III

Paper III

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

Martina Zahradníková[1], Tor Tønsberg[1] and Heidi Lie Andersen[1,2]

M. Zahradníková (corresponding author) and T. Tønsberg (co-corresponding author): [1]Department of Natural History, University Museum, University of Bergen, Allégaten 41, P.O. Box 7800, N-5020 Bergen, Norway.

[2]The Arboretum and Botanical Gardens, Department of Natural History, University Museum, University of Bergen, Allégaten 41, P.O. Box 7800, N-5020 Bergen, Norway.

Emails: Martina.Zahradnikova@uib.no, Tor.Tonsberg@uib.no

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*, molecular phylogeny, infraspecific taxonomy, lichen varieties, secondary chemistry.

Introduction

Substrate 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, V. Wirth & Vězda, 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 Britain and Ireland, species of *Fuscidea* inhabit rock or, more rarely, bark, occasionally wood, and 10 of the 11 species are either exclusively saxicolous (8 spp.) or exclusively corticolous/lignicolous (2 spp.), and only *F. cyathoides* (Ach.) V. Wirth & Vězda is capable of inhabiting both rock and bark (Gilbert *et al.* 2009). Substrate ecology and the presence/absence of soredia have been suggested as important characters for formal recognition of taxonomic entities at the species level (Hafellner & Türk, 2001; Hafellner, 2002) and the varietal level (Fries, 1831; Magnusson, 1925; Zschacke, 1927) (see Table 1).

Magnusson (1925), for example, 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). None of the *F. cyathoides* forms is longer 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, while var. *cyathoides* is grey when dry and umber-brown when wet. 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. Santesson *et al.* 2004; Inoue 1981) recognize this taxon as *F. cyathoides* var. *corticola*.

Zschacke (1927) recognized the absence of black prothallus, the larger and flatter thallus as well as the larger apothecia as 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 is treated as a synonym of var. *cyathoides* by Magnusson (1925) (as *Lecidea rivulosa* var. *corticola* (Fr.) Jatta) and by Vainio (1934) (as *L. rivulosa* f. *corticola* (Fr.) Vain), and 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 byFerencová *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 *Mycoblastus 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 morphology (esorediate, richly fertile *vs*. sorediate, sterile or sparingly fertile) and chemistry (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 was provided by BG, HO, MSC, LD, UPS, TUR, and H-Ach, as well as from private collections. As var. *sorediata* is scarce in Europe, we only managed to obtain one fresh specimen.

Morphology

To determine morphological differences between varieties, the anatomy and morphology of the apothecia and thalli were examined by light microscopy on hand-cut sections mounted in water with 10% KOH using a Carl Zeiss Axiskoskop 2 microscope. 20 specimens of *F. cyathoides*, including all the three varieties, were investigated. The following morphological characters were studied: overall diameter of the apothecia and the areoles, height of the epihymenium and the hymenium, length and width of the ascospores, and the colour of the thalli (Table 2). The ratio between length and width of spores was calculated. The 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); the first two axes were displayed as a scatterplot.

Secondary chemical compounds

Lichen substances were analysed 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 analysed 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 conducted a concatenate 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: 1x Buffer II GeneAmp® 10x 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) with the following programs: mtSSU: initial denaturation at 94°C for 5 min, touchdown of six cycles: 94°C for 30s, 62–56°C for 30 s, and 72°C in 1 min 45 s, followed by 34 cycles of 94°C for 30 s, 56°C for 30 s, 72°C in 1 min 45 s, and a final elongation at 72°C for 10 min, LSU and ITS: as for mtSSU, 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 analyser (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.) Schrader 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). For mtSSU, the model GTR+G was selected, GTR+I+G for LSU, SYM+G for ITS1, K80+I for 5.8S, HKY+G for ITS2, and GTR+I+G for the concatenate 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 neighbor-joining model with a maximum likelihood distance (e.g., Reeb *et al.* 2004). Bootstrap scores were calculated using 2,000 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 using MrBayes version 3.2.1 (Ronquist & Huelsenbeck 2003) to sample trees using a Markov 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 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 of trees) 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 equal to or above 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, 1,000 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 equal or above 70%.

Results

Morphological examination

The morphological examination (Table 2) showed that only corticolous specimens had greenish to green thalli. The colour of saxicolous specimens varied from grey to brown.

Corticolous specimens more frequently developed tuberculate apothecia (i.e., 90% of examined specimens) than saxicolous ones (i.e., 20% of examined specimens). Var. *sorediata*, represented by only one specimen, had smaller and fewer apothecia (see Table 2).

The ascospores of all the three varieties were bean-shaped. However, those of the corticolous specimens were narrower (mean 4.53 ± 1.82 µm) than saxicolous ones (mean 4.79 ± 1.21 µm), but were similar in the mean of spores 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% 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 height of hymenium and epihymenium, and width of ascospores, were both 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 of different genes, they were combined and the final aligned sequence matrix comprised 26 taxa with 2,187 characters of which 1,618 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. 1. The average −ln likelihood of the tree was 8,081.83 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.

A heuristic search using the parsimony criterion resulted in 100 MP trees of length 1,041 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 = 8,104.6499). 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 (BG-L-96931), G. Thor 18066, G. Thor 18061 and R. Haugan 1389) within the *F. cyathoides* group. All incongruences are marked with a circle in Fig. 2.

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 into the varieties of corticolous and saxicolous specimens was discovered. The specimens from Central Europe, i.e. the Czech Republic and Slovakia, formed a group separate from northwest 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 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 nor genetic differences. The observed variation between these apothecia types is not significant (see Figs. 1 and 2), confirming the statement 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 the bean-shaped spores and the tuberculate apothecia to be 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 as 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**

Beiträge zur naturkundlichen Forschung in Südwestdeutschland **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, *Beihefte zur 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, *Beihefte zur Nova Hedwigia* **79**: 553 (1984). – *Biatora rivulosa* (Ach.) Fr., *Kongliga Vetenskaps Academiens Nya Handlingar*: 269 (1822). – *Microlecia rivulosa* (Ach.) Choisy, *Bulletin mensuel de la Société Linnéenne de 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, *Beihefte zur Nova Hedwigia* **79**: 554 (1984)).

