



Noteworthy foliicolous lichens and a lichenicolous fungus collected from Okinawa Island, southern Japan

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ABSTRACT: Based on field surveys conducted from 2020 to 2024 on Okinawa Island, southern Japan, a total of 26 genera, 51 species, and one subspecies of foliicolous lichens, together with one lichenicolous fungus, were identified. Among them, seven foliicolous lichens are newly recorded from Japan, including *Badimia polillensis*, *Byssoloma brunneodiscum*, *B. melanodiscocarpum* (= *B. discordans* var. *flavescens*, syn. nov.), *Gyalectidium imperfectum*, *Porina perminuta*, *Strigula pseudosubtilissima*, and *S. smaragdula* subsp. *multiformis* (comb. & stat. nov.). An additional 39 species are newly recorded from Okinawa Island. A lichenicolous fungus, *Hemigrapha strigulae*, is reported from Asia for the first time. A total of 169 mtSSU sequences representing 48 species and eight nuITS sequences representing three species were newly generated. For 15 species, mtSSU sequences have been deposited in GenBank for the first time. These data provide the first molecular evidence for *Microtheliopsis uleana*, allowing a preliminary evaluation of its phylogenetic placement within Chaetothyriales. *Strigula smaragdula* subsp. *novae-zelandiae* (comb. & stat. nov.) is also proposed.

KEY WORDS: Asia, Ascomycota, lichenized fungi, mtSSU, nuITS, phylogeny, subspecies, taxonomy.

INTRODUCTION

Foliicolous lichens, which grow on living leaves of vascular plants, constitute taxonomically diverse groups with over 800 known species worldwide, predominantly found in subtropical and tropical regions (e.g., Santesson, 1952; Lücking, 2008).

In Japan, 41 genera and 93 species have been recorded to date (Harada *et al.*, 1999; Thor *et al.*, 2000; Suto and Ohtani, 2015, 2018; Miyazawa *et al.*, 2020, 2022, 2023; Miyazawa and Ohmura, 2023, 2024). Their distribution is primarily concentrated in warm temperate and subtropical regions, with the highest species richness observed in the Ryukyu Archipelago, southern Japan (Thor *et al.*, 2000). Currently, Iriomote Island (ca. 24°20'N, 123°49'E) harbors the greatest diversity with 36 genera and 72 species, followed by Amami-Oshima Island (ca. 28°17'N, 129°23'E) with 23 genera and 37 species, and Ishigaki Island (ca. 24°24'N, 124°11'E) with 19 genera and 34 species (Thor *et al.*, 2000; Miyazawa *et al.*, 2022). In contrast, only eight genera and eight species have been reported from Okinawa Island (ca. 26°30'N, 127°56'E), despite being the largest island (1,208 km²) in the archipelago (Thor *et al.*, 2000; Yamamoto *et al.*, 2021; Miyazawa and Ohmura, 2023, 2024; Ohmura, 2023).

In addition, three lichenicolous fungi, *Enterographa mazosiae* R. Sant. ex Matzer & R. Sant., *Koordersiella insectivora* (Hansf.) D. Hawksw. & O.E. Erikss., and *Opegrapha lichenicola* G. Thor, Lücking & Tat. Matsumoto, have been reported from foliicolous lichens in Japan (Thor *et al.*, 2000; Nakajima *et al.*, 2025).

Among them, however, only *K. insectivora* has been recorded from Okinawa Island (Nakajima *et al.*, 2025).

Okinawa Island is highly urbanized in its southern part, and approximately 15% of the island is occupied by U.S. military bases (Okinawa Prefecture Governor's Office, 2024). Such anthropogenic pressures may partly explain the island's relatively low lichen diversity. In contrast, the northern part of the island has been designated as a National Park since 2016 and is managed to minimize human impact. The natural vegetation in this area mainly consists of subtropical evergreen broad-leaved forests, characterized by *Castanopsis sieboldii* subsp. *lutchuensis* (Koidz.) H. Ohba, *Quercus miyagii* Koidz., and other members of evergreen broad-leaf trees, along with rare endemic plant species (Ministry of the Environment, 2025).

This study aims to document the diversity of foliicolous lichens including associated lichenicolous fungi through extensive field surveys on Okinawa Island, and to discuss noteworthy taxa from a taxonomic point of view.

MATERIALS AND METHODS

Collections

The field surveys on Okinawa Island were conducted between December 2020 and July 2024, covering 25 localities distributed throughout the island from north to south (Table S1). Approximately 500 specimens of foliicolous lichens were collected, of which 391 were identified to the species or subspecies level (Table S2). Additional specimens, including extra-regional collections of the same species and comparative material of closely



related taxa, were also examined. All identified voucher specimens are housed in the herbarium of the National Museum of Nature and Science (TNS), Tsukuba, Japan.

Morphology and chemistry

Morphological observations and photography were conducted using a dissecting microscope (SZX16; Olympus, Tokyo, Japan) and a differential interference contrast microscope (BX51; Olympus) with a digital camera (EOS Kiss X10i; Canon, Tokyo, Japan). Anatomical examinations were performed using hand-cut sections mounted in GAW solution (glycerin : ethanol : water, 1:1:1, Asahina 1936). When a statistically sufficient number of spores or photobiont cells were measured ($n \geq 20$), the data were presented as (minimum value–) mean value \pm standard deviation (–maximum value) (numbers).

The presence of calcium oxalate crystals was checked under the microscope by adding 25% sulfuric acid, following Thor *et al.* (2000). The K reaction of fungal tissues was tested using 5–10% KOH, and amyloidity of fungal tissues was examined using Lugol's solution (I), either directly or after pretreatment with 5–10% KOH (K/I). The UV reaction of the thallus was examined under UV light at 365 nm.

Lichen substances were examined using high-performance thin-layer chromatography (HPTLC) following Schumm and Elix (2015). Solvent system B' (*n*-hexane : methyl *tert*-butyl ether : formic acid, 140:72:18) (Culberson and Johnson, 1982) was used for the HPTLC. The spot color was checked under UV light at 254 and 365 nm and visible light, before and after spraying with 10% sulfuric acid on the HPTLC plate and charring at 90°C for 20 minutes.

DNA extraction, PCR amplification and sequencing

DNA was extracted from fresh samples according to a modified method of Izumitsu *et al.* (2012) (Miyazawa *et al.*, 2022). The voucher information is shown in Table S2. For PCR amplification, 10 μ L of PCR mix contained 1 μ L of genomic DNA extract, 0.25 μ L of each primer (10 pmol/ μ L) and 5 μ L EmeraldAmp® MAX PCR Master Mix (TaKaRa Bio Inc., Shiga, Japan). The partial sequences of the small subunit of the mitochondrial ribosomal DNA (mtSSU) and, in Strigulaceae, the internal transcribed spacer of the nuclear ribosomal DNA (nuITS) were amplified with the primer sets mrSSU1 and mrSSU3R (Zoller *et al.*, 1999) for mtSSU, and ITS1F (Gardes and Bruns, 1993) and LR1 (Vilgalys and Hester, 1990) for nuITS. The PCR conditions followed the methods of Miyazawa *et al.* (2023) for mtSSU and Ohmura *et al.* (2006) for nuITS.

The PCR products were purified according to the method of Miyazawa and Ohmura (2023). DNA sequencing was performed on an Applied Biosystems™ 3500xL Genetic Analyzer (Thermo Fisher Scientific, Tokyo, Japan) using the BigDye® Terminator v3.1 Cycle

Sequencing Kit (Thermo Fisher Scientific) following the manufacturer's instructions.

BLAST search

The similarity of the obtained DNA sequences with those registered in GenBank was tested using BLAST search (blastn) with default settings (Table S2). When the top hits showed an identity of 95% or higher, the top three sequences with the lowest E-values were presented. When the similarity was below 95%, only the top hit was shown.

Molecular phylogenetic analyses

Molecular phylogenetic analyses were conducted for *Strigula* spp., *Badimia* spp., *Byssoloma* spp., *Hemigrapha strigulae* Matzer, *Microtheliopsis uleana* Müll. Arg., and *Byssolecania* cf. *variabilis* Vězda, Kalb & Lücking, whose phylogenetic positions have been uncertain. Newly obtained sequences were aligned with selected taxa based on previous studies (cited below) using MAFFT ver. 7 (Katoh *et al.*, 2019) with default settings. Six datasets were assembled for subsequent analyses: the dataset for *Strigula* spp. was constructed following Woo *et al.* (2020, 2025) (Dataset 1, Table S3), the dataset for *Badimia* spp. followed Wang *et al.* (2023) (Dataset 2, Table S4), the dataset for *Byssoloma* spp. followed Miyazawa and Ohmura (2023) (Dataset 3, Table S5), the dataset for *Hemigrapha strigulae* was based on the phylogenetic analysis of Asterales taxa from mtSSU sequences in Ertz and Diederich (2015), supplemented with additional mtSSU sequences published by Ertz *et al.* (2016) (Dataset 4, Table S6), the dataset for *Microtheliopsis uleana* was based on Muggia *et al.* (2019) (Dataset 5, Table S7), and the dataset for *Byssolecania* cf. *variabilis* was prepared following Halda *et al.* (2022) (Dataset 6, Table S8).

After excluding gaps and missing data, the final alignments consisted of 425 sites for Dataset 1, 599 sites for Dataset 2, 591 sites for Dataset 3, 543 sites for Dataset 4, 369 sites for Dataset 5, and 460 sites for Dataset 6. Phylogenetic analyses were performed using both the Neighbor-Joining (NJ) method (Saitou and Nei, 1987) and Maximum Likelihood (ML) analyses. The best-fitting model for each dataset in the ML analyses was selected based on the lowest Bayesian Information Criterion (BIC) score. The selected models were as follows: Tamura–Nei model (Tamura and Nei, 1993) with a gamma distribution (G) for Dataset 1; Tamura 3-parameter model (Tamura, 1992) with a gamma distribution (G) for Datasets 2, 3, and 4; Tamura 3-parameter with a gamma distribution (G) and a proportion of invariant sites (+I, 27.51%) for Dataset 5; and the General Time Reversible model (Nei and Kumar, 2000) with a gamma distribution (G) and a proportion of invariant sites (+I, 24.78%) for Dataset 6.

Bootstrap values from 1,000 replicates for both NJ and ML analyses are indicated on the branches, using a



cutoff of $\geq 50\%$ or $\geq 70\%$ depending on the dataset. All calculations were performed using MEGA X (Kumar *et al.*, 2018).

RESULTS AND DISCUSSION

Based on an examination of morphology, lichen substances, and DNA sequences for the collected specimens, a total of 26 genera, 51 species, and one subspecies of follicolous lichens, as well as one lichenicolous fungus, were identified. Regarding lichens, *Badimia polillensis* (Vain.) Vězda, *Byssoloma brunneodiscum* W.C. Wang & J.C. Wei, *B. melanodiscocarpum* W.C. Wang & J.C. Wei, *Gyalectidium imperfectum* Vězda, *Porina perminuta* Vain., *Strigula pseudosubtilissima* S.H. Jiang, J.C. Wei & Lücking, and *S. smaragdula* subsp. *multiformis* (J.J. Woo, Lücking & Hur) K. Miyaz. & Y. Ohmura, comb. & stat. nov., are new records for Japan. Additionally, 39 species are newly recorded from Okinawa Island. Regarding the lichenicolous fungus, *Hemigrapha strigulae* is a new record for Asia. For the taxa that are new records for Asia or Japan, descriptions based on Japanese materials are provided.

