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Leprarioid lichens and associated lichenicolous fungi from the Commander Islands (Kamchatka Territory, Russia) including a new species *Lepraria tiinae*

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Abstract: Here, we present new records of leprarioid lichens from the Commander Islands, including one species of *Lithocalla* and six species of *Lepraria*. Notably, we describe as new to science *Lepraria tiinae*, which is quite common in coastal biotopes of the archipelago. The main distinguishing phenotypic features of this new species include large granules of the thallus, a well-developed hypothallus, dark rhizohyphae, and the production of thiophanic acid, arthothelin, and dichlorolichexanthone. Additionally, three species of lichenicolous fungi or fungi associated with leprarioid lichens were found in the studied specimens, all of which are new to the Kamchatka Territory.

Keywords: sterile lichens, secondary metabolites, protected areas, *Lithocalla*, Pacific Ocean, Beringia, the Aleutian Arc

INTRODUCTION

Leprarioid lichens are a morphological group of lichenized fungi that includes species with “leprose”, or ecorticate crustose, thallus. Such thalli consist of lichenized cortex-free soredia-like granules, usually found lying on a layer of non-lichenized hyphae or directly on the substrate (e. g., Laundon, 1992; Kukwa, 2002; Saag et al., 2009; Lendemer, 2011, 2013a). The non-lichenized part of the leprarioid thallus was traditionally interpreted as the “medulla”. However, Lendemer (2011) proposed that the non-lichenized layer consists of two parts: the first is the prothallus, which is always present at the beginning but often disappears with age, and the second is the hypothallus, which is thick and well-developed in some species, but thin or completely absent in others.

The leprarioid lichens are not limited to one genus, as leprose thalli are present in many lichen taxa that were formerly classified as *Lepraria*. In the Holarctic area, this phylogenetically heterogenic group includes representatives of various families, such as *Cladoniaceae* Zenker (*Lepraria*), *Leprocaulaceae* Lendemer & B. P. Hodk. (*Leprocaulon* Nyl.), *Ramalinaceae* C. Agardh (*Lithocalla* Orange, *Phyllopsora* Müll. Arg.), *Chrysotrichaceae* Zahlbr. (*Chrysothrix* Mont.), and the order *Verrucariales* incertae sedis (*Botryolepraria* Canals et al.) (Lendemer & Hodkinson, 2013; Wijayawardene et al., 2022; Kukwa et al., 2023). Moreover, sterile thalli, leprose at least when mature, can be observed, for example, in some species of *Haematomma* A. Massal., *Lecanora* Ach., *Lecidea* Ach., and *Leproplaca* (Nyl.) Nyl. (see Tønsberg, 1992; Harris et al., 2000; Nelsen et al., 2008; Zduńczyk & Kukwa, 2014).

The genus *Lepraria* Ach. comprises approximately 75 species (see Wijayawardene et al., 2022; Kukwa, 2023) and includes leprose lichens, as well as some fruticose species formerly placed in the genus *Leprocaulon* Nyl. (Lendemer & Hodkinson, 2013). Lichen substances are diverse within this genus, and traditionally, the composition of secondary metabolites has been a key phenotypic feature for species delimitation within the genus *Lepraria*, especially given the limited anatomical and morphological features, as well as the absence of fruiting bodies or conidia.

Despite intensive investigations in the last decades (see Saag et al., 2009; Joshi et al., 2010; Lendemer, 2010, 2011, 2013a, b; Lendemer & Hodkinson, 2013; Tsurykau et al., 2016; Orange, 2020; Barcenas-Peña et al., 2021; Kukwa at al., 2023), the diversity, distribution, and ecological features of leprarioid lichens are still insufficiently known. One of the understudied territories in this respect is the Aleutian Arc. Only two leprarioid species, *Lepraria neglecta* (Nyl.) Lettau and *L. nivalis* Laundon, have been reported from this area before (Talbot et al., 1991, 1997), both lacking data on the secondary metabolites; therefore, we consider these records as questionable.

This study provides the first description of the diversity and ecological preferences of leprarioid lichens in the Aleutian Arc. However, given the much larger area of the archipelago to the east, a higher diversity of leprarioid lichens is expected.

MATERIAL AND METHODS

The following abbreviations are used in the text: SA – sample area, AP – additional point, IS – Irina S. Stepanchikova, DH – Dmitry E. Himelbrant, AZ – Anna S. Zueva. Other names, which are less frequently used in the text, are spelled out.

The study area

The Commander Islands represent the westernmost part of the Aleutian Arc and are located in the northern part of the Pacific Ocean, approximately 190 km east of the Kamchatka Peninsula. The archipelago includes two large islands, Bering (1667 km^2) and Medny (186 km^2), as well as small islands Toporkov (0.25 km^2) and Ary Kamen' (cliff ca. 0.08 km^2), and also about 60 offshore cliffs and rocks. The Commander Islands are the surface part of an underwater volcanic range aged 40–50 million years, resulting in a typically mountainous relief, with the exception of Toporkov and the northernmost part of Bering Island. The maximum elevation on Bering Island is 755 m above sea level, and Medny Island reaches 647 m above sea level. The climate of the islands is oceanic, temperate, and very humid (Hydrometcenter of Russia, 2023), with cool summers and mild winters (average annual temperature 2–2.5°C on Bering and 2.8°C on Medny Island). The typical summer weather is cloudy, windy, and rainy, although the total annual precipitation is not extreme and ranges from 690 mm on Bering to 1210 mm on Medny Island. During frequent storms, wind speed reach 33 m/s and more (Ponomareva & Isachenkova, 1991). The Commander Islands are located within the hypoarctic zone. In the mountains different types of tundra prevail, most common of them are lichen- and moss-dwarf shrub communities (Ponomareva & Yanitskaya, 1991; Mochalova & Yakubov, 2004). Uplands, especially on Bering Island, do not have continuous plant cover, and are dominated by gravel fields with mosaic patches of tundra. Deeply incised valleys of numerous streams and creeks are occupied by tall grass meadows and, on Bering Island, by shrub communities composed of *Salix* spp. Forest vegetation is absent in the archipelago. Lichen vegetation of the rocky cliffs along the coast is shaped by seabird colonies (Mochalova & Yakubov, 2004; Commander Islands National Park, 2010–2022). The entire archipelago of the Commander Islands is designated as a national park.

Field work and herbarium studies

The first data on lichen diversity of the Commander Islands are based on collections made by E. Almquist on July 31 and August 2, 1879, as part of the Vega Expedition sponsored by A. E. Nordenskiöld (Almquist, 1887; Nylander, 1888). This collection consists of more than 250 specimens, which are stored at the herbaria of the Finnish Museum of Natural History, University of Helsinki (H, H-NYL) and the Swedish Museum of Natural History (S).

Later, Hans H. Trass investigated lichens on Medny Island (August 14, 1960), near Preobrazhenskoe (Trass, 1963), where he collected approximately 80 specimens, now stored in the lichen collection of the herbarium at the University of Tartu (TUF). However, most of the collection by H. Trass from Medny remained unidentified until our recent study. We revised all available specimens in the collections mentioned above but did not find any leprarioid lichens. Some species from the Commander Islands were mentioned in several subsequent taxonomical publications (e.g., Dombrovskaya, 1996; Printzen, 1995; Ryan, 1998; Hertel, Andreev, 2003), but they mostly are based on the same historical collections. In 2019–2022, we investigated all four islands in order to study the lichen diversity and ecology of the archipelago.

The lichen specimens were collected in field by DH and IS from 2019 to 2022, together with AZ in 2022. In total, 245 standard SA were investigated (Bering Island – 189, Medny Island – 51, Toporkov Island – 5, Ary Kamen' Island – 3) (Himelbrant et al., in prep.). SA were 10 × 10 m or in the natural boundaries of the community with a smaller area. Within SA, the lichen diversity of each substrate was described in as much detail as possible. In addition, 52 AP were

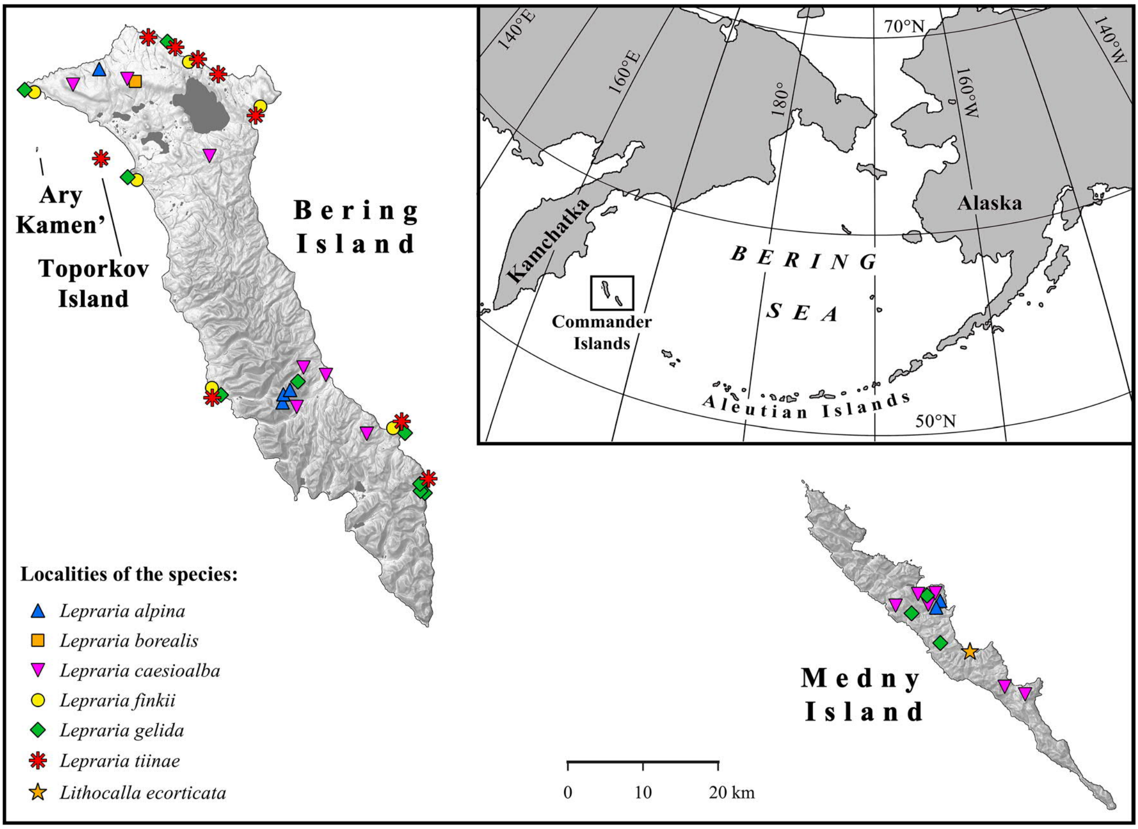

Fig. 1. Map of the study area with localities of leprarioid lichens recorded in 2019–2022.

studied (Bering Island – 32, Medny Island – 20), where only individual substrates or species were examined. We found leprarioid lichens at 37 localities, 35 SAs and 2 APs (Fig. 1), among the total 299 studied sites. In total, we collected 50 specimens of leprarioid lichens. All geographical coordinates are given in the spatial reference system WGS 84. The coordinates for old collections are approximate, as they were estimated using maps and local toponyms. These coordinates are given in square brackets.

