The Lichenologist (2025), **57**, 13–24
doi:10.1017/S0024282924000446

Standard Paper

Micarea svetlanae, a new species of the *M. prasina* group from the Russian Far East

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Abstract

A species new to science, *Micarea svetlanae*, is described from the southern part of the Russian Far East based on morphological, chemical and molecular data. This species is closely related to *M. isidioprasina*, which also has the micareic acid, the granular-isidiate thallus with Sedifolia-grey pigment, and crystalline granules in the hymenium and thallus, but differs in the cushion-shaped thallus, the presence of Sedifolia-grey pigment in the hymenium, numerous crystalline granules in the hymenium and hypothecium and 0–2(3)-septate ascospores. The results of the phylogenetic reconstruction place *M. svetlanae* in the *M. prasina* group. Morphological features and data on ecology, distribution and secondary metabolites are presented in detail in the paper. This new lichen species is named in honour of the Russian lichenologist Dr Svetlana Tchabanenko, who devoted her life to the study of lichens of the Russian Far East.

Keywords: Asia; isidiate thallus; lichens; micareic acid; new taxon; *Pilocarpaceae*; taxonomy

(Accepted 29 August 2024)

Introduction

The genus *Micarea* Fr. is a cosmopolitan group of crustose lichens, which has recently attracted increased interest among researchers around the world. According to various sources (Kirk *et al*. 2008; Lücking *et al*. 2017; Wijayawardene *et al*. 2022), the diversity of the *Micarea* is estimated at *c*. 100 species. Obviously, this number is an underestimate, since 69 *Micarea* species have been described in the last 10 years alone (Aptroot & Cáceres 2014, 2024; Brand *et al*. 2014; Córdova-Chávez *et al*. 2014; van den Boom & Ertz 2014; Brackel 2016; Guzow-Krzemińska *et al*. 2016, 2019; McCarthy & Elix 2016*a*, *b*, 2020*a*, *b*; Etayo 2017; van den Boom *et al*. 2017*a*, *b*, 2020, 2023; Elix & McCarthy 2018; Kantvilas 2018; Hyde *et al*. 2019; Kantvilas & Coppins 2019; Launis *et al*. 2019*a*, *b*; Launis & Myllys 2019; Coppins *et al*. 2021; Kantelinen *et al*. 2021, 2024; van den Boom 2021; Vondrák *et al*. 2022; Schumm & Aptroot 2024). According to our estimation, the genus *Micarea* has more than 160 species.

Today the *Micarea prasina* group is one of the most studied in the genus. Based on molecular data, it includes 32 species, of which 26 have been described over the past 10 years (Guzow-Krzemińska *et al*. 2016, 2019; van den Boom *et al*. 2017*a*, 2020; Launis *et al*. 2019*a*, *b*; Launis & Myllys 2019; Kantelinen *et al*. 2021). *Micarea corallothallina* Cáceres *et al*., *M. hyalinoxanthonica* Brand *et al*., *M. kartana* Kantvilas & Coppins and *M. melanoprasina* Brand *et al*. (Cáceres *et al*. 2013; Brand *et al*. 2014; Kantvilas 2018) probably belong to the *M. prasina* group as well, but due to the lack of molecular data their phylogenetic relationships are unclear.

The *Micarea prasina* group is characterized by effuse thalli composed of goniocysts and a 'micareoid' photobiont (a coccoid green alga with cells 4–7.5 µm diam.). Another important characteristic is the presence of the Sedifolia-grey pigment often produced in the epihymenium, pycnidial walls and dark-coloured parts of the thallus. The species of the *M. prasina* group are also characterized by immarginate apothecia of various colours, a hyaline hypothecium, branched paraphyses, and *Micarea*-type asci, with a K/I+ blue amyloid tholus and a more lightly staining axial body often with a darkly stained lining (Coppins 1983; Hafellner 1984; Czarnota 2007; Ekman *et al*. 2008; Czarnota & Guzow-Krzemińska 2010; Guzow-Krzemińska *et al*. 2016, 2019; Launis *et al*. 2019*a*, *b*). According to molecular studies (e.g. Guzow-Krzemińska *et al*. 2016, 2019; Launis *et al*. 2019*a*, *b*; Kantelinen *et al*. 2021), the *M. prasina* group is monophyletic and divided into two main lineages, namely the *M. micrococca* clade and the *M. prasina* clade, with *M. tomentosa* Czarnota & Coppins and *M. pusilla* Launis *et al*. basal to these two clades. Launis *et al*. (2019*b*) introduced a new character for species separation, the presence (Pol+) or absence (Pol−) of crystalline granules visible in polarized light in thallus and apothecia sections in the *M. prasina* group. This, combined with morphological and chemical characteristics, made possible a reliable separation of species in this group (Guzow-Krzemińska *et al*. 2019; Launis *et al*. 2019*a*, *b*; Kantelinen *et al*. 2021). For other taxa of the genus *Micarea*, the significance of this character remains poorly studied (Konoreva *et al*. 2019, 2021*a*, *b*).

In Russia, until recently most of the species with a goniocystose thallus and pale apothecia were referred to *Micarea prasina*

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Cite this article: Konoreva LA, Chesnokov SV and Frolov IV (2025) *Micarea svetlanae*, a new species of the *M. prasina* group from the Russian Far East. *Lichenologist* **57**, 13–24. https://doi.org/10.1017/S0024282924000446

Fr. s. lat. and required revision. Currently, 16 species of the *M. prasina* group are reliably known in Russia (Stepanchikova *et al.* 2017, 2020, 2022; Urbanavichene & Urbanavichus 2017, 2021; Urbanavichus & Urbanavichene 2017; Konoreva *et al.* 2019, 2020, 2021*b*; Launis *et al.* 2019*a*; Tarasova *et al.* 2020; Urbanavichus *et al.* 2020; Davydov *et al.* 2021). To study the diversity of the genus *Micarea* in southern parts of the Russian Far East, extensive material was collected that was morphologically similar to *M. isidioprasina* van den Boom *et al.* Further study of the morphology, anatomy, secondary metabolites and molecular data led to the conclusion that the specimens belong to a new species, described here as *M. svetlanae* Konoreva & Chesnokov.

Materials and Methods

Field and herbarium studies

This study is based on the fieldwork of Liudmila Konoreva and Sergey Chesnokov in the Russian Far East in 2017–2020. The specimens collected and presented in this paper are deposited in the herbaria of the Komarov Botanical Institute of the Russian Academy of Sciences (LE), the Botanical Garden-Institute of the Far Eastern Branch of the Russian Academy of Sciences (VBGI), the Polar-Alpine Botanical Garden-Institute (separate department of the Kola Science Centre of the Russian Academy of Sciences) (KPABG) and the V. F. Kuprevich Institute of Experimental Botany of the National Academy of Science (MSK). A total of 74 specimens were studied, 18 of which were sterile. More detailed information about the locations of the samples studied is presented in the Supplementary Material (available online). The material was examined using standard microscopic techniques and spot tests with 10% potassium hydroxide (K), calcium hypochlorite (C) and paraphenylenediamine (PD) (Smith *et al.* 2009). Crystalline granules were investigated using a Zeiss Axio Scope.A1 compound microscope with polarizing filters. High performance thin-layer chromatography (HPTLC) was performed at the Laboratory of Lichenology and Bryology of the Komarov Botanical Institute, according to standard procedures using solvent systems A and C (Orange *et al.* 2001). The names of the pigments observed in *Micarea* species follow Meyer & Printzen (2000). Photographs of the species were taken with a Motic SMZ-171-LED stereoscopic microscope with an attached MotiCam S6 camera and an Axio Scope.A1 with Axiocam 506 colour camera. The distribution maps were prepared using the GIS Axioma 5.1 program.