Species for which morphological and molecular examinations were insufficient, such as *Anisomeridium* sp., *Calenia* sp., *Porina* spp., and *Puiggariella* sp. were excluded from the present treatment.

In addition, a total of 169 mtSSU sequences for 48 species and eight nuITS sequences for three species from our collections were successfully obtained. For 15 taxa [*Arthonia accolens* Stirt., *Asterothyrium sasae* Y. Suto, *Bacidina pallidocarnea* (Müll. Arg.) Vězda, *Byssoloma discordans* var. *flavescens* G. Thor, Lücking & Tat. Matsumoto, *B. subleucoblepharum* G. Thor, Lücking & Tat. Matsumoto, *Coenogonium geralense* (Henn.) Lücking, *C. subluteum* (Rehm) Kalb & Lücking, *Eremothecella calamicola* Syd., *Fellhanera rhabdophylli* (Rehm) Vězda, *F. subfuscatula* Lücking, *Hemigrapha strigulae*, *Microtheliopsis uleana*, *Sporopodium flavescens* (R. Sant.) Vězda, *S. phyllocharis* (Mont.) A. Massal., and *Trichothelium assurgens* (Cooke) Aptroot & Lücking], mtSSU sequences have been submitted to GenBank for the first time. Notably, this study provides the first molecular evidence for *Microtheliopsis uleana*, allowing a preliminary assessment of its phylogenetic placement within the Chaetothyriales based on mtSSU data (see below for details). Photographs of the taxa from which these sequences were generated are provided in Figs. 7–8 and Fig. S1. We did not illustrate all specimens; instead, representative material was selected. For taxa exhibiting noticeable morphological variation, multiple specimens of the same taxon were photographed to capture the observed range of variation.

The phylogenetic trees constructed from each dataset

(Datasets 1 to 6) showed no conflict with strongly supported branches reported in previous studies (Figs. 1–6). Detailed results are shown in the notes for each species.

New combinations and new status

The Okinawa specimen and additional Japanese specimens morphologically identified as *Strigula smaragdula* Fr. (Fig. S1, panels AQ–AS) were analyzed using nuITS sequences. These samples formed a single clade with *S. multiformis* J.J. Woo, Lücking & Hur with strong support (NJ/ML = 99/90) (Fig. 1). This clade is sister to *S. novae-zelandiae* (Nag Raj) Sérus., and together these two taxa form a well-supported clade with *S. smaragdula* (NJ/ML = 100/99) (Fig. 1).

Strigula multiformis has been distinguished from *S. novae-zelandiae* by several morphological characters, including “polarilocular spores,” “numerous pycnidia arranged in radial lines,” a “thicker thallus,” and “larger macroconidia” (Sérusiaux, 1998; Ford *et al.*, 2019). Regarding the polarilocular spores, however, illustrations in the original description by Nag Raj (1981) cannot be confirmed; instead, the microconidia appear to possess a single septum with a centrally attenuated wall. A similar septum is also observed in *S. smaragdula* (Jiang *et al.*, 2020), and the macroconidia likewise show thinning of the central septal wall. These observations suggest that the “polarilocular” feature of macroconidia in *S. novae-zelandiae* may simply represent a developmental stage rather than a stable diagnostic character.

Regarding the “numerous pycnidia arranged in radial lines,” similar radially arranged pycnidia are also documented in *S. multiformis* (e.g., Fig. 5O & P in Woo *et al.*, 2020), indicating that this feature is not unique to *S. novae-zelandiae*. Thallus thickness likewise appears unreliable, as Woo *et al.* (2020) showed that thallus morphology varies depending on the phorophyte in *S. multiformis*.

The size of macroconidia also fails to separate the three taxa: *S. novae-zelandiae* (11–18 × 2.5–4.5 μm; Nag Raj, 1981; Sérusiaux 1998; Ford *et al.*, 2019), *S. smaragdula* (12–20 × 3–4 μm; Jiang *et al.*, 2020), and *S. multiformis* (15–17.5 × 2.5–3.8 μm; Woo *et al.*, 2020) all exhibit broadly overlapping dimensions. Thus, none of the morphological characters proposed so far provides a reliable basis for distinguishing these taxa.

In contrast, *S. multiformis* has been separated from *S. smaragdula* mainly by differences in ascospore and conidia size (Woo *et al.*, 2020). Ascospores of *S. smaragdula* measure 15–25 × 4–6 μm, whereas those of *S. multiformis* measure 15–20 × 3.8–5 μm. Macroconidia likewise overlap broadly (*S. smaragdula*: 12–20 × 3–4 μm; *S. multiformis*: 15–17.5 × 2.5–3.8 μm). Considering the range of variations provided in the current taxonomic concept of *S. smaragdula* (Jiang *et al.*, 2020), these size differences are mostly overlapping and do not constitute discrete diagnostic characters.

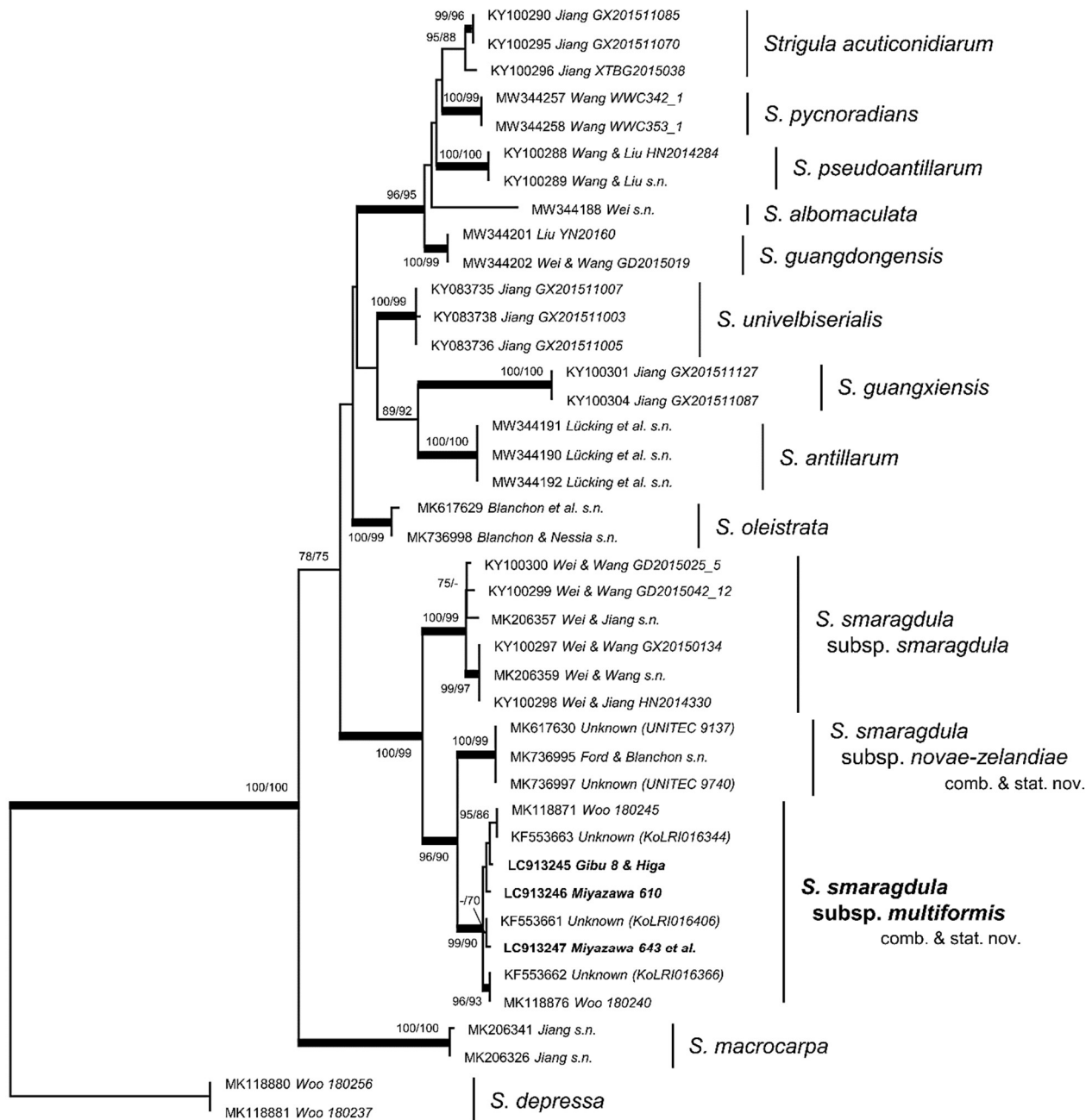


Fig. 1. ML tree based on nuITS sequences showing the phylogenetic position of *Strigula* spp., collected from Japan and shown in bold. *Strigula depressa* was used as the outgroup taxon. NJ and ML support values ($\geq 70\%$) are indicated at nodes. Branches supported by both methods with $\geq 90\%$ are highlighted with thick black lines.

The three taxa also show geographically structured but mutually exclusive distributions: continental Asia (*S. smaragdula*), Korea and Japan (*S. multiformis*), and the North Island of New Zealand (*S. novae-zelandiae*). Thus, the three lineages cannot be separated by morphology, and they are distinguishable only by geography and DNA sequence variation.

For such cases, where morphologically inseparable but

geographically and genetically differentiated metapopulations occur, Jørgensen (2019) and Lücking (2008) have argued that recognition at the subspecies rank is taxonomically appropriate, particularly in lichenized fungi. Following this reasoning, we treat the *S. smaragdula* complex as a single species comprising three subspecies: *S. smaragdula* subsp. *smaragdula*, *S. smaragdula* subsp. *multiformis*, and *S. smaragdula* subsp. *novae-zelandiae*.

