



Two New Species of the Genus *Candelariella* from China and Korea

Dong Liu^{a,b} , Lisong Wang^b , Xin Yu Wang^b  and Jae-Seoun Hur^a

^aKorean Lichen Research Institute (KoLRI), Suncheon National University, Suncheon, Korea; ^bKey Laboratory for Plant Diversity and Biogeography of East Asia, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, China

ABSTRACT

Candelariella is a widespread lineage of lichenized ascomycetes with ambiguous relationships among species that have not solved completely. In this study, several specimens belonging to *Candelariella* were collected from China and South Korea, and the internal transcribed spacer region was generated to confirm the system position of the newly collected specimens. Combined with a morphological examination and phylogenetic analysis, two new areolate species, *Candelariella rubrisoli* and *C. subsquamulosa*, are new to science. Detail descriptions of each new species are presented. In addition, *C. canadensis* is firstly reported from China mainland.

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KEYWORDS

Taxonomy; Candelariaceae;
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1. Introduction

The family Candelariaceae Hakul., primarily described by Hakulinen [1], is comprised of four genera around the world: *Candelariella* Müll. Arg. (ca. 50 spp.) with the areolate to squamulose thallus, *Candelaria* A. Massal. (9 spp.) with foliose to subfruticose thallus, *Candelina* Poelt (3 spp.) with placoid to subfoliose thallus, and *Placomaronea* Räsänen (6 spp.) with squamulose to umbilicate thallus [2–4]. Although molecular analyses have been conducted, many taxonomic questions remain to be answered. Neither *Candelariella* nor *Candelaria* was monophyletic indicated by phylogenetic analysis [4,5]. Polyspored or 8-spored asci is a very important characteristic to distinguish the species in genus *Candelariella*, but the fertile organism is frequently absent in the sorediate group, which makes species identification much more difficult. Hence, molecular data are expected to solve this issue [6].

Candelariella are estimated to be particularly diverse in Asia and America [6–12], but delimitation of the species needs to be assessed critically. The patterns in morphological diversity suggest that this genus is represented by five species in South Korea [13–20] and fourteen species in China mainland and Taiwan [7,21]. The morphological, chemical and DNA traits were integrated to elucidate the diversity of species of *Candelariella* in South Korea and Southwest of China and estimate their relationships.

2. Material and methods

2.1. Material and morphological studies

All newly collected specimens included in this study were deposited in Suncheon National University, Korean Lichen Research Institute (KoLRI). The morphology examination and anatomical characteristics were recorded under a dissecting microscope (Model SMZ 745 T; Nikon, Tokyo, Japan) and Olympus BX 50 microscope (Olympus, Tokyo, Japan), and photographs were taken using a HD-Measure LTHS-300 (Leetech Co., Seoul, South Korea) microscope and Carl Zeiss MicroImaging with Axio Cam ERc 5s imaging system (Carl Zeiss, Gottingen, Germany). The minimum (min.) and maximum values (max.) of the thallus width, soredia, apothecia, and ascospore size are recorded. The number (N) and mean values (in italics) were measured. Secondary metabolites were studied by a spot test and thin layer chromatography in solvent C, as described in [22] and [23]. UV test was performed with a UV Chamber (VL-6.LC; Viber Lourmat, Collégien, France) under a long (366 nm) wavelength.

2.2. Molecular studies

The total genomic DNA was extracted from newly collected specimens using the NucleoSpin Plant II Kit (Clontech Laboratories, Mountain View, CA) according to the manufacturer's instructions. The

CONTACT Jae-Seoun Hur  jshur1@scnu.ac.kr


 Supplemental data for this article can be accessed [here](#).

Table 1. Voucher information of the ITS and 28S sequences newly generated in this study.

Taxon	Location	Voucher	Accession No.	
			ITS	28S
<i>Candelariella canadensis</i>	China, Yunnan Province, Luquan Co.	J.-S Hur & D. Liu CH170062	MG694271	MH101756
<i>Candelariella placodizans</i>	China, Yunnan Province, Luquan Co.	J.-S Hur & D. Liu CH170084	MG694272	MH101757
<i>Candelariella rubrisoli</i>	China, Yunnan Province, Xundian Co.	J.-S Hur & D. Liu CH170039	MG694273	MH101758
<i>Candelariella subsquamulosa</i>	South Korea, Jeollanam-do, Suncheon-si	D. Liu 171419	MG694274	MH101759
<i>Candelariella subsquamulosa</i>	South Korea, Jeollabuk-do, Namwon-si	D. Liu 152676	MG694275	MH101760

internal transcribed spacer (ITS) region, including the 5.8S ribosomal RNA gene, and the 5' portion of the large subunit of the ribosomal RNA (28S) were targeted by PCR using the primers pairs, ITS4 and ITS1F [24], LR0R [25], and LR5 [26], respectively. The protocols of PCR amplification are described in the previous report [27]. Sequencing was accomplished by the genomic companies GenoTech (Daejeon, Korea) and Macrogen (Daejeon, Korea). Newly obtained sequences for the ITS region of the *Candelariella* species (Table 1) were assembled and edited using SeqMan (DNASTAR, Madison, WI) and Mega 7.0 [28], and complemented with publicly available sequences (Supplementary Table 1) into a matrix and aligned with Mafft v7.273 [29]. The ambiguous regions were identified and excluded using Gblocks 0.91b [30]. *Pycnora xanthococca* (Sommerf.) Hafellner was used as the outgroup since *Pycnora* has been recognized as a possible sister clade to Candelariaceae [31].

