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Standard Paper

Candelariella ahtii (*Candelariaceae, Ascomycota*) – a new species of lichen from Central and North-East Asia, and a key to 8-spored *Candelariella*

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Abstract

Candelariella ahtii Yakovchenko sp. nov. is described based on phenotypic and ITS nrDNA sequence data. The species, occurring on soil in the crevices and cracks of siliceous rocks, is characterized by its squamulose cushion-forming thallus of imbricate, rounded to weakly incised granules/squamules with a greenish yellow to pale yellow pulverulent upper surface, lecanorine apothecia with a plane to somewhat convex ochre-yellow disc and a permanent thick thalline margin, 8-spored asci and ellipsoid to narrowly ellipsoid ascospores with rounded ends, as well as a distribution in Central and North-East Asia. It is similar to *Candelariella citrina* but differs in having ascospores without attenuated ends and smaller squamules. *Candelariella citrina* is excluded from the lichen flora of Russia. A worldwide key to all known *Candelariella* species with 8-spored asci, including 41 names, is provided.

Keywords: *Candelariella citrina*; China; Mongolia; Russia; Russian Far East; taxonomy

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Introduction

Candelariella Müll. Arg., a cosmopolitan genus of *c.* 75 species, includes lichenized taxa on all substrata, as well as non-lichenized fungi and lichenicolous parasites. The taxa are predominately nitrophilous with most occurring on rock, bark and plant debris in various undisturbed habitats as well as urban areas (e.g. Hakulinen 1954; Westberg 2004, 2005, 2007*a*, *b*, *c*; Khodosovtsev 2005; Westberg *et al.* 2009, 2011; Westberg & Sohrabi 2012; Ismailov *et al.* 2017). It is the largest genus of *Candelariaceae*, introduced by Hakulinen (1954) with three genera, namely *Candelaria* A. Massal. (as the type), *Candelariella* and *Placomaronea* Räsänen. The family currently includes two additional genera, *Candelina* Poelt (Poelt 1974) and the recently described *Protocandelariella* Poelt *et al.* (Kondratyuk *et al.* 2020) which was tentatively proposed by Poelt (1974) and subsequently confirmed by molecular studies (Westberg *et al.* 2007; Yakovchenko *et al.* 2017; Kondratyuk *et al.* 2020).

The phylogeny of *Candelariella* still has not yet been resolved. Miadlikowska *et al.* (2006) considered that the generic circumscription in *Candelariaceae* based on the outer morphology (i.e. growth form) only partly reflects the phylogeny. The first comprehensive molecular phylogenetic study of *Candelariella* (Westberg *et al.* 2007) based on ITS nrDNA demonstrated that the overall topology of the phylogram was poorly resolved and was strongly supported only at terminal clades due to several 'good species' with distinct morphology (Westberg 2007*a*, *b*, *c*). Subsequent phylogenies based on ITS nrDNA also confirmed the polyphyletic nature of *Candelariella* and *Candelaria* and were not well-resolved; however, they were still useful at a specific level and several new species were described (Westberg *et al.* 2011; Yakovchenko *et al.* 2017; Liu *et al.* 2019; Halıcı *et al.* 2023). The addition of several molecular markers did not give the desired result since the recent phylogeny (Kondratyuk *et al.* 2020) based on mostly nrITS and a small number of additional sequences of 12S mtSSU and 28S nrLSU demonstrated that the backbone of the phylogram was still poorly supported; nevertheless, three new genera were described. Cannon *et al.* (2021) suggested that the phylogenetic relationships within non-monophyletic *Candelariella* need additional research. *Protocandelariella* is morphologically and phylogenetically distinct whereas the segregation of two other genera, *Candelinella* S. Y. Kondr. and *Opeltiella* S. Y. Kondr., requires additional phenotypic and phylogenetic evidence.

The characters thought to be taxonomically important for *Candelariella* were summarized in Hakulinen (1954), Poelt (1974) and Westberg (2005). The main taxonomically important features to define the taxa are: life strategy, thallus growth form, colour and texture of the upper surface, type of apothecia, ascospore size, shape, septation and number per ascus, presence or absence of vegetative propagules and their localization, as well as substratum and ecology.

The group of *Candelariella* s. lat. with 8-spored asci is the largest among the genus, comprising 41 lichen taxa. It is represented by lichenized or lichenicolous species with all possible variations of thallus morphology, occurring on various substrata in habitats worldwide including both the Arctic and Antarctic. While checking herbarium material from Mongolia collected by the first

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Table 1. Voucher information and GenBank Accession numbers for the specimens used in the phylogenetic analyses in this study. Newly generated sequences are shown in bold

Species	Locality	Voucher (Herbarium)	GenBank Accession number
Candelariella aggregata	USA: Colorado	*Westberg* 1080 (LD)	EF535157
C. ahtii	Russia: Altai Territory	*Davydov* 16468 (ALTB)	**PP862913**
	Mongolia: Khentii Province	*Yakovchenko* 1266 (hb. Davydov & Yakovchenko)	**PP862911**
	Russia: Primorye Territory	*Yakovchenko* 1172 (VLA)	**PP862914**
	Mongolia: Khentii Province	*Yakovchenko* 1267 (hb. Davydov & Yakovchenko)	**PP862910**
	Russia: Altai territory, Tigirek strict reserve	*Davydov* 16329 (LE-13177–holotype; H, ALTB–isotypes).	**PP862912**
C. antennaria	Turkey	?CAN0413	MG271788
C. arctica	Norway: Finnmark	*Klepsland* (O-L200509)	MK812015
C. aurella	Czech Republic	*Vondrák* & *Palice* PRA-JV23720	OK332959
C. biatorina	USA: California	*Tucker* & *Bratt* 34049 (SBBG)	EF535165
C. borealis	Canada: Nunavut	*Westberg* 2381 (LD)	EF535167
C. californica	USA: California	*Westberg* 1244 (LD)	EF535169
C. canadensis	China: Yunnan	*Hur* & *Liu* (CH170062)	MG694271
C. citrina	Mexico: Baja California Sur	*Westberg* 398 (LD)	EF535170
	USA: Colorado	*Westberg* 1063 (LD)	EF535171
	USA: Arizona	*Westberg* 745 (LD)	EF535172
	USA: Utah	*Leavitt* 19122	MZ922103
	USA: Utah	*Leavitt* 19124	MZ922104
	USA: Utah	*Leavitt* 19086	MZ922105
C. clarkii	USA: Colorado	*Tripp* & *D'az* 4876 (COLO)	KR052104
C. complanata	Mexico: Baja California Sur	*Westberg* 383 (LD)	EF535174
C. coralliza	Sweden: Oland	*Westberg* 51 (LD)	EF535175
C. corallizoides	Mexico: Baja California Sur	*Westberg* 341 (LD)	EF535176
C. corviniscalensis	USA: Colorado	*Morse* 15881 & *Ladd* (S)	GU967377
C. deppeanae	USA: Arizona	*Westberg* 585 (holotype) (LD)	EF535178
C. efflorescens	Austria: Steiermark	*Arup* L97286 (hb. Ulf Arup)	EF535180
C. faginea	Russia: Western Caucasus	*Malíček* 10177 (hb. Malíček)	MK778596
C. flava	Antarctica	*Felix Bast* 877-L-2017-CF-1	MZ919298
C. granuliformis	Canada: Nunavut	*Mattsson* 5209 (UPS)	GU967375
C. kansuensis	USA: Arizona	*Wetmore* 55470 (MIN)	EF535181
C. lutella	Norway: Troms	*Westberg* 2808 (LD)	EF535182
C. medians	Sweden: Skane	*Arup* L03165 (LD)	EF535184
C. placodizans	Canada: Nunavut	*Westberg* 206 (LD)	EF535187
C. plumbea	China	14-04-0978	MN103123
C. reflexa	Norway: Vestfold	*Lindblom* & *Blom* L61 (BG)	EF535190
C. rosulans	USA: Colorado	*Westberg* 1146 (LD)	EF535191
C. rubrisoli	China: Yunnan	*Hur* & *Liu* (CH170039)	MG694273
C. ruzgarii	Antarctica: James Ross I.	*Halıcı* (ERCH:JR 395")	NR185742
C. spraguei	USA: Colorado	*Westberg* 1037 (LD)	EF535194
C. subsquamulosa	South Korea: Jeollanam-do, Suncheon-si	*Liu* 171419	MG694274

