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

Josef P. Halda, Jung-Jae Woo, Dong Liu, Soon-Ok Oh, Yogesh Joshi and Jae-Seoun Hur

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 × 4–5 μm). 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.

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 most species grow on leaves. Research of that group has been very intensive recently and descriptions of most species grow on leaves. Research of that group has been very intensive recently and descriptions of most species grow on leaves.

KEYWORDS
Pilocarpaceae; biodiversity; lichens; phylogeny; taxonomy

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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 folicolous 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 ± 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]. Macroph images were captured with a Canon 5DSR digital SLR camera (Canon, Tokyo, Japan) and an Olympus Zuiko 20 mm macro lens (Olympus, Tokyo, Japan). Micropscopic 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 GGTCAATTAGGAACTAAA-3') and ITS4 (5'-TC CTCGGCTTATGATG-3') for ITS [25], mrSSU1 (5'-AGCAGTGGAGGATATTGGTGC-3') and mrSSU3R (5'-ATGTTGCGATCCTATAGCCC-3') for mtSSU [26]. PCR amplification was done using a T100™ 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 1-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 + G4 model for nrITS and TYM + 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
| Species name                  | Voucher                        | nrITS               | mtSSU               |
|------------------------------|--------------------------------|---------------------|---------------------|
| Aquacidia antricola          | ALV4918                         | MH817969            |                     |
| Aquacidia trachona           | Andersen 99 (BG)                | AY756456            | AY567784            |
| Bapalmia palmularis          | Lucking 16003 (BG)              | AY756457            | AY567781            |
| Byssolacia hymenocarpa       | KYW0254                         | MK946965            | MK957159            |
| Byssolacia hymenocarpa sp.   | 20180247                        | MK946967            | MK957152            |
| Byssolacia variabilis        | Lucking 16033 b (BG)            | AY756458            | AY567780            |
| Byssoloma annuum             | KeM583                          | LC648423            |                     |
| Byssoloma annuum             | HN20170295                      | MN043716            |                     |
| Byssoloma brunnединiscum    | HN20170147                      | MN05603             |                     |
| Byssoloma brunnединiscum    | HN20170165                      | MN05660             |                     |
| Byssoloma cf. leucoblepharum | KYW0184                         | MN043700            |                     |
| Byssoloma variabilis         | KeM575                          | LC648423            |                     |
| Byssoloma chlorinum          | KeM372                          | LC648410            |                     |
| Byssoloma citricola          | 50677                           | MN043707            |                     |
| Byssoloma leucoblepharum     | KeM583                          | MN05613             |                     |
| Byssoloma leucoblepharum     | KYW0184                         | MN043724            |                     |
| Byssoloma leucoblepharum     | KYW0422                         | MN043720            |                     |
| Byssoloma leucoblepharum     | HN20170108                      | MN05660             |                     |
| Byssoloma leucoblepharum     | HN20170091                      | MN05660             |                     |
| Byssoloma leucoblepharum     | 20180145                        | MK946977            | MK957174            |
| Byssoloma leucoblepharum     | 20180153                        | MK946971            | MK957166            |
| Byssoloma leucoblepharum     | KYW0405                         | MK946966            | MK957160            |
| Byssoloma leucoblepharum     | Ekman 3502 (BG)                 | AY756459            | AY567778            |