2.3. Phylogenetic analysis

The matrix was analyzed under the criterion of maximum likelihood (ML) using RAxML v7.2.6 [32] with the GTR + I + G model. The nodes supported by ML bootstrap values >70% were estimated from the consensus trees obtained from 1000 nonparametric bootstrapping pseudoreplicates. Bayesian inference (BI) was performed with MrBayes v3.1.2 [33], applying the best-fitted substitution models (GTR + T + G) based on the Akaike information criterion using jModelTest 3.7 [34]. The BIs were conducted using four chains and run for 2 million generations. The trees were sampled every 1000 generations with the first 20% of the tree discarded. The remaining trees were used to generate a majority-rule consensus tree with posterior probabilities (PP); clades with a PP value ≥ 0.95 were considered to be significantly supported.

3. Results

The matrix was comprised of 57 sequences representing 30 taxa. After excluding the ambiguous sites, 471 sites were retained for the *Candelariella* matrix. The phylogenetic analyses resolved all species of *Candelariella* that were represented by two or more

accessions as robust clades (Figure 1). Newly sequenced accessions from East Asia, were either mostly closely related to known taxa (e.g., *Candelariella placodizans*, *C. canadensis*; Figure 1), resolved as singletons (i.e., *Candelariella rubrisoli*; Figure 1), or as novel clades (i.e., *C. subsquamulosa*; Figure 1) that were proposed as new species. Seven characters (apothecia type, conidia production, asci spored type, thallus color and type, soredia and substrate type) were combined with a phylogenetic tree to examine the lineages of *Candelariella* (Figure 1), but neither 8-spored nor polyspored species of *Candelariella* were monophyletic.

3.1. Taxonomy of *Candelariella rubrisoli* D. Liu & J.-S hur, sp. nov

Mycobank No.: MB824741

Similar to *C. efflorescens*, but differs in an irregular subsquamulose thallus, usually slightly ascending from one side.

Type: China, Yunnan Province, Kunming City, Dongchuan District, Huagou Village, 25°55'23"N, 103°05'03"E, 2403 m, on *Pinus armandi*, 3 August 2017, J.-S. Hur & D. Liu CH170039 (holotype, KoLRI!). Accession number: ITS = MG694273, LSU = MH101758 (Figure 2).

Thallus corticolous, crustose, areolate to subsquamulose, irregular, scattered or several aggregation to imbricate sometimes, green yellow, (50)60–140–220(280) μm ($N=56$). Subsquamulose thalli often dissolved, and margin broke into fine, granular soredia and dispersed inward or to the lower side, covering the entire upper surface of the squamules and forming a \pm continuous leprose or pulverulent crust, which is greenish under the soredia layer due to the exposure of photobiont. Soredia granular, spherical, (30)40–54–70(80) μm ($N=85$), bright yellow to orange. Thallus layers not well developed, upper cortex (pseudocortex) indistinct, 7–10 μm thick, of 1–2 layer non-gelatinized hyphae. Photobiont chlorococcoid, ca. 6.9–11.3 μm in diam., dispersed in the thallus. Hypothallus and prothallus absent. Apothecia and pycnidia not seen.

Chemistry: K–, KC–, C–, PD–; Calycin and pulvinic acid as major substances.

Etymology: The epithet "*rubrisoli*" refers to the type location, where is famous for its red soil lands.

