Lecidea doliiformis belongs to *Micarea*, *Catillaria alba* to *Biatora*, and *Biatora ligni-mollis* occurs in Western Europe

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Abstract. The taxonomic position of several European corticolous lichen species with conspicuous pycnidia and chlorococcoid photobiont is currently unsatisfactory and is here examined with maximum parsimony, maximum likelihood and Bayesian inferences using mtSSU sequences. *Lecidea doliiformis* is resolved as a member of the *Micarea assimilata*-group and *Catillaria alba* as sister to the recently described *Biatora ligni-mollis*. Therefore, *L. doliiformis* is transferred to *Micarea* [*M. doliiformis* (Coppins & P. James) Coppins & Sérus. *comb. nov.*], and a new name is introduced for the transfer of *C. alba* into *Biatora* (*B. veteranorum* Coppins & Sérus. *nom. nov.*). *Biatora ligni-mollis*, recently described from primary forests in British Columbia (Canada), is shown to be a rare but widespread species in Western Europe (Belgium, France, Germany, Poland and Scotland) where it is not confined to undisturbed forests.

Keywords. Bacidiaceae, Micareaceae, Pilocarpaceae, Ramalinaceae, mtSSU, phylogeny.

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In the original description of *Fellhanera gyrophorica*, Sérusiaux et al. (2001) provided a rapid survey of the diagnostic characters of several European corticolous species with conspicuous pycnidia and chlorococcoid algae as photobiont. Those species are currently placed into *Bacidia*, *Catillaria*, *Fellhanera*, *Fellhaneropsis*, *Lecidea* and *Micarea*. Sérusiaux et al. (2001) further observed that many species do not belong to the genera to which they are currently assigned and should be moved elsewhere. Even in their original descriptions, the assignment of species in *Catillaria* (*C. alba*) and *Lecidea* (*L. doliiformis*) was considered provisional.

The corticolous species with conspicuous pycnidia and chlorococcoid algae are all empirically assumed to belong to four families, e.g. the Bacidiaceae, Micareaceae, Pilocarpaceae and Ramalinaceae. However, the circumscription of those families is very much unresolved as demonstrated by the phylogenetic study by Andersen & Ekman (2005). Indeed, their analysis, based on Bayesian tree sampling and maximum likelihood analysis of mtSSU

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sequences, showed that *Micarea* in its classical delimitation (Coppins 1983) is polyphyletic: besides the likely assignment of several species to other genera (*Helocarpon* and *Scoliciosporum*), at least two different taxa are involved: the *M. bauschiana*-aggregate (group I in Coppins 1983) that is close to *Psora decipiens* and all the other species (incl. the type species, *M. prasina*) forming a complex, partly unresolved, paraphyletic clade, with all sampled representatives of the Pilocarpaceae nested in it. Further, the inferences showed that the Bacidiaceae may be restricted to a core group including *Bacidia*, *Bacidina*, *Toninia* and *Scutula*, whereas the Ramalinaceae *s. str.* would include *Bilimbia*, *Cliostomum*, *Crocynia*, *Lecania* and the fruticose genus *Ramalina*. These two clades were well-supported in a 3-gene Bayesian analysis that focused on the delimitation of *Lecania* (Reese Næsborg et al. 2007).

The aim of the present study is to assess the generic affinities of the Western European endemic *Lecidea doliiformis* Coppins & P. James, the possibly widespread *Catillaria alba* Coppins & Vězda, and to report the occurrence in Western Europe of *Biatora ligni-mollis* T. Sprib. & Printzen, recently described from British Columbia, Canada (Spribille et al. 2009).

MATERIAL AND METHODS

The material was examined in tap water, in lactophenol cotton-blue (LCB; FLUKA Chemika 61335) or in Lugol's solution (IKI; Lugol's solution SIGMA L-6146); measurements always refer to water mounts. TLC and HPLC have been kindly performed by Prof. J. A. Elix (Canberra, Asutralia).

Well-preserved and freshly collected lichen specimens lacking any visible symptoms of fungal infection were used for DNA isolation. A population of each taxon dealt with in this study was sampled and three extractions of different individuals were made for each. All three sequences were identical and thus only one was included (**Table 1**). All other sequences used in the phylogenetic analyses were retrieved from GenBank, except for a sample of *Cliostomum griffithii*. The available sequence of *Micarea incrassata* (AY756449) was not included in our matrix. This species is assumed to be close to the group of *Micarea* species (group J in Coppins 1983)

Table 1. GenBank accessions numbers for mtSSU sequences used for assessing the phylogenetic affinities of *Biatoria ligni-mollis*, *B. veteranorum* (formerly *Catillaria alba*) and *Micarea doliiformis* (formerly *Lecidea doliiformis*). Newly generated mtSSU sequences are highlighted in boldface.