– *Lecidea subrivulosa* Vain., *Acta Societiatis pro Fauna et Flora Fennica* **57**: 316 (1934); type: Russia [Finlandia]: in Somerikonvuoret in Suursaari v. Hoglandia, in rupe porphyrica, 1875, Vainio (TUR-Vainio 24352 – holotypus [!]). – *Fuscidea subrivulosa* (Vain.) P. James, Poelt & May. Inoue, *Hikobia Supplement* **1**: 179 (1981). – *Fuscidea subrivulosa* (Vain.) P. James, Poelt & V. Wirth, *Bibliotheca Lichenologica* **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. n. 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, *Beihefte zur 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 (neotypus [probably lost] designated by Oberhollenzer & Wirth, in *Beihefte zur Nova Hedwigia* **79**: 554 (1984)). – *Biatorinella fagicola* (Zschacke) Deschâtres & Werner, *Bulletin de la Société Botanique de France* **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 – holotypus [!]). – *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 – lectotypus, designated here). – *Fuscidea cyathoides* var. *sorediata* (H. Magn.) Poelt, *Norwegian Journal of Botany* **25**: 127 (1978). **Syn. nov.**

(Figs 4A–D)

Thallus crustose, very variable, rimose-cracked, to reticulate, delimited, occasionally sorediate; over-all 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* green, coccoid, globose to broadly ellipsoid. *Apothecia* immersed to sessile, constricted at base, roundish, up to 1.4 mm in diam., to 1.9 mm when tuberculate, dark grey-brown to black; margin paler or concolorous with disc, rounded to strongly flexuouse; 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–)10–11(–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 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*, *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 presently published material, and Sweden (Nordin *et al.* 2010) (see Fig. 5). 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), 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), W. Scotland (Gilbert *et al.* 2009), Sweden (Nordin *et al.* 2010), Switzerland (Clerc 2004), Ukraine (Coppins *et al.* 2005) (see Fig. 6), 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, 17.11.2012, *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, 17.11.2012, *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, 8.11.2012, *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, 7.5.2011, *J. Halda* 662/2011 (JHP/13294). **Norway**: *Hordaland*, Fjell, Sotra, SW from 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, 20.3.2011, *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, saxicolous on siliceous rock wall in coastal heath, 15.11.2010, *M. Zahradníková* MZ 5 (BG-L-96931); Nordland, Nesna, Island Tomma, Valhaugen, 66°17'44.63"N, 12°49'15.31", alt. 35 m, saxicolous on bedrock in open, treeless situation, 20.6.2016, *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, 4.9.2003, *J. Halda & Z. Palice* 7903. **U.K., Scotland**: *South Aberdeenshire*: **V.C. 92,** 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, 24.5.2005, *A.M. Fryday* 9012 (MSC0050557).

Sweden: *Skåne*: S. Mellby, Stenshuvud, på block i strandskogen, 13.4.1987, *S. Ekman* 265 (LD–1132977).

Specimens examined (corticolous): **Norway**: *Rogaland*, Forsand, N side of Mt Uburen by Forsandåna, alt. 60–80 m, on *Betula pubescens* in boulder field, 29.8.2001, *J.I. Johnsen* (BG-L-89616); Sokndal, S of Årstad, alt. 60–80 m, on *Betula pubescens*, 25.8.2010, *J.I. Johnsen* (BG-L-89638). **Slovakia**: *Bukovské Mts*: Nová Sedlica - protected area Stužica, valley of Stužická rieka river, natural deciduous forest, 49°04’23”N, 22°32’25”E, alt. 608–700 m, on bark of *Fagus sylvatica*, 24.10.2013, *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*, 8.7.2004, *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*, 26.10.2013, *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*, 26.10.2013, *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*, 26.10.2013, *J. Vondrák & J. Malíček* 11476; *Muránska planina*: Nová Maša: alder stand along unnamed stream in parallel stream with Rácov Brook), 48°48’45–50”N, 20°01’45”E, alt. 770–780 m, on bark of *Alnus incana*, 17.10.1999, *A. Guttová, V. Orthová & Z. Palice* 4642. **Sweden**: *Sk. Vittsjö*: N end of Vittsjö, on roadside *Fagus* near bridge, 29.09.1987, *U. Arup & S. Ekman* L035 (LD–1157864); *Sk. N. Åkarp*: 2.5 km S Bjärnum, c. 500–700 m SSW of Lake Agnsjön, W of road, on *Fagus*, 29.9.1987, *U. Arup & S. Ekman* L036 (LD–1157444); *Skåne*: Tåssjö par., Hålskutt, 22.5.1988, *U. Arup & S. Ekman* L130 (LD–1131717); S. Mellby, Stenshuvud, på rönn i Ö-branten, 28.4.1987, *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, 20.6.2016, *T. Tønsberg* 46570 (BG-L-99902).

Acknowledgements

We thank the curators of HO, LD, UPS, H-Ach, and MSC for loan of material, Zdeněk Palice, Jan Vondrák, Jiří Malíček (all from the Academy of Science of the Czech Republic) and Josef Halda (Museum and Gallery of Orlické hory Mts., Czech Republic) for providing fresh material from Central Europe, M.R.D. Seaward (University of Bradford, England) for language improvements, Louise Lindblom, Beate Helle, and Per M. Jørgensen (all University of Bergen, Norway) for technical help with the molecular work (LL), technical help with the preparation of the distribution maps (BH) and help with botanical nomenclature (PMJ), respectively, and Kim Abel (Røyken, Norway) for taking the photos. The project was funded by the University Museum of Bergen, University of Bergen, including grants from the Grolle Olsen fund. This work is a part of the doctoral thesis of MZ. The molecular work was done in the Biodiversity Laboratories at University of Bergen.

Appendix A: Supplementary material

Supplementary data associated with this article can be found in the online version at http://###

References

Acharius, E. (1798) *Lichenographiae Suecicae Prodromus*: 62. Lincopiae, D.G. Björn.

Aptroot, A. & Sparrius, L. B. (2003) New microlichens from Taiwan. *Fungal Diversity* **14**: 1–50.

Bielczyk, U., Lackovičová, A., Farkas, E., Lőkös L., Breuss, O. & Kondratyuk, S. Ya. (2004) *Checklist of lichens of the Western Carpathians*. Kraków: W. Szafer Institute of Botany, Polish Academy of Sciences.

Bylin, A., Arnerup, J., Hogberg, N. & Thor, G. (2007) A phylogenetic study of Fuscideaceae using mtSSU rDNA. *Bibliotheca Lichenologica* **96**: 49–60.

Cezanne, R., Eichler, M. & Wirth, V. (2004) Flechten-Exkursion in die Umgebung von Bad Wildungen 04./05. 10. 2002. *Hessische Floristische Briefe* **53**: 17–28.

Christensen, S. (1994) Lichens from Bosnia-Herzegovina. *Nova Hedwigia* **59**: 441–453.

Ciurchea, D. (1998) *Catalog of lichens in Romania*. Available online at http://www.bgbm.fu-berlin.de/sipman/Zschackia/Rumania/index.htm.