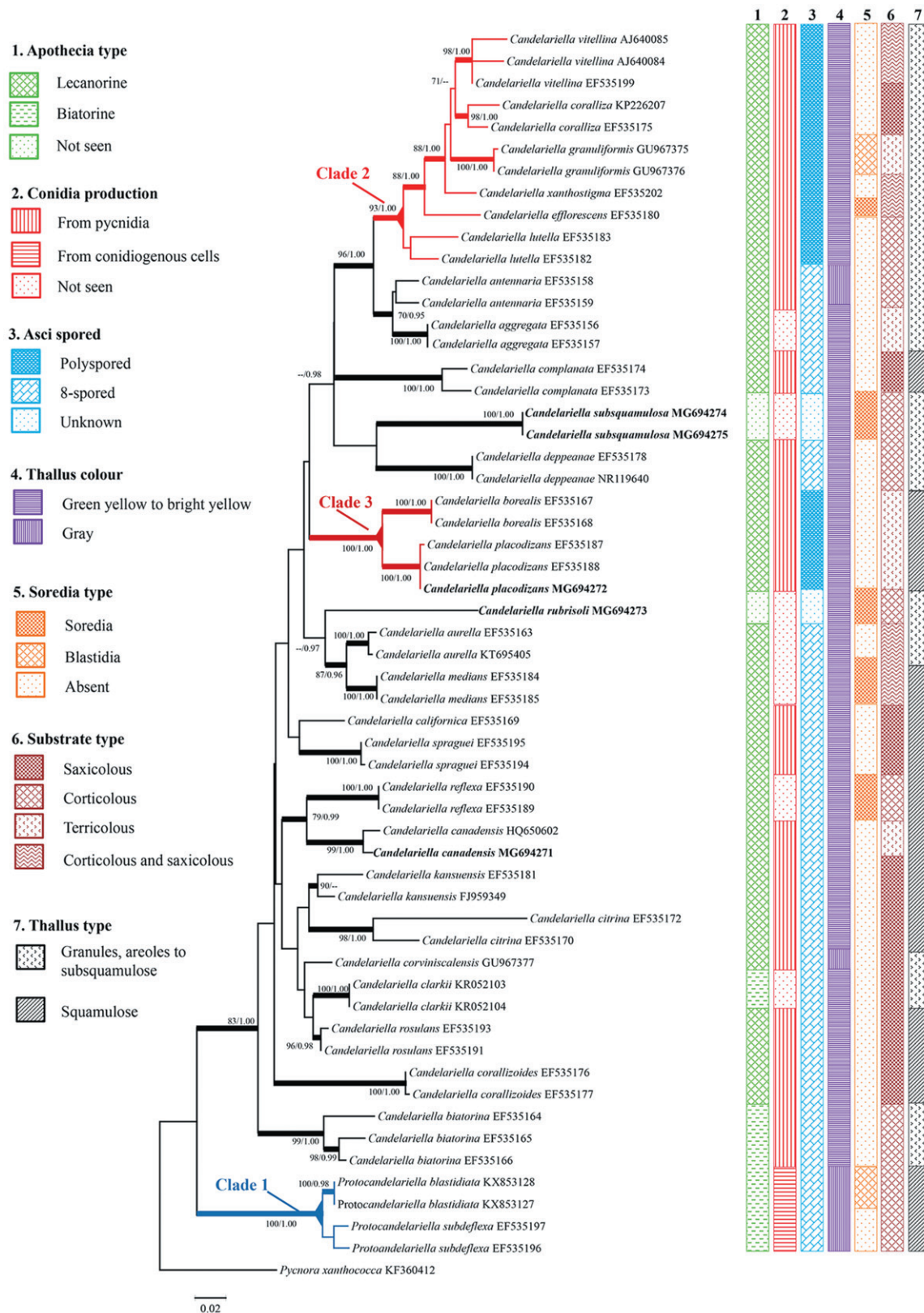


Figure 1. Most likely phylogenetic relationships among species of *Candelariella* inferred from ITS sequences with distribution of selected characters. Nodes supported by ML bootstrap values $>70\%$ and Bayesian posterior probabilities >0.95 are identified by thickened branches; the clades with polyspored asci and conidiogenous cell were marked with color.

Ecology: *Candelariella rubrisoli* was found growing on *Pinus armandi*, together with *Flavopunctelia flaventior*, *Heterodermia*, *Lepraria*, *Ochrolechia*, *Parmotrema*, *Rinodina* and *Usnea rubescens*.

Remarks: *Candelariella rubrisoli* is characterized by the areolate to subsquamulose thallus, which usually breaks and ultimately dissolves into the soredia. *Candelariella rubrisoli* resembles *C. efflorescens* R. C.