(*Continued*)

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Table 1. (*Continued*)

Species	Locality	Voucher (Herbarium)	GenBank Accession number
C. terrigena	Canada: Nunavut	*Lutzoni* & *Miadlikowska* 07.13.03-19 (DUKE)	HQ650602
C. viae-lacteae	Czech Republic	*Vondrák* 10677 (PRA)	OQ717356
C. vitellina	Norway: Oslo	*Haugan* (O-L-166987)	MK812582
C. xanthostigma	Czech Republic	Hb. Malíček 5066	OQ717357
Protocandelariella blastidiata	China: Xinjiang	*Davydov* 12272 (ALTB)	KX853126
P. subdeflexa	USA: Arizona	*Nash* 38631 (ASU)	EF535197
Pycnora xanthococca	Norway	*Timdal* 11646 (O L-163707)	KF360412

author, our attention was caught by a *Candelariella* sp. with a cushion-forming, greenish yellow pulverulent thallus growing not directly on siliceous rock surfaces but in rock crevices and easily falling down from the substratum. Morphologically and ecologically, it resembled the American taxon *Candelariella citrina* de Lesd., known mostly from North America. Anatomical investigation showed that the specimens had no citriform ascospores which are characteristic of *C. citrina*. The same material was collected during the authors' joint fieldwork in 2014 in the Altai Mountains and Russian Far East, and also found after checking herbarium material collected by the second author from China. Both morphological and molecular studies have independently confirmed its status as a new species, described here as *Candelariella ahtii*. A worldwide key to 8-spored *Candelariella* is also presented.

Materials and Methods

Sampling

Sixteen collections of fresh material of *Candelariella ahtii* were made by the authors between 2006 and 2014 and are deposited in the private herbarium of Davydov & Yakovchenko, with duplicates deposited in the herbaria ALTB and VLA. The type material was deposited in LE and ALTB as well as being prepared for transfer to H. At each location, material was collected over the sampled boulder or rock, not directly from the rock surface but on soil in cracks and crevices. For each collection, the following were recorded: GPS coordinates, elevation, surrounding environment and substratum. Additionally, specimens of *Candelariella citrina*, including the type material, were studied from the herbaria H, S, TUR and UPS as well as the private herbaria of B. McCune and J. Hollinger.

Morphology, anatomy and chemistry

Morphological observations were carried out using a stereomicroscope (Zeiss Stemi 2000-C). Apothecia and thalli were hand-sectioned with a razor blade and observed with a compound microscope (Zeiss Axio Lab.A1) after mounting in water. Measurements of the squamules, apothecia, ascospores and thalline margin are presented as the mean ($\bar{x}$) and range including 85% of the variation, bounded by the smallest and largest observed values and the sample size (n), following Westberg (2005). Other measurements are presented as (extreme minimum) minimum–maximum (extreme maximum) or the maximum value observed. Measurements were recorded to the nearest 0.5 µm. Lichen substances were studied by spot tests using potassium hydroxide solution (K), sodium hypochlorite solution (C), 1,4-p-phenylendiamine (PD), potassium iodide solution (I), and by thin-layer chromatography (TLC) with solvent systems A, B' and C, following Orange *et al.* (2001).

DNA extraction, amplification and sequencing

Between 3–5 apothecia were carefully checked for fungal infections and thoroughly cleaned of extraneous matter. DNA extraction, primers, amplification and sequencing of the internal transcribed spacer region of nuclear ribosomal DNA (ITS) followed the methods of Davydov & Yakovchenko (2017). Cycling conditions included initial denaturation at 94 °C for 5 min, 35 cycles of 95 °C for 20 s, 52 °C for 40 s, 72 °C for 60 s, and a final extension step at 72 °C for 7 min. The program Geneious v. 6.0 (Biomatters Ltd, New Zealand) was used for assembling partial and complementary sequences.

Sequence alignment and phylogenetic analyses

To test the phylogenetic relationship to other species of *Candelariella*, all obtained sequences of the putative new species were supplemented with sequences of *Candelariella* species obtained from GenBank (Table 1). Sequences were aligned with those of 35 species, preferably representing type material, from the most comprehensive phylogenetic study of *Candelariella* by Westberg *at al.* (2007) and other recent studies, where possible representing material from Eurasia (Schmull *et al.* 2011; Westberg *et al.* 2011; Tripp & Lendemer 2015; Yakovchenko *et al.* 2017; Liu *et al.* 2019; Urbanavichus *et al.* 2020; Halıcı *et al.* 2023; Vondrák *et al.* 2023). *Pycnora xanthococca* (Sommerf.) Hafellner was used as the outgroup since *Pycnora* has been suggested as the sister clade to *Candelariaceae* (Bendiksby & Timdal 2013). An ITS1-5.8S rDNA-ITS2 dataset containing the sequences listed in Table 1 was compiled and aligned using the MAFFT algorithm (Katoh *et al.* 2019) and visible deviations in position homology were then manually optimized. A total of 469 bp alignment sites were used for a heuristic search for the maximum likelihood (ML) bootstrap tree, with simultaneous inference of the optimal partitioning scheme and substitution models (TIM2e + G4 for ITS1, K2P + I for 5.8S, and TPM2u + F + G4 for ITS2 subsets) performed using the online version of IQ-TREE (Nguyen *et al.* 2015; Trifinopoulos *et al.* 2016), suggesting three initial partitions

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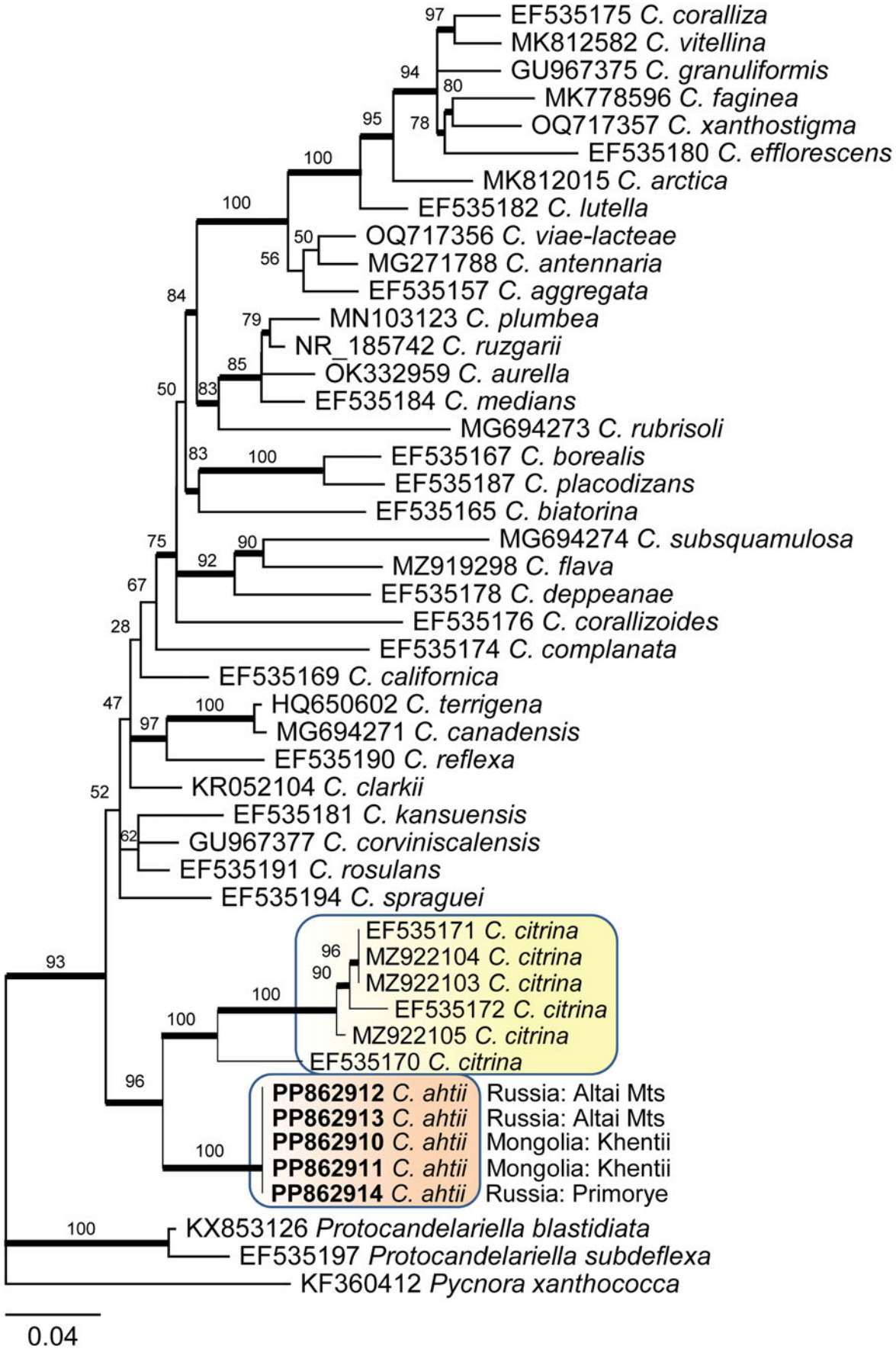

