Three new species, new combinations and a key to known species of Lobothallia (Megasporaceae)

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Abstract: Three species, Lobothallia brachyloba Paukov & I. V. Frolov, L. epiadelpha Paukov & A. Nordin and L. zogtii Paukov & Davydov, from arid regions of Eurasia (Russia, Kazakhstan, Kyrgyzstan, China and Mongolia) are described as new to science. Lobothallia brachyloba has flat, firmly attached lobes, immersed apothecia lacking a distinct thalline margin, and contains norstictic acid. Both Lobothallia epiadelpha and L. zogtii contain stictic acid and have a brown thallus and sessile apothecia. Lobothallia epiadelpha initially develops on crustose Circinaria spp, has thick lobes loosely attached to the substratum, and brown apothecial discs with constant thalline margins. Lobothallia zogtii is a free-living species with brownish black to jet black apothecial discs surrounded by a receding thalline margin. Lecanora bojidensis is synonymized with Lobothallia praeradiosa and Lobothallia helanensis is synonymized with L. subdiffracta. Three new combinations, Lobothallia hedinii (H. Magn.) Paukov, A. Nordin & Sohrabi, L. lactola (Oxner) Şenkardesler, Paukov, Davydov & Sohrabi, and L. subdiffracta (H. Magn.) Paukov, are proposed. Phylogenetic analyses of Lobothallia brachyloba, L. epiadelpha and L. subdiffracta (ITS, mtSSU) are presented, showing their relationships within Lobothallia. The lectotype of the name Aspicilia lacteola Oxner is designated. A key to 18 species of Lobothallia is provided.

Key words: Altai, Ascomycota, China, lichenized fungi, Mongolia, new taxa, South Urals, taxonomy

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Introduction

The name Lobothallia was introduced as a subgenus of Aspicilia (Clauzade & Roux 1984) and was later raised to the genus rank within Aspiciliaceae (Hafellner 1991). Initially Lobothallia included taxa from the Aspicilia radiosa group and comprised four species with marginal lobes: L. alphoplaca, L. melanaspis, L. praeradiosa and L. radiosa. However, subsequent molecular studies broadened the concept of the genus to also include non-lobate crustose species (Nordin et al. 2010; Kou et al. 2013) as proposed by Esnault (1985) using morphological and anatomical characters. Lobothallia is now recognized within Megasporaceae (Schmitt et al. 2006; Nordin et al. 2010) and is characterized by relatively small ascospores, rarely exceeding 18 μm in length, and short conidia, 3–8 μm long. Additional morpho-anatomical characters are: a low hymenium not exceeding 100 μm; an ephymenium lacking, or with small amounts, of Caesiocinerarea-green (Meyer & Printzen 2000) and consequently a reaction with N that is negative to slightly greenish (vs. strong...
N+ (emerald green) reaction in other *Megasporaceae*; a distinct sub-hypothecial algal layer (Ryan 2004; Kou et al. 2013) visible after staining with lactophenol blue (Clauzade & Roux 1985) but which may be poorly visible unless stained (Roux et al. 2016). Species of *Circinaria* and *Megaspora* with short conidia differ from *Lobothallia* in having larger spores, usually more than 20 μm in length. Species of the *Aspicilia* polychroma group (*Aspicilia candida* (Anzi) Hue, *A. polychroma* Anzi, *A. polychromoides* (J. Steiner) Hue and *A. thjanschanica* Oxner), with comparable spore length, have much longer conidia and contain substictic acid, which is currently not known in *Lobothallia* (Nordin et al. 2010). Only *Aspicilia brucei* Owe-Lars. & A. Nordin, from the *A. cinerea* group, has spores and conidia which are as small as those in *Lobothallia* (Owe-Larsson et al. 2007; Roux et al. 2011).


During the study of lichen material collected by the authors in the Astrakhan, the Orenburg region of Russia, Altai (Russian and Chinese parts) and Kazakhstan, together with herbarium specimens, we recognized that some samples belong to previously undescribed species and that four taxa known as *Aspicilia* and *Lecanora* should be placed correctly in *Lobothallia*. Here we describe three species new to science and propose new combinations in *Lobothallia*.

### Materials and Methods

**Specimens and phenotype studies**

The core material for this study was collected by the authors and deposited in herbaria ALTB, UFU and UPS. Additionally, type specimens were examined in G, H-Nyl, KW, LE, MARSSJ, S and W. Morphological observations were made using a dissecting microscope. Cross-sections of apothecia and thalli were cut by hand with a razor blade and observed after mounting in water, 10% potassium hydroxide KOH (K), 10% water solution of nitric acid HNO₃ (N), calcium hypochlorite (C) and iodine solutions (I). Measurements of spores and conidia are presented as follows: (smallest value recorded) (x − SE) – x – (x + SE) (largest value recorded), where x is the (arithmetic) sample mean, and SE the sample error of the mean. The measurements were made with a precision of 0·5 μm.

Secondary products were analyzed by applying standard thin-layer chromatography techniques (Culberson & Kristinsson 1970). Solvent systems A (toluene: 1,4-dioxane: acetic acid, 180: 45: 5), B (hexane: diethyl ether: formic acid, 140: 72: 18) and C (toluene: acetic acid, 170: 30) were used for the TLC analysis.

### Sequences and phylogenetic reconstructions

To test phylogenetic relationships with other species, nuclear internal transcribed spacer and 5.8S rDNA (ITS) and mitochondrial small subunit (mtSSU) sequences of our fresh material and other sequences retrieved from the NCBI database (GenBank) were used for molecular phylogenetic analysis. Our sampling comprised 14 species of *Lobothallia* including two putative new species, species of *Aspicilia* and *Circinaria*, as well as *Megaspora verrucosa* as an outgroup. This selection was based on the studies of Nordin et al. (2010) and a five-gene analysis by Miadlikowska et al. (2014), in which *Megaspora* forms a sister clade to *Lobothallia* and *Circinaria*. Information on the samples together with the GenBank Accession numbers are given in Table 1.

Methods used for DNA extraction, amplification and sequencing follow Davydov & Yakovchenko (2017). ITS (531 bp) and mtSSU (725 bp) matrices were aligned separately in Geneious 6.0 (Biomatters Ltd., New Zealand) using the MUSCLE algorithm (Edgar 2004). Visible deviations in position homology were manually optimized. Since the specimens for the two datasets differed, we did not concatenate the matrices. Optimal
Table 1. Species of lichens used in the phylogenetic analyses in this study together with specimen information and GenBank Accession numbers. New specimens and associated sequences are in bold.