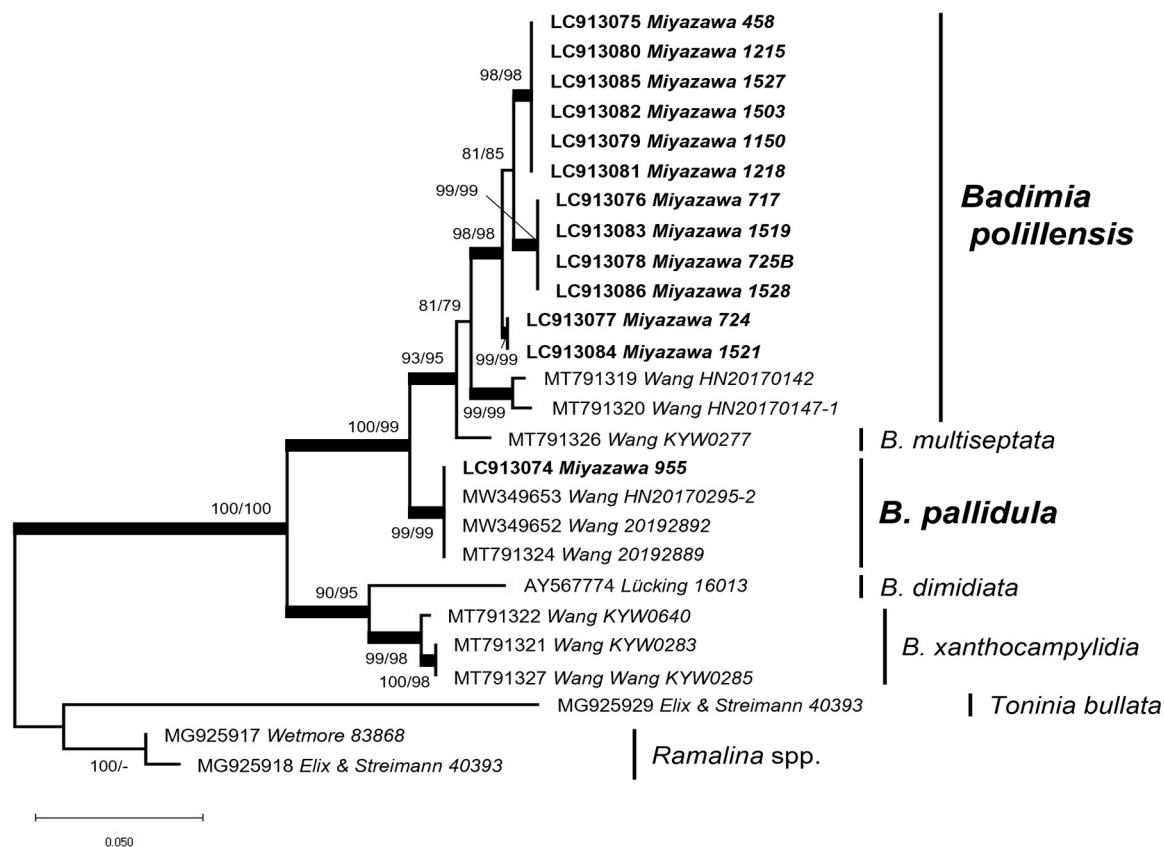


Fig. 2. ML tree based on mtSSU sequences showing the phylogenetic positions of *Badimia pallidula* and *B. polillensis*, both collected from Japan and shown in bold. *Ramalina* spp. and *Toninia bullata* were used as outgroup taxa. NJ and ML support values ($\geq 70\%$) are indicated at nodes. Branches supported by both methods with $\geq 90\%$ are highlighted with thick black lines.

Strigula smaragdula Fr. subsp. *smaragdula*, Linnaea 5: 550. 1830. **Type:** Nepal, unknown locality, on leaves of *Loranthus ligustroides*, König s.n. (lectotype: UPS, not seen).

Strigula smaragdula subsp. *smaragdula* is characterized by bright green, thickened thallus patches, basally immersed and apically erumpent perithecia partly covered by a thallus layer and with a diffuse limit between the thallus and involucrellum, fusiform, 1-septate ascospores $15\text{--}25 \times 4\text{--}6 \mu\text{m}$ in size, and bacillar, 1-septate macroconidia $12\text{--}20 \times 3\text{--}4 \mu\text{m}$ (Jiang *et al.*, 2020).

Distribution: Continental Asia (India, Nepal, and southern China; Jiang *et al.*, 2020).

Strigula smaragdula subsp. *multiformis* (J.J. Woo, Lücking & Hur) K. Miyaz. & Y. Ohmura, **comb. & stat. nov.** **Basionym:** *Strigula multiformis* J.J. Woo, Lücking & Hur, in Woo, Lücking, Oh, Jeun & Hur, Phytotaxa 443(1): 8. 2020. **Type:** SOUTH KOREA. Jeju-do (Province): Napeup warm-temperate forest, $33^{\circ}25'59.49''\text{N}$, $126^{\circ}19'49.24''\text{E}$, 89 m elev., on leaves of *Machilus thunbergii*, 26 June 2018, *Woo 180245* (holotype: KoLRI 049964, not seen)

Mycobank No.: MB862087

Distribution: Japan (this study) and South Korea (Woo *et al.*, 2020).

Specimen examined. JAPAN. RYUKYU ISLANDS (Okinawa Pref.): Seseragi-Hiroba, Nago Central Park, Agarie, Nago-city ($26^{\circ}35'16''\text{N}$, $127^{\circ}59'29''\text{E}$), 15 m elev., on *Machilus japonica*, 25 December 2020, *K. Gibu 8 & R. Higa* (TNS).

Additional specimens examined. JAPAN. HONSHU. Kazusa Prov. (Chiba Pref.): Amatsu, Kamogawa-city ($35^{\circ}08'\text{N}$, $140^{\circ}09'\text{E}$), 50 m elev., on leaf of *Machilus thunbergii*, 28 September 2020, *K. Miyazawa 610* (TNS). Izu Prov. (Shizuoka Pref.): Kawazunanataki Waterfalls, Kawazu-cho, Kamo-gun ($34^{\circ}47'\text{--}48'\text{N}$, $138^{\circ}55'\text{--}56'\text{E}$), 200–300 m elev., on leaf of a broad-leaf tree, 3 November 2020, *K. Miyazawa 643*, *K. Ohmachi*, *K. Gibu*, *T. Nada & I. Okane* (TNS).

Strigula smaragdula subsp. *novae-zelandiae* (Nag Raj) K. Miyaz. & Y. Ohmura, **comb. & stat. nov.** **Basionym:** *Discosiella novae-zelandiae* Nag Raj, Canad. J. Bot. 59(12): 2528. 1981. **Homotypic synonym:** *Strigula novae-zelandiae* (Nag Raj) Sérus., Bryologist 101(1): 150. 1998. **Type:** NEW ZEALAND, North Island, South Auckland, Papakura, Kirk's Bush, on leaves of *Beilschmiedia* sp., 20 December 1973, *B. Kendrick KNZ 32B* (holotype: PDD 40205, not seen; the photos in Nag Raj, 1981; Ford *et al.*, 2019).

Mycobank No.: MB862088

Distribution: North Island of New Zealand (Nag Raj, 1981; Sérusiaux 1998; Ford *et al.*, 2019).

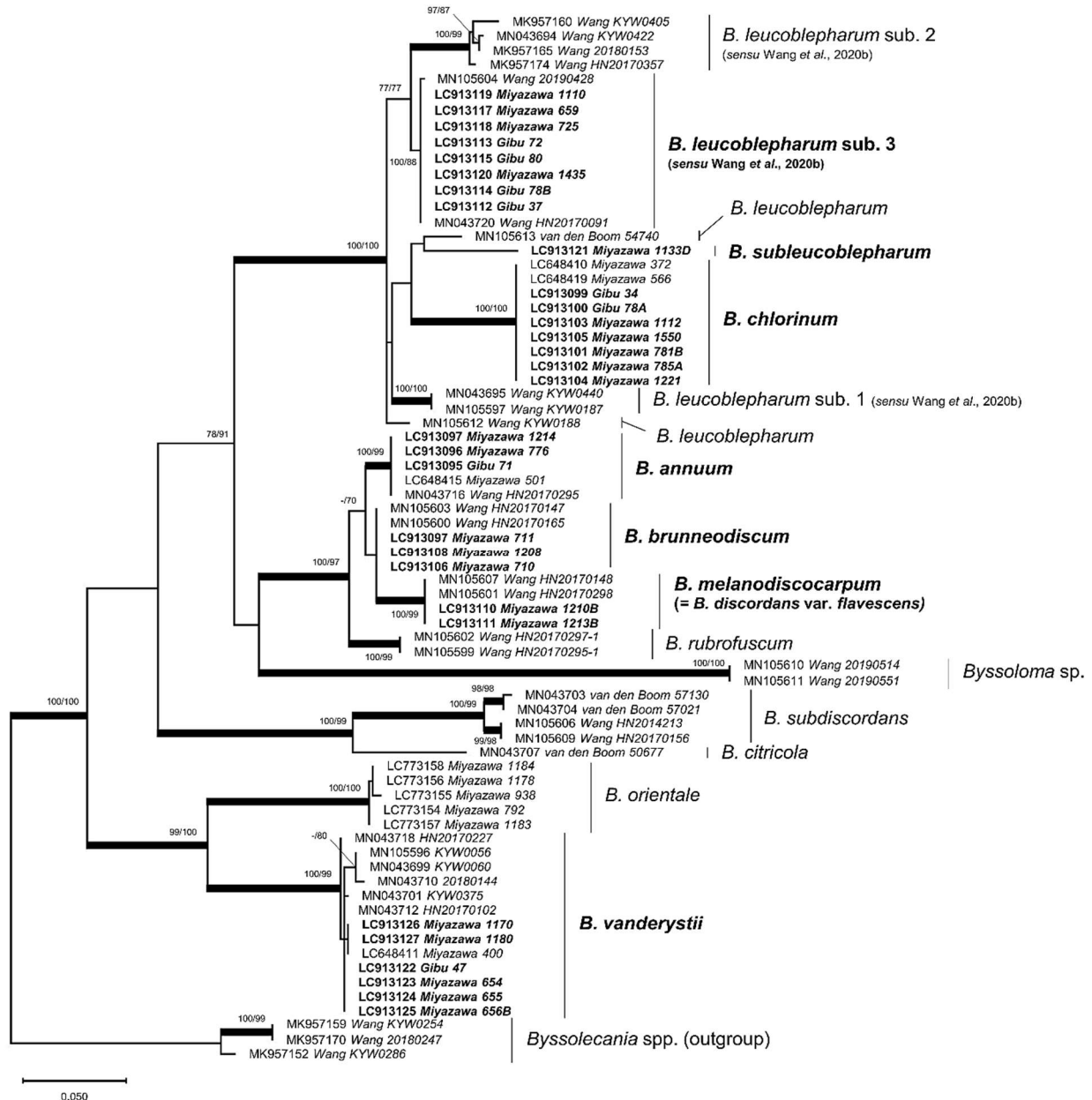


Fig. 3. ML tree based on mtSSU sequences showing the phylogenetic position of *Byssoloma* spp. collected from Okinawa Island and shown in bold. *Byssolecania* spp. were used as the outgroup. NJ and ML support values ($\geq 70\%$) are indicated at nodes. Branches supported by both methods with $\geq 90\%$ are highlighted with thick black lines.

