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Candelariella blastidiata sp. nov. (Ascomycota, *Candelariaceae*) from Eurasia and North America, and a key for grey thalli *Candelariella*

Lidia S. YAKOVCHENKO, Jan VONDRÁK, Yoshihito OHMURA, Evgeny S. KORCHIKOV, Olga S. VONDRÁKOVA and Evgeny A. DAVYDOV

Abstract: *Candelariella blastidiata* Yakovchenko sp. nov. is described. This corticolous species is characterized by biatorine yellow apothecia, a grey squamulose thallus with marginal and lower side blastidia, 8-spored asci, and a northern circumpolar distribution. *Candelariella subdeflexa* has previously been confused with *C. blastidiata*, but our analyses of phenotypic and DNA sequence data revealed *C. blastidiata* should be distinguished from *C. subdeflexa*. A worldwide key for *Candelariella* species with grey thalli is provided.

Key words: *Candelariales*, *Candelariella subdeflexa*, lichens, new species, species pair, taxonomy

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Introduction

Candelariaceae Hakul. is characterized within Lecanoromycetes primarily by the foliose or crustose thallus with pulvinic acid and related pigments which give the *Candelariaceae* its distinctive yellow to orange-yellow colour. The family has a worldwide distribution and consists of four genera with the largest, *Candelariella* Müll. Arg., comprising *c.* 50 accepted species. Among the species of *Candelariella*, a small group can be recognized that share the following features: a grey thallus, lacking lichen substances detected by high performance liquid chromatography (HPLC) and thin-layer chromatography (TLC), 8-spored asci and mostly lecanorine apothecia (Westberg 2005). The representatives of this group are predominantly found in open woodlands, steppes and prairies growing on bark, wood, plant debris or calcareous rocks, more often in dry and sun-exposed habitats. Such *Candelariella* species with a grey thallus are now frequently reported by many researchers (e.g. Malíček *et al.* 2008; Vondrák *et al.* 2008; Aptroot 2011; Westberg & Clerc 2012; Westberg & Sohrabi 2012; Yakovchenko *et al.* 2012; Gasparyan *et al.* 2014; Urbanavichus & Urbanavichene 2014; Kocakaya & Halici 2015).

Among the species with a grey thallus, *Candelariella subdeflexa* (Nyl.) Lettau is distinct in its biatorine apothecia and well-developed thallus formed by squamules with occasional conidiophores producing globose conidia on the lower side of the thallus (Westberg 2007). During a revision of *Candelariaceae* in the herbaria H, LE and TNS, the first author found several specimens identified as *Candelariella subdeflexa* with blastidiate squamules. The aim of this study is to compare these individuals with

L. S. Yakovchenko: Institute of Biology and Soil Science, Stoletiya Vladivostoka Avenue, 159, RU-690022, Vladivostok, Russia. Email: lidiyakovchenko@mail.ru
J. Vondrák: Institute of Botany, Zámek, 1, 252 43 Průhonice, Czech Republic.
Y. Ohmura: Department of Botany, National Museum of Nature and Science, 4-1-1 Amakubo, Tsukuba, Ibaraki, 305-0005, Japan.
E. S. Korchikov: Department of Ecology, Botany and Nature Protection, Samara National Research University, Academic Pavlov Str., 1, Samara, RU-443011, Russia.
O. S. Vondrákova: Laboratory Biogeography and biodiversity monitoring, Institute of steppe, Pionerskaya Str., 11, Orenburg, RU-460000, Russia.
E. A. Davydov: Altai State University, Lenin Prosp. 61, Barnaul, RU-656049, Russia.

other related taxa employing morphological, chemical and DNA sequence data. A worldwide key to grey thalline *Candelariella* is also presented.

Materials and Methods

Specimens and phenotype studies

The specimens examined are housed in ALTB, G, GZU, H, LE, PRA, SMR and TNS. Morphological observations were made using a dissecting microscope. Hand-cut sections of apothecia and thalli were observed after mounting in water. Measurements are presented as the *mean* ($\bar{x}$) and range including 85% of the variation, bounded by the smallest and largest observed values, followed by the sample size (n) following Westberg (2005).

Lichen substances were examined using thin-layer chromatography (TLC) with solvent B' (hexane: methyl tert-butyl ether: formic acid, 140 : 72 : 18) and solvent C (toluene: acetic acid, 170 : 30) (Culberson & Kristinsson 1970; Culberson & Johnson 1982) for the specimen in TNS.