<table>
<thead>
<tr>
<th>Species</th>
<th>Origin</th>
<th>Collection number or reference</th>
<th>GenBank Accession number</th>
<th>Reference</th>
</tr>
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<tr>
<td><em>Aspicilia cinerea</em></td>
<td>Sweden, Dalarna</td>
<td>Hermansson 13275 (UPS)</td>
<td>EU057899 HM060695</td>
<td>Nordin et al. 2007, 2010</td>
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<td><em>Circinaria calcarea</em></td>
<td>Sweden</td>
<td>Wedin 6500 (UPS)</td>
<td>-</td>
<td>AY853310</td>
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<tr>
<td><em>C. esculenta</em></td>
<td>Kazakhstan, Kyzylorda Region</td>
<td>Ivanov s. n. (UFU L-1743)</td>
<td>MK347507 MK348226</td>
<td></td>
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<tr>
<td><em>C. fruticulosa</em></td>
<td>Russia, Chelyabinsk Oblast</td>
<td>Paukov 3074 (UFU L-3256)</td>
<td>MK347508 MK348227</td>
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<tr>
<td><em>Lecanora bogoðensis</em></td>
<td>Russia, Astrakhan Oblast</td>
<td>Paukov 3026 (UFU)</td>
<td>MK347502 -</td>
<td>This paper</td>
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<td><em>Lobothallia alphoplasca</em></td>
<td>USA, California</td>
<td>Knudsen 826 (H)</td>
<td>KJ766429</td>
<td>Miadlikowska et al. 2014</td>
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<td><em>L. alphoplasca</em></td>
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<td>Wang 20117646 (SDNU)</td>
<td>JX476025 -</td>
<td>Kou et al. 2013</td>
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<td>JX499233 -</td>
<td>Kou et al. 2013</td>
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<tr>
<td><em>L. alphoplasca</em></td>
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<td>Nadeina et al. (KW)</td>
<td>KT456207 -</td>
<td>Kondratyuk et al. 2015</td>
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<td><em>L. brachyloba</em></td>
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<td>Tari 2311 (B)</td>
<td>JQ797481</td>
<td>Sohrabi et al. 2013</td>
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<td><em>L. controversa</em></td>
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<td>Roux 25286 (UPS)</td>
<td>HM060723</td>
<td>Nordin et al. 2010</td>
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<td>Wang 20122565 (SDNU)</td>
<td>JX476026 -</td>
<td>Kou et al. 2013</td>
</tr>
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<td><em>L. epiadelpha</em></td>
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<td>JX476031 -</td>
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<td><em>L. melanaspis</em></td>
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<td>HQ259272</td>
<td>Nordin et al. 2011b</td>
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<td>Sweden, Jämtland</td>
<td>Nordin 6622 (UPS)</td>
<td>-</td>
<td>Sohrabi et al. 2013b</td>
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<td><em>L. melanaspis</em></td>
<td>Norway</td>
<td>Owe-Larsson 8943a (UPS)</td>
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<td>Valadbeigi et al. 2011</td>
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<td><em>L. praeradiosa</em></td>
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<td>Huang 20126355 (SDNU)</td>
<td>JX499230 -</td>
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<td><em>L. praeradiosa</em></td>
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<td>Li 20126314 (SDNU)</td>
<td>JX499232 -</td>
<td>Kou et al. 2013</td>
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</table>

(Continued)
substitution models were inferred separately for ITS1, 5.8S, ITS2 and mtSSU using PartitionFinder, version 1.1.1 (Lanfear et al. 2012). The Kimura 2-parameter (K80) model was selected for the 5.8S partition, Kimura 2-parameter with gamma distribution (K80 + G) for ITS1 + ITS2, and the Hasegawa-Kishino-Yano parameter with the proportion of invariable sites and gamma-distribution (HKY + I+G) for the mtSSU. Bayesian inference with the Markov chain Monte Carlo (BMCMC) method (Larget & Simon 1999) was performed using MrBayes 3.2.3 (Ronquist et al. 2012). Three parallel Bayesian analyses were run using six chains and every 200th generation was sampled. Convergence of the chains was inferred by calculating the average standard deviation of split frequencies every 100 000 generations using a burn-in fraction of 0.5, and the runs terminated when the standard deviation of split frequencies dropped below 0.001. This was the case after 7·1 M generations for ITS and 13·9 M for the mtSSU analyses. The first 50% of trees was discarded as burn-in and a 50% majority-rule consensus tree was calculated from the remaining trees of three runs with the sumt command implemented in MrBayes 3.2.3. The most likely tree and 1000 rapid bootstrap replicates were calculated using RAxML 8.0.26 (Stamatakis 2014) by raxmlGUI software version 1.3.1 (Silvestro & Michalak 2012), applying the GTRGamma model of substitution to the subsets. The tree topologies are taken from Bayesian inference (Figs 1 & 2). Bootstrap support values and BMCMC posterior probability were noted on the best-scoring tree.

### Results

Both ITS and mtSSU sequences were successfully obtained from *Aspicilia subdiffracta* and two putative new *Lobothallia* species, described below as *Lobothallia brachyloba* and *L. epiadelpha*. The material of *Lecanora bogdænsis* gave ITS sequences only. The Bayesian 50% majority-rule consensus tree had the same topology as the maximum likelihood tree generated by RAxML for Table 1 (continued).

<table>
<thead>
<tr>
<th>Species</th>
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<th>Collection number or reference</th>
<th>GenBank Accession number</th>
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<td>KT180160</td>
<td>- Ismayil, Abbas not published</td>
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<td>KT180162</td>
<td>- Ismayil, Abbas not published</td>
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<td><em>L. pruinosa</em></td>
<td>China, Inner Mongolia</td>
<td>Wang 20123630 (SDNU)</td>
<td>JX476027</td>
<td>- Kou et al. 2013</td>
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<td><em>L. pruinosa</em></td>
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<td>Wang 20123909 (SDNU)</td>
<td>JX499231</td>
<td>- Kou et al. 2013</td>
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<td><em>L. radiosa</em></td>
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<td>-</td>
<td>MK348225 This paper</td>
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<td><em>L. radiosa</em></td>
<td>Switzerland</td>
<td>Lumbsch, 9 Aug.2004 (F)</td>
<td>-</td>
<td>DQ780274 Schmitt et al. 2006</td>
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<td><em>L. radiosa</em></td>
<td>Hungary</td>
<td>Molnar U0504/GG (DUKE)</td>
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<td>KJ766430 Miadlikowska et al. 2014</td>
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<td><em>L. radiosa</em></td>
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<td>Nordin 5889 (UPS)</td>
<td>JF703124</td>
<td>- Roux et al. 2011</td>
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<td><em>L. recedens</em></td>
<td>Sweden, Dalarna</td>
<td>Nordin 6582 (UPS)</td>
<td>HM060724</td>
<td>- Nordin et al. 2010</td>
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<td><em>L. recedens</em></td>
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<td>Nordin 6582a (UPS)</td>
<td>HQ406807</td>
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<td><em>L. subdiffracta</em></td>
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<td>Frolov 105 (UFU)</td>
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<td>Frolov 178-1 (UFU)</td>
<td>MK347503 MK348233 This paper</td>
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<td><em>Megaspora verrucosa</em></td>
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<td>Nordin 6495 (UPS)</td>
<td>-</td>
<td>HM060687 Nordin et al. 2010</td>
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<td><em>M. verrucosa</em></td>
<td>USA, Colorado</td>
<td>St. Clair C54042 (BRY)</td>
<td>KC667053</td>
<td>- Sohrabi et al. 2013a</td>
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both ITS and mtSSU and the major taxon grouping was similar in the phylogenetic reconstructions of single ITS and mtSSU (Figs 1 & 2).

Both the ITS and mtSSU phylograms combine two well-supported major clades for Lobothallia. The first major clade includes Lobothallia praeradiosa and L. recedens in the ITS tree with 1.00/93 support values (BMCMC posterior probability/bootstrap value, respectively); in the mtSSU phylogram this clade (0.97/72) additionally contains L. cernohorskyana and L. controversa. The second major clade (ITS: 0.99/75, mtSSU: 1.00/92) combines the remaining species from our selection and includes Lobothallia brachyloba and L. epiadelpha. In the ITS phylogram, both species cluster with low statistical support (0.89/66) as paraphyletic lineages to a well-supported clade combining Lobothallia praeradiosa KT180162
L. praeradiosa JX499230
L. praeradiosa JX499232
L. praeradiosa MK347501
‘Lecanora’ bogdoënsis MK347502
L. praeradiosa KT180162
L. alphoplacea JX499233
L. alphoplacea JX476025
L. alphoplacea KT456207
L. alphoplacea KT456207
L. melanospi JF825524
L. melanospi HQ259272
L. praeradiosa JX476027
L. praeradiosa JX499231
L. praeradiosa JX476030
L. praeradiosa JX476031
L. helanensis JX476031
L. helanensis JX476030
L. crassimarginata JX476026
L. crassimarginata KC007439
L. helanensis JX476031
L. helanensis JX476030
L. helanensis JX476030
L. radiosa JF703124
L. radiosa JF703124
L. radiosa JF703124
L. radiosa JF703124
L. recedens HQ406807
L. recedens HQ406807
C. fruticulosa MK347508
C. fruticulosa MK347508
C. fruticulosa MK347508
C. fruticulosa MK347508
Aspicilia cinerea EU057899
Aspicilia cinerea EU057899
Aspicilia cinerea EU057899
Aspicilia cinerea EU057899
Megaspora verrucosa KC667053
Megaspora verrucosa KC667053
Megaspora verrucosa KC667053
Megaspora verrucosa KC667053

