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CONTRIBUTIONS TO MOLECULAR PHYLOGENY OF LICHEN-FORMING FUNGI, 1. THE FAMILY CANDELARIACEAE

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Three genera new for science, i.e. *Candelinella* S. Y. Kondr. for the *Candelariella makarevichiae* group, *Opeltiella* S. Y. Kondr. for the *Candelaria fraudans* group, as well as *Protocandelariella* Poelt, D. Liu, J.-S. Hur et S. Y. Kondr. for the *Candelariella subdeflexa* group are proposed for robust monophyletic branches of the Candelariaceae on the basis of three-gene phylogeny (i.e. concatenated nrITS, 12S mtSSU and 28S nrLSU sequences). Eight new combinations, i.e. *Candelinella makarevichiae* (for *Candelariella makarevichiae* S. Y. Kondr., L. Lőkös et J.-S. Hur), *Candelinella deppeanae* (for *Candelariella deppeanae* M. Westb.), *Opeltiella fraudans* (for *Candelaria fraudans* Poelt et Oberw.), *Opeltiella fibrosoides* (for *Candelaria fibrosoides* M. Westb. et Frödén), *Opeltiella rubrisoli* (for *Candelariella rubrisoli* D. Liu et J.-S. Hur), *Opeltiella canadensis* (for *Candelariella canadensis* H. Magn.), *Protocandelariella subdeflexa* (for *Lecanora subdeflexa* Nyl.), *Protocandelariella blastidiata* (for *Candelariella blastidiata* L. Yakovchenko) are provided.

Molecular data provided for *Candelinella makarevichiae* (including holotype and isotype), as well as additional specimens of *Candelaria asiatica* from South Korea for the first time. The latter species (*Candelaria asiatica*) from China, as well as '*Candelaria*' *murrayi* from Argentina, South America are recorded for the first time. Voucher of *Candelariella vitellina* from Antarctica is also identified based on molecular phylogeny. It is for the first time shown that '*Candelaria*' *murrayi* is positioned in the outermost position to *Candelaria* s. str. branch of the phylogenetic tree of the Candelariaceae, and may belong to another genus. Status of the '*Candelariella*' medians group, the '*Candelariella*' *placodizans* group, as well as single species '*Candelariella*' *reflexa* and '*Candelaria*' *pacifica*, forming separate branches outside the *Candelariella* s. str. and *Candelaria* s. str. clades, will be clarified when additional molecular data will be accumulated. *Candelariella subsquamulosa* D. Liu et Hur, recently described from South Korea (Liu *et al.* 2019), proved to be a new synonym of *Candelinella makarevichiae.*

Key words: *Candelaria*, Candelariaceae, *Candelariella*, *Candelina*, *Candelinella*, multigene phylogeny, *Opeltiella*, *Placomaronea*, *Protocandelariella.*

INTRODUCTION

Molecular phylogeny of the representatives of the Candelariaceae are hitherto provided for separate genera, like *Candelaria* (Liu and Hur 2018, Westberg *et al.* 2007), and *Candelariella* (Kondratyuk *et al.* 2014*a*, Liu *et al.* 2019, Westberg *et al.* 2007, Yakovchenko *et al.* 2016, 2017). However, since 2007 (Westberg *et al.* 2007), all genera hitherto known for Candelariaceae were not included in the phylogenetic analysis.

The family Candelariaceae Hakul. (type genus *Candelaria* A. Massal.) hitherto includes four genera, i.e. *Candelaria* (type species *C. concolor* (Dicks.) Stein.), *Candelariella* Müll. Arg. (type species *Candelariella vitellina* (Ehrh.) Müll. Arg.), *Candelina* Poelt (type species *Candelina mexicana* (B. de Lesd.) Poelt) and *Placomaronea* Räsänen (type *P. candelarioides* Räsänen).

Candelariella hakulinenii S. Y. Kondr., L. Lőkös et J.-S. Hur, and *C. makarevichiae* S. Y. Kondr., L. Lőkös et J.-S. Hur were recently described from South Korea (Kondratyuk *et al.* 2017, 2018). However, molecular data were not included at that time, because molecular data on *C. makarevichiae* described from bark of coniferous and deciduous trees were obtained only for vouchers from bark of coniferous trees. The status of specimens of *C. makarevichiae* from bark of deciduous trees was not clarified at that time. These data of the latter species were recently published by Liu *et al.* (2019). The hypothesis about the heterogeneity of *C. makarevichiae* material is analysed hereby.

The main aim of this paper is to clarify the current position of the recently described South Korean lichen species among representatives of the Candelariaceae, as well as to clarify the status of all hitherto known genera of this family and some other species groups in the phylogenetic tree of the Candelariaceae on the basis of multigene phylogeny.

