# *Rhizocarpon vulgare*, a new species in the *R. badioatrum* species complex

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Timdal, E., Möller, E. J. & Bendiksby, M. 2024. *Rhizocarpon vulgare*, a new species in the *R. badioatrum* species complex. *Graphis Scripta* **36** (4): 89–105. Oslo. ISSN 2002-4495.

Herein, we revise the *Rhizocarpon badioatrum* species complex in the Nordic countries using molecular phylogenetics combined with morphological/anatomical and chemical data. Bayesian and Maximum Likelihood phylogenetic analyses of the nuclear ribosomal internal transcribed spacer (ITS, the fungal DNA barcode) reveals four strongly supported clades within the *R. badioatrum* species complex. Based on our assessment of the multiple sources of data included, we recognize *R. badioatrum* var. *badioatrum* and var. *vulgare* at the species level and describe the latter as the new species *R. vulgare*. *Rhizocarpon vulgare* receives support also from a phylogeny based on mitochondrial ribosomal small subunit (mtSSU). *Rhizocarpon cinereonigrum* is the phylogenetic sister species of *R. vulgare* in both the ITS and mtSSU trees. *Rhizocarpon sinense* is reported as new to Europe with specimens collected from Iceland and Norway. The secondary chemistry is shown to be largely diagnostic for the species: *R. badioatrum* is usually acid deficient, *R. vulgare* contains diffractaic acid, and *R. sinense* contains gyrophoric acid. However, the concept of *R. cinereonigrum*, which was previously based on the presence of stictic acid, is shown to be ambiguous because that compound may also occur in *R. badioatrum.* Lectotypes are designated for *Lecidea atrobadia*, *Rhizocarpon badioatrum*, *R. rivulare*, *R. sinense*.

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## Introduction

*Rhizocarpon badioatrum* (Schaer.) Th. Fr. has a wide distribution in the temperate to arctic zones of the Northern Hemisphere and also occurs in Australia, South America and Antarctica (GBIF 2024). It is a common species throughout Fennoscandia, occurring mainly on siliceous rock and crystalline schist (Westberg et al. 2021). *Rhizocarpon badioatrum* is recognised within the genus by having a brown thallus, non-amyloid medulla, 1-septate, brown ascospores, brown, K+ red epihymenium, lack of crystals (i.e., acetone-soluble lichen substances) in the apothecia, and by either lacking lichen substances or containing diffractaic acid in the medulla (cf. the key to the Nordic *Rhizocarpon* species by Timdal & Holtan-Hartwig 1988). The species is morphologically rather variable, and several infraspecific taxa have been recognised in the major European treatments of the genus. Koerber (1855) divided the species into two varieties based on morphological differences and named them *Buellia badioatra* var. *vulgaris* Körb. and var. *rivularis* Körb. This subdivision was followed by, e.g., Fries [1874; as *R. badioatrum* var. *vulgare* (Körb.) Th. Fr. and var. *rivulare* (Körb.) Th. Fr.] and by Poelt & Vězda (1981; as *R. badioatrum* var. *vulgare* and var. *badioatrum*). Vainio (1883) accepted six, and later (Vainio 1922) seven, forms of *R. badioatrum*. Malme (1914) commented on


Published 2024-06-25 by The Nordic Lichen Society, https://nhm2.uio.no/lichens/NLS.

five of Vainio's forms and stated that they seem to be more or less direct responses to different environmental conditions.

Based on Scandinavian material, Timdal & Holtan-Hartwig (1988) discovered a chemical difference between the two morphology-based varieties of Körber and later authors; var. *badioatrum* lacks lichen substances whereas var. *vulgare* contains diffractaic acid. This correlation between morphology and chemistry made Timdal & Holtan-Hartwig (1988) regard the two varieties as distinct species but because of the complex nomenclature of the group, they refrained from formal descriptions or new combinations and just referred to them as *R. badioatrum* sp. 1 and sp. 2. Further complications are (1) the identity of *R. cinereonigrum* Vain., a species morphologically similar to *R. badioatrum* sp. 2 but often recognisable by the shape of the areolae and the presence of stictic acid apparently being diagnostic (Timdal & Holtan-Hartwig 1988), and (2) a few Nordic specimens fitting *R. badioatrum* morphologically but containing gyrophoric acid and hence possibly representing *R. sinense* Zahlbr. which is otherwise known only from China (Zahlbruckner 1930, Bi et al. 2022).

This paper presents the results of a molecular study of the group, based mainly on Norwegian material in the herbarium of the Natural History Museum, University of Oslo (O). We have sequenced 32 specimens of the *R. badioatrum* species complex (including *R. cinereonigrum* and a gyrophoric acid-containing specimen) for the DNA barcode marker (ITS) and a selection of them for the mtSSU marker. Since the phylogenetic reconstructions largely corroborates the view of Timdal & Holtan-Hartwig (1988), we here formally describe *R. badioatrum* sp. 2 as the new species *R. vulgare,* confirm *R. cinereonigrum* as a distinct species and report *R. sinense* as new to Europe.

## Material and Methods

*Material*: For the phylogenetic analyses, we selected 14 specimens lacking lichen substances, 13 containing diffractaic acid, four containing stictic acid, and one containing gyrophoric acid. All were sequenced for the ITS marker and 11 for the mtSSU marker. Two of our ITS sequences of the acid deficient chemotype have been published by McCune et al. (2016: KU687450 and KU687453). Seven ITS sequences of *R. sinense* and one of *R.* sp. in GenBank were added to the dataset. To root the trees, we added one ITS sequence of *R. copelandii* (Körb.) Th. Fr. (KU687456) and one ITS and one mtSSU sequence of *R. jemtlandicum* (Malme) Malme (AF483617, AF483185) as outgroups. There are no published phylogenies showing a sister relationship between the *R. badioatrum* species complex and *R. copelandii*/*R. jemtlandicum*, but those two species are very similar to those of the *R. badioatrum* species complex and differs mainly in having a greenish, K–, epihymenium which contains crystals of lichen substances (Timdal & Holtan-Hartwig 1988). The datasets hence consisted of 42 ITS and 12 mtSSU sequences (Table 1).

In addition to the sequenced material, we have examined about 350 specimens filed under *R. badioatrum* and *R. cinereonigrum* in O. A selection of those specimens are listed in the taxonomic part. Type material was either borrowed from the herbaria in Geneva (G), Turku (TUR), and Vienna (W) or studied during a visit to Helsinki (H).

*Morphology*: The collections were studied under dissecting and compound microscopes, in the latter in water, 10% KOH (K), and lactophenol cotton blue (LCB). Polarized light was used to locate crystals of lichen substances in the apothecia and thalli. Iodine reactions in the medulla, hymenium, and asci were studied after pretreatment with K in a modified Lugol's solution where water was replaced by 50% lactic acid (KI reaction). The length and breadth of the ascospores were measured

**Table 1.** Sequences used for the phylogenetic reconstructions, with specimen ID, current species identification, original species identification, voucher information, geographical origin, and main componds. New sequences are indicated in bold. DIF: diffractaic acid, GYR: gyrophoric acid, NONE: no lichen substances, NOR: norstictic acid, STI: stictic acid.