Sequences and phylogenetic reconstructions

To test the monophyly of *Candelariella blastidiata* and its relationship with other species, ITS nrDNA sequences of fresh material and those retrieved from the NCBI database (GenBank) were used for molecular phylogenetic analysis. ITS nrDNA sequence data were used because GenBank includes a number of ITS sequences of *Candelariella*, whereas other loci are poorly represented. Furthermore, ITS single-locus genealogies are usually consistent with phenotypic data (Westberg *et al.* 2007, 2009; Westberg & Arup 2011; Tripp & Lendemer 2015). One or more different sequences of appropriate length (and preferably lacking uncertain nucleotides) were selected from every species of *Candelariella*. Our sampling comprised 26 species representing morphological variability within *Candelariella*, 10 of which were represented by two or more accessions. Information on the samples with GenBank Accession numbers is shown in Table 1.

Two apothecia or fragments of thallus (for sterile specimens) were used for DNA extraction. Samples were frozen in liquid nitrogen and made into a powder in tubes using sterile pestles. The DNeasy Plant Mini Kit (Qiagen, Germany) was used for DNA extraction following the manufacturer's instructions. The primer set was ITS1F (Gardes & Bruns 1993) and LR1 (Vilgalys & Hester 1990). PCR settings were as follows: 95 °C for 2 min, 35 cycles of 94 °C for 20 s, 53 °C for 60 s, 72 °C for 2 min, followed by 72 °C for 15 min and then maintained at 14 °C. The sequences obtained in this study and the reference sequences from GenBank were aligned by Geneious 6.0 (Biomatters Ltd., New Zealand) and manually optimized. The sequence of *Pycnora xanthococca* (Sommerf.) Hafellner was used as outgroup since *Pycnora* has been identified as a possible sister clade to *Candelariaceae* (Bendiksby & Timdal 2013). Total alignment of 461 bp was used for the maximum likelihood (ML) and Bayesian analyses. Optimal substitution models were inferred separately for ITS1, 5.8S and ITS2 using PartitionFinder version 1.1.1 (Lanfear *et al.* 2012). The symmetrical substitution model with gamma-distribution (SYM+G) was selected for the 5.8S partition and Kimura 2-parameter with proportion of invariable sites (K80+I) for ITS1+ITS2. 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 for 20 000 000 generations in six chains and every 200th generation was sampled. The first 50% of trees were discarded as burn-in and a 50% majority-rule consensus tree calculated from the remaining trees of three runs with the sumt command implemented in MrBayes 3.2.3. Bootstrap support values and BMCMC posterior probability were noted on the best scoring tree (numbers are shown only when ≥50% in both). The ML tree and 1000 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 because RAxML does not support SYM and K80 models.

Results

Six ITS sequences of blastidiate specimens of *Candelariella* were successfully obtained. They formed a monophyletic clade in the ITS phylogeny of *Candelariella* with support values of 100/1·00 (bootstrap/posterior probability) in the phylogenetic tree (Fig. 1). Variability in ITS sequences among four of the European and Russian specimens is only 1 residue, but the Chinese sequence differs from others by 3 residues. A supported sister clade (88/1·00) includes three sequences of *C. subdeflexa*. Four constant residues differentiate *C. subdeflexa* from blastidiate specimens. Both species form a group well-separated from all other included species.

The close relationship of blastidiate specimens with *C. subdeflexa* is well explained by the close morphology (i.e. grey thallus with biatorine apothecia) as well as growing in similar habitats. However, we consider the two clades as distinct and morphologically recognizable species and one of them is described here as *Candelariella blastidiata* Yakovchenko. Specimens of *C. blastidiata* studied include samples without conidiophores (European specimens) and

TABLE 1. *Locality, voucher information and GenBank Accession numbers for the species used in this study for phylogenetic analysis. New sequences are in bold.*

