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The taxonomy of the lichen *Fuscidea cyathoides* (*Fuscideaceae*, Umbilicariomycetidae, Ascomycota) in Europe

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Abstract: Based on morphometric and molecular methods, the taxonomy of the infraspecific taxa of *Fuscidea cyathoides* (Ach.) V. Wirth & Vězda, var. *corticola* (Fr.) Kalb and var. *sorediata* (H. Magn.) Poelt, has been assessed. No formal taxonomic recognition should be attributed to the morphological and ecological variation. Accordingly, var. *corticola* and var. *sorediata* are synonymized with *F. cyathoides* var. *cyathoides*. New synonyms at the specific level are *Fuscidea fagicola* (Zschacke) Hafellner & Türk and *F. stiriaca* (A. Massal.) Hafellner.

Key words: *Fuscidea fagicola*, *Fuscidea stiriaca*, infraspecific taxonomy, lichen varieties, molecular phylogeny, secondary chemistry

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Introduction

Substratum specificity is a strong feature in *Fuscidea*. However, there have been occasional reports of corticolous specimens of mainly saxicolous species. For example, *F. recensa* (Stirt.) Hertel is capable of inhabiting both rock and bark in Scandinavia (Tønsberg 1992) but corticolous specimens have not been formally recognized (Nordin *et al.* 2010). In Great Britain and Ireland, species of *Fuscidea* inhabit rock or, more rarely, bark, occasionally wood, and 9 of the 11 species are either exclusively saxicolous (8 spp.) or exclusively corticolous/lignicolous (2 spp.), with *F. cyathoides* (Ach.) V. Wirth & Vězda and *F. recensa* (Stirt.) Hertel, V. Wirth & Vězda capable of inhabiting both rock and bark (Gilbert *et al.* 2009; B. Coppins, pers. comm.). Substratum ecology and the presence/absence of soredia have been suggested as important characters for formal recognition of taxonomic entities of *F. cyathoides* at the species (Hafellner & Türk 2001; Hafellner 2002) and varietal levels (Fries 1831; Magnusson 1925; Zschacke 1927) (Table 1). Magnusson (1925) discussed seven saxicolous forms of *F. cyathoides* (as *Lecidea rivulosa* Ach.) and introduced var. *infuscata* H. Magn., separated from var. *cyathoides* based on habitat and thallus colour (see Supplementary Material Table S1, available online). None of the *F. cyathoides* forms are still recognized and Oberhollenzer & Wirth (1984) synonymized var. *infuscata* with var. *cyathoides* (see Taxonomy below).

In *F. cyathoides*, corticolous material has been attributed taxonomic rank at both infraspecific and specific levels. According to Fries (1831), *F. cyathoides* var. *corticola* (Fr.) Kalb (as *Biatora rivulosa* b. *corticola* Fr.) is distinct from var. *cyathoides* in possessing a different thallus colour (i.e. black-brown when dry and greenish when wet *vs.* grey when dry and umber brown when wet in var. *cyathoides*). Although some authors (e.g. Oberhollenzer & Wirth 1984; Gilbert *et al.* 2009) consider the corticolous variety as merely *F. cyathoides* on bark, others (e.g. Inoue 1981; Santesson *et al.* 2004) recognize this taxon as *F. cyathoides* var. *corticola*.

Zschacke (1927) recognized the absence of a black prothallus, the larger and flatter thallus as well as the larger apothecia as

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TABLE 1. *Overview of* Fuscidea cyathoides *nomenclature.*

Author(s)	Year	Name of species at: Species level	Name of species at: Varietal level	Basionym	Synonyms
Acharius, E.	1798	*Lichen cyathoides* Ach.			
Fries, E.	1831		*Biatora rivulosa* b. *corticola* Fr.		*Lecidea lightfootii* Ach.; *Lecidea rivulosa* Hepp
Massalongo, A.	1852	*Biatora stiriaca* A. Massal.			
Magnusson, H.	1925		*Lecidea rivulosa* var. *sorediata* H. Magn.		
Zschacke, H.	1927	*Lecidea fagicola* Zschacke			
Wirth, V. & Vězda, A.	1972	*Fuscidea cyathoides* (Ach.) V. Wirth & Vězda		*Lichen cyathoides* Ach.	
Kalb, K.	1976		*Fuscidea cyathoides* var. *corticola* (Fr.) Kalb	*Biatora rivulosa* b. *corticola* Fr.	*Biatorinella rivulosa* var. *corticola* (Koerb.) Werner
Poelt, J. & Buschardt, A.	1978		*Fuscidea cyathoides* var. *sorediata* (H. Magn.) Poelt	*Lecidea rivulosa* var. *sorediata* H. Magn.	
Hafellner, J. & Türk, R.	2001	*Fuscidea fagicola* (Zschacke) Hafellner & Türk		*Lecidea fagicola* Zschacke	*Biatora rivulosa* b. *corticola* Fr.
Hafellner, J.	2002	*Fuscidea stiriaca* (A. Massal.) Hafellner		*Biatora stiriaca* A. Massal.	*Fuscidea fagicola* (Zschacke) Hafellner & Türk

diagnostic characters for distinguishing *F. fagicola* (as *Lecidea fagicola* Zschacke) from *F. cyathoides* (as *L. rivulosa*). When comparing the so-called *Fagus*-type of apothecia of var. *corticola* (i.e. apothecia from specimens growing on *Fagus* in southern Europe) with those on *Betula*, the so-called *Betula*-type, Oberhollenzer & Wirth (1984) did not find any significant variation. Based on this result they concluded that *L. fagicola* most certainly is synonymous with var. *corticola*. Hafellner & Türk (2001) transferred *L. fagicola* to *Fuscidea* and placed *F. cyathoides* var. *corticola* in synonymy without any explanatory discussion.

Hafellner (2002) made the combination *F. stiriaca* (A. Massal.) Hafellner based on the basionym *Biatora stiriaca* A. Massal., which was treated as a synonym of var. *cyathoides* by Magnusson (1925) (as *L. rivulosa* var. *corticola* (Fr.) Jatta) and by Vainio (1934) (as *L. rivulosa* f. *corticola* (Fr.) Vain.), and he synonymized *F. fagicola* with *F. stiriaca*. The sorediate form, var. *sorediata* (H. Magn.) Poelt, is saxicolous and rare. It was, for example, accepted by Santesson *et al.* (2004) and Gilbert *et al.* (2009).

Molecular approaches changed the concept of species delimitation (as discussed in Resl *et al.* 2016) and provided a new approach to assess the status of sorediate lichens. In the studies of *Pseudevernia furfuracea* (L.) Zopf by Ferencová *et al.* (2010), *Mycoblastus alpinus* (Fr.) Kernst./*M. affinis* (Schaerer) Schauer by Spribille *et al.* (2011), several species of *Dirina* Fr. by Tehler *et al.* (2013) and *Rinodina degeliana* Coppins/*R. subparieta* (Nyl.) Zahlbr. by Resl *et al.* (2016) no taxonomic relevance was given to the presence of soredia. For example, Spribille *et al.* (2011) confirmed the hypothesis of Tønsberg (1992) that *M. alpinus* and *M. affinis* are conspecific using a combined matrix of two protein coding (EF1-α, MCM7) and ITS genes. These two species differ in their morphologies (esorediate, richly fertile *vs.* sorediate, sterile or sparingly fertile) and chemistries (usnic acid absent/thallus grey *vs.* usnic acid present in the (yellowish) soralia).