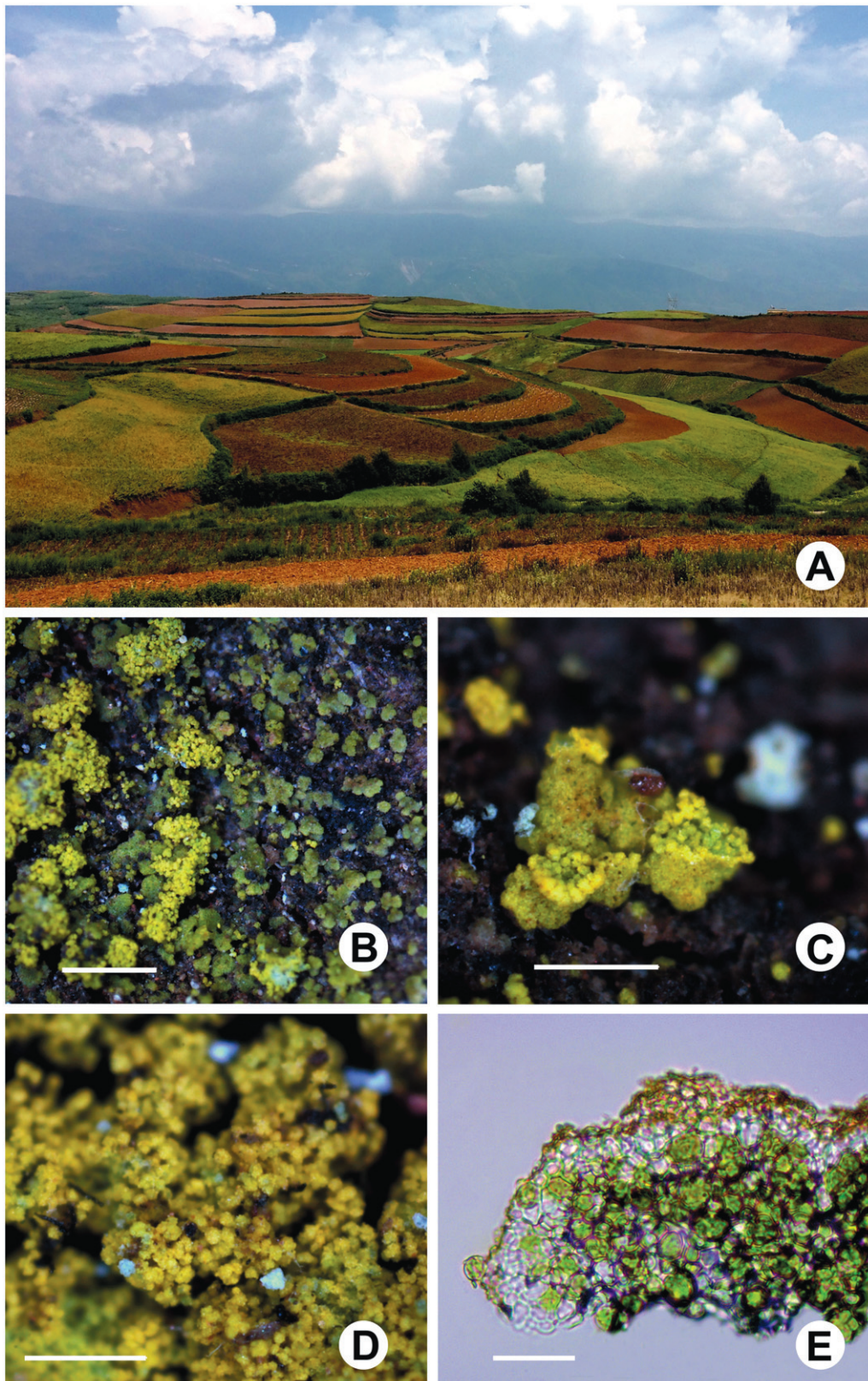


Figure 2. *Candelariella rubrisoli*. (A, B) Habit; (C) thallus breaking into soredia; (D) soredia; (E) transverse section of thallus [Scale bar: (B–D) 0.5 mm, (E) 20 μ m].

Harris & W. R. Buck, but differs in having larger soredia ((30)40–54–70(80) vs. 15–40(–50) μ m [6]). It is also similar to *C. reflexa* (Nyl.) Lettau, but differs in having smaller squamules, and to *C. xanthostigmoides* (Müll. Arg.) R. W. Rogers, which has smaller soredia ((20)18.6–32.4–46.2(60) μ m [35])

and frequently grows on the deciduous trees in North America.

Comparison with *C. sorediosa* Poelt & Reddi, the similar corticolous species was primarily described from Nepal [36], and from Taiwan [10]. However, Lendemer and Westberg [35] treated *C. sorediosa* as

a distinct species based on the examination of holotype (Poelt L434, M), which is “very meager, a few minute areoles are slightly raised from substrate, and sorediate from the margin,” this species seems even not frequently recorded in the Asia. Yakovchenko et al. [7] treated the growth direction of soredia as a significant character to distinguish the sorediate species of *Candelariella* in their key part, with a short description that the soredia dispersed to the lower side of thallus, in contrast, soredia of *C. rubrisoli* dispersed inward and lacking district direction.

Candelariella rubrisoli is similar to *C. granuliformis*, however, *C. granuliformis* usually not forming distinct soralia but breaking into blastidia and frequently occurs in terricolous habit [37]. *Candelariella rubrisoli* resembles *C. biatorina*, *C. subdeflexa*, *C. lutella*, and *C. deppeanae*, but differs in having soredia; *Candelariella rubrisoli* can be distinguished from *C. antennaria*, *C. blastidiata*, *C. oleaginescens*, and *C. aurella* in having bright yellowish areolate to subsquamulose thallus. There are no sexual propagules present, and it is hard to make clear the polyspored or 8-spored asci, however, the phylogenetic tree also suggests that *C. rubrisoli* separated from other species.

3.2. Taxonomy of *Candelariella subsquamulosa* *D. Liu & J.-S. hur, sp. nov*

Mycobank No.: MB824742

Similar to *C. reflexa*, but differs by the green to dark green thallus with the margins remaining intact (i.e., not breaking into soredia).

Type: South Korea, Jeollanam-do, Suncheon-si, Jungang-ro 225, Sunchon National University, 34°58'01"N, 127°28'48"E, 47 m, on *Cerasus* sp., 26 September 2017, D. Liu 171419 (holotype, KoLRI!). Accession number: ITS = MG694274, LSU = MH101759 (Figure 3).