Species	Locality	Voucher (Herbarium)	GenBank Acc. no.	Reference
Candelariella aggregata	USA: Colorado	*Westberg* 1080 (LD)	EF535157	Westberg *et al.* (2007)
C. antennaria	USA: Colorado	*Westberg* 1155 (LD)	EF535159	Westberg *et al.* (2007)
C. aurella	USA: Colorado	*Westberg* 1053 (LD)	EF535162	Westberg *et al.* (2007)
C. aurella	USA: Arizona	*Westberg* 150 (LD)	EF535163	Westberg *et al.* (2007)
C. biatorina	USA: California	*Tucker & Bratt* 34049 (SBBG)	EF535165	Westberg *et al.* (2007)
C. blastidiata	Russia: Repub. of Altai	*Davydov* 7716 (ALTB)	**KX853128**	This study
C. blastidiata	Russia: Orenburg Region	*Vondrák* 7428 *& Khodosovtsev* (TNS)	**KX853127**	This study (isotype)
C. blastidiata	Russia: Orenburg Region	*Vondrák* 7428 *& Khodosovtsev* (LE-L11031)	**KX853123**	This study (holotype)
C. blastidiata	Slovakia: Filakovo	*Vondrák* 10207 (PRA)	**KX853125**	This study
C. blastidiata	Slovakia: Revúca	*Vondrák* 9195 (PRA)	**KX853124**	This study
C. blastidiata	China: Xinjiang	*Davydov* 12272 (ALTB)	**KX853126**	This study
C. borealis	Canada: Nunavut	*Westberg* 2381 (LD)	EF535167	Westberg *et al.* (2007)
C. borealis	USA: Colorado	*Westberg* 1079 (LD)	EF535168	Westberg *et al.* (2007)
C. californica	USA: California	*Westberg* 1244 (LD)	EF535169	Westberg *et al.* (2007)
C. citrina	Mexico: Baja California Sur	*Westberg* 398 (LD)	EF535170	Westberg *et al.* (2007)
C. clarkii	USA: Colorado	*Tripp & D'az* 4876 (COLO)	KR052104	Tripp & Lendemer (2015)
C. complanata	Mexico: Baja California Sur	*Westberg* 383 (LD)	EF535174	Westberg *et al.* (2007)
C. coralliza	Sweden: Öland	*Westberg* 51 (LD)	EF535175	Westberg *et al.* (2007)
C. coralliza	China: Yanbian Korean Autonomous Prefecture	YK140035	KP226207	Cao *et al.* (2015)
C. corallizoides	Mexico: Baja California Sur	*Westberg* 341 (LD)	EF535176	Westberg *et al.* (2007)
C. corviniscalensis	USA: Colorado	*Morse* 15881 *& Ladd* (S)	GU967377	Westberg *et al.* (2011)
C. deppeanae	USA: Arizona	*Westberg* 585 (holotype) (LD)	EF535178	Westberg *et al.* (2007)
C. deppeanae	Mexico: Chihuahua	*Nash* 36526 (ASU)	EF535179	Westberg *et al.* (2007)
C. efflorescens	Austria: Steiermark	*Arup* L97286 (hb. Ulf Arup)	EF535180	Westberg *et al.* (2007)
C. granuliformis	Canada: Nunavut	*Mattsson* 5209 (UPS)	GU967375	Westberg *et al.* (2011)
C. kansuensis	USA: Arizona	*Wetmore* 55470 (MIN)	EF535181	Westberg *et al.* (2007)
C. kansuensis	USA: Arizona	*Westberg* s. n. (LD)	FJ959349	Westberg *et al.* (2009)
C. lutella	Norway: Troms	*Westberg* 2808 (LD)	EF535182	Westberg *et al.* (2007)
C. lutella	USA: Arizona	*Westberg* 206 (LD)	EF535183	Westberg *et al.* (2007)
C. medians	Sweden: Skåne	*Arup* L03165 (LD)	EF535184	Westberg *et al.* (2007)
C. placodizans	Canada: Nunavut	*Westberg* 206 (LD)	EF535187	Westberg *et al.* (2007)
C. placodizans	USA: Colorado	*Westberg* 1083 (LD)	EF535188	Westberg *et al.* (2007)
C. reflexa	Norway: Vestfold	*Lindblom & Blom* L61 (BG)	EF535190	Westberg *et al.* (2007)
C. rosulans	USA: Colorado	*Westberg* 1146 (LD)	EF535191	Westberg *et al.* (2007)
C. rosulans	USA: Arizona	*Westberg* 812 (LD)	EF535192	Westberg *et al.* (2007)
C. rosulans	USA: Colorado	*Westberg* 199 (LD)	EF535193	Westberg *et al.* (2007)
C. spraguei	USA: Colorado	*Westberg* 1037 (LD)	EF535194	Westberg *et al.* (2007)

Table 1 (continued)

Species	Locality	Voucher (Herbarium)	GenBank Acc. no.	Reference
C. subdeflexa	USA: South Dakota	*Lendemer* 1164 (PH)	EF535196	Westberg *et al.* (2007)
C. subdeflexa	USA: Arizona	*Nash* 38631 (ASU)	EF535197	Westberg *et al.* (2007)
C. subdeflexa	USA: Arizona	*Westberg* 660 (LD)	EF535198	Westberg *et al.* (2007)
C. terrigena	Canada: Nunavut	*Lutzoni & Miadlikowska* 07.13.03-19 (DUKE)	HQ650602	Schmull *et al.* (2011)
C. vitellina	USA: Oregon	*Westberg* 875 (LD)	EF535199	Westberg *et al.* (2007)
C. vitellina	Sweden: Öland	*Westberg* 49 (LD)	EF535200	Westberg *et al.* (2007)
C. xanthostigma	USA: California	*Nash* 32596 (ASU)	EF535201	Westberg *et al.* (2007)
C. xanthostigma	USA: Colorado	*Westberg* 1122 (LD)	EF535202	Westberg *et al.* (2007)
Pycnora xanthococca	Norway	*E. Timdal* 11646 (O L-163707)	KF360412	Bendiksby & Timdal (2013)

samples with a poorly developed layer of conidiophores at the base of the squamules (Altaian specimens: Russia, ED 7716; China, ED 12272). The Chinese specimen also shows slight morphological differences, with larger squamules and more abundant blastidia (Fig. 2A).

