



RESEARCH ARTICLE



Jejulea byssolomoides gen. et sp. nov., a Remarkable Pilocarpaceae (Lichen-Forming Ascomycetes) from Jeju Island, South Korea

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ABSTRACT

The new genus and species, Jejulea byssolomoides, is described from Jeju Island, Korea. This lichen is characterized by saxicolous, crustose, pale greenish-gray, partly finely filamentous, matt, smooth thallus, prominent convex brown to dark brown ascomata with a concolorous margin constricted at the dark brown base, 300-800 μm diameter, 200-250 μm high, without a distinct proper margin, adhering to the substratum ending in a minute byssoid white external part of cylindrical cells, fusiform 3–5 septate ascospores (17–23 \times 4–5 μ m). Phylogenetic analyses using ITS and mtSSU sequences place Jejulea in the Pilocarpaceae (Lecanorales). The new taxon is closely related to Byssoloma, a cosmopolitan group of foliicolous lichens, which is most diverse in the tropics. Like Byssoloma, Jejulea also forms a byssoid apothecial margin.

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1. Introduction

Although Jeju Island is small in size (1826 km²), it is known for its high number of endemic lichens [1–4] and lichenicolous fungi [5]. Foliicolous lichens in the Gotjawal forest area on Jeju Island have also been described [6]. So far, lichen research has focused mainly on epiphytic, saxicolous [1,2,7], and foliicolous lichens [8,9]. The river valley formed by a solid basalt base can be surprisingly interesting. The discovery of the saxicolous "Byssoloma" is another example of a remarkable endemic species occurring on these islands of the East China Sea.

Pilocarpaceae is a crustose, cosmopolitan family comprising 29 genera, with 424 species [10]. Species are characterized by biatorine or lecideine apothecia and pycnidia or campylidia type of conidiomata. The family is distributed in the tropical zone, where most species grow on leaves. Research of that group has been very intensive recently and descriptions of the new species are not rare [11]. The closest relatives of the new genus Jejulea are the genera Byssoloma, Sporopodium, Tapellaria, Fellhanera, Lasioloma, and Calopadia. The genus Byssoloma Trevis. [12] recently comprises 93 cosmopolitan foliicolous lichen species [13] with the main distribution in tropical and subtropical zones. A few species extend to temperate zones [11]. The genus is

characterized by cortical crustose thalli, a byssoid apothecial margin, loosely intricate hyphae of proper exciple, asci with I + darker, tubular structure, and colorless, 1-3 septate spores [14]. Sporopodium Mont. [15] is a genus that also occurs in tropical zones, the campylidia of these 11 species usually feature a distinct socle producing the conidia [14]. Some of the species contain secondary metabolites [16]. The genus Tapellaria [17] forms black, lecideine apothecia, anastomosing paraphyses, and campylidia producing filiform conidia. It is a predominantly foliicolous genus (25 species) with only a small number of the species growing on bark [18]. Most of the species are known from Neotropics, but Tapellaria parvimuriformis was newly described from East Asia [11]. Fellhanera Vězda [19] is a large polyphyletic genus among foliicolous lichens [11] which contains about 114 species [13]. Like the previous genera, it forms small apothecia with a thin margin, paraplectenchymatous excipulum, anastomosing paraphyses, Byssoloma type asci, ellipsoid ascospores, and pycnidial conidiomata [14]. There are other genera very close to Fellhanera: Brasilicia differs in its filiform ascospores, Bapalmuia Sérus [20] has the very same shape as ascospores but differs in its secondary chemistry [14]. Lasioloma [21] differs from Tapellaria and Calopadia in its wooly prothallus, the

pilose apothecial margins, and the centrally branched conidia, whereas Tapellaria differs in its black apothecia with purple hypothecium and anastomosing paraphyses. 10 species are corticolous with Neotropical distribution and the rest are foliicolous species with a predominantly Paleotropical distribution [22].