Foliicolous lichens new to Japan

Badimia polillensis (Vain.) Vězda, Folia Geobot. Phytotax. 21(2): 215. 1986. **Basionym:** *Bilimbia polillensis* Vain., Ann. Acad. Sci. Fenn., Ser. A, 15: 82. 1921. **Type:** Philippines. Polillo, 1909, *Robinson s.n.* (holotype: TUR-V 21548!). **Fig. 7A**

THALLUS continuous to sometimes dispersed, 5–30 mm diam. and 15–25 μm thick, densely verrucose, greenish grey with bluish tinge; verrucae wart-shaped, 75–150 μm diam., whitish green to white. APOTHECIA rounded, 0.5–0.9 mm diam. and 150–200 μm tall; disc

plane to convex when mature, yellowish white to orange, slightly translucent; margin thin, slightly prominent, concolor with disc; epithecium indistinct, slightly brown; excipulum paraplectenchymatous, colorless to slightly brown in outer margin, lacking crystals, 30–50 μm wide; hymenium colorless, K–, 40–55 μm tall; paraphyses distinct, septate, unbranched, 1–1.5 μm thick, thickened apically, up to 4 μm thick; hypothecium pale yellow, K–, 25–35 μm tall. ASCI 35–42 \times 8–15 μm . ASCOSPORES ellipsoid to fusiform, 3-septate, without or with slight constrictions at septa, colorless, (9.8–)11.6–14.3(–15.5) \times (3.0–)3.8–4.9(–5.2) μm ($n = 30$), 2.5–4 times as long as

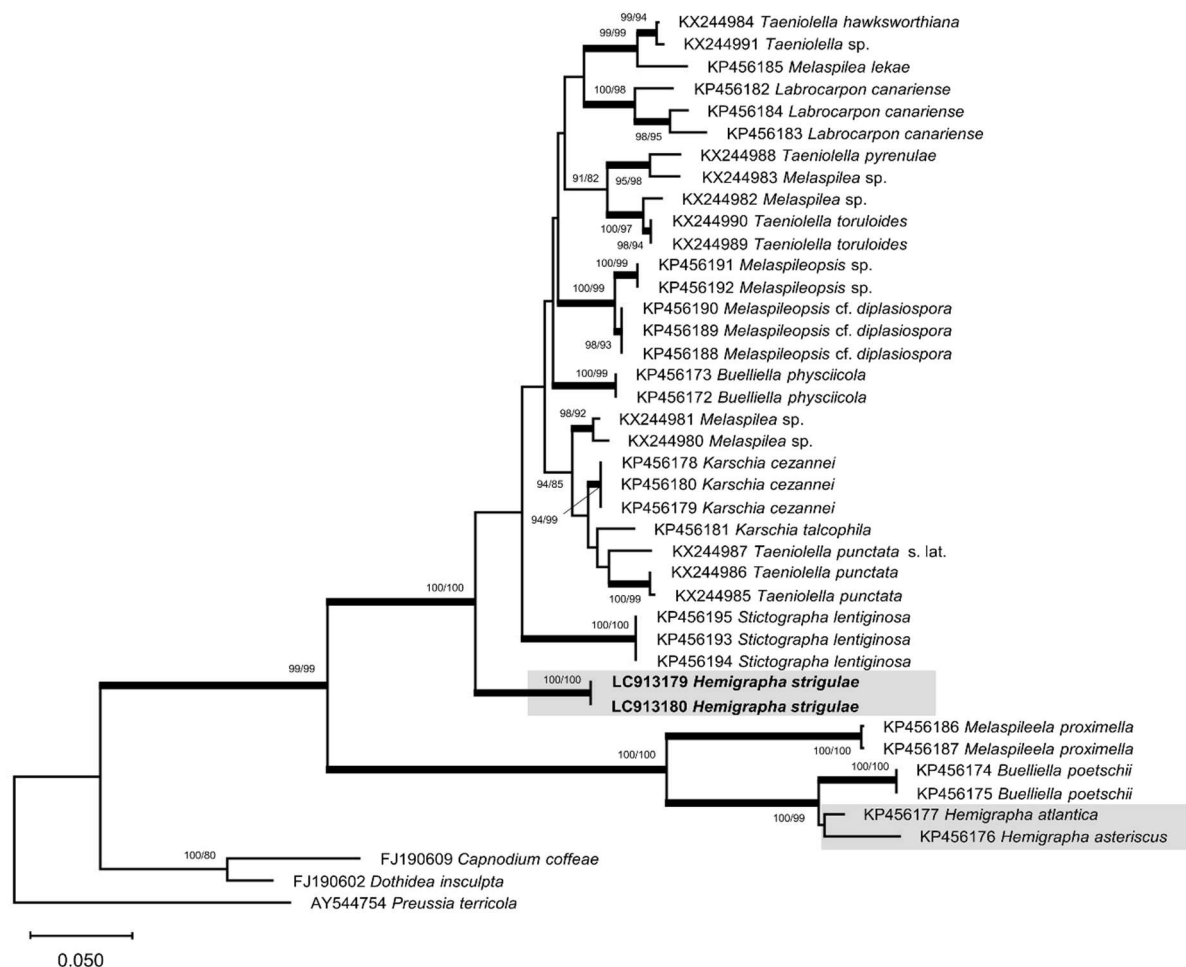


Fig. 4. ML tree based on mtSSU sequences showing the phylogenetic position of *Hemigrapha strigulae* collected from Okinawa Island and shown in bold. *Capnodium coffeae*, *Dothidea insculpta* and *Preussia terricola* were used as outgroup taxa. NJ and ML support values ($\geq 70\%$) are indicated at nodes. Branches supported by both methods with $\geq 90\%$ are highlighted with thick black lines.

broad. CAMPYLIDIA 0.7–1.0 mm wide, white to yellowish white. CONIDIA filiform, 3–7-septate (mostly indistinct), $70\text{--}90 \times 1.2\text{--}1.8 \mu\text{m}$, colorless, with 3–5 lateral appendages; lateral appendages up to 3–5 μm long and 0.8 μm wide, apically thickened (up to 2 μm wide).

Chemistry: usnic acid and zeorin were detected by HPTLC.

Badimia polillensis is characterized by the thallus with dense smaller verrucae (not extending 0.2 mm diam.) (Fig. 7A), yellowish white to orange apothecia and white campylidia (Fig. 7A), 3-septate ascospores, and usnic acid and zeorin as major substances.

The ascus size of the Okinawa Island material measured $35\text{--}42 \times 8\text{--}15 \mu\text{m}$, which is smaller than that in the protologue (Santesson, 1952) ($45\text{--}60 \times 10\text{--}12 \mu\text{m}$), but generally agrees with the protologue and the original material (holotype: TUR-V 21548!). Additionally, the campylidial conidia of the Okinawa Island material measured $70\text{--}90 \times 1.2\text{--}1.8 \mu\text{m}$, which is notably longer than the size described by Lücking (2008) based on specimens from the Neotropics ($50\text{--}65 \times 1\text{--}1.5 \mu\text{m}$).

Since campylidia were not observed in the original material and were not mentioned in the protologue, no direct comparison could be made.

BLAST results for the mtSSU sequences from the materials collected on Okinawa Island showed 95–97% identity with those of *Badimia* spp. in GenBank (Table S2). Notably, the sequences obtained from Japan showed less than 97% identity with the sequences of *B. polillensis* from China and Malaysia published by Wang *et al.* (2021) (Table S2). In the molecular phylogenetic analysis, the clade consisting of the Japanese and Chinese samples showed relatively low support (NJ/ML = 81/79) (Fig. 2). Furthermore, among the Japanese sequences, the identity ranged from 95 to 97%. However, due to the lack of morphological and chemical differences among these samples, they are treated as the same species in this study, though further detailed taxonomic examination is necessary.

Badimia polillensis is similar to *B. pallidula* (Kremp.) Vězda, but the latter has a thallus with larger and more scattered warts (Santesson, 1952; Wang *et al.*, 2021) (Fig. 7A & B). Thor *et al.* (2000) noted that some specimens

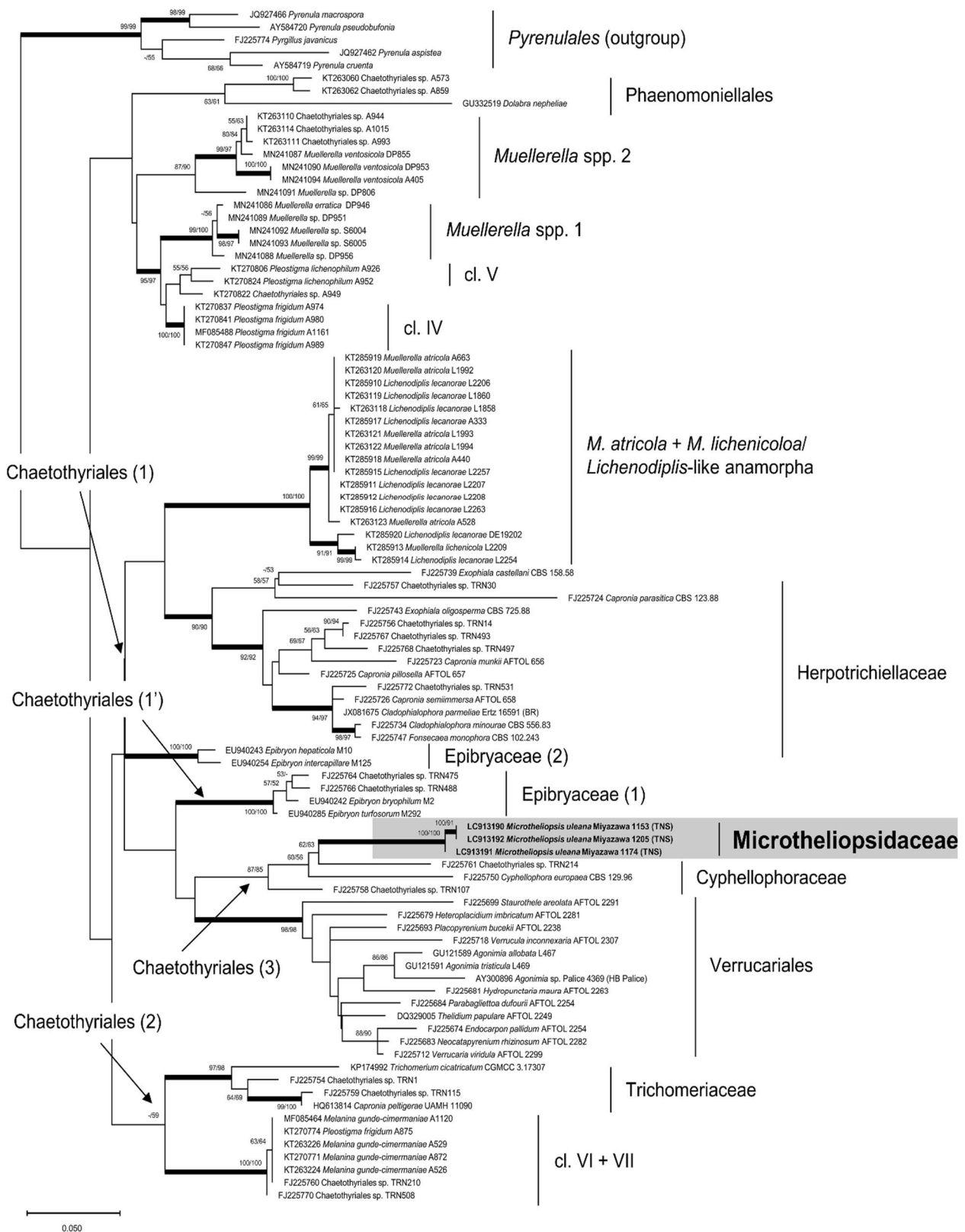


Fig. 5. ML tree based on mtSSU sequences showing the phylogenetic position of *Microtheliopsis uleana* collected from Okinawa Island and shown in bold. Members of Pyrenulales were used as outgroup taxa. NJ and ML support values ($\geq 50\%$) are indicated at nodes. Branches supported by both methods with $\geq 90\%$ are highlighted with thick black lines.

