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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 bogdoënsis* 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. lacteola* (Oxner) Şenkardeşler, 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 epihymenium lacking, or with small amounts, of Caesiocinerea-green (Meyer & Printzen 2000) and consequently a reaction with N that is negative to slightly greenish (vs. strong

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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-Larss. & 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).

The genus currently comprises 13 accepted species: *Lobothallia alphoplaca* (Wahlenb.) Hafellner, *L. cernohorskyana* (Clauzade & Vězda) A. Nordin *et al.*, *L. chadefaudiana* (Cl. Roux) A. Nordin *et al.*, *L. cheresina* (Müll. Arg.) A. Nordin *et al.*, *L. controversa* Cl. Roux & A. Nordin, *L. crassimarginata* X. R. Kou & Q. Ren, *L. helanensis* X. R. Kou & Q. Ren, *L. hydrocharis* (Poelt & Nimis) Sohrabi & Nimis, *L. melanaspis* (Ach.) Hafellner, *L. praeradiosa* (Nyl.) Hafellner, *L. pruinosa* X. R. Kou & Q. Ren, *L. radiosa* (Hoffm.) Hafellner and *L. recedens* (Taylor) A. Nordin *et al.* (Nordin *et al.* 2010; Roux 2012; Kou *et al.* 2013; Nimis 2016; Roux *et al.* 2016). Some taxa (viz. *Lobothallia cheresina* (Müll. Arg.) A. Nordin *et al.* chemotype *justii*, *L. cheresina* (Müll. Arg.) A. Nordin *et al.* chemotype *microspora*, *Lobothallia parasitica* (B. de Lesd.) ined., and *Lobothallia radiosa* (Hoffm.) Hafellner chemotype *subcircinata*) are regarded as only chemotypes (Roux 2012; Roux et al. 2017). Further species, which probably belong in *Lobothallia* from western North America, along with their validly published combinations, are likely to be forthcoming (Wheeler 2017).

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 HNO_3 (N), calcium hypochlorite (C) and iodine solutions (I). Measurements of spores and conidia are presented as follows: (smallest value recorded) ($\bar{x}$ – SE) – $\bar{x}$ – ($\bar{x}$ + SE) (largest value recorded), where $\bar{x}$ 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.*

Species	Origin	Collection number or reference	GenBank Accession number		Reference
			ITS	mtSSU	
Aspicilia cinerea	Sweden, Dalarna	*Hermansson* 13275 (UPS)	EU057899	HM060695	Nordin *et al.* 2007, 2010
Circinaria calcarea	Sweden	*Wedin* 6500 (UPS)	-	AY853310	Wedin *et al.* 2005
C. esculenta	**Kazakhstan, Kyzylorda Region**	***Ivanov* s. n. (UFU L-1743)**	**MK347507**	**MK348226**	**This paper**
C. fruticulosa	**Russia, Chelyabinsk Oblast**	***Paukov* 3074 (UFU L-3256)**	**MK347508**	**MK348227**	**This paper**
'Lecanora' bogdoënsis	**Russia, Astrakhan Oblast**	***Paukov* 3026 (UFU)**	**MK347502**	-	**This paper**
Lobothallia alphoplaca	USA, California	*Knudsen* 826 (H)	-	KJ766429	Miadlikowska *et al.* 2014
L. alphoplaca	China, Inner Mongolia	*Wang* 20117646 (SDNU)	JX476025	-	Kou *et al.* 2013
L. alphoplaca	China, Inner Mongolia	*Tong* 20117616 (SDNU)	JX499233	-	Kou *et al.* 2013
L. alphoplaca	Ukraine, Donetsk Oblast	*Nadeina* et al. (KW)	KT456207	-	Kondratyuk *et al.* 2015
L. brachyloba	**Russia, Republic of Altai**	***Frolov* 357 (UFU) holotype**	**MK347506**	**MK348228**	**This paper**
L. cernohorskyana	Iran, South Khorasan	*Tari* 2311 (B)	-	JQ797481	Sohrabi *et al.* 2013*b*
L. controversa	France, Rhône-Alpes	*Roux* 25286 (UPS)	-	HM060723	Nordin *et al.* 2010
L. crassimarginata	China, Inner Mongolia	*Wang* 20122565 (SDNU)	JX476026	-	Kou *et al.* 2013
L. crassimarginata	China, Inner Mongolia	*Tong* 20122583 (SDNU)	KC007439	-	Kou *et al.* 2013
L. epiadelpha	**Russia, Orenburg Oblast**	***Paukov* AGP20130528-06 (UFU L-1705)**	-	**MK348230**	**This paper**
L. epiadelpha	**Russia, Orenburg Oblast**	***Paukov* AGP20130529-21 (UFU L-1882)**	-	**MK348231**	**This paper**
L. epiadelpha	**Russia, Orenburg Oblast**	***Paukov* 1881 (UFU L-3189) holotype**	**MK347505**	**MK348232**	**This paper**
L. helanensis	China, Inner Mongolia	*Tong* 20122517 (SDNU)	JX476030	-	Kou *et al.* 2013
L. helanensis	China, Inner Mongolia	*Tong* 20122791 (SDNU)	JX476031	-	Kou *et al.* 2013
L. melanaspis	Sweden, Jämtland	*Nordin* 6622 (UPS)	HQ259272	-	Nordin *et al.* 2011*b*
L. melanaspis	Sweden, Jämtland	*Nordin* 6622 (UPS)	-	HM060688	Sohrabi *et al.* 2013*b*
L. melanaspis	Norway	*Owe-Larsson* 8943a (UPS)	JF825524	-	Valadbeigi *et al.* 2011
L. praeradiosa	**Russia, Orenburg oblast**	***Paukov* AGP20120606-12 (UFU L-1264)**	**MK347501**	**MK348229**	**This paper**
L. praeradiosa	China, Xinjiang	*Huang* 20126355 (SDNU)	JX499230	-	Kou *et al.* 2013
L. praeradiosa	China, Xinjiang	*Li* 20126314 (SDNU)	JX499232	-	Kou *et al.* 2013

(*Continued*)

TABLE 1 (*continued*).