2. Materials and methods

2.1. Morphological studies

Observations and measurements of photobiont cells, thallus and apothecium anatomy, asci and ascospores were made of hand-cut sections mounted in water and diluted KOH (K) solution. Asci were also observed in Lugol's Iodine (I), with and without pretreatment in K. Mean value (x) and standard deviation (SD) were calculated, and the results are given as (minimum value observed) $x \pm SD$ (maximum value observed). x, SD, and n (the total number of ascospores measured) are given within parentheses. Thin-layer chromatography (TLC; Merck, Darmstadt, Germany) was carried out according to [23]. Macro images were captured with a Canon 5DSR digital SLR camera (Canon, Tokyo, Japan) and an Olympus Zuiko 20 mm macro lens (Olympus, Tokyo, Japan). Microscopic images were captured with a Canon 5DSR digital SLR camera (Canon, Tokyo, Japan) mounted on an Olympus BX41 DIC microscope (Olympus, Tokyo, Japan). Illustrations were prepared using Adobe Photoshop. Measurements of the hymenium, hypothecium, cortex, and spore size (30-50 spores per specimen) were made in water mounts. The voucher specimen was deposited in the Korean Lichen Research Institute, Sunchon National University, Suncheon, South Korea.

2.2. DNA extraction, amplification, and sequencing

Genomic DNA was extracted from the six fresh lichen specimens using the CTAB protocol [24]. The nuclear ribosomal internal transcribed spacer (nrITS) and mitochondrial small subunit ribosomal RNA (mtSSU) regions were amplified using AccuPower® PCR PreMix (Bioneer, Daejeon, South Korea). The primers used were ITS1F (5'-CTT GGTCATTTAGAGGAAGTAA-3') and ITS4 (5'-TC CTCCGCTTATTGATATGC-3') for ITS [25], mrSS U1 (5'-AGCAGTGAGGAATATTGGTC-3') and mrS SU3R (5'-ATGTGGCACGTCTATAGCCC-3') mtSSU [26]. PCR amplification was done using a Thermal Cycler machine (Bio-Rad, Hercules, CA, USA) performed under the following conditions: an initial cycle of 5 min at 94 °C,

followed by 30 cycles of 30 s at 94 °C, 30 s at 55 °C, 10 min at 72 °C, and then finally 10 min at 72 °C for nrITS, and an initial cycle of 3 min at 94 °C, followed by 35 cycles of 1 min at 94 °C, 1 min at 52 °C, 1 min at 72 °C, and then finally 7 min at 72 °C for mtSSU.

2.3. Multiple sequence alignment

Six new sequences (nrITS and mtSSU) were obtained from this study, and their closest relatives (i.e., Byssoloma species) based on BLAST searches were retrieved from GenBank. Members representing all genera were currently accepted (Table 1). For phylogenetic analyses, sequences were assembled by ATGC version 1.03 (GENETYX Co., Tokyo, Japan) and multiple sequence alignment (MSA) was performed using MAFFT v. 7 with G-INS-1 algorithm for nrITS and L-INS-i algorithm for mtSSU [27]. Unclearly aligned position sequences were manually modified using MEGA v. 7 [28]. nrITS and mtSSU based on a combined phylogenetic tree were estimated based on Maximum-Likelihood (ML) and Bayesian Posterior Probabilities (PP). ML and PP best-fit model of nucleotide substitution and parameters were estimated by IQ-TREE 2.2.0 [29] based on Bayesian information criterion (BIC), and SYM + I + G4model for nrITS and TVM + F + I + G4 for mtSSU were chosen. ML analysis was performed using IQ-TREE 2. 2. 0 [29] and 1000 bootstrap replications. Bayesian analysis was conducted based on the Markov chain Monte Carlo method (MCMC), 10 million generations with every 100th sampling using MrBayes v. 3.2.7 [30]. The first 25% sample of trees was discarded and visualized in Figtree v. 1.4.4. Micarea micrococca and Micarea byssacea located in Pilocarpaceae were chosen as outgroups.

