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Rinodina candidogrisea, a new sorediate species from high altitudes in the Alps

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Abstract: *Rinodina candidogrisea*, a commonly sterile sorediate species, is described as new to science and reported from Austria, Germany, Italy, Slovenia and Switzerland. ITS-rRNA sequence data as well as phenotypic apothecial characters show that it belongs to the *R. roscida*-group.

Keywords: Ascomycota, epigaeic, lichenized fungi, *Megaspora verrucosa* community, phylogeny, Physciaceae, species pair

Introduction

Several *Rinodina* species are known to have switched their reproductive mode from sexual to asexual. As in other cases, this switch to the regular production of vegetative diaspores is accompanied by complete or almost complete suppression of ascoma formation, an important source for phenotypic characters for species identification. Although considerable progress has been made in recent years in our knowledge of the taxonomy of commonly sterile corticolous *Rinodina* species, resulting in the description of several new species by various authors (see Table 2), this mode of reproduction has yet to be recorded among obligately terricolous species.

The generic affiliation of a new, almost always sterile, terricolous (muscicolous to plant debris-inhabiting) *Rinodina* species has been elucidated by molecular methods. This has allowed the undoubted identification of a single fertile specimen as being conspecific with a range of known sterile material; this fertile specimen will serve as the type material.

The keys constructed by Giralt et al. (1993, blastidiate and sorediate species in Austria), Giralt et al. (1995, blastidiate and sorediate epiphytic species in southern Europe), Giralt et al. (1997, key for the Benelux-countries), Mayrhofer & Moberg (2002, key for Fennoscandia), Giavarini et al. (2009, key for Great Britain & Ireland), Giralt (2001, key for Iberian Peninsula), Boom et al. (2009, key for the Canary Islands), Sheard (1995, blastidiate and sorediate epiphytic species in temperate North America) and Sheard (2010, key for North America north of Mexico) have proved to be useful in distinguishing diagnostic characters of vegetatively reproducing *Rinodina* species.

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Material and methods

Morphological analysis

This study is based on an examination of herbarium specimens which are cited under each species treatment. External morphology was studied with a dissecting microscope (WILD M3, 6.4–40x) and anatomical studies of the thallus and ascomata were carried out under a light microscope (LEICA DMRE, 100–1000x). Sectioning was performed with a freezing microtome (LEITZ, sections of 12–15 µm), but squash preparations were also used. Preparations were mounted in water. When necessary, contrasting was performed by a pretreatment with lactic acid-cotton blue (MERCK 13741). Sections and squash preparations were not pretreated with KOH unless otherwise stated. Measurements refer to dimensions in tap water.

Images were generated by using a dissecting microscope (Leica, Wild M3Z) and an optical microscope (Zeiss, Axioskop 50). Both units were connected to a digital camera (Zeiss, Axiocam MRc5). Image stacks were processed with the public domain software 'CombineZP' (developed by Alan Hadley).

Secondary chemistry

Chemical analyses were carried out by means of standard thin layer chromatography following Culberson & Ammann (1979) and Elix et al. (1987). For a better separation of spots, TLC plates were run to a height of 15 cm.

Molecular methods

DNA extraction, amplification and sequencing

DNA extraction was performed on six thalli. The material was prepared by carefully scraping the sorediose parts of thalli and some squamules, when conspicuous, with a razor blade. The DNA isolation protocol of Cubero et al. (1999) was applied for all samples. The systematic position of the lichen was analysed with sequence data of the ITS region, amplified with the primers ITS1F (Gardes & Bruns 1993) and ITS4 (White et al. 1990).

PCR reactions were prepared for a 30 µl final volume containing 4.05 µl double-distilled water, 10x *Taq* polymerase reaction buffer (10 mM Tris pH 8.3), 25 mM $MgCl_2$, 2.5 mM of dNTPs, 0.15 µl *Taq* DNA polymerase, and 10 µM of each primer. PCR amplifications were performed under the following conditions: one initial heating step of 2 min at 94 °C linked to 30 cycles of 1 min at 94 °C, 1 min at 53 °C, 2 min at 72 °C, and one final extension step of 7 min at 72 °C after which the samples were kept at 4 °C. PCR products were purified using QIAGEN quick spin columns (Qiagen, Vienna, Austria) following the manufacturer's instructions. Complementary strands were sequenced, then run by Macrogen Inc. (Korea). The identity of the newly produced sequences was confirmed by BLAST search in GenBank (Altschul et al. 1997).

Sequence alignment and phylogenetic analysis

The ITS alignment was produced automatically with ClustalW (Hall 1999), as implemented in BioEdit 5.0.6 and then manually adjusted. The phylogenetic analyses included our newly obtained sequences and 63 additional taxa of

Physiaceae, the sequences of which were retrieved from GenBank. The ITS sequences of *Amandinea punctata*, *Buellia asterella*, *B. schaereri* and *Diploicia canescens* were selected as outgroups. The phylogenetic hypothesis was established using both a Bayesian and a maximum parsimony (MP) approach. Ambiguously aligned positions were excluded and the same nucleotide matrix was used for the Bayesian and MP analyses.

The Bayesian analysis was implemented in the program MrBayes 3.1.2 (Huelsenbeck & Ronquist 2003; Ronquist et al. 2005). The optimal nucleotide substitution model, the General Time Reversible substitution model (Rodriguez et al. 1990) with estimation of invariant sites and assuming a gamma distribution with four rate categories (GTR+I+G), was selected with the program MrModeltest 3.7 (written by J.A.A. Nylander and available at http://morphobank.ebc.uu.se/mrbayes/; Posada & Crandall 1998) using the Akaike Information Criterion and the hierarchical likelihood ratio test (Posada & Crandall, 1998). The Markov Chain Monte Carlo (MCMC) algorithm was run for two million generations, with six chains starting from a random seed and using the default temperature parameter of 0.2. Every 100th tree was sampled, while the first 200,000 generations were discarded as *burn-in*. The *burn-in* period was determined after testing for stationarity of likelihood values (i.e. by plotting log likelihood against generation and checking for the convergent diagnostic PSRF approaching 1; Ronquist et al. 2005). The consensus phylogram based on the mean branch lengths was calculated with the command *sumt* in MrBayes (see MrBayes 3.1 Manual; Ronquist et al. 2005).

The MP analysis was performed in the program PAUP* 4.0b10 (Swofford 2002). A heuristic search using 100 random addition replicates of random sequence additions was conducted with tree bisection-reconnection (TBR), branch swapping and MulTree options; gaps were treated as missing values. Bootstrapping was performed on 1000 pseudoreplicates (Felsenstein 1985). The phylogenetic trees were drawn using the program TreeView (Page 1996).

Material used for comparative studies

Abbreviations for institutional herbaria and author names follow Holmgren et al. (1990) and Brummitt & Powell (1992) respectively.

Allocetraria stracheyi (C.Bab.) Kurok. & M.J.Lai
China: SE-Tibet, prov. Xizang, E-Himalaya, SW-Namchabarwa Feng, NW above Nam La Co, 29°35’ N, 95°00’E, 4490 m, 15. IX. 1989, leg. B. Dickoré L-18 (GZU) (as TLC standard for secalonic acid A, hybocarpone).

Buellia arborea Coppins & Tønsberg
Austria: Steiermark (Styria), Niedere Tauern, Wölzer Tauern, Lachtal, Wiese bei der Reifhütte, unterhalb der alten Sprungschanze, c. 500 m SE der Reifhütte, 47°14’59’’N / 14°21’31’’E, 1590 m, GF 8752/3, Fichten-Lärchenwald, stehendes Totholz von *Larix decidua*, 13. VIII. 2000, leg. E. Sterner no. 345 (GZU) [TLC: atranorin, placodiolic acid].

Buellia griseovirens (Turner & Borrer ex Sm.) Almb.
Austria: Kärnten (Carinthia), [Südalpen], Karnische Alpen, Angerbachtal E vom Plöckenpass, c. 6 km S von Mauthen, 46°36’30’’N / 12°59’00’’E, c.

1320 m, GF 9343/4, koniferenreicher Mischwald im Talgrund, auf Borke von *Alnus incana*, 31. VIII. 2007, leg. J. Hafellner no. 70567 (GZU). – Salzburg, Nördliche Kalkalpen, Hagengebirge, Bluntautal W von Golling, c. 1 km SW der Bluntaumühle, 47°34’45’’N / 13°08’25’’E, c. 490 m, GF 8444/2, fichtenreicher Mischwald am Bachufer, auf Borke von *Fagus sylvatica*, 1. IX. 1996, leg. J. Hafellner no. 47290 (GZU). – Steiermark (Styria), Nördliche Kalkalpen, Ennstaler Alpen, Gesäuseberge S von Admont, Umgebung der Sieglalm c. 1 km N vom Schloß Kaiserau, 47°32’20’’N / 14°29’00’’E, c. 1120 m, GF 8452/4, montaner Forst mit dominanter *Picea abies*, auf Borke von *Alnus incana*, 13. IX. 2006, leg. J. Hafellner (GZU). – Tirol, Stubaier Alpen, Gschnitztal, Gschnitz am Martheierbach unterhalb St. Magdalena, c. 1210–1240 m, 11. IX. 1973, leg. J. Poelt no. 12973 (GZU). – **Italy**: Veneto, prov. Belluno: Southern Alps, Venetian Alps, Nevegal SE of Belluno, slopes exposed to NE, NE of the middle station of the chair-lift on Col Faverghera, 46°05’15’’N / 12°17’30’’E, c. 1300 m; mixed coniferous forest, limestone outcrops, on branches of *Larix decidua*, 31. VIII. 2002, leg. J. Hafellner no. 61319 (GZU). – **Canary Islands**: El Hierro, auf dem zentralen Bergrücken NE der Hoya de Fileba, c. 1,5 km NE der Abzweigung nach Santuario Virgen de los Reyes, c. 1330 m, 27°44’30’’N/17°59’W, *Pinus*-Forst, auf Stammborke von *Pinus* spec., 7. II. 1995, leg. J. Hafellner no. 48441 (GZU).