Our specimens are mainly deposited in the herbaria of St. Petersburg State University (LECB) and Komarov Botanical Institute (LE), and some were also sent to H and TUF. Additionally, we revised four old herbarium specimens, which were previously unidentified (LE, LECB).

Field photographs were taken by DH using a Sony RX100 III camera (Sony Group Corporation, Japan). Photographs of *Lepraria* thalli and their sections were taken by IS and DH using a Carl Zeiss Axioskop 40 light microscope (Carl Zeiss AG, Germany) with a QImaging MicroPublisher 5.0 RTV camera (QImaging, Canada) and a Carl Zeiss STEMI-2000 CS dissecting microscope with an AxioCam 506 color camera (Carl Zeiss AG, Germany). Measurements of granule and photobiont cell diameters for the new species are given as the average ($\bar{x}$) ± 1 standard deviation (sd) and bounded by the extreme observed values, or [min]–($\bar{x}$-sd)–$\bar{x}$–($\bar{x}$+sd)–[max]. The number of observations (n) is provided. Morphological terminology generally follows Lendemer (2011).

The nomenclature of taxa generally follows Saag et al. (2009), Orange (2020), Westberg et al. (2021) for lichens and Diederich et al. (2018) for lichenicolous fungi. We consider the members of the *Lepraria neglecta* complex as separate species following McCune et al. (2020), not Lendemer (2013a, b).

Identification of secondary metabolites

Investigation of lichen substances in all specimens was carried out using methods of high performance thin-layer chromatography (HPTLC) and high-performance liquid chromatography with UV detection (HPLC). HPTLC was performed for all specimens of leprarioid lichens, and HPLC was performed only for some specimens that were abundant enough. The full list of HPTLC and HPLC results is presented in Appendix 1. HPTLC was performed with the standard techniques of using TLC Silica gel 60 Merck (Germany) plates and solvent systems A, B, and C (Culberson, 1972; Huneck & Yoshimura, 1996; Orange et al., 2001). For HPLC analysis, air-dried samples of lichens were ground up, and secondary substances from each sample were extracted with 0.5 ml of acetone. Each extraction was carried out with constant stirring for 12 h at 20–25°C. The obtained extracts were centrifuged for 10 min at 6000 g and kept at 4°C until analysis. HPLC analyses were performed using a 1290 Series Agilent chromatograph with UV detection (Agilent Technologies, USA). For chromatographic separation, a Thermo Hypersil-Keystone C18 column (Thermo Fischer Scientific, USA) with dimensions of 150 × 2.1 mm × 5μm was used. The mobile phase consisted of (A) water: acetonitrile: formic acid (95:5:0.1 v/v), and (B) acetonitrile: water: formic acid (90:10:0.1 v/v). Analyses were performed at 30°C with a flow rate of 0.3 ml min^{-1} in the gradient elution mode. The percentage of B was programmed as follows: 5% (2 min) – 50% (5 min) – 70% (15 min) – 100% (25 min) – 100% (35 min). The volume of each injected sample was 5 μL. The spectra of eluting substances were recorded in UV at 250 nm. Identification of the lichen substances was carried out using authentic standards from the Komarov Botanical Institute collection.

DNA extraction, PCR amplification, and DNA sequencing

DNA was extracted directly from pieces of thalli, 2–5 mg per sample, using the PhytoSorb kit (Synthol, Russia) following the manufacturer's protocol. PCR amplification and sequencing were performed for two fungal markers: nucITS rDNA with primers ITS1F (Gardes & Bruns, 1993) and ITS4 (White et al., 1990), and mtSSU rDNA with primers mrSSU1 and mrSSU3R (Zoller et al., 1999).

PCR amplification was performed with the following program parameters: (1) for nucITS rDNA, an initial denaturation at 94°C for 2 min, followed by 35 cycles at 94°C for 30 s, 60°C for 1 min, and 72°C for 1 min, with a final extension at 72°C for 7 min (Guzow-Krzemińska et al., 2019); (2) for mtSSU rDNA, an initial denaturation at 94°C for 5 min, followed by 5 cycles at 94°C for 30 s, 55°C for 30 s, and 72°C for 1 min, then 30 cycles at 94°C for 30 s, 52°C for 30 s, and 72°C for 1 min, with a final extension 72°C for 5 min (Westberg et al., 2015). Amplicons were cleaned up using the Cleanup Mini kit (Evrogen JSC, Moscow, Russia) and then sequenced at the Research Park of St. Petersburg State University "Center for Molecular and Cell Technologies", as well as at the Komarov Botanical Institute RAS, and Evrogen JSC. The resulting sequences were searched against the NCBI GenBank database (https://www.ncbi.nlm.nih.gov/) using BLASTn search (Altschul et al., 1990; http://www.ncbi.nlm.nih.gov/BLAST/) to verify the sequence identity and check for possible contamination.

Sequence alignment and phylogenetic analysis

In addition to the newly generated sequences, in our phylogenetic analysis we included sequences of 43 *Lepraria* species from NCBI (Appendix 2). As the outgroup, we used two representatives of the genus *Stereocaulon* (namely, *S. subcoralloides* (Nyl.) Nyl. and *S. tomentosum* Th. Fr.), following Barcenas-Peña et al. (2021), as the genus is considered to be closely related to *Lepraria* (Ekman & Tønsberg 2002). The GenBank accession numbers and other key information about the sequences used in the alignments are provided in Table 1 (for newly generated sequences) and Appendix 2 (for sequences obtained from GenBank). The names *Lepraria cacuminum* (A. Massal.) Kümmerl. & Leuckert, *L. santosii* Argüello & A. Crespo and *Leproloma vouauxii* (Hue) J. R. Laundon were updated to their modern synonyms, *L. alpina*, *L. lobificans* Nyl., and *L. vouauxii* (Hue) R. C. Harris, respectively (Appendix 2).

Table 1. List of *Lepraria* specimens newly sequenced for this study with their nucITS rDNA and mtSSU rDNA GenBank accession numbers. All samples were collected in the Commander Islands.

Species	Voucher	GenBank accession No.	
		nucITS rDNA	mtSSU rDNA
L. finkii	DH, IS, & AZ Ber-127/L22 (LECB)	OQ779570	OQ779585
	DH, IS, & AZ Ber-172/L53 (LE L-21988)	OQ779572	OQ779588
L. gelida	DH, IS, & AZ Ber-183/L4 (LE L-21990)	OQ779574	OQ779587
L. tiinae	DH, IS, & AZ Ber-193/L11 (LE L-21956, holotype)	OQ779575	OQ779582
	DH, IS, & AZ Ber-127/L8 (LE L-21987)	OQ779576	OQ779589
	DH & IS Ber-23/L16 (LE L-22000)		OQ779584
	DH & IS Ber-71/L32 (H)		OQ779586
	DH & IS Top-02/L15 (LECB)		OQ779583

To determine the heterogeneity of the phylogenetic signal between the two loci, nucITS and mtSSU rDNA, we first constructed two separate phylogenies. They were then combined in a single multi-locus analysis. For the single-locus phylogenies, we aligned both sets of sequences independently using MAFFT 7 (Katoh & Standley, 2013; available at http://mafft.cbrc.jp/alignment/ server/) with the L-INS-i method (Katoh et al., 2005). We manually trimmed the alignments to remove unaligned terminal regions. The final nucITS alignment consisted of 83 sequences with 517 sites, of which 247 were conserved. The final mtSSU alignment consisted of 56 sequences with 583 sites, of which 506 were conserved.

We constructed single-locus nuclITS and mtSSU phylogenies using the Maximum Likelihood (ML) method. First, we used ModelFinder (Kalyaanamoorthy et al., 2017) with the Akaike Information Criterion (AIC) to determine the best-fit model for each partition. For the nucITS region following substitution models were selected: TIM3e+G4 for ITS1, TNe+G4 for ITS2, and HKY+F+I for 5.8S. For mtSSU, the model TRM3+F+G4 was selected. Phylogenetic trees were constructed using IQ-TREE with 1000 bootstraps (Nguyen et al., 2015; Chernomor et al., 2016; available at www.iqtee.org) and visualized using iTOL (Letunic & Bork, 2021; available at https://itol.embl.de/). The trees are presented in Appendix 3 and 4, with added bootstrap supports (BS values > 80%). Visual comparing the two single-locus phylogenies revealed that the mtSSU tree offered little resolution compared to the better-resolved nuclITS tree. However, no large-scale incongruences were detected.

For the final multi-locus phylogeny, we created a concatenated alignment of both nucITS and mtSSU loci as described above. We only concatenated sequences if we could verify that both nuclITS and mtSSU sequences originated from the same specimen. The alignment consisted of 83 sequences with 1100 sites, of which 756 were conserved. To construct phylogeny, we used both ML and Bayesian Analysis (BA) methods. For the ML analysis, following substitution models were selected: TIM3e+G4 for ITS1, TNe+G4 for ITS2, and HKY+F+I for 5.8S and mtSSU. The phylogenetic tree was constructed using IQ-TREE as described above. The BA phylogeny was created with MrBayes 3.2.7a (Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003; available at https://nbisweden.github.io/MrBayes/download.html) using the GTR+G+I substitution model. We used two parallel runs with four Markov chain Monte Carlo (MCMC) chains (3 heated and one cold chain), 10 million generations, and every 1000th tree sampled. The first 25% of trees was discarded as burn-in. The remaining results were summarized as a 50% majority-rule consensus tree. Convergence diagnostic as PSRF was close to 1.0 for all parameters and average deviation of split frequencies was below 0.01 (Gelman & Rubin, 1992). The BA and ML analyses resulted in congruent trees, presented in Fig. 2 along with the support values.

Fig. 2. ML tree based on concatenated nucITS rDNA and mtSSU rDNA datasets for *Lepraria* spp. Sequence and voucher information is presented in Table 1 (for newly generated sequences) and Appendix 2 (for sequences obtained from GenBank). The tree was rooted using an outgroup, which consisted of *Stereocaulon subcoralloides* and *S. tomentosum*. Bootstrap supports (BS) from ML analysis > 80% (above the line) and posterior probabilities (PP) from BA ≥ 0.95 (under the line) are indicated near the branches. The highly supported branches (BS values >80%, PP>0.95) are highlighted. The newly sequenced specimens of *Lepraria* are in bold. The taxa names are provided with the collection numbers of specimens.