MATERIAL AND METHODS

The specimens included in the comparative study were examined using standard microscopical techniques, hand-sectioned under a dissecting microscope (Nikon SMZ 645; Nikon, Tokyo, Japan). Anatomical descriptions were based on observations of these preparations under a microscope (Nikon Eclipse E200; Nikon, Tokyo, Japan, and Zeiss Scope, A1; Carl Zeiss, Oberkochen, Germany) with digital camera AxioCam ERc 5s. Sections of apothecia were tested with water and with K and IKI (10% aqueous potassium iodide) for identification. For identification of chemical substances of critical taxa standard TLC and HPTLC methods with solvent system C were carried out (Arup *et al.* 1993, Orange *et al.* 2001).

Table 1
Vouchers of the Candelariaceae for which newly generated molecular data as well as new names are identified

	Country, voucher specimen / reference	nrITS	28S nrLSU	12S mtSSU
Candelaria asiatica	China, Cao *et al.* (2015 as *Candelaria fibrosa*)	KP226208		
Candelaria asiatica	Republic of Korea, 110980 KoLRI, this paper	110980		
Candelaria asiatica	Republic of Korea, 150799 KoLRI, this paper	150799		
Candelaria asiatica	Canada, Telfer *et al.* (2015 as *Candelaria concolor*)		KT695365	
Candelaria asiatica	China, Nan *et al.* unpubl. [2012], as *Candelaria* sp. O40	JQ004686		
Candelaria asiatica	Republic of Korea, Liu *et al.* (2019)		MG694270	MH101755
Candelaria asiatica	Republic of Korea, Liu *et al.* (2019)		MG694269	MH101754
'Candelaria' murrayi	Argentina, Westberg and Arup, as *Candelaria fibrosa*		GU929923	
'Candelariella' hakulinenii	Republic of Korea, 161884 KoLRI, this paper	161884		
'Candelariella' hakulinenii	Republic of Korea, 161911 KoLRI, this paper	161911		
Candelariella vitellina	Antarctica, Canini *et al.* [unpubl.], as *Candelariella* sp.	MK536666		
Candelinella deppeanae	USA, Westberg *et al.* (2007)	EF535178		
Candelinella deppeanae	Mexico, Westberg *et al.* (2007)	EF535179		
Candelinella makarevichiae	Republic of Korea, 110993 KoLRI, this paper	110993		
Candelinella makarevichiae	Republic of Korea, 150828 KoLRI – holotype, this paper	150828		
Candelinella makarevichiae	Republic of Korea, 150829 KoLRI – isotype, this paper	150829		
Candelinella makarevichiae	Republic of Korea, 152676 KoLRI – Liu *et al.* (2019 as *Candelariella subsquamulosa*)	MG694271	MH101756	
Opeltiella aff. fibrosoides	Republic of Korea, 121797 KoLRI, this paper	121797		
Opeltiella canadensis	China, Liu *et al.* (2019 as *Candelariella canadensis*)	MG694271	MH101756	
Opeltiella fibrosoides	Peru, Westberg *et al.* (2007 as *Candelaria fibrosoides*)	EF535211		
Opeltiella fibrosoides	Peru, Westberg *et al.* (2007 as *Candelaria fibrosoides*)	EF535212		
Opeltiella fruticans	Ecuador, Westberg *et al.* (2007 as *Candelaria fruticans*)	EF535207		
Opeltiella rubrisoli	China, Liu *et al.* (2019 as *Candelariella rubrisoli*)	MG694273	MH101758	
Protocandelariella blastidiata	Russia, Yakovchenko *et al.* (2017)	KX853127		
Protocandelariella blastidiata	Russia, Yakovchenko *et al.* (2017)	KX853128		
Protocandelariella blastidiata	Czech Republic, Yakovchenko *et al.* (2017)	MH145376		MH156655
Protocandelariella subdeflexa	USA, Westberg *et al.* (2007)	EF535197		
Protocandelariella subdeflexa	USA, Westberg *et al.* (2007)	EF535198		

The consensus sequence was aligned with sequences from all related species retrieved from the GenBank database (Table 1). Phylogenetic analysis was performed using the ITS region and 28S nrLSU gene and 12S mtSSU sequences retrieved from the GenBank database. Sequence alignment was conducted in BioEdit and a phylogenetic tree was generated by the maximum parsimony (MP), minimum evolution (ME), and maximum likelihood (ML) analysis methods. Analyses were conducted using PAUP 4.0b10 on a Macintosh platform (Swofford 2003), and in Mega 5.0 (Tamura *et al.* 2011) with the number of bootstrap trials set to 1,000. The taxon sampling consists of 58 voucher specimens representing 37 species of the Candelariaceae (Fig. 1) with *Oxneria alfredii*, *O. ulophyllodes* and *O. huculica* as outgroup (Table 1). More than 210 nrDNA and mtDNA sequences submitted to GenBank within our study were included in the phylogenetic tree mentioned. Molecular data provided for *Candelinella makarevichiae* (including holotype and isotype), as well as additional specimens of *Candelaria asiatica* from South Korea for the first time. The latter species (*Candelaria asiatica*) from China, as well as '*Candelaria*' *murrayi* from Argentina, South America are recorded for the first time. Voucher of *Candelariella vitellina* from Antarctica is also identified based on molecular phylogeny.