Bacidia rosella	AY300877
Bacidia trachona	AY567784
Bacidina phacodes	AY567725
Bapalmuia palmularis	AY567781
Biatora ligni-mollis (France)	**GU138665**
Biatora ligni-mollis (Canada)	EU675998
Biatora meiocarpa	AM292710
Biatora pallens	AM292709
Biatora vernalis	DQ838753
Biatora veteranorum (France)	**GU138664**
Biatora veteranorum (Sweden)	AY567771
Bilimbia lobulata	AM292712
Bilimbia sabuletorum	AY567721
Byssoloma marginatum	AY567777
Byssoloma subdiscordans	AY567779
Calopadia foliicola	AY567782
Cliostomum corrugatum	AY567722
Cliostomum griffithii	**GU138667**
Cliostomum tenerum	AM292722
Crocynia gossypina	AY567766
Crocynia pyxinoides	AY584615
Fellhanera bouteillei	AY567787
Fellhaneropsis vezdae	AY567744
Frutidella caesioatra	AY567765
Lasioloma arachnoideum	AY567783
Lecania brialmontii	AM292726
Lecania chlorotiza	AM292727
Lecania cyrtella	AY300891
Lecania cyrtellina	AM292730
Lecania dubitans	AM292732
Lecania furfuracea	AM292734
Lecania fuscella	AM292735
Lecania gerlachei	AM293736
Lecania inundata	AM292740
Lecania naegelii	AM292741
Lecania nylanderiana	AM292742
Lecanora intumescens	AY567715
Lecidea sphaerella	AM292749
Lecidella meiococca	AY567714
Micarea adnata	AY567751
Micarea alabastrites	AY567764
Micarea assimilata	AY567739
Micarea botryoides	AY567741
Micarea cinerea	AY567763
Micarea coppinsii	AY567761
Micarea denigrata	AY567759
Micarea doliiformis	**GU138666**
Micarea elachista	AY567755

Table 1. Continued.

Micarea erratica	AY567737
Micarea hedlundii	AY567750
Micarea incrassata	AY756449
Micarea intrusa	AY567767
Micarea lapillicola	AY567735
Micarea lignaria var. *lignaria*	AY567748
Micarea lithinella	AY567734
Micarea melaena	AY567743
Micarea misella	AY567752
Micarea myriocarpa	AY567736
Micarea nitschkeana	AY567758
Micarea paratropa	AY567740
Micarea peliocarpa	AY567760
Micarea prasina	AY756452
Micarea pycnidiophora	AY567754
Micarea sylvicola	AY567768
Micarea synotheoides	AY567756
Mycobilimbia tetramera	AM292750
Psilolechia leprosa	AY567730
Psilolechia lucida	AY567729
Psora decipiens	AY567772
Pyrrhospora quernea	AY567712
Ramalina pollinaria	AM292752
Scoliciosporum chlorococcum	AY567768
Scutula miliaris	AY567790
Sphaerophorus globosus	AY256761
Sporopodium antonianum	AY567785
Toninia cinereovirens	AY567724

to which *Lecidea doliiformis* may belong, yet the sequence is nearly identical to that of *Frutidella caesioatra*, a morphologically rather similar species but that belongs to the Lecanoraceae (Andersen & Ekman 2005). The outgroup species (*Sphaerophorus globosus*) was chosen based on Miadlikowska et al. (2006). In total, 75 accessions representing 73 in- and outgroup species, were included.

We used Direct-PCR to amplify targeted loci. Hand-made sections of apothecia or pycnida were prepared with a sterile razor blade and directly placed in the PCR mix. The primers used were mtSSU1 and mtSSU3R (Zoller et al. 1999). A 50 µL PCR mix for one sample contained 5µL of PCR buffer, 5 µL of BSA (25 mg/mL), 4 µL of dNTPs (2.5 mM of each dATP, dGTP, dCTP and dTTP), 0.25 µL (5units/µL) of *Taq* polymerase, 1.25 µL of each primer (20 µM) and water. Amplifications were performed with the following cycling parameters: 94°C (10 min), 34 cycles of 94°C (30 s), 50°C (30 s) and 70°C (1 min), and a final extension of 72°C (10 min). Amplicons were sequenced by Macrogen®. Sequence fragments were assembled with Sequencher version 4.9 (Gene Codes Corporation, Ann Arbor, Michigan). Sequences were subjected to BLAST searches to detect potential contaminations.

The sequences were aligned manually using MacClade 4.05 (Maddison & Maddison 2002). Ambiguous regions were excluded from phylogenetic analyses. The final dataset is deposited in TreeBASE under the accession numbers M4911 for the matrix and S2569 for the studies. An unweighted Maximum Parsimony (MP) analysis was performed in PAUP* 4.0b10 (Swofford 2002) using heuristic searches with 1000 random addition sequence replicates, with tree-bisection-reconnection (TBR) branch-swapping, steepest descent not in effect and MulTrees option in effect. All saved trees were swapped to completion with no limit to the number of trees saved. Gaps were treated as missing data. The strength of support for individual branches was estimated using bootstrap values (MPBS) drawn from the 50% consensus tree constructed from all trees optimal saved during 1000 heuristic bootstrap pseudoreplicates (all other parameters identical to the original MP search).