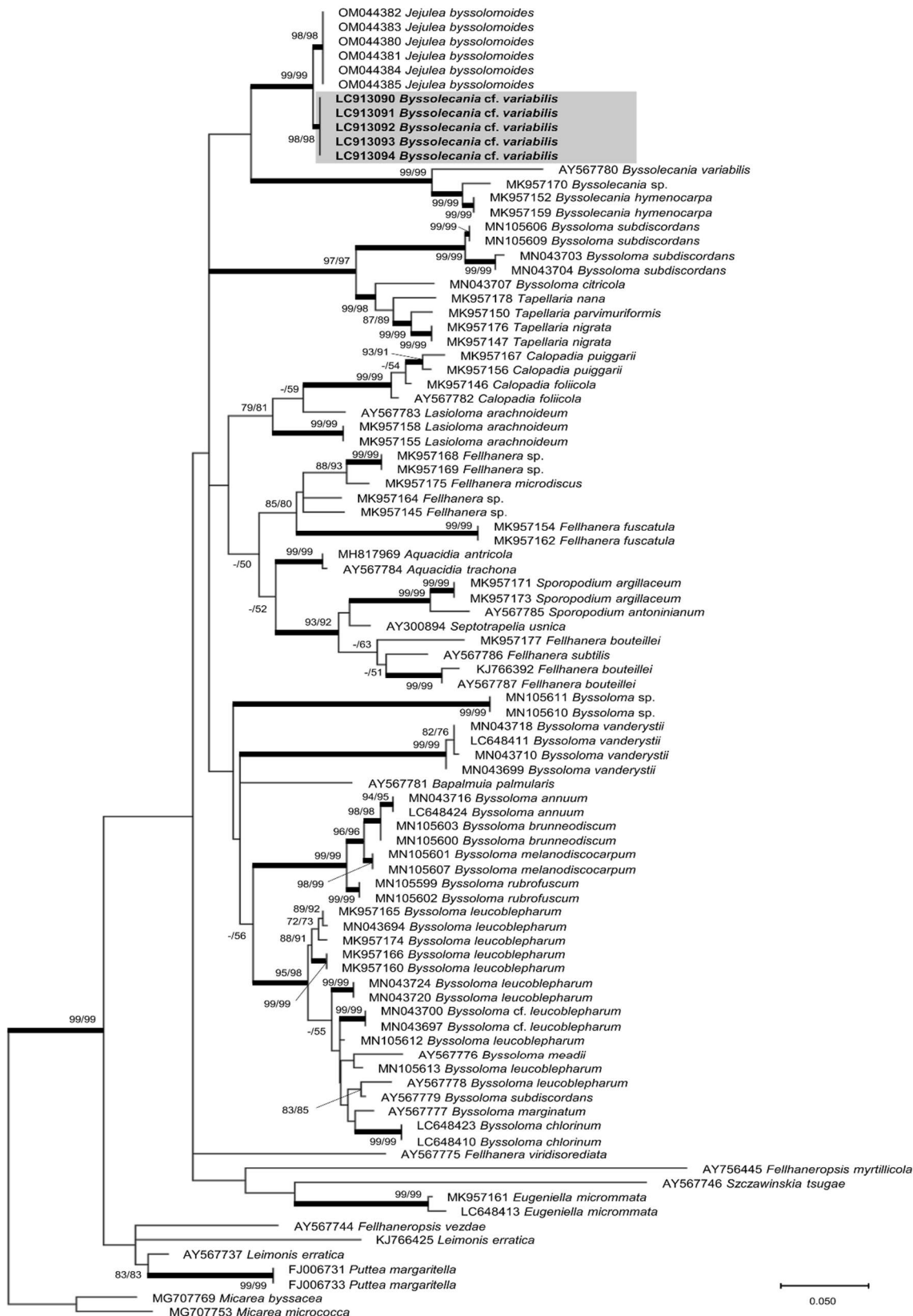


Fig. 6. ML tree based on mtSSU sequences showing the phylogenetic position of *Byssolecania cf. variabilis* collected from Okinawa Island and shown in bold. *Micarea* spp. were used as outgroup taxa. NJ and ML support values ($\geq 50\%$) are indicated at nodes. Branches supported by both methods with $\geq 90\%$ are highlighted with thick black lines.

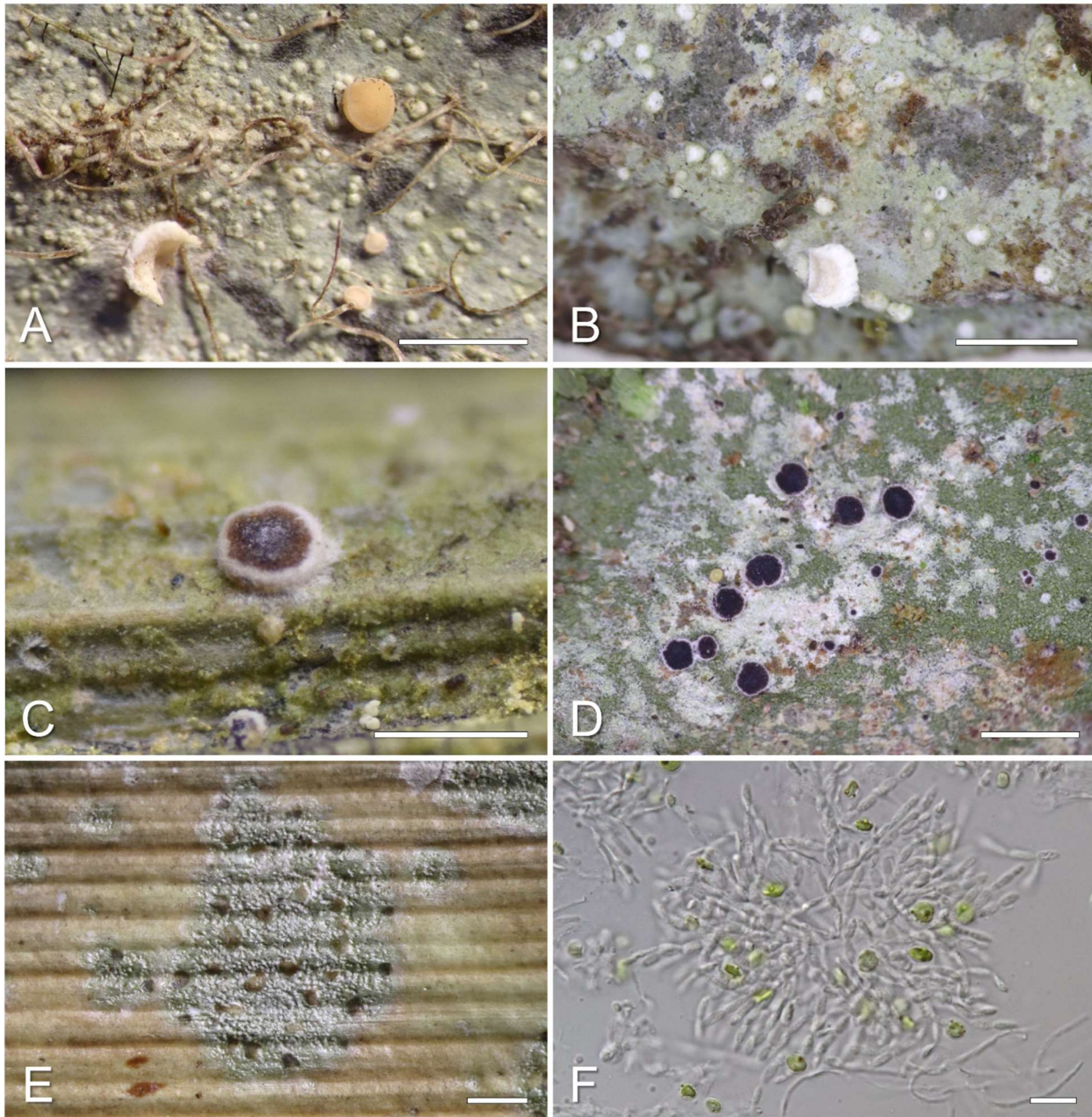


Fig. 7. Newly recorded and taxonomically reassessed foliicolous lichens from Japan. **A.** *Badimia polillensis* (K. Miyazawa 728B, K. Gibu, K. Watanabe & T. Nada, TNS). Thallus with apothecia and campylidium. **B.** *Badimia pallidula* (K. Miyazawa 955, K. Gibu & A. Ohmaki, TNS). Thallus with campylidium. **C.** *Byssoloma brunneodiscum* (K. Miyazawa 710, K. Gibu, K. Watanabe & T. Nada, TNS). Thallus with apothecium. **D.** *Byssoloma melanodiscocarpum* (syn. *B. discordans* var. *flavescens*) (K. Miyazawa 710, K. Gibu, K. Watanabe & T. Nada, TNS). **E & F.** *Gyalectidium imperfectum* (K. Miyazawa 782C, K. Gibu & T. Nada, TNS); **E.** Thallus with hyphophores. **F.** Diahyphae with algal cells. Scale bars: **A, B, D & E** = 1 mm; **C** = 0.5 mm; **F** = 10 μ m.

of *B. pallidula* from Japan resembled the type specimen of *B. polillensis*, while many others exhibited intermediate morphology between *B. polillensis* and the type specimen of *B. pallidula*. Based on this variation, they treated all these specimens as *B. pallidula*. However, our morphological observations using fresh materials and molecular phylogenetic analysis revealed two distinct clades corresponding to *B. polillensis* and *B. pallidula*

respectively (Fig. 2). Furthermore, a re-examination of *B. pallidula* specimens from Japan housed in TNS revealed that only two specimens were *B. pallidula*, while the remaining eight were *B. polillensis*, which is characterized by small, dense warts. This re-examination also confirmed that *B. polillensis* occurs not only on Okinawa Island but also on Amami-Oshima Island and Iriomote Island. In Japan, *B. polillensis* was found in relatively undisturbed