Here we aim to revise the taxonomy of *F. cyathoides* s. lat., providing a morphological, chemical and phylogenetic investigation of all three currently recognized varieties, and clarify the taxonomy of *F. cyathoides*, including the related *F. fagicola* and *F. stiriaca*.

Material and Methods

Taxon sampling

Herbarium material studied was provided by BG, HO, MSC, LD, UPS, TUR and H-Ach, as well as from private collections. As *Fuscidea cyathoides* var. *sorediata* is scarce in Europe, we managed to obtain only one fresh specimen.

Morphology

To determine morphological differences between varieties, the apothecia and thalli were examined by light microscopy in hand-cut sections mounted in water with 10% KOH using a Carl Zeiss Axioskop 2 microscope. Twenty specimens of *F. cyathoides*, including all three varieties, were investigated. The following morphological characters were studied: overall diameter of the apothecia and the areoles, height of the epihymenium and hymenium, length and width of the ascospores, and colour of the thalli (Table 2). The ratio between length and width of spores was calculated. Characters were examined using an unconstrained linear ordination, Principal Components Analysis (PCA), to explore the morphological variation. We performed the analysis with centering and standardization of characters in CANOCO 5 (Ter Braak & Šmilauer 2012).

Secondary chemical compounds

Lichen substances were analyzed by thin-layer chromatography (TLC), using the methods of Culberson & Kristinsson (1970), Culberson (1972) and Menlove (1974). All three solvents (A, B´ and C) were used, with glass plates in solvent C for the detection of fatty acids. Selected specimens were also run in solvent G for a detailed study of β-orcinol depsidone fumarprotocetraric acid and possible occurrences of the related substances protocetraric and succinprotocetraric acids (see Culberson *et al.* 1981).

DNA extraction, PCR amplification and sequencing

DNA from 10 specimens of *Fuscidea cyathoides* were analyzed together with six other *Fuscidea* species for three genes. Altogether we generated 36 new sequences, in addition to sequences of *Fuscidea* downloaded from GenBank (Table 3). DNA was extracted from apothecia or soredia with thallus using the DNeasy Plant Mini Kit (Qiagen). Although phylogenies based on ITS alone have been considered sufficient for infraspecific taxonomic investigations (e.g. Davydov *et al.* 2010; Solheim *et al.* 2013), we constructed a concatenated data set of three markers from two different genomes (mtSSU, nuITS and nuLSU). The mtSSU fragment was made with the primers mrSSU1 and mrSSU3R (Zoller *et al.* 1999), while ITS and LSU were amplified by ITS1F (Gardes & Bruns 1993), ITS4 (White *et al.* 1990) and nu-nuLSU-1125-3´ (Vilgalys & Hester 1990). The PCR master mix included: 1× Buffer II GeneAmp® 10× PCR (Applied Biosystems), 2·5 µM $MgCl_2$ (Applied Biosystems), 20 µM dNTPs (Promega), 0·6 µM of each primer, 0·036 U AmpliTaq® DNA Polymerase (Applied Biosystems), 5·0 µl of genomic DNA extract and distilled water to a total volume of 25 µl.

The PCR reactions were performed using the C1000™ Touch thermal cycler (Bio-Rad Laboratories). The following programs were used for mtSSU: initial denaturation at 94 °C for 5 min, touchdown of six cycles (94 °C for 30 s, 62–56 °C for 30 s, and 72 °C for 1 min 45 s), followed by 34 cycles of 94 °C for 30 s, 56 °C for 30 s, 72 °C for 1 min 45 s, and a final elongation at 72 °C for 10 min. The same were used for LSU and ITS, except for the annealing temperature where the touchdown ranged from 63–57 °C for six cycles, ending at 57 °C for 34 cycles.

PCR products were visualized on a 1% Red Gel-stained agarose gel under UV light and purified using Exosap-IT (GE Healthcare). The PCR products were sequenced using the PCR primers with the BigDye Terminator Cycle Sequencing Kit (Applied Biosystems) and run on an ABI Prism 3700XL DNA analyzer (Applied Biosystems) at the DNA Sequencing Laboratory, University of Bergen, Norway. The sequences were assembled in SeqMan II version 4.05 (DNASTAR).

Phylogenetic analyses

Geneious version 8.1.8 (Biomatters Ltd.) was used to align the mtSSU, LSU and ITS sequences with 65% similarity option on (Gap penalty = 14·5, Gaps extension penalty = 5), followed by manual adjustment. *Candelariella vitellina* (Hoffm.) Müll. Arg. was used as outgroup and two sequences, *Umbilicaria proboscidea* (L.) Schrad. and *U. crustulosa* (Ach.) Frey, as a sister group to *Fuscidea*.

To identify suitable substitution models for all fragments (i.e. mtSSU, LSU, ITS1, 5.8S and ITS2), a likelihood ratio test (Huelsenbeck & Crandall 1997) was performed using the software jModelTest version 2.1.7 (Posada 2008). The model GTR+G was selected for mtSSU, GTR+I+G for LSU, SYM+G for ITS1, K80+I for 5.8S, HKY+G for ITS2 and GTR+I+ G for the concatenated data set.

To detect potential conflicts between the data sets, we inspected the internodes of the phylogenetic trees with bootstrap values >70%. These were generated using the neighbour-joining model with a maximum likelihood distance (e.g. Reeb *et al.* 2004). Bootstrap scores were calculated using 2000 non-parametric replicates in the Jukes-Cantor distance model implemented in Geneious version 8.1.8 (Biomatters Ltd.).

Phylogenetic relationships were estimated from the data sets, both from each gene separately and the concatenated data, using MrBayes version 3.2.1 (Ronquist & Huelsenbeck 2003) to sample trees using a Markov

TABLE 2. *Overview of morphological characters measured on the varieties of* F. cyathoides*, given as (smallest values–)arithmetic mean ± SD(–largest values). Numbers in square brackets are the number of replicates.*