RESULTS AND DISCUSSION

TAXONOMY

Lepraria tiinae Stepanchikova & Himelbrant sp. nov. (Fig. 3 & 4)

MycoBank MB848282

Thallus thick, crustose, leprose, placodioid, with large granules (up to 0.25 mm diam.), a well-developed hypothallus, and dark rhizohyphae. The species produces thiophanic acid, arthothelin, and dichlorolichexanthone.

Holotype: Russia, Kamchatka Territory, the Commander Islands, Bering Island, N part, in the center of Zasarannaya Bay, 55˚19'08.1"N, 166˚09'21.0"E, 5 m a. s. l., on seashore rocks, over plant debris, 23.08.2022, IS, DH, & AZ Ber-193 (LE L-21956). GenBank accession numbers: OQ779575 (nrITS); OQ779582 (mtSSU).

Morphology: Thallus *cryophila*-type sensu Lendemer (2011): crustose, leprose, placodioid, forming a thick crust (up to 0.5–1.3 mm thick, besides rhizohyphae), yellowish-greenish-white in color (Fig. 3A–D). In some specimens, the lichen forms a densely folded and overlapping crust, which can exceed an overall thickness of 1.5 mm. Prothallus disappearing with age. Hypothallus well-developed, white, compact, consisting of densely arranged hyaline hyphae often incrusted by crystals that dissolve in KOH. Rhizohyphae abundant, brown to almost black, forming a distinct "waft" layer (Fig. 3E, F). In some specimens this layer is dense and occasionally forms rhizinae-like structures, which consist of 2–4 or sometimes more intertwined hyphae (Fig. 3G). Granules globose or of irregular shape, very large, [50.0]–(88.8)–135.5–(182.2)–[250.0] µm (n=100) in diam., ecorticate, in part covered with hyphae (Fig. 3E), often confluent and then almost indistinguishable as discrete units, forming compound units or continuous crust. Photobiont green, coccoid, cells globose, [4.0]–(4.8)–7.5–(10.3)–[16.0] µm (n=100) in diam.

Chemistry: 2,4,5,7-tetrachloronorlichexanthone (thiophanic acid), 2,4,5-trichloronorlichexanthone (arthothelin), 2,4-dichlorolichexanthone. All specimens were analyzed by HPTLC; the specimens LE L-21987 and TUF (Ber-36) were also analyzed by HPLC (see Appendix 1). Spot tests: K-, C+ yellow, KC+ yellow, P-, UV+ orange-yellow.

Etymology: The species is named after Tiina Randlane, an outstanding lichenologist and wonderful person, in recognition of her significant contributions to lichen studies in a wide range of taxa and regions.

Ecology and distribution: The species is found on plant debris and primary soil over rocks, rarely directly on rocks, in coastal ornithocoprophilous communities (Fig. 4). In one saxicolous specimen (LE L-22000) *Bangia*-like algae were observed inside the layer of rhizohyphae; most probably, they were not a part of lichen symbiosis but just inhabited the same rock. Accompanying species: on soil and plant debris – *Lepraria finkii*, *L. gelida*, *Ochrolechia frigida* (Sw.) Lynge, *Rinodina turfacea* (Wahlenb.) Körb., *Polycauliona candelaria* (L.) Frödén et al.; on rock – *Physcia caesia* (Hoffm.) Fürnr., *P. dubia* (Hoffm.) Lettau, *Polycauliona* spp., *Rusavskia elegans* (Link) S. Y. Kondr. et Kärnefelt, etc. *Lepraria tiinae* is known from seven modern and three historical localities on two of the Commander Islands – Bering and Toporkov (Fig. 1).

Notes: The newly described species is most closely related to *Lepraria cryophila* Lendemer by morphology and based on molecular data. Both *L. cryophila* and *L. tiinae* are characterized by placodioid thallus with a well-developed hypothallus and a weft of rhizohyphae. There are some morphological differences between these two species: *L. cryophila* has better organized and discrete granules (Lendemer, 2010, 2013a) and a loose hypothallus, while granules of *L. tiinae* are often confluent, and the hypothallus is compact. Probably, this is due to different ecological preferences: *L. cryophila* is a species occurring in cold humid habitats like rock overhangs or wet vertical rock faces (Lendemer, 2010), while *L. tiinae* seems to be a coastal ornitocoprophilous lichen. However, two species differ significantly in secondary metabolites: *L. cryophila* produces divaricatic and nordivaricatic acids (Lendemer, 2010, 2013a), while *L. tiinae* produces chloronorlichexanthones.

Among the *Lepraria* species other than *L. tiinae*, only two are known to produce xanthones, namely *Lepraria disjuncta* Lendemer and *L. xanthonica* Lendemer. However, both of them also produce usnic acid and zeorin (Lendemer, 2010), which are not recorded in *L. tiinae*. Also these species differ from *L. tiinae* in morphology:

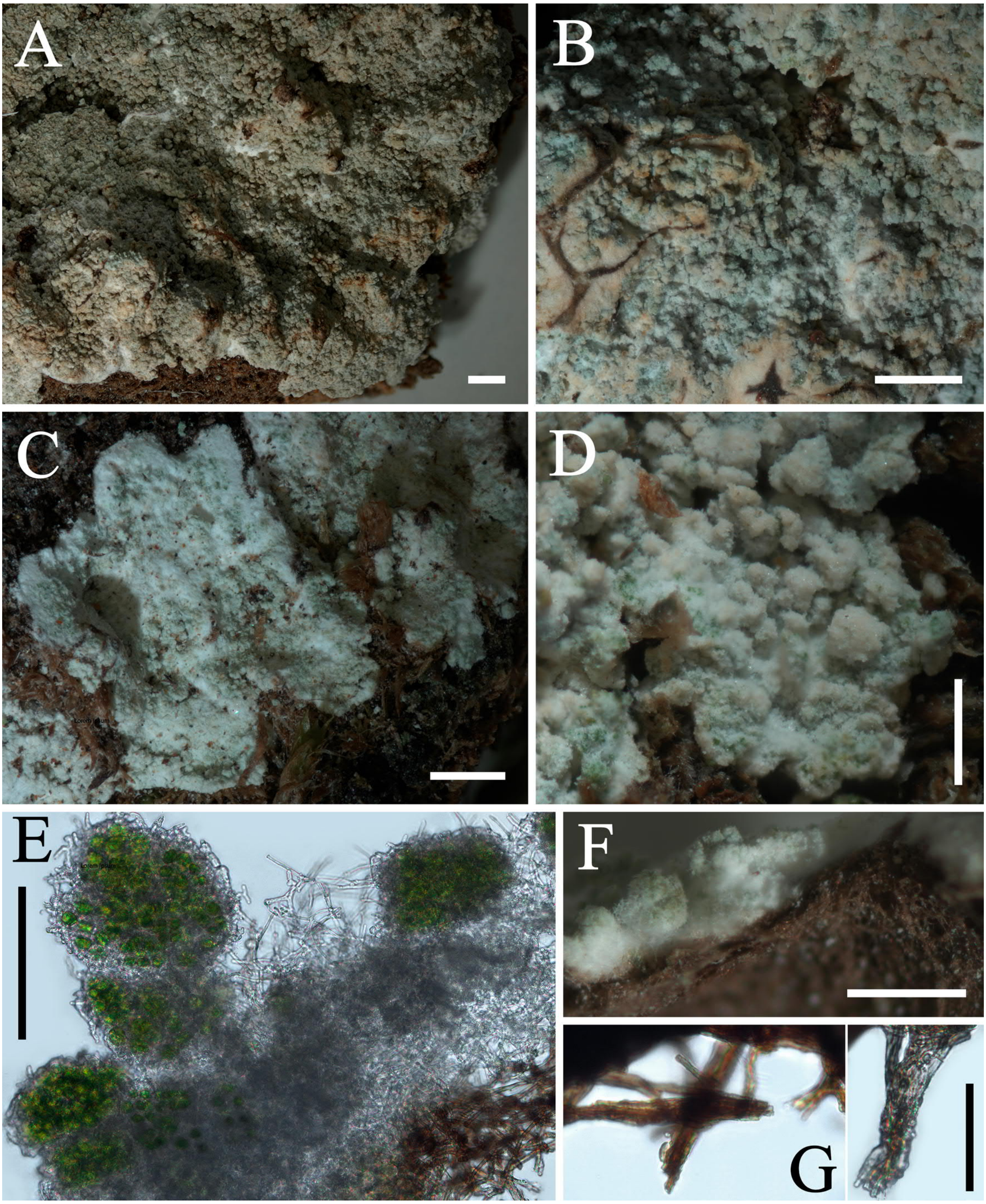

Fig. 3. *Lepraria tiinae*; A–D – thallus (A – paratype, TUF; B, D – holotype, LE L-21956; C – paratype, LE L-21987); E, F – thallus section (LE L-22000); G – rhizinae-like structures. Scale bars: A = 1 mm, B = 1 mm, C = 1 mm, D = 0.5 mm, E = 100 µm, F = 0.5 mm, G = 50 µm.

Fig. 4. *Lepraria tiinae*, type locality: Russia, Kamchatka Territory, the Commander Islands, Bering Island, N part, in the center of Zasarannaya Bay, 55˚19'08.1"N, 166˚09'21.0"E, 5 m a. s. l., seashore rocks, 23.08.2022, IS, DH, & AZ Ber-193.

both are characterized by non-stratified thalli with relatively poorly developed hypothallus and no rhizohyphae (Lendemer, 2010, 2013a). At the moment, no sequences of *L. disjuncta* and *L. xanthonica* are available for comparison.

By morphology, *L. tiinae* highly resembles species of the former genus *Leproloma* Nyl. ex Cromb. The size and arrangement of granules also makes it also apparently close to *Lepraria gelida*. However, the new species is easily distinguished from all related species by its unusual chemistry: xanthones are rare among *Lepraria*.