Figure 1. Phylogenetic relationships amongst *Candelariella* species, based on a maximum likelihood analysis of ITS1-5.8S-ITS2. The reliability of each branch was tested by ML analysis. Numbers at tree nodes indicate bootstrap values of ML. Thicker branches indicate a ML bootstrap value of ≥ 70%. GenBank Accession numbers are given in Table 1. Branch lengths represent the estimated number of substitutions per site assuming the respective models of substitution. In colour online.

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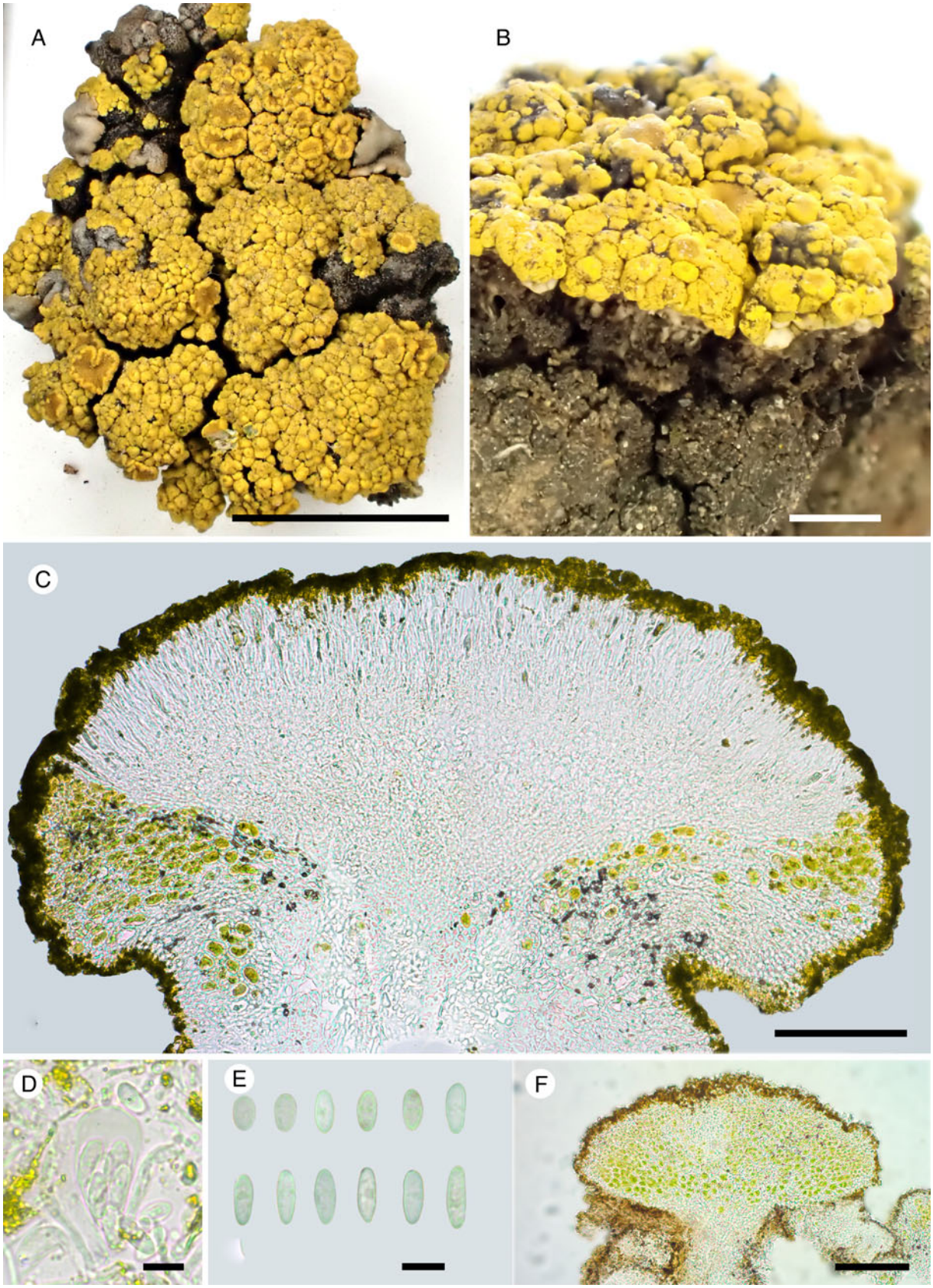

Figure 2. A–F, holotype of *Candelariella ahtii* (LE-13177). A, upper surface showing cushion-forming thallus divided by cracks. B, lower surface, showing grey lower surface constricted into a stipe. C, section of an apothecium, showing compact basal stipe formed by the *aurella*-type proper margin. D, 8-spored asci. E, ellipsoid to narrowly ellipsoid, or broadly ellipsoid, ascospores with rounded ends. F, section of a squamule. Scales: A = 5 mm; B = 1 mm; C = 50 μm; D & E = 10 μm; F = 100 μm. In colour online.