Variety	Collection number	Country	Thallus colour	Areoles diam. (mm)	Apothecia diam. (mm)	Apothecia tuberculate diam. (mm)	Hymenium (μm) [1]	Epihymenium (μm) [1]	Length of spores (μm)	Width of spores (μm)
cyathoides	ZP 7903	Ireland	dark grey	(0·23–)0·45±0·24 (–0·90) [7]	(0·63–)0·86±0·12 (–1·04) [8]		93	31	(10–)10·6±0·89 (–12) [5]	(4·5–)5·1±0·89 (–6) [5]
	JM 4928	Czech Rep.	dark grey, dark brown	(0·41–)0·68±0·23 (–0·95) [5]	(0·45–)0·85±0·27 (–1·17) [8]		62	31	(10–)10·6±0·52 (–11) [8]	5±0 [8]
	MSC0050557	Scotland	dark grey, dark brown	(0·45–)0·84±0·3 (–1·35) [10]	(0·63–)0·9±0·29 (–1·44) [6]		155	31	(7–)9·7±1·51 (–11) [6]	(4–)4·9±1·11 (–7) [6]
	JM 4866	Czech Rep.	mouse grey	(0·23–)0·41±0·15 (–0·59) [6]	(0·50–)0·93±0·25 (–1·35) [7]		68	22	(6–)10±2 (–12) [7]	(4–)4·14±0·38 (–5) [7]
	JM 4916	Czech Rep.	grey-brown	(0·23–)0·59±0·24 (–0·90) [6]	(0·50–)0·63±0·13 (–0·90) [7]		62	31	(11–)11·5±0·55 (–12) [6]	5±0 [6]
	JPH 13294	Czech Rep.	brown-grey, brown	(0·45–)1·06±0·59 (–2·03) [6]	(0·45–)0·93±0·32 (–1·35) [5]	(1·40–)1·64±0·35 (–1·89) [2]	93	31	(9–)9·9±0·99 (–11) [8]	(4–)4·88±0·64 (–6) [8]
	BG-L-96931	Norway	grey, brown-grey	(0·18–)0·41±0·26 (–0·99) [9]	(0·41–)0·55±0·11 (–0·72) [7]		78	16	(9–)9·86±0·69 (–11) [7]	(3–)4·14±0·75 (–5) [7]
	BG-L-99904	Norway	light grey, dark grey	(0·25–)0·51±0·24 (–0·88) [7]	(0·60–)0·79±0·16 (–1·12) [8]	(0·67–)0·78±0·11 (–0·88) [4]	145	32 [2]	(8–)11·55±2·19 (–14) [9]	(4·5–)4·89±0·22 (–5) [9]
	BG-L-96933	Norway	light grey, whitish	(0·14–)0·56±0·41 (–1·35) [8]	(0·45–)0·76±0·29 (–1·13) [8]		93	19	(8–)9·29±0·76 (–10) [7]	(4–)4·7±0·49 (–5) [7]
	LD-1132977	Sweden	dark grey-brown	(0·45–)1·14±0·45 (–1·94) [7]	(0·45–)0·74±0·24 (–1·13) [6]		109	16	(7–)9·33±2·08 (–11) [3]	(5–)5·5±0·87 (–6·5) [3]
sorediata	BG-L-99902	Norway	whitish, light grey	(0·25–)0·55±0·31 (–1·05) [7]	(0·16–)0·33±0·17 (–0·70) [10]		150 [2]	28 [2]	(7–)11·71±2·21 (–13) [7]	(4–)4·71±0·49 (–5) [7]
corticola	BG-L-89638	Norway	light grey	(0·50–)1·15±0·46 (–1·76) [6]	(0·54–)0·72±0·25 (–0·90) [2]	(0·94–)1·34±0·32 (–1·76) [4]	78	16	(10–)11±1·21 (–13) [6]	(4–)4·5±0·55 (–5) [6]
	JV 11476	Slovakia	dark greenish brown	(0·23–)0·38±0·1 (–0·5) [6]	(0·32–)0·48±0·12 (–0·59) [4]		53	31	(8–)8·83±0·98 (–10) [6]	(3·5–)4·1±0·49 (–5) [6]
	BG-L-89616	Norway	grey, brown	(0·45–)0·71±0·32 (–1·35) [7]	(0·45–)0·78±0·31 (–1·40) [8]		62	19	(10–)10·75±0·87 (–12) [8]	(4–)4·5±0·53 (–5) [8]
	JM 6488	Slovakia	olive-green	(0·45–)0·76±0·37 (–1·35) [5]	(0·72–)0·9±0·12 3–(1·17) [5]	(0·50–)1·24±0·53 (–1·85) [5]	62	16	(8–)9·25±1·5 (–11) [6]	(4–)4·5±0·58 (–5) [6]
	JV 11397	Slovakia	light green	(0·23–)0·63±0·24 (–0·90) [6]	(0·54–)0·83±0·17 (–0·90) [6]	(1·35–)1·51±0·22 (–1·67) [2]	68	19	(9–)10·1±1·3 (–12) [7]	(4–)4·5±0·53 (–5) [7]
	JV 11411	Slovakia	green, light green	(0·45–)0·53±0·12 (–0·77) [6]	(0·54–)0·73±0·15 (–0·90) [6]		62	19	(9–)10·3±1·38 (–13) [7]	(4–)4·6±0·53 (–5) [7]
	ZP 9629	Slovakia	mouse grey, brown	(0·45–)0·64±0·21 (–0·90) [6]	(0·50–)0·87±0·27 (–1·13) [4]	(1·31–)1·5±0·21 (–1·89) [6]	93	16	(6–)8·6±1·5 (–10) [6]	(4–)4·3±0·51 (–5) [6]
	LD-1133157	Sweden	dark grey	(0·45–)0·73±0·31 (–1·04) [7]	(0·54–)0·77±0·14 (–0·90) [6]	(1·13–)1·24±0·16 (–1·35) [2]	155	22	(10–)12·5±1·68 (–14·5) [8]	5±0 [8]
	LD-1157864	Sweden	mouse grey	(0·45–)0·89±0·38 (–1·31) [6]	(0·50–)1·03±0·3 (–1·44) [6]		124	31	10±0 [5]	(4·5–)4·8 ±0·27 (–5) [5]

TABLE 3. *List of voucher specimens with their collection details and GenBank Accession numbers, in addition to sequences included from GenBank. Newly generated sequences are indicated in bold.*

					GenBank Accession Number		
Species	Variety	Country	Substratum	Herbarium/Collector number	mtSSU	ITS	LSU
Candelariella vitellina					AY853315	AJ640085	AY853363
Fuscidea austera		Scotland	siliceous rock	MSC0050558	**KY874033**	**KY874026**	**KY874045**
F. austera		Norway		E. Timdal 4177	KJ766395	–	KJ766719
F. australis	*australis*	Tasmania, Australia	*Banksia marginata*	HO:546743	**KY874034**	**KY874022**	**KY874044**
F. cyathoides	*cyathoides*	Czech Rep.	siliceous rock	J. Malíček 4866	–	**KY874017**	–
	cyathoides	Norway	siliceous rock	BG-L-96931	**KY874030**	**KY874018**	**KY874038**
	cyathoides	Norway	siliceous rock	BG-L-96933	–	**KY874011**	–
	cyathoides	Norway		R. Haugan 1389	KJ766396	–	KJ766563
	cyathoides	Rep. of Ireland	boulders	Z. Palice 7903	–	**KY874012**	–
	cyathoides	Sweden		G. Thor 18066	EF659761	–	–
	cyathoides	Sweden		G. Thor 18061	EF659763	–	–
F. cyathoides	*corticola*	Norway	*Betula pubescens*	BG-L-89616	**KY874027**	**KY874015**	**KY874037**
	corticola	Norway	*Betula pubescens*	BG-L-89638	–	**KY874014**	–
	corticola	Slovakia	*Fagus sylvatica*	J. Malíček 6488	–	**KY874016**	**KY874039**
	corticola	Slovakia	*Fagus sylvatica*	J. Vondrák 11397	**KY874028**	**KY874019**	–
	corticola	Slovakia	*Acer pseudoplatanus*	J. Vondrák 11411	–	**KY874021**	–
F. cyathoides	*sorediata*	Norway	siliceous rock	BG-L-99902	**KY874029**	**KY874013**	**KY874046**
F. elixii		New South Wales, Australia	*Acacia melanoxylon*	HO:559235	**KY874035**	**KY874020**	**KY874043**
F. gothoburgensis		Norway	siliceous rock	BG-L-100245	**KY874036**	**KY874024**	**KY874042**
F. kochiana		Norway	siliceous rock	BG-L-96940	**KY874031**	**KY874023**	**KY874041**
F. pusilla		Norway	*Betula* sp.	BG-L-96938	**KY874032**	**KY874025**	**KY874040**
F. pusilla		Sweden		G. Thor 18063a	EF659765	–	–
F. pusilla		Sweden		G. Thor 18058	EF659767	–	–
F. stiriaca		France		A. Aptroot 55063	EF659762	–	–
Umbilicaria proboscidea					AY300920	FR799304	AY300870
U. crustulosa					AY300919	HM161499	HM161591