Candelariella blastidiata Yakovchenko sp. nov.

MycoBank No.: MB 817756

Thallus corticolous, grey, squamulose with blastidia on margins and/or the lower side of squamules 25–34 (–60) µm wide, apothecia biatorine, convex, yellow, (0·3–)0·5(–0·9) mm in diam; apothecial margin indistinct. Asci 8-spored, ascospores narrowly-ellipsoid, (7·5–) 10·0–14·5 (−15·0) × (3·5–)4·0–5·0 µm, conidiophores absent or partly-developed on the lower side of the squamules.

Type: Russia, Orenburg Region, Buzuluk District, National Park 'Buzuluksky bor', Partizanskiy Village, bank of the Borovka River, 52°59'54"N, 52°07'42"E, 80 m, on bark of *Salix*, 2009, *J. Vondrák* JV7428 & *A. Khodosovtsev* [Obermayer, *Lichenotheca Graecensis* no. 405] (LE–L11031—holotype; ALTB, ASU, B, C, CANB, CANL, E, G, GZU, H, HAL, HMAS, M, MAF, MIN, O, PRA, TNS, UPS—isotypes labelled "*C. subdeflexa*").

(Figs 2A & B, 3A–C)

Thallus squamulose. *Squamules* first prostrate to soon ascending and erect, scattered to crowded and somewhat imbricate, ±rounded, (0·2–)0·3–*0·4*–0·5(–0·7) mm long ($n = 29$) with irregularly incised margin; squamules (75–)103–*122*–141(–163) µm thick ($n = 19$); epinecral layer absent; cortex alveolate, (0–) 4–*8*–13(–25) µm thick ($n = 35$), consisting of gelatinized hyphae with ±isodiametric cells, (2·5–)4·0–*5·5*–7·0(–10·0) µm wide ($n = 30$); *algae* chlorococcoid, (18–)19–*20*–21(–25) µm diam. ($n = 20$), lower surface covered by blastidia and sometimes also with a layer of conidiophores at the base of the squamules; *conidiophores* (15–)23–*32*–41(–50) µm tall ($n = 11$). *Surface* pale grey to pale brownish grey, smooth and matt. *Vegetative propagules*: blastidia, (25–)27–*34*–41(–60) µm wide ($n = 36$), same colour as thallus or with greenish tint, marginal to spreading on the lower side of the squamules.