Clerc, P. (2004) Les champignons lichénisés de Suisse - Catalogue bibliographie complété par des données sur la distribution et l'écologie des espèces. *Cryptogamica Helvetica* **19**: 1–320. Available online at http://www.ville-ge.ch/musinfo/bd/cjb/cataloguelichen/recherche.

Coppins, B. J., Kondratyuk, S. Y., Khodosovtsev, A. Y., Zelenko, S. D. & Wolseley, P. A. (2005) Contribution to lichen flora of Ukrainian Carpathians. *Chornomors' kyi Botanical Journal* **1**: 5–23.

Culberson, C. F. (1972) Improved conditions and new data for identification of lichen products by standardized thin-layer chromatographic method. *Journal of Chromatography* **72**: 113–125.

Culberson, C. F., Culberson, W. L. & Johnson, A. (1981) A standardized TLC analysis of β-orcinol depsidones. *Bryologist* **84**: 16–29.

Culberson, C. F. & Kristinsson, H.–D. (1970) A standardized method for the identification of lichen products. *Journal of Chromatography* **46**: 85–93.

Davydov, E. A., Peršoh, D. & Rambold, G. (2010) The systematic position of *Lasallia caroliniana* (Tuck.) Davydov, Peršoh & Rambold comb. nova and considerations on the generic concept of *Lasallia* (Umbilicariaceae, Ascomycota). *Mycological Progress* **9**: 261–266.

Diederich, P. & Sérusiaux, E. (2000) *The Lichens and Lichenicolous Fungi of Belgium and Luxembourg*. An Annotated Checklist. Musée National d'Histoire naturelle, Luxembourg, pp. 1–208.

Egan, R. S. (1987) A fifth checklist of the lichen-forming, lichenicolous and allied fungi of the continental United States and Canada. *Bryologist* 90: 77–173.

Egea, J. M. (1996) Catalogue of lichenized and lichenicolous fungi of Morocco. *Bocconea* **6**: 52.

Fahselt, D. (1981) Lichen products of *Cladonia stellaris* and *Cladonia rangiferina* maintained under artificial conditions. *Lichenologist* **13**: 87–91.

Fałtynowicz, W. (1993) A checklist of Polish lichen forming and lichenicolous fungi including parasitic and saprophytic fungi occurring on lichens. *Polish Botanical Studies* **6**: 1–65.

Ferencová, Z., Del Prado, R., Pérez-Vargas, I., Hernández-Padrón, C. & Crespo, A. (2010) A discussion about reproductive modes of *Pseudevernia furfuracea* based on phylogenetic data. *Lichenologist* **42**: 449–460.

Fries, E. (1831) *Lichenographia Europaea Reformata*: Lund.

Fryday, A. M. (2008) The genus *Fuscidea* (Fuscideaceae, lichenized Ascomycota) in North America. *Lichenologist* **40**: 295–328.

Gardes, M. & Bruns, T. D. (1993) ITS primers with enhanced specificity for basidiomycetes – application to the identification of mycorrhizae and rusts. *Molecular Ecology* **2**: 113–118.

Gilbert, O. L., Purvis, O. W., Skjoddal, L. H. & Tønsberg, T. (2009) *Fuscidea* V.Wirth & Vězda (1972). In *The Lichens of the Great Britain and Ireland* (C. W. Smith, A. Aptroot, B. J. Coppins, A. Fletcher, O. L. Gilbert, P. W. James & P. A. Wolseley, eds): 407–411. British Lichen Society: London.

Hafellner, J. (2002) Ein Beitrag zur Diversität von lichenisierten und lichenicolen Pilzen im Gebiet der Gleinalpe (Steiermark, Österreich). *Fritschiana* **33**: 33–51.

Hafellner, J. & Türk, R. (2001) Die lichenisierten Pilze Österreichs – eine Checkliste der bisher nachgewiesenen Arten mit Verbreitungsangaben. *Stapfia* **76**: 1–167.

Hawksworth, D. L., James, P. W. & Coppins, B. J. (1980) Checklist of British lichen-forming, lichenicolous and allied fungi. *Lichenologist* **12**: 1–115.

Huelsenbeck, J. P. & Crandall, K. A. (1997) Phylogeny estimation and hypothesis testing using maximum likelihood. *Annual Review of Ecology and Systematics* **28**: 437–466.

Inoue, M. (1981) A taxonomic study on the Japanese species of *Fuscidea* (Lichens). *Hikobia Supplement* **1**: 161–176.

Kalb, K. (1976) Flechtenfunde aus Korsika. *Herzogia* **4**: 55–63.

Kantvilas, G. (2001) The lichen family Fuscideaceae in Tasmania. *Bibliotheca Lichenologica* **78**: 169–192.

Knežević, B. & Mayrhofer, H. (2009) Catalogue of the Lichenized and Lichenicolous Fungi of Montenegro. *Phyton* **48**: 283–328.

Kondratyuk, S. Y., Dymytrova, L. V. & Nadyeina, O. V. (2010) The third checklist of lichen-forming and allied fungi of Ukraine. In *Flora Lišajnikiv Ukraini Vol. 2, part 3* (S. Y. Kondratyuk & O. G. Roms, eds): 446–486. Kyiv: Naukova dumka.

Kroken, S. & Taylor, J. W. (2001) A gene genealogical approach to recognize phylogenetic species boundaries in the lichenized fungus *Letharia*. *Mycologia* **93**: 38–53.

Llimona, X. & Hladun, N. L. (2001) Checklist of the lichens and lichenicolous fungi of the Iberian Peninsula and Balearic Islands. *Bocconea* **14**: 153.

Magnusson, A. H. (1925) Studies in the Rivulosa-group of the genus *Lecidea*. *Göteborgs Kungliga Vetenskaps–och Vitterhets–Samhälles Handlingar* **22**: 1–50.

Massalongo, A. (1852) Licheni crostosi e materiali. *Ricerche sull´ autonomia del licheni crostosi*. Verona.

Menlove, J. E. (1974). Thin-layer chromatography for the identification of lichen substances. *British Lichen Society Bulletin* **34**: 3–5.

Nordin, A., Moberg, R., Tønsberg, T., Vitikainen, O., Dalsätt, Å., Myrdal, M. & Ekman, S. (2010) *Santesson´s Checklist of Fennoscandian Lichen-forming and Lichenicolous fungi*. Uppsala: Museum of Evolution, Uppsala University.

Oberhollenzer, H. & Wirth, V. (1984) Beitrage zur Revision der Flechtengattung *Fuscidea*. *Beihefte zur Nova Hedwigia* **79**: 562–566.