Fig. 1. Maximum likelihood (ML) phylogeny of selected Lobothallia ITS sequences. The reliability of each branch was tested by ML and Bayesian methods. Numbers at tree nodes indicate Bayesian inference with the Markov chain Monte Carlo (BMCMC) posterior probabilities (left) and ML bootstrap percentages (right). Thicker branches indicate when the bootstrap value of ML is ≥70% or the BMCMC posterior probability is ≥0.95. The Lobothallia clade is arrowed. GenBank Accession numbers are given to serve as operational taxonomic unit (OTU) names (see Table 1). For ‘Lecanora’ bogdoënsis, the quotation marks indicate the genus name prior to synonymy in the present paper. Originally produced sequences are marked in bold. Megaspora verrucosa was used as an outgroup.
crassimarginata, L. subdiffracta and L. helanensis. In the mtSSU, three sequences of L. epiadelpha form a monophyletic group (1·00/100) but its relation to other species within the second major clade lacks statistical support. Lecanora bogdoënsis is nested within the Lobothallia praeradiosa group (ITS: 1·00/100), and Lobothallia subdiffracta is placed sister to L. helanensis (ITS: 1·00/100). In the mtSSU tree (Fig. 2), Lobothallia brachyloba is sister to the second major clade, comprising Lobothallia alphoplaca, L. melanaspis, L. praeradiosa, L. subdiffracta and L. epiadelpha.

The Species

Lobothallia brachyloba Paukov & I. V. Frolov sp. nov.

MycoBank No.: MB 827340

Megaspora verrucosa was used as an outgroup.
substratum, apothecia immersed, 1–7 per areole, not crowded, lacking distinct thalline margin.

Type: Russia, Republic of Altai, Shebalino District, c. 1 km NE of village of Topuchaya, gneiss rocks on SW-slope above River Sarlyk, elev. c. 1200 m a.s.l., on gneiss, 7 July 2012, I. Frolov 357 (UFU—holotype; UPS—isotype).

(Fig. 3A & B)

Life habit lichenized, not lichenicolous.

Thallus light grey, 0·3–1·0 mm thick, placodioid, lobate in the periphery and areolate in the central part. Lobes 0·9–2·0 × 0·6–1·0 mm (length × width), flat to slightly convex, not overlapping, closely adnate to the rocky substratum, not detaching in the outer parts. Central areoles 0·5–2·0 mm, irregular in form, flat when sterile, moderately convex when fertile. Upper cortex paraplectenchymatous, (25·0–) 32·3–33·4–34·4(–42·5) μm (n = 20) over algal stacks, opaque, light brownish throughout, translucent in K, cells 4–8 μm, epinecral layer (7·5–)11·7–12·3–12·8(–17·5) μm (n = 20). Medulla (75·0–)87·5–89·4–91·2(–

Fig. 3. A & B, Lobothallia brachyloba, holotype: A, part of a thallus; B, central part of the thallus showing apothecia. C–F, Lobothallia zogtii, holotype: C & D, part of a thallus; E, central part of a thallus with apothecia; F, part of a thallus from a shady habitat. Scales = 1 mm. In colour online.
Vegetative propagules and hypothecium, algae groups visible without staining under the tissue, forming separate groups 10·5 μm (n = 20) opaque with numerous crystals. *Photobiont layer* interrupted by fungal tissue, forming separate groups 50–65 μm tall and 25–45 μm wide; almost continuous, or in groups visible without staining under the hypothecium, algae 6–14 μm diam. *Prothallus* absent. *Vegetative propagules* absent.

Apothecia cryptolecaneorine, 1–7 per areole in the outer part of the thalli, 1–2 in the central part, immersed, only slightly projecting when mature, (0.30–0.39–0.41–0.43 (–0.60) mm (n = 20); disc initially dot-like, later wider, slightly concave to flat, sparingly pruinose, dark brown, with a bulge of sterile tissue in some mature apothecia; **thalline margin** absent. *Exciple* of radiating hyphae, 10–12 μm thick, widening to 20–25 μm in the uppermost part, scarcely discernible. *Hymenium* hyaline, (65–0)–72–3–73–5–74–7 (–82·5) μm high (n = 20), yellowish blue in I; paraphyses simple, submoniliform; *epihymenium* brownish, unchanged in N, (12·5–)13·5–14·0–14·5 (–20·0) μm high (n = 20). *Hypothecium* hyaline, I+ bluish, (30·0–)37·8–38·8–39·7 (–45·0) μm high (n = 20). *Asci* clavate, Aspicilia-type; ascospores broadly ellipsoid, to almost spherical, hyaline, aseptate (10·0–)11·5–11·9–12·0 (–13·0) × (7·0–)9·5–9·8–10·0 (–12·0) μm (n = 25).

*Pycnidia* common, with punctiform ostiole; *conidia* short, bacilliform, hyaline, aseptate (5·0–)5·7–5·8–5·9 (–7·0) μm (n = 30).

**Chemistry.** *Thallus* K+ red, C–; medulla K+ red, C–; norstictic acid by TLC.

**Etymology.** The name reflects the shorter lobes of the species compared to *Lobothallia radiosa*, which can be similar in appearance.

**Ecology.** *Lobothallia brachyloba* was found on exposed acid rocks at an elevation of 1200 m a.s.l. in the boreal forest belt dominated by *Picea obovata* Ledeb. and *Pinus sibirica* Du Tour. The following species co-occurred with *L. brachyloba*: *Aspicilia cinerea*, *Bellemerea cuprea* (Nyl.) Clausade & Cl. Roux, *Lecanora cinerea* Ach. and *Protoparmeliopsis murialis* (Schreb.) M. Choisy.

**Distribution.** The species is known from one locality in the Altai mountains (Republic of Altai, Russia).

**Notes.** *Lobothallia brachyloba* is a species with a placodoid, light grey thallus and norstictic acid as a secondary metabolite. This combination of characters renders it similar to other *Lobothallia* species, such as *L. crassimarginata*, *L. praeradiosa* and to some extent *L. alphoplaea*. *Lobothallia brachyloba* differs from these species by its flat to slightly convex, closely adnate lobes and permanently immersed apothecia without a thalline margin. *Lobothallia radiosa* chemotype *radiosa* is externally similar to *L. brachyloba* but differs in having a K– thallus. The norstictic acid-containing chemotype of *Lobothallia radiosa* (= *Aspicilia subcircinata* (Nyl.) Coppens) can be separated from *L. brachyloba* by its apothecia which are crowded in the centre of the thallus, and finally form visible thalline margins (thalline margin absent in *L. brachyloba*). The central areoles of *Lobothallia radiosa* are uneven and crossed by linear depressions which divide the areoles into smaller units, while *L. brachyloba* has smooth, un-cracked central areoles.

**Lobothallia epiadelpha** Paukov & A. Nordin sp. nov.

MycoBank No.: MB 827338

*Lobothallia* with a thick, lobate, brownish thallus, containing stictic acid, initially developing on species of *Circinaria*, later free-living. Lobes are smooth, flat or slightly convex, loosely attached to the substratum, apothecia sessile.

Type: Russia, Orenburgskaya Oblast’, Gaiskiy District, 17 km to the west of Novotrotsk Town (via Akkermanovka), hills around ‘The King’s Spring’, 51°08′56″N, 58°02′32″E, elev. 299 m a.s.l., on serpentine outcrops in a dry stony steppe, 17 June 2016, A. Paukov 1881 (UFU–L3189—holotype; G, LE, M, UPS—isotypes).