Additional specimens examined. Russia, Kamchatka Territory, the Commander Islands, Bering Island: S part, in the center of Peregrebnaya Bay, 54˚50'47.3"N, 166˚38'28.0"E, 1–4 m a. s. l., vertical rocks under a colony of seabirds (*Rissa brevirostris* Bruch, 1853) in supralittoral, on plant debris, 30.07.2020, IS & DH Ber-23 (LE L-22000); W coast, cape between Perekhodnaya and Nayushka bays, Steller Arch, 54˚56'24.4"N, 166˚12'13.8"E, 0–3 m a. s. l., ornithocoprophilous community on vertical cliffs in the supralittoral zone, on soil, 09.08.2020, IS & DH Ber-36 (TUF); S part, E coast, Cape Tolsty, 54˚54'56.9"N, 166˚35'07.3"E, 44 m a. s. l., ornithocoprophilous community on sheer walls of rocky outliers facing the ocean, on soil over rock, 06.08.2021, IS & DH Ber-71 (H); N part, E coast, Drovyanaya Blizhniaya Bay, steep shore with rocky outcrops (cliffs), 55˚16'35.2"N, 166˚15'34.4"E, 21 m a. s. l., breccia rocky outcrops, on soil over rock, 27.07.2022, IS, DH, & AZ Ber-127 (LE L-21987); the northernmost part of the island, seashore W to mouth Bolshoi Rakushnik River, 55˚21'23.4"N, 166˚00'37.6"E, 2 m a. s. l., ornithocoprophilous community on conglomerate huge rocks in supralittoral, on soil over rocks, 11.08.2022, IS, DH, & AZ Ber-175 (LECB); the northernmost part SW to Emelyanovskaya Bay, 55˚20'56.4"N, 166˚02'58.8"E, 4 m a. s. l., ornithocoprophilous community on conglomerate seashore cliffs in supralittoral, on plant debris over rock, 13.08.2022, IS, DH, & AZ Ber-183 (LECB); N part, seashore between Sarannaya and Bolshaya bays NW to mouth of Sarannaya River, 55°19’34.2”N, 166°06’39.0”E, 3 m a. s. l., rocks in supralittoral, on plant debris over rock, 20.08.2022, IS, DH, & AZ Ber-186 (LECB); Cape Vkhodnoy Rif, [55°11’44”N 165°58’57”E], on soil in cracks of rock, 20.11.1928, E. A. Kardakova (LE L-21985); Toporkov Island: [55°12’N, 165°56’E], on plant debris on dead roots in cracks of rock, 25.11.1928, E. A. Kardakova (LE L-21984); SW shore, 55°12’16.2”N, 165°55’55.1”E, 2–3 m a. s. l., vertical cliffs and blocks above the littoral, under seabirds (*Rissa tridactyla* (Linnaeus, 1758), *Phalacrocorax* sp., *Fratercula* sp.) colony, on plant debris, 24.07.2020, IS & DH Top-02 (LECB).

Other leprarioid lichens

Lepraria alpina (B. de Lesd.) Tretiach & Baruffo – a species related to *Lepraria neglecta*, from which it differs by having larger thalline granules (Lendemer, 2011), the production of porphyrilic acid, and tendency to form radiating rosettes. In our material, all thalli contain atranorin, porphyrilic, and roccellic/angardianic acids (see Appendix 1). The species is commonly found in Arctic and alpine habitats, and the nearest known locality is in the Kamchatka Peninsula (Makarova & Himelbrant, 2008).

Specimens examined. Russia, Kamchatka Territory, the Commander Islands, Bering Island: central part, NW of Polovina River valley, a peak on the ridge between 747.2 and 555.4 m, 54°56’55.9”N, 166°21’11.8”E, 625 m a. s. l., rocky outcrops on the mountain top with gravel and scarce patches of *Saxifraga* sp., on soil, 17.08.2021, IS & DH Ber-a15 (LECB); mountain S of the peak 747.2 m, 54°56’00.2”N, 166°20’22.3”E, 657 m a. s. l., the mountain top, range-like outlier made of single rocks surrounded by gravel screes and patches of *Empetrum nigrum* L. tundra, on soil, 13.08.2021, IS & DH Ber-95 (LE L-21989); NE of Polovina River valley, peak 747.2 m, 54°56’35.3”N, 166°20’24.3”E, 747 m a. s. l., the mountain top, gravel tundra with patches of mosses, *Saxifraga* spp., and dwarf *Salix* spp., on soil, 17.08.2021, IS & DH Ber-104 (LECB); the northernmost part of the island, dry valley of the right inflow of Medvezhya River, 55°18’55.8”N, 165°54’33.8”E, 52 m a. s. l., nival dwarf shrub-grass tundra community in dry river bed, on soil, 12.08.2022, IS, DH, & AZ Ber-179 (LE L-21993); Medny Island: S spur of the mountain SSE of Mt. Zhirovaya, slope of the valley of the creek flowing into Gladkovskaya Bay, 54°44’26.5”N, 167°43’08.5”E, 123 m a. s. l., shrub community with *Salix* spp., *Sorbus sambucifolia* (Cham. et Schltdl.) M. Roem., and *Vaccinium ovalifolium* Smith on a forb meadow, on mosses, 11.08.2019, IS & DH Med-25 (LECB); top of the Mt. Zhirovaya, 54°45’17.5”N, 167°42’34.6”E, 446 m a. s. l., gravel tundra with patches of lichens and dwarf shrubs, on soil, 18.08.2019, IS & DH Med-37 (LECB).

Lepraria borealis Lohtander & Tønsberg – a species of the *Lepraria neglecta* group, producing atranorin and fatty acids: according to Saag et al. (2009), the most common chemotype 1 comprises atranorin, rangiformic and ± norrangiformic acid; in chemotype 2 rangiformic acid is replaced by roccellic/angardianic acid, and in chemotype 3 both fatty acids are present. Our specimen contains atranorin and jackinic/rangiformic acid, therefore it can be identified as chemotype 1. The species is widespread in Arctic and alpine regions but is relatively rarely reported. In the Kamchatka Territory, it is known from Koryakia (Himelbrant et al., 2021).

Specimen examined. Russia, Kamchatka Territory, the Commander Islands, Bering Island: N part, local depression between the peaks 160.8 m and 157.4 m, 55°18’05.2”N, 165°58’56.7”E, 131 m a. s. l., lichen-*Diapensia obovata* (F. Schmidt) Nakai tundra, on soil, 14.08.2022, IS, DH, & AZ Ber-185 (LE L-21991).

Lepraria caesioalba (B. de Lesd.) J. R. Laundon – a species of the *Lepraria neglecta* group, characterized by a bluish-grey thallus and a variable combination of secondary metabolites. We recognize three chemotypes following Leuckert et al. (1995) and Saag et al. (2009), all of which contain atranorin and fatty acids in different proportions together with fumarprotocetraric acid (chemotype 1), stictic acid group (chemotype 2), or psoromic acid (chemotype 3). In our material from the Commander Islands, we detected chemotypes 1 and 3 (Saag et al., 2009). The thalli of chemotype 1 contain atranorin, fumarprotocetraric acid, and fatty acids: roccellic/

angardianic and/or jackinic/rangiformic acid. The thalli of chemotype 3 contain atranorin and psoromic acid (see Appendix 1). The species is widespread in Arctic and alpine regions. In the Kamchatka Territory, it is known from Koryakia (Himelbrant et al., 2021).

Specimens examined. Chemotype 1 (sensu Saag et al., 2009) – Russia, Kamchatka Territory, the Commander Islands, Bering Island: NW part, W part of plateau 200.6 m (“Zabiyaka”), 55°17’40.1”N, 165°51’25.7”E, 185 m a. s. l., lichen-*Empetrum nigrum* tundra with single rocks on a flattened plateau top, on stone, 19.08.2020, IS & DH Ber-a09 (LE L-21992); Medny Island: S of Ozhidaniya Bay, valley of the stream, right side, 54°38’03.0”N, 167°54’25.8”E, 179 m a. s. l., dwarf shrub-moss-lichen tundra with an old scree, on soil, 06.08.2019, IS & DH Med-17 (LE L-21999); top of the Mt. Zhirovaya, 54°45’17.5”N, 167°42’34.6”E, 446 m a. s. l., gravel tundra with patches of lichens and dwarf shrubs, on mosses, 18.08.2019, IS & DH Med-37 (LECB); top of the unnamed mountain S to Zhirovaya Bay, 54°44’53.5”N, 167°40’37.0”E, 459 m a. s. l., rocky outcrop and gravel tundra with patches of dwarf shrubs and lichens, on soil, 18.08.2019, IS & DH Med-39 (LE L-21995); W of Lake Gladkovskoe, slope of the mountain, 54°44’08.7”N, 167°42’17.9”E, 146 m a. s. l., outliers on the slope surrounded by tundra with dwarf shrubs and lichens on solifluction steps, on stone, 20.08.2019, IS & DH Med-45 (LECB); Mt. Sen’kina, SE slope near the top, 54°43’58.8”N, 167°37’54.3”E, 411 m a. s. l., rocky outcrops and a patch of tundra with lichens and dwarf shrubs, on soil, 22.08.2019, IS & DH Med-49 (LECB). Chemotype 3 – Russia, Kamchatka Territory, the Commander Islands, Bering Island: S part, W slope of the mountain 407.4 m between Kislaya Kapusta and Komandor river valleys, 54°54’09.6”N, 166°31’05.6”E, 407 m a. s. l., gravel tundra with small patches of dwarf shrubs and *Saxifraga* spp., and with small outliers, on soil, 08.08.2021, IS & DH Ber-78 (LECB); central part, E coast, Polovina Bay, SW of the peak 130.4 m, 54°58’09.9”N, 166°25’32.5”E, 102 m a. s. l., dwarf shrub tundra, on soil, 10.08.2021, IS & DH Ber-85 (LECB); central part, watershed of the Polovina and Gladkovskaya rivers, top of the local elevation, 54°55’44.4”N, 166°22’10.2”E, 132 m a. s. l., dwarf shrub tundra with gravel spots, on soil, 12.08.2021, IS & DH Ber-92 (LECB); E part, 2.8 km W of Usovaya Bay, between the heights 226.4 and 555.4 m, 54°58’35.7”N, 166°22’41.4”E, 220 m a. s. l., dwarf shrub tundra with extensive areas of gravel on solifluction steps, on soil, 16.08.2021, IS & DH Ber-102 (LE L-21998); N part, pass between Nikolskoe and the Bay Staraya Gavan’, 55°13’16.3”N, 166°09’10.2”E, 112 m a. s. l., dwarf shrub-lichen tundra, on soil, 31.07.2022, IS, DH, & AZ Ber-134 (LECB); N part, local depression between 160.8 and 157.4 heights, 55°18’05.2”N, 165°58’56.7”E, 131 m a. s. l., lichen-*Diapensia obovata* tundra, on soil, 14.08.2022, IS, DH, & AZ Ber-185 (LECB); Medny Island: flattened N spur of Mt. Kuropatkina, 54°38’31.5”N, 167°51’52.1”E, 220 m a. s. l., gravel-lichen tundra on solifluction steps, on soil, 05.08.2019, IS & DH Med-11 (LECB); top of the Mt. Zhirovaya, 54°45’17.5”N, 167°42’34.6”E, 446 m a. s. l., gravel tundra with patches of lichens and dwarf shrubs, on soil, 18.08.2019, IS & DH Med-37 (LECB); top of the unnamed mountain SW of Mt. Zhirovaya, 54°44’59.1”N, 167°42’08.9”E, 417 m a. s. l., tundra with dwarf shrubs and lichens, with areas of disturbed soil at the top ridge, on soil, 18.08.2019, IS & DH Med-38 (LECB); top of the unnamed mountain S to Zhirovaya Bay, 54°44’53.5”N, 167°40’37.0”E, 459 m a. s. l., rocky outcrop and gravel tundra with patches of dwarf shrubs and lichens, on soil, 18.08.2019, IS & DH Med-39 (LE L-21994).