| ID | Species | Original epithet | Voucher | Geography | Main Compound | ITS | mtSSU |
|---|---|---|---|---|---|---|---|
| 1 | badioatrum | badioatrum 1 | Timdal 11289 (O-L-163350) | Norway, Telemark | NONE | **PP941850** | – |
| 2 | badioatrum | badioatrum 1 | Timdal 11398 (O-L-163459) | Norway, Hordaland | NONE | **PP941116** | – |
| 3 | badioatrum | badioatrum 1 | Timdal 11426 (O-L-163487) | Norway, Hordaland | NONE | **PP941851** | – |
| 4 | badioatrum | badioatrum 1 | Timdal 11468 (O-L-163529) | Norway, Hedmark | NONE | **PP941112** | – |
| 5 | badioatrum | cinereonigrum | Timdal 11490 (O-L-163551) | Norway, Hedmark | STI | **PP941115** | – |
| 6 | badioatrum | cinereonigrum | Timdal 11491 (O-L-163552) | Norway, Hedmark | STI | **PP941852** | **PP941871** |
| 7 | badioatrum | badioatrum 1 | Timdal 11637 (O-L-163698) | Norway, Nordland | NONE | **PP941853** | – |
| 8 | badioatrum | badioatrum 1 | Timdal 11767 (O-L-163824) | Norway, Oppland | NONE | KU687450 | – |
| 9 | badioatrum | badioatrum 1 | Timdal 11782 (O-L-163839) | Norway, Buskerud | NONE | KU687453 | – |
| 10 | badioatrum | badioatrum 1 | Timdal 12177 (O-L-170677) | Norway, Finnmark | NONE | **PP941854** | **PP941872** |
| 11 | badioatrum | badioatrum 1 | Timdal 12223 (O-L-170723) | Norway, Finnmark | NONE | **PP941855** | **PP941873** |
| 12 | badioatrum | badioatrum 1 | Timdal 12318 (O-L-170818) | Norway, Finnmark | NONE | **PP941856** | **PP941874** |
| 13 | badioatrum | badioatrum 1 | Haugan 10449 (O-L-174026) | Norway, Nordland | NONE | **PP941114** | – |
| 14 | badioatrum | badioatrum 1 | Timdal 18711 (O-L-227813) | Norway, Nordland | NONE | **PP941857** | **PP941875** |
| 15 | badioatrum | badioatrum 1 | Haugan & Timdal YAK27/06 (O-L-19248) | Russia, Magadan oblast | NONE | **PP941858** | **PP941876** |
| 16 | badioatrum | badioatrum 1 | Haugan & Timdal YAK32/24 (O-L-19365) | Russia, Magadan oblast | NONE | **PP941859** | **PP941877** |
| 17 | cinereonigrum | cinereonigrum | Haugan 8936 (O-L-165507) | Norway, Sør-Trøndelag | STI | **PP941110** | – |
| 18 | cinereonigrum | cinereonigrum | McCune 35907 (hb McCune) | USA, Oregon | STI | **PP941860** | **PP941878** |
| 19 | sinense | sinense | SDNU20210777 | China | – | OQ626899 | – |
| 20 | sinense | sinense | SDNU20210791 | China | – | OQ626900 | – |
| 21 | sinense | sinense | SDNU20150706 | China | – | MH979400 | – |
| 22 | sinense | sinense | SDNU20150715 | China | – | MH979401 | – |
| 23 | sinense | sinense | KUN46581 | China | – | MH979402 | – |
| 24 | sinense | sinense | 20181590 | China | – | MZ188998 | – |
| 25 | sinense | sinense | 20181676 | China | – | MZ188999 | – |
| 26 | sinense | badioatrum s.l. | Timdal 11749 (O-L-163802) | Norway, Sør-Trøndelag | GYR | **PP941109** | – |
| 27 | vulgare | badioatrum 2 | Timdal 11944 (O-L-170444) | Finland, Inarin Lappi | DIF | **PP941861** | **PP941879** |
| 28 | vulgare | badioatrum 2 | Timdal 11492 (O-L-163553) | Norway, Hedmark | DIF | **PP941113** | – |
| 29 | vulgare | badioatrum 2 | Timdal 11766 (O-L-163823), holotype | Norway, Oppland | DIF | **PP941862** | – |
| 30 | vulgare | badioatrum 2 | Haugan 8776 (O-L-165364) | Norway, Hedmark | DIF | **PP941863** | – |
| 31 | vulgare | badioatrum 2 | Haugan 9258 (O-L-165985) | Norway, Hedmark | DIF | **PP941864** | – |
| 32 | vulgare | badioatrum 2 | Timdal 11966 (O-L-170466) | Norway, Finnmark | DIF | **PP941865** | – |
| 33 | vulgare | badioatrum 2 | Timdal 12107 (O-L-170607) | Norway, Finnmark | DIF | **PP941866** | – |
| 34 | vulgare | badioatrum 2 | Timdal 12207 (O-L-170707) | Norway, Finnmark | DIF | **PP941867** | – |
| 35 | vulgare | badioatrum 2 | Timdal 12222 (O-L-170722) | Norway, Finnmark | DIF | **PP941868** | – |
| 36 | vulgare | badioatrum 2 | Timdal 12320 (O-L-170820) | Norway, Finnmark | DIF | **PP941108** | – |
| 37 | vulgare | badioatrum 2 | Timdal 12371 (O-L-170871) | Sweden, Lule lappmark | DIF | **PP941869** | **PP941880** |
| 38 | vulgare | badioatrum 2 | Rui & Timdal 16064 (O-L-204662) | Slovakia | DIF | **PP941111** | – |
| 39 | sp. 1 | sp. | SDNU20150553 | China | – | MH979403 | – |
| 40 | sp. 2 | badioatrum 2 | Timdal CH06/15 (O-L-206248) | China, Yunnan | DIF | **PP941870** | **PP941881** |
| 41 | copelandii | copelandii | Timdal 13108 (O-L-184521) | Norway, Hedmark | NOR | KU687456 | – |
| 42 | jemtlandicum | jemtlandicum | Haugan H1530 (O-L-119599) | Norway, Nordland | STI | AF483617 | AF483185 |

at 100× magnification and the measurements are given as X ± 1.5×SD, where X is the arithmetic mean and SD is the sample standard deviation.

*Thin-layer chromatography*: Thin-layer chromatography (TLC) was performed in accordance with the methods of Culberson (1972) and Culberson & Johnson (1982). We used solvent systems B' and/or C, and aluminium or occasionally glass plates. We have examined 238 specimens in O, including all those that were sequenced and all those that are listed in the taxonomic part.

*Sequencing*: Eleven of the new ITS sequences (KU687450, KU687453, PP941108–PP941116) were obtained through the NorBOL pipeline in the DNA barcode project OLICH (see Martinsen et al. 2019), in which DNA extraction, PCR amplification (using the primers ITS5 and ITS4 by White et al. 1990), Sanger sequencing, and preliminary sequence editing are outsourced to the Canadian Centre for DNA Barcoding (https://ccdb.ca).

We generated the remaining sequences (PP941850–PP941881) at the DNA lab at the Natural History Museum, University of Oslo in the period 2012–2020. Total genomic DNA was extracted from both fungarium and freshly collected specimens using the E.Z.N.A. SP Plant DNA Mini Kit (Omega Bio-tek, Inc., Norcross, Georgia, U.S.A.) according to the manufacturer's instructions. The sequencing followed slightly different amplification profiles over the years, but for the majority of the samples we amplified the ITS region in two parts, using the primer pairs ITS5/ITS-hypR or ITS5/ITS-lichR for ITS1 and ITS-lichF/ITS4 for ITS2 (White et al. 1990, Bendiksby & Timdal 2013) and mtSSU1/mtSSU3R for mtSSU (Zoller et al. 1999).

*Phylogenetic analyses*: The ITS and mtSSU datasets were iteratively aligned by SATé-II ver. 2.2.7 (Liu et al. 2012), using MAFFT ver. 6.717 (Katoh et al. 2005, Katoh & Toh 2008) as aligner, MUSCLE ver. 3.7 (Edgar 2004) as merger, FastTree ver. 2.1.4 (Price et al. 2010) as tree evaluator (i.e., under an approximate maximum likelihood criterion), and with the default settings in the GUI except that the number of iterations after last improvement in the maximum likelihood score was set to 10. Due to obvious alignment errors, the SATé alignments were manually improved and trimmed at the ends in BioEdit ver. 7.2.5 (Hall 1999) prior to phylogenetic analysis.

Bayesian inference (BI) and Maximum Likelihood (ML) phylogenetic hypotheses were inferred using MrBayes 3.2.7a (Huelsenbeck & Ronquist 2001, Ronquist & Huelsenbeck 2003) and RAxML 8.2.12 (Stamatakis 2014), respectively. In the Bayesian analyses, default settings were used, every 1000th generation was sampled, the burnin was set to 25%, and the posterior distribution of phylogenetic trees were summarized in 50% majority rule consensus (MRC) trees. MrBayes was terminated after the average deviation of split frequencies (ASDSF) had reached a level below 0.01. The ML analyses were run using raxmlGUI ver. 2.0.10 (Edler et al. 2021), and using the bundled software ModelTest ver. 0.1.7 (Darriba et al. 2020) to estimate the best substitution model. We ran 1000 rapid bootstrap replicates. The BI consensus trees and the ML best trees were edited in TreeGraph 2 (Stöver & Müller 2010) and inspected for topological incongruence. The ITS BI tree was collapsed at posterior probability (PP) < 0.95; the mtSSU BI tree was not collapsed. The bootstrap values (BS) above 70% in the ML trees were manually transferred to the BI trees.