Phaeorrhiza nimbosa (Fr.) H. Mayrhofer & Poelt
Austria: Steiermark (Styria), [Zentralalpen], Niedere Tauern, Wölzer Tauern, Berge, c. 8 km WNW von Pusterwald, E-Hänge des Kleinhansl, am Steig vom der Wildalmhütte zum Kleinhansl, 47°19’40’’N / 14°16’40’’E, c. 2000 m, GF 8651/4, niedere Ausbisse und kleine Schrofen aus Marmor, in erdgefüllten Spalten, 25. VIII. 2005, leg. J. Hafellner no. 73207 (as TLC standard for variolaric acid).

Rinodina colobina (Ach.) Th.Fr.
Canada: Saskatchewan, 17 km W of Hudsons Bay, picnic area by Hwy 3, 52°51’N / 102°37’W, on bark of *Populus tremuloides*, 11. VI. 2003, leg. J. W. Sheard no. 5214 (GZU).

Rinodina colobinoides (Nyl.) Zahlbr.
Bermuda: Hamilton, Botanischer Garten, c. 40 m, auf Borke eines Nadelbaumes, 18. XI. 2004, leg. F. Berger no. 19679 (GZU).

Rinodina efflorescens Malme
Austria: Steiermark (Styria), Oststeirisches Riedelland, 7 km E of the centre of Graz, 2.9 km SW of Hönigtal, 250 m W of Rot, forest area between Ragnitzstraße und Höhenstraße, 47°04’45’’N / 15°31’45’’E, 460–480 m, GF 8959/1, mixed forest, on bark of *Fagus sylvatica*, 20. III. 2006, leg. W. Obermayer no. 11070 (GZU) [TLC: pannarin, yellow pigment]. – Oberösterreich (Upper Austria), Nördliche Kalkalpen, Laussabacheralm, c. 15 km E von Windischgarsten, c. 850 m, auf Borke von *Acer pseudoplatanus*, 24. VII. 1994, leg. Z. Palice (GZU).

Rinodina griseosoralifera Coppins
Germany: Bayern (Bavaria), Berchtesgadener Land, Untersberg, Gernweg, 920 m, GF 8343, auf Borke von *Acer pseudoplatanus*, 26. VIII. 1990, leg. F. Gloßner no. 198 (GZU). – **Great Britain**: Scotland, Clackmannan (V.C. 87). Ochil Hills,

Menstrie Burn, on *Ulmus* on side of small valley, 90–150 m, 29. IV. 1984, leg. B. J. Coppins no. 10256 (E).

Rinodina pityrea Ropin & H. Mayrhofer
Germany: Baden-Württemberg, Kreis Tauberbischofsheim, Bad Mergentheim, Gewerbegebiet beim Bahnhof, c. 200 m, MTB 6524, auf Borke von *Sambucus nigra*, 16. I. 2005, leg. R. Türk no. 35566 (GZU).

Rinodina roscida (Sommerf.) Arnold
Strain I:
Austria: Steiermark (Styria), Nördliche Kalkalpen, Ennstaler Alpen, Gesäuseberge, Gsuchmauer c. 9 km SW von Hieflau, auf dem schmalen Rücken kurz W vom Gipfel, 47°32’55’’N / 14°39’55’’E, c. 2100 m, GF 8453/4, kleine Ausbisse aus Triaskalk in alpinen Matten, auf Moosen und Pflanzenresten auf dem wenig geneigten Rücken, 11. IX. 2006, leg. J. Hafellner no. 68984 (GZU) [TLC: zeorin only].
Strain II:
Austria: Oberösterreich (Upper Austria), Nördliche Kalkalpen, Ennstaler Alpen, Haller Mauern, Großer Pyhrgas SE von Spital am Pyhrn, am Steig kurz SW unterhalb vom Gipfel, 47°39’10’’N / 14°23’50’’E, c. 2160 m, GF 8352/1, niedere Kalkausbisse in alpinen Rasen, auf Moosen und Pflanzenresten, 15. X. 2006, leg. J. Hafellner no. 69260 & L. Muggia (GZU) [TLC: variolaric acid only]. – Chemistry not tested: **Austria**: Kärnten (Carinthia), [Südalpen], Karawanken, Petzen, am Weg von Siebenhütten zum Knirpssattel, c. 1950 m, auf Pflanzenresten, 30. VIII. 1992, leg. E. B. Timpe & W. Wetschnig (GZU). – Salzburg, Nationalpark Hohe Tauern, Goldberggruppe, Vorderer Gesselkopf (Geißlkopf), am Westgrat knapp unter dem Gipfel, [47°00’50’’N / 13°04’20’’E], c. 2950 m, GF 8944/3, kalkhältige Glimmerschieferblöcke auf einem steilen Westhang, auf Moosen und Pflanzenresten, 10. VIII. 1994, leg. J. Hafellner no. 33273 (GZU). – Steiermark (Styria), [Nördliche Kalkalpen], Dachstein-Massiv, Stoderzinken, N-exponierte Hänge am Gipfel, c. 2040 m, GF 8548, auf Pflanzenresten in Felsspalten von Kalkschrofen, 24. VII. 1985, leg. J. Hafellner no. 14017 (GZU). – Steiermark (Styria), Nördliche Kalkalpen, Hochschwab, Matten bei der Fleischerhütte (Biwak), c. 2100 m, an Windkanten, 15. VIII. 1975, leg. J. Hafellner no. 681 (GZU). – Tirol, Tuxer Alpen, Wattener Lizum S von Wattens, am W-Fuß der Kalkwand SSE ober der Lizumer Hütte, c. 2200 m, GF 8835/4, Kalkblockschutthalde, in erdigen Spalten großer Blöcke, 7. VII. 1992, leg. J. Hafellner no. 23447 (GZU). – **Germany**: Bayern (Bavaria), Oberbayern, Ammergauer Alpen, Gipfel der Klammspitze, 27. VI. 1965, leg. J. Poelt no. 2042 (GZU). – **Norway**: Oppland, Lom: Jotunheimen, Visdalen, W-exponierte Hänge, c. 1 km NE von Spiterstulen; W-exponierte Abbrüche, c. 1250 m; 24. VIII. 1984, leg. J. Hafellner no. 12821 & A. Ochsenhofer (herb. Hafellner). – **Slovenia**: Steiner Alpen, etwas oberhalb Kokrsko sedlo (Cojzova koča) in Richtung Grintovec, c. 1900 m, 22. VIII. 1992, leg. E. B. Timpe & W. Wetschnig (GZU). – **Spitzbergen**: Woodfjorden area, Bockfjorden, Granitblockschutthalde am SE Zungenrand des Friedrichbreen, 79°17’30’’N / 13°14’E, c. 200 m, auf Rentiergeweihen, 22. VII. 1979, leg. J. Hafellner no. 5448 (GZU). – Woodfjorden, Bockfjorden, Sinterhügel der westlichen Thermalquelle Jotunkjeldene, 79°17’30’’N / 13°17’30’’E, c. 70 m, auf Moospolstern, 22. VII.

1979, leg. J. Hafellner no. 5246 (GZU). – **Switzerland**: Graubünden, Samnaun-Gruppe, Ils Gips kurz E unterhalb des Kleinen Fimberpasses, c. 2500 m, auf Pflanzenresten, 7. VIII. 1967, leg. J. Poelt no. 5313 (GZU).

Results

Rinodina candidogrisea Hafellner, Muggia & Obermayer species nova MB 561878

Thallus albidogriseus, areolis marginalibus albidis et subsquamulosis mox ad marginem sorediosis, areolis centralibus crustaceo-dissolutis, omnino sorediatis. Soredia granulosa, grisea. Apothecia (rarissime evoluta) ut in *R. roscida* constructa. Differt a *R. roscida* thallis sorediosis, specibus aliis sorediosis in aspectu thallorum et in chemia.

Typus: Austria: Steiermark, Nördliche Kalkalpen, Ennstaler Alpen, Gesäuseberge, Gsuchmauer, c. 9 km SW von Hieflau, auf dem schmalen Rücken kurz W vom Gipfel, 47°32’55’’N / 14°39’55’’E, c. 2100 m, GF 8453/4, kleine Ausbisse aus Triaskalk in alpinen Matten, auf Moosen und Pflanzenresten auf dem wenig geneigten Rücken, 11. IX. 2006, leg. J. Hafellner no. 68273 (GZU, holotype)!

Icon.: Fig. 1 (thallus), Fig. 2 (early developmental stages of thalli), Fig. 3 (habit of apothecium, developmental stages of ascospores), Fig. 4 (pattern of chemical substances on TLC plates), Fig. 5 (phylogenetic tree).

Etymology: candidus [lat.] – pure white, because of the colour of marginal, subsquamulose areoles; griseus [lat.] – grey, a little verging to blue, because of the colour of soredia and the strongly sorediate central parts of the thalli.