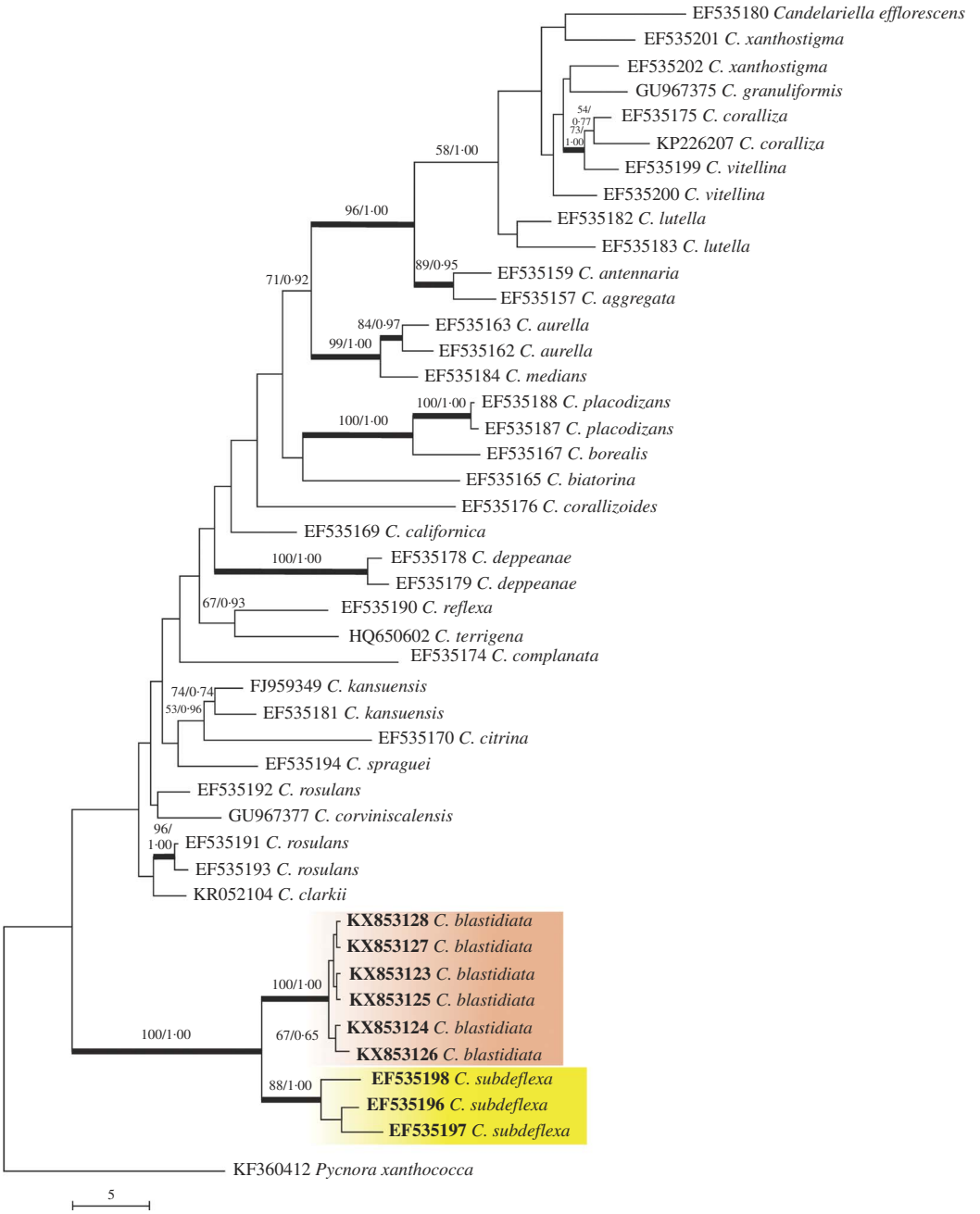

FIG. 1. Reconstruction of the *Candelariella* ITS phylogeny showing positions of *C. blastidiata* and *C. subdeflexa*. The tree was constructed by Maximum Liklihood (ML), and the reliability of each branch was tested by ML and Bayesian methods. Numbers at tree nodes indicate bootstrap values of ML (left) and BMCMC posterior probabilities (right) (only ML values ≥50% and PP values ≥0·50 are depicted). Thicker branches indicate where both the ML bootstrap value is ≥70% and the BMCMC posterior probability is ≥0·95. GenBank Accession numbers are given as OTU names (see Table 1). *Pycnora xanthococca* is the outgroup.

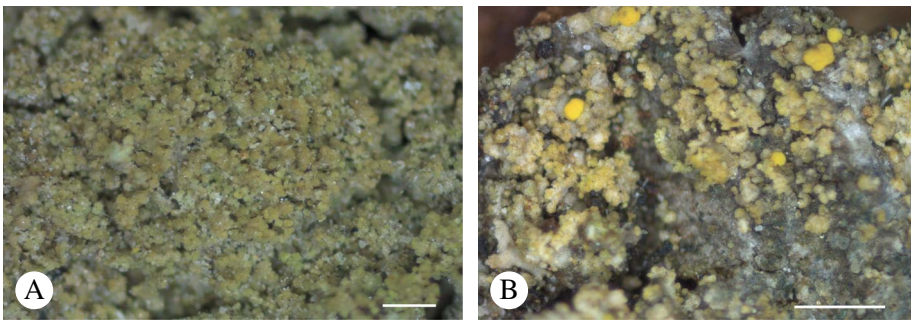

FIG. 2. *Candelariella blastidiata*. A, sterile specimen with abundant blastidia, China, Altai, ED 12272 (ALTB); B, isotype (ALTB). Scales: A = 200 µm; B = 500 µm. In colour online.

Apothecia biatorine, yellow, scattered to crowded and coalescing, (0·3–)0·4–*0·5*–0·5 (–0·9) mm diam. (n = 32); *disc* first rounded and weakly convex, becoming irregular in outline and strongly convex with age; *proper margin* not visible, hidden below margin of the convex disc, of branched and anastomosing hyphae radiating towards the margin, consisting of ±rectangular cells *c*. 4·5–10·0 × 1·5–2·5 µm (n = 10), ±similar throughout; *epihymenium* yellow-brown; *hymenium* colourless, *c*. 45·0–62·5 µm tall (n = 12); subhymenial layers colourless with oil droplets; *paraphyses* simple to branched, in midhymenium 1·5–2·5 µm wide (n = 15); tips cylindrical or weakly tapering, rarely narrowly clavate, up to 3 µm wide; *asci* clavate to widely-clavate, 8-spored, *c*. 30–50 × 12·5–15·0 µm (n = 17); *ascospores* narrowly ellipsoid, with thin septa or rarely simple, straight to slightly curved, (7·5–)10·0–*12·0*–14·5 (–15·0) × (3·5–)4·0–*5·0*–5·0 µm (n = 42).