Thallus corticolous, crustose, granular to subsquamulose, irregular, \pm round, flattened to somewhat convex, scattered or aggregation to imbricate sometimes, not dissolved, tightly attached to the substrate, (60)90–170–370(440) μm (N = 38). Upper surface green to dark green, slightly shiny under optical microscopy, margin irregular, usually not breaking into soredia. Soredia granular, spherical, (30) 40–60–70(80) μm (N = 40), bright yellow to orange, discrete or aggregation into a sorediate crust, with a thallus areole-like appearance, covering the thallus or directly widespread on the substrate. Thallus layers not well developed, upper cortex (pseudocortex) indistinct, 7–8 μm thick, of 1–2 layers of non-gelatinized hyphae. Photobiont chlorococcoid, ca. 5–10 μm in diameter, dispersed in the thallus, but usually close to the upper cortex.

Hypothallus indistinct, with silvery hyphae interwoven. Apothecia and pycnidia not seen.

Chemistry: K–, KC–, C–, PD–; Calycin and pulvinic acid as major substances.

Ecology: *Candelariella subsquamulosa* was found growing on conifer and cherry flower trees, together with buelliod lichens, *Lepraria*, and *Phaeophyscia* spp.

Etymology: The epithet “*subsquamulosa*” refers to the green to dark green subsquamulose thallus.

Additional examined specimens: South Korea. Jeollanam-do, Suncheon-si, Jungang-ro 225, Sunchon National University, 34°58'01"N, 127°28'48"E, 47 m, on *Cerasus* sp., 26 September 2017, D. Liu 171418; 1 December 2017, D. Liu 171451, 171452; Jeollabuk-do, Namwon-si, Geumjimyemyeon, 35°19'11"N, 127°16'45"E, 260 m, on pine tree, 5 June 2015, D. Liu 152676.

Remarks. *Candelariella subsquamulosa* is characterized by its green to dark green granular to subsquamulose thallus, which never breaks into the soredia and is covered with numerous bright yellow to orange soredia. This species usually grows on the bark of cherry and conifers. The color of soredia is variable, always orange on conifers or under an open area, but is yellow to yellow greenish when on a cherry tree or under low light or in the shade.

Differences among species of *Candelariella* are usually based on the following characteristics: substrate, thallus color, and type, asci 8-spored or polyspored and soredia present or absent. The genus holds ca. 50 species around the world, and five species produce soredia: *C. efflorescens*, *C. medians* (Nyl.) A. L. Sm., *C. reflexa*, *C. sorediosa*, and *C. xanthostigmoides*.

Candelariella subsquamulosa is most similar to *C. reflexa* in having soredia, and often growing on bark, but differs in having green granular to subsquamulose thalli, and an intact thallus margin. The soredia of *C. subsquamulosa* usually adhere to or are scattered over the surface and can be separated easily from the thallus or substrate. Furthermore, *C. reflexa* has much larger and indistinctly effigurate thalli, with lobes up to 0.6 mm long [6], and when well developed, it can have an almost rosette-like thallus, and be sorediate from the center of the areoles.

Candelariella subsquamulosa is also similar to *C. efflorescens*, but can be distinguished by its thallus not dissolved and obscured by soredia. In addition, the soredia of *C. efflorescens* usually form along the margin of thallus. *Candelariella efflorescens* is recorded from Europe [38], North America [6], and South Korea [18]. The species always grows on bark (mainly broadleaved trees) or bryophytes [6], but one specimen was found on siliceous rock in South