RESULTS

nrITS phylogeny

Our nrITS phylogeny confirms previous data that only species of the '*Candelariella*' *subdeflexa* group are positioned in the outermost position to all representatives of the Candelariaceae (Liu *et al.* 2019, Westberg *et al.* 2007, Yakovchenko *et al.* 2017), while members of the genera *Candelina*, *Placomaronea* are positioned among various species of the genus *Candelariella* s. l.

After nrITS phylogeny species of the genus *Candelina* (i.e. *C. mexicana* (B. de Lesd.) Poelt, the type species, and *C. submexicana* (B. de Lesd.) Poelt) form a separate robust branch which is positioned in sister position to the '*Candelariella*' *makarevichiae* group.

The five species of the genus *Placomaronea* Räsänen including the type species *P. candelarioides* Räsänen, and *P. fuegiana* M. Westb. et Frödén, *P. kaernefeltiana* M. Westb., Frödén et Wedin, *P. mendozae* (Räsänen) M. Westb., as well as *P. minima* M. Westb. et Frödén are positioned in a separate branch being in the intermediate position between the '*Candelariella*' *subdeflexa* and the other branches of the *Candelaria* s. l. and the *Candelariella* s. l. subclades.

It was stressed several times that the genus *Candelariella* Müll. Arg. is polyphyletic after molecular data (Liu and Hur 2018, Liu *et al.* 2019, Westberg *et al.* 2007, Yakovchenko *et al.* 2016, 2017). The genus *Candelariella* s. str. (i.e. the