3. Results

3.1. Phylogenetic analyses

The data set of nrITS and mtSSU consisted of 37 nrITS and 81 mtSSU sequences of Pilocarpaceae obtained from NCBI with six sequences of two-locus newly obtained from Jejulea byssolomoides (Table 1). Maximum-likelihood bootstrap value (ML) ≥70% and Bayesian Posterior Probabilities (PP) >95% were added above the branches. In the mtSSU phylogenetic tree, J. byssolomoides is closely located in a clade composed of four genera, Bapalmuia, Byssolecania, Byssoloma, Tapellaria, and formed an independent clade (Figure 1). In the nrITS phylogenetic tree, J. byssolomoides was clustered in the Byssoloma clade with Bapalmuia palmularis (Figure 2). The branch length indicates the

 Table 1. List of species and DNA sequence information employed for phylogenetic analysis.

		GenBank a	ccession no.
Species name	Voucher	nrlTS	mtSSU
Aquacidia antricola	ALV4918		MH817969
Aquacidia trachona	Andersen 99 (BG)	AY756456	AY567784
Bapalmuia palmularis	Lücking 16003 (BG)	AY756457	AY567781
Byssolecania hymenocarpa Byssolecania hymenocarpa	KYW0254 KYW0286	MK946965 MK946957	MK957159 MK957152
Byssolecania nymenocarpa Byssolecania sp.	20180247	MK946973	MK957170
Byssolecania variabilis	Lücking 16033 b (BG)	AY756458	AY567780
Byssoloma annuum	KeM583		LC648424
Byssoloma annuum	HN20170295		MN043716
Byssoloma brunneodiscum	HN20170147		MN105603
Byssoloma brunneodiscum	HN20170165		MN105600
Byssoloma cf. leucoblepharum	KYW0184		MN043700
Byssoloma cf. leucoblepharum	KYW0445 KeM575		MN043697 LC648423
Byssoloma chlorinum Byssoloma chlorinum	KeM372		LC648410
Byssoloma citricola	50677		MN043707
Byssoloma leucoblepharum	54740		MN105613
Byssoloma leucoblepharum	KYW0188		MN105612
Byssoloma leucoblepharum	HN20170108		MN043724
Byssoloma leucoblepharum	HN20170091		MN043720
Byssoloma leucoblepharum	KYW0422		MN043694
Byssoloma leucoblepharum	HN20170357	MK946977	MK957174
Byssoloma leucoblepharum	20180145	MK946971	MK957166
Byssoloma leucoblepharum	20180153	MK946970	MK957165
Byssoloma leucoblepharum Byssoloma leucoblepharum	KYW0405 Ekman 3502 (BG)	MK946966 AY756459	MK957160 AY567778
Byssoloma neucobieрнагаті Byssoloma marginatum	Tønsberg 27125 (BG)	AY756460	AY567777
Byssoloma meadii	Ekman L1130 (LD)	71730400	AY567776
Byssoloma melanodiscocarpum	HN20170148		MN105607
Byssoloma melanodiscocarpum	HN20170298		MN105601
Byssoloma rubrofuscum	HN20170295		MN105599
Byssoloma rubrofuscum	HN20170297		MN105602
Byssoloma sp.	20190551		MN105611
Byssoloma sp.	20190514		MN105610
Byssoloma subdiscordans	HN20170156		MN105609
Byssoloma subdiscordans Byssoloma subdiscordans	HN2014213 57021		MN105606 MN043704
Byssoloma subdiscordans	57130		MN043704 MN043703
Byssoloma subdiscordans	Tønsberg 25968 (BG)	AY756461	AY567779
Byssoloma vanderystii	KeM400		LC648411
Byssoloma vanderystii	HN20170227		MN043718
Byssoloma vanderystii	20180144		MN043710
Byssoloma vanderystii	KYW0060		MN043699
Calopadia foliicola	KYW0068		MK957146
Calopadia foliicola	Lücking 16011 (BG)		AY567782
Calopadia puiggarii Calopadia puiggarii	KYW0036_31764 20180158		MK957156 MK957167
Eugeniella micrommata	KeM437		LC648413
Eugeniella micrommata	KYW0046		MK957161
Fellhanera bouteillei	AFTOL-ID 4917		KJ766392
Fellhanera bouteillei	KYW0558		MK957177
Fellhanera bouteillei	Ekman 3417 (BG)	AY756463	AY567787
Fellhanera bouteillei	LIFU082-16 (versA1)	KX132990	
Fellhanera bouteillei		AF414858	
Fellhanera fuscatula	KYW0264	MK946967	MK957162
Fellhanera fuscatula	KYW0336	MK946959	MK957154
Fellhanera fuscatula	KYW0392	MK946956	
Fellhanera fuscatula Fellhanera gyrophorica	KYW0462 17826	MK946954 MN387060	
Fellhanera gyrophorica	17746	MN387000 MN387059	
Fellhanera gyrophorica	17744	MN387058	
Fellhanera gyrophorica	17267	MN387057	
Fellhanera gyrophorica	17094	MN387056	
Fellhanera microdiscus	HN20170313	MK946978	MK957175
Fellhanera sp.	20180167	MK946981	MK957169
Fellhanera sp.	20180166	MK946980	MK957168
Fellhanera sp.	20180146	MK946969	MK957164
Fellhanera sp.	20180711	MK946950	MK957145
Fellhanera subtilis Fellhanera viridicorediata	Tønsberg 28199 (BG)	AY756464	AY567786
Fellhanera viridisorediata Fellhaneropsis myrtillicola	Tønsberg 27375 (BG) Tønsberg 25311 (BG)	AY756465 AY756466	AY567775 AY756445
Fellhaneropsis myrtillicola Fellhaneropsis vezdae	Knutsson 97-229 (hb Knutsson)	A1/30400	AY567744
Jejulea byssolomoides	KoLRI057219	OM044386	OM044380
Jejulea byssolomoides	KoLRI057220	OM044387	OM044381
Jejulea byssolomoides	KoLRI057221	OM044388	OM044382