## Results

We identified four chemotypes, based on the major compounds present. They were diffractaic acid (92 specimens), gyrophoric acid (four specimens), stictic acid (32 specimens; often with accessory compounds), and no lichen substances present (110 specimens). The chemotypes of the sequenced material are given in Table 1 and indicated with colour symbols in the phylogeny (Fig. 1). In that phylogeny, specimens containing diffractaic acid occurred in clade B2 and in one singleton from

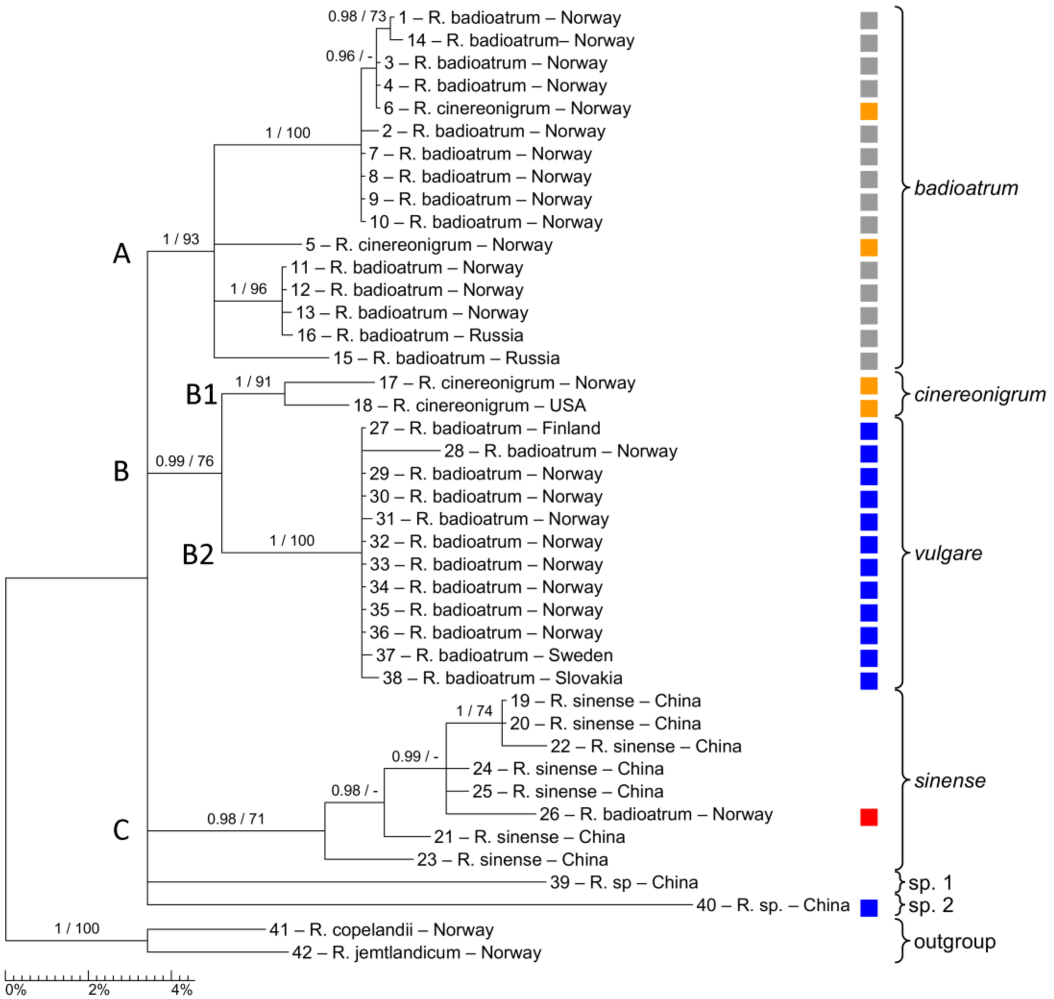


**Figure 1**. Bayesian 50% majority rule consensus tree, collapsed where PP < 0.95, of all known ITS sequences of the *Rhizocarpon badioatrum* species complex. Support values for the branches are given as PP/BS (for PP≥0.95/BS≥70%). Letters A–C indicate the major clades. Sequence numbers follow Table 1. ■: Diffractaic acid, ■: gyrophoric acid, ■: stictic acid, ■: no lichen substances.

China, the specimen containing gyrophoric acid in clade C, specimens containing stictic acid in clades A and B1, and the acid deficient specimens in clade A. For the remaining material examined by TLC, the chemotypes are indicated in the taxonomic part.

We produced 30 ITS and 11 mtSSU sequences for this paper (Table 1). The ITS alignment was 552 characters long and the ingroup included 160 variable and 106 parsimony informative sites. ModelTest estimated GTRGAMMA to be the best substitution model. The Bayesian analysis was terminated at 0.9 million generations when the ASDSF had fallen to 0.0086. The BI and ML phylogenetic hypotheses were congruent except for there being three more supported clades in the BI tree and six more supported clades in the ML tree. The Bayesian MRC tree, with the ML bootstrap

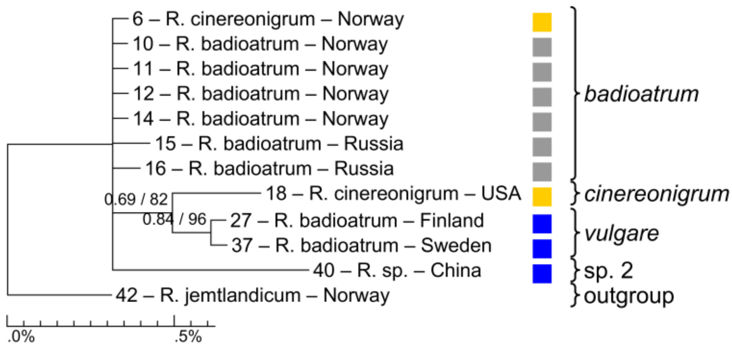


**Figure 2**. Bayesian 50% majority rule consensus tree, not collapsed, of all known mtSSU sequences of the *Rhizocarpon badioatrum* species complex. Support values for the branches are given as PP/BS (for PP≥0.95/BS≥70%). Sequence numbers follow Table 1. ■: Diffractaic acid, ■: stictic acid, ■: no lichen substances.

values above 70% superimposed, reveals three highly supported major clades, referred to as A, B, and C, and two long-branched singletons in a basal polytomy (Fig. 1). Clade A consists of two strongly supported subclades and two singletons. The acid deficient specimens were recovered in three of the clades and two of the four specimens containing stictic acid in two clades. Clade B consists of two highly supported subclades, one (B1) consisting of the two remaining specimens with stictic and one (B2) with all but one of the specimen containing diffractaic acid. Clade C consists of the GenBank sequences named *R. sinense* (chemistry unknown) and the single Norwegian specimen containing gyrophoric acid. The two unresolved accessions (Fig.1: 39 and 40) are both unidentified specimens originating from China; one retrieved from GenBank (chemistry unknown) and the other collected by us (diffractaic acid).

The mtSSU alignment was 802 characters long and the ingroup included 13 variable and 3 parsimony informative sites. ModelTest estimated GTRGAMMA to be the best substitution model. The Bayesian analysis was terminated at 2.0 million generations when the ASDSF had fallen to 0.0080. The BI and ML phylogenetic hypotheses were fully congruent. The Bayesian MRC tree, with the ML bootstrap values above 70% superimposed, reveals one clade of three specimens that is only moderately supported by ML bootstrapping and eight singletons form a basal polytomy (Fig. 2). The supported clade consists of a subclade of the two specimens with diffractaic acid and a singleton with stictic acid as their sister. The eight basal singletons consist of specimens with diffractaic acid, stictic acid, and acid deficient specimens (Fig. 2).

## Discussion

The ITS phylogeny recovered the acid deficient specimens in clade A and all but one of the diffractaic acid-containing specimens in subclade B2 (Fig. 1), with the other specimen in an unresolved position (R. sp. 2). Stictic acid-containing specimens are partly found in clade A and partly in subclade B1. We regard clade A as corresponding to *R. badioatrum* sp. 1 of Timdal & Holtan-Hartwig (1988), but with the addition of a stictic acid chemotype. The stictic acid chemotype seems to be uncommon, as all of the other examined specimens assumed to belong to clade A are acid deficient. Due to very few informative sites in the mtSSU dataset, there is no support for this species hypothesis in the mtSSU phylogeny. Regardless, based on the typification given below and the morphological features that seem consistent for this clade (i.e., *R. badioatrum* differing from *R. vulgare/R. cinereonigrum* in the colour and shape of the areolae, by the distinctness and thickness of the epihymenium, and the intensity of its reaction with K), we refer to this clade as the species *R. badioatrum* s. str.