Lepraria finkii (B. de Lesd.) R. C. Harris – a widespread species, characterized by a soft thallus with often a well-developed hypothallus, granules with projecting hyphae, and the production of atranorin, zeorin, stictic acid, and sometimes fatty acids. *L. finkii* is widespread on almost all continents and inhabits various biotopes. In the Kamchatka Territory, it is known from the Kamchatka Peninsula and Koryakia (Himelbrant et al., 2019). In the material from the Commander Islands, all thalli contain atranorin, zeorin, and the stictic acid complex; two specimens (Ber-71 and Ber-127, LECB) also contain roccellic/angardianic – and jackinic/rangiformic fatty acids (HPTLC). In the two other specimens which were analyzed by HPLC (LE L-21996 and LE L-21997) porphyrilic acid was revealed. Our material generally corresponds to the protologue description (Hue, 1924) and latter description by Lendemer (2013a), but the presence of porphyrilic acid in two specimens analyzed by HPLC is not typical for *L. finkii*. However, our specimens from the Commander Islands did not show any special morphological features separating them from *L. finkii*; moreover, in the phylogenetic tree *L. finkii* forms a well-supported clade including our specimens (Fig. 2). Further investigations are needed to understand if the population in the Commander Islands represents a new chemotype of *L. finkii* with porphyrilic acid, or it is a separate species.

Specimens examined. Russia, Kamchatka Territory, the Commander Islands, Bering Island: central part, W coast, cape between Perekhodnaya and Nayushka bays, Steller Arch, 54˚56'24.4"N, 166˚12'13.8"E, 0–3 m a. s. l., ornithocoprophilous communities on vertical cliffs in the supralittoral zone on a pebble beach, on soil, 09.08.2020, IS & DH Ber-36 (LE L-21996); N part, Severo-Zapadny Cape, second coastal terrace, 55˚17'13.5"N, 165˚45'57.3"E, 47 m a. s. l., small rocky outlier, on rock, 19.08.2020, IS & DH Ber-59 (LECB); S part, E shore, Cape Tolsty, 54˚54'56.9"N, 166˚35'07.3"E, 44 m a. s. l., ornithocoprophilous community on sheer walls of rocky outliers facing the ocean, on soil, 06.08.2021, IS & DH Ber-71 (LECB); N part, E shore, Drovyanaya Blizhniaya Bay, steep shore with rocky outcrops (cliffs), 55˚16'35.2"N, 166˚15'34.4"E, 21 m a. s. l., breccia rocky outcrops, on soil, 27.07.2022, IS, DH, & AZ Ber-127 (LECB); N part, W shore, cape 82.2 m S to Vkhodnoy Rif Cape and S to Nikolskoe, 55˚11'12.8"N, 165˚59'53.0"E, 3 m a. s. l., ornithocoprophilous community on rocks in supralittoral, on soil over rock, 09.08.2022, IS, DH, & AZ Ber-172 (LE L-21988); N part, seashore between Sarannaya and Bolshaya bays NW to mouth of Sarannaya River, 55˚19'34.2"N, 166˚06'39.0"E, 3 m a. s. l., rocks in supralittoral, on plant debris over rock, 20.08.2022, IS, DH, & AZ Ber-186 (LE L-21997); suburbs of Nikol'skoe, [55˚12'N, 166˚00'E], on soil over scree between rocks, 16.09.1928, E. A. Kardakova (LE L-21986).

Lepraria gelida Tønsberg & Zhurb. – the species is characterized by a thick thallus with large granules, sometimes forming a continuous crust, and production of porphyrilic and alectorialic acids (Kukwa & Zhurbenko, 2010). *Lepraria gelida* is widely known from the Arctic, and in Beringia it was previously reported from Koryakia, Kamchatka territory (Himelbrant et al., 2021) and Chukotka (Kristinsson et al., 2010). The specimens from the Commander Islands represent the granular-areolate morphotype (Kukwa & Zhurbenko, 2010). Thalli contain porphyrilic and alectorialic acids (by HPTLC); additionally, barbatolic and hypoalectorialic acids were revealed by HPLC (see Appendix 1). Our material looks very similar to the paratype of *L. gelida* (LE L-7552, Severnaya Zemlya Archipelago) and fully corresponds to the description of the species (Tønsberg & Zhurbenko, 2006). According to Lendemer (2013a, b), the species belongs to the *L. neglecta* group and is recognized as a chemotype of *L. neglecta*. However, further studies on wider range of material are needed to resolve the phylogenetic position of this species.

Specimens examined. Russia, Kamchatka Territory, the Commander Islands, Bering Island: S part of Peregrebnaya Bay, 54˚50'09.7"N, 166˚38'42.7"E, 0–5 m a. s. l., breccia vertical rocks with a colony of seabirds (*Rissa brevirostris*) in supralittoral, on soil, 30.07.2020, IS & DH Ber-20 (LECB); same place, 54˚50'19.3"N, 166˚38'18.5"E, 20 m a. s. l., breccia rocks above the supralittoral zone, on soil, 30.07.2020, IS & DH Ber-21 (LECB); S part, central part of Peregrebnaya Bay, mouth of the creek in deep valley, 54˚50'46.8"N, 166˚38'19.8"E, 1–5 m a. s. l., rocky bed and sides of the creek valley, on soil over rock, 30.07.2020, IS & DH Ber-22 (H); central part, W shore, cape between Perekhodnaya and Nayushka bays, Steller Arch, 54˚56'24.4"N, 166˚12'13.8"E, 0–3 m a. s. l., ornithocoprophilous communities on vertical cliffs in the supralittoral zone, on soil over rock, 09.08.2020, IS & DH Ber-36 (H); NW part, Severo-Zapadny Cape, second coastal terrace, 55˚17'13.5"N, 165˚45'57.3"E, 47 m a. s. l., small rocky outlier, on soil over rock, 19.08.2020, IS & DH Ber-59 (LECB); S part, E coast, Cape Tolsty, 54˚54'56.9"N, 166˚35'07.3"E, 44 m a. s. l., ornithocoprophilous community on sheer walls of rocky outliers facing the ocean, on soil, 06.08.2021, IS & DH Ber-71 (TU); central part, NE of Polovina River valley, peak 555.4 m, 54˚57'33.9"N, 166˚22'07.0"E, 550 m a. s. l., gravel tundra, on soil, 17.08.2021, IS & DH Ber-105 (LECB); N part, W shore, cape 82.2 m S to Vkhodnoi Rif Cape and S to Nikolskoe, 55˚11'12.8"N, 165˚59'53.0"E, 3 m a. s. l., ornithocoprophilous communities on rocks in supralittoral, on soil over rock, 09.08.2022, IS, DH, & AZ Ber-172 (LECB); the northernmost part, SW to Emelyanovskaya Bay, 55°20'56.4"N, 166°02'58.8"E, 4 m a. s. l., ornithocoprophilous community on conglomerate seashore cliffs in supralittoral, on plant debris over rock, 13.08.2022, IS, DH, & AZ Ber-183 (LE L-21990); Medny Island: between Mts Sen'kina and Stolbovaya, pass between the right inflow of the Ozernaya River and Sen'kina Bay, 54°43'29.2"N, 167°39'55.4"E, 132 m a. s. l., gravel with low range of outliers on the pass, on soil, 12.08.2019, IS & DH Med-27 (LECB); top of the Mt. Zhirovaya, 54°45'17.5"N, 167°42'34.6"E, 446 m a. s. l., gravel tundra with patches of lichens and dwarf shrubs, on soil, 18.08.2019, IS & DH Med-37 (LE L-22001); top of the unnamed mountain SW of Mt. Zhirovaya, 54°44'59.1"N, 167°42'08.9"E, 417 m a. s. l., tundra with dwarf shrubs and lichens, with patches of disturbed soil, on soil, 18.08.2019, IS & DH Med-38 (LECB); SW slope of Mt. Dorozhnaya, 54°41'27.5"N, 167°43'39.1"E, 291 m a. s. l., lichen-moss-dwarf shrub tundra, on soil, 23.08.2019, IS & DH Med-51 (LECB); SE end, vicinity of SW rookery of *Callorhinus usrinus* L., [54°30'N, 168°06'E], S slope of rocky seashore, on soil, 07.1993, S. Garbuzov (Med-SW).

LITHOCALLA aff. ECORTICATA (J. R. Laundon) Orange – formerly placed in the genus *Lepraria*, this species is characterized by a leprose yellowish-green thallus and production of usnic acid, but no zeorin (Saag et al., 2009). *Lithocalla ecorticata* has not been reported before from the Russian Far East and Beringia. The nearest known locality in Russia is in the Arkhangelsk Region (Tarasova et al., 2016). Our specimen contains usnic, isousnic, and stictic acids (see Appenix 1) and closely resembles the protologue description of *Lithocalla malouina* (Øvstedal) Fryday & Orange in both by morphology and chemistry (Fryday & Øvstedal, 2012). However, recent studies have revealed phenotypical variation and overlap between *Lithocalla ecorticata* and *L. malouina*, with the latter species being so far endemic to the Falkland Islands, while the former is more widespread (Orange, 2020). Unfortunately, we were unable to extract DNA from the specimen from the Commander Islands, and thus it is designated here as *Lithocalla* aff. *ecorticata*.

Specimen examined. Russia, Kamchatka Territory, the Commander Islands, Medny Island: E coast, S part of Korabel'naya Bay, 54°40'55.6"N, 167°47'22.4"E, 1 m a. s. l., cliffs in the supralittoral zone, under a seabird's colony (*Fratercula* sp.), on vertical seashore rock, in cracks, 08.08.2019, IS & DH Med-20 (LECB, LE L-21991, TUF).

Fungi associated with leprarioid lichens

BRYOSTIGMA EXCENTRICUM (Th. Fr.) Etayo & Pino-Bodas – lichenicolous fungus, occurring on various species of *Lepraria* (mostly *L. neglecta* s. lat. and *L. gelida*) (Zhurbenko, 2008, 2020). The characters of our specimens in general are in accordance with the protologue (Fries, 1867), with exception of larger spores which correspond to subsequent descriptions in literature (Zhurbenko et al., 2020; Etayo et al., 2023). The species is new to the Kamchatka Territory, the nearest localities are known in Chukotka (Zhurbenko, 2008).