Models of evolution for the Maximum Likelihood (ML) and Bayesian analysis were selected based on the Akaike Information Criterion (Posada & Buckley 2004) as implemented in Mr. ModelTest v2.3 (Nylander 2004). The selected model corresponds to the GTR model of nucleotide substitution (Rodríguez et al. 1990) including a proportion of invariable sites and a discrete gamma distribution with six rates categories. The ML analysis was performed using GARLI (Zwickl 2006, version 0.951 for OS X). Support for the branches was estimated using bootstrap values (MLBS) from 300 pseudoreplicates (all other parameters identical to the original ML search). Bayesian analyses were carried out using the Metropolis-coupled Markov chain Monte Carlo method (MCMCMC) in MrBayes v3.1.2 (Ronquist & Huelsenbeck 2003, Altekar et al. 2004). All Bayesian prior distributions were set to default values. A run with 5,800,000 generations starting with a random tree and employing four simultaneous chains was executed. A tree was sampled every 100th generation. We used TRACER

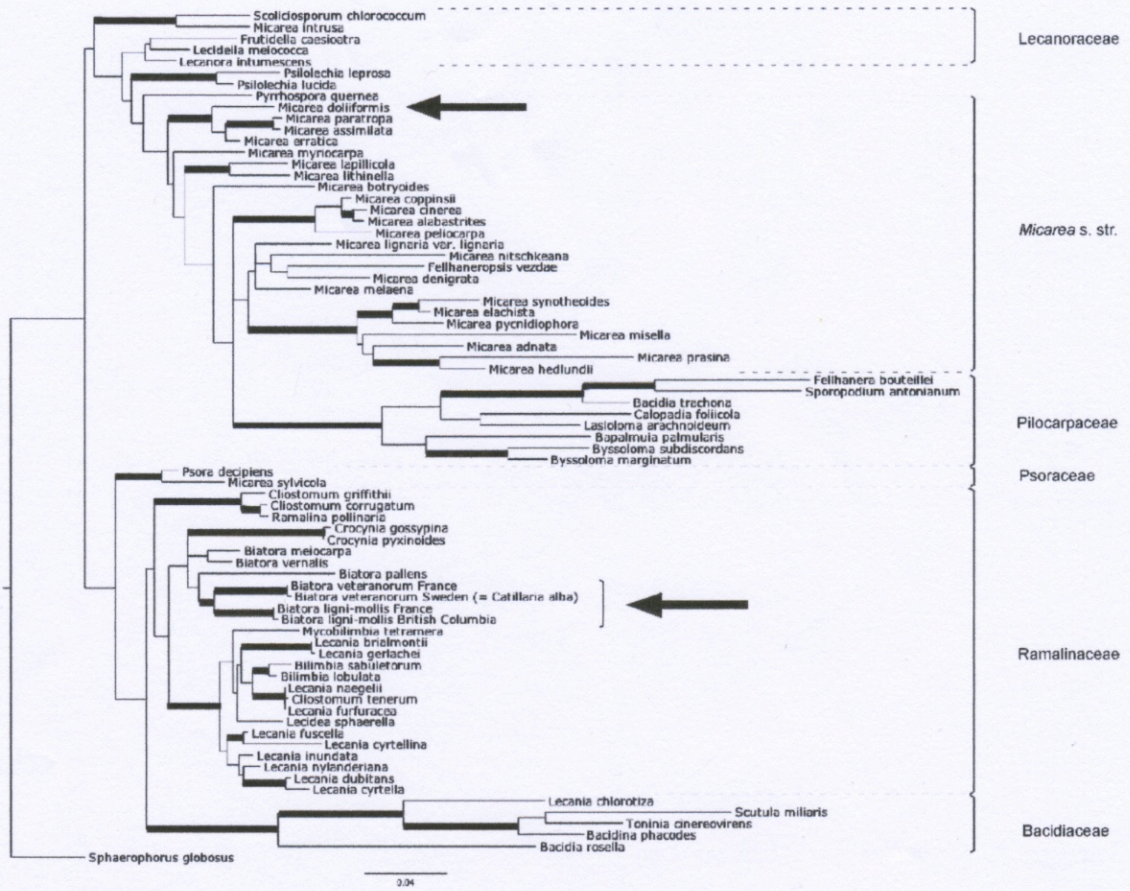

Figure 1. Phylogenetic position of *Biatora ligni-mollis*, *B. veteranorum* and *Micarea doliiformis* (arrows) in the single most likely tree (−lnL = 8942.86779) inferred from mtSSU sequences of representative species of the Bacidiaceae, Micareaceae, Pilocarpaceae and Ramalinaceae. Branches in bold are supported by MP and ML Bootstrap frequencies > 70% and Posterior Probabilities > 0.95.

v1.4.1 (Rambaut & Drummond 2007) to plot the log-likelihood values of the sample points against generation time, and determine when stationarity was achieved. Consequently the first 580,000 generations were deleted as the burn-in of the chain. A majority rule consensus tree with average branch lenghts was constructed for the remaining trees using the sumt option of MrBayes. Phylogenetic trees were visualized using TreeFig v1.2.3 (Rambaut 2009).