In clade B, the correlation between the long-branched, highly supported subclades B1 and B2 and their respective chemotypes (Fig. 1), (B1 – stictic acid vs. B2 – diffractaic acid), makes us regard B1 and B2 as separate species hypotheses. This is consistent with the mtSSU topology, although the sample size is very low (Fig. 2). Clade B1 conforms with the concept of *R. cinereonigrum* in Timdal & Holtan-Hartwig (1988), except that stictic acid-containing specimens may also be found in *R. badioatrum* (Fig.1: clade A). Clade B2 conforms with *R. badioatrum* sp. 2 of Timdal & Holtan-Hartwig (1988), and we describe it below as the new species *R. vulgare*.

Clade C appears to correspond to *R. sinense*. Unfortunately, the specimens named *R. sinensis* from China in GenBank seem to be unpublished and their chemistry is unknown. Our Norwegian specimen, collected as *R. badioatrum* (26), nests among the *R. sinensis* accessions within clade C. It contains gyrophoric acid, as does the lectotype of *R. sinense* selected below.

Two long-branched and unresolved accessions (Fig. 1: 39 and 40) apparently represent undescribed Chinese species. One of them contains diffractaic acid, indicating that the compound is not exclusive to *R. vulgare* within the *R. badioatrum* species complex. As long as that species hypothesis is not proven to occur in Europe, we use diffractaic acid as diagnostic feature in the list of Nordic material given below.

## The Species

### 1. *Rhizocarpon badioatrum* (Flörke ex Schaer.) Th. Fr. Fig. 3

*Lichenogr. scand.* 1 (2): 613 (1874). – *Lecidea badioatra* Flörke ex Schaer., *Naturwiss. Anz. allg. Schweiz. Ges. gesammten Naturwiss.* 2: 9 (1818); type: Switzerland, 'Helvetia. Lecidea badio-atra.' [added in pencil: 'Schærer', 'J-', and 'incusa' and on a separate slip: '9. Lecidea badio-atra Fl. ms. Helvet. transalpina'] (H-ACH 207 – lectotype designated here; MBT: 10020983) [TLC: no lichen substances].

*Synonym*: *Rhizocarpon rivulare* (Körb.) Müll. Arg., *Bull. herb. Boissier* 1: 53 (1893). – *Buellia badioatra* β [var.] *rivularis* Flot. ex Körb., *Syst. lich. Germ.* (3): 223 (1855). – *Buellia rivularis* (Körb.) Kremp., *Denkschr. königl.-baier. bot. Ges. Regensburg* 4: 201 (1861); type: Switzerland, 'Grimsel', Schaerer, Lich. Helv. Exs. No. 179 (G-57805 – lectotype designated here; MBT: 10020984) [TLC: no lichen substances]; O L-192631, isolectotype [TLC: no lichen substances].

*Nomenclatural note*: The author of *Lecidea badioatra* is generally regarded to be Flörke in/ex Sprengel (1821). Schaerer's (1818) earlier paper, however, contains a valid diagnostic statement in a key separating *L. badioatra* from *L. lygaea* Ach. ('Crusta areolata-verrucosa; apotheciorum margine conspicuo'). Although Schaerer (1818) attributed the name to Flörke with the author citation 'Fl. Ms.' (and later as 'Flk! in litt. anni 1815'; Schaerer 1850), we believe the text in the dichotomous key was made by Schaerer and hence the author citation should be 'Flörke ex Schaer.'. The original material must be the material studied by Schaerer prior to August 1., 1818, the date given in the paper's heading. Schaerer's herbarium in G contains only duplicates of undated material distributed in 1828 in his *Lichenes Helvetici Exsiccati* (Fasc. 7–8) No. 179, and we do not know if this is a part of the original material. But Schaerer apparently sent a specimen of *L. badioatra* to Acharius (H-ACH 207) and since Acharius died on August 14, 1819, we find it likely that this

**Figure 3**. *Rhizocarpon badioatrum*. Norway, specimen 3 in Table 1 (O L-163459). Bar = 2 mm.

specimen is a part of the original material. It is hence here chosen as the lectotype. We believe H-ACH 207 is the specimen Fries (1874: 615) referred to when he stated that Acharius, after editing *Synopsis methodica Lichenum* (Acharius 1814), received material of *R. badioatrum* collected in Switzerland from Schaerer (see further under *Lecidea incusa* Ach., below).

In the protologue of *Buellia badioatra* var. *rivularis*, Koerber (1855) cited only one collection (Schaerer, *Lich. Helv. Exs.* No. 179), but he had clearly seen more specimens since he gave a general statement of its distribution. We have not examined Körber's herbarium in L, but we have chosen the exsiccate number in G (an isosyntype) as the lectotype since it agrees with the general understanding of the taxon.

*Description*: Thallus areolate and up to 10 cm diam.; hypothallus usually well developed and black; areolae up to 2 mm diam., medium brown to dark brown, sometimes partly greyish brown, dull, contiguous, thick, usually angular or crenulate, and more or less plane; medulla KI–. Apothecia up to 1 mm diam., black, epruinose, orbicular or angular, and remaining more or less plane and marginate; excipulum reddish brown in inner part, rim brownish black, and K+ red; hypothecium brown and K–; hymenium colourless; epihymenium reddish brown and K+ red; minute red granules may be present in the epihymenium (dissolving in K); ascospores 8 per ascus, 1-septate, soon becoming dark brown, and 27–38 × 13–19 µm (n = 59). Conidiomata not seen.

*Chemistry*: No lichen substances or rarely stictic acid.

*Habitat*: On siliceous rock, often at humid sites or near lakes and rivers. In the Nordic countries, both in the lowlands and in the mountains.

*Notes*: All specimens of the *R. badioatrum* species complex not containing lichen substances belong here (i.e., to *R. badioatrum* (Flörke ex Schaer.) Th. Fr.). In addition, two specimens containing stictic acid fell into the same clade in the phylogenetic analysis based on ITS data (Fig. 1: clade A). Timdal & Holtan-Hartwig (1988; as *R. badioatrum* sp. 1 and 2) states that *R. badioatrum* often differs from *R. vulgare/R. cinereonigrum* in the colour and shape of the areolae, by the distinctness and thickness of the epihymenium, and the intensity of its reaction with K. These differences are subtle, however, and we have refrained from trying to identifying possible stictic acid-containing specimens of *R. badioatrum* s. str. without a DNA sequence. Hence, the specimens listed below are all acid deficient, except for the two sequenced specimens containing stictic acid (O L-163551, O L-163552).