Conidiogenous cells cylindrical to flask-shaped; *conidia* globose to widely teardrop-shaped, (2·5–)4·0–*5·5*–6·5(–7·5) µm diam. (n = 41). *Pycnidia* not seen.

Chemistry. Spot tests: apothecia K+ reddish, KC−, C−; thallus K−, KC−, C−. TLC: thallus, no substances; apothecia containing calycin, pulvinic acid, and pulvinic dilactone.

Etymology. The species is named with reference to the blastidia.

Ecology. *Candelariella blastidiata* was found on the bark of deciduous trees. It grows in open woodland or on solitary trees at elevations of 49–1050 m near rivers on trunks of *Acer*, *Cercidium*, *Populus*, *Tilia* and *Salix*. It often grows together with *Candelariella antennaria* Räsänen.

Distribution. *Candelariella blastidiata* is currently known from a small number of localities in Eurasia and North America: Central Europe, the European part of Russia (Orenburg, Samara Region), Siberia and the adjacent territory of China (Altai Mountains), and western North America (North Dakota and Arizona).

Additional specimens examined. **Slovakia:** *Banská Bystrica Region*: Revúca, Muráň, in village of Predná Hora, Muránská planina Mts, 48°46'21"N, 20°6'13"E, 760 m, on bark of *Tilia cordata*, 2011, *J. Vondrák* 9195 (PRA); Filakovo, Hajnáčka, Šurice, S-slope of hill Soví hrad, Cerová vrchovina upland, 48°13'34"N, 19°54'45"E, 250 m, on bark of solitary *Acer campestre* on sun-exposed rock, 2012, *J. Vondrák* 10207 (PRA).—**Russia:** *Orenburg Region*: Buzuluk District, National Park 'Buzuluksky bor', Koltubanovskiy Village, square 95, 52°53'03·13"N, 52°03'16·31"E, 64 m, on bark of *Populus tremula* and *Salix alba*, 2013, *V. P. Travkin* 167, 168 (SMR); same National Park, Borovo-opytniy Village, square 50, 52°59'52·87"N, 52°07'35·55"E, 81 m, on bark of *Salix alba*, 2015, *V. P. Travkin* 171 (SMR). *Samara Region*: Kinel District, Krasnosamarskiy Village, square 81, 52°59'45·61"N, 51°04'53·82"E, 49 m, on bark of *Populus tremula*, 2008, *E. S. Korchikov* 172, 173 (SMR). *Republic of Altai*: Ongudaisky District, Altai Mts, Terektinsky range, right bank of Bolshoi Yaloman River, 1 km upstream from its mouth, on bark of *Populus laurifolia*, 50°31'27"N, 86°33'23"E, 770 m, 2009, *E. A. Davydov* 7716 (ALTB).—**China:** *Xinjiang*: Altai Mts, Kabinsky range, at 22 km

NNE of Keldynen-Bulak settlement, the valley of Terekty River, on bark of *Populus laurifolia*, 48°28'25"N, 86°41'29"E, 1050 m, 2005, *E. A. Davydov* 12272 (ALTB).—**USA:** *North Dakota*: Mercer County, Knife River Indian Villages National Historic Site, 0·5 mi NE of headquarters (50 mi NW of Bismarck), in woods along Knife River with dead green ash and box elder and small prairie knoll, sec. 33, T 145 N, R 84 W, on boulder, 47°20'23"N, 101°23'10"W, 1998, *C. M. Wetmore* 79964/51-2000 (GZU). *Arizona*: Pinal Co., between Boyce Thompson arboretum and Picket Post Mt., upper Sonoran Desert, 33°16'N, 111°10'W, 600–800 m, at the base of trunk of *Cercidium* sp., NE-exp. (very shady), 1988, *P. Clerc* 88/394 (G00295824).

Discussion

Candelariella blastidiata is easily recognized by the grey to brownish grey squamulose thallus, composed of prostrate to ascending and erect squamules with marginal blastidia spreading on the lower side of the squamules, the presence of biatorine apothecia with 8 spores per ascus and an absent or poorly developed layer of conidiophores at the base of the squamules (Fig. 3A & B).