Partl, A. (2009) Checklist of lichens and lichenicolous fungi of Croatia. University of Osijek, Croatia, Preliminary version 1 March 2009.

Pišút, I., Guttová, A., Lackovičová, A. & Lisická, E. (1998) Lichenizované huby (lišajníky). In *Zoznam nižších a vyšších rastlín Slovenska* (*Checklist of nonvascular and vascular plants of Slovakia*) (K. Marhold & F. Hindák, eds): 229–295. Veda, Bratislava.

Poelt, J. (1970) Das Konzept der Artenpaare bei den Flechten. *Berichte der Deutschen Botanischen Gesellschaft* **4**: 187–198.

Poelt, J. (1972) Die taxonomische Behandlung von Artenpaaren bei den Flechten. *Botaniska Notiser* **125**: 77–81.

Poelt, J. & Buschardt, A. (1978) Über einige bemerkenswerte Flechten aus Norwegen. *Norwegian Journal of Botany* **25**: 123–135.

Posada, D. (2008) jModelTest: phylogenetic model averaging. *Molecular Biology and Evolution* **25**: 1253–1256.

Puntillo, D. (1996) *I Licheni di Calabria.* Museo Regionale di Scienze Naturali Torino, Monografie 22.

Randlane, T. & Saag, A. (eds) (1999) Second checklist of lichenized, lichenicolous and allied fungi of Estonia. *Folia Cryptogamica Estonica* **35**: 1–132.

Reeb, V., Lutzoni, F. & Roux, C. (2004) Contribution of RPB2 to multilocus phylogenetic studies of the euascomycetes (Pezizomycotina, Fungi) with special emphasis on the lichen-forming Acarosporaceae and evolution of polyspory. *Molecular Phylogenetics and Evolution* **32**: 1036–1060.

Resl, P., Mayrhofer, H., Clayden, S. R., Spribille, T., Thor, G., Tønsberg, T. & Sheard, J. W. (2016) Morphological, chemical and species delimitation analyses provide new taxonomic insights into two groups of *Rinodina*. *Lichenologist* **48**: 469–488.

Richardson, R. M. & Richardson, D. H. S. (1982) A systematic list with distributions of the lichen species of Western Australia, based on collections in the Western Australian Herbarium. *Western Australian Herbarium Research Notes* **7**: 17–29.

Ronquist, F. & Huelsenbeck, J. P. (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**: 1572–1574.

Roux, C. (2012) Liste des lichens et champignons lichénicoles de France. *Bulletin de la Société linnéenne de Provence*, *n° spécial* **16**: 16. Available online at http://lichenologue.org/fr/index.php.

Santesson, R., Moberg, R., Nordin, A., Tønsberg, T. & Vitikainen, O. (2004) Lichen-forming and lichenicolous fungi of Fennoscandia. Museum of Evolution, Uppsala University.

Savić, S. & Tibell, L. (2006) Checklist of the lichens of Serbia. *Mycologia Balcanica* **3**: 187–215.

Søchting, U. & Alstrup, V. (2008) *Danish Lichen Checklist*: 14. Faculty of Science, University of Copenhagen, Copenhagen.

Solheim H., Torp, T. B. & Hietala, A. M. (2013) Characterization of the ascomycetes *Therrya fuckelii* and *T. pini* fruiting on Scots pine branches in Nordic countries. *Mycological Progress* **12**: 37–44.

Spribille, T., Klug, B. & Mayrhofer, H. (2011) A phylogenetic analysis of the boreal lichen *Mycoblastus sanguinarius* (Mycoblastaceae, lichenized Ascomycota) reveals cryptic clades correlated with fatty acid profiles. *Molecular Phylogenetics and Evolution* **59**: 603–614.

Suppan, U., Prügger, J. & Mayrhofer, H. (2000) Catalogue of the lichenized and lichenicolous fungi of Slovenia. *Bibliotheca Lichenologica* **76**: 1–215.

Svoboda, D., Bouda, F., Malíček, J. & Hafellner, J. (2012) A contribution to the knowledge of lichenized and lichenicolous fungi in Albania. *Herzogia* **25**: 146–165.

Swofford, D. L. (2002) *PAUP*: Phylogenetic analysis using parsimony (and Other Methods) 4.0 beta*. Sinauer Associates, Sunderland, Mass., USA.

Tehler, A., Ertz, D. & Irestedt, M. (2013) The genus *Dirina* (Roccellaceae, Arthoniales) revisited. *Lichenologist* **45**: 427–476.

Ter Braak, C. J. F. & Šmilauer, P. (2012) *Canoco reference manual and user's guide: software for ordination (version 50) microcomputer power*. Ithaca, NY, USA.

Thomson, J. W. (1997) *American Arctic Lichens. 2. The Microlichens*. Madison, Wisconsin: The University of Wisconsin Press.

Tretiach, M. & Nimis, P. L. (1994) Una collezione di licheni dalle Foreste Casentinesi (Camaldoli, Toscana). *Notiziario della Società Lichenologica Italiana* **7**: 25–32.

Tønsberg, T. (1992) The sorediate and isidiate, corticolous crustose lichens in Norway. *Sommerfeltia* **14**: 1–331.

Urbanavichus, G. P. & Andreev, M. (2010) *A checklist of the lichen flora of Russia*. Saint Petersburg: Nauka.

Vainio, E. A. (1934) Lichenographia Fennica IV – Lecideales II. *Acta Societatis pro Fauna et flora Fennica* **57**: 314–315.

Van den Boom, P. P. G. & Giralt, M. (1999) Contribution to the flora of Portugal, lichens and lichenicolous fungi II. *Nova Hedwigia* **68**: 183–196.

Vězda, A. & Liška, J. (1999) *Katalog lišejníků České republiky* (*A catalogue of lichens of the Czech Republic*). Průhonice: Institute of Botany, Academy of Science of the Czech Republic.

Wei, J.-C. (1991) *An Enumeration of Lichens in China*. Beijing: International Academic Publishers.

Vilgalys, R. & Hester, M. (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. *Journal of Bacteriology* **172**: 4238–4246.

White, T. J., Bruns, T., Lee, S. & Taylor, J. (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In *PCR Protocols: A Guide to Methods and Applications* (M. A. Innis, D. H. Gelfand, J. J. Sninsky & T. J. White, eds): 315–322. San Diego: Academic Press.

Wirth, V. (1987) *Die Flechten Baden-Württembergs*. Stuttgart: Eugen Ulmer.

