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Taxonomy of *Bryoria* section *Implexae* (Parmeliaceae, Lecanoromycetes) in North America and Europe, based on chemical, morphological and molecular data

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Ninety-seven ingroup specimens of *Bryoria* section *Implexae* (Parmeliaceae, Lecanoromycetes) were studied using molecular, chemical, morphological and geographic characters. The molecular data included nuclear ribosomal markers (ITS, IGS) and the partial glyceraldehyde-3-phosphate dehydrogenase (GAPDH) gene. In addition to parsimony analyses, a haplotype network was constructed. Phylogenetic analyses strongly supported the monophyly of the section *Implexae*. The specimens were grouped into two monophyletic clades. Clade 1 encompassed all esorediate material from North America, whereas Clade 2 included both sorediate North American material and all European material. Relationships at the species level, however, remained unresolved, except in the case of North American *B. implexa* chemotype 1 and European *B. capillaris*. Nevertheless a number of species in each clade can be recognized using traditional morphological, chemical and ecological characters: *Bryoria friabilis*, *B. inactiva sp. nova*, *B. kockiana sp. nova* (supported also by phylogeny), *B. pikei* and *B. pseudofuscescens* in Clade 1, and *B. capillaris*, *B. fuscescens*, *B. implexa*, *B. kuemmerleana*, and *B. vrangiana* in Clade 2. In addition, North American *B. capillaris* is proposed for inclusion in *B. pikei*, while *B. chalybeiformis, B. lanestris* and *B. subcana* are used as synonyms of *B. fuscescens*.

Introduction

The lichen-forming euascomycete genus *Bryoria* (Parmeliaceae, Lecanoromycetes) is distributed mainly in forested regions of boreal to north temperate Eurasia and North America, but also more widely on all continents, especially in mountainous regions. Most species are epiphytic on conifer branches but the genus includes some epilithic taxa as well (Brodo & Hawksworth 1977). *Bryoria* is characterized by its capillary growth form, its greyish, brownish or blackish branches, and its erect, caespitose or pendent habit. Pseudocyphellae (small openings in the cortex) are common although often inconspicuous. Soralia (vegetative propagules composed both of photobiont cells and fungal hyphae) are common, whereas sexual fruiting structures are rather rare or even unknown in a few species. Secondary metabolites, especially β-orcinol depsidones such as fumarprotocetraric acid, are often present. A closely related genus *Nodobryoria* differs from *Bryoria* by its cortical structure, lack of soralia and pseudocyphellae as well as lack of secondary metabolites (Common & Brodo 1995). *Bryocaulon* differs in having anisotomic dichotomously branched lobes, white, fusiform to punctiform and often raised pseudocyphellae, and olivetoric or physodic acid (Kärnefelt 1986). *Oropogon* resembles *Bryoria* in outward appearance, but has large muriform ascospores and, in most cases, perforate pseudocyphellae; *Bryoria* has simple, hyaline ascospores and non-perforate pseudocyphellae (Esslinger 1989).

Although conspicuous and frequently collected, *Bryoria* contains many poorly understood taxa owing to its considerable morphological plasticity and rarity of fungal sexual fruiting structures. In addition, intermediate specimens having morphological characters pointing to two or more species have been documented (Brodo & Hawksworth 1977, Brodo 1978, Holien 1989, Velmala *et al*. 2009). Especially perplexing are the pendent species, which often vary greatly in color, branching pattern and presence and type of soralia and pseudocyphellae. Consequently, the species are often identified primarily on thallus chemistry which, however, can also vary even for the major compounds (Brodo & Hawksworth 1977, Brodo 1978, Holien 1989). Chemically distinct but morphologically more or less identical populations have sometimes been recognized as chemotypes (Holien 1989).

Our recent phylogenetic studies on *Bryoria* (Velmala *et al*. 2009, Myllys *et al*. 2011b, *see* also Myllys *et al*. 2011a) have led us to question the traditional systematic position of many pendent taxa, including *B. capillaris*, *B. fuscescens*, *B. implexa* (including five chemotypes *sensu* Holien 1989), *B. lanestris* and *B. subcana*. Until recently, these species were assigned to two sections within *Bryoria*, i.e., the section *Bryoria* (*B. fuscescens*, *B. lanestris* and *B. subcana*) and the section *Implexae* (*B. capillaris* and *B. implexa*), these being traditionally separated based on chemical and cortical characters (Brodo & Hawksworth 1977, Holien 1989; *see* also Table 1). However, our analyses of ITS, GAPDH and mtSSU sequences showed that neither section is monophyletic, leading us to place these taxa in an emended section *Implexae* (Table 1) characterized by pendent, non-spinulose branches (Myllys *et al*. 2011b). Within this section, the five species — or chemotypes in the case of *B. implexa* — grouped into two subclades partly congruent with secondary chemistry and distribution. Representative specimens within each of these subclades shared almost identical DNA sequences, suggesting that several taxa currently treated at the species level may be conspecific, while others, for instance North American and European *B. capillaris*, may be taxonomically distinct. However, no taxonomic changes were proposed owing to limited taxon sampling.

Here we continue our phylogenic explorations of the section *Implexae* both by sampling across a wider range of taxa and by making use of a new DNA region (IGS of the nuclear rDNA). More specifically we aim to examine morphological and chemical species concepts in *Bryoria* section *Implexae* in light of our phylogenetic findings.

Material and methods

Taxon sampling

Ninety-nine *Bryoria* specimens from North America, Europe (including Canary Islands) and Asia were used in this study (Table 2). The ingroup consisted of 97 specimens from the section *Implexae* as defined by Myllys *et al*. (2011b) and representing seven species and nine unidentified specimens. Multiple samples of each taxon were included to assess genetic and geographic variation. The specimens were identified based on morphological and chemical characters as given in Brodo and Hawksworth (1977), Holien (1989, 1991, 1992) and Goward (1999). Here it must be noted that we provisionally followed the species concept of Holien (1989) and Myllys *et al.* (2011b), whereby *B. friabilis*, *B. pseudofuscescens* and *B. vrangiana* are treated as chemotypes of "*B. implexa s. lato*", as follows: (1) chemotype 1 with psoromic acid (*B. implexa* in Brodo & Hawksworth 1977), (2) chemotype 2 with norstictic acid (*B. pseudofuscescens* in Brodo & Hawksworth 1977), (3) chemotype 3 with gyrophoric acid (*B. friabilis* in Brodo & Hawksworth 1977), (4) chemotype 4 with fumarprotocetraric acid and ± atranorin (identified as *B. fuscescens*, *B. vrangiana* or as undescribed species according to Holien 1989), and (5) chemotype 5 with fumarprotocetraric acid in soralia and ± atranorin in thallus (identified as *B. fuscescens*, *B. vrangiana* or as undescribed species according to Holien 1989); *see* also Table 3. Unfortunately we were unable to obtain fresh material of the North American [henceforth NA] endemic species *B. pseudocapillaris*, *B. salazinica* and *B. spiralifera*, all of which were included in section *Implexae* by Brodo and Hawksworth (1977). We also lacked NA material of *B. implexa* chemotype 4, but did succeed in obtaining material of the following species not

Table 1. Species and diagnostic characters for sections *Bryoria* and *Implexae* according to Brodo and Hawksworth (1977) and Myllys *et al.* (2011b). Species marked with an asterisk were either not discussed by Brodo and Hawksworth (1977) or were included in section *Divaricatae*. Species not included in Myllys *et al.* (2011b) are marked with a question mark. Myllys *et al.* (2011b) treated *Bryoria trichodes* ssp. *americana* at the species level, as *B. americana*, which belongs in section *Americanae*. The type species of each section are in boldface.

Section	Brodo & Hawksworth (1977)	Myllys *et al.* (2011b)
Bryoria	Fumarprotocetraric acid present, pseudocyphellae present or absent, soralia frequent, lateral spinules or spinulose branches rare	Fumarprotocetraric acid common, pseudocyphellae present or absent, soralia present or absent, lateral spinules or spinulose branches usually present
	B. chalybeiformis	*B. divergescens**
	B. fuscescens	*B. fastigiata**
	B. glabra	*B. furcellata**
	B. lanestris	*B. hengduanensis**
	B. subcana	*B. lactinea**
	B. trichodes* subsp. *trichodes	*B. nadvornikiana* *B. nitidula*
	B. trichodes subsp. *americana*	*B. perspinosa**
	B. vrangiana	*B. poeltii**
		*B. simplicior**
		B. trichodes
Implexae	β-orcinol depsidones other than fumarprotocetraric acid present, pseudocyphellae always present, soralia occasional, lateral spinules or spinulose branches rare	Fumarprotocetraric acid common, pseudocyphellae present or absent, soralia present or absent, lateral spinules or spinulose branches absent
	B. capillaris	*B. capillaris*
	B. friabilis	*B. chalybeiformis*?
	B. implexa	*B. fuscescens*
	B. nadvornikiana	*B. glabra*
	B. pikei *B. pseudocapillaris*	***B. implexa*** (incl. *B. friabilis*, *B. pseudofuscescens*, *B. vrangiana*)
	B. pseudofuscescens	*B. lanestris*
	B. salazinica	*B. pikei*?
	B. spiralifera	*B. pseudocapillaris*?
		B. salazinica?
		B. spiralifera?
		B. subcana

Table 2. List of specimens used in the phylogenetic analyses with voucher details and GenBank accession numbers. An asterisk indicates newly generated sequences; others were obtained from GenBank. – = n.a.

Taxon	Voucher specimen	Laboratory code	ITS	IGS	GAPDH
Bryoria capillaris	Finland, Etelä-Häme, 2003, *V. Haikonen 22228* (H)	L141	FJ668493	FJ668455	FJ668399
B. capillaris	Finland, Etelä-Savo, 2005, *L. Myllys 485* (H)	L211	GQ996287	KJ396487*	GQ996259
B. capillaris	Norway, Nord-Trøndelag, 2005, *H. Holien 10056* (TRH)	L270	GQ996288	KJ396488*	GQ996260
B. capillaris	Finland, Uusimaa, 2005, *S. Velmala 4 & L. Myllys* (H)	S2	KJ396433*	KJ396489*	KJ954306*
B. capillaris	Spain, Tenerife, 2006, *P. Keihäs s.n.* (OULU)	S192	GQ996289	KJ396490*	GQ996261
B. friabilis	Canada, British Columbia, 2006, *T. Goward 06-858* (UBC)	L355	KJ396434*	KJ396491*	KJ954307*
B. friabilis	Canada, 2011, *Dillman 11 May 11:6* (UBC)	L407	KJ396435*	KJ396492*	KJ954308*
B. friabilis	U.S.A., Alaska, 2008, *S. Jovan s.n.* (KLGO-50787)	S395a	KJ576728	KJ396493*	KJ599481
B. furcellata	Finland, Etelä-Savo, 2003, *V. Haikonen 22770* (H)	L147	HQ402711	KJ396494*	HQ402627
B. fuscescens	Finland, Etelä-Savo, 2005, *L. Myllys 464* (H)	L139	KJ396436*	KJ396495*	KJ954309*
B. fuscescens	Finland, Ahvenanmaa, 2003, *M. Stjernberg s.n.* (H)	L149	GQ996290	KJ396496*	GQ996262
B. fuscescens	Sweden, Södermanland, 2002, *Rydberg s.n.* (UPS)	L160	GQ996300	KJ396497*	GQ996272
B. fuscescens	Finland, Oulun Pohjanmaa, 2005, *P. Halonen s.n.* (OULU)	L189	GQ996305	KJ396498*	GQ996278
B. fuscescens	Norway, Sogn og Fjordane, 2005, *T. Goward 05-1205* (UBC)	L224	KJ396437*	KJ396499*	KJ954310*
B. fuscescens	Denmark, Greenland, 2004, *Hansen, Lich. Greenl. Exs. 946* (H)	L232	GQ996304	KJ396500*	GQ996277
B. fuscescens	Norway, Telemark, 2005, *S. Rui & E. Timdal 9910* (O)	L305	KJ396438*	–	–
B. fuscescens	Norway, Oppland, 2005, *R. Haugan 7636* (O)	L307	KJ396439*	–	KJ954311*
B. fuscescens	Finland, Koillismaa, 2005, *S. Velmala 25, P. Halonen & L. Myllys* (H)	S24	KJ576715	KJ396501*	KJ599468
B. fuscescens	Finland, Koillismaa, 2005, *S. Velmala 51 & P. Halonen* (H)	S56	GQ996291	KJ396502*	GQ996263
B. fuscescens	Finland, Pohjois-Karjala, 2006, *S. Velmala 101, P. Halonen & S. Laitinen* (H)	S109	KJ396440*	KJ396503*	KJ954312*
B. fuscescens	Russia, Perm Territory, 2005, *M. Schajachmetova 18.9* (H)	S157	GQ996306	KJ396504*	GQ996279
B. fuscescens	Canada, Alberta, 2006, *A. Adams 0076B & D. Hall* (UBC)	S256	GQ996307	KJ396505*	GQ996280
B. fuscescens	Canada, 2006, collector unknown (UBC)	S259	KJ396441*	KJ396506*	KJ954313*
B. fuscescens	Canada, Alberta, 2006, *A. Adams 0037_a & D. Hall* (UBC)	S260a	KJ396442*	KJ396507*	KJ954314*
B. fuscescens	Canada, Alberta, 2006, *A. Adams 0037_b & D. Hall* (UBC)	S260b	GQ996286	KJ396508*	GQ996258
B. fuscescens	Canada, Alberta, 2006, *A. Adams 0087 & D. Hall* (UBC)	S261	KJ396443*	KJ396509*	KJ954315*
B. fuscescens	Canada, Alberta, 2006, *J. Kamin 033* (UBC)	S267	KJ576716	KJ396510*	KJ599469
B. fuscescens	Canada, Alberta, 2006, *A. Adams 0089 & D. Hall* (UBC)	S272	KJ576717	KJ396511*	KJ599470
B. fuscescens	Canada, Alberta, 2006, *J. Kamin 016* (UBC)	S274	GQ996303	KJ396512*	GQ996276
B. fuscescens	Canada, Alberta, 2006, *J. Kamin 037* (UBC)	S277a	KJ576718	KJ396513*	KJ599471
B. fuscescens	Canada, Alberta, 2008, collector unknown (UBC)	S369	KJ396444*	KJ396514*	KJ954316*
B. fuscescens	Canada, Alberta, 2008, collector unknown (UBC)	S379	KJ396445*	KJ396515*	KJ954317*
B. fuscescens	Canada, Alberta, 2006, *A. Adams 1069 & D. Hall* (UBC)	S380	KJ396446*	KJ396516*	KJ954318*
B. glabra	Finland, Koillismaa, 2004, *P. Halonen s.n.* (OULU)	L186	FJ668494	FJ668456	FJ668400
B. implexa	Finland, Koillismaa, 2005, *S. Velmala 23, P. Halonen & L. Myllys* (H)	S22	GQ996294	KJ396517*	GQ996266