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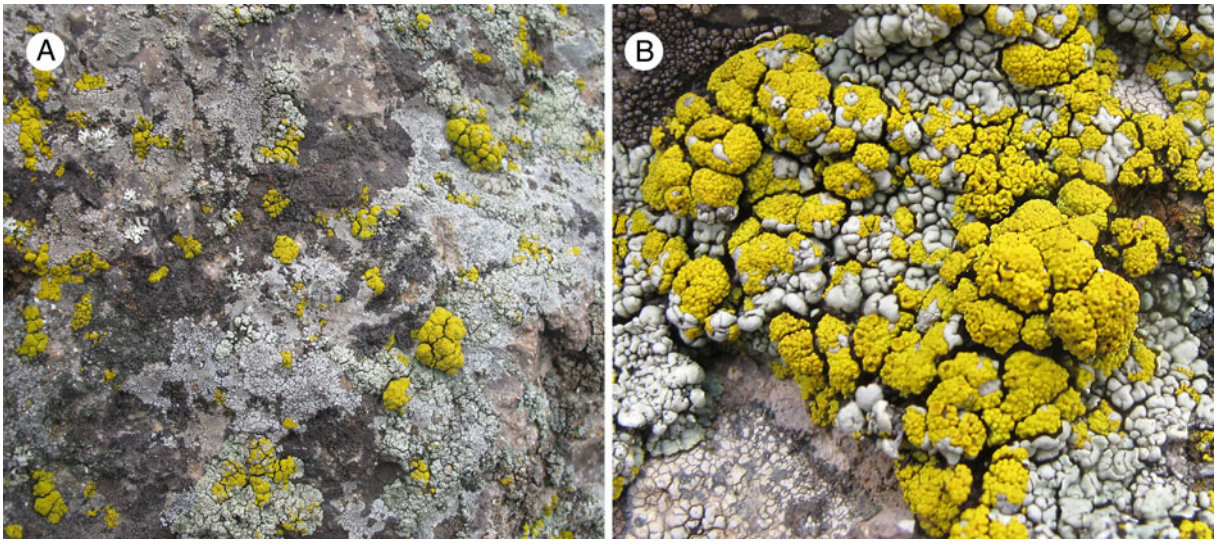

Figure 3. A & B, field photographs of *Candelariella ahtii* (LE-13177). A, *Candelariella ahtii* with neighbouring saxicolous species. B, *Candelariella ahtii*, in detail. In colour online.

(ITS1, 5.8S rDNA, ITS2). Branch lengths were assumed to be equal for all partitions. Branch support was estimated with the ultrafast bootstrap algorithm (Minh *et al.* 2013) based on 1000 bootstrap replicates and using a maximum of 1000 iterations and a minimum correlation coefficient of 0.99 as a stopping rule.

Results

The phylogenetic study

To test the monophyly and phylogenetic relationships of the putative new species, we used ITS/5.8S rDNA sequences. ITS sequences were successfully obtained from five specimens from different regions of Asia. Despite long distances between collected specimens, ITS sequences of *Candelariella ahtii* were identical and combined into a well-supported clade (100% bootstrap support (BS)) (Fig. 1). *Candelariella ahtii* clusters as sister to *C. citrina* with high support (97% BS).

Candelariella ahtii Yakovchenko sp. nov.

MycoBank No.: MB 854215

Thallus on soil in siliceous rock crevices and cracks, squamulose, up to 1.5(–2.0) mm thick, cushion-forming, split by cracks; of imbricate, large, rounded to weakly incised granules/squamules (0.15–)0.25–*0.35*–0.5(–0.8) mm diam., constricted at the base into a stipe. Vegetative propagules and prothallus are absent. Upper surface is greenish yellow to pale yellow, pulverulent, lower surface grey. Apothecia lecanorine, rounded to wavy or lobate with a flattened to somewhat convex, ochre-yellow disc, with a permanent, even to incised thalline margin. Asci 8-spored, ascospores ellipsoid to narrowly ellipsoid, rarely broadly ellipsoid, with rounded ends (8.5–)11.0–*12.5*–14.0(–16.0) × (4.5–)5.0–*5.3*–5.5(–6.0) µm. Similar to *Candelariella citrina* but differs by its ascospores with non-attenuated ends. It differs from *C. grimmiae* Poelt & Reddi by its pulvinate thallus of imbricate large granules/squamules constricted basally into a stipe and its smaller ascospores.

Type: Russia, Altai Territory, Krasnoshchokovsky District, Tigireksky Range, Tigirek Strict Reserve, 7.6 km NW from the Tigirek settlement, Chorny Kamen' Mt, 51°11′29″N, 82°56′52″E, 970 m, conglomerate rocks, on soil and lichens in rock crevices, 20 June 2014, *E. A. Davydov* 16329 & *L. S. Yakovchenko* LYF-14-33 (LE-13177—holotype; H, ALTB—isotypes).

(Fig. 2)

Thallus squamulose, loosely attached to the substrate, distinct and visible as ±continuous thick cushion-forming crust divided by deep cracks into irregular clusters up to 3.5(–5.0) mm wide and 1.5(–2.0) mm tall ($n = 35$), composed of imbricate, large granules or subsquamules/squamules, without vegetative propagules. *Prothallus* absent. *Granules/squamules* (0.15–)0.25–*0.35*–0.50(–0.80) mm diam. ($n = 155$) and up to 0.3 mm tall, convex, imbricate, rounded to weakly incised or rarely sublobate, constricted at the base, into a stipe. *Upper surface* greenish yellow to pale yellow, pulverulent, coarse, matt. *Lower surface* grey. *Pseudocortex* indistinct to thin, of (0)1–2 cell layers, 5.0–12.5 µm thick ($n = 25$), composed of non-gelatinized hyphae with ±isodiametric, thin-walled cells 3–7 µm wide ($n = 25$), in uppermost part covered by yellow-brown irregular cortical crystals, without an epinecral layer. *Algae* chlorococcoid, 5–18 µm diam. ($n = 21$).

Apothecia common, lecanorine, rounded to wavy or lobate, constricted at the base, crowded to scattered, (0.3–)0.4–*0.75*–1.2(–1.5) mm wide ($n = 105$). *Disc* ochre-yellow, plane to somewhat convex or concave in the centre, brownish tan when old. *Proper margin* not visible from the outside. *Thalline margin* of the same colour as the thallus, pulverulent, matt, persistent, at the same level as the disc or lower, entire or slightly incised to sublobate, (0.05–)0.07–*0.10*–0.15(–0.2) mm thick ($n = 55$); with a thin pseudocortex, of 1–2(–3) cell layers, 4–18 µm thick ($n = 21$), thicker at the base of apothecia, composed of thin-walled, ±isodiametric cells, 3–8 µm wide ($n = 21$), covered by 4–10 µm thick ($n = 21$) layer of yellow-brown, irregular cortical crystals. *Proper margin* indistinct to well developed and fan-shaped, 27–40 µm wide ($n = 21$) in the uppermost part, *aurella*-type, viz. of branched, thick-walled, radiating hyphae

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Figure 4. A & B, habitats of *Candelariella ahtii*. A, type locality in the Altai Mts. B, a local rocky summit with sparse *Juniperus rigida* Siebold et Zucc. surrounded by *Quercus mongolica* forest in the Russian Far East. In colour online.

with rectangular cells 5–15 × 2–3 µm ($n = 21$), which become shorter and rounded in the uppermost part and below the hypothecium form a stipe penetrating downwards through the algal layer. *Epihymenium* reddish yellow to yellow-brown, 5–12 µm tall ($n = 21$), of irregular, angular crystals; *hymenium* hyaline, 50–75 µm tall ($n = 21$); *subhymenium* hyaline, with oil droplets; *paraphyses* septate, simple or branched near the tips, 1.7–3.0 µm wide in mid-hymenium ($n = 21$) with cylindrical or clavate tips, 3.0–5.5 µm wide ($n = 21$); *asci* 8-spored, clavate to broadly clavate, 40–60 × 14–19 µm ($n = 21$), *Candelariella*-type; *ascospores* hyaline, simple,

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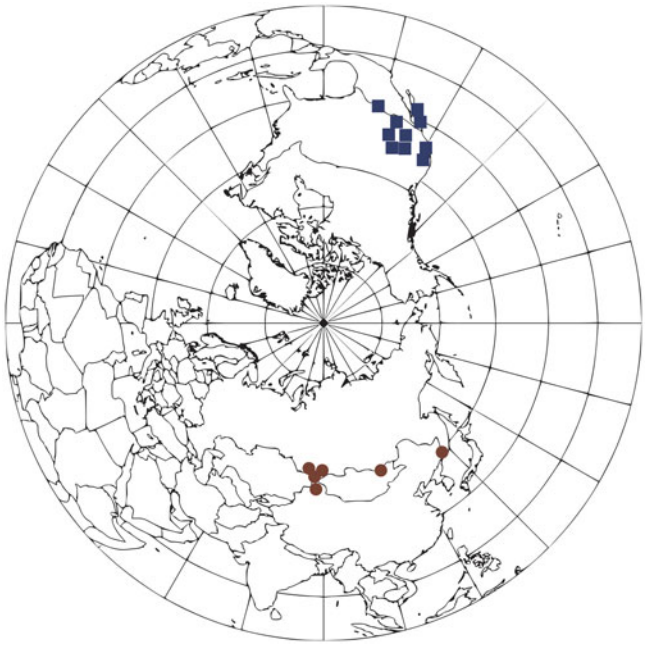

Figure 5. Distribution of *Candelariella ahtii* (●) and *C. citrina* (■) in the Northern Hemisphere. In colour online.

rarely 1-septate with thin septa, straight, ellipsoid to narrowly ellipsoid, or rarely broadly ellipsoid, with rounded ends, (8.5–)11.0–*12.5*–14.0(–16.0) × (4.5–)5.0–*5.3*–5.5(–6.0) µm (n = 145).