(continued)

Table 1. Continued.

Species name	Voucher	GenBank accession no.	
		nrlTS	mtSSU
Jejulea byssolomoides	KoLRI057222	OM044389	OM044383
Jejulea byssolomoides	KoLRI057223	OM044390	OM044384
Jejulea byssolomoides	KoLRI057224	OM044391	OM044385
Lasioloma arachnoideum	KYW0595		MK957155
Lasioloma arachnoideum	KYW0646		MK957158
Lasioloma arachnoideum	Lücking 16005 (BG)		AY567783
Leimonis erratica	AFTOL-ID 4988		KJ766425
Leimonis erratica	Arup 99192 (hb Arup)		AY567737
Micarea byssacea	289102_A97	MG521563	MG707769
Micarea micrococca	299101_A100	MG521552	MG707753
Puttea margaritella	M351		FJ006733
Puttea margaritella	M270		FJ006731
Septotrapelia usnica	26 Sept 01 Sudirman & Sipman		AY300894
Sporopodium antoninianum	Lücking 16002d (BG)		AY567785
Sporopodium argillaceum	HN20170022		MK957173
Sporopodium argillaceum	HN20170001		MK957171
Szczawinskia tsugae	Tønsberg 30044 (BG)		AY567746
Tapellaria nana	50677		MK957178
Tapellaria nigrata	KYW0539		MK957176
Tapellaria nigrata	KYW0602	MK946952	MK957147
Tapellaria parvimuriformis	KYW0181	MK946955	MK957150

DNA sequences for the new genus Jejulea (in bold) were generated in this study. All others were obtained from GenBank. The species names are followed by voucher information and GenBank accession numbers. Voucher: Specimen voucher information; nrITS: internal transcribed spacer; mtSSU: mitochondrial small subunit.

difference between the three genera. However, statistical support of the external node dividing the clustered three genera Bapalmuia, Byssoloma, and Jejulea in nrITS was not significant. Thus, the approximate taxonomic position of J. byssolomoides was confirmed in nrITS. Two genera Byssolecania and Tapellaria formed independent clades strongly supported by ML and PP.