Results and Discussion

The matrix of mtSSU sequences included 669 characters, of which 323 were constant, 73 were variable but parsimony-uninformative and 273 characters were potentially parsimony-informative. The single most-likely tree (−lnL = 8942.86779) inferred from mtSSU data (**Fig. 1**) is topologically largely congruent with that proposed by Andersen & Ekman (2005) and Reese Næsborg et al. (2007). A strongly supported clade includes all accessions of the Pilocarpaceae (MPBS = 99%; MLBS = 100%; PP = 1.0), nested within a non-supported clade containing most groups (sensu Coppins 1983) of *Micarea*, a genus here confirmed to be polyphyletic. A second large albeit ambiguous clade contains several strongly supported lineages: (1) the Bacidiaceae *s. str.* with accessions of *Bacidia*, *Bacidina*, *Scutula* and *Toninia*, as well as *Lecania chlorotiza* (MPBS = 100%; MLBS = 87%; PP = 1.0); (2) a clade with *Psora decipiens* and *Micarea sylvicola* (MPBS = 91%; MLBS = 93%; PP = 1.0); (3) a clade with the type species of *Cliostomum* and *Ramalina* (MPBS = 100%; MLBS = 100%; PP = 1.0); (4) and a clade (MPBS= 92%; MLBS= 98%; PP= 1.0) with *Bilimbia*, *Mycoblimbia*, *Lecania* except *L. chlorotiza*, and a surprizing but well-supported clade formed by *Cliostomum tenerum*,

Lecania furfuracea and *L. naegelii* (MPBS = 100%; MLBS = 98%; PP = 1.0). *Crocynia* and available accessions of *Biatora* compose a clade that is, however, supported in the Bayesian analysis (MPBS and MLBS < 70%; PP = 1.0). Similarly the family Ramalinaceae *s. str.*, e. g. excluding the Bacidiaceae (Andersen & Ekman 2005, fig. 2) is only supported by posterior probabilities and not bootstrap values (MPBS and MLBS < 70%; PP=1.0).

The two species targeted here for assessing their phylogenetic affinities are resolved within two different clades (**Fig. 1**):

- *Lecidea doliiformis* is resolved within the robust clade formed by accessions of group J of *Micarea* (Coppins 1983) and *M. erratica* (MPBS = 90%; MLBS = 86%; PP = 1.0). Species of *Micarea* compose several discrete robust lineages, such as the group of *M. alabastrites* (group C in Coppins 1983) but the genus, even after excluding *M. sylvicola*, which appears sister to *Psora decipiens*, is resolved as a potentially paraphyletic entity;
- Our accession of *Catillaria alba* is sister to the GenBank accession of the same species, and our European sample of *Biatora ligni-mollis* is identical except for a single substitution with the type-collection of that species, described from British Columbia/Canada (Spribille et al. 2009); support for the clade formed by both species is MPBS = 78%; MLBS = 83%; PP = 0.99. *Catillaria alba* and *Biatora ligni-mollis* are thus resolved as a supported pair nested within a clade supported only in the Bayesian analysis that includes all accessions of *Biatora* and both species of *Crocynia* (which form a strongly supported pair: MPBS = 100%; MLBS = 100%; PP = 1.0).

If the paraphyly of *Micarea* can be confirmed by further phylogenetic studies based on inferences from other loci, three validly published names are available for possible taxonomic recognition of segregated genera: *Fellhaneropsis* Sérus. & Coppins (Sérusiaux 1996), *Leimonis* R.C. Harris (Harris 2009) and *Szczawinskia* Funk (Holien & Tønsberg 2002). We refrain from dismembering *Micarea* without such data and conclude that *Lecidea doliiformis* is better assigned to *Micarea*. Regarding the generic position of *Catillaria alba*, we follow the option of Spribille et al. (2009) who assigned its sister species to *Biatora* (*B. ligni-mollis*) with strong support (Bayesian analysis of ITS and mtSSU sequences).

Therefore, the taxonomical conclusions of this analysis are the assignment of *Lecidea doliiformis* to *Micarea*, and that of *Catillaria alba* to *Biatora*.

The Species

Biatora veteranorum Coppins & Sérus. *nom. nov.*
Nomen novum for *Catillaria alba* Coppins & Vězda, in Vězda, Lichenes Rariores Exsiccati n° 53, 1993. Non *Biatora alba* (Schleich.) Hepp, Flechten Europas, n° 251, 1857 [= *Lecidella pulveracea* (Schaer.) H. Syd.].Type: Austria. tyrol: Hohe Tauern, Virgen, Hinteregg, ca. 1600 m, ad truncum putridum *Laricis*, Sep 1988, *A. Vězda* (holotype herb. Vězda; isotype e!).
MycoBank n°: MB 516555

Biatora veteranorum is easily characterized by its effuse thallus, with tiny, pale orange to pinkish apothecia, usually with slightly white pruinose disc, its numerous, stalked, white-pruinose pycnidia, and its ecological requirements (e. g., old dry bark or lignum, on living or dead but still standing trees). Its generic position is not easy to assess on morphological and anatomical characters. Its ascus has an amyloid layer and apical dome (tholus) with a darker tube or plug-like structure and a small non amyloid conical ocular chamber is sometimes evident according to Coppins & Vězda (1993; original description). The excipulum is distinctive with conglutinate radiating hyphae. Paraphyses are simple or branched, 1.0–1.5 µm and widening to 2.5–2.8 µm at their tips. Ascospores are ellipsoid, 1-septate, (6.5–)8–10(–11.5) × 2.3–3.0 µm, and conidia are bacilliform, simple and 2.8–3.5(–3.8) × 0.8–1.0 (–1.2) µm.