Nomenclature of vascular plants corresponds to the book '*Flora of the Kuril Islands*' (Barkalov 2009).

DNA extraction, amplification and sequencing

DNA was extracted directly from pieces of thalli or apothecia using the modified CTAB method (Guzow-Krzemińska & Węgrzyn 2000) and used for PCR amplification of mtSSU rDNA. The primers mrSSU1 and mrSSU3R (Zoller *et al.* 1999) were used as PCR and sequencing primers. PCR amplification was performed as follows: initial denaturation at 95 °C for 10 min and six cycles at 95 °C for 1 min, 62 °C for 1 min and 72 °C for 105 s, followed by 40 cycles at 95 °C for 1 min, 56 °C for 1 min and 72 °C for 1 min, and a final extension step at 72 °C for 10 min (Czarnota & Guzow-Krzemińska 2010). Amplicons were sequenced by Eurogen (Moscow, Russia; https://evrogen.ru/). Newly generated sequences were deposited in NCBI (GenBank) (Table 1).

Sequence alignment and phylogenetic analysis

The mtSSU alignment was compiled with all the species of the *Micarea prasina* group and several closely related species were used as an outgroup following Guzow-Krzemińska *et al.* (2019). The dataset was aligned online using MAFFT v. 7 (Katoh & Standley 2013; available at http://mafft.cbrc.jp/alignment/server/), with the L-INS-i method (Katoh *et al.* 2005) selected automatically by the program. To exclude ambiguously aligned positions, alignment was subsequently analyzed by the automated1 algorithm as implemented in the TrimAl software package (Capella-Gutierrez *et al.* 2009). Phylogenetic reconstruction was carried out using Bayesian inference in MrBayes v. 3.2.6 (Ronquist & Huelsenbeck 2003) and maximum likelihood (ML) in RAxML (Stamatakis *et al.* 2005) through the RAxMLGUI interface (Silvestro & Michalak 2012). Bootstrap support values were calculated on 1000 bootstrap replicates using rapid bootstrapping ('ML + rapid bootstrap' function in RAxMLGUI). The analyses were run on the CIPRES Web Portal (http://www.phylo.org/portal2/). The HKY + G model was proposed by the program jModelTest (Guindon & Gascuel 2003; Posada 2008) as the best DNA substitution model. MrBayes analysis (BI) was performed using two independent runs with four MCMC chains (three cold and one heated) in each run. Trees were sampled every 500th generation. The analysis was stopped when the average standard deviation of split frequencies between the simultaneous runs dropped below 0.01 (1 270 000 generations). The first 25% of trees was discarded as burn-in, and the remaining trees were used for construction of a 50% majority-rule consensus tree.

Results

Phylogenetic analyses

Three new mtSSU rDNA sequences were generated and 72 downloaded from GenBank. The final alignment consisted of 75 sequences and 637 characters. Since the topologies from the maximum likelihood and Bayesian analyses did not show any supported conflict, the maximum likelihood tree is presented in Fig. 1 with added posterior probabilities from the Bayesian analysis.

The phylogenetic reconstruction (Fig. 1) shows that the *Micarea prasina* group is highly supported and monophyletic (96/1.00; ML/BI). It is divided into the *M. micrococca* (Körb.) Gams ex Coppins and *M. prasina* clades, lineages of *M. hedlundii* Coppins and *M. xanthonica* Coppins & Tønsberg basal to the *M. micrococca* clade and lineages of *M. tomentosa* and *M. pusilla* forming a highly supported clade basal (not supported) to other clades. This is in agreement with previous studies (e.g. Czarnota & Guzow-Krzemińska 2010; Guzow-Krzemińska *et al.* 2016, 2019; Launis *et al.* 2019*a*, *b*; Launis & Myllys 2019; van den Boom *et al.* 2020; Kantelinen *et al.* 2021).

The *M. micrococca* clade (91/1.00) consists mostly of species containing methoxymicareic acid and is divided into two lineages of *M. byssacea* and *M. micrococca* complexes. The *M. prasina* clade (48/0.99) consists mostly of species containing micareic acid and accommodates the newly described *M. svetlanae*. Several highly supported lineages are further distinguished within this clade. The sampled specimens of *M. svetlanae* form a highly

https://doi.org/10.1017/S0024282924000446 Published online by Cambridge University Press

Table 1. *Micarea* specimens used in this study with voucher information and GenBank Accession numbers. Sequences newly generated for this study are given in bold.