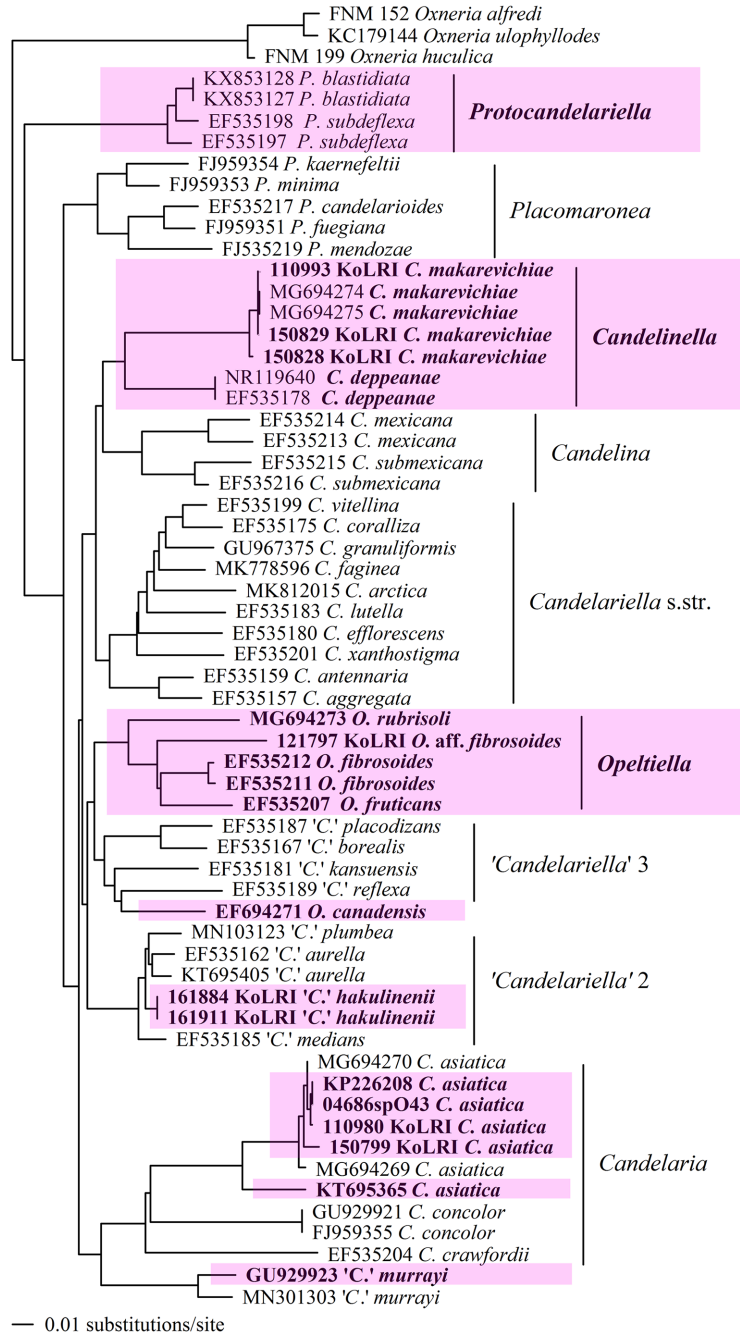

Fig. 1. Position of *Candelinella*, *Opeltiella* and *Protocandelariella* species in the phylogenetic tree of the Candelariaceae based on nrITS phylogeny

Candelariella vitellina group) includes a very small group of species based on our nrITS phylogeny (i.e. ten species: *Candelariella vitellina* (Hoff.) Müll. Arg., *C. coralliza* (Nyl.) H. Magn., *C. granuliformis* M. Westb., *C. xanthostigma* (Pers. ex Ach.) Lettau, *C. faginea* Nimis, Poelt et Puntillo, *C. lutella* (Vain.) Räsänen, *C. efflorescens* R. C. Harris et W. R. Buck, *C. arctica* (Körb.) R. Sant., *C. antennaria* Räsänen and *C. aggregata* M. Westb.). It is for the first time recorded that *C. vitellina* is a correct name for the specimen deposited as *Candelariella* sp. under GB accession number MK536666 from Antarctica.

The majority of the species hitherto included in the genus *Candelariella* s. l. is positioned in a clade together with '*Candelariella*' *medians*, '*Candelariella*' *placodizans* (Nyl.) H. Magn., '*Candelariella*' *citrina*, '*Candelariella*' *reflexa*, '*Candelariella*' *canadensis* (Fig. 1), and other single species of the *Candelariella* s. l. (i.e. '*Candelariella*' *complanata* M. Westb., '*C.*' *corviniscalensis* C. A. Morse et M. Westb., '*C.*' *rosulans* (Müll. Arg.) Zahlbr., '*C.*' *kansuensis* H. Magn., '*C.*' *spraguei* (Tuck.) Zahlbr., '*C.*' *clarkiae* E. Tripp et Lendemer [as '*clarkii*'] etc. not shown in Fig. 1), while the '*Candelariella*' *makarevichiae* group is positioned in sister position to the genus *Candelina*.

The conclusion that *Candelaria* A. Massal. is polyphyletic genus was illustrated by molecular data several times, too (Liu and Hur 2018, Westberg *et al.* 2007). However, the status of separate species of the genus *Candelaria* s. l. was hitherto not analysed in detail. From our analysis the genus *Candelaria* s. str. includes only four species, i.e. *C. concolor*, the recently described Asian *C. asiatica*, the pantropical *C. fibrosa*, and *C. crawfordii* (Fig. 1). In the original publication *C. asiatica* D. Liu et J.-S. Hur was recorded only from three localities in South Korea (Liu and Hur 2018). Molecular data of two additional specimens of *C. asiatica* from South Korea are added within this study (voucher specimens 110980 KoLRI and 150799 KoLRI), while further three specimens from China submitted under incorrect names to GenBank earlier, i.e. *C. fibrosa* voucher specimen YK 14043 (GB accession number KP226208, Cao *et al.* 2015), *Candelaria* sp. O40 (GB accession number GU929923), and *C. concolor* (GB accession number EF535206), are also identified within this study (Table 1, Fig. 1). Thus, *C. asiatica* is recorded from China for the first time here. Our nrITS phylogeny confirms previous data that '*Candelaria*' *pacifica* (not shown in Fig. 1), as well as the '*Candelaria*' *fruticans* group are positioned in a distant position from the *Candelaria* s. str. branch. '*Candelaria*' *pacifica* is positioned within the '*Candelariella*' *medians* group, while the '*Candelaria*' *fruticans* group is positioned in a somewhat outermost position to other *Candelariella* species.

