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Taxonomic delimitation of the genera *Bryoria* and *Sulcaria*, with a new combination *Sulcaria spiralifera* introduced

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Abstract: *Bryoria pseudocapillaris* and *B. spiralifera* are currently treated as members of *Bryoria* section *Implexae* although conspicuous, long and depressed pseudocyphellae characterizing both species resemble those found in the genus *Sulcaria*. Both genera belong in *Parmeliaceae* and form an alectorioid group together with *Alectoria*, *Gowardia* and *Pseudephebe*. Parsimony and Bayesian analyses of ITS, partial GAPDH and partial *Mcm7* sequence data were used to examine the phylogenetic position of *B. pseudocapillaris* and *B. spiralifera*, and in light of these results evaluate the generic delimitation of *Bryoria* and *Sulcaria*. A total of 110 specimens of 53 species containing representatives from alectorioid and closely related genera were included in the analyses. The results clearly show first, that both *B. pseudocapillaris* and *B. spiralifera* belong in *Sulcaria* rather than in *Bryoria*, and second, that they should be considered conspecific. *Bryoria pseudocapillaris* is proposed as a synonym under *B. spiralifera* and the name *Sulcaria spiralifera* comb. nov. is introduced.

Key words: alectorioid lichens, *Implexae*, pseudocyphellae, secondary chemistry

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Introduction

The lichen genus *Bryoria* Brodo & D. Hawksw., including some 30–40 currently recognized species, has traditionally been treated as a member of the 'alectorioid' lichens, characterized morphologically by a fruticose, often hair-like thallus (Brodo & Hawksworth 1977). In their revision of North American alectorioid genera, Brodo & Hawksworth (1977) segregated *Bryoria* from *Alectoria* Ach. based on differences in ascospore characters (colourless vs. brown, respectively), secondary chemistry (ß-orcinol depsidones often present vs. absent; usnic acid absent vs. present) and vegetative structures (for example, pseudocyphellae usually inconspicuous and depressed vs. conspicuous and markedly raised). They recognized five distinct sections of *Bryoria* on the basis of anatomical, chemical and morphological characters: *Bryoria*, *Divaricatae* (Du Rietz) Brodo & D. Hawksw., *Implexae* (Gyeln.) Brodo & D. Hawksw., *Subdivergentes* (Motyka) Brodo & D. Hawksw. and *Tortuosae* (Bystrek) Brodo & D. Hawksw. Section *Subdivergentes* was later transferred to the genus *Nodobryoria* Common & Brodo, differing from *Bryoria* by its cortical structure, lack of soralia and pseudocyphellae, as well as lack of secondary metabolites (Common & Brodo 1995).

In a molecular phylogeny of the genus *Bryoria*, Myllys *et al.* (2011) proposed a new infrageneric classification in which five sections were recognized, mostly corresponding to the sections of *Bryoria*, *Divaricatae*, *Implexae*, and *Tortuosae* of Brodo & Hawksworth

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(1977), but with the addition of section *Americanae* Myllys & Velmala. Section *Implexae* was amended to include most of the species assigned by Brodo & Hawksworth (1977) to sections *Bryoria* and *Implexae*. However, in contrast to other sections in *Bryoria*, genetic diversity in section *Implexae* was found to be minimal. In fact, only *B. glabra* (Motyka) Brodo & D. Hawksw. was supported as a distinct species, although some level of genetic isolation was observed between European and North American populations of *B. capillaris* (Ach.) Brodo & D. Hawksw. and *B. implexa* (Hoffm.) Brodo & D. Hawksw. These results are perhaps not surprising as taxonomic concepts within the section have been problematic, with many taxa defined almost exclusively on secondary chemistry.

The phylogenetic position of some North American taxa placed in *Implexae* by Brodo & Hawksworth (1977) remained unresolved in the absence of fresh material for DNA analyses. These include *B. pseudocapillaris* Brodo & D. Hawksw. and *B. spiralifera* Brodo & D. Hawksw., both restricted to coastal California northward to Washington and Oregon, respectively (Glavich 2003; Glavich *et al.* 2005). Brodo & Hawksworth (1977) tentatively placed these species in *Bryoria*, owing to their resemblance to certain species in section *Implexae*, while at the same time noting that their production of conspicuous long, typically depressed pseudocyphellae might equally justify their placement in *Sulcaria* Bystrek (see Bystrek 1971; Obermayer & Elix 2003). By contrast, the pseudocyphellae of other members of section *Implexae* are usually shorter, more or less inconspicuous or in some species even absent. When fertile, *Sulcaria* and *Bryoria* are readily distinguished by their spores, which are 2–4-celled and yellowish to brown versus simple and hyaline, respectively (Bystrek 1971). Unfortunately, fruiting bodies are unknown in both *B. pseudocapillaris* and *B. spiralifera* (Brodo & Hawksworth 1977).

The phylogenetic position of *Bryoria* and *Sulcaria* has varied during taxonomic studies of alectorioid lichens. Kärnefelt & Thell (1992) considered *Alectoria*, *Oropogon* Th. Fr. and *Sulcaria* to constitute a separate family, *Alectoriaceae*, based mainly on reproductive structures including their relatively large, brownish, thick-walled, often multicelled spores, their strongly amyloid asci, and the branched and anastomosing hyphae of their paraphysoids. Other traditional alectorioid genera (i.e. *Bryocaulon* Kärnefelt, *Bryoria* and *Pseudephebe* M. Choisy) lack these features and were consequently excluded from the *Alectoriaceae*. More recently, however, the multi-gene phylogenies of Crespo *et al.* (2007, 2010) have shown that both *Bryoria* and *Sulcaria* belong in the *Parmeliaceae* and form an alectorioid group together with *Alectoria* and *Pseudephebe*, although the position of *Bryoria* within the group is weakly supported. The group additionally includes the recent segregate genus *Gowardia* Halonen *et al.* (Halonen *et al.* 2009) but excludes *Bryocaulon*, *Oropogon* and *Nodobryoria*, which have an uncertain position in the *Parmeliaceae* (see Thell *et al.* 2012 for a review of the lichen family *Parmeliaceae*).

Our main objectives in this study are: 1) to examine the phylogenetic position and taxonomic status of *B. pseudocapillaris* and *B. spiralifera* and, 2) in the light of these results to evaluate the taxonomic delimitation of *Sulcaria* and *Bryoria*. These questions were addressed by means of phylogenetic analyses performed on representatives of all alectorioid genera (*sensu* Crespo *et al.* 2007, 2010; Thell *et al.* 2012) and based on three gene regions: ITS regions of the nuclear ribosomal DNA, partial glyceraldehyde-3-phosphate dehydrogenase gene (GAPDH) and partial minichromosome maintenance protein 7 gene (*Mcm7*).

Materials and Methods

Taxon selection

A total of 112 specimens were used in this study (Table 1). Seventy-one of these represented *Bryoria* (32 species), and eight represented *Sulcaria* (4 species). Taxa from all five sections of *Bryoria* were included, though in keeping with the putative placement of *B. pseudocapillaris* and *B. spiralifera* (Brodo & Hawksworth 1977), special emphasis was accorded to section *Implexae*. In addition to the six *Implexae* species used in Myllys *et al.* (2011), we also included for the first time *B. pikei* Brodo & D. Hawksw. in

TABLE 1. *Specimens used in this study with GenBank accession numbers. New sequences produced for this study are marked in bold.* Bryoria pseudocapillaris *and* B. spiralifera *specimens were submitted to GenBank as* Sulcaria spiralifera *(see discussion)*