Micarea species	Country	Collector & Herbarium	mrSSU	Reference
M. adnata	Norway	*Andersen* 48 (BG)	AY567751	Andersen & Ekman 2005
M. adnata	France	*Sérusiaux* s. n., DNA 3438 (LG)	KX459344	van den Boom *et al*. 2017*a*
M. aeruginoprasina	Azores	*van den Boom* 51445, DNA 3973, holotype (LG)	MK562024	Guzow-Krzemińska *et al*. 2019
M. azorica	Azores	*van den Boom* 51330, DNA 3976 (LG)	MK562025	Guzow-Krzemińska *et al*. 2019
M. azorica	Azores	*van den Boom* 51468 DNA 3977, holotype (LG)	MK562026	Guzow-Krzemińska *et al*. 2019
M. azorica	Azores	*van den Boom* 51733, DNA 3978 (LG)	MK562027	Guzow-Krzemińska *et al*. 2019
M. byssacea	Finland	*Launis* 289103, DNA A98 (H)	MG707768	Launis *et al*. 2019*b*
M. byssacea	Finland	*Launis* 289102, DNA A97 (H)	MG707769	Launis *et al*. 2019*b*
M. czarnotae	Finland	*Launis* 1010133, DNA A455 (H)	MG707760	Launis *et al*. 2019*b*
M. czarnotae	Finland	*Launis* 109111, DNA A604 (H)	MG707759	Launis *et al*. 2019*b*
M. elachista	Finland	*Launis* 67113, DNA A340 (H)	MG707745	Launis *et al*. 2019*b*
M. elachista	Poland	*Czarnota* & *Guzow-Krzemińska* s. n. (GPN 2986)	EF453680	Czarnota & Guzow-Krzemińska 2010
M. fallax	Finland	*Launis* 1710132, DNA A718 (H)	MK454764	Launis *et al*. 2019*a*
M. fallax	Finland	*Launis* 1010138, DNA A461 (H)	MK454765	Launis *et al*. 2019*a*
M. fallax	Finland	*Launis* 1010139, DNA A453 (H)	MK454766	Launis *et al*. 2019*a*
M. fennica	Finland	*Launis* 68, DNA A117 (H)	MK517715	Launis & Myllys 2019
M. fennica	Finland	*Launis* 3220, DNA A790 (H)	MK517716	Launis & Myllys 2019
M. flavoleprosa	Czech Republic	*Malíček* 5098, DNA A616 (PRA)	MK454756	Launis *et al*. 2019*a*
M. flavoleprosa	Czech Republic	*Malíček* 4699, DNA A614 (PRA)	MK454755	Launis *et al*. 2019*a*
M. globulosella	Finland	*Launis* 67112, DNA A240 (H)	MG707743	Launis *et al*. 2019*b*
M. globulosella	Finland	*Launis* 67114, DNA A243 (H)	MG707744	Launis *et al*. 2019*b*
M. hedlundii	Poland	*Czarnota* & *Guzow-Krzemińska* s. n. (GPN 4589)	EF453677	Czarnota & Guzow-Krzemińska 2010
M. hedlundii	Finland	*Launis* 67119, DNA A254 (H)	MG707749	Launis *et al*. 2019*b*
M. herbarum	Netherlands	*van den Boom*, 2015, 52575, DNA 4236 (hb. van den Boom, LG)	KX459349	van den Boom *et al*. 2017*a*
M. herbarum	Netherlands	*Brand*, 2014, 63193, DNA 3852 (hb. Brand, LG)	KX459350	van den Boom *et al*. 2017*a*
M. isidioprasina	Poland	*Kukwa* 17493 (UGDA)	MK562015	Guzow-Krzemińska *et al*. 2019
M. isidioprasina	Poland	*Kukwa* 17367a & *Łubek*, holotype (UGDA)	MK562016	Guzow-Krzemińska *et al*. 2019
M. isidioprasina	Germany	*van den Boom* 53248, DNA 4590 (LG)	MK562030	Guzow-Krzemińska *et al*. 2019
M. laeta	Finland	*Launis* 59153, DNA A825 (H)	MG707771	Launis *et al*. 2019*b*
M. laeta	Finland	*Launis* 49151, DNA A819 (H)	MG707772	Launis *et al*. 2019*b*
M. levicula	Reunion	*Sérusiaux* s. n., DNA 3532 (LG)	MK562019	Guzow-Krzemińska *et al*. 2019
M. levicula	Reunion	*Sérusiaux* s. n., DNA 3585 (LG)	MK562020	Guzow-Krzemińska *et al*. 2019
M. melanobola	Finland	*Launis* 286152, DNA A813 (H)	MK454772	Launis *et al*. 2019*a*
M. melanobola	Finland	*Launis* 266151, DNA A818 (H)	MK454773	Launis *et al*. 2019*a*
M. melanobola	Finland	*Launis* 11014, DNA A424 (H)	MK454774	Launis *et al*. 2019*a*
M. meridionalis	Portugal	*van den Boom*, 2015, DNA 4279 (hb. van den Boom, LG)	KX459353	van den Boom *et al*. 2017*a*
M. meridionalis	Portugal	*van den Boom*, 2015, DNA 4281 (hb. van den Boom, LG)	KX459354	van den Boom *et al*. 2017*a*
M. meridionalis	Portugal	*van den Boom*, 2015, DNA 4581 (hb. van den Boom, LG)	KX459355	van den Boom *et al*. 2017*a*

(*Continued*)

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Table 1. (*Continued*)

Micarea species	Country	Collector & Herbarium	mrSSU	Reference
M. microareolata	Finland	*Launis* 59133, DNA A565 (H)	MG707766	Launis *et al.* 2019*b*
M. microareolata	Finland	*Launis* 89133, DNA A629 (H)	MG707767	Launis *et al.* 2019*b*
M. micrococca	USA	*Launis* 146127, DNA A320 (H)	MG707754	Launis *et al.* 2019*b*
M. micrococca	Finland	*Launis* 299101, DNA A100 (H)	MG707753	Launis *et al.* 2019*b*
M. microsorediata	Poland	*Kukwa* 16994 (UGDA)	MK562011	Guzow-Krzemińska *et al.* 2019
M. microsorediata	Netherlands	*van den Boom* 50279, DNA 3711 (LG)	MK562022	Guzow-Krzemińska *et al.* 2019
M. misella	Norway	*Andersen* 73 (BG)	AY567752	Andersen & Ekman 2005
M. misella	Finland	*Launis* 108111, DNA A264 (H)	MG707742	Launis *et al.* 2019*b*
M. nigra	Portugal	*van den Boom* 53726, DNA 4573 (LG)	MK562029	Guzow-Krzemińska *et al.* 2019
M. nowakii	Finland	*Launis* 245131, DNA A684 (H)	MG707751	Launis *et al.* 2019*b*
M. nowakii	Romania	*Sérusiaux*, 2015, s. n., LG DNA 4380	KX459359	van den Boom *et al.* 2017*a*
M. nowakii	Poland	*Czarnota* & *Guzow-Krzemińska* s. n. (GPN 4688)	EF453689	Czarnota & Guzow-Krzemińska 2010
M. pauli	Poland	*Kukwa* 17544 & *Łubek* (UGDA)	MK562010	Guzow-Krzemińska *et al.* 2019
M. pauli	Poland	*Kukwa* 17240 & *Łubek*, holotype (UGDA)	MK562014	Guzow-Krzemińska et al. 2019
M. peliocarpa	USA	*Launis* 66123, DNA A324 (H)	MG707741	Launis *et al.* 2019*b*
M. prasina	Poland	*Czarnota* & *Guzow-Krzemińska* s. n. (GPN 4319)	EF453679	Czarnota & Guzow-Krzemińska 2010
M. prasina	Finland	*Launis* 199105, DNA A93 (H)	MG707748	Launis *et al.* 2019*b*
M. prasina	Finland	*Launis* 265101, DNA A92 (H)	MG707747	Launis *et al.* 2019*b*
M. pseudomicrococca	Scotland	*Launis* 171141, DNA A645 (H)	MG707758	Launis *et al.* 2019*b*
M. pseudomicrococca	Finland	*Launis* 258131, DNA A603 (H)	MG707757	Launis *et al.* 2019*b*
M. pusilla	Finland	*Launis* 1010136, DNA A470 (H)	MK454751	Launis *et al.* 2019*a*
M. pusilla	Finland	*Launis* 1010137, DNA A460 (H)	MK454752	Launis *et al.* 2019*a*
M. pycnidiophora	USA	*Tønsberg* 30881 (BG)	AY567754	Andersen & Ekman 2005
M. soralifera	Finland	*Launis* 1710131, DNA A714 (H)	MG707746	Launis *et al.* 2019*b*
M. soralifera	Poland	*Kukwa* 12999 & *Łubek* (UGDA)	KT119885	Guzow-Krzemińska *et al.* 2016
M. soralifera	Poland	*Kukwa* 13001 & *Łubek* (UGDA)	KT119886	Guzow-Krzemińska *et al.* 2016
M. stipitata	USA	*Ekman* s. n. (BG)	AY567753	Andersen & Ekman 2005
M. subviridescens	Scotland	*Czarnota* & *Guzow-Krzemińska* s. n. (GPN 3599)	EF453666	Czarnota & Guzow-Krzemińska 2010
M. svetlanae	**Russia, Shikotan Island**	***Konoreva* LK-241 (LE)**	**PP477413**	**present study**
M. svetlanae	**Russia, Sakhalin Island**	***Konoreva* LK-248 (LE)**	**PP477414**	**present study**
M. svetlanae	**Russia, Sakhalin Island**	***Konoreva* LK-342 (LE)**	**PP477415**	**present study**
M. synotheoides	Norway	*Andersen* 47 (BG)	AY567756	Andersen & Ekman 2005
M. tomentosa	Finland	*Launis* 11013, DNA A773 (H)	MG707750	Launis *et al.* 2019*b*
M. tomentosa	Poland	*Czarnota* 3949 (GPN)	EF453686	Czarnota & Guzow-Krzemińska 2010
M. viridileprosa	Poland	*Czarnota* 3436 (GPN)	EF453671	Czarnota & Guzow-Krzemińska 2010
M. viridileprosa	Netherlands	*van den Boom* 50066, DNA 3493 (hb. van den Boom, LG)	KX459366	van den Boom *et al.* 2017*a*
M. xanthonica	USA	*Tønsberg* 25674 (BG)	AY756454	Andersen 2004