Species	Origin	Collection number or reference	GenBank Accession number		Reference
			ITS	mtSSU	
L. praeradiosa	China, Xinjiang	*Mamut* s. n. (XJU)	KT180160	-	Ismayil, Abbas not published
L. praeradiosa	China, Xinjiang	*Mamut* s. n. (XJU)	KT180162	-	Ismayil, Abbas not published
L. pruinosa	China, Inner Mongolia	*Wang* 20123630 (SDNU)	JX476027	-	Kou *et al.* 2013
L. pruinosa	China, Inner Mongolia	*Wang* 20123909 (SDNU)	JX499231	-	Kou *et al.* 2013
L. radiosa	**Russia, Orenburg Oblast**	***Paukov* AGP20120605-04 (UFU L-1428)**	-	**MK348225**	**This paper**
L. radiosa	Switzerland	*Lumbsch*, 9 Aug.2004 (F)	-	DQ780274	Schmitt *et al.* 2006
L. radiosa	Hungary	*Molnar* U0504/CG (DUKE)	-	KJ766430	Miadlikowska *et al.* 2014
L. radiosa	Sweden	*Nordin* 5889 (UPS)	JF703124	-	Roux *et al.* 2011
L. recedens	Sweden, Dalarna	*Nordin* 6582 (UPS)	-	HM060724	Nordin *et al.* 2010
L. recedens	Sweden, Dalarna	*Nordin* 6582a (UPS)	HQ406807	-	Owe-Larsson *et al.* 2011
L. subdiffracta	**Russia, Republic of Altai**	***Frolov* 105 (UFU)**	-	**MK348234**	**This paper**
L. subdiffracta	**Russia, Republic of Altai**	***Frolov* 178-1 (UFU)**	**MK347503**	**MK348233**	**This paper**
Megaspora verrucosa	Sweden, Jämtland	*Nordin* 6495 (UPS)	-	HM060687	Nordin *et al.* 2010
M. verrucosa	USA, Colorado	*St. Clair* C54042 (BRY)	KC667053	-	Sohrabi *et al.* 2013*a*

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 & Shimon 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 bogdoënsis* gave ITS sequences only. The Bayesian 50% majority-rule consensus tree had the same topology as the maximum likelihood tree generated by RAxML for

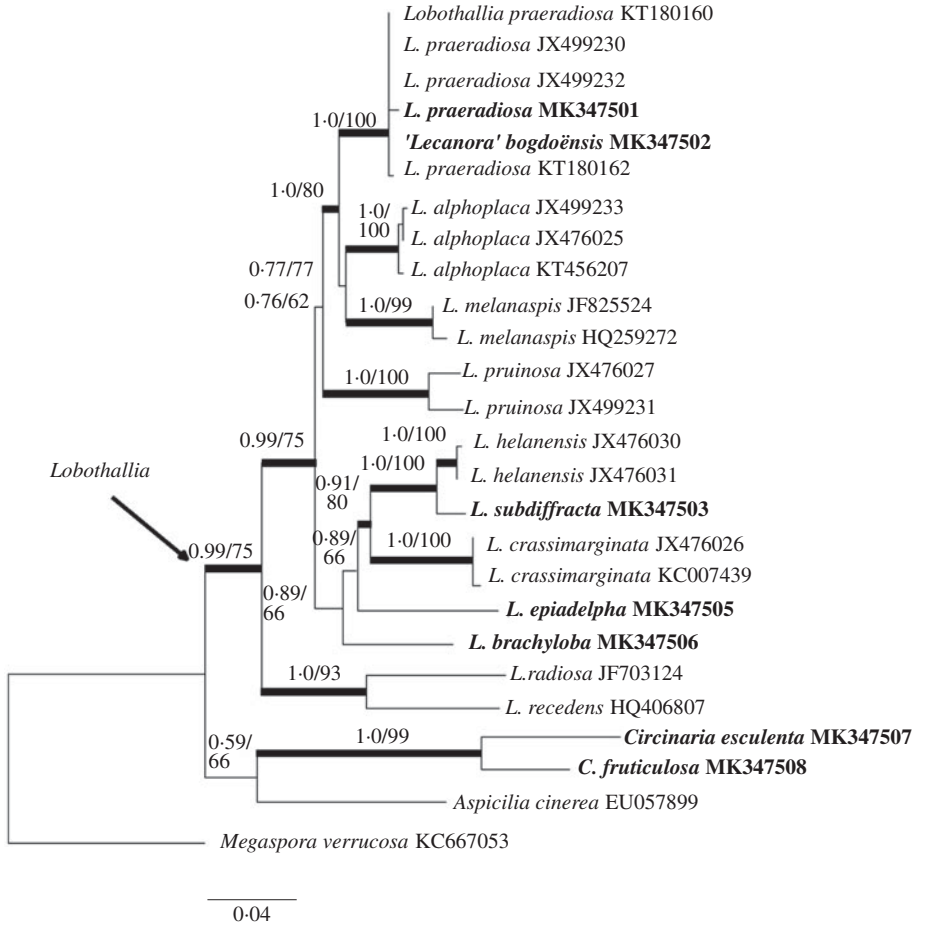

FIG. 1. Maximum likelihood (ML) phylogeny of selected *Lobothallia* ITS sequences. The reliability of each branch was tested by ML and Bayesian methods. Numbers at tree nodes indicate Bayesian inference with the Markov chain Monte Carlo (BMCMC) posterior probabilities (left) and ML bootstrap percentages (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.