chain Monte Carlo (MCMC) method in the Bayesian inference (BI). Tree sampling performed under the MCMC analysis was run for 4 000 000 generations with four parallel chains starting from a random tree, using the default setting with temperature of 0·2. Gaps were coded as a fifth character state. Sampling frequency of trees was every 10th generation, including branch lengths. The first 40 000 trees (i.e. 10% of the total number) were deleted as burn-in. A majority-rule consensus tree with average branch lengths was constructed from 360 000 trees and visualized in Geneious (Biomatters Ltd.). Significant posterior probabilities were ≥95%.

Weighted maximum parsimony (MP) and maximum likelihood (ML) analyses were carried out in PAUP*4.0b10 (Swofford 2002) to construct MP and ML trees with bootstrap support. A first heuristic search was run to find MP trees using random sequence additions with 500 replicates, and tree bisection-reconnection branch swapping (TBR). The MulTrees and steepest descent options were on, and the collapse zero-length branches option was off. Gaps were coded as a fifth character state. To estimate the branch support for the MP trees, 1000 bootstrap replicates with 10 random additions of the taxa were performed. A second heuristic search with 500 replicates under the ML criterion and the selected substitution model was run using the MP trees from the previous heuristic search as starting trees. Branch support for the ML trees was estimated by 100 bootstrap replicates with 10 random additions of the taxa. High bootstrap support was considered to be ≥70%.

Results

Morphological examination

This study showed that only corticolous specimens had greenish to green thalli and that saxicolous specimens varied from grey to brown (Table 2). Corticolous specimens developed tuberculate apothecia more frequently (90% of specimens examined) than saxicolous thalli (20% of specimens examined). Var. *sorediata*, represented by only one specimen, had smaller and fewer apothecia (Table 2). The ascospores of all three varieties were bean-shaped. However, those of the corticolous specimens were narrower (4·53 ± 1·82 μm) than saxicolous thalli (4·79 ± 1·21 μm), but were similar in length (i.e. 10·17 ± 4·79 μm and 10·24 ± 3·11 μm, respectively) (see Table 2).

PCA based on morphological characters of *F. cyathoides* did not separate corticolous and saxicolous specimens along the two first ordination axes representing 28·77% and 24·11% of the variation, respectively (Fig. 1). One character, namely the ratio between the length and width of ascospores, had a larger range for var. *cyathoides* than var. *corticola*. The heights of the hymenium and epihymenium, and width of ascospores, were all positively correlated with the size of areoles and tuberculate apothecia.

Secondary chemical compounds

Analysis of secondary chemical compounds in the fumarprotocetraric acid chemosyndrome did not reveal any chemical differences between the specimens. The major and diagnostic constituent was fumarprotocetraric acid; a trace of the satellite substance protocetraric acid was present in most specimens, whereas succinprotocetraric acid was not detected in any of the specimens tested.

Phylogeny of *Fuscidea cyathoides*

As no conflicts were detected between the data sets for different genes, they were combined and the final aligned sequence matrix comprised 26 taxa with 2187 characters, of which 1618 were constant and 361 informative. The GenBank Accession numbers are given in Table 3. The majority-rule consensus tree from the BI is displayed in Fig. 3. The average −ln likelihood of the tree was 8081·83 and the average standard deviation of split frequencies was 0·0025, indicating that two independent runs of the Markov chain search converged. The calculated likelihood parameters of the MCMC analysis are summarized in Table S2 (see Supplementary Material, available online).

A heuristic search using the parsimony criterion resulted in 100 MP trees of length 1041 with consistency index = 0·7080, homoplasy index = 0·2920, retention index = 0·6984 and rescaled retention index = 0·4945. A second heuristic search under the ML criterion and the GTR+I+G model using the MP trees as starting trees resulted in three equally best ML trees (−lnL = 8104·6499). The consensus ML tree was incongruent with the BI tree in the position of *F. kochiana* (Hepp) V. Wirth & Vězda, and five specimens (*A. Aptroot* 55063, *M. Zahradníková* MZ05

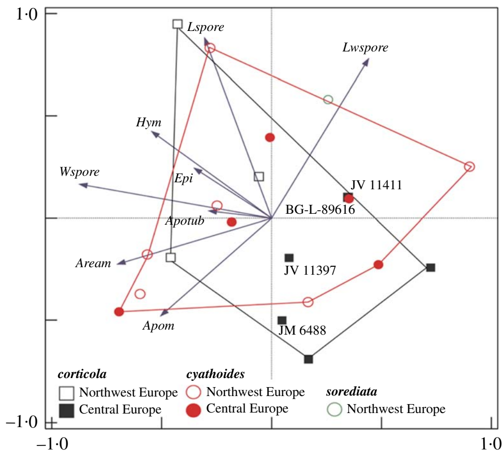

FIG. 1. Biplot of the first two principal component axes, showing morphological variation of *Fuscidea cyathoides* identified in this study. Key to variables: *Apom* = diam. (mm) of apothecia; *Apotub* = diam. (mm) of tuberculate apothecia; *Aream* = diam. (mm) of areoles; *Hym* = height (μm) of hymenium; *Epi* = height (μm) of epihymenium; *Lspore* = length (μm) of ascospores; *Wspore* = width (μm) of ascospores; *Lwspore* = ratio of *Wspore*:*Lspore*.

(BG-L-96931), *G. Thor* 18066, *G. Thor* 18061 and *R. Haugan* 1389) within the *F. cyathoides* group. All incongruences are indicated with a circle in Fig. 3.

All the samples of *Fuscidea* included here formed a monophyletic group. All three varieties of *F. cyathoides* were clustered in one subgroup with PP = 0·99, MP = 97%, ML = 99% support. Within this subgroup, no clear classification in the varieties of corticolous and saxicolous specimens was discovered. The specimens from Central Europe (i.e. the Czech Republic and Slovakia) formed a separate group to those from North-West Europe (i.e. Norway and the Republic of Ireland).