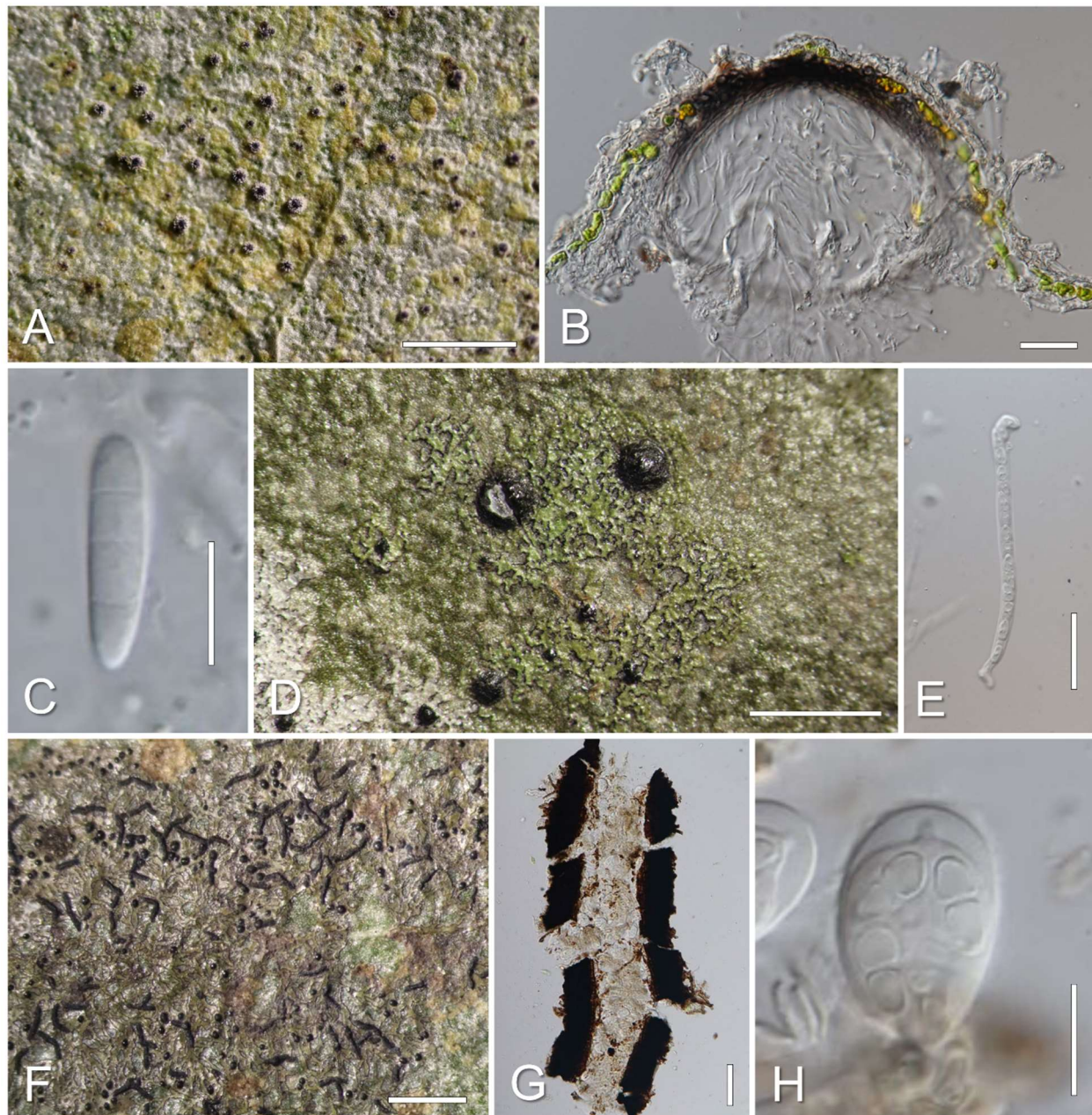


Fig. 8. Newly recorded foliicolous lichens and a lichenicolous fungus from Japan. **A–C.** *Porina perminuta* (K. Miyazawa 1237, TNS); **A.** Thallus with perithecia. **B.** Vertical section of perithecium. **C.** Ascospore. **D & E.** *Strigula pseudosubtilissima* (K. Miyazawa 1211, TNS); **D.** Thallus with perithecia. **E.** Ascus with ascospores. **F–H.** *Hemigrapha strigulae* (K. Miyazawa 1522 & Y. Ohmura, TNS); **F.** Thyriothecoid ascomata on thallus of *Strigula* sp. **G.** Mashed ascoma. **H.** Fissitunicate ascus with 1-septate ascospores. Scale bars: **A, D & F** = 1 mm; **B & E** = 20 μ m; **C & H** = 10 μ m; **G** = 50 μ m.

subtropical forests on Ryukyu Islands, whereas *B. pallidula* has been found in temperate Kyushu, suggesting potential habitat differences between the two species.

Badimia polillensis has been reported from Asia [China, Indonesia, Malaysia, and the Philippines (Santesson, 1952; Wang *et al.*, 2021)], Africa [Republic of Côte d'Ivoire (Santesson and Lücking, 1999)], and the Neotropics (Lücking, 2008), indicating that this species is pantropical. The known distribution is extended to Japan.

Specimens examined. JAPAN. RYUKYU ISLANDS (Okinawa Pref.): along Hiji River path between Hiji Waterfall Camp site and Hiji Waterfall, Kunigami-son, Kunigami-gun, Okinawa Island (26°43–44'N, 128°10–11'E), 20–100 m elev., on *Aidia canthioides*, 13 March 2021, K. Miyazawa 717, K. Gibu, K. Watanabe & T. Nada (TNS); *ibid.*, on *Ardisia quinquegona*, K. Miyazawa 721, K. Gibu, K. Watanabe & T. Nada (TNS); *ibid.*, on *Neolitsea sericea*, K. Miyazawa 724, K. Gibu, K. Watanabe & T. Nada (TNS), K. Miyazawa 725 *pr.p.*, K. Gibu, K. Watanabe & T. Nada (in collection of *Byssoloma leucoblepharum*) (TNS); *ibid.*, on *Arenga engleri*, K. Miyazawa 726C, K. Gibu, K. Watanabe & T. Nada (TNS); *ibid.*, on *Lasianthus hirsutus*, K. Miyazawa 728B, K. Gibu,



K. Watanabe & T. Nada (TNS); around Lake Kuina, Aha, Kunigami-son, Kunigami-gun, Okinawa Island (26°43'16"N, 128°15'57"E), 190 m elev., on *Distylium racemosum*, 15 November 2022, *K. Miyazawa 1150* (TNS); Takae, Higashi-son, Kunigami-gun (26°40'02"N, 128°14'42"E), 85 m elev., on broad-leaf tree along a stream, 15 November 2022, *K. Miyazawa 1157* (TNS); Takazato, Ohgimi-son, Kunigami-gun, Okinawa Island (26°41'28"N, 128°10'42"E), 140 m elev., on *Ardisia quinquegona* along a stream, 16 November 2022, *K. Miyazawa 1215* (TNS); *ibid.*, on *Turpinia ternata* along a stream, *K. Miyazawa 1218* (TNS); *ibid.*, on *Ilex warburgii* along a stream, *K. Miyazawa 1220* (TNS); Yona Field, University of the Ryukyus, Iji, Kunigami-son, Kunigami-gun, Okinawa Island (26°45'03"N, 128°12'43"E), 190 m elev., on *Machilus japonica* along the stream, 10 March 2023, *K. Miyazawa 1503 & Y. Ohmura* (TNS); *ibid.* (26°45'34"N, 128°13'00"E), 210 m elev., on *Turpinia ternata*, 10 March 2023, *K. Miyazawa 1508 & Y. Ohmura* (TNS); *ibid.*, on *Machilus japonica*, *K. Miyazawa 1515 & Y. Ohmura* (TNS), *K. Miyazawa 1517A & Y. Ohmura* (TNS), *ibid.*, on *Ilex warburgii*, *K. Miyazawa 1519 & Y. Ohmura* (TNS); *ibid.*, on *Distylium racemosum*, *K. Miyazawa 1521 & Y. Ohmura* (TNS); *ibid.*, on *Ardisia quinquegona*, *K. Miyazawa 1527 & Y. Ohmura* (TNS), *ibid.*, on a fern, *K. Miyazawa 1528 & Y. Ohmura* (TNS).

Additional specimens examined. [*Badimia polilensis* (Vain.) Vězda] JAPAN. AMAMI ISLANDS (Kagoshima Pref.): 7 km SW of Nishinakama village, ca. 100–200 m N of Yagachi River, near the road, Sumiyo-cho, Oshima-gun, Amami-Oshima Island, (28°13'N, 129°21'E), 60–80 m elev., on a broad-leaf tree in dense subtropical deciduous forest, 5 February 1995, *G. Thor 12999 pr.p.* (in collection of *Strigula subtilissima*) (TNS). RYUKYU ISLANDS (Okinawa Pref.): along mountain path between Ohtomi-guchi Entrance and Daiichi Yamagoyato, Iriomote Island, Yaeyama Islands (24°19'32"N, 123°50'55"E), 190 m elev., on *Distylium racemosum*, 19 November 2019, *K. Miyazawa 458 & Y. Ohmura* (TNS); along trail in the mountains along Urauchi river from 500 m N of southernmost starting point 6 km NW of Ohara village to small camping site between two streams 2.5 km NNE of starting point (7.5 km NNW of Ohara village), Taketomi-cho, Yaeyama-gun (24°18–20'N, 123°51'E), 160–220 m elev., on a broad-leaf tree, 10 February 1995, *G. Thor 13151* (TNS), *G. Thor 13163 pr.p.* (in collection of *Porina rufula*) (TNS), *G. Thor 13163* (TNS); along 1.5 km long trail to Maryudo waterfall from starting point at Urauchi river 5 km SSW of Funaura village, Taketomi-cho, Yaeyama-gun (24°21–22'N, 123°48'E), 5–60 m elev., on a palm, 13 February 1995, *G. Thor 13344* (TNS), *G. Thor 13338 pr.p.* (in collection of *Sporocybomyces leucotrichoides*) (TNS); *ibid.*, on broad-leaf tree, *G. Thor 13379* (TNS).

[*Badimia pallidula* (Kremp.) Vězda] JAPAN. KYUSHU. Hyuga Prov. (Miyazaki Pref.): Inohae Valley, Kitagawachi, Kitagou-cho, Nichinan-City (31°43'N, 131°22'E), ca. 100 m elev., on *Ilex latifolia*, 1 October 2021, *K. Miyazawa 955, K. Gibu & A. Ohmaki* (TNS). Higo Prov. (Kumamoto Pref.): Mt. Ichibusu, on *Thujopsis dolabrata*, 1 November 1963, *S. Kurokawa 63093* (TNS).

Byssoloma brunneodiscum W.C. Wang & J.C. Wei, Lichenologist 52(5): 391. 2020b. **Type:** CHINA, Hainan Prov., Ledong Co., Jianfeng Ridge, Mingfeng Valley, 18°44'N, 108°50'E, 960 m elev., on leaves, 6 September 2017, *W.C. Wang 139422* [holotype: HMAS, not seen; the photos in Wang *et al.* (2020b)!].

Fig. 7C

Thallus crustose, irregular in shape, continuous, smooth, light green to grayish green, UV+ brick red, 15–45 mm diam., 10–15 µm thick. Apothecia rounded, sessile, constricted at the base, 0.3–0.7 mm diam., 90–120 µm tall; margin byssoid but compact, persistent, not spreading laterally over thallus surface, 30–50 µm wide, white to brownish white, composed of loosely woven colorless hyphae with abundant colorless crystals, which dissolve in K, K–; disc plane to slightly convex, brown to dark brown; epithecium colorless to pale brown, ca. 5 µm

tall; hymenium 50–60 µm tall, colorless, with scattered reddish brown pigment; hypothecium 20–30 µm tall, reddish brown, K–; apothecial base reddish brown, K–; paraphyses indistinct. ASCI clavate, 8-spored, I+ dark blue with the tubular structure at the apices, tholus amyloid of 'Byssoloma-type' (Hafellner, 1984), 34–52 × 10–13 µm. ASCOSPORES oblong, 3-septate, with or without slight constriction at septa, colorless, (9.2–)11.0–12.9(–13.5) × (2.4–)2.7–3.5(–3.9) µm (n = 30), 3–5.5 times as long as broad. PYCNIDIA sessile, wart-shaped, 50–85 µm diam., cream-colored, covered by whitish loose hyphal tissue at the base. CONIDIA pyriform, aseptate, colorless, (3.7–)3.9–4.6(–4.7) × (1.4–)1.5–1.8(–2.0) µm (n = 20). PHOTOBIONT trebouxoid, subglobose, (4.8–)5.2–6.7(–8.1) × (3.2–)3.8–5.3(–6.2) µm (n = 20).