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 radiosa* 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*

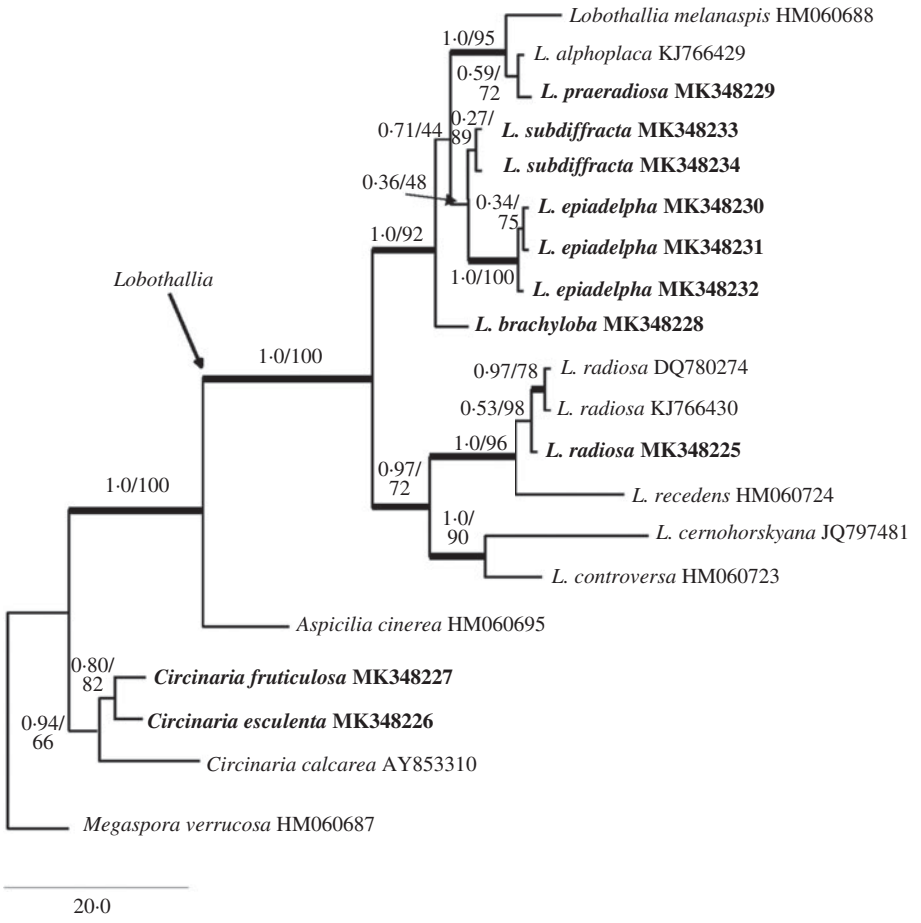

FIG. 2. Maximum likelihood (ML) phylogeny of selected *Lobothallia* mtSSU sequences. The reliability of each branch was tested by ML and Bayesian methods. Numbers at tree nodes indicate Bayesian inference with the Markov chain Monte Carlo (BMCMC) posterior probabilities (left) and ML bootstrap percentages (right). Thicker branches indicate when the bootstrap value of ML is ≥70% or the BMCMC posterior probability is ≥0·95. *Lobothallia* clade is arrowed. GenBank Accession numbers are given to serve as operational taxonomic unit (OTU) names (see Table 1). 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

Lobothallia with a thin, lobate, grey thallus, containing norstictic acid. Lobes flat, firmly attached to the