Discussion

Neither the chemistry nor the molecular data show evidence for differentiation within *F. cyathoides*. Our results suggest that the bean-shaped spores becoming brownish

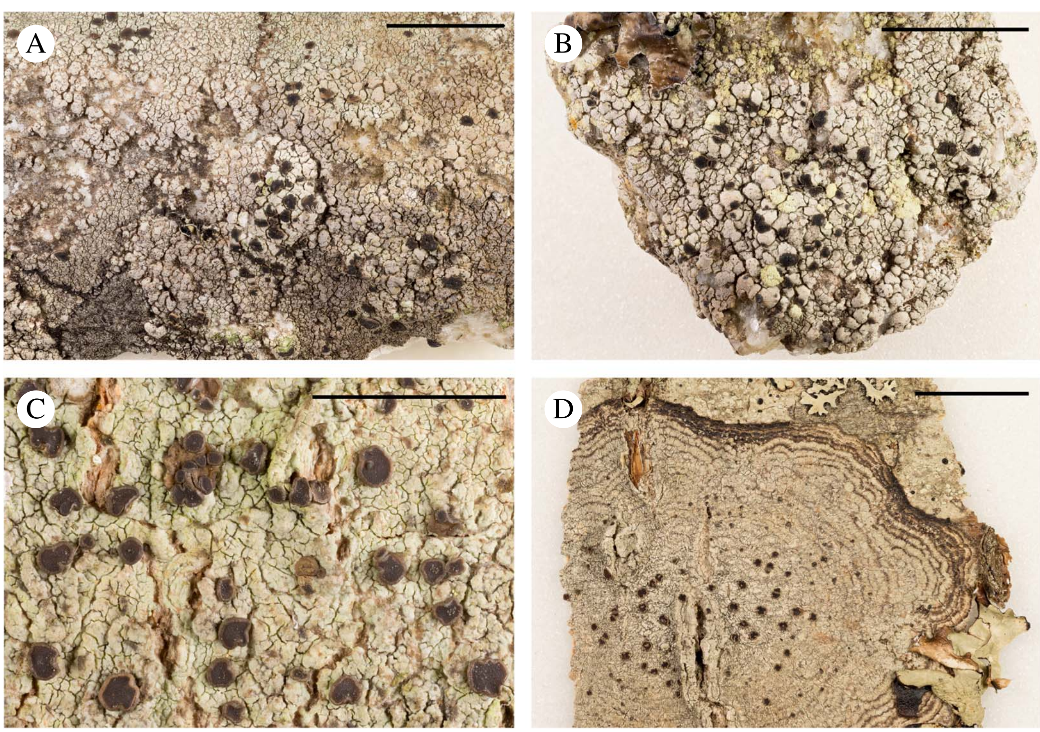

FIG. 2. *Fuscidea cyathoides*.; A, saxicolous and esorediate specimen (Norway, TT 46572, BG-L-99904); B, saxicolous and sorediate specimen (Norway, TT 46570, BG-L-99902). C & D, corticolous; C, on *Fagus sylvatica*, Slovakia (JV 11397); D, on *Alnus incana*, Norway (TT 26205, BG-L-70280). Scales: A, B & D = 2 cm; C = 0·5 cm. Photographs by Kim Abel.

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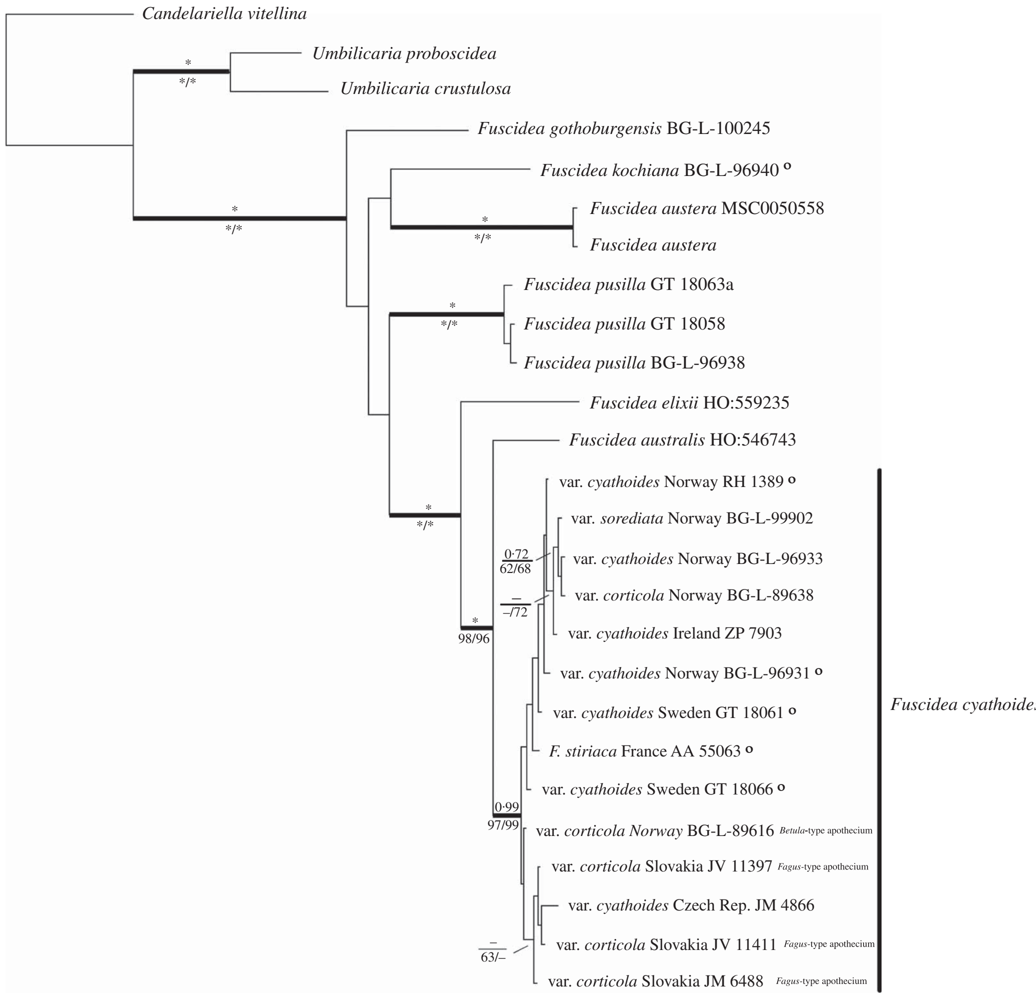

FIG. 3. Phylogenetic relationships of esorediate and sorediate, saxicolous and corticolous specimens of *Fuscidea cyathoides*, shown here as a 50% majority-rule consensus tree of a B/MCMC analysis based on the concatenated data set (–ln = 8081·83) of mtSSU, LSU and ITS. Posterior probabilities (PP) are displayed above, and MP and ML bootstrap values are displayed below, the branches; asterisks indicate a value of 100%. A circle indicates incongruent topology with the ML tree.

when mature and the production of fumarprotocetraric acid are the only diagnostic characters for the recognition of *F. cyathoides*.