B. implexa	Finland, Koillismaa, 2005, *S. Velmala 35a, P. Halonen & L. Myllys* (H)	S36	KJ576719	KJ396518*	KJ599472
B. implexa	Finland, Koillismaa, 2005, *S. Velmala 37, P. Halonen & L. Myllys* (H)	S39	GQ996293	KJ396519*	GQ996265
B. implexa	Finland, Koillismaa, 2005, *S. Velmala 35c, P. Halonen & L. Myllys* (H)	S67	KJ396447*	KJ396520*	KJ954319*
B. implexa	Russia, Murmansk Region, 2005, *G. Urbanavichus 05-1270* (KPABG)	S168	KJ396448*	KJ396521*	KJ954320*
B. inactiva	Canada, British Columbia, 2005, *T. Goward 05-05* (UBC)	L206	GQ996283	KJ396522*	GQ996255
B. inactiva	Canada, British Columbia, 2011, *T. Goward 11-52* (UBC)	L323b	KJ396449*	KJ396523*	KJ954321*
B. inactiva	Canada, British Columbia, 2011, *T. Goward 11-61* (UBC)	L347	KJ396450*	KJ396524*	KJ954322*
B. inactiva	Canada, British Columbia, 2006, *T. Goward 06-112* (UBC)	L358	KJ396451*	KJ396525*	KJ954323*
B. inactiva	Canada, British Columbia, 2007, *T. Goward 07-02-0028* (UBC)	S239a	GQ996284	KJ396526*	GQ996256
B. inactiva	U.S.A., Alaska, *Berg 3082* (UBC)	S384	KJ576724	KJ396527*	KJ599479
B. inactiva	Canada, British Columbia, 2009, *T. Goward s.n.* (UBC)	S392a	KJ396452*	KJ396528*	KJ954324*
B. kockiana	U.S.A., Alaska, 2011, *D. Nossov 20019-1* (UBC)	L394	KJ396453*	KJ396529*	KJ954325*
B. kockiana	U.S.A., Alaska, 2011, *D. Nossov 90002-1* (UBC)	L396	KJ396454*	KJ396530*	KJ954326*
B. kuemmerleana	Iran, East Azarbaijan, 2005, *M. Sohrabi 4656* (H)	L244a	GQ996295	KJ396531*	GQ996267
B. kuemmerleana	Norway, Nord-Trøndelag, 2005, *H. Holien 10177* (TRH)	L274	GQ996296	KJ396532*	GQ996268
B. kuemmerleana	Norway, Nord-Trøndelag, 2005, *H. Holien 10175* (TRH)	L275	KJ396455*	KJ396533*	KJ954327*
B. kuemmerleana	Sweden, Härjedalen, 2005, *F. Högnabba 593* (H)	S128	KJ576720	KJ396534*	KJ599473
B. kuemmerleana	Russia, Perm Territory, 2004, *A. V. Melekhin 6506* (H)	S160	KJ396456*	KJ396535*	KJ954328*
B. pikei	Canada, British Columbia, 2005, *T. Goward 05-23* (UBC)	L197	KJ396457*	KJ396536*	KJ954329*
B. pikei	Canada, British Columbia, 2005, *T. Goward 05-20* (UBC)	L200	KJ396458*	KJ396537*	KJ954330*
B. pikei	Canada, British Columbia, 2005, *T. Goward 05-19* (UBC)	L209	GQ996281	KJ396538*	GQ996253
B. pikei	Canada, British Columbia, 2005, *T. Goward 05-18* (UBC)	L210	KJ576714	KJ396539*	KJ599467
B. pikei	Canada, British Columbia, 2008, *C. Björk 17006* (UBC)	L374	KJ396459*	KJ396540*	KJ954331*
B. pikei	Canada, British Columbia, 2009, *C. Björk 18116* (UBC)	L376	KJ396460*	KJ396541*	KJ954332*
B. pikei	Canada, British Columbia, 2009, *T. Goward 09-323b* (UBC)	L377	KJ396461*	KJ396542*	KJ954333*
B. pikei	Canada, British Columbia, 2009, *T. Goward 09-365* (UBC)	L421	KJ396462*	KJ396543*	KJ954334*
B. pikei	Canada, British Columbia, 2007, *T. Goward 07-02-0010* (UBC)	S221	KJ396463*	KJ396544*	KJ954335*
B. pikei	Canada, British Columbia, 2008, *K. McKeown s.n.* (UBC)	S362	KJ396464*	KJ396545*	KJ954336*
B. pikei	Canada, British Columbia, 2008, *T. Goward s.n.* (UBC)	S368	KJ396465*	KJ396546*	KJ954337*
B. pikei	Canada, Alberta, 2008, *C. Lane 0017_XEV004_17a* (UBC)	S382	KJ396466*	KJ396547*	KJ954338*
B. pikei	Canada, Alberta, 2008, *C. Lane 0017_XEV004_17b* (UBC)	S383a	KJ396467*	KJ396548*	KJ954339*
B. pikei	U.S.A., Alaska, *Berg 3051* (UBC)	S390	KJ396468*	KJ396549*	KJ954340*
B. pikei	U.S.A., Oregon, 2008, *T. Spribille 29879* (hb. Spribille)	S394	KJ576727	KJ396550*	KJ599480
B. pseudofuscescens	Canada, British Columbia, 2007, *T. Goward 07-02-0011* (UBC)	S222	KJ396469*	KJ396551*	KJ954341*
B. pseudofuscescens	Canada, British Columbia, 2007, *T. Goward 07-02-0021* (UBC)	S232	KJ396470*	KJ396552*	KJ954342*
B. pseudofuscescens	Canada, British Columbia, 2007, *T. Goward s.n.* (UBC)	S370	KJ396471*	KJ396553*	KJ954343*
B. pseudofuscescens	Canada, British Columbia, 2007, *T. Goward s.n.* (UBC)	S371	KJ396472*	KJ396554*	KJ954344*
B. pseudofuscescens	U.S.A., Alaska, *Berg 5555* (UBC)	S377	KJ396473*	KJ396555*	KJ954345*
B. pseudofuscescens	U.S.A., Alaska, *Berg 3242* (UBC)	S386	KJ576725	KJ396556*	KJ599478
B. pseudofuscescens	U.S.A., Alaska, *Berg 3242-A* (UBC)	S387	KJ576726	KJ396557*	KJ599477

continued

Table 2. Continued.

Taxon	Voucher specimen	Laboratory code	ITS	IGS	GAPDH
B. vrangiana	Norway, Nord-Trøndelag, 2005, *H. Holien 10039* (TRH)	L272	GQ996299	KJ396558*	GQ996271
B. vrangiana	Norway, Nord-Trøndelag, 2005, *H. Holien 10439* (TRH)	L273	KJ396474*	KJ396559*	KJ954346*
B. vrangiana	Norway, Nord-Trøndelag, 2005, *H. Holien 10040* (TRH)	L279	KJ396475*	KJ396560*	KJ954347*
B. vrangiana	Norway, Nord-Trøndelag, 2005, *H. Holien 10409* (TRH)	L286	KJ396476*	KJ396561*	KJ954348*
B. vrangiana	Norway, Nord-Trøndelag, 2005, *H. Holien 10176* (TRH)	L300	GQ996301	KJ396562*	GQ996274
B. vrangiana	Finland, Uusimaa, 2005, *S. Velmala 08 & L. Myllys* (H)	S6	KJ396477*	KJ396563*	KJ954349*
B. vrangiana	Finland, Koillismaa, 2005, *S. Velmala 11b, P. Halonen & L. Myllys* (H)	S10	GQ996297	KJ396564*	GQ996269
B. vrangiana	Finland, Koillismaa, 2005, *S. Velmala 31b, P. Halonen & L. Myllys* (H)	S32	GQ996298	KJ396565*	GQ996270
B. vrangiana	Finland, Koillismaa, 2005, *S. Velmala 40, P. Halonen & L. Myllys* (H)	S42	KJ396478*	KJ396566*	KJ954350*
B. vrangiana	Finland, Koillismaa, 2005, *S. Velmala 41, P. Halonen & L. Myllys* (H)	S43	KJ396479*	KJ396567*	KJ954351*
B. vrangiana	Finland, Koillismaa, 2005, *S. Velmala 43a, P. Halonen & L. Myllys* (H)	S45	GQ996302	KJ396568*	GQ996275
B. vrangiana	Finland, Koillismaa, 2005, *S. Velmala 44, P. Halonen & L. Myllys* (H)	S47	KJ576723	KJ396569*	KJ599476
B. vrangiana	Finland, Koillismaa, 2005, *S. Velmala 52 & P. Halonen* (H)	S57	KJ576722	KJ396570*	KJ599475
B. vrangiana	Finland, Koillismaa, 2005, *S. Velmala 54 & P. Halonen* (H)	S59	KJ396480*	KJ396571*	KJ954352*
B. vrangiana	Finland, Varsinais-Suomi, 2005, *S. Velmala 57, L. Myllys & A. Puolasmaa* (H)	S62	KJ576721	KJ396572*	KJ599474
B. vrangiana	Finland, Kainuu, 2005, *S. Velmala 66, P. Halonen & P. Keihäs* (H)	S72	KJ396481*	KJ396573*	KJ954353*
B. vrangiana	Russia, Perm Territory, 2003, *Y. A. Ateeva 5055* (H)	S164	GQ996285	KJ396574*	GQ996257
B. vrangiana	Russia, Perm Territory, 2003, *A. V. Melekhin 10123* (H)	S166	GQ996308	KJ396575*	GQ996273
B. vrangiana	Finland, Oulun Pohjanmaa, 2006, *P. Halonen s.n.* (OULU)	S196	KJ396482*	KJ396576*	KJ954354*
B. vrangiana	Finland, Kainuu, 2008, *L. Myllys 512* (H)	S341b	KJ396483*	KJ396577*	KJ954355*
B. vrangiana	Canada, Alberta, 2008, *C. Lane 0017_XEV001_79* (UBC)	S385	KJ396484*	KJ396578*	KJ954356*
B. vrangiana	Norway, Møre og Romsdal, 2008, *H. Holien 11496* (TRH)	S396	KJ576729	KJ396579*	KJ599482
Bryoria sp.	U.S.A., Alaska, 2011, *S. Jaan 90088-21* (UBC)	L392	KJ396485*	KJ396580*	KJ954357*
Bryoria sp.	U.S.A., Alaska, 2011, *D. Nossov 90077-1* (UBC)	L395	KJ396486*	KJ396581*	KJ954358*

available for our previous study (Myllys *et al.* 2011b): *B. chalybeiformis*, NA material of *B. implexa* chemotype 1 and *B. pikei*. *Bryoria furcellata* was used as outgroup, based on its known placement in section *Bryoria*, a sister clade to the section *Implexae* (Myllys *et al.* 2011b). *Bryoria glabra*, which appeared as a basal taxon in the section *Implexae*, was also included in the analyses.

Thin layer chromatography

Secondary metabolites were examined with thin layer chromatography (TLC) according to the methods in Orange *et al.* (2001). The metabolites were extracted in acetone using branches 1–3 cm long and spotted with 75 mm/75 μl glass capillary tubes (Hirschmann Laborgeräte) on 10 × 20 cm 60 F_{254} silica gel TLC-plates (Merck). The plates were run in solvents A and B (for solvent B, formulas from both Culberson 1972 and Mietzsch *et al.* 1994 according to Orange *et al.* 2001 were used).

The presence of fumarprotocetraric acid has been considered an important diagnostic character especially in *B. fuscescens s. lato* (Brodo & Hawksworth 1977): *B. fuscescens* and *B. subcana* typically contain fumarprotocetraric acid in the soralia, medulla and outer cortex of the thallus, while this compound is present only in the soralia in *B. glabra*, *B. chalybeiformis* and *B. lanestris*. Outside *B. fuscescens s. lato*, fumarprotocetraric acid has been reported in the thallus of *B. implexa* chemotype 4 as well as in the soralia of *B. capillaris* and *B. implexa* chemotypes 3 and 5 (Holien 1989). For this reason, branches without soralia were used for TLC and soralia were tested separately with *para*-phenylendiamine (PD) spot tests which produces a red reaction in the presence of fumarprotocetraric acid. In the case of heavily sorediate thalli, we performed TLC on sorediate branches and then spot-tested both branches and soralia with PD.

DNA extraction, amplification and sequencing

DNA extraction, amplification and sequencing were performed as described by Myllys *et al.* (2011b). Three DNA regions were used: (1) the internal transcribed spacers of the nuclear rDNA including the 5.8S region (ITS); (2) partial sequences from the intergenic spacer of the nuclear rDNA (IGS); and (3) partial sequences from the protein-coding glyceraldehyde-3-phosphate dehydrogenase gene (GAPDH).

Primers used for PCR amplification were as follows: (1) for the ITS region: ITS1-F (Gardes & Bruns 1993) and ITS4 (White *et al.* 1990) or ITS1-LM (Myllys *et al.* 1999) and ITS2-KL (Lohtander *et al.* 1998); (2) for the IGS region: IGS12B (Printzen & Ekman 2002) and SSU72R

Table 3. Members of *Bryoria* section *Implexae* examined in the present study.