*Selected additional specimens examined*: **Finland**. *Päre-Pohjanmaa*: Simo, Rajasuo, prope lacum Syvälahdenjärvi, ad saxum graniticum, 1942-07-31, V. Räsänen, Räsänen, Lich. Fenn. Exs. 817 (O L-187351). *Uusimaa*: Helsinge, Dickursby, ad saxa in flumine, J.P. Norrlin, Nyander & Norrlin, Herb. Lich. Fenn. 727 (O L-187350). **Iceland**. *Akureyri*: Akureyri, nær sildoljefabriken, 1937-07-20, B. Lynge (O L-187443); *Eyjafjarðarsýsla*: Reistarárskarð, 1937-07-11, B. Lynge (O L-187450); *Nordur-Mulasysla*: Skjöldolfsstaðir, 1939-08-09, B. Lynge (O L-187446); *Reykjavik*: Effersey, 1937-07-05, B. Lynge (O L-187447). **Italy**. *Sondrio*: in alpibus Bormiensibus, vulgaris ad rupes, et saxa granitica humida, M. Anzi, Anzi, Lich. Lang. 191 (O L-187461); *Trentino*: im Thale unterhalb des Col Briccon unweit des Baches ober dem Travignolo bei Paneveggio in Südtirol, auf einem Porphyrblocke, 1888-07-17, F. Arnold, Arnold, Lich. Exs. 1395 (O L-187469). **Norway**. *Akershus*: Aurskog-Høland, c. 1.2 km ESE of Søndre Ovlin, 59.9801°N, 11.7328°E, 230 m alt., 1987-08-09, E. Timdal, 4951 (O L-162367); *Buskerud*: Hol, Haugestøl: Follaskaret, 60.6065°N, 7.8046°E, 1915-09, B. Lynge (O L-89889); Krødsherad, Laksegjuv, E of Ringnessætra, 60.2946°N, 9.5517°E, 600 m alt., 1982-06-15, E. Timdal, 3389b (O L-89858); Sigdal, Mt Holmevassnatten, 60.3001°N, 9.3288°E, 1100 m alt., on rock in brook, 2010-08-14, E. Timdal, 11782 (O L-163839); *Finnmark*: Alta, N end of lake Avzejavri, 69.7472°N, 23.3807°E, 300 m alt., on boulder at edge of birch forest, 2011-07-03, E. Timdal, 12318 (O L-170818); Båtsfjord, Båtsfjorddalen, hill E of river Storelva, 70.5763°N, 29.6545°E, 120 m alt., 1986-07-25, E. Timdal, 4687 (O L-89663); Berlevåg, c. 2 km S of Kjölneset, 1966-08-01, R. Moberg, 621 (UPS); Kautokeino, 2 km N of Biilacorut, 69.6504°N, 23.5264°E, 480 m alt., rock wall in the alpine region, 2011-07-04, E. Timdal, 12341 (O L-170841); Porsanger, Skoganvarri, S shore of lake Bajitjavri, 69.8338°N, 25.0893°E, on boulders in talus slope, 2011-06-30, E. Timdal, 12223 (O L-170723); Tana, S slope of Mt Rasttigaisa, 69.9901°N, 26.2973°E, 740 m alt., submerged in brook in the alpine region, 2011-06-28, E. Timdal, 12177 (O L-170677); *Hedmark*: Engerdal, South shore of lake Isteren, 61.9153°N, 11.8016°E, 645 m alt., on rocks at the sea shore, 2010-08-04, E. Timdal, 11490 (O L-163551); ibid., E. Timdal, 11491 (O L-163552); Grue, Shore of lake Røgden N of Neverhaugen, 60.4371°N, 12.4588°E, 280 m alt., siliceous boulder, 2010-09-30, R. Haugan, 9276 (O L-166003); Ringsaker, Godlidalen, between Mt Kotuva and Mt Taterungskampen, 61.2628°N, 10.8738°E, on a temporarily inundated rock in a small river, 1996-08-24, R. Haugan, 5302 (O L-44977); Trysil, just SW of bridge over river Trysilelva at Fossheim, 61.1777°N, 12.4477°E, 350 m alt., on rock near the river, 2010-08-03, E. Timdal, 11468 (O L-163529); Tynset, Gammeldalen, Kløftet, 62.2743°N, 10.9941°E, 750 m alt., on rocks in the river, periodically inundated, 1989-05-26, R. Haugan et al., 7241 (O L-152573); Våler, Kristensonkoia, 60.9292°N, 12.0758°E, 460 m alt., siliceous rock in roadcut, 2010-09-20, R. Haugan, 9352 (O L-166089); Åmot, N Glesåa, i kløfta N for Granbergbua og mot S Storåsen, 61.4284°N, 11.4088°E, 585 m alt., bekkekløft med gammel granskog og bergvegger. På steiner i elva, 2004-08-13, R. Haugan, åmot13804c5 (O L-131757); *Hordaland*: Ullensvang, E slope of Dyrskarnuten, 59.8462°N, 7.0581°E, 1060 m alt., rock outcrop in alpine zone, 2010-07-27, E. Timdal, 11398 (O L-163459); Ullensvang, Middyrelva, 59.8532°N, 7.0563°E, 1060 m alt., on rocks by the river, 2010-07-27, E. Timdal, 11426 (O L-163487); Ulvik, Finse: Sandalshøgen, 60.6176°N, 7.5264°E, Aug-15, B. Lynge (O L-89917); Voss, Lønehorgje, 1919-07, B. Lynge (O L-89908); *Møre og Romsdal*: Rauma, E of Skirimoen, 62.4284°N, 7.9466°E, 130 m alt., siliceous boulder, 2010-10-02, R. Haugan, 9311 (O L-166038); *Nordland*: Bindal, Kollbotnet, Digermulen, 65.0274°N, 12.1903°E, 10 m alt., calcareous seashore rock, 2011-08-14, R. Haugan, 10449 (O L-174026); Bodø, Skjerstad: Snelifossen waterfall, 9 km S of Misvær, 67.0352°N, 15.0574°E, 270 m alt., on rock in the marginal zone of the river, 1990-07-16, R. Haugan, 1560 (O L-38129); Bodø, Skjerstad: Snelifossen waterfall, 9 km S of Misvær, 67.0352°N, 15.0574°E, 270 m alt., on rock in the marginal zone of the river, 1990-07-16, R. Haugan, 1561b (O L-89668); Hattfjelldal, Kjerringtinden, 65.7438°N, 13.8969°E, 670 m alt., siliceous rock outcrop in low alpine meadow, 2011-08-18, R. Haugan, 10571 (O L-174148); Hemnes, Korgfjellet, NE slope of hill S of the pass (just on the, 66.0527°N, 13.6987°E, 580 m alt., rock wall, facing E, 2010-08-09, E. Timdal, 11732 (O L-163785); Saltdal, river Graddiselva, 500 m WNW of Graddis fjellstue, 66.7448°N, 15.7305°E, 430 m alt., rocks by the river, 2010-08-08, E. Timdal, 11637 (O L-163698); Saltdal, by the road to Skaiti, 66.7725°N, 15.6975°E, 550 m alt., on vertical/overhanging, SW-facing, exposed rock wall in sub-/low alpine zone, 2020-08-09, E. Timdal, 18711 (O L-227813); Vefsn, along river E of Tennvatnet, 66.0512°N, 13.6445°E, 380 m alt., humid riverside rock, 2011-08-19, R. Haugan, 10624 (O L-174201); *Nord-Trøndelag*: Steinkjer, old copper mines 1.5 km E of Mokk, 63.9653°N, 12.1331°E, 500 m alt., 2011-08-09, M. Bendiksby et al., 12419 (O L-175698); *Oppland*: Dovre, Fokstua: Graahø, 62.0958°N, 9.2930°E, 1925-08, B. Lynge (O L-89876); Etnedal, S of the bridge at Steinsrud, W side of river Etna, 60.9482°N, 9.6260°E, 390 m alt., on rock outcrop close to the river, 2011-05-29, R. Haugan & E. Timdal, 11923 (O L-169831); Gausdal, Holsbrua, just W of the bridge, 61.1789°N, 9.8707°E, 760 m alt., on schistose rock close to the river, 2011-05-29, R. Haugan & E. Timdal, 11917 (O L-169825); Lillehammer, Svarverudberget, 61.2316°N, 10.4207°E, 270 m alt., siliceous rock in boulderscree, 2010-09-16, R. Haugan, 8956 (O L-165525); Lom, Visdalen, scree E of Kyrkjeglupen, 61.5508°N, 8.3132°E, 1500 m alt., on large boulder, 1990-08-26, R. Haugan, H1734 (O L-19696); Østre Toten, Jenssætra, along brook Jenssæterelva, 60.5470°N, 10.8519°E, 420 m alt., rock in the brook, 2011-05-12, R. Haugan, 9856 (O L-173192); Sel, Høvringen, 61.8890°N, 9.4781°E, 940 m alt., rock outcrop by river, 2010-08-10, E. Timdal, 11767 (O L-163824); Skjåk, Tora river gorge, 62.0197°N, 7.8649°E, 860 m alt., siliceous rock, 2000-08-11, R. Haugan, 8549 (O L-159746); *Oslo*: Nordmarka: Sandungen, 60.1211°N, 10.6151°E, 1906-04-12, B. Lynge (O L-89834); *Sør-Trøndelag*: Oppdal, Dovre: Søndre Knutshø (høifjeldet), 62.3064°N, 9.6847°E, 1916-08-18, B. Lynge (O L-89924); Røros, Skaarhammerdalen, 62.5739°N, 11.3170°E, 650 m alt., 1919-07-28, A.H. Magnusson, 3665 (O L-89707); *Telemark*: Vinje, Grungebru, 59.6987°N, 7.8122°E, 540 m alt., boulders in N-facing slope, near lake, 2010-06-30, E. Timdal, 11289 (O L-163350); *Troms*: Balsfjord, valley between Mt Istind and Mt Lemmetfjell, 69.1482°N, 19.8798°E, 500 m alt., 1984-05-31, E. Timdal, 4141 (O L-89661); Bardu, Tromsø amt: Indset, 68.6580°N, 18.8207°E, 1911-06-09, B. Lynge (O L-113878); Kåfjord, Kåfjorddalen, Miessevárri, N of lake Miesevárlouhkát, 69.4003°N, 21.0185°E, 590 m alt., sliliceous rock outcrop, 2014-07-07, R. Haugan, 141718 (O L-198768); Målselv, Rostafjeld, 1862, J.M. Norman (O L-89926). **Russia**. *Karelia Rep.*: Karelia Ladogensis: Kurkijoki, insula Pätäkänsaari prope ins. Heposaari, ad rupem apricam prope lacum Laatokka, 1938-03-25, V. Räsänen, Räsänen, Lich. Fenn. Exs. 648 (O L-187352); *Magadan Oblast*: Yagodninskii region: c. 20 km SSE of Orotukan, 62.10°N, 151.85°E, 610 m alt., rock wall, 1992-07-27, R. Haugan & E. Timdal, YAK27/06 (O L-19248); Magadan: hill c. 1-2 km N of Snezhnaya Dolina (=town c. 20 km N of Magadan), 59.7667°N, 150.8333°E, 1992-07-30, R. Haugan & E. Timdal, YAK32/24 (O L-19365); *Novaya Zemlya*: Solbugten i Mashigin, 1921-08-25, B. Lynge (O L-187437). **Svalbard**. Spitsbergen, Virgohamna, 79.70°N, 10.95°E, 1928-07-07, O.A. Høeg (O L-187415). **Sweden**. *Jämtland:* Handöl, Handölsfallet, 1910-07-22, G.O. Malme (O L-187451); *Norrbotten*: Karesuando: Guolbanåive, 1910-07-09, B. Lynge (O L-187340); *Torne Lappmark*: stream 800 m WNW of Tornehavn, 68.4345°N, 18.6515°E, 350 m alt., on rocks by the stream, 2014-07-08, E. Timdal, 13470-2 (O L-195681). **Switzerland.** *Uri*: im Maderanerthal, an Granitfelsen, P. Hepp, Hepp, Flecht. Eur. 753 (O L-187336).

