Two new *Rinodina* lichens from South Korea, with an updated key to the species of *Rinodina* in the far eastern Asia

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Abstract

*Rinodina salicis* Lee & Hur and *Rinodina zeorina* Lee & Hur are described as new lichen-forming fungi from forested wetlands or a humid forest in South Korea. *Rinodina salicis* is distinguishable from *Rinodina excrescens* Vain., the most similar species, by its olive-gray thallus with smaller areoles without having blastidia, contiguous apothecia, non-pruinose discs, paler disc color, wider ascospores in the *Pachysporaria*-type II, and the absence of secondary metabolites. *Rinodina zeorina* differs from *Rinodina hypobadia* Sheard by areolate and brownish thallus, non-pruinose apothecia, colorless and wider parathecium, narrower paraphyses with non-pigmented and unswollen tips, longer and narrower ascospores with angular to globose lumina, and the absence of pannarin. Molecular analyses employing internal transcribed spacer (ITS) sequences strongly support the two new species to be unique in the genus *Rinodina*. An updated key is provided to assist in the identification of all 63 taxa in *Rinodina* of the far eastern Asia.

Keywords

Biodiversity, corticolous, phylogeny, Physciaceae, taxonomy

Introduction

*Rinodina*, the largest genus in the family Physciaceae, comprises about three hundred species worldwide (Sheard et al. 2017; Wijayawardene et al. 2020). Several infrageneric groups have been studied since Malme (1902) introduced the ascospore-type
concept for the groups in *Rinodina* (Poelt 1965; Grube and Arup 2001). Although the classification based on different ascospore types has been coarsely accepted, the variety of ascospores does not always correspond to the infrageneric classification. As the pattern of ascospore ontogeny is considered more important than the spore type itself, it is understood that the ascospore types should be respected in developmental stages of a spore (Giralt 1994; Grube and Arup 2001; Sheard 2010; Resl et al. 2016).

The *Rinodina* has been studied in Europe (Mayrhofer and Poelt 1979; Giralt et al. 1995; Giralt 2001; Mayrhofer and Moberg 2002), North America (Sheard and Mayrhofer 2002; Sheard 2004, 2010, 2018; Sheard et al. 2011, 2012; Lendemer et al. 2012, 2019; Morse and Sheard 2020), islands of South America (Bungartz et al. 2016), Australia to New Zealand (Mayrhofer 1983, 1984b; Kaschik 2006; Elix 2011; Elix et al. 2020), Asia to Russian Far East (Mayrhofer 1984a; Galanina et al. 2011; Lendemer et al. 2012; Sheard et al. 2017; Galanina et al. 2018; Galanina and Ezhkin 2019; Zheng and Ren 2020; Galanina et al. 2021; Kumar et al. 2021), and South Africa (Matzer and Mayrhofer 1996; Mayrhofer et al. 2014). Molecular works have been accomplished over the continents (Grube and Arup 2001; Wedin et al. 2002; Nadyeina et al. 2010; Resl et al. 2016).

Sheard et al. (2017) achieved the first and comprehensive study on the genus *Rinodina* of the far eastern Asia (Korea, Japan, and Russian Far East). Several studies announced further more species in the genus, such as *R. badiexcipula* Sheard, *R. convexula* H. Magn., *R. occulta* (Körb.) Sheard, *R. oxneriana* S.Y. Kondr., Lőkös & Hur and *R. tephraspis* (Tück.) Herre from South Korea (Kondratyuk et al. 2016, 2017; Yakovchenko 2018; Kondratyuk et al. 2020) and *R. colobinoides* (Nyl.) Müll. Arg., *R. herrei* H. Magn., *R. laevigata* (Ach.) Malme, and *R. parasitica* H. Mayrhofer & Poelt from the Kuril Islands and the Magadan region, Russian Far East (Galanina and Ezhkin 2019; Galanina et al. 2021). Among them, *R. oxneriana* was discovered as a new species and other eight species were reported as new records to the far eastern Asia. The species of *Rinodina* in the far eastern Asia are mainly corticolous and the main genera of the substrate trees are *Quercus*, *Picea*, *Salix*, *Betula* and *Alnus* (Fig. 1) (Lendemer et al. 2012; Sheard et al. 2012; Joshi et al. 2013; Kondratyuk et al. 2013, 2016, 2017, 2020; Apton and Moon 2014; Sheard et al. 2017; Yakovchenko et al. 2018; Galanina and Ezhkin 2019; Gananina et al. 2021). Those main substrates vigorously grow in a humid forest, a valley or a wetland, and particularly the genera *Salix* and *Alnus* often inhabit the water. Inhabiting those tree barks, diverse *Rinodina* species are easily detected in shaded forests and forested wetlands in which are one of the representative lichens of the ecosystems.

This study describes two new lichen-forming fungi in the genus *Rinodina*. Field surveys for the lichen biodiversity in the forested wetlands of South Korea were carried out during the summer of 2020, and a couple of specimens of *Rinodina* were collected from barks of *Quercus* and *Salix*, the most common genera of the substrates for corticolous *Rinodina* species in the far eastern Asia, in a humid forest and a forested wetland on mountains (Fig. 2). The specimens were comprehensively analyzed in ecology, morphology, chemistry and molecular phylogeny and did not correspond to any
Figure 1. Substrates of *Rinodina* species in the far eastern Asia. *Rinodina* species of the far eastern Asia occur mainly on bark, and the genera *Quercus*, *Picea*, *Salix*, *Betula* and *Alnus* are the main substrates for corticolous *Rinodina* species of the far eastern Asia.

previously known species. We describe them as new species, *Rinodina salicis* and *R. zeorina*, and this discovery contributes to the taxonomy with overall 63 taxa in the genus *Rinodina* of the far eastern Asia. The type specimens are deposited in the herbarium of the Baekdudaegan National Arboretum (KBA, the herbarium acronym in the Index Herbariorum), South Korea.
Materials and methods

Morphological and chemical analyses

Hand sections were prepared manually with a razor blade under a stereomicroscope (Olympus optical SZ51; Olympus, Tokyo, Japan), scrutinized under a compound microscope (Nikon Eclipse E400; Nikon, Tokyo, Japan) and pictured using a software program (NIS-Elements D; Nikon, Tokyo, Japan) and a DS-Fi3 camera (Nikon, Tokyo, Japan) mounted on a Nikon Eclipse Ni-U microscope (Nikon, Tokyo, Japan). The ascospores were examined at 1000× magnification in water. The length and width of the ascospores were measured and the range of spore sizes was shown with average, standard deviation (SD), length-to-width ratio, and the number of measured spores. Thin-layer chromatography (TLC) was performed using solvent systems A and C according to standard methods (Orange et al. 2001).