(Fig. 4A–F)

**Life habit** lichenized, initially lichenicolous, developing mainly on *Circinaria* spp., later overgrowing the host and free-living. *Thallus* brown, up to 1·5 mm thick, lobate in the periphery and squamulose in the central part.
FIG. 4. A–F, Lobothallia epiadelpha: A, part of a thallus with wide lobes, holotype; B, young specimen overgrowing Circinaria maculata, isotype; C, Lobothallia epiadelpha on C. maculata, isotype; D, section of thallus, holotype; E, section of apothecium coloured by iodine solution, holotype; F, type locality in the Orenburg Oblast. G & H, Lobothallia hedinii, holotype: G, outer part of a thallus; H, apothecia. Scales: A, B, G & H = 1 mm; C = 1 cm; D & E = 50 μm. In colour online.
**Lobes** relatively short and wide, 1·0–2·3 × 0·5–2·7 mm (length × width), flat to moderately convex, white-bordered, smooth or with irregular cracks, widened paw-like and incised in the outermost part to form 2–3 lobules or entire, overlapping, attached to the rocky substratum only by their base, but when parasitic usually firmly attached to the host, lower side whitish to light brownish. *Central squamules* 0·8–2·7 mm, irregular in form, constricted at the base, slightly overlapping, moderately convex. *Upper cortex* parapectenanchymatous, (22·5–30·1–31·3–32·6–(41·5) μm high (n = 15) over algal stacks, brownish in its outermost part (Subdepressa-brown; see Roux et al. 2011), cells 7–9 μm, epinecral layer (8·5–)12·3–12·8–13·4–(16·0) μm high (n = 15). *Medulla* I–, K+ yellow. *Lower cortex* whitish. *Photobiont layer* interrupted by fungal tissue, forming algal stacks (Vondrák & Kubásek 2013), 100–125 μm tall and 28–66 μm wide; spherical algal groups (21·0–)31·0–32·7–34·4–(41·5) μm (n = 10) present under hypothecium. *Photobiont* chlorococcoid, algae 7–20 μm diam. *Prothallus* absent. *Vegetative propagules* absent.

*Apothecia* lecanorine, 1–4 per squamule, initially immersed, later sessile, constricted at the base, rounded or elliptic in outline, (0·5–)0·8–0·9–1·0–(1·5) mm diam. (n = 25); *disc* initially dot-like, later wide, flat to slightly convex, pruinose when young, black to chestnut brown in older apothecia; *thalline margin* appearing in dot-like apothecia as a dark zone around the disc, later well developed, thick, 0·15–0·25 mm, projecting, dark, concolorous with the disc, in older apothecia becoming lighter and receding. *Excipl* of radiating hyphae, 12–20 μm, widening to 45–50 μm in the uppermost part. *Hymenium* hyaline, (60·5–)66·8–68·2–69·6–(77·0) μm high (n = 15), unchanged in I; *paraphyses* moniliform with 3–7 apical cells 5·0–6·5 μm thick; *epihymenium* brownish, N+ weakly greenish, giving an impression of a parapectenanchymatous tissue because of swollen upper cells of the paraphyses, (13·5–)17·3–18·0–18·6–(22·5) μm high (n = 15). *Hypothecium* hyaline, I+ weakly bluish, (26·0–)30·0–31·1–32·0–(40·0) μm high (n = 15). *Asci* clavate, *Aspicilia*-type; *ascospores* broadly ellipsoid, hyaline, aseptate (10·0–11·9–12·1–12·4–(14·5) × (6·0–)9·0–9·2–9·5–(11·8) μm (n = 30).

*Pycnidia* common, with punctiform ostiole; *conidia* short, bacilliform, hyaline, aseptate (5·0–)5·8–5·9–6·0–(7·0) μm long (n = 32).

**Chemistry.** Thallus K–, C–; medulla K+ yellow, C–; stictic acid complex by TLC, nortistic acid as a minor substance found in one specimen.

**Etymology.** The name refers to the parasitic life habit of the species, which grows on representatives of the same family *Megasporaceae*.

**Ecology.** *Lobothallia epiadelpha* was found in arid conditions on exposed siliceous rocks (schistose and serpentine) in steppe communities at elevations 200–1200 m a.s.l. It grows predominantly as a free-living saxicolous lichen but younger thalli commonly overgrow species of *Circinaria*, mainly *Circinaria maculata* (H. Magn.) Q. Ren (Fig. 4C). The following species co-occurred with *Lobothallia epiadelpha*: *Acarospora irregularis* H. Magn., *Aspicilia cinerea* (L.) Körb., *Bellemerea cupreatra*, *Candelariella vitellina* (Ehrh.) Müll. Arg., *Circinaria* spp., *Lecanora argopholis* (Ach.) Ach., *Protoparmeliopsis muralis*, *Rusavskia* spp. and *Xanthoparmelia delisei* (Duby) O. Blanco et al.

**Distribution.** The species is known from three localities in the Orenburg Oblast’ of Russia, and Central and Eastern Kazakhstan.

**Notes.** *Lobothallia epiadelpha* may be confused with *Lobothallia radios* chemotype *parasitica* due to its lichenicolous habit and stictic acid as a secondary metabolite. The latter taxon differs by its thinner thallus with closely adnate not overlapping lobes, and the immersed apothecia with smaller discs (up to 0·6 mm), which are numerous in each areole. It is known only from Mediterranean and sub-Mediterranean regions and grows on other hosts (Bouly de Lesdain 1931; Loppi & Mariotti 1995) or may be free-living (Roux et al. 2017).
**2019**

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Additional material examined. **Russia**: Orenburgskaya Oblast': Gaikisky District, vicinity of Novotroitsk Town, 9·5 km to the SW of Khabarnoye settlement, 51°06′28″−7′N, 58°06′35″−6″E, 205 m, serpentine outcrops in steppe, 2013, A. Paukov AGP20130528−06 (UFU−L1705); 1 km to the east of Karagay-Pokrovka Village, steep slope on a bank of a brook confluent to Guberlya River, 51°37′54″−8′N, 57°55′45″−8″E, 413 m, slate outcrops in steppe, 2013, A. Paukov AGP20130529−21 (UFU−L1882). — **Kazakhstan**: Shyghys Kazakhstan: along the road NE of Alekseyevka, 48°29′′−9″N, 85°52′′−8″E, 1200 m, on schistose rocks, 1993, R. Moberg & A. Nordin K22:19 (UPS−L078051). Karagandinskaya Oblast': Shetskiy District, rocky outcrops in steppe along the road Zharyk-Unrek, 48°51′′−1″N, 72°55′′−16″E, 2018, I. Frolov K1:2145 (UFU).

**Lobothallia zogtii** Paukov & Davydov sp. nov.

MycoBank No.: MB 827339

*Lobothallia* with a thick, lobate, brownish, non-parasitic thallus, containing stictic acid. Lobes with deep cracks, slightly to strongly convex, firmly attached to the substratum; apothecia sessile, pruinose; disc brownish black to jet black, chestnut brown when wet; thalline margin white pruinose, brownish black to jet black, centrally distinctly constricted, usually but not consistently present under the hypothecium. Prothallium chlorococcoid, algae 8–17 μm diam. *Prothallus* absent. Vegetative propagules absent.