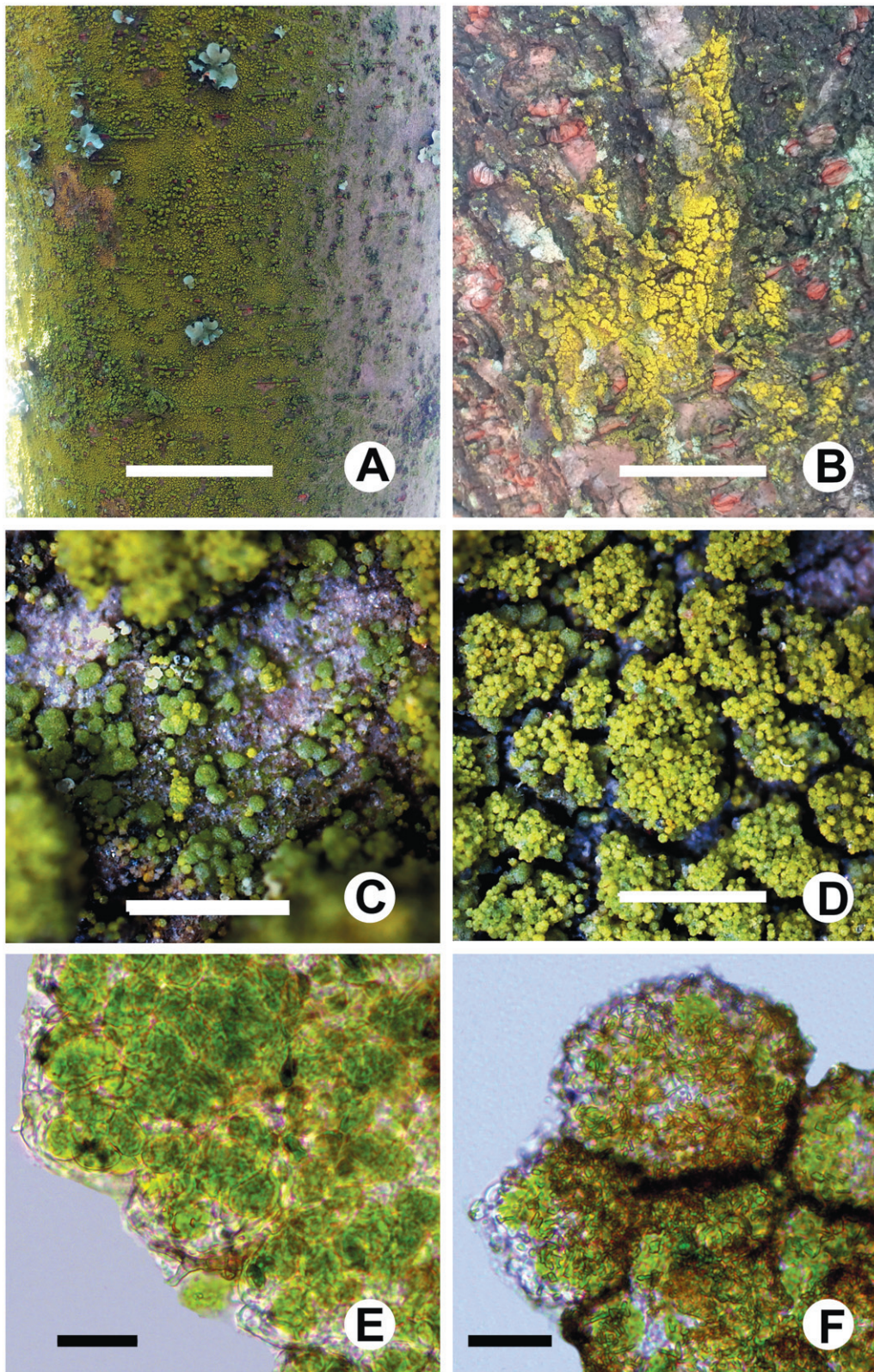


Figure 3. *Candelariella subsquamulosa*. (A, B) Habitat; (C) thallus; (D, F) soredia; (E) transverse section of thallus [Scale bar: (A, B) 2 cm, (C, D) 0.5 mm, (E, F) 20 μ m].

Korea [18]. In contrast, *C. subsquamulosa* was only found in colonizing bark.

Candelariella subsquamulosa also resembles also the sorediate species *C. medians*, which occurs in North Africa, Europe, Southwest Asia, and China [9,21,39], but *C. medians* forms placoid thalli, and is

usually found on nitrogen-enriched rocks, particularly where birds often rest and leave their droppings [39].

Candelariella subsquamulosa differs from the other soradiate species, *C. xanthostigmoides*, in thallus not dissolved into soredia, and in soredia without obvious spreading direction, comparison with *C.*

xanthostigmoides, soredia of latter appears to begin at the margin, spreading inward [35].

3.3. Taxonomy of *Candelariella canadensis* H. Magn.

Ark. Bot. ser. 2, 2: 216 (1952)

= *Candelariella hudsonica* Hakul., Ann. Bot. Soc. Zool.-Bot. Fenn. "Vanamo" 27: 49 (1954), synonymized in [40].

= *Candelariella nepalensis* Poelt & Reddi, Khumbu Himal [Universitätsverlag Wagner, Innsbruck-München] 6: 8 (1969), synonymized in [40].

Thallus composed of large granules 100–400 µm ($N=30$), aggregation or becoming large then forming lobes, up to 1–3 mm wide, ± rosettes adnate to the substrate; surface yellow to dark yellow, smooth in the lobe center and pulverulent near the lobe margin and granules. Thallus 200–330 µm thick, pseudocortex uneven, 9.6–12 µm. Photobiont chlorococcoid, ca. 5–10 µm diam. Apothecia lecanorine, 0.33–0.59–0.86 mm ($N=17$) diam., thalline margin to 160 µm thick, entire when young, becoming incised and ultimately with few granules remaining. Proper margin 25–106 µm thick, composed of radiating hyphae with elongated cells. Disc yellow to brown, flat at first, or turning convex or even globose sometimes. Hymenium 60–82 µm thick. Paraphyses simple, sometimes branch on the tip, swollen at the tip but not blacken, up to 5.5 µm wide. Asci clavate, 8-spored, 58.7(58.8)–62.6–66.5(69) × (10.1)10.5–12.7–14.6(15.2) µm ($N=16$). Ascospores colorless, narrowly ellipsoid, simple, or with thin septa, or with oil droplets sometimes, the end usually attenuated, 13.1(13.3)–15.2–17.3(17.5) × (5.1)5.9–6.6–7.4(8) µm ($N=37$). Pycnidia not seen (Figure 4(A,C–F)).