Isolation, DNA extraction, amplification, and sequencing

Hand-cut sections of ten to twenty ascomata per collected specimen were prepared for DNA isolation and DNA was extracted with a NucleoSpin Plant II Kit in line with the manufacturer’s instructions (Macherey-Nagel, Düren, Germany). PCR amplifications

Figure 2. Specific collection sites for two new species A habitat/landscape for R. salicis B habitat/landscape for R. zeorina C location for R. salicis (a black star); locations for R. zeorina (two black diamonds).
for the internal transcribed spacer region (ITS1-5.8S-ITS2 rDNA) RNA genes were achieved using Bioneer’s AccuPower PCR Premix (Bioneer, Daejeon, Korea) in 20-μl tubes with 16 μl of distilled water, 2 μl of DNA extracts and 2 μl of the primers ITS5 and ITS4 (White et al. 1990). The PCR thermal cycling parameters used were 95 °C (15 sec), followed by 35 cycles of 95 °C (45 sec), 54 °C (45 sec), and 72 °C (1 min), and a final extension at 72 °C (7 min) based on Ekman (2001). The annealing temperature was occasionally altered by ±1 degree in order to get a better result. PCR purification and DNA sequencing were accomplished by the genomic research company Macrogen (Seoul, Korea).

**Phylogenetic analyses**

All ITS sequences (Table 1) were aligned and edited manually using ClustalW in Bi-oedit V7.2.6.1 (Hall 1999). All missing and ambiguously aligned data and parsimony-uninformative positions were removed and only parsimony-informative regions were finally analyzed in MEGA X (Stecher et al. 2020). The final alignment comprised 974 bp in which 167 variable regions were detected. The phylogenetically informative regions were 523. Phylogenetic trees with bootstrap values were obtained in RAxML GUI 2.0 beta (Edler et al. 2019) using the maximum likelihood method with a rapid bootstrap with 1000 bootstrap replications and GTR GAMMA for the substitution matrix. The posterior probabilities were obtained in BEAST 2.6.4 (Bouckaert et al. 2019) using the GTR 121343 model, as the appropriate model of nucleotide substitution produced by the bayesian model averaging methods with bModelTest (Bouckaert and Drummond 2017), empirical base frequencies, gamma for the site heterogeneity model, four categories for gamma, and a 10,000,000 Markov chain Monte Carlo chain length with a 10,000-echo state screening and 1000 log parameters. Then, a consensus tree was constructed in TreeAnnotator 2.6.4 (Bouckaert et al. 2019) with no discard of burnin, no posterior probability limit, a maximum clade credibility tree for the target tree type, and median node heights. All trees were displayed in FigTree 1.4.2 (Rambaut 2014) and edited in Microsoft Paint. The bootstrapping and posterior probability analyses were repeated three times for the result consistency and no significant differences were shown for the tree shapes and branch values. The phylogenetic trees and DNA sequence alignments are deposited in TreeBASE under the study ID 28192. Overall analyses in the materials and methods were accomplished based on Lee and Hur (2020).

**Results and discussion**

**Phylogenetic analyses**

An independent phylogenetic tree for the genus *Rinodina* and related genera was produced from 67 sequences from GenBank and 11 newly generated sequences for the two new species and related species (Table 1). The two new species were positioned in the genus *Rinodina* in the ITS tree. The ITS tree describes that *R. salicis*, a new species, is com-
Table 1. Species list and DNA sequence information employed for phylogenetic analysis.