*Apothecia* lecanorine, 1–2 per squamule, but sometimes forming 3–4 unclearly separated apothecia due to cracking of the primary discs, initially immersed, soon sessile, constricted at the base, rounded or elliptic in outline, (0·5−)1−2−1·3−1·4(−2·5) mm (n = 20); disc initially dot-like, later wide, slightly convex, pruinose, brownish black to jet black, chestnut brown when wet; *thalline margin* 0·10−0·20 mm thick, projecting when young, concolorous with the thallus, in older apothecia becoming dark and receding, not higher than the disc, sometimes with white pruina. *Exciple* of radiating hyphae, 17–25 μm, widening to 45–50 μm in the uppermost part. *Hymenium* hyaline, (70−0−)81·1−82·7−84·2(−95·0) μm high (n = 20), unchanged in I; *paraphyses* moniliform, with 3–7 apical cells 7–9 μm thick; *epithecium* brownish, unchanged in N, (12·5−)16·6−17·3−18·1(−22·5) μm high (n = 20). *Hypothe- ci um* hyaline, I+ weakly bluish, (25·0−)34·2−35·3−36·5(−45·0) μm high (n = 20). *Asci* clavate, *Aspicilia*-type; *ascospores* broadly ellipsoidal, hyaline, aseptate (10·0−)11·2−11·4−11·7(−14·0) × (7·0−)7·9−8·0−8·1(−9·0) μm (n = 25).

*Pycnidia* common, with punctiform ostiole; *conidia* short, bacilliform, hyaline, aseptate (5·0−)5·8−6·0−6·1(−7·0) μm (n = 35).

**Chemistry.** Thallus K−, C−; medulla K+ yellow, C−; stictic acid complex by TLC.

**Etymology.** The name refers to the Mongolian botanist U. Zogt, who collected the type specimen.

(Fig. 3C−F)

*Thallus* brown, 1·5−2·5 mm thick, lobate in the periphery and squamulose-areolate in the central part. *Lobes* 1·5−3·5 × 1·0−2·5 mm (length × width), moderately to strongly convex, white-bordered, with irregular deep depressions forming a reticulate pattern (smooth in shade), not overlapping, transversely cracking towards the centre of the thallus to form areoles, closely adnate to the rocky substratum, with outer part (c. 0·5−1·0 mm) unattached, lower side whitish to light brownish. *Lower cortex* indefinite. *Central areoles* 1·0−1·7 mm, irregular in form, moderately convex, with irregular depressions forming a reticulate pattern, sometimes even forming cracks subdividing the areoles (in shade the areoles are convex and smooth). *Upper cortex* paraplectenchymatous, (62·5−)76·9−79·3−81·8(−100·0) μm (n = 15) over algal groups, outer 10 μm of cortex brownish, with ‘Subdepressa-brown’ cells 5–8 μm, epinuclear layer (17·5−)21·3−23·7−26·0(−42·5) μm (n = 20). *Medulla* I−, K+ yellow. *Photobiont layer* interrupted by a fungal tissue, forming separate columns 125–300 μm tall and 75–125 μm wide; algal layer under hypothecium is visible without staining as spherical algal groups (25·0−)35·5−37·2−38·8(−50·0) μm (n = 21) usually but not consistently present under the hypothecium. *Photobiont* chlorococcoid, algae 8–17 μm diam. *Prothallus* absent. Vegetative propagules absent.

*Additional material examined. Russia*: Orenburgskaya Oblast': Gaikisky District, vicinity of Novotroitsk Town, 9·5 km to the SW of Khabarnoye settlement, 51°06′28″−7′N, 58°06′35″−6″E, 205 m, serpentine outcrops in steppe, 2013, A. Paukov AGP20130528−06 (UFU−L1705); 1 km to the east of Karagay-Pokrovka Village, steep slope on a bank of a brook confluent to Guberlya River, 51°37′54″−8′N, 57°55′45″−8″E, 413 m, slate outcrops in steppe, 2013, A. Paukov AGP20130529−21 (UFU−L1882). — **Kazakhstan**: Shyghys Kazakhstan: along the road NE of Alekseyevka, 48°29′′−9″N, 85°52′′−8″E, 1200 m, on schistose rocks, 1993, R. Moberg & A. Nordin K22:19 (UPS−L078051). Karagandinskaya Oblast’: Shetskiy District, rocky outcrops in steppe along the road Zharyk-Unrek, 48°51′′−1″N, 72°55′′−16″E, 2018, I. Frolov K1:2145 (UFU).

**Lobothallia zogtii** Paukov & Davydov sp. nov.

MycoBank No.: MB 827339

*Lobothallia* with a thick, lobate, brownish, non-parasitic thallus, containing stictic acid. Lobes with deep cracks, slightly to strongly convex, firmly attached to the substratum; apothecia sessile, pruinose; disc brownish black to jet black, chestnut brown when wet; *thalline margin* 0·10−0·20 mm thick, projecting when young, concolorous with the thallus, in older apothecia becoming dark and receding, not higher than the disc, sometimes with white pruina. *Exciple* of radiating hyphae, 17−25 μm, widening to 45−50 μm in the uppermost part. *Hymenium* hyaline, (70−0−)81·1−82·7−84·2(−95·0) μm high (n = 20), unchanged in I; *paraphyses* moniliform, with 3−7 apical cells 7−9 μm thick; *epithecium* brownish, unchanged in N, (12·5−)16·6−17·3−18·1(−22·5) μm high (n = 20). *Hypothe- ci um* hyaline, I+ weakly bluish, (25·0−)34·2−35·3−36·5(−45·0) μm high (n = 20). *Asci* clavate, *Aspicilia*-type; *ascospores* broadly ellipsoidal, hyaline, aseptate (10·0−)11·2−11·4−11·7(−14·0) × (7·0−)7·9−8·0−8·1(−9·0) μm (n = 25).

*Pycnidia* common, with punctiform ostiole; *conidia* short, bacilliform, hyaline, aseptate (5·0−)5·8−6·0−6·1(−7·0) μm (n = 35).

**Chemistry.** Thallus K−, C−; medulla K+ yellow, C−; stictic acid complex by TLC.

**Etymology.** The name refers to the Mongolian botanist U. Zogt, who collected the type specimen.
Ecology. _Lobothallia zogtii_ was found in arid steppe communities on exposed siliceous rocks at elevations 1200–1800 m a.s.l. Accompanying species are _Anaptychia desertorum_ (Rupr.) Poelt, _Candelariella rosulans_ (Müll. Arg.) Zähr., _Lecidea tessellata_ Flörke and _Protoparmeliopsis peltata_ (Ramond) Arup et al.

**Distribution.** The species is known from two localities in the Xinjiang Autonomous Region of China.

**Notes.** _Lobothallia zogtii_ might be confused with _L. epiadelpha_ due to its general appearance, the colour of the thallus and the presence of stictic acid as its main secondary metabolite. However, it has not been found overgrowing other lichens and it has narrower and convex, adnate, non-overlapping lobes with a definite reticulate pattern, formed by depressions of the upper cortex. This pattern, however, is poorly visible or even absent in thalli from shady microhabitats although it can be found in lobes of the same specimens on an exposed side of the stone substratum. Compared to _L. epiadelpha_, apothecia of _Lobothallia zogtii_ are larger, usually 1–2 per areole, and have blackish (brown in shade) convex discs with receding margins, projecting in younger apothecia only.

Additional material examined. **China:** Xinjiang: foothills of Mongolian Altai range at the 40th km of the Qinghe-Altaí road (30 km SW of Qinghe), desert steppe slopes, on rocks, *Achnatherum splendens* community in meso-depressions, 46°30′–46°5′N, 90°03′–90°05′E, 1280 m, 2007, E. A. Davydov 16027 (ALTB).

**New combinations**

In his works on the lichens of China, Magnusson (1940, 1944) described among others two species, *Lecanora hedini* H. Magn. and _L. subdiffracta_ H. Magn., which were subsequently moved to _Aspicilia_ (Oxner 1972; Wei 1991). A year before Magnusson, Oxner himself described _Aspicilia lacteola_ Oxner from Kyrgyzstan (Oxner 1939). Cretzoiou (1941) was one of the lichenologists who treated _Aspicilia_ as a section in the genus _Lecanora_. For this reason, he proposed the name _L. oxneri_ Cretz. when transferring _A. lacteola_ into _Lecanora_ to avoid a homonymy with _L. lacteola_ Müll. Arg. Our study of the types of these species in S and KW has convinced us that their correct placement is in _Lobothallia_.