Species name/identification according to Brodo and Hawksworth (1977)	*Bryoria implexa* chemotype according to Holien (1989)	Diagnostic substance
B. implexa	1	psoromic acid
B. pseudofuscescens	2	norstictic acid
B. friabilis	3	gyrophoric acid
B. fuscescens/*B. vrangiana*/*Bryoria* sp.	4	fumarprotocetraric acid
B. fuscescens/*B. vrangiana*/*Bryoria* sp.	5	no substances or atranorin
B. capillaris	–	barbatolic acid
B. chalybeiformis	–	no substances (fumarprotocetraric acid in soralia)
B. fuscescens	–	fumarprotocetraric acid
B. pikei	–	alectorialic acid
B. lanestris	–	no substances (fumarprotocetraric acid in soralia)
B. subcana	–	fumarprotocetraric acid

(Gargas & Taylor 1992); and (3) for the GAPDH region: Gpd1-LM and Gpd2-LM (Myllys *et al*. 2002). The same primers were used in DNA sequencing except for the ITS region for which the primer ITS5 (White *et al*. 1990) was used together with ITS2-KL.

Chemical, geographic and morphological characters

We included one distributional geographic, eight morphological and nine chemical characters in our phylogenetic reconstruction (Table 4), in keeping with traditional species concepts in *Bryoria* (*see* e.g. Brodo & Hawksworth 1977, Holien 1989, 1991, 1992 and Goward 1999). In light of the wide infraspecific morphological variation in this genus, as well as the potential for hitherto unknown species, we coded these characters primarily according to the condition actually observed in our material; hence the character states recorded here may not conform in all regards with earlier published descriptions. Chemical compounds were grouped according to their biosynthetic origin, with each biosynthetic group treated as a separate character (characters 1, 5 and 9). Psoromic acid (character 4) has been reported from the apothecia of several species (Brodo & Hawksworth 1977, Holien 1989), but was coded as present only when occurring in the thallus. Character 10, the presence or absence of soralia, was often difficult to interpret because of intermixed specimens. In such cases, several esorediate and sorediate branches were separately spot-tested to ascertain which part was originally used for TLC and DNA extraction. PD was used to detect fumarprotocetraric acid (brick red reaction) and psoromic acid (bright yellow reaction, at least in high concentration), and potassium hydroxide (KOH) to detect barbatolic acid (yellow reaction) and norstictic acid (dark red reaction). In some specimens pseudocyphellae (character 11) were difficult to distinguish from young soralia, and were coded as missing data. The morphological data matrix is given in Appendix 1.

Sequence alignment and data analyses

Altogether 202 new DNA sequences were generated in connection with this study: 54 ITS, 95 IGS and 53 GAPDH sequences (*see* Table 2). SeqMan II for Macintosh (DNASTAR, Inc., Madison, Wisconsin, U.S.A.) was used to edit and assemble the chromatograms. The sequences were aligned with MUSCLE 3.7 using default parameters (Edgar 2004) on Hippu server system at the CSC — IT Center for Science, Finland (http://www.csc.fi/english). The alignments for each marker were manually optimized and con-

Table 4. Chemical, morphological and geographic characters and character states used in this study.

1.	β-orcinol depsidones: absent (0), present (1), *see* characters 2–4
2.	Fumarprotocetraric acid: absent (0), present only in soralia (1), present in thallus (2)
3.	Norstictic acid: absent (0), present (1)
4.	Psoromic acid: absent (0), present (1)
5.	β-orcinol depsides: absent (0), present (1), see characters 6–8
6.	Atranorin and/or chloroatranorin: absent (0), present (1)
7.	Alectorialic acid: absent (0), present (1)
8.	Barbatolic acid: absent (0), present (1)
9.	Gyrophoric acid (= orcinol depside): absent (0), present (1)
10.	Soralia: absent (0), present (1)
11.	Pseudocyphellae: absent or very rare (0), present (1)
12.	Pseudocyphellae color: brownish white (0), white (1)
13.	Pseudocyphellae surface: slightly depressed or plane (0), partly raised (1)
14.	Pseudocyphellae shape: linear (0), elongate-fusiform (1)
15.	Thallus color: gray to pale brown (0), brown (1), dark brown to black (2)
16.	Apothecia: absent (0), present (1)
17.	Branching angles: mainly acute (0), mainly obtuse (1), both (2)
18.	Origin: North America (0), Europe or Asia (1)

catenated for the combined analyses using MacClade 4.08 (Maddison & Maddison 2005).

Phylogenetic analyses using Maximum Parsimony as an optimality criterion were performed on concatenated sequence matrices. Since we could not obtain IGS and/or GAPDH sequences from the two *B. chalybeiformis* specimens, two combined datasets consisting exclusively of molecular characters were analyzed: (1) ITS, IGS and GAPDH dataset with 97 specimens, i.e. without *B. chalybeiformis* (pruned dataset), and (2) ITS, IGS and GAPDH dataset with all 99 specimens (large dataset). In addition, a third analysis was performed where chemical, distributional and morphological characters were combined with the pruned dataset. The parsimony analyses were performed with TNT ver. 1.1 for Windows (Goloboff *et al.* 2008) using the New Technology Search (including sectorial searches, tree drifting, ratchet and tree fusing) and default parameters except for the following settings: random addition sequence (RAS) with 500 replicates and 15 iterations for the ratchet. Gaps were treated as missing data and, for comparison, all analyses were also performed with gaps as fifth character. Clade support was assessed with Jackknifing as implemented in TNT using 1000 repetitions and the New Technology Search as described above.

To estimate intraspecific haplotype relationships a haplotype network analysis was performed with TCS 1.21 (Clement *et al.* 2000) on the pruned dataset. *Bryoria furcellata* and *B. glabra* were excluded from the analysis. Gaps were treated as missing data and the probability of parsimony was set at 95%.

To test for potential conflict among the different DNA regions, parsimony analysis was performed on each individual marker. Since the resulted consensus trees showed no conflicting groups by visual inspection, combined dataset including all regions were used in the phylogenetic and haplotype analyses.

Results

Phylogenetic analyses

The pruned dataset with 97 specimens contained 1855 characters of which 75 (4.0%) were parsimony informative. TNT analysis resulted in 413 most parsimonious trees of 230 steps. The section *Implexae* is clearly monophyletic with a 100% jackknife support value (Fig. 1). The ingroup is divided into two strongly or moderately supported (90% and 82% jackknife values) clades, partly based on the geographic origin of the specimens: Clade 1 includes all esorediate NA specimens (*B. capillaris*, *B. implexa* chemotypes 1, 2 and 3, *B. pikei* and *Bryoria* spp.), whereas Clade 2 includes all European and Asian specimens (*B. capillaris*, *B. fuscescens*, *B. implexa*, *B. lanestris* and *B. subcana*) as well as sorediate NA specimens (*B. fuscescens*, *B. implexa* chemotype 5 and *B. lanestris*). Clade 1 includes two strongly supported (99% jackknife values) subclades: one with NA *Bryoria implexa* chemotype 1 specimens and two *Bryoria* sp. specimens, and one with all the other specimens. Otherwise the subclades in Clade 1 are mostly poorly supported and do not correlate with traditional chemical or morphological markers. The relationships in Clade 2 are mostly unresolved; 24 out of the 59 specimens in the clade grouped in a subclade with the 55% jackknife value, and further into smaller clades. Here too, however, the subclades do not correlate with current taxonomic concepts.

The large data set with 99 specimens contained 1855 characters of which 75 (4.0%) were parsimony informative. TNT analysis resulted in 127 most parsimonious trees of 230 steps. Again the ingroup is monophyletic (Fig. 2) but only Clade 1 appeared with the 52% jackknife value. Otherwise the topologies are the same as in the pruned tree. The poorer resolution, i.e. the lack of Clade 2, and poorer support values as compared with those in the pruned tree are most probably due to the two *B. chalybeiformis* specimens which include large amount of missing data (missing IGS and/or GAPDH sequences), since the datasets are otherwise identical.

The third dataset with geographic, chemical and morphological data combined with the pruned dataset contained 1873 characters of which 93 (5.0%) were parsimony informative. TNT analysis resulted in 116 trees of 407 steps. The ingroup is monophyletic (Fig. 3), and both Clades 1 and 2 appear but are more poorly resolved than in the molecular trees. A subclade

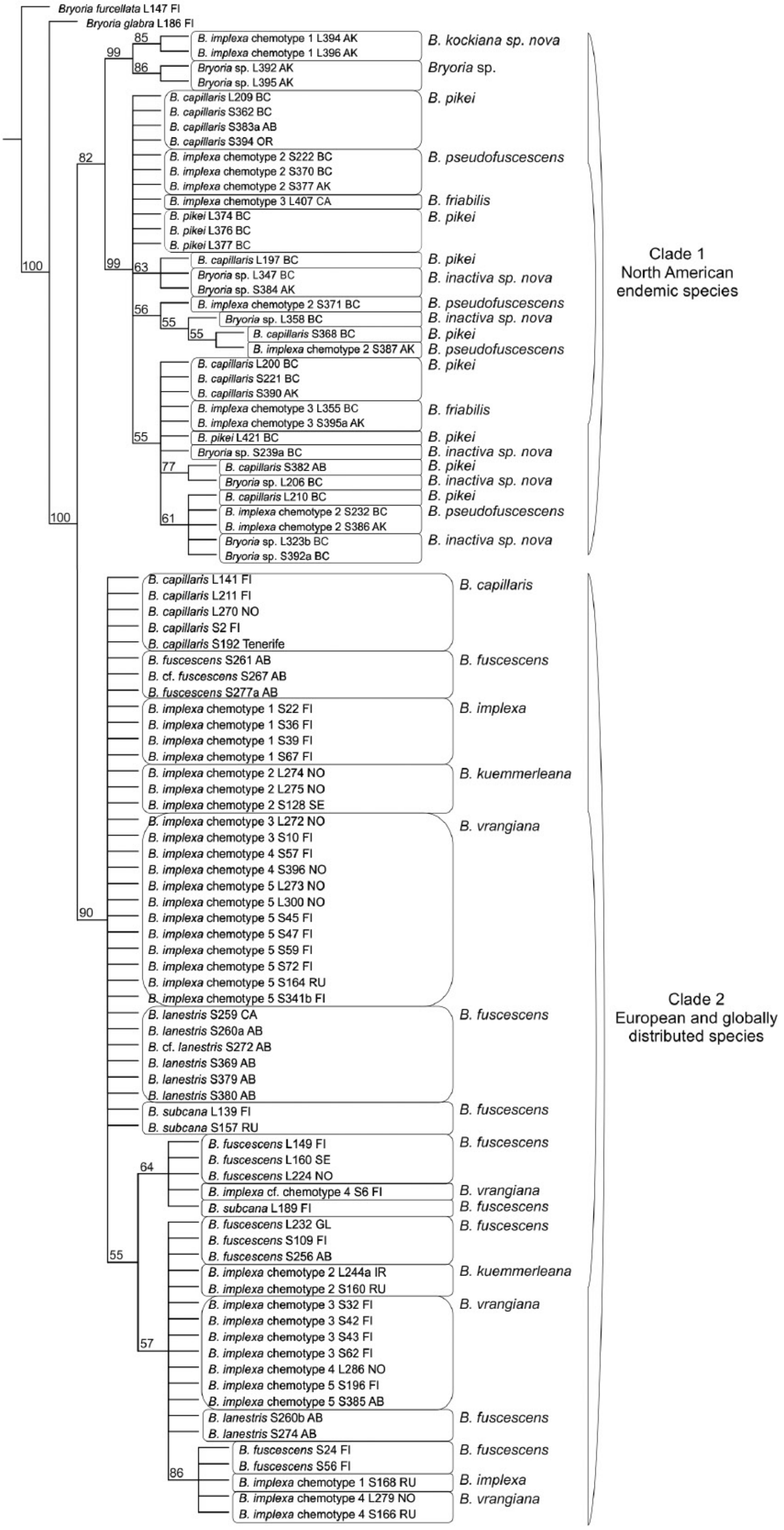

Fig. 1. Strict consensus tree based on the pruned dataset of ITS, IGS and GAPDH regions. Jackknife support values exceeding 50% are shown above the nodes. Laboratory code is given after the taxon name, followed by the locality (AB = Alberta, Canada; AK = Alaska, U.S.A.; BC = British Columbia, Canada; FI = Finland; GL = Greenland, Denmark; IR = Iran; NO = Norway; OR = Oregon, U.S.A., RU = Russia; SE = Sweden). Taxon names given in boxes with rounded corners follow recent taxonomic concepts. Names on the right are new names proposed in this study.