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Figure 1. Phylogenetic reconstruction of the *Micarea prasina* group, based on maximum likelihood analysis (ML) of mtSSU. The reliability of each branch was tested by ML and Bayesian methods. Numbers at tree nodes indicate bootstrap values of ML (left) and BMCMC posterior probabilities (right). Thicker branches indicate when both the bootstrap value of ML is ≥ 70% and the BMCMC posterior probability is ≥ 0.95. Newly sequenced specimens are indicated in bold and voucher information for all specimens is provided in Table 1. Branch lengths represent the estimated number of substitutions per site assuming the respective models of substitution. In colour online.

supported clade (100/1.00) sister without support to the clade comprising *M. isidioprasina* and *M. flavoleprosa* Launis *et al.* (Fig. 1).

Taxonomy

Micarea svetlanae Konoreva & Chesnokov sp. nov.

MycoBank No.: MB 853375

Similar to *M. isidioprasina* due to the presence of micareic acid, the granular-isidiate thallus with Sedifolia-grey, and crystalline granules in the thallus and hymenium, but differing in the cushion-shaped thallus, with cushions up to 0.6 mm diam. and 0.4 mm high, the presence of Sedifolia-grey pigment in the hymenium, numerous crystalline granules in the hymenium and hypothecium and 0–2(–3)-septate ascospores.

Type: Russia, Khabarovsk Territory, Ulchsky District, upper reaches of the Levyi Psyu River, 51°48′04.5″N, 141°03′47.1″E, 266 m a.s.l., spruce-fir fern-blueberry forest, on rotten fir wood, 25 September 2018, *S. V. Chesnokov* 193 (LE L-26024—holotype).

(Figs 2–5)

Thallus crustose, granular-isidiate, pale to dark green, sometimes a transition from very pale to dark olive can be seen within a single specimen (depending on light conditions) (Fig. 2A, B, E & F). Non-isidiate parts rare, granular or minutely areolate, areoles up to 0.05 mm diam., green, soon developing isidia. *Isidia* consisting of chains of goniocysts, coralloid, up to 175 µm tall and 25 µm wide (Figs 2A–H, 3B, D & F), forming an almost continuous layer over the substratum. Denser clusters of isidia forming a thick cushion-like thallus, which is then divided by fissures into