3.2. Taxonomy

Jejulea byssolomoides J.P. Halda, J.-J. Woo & J.-S. Hur gen. et sp. nov. (Figure 3).

MycoBank No.: MB#842471 (genus) and MB#842472 (species).

Jejulea byssolomoides belongs to the Pilocarpaceae and is phylogenetically related to Byssoloma leucoblepharum, Byssoloma subdiscordans, Byssoloma marginatum, and B. palmularis but differs by the combination of the following characters: fusiform 3-5 septate ascospores $(17-23 \times 4-5 \mu m)$, an indistinct proper margin with a white byssoid external part of cylindrical cells (20-25 µm), dark brown hypothecium and absence of pycnidia.

3.3. Type

South Korea, Yeongcheon-dong, Seogwipo, Jeju-si, Jeju-do, 33°18′0.79"N 126°34′34.54"E, alt. 307 m, on the vertical face of a sheltered basalt rock along a stream, 18 August 2015, J. P. Halda, S.-O. Oh & D. Liu 152633 (KoLRI 036855 - Holotype, KoLRI 036876, 036882, 036883, 036886, 036887, 036888,

036889, 036891, 036893, 057219, 057220, 057221, 057222, 057223, 057224 - *Isotypes*).

3.4. Etymology

The name of the genus refers to Jeju Island, the type locality. The epithet "byssolomoides" points to the closest relative genus, Byssoloma.

3.5. Morphology

Thallus thin, crustose, superficial, spreading, 1-8 cm diameter, $20-40 \mu m$ thick, spreading, pale greenish-gray, partly finely filamentous, matt, smooth; hypothallus indistinct. Algal cells chlorococcoid, spherical 6-15(-17) μ m diameter interstitial hyphae short-celled, $2-3 \mu m$ thick. Apothecia biatorine, applanate, orbicular, 300-800 μm diameter, $200-250 \,\mu\text{m}$ high, often grows in small groups of 2-4 ascomata. Excipulum well-developed, margin indistinct, becoming thinner outwards and adhering to the substratum ending in a minute white external part of cylindrical cells $(20-25 \mu m)$; disk $250-750 \mu m$ diameter, almost flat, not elevated at the margin, brown to dark brown, blackish from the center, epruinose. Proper exciple obviously thinner or tapering outwards as a minute white hyphal rim, colorless, subgelatinous; hyphae branched and anastomosing, uninflated (ca. 2 µm wide lumina), embedded in a gelatinous matrix, generally oriented toward the tapering edge. Hypothecium ca. $100 \,\mu m$ thick at the center, dark brown to partly black, subparaplectenchymatous, composed of more or less vertically



Figure 1. The phylogenetic tree was based on mtSSU sequences. Maximum-likelihood bootstrap value (ML) \geq 70% and Bayesian Posterior Probabilities (PP) \geq 95% were marked above branches. Thickened branches indicate ML/PP = 100/1.00. The newly obtained sequence of Jejulea byssolomoides used in this study is shown in bold.

cells, darker subhymenium. arranged than Subhymenium $15-20 \,\mu\text{m}$ thick, brown. Hymenium 40–75 μm thick, pale brown, dark brown below; paraphyses sparsely branched and anastomosing, with $1-2 \mu m$ diameter lumina. Asci clavate, with a blurred IKI + layer and a tholus with an IKI + blue inner

tube (*Byssoloma*-type), ca. $35 \times 12 \,\mu\text{m}$. Ascospores 8 per ascus, fusiform, 3-5 septate sometimes with perispore 1–2 μ m thick, (14–)17–23(–26) × (3–)4–5(–6) μ m [$x = 19.6 \times 4.4 \mu$ m; SD 3.3; 0.6 μ m; n = 48; l/wratio = 4.5], colorless, sometimes slightly constricted at the septa. Pycnidia not observed.