Wirth, V. & Vĕzda, A. (1972) Zur Systematik der *Lecidea cyathoides*-Gruppe. *Beiträge zur naturkundlichen Forschung in Südwestdeutschland* **31**: 91–92.

Yildiz, A., John, V. & Yurdakul, E. (2002) Lichens from the Çangal Mountains (Sinop, Turkey). *Cryptogamie Mycologie* **23**: 81–88.

Zoller, S., Scheidegger, C. & Sperisen, C. (1999). PCR primers for the amplification of mitochondrial small subunit ribosomal DNA of lichen-forming ascomycetes. *Lichenologist* **31**: 511–516.

Zschacke, H. (1927) *Korsische Flechten, gesammelt in den Jahren 1914–16*. Berlin: Botanischer Verein der Provinz Brandenburg.

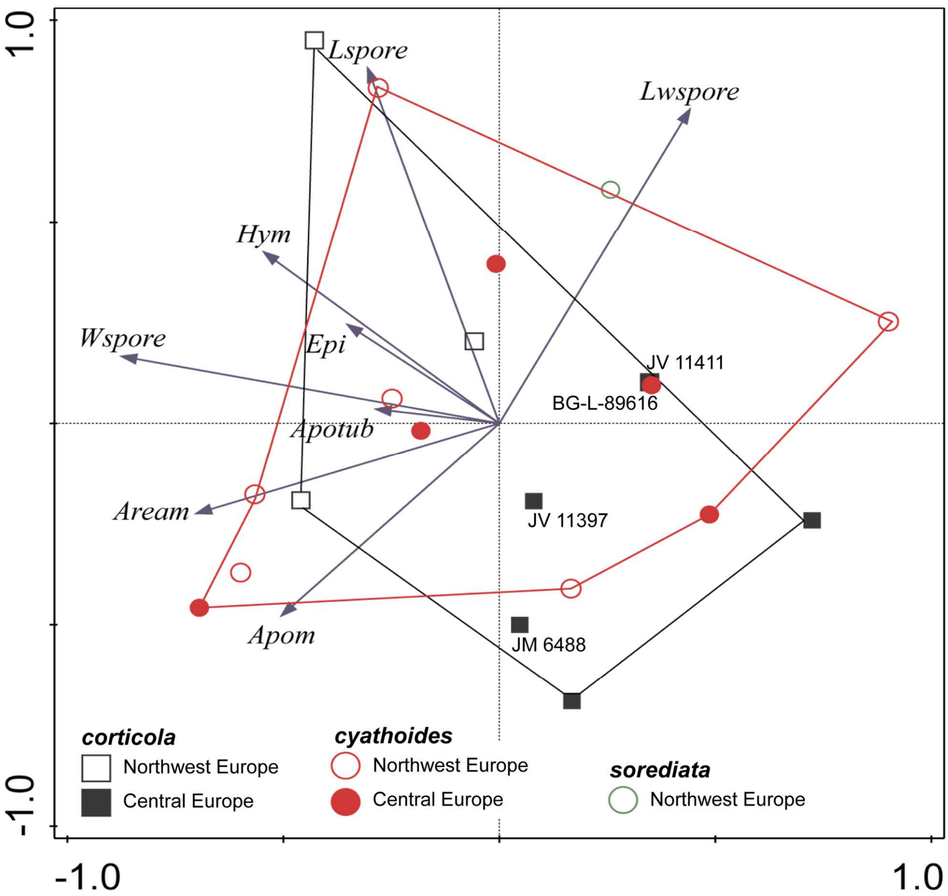

Figure 1. Biplot of the two first principal component axes, showing morphological variation of the studied specimens of *F. cyathoides*. Abbreviations of the variables: *Apom* = diam. (mm) of apothecia; *Apotub* = diam. (mm) of tuberculate apothecia; *Aream* = diam. (mm) of areolum; *Hym* = width (μm) of hymenium; *Epi* = width (μm) of epihymenium; *Lspore* = length (μm) of ascospores; *Wspore* = width (μm) of ascospores; *Lwspore* = ratio of *wspore* : *lspore*.

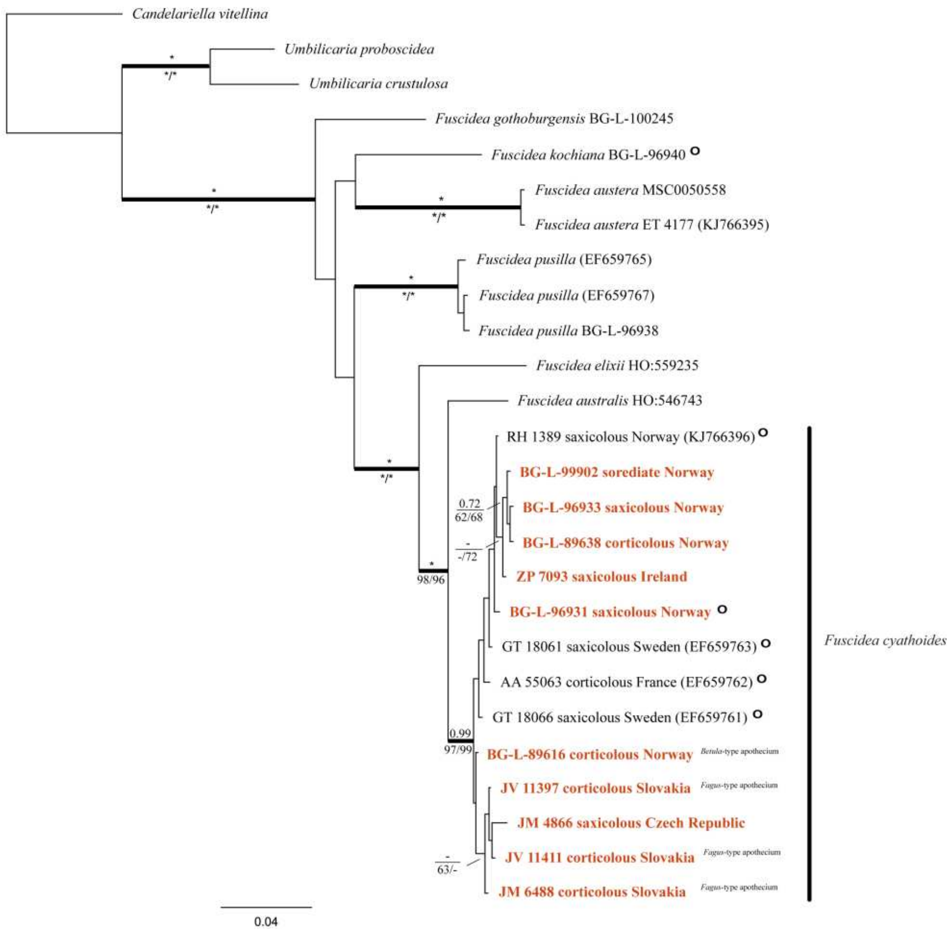

Figure 2. Phylogenetic relationships of esorediate and sorediate, saxicolous, and corticolous specimens of *Fuscidea cyathoides*, shown here as a 50% majority rule consensus tree of a B/MCMC analysis based on the concatenate data set (–ln = 8,081.83) of mtSSU, LSU and ITS. Posterior probabilities (PP) are displayed above the branches; MP and ML bootstrap values are displayed under the branches; asterisks indicate value of 100%. A circle indicates incongruent topology with the ML tree.