Our findings agree with Bylin *et al.* (2007), where corticolous and saxicolous specimens of *F. cyathoides* were grouped together, but with less sampling and MP bootstrap support lower than 80%. Moreover, *Fuscidea stiriaca* was clustered with var. *cyathoides* (MP = 100%).

The included representatives with apothecia of both the *Fagus*- and *Betula*-types show no morphological or genetic differences. The observed variation between these apothecium types is not significant (see Figs 1 & 3), confirming the report of Oberhollenzer & Wirth (1984). In the PCA, the *Betula*-type (BG-L-89616) and the *Fagus*-type (JV 11397, JV 11411 and JM 6488) are not separated from each other; furthermore, specimens

BG-L-89616 and JV 11411 are found to overlap. We consider the colour and the presence of crystals in the apothecia as adaptations to localities with direct light exposure. It should be noted that Fahselt (1981) found that levels of perlatolic and fumarprotocetraric acids in populations of *Cladonia stellaris* (Opiz) Pouzar & Vězda and *C. rangiformis* Hoffm., respectively, were influenced by light intensity. Massalongo (1852) suggested that the bean-shaped spores and tuberculate apothecia were diagnostic for *F. stiriaca* (as *Biatora stiriaca*) (see Fig. 1). This cannot be supported since both characters are also present in var. *cyathoides*.

In the present study var. *sorediata* has the smallest apothecia (see Table 2), but this feature is considered to be a result of a biological energy saving strategy (see Tønsberg 1992) and should not be used as a diagnostic character for species forming species pairs *sensu* Poelt (1970, 1972).

To conclude, no significant genetic difference between specimens reflecting the morphological and ecological variations was found in *F. cyathoides.* Therefore, we synonymize var. *corticola* and var. *sorediata* with the typical form. *Fuscidea fagicola* and *F. stiriaca* are synonymized with *F. cyathoides.*

Taxonomy

Fuscidea cyathoides (Ach.) V. Wirth & Vězda

Beitr. nat. kdl. Forsch. in Südwestdtschl. **31:** 92 (1972).—*Lichen cyathoides* Ach., *Lichenographiae Suecicae Prodromus*: 62 (1798); type: Sweden, in saxis et rupibus (H-Ach 273 F & G—lectotypus [!] in Oberhollenzer & Wirth, *Beih. Nova Hedwigia* **79:** 552 (1984)).—*Lecidea cyathoides* (Ach.) Ach., *Methodus qua Omnes Detectos Lichenes*: 51 (1803).—*Biatora cyathoides* (Ach.) Oxner, *Flora of Lichens of the Ukraine* **2:** 78 (1968).

Lecidea rivulosa Ach., *Methododus qua Omnes Detectos Lichenes*: 38 (1803); type: Sweden, in saxis et rupibus (H-Ach 273 C—lectotypus [!] in Oberhollenzer & Wirth, *Beih. Nova Hedwigia* **79:** 553 (1984)).—*Biatora rivulosa* (Ach.) Fr., *Kongliga Vetenskaps Academiens Nya Handlingar*: 269 (1822).—*Microlecia rivulosa* (Ach.) Choisy, *Bull. Mens. Soc. Linn. Lyon* **18:** 151 (1949).

Lecidea rivulosa Ach. var. *infuscata* H. Magn., *Kongliga Götheborgska Vetenskaps Samhällets Handlingar, Vetenskskaps Afd.* **29:** 27 (1925); type: Norway, Hordaland: Mosterhavn, Aug. 1910, Havaas, Havaas, *Lich. Norv. Occ.* 43 (UPS—lectotypus [!] in Oberhollenzer & Wirth, *Beih. Nova Hedwigia* **79:** 554 (1984)).

Lecidea subrivulosa Vain., *Acta Soc. Fauna Fl. Fenn.* **57:** 316 (1934); type: Russia [Finlandia]: in Somerikonvuoret in Suursaari v. Hoglandia, in rupe porphyrica, 1875, *Vainio* (TUR-Vainio 24352—holotype [!]).—*Fuscidea subrivulosa* (Vain.) P. James, Poelt & May. Inoue, *Hikobia Supplement* **1:** 179 (1981).—*Fuscidea subrivulosa* (Vain.) P. James, Poelt & V. Wirth, *Biblioth. Lichenol.* **16:** 154 (1981), nom. inval., Art. 41.4 (Melbourne).

Biatora rivulosa b. *corticola* Fr., *Lichenographia Europaea Reformata*: 272 (1831); type: Sweden, Småland: Femsjö, on bark, *E. Fries*: *Exs. Lich. Suec.* no. 39 (1818) (UPS—lectotypus [!] in Inoue, *Hikobia Supplement* **1:** 178 (1981) as "holotypus").—*Fuscidea cyathoides* var. *corticola* (Fr.) Kalb, *Herzogia* **4:** 57 (1976). **Syn. nov.**

Lecidea fagicola Zschacke, *Verhandlungen des Botanischen Vereins der Provinz Brandenburg* **69:** 11 (1927); type: Frankreich, Corsica: Vizzavona, *H. Zschacke* (B—holotypus [lost, see Oberhollenzer & Wirth, *Beih. Nova Hedwigia* **79:** 554 (1984)]; Frankreich, Corsica, Distr. Evissa: Silva Aitone, in valle rivi Aitone, *c.* 1300 m, *Fagicola*, 30 June 1969, *J. Lambinon, Y. Rondon, A. Vězda* (neotype [probably lost] designated by Oberhollenzer & Wirth, in *Beih. Nova Hedwigia* **79:** 554 (1984)).—*Biatorinella fagicola* (Zschacke) Deschâtres & Werner, *B. Soc. Bot. Fr.* **121:** 305 (1974).—*Fuscidea fagicola* (Zschacke) Hafellner & Türk, *Stapfia* **76:** 152 (2001). **Syn. nov.**

Biatora stiriaca A. Massal., *Ricerche sull´ autonomia del licheni crostosi*: 125 (1852); type: Italia, vive sui faggi nelle Stiria, legit. Welwic. (VER—holotype [!]).—*Lecidea stiriaca* (A. Massal.) Jatta, *Sylloge Lichenum Italicorum* **39:** 328 (1900).—*Fuscidea stiriaca* (A. Massal.) Hafellner, *Fritschiana* **33:** 42 (2002). **Syn. nov.**

Lecidea rivulosa var. *sorediata* H. Magn., *Göteborgs Kunglige Vetenskaps- och Vitterhets-Samhälles Handlingar, Ser. 4* **29:** 29 (1925); type: Sweden, Västergötland: par. Frölunda, Näset, on sunny boulder, 24 August 1924, *A. H. Magnusson* 9237 A (UPS, L-763155—lectotype, designated here).—*Fuscidea cyathoides* var. *sorediata* (H. Magn.) Poelt, *Norw. J. Bot.* **25:** 127 (1978). **Syn. nov.**

(Fig. 2A–D)

Thallus crustose, very variable, rimose-cracked to reticulate, delimited, occasionally sorediate; overall colour in saxicolous habitats from light grey to dark grey or brown, in corticolous habitats greyish or brownish green to olive-green. *Areoles* discrete, irregular, convex, highly variable in size, becoming secondarily cracked. *Soralia* rarely present, yellowish, sometimes tinged with brown, bursting from the apices of the areoles. *Prothallus* distinct, dark brown or black visible, ramifying the thallus, often forming mosaics. *Photobiont Apatococcus fuscideae* A. Beck & Zahradn., green, coccoid, globose to broadly ellipsoid.