The presence of biatorine apothecia and blastidia distinguishes *C. blastidiata* from other corticolous and lignicolous species with grey thalli: *Candelariella antennaria* Räsänen, *C. viae-lacteae* G. Thor & V. Wirth, *C. boikoi* Khodos. & S. Y. Kondr. and forms of *C. aurella* (Hoffm.) Zahlbr. with an eroded non-yellow thallus. It differs from *C. subdeflexa* by having blastidia and the absence of an epinecral layer. In addition, the layer of conidiophores on the lower side of the squamules is absent or poorly developed in *C. blastidiata*, whereas it is prominent in *C. subdeflexa* (Fig. 3D). In North America

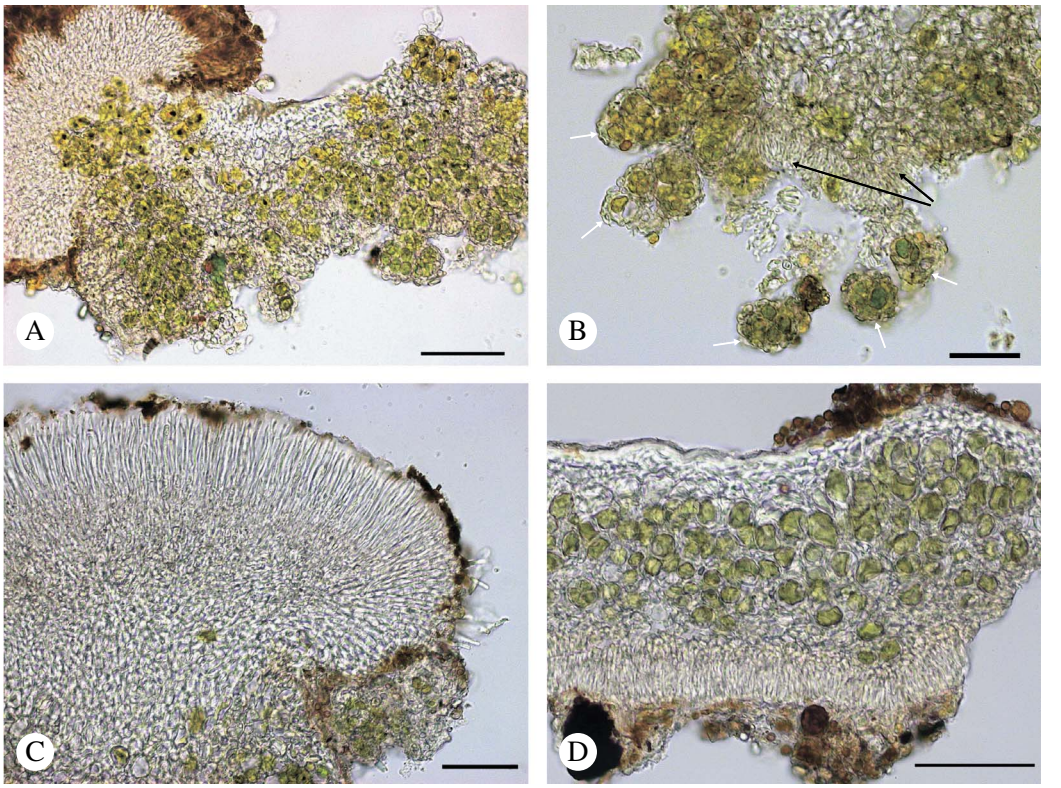

FIG. 3. A–C, *Candelariella blastidiata*, vertical sections through thallus; A, thallus with blastidia; B, lower part of thallus (white arrows, blastidia; black arrows, conidiophores); C, apothecium. D, *Candelariella subdeflexa*, vertical section through thallus with conidiophores on the lower side, lectotype (H–9506465). Scales: A = 100 µm; B–D = 50 µm. In colour online.

both species occur together in North Dakota. They could be easily distinguished from each other morphologically: North American specimens of *C. subdeflexa* typically have a well-developed thallus composed of thick, shiny squamules forming a thick imbricate crust (Westberg & Clerc 2012) while *C. blastidiata* is distinguished by having flattened, matt squamules with marginal or lower-side blastidia.

Candelariella blastidiata can be found sterile and then its grey thallus is not likely to be identified as *Candelariella*. In a sterile state, *C. blastidiata* could be confused with *C. viae-lacteae* G. Thor & V. Wirth. *Candelariella antennaria* with lecanorine apothecia might grow among squamules of sterile *C. blastidiata* and the combination of both species could be erroneously identified as *C. viae-lacteae*, which is characterized by lecanorine apothecia and a thallus composed of crowded granules resembling blastidia (Thor & Wirth 1990; Khodosovtsev *et al.* 2004; Khodosovtsev 2005). In such cases *C. blastidiata* is distinguished from *C. viae-lacteae* by permanent squamules while the thallus of *C. viae-lacteae* soon dissolves into granular blastidia. Some unrelated species (e.g. *Caloplaca substerilis* Vondrák *et al.*; Vondrák *et al.* 2013) might also be very similar to sterile crusts of *Candelariella. blastidiata*.