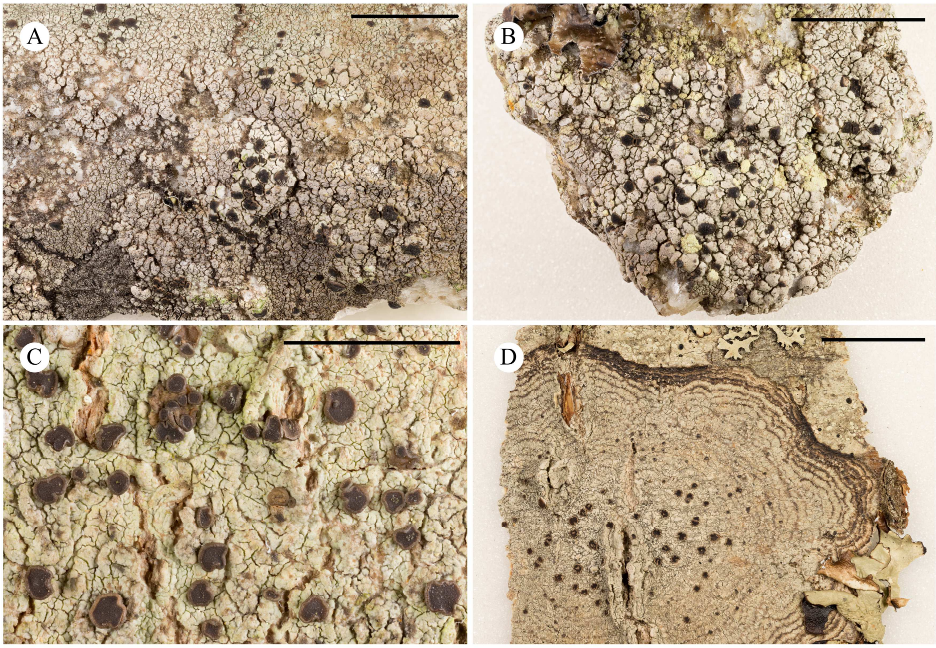

Figure 3. *Fuscidea cyathoides*. A: saxicolous and sorediate specimen, B: saxicolous and esorediate; C−D: corticolous. A, Norway (TT 46570, BG-L-99902); B, Norway (TT 46572, BG-L-99904); C, on *Fagus sylvatica*, Slovakia (JV 11397); D, on *Alnus incana*, Norway (TT 26205, BG-L-70280). Scale: A, B, D = 2 cm, C = 0.5 cm. Photos by Kim Abel.

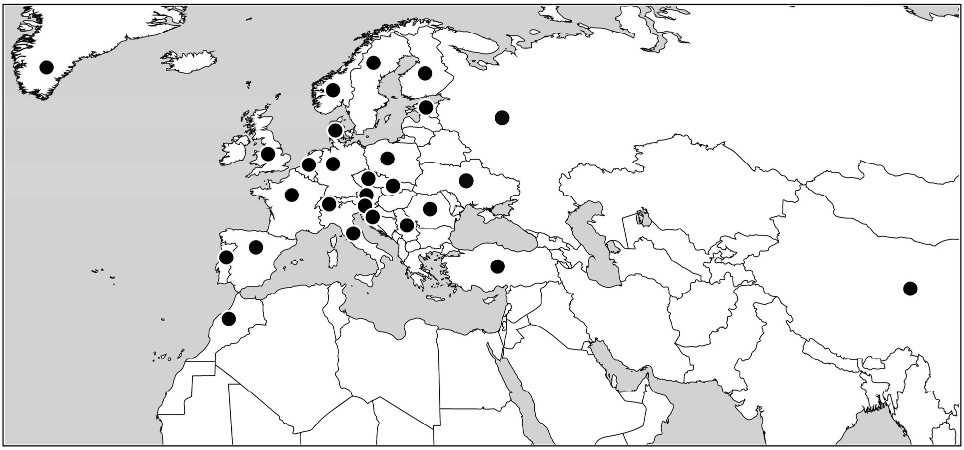

Figure 4. Distribution of saxicolous, esorediate and sorediate forms of *Fuscidea cyathoides* based on the examined material and the literature.

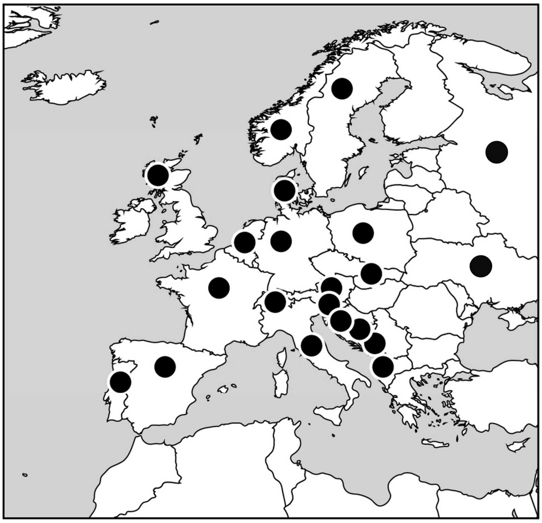

Figure 5. Distribution of corticolous forms of *Fuscidea cyathoides* based on the examined material and the literature.

Table 1. Overview of *Fuscidea cyathoides* nomenclature.