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Apothecia immersed to sessile, constricted at base, roundish, up to 1·4 mm diam., to 1·9 mm when tuberculate, dark grey-brown to black; margin paler or concolorous with disc, rounded to strongly flexuous; *disc* black, mostly flat. *Epihymenium* brown; *hymenium* pale or faintly brownish; *hypothecium* hyaline. *Asci* clavate, of the *Fuscidea*-type. *Ascospores* simple, colourless, sometimes elliptical when young, bean-shaped when mature, brownish (6·0–)10·0–11·0(–14·5) × (3–)4–5(–7) µm.

Pycnidia abundant, brown, immersed to emergent with a thin thalline rim. *Conidia* bacilliform 3–4 × 1·5–2·0 µm.

Chemistry. Fumarprotocetraric acid (major), protocetraric acid (trace, usually present). Spot tests: K+ orange-yellow, Pd+ rust red, UV−.

Distribution and ecology. *Fuscidea cyathoides* is mainly saxicolous on coarse-grained, nutrient-deficient, siliceous rocks; occasionally it is corticolous on trunks and branches of *Acer*, *Alnus*, *Betula*, *Castanea*, *Fagus*, *Ilex* (B. Coppins, pers. comm.), *Quercus* and *Sorbus*.

The typical form (saxicolous esorediate) of *Fuscidea cyathoides* has been reported from Austria (Hafellner & Türk 2001), Belgium and Luxembourg (Diederich & Sérusiaux 2000), the British Isles (Hawksworth *et al.* 1980; Gilbert *et al.* 2009), China (Wei 1991), Croatia (Partl 2009), Czech Republic (Vězda & Liška 1999), Denmark (Søchting & Alstrup 2008), Estonia (Randlane & Saag 1999), Finland (Nordin *et al.* 2010), France (Roux 2012), Germany (Wirth 1987), Greenland (Thomson 1997), Italy (Puntillo 1996), Morocco (Egea 1996), Norway (Nordin *et al.* 2010), Poland (Fałtynowicz 1993), Portugal (van den Boom & Giralt 1999; Llimona & Hladun 2001), Romania (Ciurchea 1998), Russia (Urbanavichus & Andreev 2010), Serbia (Savić & Tibell 2006), Slovakia (Pišút *et al.* 1998), Slovenia (Suppan *et al.* 2000), Spain (Llimona & Hladun 2001), Sweden (Nordin *et al.* 2010), Switzerland (Clerc 2004), Turkey (Yildiz *et al.* 2002) and Ukraine (Kondratyuk *et al.* 2010). The saxicolous sorediate form is known from the British Isles (Hawksworth *et al.* 1980), Denmark (Søchting & Alstrup 2008), France (Roux 2012), Poland (Fałtynowicz 1993), Norway (Poelt & Buschardt 1978; and material to be published), and Sweden (Nordin *et al.* 2010) (see Fig. 4). The records from North America and Tasmania (Richardson & Richardson 1982; Egan 1987) were later rejected as they were based on misidentifications (Kantvilas 2001; Fryday 2008).

The corticolous form has been reported from Albania (Svoboda *et al.* 2012), Austria (Hafellner & Türk 2001), Belgium and Luxembourg (Diederich & Sérusiaux 2000), Bosnia-Herzegovina (Christensen 1994), the British Isles (Gilbert *et al.* 2009; B. Coppins, pers. comm.), Croatia (Partl 2009), Denmark (Søchting & Alstrup 2008), France (Roux 2012), Germany (Cezanne *et al.* 2004), Italy (Tretiach & Nimis 1994), Poland (Faltynowicz 1993), Portugal (van den Boom & Giralt 1999; Llimona & Hladun 2001), Montenegro (Knežević & Mayrhofer 2009), Norway (Nordin *et al.* 2010), Russia (Urbanavichus & Andreev 2010), Slovakia (Bielczyk *et al.* 2004), Slovenia (Suppan *et al.* 2000), Spain (Llimona & Hladun 2001), Sweden (Nordin *et al.* 2010), Switzerland (Clerc 2004) and Ukraine (Coppins *et al.* 2005) (see Fig. 5), as well as from Taiwan (Aptroot & Sparrius 2003).

Specimens examined (*saxicolous, esorediate*). **Czech Republic:** *Central Bohemia*: Distr. Beroun, Brdy Mts, Neřežín - Malá Víska, upper part of Krkavčina Mt., forested (*Picea*, *Betula*, *Larix* etc.) rocky hill, 49°45'55"N, 13°53'36"E, alt. 570–600 m, on siliceous boulder, 2012, *J. Malíček* 4916; Distr. Beroun, Brdy Mts, Neřežín, Jindřichova skála Mt., 1 km SE of Malá Víska, rock with E-exposed boulder scree, 49°46'05"N, 13°52'55"E, alt. 550–580 m, on siliceous boulder, 2012, *J. Malíček* 4928. *Western Bohemia*: Distr. Rokycany, Brdy Mts, Strašice - Lipovsko Mts (651 m), 3 km SE of town, rock with boulder scree on S-exposed slope, 49°42'53"N, 13°47'11"E, alt. 620–640 m, on siliceous rock, 8 xi 2012, *J. Malíček* (4866). *Moravský kras*: Mohelno, 49°06'08·80"N, 16°11'05·20"E, alt. 344 m, in deciduous forest on shaded siliceous rock, 2011, *J. Halda* 662/2011 (JHP/13294).—**Norway:** *Hordaland*: Fjell, Sotra, SW of Landro, Ingholet, 100 m from cemetery, 60°25'6"N, 4°58'31·2"E, alt. 35–45 m, saxicolous on SW-facing vertical siliceous stone wall, 2011, *M. Zahradníková* MZ 30 (BG-L-96933); Fjell, Sotra, W of the road between Skålvik and Sekkingstad, S of road jct to Algrøyna, 60°20'06·6"N, 4°59'42·0"E, alt. 40–70 m,