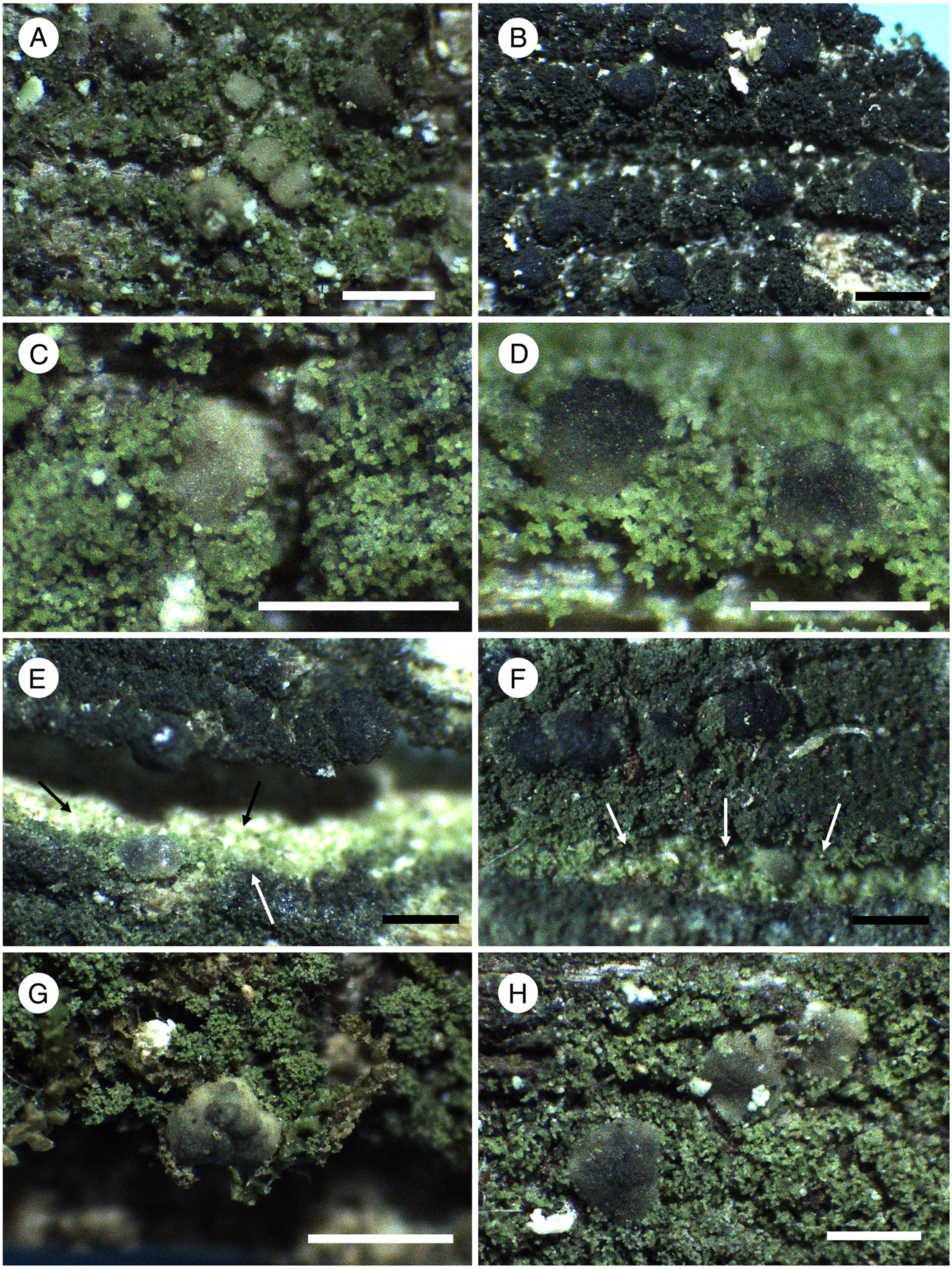

Figure 2. Morphological variability of *Micarea svetlanae* Konoreva & Chesnokov. A, thallus and apothecia without Sedifolia-grey. B, thallus and apothecia with high content of Sedifolia-grey. C & D, subconvex apothecia immersed in the thallus. E & F, differently coloured areas of the same specimens; arrows indicate pale-coloured thallus (without Sedifolia-grey) in the crack. G, tuberculate apothecium. H, adnate apothecia. Scales: A–F & H = 0.5 mm; G = 1 mm. In colour online.

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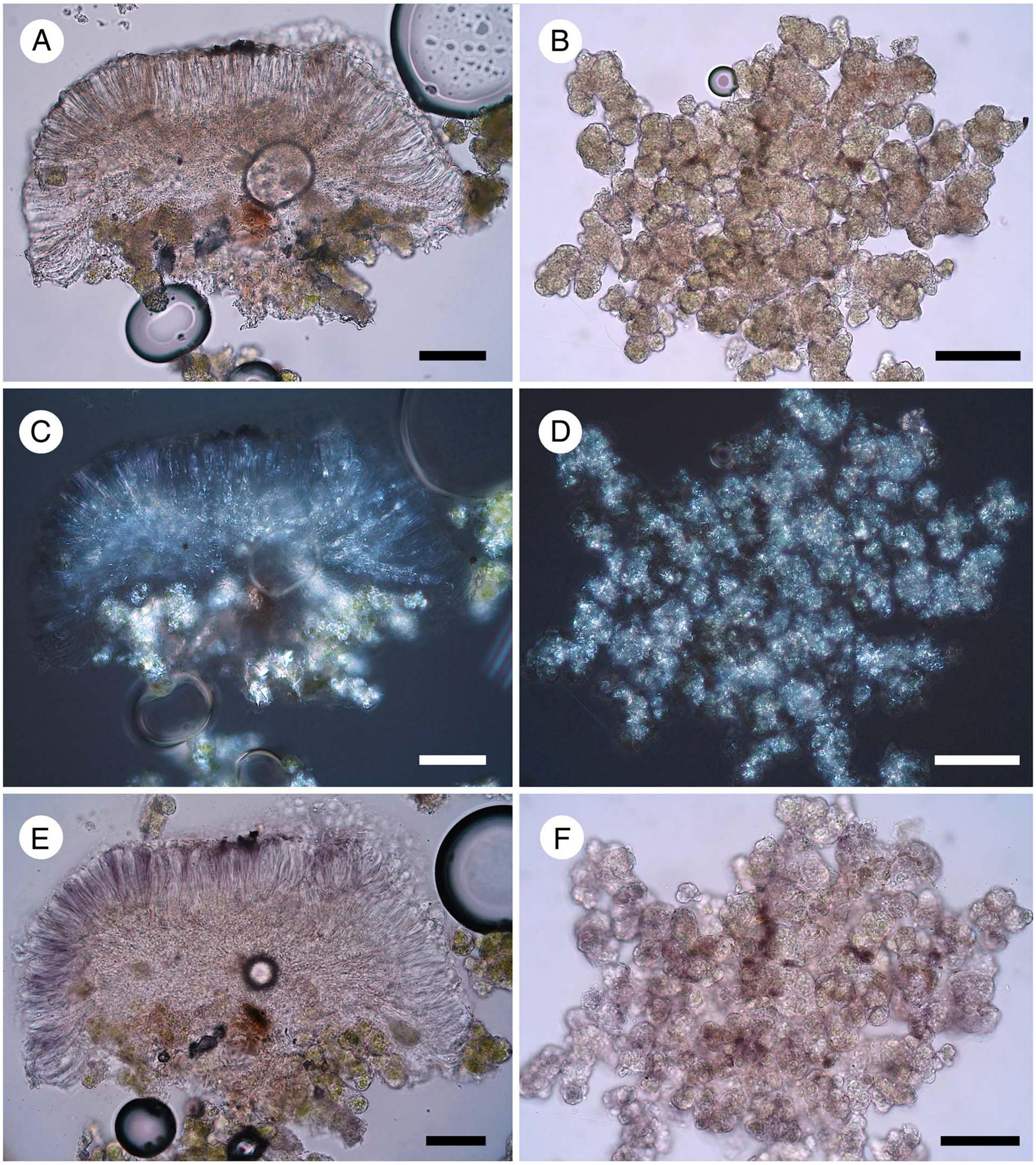

Figure 3. Section of the apothecium and thallus of *Micarea svetlanae*. A & B, in transmitted light. C & D, in polarized light. E & F, in transmitted light after reaction with K. Scales = 50 µm. In colour online.

separate dense cushions up to 0.4 mm tall and 0.6 mm diam. (Fig. 4F & H). The cushions, like the isidia, are made up of numerous goniocysts. *Prothallus* not visible. *Photobiont* micareoid, cells thin walled, 4–7 µm diam., clustered in compact groups, single goniocysts up to 25 µm diam. (Fig. 3B).

Apothecia immarginate, adnate to convex, 0.2–0.5 mm diam., often tuberculate and then up to 0.8 mm diam., pale cream to grey or dark grey, often different colours present within a single apothecium (Fig. 2A–H). When the apothecia develop among the cushions of the thallus, they appear immersed (Fig. 2C & D). *Epihymenium* hyaline; *hymenium* up to 65 µm high, hyaline (pale-coloured form) to pale greyish olive (in dark-coloured forms); *hypothecium* hyaline (Fig. 3A); *paraphyses* sparse, branched, anastomosing, 1.0–1.2(–1.5) µm wide, tips not widened and not pigmented (Fig. 5B); *asci* cylindrical, 40–50 × 10–12(–17) µm ($n = 30$), 8-spored (Fig. 5B); *ascospores* ellipsoidal to ovoid, 0-2(–3)-septate, 10–15 × 3.0–5.0(–6) µm ($n = 96$) (Fig. 5A).

Pycnidia not observed.