			GenBank accession numbers		
Taxon	Locality	Voucher specimen and sequence ID	ITS	GAPDH	*Mcm7*
Alectoria imshaugii	Canada, British Columbia	*T. Goward* 05-32 (UBC), H131	EU282496	EU282511	**KJ948003**
A. imshaugii	USA, Washington	*C. Björk* 15571 (UBC), L428	**KJ947931**	–	–
A. imshaugii	USA, Washington	*C. Björk* 16672 (UBC), L429	**KJ947932**	–	**KJ948004**
A. ochroleuca	Iceland, Norður-Island	*P. Keihäs* 667 (OULU), L430	**KJ947933**	**KJ947977**	**KJ948005**
A. ochroleuca	Russia, Murmansk Region	*P. Uotila* 49194 (H), L519	**KJ947934**	**KJ947978**	**KJ948006**
A. sarmentosa	Finland, Oulun Pohjanmaa	*P. Halonen* s.n. (OULU), H29	EU282494	EU282509	**KJ948007**
A. sarmentosa	Canada, British Columbia	*T. Goward* 05-38 (UBC), H132	EU282495	EU282510	**KJ948008**
A. sarmentosa subsp. *vexillifera*	Finland, Oulun Pohjanmaa	*P. Halonen* s.n. (OULU), H28	EU282493	EU282508	**KJ948009**
A. sarmentosa subsp. *vexillifera*	Canada, British Columbia	*T. Goward* 01-542 (UBC), H130	EU282492	EU282507	**KJ948010**
A. vancouverensis	Finland, Oulun Pohjanmaa	*P. Halonen* s.n. (OULU), H127	EU282498	EU282513	**KJ948011**
A. vancouverensis	Canada, British Columbia	*T. Goward* 01-810 (UBC), H128	EU282497	EU282512	**KJ948012**
Bryocaulon divergens	USA, Alaska	*S. S. Talbot* & *J. Myers* UNI062-34 (H), L475	**KJ947935**	**KJ947979**	**KJ948013**
B. divergens	Russia, Murmansk Region	*L. A. Konoreva* s.n. (H), L478	**KJ947936**	**KJ947980**	**KJ948014**
B. divergens	Russia, Murmansk Region	*L. A. Konoreva* s.n. (H), L479	**KJ947937**	**KJ947981**	**KJ948015**
Bryoria americana	Canada, British Columbia	*T. Goward* 02-165 (UBC), L199	HQ402678	HQ402606	**KJ948016**
B. americana	Finland, Kainuu	*S. Velmala* 63 & *P. Halonen* (H), S69	HQ402677	HQ402605	**KJ948017**
B. bicolor	Finland, Etelä-Häme	*M. Kuusinen* 1063 & *R. Lampinen* (H), L183	HQ402691	HQ402612	**KJ948018**
B. bicolor	Finland, Koillismaa	*S. Velmala et al.* 24 (H), S23	HQ402689	HQ417113	**KJ948019**
B. capillaris	Finland, Etelä-Häme	*V. Haikonen* 22228 (H), L141	FJ668493	FJ668399	**KJ948020**
B. capillaris	Canada, British Columbia	*T. Goward* 05-19 (UBC), L209	GQ996281	GQ996253	**KJ948021**
B. capillaris	Finland, Etelä-Savo	*L. Myllys* 485 (H), L211	GQ996287	GQ996259	**KJ948022**
B. capillaris	USA, Oregon	*C. Björk* 21120 (UBC), L369	**KJ947938**	**KJ947982**	**KJ948023**
B. confusa	China, Yunnan	*L. S. Wang* 06-26974 (KUN-L), S292	HQ402686	HQ417112	**KJ948024**
B. divergescens	China, Yunnan	*L. S. Wang* 06-26244 (KUN-L), S284	HQ402705	–	**KJ948025**
B. fastigiata	China, Yunnan	*L. S. Wang et al.* 06-26696 (KUN-L), S288	HQ402706	–	**KJ948026**
B. flocculosa	China, Yunnan	*L. S. Wang* & *J. Wang* 09-30973 (H), L498b	**KJ947939**	–	**KJ948027**
B. fremontii	Canada, British Columbia	*T. Goward* 05-04 (UBC), L205	FJ668503	FJ668408	**KJ948028**
B. fremontii	Finland, Koillismaa	*S. Velmala et al.* 13b (H), S13	FJ668498	FJ668404	**KJ948029**
B. furcellata	Canada, Manitoba	*T. Ahti* 63217 (H), L138	HQ402721	HQ402602	**KJ948030**
B. furcellata	Finland, Etelä-Savo	*V. Haikonen* 22770 (H), L147	HQ402722	HQ402627	**KJ948031**
B. fuscescens	Finland, Ahvenanmaa	*M. Stjernberg* s.n. (H), L149	GQ996290	GQ996262	**KJ948032**
B. fuscescens	USA, Alaska	*D. Nossov* 90098-14 (UBC), L397	**KJ947940**	**KJ947983**	**KJ948033**
B. fuscescens	USA, Alaska	*S. Jovan* 90088-24 (UBC), L398	**KJ947941**	**KJ947984**	**KJ948034**
B. fuscescens	Finland, Koillismaa	*S. Velmala* 51 & *P. Halonen* (H), S56	GQ996291	GQ996263	**KJ948035**
B. glabra	Finland, Koillismaa	*P. Halonen* s.n. (OULU), L186	FJ668494	FJ668400	**KJ948036**
B. glabra	Canada, British Columbia	*T. Goward* 07-02-0033 (UBC), S244	HQ402728	HQ402632	**KJ948037**
B. hengduanensis	China, Yunnan	*L. S. Wang et al.* 06-26692 (KUN-L), S287	HQ402704	–	**KJ948038**
B. implexa chemotype 1	Finland, Koillismaa	*S. Velmala et al.* 23 (H), S22	GQ996294	GQ996266	**KJ948039**
B. implexa chemotype 1	Finland, Koillismaa	*S. Velmala et al.* 37 (H), S39	GQ996293	GQ996265	**KJ948040**
B. implexa chemotype 2	Canada, British Columbia	*T. Goward* 05-31 (UBC), L240b	GQ996282	GQ996254	**KJ948041**
B. implexa chemotype 2	Iran, East-Azarbaijan	*M. Sohrabi* 4656 (H), L244a	GQ996295	GQ996267	**KJ948042**