| No. | Species                  | ID (ITS)     | Voucher                  |
|-----|--------------------------|--------------|--------------------------|
| 1   | Amandinea lignicola      | JX878521     | Tønsberg 36426 (BG)      |
| 2   | Amandinea punctata       | HK650627     | AFTOL-ID 1306            |
| 3   | Buellia badia            | MG250192     | TS1767 (LCU)             |
| 4   | Buellia bucongensis      | MF399800     | KolRI 041680             |
| 5   | Buellia numerosa         | LC153799     | CBM:Wazanuki L01034      |
| 6   | Rinodina afghanica       | MT260860     | 500103 (XJU-L)           |
| 7   | Rinodina alba            | GU553290     | GZU 000272655            |
| 8   | Rinodina albana          | GU553297     | GZU 000272651            |
| 9   | Rinodina anomala         | MN587028     | Sipman 6294              |
| 10  | Rinodina archata         | DQ492929     | H. Mayrhofer 15752 (GZU) |
| 11  | Rinodina atrocinerea     | AF540544     | H. Mayrhofer 13.740 & U. Arup (GZU) |
| 12  | Rinodina balanina        | KY266842     | O-L-195705               |
| 13  | Rinodina bischoffi       | DQ849291     | M. Lambauer 0044 (GZU)   |
| 14  | Rinodina cacaoitana      | DQ849295     | H. Mayrhofer 10770 (HO)  |
| 15  | Rinodina calcarea        | GU553292     | GZU 000272654            |
| 16  | Rinodina cana            | MN587029     | Sipman 63008             |
| 17  | Rinodina capensis        | DQ849296     | W. Obermayer 09230 (GZU) |
| 18  | Rinodina confregosa      | DQ849297     | W. Obermayer 09091 (GZU) |
| 19  | Rinodina congrugusula    | DQ849298     | M. Lambauer 0944 (GZU)   |
| 20  | Rinodina degeliana       | KX015681     | Tønsberg 42631           |
| 21  | Rinodina destituta       | KT695382     | BIOUG24047-H02           |
| 22  | Rinodina disjuncta       | MK812529     | TRH-L-15387              |
| 23  | Rinodina efforescens     | KX015683     | Malicek 5462             |
| 24  | Rinodina exigua          | GU553294     | GZU 000272652            |
| 25  | Rinodina gallowayi       | DQ492929     | M. Lambauer 0125 (GZU)   |
| 26  | Rinodina gennarii        | AJ544187     | B44435                   |
| 27  | Rinodina glauca          | GU553295     | GZU 000272662            |
| 28  | Rinodina berteliana      | DQ849300     | M. Lambauer 0177 (GZU)   |
| 29  | Rinodina immersa         | DQ849301     | M. Lambauer 0129 (GZU)   |
| 30  | Rinodina interpolata     | AF250809     | M263                     |
| 31  | Rinodina jamesii         | DQ849303     | H. Mayrhofer 10810 (GZU) |
| 32  | Rinodina lecanorina      | AF540545     | H. Mayrhofer 13.120 (GZU) |
| 33  | Rinodina lepida          | AY143413     | Trinkaus 137             |
| 34  | Rinodina luridata        | DQ49304      | H. Mayrhofer 12122 (GZU) |
| 35  | Rinodina luridescens     | AJ544183     | B42835                   |
| 36  | Rinodina metaboliza      | MT260864     | 20080224 (XJU-L)         |
| 37  | Rinodina milvina         | GU553299     | KW 63379                 |
| 38  | Rinodina mniaroea        | KX015689     | Spribeille 21010 (GZU)   |
| 39  | Rinodina mniaroea        | KX015691     | V. Wagner, 15.07.06/1 (GZU) |
| 40  | Rinodina mniaroea        | KX015692     | Spribeille 20391 (GZU)   |
| 41  | Rinodina moziana         | DQ49307      | H. Mayrhofer 6729 (GZU)  |
| 42  | Rinodina moziana var. moziana | DQ49305 | M. Lambauer 0214 (GZU) |
| 43  | Rinodina nimsini         | AJ544184     | B42685                   |
| 44  | Rinodina obnascens       | AJ544185     | B42477                   |
| 45  | Rinodina oleae           | DQ49308      | M. Lambauer 0178 (GZU)   |
| 46  | Rinodina oleace          | GU553301     | GZU 000272565            |
| 47  | Rinodina olivaceobrunnea | AF540547     | J. Rommeke 2.09.0300 (GOET) |
| 48  | Rinodina orcadata        | DQ49309      | H. Mayrhofer 15754 (GZU) |
| 49  | Rinodina orientalis      | MW832807     | BDNA-L-0000284           |
| 50  | Rinodina orientalis      | MW832808     | BDNA-L-00000653          |
| 51  | Rinodina orientalis      | MW832809     | BDNA-L-0000774           |
| 52  | Rinodina oxydata         | DQ49313      | H. Mayrhofer 11406 (GZU) |
| 53  | Rinodina plana           | AF250812     | E34                     |
| 54  | Rinodina pyrina          | AF540549     | P. Bilovitz & H. Mayrhofer 483 (GZU) |
| 55  | Rinodina ramboldii       | DQ49315      | G. Rambold 5094 (M)      |
| 56  | Rinodina reagens         | DQ49316      | M. Lambauer 0218 (GZU)   |
| 57  | Rinodina roborri         | MK811851     | O-L-206765               |
| 58  | Rinodina rosida          | DQ49317      | S. Kholod plot515 (GZU)  |
| 59  | Rinodina salicina        | MW832810     | BDNA-L-0000558           |
| 60  | Rinodina salicina        | MW832811     | BDNA-L-00000560          |
| 61  | Rinodina septentrionalis | GU553303     | GZU 000272561            |
| 62  | Rinodina sheardii        | MK778639     | J. Malicek 10238         |
| 63  | Rinodina sheardii        | MK778640     | J. Vondrak 15298 (PRA)   |
DNA sequences which were generated in this study, i.e., two new species such as *Rinodina salicis* and *R. zeorina*, and another compared species, *R. orientalis*, are presented in bold. All others were obtained from GenBank. The species names are followed by GenBank accession numbers and voucher information. ITS, internal transcribed spacer; Voucher, voucher information.

ing alone in a single clade. Several species such as *R. mniaroea* (Ach.) Körb., *R. rosicida* (Sommerf.) Arnold, *R. bischoffii* (Hepp) A. Massal., *R. luridata* (Körb.) H. Mayrhofer, Scheid. & Sheard, *R. metaboliza* Vain., *R. albana* (A. Massal.) A. Massal., *R. afghanica* M. Steiner & Poelt, *R. zwackhiana* (Kremp.) Körb., *R. calcula* (Hepp ex Arnold) Arnold, *R. immersa* (Körb.) J. Steiner, *R. tunicata* H. Mayrhofer & Poelt, *Rinodinella controversa* (A. Massal.) H. Mayrhofer & Poelt, and *R. dubyanoides* (Hepp) H. Mayrhofer & Poelt, are situated close to the new species; this particular clade lacks statistical support (bootstrap value of 58 and a posterior probability of 0.75). *Rinodina zeorina*, the other new species, was located in a clade with *R. sheardii* Tønsberg, represented by a bootstrap value of 89 and a posterior probability of 0.88 (not shown) for the branch (Fig. 3).

**Taxonomy**

*Rinodina salicis* B.G. Lee & J.-S. Hur sp. nov.

No: MB839186

Fig. 4

**Diagnosis.** *Rinodina salicis* differs from *R. excrescens* by olive-gray thallus with smaller areoles without blastidia, contiguous apothecia, the absence of pruina on disc, paler disc color, wider ascospores in the *Pachysporaria*-type, and the absence of secondary metabolites.

**Type.** South Korea, Gangwon Province, Gangneung, Seongsan-myeon, Eoheul-ri, a forested wetland, 37°43.61′N, 128°48.13′E, 212 m alt., on bark of *Salix koreensis* Andersson, 02 June 2020, B.G.Lee & H.J.Lee 2020-000358 (holotype: BDNA-L-0000558; GenBank MW832810 for ITS); same locality, on bark of *Salix koreensis*, 02 June 2020, B.G.Lee & H.J.Lee 2020-000360, with Caloplaca gordejevii (Tomin) Oxner, Lecanora sp., and Phaeophyscia sp. (*paratype*: BDNA-L-0000560; GenBank MW832811 for ITS).

Thallus corticolous, crustose, minutely bullate, some developing to conglomerate and continuous, rarely lobulated, thin, grayish-green to olive green, margin indeter-
Figure 3. Phylogenetic relationships among available species in the genus *Rinodina* based on a maximum likelihood analysis of the dataset of ITS sequences. The tree was rooted with the sequences of the genera *Amandinea* and *Buellia*. Maximum likelihood bootstrap values ≥ 70% and posterior probabilities ≥ 95% are shown above internal branches. Branches with bootstrap values ≥ 90% are shown as fatty lines. Two new species, *R. salicis* and *R. zeorina* are presented in bold as their DNA sequences were produced from this study. All species names are followed by the Genbank accession numbers.
Rinodina species of the far eastern Asia

Thallus olive-gray composed of tiny areoles and non-pruinose apothecia E well-developed amphitheium and algal layer extending to the base F asci clavate with eight spores G ascospores simple in the beginning and developed 1-septate, Pachysporaria-type II, rarely Physcia-type at mature. Scale bars: 1 mm (A–D); 200 μm (E); 10 μm (F, G).