It is for the first time illustrated that the '*Candelaria*' *murrayi* (Dodge) Poelt is positioned in the outermost position to the *Candelaria* s. str. clade. The level of support of the *Candelaria* s. str. subclade and the '*Candelaria*' *murrayi* branch

is rather low. From our data there are two sequences of '*Candelaria*' *murrayi* submitted to the GenBank, one under the correct name (GB accession number MH301303) and another specimen submitted under the incorrectly identified name *Candelaria fibrosa* (GB accession number GU929923). '*Candelaria*' *murrayi* is recorded from South America for the first time here on the basis of voucher specimens submitted to the GenBank under the incorrect name of *Candelaria concolor* (see Table 1). These two sequences are identical. Thus, '*Candelaria*' *murrayi* is recorded here from Argentina, South America for the first time. The "*Candelaria*' *murrayi* branch is probably monotypic, which will be a member of another genus. The situation is similar with the monotypic genus *Martinjahnsia* S. Y. Kondr., Fedorenko, S. Stenroos, Kärnefelt, Elix, Hur et A. Thell and the genus *Xanthoria* s. str. (Fedorenko *et al.* 2012), as well as the monotypic genera *Jesmurraya* S. Y. Kondr., Fedorenko, S. Stenroos, Kärnefelt, Elix, Hur et A. Thell and *Golubkovaea* S. Y. Kondr., Kärnefelt, Elix, A. Thell et Hur (Ahti *et al.* 2015, Fedorenko *et al.* 2012, Kondratyuk *et al.* 2014*b*), as well as the genus *Oxneria* s. str. in the Teloschistaceae.

Unfortunately, data on 12S mtSSU and 28S nrLSU sequences are still missing for the genera *Candelina* and *Placomaronea*.

Combined phylogeny

On the basis of three-gene phylogeny (i.e. concatenated nrITS, 12S mtSSU and 28S nrLSU sequences) carried out within this study from data hitherto available for the representatives of the Candelariaceae there are the following separate branches of the phylogenetic tree of the Candelariaceae: the *Candelariella* s. str. / the '*Candelariella*' *medians* group subclade, the *Candelaria* s. str. / '*Candelaria*' *murrayi* subclade; *Candelina* / the '*Candelariella*' *makarevichiae* group subclade, the *Placomaronea* subclade, and the '*Candelariella*' *deflexa* group (Fig. 2).

The following three new genera, i.e. *Candelinella* S. Y. Kondr., for the '*Candelariella*' *makarevichiae* group, *Opeltiella* S. Y. Kondr. for the '*Candelaria*' *fraudans* group, as well as *Protocandelariella* Poelt, D. Liu, J.-S. Hur et S. Y. Kondr. for the '*Candelariella*' *subdeflexa* group are proposed as the monophyletic branches of the Candelariaceae, i.e. having the highest level of support after combined phylogenetic analysis based in concatenated nrITS, 12S mtSSU and 28S nrLSU sequences.*

* It should be mentioned that data on nrITS sequences of single species '*Candelaria*' *pacifica*, '*Candelariella*' *hakulinenii*, etc. showing closer relations to the '*Candelariella*' *medians* group are not included in the final phylogenetic tree. Clarifying the status of all taxa mentioned is pending accumulation of further molecular data.