Full description: Thallus crustose; individual thalli usually less than 3 cm in diam., with white marginal zone and grey centre; marginal areoles somewhat enlarged to tiny subsquamulose, scattered, white, only marginally sorediate; more central areoles densely arranged, entirely sorediate and appearing grey with naked eye or under the hand lenses. Photobiont a coccal green alga, probably a species of *Trebouxia*. Soredia granular, greyish, 30–55 µm in diam., without distinctly protruding hyphae under the dissecting microscope, under the light microscope terminal cells of peripherical hyphae clavate to globose, with hyaline to brownish papillate walls, K–. Thalli usually sterile. Apothecia [so far observed only on a single specimen (type)] scattered, adpressed, 0.3–0.7mm in diam., with thick margin, margins and discs pruinose; in longitudinal section with thalline margin, the margin not distinctly corticate but encrusted with a dense layer of Ca-oxalate crystals. Hymenium not inspersed, c. 100 µm high. Paraphyses with few ramifications in the upper part, c. 2 µm in diam., with slightly enlarged tips surrounded by brownish gel and Ca-oxalate crystals. Asci 8-spored, 70–80 × 24–30 µm. Ascospores 2-celled, of *Physcia*-type, with spore ontogeny of type A (compare Mayrhofer & Moberg 2002: 43); in certain stages of development with distinct torus, 23–26.3–28 × 10–11.6–12.5 µm. Pycnidia not observed.

Secondary chemistry: TLC: (1) Zeorin (in all samples), (2) unknown fatty acid (in all samples; (2-)3/1(-2)/2(-3)), (3) variolaric acid (in some samples),

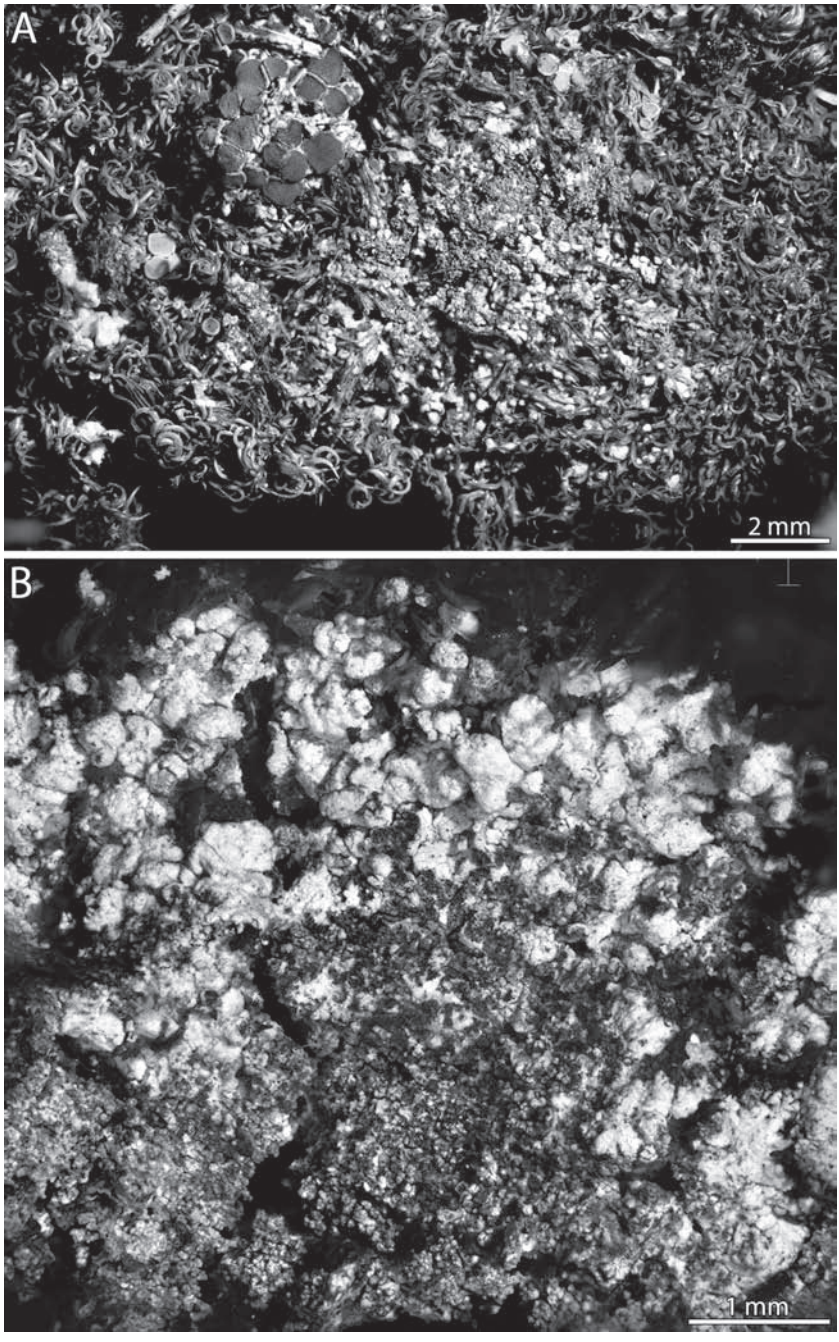

Fig. 1. *Rinodina candidogrisea* A: Overview of sterile upper left thallus in type specimen bordered by three muscicolous *Caloplaca* species. B: Close-up of a thallus showing the whitish marginal areoles and the grey central part. A from holotype, B from Hafellner 68270 (photo: W. Obermayer, 15. II. 2011).

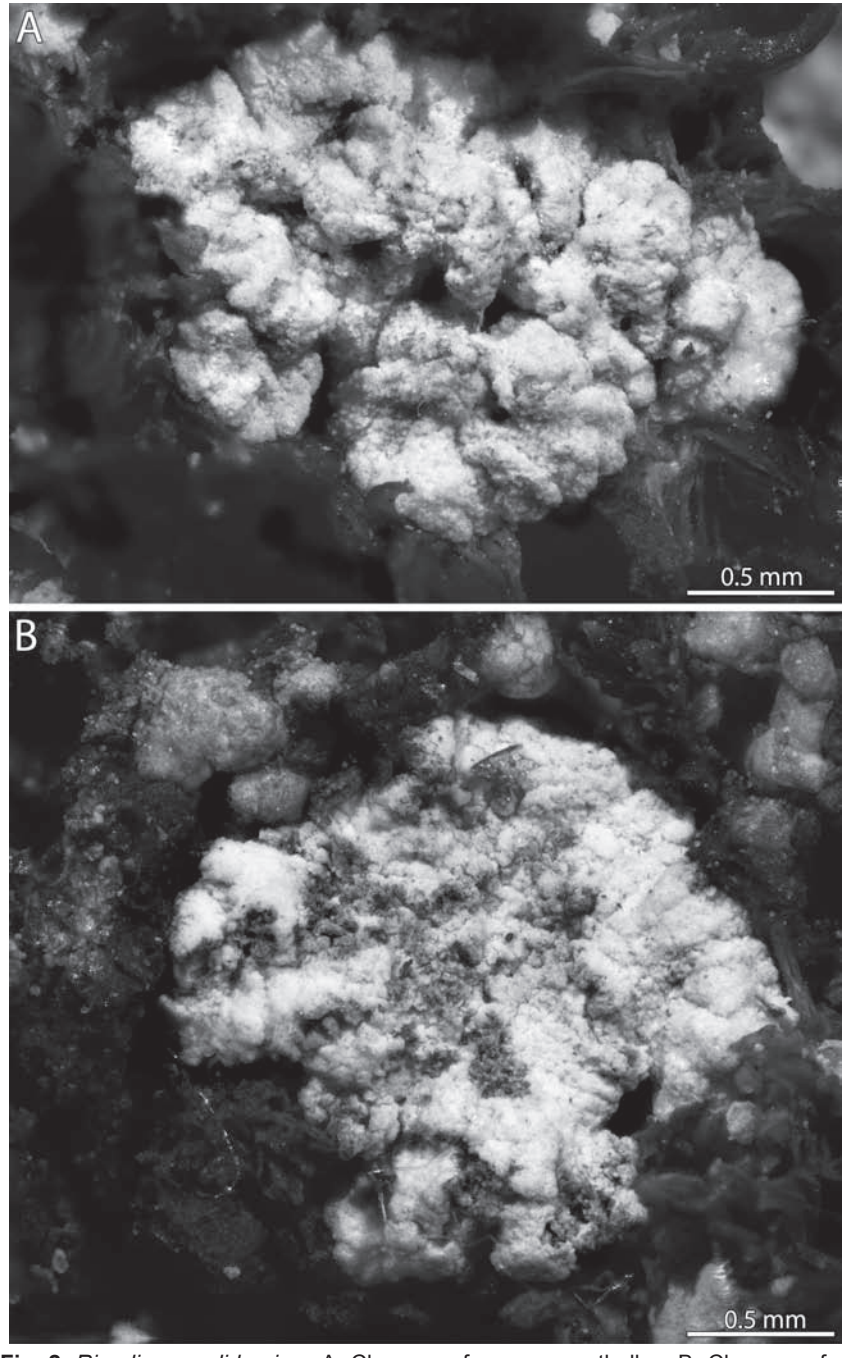

Fig. 2. *Rinodina candidogrisea* A: Close up of very young thallus. B: Close up of a thallus with already some soralia developed. A, B from Hafellner 68270 (photo: W. Obermayer, 15.II.2011).