Figure 4. Rinodina salicis (BDNA-L-0000558, holotype) in morphology A–D habitus and apothecia. Thallus olive-gray composed of tiny areoles and non-pruinose apothecia E well-developed amphitheium and algal layer extending to the base F asci clavate with eight spores G ascospores simple in the beginning and developed 1-septate, Pachysporaria-type II, rarely Physcia-type at mature. Scale bars: 1 mm (A–D); 200 μm (E); 10 μm (F, G).

minate, vegetative propagules absent, areoles 0.1–0.2 mm diam., 85–90 μm thick; cortex hyaline, 10 μm thick, cortical cells 5–9 μm diam.; medulla 60–65 μm thick, intermixed with algal cells, without crystals (PL–); photobiont coccoid, cells globose, 5–15 μm. Prothallus absent.

Apothecia abundant, rounded, often contiguous, emerging on the surface of thallus and sessile when mature, constricted at the base, 0.2–1.3 mm diam. Disc flat, not pruinose, pale brown or dark brown from early stages, 220–260 μm thick; margin persistent, generally entire or somewhat flexuous, a little crenulate, thalline margin concolorous to thallus but proper margin near disc distinctly pale brown. Amphitheium well-developed, with small crystals in both cortical layer and the algal-containing medulla, crystals extending to the base, not dissolving in K, 60–70 μm wide laterally, algal layers continuous to the base or solitary, algal cells 5–15 μm diam., cortical layer hyaline, 10–20 μm thick. Paratheicum hyaline but light brown at periphery, 45–50 μm wide laterally and 70–80 μm wide at periphery. Epithymenium brown, not granular, pigment slightly paler in K but not diluted, 5–10 μm high. Hymenium hyaline, 70–90 μm high. Hypotheicum generally hyaline, with pale yellow pigment, prosoplectenchymatous (irregular), 70–80 μm high. Oil droplets are present mainly in hypotheicum and a little in hymenium. Paraphyses septeate, anastomosing, 1–1.5 μm wide, simple or branched at tips, tips swollen, pigmented, epithymenium pigmented by paraphysial tips, 4.5–7.5 μm wide. Asci clavate, 8-spored, 68–90 × 20–25 μm (n
Ascospores ellipsoid, 1-septate, *Pachysporaria*-type II, rarely *Physcia*-type, Type A development, hyaline when young and light brown to brown in mature, 14–24 × 8–13.5 μm (mean = 18.2 × 10.5 μm; SD = 2.12(L), 1.19(W); L/W ratio 1.2–2.4, ratio mean = 1.7, ratio SD = 0.2; n = 105). Pycnidia not detected.

**Chemistry.** Thallus K–, KC–, C–, Pd–. Hymenium I+ purple-blue. UV–. No lichen substance was detected by TLC.

**Distribution and ecology.** The species occurs on the bark of *Salix koreensis*. The species is currently known from the type collections.

**Etymology.** The species epithet indicates the lichen's substrate preference, namely the substrate tree *Salix koreensis*.

**Notes.** The new species is similar to *R. excrescens* and *R. bullata* Sheard & Lendemer in having bullate thallus. However, the new species differs from *R. excrescens* by olive-gray thallus with smaller areoles without having blastidia, contiguous apothecia, the absence of pruina on disc, paler disc color, ascospore type, larger ascospore, and the absence of secondary metabolites (Sheard 1966; Sheard et al. 2012).

The new species is closer to *R. bullata* in having small bullate areoles without having blastidia. However, the new species differs from the latter by olive-gray thallus, contiguous and larger apothecia, proper margin with pale brown color, crystals present in both cortex and medulla in amphithecium, larger ascospores, K– reaction on thallus, and the absence of lichen substance (Sheard et al. 2012, 2017).

The new species is comparable to *R. granulans* Vain. as the latter represents thallus with minute areoles. However, the new species differs from the latter by thallus color, slightly smaller areoles without blastidia, abundance of apothecia without pruina, *Pachysporaria*-type II ascospores, K– reaction on thallus, and the absence of lichen substance (Giralt et al. 1994; Galanina et al. 2011). Reference Table 2 provides the key characteristics distinguishing *R. salicis* from the compared species above.

**Table 2.** Comparison of *Rinodina salicis* with closely-related species.

| Species            | *Rinodina salicis* | *Rinodina bullata* | *Rinodina excrescens* | *Rinodina granulans* |
|--------------------|--------------------|--------------------|-----------------------|----------------------|
| **Thallus growth form** | bullate without blastidia | bullate without blastidia | bullate with blastidia | bullate with blastidia, forming leprose crust |
| **Areoles (mm in diam.)** | 0.1–0.2 | 0.1–0.15(–0.2) | up to c. 1.98 | (0.1–)0.2–0.3(–0.5) |
| **Thallus color** | olive-gray | light gray | gray | gray to gray-brown |
| **Apothecia (mm in diam.)** | 0.2–1.5 | 0.3–0.6 | up to c. 1.26 | up to 0.3 |
| **Apothecia contiguity** | often contiguous | not contiguous | not contiguous | not contiguous |
| **Apothecia abundance** | abundant | abundant | abundant | abundant |
| **Pruina** | absent on disc | – | often present on disc | often present on disc |
| **Disc color** | pale to dark brown | brown | brown to black | reddish brown |
| **Proper margin** | pale brown | indistinct | – | indistinct |
| **Crystals in amphithecium** | present in medulla and cortex | present in cortex | – | present |
| **Ascospore type** | *Pachysporaria*-type II | *Pachysporaria*-type II | *Physcia*-type | *Physcia*-type to *Milvina*-type |
| **Ascospores (μm)** | 14–24 × 8–13.5 | 14.5–16.5 × 8–9 | 17.5–19.5 × 8.5–9.5 | 18–25 × 10–14 |
| **Spot test** | thallus K– | thallus K+ yellow | thallus K– | thallus K+ faint yellow |
| **Substance** | absent | atranorin | panarin, (rarely zeorin) | panarin |
| **Reference** | BDNA-L-0000558 (holotype), BDNA-L-0000560 (paratype) | Sheard et al. 2012, 2017 | Sheard 1966; Sheard et al. 2012, 2017 | Giralt et al. 1994; Galanina et al. 2011 |

The morphological and chemical characteristics of several species close to the new species are referenced from the previous literature. All information on the new species is produced from type specimens (BDNA-L-0000558 and BDNA-L-0000560) in this study.
**Rinodina zeorina** B.G. Lee & J.-S. Hur sp. nov.
No: MB839187
Fig. 5

**Diagnosis.** *Rinodina zeorina* differs from *R. hypobadia* by areolate, brownish thallus, apothecia without pruina, hyaline and wider parathecium, narrower paraphyses with hyaline and unswollen tips, longer and narrower ascospores with just angular to globose lumina, and the absence of pannarin.