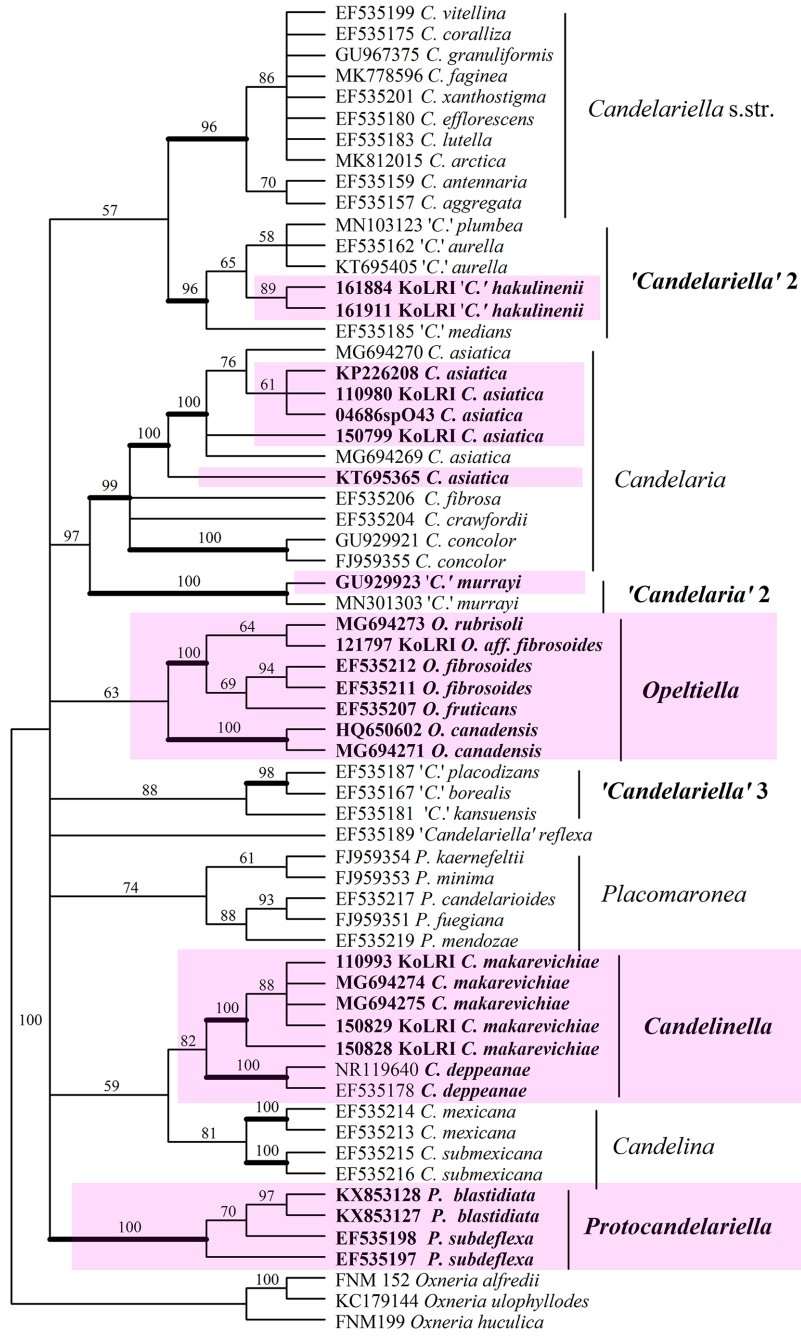

Fig. 2. Position of *Candelinella, Opeltiella* and *Protocandelariella* species in the phylogenetic tree of the Candelariaceae based on combined multigene phylogeny

New taxa

Candelinella S. Y. Kondr., *gen. nova*

MycoBank No.: MB 836762

Similar to the genus Candelina, *but differs in having from indistinct areole to squamulose thallus, not being firmly attached to the substrate, and in having simple to 1-septate, narrowly ellipsoid to oblong ascospores, as well as in the lack of lower cortex and medulla, and in the lack of distinctly lobed thallus in the peripheral portion.*

Type species: *Candelinella makarevichiae* (S. Y. Kondr., L. Lőkös et J.-S. Hur) S. Y. Kondr.

Thallus small, crustose, granular to areolate or squamulose; areoles convex, rounded to angular or irregular in outline, scattered to crowded, sometimes aggregated into thicker crusts, green yellow to orange yellow, smooth.

Apothecia lecanorine, darker yellow than the thallus, round, soon becoming strongly convex, where thalline margin seems to be excluded / disappearing, while it is well developed in section; paraphyses simple, cylindrical or with slightly swollen tips; hypothecium hyaline, asci 8-spored, ascospores hyaline, simple to 1-septate, narrowly ellipsoid to oblong; conidia hyaline, oblong to ellipsoid.

Chemistry: calicin, pulvinic acid, pulvinic dilactone, and vulpinic acid.

Etymology: The genus *Candelinella* is named after similarity to the genus *Candelina* based on combined multigene phylogeny and nrITS phylogeny.

Distribution and ecology: The genus hitherto includes two species, i.e. *Candelinella makarevichiae* from East Asia and *C. deppeanae* distributed in southwestern North America. The latter species (i.e. *C. deppeanae*) might belong to another genus as the level of support of the *Candelinella* subclade is rather low. They grow on bark or on decorticated trunks of both coniferous (*Juniperus deppeana* and *Pinus* spp.) and deciduous trees (oak, cherry trees, etc.) and shrubs, from desert scrub, riparian woodland, canyons to pine forests up to 2,100 m a.s.l.

Taxonomic notes: The genus *Candelinella* is positioned in sister position to the genus *Candelina* based on combined multigene phylogeny (Fig. 2) and based on nrITS phylogeny (Fig. 1). The genus *Candelinella* is similar to the genus *Candelina*, but differs in having indistinct areolate to squamulose thallus, not being firmly attached to the substrate, and in having simple to 1-septate, narrowly ellipsoid to oblong ascospores (vs. simple and often slightly curved (bean-like)), as well as in the lack of lower cortex and medulla (vs. lower cortex and white or yellow medullar well developed), and in the lack of distinctly lobed thallus in the peripheral portion.

When *Candelinella makarevichiae* was described it was recorded from the bark of deciduous as well as coniferous trees. However, molecular data were obtained for this species only from material from the bark of coniferous trees. The question whether the material from the bark of deciduous trees is conspecific with the material from the bark of coniferous trees was still open at that time (Kondratyuk *et al.* 2018). Liu *et al.* (2019) provided data on specimens of this species on the bark of both coniferous and deciduous trees. Materials from both groups of phorophytes were found within this study to be the same.