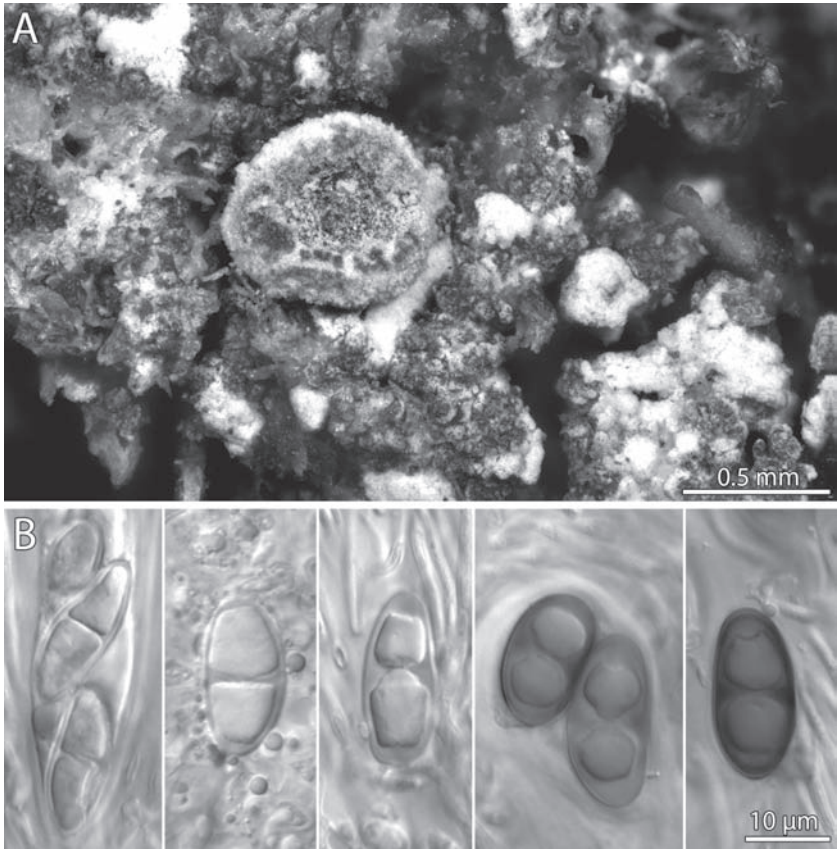

Fig. 3. *Rinodina candidogrisea* A: Fertile portion of upper left thallus in type specimen. B: Ascospores in various stages of development, illustrating type A ascospore ontogeny. From holotype in GZU (photo: W. Obermayer, 15.II.2011).

(4) unknown yellow pigment (in a few samples; (3-)4/2/3(-4)); for pattern of spots on TLC plates see Fig. 4. Spot tests: Cortex: K–, P–, C–; UV+ whitish (especially marginal lobes). Medulla (when white): C–, K– and P– or faintly yellow (samples with a yellow medulla or yellow soredia are K+ purple). Thus,

Table 1. *Rinodina candidogrisea*. Specimen data and Genebank accession nos. – all specimens deposited in GZU.

Specimen ID no.	Origin of specimen	DNA extr. no.	Genebank acc. no.
Hafellner 73530	Austria, Carinthia, Koralpe	L1020	JN211108
Hafellner 76033	Austria, Styria, Totes Gebirge	L1022	JN211109
Hafellner 75179	Germany, Bavaria, Chiemgauer Alpen	L1019	JN211107

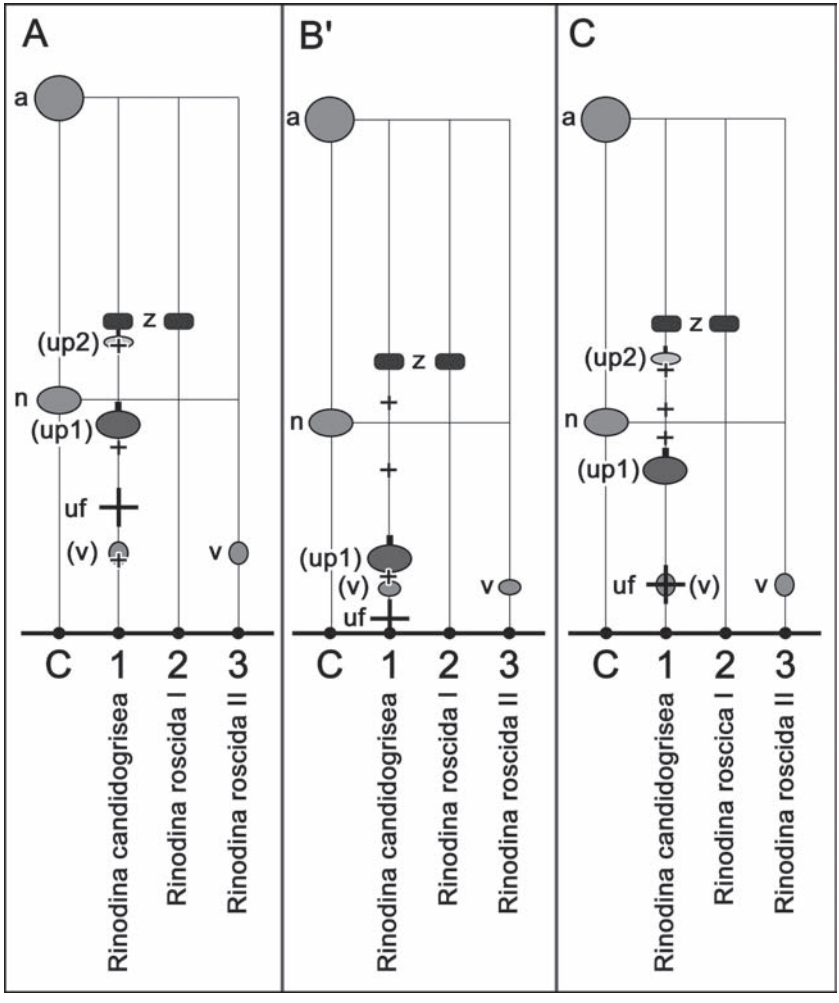

Fig. 4. Schematic drawing of TLC plates showing the spot pattern of *Rinodina candidogrisea* in solvent systems A, B' and C, compared with two chemical strains of *R. roscida*; C = standard from *Cladonia symphycarpia* (designed by W. Obermayer, 10.I.2011). Symbols: a = atranorin, n = norstictic acid, v = variolaric acid, z = zeorin; uf = strongly concentrated, unknown fatty acid (accompanied by some low concentrated fatty acids (given in smaller crosses); up1 = unknown pigment 1, up2 = unknown pigment 2; symbols for substances without parentheses = substance constantly present; symbols for substances given in parentheses = substance facultatively present.

R. candidogrisea occurs in four chemical strains: Strain I (including the type): (1) + (2), strain II: (1) + (2) + (3), strain 3: (1) + (2) + (4), and strain IV: (1) + (2) + (3) + (4).

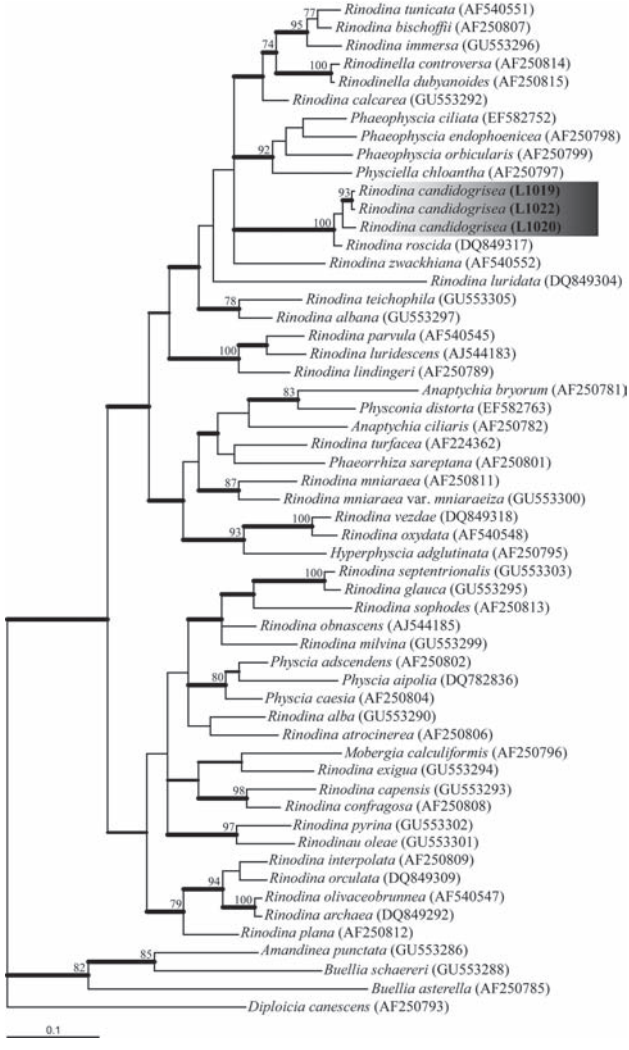

Fig. 5. Bayesian consensus tree of an ITS sequence analysis of selected Physciaceae showing the phylogenetic position of *Rinodina candidogrisea*. Bayesian posterior probabilities > 95% are indicated by the thickness of the branches; MP bootstrap values > 75% are reported above the branches. NCBI accession numbers are reported for all the taxa, and newly produced sequences are in bold.

Table 2. Comparative table of thalline characters of holarctic vegetatively reproducing crustose Physciaceae (epiphytic and terricolous species only). Publications containing an illustration of habit are marked with an asterisk* (Data from cited references and own observations).