Such a combination of characters could point to the Pilocarpaceae, and particularly the genera *Byssoloma* and *Fellhanera*, which show diverse excipulum and pycnidia types (Sérusiaux 1995), or *Cliostomum* as circumscribed by Ekman (1997). Inferences from mtSSU sequences clearly point to a close relationship with *Biatora ligni-mollis* (see below). Spribille et al. (2009) adopted the genus *Biatora* for both species although the ascus type and the conspicuous pycnidia might be incongruent. With the data currently available and pending further research on the genus (Printzen in prep. *fide* Spribille et al. 2009), the most appropriate generic position for *Catillaria alba* is *Biatora*.

When combined into *Biatora*, *Catillaria alba* requires a new name as the combination *Biatora alba* has already been used for a putative synonym of

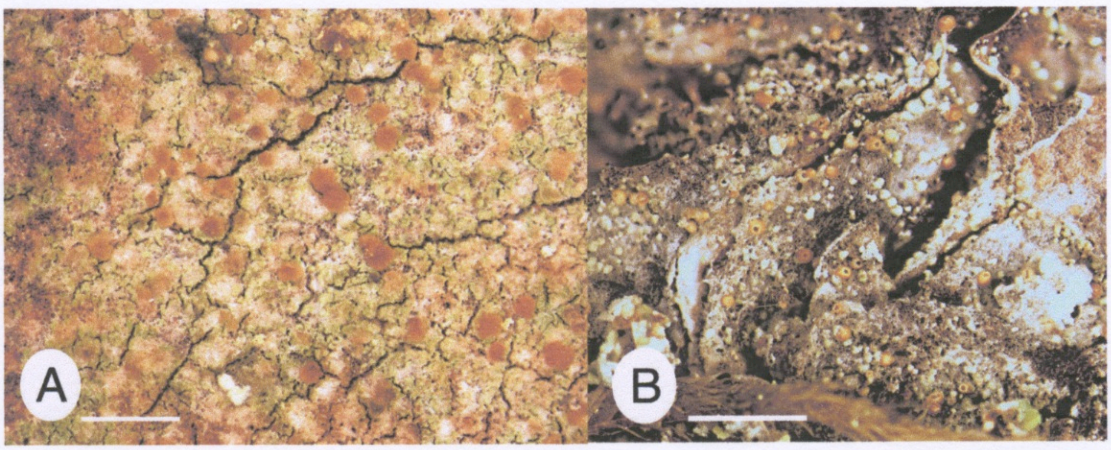

Figure 2. *Biatora ligni-mollis* (France, Vosges, NE of Le Tholy, Aug 2006, *E. Sérusiaux* s. n., LG). **A.** Thallus with apothecia. **B.** Thallus with pycnidia. Scale bar = 1 mm.

Lecidella pulveracea. The epithet *veteranorum* refers to the habitat of the species, e. g. bark or exposed lignum of very old trees.

Biatora veteranorum was originally reported from Austria, Denmark, Germany, Italy, Spain and Scotland. Its range now also includes the Czech Republik and Slovakia (Palice 1999) and Poland (Czarnota 2003). A tentative identification from Rwanda is mentionned in Killmann & Fischer (2005). Berger (2000: 450, Fig. 16) published a splendid color picture.

Specimen sampled for DNA: FRANCE. Dépt. Vosges, NE de Xonrupt-Longemer, Défilé de Straiture, 850–900m, futaie d'*Abies alba* sur éboulis, tronc d'un vieux *Abies*, Aug 2006, *E. Sérusiaux* s.n. with Olivier Bricaud, Valérie Reeb and Claude Roux (LG).

Biatora ligni-mollis T. Sprib. & Printzen, Bryologist 112: 121, 2009. **Fig. 2**

TYPE. CANADA. BRITISH COLUMBIA; Selkirk Mts, Incomappleux River drainage, 700 m, on soft snag in old-growth forest, Aug 2003, *Spribille 12692, C. R. Björk & C. Pettitt* (holotype: CANL; isotypes: BG, FR).

Description of European material. Thallus thin, continuous, whitish to pale green, distinctly granulose or farinose, partly endophloeodal, without prothallus. Photobiont: a chlorococcoid alga, with spherical green cells, 8–14 µm diam. Apothecia usually present, scattered over the thallus or in groups, sometimes contiguous but not agglomerated, round, 0.15–0.40 mm diam., with a slightly constricted base; disc dark orange to pale reddish brown, flat and becoming slightly convex in old apothecia; margin distinct in young and mature apothecia but hardly present in old ones, slightly paler and sometimes slightly sinuose; excipulum hyaline, 40–45 µm thick, with radiately arranged, thick-walled hyphae, with small crystals in the protoplasma, disappearing in K; hypothecium hyaline; hymenium hyaline, 40–60 µm high, sometimes with vertical rows of tiny hyaline crystals, especially in the upper parts; paraphyses rather few, usually shorter than the asci, simple, not swollen at their tips, ca. 1 µm thick; asci 25–35 × 7–10 µm, clavate or sometimes slightly turbinate, with an amyloid outer layer and tholus, an IKI+ dark blue tube like structure usually seen; ascospores 8/ascus, narrowly ellipsoid with rather rounded ends, straight or slightly arcate, distorted ones not rare, with a very thin wall, 1–2(–3) septate, 8–12 × 2.0–3.5 µm. Pycnidia always present, sessile, conspicuous but quite small (ca. 0.1 mm diam.), globose usually with a wide open ostiole, of the same color as the apothecia but paler and thus pale orange to brownish; cavity unilocular and lined with the conidiogenous layer; conidiophores made of hyaline, elongate cells; conidiogenous cells elongate or sometimes ampulliform. Conidia of two types, not produced in the same pycnidia: (a) bacilliform, 3.5–5.5 × 0.8–1.5 µm; (b) ovoid, with a slightly pointed

end, 2.5–3.0 × ca. 2 µm. Chemical tests (TLC & HPLC performed by J. A. Elix): lobaric acid (major) and roccellic acid (major), no accessory compounds detected.