Chemistry. Micareic acid detected by HPTLC; K−, C−, KC−, PD−. Sedifolia-grey pigment (K+ violet, C+ violet) present in hymenium (Fig. 3E) and dark-coloured areas of the thallus (Fig. 3F), sometimes

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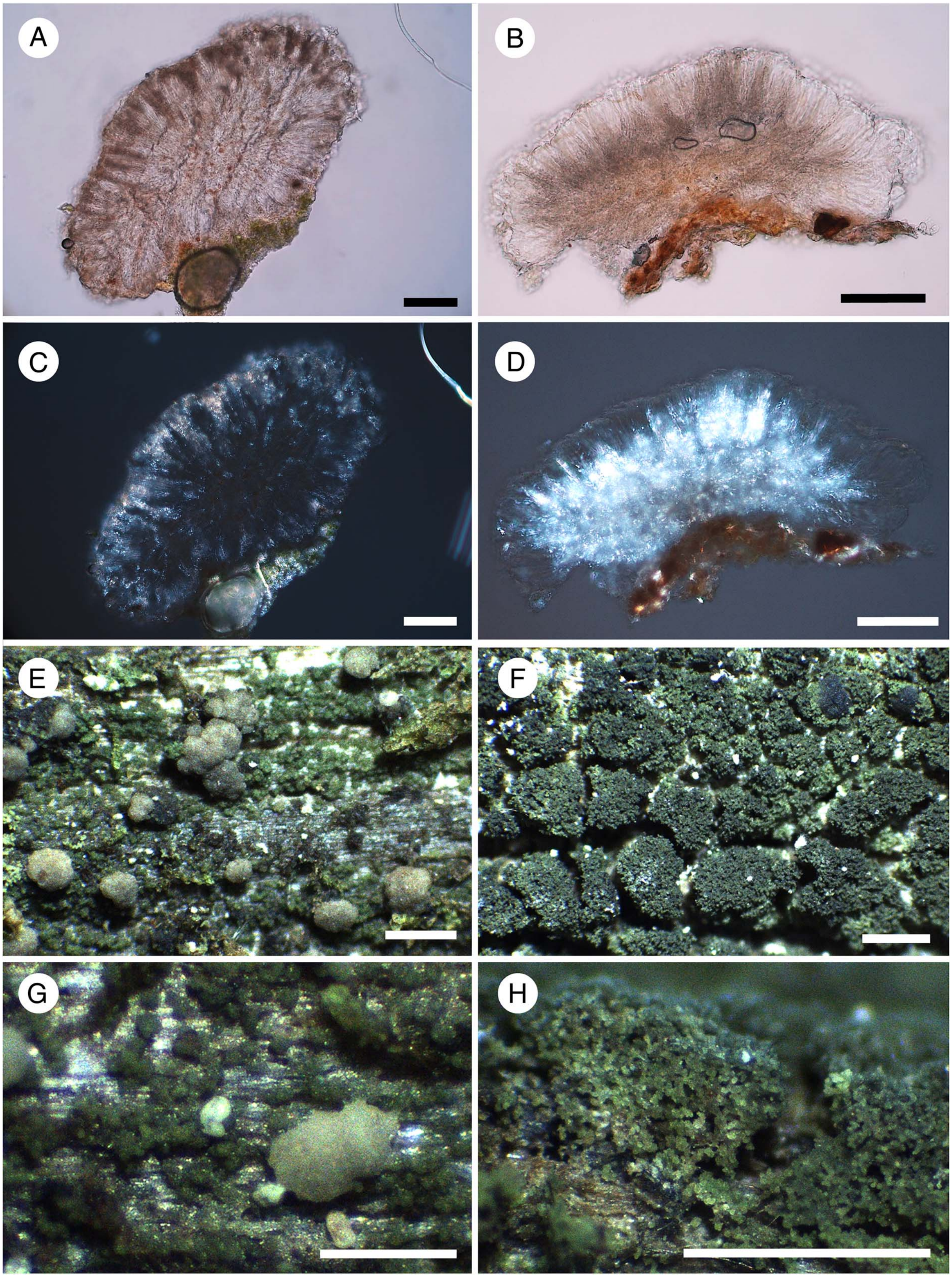

Figure 4. Comparison of anatomy (A–D) and morphology (E–H) of *Micarea prasina* (A, C, E, G) and *M. svetlanae* (B, D, F, H). A & B, localization of crystalline granules in transmitted light. C & D, localization of crystalline granules in polarized light. E, granular warty thallus and subglobose apothecia of *M. prasina*. F, cushion-like thallus, divided by fissures into separate dense cushions and apothecia of *M. svetlanae* immersed in the thallus. G, granular warty thallus of *M. prasina*. H, section through a thallus cushion of *M. svetlanae*. Scales: A–D = 50 µm; E & F = 0.5 mm; G = 0.4 mm; H = 1 mm. In colour online.

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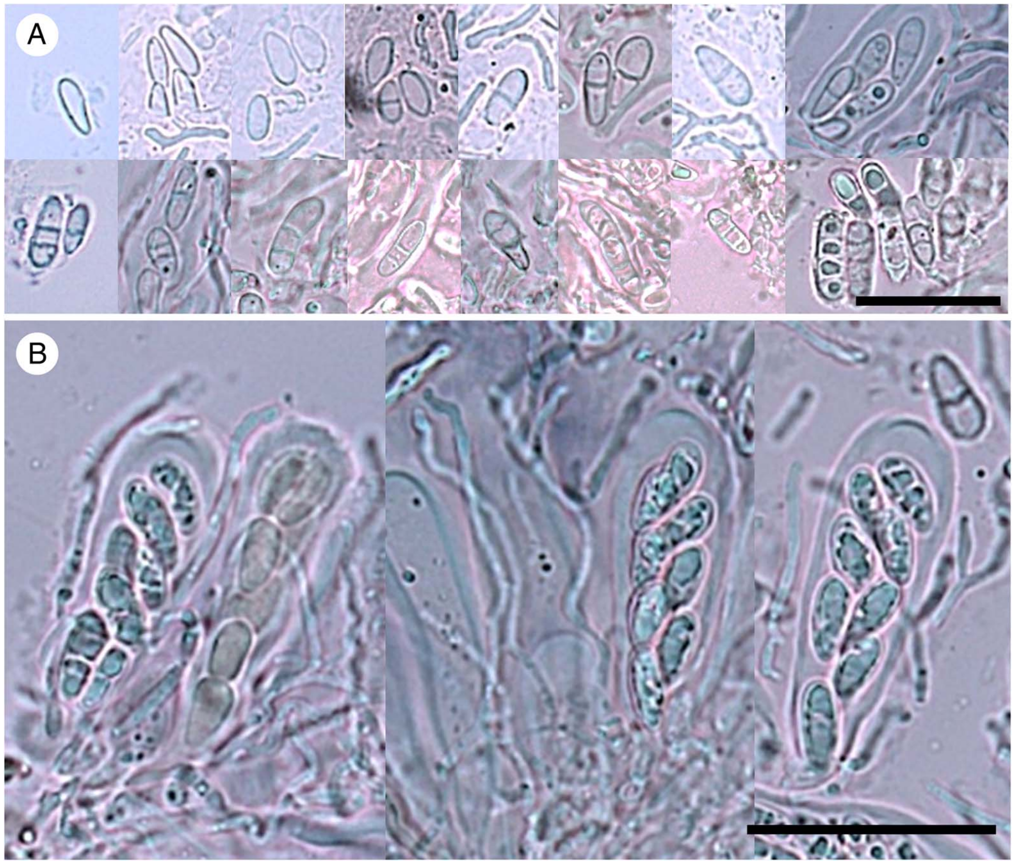

Figure 5. Asci, ascospores and paraphyses of *Micarea svetlanae*. A, variability of ascospores. B, asci with ascospores and anastomosing paraphyses. Scales: A = 20 µm; B = 25 µm. In colour online.

indistinct. Crystalline granules (studied in polarized light) abundant, visible in hymenium, hypothecium and thallus, soluble in K (Figs 3C & D, 4D).