Taxon	Thallus	Mode of vegetative reproduction	veget. diaspores	Secondary chemistry (by TLC)	Spot tests	Ascospore type	Selected references
R. albertana Sheard	thin, discontinuous with discrete areoles, or areoles coalescing forming a continuous to rimose crust, grey	blastidiate and/ or consorediate, marginal then spreading to surface	blastidia papillate, consoredia breaking into soredia, all darker than the thallus	-	none	*Dirinaria*	Sheard 2010
R. candidogrisea Hafellner, Muggia & Obermayer	crustose, marginal areoles subsquamulose	sorediate, soralia, numerous, marginally on marginal areoles, superficially in central areoles, there also confluent	soredia whitish to rarely yellowish, with blackish tinge	zeorin, unident. fatty acid, accessory variolaric acid and/ or orange pigment in medulla	usually none, yellowish medulla if present K+ purple	*Physcia*	this publication
R. colobina (Ach.) Th.Fr.	verrucose to granulose, often blastidiate, dark grey-brownish	blastidiate	blastidia eroding in soredia	-	Cortex K+, C+, N+ violet	*Pachysporaria*-*Physcia*-*Mischoblastia*-intermediate	Giralt 2001, Mayrhofer & Moberg 2002*, Sheard 2010
R. colobinoides (Nyl.) Zahlbr.	blastidiate, greenish-white to olivaceous	blastidiate	blastidia eroding in soredia	yellow-orange pigment in medulla	orange parts K+ purple-rose	*Pachysporaria*	Giralt 2001, Giavarini et al. 2009, Sheard 2010
R. dalmatica Zahlbr.	areolate, ochraceous to brownish, areoles becoming completely blastidiate	blastidiate	blastidia whitish brown, olivaceous or brown	pannarin, unknown pigment	K+ yellowish, Pd+ orange	*Pachysporaria*	Giralt et al. 1994, 1995*
R. degeliana Coppins	crustose to subsquamulose, areoles grey-white	sorediate, marginal, pure white	soredia	atranorin, chloroatranorin, zeorin, terpenoids	K+ yellow, Pd+ yellow	*Physcia*[1] / *Dirinaria*[2]	Tønsberg 1992a*, Mayrhofer & Moberg 2002*[1], Giavarini et al. 2009[2], Sheard 2010

R. disjuncta Sheard & Tønsb.	areolate, areoles plane than convex	laminal, consorediate to blastidiate sometimes transforming into irregularly shaped soralia	blastidia occasionally breaking into soredia, lighter grey than thallus	sphaerophorin, isosphaeric acid	soralia UV(lw)+ blue-white	*Physcia-Physconia*-intermediate	Tønsberg 1992a*, Sheard 2010
R. efflorescens Malme	areolate, areoles scattered to contiguous, usually as minute flattened squamules, brown-white to brown-grey	sorediate, laminal to marginal, scattered, sometimes confluent but not continuous leprose	whitish to greenish-yellow, often with brown tinge	pannarin, secalonic acid A, zeorin[3]	Pd+ red	*Physcia*[1] / *Milvina*[2]	Tønsberg 1992a, Giralt et al. 1994, 1995*, Giralt 2001, Mayrhofer & Moberg 2002*[1] Giavarini et al. 2009[2] Sheard 2010[3]
R. ericina var. *boomii* Giralt	thin continuous, pale grey to ochraceous	sorediate, soralia at first discrete and crateriform, later confluent to a leprose crust,	soredia white-grey to pale blue-grey	atranorin, diploicin	K+ yellow	*Dirinaria*	Giralt 2000, 2001
R. evae Fos & Giralt	areolate, areoles grey, greenish-grey to pale brownish-grey, irregularly rounded to slightly lobate subsquamulose, hirsute	blastidiate on the surface and margin of areoles	blastidia spherical to ovoid, concolorous with thallus and sparsely hirsute	-	none	*Pachysporaria*	Fos & Giralt 2009*
R. excrescens Vain.	areolate (minute sublobulate squamules), areoles scattered to contiguous, grey to grey-brown	mostly blastidiate	blastidia large, scattered or confluent	atranorin[1], pannarin	K+ yellow, Pd+ orange	*Physcia*	Giralt et al. 1994*[1], Sheard 2010
R. flavosoralifera Tønsberg	crustose, areoles scattered, dull with brownish tinge	sorediate, soralia punctiform or rarely marginal	soredia dull yellow, often with brownish tinge	arthothelin, thiophanic acid	C+ orange, UV+ orange-red	only known in immature state	Tønsberg 1992a, Mayrhofer & Moberg 2002* Giavarini et al. 2009

Taxon	Thallus	Mode of vegetative reproduction	veget. diaspores	Secondary chemistry (by TLC)	Spot tests	Ascospore type	Selected references
R. furfuracea H.Magn.	discontinuous, thin, smooth, whitish, whitish brown or greenish	blastidiate	blastidia forming a leprose-granulose crust	-	none	*Physcia-Physconia*-intermediate	Giralt et al. 1995, Giralt 2001
R. granulans Vain.	crustose, areolate, whitish to whitish-grey	blastidiate	blastidia small confluent leprose, whitsh or with brown tinge	pannarin	K+ yellow, Pd+ orange	*Physcia-Milvina*-intermediate	Giralt et al. 1994*, 1995
R. griseosoralifera Coppins	crustose, areoles scattered to contiguous, convex, sometimes subsquamulose	sorediate, soralia numerous, discrete, convex, erupting from upper surface, sometimes confluent but not continuous leprose	soredia blue-grey, colour fading in the herbarium	atranorin, zeorin	K+ faint yellow, Pd+ light yellow	*Pachysporaria*	Coppins 1989, Tønsberg 1992a, Giralt 2001, Mayrhofer & Moberg 2002* Giavarini et al. 2009, Sheard 2010
R. herrei H.Magn.	continuos then rimose to areolate, areoles with raised margins	blastidiate at the margins of the areoles	blastidia papillate, often composed of consoredia	-	none	*Physcia*, then *Michoblastia*, finally *Pachysporaria*	Sheard 2010
R. inflate Kalb	areolate, areoles up to subsquamulose	sorediate, soralia at margins and upper surface	soredia whitish	atranorin	K+ yellow	*Pachysporaria*	Kalb 1976
R. *isidioides* (Borr.) H.Olivier	crustose to subsquamulose, whitish, pale whitish grey or greyish green	isidiate	isidia thin, coralloid, long, cylindrical, often brownish at the top	atranorin, zeorin	K+ yellow	*Pachysporaria*, sometimes with additional septa	Giralt et al. 1995*, Giralt 2001
R. *juniperina* Sheard	thick, composed of minute verrucae, then continuous to areolate, dark grey to grey-green or bownsih	consorediate along cracks and upturned margins of areoles	consoredia breaking into soredia	-	none	*Physcia*	Sheard & Mayrhofer 2003, Sheard 2010

R. malangica (Norm.) Arnold	areolate, well developed, areoles sublobate, yellowish brown, olivaceous, greybrown to grey green	blastidiate	blastidia coralloid	-	none	*Physcia*	Ropin & Mayrhofer 1993, Giralt et al. 1995, Giralt 2001
Rinodina nimisii Giralt & H.Mayrhofer	crustaceous, well-developed, continuous, smooth, greyish-green, brownish or olivaceous	blastidiate	blastidia with a slightly pruinose and rugose appearance	-	none	*Dirinaria*, strongly warted	Giralt et al. 1995*, Giralt 2001
R. pachysperma H.Magn.	continuous to rimose-areolate, grey to grey-brown, areoles rugose to granular	occasionally with consoredia	consoredia breaking into soredia	-	none	*Pachysporaria*	Sheard 2010
R. papillata H.Magn.	thin continuous to rimose-areolate, grey to ochraceous	blastidiate at the margins of the areoles	blastidia globose to cylindric	-	none	*Pachysporaria*	Sheard 2010
R. perreagens Sheard	thin discontinuous, then rimose-areolate, grey	sorediate, sometimes also blastidiate, soredia effuse, lighter than thallus	blastidia when present elongated	panarin + further xanthones	K+ faint yellow, Pd+ orange	*Pachysporaria*	Sheard & Mayrhofer 2003, Sheard 2010
R. pityrea Ropin & H.Mayrhofer	thin, continuous to cracked to granular, dark grey to blackish, often blastidiate	entirely blastidiate	blastidia small	-	none	*Tunicata*	Ropin & Mayrhofer 1995, Giralt 2001, Mayrhofer & Moberg 2002*
R. poeltiana Giralt & W.Obermayer	areolate, areoles grey to brown-grey	blastidiate at surface and margins of areoles	blastidia confluent, dark brown, forming a continuous crust	-	none	*Pachysporaria*	Giralt et al. 1993, Sheard 2010

Taxon	Thallus	Mode of vegetative reproduction	veget. diaspores	Secondary chemistry (by TLC)	Spot tests	Ascospore type	Selected references
R. *santae-monicae* H.Magn. (syn. *R. thomsonii* Sheard)	thin, rimose then areolate, grey to greenish-brown	occasionally consorediate or blastidiate at margins of areoles	consoredia or blastidia breaking into consoredia	-	none	*Dirinaria*	Sheard 1995, 2010
R. sheardii Tønsberg	continuous to areolate, areoles glaucous to whitish	sorediate, soralia discrete, irregularly rounded, sometimes convex, yellowish to pale brown	soredia	thiomelin + additional chlorinated xanthones, atranorin, zeorin, secalonic acid A	C+ orange	*Physcia*	Tønsberg 1992b, Mayrhofer & Moberg 2002*, Sheard 2010
R. stictica Sheard & Tønsberg	usually endophloeodal in esorediate parts, then areolate, grey	sorediate, soralia discrete, on the surface of the areoles, rarely confluent, pale green to greyish-bluish	soredia or consoredia	atranorin, chloroatranorin, zeorin, stictic acid	K+ yellow, Pd+ orange-red	*Physcia-Pachysporaria intermediate*	Sheard & Tønsberg 1995*, Mayrhofer & Moberg 2002*, Sheard 2010
R. turfaceoides P.Boom, H.Mayrhofer, Elix & Giralt	areolate, areoles distinct and discrete when young, whitish grey to pale brownish grey, subconvex to convex, rapidly becoming contiguous to fused	blastidiate from the centre of the areoles	blastidia confluent, forming a thick leprose crust, pale to dark greyish brown	sphaerophorin + 4 unidentified quinoid substances, variolaric acid	K+ yellowish	*Physcia*	Giralt et al. 2001*
R. wetmorei Sheard	thin continuous, then rimose, dark grey to ochraceous	effuse consorediate	consoredia slightly darker than thallus, more brownish	-	none	*Mischoblastia*	Sheard 2010
R. willeyi Sheard & Giralt	areolate, grey, areoles sometimes with raised margins	sorediate, soralia at margins of the areoles becoming discrete and convex	soredia concolorous with thallus or somewhat lighter	pannarin, zeorin	Pd+ orange	*Pachysporaria*	Sheard 1995, 2010