Biatora ligni-mollis was first collected in the 19th century by the German botanist Carl Albert Kemmler (1813–1888) who made it available to F. C. G. Arnold, a famous lichenologist from Southern Germany. The material was distributed in his Exsiccati, under the name of *Biatora albohyalina* (Nyl.) Bagl. & Car. This species is not accepted in that genus by Printzen (1995) and can be easily distinguished from *Biatora ligni-mollis* by its semi-immersed pycnidia with a conspicuous glut of filiform conidia, 25–50 × 1.5–2.0 µm.

The European material differs somewhat from the original collections from British Columbia by several characters: a single substitution in the mtSSU sequence, apothecia more orange brown (vs rufous brown in Spribille et al. 2009) and less abundant (vs "strikingly high density of apothecia, to 170 apothecia per cm^2" that has not been seen in European samples), 1–2(–3) septate spores (vs 0–1 septate in British Columbia samples) and the production of lobaric and roccellic acids (lobaric acid only in British Columbia samples). Such differences may indicate that two different species could be distinguished, but without further data, we refrain from describing a new species.

In British Columbia (Canada), *Biatora ligni-mollis* is found on soft, punky wood of conifer snags in humid old-growth forests and is assumed to be confined to such habiats (Spribille et al. 2009). In Western Europe, it is a rare, but possibly overlooked, species growing on old bark or lignum of deciduous or conifers trees, either decorticated or still alive, in forest stands, sometimes at their outskirts. The localities where the species has been found are not pristine forests but nevertheless can be described as habitats with old trees and enjoying a long ecological continuity (Coppins & Coppins 2002).

The discovery of *Biatora ligni-mollis* throughout Western Europe (Belgium, France, Germany, Poland and Scotland; our data already made available to Hitch 2009) is a further example of the disjunct distribution of several lichen species between Western Europe (incl. the Mediterranean area and Macaronesia) and the western parts of North America. Another recently documented example is the occurrence of *Pyrenula acutispora* in Western Europe (British Isles and France), Macaronesia (Canary Islands, Madeira and the Azores) and British Columbia (Sérusiaux & Coppins 2008).

Specimen sampled for DNA: FRANCE. Dépt. Vosges, O de Gérardmer, NE de Le Tholy, hêtraie-sapinière en bord de ruisseau, 650–660 m, sur *Abies*, Aug 2006, *E. Sérusiaux* (LG, E) [AFL Field Session]. ***Other specimens examined:*** BELGIUM. Forêt d'Anlier, near Rulles, on old *Quercus* in old, open wood (*Quercus-Fagus*), 450 m, Mar 1989, *A. M. Brand 20094* (LG, hb Brand). FRANCE. Dépt. Vosges, 2 km NE of Gérardmer, valley of Vologne, Pointe des Fées, on *Abies* at roadside in wooded valley, 650 m, July 1984, *A. M. Brand 11987* (hb Brand). Ibid., 10.5 km SSE of Gérardmer, S of Col Brammont, N of Pourri Faing, on wood of dead *Abies* trunk in open place, in woodland on SE slope, 1100 m, Jul 1984, *A. M. Brand 11859B* (hb Brand). Ibid., NE de Gérardmer, défilé de Straiture, futaie d'*Abies* sur la ligne de crête, avec éboulis de gros blocs et de nombreux arbres couchés, 900–1000 m, Sep 2005, *E. Sérusiaux* s.n. (LG). Dépt. Pyrénées-Atlantiques, S of Arette, S slope of Pic Soulaing, on dead wood of a standing trunk of *Abies* in *Abieto-Fagetum*, 1400 m, *A. M. Brand 28245* (hb Brand). GERMANY. Württemberg, bei Geifertshofen, Oberamt Geildorf, an einer alten Tanne in einer Waldschlucht, Aug 1862, *Kemmler* in Arnold Exsiccati n° 543, sub *Biatora albohyalina* Nyl. (L). UNITED KINGDOM. SCOTLAND. East Ross (V.C. 106), Strathbran, Chullin, S-facing oak-birch wood on rocky slope, on underside of large *Quercus* trunk projecting from a steep slope, Jun 1986, *B. J. Coppins 11936* & *R. G. Woods* (E). POLAND. S of Suwalki, Augustow Forest, Starozyn Nature Reserve, on trunk of an old *Carpinus betulus* in hardwood forest, Aug 2005, *J. Motiejunaite 7692* (BILAS).

Micarea doliiformis (Coppins & P. James) Coppins & Sérus. *comb. nov.*

BASIONYM: *Lecidea doliiformis* Coppins & J. James, Lichenologist 24: 361, 1992. TYPE. UNITED KINGDOM. ENGLAND: Dorset (V.C.9), Brownsea Island, on bark of a large *Pinus*, 30 Aug 1983, *P. W. James & V. J. Giavarini* (holotype BM!; isotype E!).