Chemistry: 2,5,7-trichloro-3-O-methylnorlichexanthone was detected by HPTLC.

Byssoloma brunneodiscum is characterized by a light green thallus, compact byssoid apothecial margin, not spreading laterally over thallus surface (Fig. 7C), brown disc due to having reddish brown hymenium and hypothecium (at least partly), 3-septate ascospores, and the presence of 2,5,7-trichloro-3-O-methylnorlichexanthone as the major substance (Wang *et al.*, 2020b).

While the material collected on Okinawa Island mostly agrees with the protologue (Wang *et al.*, 2020b), there are noticeable differences in the sizes of the pycnidia and conidia. The pycnidia of the Okinawa specimens measured 50–85 µm diam., whereas the protologue reports a diameter of only 10–13 µm, approximately five to six times smaller. Similarly, the conidia measured 3.7–4.7 × 1.4–2.0 µm, compared to 2–2.5 × 1.5 µm reported in the protologue. However, these differences are likely attributable to measurement errors in Wang *et al.* (2020b). According to the figure in the protologue (Wang *et al.*, 2020b), the conidium size calculated from the scale was 3.9–5.8 × 1.4–1.9 µm, which are consistent with those of the Okinawa material. Furthermore, pycnidia described as wart-shaped in the genus *Byssoloma* are usually 50–200 µm diam. (e.g., Lücking, 2008; Elix and McCarthy, 2018; Miyazawa and Ohmura, 2023), making the 10–13 µm reported by Wang *et al.* (2020b) highly unusual and possibly due to reporting errors.

BLAST results for the mtSSU sequences of the Okinawa material showed 99% identity with those of *B. brunneodiscum* in GenBank, including that of the type specimen (Table S2), and molecular phylogenetic analyses based on the mtSSU sequences placed the Okinawa material in the same clade with the holotype sequence of *B. brunneodiscum* (Fig. 3). Diagnostic morphological features, lichen substances, and the mtSSU sequences are mostly consistent with those of *B. brunneodiscum*, supporting the identification of the Okinawa material as this species.



Byssoloma brunneodiscum closely resembles *B. annuum* (Vain.) G. Thor, Lücking & Tat. Matsumoto, but the latter can be distinguished by its orange-yellow apothecia with a colorless hypothecium. While intermediate disc colors are occasionally observed, the color of the hypothecium remains stable. In some cases, *B. brunneodiscum* can be confused with species of *Fellhanera*, particularly due to its compact apothecial margin. It can be distinguished by the presence of a byssoid margin, visible under a dissecting microscope. One exception is *Fellhanera albidocincta* (Vain.) Lücking (holotype: TUR-V 21560!), which has cylindrical hyphae forming the outer excipulum margin and a pilose apothecial margin, making it difficult to differentiate from *B. brunneodiscum*. Nonetheless, our HPTLC analysis revealed distinct chemical patterns between the two taxa. In *F. albidocincta*, several spots were detected with HPTLC in solvent system B' at Rf class 5–6, presumably corresponding to xanthenes, which were clearly different from 2,5,7-trichloro-3-O-methylnorlichexanthone, the major substance found in *B. brunneodiscum*.

Byssoloma brunneodiscum has been reported only from Hainan Island, China, where it grows at 960 m elevation on a mountain (Wang *et al.*, 2020b). In Japan, *B. brunneodiscum* was found at 20–140 m elevation in lowland forests.

Specimens examined. JAPAN. RYUKYU ISLANDS (Okinawa Pref.): along Hiji River path between Hiji Waterfall Camp site and Hiji Waterfall, Kunigami-son, Kunigami-gun, Okinawa Island (26°43–44'N, 128°10–11'E), 20–100 m elev., on *Arenga engleri*, 13 March 2021, K. Miyazawa 710, K. Gibu, K. Watanabe & T. Nada (TNS), K. Miyazawa 711, K. Gibu, K. Watanabe & T. Nada (TNS); Takazato, Ohgimi-son, Kunigami-gun (26°41'28"N, 128°10'42"E), 140 m elev., *Symplocos* sp. along a stream, 16 November 2022, K. Miyazawa 1208 (TNS).

Byssoloma melanodiscocarpum W.C. Wang & J.C. Wei, Lichenologist 52(5): 394. 2020b. **Type:** CHINA, Hainan Prov., Wuzhishan City, Wuzhishan National Forest Park, 18°54'N, 109°41'E, on leaves, 8 September 2017, 800 m elev., W.C. Wang 139744 [holotype: HMAS, not seen; the photos in Wang *et al.* (2020b)!].

= *Byssoloma discordans* (Vain.) Zahlbr. var. *flavescens* G. Thor, Lücking & Tat. Matsumoto, Symb. Bot. Upsal. 32(3): 30. 2000. (**Syn. nov.**) **Type:** JAPAN, Iriomote Island, Yaeyama Islands (Okinawa Pref.), along trail in the mountains along Urauchi river from small camping site between two streams 7.5 km NNW of Ohara village (2.5 km NNE of the southernmost starting point of the trail), and along trail to 500 m N of southernmost starting point 6 km NW of Ohara village, Taketomi-cho, Yaeyama-gun, on *Cheiropleuria bicuspis*, 24°18–20'N, 123°51'E, 160–220 m elev., 12 February 1995, Thor 13303 (holotype: TNS!; isotype: UPS!).

Fig. 7D

THALLUS crustose, irregular in shape, continuous, smooth, grayish green, UV+ brick red, 7–30 mm diam., 10–15 µm thick. **APOTHECIA** rounded, sessile, constricted at the base, 0.3–0.6 mm diam., 150–200 µm tall; margin byssoid but compact, persistent, not spreading laterally over thallus surface, 20–60 µm wide, white, composed of loosely woven colorless hyphae with abundant grey to grayish yellow crystals, which dissolve in K, K+ yellow; disc plane to slightly convex, pure black

to greyish black or purplish black; epithecium pale brown, ca. 5 µm tall; hymenium 30–50 µm tall, colorless; hypothecium 15–25 µm tall, reddish brown, K+ olive-black; apothecial base grey to grayish yellow due to crystals, K–; paraphyses indistinct. ASCI clavate, 8-spored, I+ dark blue with the tubular structure at the apices, tholus amyloid of 'Byssoloma-type' (Hafellner, 1984), 32–40 × 10–13 µm. ASCOSPORES oblong, 3-septate, with or without slight constrictions at septa, colorless, (9.7–)10.3–12.5(–13.4) × (2.9–)3.0–3.6(–3.8) µm (n = 20), 3–4.5 times as long as broad. PYCNIDIA not seen. PHOTOBIONT trebouxioid, subglobose, (4.9–)5.8–7.5(–9.1) × (3.7–)4.9–6.5(–7.1) µm (n = 50).

The material from Okinawa Island agrees well morphologically with the original material of *Byssoloma discordans* var. *flavescens* from Iriomote Island, as described by Thor *et al.* (2000). This identification is further supported by their HPTLC profile, which shows the presence of thiophanic acid. However, the material from Okinawa Island also closely resembles *B. melanodiscocarpum*, described by Wang *et al.* (2020b) from China and Thailand. Wang *et al.* (2020b) distinguished *B. melanodiscocarpum* from *B. discordans* var. *flavescens* by its continuous, smooth green thallus, pure black apothecia, presence of crystals in the excipulum, and K+ olive-black hypothecium. Upon re-examination of both the material from Okinawa Island and the original material of *B. discordans* var. *flavescens*, it was found that the disc color ranged from black to greyish black to blackish brown, sometimes with a purple tinge. Moreover, both materials possess a continuous, smooth thallus ranging from green to greenish-grey, as well as K+ olive-black hypothecium, making them difficult to distinguish morphologically. The observed variation in disc color falls within the range of intraspecific variation.

Wang *et al.* (2020b) also stated that *B. discordans* var. *flavescens* has crystals in the excipulum, whereas *B. melanodiscocarpum* lacks them. However, this distinction appears to be merely terminological, as they referred to the crystals as 'granular substances', which essentially represent the same feature. These crystals dissolve in K and produce a yellow reaction, a characteristic consistent with *B. discordans* var. *flavescens*. Furthermore, *B. melanodiscocarpum* also contains thiophanic acid (Wang *et al.*, 2020b), aligning with the chemical profile of *B. discordans* var. *flavescens*.

The molecular phylogenetic analyses of the genus *Byssoloma*, based on mtSSU sequences, strongly supported a single clade comprising both *B. discordans* var. *flavescens* and *B. melanodiscocarpum*, including the sequence from the type specimen of the latter (MN105601), with high support values (NJ/ML = 100/99) (Fig. 3). Based on morphological, chemical, and molecular evidence, we conclude that *B. discordans* var. *flavescens* and *B. melanodiscocarpum* are conspecific.

Byssoloma melanodiscocarpum was originally



described from China and Thailand (Wang *et al.*, 2020b) and the distribution now extends to Japan (Okinawa Island and Iriomote Island). In Japan, this species has been found exclusively in humid, subtropical forests with little anthropogenic disturbance, and it is considered to be rare.

This species resembles *B. subdiscordans* in having ascomata with a dark disc and a white byssoid margin. However, *B. subdiscordans* can be distinguished by its white thallus with corticiform layer, byssoid apothecial margin that spreads laterally over the thallus, and pure black disc.

Specimens examined. JAPAN. RYUKYU ISLANDS (Okinawa Pref.): Takazato, Ohgimi-son, Kunigami-gun, Okinawa Island (26°41'28"N, 128°10'42"E), 140 m elev., on *Cheiropleuria integrifolia* along a stream, 16 November 2022, K. Miyazawa 1210B (TNS), K. Miyazawa 1213B (TNS); along Hiji River path between Hiji Waterfall Camp site and Hiji Waterfall, Kunigami-son, Kunigami-gun, Okinawa Island (26°43'44"N, 128°10'11"E), 20–100 m elev., on *Aidia canthioides*, 13 March 2021, K. Miyazawa 718, K. Gibu, K. Watanabe & T. Nada (TNS).

Additional specimens examined. JAPAN. RYUKYU ISLANDS (Okinawa Pref.): along the trail in the mountains along the Urauchi river from the small camping site between two streams 7.5 km NNW of Ohara village (2.5 km NNE of the southernmost starting point of the trail) and along trail to 500 m N of the southernmost starting point 6 km NW of Ohara village, Taketomi-cho, Yaeyama-gun, Iriomote Island (24°18'–20'N, 123°51'E), 160–220 m elev., 12 February 1995, on a broad-leaf tree in dense, humid, old-growth, subtropical to tropical deciduous forest, *G. Thor 13300* (TNS); along the trail in the mountains along Urauchi river from 500 m N of southernmost starting point 6 km NW of Ohara village to small camping site between two streams 2.5 km NNE of starting point (7.5 km NNW of Ohara village), Taketomi-cho, Yaeyama-gun, Iriomote Island (24°18'–20'N, 123°51'E), 160–220 m elev., 10 February 1995, on small tree in dense humid, old-growth, subtropical to tropical deciduous forest, *G. Thor 13164* (as *Byssoloma subdiscordans*) (TNS); along 1.5 km long trail to Maryudo waterfall from the starting point at Urauchi river 5 km SSW of Funaura village, Taketomi-cho, Yaeyama-gun, Iriomote Island (24°21'–22'N, 123°48'E), 5–60 m elev., 13 February 1995, on a palm in dense humid, old-growth, subtropical to tropical deciduous forest, *G. Thor 13338* *pr.p.* (in collection of *Sporocybomyces leucotrichoides*) (TNS), *G. Thor 13339* (TNS).