Pycnidia not seen.

Chemistry. Thallus and disc K+ weakly reddish, KC−, C−, P−; hymenium I+ blue; medulla I−. Calycin, pulvinic acid, pulvinic dilactone and vulpinic acid detected by TLC.

Etymology. The species is named after the great Finnish lichenologist, Teuvo Ahti, dear friend of the authors, with gratitude for his kindness, responsiveness, care and help, as well as with appreciation for his remarkable contribution to the study of *Cladonia* worldwide.

Ecology. Candelariella ahtii occurs in open siliceous outcrops on boulders or rocks, not directly on the rock surface but on soil in cracks and crevices, sometimes covering saxicolous lichens growing nearby (Fig. 3). It has been recorded at elevations between 390 and 2550 m, but it seems to prefer moderate elevations since most records are found at *c.* 1000 m a.s.l. In the area of investigation, three vegetation belts are found within this elevational range: forest, montane steppe and alpine. It is mostly recorded in open habitat in alpine or mountain steppe belts. Part of the location is located in the forest belt where the surrounding areas are wooded, mainly *Larix sibirica* Ledeb. (in Central Asia), *Quercus mongolica* Fisch. ex Ledeb. or mixed broad-deciduous forest (in the Far East). In these forested habitats, *Candelariella ahtii* occurs in well-lit open sites, mostly on the upper part of large boulders and rock massifs, but never in very shady areas (Fig. 4).

Candelariella ahtii rarely occurs monospecifically, but is often mixed with *C. vitellina* s. lat. It also occurs with *Acarospora badiofusca* (Nyl.) Th. Fr., *Circinaria* sp., *Dimelaena oreina* (Ach.) Norman, *Lecanora achariana* A. L. Sm., *Montanelia tominii* (Oxner) Divakar *et al.*, *Rhizocarpon geographicum* (L.) DC., *R. subgeminatum* Eitner, *Rhizoplaca chrysoleuca* (Sm.) Zopf, *R. subdiscrepans* (Nyl.) R. Sant. and *Rimularia badioatra* (Kremp.) Hertel & Rambold.

Distribution. Candelariella ahtii is distributed in Central and North-East Asia. To date this lichen has been collected from several localities in Mongolia, China and Russia (Altai Mountains and Russian Far East). It is known from 43–51°N and 83–133°E with the distance from the most remote localities *c.* 3800 km (Fig. 5).

Additional specimens examined. **Russia:** *Primorye Territory*: Khankaisky District, 15 km S from the Komissarovo settlement, Pogranichnyi Range, top of Siniaya Mt, 44°51′37.5″N, 131°42′34″E, 650 m, on soil and other lichens in rocks crevices, 2013, *L. S. Yakovchenko* 1172 (VLA); *ibid.*, 2014, *E. A. Davydov* 16310, 16328, 16483 & *L. S. Yakovchenko* (hb. Davydov & Yakovchenko); Chuguevsky District, Sikhote-Alin' Range, at the right bank of the Egerskaya River between Verkhniaya Breevka and Arkhipovka, Parshivaya Mt, 43°46′03.5″N, 133°48′33.5″E, 480 m, siliceous rock outcrops at the summit, surrounded by *Quercus mongolica* forest, on soil in rock crevices, 2017, *E. A. Davydov* 17417 & *L. S. Yakovchenko* (hb. Davydov & Yakovchenko). *Altai Territory*: Ust'-Kalmansky District, 3 km W from the Ogni settlement, foothills of the Altai Mts, right bank of the Zemlyanukha River, 51°53′40″N, 83°29′05″E, 390 m, open siliceous outcrops of the top of the hill, SW slope, on soil in rock crevices, 2014, *E. A. Davydov* 16330, 16481, 16468 & *L. S. Yakovchenko* (ALTB). *Republic of Altai*: Kosh-Agachsky District, Altai Mts, Sailjugem range, watershed of Bayan-Chagan and Sarzhemoty Rivers, 4 km S of its junction, mountain rocky steppe, on soil in rock crevices and saxicolous lichens, 49° 32′06″N, 88°45′31″E, 2550 m, 2014, *E. A. Davydov* 16312 & *L. S. Yakovchenko* (ALTB). *Republic of Tuva*: Mongun-Taiginsky District, Mongun-taiga massif, left side of the Toolaity River valley, 5 km upstream of the Eski-Toolaity Lake, 50°11′36″N, 90°08′46″E, 2550 m, mountain tundras, stonefield, on soil in rock crevices, 2014, *E. A. Davydov* 16308 & *L. S. Yakovchenko* (ALTB); *ibid.*, headwaters of the Orta-Shegetei River, 4.5 km upstream of the Sive-Khol′ Lake, 50°09′10″N, 90°01′21″E, 2480 m, stonefield, on crevices of the rocks, 2014, *E. A. Davydov* 16315 & *L. S. Yakovchenko* (ALTB).—**China:** *Xinjiang*: Mongol'sky Altai Range, upper reaches of Khara-Belchir-he, west slope of Kara-Balchigtau Mt (3215 m), 46°42′08″N, 90°58′29″E, 2400 m, *Larix sibirica* forest, on soil in rock crevices, 2007, *E. A. Davydov* 16314 (ALTB); Zimunai County, Saur Range, N slope, valley of Ul'kun-Ulyasty near the border with Kazakhstan, 15 km to the north of Mustau peak (3816 m a.s.l.), 40 km S of Zimunai, 47°10′30″N, 85°38′28″E, 2410 m, degraded alpine meadow along the road, on soil in rock crevices, 2007, *E. A. Davydov* 16316 (ALTB).—**Mongolia:** *Khentii Province*: 28 km SW from Dadal, Shulub-Ula Mt, 48° 56′59″N, 111°22′08″E, 1100 m, granite boulders in the mountain steppe, on soil in rock crevices, 2006, *L. S. Yakovchenko* 1266 (hb. Davydov & Yakovchenko); the same massif, 48°56′42″N, 111°22′03″E, 1066 m, granite boulders in the mountain steppe, on soil in rock crevices, 2006, *L. S. Yakovchenko* 1267 (hb. Davydov & Yakovchenko).

Candelariella citrina de Lesd.

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Ann. Cryptog. Exot. **5**, 120 (1932); type: USA, New Mexico, Environments de Las Vegas, Thunderbird Ranch, alt.: 1950 m, 5. II. 1929 *Arsene Brouard* (L-106306) 190850 (UPS—lectotype!).

Candelariella terrigena Räsänen, *Anales Soc. Ci. Argent.* **128**, 137 (1939); type: USA, Colorado, Gregory Canyon near Boulder, ad terram argillaceam, 16 Jul 1931 [1921?], *C. C. Plitt* (the second piece from the right) (H—lectotype!).