TABLE 1. *Continued*

			GenBank accession numbers		
Taxon	Locality	Voucher specimen and sequence ID	ITS	GAPDH	*Mcm7*
Bryoria implexa chemotype 2	Canada, British Columbia	*T. Goward* 06-1066a (UBC), L379a	**KJ947942**	**KJ947985**	**KJ948043**
B. implexa chemotype 3	Finland, Koillismaa	*S. Velmala et al.* 11b (H), S10	GQ996297	GQ996269	**KJ948044**
B. implexa chemotype 3	Finland, Koillismaa	*S. Velmala et al.* 31b (H), S32	GQ996298	GQ996270	**KJ948045**
B. implexa chemotype 3	Canada, British Columbia	*T. Goward* 09-527 (UBC), L422b	**KJ947943**	–	**KJ948046**
B. implexa chemotype 4	Russia, Perm Territory	*A. V. Melekhin* 10123 (H), S166	GQ996308	GQ996273	**KJ948047**
B. implexa chemotype 4	Finland, Pohjois-Karjala	*S. Velmala et al.* 90 (H), S97	**KJ947944**	–	–
B. implexa chemotype 5	Finland, Koillismaa	*S. Velmala et al.* 43a (H), S45	GQ996302	GQ996275	**KJ948048**
B. implexa chemotype 5	Russia, Perm Territory	*Y. A. Ateeva* 5055 (H), S164	GQ996285	GQ996257	**KJ948049**
B. indonesica	New Zealand, Gisborne	*M. Wedin* 4058 (UPS), L172	HQ402688	–	–
B. indonesica	New Zealand, Gisborne	*M. Wedin* 4057 (UPS), L173	HQ402687	–	–
B. lactinea	China, Yunnan	*L. S. Wang* 06-26966 (KUN-L), S279	HQ402699	–	**KJ948050**
B. lactinea	China, Yunnan	*L. S. Wang et al.* 06-26541 (KUN-L), S293	HQ402700	–	–
B. lanestris	Canada, Alberta	*J. Kamin* 016 (UBC), S274	GQ996303	GQ996276	**KJ948051**
B. nadvornikiana	Iran, East-Azarbaijan	*M. Sohrabi* 4510 (H), L245	HQ402720	HQ402626	**KJ948052**
B. nadvornikiana	Finland, Kainuu	*S. Velmala et al.* 73 (H), S79	HQ402718	HQ402624	**KJ948053**
B. nitidula	Sweden, Ångermanland	*J. Granbo* s.n. (UPS), L163	HQ402713	HQ402621	**KJ948054**
B. nitidula	Greenland	*F. Högnabba* 752 (H), S121	HQ402711	HQ402619	**KJ948055**
B. perspinosa	China, Yunnan	*L. S. Wang et al.* 06-26547 (KUN-L), S296	HQ402698	–	–
B. pikei	Canada, British Columbia	*T. Goward* 09-323a (UBC), L420	**KJ947945**	–	**KJ948056**
B. poeltii	China, Yunnan	*L. S. Wang et al.* 06-26697 (KUN-L), S295	HQ402701	HQ402617	**KJ948057**
B. pseudocapillaris	USA, California	*C. Björk* 23547 (UBC), L378	**KJ947946**	**KJ947986**	**KJ948058**
B. pseudocapillaris	USA, California	*D. Glavich* 550 (Siuslaw National Herbarium), L510	**KJ947947**	–	**KJ948059**
*B. pseudocapillaris**	USA, California	*D. Glavich* s.n. (Siuslaw National Herbarium), L518a	–	–	**KJ948060**
B. rigida	China, Yunnan	*L. S. Wang* 06-26208 (KUN-L), S289	HQ402703	–	**KJ948061**
B. simplicior	Russia, Sakha Republic	*T. Ahti* 61399 (H), L231b	HQ402716	HQ402601	**KJ948062**
B. simplicior	Finland, Koillismaa	*S. Velmala et al.* 30 (H), S30b	HQ402714	HQ402622	**KJ948063**
B. smithii	India, Uttarkhand	*L. Tibell* 23319 (UPS), L174	HQ402685	HQ402610	**KJ948064**
B. smithii	Finland, Varsinais-Suomi	*S. Velmala et al.* 60 (H), S65	HQ402684	HQ402609	**KJ948065**
B. spiralifera	USA, California	*C. Björk* 23483 (UBC), L385	**KJ947948**	**KJ947987**	**KJ948066**
B. spiralifera	USA, California	*T. Carlberg* 02957 (H), L508a	**KJ947949**	**KJ947988**	**KJ948067**
B. spiralifera	USA, California	*T. Carlberg* 02957 (H), L508b	**KJ947950**	–	**KJ948068**
B. spiralifera	USA, Oregon	*D. Glavich* s.n. (Siuslaw National Herbarium), L516	**KJ947951**	–	**KJ948069**
*B. spiralifera**	USA, California	*T. Carlberg* 02959 (H), L509b	–	–	**KJ948070**
B. subcana	Finland, Oulun Pohjanmaa	*P. Halonen* s.n. (OULU), L189	GQ996305	GQ996278	**KJ948071**
B. subcana	Russia, Perm Territory	*M. Schajachmetova* 18.9 (H), S157	GQ996306	GQ996279	**KJ948072**
B. tenuis	Sweden, Dalarna	*J. Hermansson* 12855d (UPS), L164	HQ402695	HQ402616	**KJ948073**
B. tenuis	Finland, Kainuu	*S. Velmala et al.* 64 (H), S70	HQ402694	HQ402615	**KJ948074**
B. trichodes	Canada, Newfoundland	*T. Ahti* 60134 (H), L230	HQ402710	–	**KJ948075**
B. trichodes	Russia, Kamchatka	*T. V. Khakimullina* s.n. (H), L505	**KJ947952**	–	**KJ948076**
B. variabilis	China, Yunnan	*L. S. Wang* 04-23184 (KUN-L), S286	HQ402683	–	–
B. sp. 1	USA, Alaska	*K. Dillman* 11:3 (UBC), L411	**KJ947953**	**KJ947989**	**KJ948077**

TABLE 1. *Continued*

Taxon	Locality	Voucher specimen and sequence ID	GenBank accession numbers		
			ITS	GAPDH	*Mcm7*
Bryoria sp. 1	USA, Alaska	*K. Dillman* 09:264 (UBC), L413	**KJ947954**	–	**KJ948078**
B. sp. 2	USA, Alaska	*K. Dillman* 11:5 (UBC), L404	**KJ947955**	–	**KJ948079**
B. sp. 2	USA, Alaska	*S. S.* & *S. Talbot* 116 (UBC), L488	**KJ947956**	–	**KJ948080**
Cladonia mitis	Finland, Uusimaa	*L. Myllys* 240513-1 (H), L526	**KJ947957**	**KJ947990**	**KJ948081**
Gowardia arctica	Canada, Nunavut	*J.-E. Mattsson* 5115 (UPS), L171	EU282504	(EU282520)†	–
G. arctica	Russia, Nenetsia	*A. Pajunen* s.n. (OULU), S146	EU282503	EU282519	**KJ948082**
G. nigricans	Finland, Inarin Lappi	*H. Hyvärinen* s.n. (OULU), H79	EU282499	EU282514	**KJ948083**
G. nigricans	Finland, Enontekiön Lappi	*R. Virtanen* s.n. (OULU), S201	EU282501	EU282517	**KJ948084**
Nodobryoria abbreviata	USA, California	*K. Knudsen* 1305 (H), L152	HQ402675	**KJ947991**	**KJ948085**
N. abbreviata	USA, Idaho	*Anderson & Shushan Lich. W. North America Exs.* 146 (H), L477	**KJ947958**	–	**KJ948086**
N. oregana	Canada, British Columbia	*T. Goward* 05-26 (UBC), L198a	**KJ947959**	**KJ947992**	**KJ948087**
N. subdivergens	Greenland	*J.-E. Mattsson* 5004 (UPS), L181	**KJ947960**	–	**KJ948088**
Platismatia glauca	Finland, Uusimaa	*L. Myllys* 080413-1 (H), L520	**KJ947961**	**KJ947993**	**KJ948089**
Pseudephebe minuscula	Russia, Franz Josef Land	*S. S. Kholod* s.n. (H), L525	**KJ947962**	–	**KJ948090**
P. pubescens	USA, Alaska	*T. Ahti* 63704 (H), L221	HQ402676	HQ402604	**KJ948091**
P. pubescens	USA, Alaska	*T. Ahti* 70048 & *S. S. Talbot* (H), L487	**KJ947963**	**KJ947994**	**KJ948092**
P. pubescens	USA, Alaska	*T. Ahti* 70044 & *S. S. Talbot* (H), L491	**KJ947964**	**KJ947995**	**KJ948093**
P. pubescens	Russia, Franz Josef Land	*S. S. Kholod* s.n. (H), L524	**KJ947965**	**KJ947996**	**KJ948094**
Pseudevernia furfuracea	Finland, Uusimaa	*L. Myllys* 080413-2 (H), L521	**KJ947966**	**KJ947997**	**KJ948095**
Sulcaria badia	USA, California	*C. Björk* 23688 (UBC), L391	**KJ947967**	**KJ947998**	**KJ948096**
S. badia	USA, California	*T. Carlberg* 02955 (H), L511	**KJ947968**	–	**KJ948097**
S. badia	USA, California	*T. Carlberg* 02954 (H), L512	**KJ947969**	**KJ947999**	**KJ948098**
S. isidiifera	USA, California	*R. Riefner* 20-293 (H), L151	HQ402674	–	**KJ948099**
S. isidiifera	USA, California	*J. Hollinger* 4628c (H, UBC), L476	**KJ947970**	**KJ948000**	**KJ948100**
S. sulcata	China, Yunnan	*L. S. Wang* & *M. M. Liang* 11-32136 (H), L492	**KJ947971**	–	**KJ948101**
S. sulcata f. *vulpinoides*	China, Yunnan	*D. L. Niu et al.* 12-35586 (H), L494a	**KJ947972**	**KJ948001**	**KJ948102**
S. virens	China, Yunnan	*L. S. Wang* & *M. M. Liang* 11-32117 (H), L493	**KJ947973**	–	–
Usnea chaetophora	Finland, Pohjois-Savo	*K. Jääskeläinen* s.n. (H), S360	**KJ947974**	–	**KJ948103**
U. dasopoga	Finland, Uusimaa	*L. Myllys* 080413-4 (H), L523	**KJ947975**	**KJ948002**	**KJ948104**
U. hirta	Finland, Uusimaa	*L. Myllys* 080413-3 (H), L522	**KJ947976**	–	**KJ948105**

[*] *Mcm7* sequences were obtained from these specimens but not used for analyses because ITS and GAPDH sequences lacking.