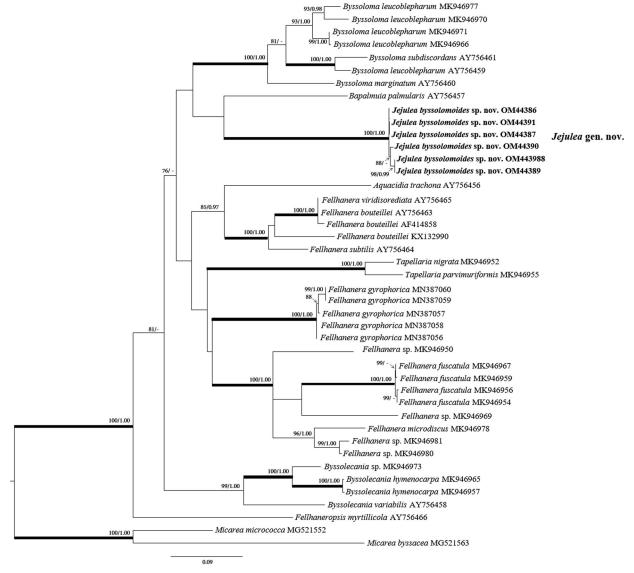


Figure 2. The phylogenetic tree was based on nrITS sequences. Maximum-likelihood bootstrap value (ML) \geq 70% and Bayesian Posterior Probabilities (PP) \geq 95% were marked above branches. Thickened branches indicate ML/PP = 100/1.00. The newly obtained sequence of *Jejulea byssolomoides* used in this study is shown in bold.

3.6. Chemistry

No lichen product was detected by TLC.

3.7. Ecology and distribution

Known from the type locality in Seogwipo, Jeju Island, South Korea. The species was found growing on shaded volcanic rocks (basalt) along a stream protected by the forest's margin together with Coenogonium lueckingii, Flakea papillata, Porina curnowii, P. eminentior, P. leptalea, P. mastoidea, Strigula nipponica, Verrucaria aethiobola, and Willeya iwatsukii. Jeju Island is a shield volcano that is composed of basaltic lava flows and minor pyroclastic rocks. The climate is characterized by hot humid summers and cool winters as a result of the influence of the East Asian monsoon.

3.8. Remarks

Byssoloma (see above) with its white byssoid margin of apothecia and septate ascospores but differs in the different ascus type and in having a true exciple of palisade plectenchyma. No species of the genus *Byssoloma* have been confirmed from Korea. Among saxicolous East-Asian species *Gyalideopsis lunata* [31] differs in its colorless hymenium and hypothecium, hyaline proper margin, and shorter submuriform to muriform ascospores $(12-17 \times 7-10 \, \mu \text{m})$ vs. 3–5 septate, $17-23 \times 4-5 \, \mu \text{m}$ in *J. byssolomoides*).

The closest related species *B. leucoblepharum* and *B. subdiscordans* differ in ecology: they grow especially on leaves of evergreen shrubs and trees, and also in morphology: thinner thallus, smaller pale to black apothecia $300-600\,\mu\mathrm{m}$ diameter, disk plane, with a persistent densely byssoid white margin.