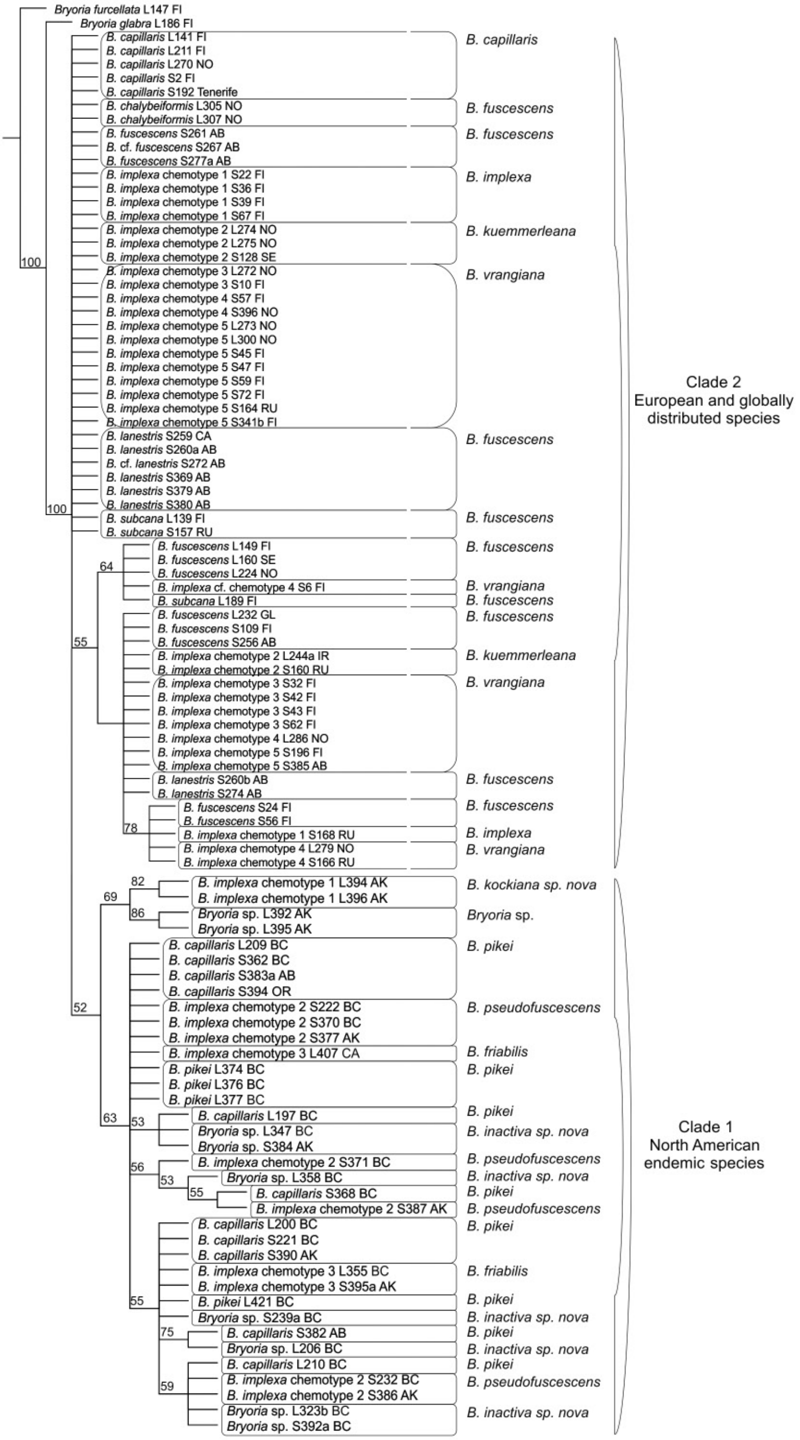

Fig. 2. Strict consensus tree based on the large dataset of ITS, IGS and GAPDH regions. Jackknife support values exceeding 50% are shown above the nodes. Laboratory code and locality (for abbreviations *see* Fig. 1) are given after the taxon name. Taxon names given in boxes with rounded corners follow recent taxonomic concepts. Names on the right are new names proposed in this study.

in Clade 1 including *B. implexa* chemotype 1 and two *Bryoria* sp. specimens is strongly supported. Within this subclade NA *B. implexa* chemotype 1 appears as monophyletic, a result obtained also from analyses of molecular data only. European *B. capillaris* in Clade 2 is recovered, otherwise

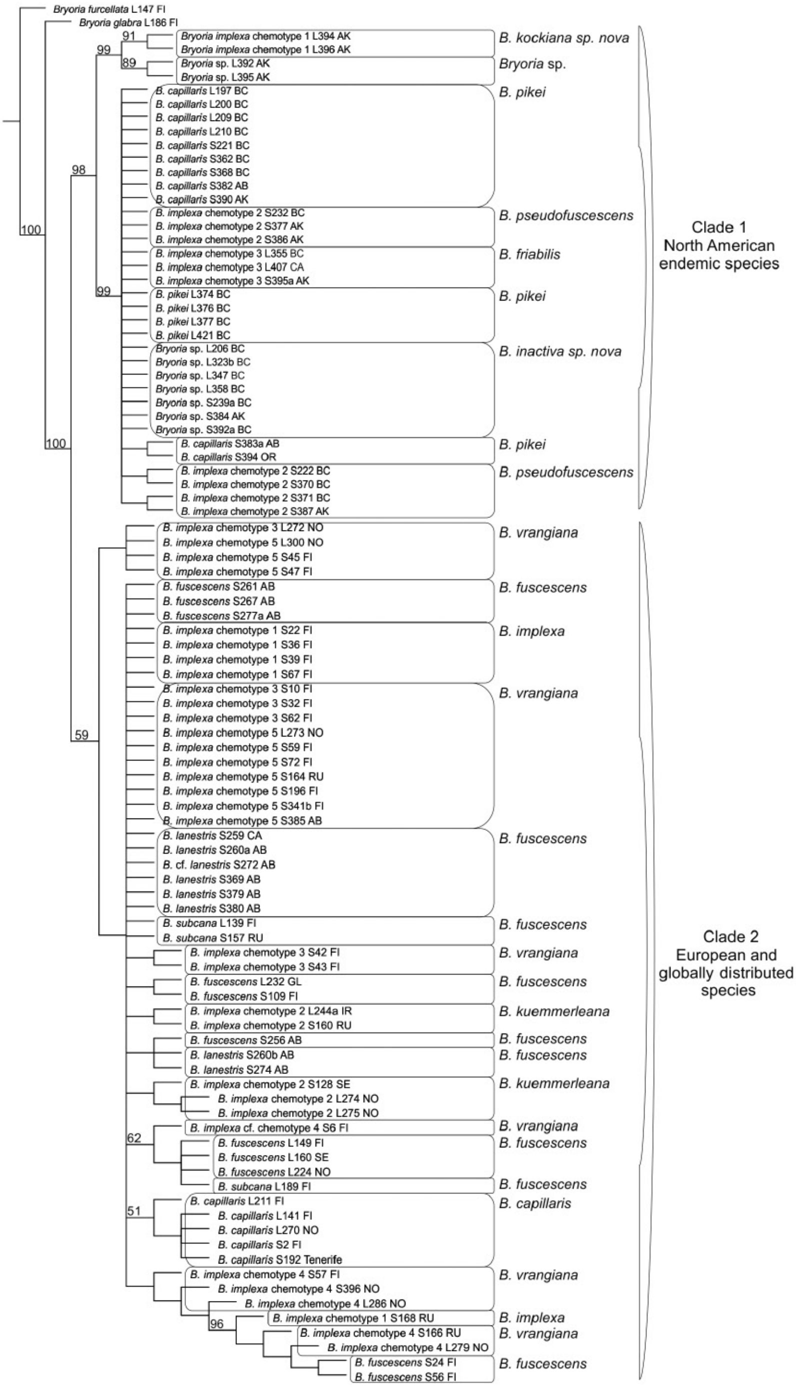

Fig. 3. Strict consensus tree based on the combined dataset of the pruned dataset and chemical, geological and morphological characters. Jackknife support values exceeding 50% are shown above the nodes. Laboratory code and locality (for abbreviations *see* Fig. 1) are given after the taxon name. Taxon names given in boxes with rounded corners follow recent taxonomic concepts. Names on the right are new names proposed in this study.

the taxa are nonmonophyletic. None of the nonmolecular characters examined were synapomorphic for any group.

The analyses with gaps treated as fifth character had identical tree topologies for all three data sets (trees not shown).

Haplotype network

The haplotype network produced 33 haplotypes from 95 specimens. Specimens differing only by missing or ambiguous characters were not counted as haplotypes. The maximum number

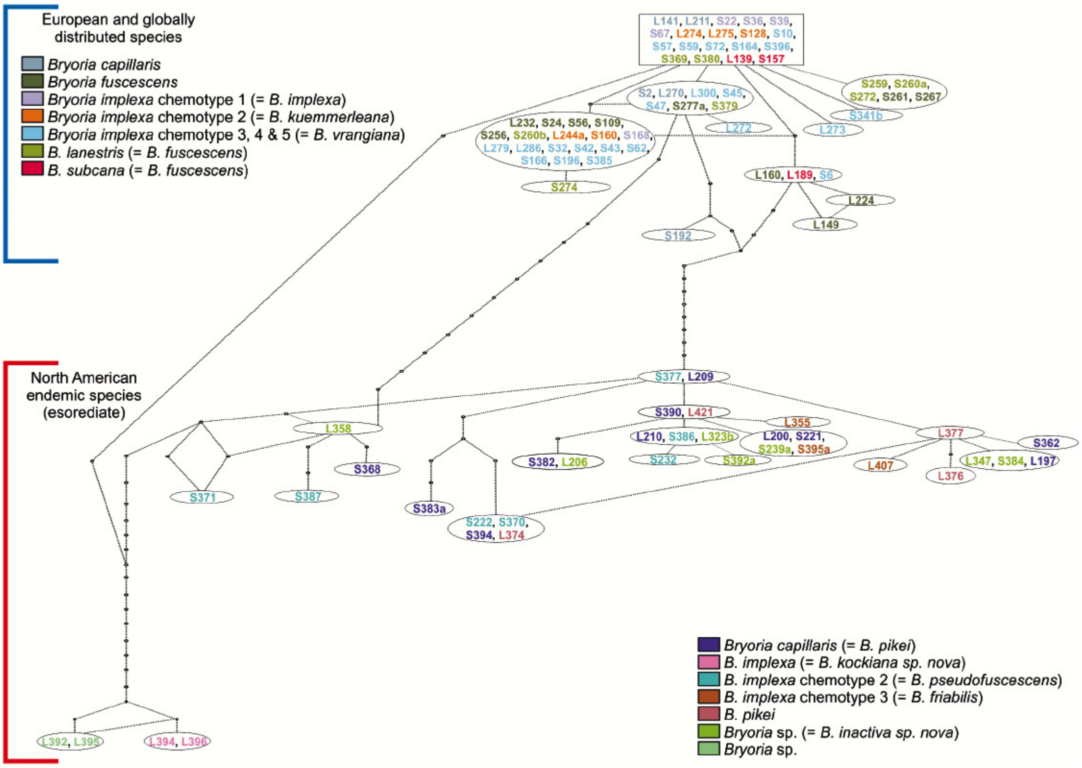

Fig. 4. Haplotype network of 95 specimens of *Bryoria* section *Implexae*. Specimens are marked with laboratory codes, each taxon with different color. Ancestral haplotype is enclosed in a box and derived haplotypes in ovals. Each line represents one mutation and open circles indicate missing (unsampled and/or extinct) haplotypes.

of connection steps was 19. The network shows a taxonomic pattern similar to the pattern in the phylogenetic trees as no haplotypes were shared among Clades 1 and 2 (Fig. 4). The haplotypes are, however, shared with different taxa inside Clades 1 and 2 except for the NA *B. implexa* chemotype 1 as well as two *Bryoria* sp. specimens. A haplotype belonging to Clade 2 is placed in an ancestral position.

Discussion

This study confirms our earlier finding that specimens traditionally placed in *B. capillaris*, *B. chalybeiformis*, *B. fuscescens*, *B. implexa*, *B. lanestris* and *B. subcana* group into two strongly supported monophyletic clades. Resolution within the two clades, however, is strikingly low, especially in light of well-defined morphological and particularly chemical characters. The few monophyletic groups found within the clades were mostly poorly supported and did not correlate with morphological or chemical characters. The only exception to this is the monophyly of NA *B. implexa* chemotype 1 and the monophyly of European *B. capillaris*, although the latter was only weakly supported in an analysis based on combined molecular and nonmolecular data. This low resolution is explained by the sequences themselves, which were in most cases practically identical, rather than by incongruence between different DNA regions. The result can most probably be explained by the recent speciation event of the studied taxa. However, our results are somewhat surprising inasmuch as the gene regions used in this study have successfully been applied in the delimitation of other assemblages of closely related taxa (e.g. Myllys *et al*. 2002, Lindblom & Ekman 2007). Similar findings have been reported for another fruticose lichen-forming taxon, i.e. *Cladonia arbus-*

cula, where morphological variation and genetic variability of the mycobiont were found to be unlinked (Piercey-Normore *et al.* 2010). In that case, the authors concluded that *C. arbuscula s. lato* represents a single species whose considerable infraspecific morphological variation may be attributable to such factors as environmental conditions, presence of different photobionts, or different mechanisms of thallus development (*see* Goward 2009).

Even so, it is clear that while the *presence* of molecular markers can be taken as strong circumstantial evidence, their *absence* must be regarded as inconclusive. In the present case, we are reluctant to accept that all specimens in each of the two clades are conspecific. Such a conclusion would be at variance, for example, with the consistently observed close agreement between chemical constituents, thallus morphology and, in some cases, ecological preference. Accordingly it seems appropriate here to adopt species concepts based on traditional character sets, notwithstanding the lack of any corroborating genetic evidence. Below, we discuss the morphology, chemistry and taxonomy of each taxon here accorded species status. We also clarify our taxonomic concept in light of current species delimitation. Note that the species delimitation adopted here is somewhat at variance with that presented in Myllys *et al.* (2011a).

Clade 1

Clade 1 includes all NA specimens of *B. capillaris*, *B. pikei*, *B. implexa* chemotypes 1, 2 and 3 as well as two unidentified *Bryoria* specimens from Alaska. Also included is a new *Bryoria* species (*B. inactiva sp. nova*) earlier referred to as *Bryoria* sp. and here represented by seven specimens. It can be observed that all taxa in Clade 1 lack soralia. As discussed above, the relationships between these species remain mainly unresolved in the phylogenetic analyses. However, all the analyses support monophyly of NA *B. implexa* chemotype 1. By contrast, the only NA specimen representing *B. implexa* chemotype 5 (specimen S385) groups with Clade 2.

The results reported here agree with those of our previous study (Myllys *et al.* 2011b), in which NA and European populations of *B. capillaris* and *B. implexa* (chemotype 2) were in both cases found to be genetically distinct. This result is corroborated by morphological and chemical differences, insofar as both *B. capillaris* and *B. implexa s. lato* in Europe are frequently sorediate and contain atranorin, while NA specimens hitherto attributed to the same species are esorediate and lack atranorin (Brodo & Hawksworth 1977, Holien 1989).

Based on the haplotype analysis, taxa in Clade 2 are ancestral to the strictly NA species. The result suggests that an ancestor of strictly NA species lost its sorediate mode of dispersal.

As explained in Material and methods, we at first provisionally followed Holien's taxonomic concept for both European and NA material of *B. implexa s. lato* where Holien (1989) treated *B. friabilis* and *B. pseudofuscescens* as chemotypes of *B. implexa* as he found no morphological characters by which to discriminate these species, at least in the Norwegian material. Based, however, on subsequent careful examination of the type and additional herbarium material, we are now inclined to agree with Brodo and Hawksworth (1977) that NA *B. implexa* chemotypes 1, 2 and 3 warrant recognition as separate species, i.e. *B. kockiana sp. nova*, *B. pseudofuscescens* and *B. friabilis*, respectively. Here it can be noted that we need additional material to examine the status of two unidentified specimens grouping with *B. kockiana* (= NA *B. implexa* chemotype 1). They resemble *B. kockiana* in having broad pseudocyphellae but differ from this species in chemistry (no lichen substances) and in darker color.