**Type.** South Korea, North Gyeongsang Province, Bonghwa-gun, Seokpo-myeon, Mt. Cheongok, 37°01.89′N, 128°58.65′E, 1,104 m alt., on bark of *Quercus mongolica*, 16 June 2020, B.G. Lee & H.J. Lee 2020-000733, with *Biatora* sp., *Lecidella euphorea* (Flörke) Kremp., *Pertusaria multipuncta* (Turner) Nyl., and *Sagiolechia* sp. (holotype: BDNA-L-0000933; GenBank MW832817 for ITS).

Thallus corticolous, crustose, areolate, rimose to continuous, thin, light gray to light brownish gray, margin indeterminate or determinate with prothallus, vegetative propagules absent, 160–250 mm diam., 80–170 μm thick, areoles 0.1–0.5 mm diam.; cortex brown, 5–8 μm thick, with epinecral layer, hyaline, 3–7 μm thick; medulla 35–40 μm thick, intermixed with algal cells, without crystals (PL–); photobiont coccosid, cells globose, 5–9 μm. Prothallus absent or brownish black when present.

Apothecia abundant, rounded, erumpent in the beginning and sessile when mature, constricted at the base, 0.2–0.6 mm diam. Disc flat, not pruinose but epinecral debris shown in water, black to dark brown from early stages, 150–200 μm thick; margin persistent, prominent, generally entire or a little crenulate, concolorous to thallus. Amphithecium well-developed, with small crystals in the algal-containing medulla and particularly near the base, dissolving in K, 70–90 μm wide laterally, algal cells evenly distributed from periphery to base, 10–15 μm diam., cortical layer brownish, cortical cells granular, 2–3 μm diam., with epinecral layer, up to 5 μm thick. Parathecium hyaline but light brown at periphery, 5–10 μm wide laterally and 20–50 μm wide at periphery. Epihymenium red-brown, small granules not dissolving in K, 8–10 μm high. Hymenium hyaline, 90–95 μm high. Hypothecium brown with olive pigment in upper part, prosoplectenchymatous (irregular), 60–65 μm high. Oil droplets present a little in hypothecium. Paraphyses septate, anastomosing, 0.5–1 μm wide, simple or branched at tips, tips generally not swollen or little swollen, not pigmented, epihymenium pigmented by small granules, not by paraphysial tips, up to 1.5 μm wide. Asci clavate, 8-spored, 60–75 × 15–21 μm (n = 3). Ascospores ellipsoid, 1-septate, *Dirinaria*-type but lumina angular to globose, Type B development not detected, septum inflated a little or not, without a torus, hyaline when young and generally brown or dark brown in mature, 11–20 × 5–8.5 μm (mean = 15.4 × 7.1 μm; SD = 1.77(L), 0.70(W); L/W ratio 1.5–3.4, ratio mean = 2.2, ratio SD = 0.3; n = 105). Pycnidia raised, asymmetric, 175–225 μm wide. Pycnoconidia bacilliform, 3–4 × 0.5 μm.

**Chemistry.** Thallus K–, KC–, C–, Pd–. Hymenium I+ blue. UV–. Zeorin was detected by TLC.

**Distribution and ecology.** The species occurs on the bark of *Quercus mongolica*, *Tilia amurensis* Rupr., and *Maackia amurensis* Rupr. & Maxim. The species is currently known from a humid forest and a forested wetland of two mountainous sites.
**Etymology.** The species epithet indicates that the lichen’s substance, zeorin, is a major compound.

**Notes.** The new species is similar to *R. hypobadia*, *R. sheardii*, and *R. sp. A* in having a pigmented hypothecium. However, the new species differs from *R. hypobadia* by areolate, brownish thallus, apothecia without pruina, hyaline and wider paratheicum, narrower paraphyses with hyaline and unswollen tips, longer and narrower ascospores with just angular to globose lumina, and the absence of pannarin (Sheard et al. 2017).

The new species differs from *Rinodina sheardii* by the absence of vegetative propagules, and *Dirinaria*-type ascospores in smaller size (Sheard et al. 2017).

The new species differs from *Rinodina sp. A* by a wider paratheicum, narrower paraphyses with swollen tips, smaller ascospores *Dirinaria*-type, and the absence of pannarin (Sheard et al. 2017).
Table 3. Comparison of *Rinodina zeorina* with closely-related species.

| Species | Rinodina zeorina | Rinodina hypobadia | Rinodina manshurica | Rinodina sheardii | Rinodina aff. oleae | Rinodina sp. A |
|---------|------------------|--------------------|---------------------|------------------|---------------------|----------------|
| Thallus growth from | areolate, rimose to continuous | rimose, not areolate | rimose, rimose-areolate | ±areolate to continuous | continuous, rimose-areolate | continuous to areolate |
| Thallus color | light gray to light brownish gray | light to dark gray | gray-brown | yellow, yellow-brown, or pale brown or greenish | (dark gray to olive-green) | dark gray to gray-brown |
| Pruina | absent, but epinecral debris shown in water | slightly pruinose | absent | absent | (absent) | – |
| Parathecium color | hyaline and light brown at periphery | red-brown | – | red-brown to brown | (hyaline to brownish) | – |
| Parathecium at periphery (μm) | 20–50 | 10–20 | c. 20 | c. 30 | (up to 30) | c. 25 |
| Paraphyses (μm) | up to 1.5 | 2–2.5 | 2.0 | 2.0 | (1–2) | 3.0 |
| Paraphysial tips | not or little swollen, not pigmented | 3–4 μm, lightly pigmented | c. 3 μm, light pigmented | c. 3 μm | – | c. 4.5 μm, pigmented |
| Hypothecium color | brown with olive pigment | reddish or chestnut brown | hyaline | dilute brown to red-brown | hyaline | light brown |
| Crystals in amphithecium | present in medulla | present in both cortex and medulla | absent | present | – | present in medulla |
| Ascospore type | *Dirinaria*-type with angular-globose lumina | *Dirinaria*-type with *Physcia*- or *Physconia*-like lumina | *Dirinaria*-type, with *Physcia*-like lumina | *Pachysporaria*-type I | *Dirinaria*-type with *Physcia*-like lumina | *Pachysporaria*-type I |
| Ascospores (μm) | 11–20 × 5–8.5 | 12.5–18.5 × 6.5–10 | 14–16.5 × 7.5–8.5 | 16–35 × 8–17 | 15.5–19 × 6.5–9.5 | 22–28.5 × 10.5–15.5 |
| Pycnidia | 175–225 | up to 300 | – | – | – | – |
| Pycnoconidia (μm) | 3–4 × 0.5 | 3.5 × 1.0 | – | – | (4–5 × 1) | – |
| Substance | zeorin | pannarin, zeorin | absent | zeorin | (absent) | pannarin, zeorin |
| Reference | BDNA-L-0000933 (holotype), BDNA-L-0000642, BDNA-L-0000646, BDNA-L-0000650, BDNA-L-0000651, BDNA-L-0000668 | Sheard et al. 2017 | Sheard et al. 2017 | Tønsberg 1992; Sheard et al. 2017 | Joshi et al. 2013; Smith et al. 2009; Sheard et al. 2017 | Sheard et al. 2017 |