Candelariella terrigena var. *placodimorpha* Hakul., *Arch. Soc. Zool.-Bot. Fenn. 'Vanamo'* **13**, 54 (1958); type: USA, New Mexico, Valencia Co., lava flows and sandstone ledges along San Jose River, 3.5 miles SE of Correo on road to Las Lunas, *c.* 5500 ft, 27 Mar 1956, *S. Shushan* & *W. A. Weber* S6893 (TUR—holotype!).

Additional specimens examined. **USA:** *Nevada*: Washoe, Dogskin Mountain, south-eastern end of mountain, open north face of small granite outcrop at top of small ridge, with a few scattered *Juniperus osteosperma*, *Artemisia tridentata* and *Pinus andersonii*, 39.8473°N, 119.7647°W, 1800 m, granite, 2016, *J. Hollinger* 6993; Lincoln, Hiko Range, Crystal Wash, *c.* 5.5 km ENE of jct. of Hwys 93 and 25, at foot of N-facing cliff in small rhyolite-tuff canyon, 37.5441°N, 115.1712°W, 1248 m, vertical shaded tuff, 2018, *J. Hollinger* 6994. *California*: Siskiyou County, 41.9786°N, 122.4488°W, 755 m, NW of Iron Gate Reservoir, Horseshoe Ranch Wildlife Area, open savannah and woodland with andesite outcrops, on soil and mosses over rocks, March 2017, *B. McCune* 37341 with NW lichenologists; Orange Co., south slope of Santa Ana Mts, below Silverado near the boundary of Cleveland National Forest, on sandstone rocks at the river, elev. *c.* 700 m, 1966, *R. Santesson* 17723 (F69994-S). *Arizona*: Maricopa, White Tank Mountains, county regional park, habitat on granite, 1975, *T. H. Nash* 9808 (F69998–S). *Texas*: Brewster County, Big Bend National Park, low hill just SE of headquarters at Panther Junction, along north-facing hillside among boulders in desert, elev. 3800 ft, 1980, *C. M. Wetmore* 40838 (F69997-S).

Discussion

Phylogenetic position and diagnostic traits

Candelariella ahtii clusters as sister to morphologically and ecologically similar *C. citrina*, both having a squamulose thallus with a greenish yellow pulverulent surface, similar type and size of apothecia, and ascospores of similar size, but the latter species has citriform to broadly fusiform ascospores with one or both ends pointed (Westberg 2007*c*), whereas those of *C. ahtii* are ellipsoid, or narrowly ellipsoid to broadly ellipsoid, with rounded ends. *Candelariella ahtii*, in contrast to *C. citrina*, usually has a cushion-forming thallus of imbricate, large granules or squamules divided by deep cracks, whereas *C. citrina* rarely forms a continuous crust (Westberg 2007*c*), although specimens examined from Nevada (*J. Hollinger* 6993) showed a similar thallus morphology to *C. ahtii*. In addition, the size of the squamules is smaller (up to 0.5(–0.8) mm long in *C. ahtii* and up to 0.6(–1.3) mm long in *C. citrina*); the ascospores with equal maximum length (up to 16 µm) are narrower (up to 5.5(–6) µm in *C. ahtii* and up to 6.5(–7) µm in *C. citrina*). *Candelariella grimmiae* described from Nepal (Poelt & Reddi 1969) is similar to *C. citrina* (Westberg 2007*c*) and *C. ahtii* in having a squamulose thallus with a greenish yellow to ginger yellow heavy pulverulent surface, even characterized as 'sorediate in some areas, but without the formation of distinct sorale' in the protologue, and occurring on soil over gneiss. The ascospore size given in the protologue is (13.0–)15.0–18.5 × (4.5–)5.0–6.5 µm which is larger than those observed in *C. ahtii* and *C. citrina*. Unfortunately, the shape of the ascospores and the shape of the ends, which are key characters in this case, are not given in the protologue. We agree with Westberg (2007*c*) that additional material is needed to confirm the independent status of these species. *Candelariella grimmiae* is distinguished from *C. ahtii* by its larger thallus of prostrate well-developed squamules with deeply incised ascending margins, whereas *C. ahtii* usually forms a cushion-forming crust of imbricate granules or squamules divided by cracks into irregular clusters, and the size of the squamules is smaller than given for *C. grimmiae*. The thallus of thick cushions up to 2 mm thick divided by cracks is also known in the saxicolous *C. coralliza* (Nyl.) H. Magn. but this has polysporous asci; when sterile the species is distinguished by its thallus composed of deeply incised coralloid squamules, which are even considered to be isidia (Khodosovtsev 2005). *Candelariella ahtii* is often found together with *C. vitellina* s. lat., which also possesses a thallus in the form of a thick pulvinate crust, but differs in its polyspored asci with oblong, smaller, up to 12.5(–14.0) µm long ascospores. *Candelariella vitellina* s. lat. was often found sterile but could be well distinguished from *C. ahtii* by its smaller, up to 0.2 mm long squamules with serrated margins and an orange-yellow smooth upper surface. *Candelariella ahtii* differs from terricolous and muscicolous *C. canadensis* H. Magn. by its thallus morphology and apothecia with a flattened disc and a permanent, thick thalline margin. *Candelariella rosulans* (Müll. Arg.) Zahlbr. has a similar apothecial morphology to *C. ahtii* but is distinguished by its significantly larger ascospores, different thallus morphology and ecological preferences.

Distribution and ecology

The ecology of *Candelariella ahtii* seems to be quite similar to that of *C. citrina* (Westberg 2005, 2007*c*), a related species from the Americas which is common in open habitats at moderate elevations, reaching up to at least 2200 m, but with a wider range of substrata, growing not only on soil and other lichens but also on saxicolous mosses (Westberg 2007*c*). We have found *C. ahtii* growing on *Montanelia tominii*, *Rhizoplaca chrysoleuca* and *R. subdiscrepans* only in two locations in the Russian Far East (North-East Asia) and the Altai Mts (Central Asia) and have never seen it on mosses. In addition, we usually found *C. ahtii* mixed with and on *C. vitellina* s. lat., on the same rock face in locations at moderate and high elevations. Both species grow on soil in rock crevices although normally *Candelariella vitellina* s. str. grows on siliceous rock and is less often found on a variety of substrata with the exception of soil (Westberg 2007*b*).

Morphological and molecular phylogenetic data support the close relationship of *C. ahtii* and *C. citrina*. Since all our ITS sequences of *C. ahtii* are from Asia and *C. citrina* sequences from NCBI are from North America, our results might be interpreted as an existence of two vicarious species that differ in geographical range and ascospores shape. We cannot deny this possibility despite the limited availability of specimens. Nevertheless, the record of *C. citrina* from Siberia (Urbanavichus 2010) is considered dubious and should be excluded from the lichen flora of Russia.

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Worldwide key to the 8-spored *Candelariella* s. lat.

All 41 known *Candelariella* s. lat. species (including two of *Protocandelariella*) with 8-spored asci are included in the key. Other than names with an asterisk (*), all taxa either have a distinct morphology and/or molecular data, or type material and/or relevant herbarium material studied by the first author in ALTB, F, GZU, H, H-ACH, H-NYL, HIRO, KPABG, LE, NIBR, S, TDZ, TNS, TUR, VBGI, VLA and UPS. Although some little-known species with 8-spored asci have not been studied by us, they are also included. Distribution data is given for each species as suggested by studied herbarium material or reliable literature data.