[†] GAPDH sequence (EU282520) for *Gowardia arctica* specimen L171 was published by Halonen *et al.* (2009) but is not included in this study because it lacks the *Mcm7* sequence.

our analyses. That taxon is endemic to North America and was originally classified in section *Implexae*, as defined by Brodo & Hawksworth (1977).

In addition to specimens of *Bryoria* and *Sulcaria*, we also included representatives of all alectorioid genera (*sensu* Crespo *et al.* 2007, 2010; Thell *et al.* 2012), that is *Alectoria* (11 specimens/4 species), *Gowardia* (4/2) and *Pseudephebe* (5/2), *Bryocaulon divergens* (Ach.) Kärnefelt (3) and *Nodobryoria* (4/3). According to Thell *et al.* (2012), these last two genera have an uncertain position in the *Parmeliaceae* but, as they have traditionally been grouped with the alectorioid lichens (Brodo & Hawksworth 1977), we include them here. *Cladonia mitis* Sandst. (*Cladoniaceae*, *Lecanorales*) was used as outgroup. *Pseudevernia furfuracea* (L.) Zopf from the Hypogymnioid clade, three *Usnea* species from the Usneoid clade [see Thell *et al.* (2012) for definition of these clades] and *Platismatia glauca* (L.) W. L. Culb. & C. F. Culb. (uncertain position in *Parmeliaceae*) were also included in the analyses to test the monophyly of the alectorioid group.

Secondary chemistry

All *Bryoria* and *Sulcaria* specimens used in our phylogenetic analyses were examined for secondary compounds with thin-layer chromatography (TLC) using solvents A and B (Orange *et al.* 2001). Methods were as those described in Myllys *et al.* (2011).

Molecular methods

Total genomic DNA was extracted using the methods described in Myllys *et al.* (2011). Sequences from three gene regions were generated for this study: the complete nuclear ribosomal internal transcribed spacer region (ITS), *c.* 1 kb of the glyceraldehyde-3-phosphate dehydrogenase gene (GAPDH) and *c.* 0·6 kb of the minichromosome maintenance protein 7 gene (*Mcm7*). ITS and GAPDH were selected based on our previous studies (i.e. Velmala *et al.* 2009; Myllys *et al.* 2011), while *Mcm7* has been shown to be promising at the species-level and genus-level studies of Spribille *et al.* (2011*a*, *b*) and Sadowska-Deś *et al.* (2013).

PCR profiles for ITS regions and GAPDH gene followed those described in Myllys *et al.* (2011), and PCR profiles for *Mcm7* followed those described in Schmitt *et al.* (2009).

Sequence alignment and phylogenetic analyses

We aligned our DNA sequences with MUSCLE 3.7 using default parameters (Edgar 2004) on Hippu server system at CSC – IT Center for Science, Finland (http://www.csc.fi/english). We constructed three separate data sets to avoid the introduction of missing data in the analyses: ITS data set included 110 terminals, combined ITS+*Mcm7* data set 101 terminals, and combined ITS+*Mcm7*+GAPDH data set 76 terminals (see Table 1). Each data set was subjected to parsimony and Bayesian analyses. Parsimony analyses were performed in TNT version 1.1 for Windows (Goloboff *et al.* 2008) using the option traditional search with the following settings: random addition of sequences with 100 replicates and TBR branch swapping algorithm. Ten trees were saved for each replicate. The bootstrapping method as implemented in TNT was used with 1000 replicates to estimate node support. The program jModelTest2 version 2.1.1 (Guindon & Gascuel 2003; Darriba *et al.* 2012) was used to estimate an optimal evolutionary model for Bayesian analyses by calculating AIC (Akaike Information Criterion) scores for each gene region. For the ITS region, evolutionary model was estimated separately for each partition. Models with the lowest AIC scores were used in the analyses. For ITS1, ITS2, *Mcm7* and GAPDH the model GTR+I+G was selected, whereas the model K80 was used for the 5.8S. Bayesian analyses were performed on all three data sets using MrBayes version 3.2.2 (Huelsenbeck & Ronquist 2001). For the ITS and ITS+*Mcm7* data sets two parallel runs of 10 000 000 generations for ITS and 15 000 000 generations for ITS+*Mcm7* were performed using four chains and sampling every 500th tree. The first 25% of samples, corresponding to 5000 samples for ITS and 7500 samples for ITS+*Mcm7*, was discarded as burn-in. For the ITS+*Mcm7*+GAPDH data set, two parallel runs of 20 000 000 generations were performed, also using four chains but sampling every 1000th tree. The number of samples discarded as burn-in for this data set was 5000. The temperature parameter was set to 0·05 for all three analyses.

Results

We produced 173 new sequences for this study: 46 ITS sequences, 103 *Mcm7* sequences and 26 GAPDH sequences. The remaining 114 sequences used in the analyses are from our earlier studies (Halonen *et al.* 2009; Velmala *et al.* 2009; Myllys *et al.* 2011).

Since the topologies of the TNT and Bayesian analyses did not show any strongly supported conflicts, only the trees obtained from the TNT analyses are shown (Figs 1–3).

The combined matrix of ITS, *Mcm7* and GAPDH data sets with 76 terminals included 2147 characters, of which 663 were parsimony-informative. The strict consensus of the 18 trees obtained from the TNT analysis is given in Figure 1. *Usnea dasopoga* (Ach.) Nyl. is basal to the remaining taxa, otherwise the intergeneric relationships remain mostly unsupported. Only *Gowardia* and *Alectoria* form a strongly supported monophyletic group. The alectorioid group is not monophyletic as *Pseudevernia furfuracea* forms a sister group to *Bryoria*, *Platismatia glauca* groups with *Sulcaria*, *Bryocaulon divergens* is