Specimens examined. Russia, Kamchatka Territory, the Commander Islands, Bering Island: central part, NW of Polovina River valley, mountain S of the peak 747.2 m, 54°56'00.2"N, 166°20'22.3"E, 657 m a. s. l., the mountain top, range-like outlier made of single rocks surrounded by gravel screes and patches of *Empetrum nigrum* tundra, on thallus of *Lepraria alpina* on soil, 13.08.2021, IS & DH Ber-95 (LECB); the northernmost part, SW to Emelyanovskaya Bay, 55°20'56.4"N, 166°02'58.8"E, 4 m a. s. l., ornithocoprophilous community on conglomerate seashore cliffs in supralittoral, on thallus of *L. gelida* on plant debris over rock, 13.08.2022, IS, DH, & AZ Ber-183 (LECB); suburbs of Nikol'skoe, [55°12'N 166°00'E], on soil over scree between rocks, 16.09.1928, E. A. Kardakova (LE L-21986, sub *L. finkii*); Medny Island: top of the unnamed mountain S of Zhirovaya Bay, 54°44'53.5"N, 167°40'37.0"E, 459 m a. s. l., rocky outcrop and gravel tundra with patches of dwarf shrubs and lichens, on thallus of *L. caesioalba* chemotype 1 on soil, 18.08.2019, IS & DH Med-39 (LECB).

RHYMBOCARPUS NEGLECTUS (Vain.) Diederich & Etayo – a lichenicolous fungus confined to the species of *Lepraria neglecta* group. The material from the Commander Islands corresponds to the protologue description (Diederich & Etayo, 2000), the species was found on *L. alpina* and *L. caesioalba*. The species is new to the Kamchatka

Territory, the nearest localities are known in Chukotka (Zhurbenko, 2007).

Specimens examined. Russia, Kamchatka Territory, the Commander Islands, Bering Island: the northernmost part, dry valley of the right inflow of Medvezhya River, 55˚18'55.8"N, 165˚54'33.8"E, 52 m a. s. l., nival dwarf shrub-grass tundra community in dry river bed, on thallus of *Lepraria alpina* on soil, 12.08.2022, IS, DH, & AZ Ber-179 (LECB); Medny Island: top of the unnamed mountain S to Zhirovaya Bay, 54˚44'53.5"N, 167˚40'37.0"E, 459 m a. s. l., rocky outcrop and gravel tundra with patches of dwarf shrubs and lichens, on thallus of *L. caesioalba* chemotype 1 on soil, 18.08.2019, IS & DH Med-39 (LECB).

Enigmatic lichenicolous "lichen" (sensu Zhurbenko, 2019) – an unidentified lichenicolous fungus (probably lichenized). Morphologically it resembles species of the lichenicolous genus *Sphaerellothecium* Zopf and is characterized by black superficial vegetative hyphae and superficial subglobose brown-black paraplectenchymatous "bodies" with no any spores, but filled with green algal cells. Our material fully conforms to the description and pictures published by Zhurbenko (2019) – all our specimens have "bodies" described above. The fungus is tentatively known from a range of arctic terricolous lichens. Zhurbenko & Triebel (2008) reported the fungus as "undetermined fungal taxon with a primitive lichenization" from thalli of *Lecidoma demissum* (Rutstr.) Gotth. Schneid. & Hertel and species of *Stereocaulon* Hoffm. from Bol'shevik Island, Krasnoyarsk Territory. Later Zhurbenko (2019) found it on *Siphula ceratites* (Wahlenb.) Fr. from Bely Island, Yamal-Nenets Autonomous Area. (Zhurbenko & Triebel, 2008). *Lepraria* spp. are reported here as new "hosts" for this fungus. Our attempts to extract DNA from the mycelium were unsuccessful. Based on our observations, it is the most common lichenicolous fungus inhabiting 18% of specimens of leprarioid lichens in the Commander Islands.

Specimens examined. Russia, Kamchatka Territory, the Commander Islands, Bering Island: mountain S of the peak 747.2 m, 54˚56'00.2"N, 166˚20'22.3"E, 657 m a. s. l., the mountain top, range-like outlier made of single rocks surrounded by gravel screes and patches of *Empetrum nigrum* tundra, on *Lepraria alpina*, 13.08.2021, IS & DH Ber-95 (LE L-21989); NE of Polovina River valley, peak 747.2 m, 54˚56'35.3"N, 166˚20'24.3"E, 747 m a. s. l., the mountain top, gravel tundra with patches of mosses, *Saxifraga* spp., and dwarf *Salix* spp., on *Lepraria alpina*, 17.08.2021, IS & DH Ber-104 (LECB); S part, W slope of the mountain 407.4 m between Kislaya Kapusta and Komandor river valleys, 54˚54'09.6"N, 166˚31'05.6"E, 407 m a. s. l., gravel tundra with small patches of dwarf shrubs and *Saxifraga* spp., and with small outliers, on *L. caesioalba* , 08.08.2021, IS & DH Ber-78 (LECB); central part, E coast, Polovina Bay, SW of the peak 130.4 m, 54˚58'09.9"N, 166˚25'32.5"E, 102 m a. s. l., dwarf shrub tundra, on *L. caesioalba*, 10.08.2021, IS & DH Ber-85 (LECB); central part, watershed of the Polovina and Gladkovskaya rivers, top of the local elevation, 54˚55'44.4"N, 166˚22'10.2"E, 132 m a. s. l., dwarf shrub tundra with gravel spots, on *L. caesioalba*, 12.08.2021, IS & DH Ber-92 (LECB); E part, 2.8 km W of Usovaya Bay, between the heights 226.4 and 555.4 m, 54˚58'35.7"N, 166˚22'41.4"E, 220 m a. s. l., dwarf shrub tundra with extensive areas of gravel on solifluction steps, on *L. caesioalba*, 16.08.2021, IS & DH Ber-102 (LE L-21998); N part, local depression between 160.8 and 157.4 heights, 55˚18'05.2"N, 165˚58'56.7"E, 131 m a. s. l., lichen-*Diapensia obovata* tundra, on *L. caesioalba*, 14.08.2022, IS, DH, & AZ Ber-185 (LECB); Medny Island: top of the Mt. Zhirovaya, 54˚45'17.5"N, 167˚42'34.6"E, 446 m a. s. l., gravel tundra with patches of lichens and dwarf shrubs, on *Lepraria alpina* and *L. caesioalba.* 18.08.2019, IS & DH Med-37 (LECB); SW slope of Mt. Dorozhnaya, 54˚41'27.5"N, 167˚43'39.1"E, 291 m a. s. l., lichen-moss-dwarf shrub tundra, on *Lepraria gelida*, 23.08.2019, IS & DH Med-51 (LECB).

Here, we report seven leprarioid lichens from the Commander Islands: *Lepraria alpina*, *L. borealis*, *L. caesioalba*, *L. finkii*, *L. gelida*, *L. tiinae*, and *Lithocalla ecorticata*.

The newly sequenced specimens collected in Commander Islands were recovered in three different clades within the *Lepraria* phylogeny (Fig. 2). The two sequences of *L. tiinae* formed a highly supported clade (BS value = 100%, PP = 1), which was sister to *L. cryophila* (also forming a well-supported clade). The two newly sequenced specimens of *L. finkii* grouped together with the two existing *L. finkii* specimens, forming a single well-supported clade (BS value = 91%, PP = 0.97). *Lepraria gelida* was not recovered within the *L. neglecta* group, even though it was recognized as a chemotype of *L. neglecta* by some authors as mentioned above (see Lendemer, 2013a, b). Instead, it was recovered within a well-supported lineage (BS value = 90%, PP = 1) together with *L. chileana*, *L. eburnea*, and *L. nivalis*. Further studies are needed to resolve phylogenetic relationships of this species.

The newly described lichen, *Lepraria tiinae*, is identified as a species with distinctive chemistry, morphology, and ecology. It is most closely related to *L. cryophila*; their relationship is confirmed by the results of phylogenetic analysis (Fig. 2). In terms of morphology, *L. tiinae* shows some resemblance to *L. cryophila* (see Lendemer, 2011, 2013a) and as *L. gelida* (see Table 2), as well as to some species within the "*Leproloma*" group (see the species description). The metabolite composition of *L. tiinae* is unique: such chemistry is more typical for *Lecanora* and *Lecidella* species, which, however, morphologically are very distant from the newly described *Lepraria*. *Lepraria tiinae* has been found in several localities on two islands within the Commander Archipelago, and we anticipate that it may be more widespread, at least across the Aleutian Arc.

Leprarioid lichens are rare in the Commander Islands, and we estimate their total frequency of occurrence as low, accounting for 14.3% (35 of 245 SA). Only one leprarioid species, *Lepraria tiinae*, was found on a small Toporkov Island. Four species were observed on Medny Island, namely *L. alpina*, *L. caesioalba*, *L. gelida*, *Lithocalla ecorticata*, while six species were recorded on Bering Island, the largest island of the archipelago. These include *Lepraria alpina*, *L. borealis*, *L. caesioalba*, *L. finkii*, *L. gelida*, and *L. tiinae*. No leprarioids were discovered on Ary Kamen' Isand. The most common species in the archipelago are *L. caesioalba* (14 SA, accounting for 5.7% of all localities investigated in 2019–2022) and *L. gelida* (13 SA, accounting for 5.3%), *L. tiinae, L. finkii,* and *L. alpina* are less frequently found, on 9, 6 and 6 SA, respectively. *Lepraria borealis* and *Lithocalla ecorticata* were each observed only once (Fig. 2).

The *Lepraria* species in the Commander Islands primarily grow on soil and plant debris, occasionally on rocks and mosses, and prefer different habitats: *Lepraria alpina*, *L. borealis*, and *L. caesioalba* were exclusively found in tundra areas, while *L. finkii*, *L. tiinae*, and *Lithocalla ecorticata* were exclusively recorded in coastal ornithocoprophilous communities. *Lepraria gelida*, on the other hand, was found in both types of communities.

It is noteworthy that *Lepraria finkii* and *L. tiinae* were not recorded on Medny Island. This probably could be explained by the differences in shoreline landscapes of the Commander Islands. Medny and Ary Kamen' Islands consist of firm volcanic rocks, and their coastal line mostly consist of high and very steep cliffs, either naked or covered by Teloschistaceae. In contrast, on Bering and Toporkov sedimentary rocks are common along seashores. These rocks are not as high and steep, and they are more suspected to weathering, resulting in many cracks where plant debris and primary soil accumulate, making them more suitable for *Lepraria* spp.

In addition to the species reported above, we found three fungal species, associated with lichens. *Bryostigma excentricum* and *Rhymbocarpus neglectus* were recorded in a few localities and represent widespread lichenicolous fungi. Moreover, in nine specimens we found an "Enigmatic lichenicolous "lichen" (Zhurbenko, 2019). This unusual fungus was recorded on Bering and Medny Islands, inhabiting different hosts (*Lepraria alpina*, *L. caesioalba*, *L. gelida*), and was the most common among all recorded fungi, which were associated with leprarioid lichens in the Commander Islands.