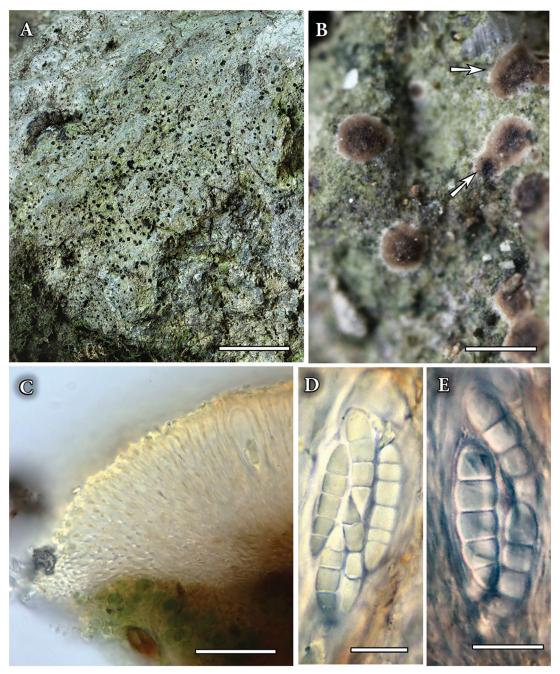


Figure 3. Jejulea byssolomoides (KoLRI 36855, holotype). (A, B) Thallus with ascomata (arows); (C) Cross section of ascoma; (D, E) Detail of mature ascospores in ascus (mounted in water). Scales: (A) $-10 \, \text{mm}$, (B) $-1000 \, \mu \text{m}$, (C) $-50 \, \mu \text{m}$, (D, E) $-10 \, \mu \text{m}$.

Excipulum made of colorless loosely woven hyphae, $50-150 \,\mu\text{m}$ broad. Hypothecium $20-50 \,\mu\text{m}$ high, light dark brown. Apothecial aeruginous. Hymenium 45–60 μm high, colorless. Asci $35-55 \times 9-12 \,\mu\text{m}$. Ascospores oblong, 3-septate, without constrictions at the septa, $10-18 \times 2.5-3.5 \mu m$ (3-5 μm in B. subdiscordans), colorless. Pycnidia subglobose to cup-shaped, 0.1-0.15 mm diameter, brownish-gray with a black center. Conidia pyriform, non-septate, $4-5 \times 1.2-1.8 \,\mu\text{m}$, colorless. *Byssoloma* marginatum forms a compact apothecial margin because the excipulum is composed of hyphae embedded in the gelatinous matrix. The apothecial disk is colored dark grayish brown and ascospores $(10-16 \times 3-4 \,\mu\text{m})$, 3-septate, colorless.

4. Discussion

Its geographical isolation and the special climatic conditions on Jeju Island are the main factors determining the emergence of new species of lichenized fungi, of which several dozen have been described herein in recent years (e.g., Caloplaca chejuensis, Fellhanera chejuensis, Fauriea jejuensis, Graphis jejuensis, Orientophila chejuensis, and Protoparmeliopsis chejuensis).

Jejulea byssolomoides is a distinct and mainly lichen-inhabiting lineage in the Pilocarpaceae characterized by its saxicolous thallus having a larger and wide 3–5 septate, $17-23 \times 4-5 \mu m$ ascospores so it cannot be confused with any other species of Pilocarpaceae. Other lichen genera with a byssaceous

ascomata growth form and a chlorococcoid photobiont such as Byssoloma Trevis., Bapalmuia Sérus., Mont., Tapellaria Sporopodium Müll. Arg., Fellhanera Vězda, Lasioloma Santesson, and Calopadia Vězda are phylogenetically unrelated, with different types of fruiting bodies and sizes of ascospores. The new species also resembles the saxicolous Septotrapelia usnica known from Indonesia, Singapore, and Sri Lanka [32], but the species contains usnic acid and zeorin and forms a granulose thallus, slightly bent, 3-septate ascospores not constricted at the septa $(21-27 \times 5-6 \,\mu\text{m})$ [33].

Ascomata with hairy margins are not common among lichens. They are known in some species in the family *Porinaceae* which produce hairy perithecial ascomata (*Trichothelium*) and in *Pilocarpaceae* (*Lasioloma*, *Byssoloma*) [14]. The saxicolous *Gyalidea* species, also known from coastal Korea, differ in the absence of white cylindrical cells growing from the margin of the excipulum, a different type of ascus (lightly thickened apical tholus, KI-, a small ocular chamber) [34] and in the different shape and size of the ascospores (1-septate to muriform) [2,35].

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