1 Lichenicolous . . . 2
Not lichenicolous . . . 3

2(1) Apothecia biatorine, thallus absent, on *Candelina submexicana* (de Lesd.) Poelt; N America . . . . **C. lichenicola** M. Westb.
Apothecia lecanorine, thallus absent or present then grey amorphous, on *Lecanora populicola* (DC.) Duby; Europe, Asia (Caucasus) . . . **C. superdistans** (Nyl.) Malme

3(1) Thallus distinctly placodioid, on rocks . . . 4
Thallus indistinct, areolate, subsquamulose, squamulose, rosulate, never with elongated marginal lobes, on various substrata . . . 6

4(3) Lobes strongly convex and short, 1–2 mm long, pruinose in the central part; Europe, Asia (Caucasus, SW Asia) . . . **C. rhodax** Poelt & Vězda
Lobes flattened and long, up to 3–5 mm long, with or without pruina; different regions . . . 5

5(4) With granular areoles in the centre of the thallus, disintegrating into isidious soredia or blastidia, usually pruinose; Europe, Africa, Asia . . . **C. medians** (Nyl.) A. L. Sm.
Without vegetative propagules, usually epruinose; Europe, Asia . . . **C. senior** Poelt

6(3) Apothecia biatorine . . . 7
Apothecia lecanorine or pseudolecanorine . . . 10

7(6) Thallus endolithic; N America . . . **C. corviniscalensis** C. A. Morse & M. Westb.
Thallus apparent, corticolous; various regions . . . 8

8(7) Thallus yellow, crustose; Asia, N America . . . **C. biatorina** M. Westb.
Thallus grey, squamulose; different regions . . . 9

9(8) Thallus without blastidia, often shiny, conidiophores present on the lower side of the squamules, forming a ±continuous layer; Europe, Africa, Asia, N America, New Zealand . . . **P. subdeflexa** (Nyl.) Poelt *et al.*
Thallus with blastidia, matt, conidiophores absent from the lower side of the squamules or poorly developed at the base of the squamules; Europe, Asia, N America . . . **P. blastidiata** (Yakovch.) D. Liu *et al.*

10(6) Thallus grey or apparently lacking . . . 11
Thallus yellow . . . 21

11(10) On rocks . . . 12
On bark, wood, plant debris . . . 18

12(11) Thallus indistinct, present as a thalline margin which is often partly excluded to indistinct . . . 13
Thallus distinct, areolate, subsquamulose, squamulose, amorphous crustose, thalline margin distinct . . . 14

13(12) Ascospores (11.0–)12.0–16.0(–16.5) × 4.0–5.0(–6.0) µm, apothecia 0.3–0.55(–0.7) mm wide with yellow thalline margin, often partly excluded; cosmopolitan . . . **C. aurella** (Hoffm.) Zahlbr. (grey thallus morphotype)
Ascospores (9.0–)10.0–13.0 × (5.5–)6.0–7.0(–8.0) µm, apothecia 0.5–1.6 mm wide with whitish to greyish thalline margin, suppressed to the lower side of apothecia; N America . . . **C. immarginata** M. Westb.

14(12) Thallus subsquamulose to squamulose, thick, apothecia with thick, crenulated and convoluted thalline margin . . . 15
Thallus areolate to amorphous crustose, thin, apothecia with thin, even to somewhat crenulated thalline margin . . . 16

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15(14) On calcareous rocks or granite, inland, mountain to Arctic-alpine; Europe, Asia, N America, Antarctic . . . . . **C. plumbea** Poelt & Vězda
On siliceous rocks, coastal, temperate; E Asia (South Korea) . . . . . **C. hakulinenii** S. Y. Kondr. *et al.*

16(14) Thallus of convex areoles, thalline margin yellow, often partly excluded; cosmopolitan . . . . . **C. aurella** (Hoffm.) Zahlbr. (grey thallus morphotype)
Thallus of flattened areoles or amorphous crustose, thalline margin grey, persistent; various regions 17

17(16) On siliceous rocks, amphibious in splash zone of high mountain streams, inland; C Asia (Russia) . . . . . **C. aquatica** Yakovch. *et al.*
On calcareous rocks, not amphibious or connected with streams, temperate to mountain; Europe, Africa, Asia . . . . . **C. oleaginescens** Rondon

18(11) Apothecia large, (0.3–)0.5–1.2(–1.5) mm diam., aggregate. On plant debris or shrubs in steppes and salt marshes; Europe, C Asia . . . . . **C. boikoi** Khodos. & S. Y. Kondr.
Apothecia smaller, 0.2–0.8(–1.0) mm diam., scattered to aggregate. On bark, wood in various habitats; various regions . . . 19

19(18) Thallus uniformly composed of crowded spherical granules, unbranched to coralloid; Europe, Asia . . . . . **C. viae-lacteae** G. Thor & V. Wirth
Thallus indistinct and seen only at the base of apothecia to amorphous crustose or areolate; various regions 20

20(19) Thallus indistinct to areolate, of convex areoles, thalline margin entirely yellow, often partly excluded, proper margin of *aurella*-type, of elongated, thick-walled cells forming a compact stipe penetrating through algal layer; on wood; cosmopolitan . . . . . **C. aurella** (Hoffm.) Zahlbr. (grey thallus morphotype)
Thallus indistinct to amorphous crustose, thalline margin yellow, often greyish in the outer side, persistent, proper margin of *aggregata*-type, of more or less isodiametrical, thin-walled cells not forming a compact stipe; on bark, rarely on wood; Europe, Asia, N America . . . . . **C. antennaria** Räsänen

21(10) Thallus with vegetative propagules 22
Thallus without vegetative propagules 27

22(21) Thallus squamulose to subsquamulose-granulate 23
Thallus of minute areoles 25

23(22) Soredia laminal, formed in crateriform soralia; thallus distinctly squamulose, squamules up to 1(–2) mm wide, rosette with loosely attached margins; corticolous, temperate; Europe, Asia (Caucasus) . . . . . **C. reflexa** Poelt & Vězda
Soredia marginal, dispersed inward or to the lower side of the subsquamules; thallus subsquamulose to granulose, subsquamules up to 0.5 mm wide, ascending from the one margin 24

24(23) Subsquamules 0.2–0.5 mm wide; soredia (–20)30–50(–60) µm diam., dispersed to the lower side of the subsquamules; thallus never totally dissolved into sorediate crust; corticolous and muscicolous; high mountains; E Asia and S Asia (Nepal, Taiwan) . . . . . ***C. sorediosa** Poelt & Reddi
Subsquamules (–0.05)0.06–0.2(–0.3) mm wide; soredia (–30)40–70(–80) µm diam., dispersed to the lower side of the subsquamules or inward, soon forming a ±continuous sorediate crust; corticolous, temperate, mountain; Europe, S Asia (China) . . . . . **C. rubrisoli** D. Liu & Hur

25(22) Soredia 20–60(–70) µm diam., apothecia up to 0.25(–0.3) mm diam., ascospores (11.0–)11.2–*13.3*–15.4(–17.7) × (3.8–)4.2–*5.0*–5.9(–7.2) µm, corticolous, temperate; Asia (Caucasus, Japan), N America, Australia . . . . . **C. xanthostigmoides** (Müll. Arg.) R. W. Rogers
Soredia 20–50 µm diam., apothecia up to 0.55 mm diam., ascospores (12.0–)14.0–21.0 × (4.5–)5.0–8.0(–10.5) µm, corticolous; Southern Hemisphere 26

26(25) Soredia *c.* 25 µm diam., thalline margin persistent and non-sorediate, asci 8-spored, ascospores simple, fusiform to rhomboidal with rounded ends, (14.0–)18.0–21.0 × 5.0–6.0 µm; Africa (Réunion) . . . . . **C. flavosorediata** Kalb & Aptroot
Soredia 20–50 µm diam., thalline margin soon disappearing and becoming granular-sorediate, asci 4–8-spored, ascospores simple to 1(–2)-septate, elongate to broadly ellipsoid, (12.0–)14.0–19.0(–21.0) × (4.5–)5.0–8.0(–10.5) µm; S America (Chile) . . . . . **C. magellanica** Etayo

27(21) On bark and wood 28
On rocks, soil, mosses, plant debris and other lichens 30

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28(27) Thallus uniformly granular, on bark and wood; N America . . . . . **C. deppeanae** M. Westb.
Thallus areolate, squamulose to indistinct, saxicolous species occasionally growing on bark or wood; various regions 29

29(28) Thallus areolate, small granulate to indistinct, apothecia up to 0.55(–0.7) mm wide, with somewhat convex disc and partly excluded thalline margin, ascospores mostly narrowly ellipsoid; cosmopolitan . . . . . **C. aurella** (Hoffm.) Zahlbr.
Thallus mostly squamulose, sometimes indistinct, apothecia up to 1.2(–2.2) mm wide, with flat to somewhat convex disc and persistent thalline margin, ascospores mostly oblong; Europe, Asia, N America, Australia . . . **C. rosulans** (Müll. Arg.) Zahlbr.