| Byssoloma marginatum         | Tønsberg 27125 (BG)             | AY756460            | AY567777            |
| Byssoloma meadii             | Ekman L1130 (LD)                | MN105611            |                     |
| Byssoloma melanodiscocarpum  | HN20170148                      | MN105607            |                     |
| Byssoloma melanodiscocarpum  | HN20170298                      | MN105601            |                     |
| Byssoloma rubrofuscum        | HN20170295                      | MN105399            |                     |
| Byssoloma rubrofuscum        | HN20170297                      | MN105602            |                     |
| Byssoloma sp.                | 20190531                        | MN105610            |                     |
| Byssoloma sp.                | 20190514                        | MN105609            |                     |
| Byssoloma subdiscordans      | HN20170156                      | MN105609            |                     |
| Byssoloma subdiscordans      | HN2014213                       | MN105606            |                     |
| Byssoloma subdiscordans      | 57023                           | MN1043704           |                     |
| Byssoloma subdiscordans      | 57130                           | MN1043703           |                     |
| Byssoloma subdiscordans      | Tønsberg 25968 (BG)             | AY756461            | AY567779            |
| Byssoloma vanderystii        | KeM400                          | LC648411            |                     |
| Byssoloma vanderystii        | HN20170227                      | MN1043718           |                     |
| Byssoloma vanderystii        | 20180148                        | MN1043710           |                     |
| Byssoloma vanderystii        | KYW0060                         | MN1043699           |                     |
| Calopadia foliicola          | KYW0068                         | MK957146            |                     |
| Calopadia foliicola          | Lucking 16011 (BG)              | AY567782            |                     |
| Calopadia puiggarii          | KYW0036_31764                   | MK957156            |                     |
| Calopadia puiggarii          | 20180158                        | MK957167            |                     |
| Eugeniella micrommata        | KeM437                          | LC648413            |                     |
| Eugeniella micrommata        | KYW0046                         | MK957161            |                     |
| Fellhanera bouteillei        | AF301-974                       | KJ76392             |                     |
| 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                         | MK946954            |                     |
| Fellhanera hyophorica         | 17826                           | MN587060            |                     |
| Fellhanera hyophorica         | 17744                           | MN587059            |                     |
| Fellhanera hyophorica         | 17744                           | MN587058            |                     |
| Fellhanera hyophorica         | 17267                           | MN587057            |                     |
| Fellhanera hyophorica         | 17094                           | MN587056            |                     |
| Fellhanera microdiscus        | HN20170313                      | MK946978            | MK957175            |
| Fellhanera sp.               | 20180167                        | MK946981            | MK957169            |
| Fellhanera sp.               | 20180166                        | MK946980            | MK957158            |
| Fellhanera sp.               | 20180146                        | MK946969            | MK957164            |
| Fellhanera sp.               | 20180711                        | MK946950            | MK957145            |
| Fellhanera subtilis           | Tønsberg 28199 (BG)             | AY756464            | AY567786            |
| Fellhanera viridisorediata    | Tønsberg 27375 (BG)             | AY756465            | AY567775            |
| Fellhaneropsis myristicola    | Tønsberg 25311 (BG)             | AY756466            | AY567745            |
| Fellhaneropsis vezdae         | Knutsson 97-229 (hb Knutsson)   | AY567744            |                     |