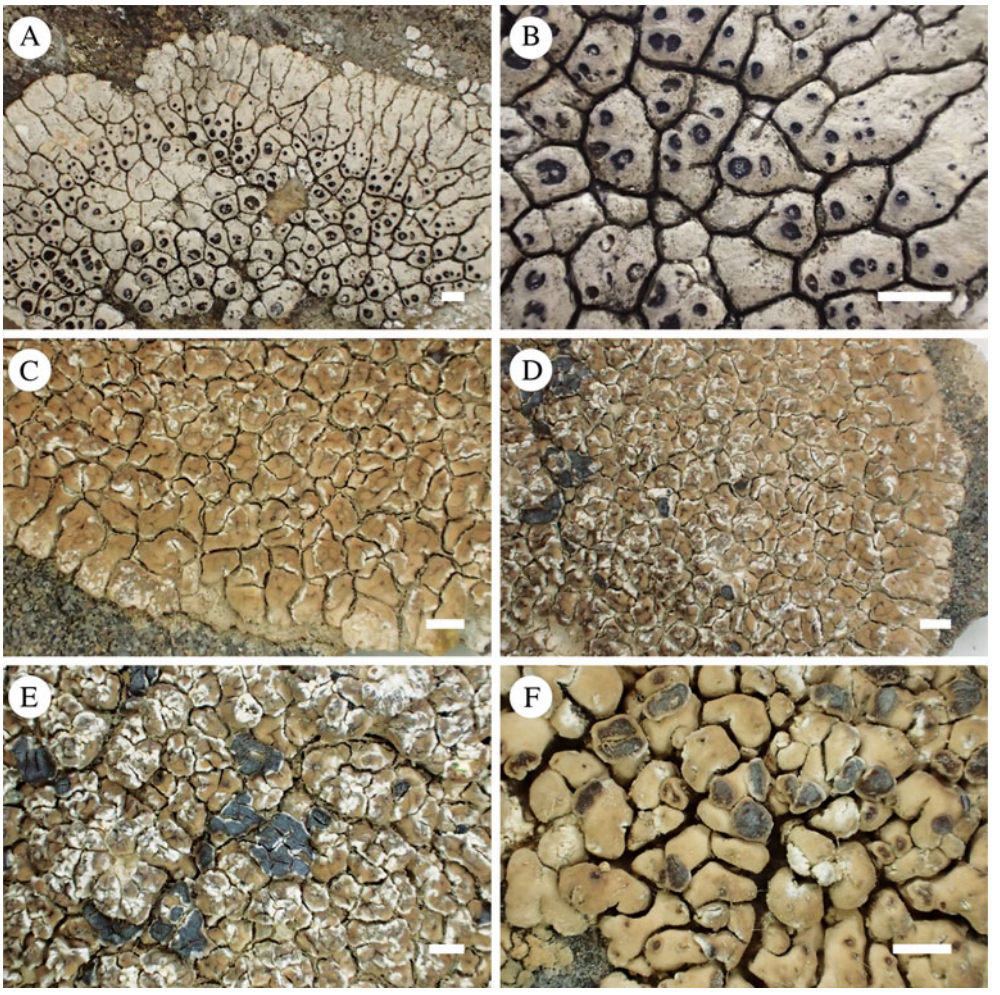

FIG. 3. A & B, *Lobothallia brachyloba*, holotype: A, part of a thallus; B, central part of the thallus showing apothecia. C–F, *Lobothallia zogtii*, holotype: C & D, part of a thallus; E, central part of a thallus with apothecia; F, part of a thallus from a shady habitat. Scales = 1 mm. In colour online.

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–L3254—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(–

105·0) 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 cryptolecanorine, 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 cupreoatra* (Nyl.) Clauzade & Cl. Roux, *Lecanora cenisia* Ach. and *Protoparmeliopsis muralis* (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 placodioid, 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. alphoplaca*. *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.) Coppins) 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 Novotroitsk Town (via Akkermanovka), hills around 'The King's Spring', 51°08′56·1″N, 58°02′32·0″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.

