat. Young apothecia of *L. schizochromatica* can also be confused with those of *Cliostomum griffithii*, which likewise have a greyish exciple and beige disc, but that species can be easily distinguished by its 1-septate ascospores and *Bacidia*-type asci, and it frequently possesses large pycnidia with a K+ purple pigment. The most likely species to be confused with *L. schizochromatica* is *L. filamentosa*. This species differs in having larger ascospores averaging 10–16×3.5–5.5 µm. Young apothecia of both species are usually pale beige to ochre and darken with age until they may eventually become completely black. In *L. schizochromatica*, the margin is usually darker than the disc and the first part to become black (Fig. 1 a, c, d), whereas margin and disc in *L. filamentosa* usually do not differ markedly or the margin is paler. Young apothecia of *L. filamentosa* usually have a lecanorine amphithegium that is lacking in *L. schizochromatica*. Specimens of *L. schizochromatica* with black apothecia contain higher concentrations of the pigment *cinereorufa* green (K+ greenish, HNO₃+ reddish in section) and are usually found in highly exposed sites. *Cinereorufa* green is also present in shade specimens but is then often confined to the margins.

Several specimens of *L. schizochromatica* exposed to sunlight, particularly on exposed wood at high elevations, are aberrant in either lacking fine crystals in the excipulum (*McCune 12721*, hb. McCune) or in having slightly larger ascospores 11–14×3.5–5.0 µm and a thicker lateral exciple, 90–170 µm wide (*Spribille 20071*, CANL). Some specimens from southern areas are also aberrant, as with two specimens from California that can only tentatively be assigned here on account of the presence of fine crystals in the hymenium (Trinity Co., *Spribille 18405*, GZU) or strongly swollen paraphyses (Del Norte Co., *Muggia s.n.*, TSB-38880). More specimens and study is required to assess variability at the geographical and ecological fringes of this species group.

Distribution and ecology Lecanora schizochromatica occurs in open, well-ventilated habitats on bark and wood of conifers from sea level (in Alaska) to the timberline (to 2,400 m asl). It is a reliable member of a well characterized and colourful species assemblage comprised to a large degree of species endemic to western North America or with their main global distribution there, including *Bryoria fremontii* (Tuck.) Brodo & D. Hawksw., *Kaernefeltia merrillii* (Du Rietz) A. Thell & Goward, *Vulpicida canadensis* (Räsänen) J.-E. Mattsson & M.J. Lai, *Tuckermannopsis platyphylla* (Tuck.) Hale, *T. orbata* (Nyl.) M.J. Lai, *Hypogymnia imshaugii* Krog s.lat., *H. occidentalis* L. H. Pike, *Lecanora laxa* (Śliwa & Wetmore) Printzen, *Ramboldia gowardiana* (T. Sprib. & Hauck) Kalb, Lumbsch & Elix, and *Lecidea rubrocastanea* T. Sprib. & Printzen.

Acknowledgments Our thanks are due to the curators of BM, CANL, FH and GLAM and to Curtis Björk, Trevor Goward, Bruce McCune, and Lucia Muggia for allowing us to cite their material. We are also grateful to Lucia Muggia and an anonymous referee for their valuable comments. S.P.O. is indebted to the Ministerio de Educación y Ciencia (Spain) for a postdoctoral grant and C.P. to the Deutsche Forschungsgemeinschaft for funding the project PR 567/9-1. Z.P. acknowledges the Grant Agency of the Academy of Sciences of the Czech Republic (KJB600050635), and continuing support by the Academy of the Czech Republic (AV0Z60050516) and by the Ministry of Education, Youth and Sports of the Czech Republic (0021620828). Z.P. also thanks Fredrik Jonsson who first showed him the species in the field.