Brodo and Hawksworth (1977) considered *B. capillaris* and *B. pikei* to be distinct taxa in spite of existence of some intermediate forms. However, we will treat them as conspecific, since the diagnostic morphological characters of NA *B. capillaris* and *B. pikei* overlap and are not consistent with chemical characters.

Bryoria friabilis Brodo & D. Hawksw. (Fig. 5A)

Opera Bot. 42: 118. 1977. — TYPE: U.S.A. Washington, [Thurston County], Gate, 14 Oct. 1911 *A. S. Foster s.n.* (holotype NY!).

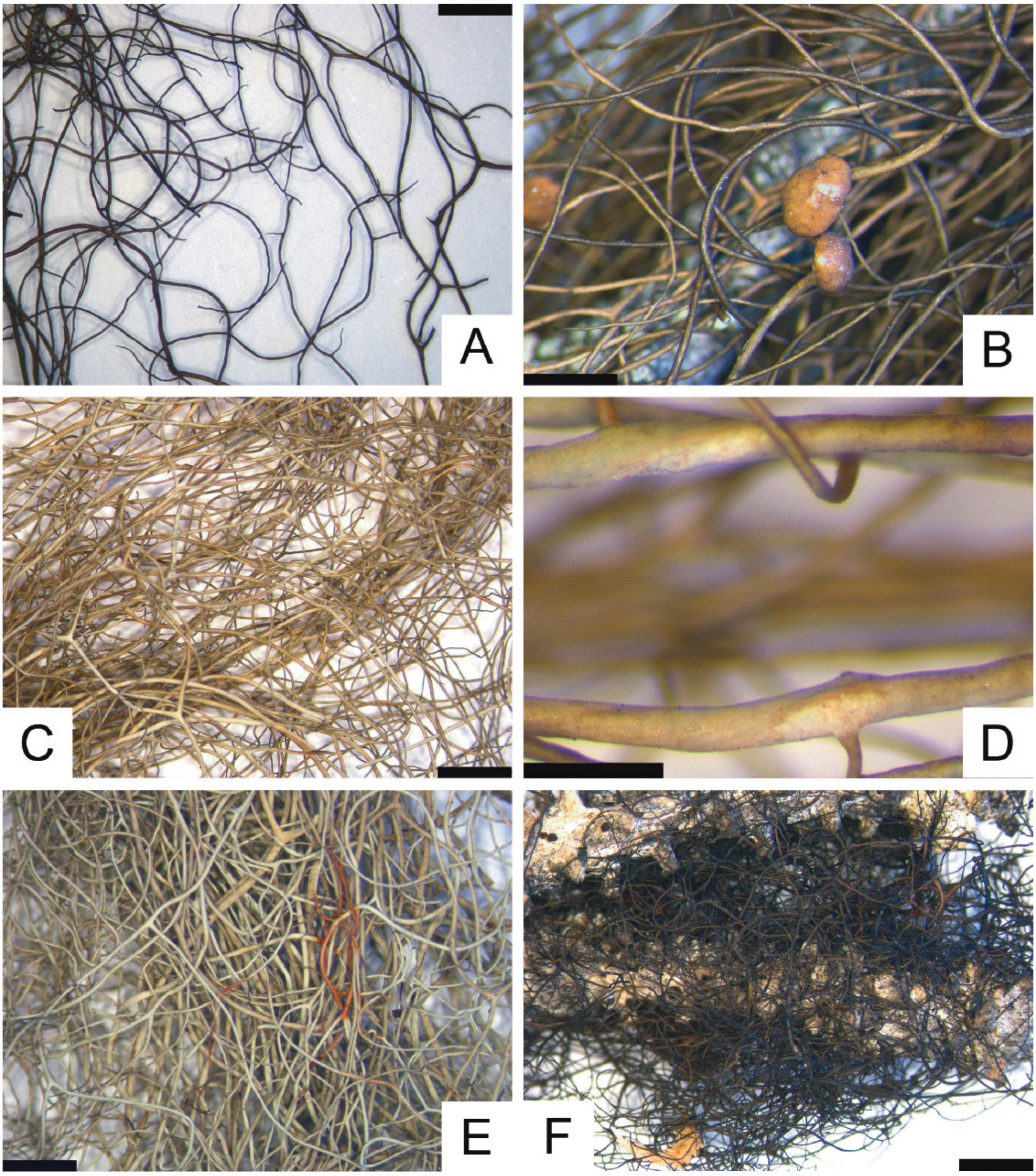

Fig. 5. North American species of *Bryoria* section *Implexae* examined in this study. — **A**: *B. friabilis* with short side branches (specimen *L407*). — **B**: *B. inactiva* with apothecia and white pseudocyphellae (specimen *S392*). — **C**: *B. kockiana* (specimen *L394*, holotype). — **D**: *B. kockiana* with broad pseudocyphellae (specimen *L394*, holotype). — **E**: *B. pikei*, pale morphotype showing C+ red reaction (alectorialic and gyrophoric acids, specimen *L374*). — **F**: *B. pseudofuscescens* (specimen *S377*). Scale bars: 2 mm for **A**, **C**, **E** and **F**; 1 mm for **B**; 500 *μ*m for **D**.

A detailed description of *B. friabilis* is given by Brodo and Hawksworth (1977: 118).

Chemistry: All portions of thallus K–, C+ red, KC+ red, PD–; gyrophoric acid. Apothecia K+ yellow, C+ red, KC+ red, PD+ yellow; alectorialic acid.

Notes: According to Brodo and Hawksworth (1977) *B. friabilis* is characterized by its uneven, foveolate and brittle branches, its mainly isotomic dichotomous branching with obtuse angles, its short side branches and abundant, brownish to white and broadly fusiform pseudocyphellae, its pale color (rarely shiny cervine brown) which darkens in storage, and its absence of soredia. However, some of the gyrophoric acid-containing specimens studied by us are at variance with this description, e.g., in having a shiny cortex and even branches with at most only narrowly fusiform pseudocyphellae. In the absence of chemical testing, such specimens might be mistaken for *B. pseudofuscescens*, though all four specimens included in our analyses differ from that species, e.g., in having short side branches and broader branch angles.

SELECTED SPECIMENS EXAMINED: **Canada**. British Columbia, Vancouver Island, Carmanah Valley, 1991 *T. Goward 91-536A* (UBC), Coquihalla Valley, 13 km SW of highway summit, 1991 *T. Goward 91-842A* (UBC).

Bryoria inactiva Goward, Velmala & Myllys, *sp. nova* (Fig. 5B)

MB 804513. — TYPE: Canada. British Columbia, Clearwater Valley, 0.5 km S of Philip Creek, “Edgewood West”, 715 m, 9 Nov. 2011 *T. Goward 11-61* (holotype UBC!).

ETYMOLOGY: *Inactiva* refers to the absence of spot test reactions in the thallus owing to a lack of secondary substances.

Thallus up to 10–15 cm long, pendent, branches olivaceous brown to dark brown, concolorous throughout or in part with blackened portions, weakly shiny to glossy, pliant to occasionally rather brittle, 0.03–0.2(–0.3) mm diam. Branching predominantly isotomic dichotomous, without distinct main branches, angles between branches mainly acute, except often in part rounded in basal portions. Soralia, isidia and spinules absent. Pseudocyphellae sparse, rarely absent, brownish white, rarely white, linear, rarely elongate-fusiform, often somewhat depressed, 0.4–0.6(–1.7) mm long by 0.02–0.03(–0.1) mm wide. Pycnidia unknown. Apothecia infrequent, disc pale brown to brown, 0.4–0.9 mm diam., convex. Hymenium 42 μm high. Spores hyaline, ellipsoid, 8 × 3–5 μm.

CHEMISTRY: All portions of thallus K–, C–, KC–, PD–; secondary substances absent. Apothecia K–, C–, KC–, PD+ yellow; psoromic acid.

DISTRIBUTION AND HABITAT: Endemic to cordilleran northwest North America. As currently delimited, known only from British Columbia and Alaska between 52°N and 60°N. In the southern, holotypic portion of its range, this species appears to be restricted to humid intermontane regions, though northward it extends outward to the coast — conceivably as a separate species. Restricted to the branches of conifers (*Picea engelmannii* × *glauca*, *Pseudotsuga menziesii*, *Tsuga heterophylla*) in open, well ventilated forests. Presently known only from the lower oroboreal subzone below about 700 m a.s.l., as well as from the southern boreal subzone (*sensu* Tuhkanen 1984). In southern portions of its range, this species grows in low-lying areas near open wetlands, where it presumably benefits from frequent nighttime fog or dew.

NOTES: *Bryoria inactiva* is a nonsorediate species distinguished by its even, typically shiny olivaceous branches that typically bear at least some linear, often whitish, somewhat depressed pseudocyphellae. This species is readily distinguished from other nonsorediate North American members of the section *Implexa* by its strictly linear (= non-fusiform) pseudocyphellae and especially its lack of secondary substances.

Bryoria inactiva may also be confused with nonsorediate forms of the more widely distributed *B. lanestris* (now *B. fuscescens*, *see* discussion below); and apparently this accounts for at least some of the material of that species reported by Brodo and Hawksworth (1977) from “the coastal ranges” of British Columbia. Both lichens, for example, have long, slender, distinctly “hair-like” branches scarcely exceeding 0.2 mm in diameter even in basal portions. *Bryoria lanestris*, however, is a darker, almost black species consisting of rather matt, mostly anisotomic branches quite variable in thickness, and tending to fragment in the herbarium packet. Nonsorediate forms of *B. americana* may also somewhat resemble *B. inactiva*, but differ in having reddish brown, often in part blackish branches with spinulose side branches.

SELECTED SPECIMENS EXAMINED (paratypes): **Canada**. British Columbia, Kispiox Valley, Date Creek, 2006 *T. Goward 06-112*, *06-177* (UBC), Vancouver Island, Sproat Lake, 2009 *T. Goward 09-445* (UBC), Clearwater Valley, 0.5 km south of Philip Creek, 2010 *T. Goward 10-13* (UBC).

Bryoria kockiana Velmala, Myllys & Goward, *sp. nova* (Fig. 5C and D)

MB 804514. — TYPE: U.S.A. Alaska, Fairbanks North Star Borough, 26 July 2011 *D. Nossov 20019-1* (holotype UBC!; isotype H!).

ETYMOLOGY: *Bryoria kockiana* is named in honor of Henry Kock (1952–2005), a noted Ontario horticulturalist. The name was chosen by his widow, wildlife artist Anne Hansen, after placing the winning bid in an environmental fund-raising auction for the right to name this species. Earnings went toward creation of a wildlife crossing near Wells Gray Provincial Park, British Columbia.

Thallus up to 15(–27) cm long, pendent, branches greyish brown or pale brown to brown, dull to slightly shiny, mainly even, rarely twisted or compressed, 0.1–0.2 mm diam. Branching mainly isotomic dichotomous, without distinct main branches, angles between branches acute to obtuse. Soralia, isidia and spinules absent. Pseudocyphellae conspicuous, brownish white to white, broad, elongate-fusiform, usually slightly raised, 0.2–1.0 mm long by 0.1 mm wide. Pycnidia unknown. Apothecia unknown.

CHEMISTRY: Thallus K– or K+ pale yellow, C–, KC–, PD+ yellow; psoromic acid, sometimes also atranorin.

DISTRIBUTION AND HABITAT: Endemic to North America. On branches of conifers. For more detailed information, *see* under *B. implexa* in Brodo and Hawksworth (1977: 121).

NOTES: Until now, North American material of *Bryoria* with psoromic acid in the vegetative tissues has been attributed to *B. implexa* (Brodo & Hawksworth 1977). Based, however, on our phylogenetic analyses, *B. implexa s. stricto* is restricted to Eurasia (the type is probably from Germany or Russia), whereas its North American counterpart represents an undescribed species here named *B. kockiana*. Only two specimens of *B. kockiana* species were available to us, though a third specimen (*T. Goward 08-1040*) shared an almost identical ITS profile, differing in only one base pair. In North America, *B. kockiana* is readily distinguished from other nonsorediate species by its production of psoromic acid in the thalline portions. (Note: Other *Bryoria* species contain psoromic acid in the apothecia, but only in *B. kockiana* does this substance occur in vegetative portions of the thallus). *Bryoria kockiana* is also unique among inland boreal species in having broad and plane or raised pseudocyphellae. Note, however, that Brodo and Hawksworth (1977) reported the pseudocyphellae in this species as "usually depressed". As discussed earlier, Brodo and Hawksworth (1977) separated NA and European *B. capillaris* and *B. implexa* populations partly by their chemistry: while European specimens in both species contained atranorin, NA specimens lacked the substance. However, one NA specimen included in our study (L394) contained traces of atranorin in addition to psoromic acid.

ADDITIONAL SPECIMENS EXAMINED (paratype): **Canada**. British Columbia, Fort Nelson area, 1982 *T. Goward 82-1040* (UBC).

Bryoria pikei Brodo & D. Hawksw. (Fig. 5E)

Opera Bot. 42: 125. 1977. — TYPE: U.S.A. Oregon, Marion County, Silver Creek Falls State Park, *prope* Winter Falls, *orientem versus a* Salem, 44°54′N, 122°39′W, 1450 ft, 9 April 1972 *L. Pike 2475* (holotype *CANL 38271*!).

Thallus up to 15(–30) cm long, pendent, branches pale grayish to pale brown, sometimes dark brown where exposed, dull to occasionally weakly shiny, often variegated (i.e., with both pale and dark clusters of branches), dark pigments conspicuously streaked or not (checked at 40×), usually appearing pruinose, generally rather pliant, 0.1–0.3(–0.5) mm diam. Branching isotomic dichotomous to occasionally anisotomic dichotomous, usually without distinct main branches, angles between branches mainly acute. Soralia, isidia and spinules absent. Pseudocyphellae sparse, brownish white, rarely white, elongate-fusiform, rarely linear, 0.2–1.0(–1.4) mm long by 0.03–0.2 mm wide. Pycnidia unknown. Apothecia infrequent, disc pale brown to brown, 0.5–1.1 mm diam., plane, becoming convex. Hymenium 38–45 μm high. Spores hyaline, ellipsoid, 5–7 × 4–5 μm.