The new species can be compared with *R. manshurica* and *R. aff. oleae* in having erumpent apothecia, small ascospores (<21 μm long) with swollen septum among corticolous species. However, the new species differs from *R. manshurica* by crystals present in the amphithecium, wider parathecium, narrower paraphyses without swollen tips, pigmented hypothecium, and longer and narrower ascospores (Tønsberg 1992; Sheard et al. 2017). The new species is distinguished from *R. aff. oleae* by narrower ascospores, and pigmented hypothecium (vs. hyaline hypothecium) (Sheard et al. 2017). Reference Table 3 provides the key characteristics distinguishing *R. zeorina* from the compared species above.

The new species is compared further with other *Rinodina* species having the substance zeorin, *R. ascociscana* (Tuck.) Tuck., *R. buckii* Sheard, *R. efflorescens* Malme, *R. luteonigra* Zahlbr., *R. subalbida* (Nyl.) Vain., *R. subminuta* H. Magn., and *R. willeyi*...
Sheard & Giralt. However, all of them are different from the new species because those species represent larger ascospores in _Physcia_ - to _Physconia_-type for _R. ascocisca_; sorediate thallus, mostly light brown hypothecium and _Teichophila_-type ascospores and the presence of pannarin for _R. buckii_; sorediate thallus, colorless hypothecium, _Pachysporaria_-type ascospores and the presence of pannarin and secalonic acid A for _R. efflorescens_; colorless hypothecium, larger ascospores in _Pachysporaria_-type and the presence of thiomelin for _R. luteonigra_; larger spores in _Pachysporaria_-type and the presence of pannarin for _R. subalbida_; larger spores in _Physcia_-type for _R. subminuta_; sorediate thallus and the presence of pannarin for _R. willeyi_ (Sheard et al. 2012, 2017).

**Additional specimens examined.** South Korea, Gangwon Province, Pyeongchang-gun, Daegwallyeong-myeon, Heonggye-ri, a forested wetland, 37°46.00’N, 128°42.33’E, 1,047 m alt., on bark of _Maackia amurensis_, 03 June 2020, B.G. Lee & H.J.Lee 2020-000442, with _Buellia disciformis_ (Fr.) Mudd, _Buellia_ sp., _Catillaria nigroclavata_ (Nyl.) J. Steiner, _Lecanora megalochelia_ (Hue) H. Miyaw., _Lecanora symmica_ (Ach.) Ach., _Lecidella euphora_, and _Lambiella cf. caeca_ (J. Lowe) Resl & T. Sprib. (BDNA-L-0000642; GenBank MW832812 for ITS); same locality, 37°46’0.02”N, 128°42’19.58”E, 1,047 m alt., on bark of _Maackia amurensis_, 03 June 2020, B.G. Lee & H.J.Lee 2020-000446 (BDNA-L-0000646; GenBank MW832813 for ITS); same locality, 37°46.00’N, 128°42.33’E, 1,047 m alt., on bark of _Maackia amurensis_, 03 June 2020, B.G. Lee & H.J.Lee 2020-000446 (BDNA-L-0000646; GenBank MW832814 for ITS); same locality, 37°46.00’N, 128°42.33’E, 1,047 m alt., on bark of _Maackia amurensis_, 03 June 2020, B.G. Lee & H.J.Lee 2020-000450 (BDNA-L-0000650; GenBank MW832815 for ITS); same locality, 37°46.00’N, 128°42.33’E, 1,047 m alt., on bark of _Tilia amurensis_, 03 June 2020, B.G. Lee & H.J.Lee 2020-000468, with _Amandinea punctata_ (Hoffm.) Coppins & Scheid., _Bacidia aff. beckhausii_ Körb., _Catillaria sp._, _Micarea prasina_ Fr., _Phaeophyscia limbata_ (Poelt) Kashiw., _Rinodina cf. oleae_ Bagl., _Traponora aff. varians_ (Ach.) J. Kalb & Kalb (BDNA-L-0000668; GenBank MW832816 for ITS).

**Key to the species of Rinodina from the far eastern Asia (63 taxa)**

Eleven more species have been recorded since Sheard et al. (2017), such as _Rinodina badiexcipula_, _R. colobinoides_, _R. convexula_, _R. herrei_, _R. laevigata_, _R. occulta_, _R. oxneriana_, _R. parasitica_, _R. tephraspis_ and two new species from this study (Kondratyuk et al. 2016, 2017; Yakovchenko et al. 2018; Galanina and Ezhkin 2019; Kondratyuk et al. 2020; Galanina et al. 2021). Particularly, _R. laevigata_ of Aptroot and Moon (2014) was rejected by Sheard et al. (2017), but Galanina et al. (2021) confirmed the species in the far eastern Asia. This key includes all above species except for _R. convexula_ because the species was just announced for a new record to Korea without any specific description for reference (Kondratyuk et al. 2020). _Rinodina confragosa_ (Ach.) Körb., _R. milvina_ (Wahlenb.) Th. Fr., and _R. olivaceobrunnea_ C.W. Dodge & G.E. Baker were reported from Korea and Russian Far East (Kondratyuk et al. 2016; Galanina et al. 2021) as expected to occur (Sheard et al. 2017). All expected species are remained with an asterisk mark(*).