**Lobothallia hedini (H. Magn.) Paukov, A. Nordin & Sohrabi comb. nov.**

MycoBank No.: MB 827675


(Fig. 4G & H)

The species can be recognized by the following set of characters: brown, white-pruinose thallus with norstictic acid; straight, parallel, simple or dichotomous convex lobes; immersed apothecia 1–2(3) per areole. _Lobothallia pruinosa_ most closely corresponds to this set of characters but has flat lobes, not arranged in parallel. Other _Lobothallia_ species with convex lobes differ from _Lobothallia hedini_ in their appressed apothecia.

**Lobothallia lacteola (Oxner) Şenkardeşler, Paukov, Davydov & Sohrabi comb. nov.**

MycoBank No.: MB 827678


(Fig. 5D)

_Lobothallia lacteola_ differs from other species of the genus by the following set of
Fig. 5. A, holotype of Lobothallia subdiffracta, part of a thallus (S); B, L. reedens, Sweden, Dalarna, A. Nordin 6587 (UPS); C, L. controversa, Russia, Altaiskiy Krai, E. A. Datsykov 17606 & L. S. Yakovchenko (ALTB); D, lectotype of L. lacteola (KW); E, L. radiosa chemotype parasitica, isotype of Lecanora parasitica (LE); F, L. radiosa chemotype radiosa, Russia, Orenburg Oblast, A. Paukov AGP20120606-11 (UFU); G & H, L. radiosa chemotype subcircinata, France, Pyrénées-Orientales (photograph: S. Poumarat). Scales = 1 mm. In colour online.
characters: calcareous, circular, white, fari-
nose, distinctly rimose-areolate thallus with
indefinitely radically cracked or plicate mar-
gins; immersed apothecia with black, pruinose
disc and prominent thalline margin; norstictic
acid as a major secondary metabolite, which is
occasionally accompanied by connorstictic
acid as a minor component. Additional char-
acters are simple and non-moniliform par-
aphyses and 6–8-spored asci with shortly
ellipsoid to globose ascospores 10·0–11·5 ×
7·5–11·5 μm in size.

The species is similar to Lobothallia controversa
Cl. Roux & A. Nordin but differs chemically in
the absence of terpenes. The thalline margin of
L. lacteola projects clearly in mature apothecia
while it is absent in L. controversa.

Lobothallia lacteola is known from two
localities in Kyrgyzstan and one locality in
Russia (Altaiiskiy Krai), where it inhabits
exposed limestone rocks. The species is
guarded here as new to Russia.

Additional material examined. Russia: Altaiiskiy Krai:
Tigirelskiy Range, right bank of Inya River, 2 km
upstream from Tigirek settlement, Inskaya mountain,
SE slope, limestone, 51°09′ N, 83°04′ E, 1996,
E. A. Datsyuk 5008 (ALTB).

Lobothallia subdiffracta (H. Magn.)
Paukov comb. nov.

MycoBank No.: MB 827676

Lecanora subdiffracta H. Magn. Lichens from Central Asia
2: 40 (1940).—Aspicilia subdiffracta (H. Magn.)
J. C. Wei, Enumeration of Lichens in China (Beijing)
1991: 34 (1991); type: China, Inner Mongolia, Beli-
Miao, 41°30′ N, 110°10′ E, 1929, Bohlin (S—holotype!).

Lobothallia helanensis X. R. Kou & Q. Ren, Mycotaxon
123: 245 (2013); type: China, Inner Mongolia, Mt.
Helan, elev. 1500 m, 2011, D. B. Tong 20122517
(SDNU—holotype, not seen), syn. nov.

(Fig. 5A)

The holotype of Lecanora subdiffracta kept in
S is a small specimen. Nonetheless it bears all
the characters typical of this species, namely a
thick, non-lobate squamulose thallus, dark,
white-bordered squamules and apothecia
with incised margins, which agree with
Lobothallia helanensis. On the basis of the simi-
larly of the species in the ITS and mtSSU
regions, as well as their morphological and
anatomical similarity, we conclude that these
two taxa represent the same species, with sub-
diffracta as an earlier epithet. In addition to
the type localities of Lobothallia subdiffracta
and L. helanensis in China, the species is widely
distributed in arid conditions in Russia
(Republic of Altai) and Mongolia.

Material examined. Russia: Republic of Altai:
Kosh-Agachskiy District, SE part of Kuray Ridge, NE of
village of Chagan-Uzun, 2000 m, 2012, I. Frolov 105
(UFU); 10 km S of Tarkhata, valley of Tarkhata brook,
Schistose rocks at the brook, 2200 m, 2012, I. Frolov 178
(UFU); Chuiskaya Steppe, right bank of the Tydtyaryk
River near its junction with Chuya River, rock outcrops,
dry steppe, 50°04′18″ N, 88°24′50″ E, 1760 m, on rocks,
2016, A. Paukov 1952 (UFU).—Mongolia: Dschungarischer Gobi: Argalant mountains, near Ubcchu-Bulak, 1700 m, on rocks,

Lobothallia controversa

New synonym

Lobothallia praeradiosa (Nyl.) Haeflerner

MycoBank No.: MB 354542

Nyl., Flora (Regensburg) 67: 389 (1884); type: Hungary,
prope Budapest, 1882, Lojka (G—isotype!).

Lecanora bogdoënsis Tomin, Priroda i sel’khoz kho-
zyaistvo zasushlivykh oblastey SSSR 1–2; 48[4] (1927),
syn. nov.—Placocanora bogdoënsis (Tomin) Kopach.,
Nov. Sist. Nizh. Rast. 9: 295 (1972), syn. nov.—Proto-
J. 69: 876 (2012), syn. nov. (W-L282—isotype!).

(Fig. 6F & G)

Lecanora bogdoënsis Tomin was segregated
from lobate Lecanora alphoplaca on the
grounds of its wider and more flattened
lobes and wider conidia (Tomin 1927). The
species was later moved to Placocanora
(Kopacevskaja 1972) and Protoparamelopsis
(Kondratyuk et al. 2012). However, the
absence of usnic acid, isousnic acid or
xanthones along with small spores and short
conidia imply an affiliation with Lobothallia.
ITS sequences as well as the morphology and
Fig. 6. A, Lobothallia chadefaudiana, Vézda, Lich. Sel. Exs. 1638 (W); B, L. cernohorskyana, Vézda, Lich. Sel. Exs. 895 (W); C, L. cheresina chemotype cheresina, Greece, Rhodos, I. Pišút s. n. (SAV); D, L. cheresina chemotype justii, type of Lecanora justii (W); E, L. alphoplaca, Russia, Bashkortostan, A. Paukov AGP20100525-37 (UFU); F, L. praeradiosa, isotype of Lecanora praeradiosa (G); G, isotype of Lecanora bogdoënsis (W); H, L. melanaspis, Russia, Altaiskiy Krai, E. A. Davydov 5907 (ALTB). Scales = 1 mm. In colour online.
conidial width of the material collected by the authors in the locus classicus agree with those of Lobothallia praeradiosa, with which we synonymize Lecanora bogdoënsis here.

Notes on Lobothallia radiosa (incl. Aspicilia parasitica B. de Lesd.), stictic acid chemotype

Aspicilia parasitica B. de Lesd.


(Fig. 5E)

Aspicilia parasitica has been the subject of two different interpretations: Esnault (1985) and Loppi & Mariotti (1995) consider it as a species distinct from Lobothallia radiosa due to its chemistry (stictic acid) and its parasitism on various species of Aspicilia (Loppi & Mariotti 1995). The parasitic nature of the species was considered to be an essential attribute because of the existence in Algeria of a non-parasitic chemotype of L. radiosa with stictic acid (Esnault 1985).