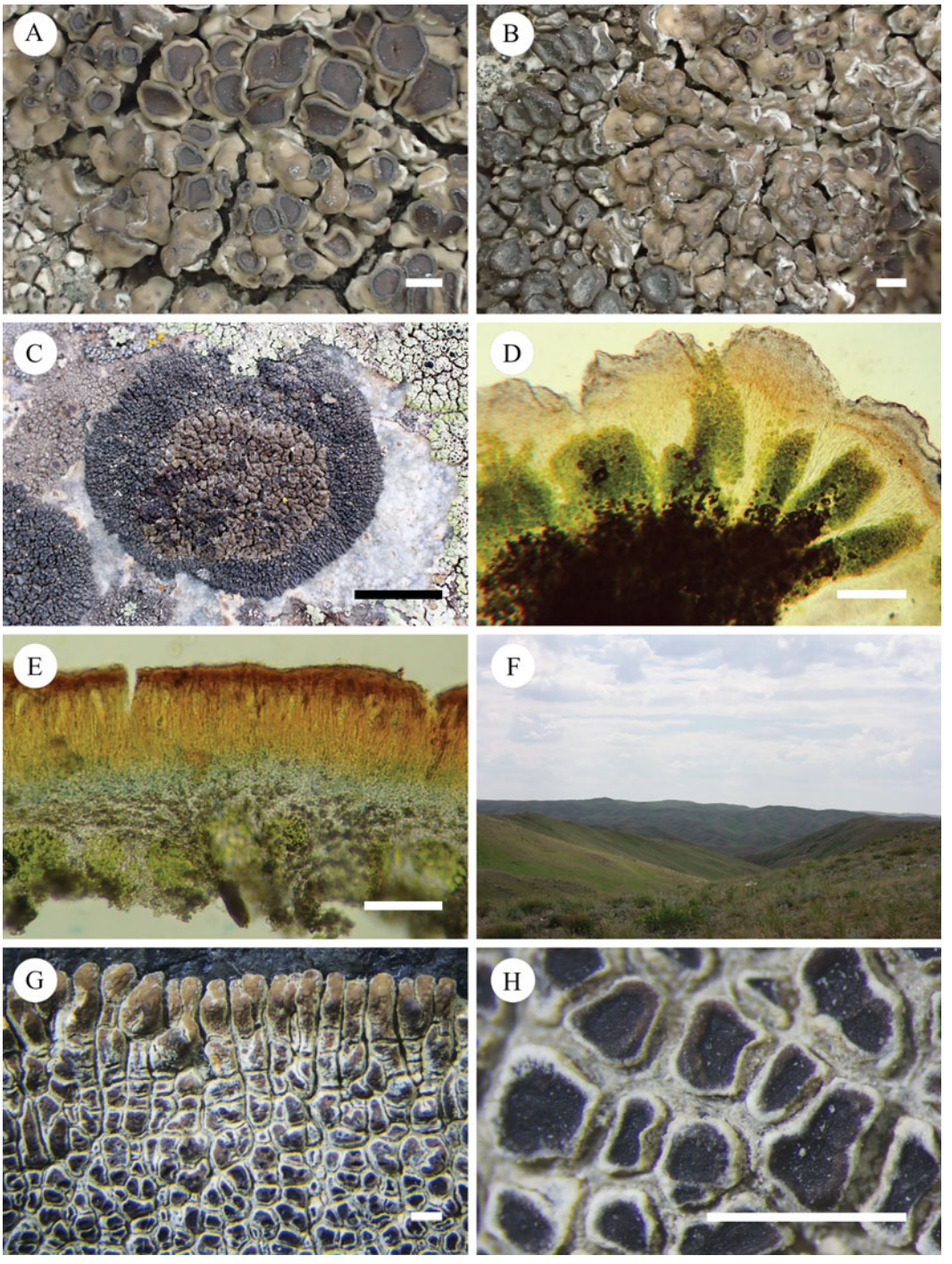

Fig. 4. A–F, *Lobothallia epiadelpha*: A, part of a thallus with wide lobes, holotype; B, young specimen overgrowing *Circinaria maculata*, isotype; C, *Lobothallia epiadelpha* on *C. maculata*, isotype; D, section of thallus, holotype; E, section of apothecium coloured by iodine solution, holotype; 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* paraplectenchymatous, (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. *Exciple* 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 paraplectenchymatous 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, norstictic 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 cupreoatra*, *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 radiosa* 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).

Additional material examined. **Russia:** *Orenburgskaya Oblast'*: Gaiskiy 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′N, 85°52′E, 1200 m, on schistose rocks, 1993, *R. Moberg & A. Nordin* K22:19 (UPS–L078045); along the road S of Ajaguz, 48°35′N, 80° 39′E, 850 m, on open rocks, 1993, *R. Moberg & A. Nordin* K28:07 (UPS–L078051). *Karagandinskaya Oblast'*: Shetskiy District, rocky outcrops in steppe along the road Zharyk-Unrek, 48°51′N, 72°55′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, convex, surrounded by a receding thalline margin.

Type: China, Dzhungarian Gobi, Baitag-Bogd-Ula, elev. 1800 m a.s.l., on rocks, 19 July 1981, *U. Zogt* 5259 (LE—holotype, isotype). Determined as *Aspicilia melanaspis* (Ach.) Poelt & Leuckert.

(Fig. 3C–F)

Life habit lichenized, not lichenicolous.

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, epinecral 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.

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; *epihymenium* brownish, unchanged in N, (12·5–)16·6–*17·3*–18·1(–22·5) µm high ($n = 20$). *Hypothecium* hyaline, I+ weakly bluish, (25·0–)34·2–*35·3*–36·5(–45·0) µm high ($n = 20$). *Asci* clavate, *Aspicilia*-type; *ascospores* broadly ellipsoid, 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.) Zahlbr., *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-Altai road (30 km SW of Qinghe), desert steppe slopes, on rocks, *Achnatherum splendens* community in meso-depressions, 46°30′46·5″N, 90°03′31·5″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 hedinii* 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). Cretzoiu (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 hedinii (H. Magn.) Paukov, A. Nordin & Sohrabi comb. nov.

MycoBank No.: MB 827675

Lecanora hedinii H. Magn. *Lichens from Central Asia* **1:** 98 (1940).—*Aspicilia hedinii* (H. Magn.) Oxner, *Nov. Sist. Nizsh. Rast.* **9:** 288 (1972); type: China, Kansu Prov., Eh-ma-ta-ch'üan, 1931, *Bohlin* 55a (S—holotype!).

Lecanora hedinii f. *pruinosa* H. Magn., *Lichens from Central Asia* **1:** 100 (1940).—*Aspicilia hedinii* f. *pruinosa* (H. Magn.) J. C. Wei, *Enumeration of Lichens in China (Beijing)* **1991:** 32 (1991); type: China, Kansu Prov., Eh-ma-ta-ch'üan, 1931, *Bohlin* 55b (S—holotype!), syn. nov.

(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 hedinii* in their appressed apothecia.

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

MycoBank No.: MB 827678

Aspicilia lacteola Oxner, *Zhurnal Institutu Botaniki AN URSR* **20**(28)**:** 118 (1939); type: Kyrgyzstan (Kirgizskaya SSR), Dzhelalabadskiy kanton, spurs of Fergana ridge, vicinity of Arslan-Boba, 1928, *Lazarenko* (KW 23609!—lectotype, designated here, MycoBank typification MBT 386683). HPTLC: norstictic acid. (Other syntype traced: Kyrgyzstan (Kirgizskaia SSR), Dzhelalabadskyi kanton, spurs of Fergana ridge, limestones in the vicinity of Gava Village, 1928, *Lazarenko* (KW 23608!). HPTLC: norstictic and connorstictic acids).

Lecanora oxneri Cretz., *Bull. Grăd. Bot. Univ. Cluj* **21:** 139 (1941), syn. nov. (KW 23609!—type).