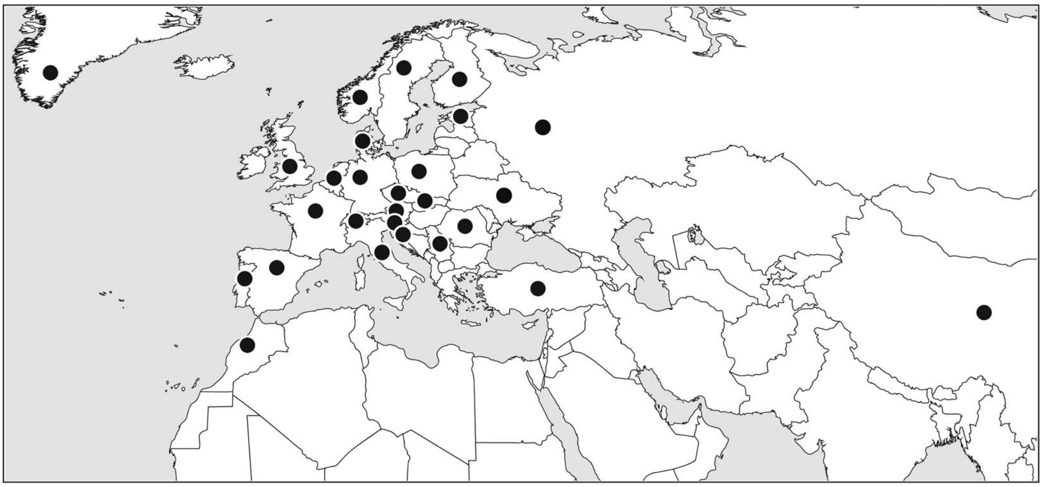

FIG. 4. Distribution of saxicolous, esorediate and sorediate forms of *Fuscidea cyathoides* based on the material examined and the literature.

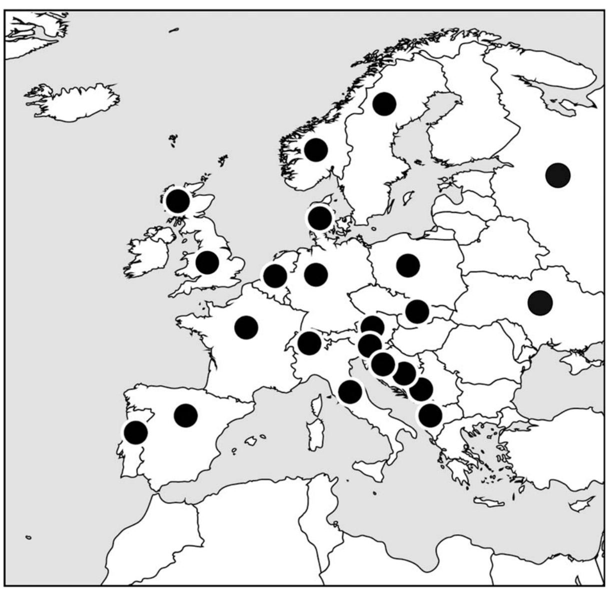

FIG. 5. Distribution of corticolous forms of *Fuscidea cyathoides* based on the material examined and the literature.

saxicolous on siliceous rock wall in coastal heath, 2010, *M. Zahradníková* MZ 5 (BG-L-96931). *Nordland*: Nesna, Tomma Island, Valhaugen, 66°17'44·63"N, 12°49'15·31"E, alt. 35 m, saxicolous on bedrock in open, treeless situation, 2016, *T. Tønsberg* 46572 *& A. Botnen* (BG-L-99904).—**Ireland:** *Co. Kerry*: Macgillycuddy's Reeks, Gaddagh River valley NE of Carrauntoohil (Corrán Tuathail) [1039 m], *c.* 14 km WSW of Killarney, 52°00'50·0"N, 9°42'49·0"W, alt. 225 m, on boulders near the brook, 2003, *J. Halda & Z. Palice* 7903.—**Great Britain:** *Scotland*: **V.C. 92,** South Aberdeenshire: Braemar, Invercauld Estate, Craig Leek, NE-E facing crags, partly limestone, 57°01'24·0"N, 3°39'60·0"W, alt. 425 m, on siliceous rock in pasture below crags, 2005, *A. M. Fryday* 9012 (MSC0050557).—**Sweden:** *Skåne*: S. Mellby, Stenshuvud, på block i strandskogen, 1987, *S. Ekman* 265 (LD–1132977).

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Specimens examined (*corticolous*): **Norway:** *Rogaland*: Forsand, N side of Mt. Uburen by Forsandåna, alt. 60–80 m, on *Betula pubescens* in boulder field, 29 viii 2001, *J. I. Johnsen* (BG-L-89616); Sokndal, S of Årstad, alt. 60–80 m, on *Betula pubescens*, 25 viii 2010, *J. I. Johnsen* (BG-L-89638).—**Slovakia:** *Bukovské Mts*: Nová Sedlica, protected area Stužica, valley of Stužická Rieka, natural deciduous forest, 49°04'23"N, 22°32'25"E, alt. 608–700 m, on bark of *Fagus sylvatica*, 2013, *J. Malíček & J. Vondrák* 6488; Nová Sedlica, beech forest on the crest Čiertáž - Hrúbky - Kremenec, 49°05'34·2"N, 22°22°31'36·6"E, alt. 1110 m, on bark of *Fagus*, 2004, *Z. Palice & J. Šárová* 9629; Nová Sedlica, protected area Stužica, 49°4'24"N, 22°32'35"E, alt. 600–1200 m, on bark of *Acer pseudoplatanus*, 2013, *J. Vondrák & J. Malíček* 11411; Ulič, Nová Sedlica, protected area Stužica, 49°04'24"N, 22°32'35"E, alt. 600–1200 m, on bark of *Fagus sylvatica*, 2013, *J. Vondrák & J. Malíček* 11397; Ulič, Nová Sedlica, protected area Stužica, 49°04'24"N, 22°32'35"E, alt. 1000–1200 m, on bark of *Fagus sylvatica*, 2013, *J. Vondrák & J. Malíček* 11476. *Muránska planina*: Nová Maša, alder stand along unnamed stream in parallel with Rácov brook, 48°48'45–50"N, 20°01'45"E, alt. 770–780 m, on bark of *Alnus incana*, 1999, *A. Guttová, V. Orthová & Z. Palice* 4642.—**Sweden:** *Skåne*: Vittsjö, N end of Vittsjö, on roadside *Fagus* near bridge, 1987, *U. Arup & S. Ekman* L035 (LD–1157864); N Åkarp, 2·5 km S Bjärnum, *c.* 500–700 m SSW of Lake Agnsjön, W of road, on *Fagus*, 1987, *U. Arup & S. Ekman* L036 (LD–1157444); Tåssjö par., Hålskutt, 1988, *U. Arup & S. Ekman* L130 (LD–1131717); S. Mellby, Stenshuvud, på rönn i Ö-branten, 1987, *S. Ekman* L146 (LD–1133157).

Specimens examined (*saxicolous, sorediate*): **Norway:** *Nordland*: Nesna, Tomma, Valhaugen, 66°17'44·77"N, 12°49'15·31"E, alt. 35–40 m, saxicolous in shallow crevice (with seeping water) in bedrock in open, treeless situation, 2016, *T. Tønsberg* 46570 (BG-L-99902).

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Supplementary material

For supplementary material accompanying this paper visit https://doi.org/10.1017/10.1017/S0024282917000524

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