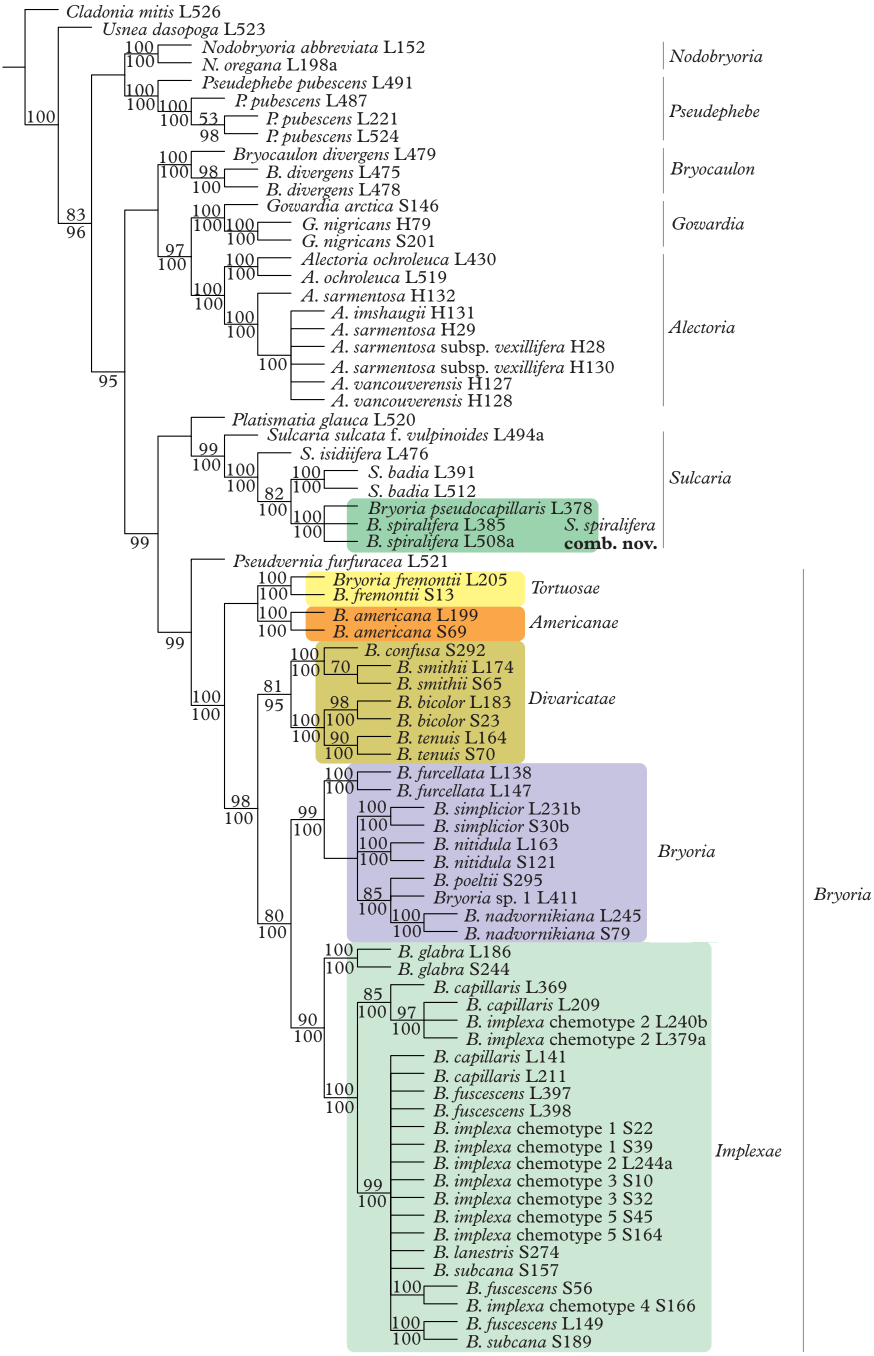

FIG. 1. Molecular phylogeny of alectorioid lichens focusing on *Bryoria* and *Sulcaria*. Strict consensus obtained from TNT analysis based on a combined ITS, *Mcm7* and GAPDH data set. Bootstrap values ≥50% obtained from TNT analysis are shown above nodes and BPP values ≥90% obtained from Bayesian analysis are shown below nodes. Five *Bryoria* sections and positions of *B. pseudocapillaris* and *B. spiralifera* are indicated in coloured boxes.

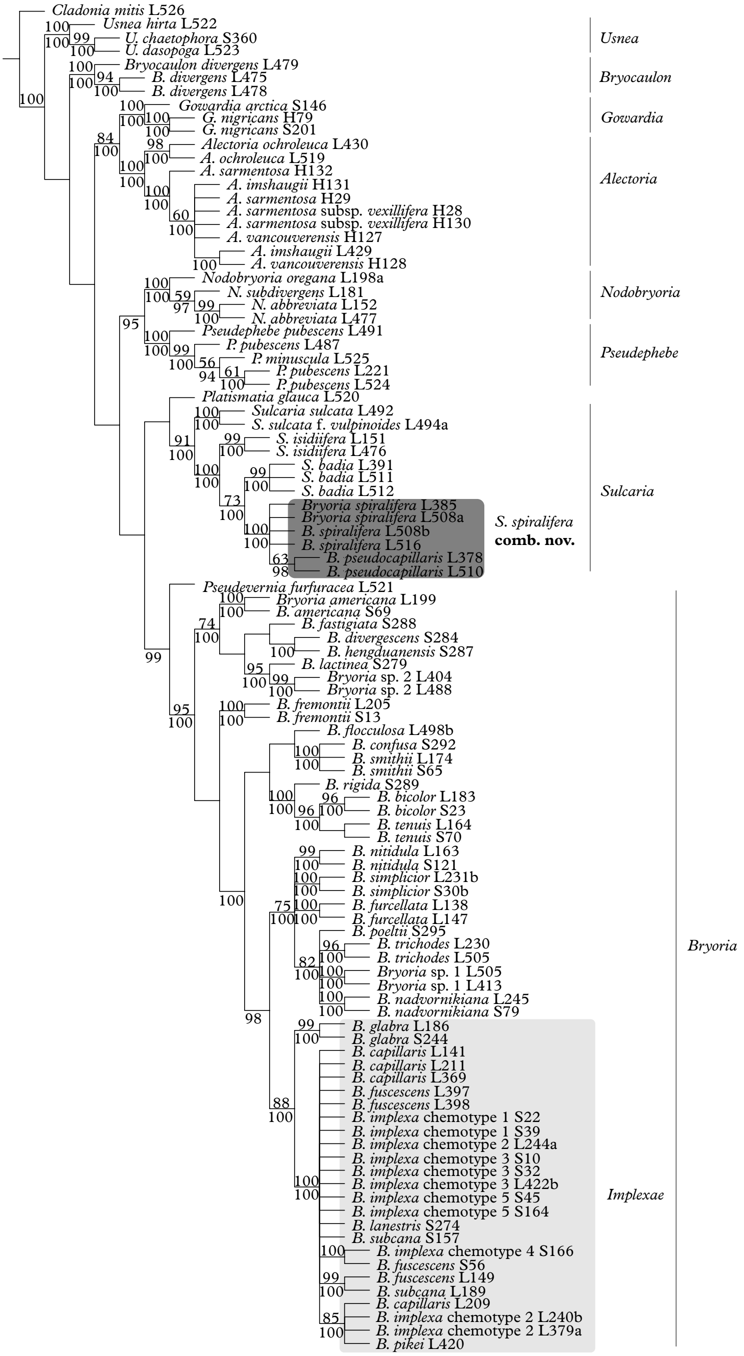

FIG. 2. Molecular phylogeny of alectorioid lichens focusing on *Bryoria* and *Sulcaria*. Strict consensus obtained from TNT analysis based on a combined ITS and *Mcm7* data set. Bootstrap values ≥50% obtained from TNT analysis are shown above nodes and BPP values ≥90% obtained from Bayesian analysis are shown below nodes. *Bryoria* section *Implexae* and positions of *B. pseudocapillaris* and *B. spiralifera* are indicated in coloured boxes.

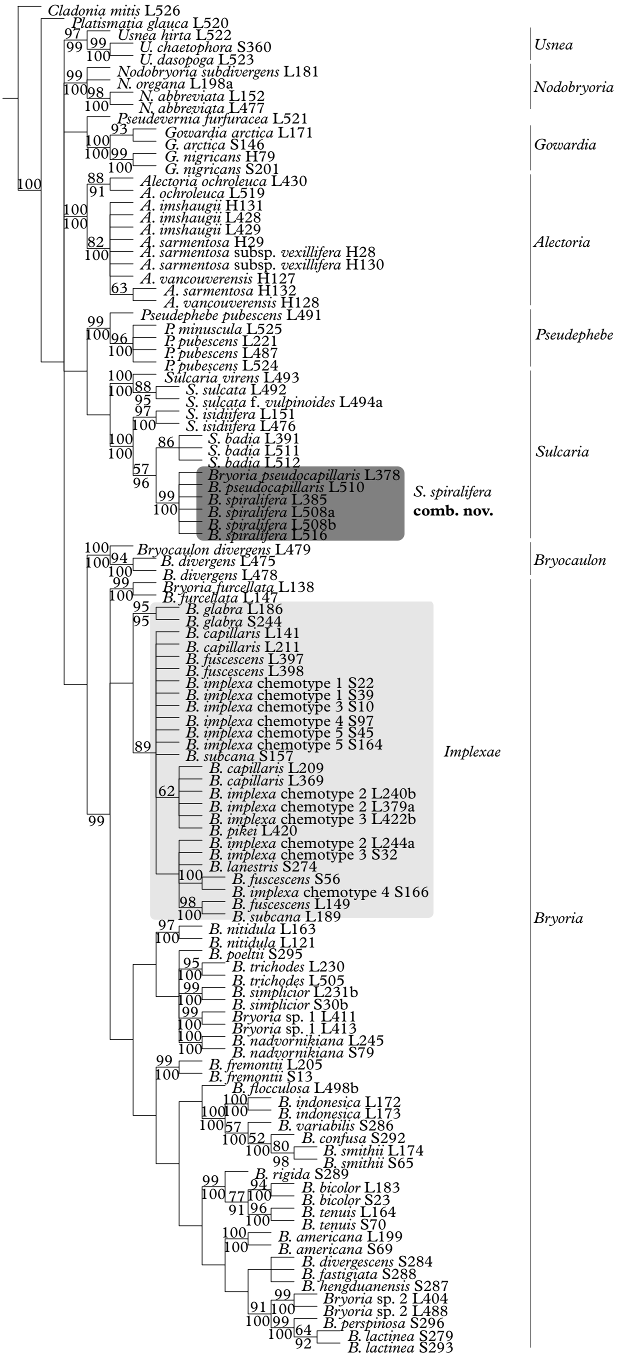

FIG. 3. Molecular phylogeny of alectorioid lichens focusing on *Bryoria* and *Sulcaria*. Strict consensus obtained from TNT analysis based on ITS data set. Bootstrap values ≥50% obtained from TNT analysis are shown above nodes and BPP values ≥90% obtained from Bayesian analysis are shown below nodes. *Bryoria* section *Implexae* and positions of *B. pseudocapillaris* and *B. spiralifera* are indicated in coloured boxes.