CHEMISTRY: Chemotype 1: Thallus K+ yellow, C– or C+ red, KC– or KC+ red, PD+ yellow; barbatolic acid, sometimes also alectorialic acid in lesser amounts. Apothecia K–, C–, KC–, PD+ yellow; psoromic acid. Chemotype 2: K+ yellow, C+ red, KC+ red, PD+ yellow; alectorialic and gyrophoric acids. Apothecia K–, C–, KC–, PD+ yellow; psoromic acid.

DISTRIBUTION AND HABITAT: Endemic to North America. Widespread, in the west ranging from northern California to coastal Alaska, extending inland into intermontane British Columbia and adjacent portions of the American Pacific Northwest, otherwise mostly restricted to Canada (*see* map of *B. capillaris* and *B. pikei* in Brodo and Hawksworth 1977: 116, 123). Common on conifers and other acid-bark trees in open to shaded forests, especially near wetlands and other localities subject to frequent mist, dew or high atmospheric humidity, mostly north temperate to middle (oro)boreal.

NOTES: Brodo and Hawksworth (1977) distinguished *B. pikei* from *B. capillaris* based on the former's shiny, uniformly olivaceous, even branches and presence of alectorialic acid as major substance (sometimes secondarily accompanied by barbatolic and/or gyrophoric acid), versus the latter's mostly dull, greyish, even to uneven branches, and presence of barbatolic as major substance (often secondarily with alectorialic acid). However, careful examination of a rich assortment of North American specimens (ca. 80), has failed to reveal any consistent correlation between thallus morphology and chemistry, e.g., specimens with barbatolic acid can be shiny, while specimens with alectorialic acid can be distinctly two-tone. For this reason, we prefer to unite within *B. pikei* all NA material hitherto attributed to the European species, *B. capillaris*.

Bryoria pikei differs from other nonsorediate NA species included in this study by its combination of typically pale, frequently variegated, often pruinose branches and, especially, the presence of barbatolic and/or alectorialic acids (= K+ persistent yellow). Other NA esorediate species producing barbatolic or alectorialic acid, i.e., *B. pseudocapillaris*, also nonsorediate and with barbatolic and alectorialic acids, has longer and more striking pseudocyphellae. *Bryoria nadvornikiana* produces barbatolic acid, but is sorediate and usually conspicuously spinulose.

Apothecia have not previously been reported from *B. pikei s. stricto*, but they occur in our *L377* and *T. Goward 09-323*; *see* description.

SELECTED SPECIMENS EXAMINED: **Canada**. British Columbia, Clearwater Valley, 0.5 km S of Philip Creek, "Edgewood West", 2006 *T. Goward 05-06* (UBC), Vancouver Island, Broughton, 2004 *K. G. Wright 2004-59* (UBC), Saltspring Island, 2009 *T. Goward 09-323a* (UBC).

Bryoria pseudofuscescens (Gyeln.) Brodo & D. Hawksw. (Fig. 5F)

Opera Bot. 42: 127. 1977. — *Alectoria pseudofuscescens* Gyeln., Ann. Hist.-Nat. Mus. Natl. Hung. 28: 283. 1934. — TYPE: U.S.A. Oregon, [Benton County], Corvallis, Dec. 1931 *F. P. Sipe 669* (holotype *BP 33958*!).

Alectoria norstictica Motyka, Bryologist 67: 33. 1964, *nom. inval.*; Motyka *ex* Krog in Norsk Polarinst. Skrifter 144: 139. 1968, *nom. inval.* (*see* notes below). — Synonymized by Brodo & Hawksworth (1977: 127).

Alectoria subtilis Motyka, Bryologist 67: 32. 1964, *nom. inval.*; Motyka *ex* Krog in Norsk Polarinst. Skrifter 144: 139. 1968, *nom. inval.* (*see* notes below). — Synonymized by Brodo and Hawksworth (1977: 127).

For species description of *B. pseudofuscescensee see* Brodo and Hawksworth (1977: 127).

CHEMISTRY: All portions of thallus K+ red or yellow becoming dingy orange, C–, KC–, PD+ yellow; norstictic acid, sometimes also connorstictic acid. Apothecia K–, C–, KC–, PD+ yellow; psoromic acid.

NOTES: According to Brodo and Hawksworth (1977) *B. pseudofuscescens* is a variable taxon characterized by the presence of norstictic acid, usually darkening to dark brown or black but sometimes pale thallus, isotomic dichotomous branching at least at the base, variable branch angles, esorediate uneven to even branches with usually abundant, brownish to white, short to elongate fusiform, depressed pseudocyphellae. Based on the NA material, Brodo and Hawksworth (1977) considered *B. implexa s. stricto* to be closely related to *B. pseudofuscescens* but found the two taxa distinguishable based on differences in chemistry (psoromic acid in *B. implexa vs.* norstictic acid in *B. pseudofuscescens*) and to some extent in thallus color (darker in *B. pseudofuscescens*). To us, some norstictic acid containing specimens resemble *B. inactiva* in color and in having linear and depressed pseudocyphellae. In those cases chemical characters are the only way to separate the two species. In addition, some *B. pseudofuscescens* specimens have broad pseudocyphellae and/or uneven and twisted branches and are somewhat brittle and thus resemble *B. friabilis*. These specimens, however, lack short side branches which are present in *B. friabilis*.

Hawksworth (1972) indicated "lectotypes" for *Alectoria norstictica* and *A. subtilis*; but because those names were invalidly published they have no nomenclatural status and cannot have types (Art. 6.3). The holotype of *B. pseudofuscescens* is most probably a mixed collection since some of the branches bear soralia.

Clade 2

Clade 2 comprises all European material of *B. capillaris*, *B. chalybeiformis*, *B. fuscescens*, *B. implexa s. lato*, *B. lanestris* and *B. subcana* as well as NA specimens traditionally referred to *B. fuscescens, B. implexa* chemotype 5 and *B. lanestris*. With rare exceptions, all of this material is characterized by the presence of soralia. Differences between European *B. capillaris* and NA *B.* "*capillaris*" (= *B. pikei*) have already been discussed.

Based on our examination of other members of Clade 2, we propose that European *B. implexa s. lato* should be divided into three taxonomic entities: (1) *B. implexa* (= "*B. implexa* chemotype 1"), with psoromic acid and conspicuous, mostly striking white pseudocyphellae, (2) *B. kuemmerleana* (= "*B. implexa* chemotype 2"), with norstictic acid and pruinose thallus, and (3) *B. vrangiana* (= "*B. implexa* chemotypes 3, 4 and 5"), with gyrophoric or fumarprotocetraric acid or having no substances and brownish rather than white pseudocyphellae. Based on our material (specimen S385), *B. vrangiana* appears to occur in North America (acid-deficient chemotype). In addition, we propose *B. chalybeiformis*, *B. lanestris* and *B. subcana* to be treated as synonyms of *B. fuscescens* (*see* discussion under *B. fuscescens*).

Bryoria capillaris (Ach.) Brodo & D. Hawksw. (Fig. 6A)

Opera Bot. 42: 115. 1977. — *Parmelia jubata* var. *capillaris* Ach., Methodus: 273. 1803. — TYPE: Sweden (lectotype *H-ACH 1799A*! chosen by Hawksworth 1972: 209).

Thallus up to 30 cm long, pendent, branches whitish gray to grey, sometimes brownish, dull to occasionally slightly shiny where exposed, mainly even, sometimes twisted and compressed, up to 0.07–0.4 mm diam. Branching isotomic dichotomous to anisotomic dichotomous, without distinct main branches, angles between branches mainly acute. Soralia absent or more often present, sometimes abundant, tuberculate. Isidia and spinules absent. Pseudocyphellae absent or present, inconspicuous, white, fusiform or sometimes linear, plane or occasionally slightly depressed, up to 0.2–0.7 mm long by 0.03–0.1 mm wide. Pycnidia unknown. Apothecia rare. *See* description under *B. capillaris* in Holien (1989: 246) for a detailed account of ascoma and spore characters.

CHEMISTRY: Thallus K+ yellow, C+ red or C–, KC+ red, PD+ yellow; barbatolic acid, sometimes also alectorialic acid and atranorin, rarely with alectorialic acid only. Soralia PD+ red; fumarprotocetraric acid. Apothecia K–, C–, KC–, PD+ yellow; psoromic acid.

DISTRIBUTION AND HABITAT: Common in Scandinavia, but becoming rarer in the north, and in much of the rest of Europe, also present in the boreal Asia as well as at higher elevations in the Canary Islands and Iran. Grows on both coniferous and deciduous trees, occasionally on rocks. Seems to prefer shaded and humid spruce forests.

NOTES: *Bryoria capillaris* is readily distinguished from other sorediate *Bryorias* by its pale grey thallus, inconspicuous pseudocyphellae and presence of barbatolic acid. Holien (1989) reported specimens of *B. capillaris* with alectorialic acid only, but no such chemotype was found by us. When the existing DNA data is complemented with morphological data, our analyses support *B. capillaris* as monophyletic.

Bryoria fuscescens (Gyeln.) Brodo & D. Hawksw. (Fig. 6B and C)

Opera Bot. 42: 83. 1977. — *Alectoria fuscescens* Gyeln., Nyt Mag. Naturvidensk. 70: 55. 1932 ('1931'), *nom. cons. prop.* (Hawksworth & Jørgensen 2013). — TYPE: Russia. Karelia ladogensis, Sortavala, Mäkisalo, *K. Linkola s.n.* (holotype lost, not in BP, H); Finland. Tavastia australis, Hollola, Sep.

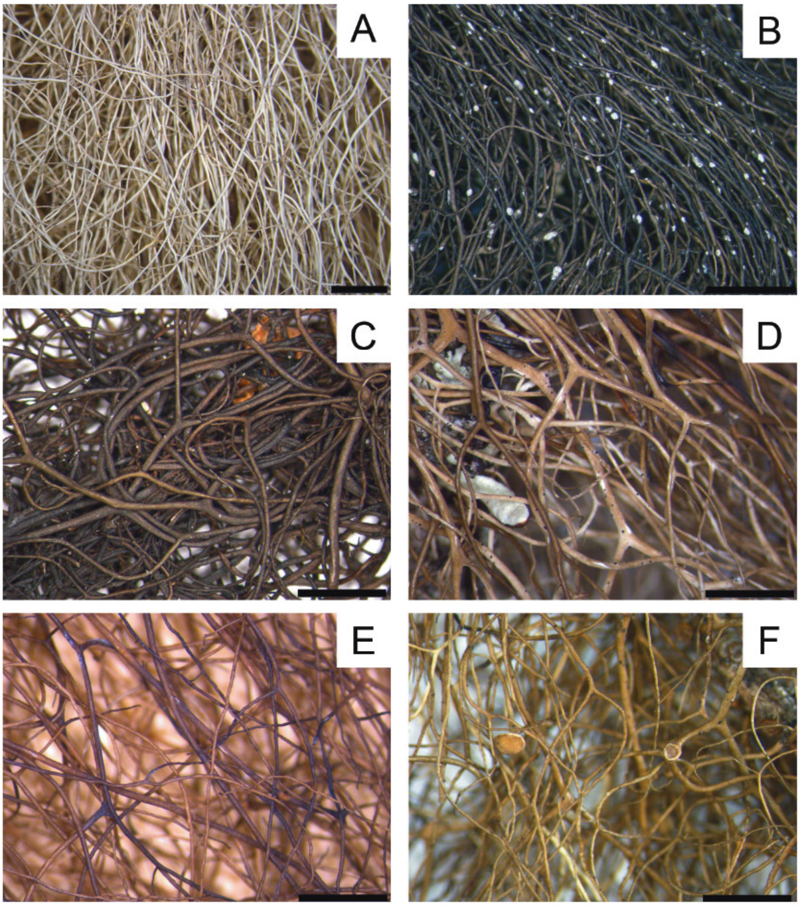

Fig. 6. European and globally distributed species of *Bryoria* section *Implexae* examined in this study. — **A**: *B. capillaris* with pale grey thallus branches (specimen *L211*). — **B**: *B. fuscescens*, slender and sorediate morph (specimen *S379*). — **C**: *B. fuscescens*, more robust morph (specimen *L307*). — **D**: *B. implexa* with striking white pseudocyphellae (specimen *S67*). — **E**: *B. kuemmerleana* with pruinose branches and elongate fusiform pseudocyphellae (specimen *L275*). — **F**: *B. vrangiana* with apothecia (specimen *S42*). Scale bars = 2 mm.

1882 *J. P. Norrlin s.n.*, Norrlin & Nylander, *Lich. Fenn. Exs. no. 466* (lectotype *BP 33947*! chosen by Hawksworth 1972: 217; isolectotypes BM, CANL, H!).

Bryoria chalybeiformis (L.) Brodo & D. Hawksw., Opera Bot. 42: 81. 1977. — *Lichen chalybeiformis* L., Sp. Pl. 2: 1155. 1753, *nom. rej. prop.* (Hawksworth & Jørgensen 2013). — Type (cons.): Without locality, herb. Linnaeus (*LINN 1273.291* [image!]).

Bryoria lanestris (Ach.) Brodo & D. Hawksw. Opera Bot. 42: 88. 1977. — *Alectoria jubata* var. *lanestris* Ach., Lichenogr. Universalis: 593. 1810. — *Alectoria lanestris* (Ach.) Gyeln., Nyt Mag. Naturvidensk. 70: 58. 1932 ('1931'). — Type: Switzerland ("Helvetia"). [*J. C. Schleicher*] *926* (lectotype *H-ACH 1808A*! chosen by Hawksworth 1972: 222 as 'holotype').

Bryoria subcana (Nyl. *ex* Stizenb.) Brodo & D. Hawksw., Opera Bot. 42: 91. 1977. — *Alectoria prolixa* var. *subcana* Nyl. *ex* Stizenb., Ann. Naturhist. Mus. Wien 7: 129. 1892. — *Alectoria subcana* (Nyl. *ex* Stizenb.) Gyeln., Magyar Bot. Lapok 30: 54. 1931, *nom. rej. prop.* (Hawksworth & Jørgensen 2013). — Type: United Kingdom. Scotland, 1875 *J. M. Crombie s.n.* (lectotype *H-NYL 35835*! chosen by Hawksworth 1972: 249).