Etymology. The species is named in honour of the Russian lichenologist, Dr Svetlana Tchabanenko (Chabanenko), who devoted her life to the study of lichens of the Russian Far East.

Habitat and distribution. Throughout its geographical range, *Micarea svetlanae* grows abundantly on lignum of coniferous trees *Abies nephrolepis* (Trautv. et Maxim.) Maxim., *A. sachalinensis* Fr. Schmidt, *Larix kamtschatica* (Rupr.) Carr., *Picea jezoensis* (Siebold et Zucc.) Carr. and *Taxus cuspidata* Siebold et Zucc.) and sometimes on the bark of fallen deadwood of *Abies sachalinensis*, *Pinus koraiensis* Siebold & Zucc. and *Salix* sp. in coniferous forests dominated by *Abies sachalinensis*, *Larix kamtschatica* and *Picea jezoensis* with *Juniperus* sp., *Sasa kurilensis* (Rupr.) Makino & Shibata, mosses and deadwood or in mixed forests with the same composition of conifers and *Betula ermanii* Cham. The new species often grows together with *Micarea prasina*, *M. nowakii* Czarnota & Coppins, *M. laeta* Launis & Myllys, *Trapelia corticola* Coppins & P. James and *Cladonia* spp. *Micarea svetlanae* is known only from the Russian Far East, namely Primorye and Khabarovsk Territories as well as Sakhalin and the Kuril Islands (Shikotan, Kunashir and Iturup) (Fig. 6). It is likely that the species range in Russia is limited to southern parts of the Russian Far East, since *M. svetlanae* was not found during our intensive field studies in the Magadan Region, Kamchatka Territory and Paramushir Island. In addition, it is likely that the species may be found in Japan, Korea and China.

Selected specimens examined. **Russia:** *Primorye Territory*: Dal'negorsk District, 8 km north-west of Krasnorechensky village, left bank of the Rudnaya River, 44°39′37.4″N, 135°15′05.6″E, 932 m, 2020, *L. A. Konoreva* 64 (LE L-26044); Terneysky District, Sikhote-Alin Nature Reserve, vicinity of the cordon Yasnaya, right bank of the Yasnaya River, 45°14′25.2″N, 136° 29′21.5″E, 116 m, 2020, *L. A. Konoreva* 193 (KPABG 21307). *Sakhalin Region*: Iturup Island, Ostrovnoy Reserve, Stokap volcano, Craternyi stream, 44°50′25.9″N, 147°17′44.7″E, 369 m, 2017, *L. A. Konoreva* 619 (LE L-26012); Kunashir Island, Kurilsky Nature Reserve, vicinity of the cordon Saratovsky, 44°15′41.4″N, 146°06′26.0″E, 10 m, 2019, *L. A. Konoreva* 50 (VBGI 170161); *ibid*., left bank of the River Saratovskaya, 44°16′21.7″N, 146°06′36.4″E, 28 m, 2019, *S. V. Chesnokov* 17 (LE L-26039, MSK); Sakhalin Island, Korsakovsky District, natural monument 'Lagoon Busse', surroundings of the Vyselkovoe Lake, 46°33′57.1″N, 143°16′54.7″E, 26 m, 2017, *L. A. Konoreva* 220, 230 (LE L-26016, LE L-26017; GenBank No. PP477414); vicinity of Yuzhno-Sakhalinsk city, Susunaisky ridge, Chekhov peak, Voroniy kamen' viewing platform, 46°58′38.3″N, 142°49′25.7″E, 352 m, 2017, *L. A. Konoreva* 248 (LE L-26020; GenBank No. PP477415); Tomarinsky District, Krasnogorsky nature reserve, vicinity of the Uglovogo Lake, 48°33′39.9″N, 141°58′15.0″E, 37 m, 2017, *L. A. Konoreva* 88 (VBGI 170158); Shikotan Island, vicinity of Tserkovnaya Bay, 43°44′16.5″N, 146°41′06.7″E, 30 m,

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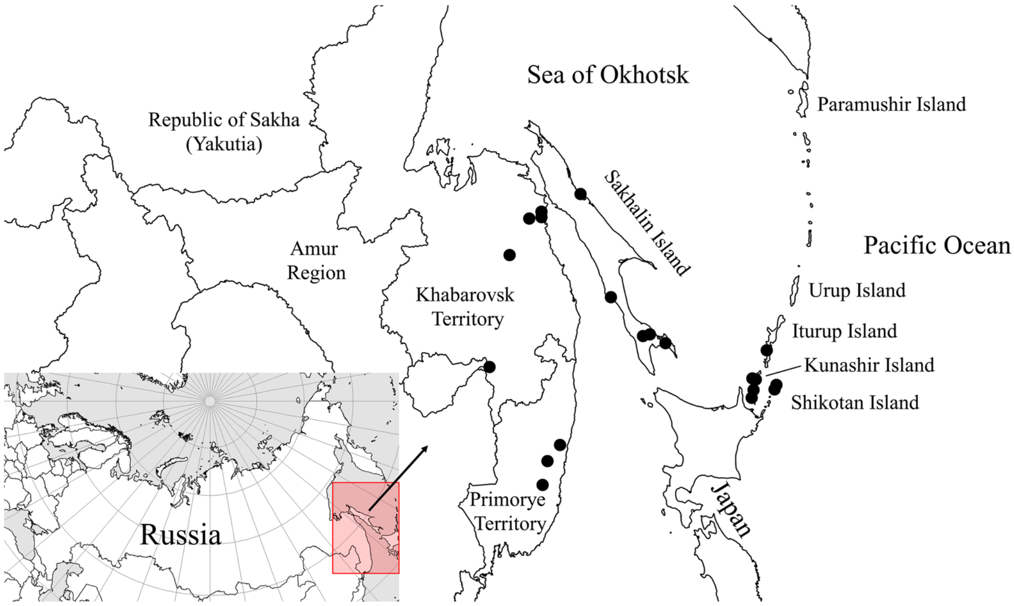

Figure 6. Known distribution of *Micarea svetlanae* in the Russian Far East. In colour online.