### 2. *Rhizocarpon cinereonigrum* Vain. Fig. 4

*Acta Soc. Fauna Fl. fenn.* 53, 1: 332 (1922).

*Type*: Finland, Etelä-Häme, Tammela, Kuusto, ad saxa diabasicum, 1867, Kullhem A. (TUR V-22009, holotype).

*Nomenclatural note*: The holotype is the only specimen cited by Vainio (1922) in the protologue. It consists of a few, small pieces which we regarded as too scanty for TLC examination. The assumption that it contains stictic acid is based on Vainio's (1922) description: 'Thallus … verrucis … intus albis et KHO lutescentibus' (Thallus … by warts … [that are] inside white and K+ yellow). We confirm Vainio's statement that the epihymenium is dark reddish brown, K+ red, and

**Figure 4**. *Rhizocarpon cinereonigrum*. Norway, specimen 17 in Table 1 (O L-165507). Bar = 2 mm.

we did not observe crystals in the epihymenium (i.e., the holotype belongs in the *R. badioatrum* species complex, not in *R. copelandii* or *R. jemtlandicum* which have a greenish, K–, epihymenium containing crystals of lichen substances). Specimens containing stictic acid occur both in clade A and subclade B1 of the ITS phylogeny (Fig. 1). There are slight morphological differences between these clades (cfr. Timdal & Holtan-Hartwig 1988, as *R. badioatrum* sp. 1 and 2, respectively), however, and we tentatively place the holotype of *R. cinereonigrum* in subclade B1, which we think is in best agreement with the use of the name. The scanty condition of the holotype could have justified an epitypification, but our two sequenced specimens are not ideal as we think they are collected in areas too far from that of the holotype.

*Notes*: The morphological characterization of *R. cinereonigrum* by Timdal & Holtan-Hartwig (1988) may not be valid, as their concept of the species included stictic acid-containing specimens which are here placed in *R. badioatrum* s. str. We have not attempted a revision of the 28 stictic acid-containing specimens in O that are not sequenced. This would have required comprehensive sequencing to establish any morphological differences; a work that is outside the scope of this paper and probably currently impossible due to the age of the material. Hence, the list of examined specimens is restricted to the two sequenced specimens.

*Additional specimens examined*: **Norway.** *Sør-Trøndelag*: Orkland, Fjordadalen, 63.5530°N, 9.5978°E, 180 m alt., siliceous boulder in boulderscree, 2010-07-11, R. Haugan, 8936 (O L-165507). **USA**. *Oregon*: Linn Co., Lava flow on Highway 126, 44.4108°N, 122.0025°W, 925 m alt., ca. 3000 year-old lava flow with scattered *Pseudotsuga*, *Tsuga heterophylla*, *Taxus brevifolia*, and *Castanopsis chrysophylla*; on rock, basalt, B. McCune, 35907 (hb McCune).

**Figure 5**. *Rhizocarpon sinense*. Norway, specimen 26 in Table 1 (O L-163802). Bar = 2 mm.

### 3. *Rhizocarpon sinense* Zahlbr. Fig. 5

in Handel-Mazzetti, *Symbolae Sinica* 3: 124 (1930).

*Type*: China, Yunnan, 'prov. Yünnan bor.-occid., ad confines Tibeticas sub jugo Doker-la, 4225 m alt., in regionis alpinae saxis, substr. granitico, schistaceo, quarzti', 1915-09-17, H. v. Handel-Mazzetti 8088 (W, lectotype designated here; MBT: 10020985) [TLC: gyrophoric acid].

*Nomenclatural note*: Three specimens are mentioned in the protologue: Handel-Mazzetti 1012, 2647, and 8088. No. 1012 was not found in W and No. 2647 does not contain any *Rhizocarpon* species (but mainly a *Lecidella* sp.). No. 8088 is a *Rhizocarpon* fitting the description and is here chosen as the lectotype.

*Notes*: We assume gyrophoric acid is diagnostic for *R. sinense* and hence use that name for clade C. In addition to the sequenced specimen from Norway, we also report three additional specimens in O containing gyrophoric acid from Iceland and Norway. No diagnostic morphological features are evident in the limited material at hand.

*Additional specimens examined*: **Iceland**. *Strandasysla*: Granumyrartunga, 1937-07-21, B. Lynge (O L-187448). **Norway.** *Nordland*: Saltdal, 'Saltd.‘, 1824-06, S.C. Sommerfelt (O L-162323); Steigen, Løvø, J.M. Norman (O L-162335); *Sør-Trøndelag*: Oppdal, river Driva between Grønbakken and Kongsvoll, 62.2842°N, 9.5979°E, 910 m alt., rock outcrop by the river, 2010-08-10, E. Timdal 11749 (O L-163802)

**Figure 6**. *Rhizocarpon vulgare*, holotype. Norway, specimen 29 in Table 1 (O L-163823). Bar = 2 mm.

### 4. *Rhizocarpon vulgare* Timdal, E.J. Möller & Bendiksby, sp. nov. Fig. 6

*MycoBank No.*: MB854461.

*Diagnosis*: Differs from the other currently recognized species of the *Rhizocarpon badioatrum* species complex in containing diffractaic acid.

*Type*: Norway, Oppland, Sel, Høvringen, 61.8890N, 9.4781E, 940 m alt., rock outcrop by river, 2010-08-10, E. Timdal 11766 (O-L-163823, holotype) [TLC: diffractaic acid; ITS: PP941862].

*Possible synonym*: *Rhizocarpon badioatrum* β [var.] *vulgare* (Körb.) Th. Fr., *Lichenogr. scand.* 1 (2): 614 (1874). – *Buellia badioatra* α [var.] *vulgaris* Körb., *Syst. lich. Germ.* (3): 223 (1855), nom. illeg. (Art. 52.1); type: not designated.

*Nomenclatural note*: *Buellia badiaoatra* α [var.] *vulgaris* Körb. is an illegitimate, superfluous name as the taxon originally included the synonyms *Lecidea confervoides* α (= var. *candida* Schaer.) and ε (= var. *fuscoatra* [L.] Schaer.) in Schaerer (1850: 113).

*Description*: Thallus areolate and up to 10 cm diam.; hypothallus usually well-developed and black; areolae up to 1 mm in diam., greyish brown to dark brown, dull, usually more or less contiguous, orbicular or angular to slightly crenulate, and plane to moderately convex; medulla KI–. Apothecia up to 1 mm in diam., black, epruinose, orbicular, and remaining more or less plane and marginate; excipulum blackish brown, and K+ red or K–; hypothecium brown and K–; hymenium colourless;

epihymenium dark brown and K+ red; no crystals or granules in the apothecia; ascospores 8 per ascus, 1-septate, soon becoming dark brown, and 26–35 × 12–17 μm (n = 65). Conidiomata not seen.

*Chemistry*: Diffractaic acid by TLC; spot tests: medulla PD–, K–, C–.

*Habitat*: On siliceous rock in open locations. In the Nordic countries, occurring both in the lowlands and in the mountains.

*Notes*: The species differs from *R. badioatrum* in often forming more rounded, convex, and greyish areolae; in having a more narrow and more sharply delimited epihymenium with a less intense K+ red reaction; and in containing diffractaic acid (cf. Timdal & Holtan-Hartwig 1988). We assume diffractaic acid is diagnostic for the species in the Nordic countries, and the list below is a selection among the 92 specimens examined by TLC. However, there is a specimen from China containing diffractaic acid well outside the *R. vulgare*-clade in our phylogeny (Fig. 1: specimen 40). More sequenced specimens should establish the distribution of the Chinese taxon.