The majority of species reported in this paper, with the exception of *Lithocalla* aff. *ecorticata* and the newly described *Lepraria tiinae*, are widespread in the Northern Holarctic, especially in Arctic, Subarctic, and alpine habitats. However, all of them are new to the Aleutian Arc. This reflects that the islands of the North Pacific are still understudied in terms of lichen diversity and deserve further research.

Table 2. Distinguishing features of the new species *Lepraria tiinae* from closely related or phenotypically similar taxa.

Taxa	*Lepraria tiinae*	*Lepraria cryophila*	*Lepraria gelida*	*Lepraria disjuncta*	*Lepraria xanthonica*
Granules	>1.0 mm in diameter, often confluent	Average 30 µm in diameter, discrete, readily dividing, but forming compound units	>1.0 mm in diameter, often confluent	Average 90 µm in diameter, discrete, readily dividing	Average 30–40 µm in diameter, discrete, readily dividing
Hypothallus	Well-developed, compact	Well-developed, loose	Well-developed, compact	Poorly developed, loose	Thin, loose, extending outward from the edge of the thallus
Rhizohyphae	Brown to blackish	Pale to dirty brownish	Absent	Absent	Absent
Secondary metabolites (detected by TLC/ HPTLC)	Thiophanic acid, arthothelin, 2,4-dichlorolichexanthone	Divaricatic acid, nordivaricatic acid, ± atranorin (trace)	Alectorialic acid, porphyrilic acid	Usnic acid, zeorin, thiophanic acid, arthothelin, traces of other unidentified substances	Usnic acid, zeorin, 5,7- dichloro-3-O-methylnorlichexanthone, 3-O-methylasemone
Secondary metabolites (detected by HPLC)	Thiophanic acid, arthothelin, 2,4-dichlorolichexanthone	Divaricatic acid, nordivaricatic acid, ± atranorin (trace)	Alectorialic acid, hypoalectorialic acid, barbatolic acid, porphyrilic acid	Usnic acid, thiophanic acid, arthothelin, and zeorin (not always detectable in HPLC analysis)	Usnic acid, 5,7-dichloro-3-O-methylnorlichexanthone, 3-O-methylasemone, and zeorin (not always detectable in HPLC analysis)
Ecology	On rocks and primary soil in coastal ornitocoprophilous communities	On non-calcareous rocks in cool humid habitats (rock overhangs etc.)	On rocks and primary soil in tundra and open Arctic communities, also reported from coastal area	On rocks in cool humid habitats (rock overhangs etc.)	On non-calcareous rocks in cool humid habitats (rock overhangs etc.)
References	Reported in this paper	Lendemer, 2010, 2013a	Tønsberg & Zhurbenko, 2006; Kukwa & Zhurbenko, 2010; this paper	Lendemer, 2010	Lendemer, 2010

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Appendix 1. Data on secondary metabolites composition of the studied specimens of leprarioid lichens from the Commander Islands.

Species	SA no.	Herbarium	HPTLC no.	Substances detected by HPTLC	Substances detected by HPLC
Lepraria alpina	Ber-104	LECB s. n.	L30	atranorin, porphyrilic and roccellic/angardianic acids	-
	Ber-179	LE L-21993	L5, L52	atranorin, angardhianic acid	atranorin, porphyrilic and angardhianic acids
	Ber-95	LE L-21989	L33, L35	atranorin, porphyrilic and roccellic/angardianic acids	-
	Ber-a15	LECB s. n.	L41	atranorin, porphyrilic and roccellic/angardianic acids	-
	Med-25	LECB s. n.	9/Kor1	porphyrilic acid, atranorin, cf. roccellic/angardianic acid	-
	Med-37	LECB s. n.	L7	atranorin, porphyrilic and roccellic/angardianic acids	-
Lepraria borealis	Ber-185	LE L-21991	L27	atranorin, jackinic/rangiformic acid	atranorin, jackinic/rangiformic acid
Lepraria caesioalba chemotype 1	Ber-a09	LE L-21992	L1	atranorin, roccellic/angardhianic and fumarprotocetraric acids	atranorin, angardhianic and fumarprotocetraric acids
	Med-17	LE L-21999	L23	atranorin, roccellic/angardhianic and fumarprotocetraric acids	-
	Med-37	LECB s. n.	8/Kor1	atranorin, jackinic/rangiformic and fumarprotocetraric acids	-
	Med-39	LE L-21995	L13	atranorin, unknowns (contamination?)	atranorin, fumarprotocetraric, roccellic/ angardhianic and jackinic/rangiformic acid
	Med-45	LECB s. n.	L26	atranorin, fumarprotocetraric, roccellic/angardgianic and jackinic/rangiformic acids	-
	Med-49	LECB s. n.	L44	atranorin, roccellic/angardhianic and fumarprotocetraric acids	-
Lepraria caesioalba chemotype 3	Ber-102	LE L-21998	L39	atranorin, psoromic acid	-
	Ber-134	LECB s. n.	L12	atranorin, psoromic acid	-
	Ber-185	LECB s. n.	L51	atranorin, psoromic acid	-
	Ber-78	LECB s. n.	L45	atranorin, psoromic acid	-
	Ber-85	LECB s. n.	L28	atranorin, psoromic acid	-
	Ber-92	LECB s. n.	L49	atranorin, psoromic acid	-
	Med-11	LECB s. n.	L20	atranorin, psoromic acid	-
	Med-37	LECB s. n.	L48	atranorin, psoromic acid	-
	Med-38	LECB s. n.	L42	atranorin, psoromic acid	-
	Med-39	LE L-21994	L24	atranorin, psoromic acid	atranorin, psoromic acid

Species	SA no.	Herbarium	HPTLC no.	Substances detected by HPTLC	Substances detected by HPLC
Lepraria finkii	Ber-127	LECB s. n.	L22	atranorin, zeorin, stictic acid complex, roccellic/angardhianic and jackinic/rangiformic acids	-
	Ber-172	LE L-21988	L19, L53	atranorin, zeorin, stictic acid complex, cf. roccellic/ angardhianic acid	-
	Ber-186	LE L-21997	L3	atranorin, zeorin, stictic acid	atranorin, zeorin, stictic acid, porphyrilic acid
	Ber-36	LE L-21996	L10	atranorin, zeorin, stictic acid	atranorin, zeorin, stictic acid, porphyrilic acid
	Ber-59	LECB s. n.	L50	atranorin, zeorin, stictic acid complex	-
	Ber-71	LECB s. n.	L29	atranorin, zeorin, stictic acid complex, roccellic/angardhianic and jackinic/rangiformic acids	-
Lepraria gelida	Ber-105	LECB s. n.	L46	porphyrilic and alectorialic acids	-
	Ber-172	LECB s. n.	L19a	porphyrilic and alectorialic acids	-
	Ber-183	LE L-21990	L4	porphyrilic and alectorialic acids	porphyrilic, barbatolic, hypoalectorialic and alectorialic acids
	Ber-20	LECB s. n.	L37	porphyrilic and alectorialic acids	-
	Ber-21	LECB s. n.	L9	porphyrilic and alectorialic acids, unknowns (contamination?)	-
	Ber-22	H	L17	porphyrilic and alectorialic acids	-
	Ber-36	H	L10b	porphyrilic and alectorialic acids	-
	Ber-59	LECB s. n.	L14, L38	porphyrilic and alectorialic acids	-
	Ber-71	TUF	L31	porphyrilic and alectorialic acids	-
	Ber-71	LECB s. n.	L32a	porphyrilic and alectorialic acids	-
	Med-27	LECB s. n.	L21	porphyrilic and alectorialic acids	-
	Med-37	LE L-22001	L47	porphyrilic and alectorialic acids	-
	Med-38	LECB s. n.	L43	porphyrilic and alectorialic acids	-
	Med-51	LECB s. n.	L36	porphyrilic and alectorialic acids	-
	-	LECB s. n.	L25	porphyrilic and alectorialic acids	-

Species	SA no.	Herbarium	HPTLC no.	Substances detected by HPTLC	Substances detected by HPLC
Lepraria tiinae	Ber-127	LE L-21987	L8	thiophanic acid, arthothelin and 2,4-dichlorolichexanthone	thiophanic acid, arthothelin, 2,4-dichlorolichexanthone
	Ber-175	LECB s. n.	L18	thiophanic acid, arthothelin and 2,4-dichlorolichexanthone	-
	Ber-183	LECB s. n.	L6	thiophanic acid, arthothelin and 2,4-dichlorolichexanthone	-
	Ber-186	LECB s. n.	L2	thiophanic acid, arthothelin and 2,4-dichlorolichexanthone	-
	Ber-193	LE L-21956 (holotype)	L11	thiophanic acid, arthothelin and 2,4-dichlorolichexanthone	-
	Ber-23	LE L-22000	L16	thiophanic acid, arthothelin and 2,4-dichlorolichexanthone	-
	Ber-36	TUF	L10a	thiophanic acid, arthothelin and 2,4-dichlorolichexanthone	thiophanic acid, arthothelin, 2,4-dichlorolichexanthone; contamination from *L. finkii*: atranorin, stictic acid, porphyrilic acid
	Ber-71	H	L32	thiophanic acid, arthothelin and 2,4-dichlorolichexanthone; contamination from *L. gelida*: porphyrilic and alectorialic acids	-
	Top-02	LECB s. n.	L15	thiophanic acid, arthothelin and 2,4-dichlorolichexanthone	-
Lithocalla aff. *ecorticata*	Med-20	LECB s. n.	Kor1/12	usnic and stictic acids	usnic, isousnic and stictic acids

Appendix 2. Sequence and voucher information for data obtained from GenBank.