References

- Arup U, Grube M (1998) Molecular systematics of *Lecanora* subgenus *Placodium*. *Lichenologist* 30:415–425
- Arup U, Grube M (2000) Is *Rhizoplaca* (Lecanorales, lichenized Ascomycota) a monophyletic genus? *Can J Bot* 78:318–327
- Brodo IM (1984) The North American species of the *Lecanora subfusca* group. In: Hertel H, Oberwinkler F (eds) Beiträge zur Lichenologie. Festschrift J. Poelt. Beiheft zur Nova Hedwigia 79. Cramer, Vaduz, pp 63–185
- Brodo IM, Elix JA (1993) *Lecanora jamesii* and the relationship between *Lecanora* s. str. and *Straminella*. *Bibl Lichenol* 53:19–25
- Brodo IM, Owe-Larsson B, Lumbsch HT (1994) The sorediate, saxicolous species of the *Lecanora subfusca* group in Europe. *Nord J Bot* 14:451–461
- Bunnell FL, Spribille T, Houde I, Goward T, Björk C (2008) Lichens on down wood in logged and unlogged forest stands. *Can J For Res* 38:1033–1041
- Castresana J (2000) Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. *Mol Biol Evol* 17:540–552
- Choisy M (1929) Genres nouveaux pour la lichénologie dans le groupe des Lécanoracées. *Bull Soc Bot Fr* 76:521–527
- Choisy M (1949) Catalogue des lichens de la région lyonnaise. [Fasc. 2]. *Bull Mens Soc Linn Lyon* 18:137–152
- Culberson CF (1972) Improved conditions and new data for the identification of lichen products by a standardized thin-layer chromatographic method. *J Chromatogr* 72:113–125
- Culberson CF, Johnson A (1982) Substitution of methyl *tert.* butyl ether for diethyl ether in standardized thin-layer chromatographic method for lichen products. *J Chromatogr* 238:438–487
- DeBolt A, McCune B (1993) Lichens of Glacier National Park, Montana. *Bryologist* 96:192–204
- Dickhäuser A, Lumbsch HT, Feige GB (1995) A synopsis of the *Lecanora subcarnea* group. *Mycotaxon* 56:303–323
- Edgar RC (2004) MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Res* 32:1792–1797
- Eigler G (1969) Studien zur Gliederung der Flechtengattung *Lecanora*. *Diss Bot* 4:1–195
- Eigler G, Poelt J (1965) Flechtenstoffe und Systematik der lobaten Arten der Flechtengattung *Lecanora* in der Holarktis. *Österr Bot Z* 112:285–294
- Elix JA, Giralto M, Wardlaw JH (2003) New chloro-depsides from the lichen *Dimelaena radiata*. *Bibl Lichenol* 86:1–7
- Fink B (1935) The lichen flora of the United States. University of Michigan Press, Ann Arbor
- Frøberg L (1997) Variation in the *Lecanora dispersa* group in South Sweden. *Symb Bot Ups* 32:29–34
- Gardes M, Bruns TD (1993) ITS primers with enhanced specificity for basidiomycetes - application to the identification of mycorrhizae and rust. *Mol Ecol* 2:113–118
- Grube M, Baloch E, Arup U (2004) A phylogenetic study of the *Lecanora rupicola* group (Lecanoraceae, Ascomycota). *Mycol Res* 108:506–514
- Guderley R (1999) Die *Lecanora subfusca*-Gruppe in Süd- und Mittelamerika. *J Hattori Bot Lab* 87:131–257
- Guindon S, Gascuel O (2003) A simple, fast, and accurate algorithm to estimate large phylogenies by maximum likelihood. *Syst Biol* 52:696–704
- Hafellner J, Türk R (2001) Die lichenisierten Pilze Österreichs—eine Checkliste der bisher nachgewiesenen Arten mit Verbreitungsangaben. *Stapfia* 76:1–167
- Hansen ES (2004) Notes on some new and interesting Greenland lichens VI. *Graph Scr* 15:1–6
- Hauck M, Spribille T (2005) The significance of precipitation and substrate chemistry for epiphytic lichen diversity in spruce-fir forests of the Salish Mountains, northwestern Montana. *Flora* 200:547–562