Table 2. Morphological, anatomical, chemical and ecogeographical characters of *Frutidella caesioatra* and members of the *Micarea assimilata* gr.

Name	Thallus (incl. chemistry and photobiont) and apothecia	Exciple, hamathecium and epithecium	Asci and ascospores	Pycnidia and conidia	Habitat and distribution
Frutidella caesioatra	Thallus rather thick, strongly warted of dense subglobose, ± isidioid granules 0·1–0·2 mm diam., grey to dark grey or almost black, whitish when eroded thick with dense, subglobose granules. Photobiont cells 6–12 µm diam. Producing sphaerophorin Apothecia subglobose, (0.3)0.5–1(–1.2) mm diam. bluish black with blue-grey pruina, especially when wet	Exciple well-developed, of radiating conglutinated hyphae. Hypothecium ± colourless to reddish brown to almost violet, K+ reddish orange. Paraphyses 1.3–1.8 µm thick, sparsely branched and sometimes anastomosed, apices with individual, colourless gel-coats	Asci *Lecanora*-type. Ascospores simple, ellipsoid, (12–)15–19(–24) × 5–7(–9) µm	Pycnidia immersed or half immersed, globose or pear-shaped. Conidia filiform, 15–25 × 0.7–1 µm	Muscicolous over acid soil, in alpine habitats, circumpolar in both hemispheres
Micarea assimilata	Like *M. incrassata*, but areoles usually whitish and apothecia more prominent	Hypothecium purple-brown, K ± purple intensifying or (especially above) K ± dark green	Asci *Micarea*-type. Ascospores (10–)12–16(–19) × 3–5 µm, 0(–1)-septate	Unknown	Similar habitats to *M. incrassata*. N. Scotland. Europe, Macaronesia, N. America, Australia
Micarea doliiformis	Thallus effuse, often wide-spreading, finely granular but granules often proliferating to form a thickish crust, dull green-grey or whitish grey; granules 30–60(–80) µm diam. Photobiont cells 7–14 µm diam. No products. Apothecia 0·2–0·5 mm diam., rare, convex to subglobose, pale pinkish brown with whitish pruina	Exciple absent. Epithecium pale brownish due to dense minute crystals that dissolve in K. Hymenium 45–50 µm tall, colourless or with pale brown vertical streaks. Hypothecium reddish brown, K+ yellowish brown. Paraphyses 0·7–1·5 µm wide, but widening to 2·5(–3) µm in the epithecium, branched and anastomosed, apices colourless	Asci *Micarea*-type. Ascospores (7–)8–11 × 2·7–3·7 µm, ovoid- to oblong-ellipsoid	Pycnidia 0.08–0.16 mm diam., 0.14–0.30 mm tall, numerous, sessile or ± stalked, somewhat barrel-shaped, grey-brown to dark grey, usually thinly white-tomentose, ostiole often gaping; wall dull brown, K-, N+ reddish brown, but green (K+ intensifying, N+ red) around the ostiole. Conidia 3·5–4·7 × 1·5–2 µm, shortly oblong or wider at proximal end, mostly biguttulate	On dry, often sheltered, rough acid bark or long-exposed wood (especially *Quercus*) in woodland or sheltered parkland. British Isles Western France and Spain/Navarra. Known only from Europe

Table 2. Continued.

Name	Thallus (incl. chemistry and photobiont) and apothecia	Exciple, hamathecium and epithecium	Asci and ascospores	Pycnidia and conidia	Habitat and distribution
Micarea erratica	Thallus thin, greyish, usually continuous with conspicuous, fimbriate and black prothallus; photobiont cells 6-12 µm. No products Apothecia (0·15–)0·2–0·4(–0·7) mm diam., sessile, constricted at the base, disc concave to ± flat, rarely somewhat convex, black	Exciple persistent, raised, rarely finally excluded, blue-black at outer edge, pale brownish (K+ purplish) within. Epithecium dark greenish blue to greenish brown, K+ green intensifying, N+ purple-red. hypothecium dark brown Paraphyses ca. 1·5–2·5(–3) µm wide, sparsely branched and anastomosed	Asci *Micarea*-type. Ascospores narrowly ellipsoid, rather abruptly truncated at the ends, (6–)7–9(–10) × (2–)3–4(–5) µm	Pycnidia 80–150 µm diam., often abundant, sometimes only those present, black, scattered on the prothallus or partly immersed in the thallus. Conidia 3–5 × 1·5 µm, ± cylindrical	On pebbles, flints and stable singles, rarely on wood, also in ruderal habitats. Subcosmopolitan (not known from Africa)
Micarea incrassata	Thallus dull grey-white, grey-brown to dark grey, matt, of confluent convex-verrucose areoles ca. 80–300 µm diam. Photobiont cells 4–7 µm. Cephalodia usually present, areole-like, brown, scattered, with *Nostoc* (cells 3–5 µm diam.); clusters of *Stigonema* often amongst the areoles. No products. Apothecia 0·3–0·8(–1) mm diam., convex, usually partly immersed by surrounding areoles, black	Exciple indistinct. Hymenium 45–50 µm tall, the uppermost part dark greenish, K-, N ± red. Hypothecium ca. 150–400 µm tall, dark red-brown (no purple tinge) K-, N ± bright orange-brown. Paraphyses (1–)1·5–2 µm wide, numerous, sparingly branched, the apices sometimes to 3 µm	Asci *Micarea*-type. Ascospores (10–)12–17 × 4–4·8 µm, ellipsoid to oblong-ovoid or oblong-fusiform, 0– to 1(–2)-septate	Pycnidia 30–60 µm, rare, immersed, blackish. Conidia 6–9 × 1–1·3 µm, ± bacilliform	On soil in heathlands in montane or coastal areas, mainly in alpine habitats; circumpolar in both hemispheres
Micarea paratropa	Like *M. assimilata*, but on rocks. *Nostoc*-containing cephalodia not known, but *Stigonema* clusters usually present between areoles	Like *M. assimilata* but hymenium greenish, K+ violet	Asci *Micarea*-type. Ascospores 9–16(–17) × 4–5 µm, simple	Unknown	On small stones in turf around late snow-beds. Scotland and Norway