Thallus to 30 cm long, decumbent to pendent or subpendent, branches grayish brown, olivaceous brown to blackish brown, sometimes with blackened fragmentation areas, dull to shiny, branches even to uneven, sometimes extremely brittle, may become robust, twisted, compressed and foveolate especially when growing on rocks or in exposed localities, 0.07–0.5(–0.9) mm diam. Branching irregular, usually isotomic dichotomous, sometimes anisotomic dichotomous towards the apices, without distinct main branches, angles between branches mainly acute. Isidia and spinules absent. Soralia frequent, often abundant, tuberculate or fissural, white or white with black spots, occasionally spinulose. Pseudocyphellae absent. Pycnidia uncommon, usually aggregated, black and shiny. Apothecia rare, disc brown to dark brown, up to 2 mm diam., concave or plane, sometimes becoming convex.

Spores ellipsoid, 6–9 × 4–5 μm.

CHEMISTRY: Thallus K–, C–, KC–, PD– or PD+ red; substances absent or with fumarprotocetraric acid, sometimes also chloroatranorin. Soralia PD+ red; fumarprotocetraric acid. Apothecia K–, C–, KC–, PD+ yellow; psoromic acid.

DISTRIBUTION AND HABITAT: This is a common species in north temperate to boreal and oroboreal forests throughout the northern hemisphere. Also present in Africa at least in mountainous areas. Most common on coniferous trees, but frequently found also on deciduous trees and rocks or more rarely on the ground.

NOTES: *Bryoria chalybeiformis*, *B. lanestris* and *B. subcana* are here used as synonyms of *B. fuscescens*, and each of these names is briefly discussed below.

Bryoria fuscescens is one of the most variable species in the genus, resulting in description of several forms, varieties and even species (*see* for instance Bystrek 1963). Typically it has a richly sorediate, subpendent to pendent, olivaceous brown thallus that lacks pseudocyphellae and produces fumarprotocetraric acid.

Bryoria subcana is characterized by its pale color and strong PD+ red cortical reaction (Hawksworth 1972); but otherwise it falls within the traditional concept of *B. fuscescens*. The species has been accepted as distinct and discussed by Brodo and Hawksworth (1977) in North America and Holien (1991) in Scandinavia. We tested the lectotype (H-NYL 35835) in addition to authentic herbarium material but were unable to discern a conspicuously strong PD reaction. Fumarprotocetraric acid is well known to vary in concentration in *B. fuscescens s. lato*, as mentioned below, hence in our view *B. subcana* is appropriately regarded as a “shade” morph.

Bryoria lanestris resembles *B. fuscescens* but is darker, has thin, uneven, fragile branches, and contains fumarprotocetraric acid in the soralia alone. However, as pointed out by Brodo and Hawksworth (1977), both the cortex and medulla of *B. fuscescens* may likewise occasionally react PD–, indicating an uneven distribution or lack of fumarprotocetraric acid in the thallus. Material examined by us included some specimens in which fumarprotocetraric acid was present in the soralia alone but as such thalli were neither dark brown nor had brittle branches we conclude that *B. lanestris* and *B. fuscescens* should be considered conspecific.

Bryoria chalybeiformis has traditionally been characterized by its stout, prostrate, irregular habit, its dark thallus color, and its predominant occurrence over rock or ground in arctic-alpine regions; it produces fumarprotocetraric acid exclusively in the soralia (Krog 1980). We earlier expressed the view that such material may in fact represent a mere environmental adaptation to exposed habitats (Myllys *et al.* 2011b), but were reluctant to make taxonomic adjustments owing to insufficient material. We have now examined numerous specimens consistent with the usual delimitation of *B. chalybeiformis*, and conclude that thallus morphology and secondary chemistry are at most only weakly correlated. For instance, the other specimen (*L307*) assigned to *B. chalybeiformis* in the present phylogenetic analysis contained gyrophoric acid. Actually the lack of corroboration between morphology and chemistry was obvious already in the typification: the first lectotype of *B. chalybeiformis* (*LINN 1273.90*) selected by Howe (1912) contained fumarprotocetraric acid in the thallus and hence fell within the traditional concept of *B. fuscescens* (*see* Krog 1980). Consequently, Jørgensen *et al.* (1994) proposed that the name *chalybeiformis* be conserved with a new type. Recently, a proposal was made to conserve the name *Alectoria fuscescens* against *Lichen chalybeiformis* and *Alectoria subcana* (Hawksworth & Jørgensen 2013). Although we would prefer to use the name *Lichen chalybeiformis* (*Bryoria chalybeiformis*), being the oldest one in the *B. fuscescens* group and widely in use, we follow the proposal according to the recommendation of the Code (Rec. 56A.1).

Bryoria glabra is another brown species in the section *Implexae* without pseudocyphellae but it differs from *B. fuscescens* by having regularly oval, white soralia and obtuse and rounded branch angles, at least in the basal portions of the thallus.

Bryoria implexa (Hoffm.) Brodo & D. Hawksw. (Fig. 6D)

Opera Bot. 42: 121. 1977. — *Usnea jubata* [unranked] *im-*

plexa Hoffm., Deutschl. Fl. 2: 134. 1796. — Neotype: Without locality (neotype *MW-Hoffm. 8569* chosen by Hawksworth 1969: 395).

Thallus up to 15 cm long, pendent, branches pale brown to brown, dull to slightly shiny, mainly even, rarely twisted or compressed, up to 0.07–0.4 mm diam. Branching mainly isotomic dichotomous, without distinct main branches, angles between branches acute to obtuse. Isidia and spinules absent. Soralia absent or present, tuberculate or fissural. Pseudocyphellae conspicuous, (distinctively) white, elongate-fusiform, sometimes twisted, usually slightly raised, up to 0.2–1.2 mm long by 0.03–0.2 mm wide. Pycnidia unknown. Apothecia rare, disc brown, sometimes pruinose, to 1 mm diam., convex. Epihymenium with many crystals of psoromic acid, hymenium 80 μm high. Spores globose to subglobose, 4–7 × 3.5–5 μm.

Chemistry: Thallus and soralia K– or K+ pale yellow, C–, KC–, PD+ yellow; psoromic acid, sometimes also atranorin. Apothecia K–, C–, KC–, PD+ yellow; psoromic acid.

Distribution and habitat: World distribution insufficiently known but it is widespread in Europe, apparently absent in North America. In Scandinavia it becomes more common northward. Apparently prefers oldgrowth forests, where it grows mostly on coniferous trees.

Notes: As in the case of *B. pikei* and *B. capillaris* (both with alectorialic acid), and in that of *B. pseudofuscescens* and *B. kuemmerleana* (both with norstictic acid), so too NA and European specimens with psoromic acid in vegetative portions of the thallus belong to different species, i.e., *B. kockiana* and *B. implexa*, respectively.

Bryoria implexa is readily distinguished from other European species both by the presence of psoromic acid in vegetative portions of the thallus and, with slightly less certainty, by the strikingly white color of its pseudocyphellae, which are also elongate and fusiform.

Selected specimens examined: **Finland**. Kainuu, Kuhmo, Elimyssalo, 1987 *M. Kuusinen 971* (H), Vaala, Rokua, 2006 *M. Kuusinen s.n.* (H); Koillismaa, Kuusamo, Virkkula, 2005 *Velmala 29, Halonen & Myllys* (H), Juuma, 2005 *S. Velmala 47 & P. Halonen* (H), Merenvaara, 2005 *S. Velmala 55 & P. Halonen* (H). **Norway**. Sør-Trøndelag, Meldal, SW of Gravråk, 1992 *H. Holien 5422a* (TRH), Trondheim, Bymarka, Lian, 2000 *H. Holien 8432* (TRH); Nord-Trøndelag, Lierne, Julestrømmen, 1990 *H. Holien 3616* (TRH). **Spain**. Community of Madrid, Navacerrada, La Barranca mountain valley, close to de Pino a Pino recreational park, 2012 *L. Myllys 06112012-7* (H).

Bryoria kuemmerleana (Gyeln.) Brodo & D. Hawksw. (Fig. 6E)

Opera Bot. 42: 155. 1977. — *Alectoria kuemmerleana* Gyeln., Nyt Mag. Naturvidensk. 70: 49. 1932 ('1931'). — Type: Slovakia. High Tatra Mts., "Com. Szepes, "Stösschen" lejtőjén a Magas Tátrában", 1380 m a.s.l., 17 July 1917 *G. Timkó 3264* (holotype *BP 33952*!).

Thallus up to 20 cm long, pendent, branches pale brown to dark brown, sometimes with blackened fragmentation areas, dull to slightly shiny, pruinose (best seen in basal portions and flattened branch angles of well developed specimens), branches usually even or sometimes partly compressed and foveolate, up to 0.07–0.4(–0.5) mm diam. Branching mainly isotomic dichotomous, without distinct main branches, angles between branches acute to obtuse. Isidia and spinules absent. Soralia present or absent, mostly tuberculate but sometimes fissural, often dark grayish. Pseudocyphellae conspicuous, brownish white, elongate fusiform, sometimes twisted, mainly plane but sometimes somewhat depressed or partly raised, up to 0.2–0.7(–0.9) mm long by 0.03–0.2 mm wide. Apothecia rare, convex, disc brownish, distinctly pruinose with paler margin, up to 2 mm diam. Epihymenium with many crystals of psoromic acid. Spores globose to subglobose to broadly ellipsoid, 4–7 × 4–5 μm.

Chemistry: Thallus and soralia K+ red, C–, KC–, PD+ yellow; norstictic acid, sometimes also connorstictic acid and atranorin. Apothecia K–, C–, KC–, PD+ yellow; psoromic acid.

Distribution and habitat: Rather common in Scandinavia (although probably never reported under this name) and probably also elsewhere in the northern boreal zone, except in North America where it appears to be absent. In Scandinavia it seems to be more common northwards. Grows mainly on coniferous, also on deciduous trees, perhaps especially in old growth forests.

Notes: *Bryoria kuemmerleana* is a name first used by Gyelnik (as *Alectoria kuemmerleana*) for a European taxon containing norstictic acid. This name is adopted here since the type specimen represents the taxon studied by us. Typical material of *B. kuemmerleana* is recognized by its pruinose thallus and production of norstictic acid; although specimens in which the pruina is scanty or lacking must be checked with K to be discriminated from other European species with elongate fusiform pseudocyphellae, i.e. *B. implexa* and *B. vrangiana*.

SELECTED SPECIMENS EXAMINED: **Finland**. Enontekiön Lappi, Enontekiö, Ounastunturi, 1936 *V. Räsänen s.n.* (H). **Norway**. Buskerud, Ringerike, Oppkuven, 1997 *H. Holien 7143a* (TRH); Hedmark, Stor-Elvdal, SE of Mt Ledsagaren by river Hira, 1994 *H. Holien 6422* (TRH); Sør-Trøndelag, Agdenes, E of Ingdalsætra by river Sæterelva, 1995 *H. Holien 6549* (TRH); Nord-Trøndelag, Grong, Ekermyra, 1981 *H. Holien 1037-81* (TRH), Overhalla, SW of Risvik, Flenga, 1997 *H. Holien 7245* (TRH), Høylandet, Kongsmoen, N-facing slope by river Bjøråa, 1998 *H. Holien 7322a* (TRH), Steinkjer, Dalbygda, 2005 *H. Holien 10442* (TRH). **Spain**. Community of Madrid, Navacerrada, La Barranca mountain valley, close to de Pino a Pino recreational park, 2012, *L. Myllys 06112012-14* (H).

Bryoria vrangiana (Gyeln.) Brodo & D. Hawksw. (Fig. 6F)

Opera Bot. 42: 97. 1977. — *Alectoria vrangiana* Gyeln., Magyar Bot. Lapok 31: 46. 1932. — TYPE: Sweden. Prov. Dalecarlia [Dalarna], par. Loksund [Leksand], Laknäs, 14 July 1931 *E. P. Vrang 263* (holotype *BP 33.967*!; isotype *BP 33.968*).

Thallus up to 30 cm long, pendent, branches brown, rarely pale brownish, sometimes dark brown, often with a few blackened fragmentation areas, usually slightly shiny, mainly even, may become twisted and compressed especially when growing in exposed localities, 0.07–0.4(–0.5) mm diam. Branching isotomic dichotomous, without distinct main branches, angles between branches mainly obtuse. Isidia and spinules absent. Soralia usually present, tuberculate or sometimes fissural. Pseudocyphellae inconspicuous, brownish white, mainly elongate fusiform, mostly plane, 0.1–1.0 mm long by 0.03–0.2 mm wide. Pycnidia unknown. Apothecia locally quite common, disc brown, up to 1.7 mm diam., concave. Hymenium 80 μm. Spores globose to subglobose to ellipsoid, 8 × 3.5–5 μm.

CHEMISTRY: Chemotype 1: Thallus K–, C+ red, KC+ red, PD–; gyrophoric acid, sometimes also atranorin. Soralia sometimes PD+ red; with or without fumarprotocetraric acid. Apothecia K–, C–, KC–, PD+ yellow; psoromic acid. Chemotype 2: Thallus and soralia K–, C–, KC–, PD+ red; fumarprotocetraric acid, sometimes also protocetraric and confumarprotocetraric acids and atranorin. Apothecia K–, C–, KC–, PD+ yellow; psoromic acid. Chemotype 3: Thallus K– or K+ pale yellow, C–, KC–, PD– or PD+ pale yellow; sometimes atranorin. Soralia K–, C–, KC–, PD+ red; fumarprotocetraric acid, sometimes also protocetraric and confumarprotocetraric acids. Apothecia K–, C–, KC–, PD+ yellow; psoromic acid.

DISTRIBUTION AND HABITAT: Common species in Scandinavia where it is seemingly widespread. Possibly rather common also elsewhere in the boreal zone. In addition to Europe, only chemotype 3, i.e. the acid-deficient form has been found in North America (specimen *S385*). Grows on both coniferous and deciduous trees, and is also found on rocks.