- Hedlund T (1892) Kritische Bemerkungen über einige Arten der Flechtengattungen *Lecanora* (Ach.), *Lecidea* (Ach.) und *Micarea* (Fr.). *Bihang till Kungliga Svenska Vetenskaps-Akademiens Handlingar*, ser. 3, 18:1–104
- Houde I, Leech S, Bunnell FL, Spribille T, Björk C (2007) Old forest remnants contribute to sustaining biodiversity: the case of the Albert River valley. *B C J Ecosyst Manage* 8:43–52
- Huelsenbeck JP, Ronquist F (2003) MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19:1572–1574
- Kalb K (1991) Lichenes Neotropici: Fascicle XX (No. 451–475). Neumarkt/ Opf
- Laundon JR (2003a) Six lichens of the *Lecanora varia* group. *Nova Hedwigia* 76:83–111
- Laundon JR (2003b) The status of *Lecanora zosterae* in the British Isles. *Lichenologist* 35:97–102
- Lendemer JC, Knudsen K (2009) Two new usnic acid containing species of *Lecanora* from western North America. *Opusc Philolichenum* 6:73–80
- Leuckert C, Poelt J (1989) Studien über die *Lecanora rupicola*-Gruppe in Europa (Lecanoraceae). *Nova Hedwigia* 49:121–167
- Lumbsch HT (1994) Die *Lecanora subfusca*-Gruppe in Australasien. *J Hattori Bot Lab* 77:1–175
- Lumbsch HT, Elix JA (2004) *Lecanora*. In: McCarthy PM, Mallett K (eds) *Flora of Australia*, vol 56A, Lichens 4. ABRIS, CSIRO Australia, Melbourne, pp 12–62
- Lumbsch HT, Plümper M, Guderley R, Feige GB (1997) The corticolous species of *Lecanora sensu stricto* with pruinose apothecial discs. *Symb Bot Ups* 32:131–161
- Lumbsch HT, Schmitt I, Lücking R, Wiklund E, Wedin M (2007) The phylogenetic placement of Ostropales within Lecanoromycetes (Ascomycota) revisited. *Mycol Res* 111:257–267
- Martínez I, Aragón G (2004) The *Lecanora varia* group in Spain: species with amphithecial cortex. *Bryologist* 107:222–230
- McCune B (1982) Lichens of the Swan Valley, Montana. *Bryologist* 85:13–21
- Meyer B, Printzen C (2000) Proposal for a standardized nomenclature and characterization of insoluble lichen pigments. *Lichenologist* 32:571–583
- Miyawaki H (1988) Studies on the *Lecanora subfusca* group in Japan. *J Hattori Bot Lab* 64:271–326
- Motyka J (1995) *Porosty (Lichenes)*. Tom I. Rodzina Lecanoraceae, Lubelskie Towarzystwo Naukowe, Lublin
- Motyka J (1996a) *Porosty (Lichenes)*. Tom II. Rodzina Lecanoraceae.—Lubelskie Towarzystwo Naukowe, Lublin
- Motyka J (1996b) *Porosty (Lichenes)*. Tom III. Rodzina Lecanoraceae.—Lubelskie Towarzystwo Naukowe, Lublin

- Noble WJ (1982) *The Lichen Flora of the Coastal Douglas-fir Dry Subzone of British Columbia*. PhD Thesis, University of British Columbia, Vancouver
- Nylander W (1873) Addenda nova ad Lichenographiam europaeam. Continuatio sexta decima. *Flora* 56:289–300
- Nylander JAA (2004) MrModeltest v2. Evolutionary Biology Centre, Uppsala University, Program distributed by the author
- Page RDM (1996) TreeView: An application to display phylogenetic trees on personal computers. *Comput Appl Biosci* 12:357–358
- Poelt J (1952) Die *Lecanora subfusca*-Gruppe in Süddeutschland. *Ber Bayer Bot Ges* 29:58–69
- Poelt J (1958) Die lobaten Arten der Flechtengattung *Lecanora* Ach. sensu ampl. in der Holarktis. *Mitt Bot Staatssamml Mün* 2:411–573
- Poelt J (1966) Die lobaten Arten der Sammelgattung *Lecanora*. Lichenes, Lecanoraceae. (Flechten des Himalaya 1). *Khumbu Himal* 1:187–202