Author	Year	Name of species at: Species level	Variety level	Basionym	Synonyms
Acharius E.	1798	*Lichen cyathoides* Ach.			
Fries E.	1831		*Biatora rivulosa* b. *corticola* Fr.		*Lecidea Lightfootii* Ach.; *Lecidea rivulosa*
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 &		*Lichen cyathoides* Ach.	
Kalb K.	1976		*Fuscidea cyathoides* var. *corticola* (Fr.) Kalb	*Biatora rivulosa* b. *corticola* Fr.	*Biatorinella rivulosa* var. *corticola*
Poelt J. & Buschardt	1978		*Fuscidea cyathoides* var. *sorediata* (H. Magn.)	*Lecidea rivulosa* var. *sorediata* H.	
Hafellner J. & Türk R.	2001	*Fuscidea fagicola* (Zschacke) Hafellner &		*Lecidea fagicola* Zschacke	*Biatora rivulosa* b. *corticola* Fr.
Hafellner J.	2002	*Fuscidea stiriaca* (A. Massal.) Hafellner		*Biatora stiriaca* A. Massal.	*Fuscidea fagicola* (Zschacke) Hafellner &

Table 2. Overview of morphological characters measured on the studied specimens of *F. cyathoides*, given as (smallest values–)arithmetic mean ± s.d.(–largest values) (number of measurements).

Variety	Collection number	Country	Thallus colour	Areoles ⌀ [mm]	Apothecia ⌀ [mm]	Apothecia tuberculate ⌀ [mm]	Hymenium [µm]	Epihymenium [µm]	Length of spores [µm]	Width of spores [µm]
cyathoides	ZP 7903	Ireland	dark grey	(0.23–)0.45(±0.24)(–0.90) (n = 7)	(0.63–)0.86(±0.12)(–1.04) (n = 8)		93 (n = 1)	31 (n = 1)	(10–)10.6(±0.89)(–12) (n = 5)	(4.5–)5.1(±0.89)(–6) (n = 5)
	JM 4928	Czech Rep.	dark grey, dark brown	(0.41–)0.68(±0.23)(–0.95) (n = 5)	(0.45–)0.85(±0.27)(–1.17) (n = 8)		62 (n = 1)	31 (n = 1)	(10–)10.6(±0.52)(–11) (n = 8)	5(±0) (n = 8)
	MSC0050557	Scotland	dark grey, dark brown	(0.45–)0.84(±0.3)(–1.35) (n = 10)	(0.63–)0.9(±0.29)(–1.44) (n = 6)		155 (n = 1)	31 (n = 1)	(7–)9.7(±1.51)(–11) (n = 6)	(4–)4.9(±1.11)(–7) (n = 6)
	JM 4866	Czech Rep.	mouse grey	(0.23–)0.41(±0.15)(–0.59) (n = 6)	(0.50–)0.93(±0.25)(–1.35) (n = 7)		68 (n = 1)	22 (n = 1)	(6–)10(±2)(–12) (n = 7)	(4–)4.14(±0.38)(–5) (n = 7)
	JM 4916	Czech Rep.	grey-brown	(0.23–)0.59(±0.24)(–0.90) (n = 6)	(0.50–)0.63(±0.13)(–0.90) (n = 7)		62 (n = 1)	31 (n = 1)	(11–)11.5(±0.55)(–12) (n = 6)	5(±0) (n = 6)
	JPH 13294	Czech Rep.	brown-grey, brown	(0.45–)1.06(±0.59)(–2.03) (n = 6)	(0.45–)0.93(±0.32)(–1.35) (n = 5)	(1.40–)1.64(±0.35)(–1.89) (n = 2)	93 (n = 1)	31 (n = 1)	(9–)9.9(±0.99)(–11) (n = 8)	(4–)4.88(±0.64)(–6) (n = 8)
	BG-L-96931	Norway	grey, brown-grey	(0.18–)0.41(±0.26)(–0.99) (n = 9)	(0.41–)0.55(±0.11)(–0.72) (n = 7)		78 (n = 1)	16 (n = 1)	(9–)9.86(±0.69)(–11) (n = 7)	(3–)4.14(±0.75)(–5) (n = 7)
	BG-L-99904	Norway	light grey, dark grey	(0.25–)0.51(±0.24)(–0.88) (n =7)	(0.60–)0.79(±0.16)(–1.12) (n = 8)	(0.67–)0.78(±0.11)(–0.88) (n = 4)	145 (n = 1)	32 (n = 2)	(8–)11.55(±2.19)(–14) (n = 9)	(4.5–)4.89(±0.22)(–5) (n = 9)
	BG-L-96933	Norway	light grey, whitish	(0.14–)0.56(±0.41)(–1.35) (n = 8)	(0.45–)0.76(±0.29)(–1.13) (n = 8)		93 (n = 1)	19 (n = 1)	(8–)9.29(±0.76)(–10) (n = 7)	(4–)4.7(±0.49)(–5) (n = 7)
	LD-1132977	Sweden	dark grey-brown	(0.45–)1.14(±0.45)(–1.94) (n = 7)	(0.45–)0.74(±0.24)(–1.13) (n = 6)		109 (n = 1)	16 (n = 1)	(7–)9.33(±2.08)(–11) (n = 3)	(5–)5.5(±0.87)(–6.5) (n = 3)
sorediata	BG-L-99902	Norway	whitish, light grey	(0.25–)0.55(±0.31)(–1.05) (n = 7)	(0.16–)0.33(±0.17)(–0.70) (n = 10)		150 (n = 2)	28 (n = 2)	(7–)11.71(±2.21)(–13) (n = 7)	(4–)4.71(±0.49)(–5) (n = 7)
corticola	BG-L-89638	Norway	light grey	(0.50–)1.15(±0.46)(–1.76) (n = 6)	(0.54–)0.72(±0.25)(–0.90) (n = 2)	(0.94–)1.34(±0.32)(–1.76) (n = 4)	78 (n = 1)	16 (n = 1)	(10–)11(±1.21)(–13) (n = 6)	(4–)4.5(±0.55)(–5) (n = 6)
	JV 11476	Slovakia	dark greenish brown	(0.23–)0.38(±0.1)(–0.5) (n = 6)	(0.32–)0.48(±0.12)(–0.59) (n = 4)		53 (n = 1)	31 (n = 1)	(8–)8.83(±0.98)(–10) (n = 6)	(3.5–)4.1(±0.49)(–5) (n = 6)
	BG-L-89616	Norway	grey, brown	(0.45–)0.71(±0.32)(–1.35) (n = 7)	(0.45–)0.78(±0.31)(–1.40) (n = 8)		62 (n = 1)	19 (n = 1)	(10–)10.75(±0.87)(–12) (n = 8)	(4–)4.5(±0.53)(–5) (n = 8)
	JM 6488	Slovakia	olive-green	(0.45–)0.76(±0.37)(–1.35) (n = 5)	(0.72–)0.9(±0.12)3–(1.17) (n = 5)	(0.50–)1.24(±0.53)(–1.85) (n = 5)	62 (n = 1)	16 (n = 1)	(8–)9.25(±1.5)(–11) (n = 6)	(4–)4.5(±0.58)(–5) (n = 6)
	JV 11397	Slovakia	light green	(0.23–)0.63(±0.24)(–0.90) (n = 6)	(0.54–)0.83(±0.17)(–0.90) (n = 6)	(1.35–)1.51(±0.22)(–1.67) (n = 2)	68 (n = 1)	19 (n = 1)	(9–)10.1(±1.3)(–12) (n = 7)	(4–)4.5(±0.53)(–5) (n = 7)
	JV 11411	Slovakia	green, light green	(0.45–)0.53(±0.12)(–0.77) (n = 6)	(0.54–)0.73(±0.15)(–0.90) (n = 6)		62 (n = 1)	19 (n = 1)	(9–)10.3(±1.38)(–13) (n = 7)	(4–)4.6(±0.53)(–5) (n = 7)
	ZP 9629	Slovakia	mouse grey, brown	(0.45–)0.64(±0.21)(–0.90) (n = 6)	(0.50–)0.87(±0.27)(–1.13) (n = 4)	(1.31–)1.5(±0.21)(–1.89) (n = 6)	93 (n = 1)	16 (n = 1)	(6–)8.6(±1.5)(–10) (n = 6)	(4–)4.3(±0.51)(–5) (n = 6)
	LD-1133157	Sweden	dark grey	(0.45–)0.73(±0.31)(–1.04) (n = 7)	(0.54–)0.77(±0.14)(–0.90) (n = 6)	(1.13–)1.24(±0.16)(–1.35) (n = 2)	155 (n = 1)	22 (n = 1)	(10–)12.5(±1.68)(–14.5) (n = 8)	5(±0) (n = 8)
	LD-1157864	Sweden	mouse grey	(0.45–)0.89(±0.38)(–1.31) (n = 6)	(0.50–)1.03(±0.3)(–1.44) (n = 6)		124 (n = 1)	31 (n = 1)	10(±0) (n = 5)	(4.5–)4.8(±0.27)(–5) (n = 5)