Roux et al. (2017) considered Aspicilia parasitica to be a chemotype of L. radiosa with a K+-yellow thallus containing stictic acid. Even though the parasitism of this chemotype is quite common, it is not at all constant (especially in the Southern Alps or in young thalli which often begin their development unattached to other lichens). Otherwise, the chemotype radiosa, which is devoid of secondary chemistry, parasitizes other Aspicilia s. lat. (especially in le Var and in Corsica).

Lobothallia radiosa with stictic acid (chemotype parasitica), which is also known from the Pyrénées-Orientales (Roux et al. 2017), has a more southern distribution (Mediterranean and sub-Mediterranean) than chemotype radiosa, but their ranges widely overlap. Esnault (1985: 116) provided two other distinguishing characters of the chemotype parasitica, namely a darker colour of the thallus and the presence of an amorphous cortical coating (epinecral layer). The examination of several specimens of Lobothallia radiosa (chemotype radiosa (Fig. 5F), without or with a trace amount of norstictic acid; chemotype subcirkinita with norstictic acid (Fig. 5G & H); chemotype parasitica, including isotype material, which parasitizes Aspicilia proluta, collected by Sbarbana) has shown unambiguously that these two characters are not informative. The colour of the thallus is variable and the presence of an epinecral layer occurs in all the specimens examined but its thickness varies, depending on the part of the thallus examined, from 0 to 30 µm. Hence, we follow here the view of Roux et al. (2017) and include Aspicilia parasitica in Lobothallia radiosa.

Selected specimens examined. Chemotype radiosa. France: Pyrénées-Orientales: Jujols, beginning of the Garrigue trail, 1025 m, on inclined or subvertical surfaces (10–80°), non-calcareous schist, 2007, C. Roux 25139 (MARRSJ); Nohèdes, in the immediate vicinity of the Nohèdes Nature Reserve, 170 m to the NW of Cortal, 1030 m, on small non-calcareous shale walls, 2009, C. Illeger, 25614 (MARRSJ).—Italy: Liguria Occidentale: Spotorno (Savona), in regione ‘Castello’, ad rupeis schistoseis, 1962, C. Sbarbana (Vezda, Lichenes Selecti Exsiccati no 167; sub ‘Lecanora parasitica (B. de Lesd.) Zahlbr.’), but the specimen in MARRSJ is not parasitic and K-.


Chemotype subcirkinita. France: Alpes-de-Haute-Provence: Uvernet-Four, bottom of the Bachelard Gorges to the N of Uvernet-Four and the Courriers bridge, along the D902 road, 1250 m, on calcareous rock block (flysch du Pelat), shaded by Pinus sylvestris, 2010, C. Roux 26930 (MARRSJ); Thoard, near the Siron Peak, on exposed limestone outcrops, 1650 m, 1965, G. Clauzade (hb. G. Clauzade in MARRSJ). Alpes-Maritimes: Saint-Sauveur-sur-Tinée, a little to the S of the village, on the edge of the road (D2205), 483 m, on large rocks in a red pelites location, 2013, C. Roux 6337 (MARRSJ).

Additional species reported

Lobothallia controversa Cl. Roux & A. Nordin

The systematic position of this species was clarified only recently (Roux et al. 2016). It is the only known representative of Mega-
sporaceae containing terpenes. Lobothallia controversa belongs to the group of species with a thick, whitish, rimose-areolate thal-
lus. It differs from morphologically similar taxa by its apothecia which are pruinose, irregular in outline and without margins. Lobothallia controversa is known from Algeria and France (Roux et al. 2016) and has been recently collected in the Altai region. The species is reported here as new to Russia and Asia.


Discussion

Lobothallia is the third largest genus within Megasporaceae, currently comprising 18 species. It is widely distributed in arid and moun-
tainous regions of the Northern Hemisphere but the number of species reported in different parts of Eurasia varies. The highest diversity of Lobothallia (12 species) is currently known from the Altai Mountains (Sedelnikova 1990; Davydov 2014; Paukov et al. 2018) and adja-
cent territories of China (Magnusson 1940, 1944; Wei 1991; Kou et al. 2013). Six of these, viz. Lobothallia brachyloba, L. crassimargina, L. hedini, L. pruinosa, L. subdiffracta and L. zogtii, are known only in a small number of localities in this region. The Alps, together with the Mediterranean and sub-
Mediterranean regions, have 10 species of Lobothallia (Roux 2012; Roux et al. 2016; Nimis et al. 2018), while territories situated north of latitude 50°N maintain a much lower diversity of Lobothallia. Only five species are known both from Fennoscandia and the Ural Mountains, with none endemic to these regions (Paukov & Trapeznikova 2005; Paukov 2009; Nordin et al. 2011a).

The highest known diversity of Lobothallia in Eurasia occurs in areas which belong to the Mediterranean and to a lesser extent the temperate and boreal bioclimates, according to Rivas-Martínez et al. (2004). Equivalent regions which could be similarly high in diversity of this genus are south-
western Asia and arid parts of southern Asia, which lie between the Mediterranean region and Altai and belong to the same type of bioclimate. However, seven and six species are currently known from Turkey and Iran, respectively (John 1996; Seaward et al. 2008; Kinalioğlu 2010; Sohrabi et al. 2013b). This may be connected with the Cenozoic history of the continent during the Oligocene and middle Miocene epochs, when western Asia was continuously being modified by the rise and subsequent retreat of the Tethys Sea (Popov et al. 2004). These geological events, which also appear to cor-
relate with diversification times in some other lichen genera (Leavitt et al. 2012; Cornejo & Scheidegger 2018), might have played a role in the lower diversity of Lobothallia in western Asia.

Key to species of Lobothallia

The characters in the following key are based on our observations and measurements, and on additional information from Clauzade & Roux (1985), Ryan (2004) and Kou et al. (2013).

1 Marginal lobes absent or indistinct; thalli may have incised, plicate margins or tiny, infrequent and irregular lobules. In radial specimens the ‘lobes’ are formed by cracking of the peripheral zone by splits moving from the central parts of thalli

2 Marginal lobes constant and well developed. In closely adnate specimens the splits originate mostly from the outside of the thalli