**Note:** Continued
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 leuco-blepharum*, *Byssoloma subdiscordans*, *Byssoloma marginatum*, and *B. palmularis* but differs by the combination of the following characters: fusiform 3–5 septate ascospores (17–23 × 4–5 μm), 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, 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 μm thick, spreading, pale greenish-gray, partly finely filamentous, matt, smooth; hypothallus indistinct. Algal cells chlorococcoid, spherical 6–15(17) μm diameter interstitial hyphae short-celled, 2–3 μm thick. Apothecia biatorine, applanate, orbicular, 300–800 μm diameter, 200–250 μm 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 μm); disk 250–750 μm 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 μm thick at the center, dark brown to partly black, subparaplectenchymatous, composed of more or less vertically

| Species name                           | Voucher       | nrITS          | mtSSU          |
|----------------------------------------|---------------|----------------|----------------|
| *Jejulea byssolomoides*                | KoLRI057222   | OM044389       | OM044383       |
| *Jejulea byssolomoides*                | KoLRI057223   | OM044390       | OM044384       |
| *Jejulea byssolomoides*                | KoLRI057224   | OM044391       | OM044385       |
| *Lasioloma arachnoideum*               | KYW0595       | MY0957155      |               |
| *Lasioloma arachnoideum*               | KYW0646       | MY0957158      |               |
| *Lasioloma arachnoideum*               | Lucking 16005 (BG) | AY567783     |               |
| *Leimonis erraticus*                   | AF001499      | KJ76425        |               |
| *Leimonis erraticus*                   | Arup 99192 (hb Arup) | AY567737     |               |
| *Micarea byssacea*                     | 289102_A97    | MG521563       | MG070769       |
| *Micarea micrococcus*                  | 299101_A100   | MG521552       | MG070753       |
| *Puttea margaretilla*                  | M351          | FJ006733       |               |
| *Puttea margaretilla*                  | M270          | FJ006731       |               |
| *Septotrapelia usnica*                 | 26 Sept 01 Sudirman & Sipman | AY300894   |               |
| *Sporopodium antoninianum*             | Lucking 16002d (BG) | AY567785     |               |
| *Sporopodium argillaceum*              | HN20170022    | MY0957176      |               |
| *Sporopodium argillaceum*              | HN20170001    | MY0957171      |               |
| *Szczawinskaia tsugae*                 | Tensberg 30044 (BG) | AY567746     |               |
| *Tapellaria nana*                      | SO677         | MY0957178      |               |
| *Tapellaria nigrata*                   | KYW0539       | MY0957176      |               |
| *Tapellaria nigrata*                   | KYW0602       | MK946952       | MK947147       |
| *Tapellaria parvimaniformis*           | KYW0181       | MK946955       | MK947150       |

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.
arranged cells, darker than subhymenium. Subhymenium 15–20 µm thick, brown. Hymenium 40–75 µm thick, pale brown, dark brown below; paraphyses sparsely branched and anastomosing, with 1–2 µm diameter lumina. Asci clavate, with a blurred IKI þ layer and a tholus with an IKI þ blue inner tube (Byssoloma-type), ca. 35 × 12 µm. Ascospores 8 per ascus, fusiform, 3–5 septate sometimes with perispore 1–2 µm thick, (14–)17–23×(6–)26 × (3–)4–5(–6) µm [x = 19.6 × 4.4 µm; SD 3.3; 0.6 µm; n = 48; l/w ratio = 4.5], colorless, sometimes slightly constricted at the septa. Pycnidia not observed.

Figure 1. The phylogenetic tree was based on mtSSU sequences. Maximum-likelihood bootstrap value (ML) ≥70% and Bayesian Posterior Probabilities (PP) ≥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

Jejulea byssolomoides superficially resembles 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 submuriiform to muriform ascospores (12–17 × 7–10 μm vs. 3–5 septate, 17–23 × 4–5 μm 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 μm diameter, disk plane, with a persistent densely byssoid white margin.
Excipulum made of colorless loosely woven hyphae, 50–150 μm broad. Hypothecium 20–50 μm high, light to dark brown. Apothecial base aeruginous. Hymenium 45–60 μm high, colorless. Asci 35–55 × 9–12 μm. Ascospores oblong, 3-septate, without constrictions at the septa, 10–18 × 2.5–3.5 μm (3–5 μm in B. subdiscordans), colorless. Pycnidia sub-globose to cup-shaped, 0.1–0.15 mm diameter, brownish-gray with a black center. Conidia pyriform, non-septate, 4–5 × 1.2–1.8 μm, 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 × 3–4 μm), 3-septate, colorless.

**Figure 3.** *Jejulea byssolomoides* (KoLRi 36855, holotype). (A, B) Thallus with ascomata (arrows); (C) Cross section of ascoma; (D, E) Detail of mature ascospores in ascus (mounted in water). Scales: (A) – 10 mm, (B) – 1000 μm, (C) – 50 μm, (D, E) – 10 μm.

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 × 4–5 μm 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., Bapalmia Sérus., Sporopodium Mont., Tapellaria Müll. Arg., Fellihanera Vézda, Lasioloma Santesson, and Calopadia Vézda 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 × 5–6 μm) [33].

Ascomata with hairy margins are not common among lichens. They are known in some species in the family Porinaceae which produce hairy perithelial ascomata (Trichothecium) 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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