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

Species	Variety	Country	Substrate	Collection/Accession number	GenBank Accesion Number		
					mtSSU	ITS	LSU
Candelariella vitellina					AY853315	AJ640085	AY853363
Fuscidea austera		Scotland	siliceous rock	MSC0050558	**KY874033**	**KY874026**	**KY874045**
Fuscidea austera		Norway		E. Timdal 4177	KJ766395	–	KJ766719
Fuscidea australis	*australis*	Tasmania	*Banksia marginata*	HO:546743	**KY874034**	**KY874022**	**KY874044**
Fuscidea 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	–	–
Fuscidea 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**	–
Fuscidea cyathoides	*sorediata*	Norway	siliceous rock	BG-L-99902	**KY874029**	**KY874013**	**KY874046**
Fuscidea elixii		New South Wales	*Acacia melanoxylon*	HO:559235	**KY874035**	**KY874020**	**KY874043**
Fuscidea gothoburgensis		Norway	siliceous rock	BG-L-100245	**KY874036**	**KY874024**	**KY874042**
Fuscidea kochiana		Norway	siliceous rock	BG-L-96940	**KY874031**	**KY874023**	**KY874041**
Fuscidea pusilla		Norway	*Betula* sp.	BG-L-96938	**KY874032**	**KY874025**	**KY874040**
Fuscidea pusilla		Sweden		G. Thor 18063a	EF659765	–	–
Fuscidea pusilla		Sweden		G. Thor 18058	EF659767	–	–
Fuscidea stiriaca		France		A. Aptroot 55063	EF659762	–	–
Umbilicaria proboscidea					AY300920	FR799304	AY300870
Umbilicaria crustulosa					AY300919	HM161499	HM161591

Appendix A: Supplementary material

Table S1. Infraspecific taxa of *Fuscidea cyathoides* (as *Lecidea rivulosa* Ach.) according to Magnusson (1925).

F. cyathoides var. *cyathoides* (as *Lecidea rivulosa* Ach.)	Thallus	Apothecia	Habitat
f. *lobaluta* Nyl.	thick, with convex areoles	up to 2 mm, margin lobate	locality rich in nitrogen
f. *depressa* Leight.	areolate-rimose, areoles flat or subtly concave	sessile	
f. *obscurior* Cromb.	areolate-rimose, dark grey with brownish-black hypothallus	sessile	
f. *depauperata* Leight.	thin and fading, hypothallus blackish	sessile	
f. *falsaria* Ach.	thick with verrucose areoles, greyish-brown		
f. *cyathoides* Ach.	rimose, whitish-grey	sessile, concave, flexuous with thin greyish pruina	very shaded
f. *sylvatica* Anzi.	smooth or finely rimose-areolate, whitish or greyish when fresh, intersecting hypothalline lines visible	rare, sessile, small	shaded
var. *infuscata* H. Magn.	thick, cracky with plane areoles, dark brown	appressed, only slightly rising above thallus, usually flat	in open situation along the coast

Table S2. Calculated likelihood parameters of individual data sets of the MCMC analysis. The values indicate the mean and, in brackets, the variance.

Parameters	mtSSU	LSU	ITS1	5.8 S	ITS2
Frequency A	0.3317 (0.0002)	0.2553 (0.0002)			0.1852 (0.0006)
Frequency C	0.1521 (0.0001)	0.2272 (0.0001)			0.2965 (0.0009)
Frequency G	0.2118 (0.0002)	0.2980 (0.0002)			0.2836 (0.0009)
Frequency T	0.3045 (0.0002)	0.2196 (0.0001)			0.2347 (0.0007)
Gamma shape (G)	0.2740 (0.0016)	1.7940 (1.3397)	0.2411 (0.0045)		0.3632 (0.0105)
Proportion of invariant sites (I)		0.6428 (0.0007)		0.6428 (0.0007)	
R-matrix [A-C]	0.1071 (0.0006)	0.06532 (0.0002)	0.1387 (0.0009)		
R-matrix [A-G]	0.2934 (0.0018)	0.1732 (0.0007)	0.1976 (0.0011)		
R-matrix [A-T]	0.0968 (0.0004)	0.0499 (0.0002)	0.1057 (0.0007)		
R-matrix [C-G]	0.1518 (0.0002)	0.0476 (0.0001)	0.0670 (0.0005)		
R-matrix [C-T]	0.3765 (0.0022)	0.5986 (0.0014)	0.4490 (0.0016)		
R-matrix [G-T]	0.1111 (0.0005)	0.0654 (0.0002)	0.0501 (0.0004)		
Kappa (K)				3.9198 (0.4114)	3.9198 (0.4114)