Thus, it is for the first time shown that *Candelariella subsquamulosa* D. Liu et Hur, recently described from South Korea (Liu *et al.* 2019), is a new synonym of *C. makarevichiae*. The nrITS sequences of the holotype and isotype specimens of *C. makarevichiae* as well as of the holotype and paratype of *C. subsquamulosa* are the same (Table 1, Fig. 1). Based on nrITS phylogeny they are positioned in the same branch with the highest level of support. Thus, the conclusion that *C. subsquamulosa* is a new synonym of the *Candelinella makarevichiae* is drawn here.

Opeltiella S. Y. Kondr., *gen. nova*

MycoBank No.: MB 836763

Similar to Candelaria, *but differs in having 8-spored asci as well as in the lack of lower cortical layer and true rhizines.*

Type species: *Opeltiella fruticans* (Poelt et Oberw.) S. Y. Kondr.

Thallus areolate to subsquamulose or subfoliose, adnate to ascending or more or less erect (in *O. fruticans*), irregularly incised. Upper surface yellow, matt, smooth; soredia and isidia lacking or with sorediate lower surface (in *O. fruticans*) or thalline areoles breaks and ultimately dissolves into soredia. Lower surface white, ecorticate, arachnoid to tomentose with a thick mat of hyphal strands, true rhizines lacking.

Apothecia lecanorine, disc more or less flat, thalline margin persistent; asci 8-spored; ascospores simple to 1-septate, narrowly ellipsoid; conidia ellipsoid, 2.0–3.5 × 1.5 μm.

Chemistry: calycin (major substance), pulvinic and vulpinic acids, and pulvinic acid lactone.

Etymology: The name *Opeltiella*, similarly to the genus name *Opeltia* S. Y. Kondr. et L. Lőkös of the subfamily Caloplacoideae of the Teloschistaceae, originates from an anagram of the generic name *Poeltia* Grolle (Gymnomitriaceae, Marchantiophyta) dedicated to Josef Poelt (1924–1995), one of the greatest lichenologist in the history of the science, and the co-author of the type species of this genus.

Distribution and ecology: The genus hitherto includes four species, two of which are known from South America, as well as one species from Eastern Asia and one more from North America. Four species are confirmed as being members of the *Opeltiella* branch from the multigene phylogeny. However, one species, i.e. *Opeltiella canadensis*, may be included in another genus in the future. Species are known from dead shrubs and cacti sometimes together with *Teloschistes hosseusianus* Gyelnik in dry pasture land at high altitude (*ca* 2,200 m a.s.l.), as well as on bark of deciduous trees and from pine tree (*Pinus armandi*) in lowlands and in coastal zone.

Taxonomic notes: Our data of multigene phylogeny confirm that the genus *Opeltiella*, which is proposed here for the '*Candelaria*' *fruticans* group, as a separate robust monophyletic branch is positioned separately / distantly from *Candelaria* s. str., including only polyspored species with well-developed lower cortical layer and with true rhizines (Fig. 2). In our nrITS phylogeny *Opeltiella* was positioned in sister position to the '*Candelariella*' *placodizans* group (Fig. 1).

Protocandelariella Poelt, D. Liu, J.-S. Hur et S. Y. Kondr., *gen. nova*

MycoBank No.: MB 836764

Similar to the genus Candelariella, *but differs in having squamulose thallus and in having conidia from conidiogenous cells on the lower surface.*

Type species: *Protocandelariella subdeflexa* (Nyl.) Poelt, D. Liu, J.-S. Hur et S. Y. Kondr.

Thallus squamulose, sometimes poorly developed and then granular to indistinct, pale grey to pale brownish grey, somewhat shiny, cortical layer consisting of two layers, i.e. the upper dead compressed hyphae (or without), lower part paraplectenchymatous, without or with blastidia on margins and / or the lower side of squamules.

Apothecia biatorine, usually abundant, disc pale yellow to yellow, somewhat convex to very convex, yellow; asci 8-spored, ascospores hyaline, simple to 1-septate, narrowly ellipsoid to ovoid. Conidiomata usually lacking, instead the lower surface of the squamules are covered by conidiophores, conidia hyaline, more or less globose.

Chemistry: calycin, pulvinic acid, pulvinic dilactone and vulpinic acid. Apothecial disc K+ reddish, KC–, C–.

Etymology: It is named after its similarity to the genus *Candelariella*.

Distribution and ecology: So far two species belong to this genus, which are hitherto known from North America, southern and central Europe, North Africa, Asia and New Zealand. They grow mostly on the bark of broad-leaved trees, sometimes on wood.