MycoBank n°: MB 516556

Lecidea doliiformis was described in the framework of the first edition of The Lichen Flora of Great Britain and Ireland (Coppins et al. 1992) and was mentioned only from – but throughout – the British Isles (England, Ireland, Scotland and Wales). It is easily recognized by its wide-spreading granular thallus, its numerous, conspicuous (0.08–0.16 mm wide and 0.14–0.3 mm high), greyish to dark grey and usually thinly white-tomentose pycnidia producing simple, oblong, 3.5–4.7 × 1.5–2.0 µm conidia, and, when present, its subglobose, pale brown to pinkish (usually with whitish pruina) apothecia producing simple, ovoid to ellipsoid ascospores, 7–11 × 2.7–3.7 µm. Excipulum is absent and paraphyses are branched and anastomosed, 0.7–1.5 µm wide and widening to 2/5 µm in the epithecium. Typically, the epithecium is filled with minute crystals that dissolve in K. It grows on dry, sheltered, rough acid bark in woodland and parkland.

Comments on its generic position were quite clear in its original description (Coppins et al. 1992): "it is certainly not congeneric with *Lecidea fuscoatra*, the type species of *Lecidea*" and its affinities with *Micarea* were already detected because of absence of excipulum and branched paraphyses. However, its assignement to *Micarea* was rejected because of the combination of granular epithecium and trebouxioid photobiont. Inferences from mtSSU sequences provide strong support for its affinities with several species of *Micarea*, namely *M. assimilata* (Nyl.) Coppins, *M. erratica* (Körb.) Hertel, Rambold & Pietschm., and *M. paratropa* (Nyl.) Alstrup. *Micarea assimilata* and *M. paratropa* are usually assumed to be closely related to *M. incrassata* (Coppins 1983). An accession of the latter from GenBank is nearly identical with *Frutidella caesioatra* (Schaer.) Kalb, a monotypic genus originally assigned to the Ramalinaceae (Lumbsch & Hundorf 2007) and not surprisingly the two are resolved as sister-taxa in a Bayesian analysis (results not shown). Revision of the corresponding voucher material (Norway, Nord-Trøndelag, 28 July 1992, *T. Tønsberg* 17593, BG!) confirms it actually is a typical collection of *Micarea incrassata*. We suspect some confusion as it is much unlikely that these two species are closely related (Kalb 1994), given the clear morphological, anatomical, chemical and differentiation ecogeographical differentiation of *Frutidella caesioatra* and *M. doliiformis*, as well as other members of the *M. assimilata*-group (**Table 2**).

The genus *Leimonis* R.C. Harris has recently been introduced to accommodate *Micarea erratica* (Harris 2009), but further studies are required to establish if the circumscription of the genus should be broaden to include other species, such as *M. assimilata* and *M. doliiformis*, even if they differ by their reduced excipulum.

Outside the British Isles, *Micarea doliiformis* is known only from Spain/Navarra (van den Boom et al. 1995) and western France (Aptroot et al. 2007; see further data below); quite surprisingly it is not yet known from other oceanic regions, either in Macaronesia or in W Norway.

Specimen sampled for DNA: UNITED KINGDOM. WALES: Glamorgan (V.C. 41), Cardiff, Lisvane, Parc Cefn Onn, alt. 100 m, on rain-sheltered bark of trunk of *Pinus sylvestris* in woodland, Sep 2006, *A. Orange* (LG, NMW). ***Additional specimens examined:*** FRANCE [all specimens in herb. Brand]: Finistère dept., Locmaria-Berrien, very old *Quercus* in village, Jul 1978, *M. Brand* 7500; *c.* 4.5 km SW of Landar, old *Quercus* in woodland, Jul 1997, *M. Brand 36478*; 5 km NE of Quimper, Stangala, on *Quercus* in wood, Jul 1997, *M. Brand 36766 & 36786*; 14 km SSE of Quimper, Chapelle de Perguet, on decorticated old *Taxus* in churchyard, Jul 1997, *M. Brand 36963*; 3 km S of Quimperlé, forêt de Carnoët, on bark, Apr 1999, *M. Brand* 38493. Dépt. Ile-et-Vilaine, Mont-Dol, on very old *Castanea*, Apr 1999, *M. Brand 37872*. Dépt. Morbihan, 6 km NE of Lorient, on old *Castanea*, Apr 1999, *M. Brand 38312*.

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