NOTES: According to the original description of *B. vrangiana* by Gyelnik (as *Alectoria vrangiana*), the species lacks pseudocyphellae and gives a negative color reaction when spotted with KC (potassium hydroxide followed by calcium hypochlorite) indicating the lack of gyrophoric acid. Later, however, Krog (1979) carefully examined the type material both morphologically and chemically and found it to have pseudocyphellae and contain gyrophoric acid (KC+ red). The partly erroneous description by Gyelnik is understandable since pseudocyphellae can easily be overlooked especially when they are inconspicuous and close to the color of the thallus, as is the case with *B. vrangiana*. In addition, as already stated by Krog (1979), the presence of gyrophoric acid can be missed when tested only with lichen spot tests, since the thallus does not always give a positive color reaction. Since the material studied by us falls within the morphological and chemical description (as emended by Krog), here we have adopted the name *B. vrangiana*.

Bryoria vrangiana is distinguished from other sorediate species by its brownish white, mainly elongate fusiform pseudocyphellae and chemical characters. Specimens with only few pseudocyphellae are difficult to distinguish from *B. fuscescens*. Soralia are, however, more abundant in *B. fuscescens*. The species is here divided into three chemotypes: chemotype 1 with gyrophoric acid, chemotype 2 with fumarprotocetraric acid, and chemotype 3 without lichen acids or sometimes with atranorin. Compared with *B. vrangiana*, *B. implexa* has more conspicuous and whiter pseudocyphellae and *B. kuemmerleana* has pruinose branches. *Bryoria glabra* also lacks lichen acids, but differs from *B. vrangiana* both in its more obtuse branch angles — check basal portions — and in the absence of pseudocyphellae.

SELECTED SPECIMENS EXAMINED: **Finland**. Uusimaa, Kirkkonummi, Kvarnby, 2005 *S. Velmala 9 & L. Myllys* (H); Etelä-Häme, Hauho, Joenkylä, 1987 *M. Kuusinen 1116* (H); Etelä-Savo, Valkeala, Heikkilä, 1986 *M. Kuusinen 676* (H), Valkeala, Selänpää, 2005 *L. Myllys 491* (H); Koillismaa, Kuusamo, Juuma, 2005 *S. Velmala 48 & P. Halonen* (H). **Norway**. Oppland, Ringebu, E-facing slope of Skjerdingfjell, Skardsæterlia, 1994 *H. Holien 6197* (TRH); Hedmark, Stor-Elvdal, SE of Mt Ledsagaren, 1994 *H. Holien 6454* (TRH); Sør-Trøndelag, Roan, along brook Dalamarktjørnbekken, 1985 *H. Holien 35b-85* (TRH), Trondheim, E of lake Leirsjøen by Leirelva, 2002 *H. Holien 9352* (TRH); Nord-Trøndelag, Flatanger, along river Lislstøelva, 1981 *H. Holien 853-81* (TRH), Høylandet, W of lake Storgrønningen, 1987 *H. Holien 2707a* (TRH), Namdalseid, NW of lakelet Øyenskaveltjørn, 1981 *H. Holien 428-81* (TRH), Namsskogan, Storbjørhusdalen, along brook from Tverrdalen, 1992 *H. Holien 5121* (TRH), Leksvik, 2005 *H. Holien 10178* (TRH), Verdal, E of Vera, Strådalen by river Strådøla, 2008 *H. Holien 11576* (TRH); Nordland, Rana, Dunderlandsdalen, NW-facing slope SW of Lian, 1991 *H. Holien 4258a* (TRH), Sømna, SW of Sømnes, 2002 *H. Holien 8989* (TRH); Troms, Målselv, 2005 *H. Holien 10302* (TRH). **Russia**. Perm Territory, Dobryanka district, 2005 *S. M. Schajachmetova 5668*, *5598* (H). **Sweden**. Härjedalen, Härjedalen, 2005 *F. Högnabba 594* (H). **Spain**. Community of Madrid, Navacerrada, La Barranca mountain valley, close to de Pino a Pino recreational park, 2012 *L. Myllys 06112012-9* (H).

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Appendix 1. Data matrix of chemical, morphological and geographic characters (*see* Table 4 for explanation of characters). – = missing data.

Specimen	Character																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
B. capillaris L141	0	0	0	0	1	0	1	1	0	0	0	–	–	–	0	0	2	1
B. capillaris L211	1	1	0	0	1	0	1	1	0	1	0	–	–	–	0	0	0	1
B. capillaris L270	0	0	0	0	1	–	–	1	0	1	0	–	–	–	0	0	0	1
B. capillaris S2	0	0	0	0	1	0	1	1	0	1	0	–	–	–	0	0	0	1
B. capillaris S192	0	0	0	0	1	1	1	1	0	0	1	0	0	0	0	0	0	1
B. friabilis L355	0	0	0	0	0	0	0	0	1	0	1	0	0	0	2	0	2	0
B. friabilis L407	0	0	0	0	0	0	0	0	1	0	1	0	0	1	1	0	2	0
B. friabilis S395a	0	0	0	0	0	0	0	0	1	0	1	1	0	1	1	–	1	0
B. furcellata L147	1	2	0	0	0	0	0	0	0	1	0	–	–	–	2	0	0	1
B. fuscescens L139	1	2	0	0	0	0	0	0	0	1	0	–	–	–	0	0	0	1
B. fuscescens L149	1	2	0	0	0	0	0	0	0	1	0	–	–	–	1	0	0	1
B. fuscescens L160	1	2	0	0	1	1	0	0	0	1	0	–	–	–	1	0	0	1
B. fuscescens L189	1	2	0	0	0	0	0	0	0	1	0	–	–	–	0	0	0	1

continued

Appendix 1. Continued.

Specimen	Character																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
B. fuscescens L224	1	2	0	0	0	0	0	0	0	1	0	–	–	–	2	0	0	1
B. fuscescens L232	1	1	0	0	1	1	0	0	0	1	0	–	–	–	2	0	2	1
B. fuscescens S24	1	1	0	0	0	0	0	0	0	1	0	–	–	–	2	0	0	1
B. fuscescens S56	1	2	0	0	0	0	0	0	0	1	0	–	–	–	2	0	0	1
B. fuscescens S109	1	2	0	0	1	1	0	0	0	1	0	–	–	–	0	0	0	1
B. fuscescens S157	1	2	0	0	1	1	0	0	0	1	0	–	–	–	1	0	2	1
B. fuscescens S256	1	1	0	0	0	0	0	0	0	1	0	–	–	–	1	0	0	0
B. fuscescens S259	1	1	0	0	0	0	0	0	0	1	0	–	–	–	2	0	0	0
B. fuscescens S260a	1	1	0	0	0	0	0	0	0	1	0	–	–	–	2	0	0	0
B. fuscescens S260b	1	1	0	0	0	0	0	0	0	1	0	–	–	–	2	0	0	0
B. fuscescens S261	1	1	0	0	0	0	0	0	0	1	0	–	–	–	1	0	0	0
B. fuscescens S267	1	1	0	0	0	0	0	0	0	1	0	–	–	–	1	0	0	0
B. fuscescens S272	1	1	0	0	0	0	0	0	0	1	0	–	–	–	2	0	0	0
B. fuscescens S274	0	0	0	0	0	0	0	0	0	1	0	–	–	–	2	0	0	0
B. fuscescens S277a	1	1	0	0	0	0	0	0	0	1	0	–	–	–	2	0	0	0
B. fuscescens S369	1	1	0	0	0	0	0	0	0	1	0	–	–	–	2	0	0	0
B. fuscescens S379	1	1	0	0	0	0	0	0	0	1	0	–	–	–	2	0	0	0
B. fuscescens S380	1	1	0	0	0	0	0	0	0	1	–	–	–	–	2	0	0	0
B. glabra L186	1	1	0	0	0	0	0	0	0	1	0	–	–	–	1	0	2	1
B. implexa S22	1	0	0	1	1	1	0	0	0	1	1	1	1	1	1	0	2	1
B. implexa S36	1	0	0	1	0	0	0	0	0	0	1	1	0	1	0	0	0	1
B. implexa S39	1	0	0	1	0	0	0	0	0	1	1	1	1	1	1	0	0	1
B. implexa S67	1	0	0	1	1	1	0	0	0	0	1	1	1	1	1	0	2	1
B. implexa S168	1	0	0	1	1	1	0	0	0	1	1	–	–	–	1	1	0	1
B. inactiva L206	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0
B. inactiva L323b	0	0	0	0	0	0	0	0	0	0	1	1	0	0	1	0	2	0
B. inactiva L347	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	1	2	0
B. inactiva L358	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	2	0
B. inactiva S239a	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	2	0
B. inactiva S384	0	0	0	0	0	0	0	0	0	0	1	1	0	0	2	0	0	0
B. inactiva S392a	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1	0	0
B. kockiana L394	1	0	0	1	1	1	0	0	0	0	1	1	1	1	0	0	0	0
B. kockiana L396	1	0	0	1	0	0	0	0	0	0	1	0	1	1	1	0	0	0
B. kuemmerleana L244a	1	0	1	0	1	1	0	0	0	1	1	0	0	1	2	0	0	1
B. kuemmerleana L274	1	0	1	0	1	1	0	0	0	1	1	0	1	1	1	0	1	1
B. kuemmerleana L275	1	0	1	0	1	1	0	0	0	1	1	0	0	1	1	0	1	1
B. kuemmerleana S128	1	0	1	0	1	1	0	0	0	1	1	0	0	1	1	0	2	1
B. kuemmerleana S160	1	0	1	0	1	1	0	0	0	1	1	0	1	1	1	0	0	1
B. pikei L197	0	0	0	0	1	0	1	1	0	0	1	0	0	1	1	1	0	0
B. pikei L200	0	0	0	0	1	0	1	1	0	0	1	0	0	1	1	1	0	0
B. pikei L209	0	0	0	0	1	0	1	1	0	0	1	0	0	1	1	1	0	0
B. pikei L210	0	0	0	0	1	0	1	1	0	0	1	0	0	1	1	0	2	0
B. pikei L374	0	0	0	0	1	0	1	0	1	0	1	0	0	1	2	0	0	0
B. pikei L376	0	0	0	0	1	0	1	0	1	0	1	0	0	1	1	0	0	0
B. pikei L377	0	0	0	0	1	0	1	0	1	0	1	1	0	1	0	1	2	0
B. pikei L421	0	0	0	0	1	0	1	0	1	0	1	0	1	1	0	0	0	0
B. pikei S221	0	0	0	0	1	0	1	1	0	0	1	0	0	1	0	0	0	0
B. pikei S362	0	0	0	0	1	0	1	1	0	0	1	0	0	0	1	0	0	0
B. pikei S368	0	0	0	0	1	0	1	1	0	0	1	0	0	1	1	1	0	0
B. pikei S382	0	0	0	0	1	0	1	1	0	0	1	0	0	1	0	0	0	0
B. pikei S383a	0	0	0	0	1	0	1	1	0	0	1	1	0	1	0	0	0	0
B. pikei S390	0	0	0	0	1	0	1	1	0	0	1	–	–	–	1	0	0	0
B. pikei S394	0	0	0	0	1	0	1	1	0	0	1	0	0	1	0	0	0	0

continued

Appendix 1. Continued.

Specimen	Character																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
B. pseudofuscescens S222	1	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0	0	0
B. pseudofuscescens S232	1	0	1	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0
B. pseudofuscescens S370	1	0	1	0	0	0	0	0	0	0	1	1	0	1	1	0	0	0
B. pseudofuscescens S371	1	0	1	0	0	0	0	0	0	0	1	1	0	1	2	0	0	0
B. pseudofuscescens S377	1	0	1	0	0	0	0	0	0	0	1	1	0	0	2	0	0	0
B. pseudofuscescens S386	1	0	1	0	0	0	0	0	0	0	1	1	0	1	2	0	0	0
B. pseudofuscescens S387	1	0	1	0	0	0	0	0	0	0	1	1	0	1	2	1	2	0
B. vrangiana L272	1	1	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
B. vrangiana L273	1	1	0	0	0	0	0	0	0	1	1	0	0	1	1	0	2	1
B. vrangiana L279	1	2	0	0	0	0	0	0	0	1	1	0	0	1	1	0	2	1
B. vrangiana L286	1	2	0	0	1	1	0	0	0	1	1	0	0	1	1	1	1	1
B. vrangiana L300	1	1	0	0	0	0	0	0	0	1	1	0	0	1	1	1	1	1
B. vrangiana S6	1	2	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	1
B. vrangiana S10	0	0	0	0	0	0	0	0	1	0	1	0	0	–	1	0	2	1
B. vrangiana S32	1	1	0	0	1	1	0	0	1	1	1	0	0	1	2	0	0	1
B. vrangiana S42	1	1	0	0	0	0	0	0	1	1	1	0	0	1	1	1	2	1
B. vrangiana S43	1	1	0	0	0	0	0	0	1	1	1	0	0	1	1	0	2	1
B. vrangiana S45	1	1	0	0	0	0	0	0	0	1	1	0	0	1	1	1	2	1
B. vrangiana S47	1	1	0	0	0	0	0	0	0	1	1	0	0	1	1	1	0	1
B. vrangiana S57	1	2	0	0	1	1	0	0	0	0	1	0	0	1	1	1	2	1
B. vrangiana S59	1	1	0	0	1	1	0	0	0	1	1	0	0	1	1	0	2	1
B. vrangiana S62	1	1	0	0	1	1	0	0	1	1	1	0	0	1	1	0	0	1
B. vrangiana S72	1	1	0	0	0	0	0	0	0	1	1	0	0	0	2	0	1	1
B. vrangiana S164	1	1	0	0	1	1	0	0	0	1	1	0	0	1	2	0	0	1
B. vrangiana S166	1	2	0	0	1	1	0	0	0	1	1	0	0	1	1	0	0	1
B. vrangiana S196	1	1	0	0	0	0	0	0	0	1	1	0	0	1	1	0	0	1
B. vrangiana S341b	1	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	1	1
B. vrangiana S385	1	1	0	0	0	0	0	0	0	1	1	0	0	0	1	0	2	0
B. vrangiana S396	1	2	0	0	1	1	0	0	0	1	1	0	0	1	1	1	0	1
Bryoria sp. *L392*	0	0	0	0	0	0	0	0	0	0	1	0	0	1	1	0	0	0
Bryoria sp. *L395*	0	0	0	0	0	0	0	0	0	0	1	0	0	1	2	0	0	0