2017, *L. A. Konoreva* 369, 374 (LE L-26015, LE L-26022; GenBank No. PP477413). *Khabarovsk Territory*: Ulchsky District, 1.7 km west of Tabo Mt, 51°39′21.4″N, 140°53′45.9″E, 111 m, 2018, *S. V. Chesnokov* 149, 150, 151 (KPABG 21303, KPABG 21304, MSK); Khabarovsk District, Bolshekhehtsirsky reserve, Bykova River, vicinity of the 'Bykovka' cordon, 48°14′27.7″N, 134°48′54.1″E, 253 m, 2018, *S. V. Chesnokov* 205 (LE L-26030).

Table 2. A comparison of the characteristics of *Micarea svetlanae* with related species having micareic acid.

Morphological characters	*M. svetlanae*	*M. flavoleprosa*[2]	*M. isidioprasina*[1]	*M. prasina*[2]
Thallus colour	Pale green, green to dark olive green	Yellowish green, whitish green to olive green, bright yellow-green	Green to olive green	Bright green to olive green
Thallus structure	Granular-isidiate, isidia abundantly branched to coralloid, often denser clusters of isidia form a thick cushion-like thallus, which is then divided by fissures into separate dense cushions	Granular or farinose, composed of minute soredia or small goniocysts, which often coalesce to form larger granules	Granular-isidiate, isidia abundantly branched to coralloid, crowded, evenly dispersed over the substratum and do not form cushions	Granular or softly isidiate, goniocysts often coalesce forming larger granules
Apothecia	Usually numerous, pale cream to partly grey or dark grey, adnate to convex, often tuberculate	Rare, cream white, adnate to hemispherical	Rare, white to beige, some patchily grey, convex	Often numerous, creamy white, pale grey to partly dark grey, sometimes brownish, hemispherical to sometimes subglobose, simple or tuberculate
Sedifolia-grey pigment	Present in hymenium and dark-coloured areas of the thallus	Absent	Apparently absent in apothecial sections, present in the outermost parts of some isidia	Present in epihymenium, absent in the thallus
Crystalline granules (visible in polarized light)	Present in hymenium, hypothecium and thallus	Absent in apothecial section, present in thallus	Present rather sparsely in hymenium (as strands between asci and paraphyses) and abundantly in thallus	Present in epihymenium and sometimes also hymenium as strands and thallus
Ascospore septation	0–2(–3)-septate	0–2-septate	0–1-septate	0–1-septate
Ascospore size (µm)	10–15 × 3.0–5.0(–6) µm	(10–)12–16 × 4–6 µm	11–14 × 3.5–4.5 µm	8–12(–14) × 3–4.5(–5) µm

Distinctive features of species according Guzow-Krzemińska *et al.* (2019)[1] and Launis *et al.* (2019*a*)[2].

https://doi.org/10.1017/S0024282924000446 Published online by Cambridge University Press

Discussion

Micarea svetlanae belongs to the *M. prasina* group and contains micareic acid as the main secondary metabolite. The most characteristic features of this species are the isidia-like granules forming a rather thick cushion-shaped thallus, 0–2(–3)-septate ascospores, Sedifolia-grey pigment in the hymenium, and crystalline granules in the hymenium and hypothecium visible in polarized light.

Micarea isidioprasina and *M. flavoleprosa* are closely related to *M. svetlanae*. However, *M. flavoleprosa* is easily distinguished by its yellowish green to whitish green thallus, composed of minute soredia or small goniocysts which often coalesce to form larger granules, and the absence of Sedifolia-grey pigment in the apothecia and thallus (Launis *et al.* 2019*a*).

The most difficult to separate from *M. svetlanae* is *M. isidioprasina*, which also has a granular-isidiate thallus with Sedifolia-grey pigment, and crystalline granules in the hymenium and thallus. However, the isidia of *M. isidioprasina* are evenly dispersed over the substratum and do not form cushions, and its spores are 0–1-septate (Guzow-Krzemińska *et al.* 2019), whereas *M. svetlanae* has a cushion-shaped thallus, often cracked into individual cushions, and 0–2(–3)-septate spores (Table 2).

At the initial stages of its development, *Micarea svetlanae* may be similar to *M. prasina* with a slightly isidiate thallus, but the goniocysts of the latter species tend to merge into larger, never coralloid-branch granules. In addition, the Sedifolia-grey pigment is present in the epihymenium of *M. prasina*, crystalline granules visible in polarized light are present in the epihymenium and sometimes also in the hymenium as strands, but never in hypothecia, and its ascospores are 0–1-septate (Launis *et al.* 2019*a*; Fig. 4A–H, Table 2).

Pale forms of *Micarea svetlanae* (with or without traces of Sedifolia-grey) may resemble *M. levicula* (Nyl.) Coppins, *M. microsorediata* Brand *et al.*, *M. pauli* Guzow-Krzemińska *et al.*, *M. viridileprosa* Coppins & van den Boom and *M. xanthonica* Coppins & Tønsberg, but they are easily distinguished from these species by the presence of micareic acid. Both *M. microsorediata* and *M. pauli* produce methoxymicareic acid (Guzow-Krzemińska *et al.* 2019), *M. levicula* and *M. viridileprosa* produce gyrophoric acid (van den Boom & Coppins 2001), and *M. xanthonica* contains thiophanic acid and other xanthones as the main secondary metabolites (Coppins & Tønsberg 2001). In addition, *M. microsorediata* and *M. viridileprosa* form soralia, and *M. levicula*, *M. microsorediata*, *M. pauli* and *M. viridileprosa* never produce 2–3-septate ascospores.

Specimens of *Micarea svetlanae* with adnate apothecia and crystalline granules in the hymenium may be mistakenly identified as *M. byssacea* (Th. Fr.) Czarnota *et al.*, and light forms as *M. microareolata* Launis *et al.* However, these species are distinguished by the production of methoxymicareic acid, the absence of isidia-like coralloid-branching goniocysts and 0–1-septate ascospores (Czarnota & Guzow-Krzemińska 2010; Launis *et al.* 2019*b*).

Acknowledgements. The study was carried out in the framework of the institutional research projects 'Cryptogamic biota of Pacific Asia: taxonomy, biodiversity, species distribution' of the Botanical Garden-Institute of the Far Eastern Branch of the Russian Academy of Sciences (work by S. Chesnokov and L. Konoreva) and 'Flora and taxonomy of algae, lichens and bryophytes of Russia and phytogeographically important regions of the world' no. 121021600184-6 (work by S. Chesnokov). Ivan Frolov worked within the framework of the national project of the Botanical Garden-Institute (Russian Academy of Sciences, Ural Branch) and the project 122040800089-2 of the Botanical Garden-Institute FEB RAS. We are grateful to Curtis Björk (University of British Columbia, Canada) for the linguistic revision of the manuscript and to anonymous reviewers for valuable comments.

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Supplementary Material. The Supplementary Material for this article can be found at https://doi.org/10.1017/S0024282924000446.

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