Chemistry: Thallus K–, KC–, C–, PD–, apothecia disc K slightly red; Calycin and pulvinic acid as major substances.

Ecology: *Candelariella canadensis* was found growing on the moss over rock or directly grow on the rock.

Examined specimen: CHINA, Yunnan Province, Kunming City, Luquan Co., near the peak of Jiaozi Snow Mt., 26°5'6"N, 102°51'9"E, 3970 m, on moss, 3 August 2017, J.-S. Hur & D. Liu CH170062 (KoLRI). Accession number: ITS = MG694271, LSU = MH101756.

Remarks: *Candelariella canadensis* is characterized by the well-developed pulverulent thallus and often convex apothecia with the granules scattered around the margin. [41] treated this species as a synonym of *C. terrigena*, whereas Westberg treated as a synonym of *C. citrina*, based on the examination of holotypes of *C. terrigena* and *C. terrigena*

var. *placodimorpha* collected from Colorado (C. C. Plitt, H) and New Mexico (S. Shushan & W. A. Weber S6893, TUR), and considered the type specimen of *C. terrigena* to be a mixture of two species, including *C. rosulans* (dark yellow thallus and narrowly ellipsoid spores) and *C. citrina* (greenish thallus and shorter, ovoid to citriform spores) [12]. Then Westberg investigated the initial cited specimens and holotype of *C. canadensis* (Freucher 1469, lectotype, C), *C. hudsonica* (CANL No. 12961, holotype) and *C. nepalensis* (Poelt L441, holotype, M), and concluded that the latter two species were conspecific [40]. Our phylogenetic tree shows that our specimen collected from Jiaozi Snow Mountains forms a clade with *C. terrigena* (HQ650602), the specimen used in [42] may be a misidentification of *C. canadensis*, this species was reported as *C. nepalensis* from Taiwan growing on moss and soil over 3000 m altitude [10], and is here recorded as new from mainland of China. Morphology, anatomy, and chemistry of Chinese material match the description [40], but have longer asci (58.7(58.8)–62.6–66.5(69) × (10.1)10.5–12.7–14.6(15.2) vs. 52–57 × 13–17 µm). As a conclusion, GenBank sequence of *C. terrigena* (HQ650602) may be a misidentification of *C. canadensis*.

3.4. Taxonomy of *Candelariella placodizans* (Nyl.) H. Magn.

In Lyngby, Rep. Fifth Thule Exped. 1921–24, 2: 23 (1935)

= *Candelariella himalayana* Poelt & Reddi, Khumbu Himal [Universitätsverlag Wagner, InnsbruckMünchen] 6: 8 (1969), synonymized in [40].

Candelariella placodizans is characterized by squamulose thallus, upper surface of squamules yellow to bright pulverulent, and the lecanorine apothecia with polyspored asci. This species usually appear in the alpine and subalpine habitats on moss or plant debris [6]. Our specimen lacks apothecia but the thallus morphology, chemistry, and ecology are consistent with the description in [6]. It is also robustly resolved based on ITS data in the *C. placodizans* clade (Figure 4(B)).

Chemistry: Thallus K–, KC–, C–, PD–; Calycin and pulvinic acid as major substances.

Ecology: *Candelariella placodizans* is an arctic alpine lichen that grows on terricolous bryophytes. In China, it was found in the rocky areas of mountains in Taiwan over 3240 m [7] and in Yunnan over 3900 m, where it occurred with *C. canadensis*.

Examined specimens: China, Yunnan Province, Kunming City, Luquan Co., near the peak of Jiaozi Snow Mt., 26°5'6"N, 102°51'9"E, 3970 m, on moss,