sister to the *Gowardia-Alectoria* clade, and *Nodobryoria* specimens group with *Pseudephebe*. The close relationship of *Pseudevernia* and *Bryoria* is supported in the Bayesian analyses (see Fig. 1 for BPP values obtained from the Bayesian analysis). Otherwise these relationships receive no support. In contrast, infrageneric relationships are mostly well resolved. All *Bryoria* sections discussed in Myllys *et al.* (2011) are either strongly supported (i.e. sections *Americanae*, *Bryoria*, *Implexae* and *Tortuosae*), or moderately supported (i.e. section *Divaricatae*) monophyletic groups. Interestingly, the specimens of *Bryoria pseudocapillaris* and *B. spiralifera* do not group with members of *Implexae*. Instead, they form a sister group to *Sulcaria badia* Brodo & D. Hawksw. in the *Sulcaria* clade.

The parsimony analysis of the combined ITS+*Mcm7* data with 101 terminals resulted in 290 trees. Of the aligned 1161 characters, 390 were parsimony-informative. In a strict consensus, three *Usnea* species form a basal group followed by *Bryocaulon*, but these relationships received no support (Fig. 2). *Pseudevernia furfuracaea*, *Platismatia glauca* and *Nodobryoria* spp. are nested inside the alectorioid clade as in the tree obtained from ITS+*Mcm7*+GAPDH analysis. Direct comparison of the trees obtained from different analyses is not possible because of different taxon sampling but generally the relationships within *Bryoria* are more poorly resolved or more poorly supported than in the ITS+*Mcm7*+GAPDH tree. All five sections recognized by Myllys *et al.* (2011) are monophyletic except section *Bryoria*, which is divided into two separate clades, one of which groups with section *Americanae*. Again, *Bryoria* is polyphyletic because *B. pseudocapillaris* and *B. spiralifera* group with *Sulcaria*.

The TNT analysis of the ITS data set included 575 characters of which 216 were parsimony informative. In the strict consensus of the 133 equally parsimonious trees, intergeneric relationships remain unresolved with the following exceptions: *Pseudevernia furfuracea* forms a sister clade to *Gowardia*, *Pseudephebe* and *Sulcaria* group together, and *Bryocaulon* appears as a sister clade to *Bryoria* but none of these groupings receives any support (Fig. 3). Relationships within *Bryoria* are poorly supported and sections *Bryoria* and *Divaricatae* of Myllys *et al.* (2011) are not monophyletic. *Bryoria pseudocapillaris* and *B. spiralifera* form a strongly supported monophyletic group together with *S. badia* and *S. isidiifera* Brodo in the *Sulcaria* clade.

Discussion

Delimitation of *Bryoria* and *Sulcaria* and the phylogenetic position of *B. pseudocapillaris* and *B. spiralifera*

The monophyly of the genus *Bryoria* as traditionally proposed (i.e. Brodo & Hawksworth 1977) could not be recovered by our analyses. This is due to the position of *B. pseudocapillaris* and *B. spiralifera*, which in all three analyses grouped with members of *Sulcaria* (see Figs 1–3). The results clearly show that both species should be removed from *Bryoria* and placed in *Sulcaria*. This finding is based on data for all three data sets of two specimens of *B. pseudocapillaris* and four of *B. spiralifera*. Additional *Mcm7* sequences were obtained from one *B. pseudocapillaris* specimen (specimen L518a, see Table 1) and one *B. spiralifera* specimen (specimen L509a); again, these confirm the position of both species in *Sulcaria*.

This finding is by no means a surprise as Brodo & Hawksworth (1977) had already noted a close resemblance between the pseudocyphellae of *Sulcaria* and those of *B. pseudocapillaris* and *B. spiralifera*. Their decision to place these species in *Bryoria* section *Implexae* was prompted by a shared morphological and chemical resemblance to certain forms of *B. capillaris* and *B. kuemmerleana* (Gyeln.) Brodo & D. Hawksw. (syn. *B. implexa*; see Holien 1989). On the other hand, *B. pseudocapillaris* and *B. spiralifera* differ significantly from other members of section *Implexae*, for example, in their striking pseudocyphellae, stiff habit and perpendicular side branches (Brodo & Hawksworth 1977). This last feature especially is characteristic of all four species currently placed in *Sulcaria* (Brodo & Hawsksworth 1977; Brodo 1986). Likewise, the restricted occurrence of *B. pseudocapillaris* and *B. spiralifera* along the American west coast (Glavich 2003) is more characteristic of *Sulcaria* than of *Bryoria*, a genus typical of cool temperate and boreal regions.

The almost complete lack of genetic variation between *Bryoria pseudocapillaris* and *B. spiralifera* specimens (= 99–100% similar ITS sequences) raises the question of whether they may in fact belong to a single species. Brodo & Hawksworth (1977) identified secondary chemistry as their most reliable diagnostic point of distinction, that is, alectorialic and barbatolic acids and an unknown substance in *B. pseudocapillaris* versus atranorin and norstictic and connorstictic acids in *B. spiralifera*. Additionally, *B. pseudocapillaris* is described as an essentially pale species with long linear pseudocyphellae, while *B. spiralifera* is characterized by its more variable colour and often spiral pseudocyphellae (Fig. 4A & B). With more extended sampling, Glavich (2003) found that these morphological traits were often good predictors for the identification of the two species, but at the same time noted the existence of intermediate forms. Overlapping characters were observed in both thallus colour (ranging from pale to brown in both species) and morphology of pseudocyphellae (variation ranging from linear to spiralling in both species, see also Fig. 4C). The only exception is a dark brown coloration found only in some *B. spiralifera* specimens (Glavich 2003). The combination of a similar DNA profile and lack of distinct species boundaries strongly suggests that these two taxa are in fact chemical variants of a single species. In our view, *B. pseudocapillaris* is more appropriately treated as a synonym of *B. spiralifera*, and the name *Sulcaria spiralifera* (Brodo & D. Hawksw.) Myllys, Velmala & Goward is proposed (see below).

Our analyses show that *Sulcaria* is divided into two allopatric subclades (Figs 1–3), the first restricted to Asia and the second to North America. The original treatment of *Sulcaria* included only the Asian subclade, that is, *S. sulcata* (Lév.) Bystrek and *S. virens* (Taylor) Bystrek ex Brodo & D. Hawksw (Bystrek 1971). Both are widely distributed in the Himalayas and adjacent regions, and have more recently been reported from Japan (Awasthi & Awasthi 1985; Obermayer & Elix 2003).

Brodo & Hawksworth (1977) tentatively placed the sterile North American species *S. badia* in *Sulcaria*, based on its conspicuous, long, sulcate pseudocyphellae, though these are less well developed than in Asian members of the genus. Our analyses confirm the position of *S. badia* in *Sulcaria* and show that it is closely related to *S. spiralifera*. In fact, ITS sequence comparison revealed 98% sequence similarity between these two species. While we acknowledge that a 3% divergence for ITS sequences has usually been accepted as the minimum threshold for delimiting fungal species (but see Begerow *et al.* 2010), our analyses of *S. badia* consistently form a strongly supported monophyletic group separate from *S. spiralifera*. Hence we adopted a phylogeny-based approach instead of a similarity-based identification and treat *S. badia* as a distinct species. In fact, *S. badia* is usually easily recognized by its distinctive chestnut brown colour, extremely long pseudocyphellae extending the length of the branches, and production of atranorin alone; norstictic and connorstictic acids are lacking (Brodo & Hawksworth 1977; Peterson *et al.* 1998).