Buellia arborea Coppins & Tønsberg	mostly endosubstratal to whitish	sorediate, soralia well delimitied, flat to concave	soredia blue-green to brownish	atranorin, placodiolic acid	K+ yellow, Pd+/- yellow	*Callispora*	Tønsberg 1992a*, Foucard et al. 2002* Mayrhofer & Moberg 2002, Coppins et al. 2009
B.griseovirens (Turner & Borrer ex Sm.) Almb.	continuous to areolate, greyish	sorediate, soralia discrete, rarely confluent, greyish white to yellowish, with bluish-greenish tingue	soredia with some brown pigmented hyphae	atranorin, norstictic acid	K+ yellow > red (micro-scope), Pd+ yellow to orange, C+/- yellow	3-septate to submuriform	Foucard et al. 2002* Coppins et al. 2009
B. pulverea Coppins & P.James	powdery granular, dull grey-green to dark brown-grey	sorediate, soralia irregular patchy	soredia	alectorialic acid	C+ pink, KC+ red, Pd+/- yellow	*Amandinea*	Coppins & James 1978*, Alstrup 2001* Coppins et al. 2009
B. violaceofusca G.Thor & Muhr	endophloeodal to granular. pale grey to whitish	sorediate, soralia scattered, maculiform to confluent, dark brownish with violet tinge	outer soredia with dark brown to blackish hyphae	-	none	unknown	Thor & Muhr 1991*, Foucard et al. 2002*

Phylogenetic analysis: Three new ITS sequences (Table 1) from the six DNA extractions were obtained. The Bayesian and MP analyses resulted in the same tree topology, the consensus tree obtained from the Bayesian analysis being reported here. *R. candidogrisea* is in our phylogenetic hypothesis monophyletic and sister to *R. roscida*. The two lichens form a fully supported clade, still unresolved in the larger clade which includes saxicolous calcareous *Rinodina* spp. (forming a fully supported own clade), *Phaeophyscia* spp. and *Physciella chloantha* (Fig. 5).

Ecology and associated species: *Rinodina candidogrisea* is a terricolous (muscicolous) species with a clear preference to sites with an increased level of nitrogen. In the Alps it is therefore found on exposed blocks, rocky heads and on the top of cliffs (mainly Mesozoic limestone, rarely marble or basic siliceous rocks) manured by birds. In such places it grows on bryophyte cushions or bryophytes and plant remains established along fissures. *R. candidogrisea* can also grow on protruding cushions in alpine vegetation (e.g. in the association Caricetum firmae). In environments poor in rock outcrops such cushions are also frequently used by birds as lookouts. In both types of site we observed similar sets of accompanying species, e.g. *Agonimia gelatinosa*, *A. tristicula*, *Bilimbia microcarpa*, *Caloplaca cerina* var. *muscorum*, *C. stillicidiorum*, *C. epiphyta*, *C. tiroliensis*, *Candelariella aurella*, *Cladonia pyxidata*, *Collema fuscovirens*, *C. tenax*, *Leptogium intermedium*, *Megaspora verrucosa*, *Physconia muscigena*, *Rinodina roscida*, *Thamnolia vermicularis* and *Xanthoria elegans* (see also Table 3). Communities with similar species with evidently comparable environmental stand characteristics have been described in the past as associations under the names "Aspicilietum verrucosae Frey 1927", i.e. the *Megaspora verrucosa* community (e.g. Klement 1955: 168 f., Asta et al. 1972: 76 ff., Asta 1975: 177 f., Casares 1988) or Caloplacetum tiroliensis (Kalb 1970).

Ornithocoprophilous sites have been investigated at various localities in the Arctic and in mountain ranges in the boreal and temperate biomes (e.g. Asta et al. 1972, 1973, Creveld 1981, Sancho 1988, Olech 1990). However, such studies concentrated on purely saxicolous communities and omitted species encrusting bryophytes and remnants of vascular plants. Both niches share several nitrophilic species which can grow both on rock and organic substrata, e.g. *Physcia caesia*, *Candelariella aurella* and *Xanthoria elegans*. Therefore the syntaxonomy of these communities is controversial (see e.g. Creveld 1981: 125 ff.).

Normally other whitish to grey sorediate crustose lichens are lacking in this synusia but may be present in other synusiae developed nearby, usually living under a different regime of moisture and nutrition (e.g. *Lecanora bryopsora*, *Ochrolechia inaequatula* auct., *Pertusaria albescens*[!], *Lepraria* sp. div.).

Discussion: Several sorediate *Rinodina* species are already known. In the cast of the recent treatment of Britain and Ireland (Giavarini et al. 2009), eight asexually reproducing species are included, whereas in the Nordic Lichen Flora (Mayrhofer & Moberg 2002), 13 (2 saxicolous and 11 epiphytic) species commonly or frequently sterile taxa are treated. According to Sheard (2010), 23 (3 saxicolous and 20 epiphytic) sterile taxa are known from holarctic North America, the majority of which grow on bark or wood. From the species known to occur in Europe, only *R. efflorescens*, *R. flavosoralifera* and *R. griseosoralifera* are known to regularly colonize epiphytic bryophyte mats.

Table 3. Accompanying species in selected specimens of *Rinodina candidogrisea* preserved in GZU (for corresponding localities see section "Specimens examined").

Specimen ID no.	Origin of specimen	Species growing aside to thalli of *R. candidogrisea*
75688	Austria, Upper Austria, Totes Gebirge	*Cladonia pyxidata*, *Leptogium intermedium*
76229	Austria, Styria, Totes Gebirge	*Agonimia tristicula*, *Caloplaca epiphyta*, *Collema undulatum*, *Toninia* sp., *Cercidospora* sp.
69583	Austria, Styria, Ennstaler Alpen	*Caloplaca cerina* var. *muscorum*, *C. tiroliensis*, *Cladonia symphycarpia*, *Collema fuscovirens*, *Physconia muscigena*
68273 (type)	Austria, Styria, Ennstaler Alpen	*Agonimia gelatinosa*, *Caloplaca ammiospila*, *C. cerina* var. *muscorum*, *C. tiroliensis*, *Megaspora verrucosa*, *Rinodina roscida*
68272	Austria, Styria, Ennstaler Alpen	*Agonimia gelatinosa*, *A. tristicula*, *Bilimbia microcarpa*, *Cladonia pyxidata*, *Thamnolia vermicularis*, *Caloplaca* sp. sored. (non *C. epiphyta*)
70239	Austria, Styria, Koralpe	*Agonimia gelatinosa*, *Collema tenax*, *Leptogium intermedium*
76882	Austria, Carinthia, Karnische Alpen	*Caloplaca epiphyta*, *C. stillicidiorum*, *Candelariella aurella*, *Leptogium* cf. *intermedium*, *Physconia muscigena*, *Xanthoria elegans*
75201	Italy, prov. Bolzano, Dolomiti	*Caloplaca cerina* var. *muscorum*, *Collema tenax*, *Megaspora verrucosa*
75277	Slovenia, Julian Alps	*Caloplaca stillicidiorum* infected with *Stigmidium cerinae*
75302	Slovenia, Julian Alps	*Agonimia gelatinosa*, *Leptogium intermedium*

In previous phylogenetic analyses (Nadyeina et al. 2010, Kaschik 2006, Grube & Arup 2001), terricolous *Rinodina* species were not recovered as a monophyletic group but are scattered over several species groups. The commonest arctic-alpine terricolous species, *R. olivaceobrunnea, R. mniaraea, R. roscida* and *R. turfacea*, are distributed over three different clades. The clade including *R. roscida* is diverse with regard to the ascospore types, but shows little ecological variability, since almost all of its taxa prefer calcium-influenced substrata.

The addition of our new sequence data into a dataset of previously analysed Physciaceae (Nadyeina et al. 2010, Kaschik 2006) shows *R. candidogrisea* to be the sister taxon of *R. roscida* (Fig. 5). This is congruent with phenotypic characters of morphology and secondary chemistry (see below). The ascomata of the single fertile specimen so far detected, recall perfectly young apothecia of *R. roscida* and the characters visible in cross sections of apothecia are very

similar to those of *R. roscida*, including the identical ascospore type (*Physcia*-type) (Mayrhofer & Moberg 2002). However, as *R. candidogrisea* has only been found fertile once, the variability of the apothecial characters cannot be assessed and mean values, e.g. of spore measures, may well differ to a certain extent from those calculated from the type specimen alone.

For several specimens of *R. roscida* studied for comparison, we observed marginal areoles similar to those in *R. candidogrisea*, but *R. roscida* never produces marginal soralia on such areoles. Because of this, we regard *R. roscida*-*R. candidogrisea* as a species pair in the sense of Poelt (1970). Both species occupy the same ecological niche, as demonstrated by the fact that at several of the localities mentioned below *R. roscida* was also collected, and that it even turns up among the accompanying taxa on samples of the species described here as new (see Table 3).