(Fig. 5D)

Lobothallia lacteola differs from other species of the genus by the following set of

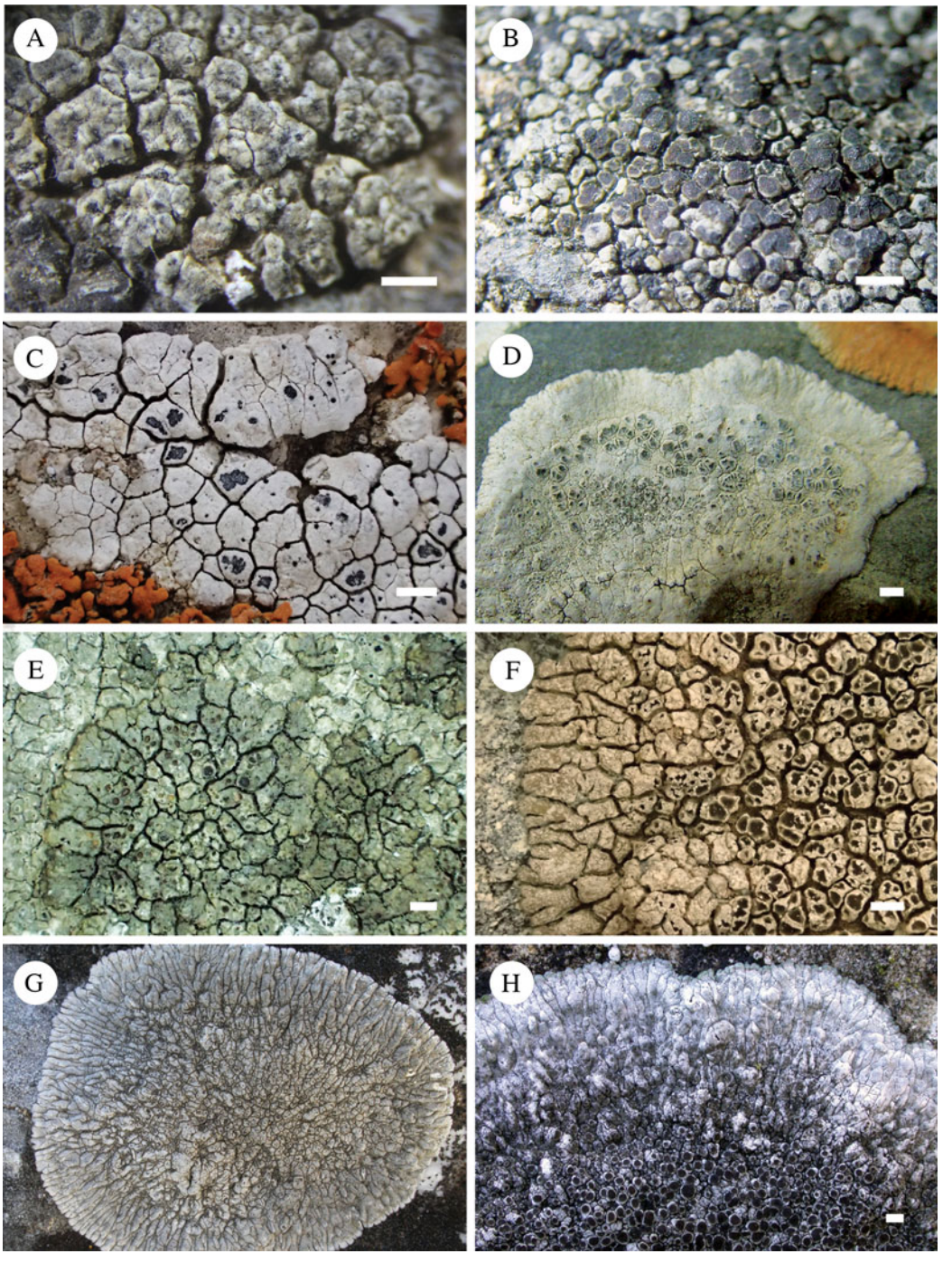

FIG. 5. A, holotype of *Lobothallia subdiffracta*, part of a thallus (S); B, *L. recedens*, Sweden, Dalarna, *A. Nordin* 6587 (UPS); C, *L. controversa*, Russia, Altaiskiy Krai, *E. A. Davydov* 17606 & *L. S. Yakovchenko* (ALTB); D, lectotype of *L. lacteola* (KW); E, *L. radiosa* chemotype *parasitica*, 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, farinose, distinctly rimose-areolate thallus with indefinitely radially cracked or plicate margins; 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 characters are simple and non-moniliform paraphyses 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 (Altaiskiy Krai), where it inhabits exposed limestone rocks. The species is regarded here as new to Russia.

Additional material examined. **Russia:** *Altaiskiy Krai*: Tigirekskiy 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. Davydov* 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 similarity 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 *subdiffracta* 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 Tydtuyaryk 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:** *Dschungarian Gobi*: Argalant mountains, near Ubchu-Bulak, 1700 m, on rocks, 1973, *N. S. Golubkova & U. Zogt* (LE–L406). *Gobi-Altai Aimak*: Gobi-Alyk-Nuur steppe, Adgi-Bogdo ridge, 1500 m, on granite, 1973, *N. S. Golubkova & U. Zogt* (LE–L432); Ih-Bogdo-Ula ridge, Dzhargatantyn-Ama canyon, 2600 m, on rocks, 1973, *N. S. Golubkova & U. Zogt* (LE–L555). *South-Gobi Aimak*: Servey ridge, on rocks, 1973, *N. S. Golubkova & U. Zogt* (LE–L763).

New synonym

Lobothallia praeradiosa (Nyl.) Hafellner

MycoBank No.: MB 354542

Acta Bot. Malacit. **16:** 138 (1991).—*Lecanora praeradiosa* Nyl., *Flora (Regensburg)* **67:** 389 (1884); type: Hungary, prope Budapest, 1882, *Lojka* (G—isotype!).