*Selected additional specimens examined*: **Finland**. *Inarin Lappi*: NE shore of lake Inari, 69.2540°N, 27.9278°E, exposed, acidic rock, 2011-06-22, E. Timdal, 11944 (O L-170444). **Norway**. *Akershus*: Aurskog-Høland, c. 1 km E of Søndre Mangen, 59.9521°N, 11.7842°E, 195 m alt., 1987-08-09, E. Timdal, 4955 (O L-162366); Bærum, Kolsås, 59.9255°N, 10.5214°E, 1928-06-17, B. Lynge (O L-89972); Lillestrøm, S of Klokkerud, 59.9116°N, 11.1848°E, 180 m alt., siliceous rock in open pine forest, 2010-05-06, R. Haugan, 9497 (O L-166348); Nordre Follo, knoll SE of Sandbakken (Oslo), 59.8236°N, 10.9350°E, 240 m alt., rock in pine forest, 1980-04-29, E. Timdal, 1073b (O L-16396); *Buskerud*: Hol, i skoggrænsen under Oddenakken, 1915-07, B. Lynge (O L-90001); *Finnmark*: Alta, N end of lake Avzejavri, 69.7472°N, 23.3807°E, 300 m alt., on boulder at edge of birch forest, 2011-07-03, E. Timdal, 12320 (O L-170820); Båtsfjord, top of Båtsfjorddalen, 70.5357°N, 29.6936°E, 240 m alt., rock outcrop, silicate rock, 2011-06-26, E. Timdal, 12107 (O L-170607); Karasjok, E shore of lake Dievaljavri, 69.5195°N, 25.4568°E, 310 m alt., on lacustrine rock field, 2011-06-30, E. Timdal, 12207 (O L-170707); Kautokeino, 2 km N of Biilacorut, 69.6504°N, 23.5264°E, 480 m alt., rock wall in the alpine region, 2011-07-04, E. Timdal, 12343 (O L-170843); Porsanger, Skoganvarri, S shore of lake Bajitjavri, 69.8338°N, 25.0893°E, on boulders in talus slope, 2011-06-30, E. Timdal, 12222 (O L-170722); Sør-Varanger, hillside NE of Ferdesmyra, 69.7585°N, 29.3105°E, 100 m alt., vertical rock wall and boulders, acidic rock, 2011-06-22, E. Timdal, 11966 (O L-170466); Vadsø, Skallneset, 70.1380°N, 30.3329°E, 20 m alt., boulders in rock field, 2011-06-25, E. Timdal, 12063 (O L-170563); *Hedmark*: Alvdal, Østerdalen: Lille Elvedalen, 1910-08-24, B. Lynge (O L-89992); Eidskog, between Enderud and lake Fjølungen, 60.0784°N, 12.2411°E, 220 m alt., 1987-08-16, E. Timdal, 4971 (O L-162369); Elverum, Hellemundsberget, 60.7836°N, 11.5943°E, 270 m alt., siliceous rock, 2010-06-09, R. Haugan, 8874 (O L-165451); Engerdal, South shore of lake Isteren, 61.9153°N, 11.8016°E, 645 m alt., on rocks at the sea shore, 2010-08-04, E. Timdal, 11492 (O L-163553); Grue, Shore of lake Røgden N of Neverhaugen, 60.4384°N, 12.4589°E, 280 m alt., siliceous boulder, 2010-09-30, R. Haugan, 9285 (O L-166012); Kongsvinger, Føttaskjæra, 60.3672°N, 12.0439°E, 200 m alt., siliceous rock in open pine forest, 2010-04-27, R. Haugan, 9487 (O L-166338); Nord-Odal, Songkjølen, between Ulvtjernet and Steintjernet, 60.3343°N, 11.5182°E, 450 m alt., siliceous boulder in pine forest, 2010-10-20, R. Haugan, 9002 (O L-165654); Stange, Kleiverud, 60.5508°N, 11.2490°E, 170 m alt., siliceous rock, 2010-04-15, R. Haugan, 9015 (O L-165665); Stor-Elvdal, W of Rødfjellet, 61.6396°N, 10.9054°E, 500 m alt., rock in boulderscree, 2010-06-29, R. Haugan, 8776 (O L-165364); Trysil, just SW of bridge over river Trysilelva at Fossheim, 61.1777°N, 12.4477°E, 350 m alt., on rock near the river, 2010-08-03, E. Timdal, 11469 (O L-163530); Tynset, Kvikne, SW of Breivadsetra, 62.6622°N, 10.1691°E, 1998-04-13, R. Haugan, 7473b (O L-168195); Åmot, W of Åsta bridge, along the river, 61.0771°N, 11.3452°E, 240 m alt., basic rock, 2010-05-26, R. Haugan, 9403 (O L-166152); Åsnes, NE of Glorviktjerna, 60.7571°N, 12.3169°E, 240 m alt., boulder in open pine forest, 2010-09-29, R. Haugan, 9258 (O L-165985); *Oppland*: Gausdal, Holsfossen, 61.1792°N, 9.8718°E, 760 m alt., mica schist on river bank, 2011-05-29, R. Haugan & E. Timdal, 9986 (O L-173361); Gran, Brandbu, 59.9689°N, 10.5010°E, 1908-04-20, B. Lynge (O L-113546); Lillehammer, Svarverudberget, 61.2316°N, 10.4207°E, 270 m alt., siliceous rock in boulderscree, 2010-09-16, R. Haugan, 8958 (O L-165527);

Ringebu, Jammerdalshøgda, 61.5930°N, 10.3338°E, 1090 m alt., 2011-08-07, M. Bendiksby et al., 12458 (O L-175737); Vang, N slope of Melviknøse, 61.2780°N, 8.1637°E, 1130 m alt., siliceous boulder in alpine heath, 2011-06-13, R. Haugan, 10188 (O L-173703); Vestre Toten, Shore of lake Einavannet W of Stormyra nature reserve, 60.5189°N, 10.6400°E, 400 m alt., sunny siliceous rock, 2011-05-13, R. Haugan, 9864 (O L-173200); Østre Toten, Jenssætra, along brook Jenssæterelva, 60.5470°N, 10.8519°E, 420 m alt., vertical siliceous rock, humid situated, 2011-05-12, R. Haugan, 9855 (O L-173191); *Oslo*: Sjådalen, 59.9726°N, 10.7224°E, 300 m alt., on sunny rocks, 1947-07-20, A.H. Magnusson, 20876 (O L-89979); *Troms*: Balsfjord, Vassdalsfjellet, 69.0760°N, 19.8082°E, 480 m alt., 1984-06-11, E. Timdal, 4161 (O L-89662); Bardu, Indset, 68.6583°N, 18.8403°E, 1911-06-09, B. Lynge (O L-90007); Ibestad, Havnvik, 68.7793°N, 17.1702°E, 1914-08-24, B. Lynge (O L-90011). **Slovakia**, High Tatra Mountains, trail from Chata pri Zelenom plese to lake Biele pleso, 49.2135°N, 20.2238°E, 1570 m alt., on vertical face of boulder by the trail, acid rock, 2016-05-25, S. Rui & E. Timdal, 16064 (O L-204662). **Sweden**. *Lule Lappmark*: W of Stora Luleälven, at route 45 crossing the railway NW of Ligga, 66.8028°N, 19.8716°E, on stone on the ground in pine forest, 2011-07-05, E. Timdal, 12371 (O L-170871); *Närke*: Stenkullen i Askersunds landsförs., 1869, P.J. Hellbom (O L-187459); *Södermanland*: St. Malm, Brännkärr, 1900-06-22, G.O. Malme (O L-187458); *Uppland*: Wärmdö v. Stockholm, 1910-10, B. Lynge (O L-187455); *Västerbotten*: by route E4 between Granberget and Klintsjön, 64.1968°N, 21.0047°E, 60 m alt., boulder in open, dry pine forest, 2014-06-28, E. Timdal, 13368-4 (O L-195478).

## Excluded species

Three additional species are listed as synonyms of *R. badioatrum* in Zahlbruckner (1926–1927):

● *Rhizocarpon atroalbum* (L.) Arnold, *Flora* 54: 148 (1871). – *Lichen atro-albus* L., *Sp. Pl.*: 1141 (1753), nom. utique rej. (ICN, Appendix V. B); type: not designated.