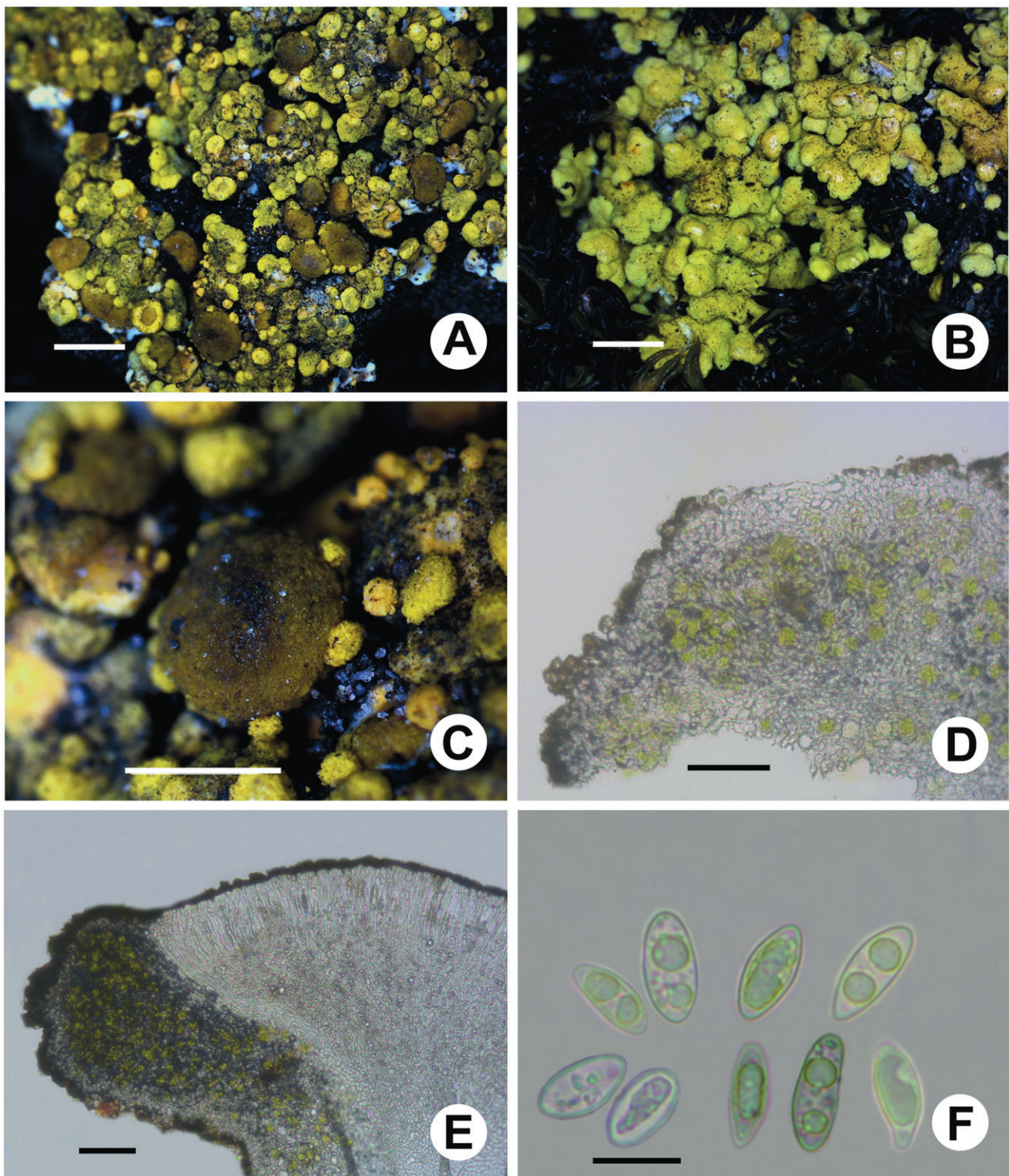


Figure 4. Species of *Candelariella* in China. (A, C–F) *Candelariella canadensis*. (A) Habit; (C) apothecia; (D) transverse section of thallus; (E) transverse section of apothecia; (F) ascospores; (B) *Candelariella placodizans* [Scale bar: (A–C) 0.5 mm, (D) 20 μ m, (E) 50 μ m, (F) 10 μ m].

3 August 2017, J.-S. Hur & D. Liu CH170084 (KoLRI). Accession number: ITS = MG694272, LSU = MH101757.

4. Discussion

Poelt recognized *Candelariella subdeflexa* was a unique and suggested it a “protocandelariella” in family Candelariaceae [43], and the morphology and

molecular phylogeny strongly supported the close relationship between *Candelariella blastidia* and *C. subdeflexa*, which formed a single clade and was separated from the other species in Candelariaceae, Clade 1 [4,44]. These two species produce conidia from conidiogenous cells on the lower surface, and differ from the other species of *Candelariella* in producing conidia from the pycnidia on the upper surface. In addition, soredia or blastidia, apothecia

type, and thallus color have a positive role in distinguishing species, but was not significant for distinguishing the potential different groups of 8-spored species of *Candelariella* prior to this study [4].

Candelariella in a broad sense is characterized by granules to squamulose thalli, 8-spored or polyspored asci, given lower support of the main clade. The relationship among 8-spored species remains ambiguous but species with polyspored asci are separated into two single clades with strong support. Clade 2, *Candelariella* s. str., with the type species *C. vitellina*, is characterized by granulose, areolate to subsquamulose thalli. Clade 3 is characterized by squamulose thalli and usually occurs on the bryophytes in the rocky mountainous areas above the tree line (i.e., >3000 m).

The 8-spored or polyspored asci is a significant character to distinguish the species of *Candelariella* and *Candelaria*, however, the apothecia usually rarely present in sorediate species, which makes the delimitation incredible only from the size of the squamules or soredia. For this case, molecular data is a potential method for the discovery of species and their relationship within the genus *Candelariella*.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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ORCID

Dong Liu  <http://orcid.org/0000-0002-7220-2272>
Lisong Wang  <http://orcid.org/0000-0003-3721-5956>
Xin Yu Wang  <http://orcid.org/0000-0003-2166-6111>

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