In *R. candidogrisea*, the triterpenoid zeorin (identity confirmed with extractions of *R. roscida*) and an unknown fatty acid (given as 'uf' in Fig. 4) have turned out to be constant and to give large spots on TLC-plates in all investigated samples. In 10 of the 20 (including the type) specimens analysed, zeorin and the unknown fatty acid occurred alone. The terpenoid zeorin is a relatively common lichen substance; for example, it is known in seven vegetatively reproducing non-saxicolous species of *Rinodina* (compare Table 2). The most intense fatty acid spot ('uf', Rf classes (2–)3/1(–2)/2(–3)) was always accompanied by 2–3 further, weak fatty acid-like spots (see Fig. 4, small crosses). Variolaric acid (its identity proved with extractions of *R. roscida* and *Phaeorrhiza nimbosa*, Fig. 4) was detected in 7 of 20 samples; this substance is reported in the blastidiate *Rinodina turfaceoides* (compare Table 2). Five (of 20) of the specimens contained a yellow pigment ('up1' in Fig. 4) with running heights of (3–)4/2/3(–4). This substance was compared with secalonic acid A (which is also reported as occurring in species of *Rinodina*, including the sorediate species *R. efflorescens* and *R. sheardii*, see Table 2), but runs below that substance in all three solvent systems. TLC characteristics of the yellow pigment are: strong yellow in daylight, visible in UV(short) before treatment, orange in UV(long) before treatment, brownish to slightly olive-green in daylight (and orange-yellow in UV_{long}) after treatment with sulphuric acid. The substance gives a K+ purple reaction and thus is supposed to be related biochemically to anthraquinones. A much lower concentrated yellowish pigment ('up2'; 5/?/5) may occur. Only one of 20 samples (Hafellner 70239) contained all the four main secondary compounds mentioned.

Further affinities could be detected in their secondary chemistry between *R. candidogrisea* and *R. roscida*. Interestingly, *R. roscida* occurs in two chemical strains, one with zeorin and the other with variolaric acid (Mayrhofer & Moberg 2002; Fig. 4 in this publication). Both these substances can also occur in *R. candidogrisea* – zeorin constantly, variolaric acid occasionally – however, *R. candidogrisea* always contains, in addition, a fatty acid unknown in *R. roscida*.

No other sorediate *Rinodina* species have been observed in the same habitat. On the other hand, *R. candidogrisea* has not been found in other habitats, such as on bark or on corticolous bryophyte mats in deciduous forests in lower vegetation belts or coniferous forests under a strong oceanic influence, which constitute the main niches for most of the other sorediate *Rinodina* species.

In fact, we regard it as hardly possible that *R. candidogrisea* may grow under such entirely different microclimatic conditions. Therefore confusion with other sterile *Rinodina* species is unlikely. Even when we neglect the different ecologies, there are sufficient characters of morphology and secondary chemistry by which *R. candidogrisea* can be distinguished from other holarctic sorediate *Rinodina* species (see Table 2 for selected phenotypic characters). Of these, *R. colobina*, *R. degeliana*, *R. efflorescens*, *R. griseosoralifera*, *R. pityrea* and *R. sheardii* are also recorded from the Eastern Alps area (Hafellner & Türk 2001, Türk & Hafellner 2010, Nimis 1993, Suppan et al. 2000, Feuerer 2010).

The colour of soredia of *R. candidogrisea* recalls somewhat that of *Buellia arborea*, but the exposed soredia of that species contain an olive pigment in the external hyphae responsible for their commonly blackish tinge (Coppins et al. 2009).

Distribution: The species seems to be relatively common in the Alps, where it occurs from the upper montane to the alpine vegetation belt on sites within an altitudinal range between c. 1700 and 2500 m. It is most likely to be present in other Central European mountain chains, and its occurence in similar habitats in, for example, Scandinavia, NW-Spitsbergen and Greenland is to be expected. In these regions, vast areas are dominated by calcareous rock types, the fertile *Rinodina roscida* is also present (Santesson et al. 2004, Elvebakk & Hertel 1997, Kristinsson et al. 2010), and the lichen community in which *R. candidogrisea* typically grows is also known to occur (Frey 1927). However, there is no sorediate lichen species known so far that fits the set of characters as described above, neither from Scandinavia (Mayrhofer & Moberg 2002), the Svalbard archipelago (Øvstedal et al. 2009) and Greenland, nor other parts of the Arctic (Kristinsson et al. 2010).

Further specimens seen (representing paratypes) (a star * indicates specimens used for sequenzing, a cross + indicates specimens used for TLC):

Austria: Kärnten (Carinthia), [Zentralalpen], Steirisches Randgebirge, Koralpe E von Wolfsberg, Steinschneider, sanft geneigter W-Rücken unterhalb der Relaisstation, 46°47’48’’N / 14°57’13’’E, c. 1980 m, GF 9255/2, niedere Felsrippe in alpinen Rasen, mineralreicher Marmor, auf Moosen und Pflanzenresten, 11. VI. 2009, leg. J. Hafellner no. 73530 (GZU)*+. – Kärnten (Carinthia), Südalpen, Karnische Alpen, Gartnerkofel, c. 8 km SW von Hermagor, markante kurze Felsrippe im Südhang etwa halbwegs zwischen Südsattel und Gipfel, 46°34’15’’N / 13°18’20’’E, c. 2100 m, GF 9445/2, Felsrippe aus Triaskalk in alpinen Rasen, auf Moosdecken in Gesteinsfugen, 1. IX. 2007, leg. J. Hafellner no. 76882 (GZU)+. – Oberösterreich (Upper Austria), Nördliche Kalkalpen, Totes Gebirge, Warscheneck Massiv, Kuppe (Kote 2137) SW über der Speikwiese, etwas NW unterhalb des Gipfels, 47°39’25’’N / 14°15’25’’E, c. 2130 m, GF 8351/2, niedere Triaskalkausbisse im Caricetum firmae, auf Moosen und Pflanzenresten, 5. VI. 2010, leg. J. Hafellner no. 75688 (GZU)*+. – Steiermark (Styria), Nordalpen, Nördliche Kalkalpen, Totes Gebirge, Hochtausing N über Wörschach, im obersten Teil des W-Grates kurz unterhalb des Gipfels, 47°35’05’’N / 14°09’20’’E, c. 1810 m, GF 8450/2, S-exp. Schrofen aus Triaskalk zwischen Rasenfragmenten und *Pinus mugo*-Flecken, auf

felshaftenden Moosen, 3. X. 2010, leg. J. Hafellner no. 76229 (GZU)*+. – Steiermark (Styria), Nordalpen (Nördliche Kalkalpen), Totes Gebirge, Hochangern-Massiv N von Liezen, Nazogl, knapp NE vom Gipfel auf dem Rücken gegen den Angerkogel, 47°36'45''N / 14°13'50''E, c. 2050 m, GF 8351/3, alpine Rasen (Caricetum firmae) mit kleinen Felsausbissen und Blöcken (Triaskalk), auf Pflanzenresten, 10. VIII. 2010, leg. J. Hafellner no. 76033 & L. Muggia (GZU)*+. – Steiermark (Styria), Nordalpen (Nördliche Kalkalpen), Ennstaler Alpen, Gesäuseberge E von Admont, Gr. Buchstein, Nordsattel zwischen dem Gipfel und der Admonter Frauenmauer, 47°36'50''N / 14°35'55''E, c. 2065 m, GF 8353/4, Polsterseggen-Silberwurzspaliere und niedere Kalkabbrüche, auf Pflanzenresten in den W-seitigen Abbrüchen, 19. VI. 2005, leg. J. Hafellner no. 68270 (GZU)+. – Steiermark (Styria), Nördliche Kalkalpen, Ennstaler Alpen, Gesäuseberge SE von Admont, niedere Kuppe zwischen Riffel und Kalbling, 47°33'05''N / 14°31'05''E, c. 2000 m, GF 8453/1, kleine Ausbisse aus Triaskalk in alpinen Rasen, N-exponiert auf Moosen und Pflanzenresten, 13. IX. 2006, leg. J. Hafellner no. 69966 (GZU)+. – Steiermark (Styria), Nördliche Kalkalpen, Ennstaler Alpen, Gesäuseberge E von Admont, Hochtor, am W-Grat kurz unter dem Gipfel, 47°33'40''N / 14°37'55''E, c. 2330 m, GF 8453/2, niedere Kalkschrofen und Fragmente von Spalierweiden-Matten, N-seitig auf Moosen und Pflanzenresten, 24. IX. 2005, leg. J. Hafellner no. 68272 (GZU)+. – Steiermark (Styria), Nördliche Kalkalpen, Ennstaler Alpen, Gesäuseberge, Hochzinödl, c. 6.5 km SW von Hieflau, NE über der Hess-Hütte, etwas SW unterhalb vom Gipfel, 47°33'58''N / 14°40'01''E, c. 2185 m, GF 8454/1, mit Rasenbändern durchsetzte Felsausbisse aus Triaskalk, auf Moosen und Pflanzenresten, 20. V. 2007, leg. J. Hafellner no. 68603, L. Muggia & A. Hafellner (GZU)+. – Steiermark (Styria), Nördliche Kalkalpen, Ennstaler Alpen, Lugauer SW von Hieflau, W-Gipfel, in der Umgebung des Gipfelkreuzes, 47°33'12''N / 14°43'20''E, c. 2210 m, GF 8454/1, Caricetum firmae-Fragmente und Kalkschrofen, auf Felsköpfen am Grat, auf Pflanzenresten, 3. VII. 2005, leg. J. Hafellner no. 69572, 69583 (GZU)+. – Steiermark (Styria), Nordalpen (Nördliche Kalkalpen), Mürzsteger Alpen, Veitsch Alpe N von Kindberg, am S-Rand des Plateaus N über dem Breitriegel, 47°38'50''N / 15°25'20''E, c. 1840 m, GF 8358/4, kleine Ausbisse aus Triaskalk in Caricetum firmae, auf Pflanzenresten, 30. IX. 2006, leg. J. Hafellner no. 76438 & L. Muggia (GZU)+. – Steiermark (Styria), Nordalpen, Mürzsteger Alpen, Proles Massiv, Kleiner Proles, c. 6.3 km NW von Mürzsteg, Geländerippe kurz S unterhalb vom Gipfel, 47°43'25''N / 15°26'50''E, c. 1570 m, GF 8258/4, niedere Schrofen aus Triaskalk und Rasenbänder, auf Moosen und Pflanzenresten, 1. VIII. 2008, leg. J. Hafellner no. 77078, L. Muggia & A. Hafellner (GZU). – Steiermark (Styria), Nordalpen, Mürzsteger Alpen, Schneealpe, Windberg, c. 7 km NW von Kapellen, knapp S unterhalb vom Gipfel, c. 1890 m, 47°42'15''N / 15°35'45''E, GF 8259/4, niedere Schrofen aus Triaskalk in Caricetum firmae, auf Moosen und Pflanzenresten, 25. VII. 2008, leg. J. Hafellner no. 77079 (GZU). – Steiermark (Styria), Niedere Tauern, Wölzer Tauern, Rettlkirchspitze NW von Oberwölz, am N-Fuß, c. 1 km W der Neunkirchner Hütte, 47°16'15''N / 14°08'00''E, c. 1720 m, GF 8750/2, Marmorschrofen in subalpinen Weiderasen, auf Moosen und Pflanzenresten, 24. VIII. 2002, leg. J. Hafellner no. 76439a & J. Miadlikowska (GZU)+. – Steiermark (Styria), [Zentralalpen], Niedere Tauern,