Overall, 63 taxa of _Rinodina_ are currently recorded or expected to the far eastern Asia (Korea, Japan and Russian Far East).
|   | Substratum rock .................................................................................................................. |
|---|-------------------------------------------------------------------------------------------------------------------------------------|
| 2 |                                                                                                                                     |
| 3 | Thalli effigurate, typically with isidia; when fertile spores belong to the Physcia*-type; associated with seabird colonies; northern. |
| 4 | Thalli not effigurate, vegetative propagules blastidia with budding soredia; spores Pachysporaria*-type II; not coastal; southern.     |
| 5 | Medulla orange, K+ red-violet; spores Pachysporaria*-type I, ultimately developing satellite apical lumina.                           |
| 6 | Medulla not orange, not K+ red-violet; spores of various types but never developing apical lumina.                                 |
| 7 |                                                                                                                                     |
| 8 | Apothecia 0.1–0.3 mm diam., hymenium 80–100 μm high, hypothecium 65–135 μm high, asci 75–80 × 16–19 μm, spores 17–27 × 8–13 μm.     |
| 9 | Thallus plane; spores averaging <21 μm in length, rarely swollen at septum.                                                           |
| 10|                                                                                                                                     |
| 11|                                                                                                                                     |
| 12|                                                                                                                                     |
| 13|                                                                                                                                     |
| 14|                                                                                                                                     |
| 15|                                                                                                                                     |
| 16|                                                                                                                                     |
15 Thallus thick, dark brown; spores constricted at septum when mature, *Milvina*-type; secondary metabolites absent .......................................................\textit{R. milvina}  
- Thallus thin, gray to light brown; spores *Physconia*-type; thalline margin C+ red (under microscope), gyrophoric acid in medulla ........................................ \textit{R. sicula}  
16 Apothecial discs pruinose; spores *Pachysporaria*-type ...........................\textit{R. compensata}  
- Apothecial discs not pruinose; spores *Pachysporaria*-to *Milvina*-like  \textit{R. kozukensis}  
17 On soil, decaying ground vegetation, wood, bone or lichenicolous ........................ \textit{18}  
- Strictly corticolous or lignicolous ................................................................. \textit{27}  
18 Spores 1-septate ................................................................................................ \textit{19}  
- Spores 3-septate or submuriform ..................................................................... \textit{20}  
19 Spores *Teichophila*-type .................................................................................. \textit{R. herrei}  
- Spores *Physcia*-type, rarely with apical satellite lumina .............................. \textit{21}  
20 Spores strictly 3-septate, type B development (apical wall thickened prior to septum formation); secondary metabolites absent ................................ \textit{R. conradii}  
- Spores 3-septate at first, typically becoming submuriform, type A development (apical wall thickening after septum formation); deoxylichesterinic acid present ................................................ \textit{R. intermedia}  
- Strictly lichenicolous, on *Aspicilia* or *Rhizocarpon* .................................. \textit{R. parasitica}  
- Generally not lichenicolous ....................................................................... \textit{22}  
22 Sphaerophorin crystals in medulla (sometimes lichenicolous)............. \textit{R. turfacea}  
- Sphaerophorin lacking in medulla (never lichenicolous) .......................... \textit{23}  
23 Cortex K+ yellow or medulla orange, K+ red ........................................ \textit{24}  
- Cortex reaction absent ................................................................................ \textit{25}  
24 Thallus light gray; K+ yellow, atranorin in cortex .......................... \textit{R. mniaroeiza*}  
- Thallus a shade of brown; medulla orange, K+ red, skyrin or other anthraquinones present ............................................................. \textit{R. cinnamomea*}  
25 Spores averaging <23 μm in length .................................................. \textit{R. olivaceobrunnea}  
- Spores averaging >23 μm in length .......................................................... \textit{26}  
26 Thallus and apothecia not pruinose; apothecial discs becoming convex, thalline margin then excluded; spores averaging 24.5–25.5 μm in length, l/w ratio 2.0–2.2 .................................................. \textit{R. mniaroea}  
- Thallus and apothecia typically pruinose; apothecial discs plane or concave, not convex, thalline margin never excluded; spores averaging 30–32 μm in length, l/w ratio 2.2–2.5 .......................................................... \textit{R. roscida}  
27 Vegetative propagules present ............................................................. \textit{28}  
- Vegetative propagules absent ................................................................ \textit{37}  
28 Thallus typically golden yellow ............................................................... \textit{29}  
- Thallus a shade of gray or brown ............................................................. \textit{30}  
29 Thallus with small, dense isidia; very rarely with apothecia; spores *Pachysporaria*-type I ................................................................. \textit{R. chrysidiata}  
- Thallus with marginal, labriform soralia, sometimes becoming pustulate; frequently, but not always, with apothecia; spores *Physcia*-type \textit{R. xanthophae}  
30 Phyllidia present ................................................................................... \textit{R. oxneriana}  
- Blastidia or soredia present ................................................................... \textit{31}
Rinodina species of the far eastern Asia