Taxonomic notes: The genus *Protocandelariella* is similar to the genus *Candelariella*, but differs in having squamulose thallus and in having conidia from conidiogenous cells on the lower surface (vs. conidia produced by the pycnidia on the upper surface).

Protocandelariella species produce conidia from conidiogenous cells on the lower surface of thalline squamules and differ from the other species of the genus *Candelariella* as well as other genera of the Candelariaceae producing conidia by the pycnidia on the upper surface. Results of our nrITS phylogeny confirm previous data (Liu *et al.* 2019, Westberg *et al.* 2007, Yakovchenko *et al.* 2017) that only the *Protocandelariella* (and sometimes the *Placomaronea* branch as well) is positioned in the outermost position to all members of the Candelariaceae (Fig. 1). The *Protocandelariella* is positioned as a separate robust monophyletic branch based also on multigene phylogeny (Fig. 2).

Poelt (1974) recognised '*Candelariella*' *subdeflexa* as a unique species among the representatives of the genus *Candelariella*. Poelt's name as a 'protocandelariella' in the family Candelariaceae is here used for the new genus, which has confirmation from morphological as well as from molecular points of view. The *Protocandelariella* includes *P. subdeflexa*, the type species, and recently described '*Candelariella*' *blastidiata* Yakovchenko. Morphological and molecular phylogenetic data support the close relationship of *P. subdeflexa* and *P. blastidiata* representing a so-called 'species pair' (Poelt 1970), where *P. subdeflexa* reproduces by sexual propagules and *P. blastidiata* mostly by vegetative ones. Both species also possess asexual conidia as additional propagules; however, the production of conidia appears to be less effective in *P. blastidiata*.

New combinations

Candelinella deppeanae (M. Westb.) S. Y. Kondr., *comb. nova* – MycoBank No.: MB 836765 – Basionym: *Candelariella deppeanae* M. Westb., Bryologist 110(3): 406 (2007).

Candelinella makarevichiae (S. Y. Kondr., L. Lőkös et J.-S. Hur) S. Y. Kondr., *comb. nova* – MycoBank No.: MB 836766 – Basionym: *Candelariella makarevichiae* S. Y. Kondr., L. Lőkös et J.-S. Hur, Acta Bot. Hung. 60(1–2): 134 (2018). – New synonym: *Candelariella subsquamulosa* D. Liu et J.-S. Hur [as J.-S hur], Mycobiology 47 (1): 44 (2019).

Opeltiella canadensis (H. Magn.) S. Y. Kondr., *comb. nova* – MycoBank No.: MB 836767 – Basionym: *Candelariella canadensis* H. Magn., Ark. Bot., Ser. 2, 2 (no 2): 216 (1952).

Opeltiella fibrosoides (M. Westberg et Frödén) S. Y. Kondr., *comb. nova* – MycoBank No.: MB 836768 – Basionym: *Candelaria fibrosoides* M. Westberg et Frödén, Bibl. Lichenol. 95: 551 (2007).

Opeltiella fruticans (Poelt et Oberw.) S. Y. Kondr., *comb. nova* – MycoBank No.: MB 836769 – Basionym: *Candelaria fruticans* Poelt et Oberw., Phyton, Horn 16(1–4): 202 (1974).

Opeltiella rubrisoli (D. Liu et J.-S. Hur) S. Y. Kondr., *comb. nova* – MycoBank No.: MB 836812 – Basionym: *Candelariella rubrisoli* D. Liu et J.-S. Hur [as J.-S hur], Mycobiology 47(1): 41 (2019).

Protocandelariella blastidiata (L. Yakovchenko) D. Liu, J.-S. Hur et S. Y. Kondr., *comb. nova* – MycoBank No.: MB 836770 – Basionym: *Candelariella blastidiata* L. Yakovchenko, Lichenologist 49(2): 120 (2017).

Protocandelariella subdeflexa (Nyl.) Poelt, D. Liu, J.-S. Hur et S. Y. Kondr., *comb. nova* – MycoBank No.: MB 836771 – Basionym: *Lecanora subdeflexa* Nyl., Flora, Regensburg 62: 355 (1879) ≡ *Candelariella subdeflexa* (Nyl.) Lettau, Hedwigia 52: 355 (1912).

CONCLUSIONS

Thus, seven genera, i.e. *Candelaria, Candelariella, Candelina, Candelinella, Opeltiella, Placomaronea* and *Protocandelariella,* found hitherto to have support from the combined phylogeny of the Candelariaceae based on nrITS, 12S mtSSU and 28S nrLSU sequences. Accumulation of the further data will help to clarify the status of the '*Candelariella*' *medians* group, the '*Candelariella*' *reflexa* group as well as other taxa of the genus *Candelariella* s. l.

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