Species	Voucher: collectors, collection no., herbarium	Country, region	nrITS	mtSSU
Lepraria achariana Flakus & Kukwa	M. Kukwa 18556 (UGDA)	Bolivia	MK629283	-
L. atlantica Orange	A. Orange 15462 (PRA)	United Kingdom	EF619550	-
L. atlantica	A. Orange 11829 (BG, isotype)	Ireland	AF517887	-
L. bergensis Tønsberg	T. Tønsberg 28875 (BG, holotype)	Norway	AF517900	AY756371
L. caerulescens (Hue) Botnen & Øvstedal	F. Grewe 596	Antarctica	MZ820319	MZ820350
L. caerulescens	F. Grewe 571	Antarctica	MZ820318	MZ820349
L. caesiella R. C. Harris	J. C. Lendemer 17484 (NY-1105936)	USA, Pennsylvania	JQ070280	KC184018
L. caesiella	J. C. Lendemer 24652 (NY-1216277)	USA, Pennsylvania	JQ070285	-
L. caesioalba (B. de Lesd.) J. R. Laundon	M. P. Nelsen 3966 (WIS)	USA	EU008610	EU008636
L. celata Slav.-Bay.	S. Slavíková-Bayerová 3525 (PRA)	Ukraine	EF619543	-
L. celata	S. Slavíková-Bayerová 3448 (PRA; holotype)	Ukraine	DQ401100	-
L. chileana Grewe et al.	T. Widhelm, M. von Konrat & J. Larrain 4462 (F, paratype)	Chile, Los Lagos Region, Grande de Chiloe Island	MZ820316	MZ820347
L. crassissima (Hue) Lettau	J. Vondrak 20641 (PRA)	Czech Republic	OK332991	OK465602
L. crassissima	T. Tønsberg 28881 (BG)	Norway	AF517902	-
L. cryophila Lendemer	J. C. Lendemer 24714 (NY-1216216)	USA, Pennsylvania	JF739382	-
L. cryophila	J. C. Lendemer 23965 (NY-1205728)	USA, Pennsylvania	JF739381	-
L. cryophila	Lewis 565 (NY)	Canada, Ontario	-	KC183957
L. cryptovouauxii Kukwa et al.	A. Flakus 17683 & P. Rodriguez (KRAM)	Bolivia	MK629272	-
L. cryptovouauxii	M. Kukwa 14848a (UGDA, holotype)	Bolivia	NR_171750	-
L. cupressicola (Hue) J. R. Laundon	Y. Ohmura YO6801 (TNS YO6801)	Japan	LC669643	-
L. cupressicola	S.-O. Oh & J. S. Park KL21-0472 (KHL0035543)	South Korea	OL472380	-
L. eburnea J. R. Laundon	F. Grewe & T. Widhelm 3482	New Zealand	MZ820313	MZ820344
L. eburnea	A. P. Dornes s.n. (KR-M-0051895)	Germany	MW325698	-
L. eburnea	A. Fryday 9365 (MSC)	USA, California	-	KC184080

Species	**Voucher: collectors, collection no., herbarium**	**Country, region**	**nrITS**	**mtSSU**
L. elobata Tønsberg	J. C. Lendemer 9804 (NY-953120)	USA, New York	JQ070297	KC184075
L. elobata	S. Slavíková-Bayerová 3449 (PRA)	Ukraine	EF619545	-
L. elobata	Harris 55713 (NY)	USA, Connecticut	-	KC184074
L. finkii (B. de Lesd.) R. C. Harris	T. Widhelm, M. von Konrat & J. Larrain 4406	Chile	MZ820308	MZ820339
L. finkii (as *L. lobificans*)	E. Fraker et al. 889 (DUKE 47683)	USA, North Carolina	HQ650623	DQ986869
L. friabilis Lendemer et al.	J. C. Lendemer 20283 (NY-1152714)	USA, North Carolina	JQ070277	KC184066
L. friabilis	J. C. Lendemer 21344 (NY-1150273)	USA, Georgia	JQ070278	KC184072
L. granulata Slavíková	S. Slavíková-Bayerová 3325 (PRA)	Bulgaria	DQ914540	-
L. granulata	S. Slavíková-Bayerová 3243 (PRA)	Bulgaria	DQ914539	-
L. harrisiana Lendemer	J. C. Lendemer 20437 (NY-1152904)	USA, Virginia	JQ070294	KC184070
L. harrisiana	J. C. Lendemer 20191 (NY-1152438)	USA, New Jersey	JQ070293	KC184065
L. hodkinsoniana Lendemer	J. C. Lendemer 18478 (NY-1107055)	USA, Pennsylvania	JF739366	KC184031
L. hodkinsoniana	J. C. Lendemer 20482 (NY-1152860)	USA, Virginia	JF739364	KC184073
L. humida Slav.-Bay. & Orange	R. C. Harris 55530 (NY-1103934)	USA, Maine	KC209157	KC184026
L. humida	A. Orange 15754 (PRA; holotype)	United Kingdom	DQ401101	-
L. humida	J. C. Lendemer 22848 (NY)	USA, Maine	-	KC183978
L. impossibilis Sipman	M. Kukwa 16858 (UGDA)	Bolivia	MK629280	-
L. impossibilis	M. Kukwa 16828 (UGDA)	Bolivia	MK629281	-
L. incana (L.) Ach.	M. Kukwa 4597 (DUKE 47722)	Poland	HQ650646	DQ986812
L. incana	L. Myllys & K. Lohtander 299 (TUR)	Finland	MK179693	-
L. isidiata (Llimona) Llimona & A. Crespo	A. Argüello & A. Crespo s.n. (MAF-Lich 13999)	Spain	DQ341287	-
L. isidiata	A. Argüello & A. Crespo s.n. (MAF-Lich 14000)	Spain	DQ341288	-
L. jackii Tønsberg	J. Vondrak 26130 (PRA)	Czech Republic	OQ717483	OQ683044
L. jackii	J. Vondrak 23804 (PRA)	Czech Republic	OQ717922	OQ646292

Species	Voucher: collectors, collection no., herbarium	Country, region	nrITS	mtSSU
L. lobificans Nyl. (as *L. santosii* Argüello & A. Crespo)	A. Crespo s.n. (MAF-Lich 14003, holotype)	Spain, Canary Islands, Tenerife	NR_119575	-
L. lobificans (as *L. santosii*)	L. Vančurová & J. Malíček A136	Spain, Canary Islands, La Gomera	OL625393	-
L. membranacea (Dicks.) Vain.	L. Myllys & K. Lohtander 272 (TUR)	Finland	KF682452	-
L. membranacea	Lendemer 28306A (NY)	Canada, Quebec	-	KC183973
L. membranacea	Lewis 450 (NY)	Canada, Ontario	-	KC183961
L. neglecta (Nyl.) Erichsen	S. Beeching 10499 (NY-1218204)	USA, Georgia	KC209147	KC183956
L. neglecta	R. Rosentreter 16535 (NY-1079668)	USA, Idaho	KC209164	KC184011
L. neozelandica Barcenas-Peña et al.	F. Grewe & T. Widhelm 3009	New Zealand	MT371885	MT371889
L. neozelandica	F. Grewe & T. Widhelm 3013	New Zealand	MT371883	MT371886
L. nivalis J. R. Laundon	T. Tønsberg 27804 (BG)	USA	AF517895	-
L. normandinoides Lendemer & R. C. Harris	J. C. Lendemer 23681 (NY-1148496)	USA, New York	JQ627120	KC184093
L. normandinoides	J. C. Lendemer 18674 (NY-1118078)	USA, Pennsylvania	JQ627115	KC184030
L. nothofagi Elix & Kukwa	T. Widhelm, M. von Konrat & J. Larrain 4006	Chile	MZ820312	MZ820343
L. nothofagi	F. Grewe 267	Antarctica	MZ820310	MZ820341
L. oxybapha Lendemer	J. C. Lendemer 23199 (NY-1148377)	USA, Maine	JQ627127	KC184089
L. oxybapha	J. C. Lendemer 18627 (NY-1117630)	USA, Pennsylvania	JQ627126	KC184029
L. pacifica Lendemer	B. McCune 29887 (NY-1079488)	USA, Oregon	JF739375	KC184007
L. pacifica	Lendemer 19566 (NY-1133225)	USA, California	JF739377	KC184043
L. rigidula (B. de Lesd.) Tønsberg	T. Tønsberg 28222 (BG)	Norway	AF517914	-
L. rigidula	S. Bayerová 3655 (PRA)	Ukraine	EF619561	-
L. rigidula	Lendemer 19577 (NY)	USA, California	-	KC184055
L. rigidula	Lendemer 19707 (NY)	USA, California	-	KC184036
L. sipmaniana (Kümmerl. & Leuckert) Kukwa	M. Kukwa 10997 (UGDA)	Bolivia	MK629274	-
L. sipmaniana	M. Kukwa 11332 (UGDA)	Bolivia	MK629275	-
L. straminea Vain.	F. Grewe 286	Antarctica	MZ820323	MZ820354
L. straminea	F. Grewe 283	Antarctica	MZ820320	MZ820351

Species	**Voucher: collectors, collection no., herbarium**	**Country, region**	**nrITS**	**mtSSU**
L. sylvicola Orange	A. Orange 15017 (PRA)	United Kingdom	EF619580	-
L. sylvicola	A. Orange 15013 (NMW C.2004.002.142, holotype)	United Kingdom	DQ401102	-
L. toensbergiana Slav.-Bay. & Kukwa	J. Zelinková et al. s.n. (herb. Zelinková)	Czech Republic	EF619562	-
L. toensbergiana	S. Bayerová 2123 (herb. Bayerová)	Czech Republic	AY560835	-
L. ulrikii Grewe et al.	F. Grewe & T. Widhelm 3037 (AK, holotype; F, isotype)	New Zealand	MZ820307	MZ820338
L. ulrikii	F. Grewe & T. Widhelm 2246	Australia	MZ820304	MZ820335
L. umbricola Tønsberg	Z. Palice 32399 (PRA)	Czech Republic	OQ717924	OQ646293
L. umbricola	A. Orange 15174 (PRA)	United Kingdom	EF619582	-
L. vouauxii (Hue) R. C. Harris	K. Mark (WSL BC-133-2)	Switzerland	KX132973	-
L. vouauxii	T. Tønsberg 28865 (BG)	Norway	AF517906	-
L. vouauxii	R. C. Harris 56396 (NY)	USA, Tennessee	-	KC184095
L. vouauxii	J. C. Lendemer 20381 (NY)	USA, Virginia	-	KC184071
Stereocaulon subcoralloides (Nyl.) Nyl.	S. Talbot 167 (WIS)	USA, Alaska	EU008633	EU008656
Stereocaulon tomentosum Fr.	S. Talbot 400 (WIS)	USA, Alaska	EU008634	EU008657

Appendix 3. ML tree based on nucITS rDNA dataset for *Lepraria* spp. Sequence and voucher information is presented in Table 1 (for newly generated sequences) and Appendix 2 (for sequences obtained from GenBank). The tree was rooted using an outgroup, which consisted of *Stereocaulon subcoralloides* and *S. tomentosum*. Bootstrap supports (BS) from ML analysis > 80% are indicated near the branches. The newly sequenced specimens of *Lepraria* are in bold. The taxa names are provided with the collection numbers of specimens.

Appendix 4. ML tree based on mtSSU rDNA dataset for *Lepraria* spp. Sequence and voucher information is presented in Table 1 (for newly generated sequences) and Appendix 2 (for sequences obtained from GenBank). The tree was rooted using an outgroup, which consisted of *Stereocaulon subcoralloides* and *S. tomentosum*. Bootstrap supports (BS) from ML analysis > 80% are indicated near the branches. The newly sequenced specimens of *Lepraria* are in bold. The taxa names are provided with the collection numbers of specimens.