- Poelt J (1983) *Bryonora*, eine neue Gattung der Lecanoraceae. *Nova Hedwigia* 38:73–111
- Poelt J, Leuckert C, Roux C (1995) Die Arten der *Lecanora dispersa*-Gruppe (Lichenes, Lecanoraceae) auf kalkreichen Gesteinen im Bereich der Ostalpen-eine Vorstudie. *Bibl Lichenol* 58:289–333
- Printzen C (2001) Corticolous and lignicolous species of *Lecanora* (Lecanoraceae, Lecanorales) with usnic or isousnic acid in the Sonoran Desert Region. *Bryologist* 104:382–409
- Printzen C, May P (2002) *Lecanora ramulicola* (Lecanoraceae, Lecanorales), an overlooked lichen species from the *Lecanora symmicta* group. *Bryologist* 105:63–69
- Rambaut A, Drummond AJ (2007) Tracer v1.4, Available from <http://beast.bio.ed.ac.uk/Tracer>
- Ryan BD (1989a) *Lecanora* sect. *Petrasterion* (lichenized Ascomycotina) in North America: *Lecanora weberi* Ryan, sp. nov. (subsect. Pseudocorticatae), from Colorado. *Mycotaxon* 36:9–14
- Ryan BD (1989b) A monograph of *Lecanora* subgen. *Placodium* sect. *Endochloris* (lichenized Ascomycotina). *Bryologist* 92:513–522
- Ryan BD (1998) A monograph of *Lecanora* subg. *Placodium* sect. *Arctoxanthae* (lichenized Ascomycotina). In: Glenn MG, Harris RC, Dirig R, Cole MS (eds) *Lichenographia Thomsoniana: North American Lichenology in Honor of John W. Thomson*. Mycotaxon, Ithaca, pp 105–131
- Ryan BD, Nash TH III (1997) Systematics of *Lecanora* subgenus *Placodium* (lichenized Ascomycotina) in North America: an overview, with keys. *Nova Hedwigia* 64:111–127
- Ryan BD, Lumbsch HT, Messuti MI, Printzen C, Śliwa L, Nash TH III (2004) *Lecanora*. In: Nash TH III, Ryan BD, Diederich P, Gries C, Bungartz F (eds) *Lichen Flora of the Greater Sonoran Desert Region*, vol 2, Lichens Unlimited. Arizona State University, Tempe, Arizona, pp 176–286
- Śliwa L (2007) A revision of the *Lecanora dispersa* complex in North America. *Polish Bot J* 52:1–70
- Śliwa L, Wetmore CM (2000) Notes on the *Lecanora varia* group in North America. *Bryologist* 103:475–492
- Spribille T (2006) Materials for an epiphytic crustose lichen flora of northwest North America. Diplom thesis, University of Göttingen
- Spribille T, Printzen C (2007) *Lecidea rubrocastanea*, a new lichen species from conifer bark and wood in interior western North America (Lecanorales, lichenized Ascomycetes). *Lichenologist* 39:339–347
- Spribille T, Thor G, Bunnell FL, Goward T, Björk CR (2008) Lichens on dead wood: species-substrate relationships in the epiphytic lichen floras of the Pacific Northwest and Fennoscandia. *Ecography* 31:741–750
- Tuckerman E (1888) A synopsis of the North American lichens. Part. II. Comprising the Lecideacei, and (in part) the Graphidacei. Anthony, New Bedford, MA
- van den Boom PPG, Brand AM (2008) Some new *Lecanora* species from western and central Europe, belonging to the *L. saligna* group, with notes on related species. *Lichenologist* 40:465–497
- Weber WA, Wittmann R (1992) Catalog of the Colorado Flora: a Biodiversity Baseline. University Press of Colorado, Boulder
- White TJ, Bruns T, Lee S, Taylor JW (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (eds) *PCR protocols: a guide to methods and applications*. Academic, New York, pp 315–322
- Zahlbruckner A (1926) Lichenes (Flechten). Spezieller Teil. In: Engler A (ed) *Die natürlichen Pflanzenfamilien*. Engelmann, Leipzig, pp 61–263