Lecanora bogdoënsis Tomin, *Pririoda i sel'skoye khozyaystvo zasushlivykh oblastey SSSR* **1–2:** 48[4] (1927), syn. nov.—*Placolecanora bogdoënsis* (Tomin) Kopach., *Nov. Sist. Nizsh. Rast.* **9:** 295 (1972), syn. nov.—*Protoparmeliopsis bogdoënsis* (Tomin) S. Y. Kondr., *Ukr. Bot. Ž.* **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 *Placolecanora* (Kopaczevskaja 1972) and *Protoparmeliopsis* (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

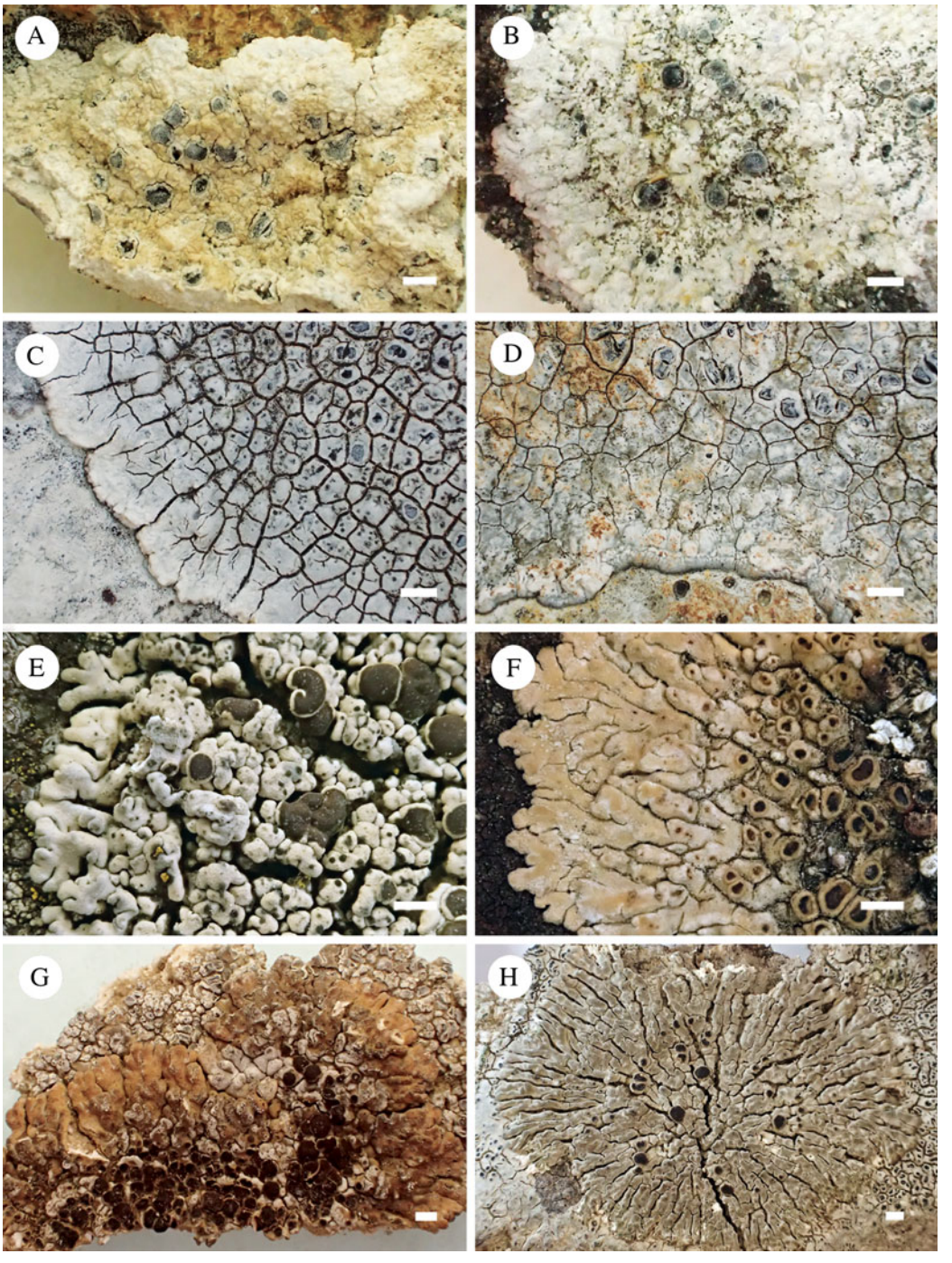

FIG. 6. A, *Lobothallia chadefaudiana*, Vězda, *Lich. Sel. Exs*. 1638 (W); B, *L. cernohorskyana*, Vězda, *Lich. Sel. Exs*. 895 (W); C, *L. cheresina* chemotype *cheresina*, Greece, Rhodos, *I. Pišút* s. n. (SAV); D. *L. cheresina* chemotype *justii*, type of *Lecanora justii* (W); E, *L. alphoplaca*, 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.

Bull. Soc. Bot. France **78:** 728 (1931); type: Italia, Genova, val Bisagno, Bosco del Serina, sur roche siliceuse, 1930, *Sbarbaro* (LE—isotype!).

(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 *subcircinata* with norstictic acid (Fig. 5G & H); chemotype *parasitica*, including isotype material, which parasitizes *Aspicilia proluta*, collected by Sbarbaro) 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 (MARSSJ); 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. Roux* 25614 (MARSSJ).—**Italy:** *Liguria Occidentale*: Spotorne (Savona), in regione 'Castelo', ad rupes schistosas, 1962, *C. Sbarbaro* (Vězda, *Lichenes Selecti Exsiccati* no 167; sub '*Lecanora parasitica* (B. de Lesd.) Zahlbr.'), but the specimen in MARSSJ is not parasitic and K–.