31 Thallus mainly blastidiate, blastidia 35–60 μm diam. ..................R. colobinoides
   – Thallus generally not blastidiate, but sorediate or sometimes blastidiate ........32
32 Blastidia present at margin, no substance, spores Teichophila-type ..........R. herrei
   – Soredia and/or blastidia present, atranorin or pannarin present, spores in various
     types ............................................................................................................33
33 Thallus light gray; soralia labriform at first, soredia whitish; K+, P+ yellow, cortical
     atranorin present, pannarin absent .......... R. subparieta (syn. R. degeliana)
   – Thallus darker gray; soredia never whitish; K−, P+ cinnabar, atranorin absent, pannarin present ..........................................................34
34 Thallus usually of convex to bullate areoles; blastidia often present, sometimes
     breaking into soredia; zeorin typically absent, when fertile pannarin also in epiphy-
     menium ........................................................................................................35
35 Soredia typically yellowish, secalonic acid A present; spores Physcia-type when
     fertile, averaging <20 μm in length .........................................................R. efflorescens
   – Soredia never yellowish, secalonic acid A absent; spores not Physcia-type, aver-
     ging >20 μm in length ...........................................................................36
36 Thallus minutely verrucose, verrucae central on areoles, quickly forming raised
     soralia, later spreading over thallus surface; soredia >40 μm diam.; spores
     Teichophila-type ....................................................................................R. buckii
   – Thallus with plane areoles, soredia developing marginally on areoles, never raised
     centrally on verrucae, later spreading over thallus surface; soredia <40 μm diam.;
     spores Pachysporaria-type I .................................................................R. willeyi
37 Ascospores 3-septate or submuriform ..................................................38
   – Ascospores 1-septate, rarely with satellite apical cells .............................39
38 Spores strictly 3-septate, type B development (apical wall thickened prior to sep-
     tum formation); secondary metabolites absent ....................................R. conradii
   – Spores 3-septate at first, becoming submuriform, type A development (apical wall
     thickening after septum formation); deoxylichesterinic acid present ............
     ..............................................................................................................39
39 Thallus brightly pigmented; xanthone present, UV+ orange ....................40
   – Thallus a shade of gray or brown; xanthone absent, UV− .......................41
40 Thallus citrine, thiomelin present; spores averaging 31.0–34.5×16.0–17.5 μm, Pach-
     ypsoraria-type I; not sorediate; subtropical, Tsushima Island, Japan ..........R. luteonigra
   – Thallus golden yellow, secalonic acid A present; spores averaging 23.5–28.5×2.0–15.0 μm, Physcia-type; frequently sorediate; temperate, widely distributed ........
     ...........................................................................................................41
41 Thallus K+ yellow or P+ cinnabar, atranorin or pannarin present ...............42
   – Thallus K−, P−, both atranorin and pannarin absent ..................................43
42 Thallus K+ yellow, atranorin present, pannarin absent .............................44
   – Thallus P+ cinnabar, pannarin present, atranorin absent ..........................45
43 Spores averaging >33 μm long, Pachysporaria-type I .........................R. megistospora
   – Spores averaging <33 μm long, Physcia- or Physcionia-type ....................46
44 Spores averaging >26 μm long, strictly Physcia-type; never sorediate; distribution limited to coastal foreshores .............................................. R. macrosora
45 Hypothecium pigmented dark reddish brown; spores Dirinaria-type, (12–)14–16.5(–18)× (6.5–)7.0–8.5(–9.5) μm, lightly pigmented ........... R. hypobadia
46 Spores averaging <20 μm in length, Physcia-type; thallus becoming bullate, often with minute blastidia .............................................. R. excrescens
47 Thallus persistently plane; epihymenium lacking crystals, P−; spores averaging >29 μm ............................................................... R. tenuis (syn. R. adirondackii)
48 Epihymenium typically possessing pannarin crystals, P+ cinnabar; spores lacking apical canals; widely distributed in Japan and adjacent mainland..... R. subalbida
49 Spores 16 per ascus ..................................................................... R. polyspora
50 Medulla with sphaerophorin crystals, PL+ ...................................... 51
51 Thallus dark gray, typically dark brown; areoles becoming contiguous, plane, 0.40–0.55 mm wide; spores averaging 26.5–27.5 × 13.5–14.5 μm .......... R. badiexcipula
52 Spores swollen at septum, more so in KOH, type B development (apical wall thickening prior to septum formation), Dirinaria-type .......................... 53
53 Thallus gray to ochraceous, rugose, areoles to 0.7 mm wide; apothecia to 0.8 mm in diam., discs plane, never convex; spores averaging 15.5–18.0 × 8.0–8.5 μm, l/w ratio 1.9–2.1 .............................................. R. mongolica
54 Spores lacking wall thickening at maturity (septal and apical thickenings may be present briefly in immature spores) ....................................... 55
55 Thallus gray to ochraceous, rugose, areoles to 0.7 mm wide; apothecia to 0.8 mm in diam., discs plane, never convex; spores averaging 15.5–18.0 × 8.0–8.5 μm, l/w ratio 1.9–2.1 .............................................. R. mongolica
56 Apothecia not erumpent; spores averaging 17.5–21.5 × 9–11 μm .... R. metaboliza
57 Apothecia erumpent; spores smaller .............................................
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57 Hypothecium pigmented with brown, spores 11–20 × 5–8.5 μm, zeorin present ................................................................. R. zeorina

– Hypothecium colorless, spores 15.5–18 × 8–9 μm, no substance ................................................................. 58

58 Spores averaging 15.5–16.0 μm in length................................................................. R. manshurica

– Spores averaging 16.5–18.0 μm in length................................................................. R. aff. oleae

59 Spores averaging >22 μm in length................................................................ R. ascociscana (syn. R. akagiensis, R. melancholica)

60 Margins of apothecia often radially cracked; spores Physcia- to Physconia-type ...

................................................................. R. ascociscana (syn. R. akagiensis, R. melancholica)

– Margins of apothecia not radially cracked; spores Pachysporaria-type I .................. R. dolichospora

61 Spores Pachysporaria-type II ................................................................. R. salicis

– Spores Physcia- or Physconia-type ........................................................................ 62

62 Spores Physcia- to Physconia-type, some lumina becoming rounded at apices, at maturity thin-walled ................................................................. 63

– Spores strictly Physcia-type, apical walls remaining thick................................................ 67

63 Thallus dark brown, spores darkly pigmented at maturity, torus prominent; oro-arctic to coastal ................................................................. 64

– Thallus a shade of gray, sometimes brownish, spores typically pigmented at maturity, torus present but not prominent; boreal ........................................... 66

64 Thallus inconspicuous; apothecia mostly crowded, typically broadly attached ....

................................................................. R. olivaceobrunnea*

– Thallus of dispersed or contiguous areoles; apothecia mostly dispersed, narrowly or broadly attached ................................................................. 65

65 Ascospores 20–21.5 × 10–11.5 μm, thallus well-developed, flat, scurfy or thick rugose areolate, apothecia broadly attached in the beginning then becoming narrow and even stipitate, discs convex when mature ................................................................. R. sibirica

– Ascospores 18.5–19.5 × 8.5–9.0 μm, thallus poorly developed, evanescent, thin or scabrid, sometimes areolate, apothecia broadly attached to thallus, discs typically flat ................................................................. R. laevigata

66 Thallus thick, rugose, areolate; apothecia crowded, discs persistently plane, thalline margins persistent ................................................................. R. archaea*

– Thallus thin, plane, continuous or rimose-areolate; apothecia dispersed, discs becoming convex, often excluding thalline margin ................................................................. R. trevisanii*

67 Spores averaging >18 μm long, zeorin present........................................................ R. subminuta

– Spores averaging <18 μm long, zeorin absent ........................................................ 68

68 Apothecia erumpent at first, discs often becoming strongly convex; spores with lightly pigmented tori at maturity ................................................................. R. orientalis

– Apothecia never erumpent, discs persistently plane; spores with very dark, prominent tori at maturity ................................................................. 69

69 Apothecia crowded, broadly attached; thalli associated with leaf scars or other mesic microhabitats; areoles plane, contiguous, to >0.2 mm in diam. ..... R. freyi

– Apothecia mostly scattered, narrowly attached; thalli typically in more xeric microhabitats; areoles convex, scattered, to 0.2 mm in diam. ..... R. septentrionalis
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