30(27) On rocks 31
On plant debris, soil, mosses and other lichens 41

31(30) On calcareous rocks 32
On siliceous rocks 35

32(31) Thallus well developed, squamulose 33
Thallus poorly developed, areolate to indistinct 34

33(32) Thallus shiny, cortex pseudoparenchymatous, 25–60 µm thick, gelatinous epicortex present; Asia, N America . . . . . **C. kansuensis** H. Magn.
Thallus matt, cortex indistinct to pseudoparenchymatous, up to 25 µm thick, gelatinous epicortex absent; Europe, Asia, N America, Australia . . . . . **C. rosulans** (Müll. Arg.) Zahlbr.

34(32) Apothecia 0.3–0.55(–0.7) mm diam., rounded, with partly excluded thalline margin and soon somewhat convex disc, always on calcareous rocks; cosmopolitan . . . . . **C. aurella** (Hoffm.) Zahlbr.
Apothecia 0.4–1.2(–2.2) mm diam., rounded to wavy, with persistent thalline margin and usually flattened disc, rarely on calcareous rocks; Europe, Asia, N America, Australia . . . . . **C. rosulans** (Müll. Arg.) Zahlbr.

35(31) Thallus usually of deeply incised squamules with finger-like lobes, scattered or forming effigurate to minutely shrubby thalli; N America . . . . . **C. corallizoides** M. Westb.
Thallus otherwise; various regions 36

36(35) Ascospores acicular, (30.5–)34.5–48.0(–57.0) × 3–4(–5) µm; Asia, N America . . . . . **C. spraguei** (Tuck.) Zahlbr.
Ascospores much smaller, ellipsoid to oblong; various regions 37

37(36) Thallus greenish yellow to pale yellow 38
Thallus yolk yellow to orange-yellow 39

38(37) Apothecia immersed, pseudolecanorine, ascospores narrowly to broadly ellipsoid, (8.0–)11.0–17.0 × 3.5–5.0(–7.0) µm; N America . . . . . **C. clarkii** E. Tripp & Lendemer
Apothecia sessile, lecanorine with strongly convex, globose disc and soon excluded thalline margin, ascospores narrowly ellipsoid, 15–22 × 4.5–6 µm; N America . . . . . **C. californica** M. Westb.

39(37) Thallus of flattened, rounded, peltate squamules with smooth upper surface; N America, S America . . . . . **C. complanata** M. Westb.
Thallus indistinct or of convex areoles/lobate squamules with smooth to pulverulent upper surface; various regions 40

40(39) Thallus surface pulverulent, ascospores 8–13(–15) × 4–5(–6) µm, asci 35–55 × 11–16 µm, hymenium 45–60 µm tall; Australia . . . . . **C. australiensis** McCarthy & Elix
Thallus surface smooth to coarse, ascospores (11–)14–22(–25) × (4–)5–6(–8) µm, asci 40–64 × 12–22 µm, hymenium 50–90 µm tall; Europe, Asia, N America, Australia . . . . . **C. rosulans** (Müll. Arg.) Zahlbr.

41(30) Ascospores acicular, (30.5–)34.5–48.0(–57.0) × 3–4(–5) µm, saxicolous species occasionally growing on soil and mosses in rock crevices; Asia, N America . . . . . **C. spraguei** (Tuck.) Zahlbr.
Ascospores much smaller, ellipsoid to oblong, always on plant debris, soil, mosses, other lichens; various regions 42

42(41) Apothecia numerous and dominant, thallus poorly developed, of scattered granules/small squamules, 0.1–0.35 mm wide or reduced to the margin of apothecia 43
Apothecia present or not, thallus well developed, squamulose of scattered to crowded and imbricate granules/squamules 45

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43(42) Apothecia large, up to 2.0 mm diam., finally lobate, with a thick, persistent, raised thalline margin, proper margin of *aurella*-type, ascospores (18.0–)20.0–28.0(–32.0) × 5.0–6.5(–7.8) µm, on plant debris, soil; Arctic-alpine: Europe, Asia (Caucasus) . . . . . **C. commutata** Otte & M. Westb.
Apothecia smaller, 0.3–0.6(–1) mm diam., rounded with a thin persistent to excluded thalline margin, proper margin of *aggregata*-type, ascospores (9.0–)11.0–19.0(–24.0) × 4.0–7.5(–9.0) µm; various regions 44

44(43) Ascospores (9.0–)11.0–*13.5*–16.0(–19.0) × (4.0–)4.5–*6.0*–7.5(–9.0) µm, phylogenetic sister species to *C. aurella* s. lat.; Antarctic . . . . . **C. ruzgarii** Halıcı *et al.*
Ascospores (10.5–)13.0–19.0(–24.0) × (4.0–)4.5–6.0(–7.5) µm, phylogenetically outside of *C. aurella* s. lat. group, on mosses, plant debris; Europe, Asia, N America . . . . . **C. aggregata** M. Westb.

45(42) Thallus squamulose, rosette-like, granulose, of scattered to converged granules or subsquamules/squamules but not forming a pulvinate crust 46
Thallus cushion-forming, of imbricate, ±uniform granules/subsquamules/squamules forming a thick pulvinate crust divided by cracks 49

46(45) Upper surface dark yellow, smooth to pulverulent, apothecia with convex disc and indistinct thalline margin when mature, Arctic-alpine; Europe, E Asia and S Asia (Nepal, Taiwan), N America . . . . . **C. canadensis** H. Magn.
Upper surface citrine green, greenish yellow, pale yellow, ginger yellow, heavy pulverulent, apothecia with flattened disc and persistent thalline margin; various regions 47

47(46) Ascospores ovoid to citriform, broadly fusiform or teardrop-shaped with at least one end pointed; mostly N America, rarely S America . . . . . **C. citrina** de Lesd.
Ascospores ellipsoid to narrowly ellipsoid, rarely broadly ellipsoid without pointed ends; various regions 48

48(47) Squamules large, 0.7–1.0 mm long, deeply incised to lobate, prostrate with finally ascending (almost vertical) margins; E Asia and S Asia (Nepal, Taiwan) . . . . . ***C. grimmiae** Poelt & Reddi
Squamules (0.15–)0.25–*0.35*–0.5(–0.8) mm long, non-incised to shallowly incised, with adpressed margins; C Asia, NE Asia (Russia) . . . . . **C. ahtii** Yakovch.

49(45) Thallus yellow, yellow-orange, of small, 0.06–0.1 mm wide, ecorticate or corticated granules, on mosses and on other lichens; Antarctic . . . . . **C. flava** (C. W. Dodge & G. E. Baker) Gastello & Nimis
Thallus of citrine green, greenish yellow, pale yellow, pulverulent, large, 0.15–0.8(–1.3) mm long granules or subsquamules/squamules, on soil in rock crevices, rarely on other lichens and mosses; different regions 50

50(49) Ascospores ovoid to citriform, broadly fusiform or teardrop-shaped with at least one end pointed, squamules up to 0.6(–1.3) mm long; mostly N America, rarely S America . . . . . **C. citrina** de Lesd.
Ascospores ellipsoid to narrowly ellipsoid, rarely broadly ellipsoid, without pointed ends, squamules up to 0.5(–0.8) mm long; C Asia, NE Asia . . . . . **C. ahtii** Yakovch.

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