Chemotype *parasitica* (parasitic). **France:** *Alpes-Maritimes*: Saorge, bottom of the Mérim Valley, 930 m, on a steeply sloping slab of non-calcareous Permian red sandstone, on *Aspicilia viridescens* (A. Massal.) Hue, 2011, *C. Roux* 26926 (MARSSJ).—**Italy:** *Liguria occidentale*: Val Bisagno, S. Eusebio sub castaneis, on *Aspicilia proluta*, *C. Sbarbaro* (hb. Bouly de Lesdain in MARSSJ, topotypus or isotypus).

Chemotype *parasitica* (not parasitic). **France:** *Pyrénées-Orientales*: Jujols, beginning of the Garrigue trail, 1025 m, on inclined or subvertical surfaces (10–80°), non-calcareous schist, 2007, *C. Roux* 25154 (MARSSJ).

Chemotype *subcircinata*. **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 (MARSSJ); Thoard, near the Siron Peak, on exposed limestone outcrops, 1650 m, 1965, *G. Clauzade* (hb. G. Clauzade in MARSSJ). *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 (MARSSJ).

Additional species reported

Lobothallia controversa Cl. Roux & A. Nordin

Herzogia **29**: 588 (2016); type: France, Bas-Vivarais, Ardèche, Rochecolombe, 2008, *Bricaud, Bauvet & Roux* (UPS-L205562—holotype).

(Fig. 5C)

The systematic position of this species was clarified only recently (Roux *et al.* 2016). It is the only known representative of *Megasporaceae* containing terpenes. *Lobothallia controversa* belongs to the group of species with a thick, whitish, rimose-areolate thallus. 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.

Material examined. **Russia:** *Altaiskiy Krai*: Krasnoshchëkovskiy District, Tigirekskiy Range, Tigirekskiy Nature Reserve, Khankharinskiy cluster, left bank of the 'Dragunskiy klyuch' stream, 5·8 km NW of the community of Tigirek, 51°11′09″N, 82°58′30″E, 870 m, 2014, *E. A. Davydov* 17606 & *L. S. Yakovchenko* (ALTB).

Discussion

Lobothallia is the third largest genus within *Megasporaceae*, currently comprising 18 species. It is widely distributed in arid and mountainous 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 adjacent territories of China (Magnusson 1940, 1944; Wei 1991; Kou *et al.* 2013). Six of these, viz. *Lobothallia brachyloba*, *L. crassimarginata*, *L. hedinii*, *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.* 2011*a*).

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.* 2013*b*). 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 correlate 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

2(1) On calcareous rocks. Thallus off-white, partly with yellowish or greyish tinge . . . 3
On siliceous rocks. Thallus light grey, dark grey, olive grey to brownish 9

3(2) Thallus ±continuous with granules on the surface or consisting of areoles with multiple cracks and having granulate appearance. Norstictic acid or no lichen substances 4
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 5

4(3) 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 . . . . . **Lobothallia chadefaudiana** (Fig. 6A)
Contains norstictic acid, K+ red. Thallus up to 0·5 mm thick, rimose to areolate; areoles have granulate appearance. Apothecia appressed, becoming constricted at the bases with time . . . . . **Lobothallia cernohorskyana** (Fig. 6B)

5(3) Thallus contains terpenes and ±norstictic or stictic acid, 1–4 mm thick. Apothecia without visible thalline margin . . . . . **Lobothallia controversa** (Fig. 5C)
Thallus contains no terpenes 6

6(5) 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 . . . . . **Lobothallia lacteola** (Fig. 5D)
Thallus whitish, commonly with grey tinge, thin to thick, sometimes semi-immersed, not farinose, with definite cracks up to the margins. Orbicular specimens usually with long, straight, open, radially arranged cracks. Lacking prominent thalline margin. Secondary metabolites absent or thallus contains stictic/norstictic acids 7

7(6) Contains no detectable secondary metabolites . . . . . .**Lobothallia cheresina** chemotype **cheresina** (Fig. 6C)
Norstictic or stictic acid present 8

8(7) Stictic acid as a main secondary metabolite . . . . . **Lobothallia cheresina** chemotype **justii** (Fig. 6D)
Norstictic acid as a main secondary metabolite . . . . . .**Lobothallia cheresina** chemotype **microspora**

9(2) Thallus areolate, light to dark grey to brownish. Thalline margin of apothecia smooth, projecting, later receding. Disc brownish. Europe, Caucasus . . . . . .**Lobothallia recedens** (Fig. 5B)
Thallus squamulose, light to dark grey to olive grey, pruinose. Squamules with deep cracks, outer squamules usually slightly enlarged. Thalline margin incised. Disc blackish. China (Gansu, Inner Mongolia); Russia (Altai), Mongolia . . . . . **Lobothallia subdiffracta** (Fig. 5A)

10(1) Thallus with stictic acid as a main lichen substance 11
Thallus with norstictic acid as a main lichen substance or secondary metabolites absent 13

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 12

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 14

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) 16

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 15

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 hydrocharis**

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 17

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 hedinii** (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). Norstictic acid . . . . . **Lobothallia crassimarginata**
Lobes flat or slightly convex, whitish, greyish to brownish or brownish grey, often pruinose. Apothecia single or crowded, with narrower margins 21

21(20) Lobes flat, grey to brownish, short, 1–2 mm long, 0·7–1 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. Norstictic acid. China . . . . . **Lobothallia pruinosa**
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 norstictic acid. Widespread . . . . . **Lobothallia radiosa**, see also couplet 19 (Fig. 5F–H)

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