● *Lecidea incusa* Ach., *Synops. Lich.*: 33 (1814); type: 'Helvetia. Lecidea incusa.' [added in pencil: Schleich 152, a' and 'badio-at'] (H-ACH 202 – holotype) [= *Acarospora* sp.].

We believe H-ACH 202 is the specimen Fries (1874: 615) referred to when he stated that the miserable and very minute specimen of *L. incusa* in Acharius' herbarium is an *Acarospora* species, and that material of *R. badioatrum* was added later to the herbarium (H-ACH 207, see note under *R. badioatrum*, above).

● *Lecidea atrobadia* Nyl., *Flora* **55**: 361 (1872); type: 'Scotia. No 6 ad saxa quartzosa apud cacumen montis Ben-y-gloe. Crombie' (H-NYL 10000 – lectotype designated here; MBT: 10020982) [TLC: Stictic acid] [= *R. polycarpum* (Hepp) Th. Fr.].

The lectotype belongs in *Rhizocarpon polycarpum*, and *L. atrobadia* actually predates *R. polycarpum* which has priority at species level only from 1874. The nomenclature of that species is beyond the scope of this paper, however.

**Acknowledgements**: We acknowledge generous financial support (project Nos. 70184216, 70184227) from the Norwegian Taxonomy Initiative (NTI; Norske Artsprosjektet) administered by The Norwegian Biodiversity Information Centre (NBIC; Artsdatabanken). The Norwegian Barcode of Life (NorBOL) funded the sequencing at the Canadian Centre for DNA Barcoding. We also thank the curators of G, TUR, and W for the loan of type specimens, H for access to Acharius' and Nylander's collections during our visit, to Bruce McCune for loan of material, and to Sonja D. Kistenich for work at the DNA laboratory at Natural History Museum in Oslo.

## References


Acharius, E. 1814. *Synopsis methodica lichenum*. Lund, 392 pp.

Bendiksby, M. & Timdal, E. 2013. Molecular phylogenetics and taxonomy of *Hypocenomyce* sensu lato (Ascomycota: Lecanoromycetes): Extreme polyphyly and morphological/ ecological convergence. *Taxon* **62**: 940–956. https://doi.org/10.12705/625.18.

Bi, Y.-X., Zhang, Y. M., Zhao, Z.-T. & Hu, L. 2022. Four species of *Rhizocarpon* subg. *Phaeothallus* in China. *Mycotaxon* **137**: 701–713.

Culberson, C. F. 1972. Improved conditions and new data for the identification of lichen products by a standardized thin-layer chromatographic method. *Journal of Chromatography* **72**: 113–125. https://doi.org/10.1016/0021-9673(72)80013-X.

Culberson, C. F. & Johnson, A. 1982. Substitution of methyl tert.-butyl ether for diethyl ether in standardized thin-layer chromatographic method for lichen products. *Journal of Chromatography* **238**: 483–487. https://doi.org/10.1016/S0021-9673(00)81336-9.

Darriba, D., Posada, D., Kozlov, A. M., Stamatakis, A., Morel, B. & Flouri, T. 2020. ModelTest-NG: A new and scalable tool for the selection of DNA and protein evolutionary models. *Molecular Biology and Evolution* **37**: 291–294. https://doi.org/10.1093/molbev/msz189.

Edgar, R. C. 2004. MUSCLE: a multiple sequence alignment method with reduced time and space complexity. *BMC Bioinformatics* **5**: 113. https://doi.org/10.1186/1471-2105-5-113.

Edler, D., Klein, J., Antonelli, A. & Silvestro, D. 2021. raxmlGUI 2.0: A graphical interface and toolkit for phylogenetic analyses using RAxML. *Methods in Ecology and Evolution* **12**: 373–377. https://doi.org/10.1111/2041-210X.13512.

Fries, T. M. 1874. *Lichenographia Scandinavica. Vol. I, Pars II*. Uppsala, pp 325–639.

GBIF 2024. *Global Biodiversity Information Facility*. https://www.gbif.org.

Hall, T. A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* **41**: 95–98.

Huelsenbeck, J. P. and Ronquist, F. 2001. MRBAYES: Bayesian inference of phylogeny. *Bioinformatics* **17**: 754–755. https://doi.org/10.1093/bioinformatics/17.8.754.

Katoh, K. & Toh, H. 2008. Recent developments in the MAFFT multiple sequence alignment program. *Briefings in Bioinformatics* **9**: 286–298. https://doi.org/10.1093/bib/bbn013.

Katoh, K., Kuma, K.-I., Toh, H. & Miyata, T. 2005. MAFFT version 5: improvement in accuracy of multiple sequence alignment. *Nucleic Acids Research* **33**: 511–518. https://doi.org/10.1093/nar/gki198.

Koerber, G. W. 1855. *Systema Lichenum Germaniae.* Breslau, 458 pp.

Liu, K., Warnow, T. J., Holder, M. T., Nelesen, S. M., Yu, J., Stamatakis, A. P. & Linder, C. R. 2012. SATé-II: very fast and accurate simultaneous estimation of multiple sequence alignments and phylogenetic trees. *Systematic Biology* **61**: 90–106. https://doi.org/10.1093/sysbio/syr095.

Malme, G. O. A. 1914. Västra Jämtlands *Rhizocarpon*-Arter. *Svensk Botanisk Tidskrift* **8**: 273–294.

Marthinsen, G., Rui, S. & Timdal, E. 2019. OLICH: A reference library of DNA barcodes for Nordic lichens. *Biodiversity Data Journal* **7**, e36252. https://doi.org/10.3897/BDJ.7.e36252.

McCune, B., Timdal, E. & Bendiksby, M. 2016. *Rhizocarpon quinonum*, a new anthraquinone-containing species from the Alaska Peninsula. *The Lichenologist* **48**: 367–375.

Poelt, J. & Vězda, A. 1981. Bestimmungsschlüssel europäischer Flechten. Ergänzungsheft II. *Bibliotheca Lichenologica* **16**: 1–390.

Price, M. N., Dehal, P. S. & Arkin, A. P. 2010. FastTree 2 – approximately maximum-likelihood trees for large alignments. *PloS One* **5**: e9490. https://doi.org/10.1371/journal.pone.0009490.

Ronquist, F. & Huelsenbeck, J. P. 2003. MRBAYES 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* **19**: 1572–1574. https://10.1093/bioinformatics/btg180.

Schaerer 1818. Lecidearum Helvetiae enumerationem ordine analytico. *Naturwissenschaftlicher Anzeiger der allgemeinen Schweizerischen Gesellschaft für die gesammten Naturwissenschaften* **2**: 9–12.

Schaerer, E. 1850. *Enumeratio critica lichenum Europaeorum*. Bern, 327 pp.

Sprengel, C. 1821. Species plantarum minus cognitae. *Sprengel's neuen Entdeckungen im ganzen Umfange der Pflanzenkunde* **2**: 95–175.

Stamatakis, A. 2014. RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. *Bioinformatics* **30**: 1312–1313. https://doi.org/10.1093/bioinformatics/btu033.

Stöver, B. C. & Müller, K. F. 2010. TreeGraph 2: Combining and visualizing evidence from different phylogenetic analyses. *BMC Bioinformatics* **11**, 7. https://doi.org/10.1186/1471-2105-11-7.

Timdal, E. & Holtan-Hartwig, J. 1988. A preliminary key to *Rhizocarpon* in Scandinavia. *Graphis Scripta* **2**: 41–54.

Vainio, E. A. 1883. Adjumenta ad lichenographiam Lapponiae fennicae atque Fenniae borealis. *Meddel. Societas pro Fauna et Flora Fennica* **10**: 1–230.

Vainio, E. A. 1922. Lichenographia fennica II. Baeomyceae et Lecideales. *Acta Soc. pro Fauna et Flora Fennica* **53, 1**: 1–340.

Westberg, M., Moberg, R., Myrdal, M., Nordin, A. & Ekman, S. 2021. *Santesson's Checklist of Fennoscandian Lichen-Forming and Lichenicolous Fungi*. Uppsala University, Museum of Evolution. https://www.uu.se/download/18.f5bb9da18bfb174bad34bb8/1701866711564/Santesson's%20Checklist%20-%20Westberg%20et%20al.%202021%20PDF-A1b.pdf

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

Zahlbruckner, A. 1926–1927. *Catalogus Lichenum Universalis. Band IV*. Gebrüder Borntraeger, Leipzig, 754 pp.

Zahlbruckner, A. 1930. Lichenes. *In:* Handel-Mazzetti, H. (ed.), *Symbolae sinicae. III. Teil*. J. Springer, Wien, 254 pp.

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. https://doi.org/10.1017/S0024282999000663.