Morphological and molecular phylogenetic data support the close relationship of *C. subdeflexa* and *C. blastidiata* representing a so-called "species pair" (Poelt 1970) where *C. subdeflexa* reproduces by sexual propagules and *C. blastidiata* mostly by vegetative ones. Both species also possess asexual conidia as additional propagules; however, production of conidia appears to be less effective in *C. blastidiata*. Divergence by switching between reproductive modes has been shown for species in different families, such as *Parmeliaceae* (Poelt 1970; Miądlikowska *et al.* 2011), *Physciaceae* (Hafellner *et al.* 2012), *Teloschistaceae* (Vondrák *et al.* 2016) and *Umbilicariaceae* (E. A. Davydov, D. Peršoh & G. Rambold, unpublished data), and often results in a reduction of sexual reproduction in species with vegetative propagules. As all our ITS sequences of *C. blastidiata* are from Eurasia and the two *C. subdeflexa* sequences are from North America, our results might be alternatively interpreted as an existence of two species that differ in geographical range and that have a blastidiate or non-blastidiate appearance. We cannot deny this possibility because of the limited availability of specimens.

Further specimens of *C. blastidiata* could probably be found amongst those labelled as "*Candelariella subdeflexa*" in herbaria. Specimens of *C. subdeflexa* from southern and central Europe (e.g. Austria, France, Germany, Italy, Spain and Switzerland) and from North Africa (Algeria) (Westberg & Clerc 2012) should be re-evaluated. The record from Russia (Obermayer 2012) is based on *C. blastidiata*, so *C. subdeflexa* should be excluded from the lichen flora of Russia.

Selected specimens of Candelariella subdeflexa *examined.* **Algeria:** *Constantine*: An Baumrinden am Wege gegen Balna bei Canstantine, 500 m, 1888, *Flagey* 1433 (H).—**Afghanistan:** *Samangan*: Kotal-i-Mirza Atbili Pass on the road from Pule-Khumri to Samangan (Aybak), N-facing slope, silt, at the base of a stump of *Pistacia vera*, 1250 m, 1972, *P. Uotila* 16702 (H).—**USA:** *North Dakota*: Ward County, 5·5 mi NNE of Sawyer (14 mi ESE of Minot), in grove of box elder (*Acer negundo*) and green ash (*Fraxinus pennsylvanica*) surrounded by cultivated fields, 48°06'N, 101°03'W, 470 m, 1979, *T. D. Trana* 9940 [distributed by *C. M. Wetmore*] 37-98 (GZU). *Minnesota*: Becker County, 1 mi N of Stinking Lake (18 mi NW of Detroit lakes), lone stream near farm with box elder and bur oak, sec. 18, T 140 N, R 43 W, 1978, *C. M. Wetmore* 35958 (H); Clay County, 8 mi NW of Hawley (18 mi NE of Moorhead), near gravel pit in grove of trees with box elder, cottonwood and willow, sec. 13, T 140 N, R 45 W, 1978, *C. M. Wetmore* 35984/233-81 (GZU).

Key to *Candelariella* with a grey thallus

1 On rocks, apothecia lecanorine 2
On bark, wood, plant debris, apothecia lecanorine or biatorine 4

2(1) Thallus indistinct to areolate with convex areoles, apothecia with yellow thalline margin, often partly excluded . . . . . **C. aurella** (Hoffm.) Zahlbr. (grey thallus morphotype)
Thallus distinct, areolate to squamulose, thalline margin persistent, greyish in the outer side 3

3(2) Thallus areolate, thin; apothecia with thin, even thalline margin . . . . . **C. oleaginescens** Rondon
Thallus subsquamulose to squamulose, thick; apothecia with thick, crenulated and convoluted thalline margin . . . . . **C. plumbea** Poelt & Vězda

4(1) On plant debris or shrubs in steppes and salt marshes. . . . . **C. boikoi** Khodos. & S. Y. Kondr.
On bark, wood in various habitats. 5

5(4) Apothecia lecanorine 6
Apothecia biatorine 8

6(5) Thallus uniformly composed of crowded spherical granules, unbranched to coralloid . . . . . **C. viae-lacteae** G. Thor & V. Wirth
Thallus indistinct and seen only at the base of apothecia to amorphous crustose or areolate. 7

7(6) Thallus indistinct to amorphous crustose; thalline margin yellow, often greyish in the outer side, persistent; proper exciple does not form a stipe downward through the algal layer; on bark, rarely on wood. . . . . **C. antennaria** Räsänen
Thallus indistinct to areolate with convex areoles; thalline margin entirely yellow, often partly excluded; proper exciple forms a distinct stipe penetrating downward through the algal layer; mostly on wood . . . . . **C. aurella** (Hoffm.) Zahlbr. (grey thallus morphotype)

8(5) Thallus without blastidia, often shiny, conidiophores on the lower side of the squamules present . . . . . **C. subdeflexa** (Nyl.) Lettau
Thallus with blastidia, matt, conidiophores on the lower side of the squamules absent or poorly developed at the base of the squamules . . . . . **C. blastidiata** Yakovchenko

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