10
<table>
<thead>
<tr>
<th>Step</th>
<th>Condition</th>
<th>Lichen Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>2(1)</td>
<td>On calcareous rocks. Thallus off-white, partly with yellowish or greyish tinge</td>
<td>Lobothallia chadefaudiana (Fig. 6A)</td>
</tr>
<tr>
<td>2(2)</td>
<td>On siliceous rocks. Thallus light grey, dark grey, olive grey to brownish</td>
<td>Lobothallia cernohorskyana (Fig. 6B)</td>
</tr>
<tr>
<td>3(2)</td>
<td>Thallus ±continuous with granules on the surface or consisting of areoles with multiple cracks and having granulate appearance. Norstictic acid or no lichen substances</td>
<td>Lobothallia controversa (Fig. 5C)</td>
</tr>
<tr>
<td>3(3)</td>
<td>Thallus rimose-areolate to distinctly areolate at least in the central part. Areoles not granulate, with smooth or farinose upper surface. Terpenes, norstictic, stictic acid or no lichen substances</td>
<td>Lobothallia lacteola (Fig. 5D)</td>
</tr>
<tr>
<td>4(3)</td>
<td>Lacks lichen substances, K−. Thallus thick, up to 1·5 mm, continuous to rimose, with rough yellowish granules on the surface. Apothecia immersed, separated from the thallus by thin cracks</td>
<td>Lobothallia cheresina chemotype cheresina (Fig. 6C)</td>
</tr>
<tr>
<td>5(3)</td>
<td>Thallus contains terpenes and ±norstictic or stictic acid, 1–4 mm thick. Apothecia without visible thalline margin</td>
<td>Lobothallia controversa (Fig. 5C)</td>
</tr>
<tr>
<td>6(5)</td>
<td>Thallus off-white, thick, 0·5–2·0 mm, superficial, with ±farinose, continuous or finely cracked, plicate margins, lacking long and straight radial cracks. Thalline margin finally prominent. Contains norstictic and ±connorstictic acids</td>
<td>Lobothallia lacteola (Fig. 5D)</td>
</tr>
<tr>
<td>7(6)</td>
<td>Contains no detectable secondary metabolites</td>
<td>Lobothallia cheresina chemotype cheresina (Fig. 6C)</td>
</tr>
<tr>
<td>8(7)</td>
<td>Stictic acid as a main secondary metabolite</td>
<td>Lobothallia cheresina chemotype justii (Fig. 6D)</td>
</tr>
<tr>
<td>9(2)</td>
<td>Thallus areolate, light to dark grey to brownish. Thalline margin of apothecia smooth, projecting, later receding. Disc brownish. Europe, Caucasus</td>
<td>Lobothallia recedens (Fig. 5B)</td>
</tr>
<tr>
<td>10(1)</td>
<td>Thallus with stictic acid as a main lichen substance</td>
<td>Lobothallia subdiffracta (Fig. 5A)</td>
</tr>
<tr>
<td>11(1)</td>
<td>Thallus with norstictic acid as a main lichen substance or secondary metabolites absent</td>
<td>Lobothallia subdiffracta (Fig. 5A)</td>
</tr>
</tbody>
</table>
11(10) Thallus light grey to dark or brownish grey, growing on non-calciphilous Aspicilia species, closely attached to the host or occasionally not parasitic. Apothecia immersed or slightly projecting, up to 0·6 mm, abundant and crowded in the central parts of thalli. Mediterranean region. Lobothallia radiosa chemotype parasitica (Fig. 5E) Thallus olive brownish to shades of brown, without hints of grey, free-living or parasitic in the early stages of development. Mature apothecia larger than 0·8 mm, sessile, constricted at the base, not crowded. South Urals (Russia), Kazakhstan, Xinjiang Autonomous Region of China. Lobothallia radiosa (Fig. 5E)

12(11) Young thalli parasitic on Circinaria maculata, later free-living. Lobes of non-parasitic thalli loosely attached, overlapping, smooth or with unclear cracks. Apothecia with dark brown flat discs. Thalline margin permanent, thick. Lobothallia epiadelpha (Fig. 4A–E) Thalli free-living, lobes firmly attached to the substratum, not overlapping, with definite deep cracks forming a reticulate pattern in exposed habitats. Apothecia with brownish black to jet black, finally convex discs. Thalline margin receding in mature apothecia. Lobothallia zogtii (Fig. 3C–F)

13(10) Thalli entirely or partly loosely attached to the substratum or at least outer 1–4 mm of lobes not adherent. Lobes ± overlapping. Mature apothecia sessile with constricted base. Thalli closely adnate to the substratum almost up to the margins, lobes not overlapping. Mature apothecia immersed to projecting (but check Lobothallia radiosa in couplets 19 and 21). Lobothallia alphoplaca (Fig. 6E) Thallus lacks secondary metabolites. Lobes dark grey, greenish when wet, repeatedly branching. In wet habitats. Lobothallia melanaspis (Fig. 6H) Thalli with norstictic acid. In dry habitats. Lobothallia praeradiosa (Fig. 6F)

14(13) Thallus lacks secondary metabolites. Lobes dark grey, greenish when wet, repeatedly branching. In wet habitats. Lobothallia melanaspis (Fig. 6H) Thallus with norstictic acid. In dry habitats. Lobothallia praeradiosa (Fig. 6F)

15(14) Thalli loosely attached to the substratum, separate lobes or even whole thalli can be detached almost intact (less evident in younger specimens). Lobes strongly convex to almost cylindrical, whitish grey, rarely with light shades of brown, side margins of lobes never arranged in parallel. Central ‘areoles’ bullate with strongly swollen tips and constricted bases. Lobothallia alphoplaca (Fig. 6E) Thalli normally closely adnate to the substratum with only outer 1–4 mm of lobes not adherent (but specimens overgrowing lichens/mosses or older parts of thalli may strongly resemble the previous species as these areas are easily detachable). Lobes flat to moderately convex, grey to distinctly brownish, often with side margins arranged in parallel in the closely adnate parts. Central ‘areoles’ flat to moderately convex or uneven, not bullate. Lobothallia praeradiosa (Fig. 6F)

16(13) On inundated rocks in summer-dry creeks. Thallus lead or bluish grey, without pruina. Areoles angular, apothecia dark, 1–6 on areole, 0·5–1 mm diam., immersed, immarginate or rarely with indistinct dark margins. Sardinia. Lobothallia alphoplaca (Fig. 6E) Thalli normally closely adnate to the substratum with only outer 1–4 mm of lobes not adherent (but specimens overgrowing lichens/mosses or older parts of thalli may strongly resemble the previous species as these areas are easily detachable). Lobes flat to moderately convex, grey to distinctly brownish, often with side margins arranged in parallel in the closely adnate parts. Central ‘areoles’ flat to moderately convex or uneven, not bullate. Lobothallia praeradiosa (Fig. 6F)

In dry, not inundated habitats. Thalli variously coloured, grey, whitish, brownish, often pruinose. Apothecia with margins, if immarginate, less than 0·6 mm diam. Distribution various. Lobothallia hydrocharis
17(16) Apothecia immersed to slightly projecting, normally less than 0·6 mm ........ 18
Mature apothecia projecting to sessile (if slightly projecting, then more than
0·6 mm) ................................................. 20

18(17) Thallus brown, white-pruinose. Lobes strongly convex, simple to dichotomous, with ±straight and parallel margins. Apothecia 1–2 on areole. Contains norstictic acid. China (Gansu) .................. **Lobothallia hedini** (Fig. 4G & H)
Thallus light to dark grey, whitish, rarely brownish, pruinose or not. Lobes flat, apothecia 1–7 on areole. Contains norstictic acid or no secondary metabolites ..................... 19

19(18) Thallus light grey, epruinose, contains norstictic acid. Apothecia immersed, circular, without margins, always smaller than the areole. Central areoles with ±smooth surface .............. **Lobothallia brachyloba** (Fig. 3A & B)
Thallus from chalky white to dark grey with brownish tint, pruinose when growing on limestone, without (chemotype *radiosa*) or with (chemotype *subcircinata*) norstictic acid. Apothecia immersed to slightly projecting, finally with visible margins, crowded on central areoles and angular. Central areoles with uneven surface and crossed by depressions or cracks which finally divide them into smaller units and, in turn, have single apothecia .................. **Lobothallia radiosa** (Fig. 5F–H)

20(17) Lobes strongly convex, short, 1–2 mm, dichotomous or simple, grey, nonpruinose. Apothecia with blackish discs and thick, permanent thalline margin (thickness equal to or more than the radius of the disc). Norstctic acid ..............

21(20) Lobes flat or slightly convex, whitish, greyish to brownish or brownish grey, often pruinose. Apothecia single or crowded, with narrower margins ........ 21

20(17) Lobes strongly convex, short, 1–2 mm, dichotomous or simple, grey, nonpruinose. Apothecia with blackish discs and thick, permanent thalline margin (thickness equal to or more than the radius of the disc). Norstctic acid ..............

21(20) Lobes flat, grey to brownish, short, 1–2 mm long, 0·7–1·2 mm wide. Pruina on the margins of areoles or covering whole surface and discs of apothecia. Apothecia solitary, slightly projecting, discs 0·7–1·2 mm. Norstctic acid. China .............. **Lobothallia crassimarginata**
Lobes flat to moderately convex, chalky white to brownish grey, 3–5 mm long, 0·5–1·5 mm wide, with or without pruina. Apothecia initially crowded and angular, extended period immersed, later projecting to broadly sessile 0·5–1·5 mm. No lichen substances or norstctic acid. Widespread ................... **Lobothallia radiosa**, see also couplet 19 (Fig. 5F–H)

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