In addition to *S. badia* and *S. spiralifera*, the North American clade includes *S. isidiifera*. This species is known only from the type locality in southern California and is distinguished by its caespitose habit, longitudinally split branches, the presence of isidia and soredia, and production of protocetraric acid (Brodo 1986).

Topologies obtained from our three analyses are not directly comparable because of different taxon sampling but generally, as expected, the ITS tree and in part the ITS+*Mcm7* tree were less resolved than the combined phylogeny obtained from the three data sets (Figs 1–3). For example, five *Bryoria* sections appearing in the combined phylogeny of ITS+*Mcm7*+GAPDH data were not always recovered as monophyletic in the ITS or in the ITS+*Mcm7* trees. However, we agree with Nixon & Carpenter (1996) that phylogenetic hypotheses based on simul-

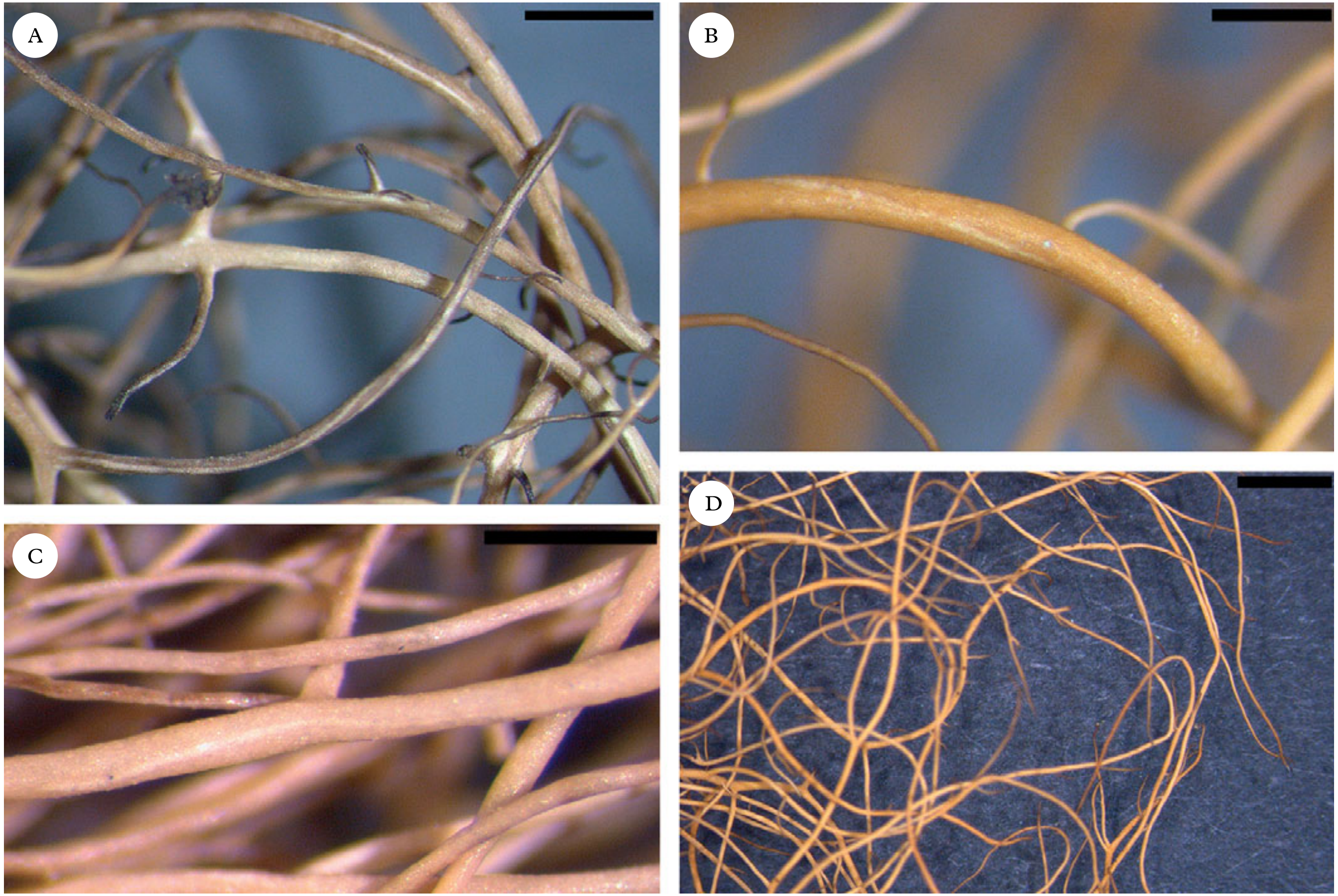

Fig. 4. *Sulcaria spiralifera*. A, typical norstictic chemotype, specimen L508a with dark brown, partly pruinose branches and spiral pseudocyphellae; B, typical alectorialic and barbatolic chemotype, specimen L510 with pale branches and spiral pseudocyphellae; C, norstictic chemotype with pale branches and straight pseudocyphellae (specimen L516); D, general habit with spinulose side branches (specimen L510). Scales: A = 1 mm; B & C = 0·5 mm; D = 2 mm.

taneous analysis of multiple data sets have the highest explanatory value, and consider the combined tree of three data sets the most reliable hypothesis of evolution. For some taxa for which GAPDH sequences could not be obtained, we still have to rely on the results obtained from the ITS and/or *Mcm7* sequences. According to our ITS and combined ITS+*Mcm7* analyses, for example, *Bryoria* contains two unidentified specimens (specimens L404 and L488), which most probably represent a new species. A formal species description, however, must await additional collections and a careful study of morphological variation. These specimens, both collected from North America, group with *B. lactinea* (Nyl.) Brodo & D. Hawksw. in the ITS+*Mcm7* tree and form a sister group to the *B. lactinea*-*B. perspinosa* clade in the ITS tree (only ITS data available for the latter species) (Figs 2 & 3). Both *B. lactinea* and *B. perspinosa* (Bystrek) Brodo & D. Hawksw. are Asian species and were referred to section *Bryoria* in Myllys *et al.* (2011), but were not present in our ITS+*Mcm7*+GAPDH analysis.

Here it can also be noted that two other specimens (specimens L411 and L413) collected from North America most probably represent yet another undescribed species. The combined ITS+*Mcm7*+GAPDH analysis suggests that it belongs in section *Bryoria* and is most closely related to *B. nadvornikiana* (Gyeln.) Brodo & D. Hawksw. and *B. poeltii* (Bystrek) Brodo & D. Hawksw. (Fig. 1).

The addition of *Mcm7* data, not used in our previous study on the phylogeny of the genus *Bryoria* (Myllys *et al.* 2011), did not shed any further light on the relationships in section *Implexae*. Resolution within this section is still low, and two subclades appearing in the combined phylogeny of ITS+*Mcm7*+GAPDH data (Fig. 1) are partly congruent with secondary chemistry and distribution.

In the combined ITS+*Mcm7* tree (GAPDH data not available), the North American endemic *B. pikei*, not present in our previous study (Myllys *et al.* 2011), falls within section *Implexae*, together with North American specimens of *B. capillaris* and *B. implexa* (chemotype 2) (Fig. 2) and close to other specimens of *B. capillaris*, *B. fuscescens* (Gyeln.) Brodo & D. Hawksw., *B. glabra*, *B. implexa*, *B. lanestris* (Ach.) Brodo & D. Hawksw., and *B. subcana* (Nyl. ex Stizenb.) Brodo & D. Hawksw. With the exception, however, of *B. glabra*, none of these taxa are confirmed as distinct species. We are now examining the taxonomy of section *Implexae* with extended taxon sampling and suggest that a number of species can be recognized on traditional morphological, chemical and ecological characters notwithstanding the apparent lack of corroborating DNA evidence (Velmala *et al.* 2014).

Phylogeny of alectorioid lichens

Although this study focused primarily on the delimitation of *Bryoria* and *Sulcaria*, it may be useful to briefly discuss the phylogeny of other alectorioid lichens included in our analyses.