Wölzer Tauern, Berge NW von Pusterwald, Nordhänge des Bergrückens zwischen Schönfeldspitz und Hirnkogel, Feldkar, 47°21’00’’N / 14°14’00’’E, c. 1790 m, GF 8651, große, erratische Marmorblöcke im sanft geneigten Quellbett unter den markanten hellgrauen Marmorabbrüchen, S-seitig auf Moosen und Pflanzenresten, 15. VIII. 2009, leg. J. Hafellner no. 73714 (GZU). – Steiermark (Styria), [Zentralalpen], Niedere Tauern, Wölzer Tauern, Berge, c. 8 km WNW von Pusterwald, E-Hänge des Kleinhansl, am Steig vom der Wildalmhütte zum Kleinhansl, 47°19’40’’N / 14°16’40’’E, c. 2000 m, GF 8651/4, niedere Ausbisse und kleine Schrofen aus Marmor, auf Moosen und Pflanzenresten, 25. VIII. 2005, leg. J. Hafellner no. 73178 (GZU)$^{+}$. – Steiermark (Styria), [Zentralalpen], Steirisches Randgebirge, Koralpe, Sattel zwischen Moschkogel und Hühnerstütze, etwas S über dem Sattel, c. 0.5 km E der Grillitschhütte, 46°48’55’’N / 14°59’30’’E, c. 1760 m, GF 9155/4, Marmorausbisse am sanft geneigten N-Hang im Bereich der Waldgrenze, auf Moosen und Pflanzenresten, 17. VI. 2007, leg. J. Hafellner no. 70239 & L. Muggia (GZU)$^{+}$. – Vorarlberg, Rätikon, Hänge zwischen Lünersee und Gafalljoch, c. 14 km SSW von Bludenz, Geländerippe an den E-Abhängen der Kanzelköpfe, W gegenüber der Zollhütte, 47°02’35’’N / 09°45’10’’E, c. 2150 m, GF 8924/4, kleine Kalkausbisse in zwergstrauchreichen Weiderasen, S-exponiert auf Moosen und Pflanzenresten, 29. VIII. 2008, leg. J. Hafellner no. 73108 (GZU). – **Germany**: Bayern (Bavaria), Nordalpen, Chiemgauer Alpen, Kampenwand, c. 22 km SE von Rosenheim, S über der Steinlingalm, im Gratbereich W unter dem Gipfelkreuz, 47°45’20’’N / 12°22’00’’E, c. 1640 m, am S-Fuß der Abbrüche des Gipfelaufbaus, Triaskalk auf Moosen, 28. VIII. 2009, leg. J. Hafellner no. 77077 (GZU). – Bayern (Bavaria), Nordalpen, Chiemgauer Alpen, Hochgern, c. 16 km SW von Traunstein, oberste N-Hänge knapp unter dem Gipfel, 47°45’04’’N / 12°30’53’’E, c. 1700 m, niedere Kalkausbisse im Bereich der Waldgrenze, auf Moosen und Pflanzenresten, 27. VIII. 2009, leg. J. Hafellner no. 75179 (GZU)*$^{+}$. – **Italy**: Trentino-Alto Adige, prov. Bolzano (Südtirol), Southern Alps, Dolomiti, M. Seceda (Geisler Spitzen) NE of Ortisei (St. Ulrich), on the ridge to W, above Forc Pana (Pana Scharte), 46°36’05’’N / 11°44’05’’E, c. 2500 m; low outcrops of limestone in alpine vegetation, on bryophytes and plant debris, 2. IX. 2002, leg. J. Hafellner no. 75201 (GZU)$^{+}$. – Friuli-Venezia Giulia, Prov. Udine: [Southern Alps], Carnic Alps, area of Passo Pramollo (Naßfeldpaß), c. 6 km N of Pontebba, monte Carnizza (Garnitzenberg) E above the pass, limestone cliffs on the ridge W of the summit, 46°33’35’’N / 13°17’36’’E, c. 1840 m, rocks of palaeozoic limestone, on plant remnants, 6. VIII. 2007, leg. J. Hafellner no. 76199 (GZU)$^{+}$. – **Slovenia**: Southern Alps, Julian Alps, massif of Mangart NE of Bovec, beginning of the trail to the Planinski mejni prehod (Mangart saddle), 46°26’45’’N / 13°39’00’’E, c. 1980 m, alpine vegetation fragments and large boulders of limestone, on plant remnants, 5. VII. 2003, leg. J. Hafellner no. 75277 (GZU)$^{+}$. – Southern Alps, Julian Alps, massif of Mangart NE of Bovec, NE slopes of Mali vrh S opposite to Mangartska koča (Mangart refuge), 46°26’00’’N / 13°38’35’’E, c. 1960 m, alpine vegetation fragments and rocks of limestone, on plant remnants, 5. VII. 2003, leg. J. Hafellner no. 75302 (GZU)$^{+}$. – **Switzerland**: Kanton Graubünden, Rhätische Alpen, Albula-Pass, Hänge um das Hospiz, 2300–2350 m, Kalkschiefer, auf kleinen Moospolstern, 25. VIII. 1980, leg. J. Poelt (GZU, separated admixture of a specimen of *Caloplaca epiphyta*).

Further specimens seen (non-type material):

Austria: Kärnten (Carinthia), Südalpen, Karnische Alpen, Gartnerkofel, c. 8 km SW von Hermagor, auf dem westlichen Seitengipfel, 46°34’20’’N / 13°18’15’’E, c. 2180 m, GF 9445/2, Ausbisse aus Triaskalk in alpinen Rasen, auf Moosen und Pflanzenresten, 1. IX. 2007, leg. J. Hafellner no. 75820 (GZU). – Steiermark (Styria), Nördliche Kalkalpen, Dachstein-Gruppe, Stoderzinken, N-exponierte Hänge knapp unter dem Gipfel, 47°27’30’’N / 13°49’40’’E, 2040–2050 m, GF 8548/2, Caricetum firmae und Caricetum rupestris über triadischen Kalkschrofen, auf Pflanzenresten, 28. VII. 2010, leg. J. Hafellner no. 75987 (GZU). – Steiermark (Styria), Nordalpen (Nördliche Kalkalpen), Ennstaler Alpen, Haller Mauern, Scheiblingstein N von Admont, NW-seitig am SW-Grat kurz unter dem Gipfel, 47°39’10’’N / 14°25’25’’E, c. 2180 m, GF 8352/2, felsdurchsetzte alpine Rasen, Triaskalk, auf Moosen und Pflanzenresten, 9. VI. 2007, leg. J. Hafellner no. 68644, L. Muggia & A. Hafellner (GZU). – Steiermark (Styria), Nordalpen (Nördliche Kalkalpen), Ennstaler Alpen, Haller Mauern N von Admont, Hexenturm, im Gipfelbereich, 47°38’47’’N / 14°28’55’’E, c. 2170 m, GF 8352/4, Kalkschrofen mit lückiger alpiner Vegetation, N-exponiert auf Moosen und Pflanzenresten, 9. IX. 2006, leg. J. Hafellner no. 69487 (GZU). – Steiermark (Styria), Nördliche Kalkalpen, Ennstaler Alpen, Tamischbachturm NW von Hieflau, auf dem Gipfel, kurz NE unter dem Gipfelkreuz, 47°36’55’’N / 14°42’00’’E, c. 2030 m, GF 8354/3, Kalkschrofen und Rasenfragmente, auf Moosen und Pflanzenresten in schattigen Felsspalten, 23. VII. 2005, leg. J. Hafellner no. 68271 (GZU). – **Italy**: Piemonte, Prov. Cuneo, [Western Alps], Alpi Cozie, W ridge of Monte Nebin, c. 1 km E of Colle di Sampeyre, 44°32’40’’N / 07°08’20’’E, c. 2380 m, outcrops of calcareous schists on slope exposed to the S, on plant remnants, 26. VII. 2000, leg. J. Hafellner no. 75633 (with P. L. Nimis & M. Tretiach) (GZU). – **Slovenia**: Southern Alps, Julian Alps, massif of Mangart NE of Bovec, on the Planinski mejni prehod (Mangart saddle), at the base of the rock faces of the mountain Travnik, 46°26’45’’N / 13°39’20’’E, c. 2100 m, alpine vegetation and rocks of limestone, on plant remains, 5. VII. 2003, leg. J. Hafellner no. 75212 (GZU).

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