As currently defined by Thell *et al.* (2012), the alectorioid group comprises *c.* 66 species from five genera (i.e., *Alectoria*, *Bryoria*, *Gowardia*, *Pseudephebe* and *Sulcaria*). Our analyses, however, do not support the monophyly of this group. The combined phylogeny of ITS+*Mcm7*+GAPDH data suggests that *Pseudevernia furfuracea* (a sister group to *Bryoria*), *Platismatia glauca* (sister to *Sulcaria*), *Bryocaulon* (sister to *Alectoria* and *Gowardia*) and *Nodobryoria* (sister to *Pseudephebe*) belong here also (Fig. 1). Our results, however, should be treated with caution as none of the above-mentioned groupings received any support. Clearly more comprehensive taxon sampling, also from parmelioid genera, is needed to assess the relationships among the alectorioid genera. Meanwhile, it is interesting to note a close, although unsupported relationship of *Pseudephebe* and *Nodobryoria*. *Nodobryoria* resembles *Pseudephebe* in cortical structure, in lacking secondary substances, and in having similar conidia (Common & Brodo 1995). According to Thell *et al.* (2012), *Nodobryoria* has an uncertain position in *Parmeliaceae*, though this is perhaps not surprising given that none of its three species have been represented in the recent large-scale molecular phylogenies. The present study, by contrast, includes all three species: two North American endemics, *N. abbreviata* (Müll. Arg.)

Common & Brodo and *N. oregana* (Tuck.) Common & Brodo, and *N. subdivergens* (E. Dahl) Common & Brodo, found also in Greenland (Brodo & Hawksworth 1977; Brodo & Alstrup 1981).

Alectoria was fairly well represented in our analyses, which included four of the seven species described so far. Diagnostic characters include the presence of conspicuous, white, markedly raised pseudocyphellae and the production of usnic acid, a substance lacking in the recent segregate genus *Gowardia* (Halonen *et al.* 2009). Our analyses did not recover the monophyly of *A. imshaugii* Brodo & D. Hawksw., *A. sarmentosa* (Ach.) Ach. and *A. vancouverensis* (Gyeln.) Brodo & D. Hawksw. (Figs 1–3). While *A. imshaugii* is easily recognized by its caespitose growth form and production of isidia, *A. sarmentosa* and *A. vancouverensis* are pendent species differing mainly in their chemistry, thallus anatomy and colour. Brodo & Hawksworth (1977) did not question the distinctiveness of the three taxa but acknowledged the presence of intermediate forms. Our results suggest that the species may be conspecific. For now, however, we refrain from venturing any definite taxonomic conclusions pending further study with additional taxon sampling.

Taxonomy

Sulcaria spiralifera (Brodo & D. Hawksw.) Myllys, Velmala & Goward comb. nov.

MycoBank No.: MB809146

Bryoria spiralifera Brodo & D. Hawksw., *Opera Bot.* **42:** 131 (1977); type: USA, California, Humboldt County, pine forest near Manila, on *Pinus contorta*, 1972, *S. Dowty* 137 (CANL 38403—holotype, seen).

New synonym: *Bryoria pseudocapillaris* Brodo & D. Hawksw., *Opera Bot.* **42:** 126 (1977); type: USA, Oregon, Curry County, Cape Blanco, 8 miles north of Port Orford, headland rocks and isolated trees on windswept summit, on sitka spruce at headland at 100 feet, 1974, *I. M. Brodo* 20539 (CANL 50596—holotype, seen; BM—isotype, not seen).

(Fig. 4A–D)

Thallus subpendent to pendent, 4–12 cm long, pale brown to dark brown, cortex dull or slightly shiny, often pruinose in norstictic-acid chemotype; branching mostly irregular, without distinct main branches, angles between the branches mainly acute, 0·10–0·35 mm diam., with spinulose side branches near apices; *pseudocyphellae* usually conspicuous, white, linear, straight or spiralling around branches, sometimes furrowed, abundant or sparse, 1–4 mm long; *soralia* and *isidia* lacking.

Apothecia and *conidiomata* unknown.

Chemistry. Chemotype 1: cortex and medulla K+ yellow, containing alectorialic acid, barbatolic acid and an unknown substance (Rf class 2–3 in solvent A and Rf class 3–4 in solvent B). Chemotype 2: cortex and medulla K+ yellow becoming red, containing norstictic acid, connorstictic acid and atranorin.

Distribution and habitat. Sulcaria spiralifera is a rare but sometimes locally abundant species endemic to the west coast of North America, from northern California to Washington. It grows in open or shady maritime forests on *Pinus contorta*, *Picea sitchensis* and on various shrubs and deciduous trees.

Comments. Bryoria pseudocapillaris and *B. spiralifera* were described in the same publication by Brodo & Hawksworth (1977). We chose to use the name *B. spiralifera*, since it better describes the morphology of this species.

Additional specimens examined. All specimens deposited in Siuslaw National Forest Herbarium unless stated otherwise **USA:** *California*: Del Norte County, Lake Earl State Park, on *Pinus contorta* var. *contorta*, 41°52′17·76″N, 124°11′56·04″W, sea level, 2000, *D. Glavich* 592; Humboldt County, Humboldt Bay National Wildlife Refuge, on *Pinus contorta* var. *contorta*, 40°52′49·44″N, 124°8′50·28″W, sea level, 2000, *D. Glavich* 581; Humboldt County, Humboldt Bay National Wildlife Refuge, 40°52′49·40″N, 124°8′50·5″W, 2001, *L. Geiser* 7075; Humboldt County, Humboldt Bay National Wildlife Refuge, on branch of *Picea sitchensis*, 41°48′43·56″N, 124°10′46·92″W, sea level, 2000, *D. Glavich* 546; Humboldt County, Trinidad State beach, 41°4′9·984″N, 124°9′10·08″W, 30 m, 1999, *D. Glavich* 0004 (hb. D. A. Glavich); Humboldt County, Redwood National Park, on *Pinus contorta* var. *contorta*, 41°42′26·28″N, 124°8′32·64″W, 76 m, 2000, *D. Glavich* 593. *Oregon*: Coos County, Siuslaw National Forest, on branch of *Vaccinium ovatum*, 43°16′8·4″N, 124°9′27·72″W, 8 m, 2000, *A. Mikulin* 1006; Coos County, Siuslaw National Forest, 43°16′8·4″N, 124°9′27·72″W, 8 m, 2000, *A. Mikulin* 1866; Coos County, Siuslaw National Forest, on branch of *Vaccinium ovatum*, 43°28′45·48″N, 124°14′54·24″W, 20 m, 2000, *A. Mikulin* 1030; Coos County, Siuslaw National Forest, on trunk of *Pinus contorta* var. *contorta*, 43°28′45·48″N, 124°14′54·24W, 20 m, 2000, *A. Mikulin* 1031; Coos County, Siuslaw National Forest, on twig of *Picea sitchensis*, 43°26′32·28″N, 124°16′22·08″W, 21 m, 2000, *A. Mikulin* 1001; Coos County, Oregon Dunes National Recreation Area, on branch of *Pinus contorta* var. *contorta*, 43°28′27·48″N, 124°13′48·36″W, 32 m, 2001, *A. Mikulin* 1224; Coos County, Oregon Dunes National Recreation Area, on branch of *Pinus contorta* var. *contorta*, 43°26″27·60″N, 124°14′49·92″W, 29 m, 2000, *A. Mikulin* 1051; Curry County, on *Picea sitchensis*, 42°50′13·20″N, 124°31′54·48″W, 2001, 15 m, *D. Glavich* 552; Lane County, north of Florence, on *Picea sitchensis* branch, 44°3′58·32″N, 124°6′52·56″W, 12 m, 2003, *D. Glavich* 603; Lane County, north of Florence, on *Picea sitchensis*, 44°3′59·04″N, 124°6′56·52″W, 6 m, 2003, *L. Geiser* 713 (Siuslaw National Forest Herbarium); Lane County, south of Florence, on *Picea sitchensis* branch, 43°52′30″N, 124°8′31·20″W, sea level, 2003, *A. Ingersoll* 953. *Washington*: Island County, Deception Pass State Park, on *Picea sitchensis* branch, 48°23′52·44″N, 122°39′47·52″W, 2 m, 2000, *A. Mikulin* 1260.

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