Gyalectidium imperfectum Vězda, Nova Hedwigia 58(1–2): 131. 1994. **Type:** AUSTRALIA, Queensland: Yungaburra road, 2 km southeast of Atherton, 17°16'S, 145°29'E, 850 m elev., 1983, *Streimann s.n.* (holotype: CBG 8302429, not seen). **Fig. 7E & F**

THALLUS crustose, more or less circular, forming rounded to irregular patches, up to 5 mm diam., 20–55 µm thick, with corticiform layer, finely but irregularly verrucose due to incrustation with calcium oxalate crystals, greenish to whitish grey; prothallus present, membranaceous, pale grey. **ASCOMATA** rounded, 0.2–0.35 mm diam., 80–90 µm tall; disc plane, yellowish brown; margin rather thick, slightly prominent, smooth, pale green to brown; epithecium ca. 10 µm tall with epithecial algae; excipulum ca. 10 µm wide; hymenium 55–65 µm tall. **ASCI** monosporous, 35–55 × 20–30 µm. **ASCOSPORES** ellipsoid, muriform, colorless, 33–49 × 14–20 µm. **CONIDIOMATA** hyphophoral, laminal, formed on thallus surface or near margin, their scales strongly reduced or absent, 0.05–0.1 mm long and wide,

translucent and membranaceous; diahyphal mass, composed of moniliform hyphae, terminal segments sausage-like shaped, cells 5–10 × 1.5–2.5 µm. Photobiont related to Watanabeales, green, with a subparietal chloroplast bearing a conspicuous central pyrenoid, spherical, 5–12 µm diam. in thallus; spherical to ellipsoid, 4–9 µm diam. in diahyphal mass and 3–7 µm diam. in epithecial tissue.

Chemistry: no lichen substance was detected by HPTLC.

The morphological and chemical features of material from Okinawa Island agree well with the protologue (Vězda, 1994) and descriptions provided by Ferraro *et al.* (2001). In addition, the BLAST results for the mtSSU sequences of the material from Okinawa Island showed 97–99% identity with those of *G. imperfectum* in GenBank (Table S2).

This species is characterized by its adnate, spot-like, dark brownish-grey hyphophores lacking a distinct scale (Fig. 7E). Similar hyphophoral structures are also known in *G. membranaceum* Sérus. & Lücking but differ in being much thinner and membranous, and the thallus of that species is distinctly areolate rather than finely verrucose (Ferraro *et al.*, 2001). Among the specimens collected from Okinawa Island, those bearing only apothecia and lacking hyphophores were predominant. The morphology of these apothecia agreed well with that of *G. filicinum* Müll. Arg. (lectotype: G-00291727!), and they were initially identified as this species. However, the hyphophores are different in these species, and the mtSSU sequences of our samples matched those of *G. imperfectum* (Table S2). Thus, they were identified as *G. imperfectum*.

The type locality of *G. filicinum* is in the Neotropics, and the Japanese specimens of *G. filicinum* reported from Amami-Oshima Island to Iriomote Island by Thor *et al.* (2000), based solely on apothecial morphology, require re-examination using DNA sequence data. *Gyalectidium imperfectum* may be confused with other foliicolous species having adnate, spot-like apothecia, such as *Echinoplaca* s. lat., but the hyphophore of *G. imperfectum* is characterized by its lacinate ledge and mass of diahyphae.

Gyalectidium imperfectum has been reported from Asia [New Caledonia, Taiwan (Lebreton *et al.*, 2025), and Vietnam (Aptroot and Sparrus, 2006)], Oceania [Australia as type locality (Ferraro *et al.*, 2001)], the Neotropics (Lücking, 2008), and Africa [Democratic Republic of the Congo (Ferraro *et al.*, 2001)], and thus shows a pantropical distribution. This species is new to Japan, where it was found on leaves of *Ardisia quinquegona* Blume, *Arenga engleri* Becc., *Ficus ampelas* Burm. f., and *Turpinia ternata* Nakai in a single locality at 20–40 m elevation. Because the thalli of *G. imperfectum* are tiny and inconspicuous, this species may easily be overlooked in the field. Further careful surveys in similar habitats are needed to reveal its distribution in Japan.



Specimens examined. JAPAN. RYUKYU ISLANDS (Okinawa Pref.): along Henan River path between parking space and Ta-taki Waterfall, Tsuha, Ohgimi-son, Kunigami-gun, Okinawa Island (26°37'–38'N, 128°05'33'–36'E), 20–40 m elev., on *Turpinia ternata*, 14 March 2021, K. Miyazawa 745 pr.p., K. Gibu & T. Nada (in collection of *Puiggariella* sp.) (TNS), K. Miyazawa 747, K. Gibu & T. Nada (TNS), K. Miyazawa 771, K. Gibu & T. Nada (TNS); *ibid.*, on *Ficus ampelas*, K. Miyazawa 748D, K. Gibu & T. Nada (TNS), K. Miyazawa 750D, K. Gibu & T. Nada (TNS); *ibid.*, on *Ardisia quinquegona*, K. Miyazawa 755 pr.p., K. Gibu & T. Nada (in collection of *Spinomyces albostrigosus*) (TNS), K. Miyazawa 758 pr.p., K. Gibu & T. Nada (in collection of *Calenia* sp.) (TNS); *ibid.*, on *Arenga engleri*, K. Miyazawa 782C, K. Gibu & T. Nada (TNS); *ibid.* (26°38'02"N, 128°05'40"E), on *Arenga engleri*, K. Miyazawa 785B, K. Gibu & T. Nada (TNS).

Porina perminuta Vain., Univ. Calif. Publ. Bot. 12(1): 14. 1924. **Type:** FRENCH POLYNESIA, Tahiti, Faaa District, on leaves of mango trees, 1 January 1922, Setchell & Parks 5085 (holotype: TUR-V 31441; isotypes: M, NY, PC, UPS, not seen). **Fig. 8A–C**

THALLUS crustose, dispersed into rounded, ca. 0.2 mm diam., confluent patches, smooth, greenish to yellowish grey due to variation of carotenoids in photobiont cells, matt to slightly nitidous, up to ca. 20 mm diam. and 6–11 µm thick; prothallus inconspicuous. PERITHECIA sessile, subglobose, slightly constricted at the base, greyish black to pure black, surface tomentose with dense, short greyish hairs, 85–135 µm diam., 90–140 µm tall, matt to slightly nitidous; excipulum dark brown, K–, 5–15 µm thick; involucrellum not distinctly separated from excipulum, brownish black to purplish black, K–, 7–11 µm thick, externally covered by thallus layer (6–11 µm thick); the hairs on the perithecial surface up to 30 µm long, formed by free or coherent hyphae; paraphyses unbranched, septate, 0.7–1.0 µm wide. ASCI obclavate, 48–54 × 8–10 µm. ASCOSPORES 8 per ascus, fusiform with rounded ends, 3-septate, without constrictions at septa, colorless, (17.5–)18.7–21.6(–23.4) × (3.6–)3.8–4.4(–4.5) µm (n = 20), 3.5–7 times as long as broad. PYCNIDIA not seen. PHOTOBIONT trentepohlioid, forming continuous plates; cells angular, slightly rounded around perithecia, green but amount of orange carotenoids is variable, (8.4–)9.7–15.7(–20.0) × (3.3–)3.8–6.2(–9.3) µm (n = 30).

Chemistry: no lichen substance was detected by HPTLC.

Porina perminuta is characterized by small blackish perithecia (up to 135 µm diam.) with short whitish hairs (Fig. 8A & B) and 3-septate ascospores (Fig. 8C). The morphological and chemical features of the specimen collected from Japan are consistent with the type specimen, the protologue (Vain, 1924), and the description provided by Santesson (1952), including ascospore dimensions [17.5–23.4 × 3.6–4.5 µm vs. 17–21 × 3.5–4.5 µm in Santesson (1952)]. The asci of the Japanese material tend to be longer (48–54 µm) than those reported by Santesson (1952) (30–40 µm), although no statistical comparison was performed. Given the absence of other distinguishing morphological features

and the 100% identity in BLAST comparison with the sequence of *P. perminuta* from Mauritius, Africa in GenBank (Table S2), the difference in ascus size is interpreted as intraspecific variation.

Porina perminuta resembles *P. thaxteri* R. Sant. in having 3-septate ascospores, but the latter has larger perithecia [200–300 µm diam. (Santesson, 1952) vs. up to 135 µm diam. in *P. perminuta*], with the ostiolum covered by thallus tissue. *Porina perminuta* is also similar to *P. nitidula* Müll. Arg. and *P. trichothelioides* R. Sant. in having papillose blackish perithecia. However, *P. nitidula* is distinguished from *P. perminuta* in having larger perithecia (150–250 µm vs. up to 135 µm diam. in *P. perminuta*) and larger 5-septate ascospores (20–32 × 3.5–5.5 µm: Santesson, 1952 vs. 17.5–23.4 × 3.6–4.5 µm in *P. perminuta*). *Porina trichothelioides* is distinct from *P. perminuta* in having larger 7-septate ascospores (28–32 × 4–5 µm; Santesson, 1952).

This species was reported from Asia [the Philippines (Santesson, 1952) and Taiwan (Aptroot *et al.*, 2003)], Oceania [French Polynesia (type locality; Vain, 1924) and Vanuatu (McCarthy, 2003)], and Africa [Mauritius (Ertz and Diederich, 2022), République de Côte d'Ivoire (Santesson and Lücking, 1999), and Seychelles (Schumm and Aptroot, 2010)], suggesting that it is a paleotropical species. In Japan, *P. perminuta* was found on Okinawa Island and Miyako Island where it grows on leaves of *Arenga engleri*, *Euonymus japonicus* Thunb. and *Ficus* sp. in a forest near the coast. This species is reported as new to Japan. At present, Okinawa Island is the northernmost locality of the species in the world.

Specimen examined. JAPAN. RYUKYU ISLANDS (Okinawa Pref.): Horohoro-no-mori, Gushikami, Yaese-cho, Shimajiri-gun, Okinawa Island (26°07'14"N, 127°44'54"E), 45 m elev., on *Euonymus japonicus*, 17 November 2022, K. Miyazawa 1237 (TNS).

Additional specimens examined. JAPAN. RYUKYU ISLANDS (Okinawa Pref.): Tomaiutaki, Yonaha, Shimoji, Miyakojima-city, Miyako Island (24°45'04"N, 125°16'05"E), 3 m elev., on *Arenga engleri*, 29 February 2024, Y. Tochihara 1 (TNS); *ibid.*, on *Ficus* sp., Y. Tochihara 2 (TNS).

Strigula pseudosubtilissima S.H. Jiang, J.C. Wei & Lücking, in Jiang, Lücking, Liu & Wei, Xavier-Leite, Portilla, Ren & Wei, J. Fungi 8(2): 19. 2022. **Type:** CHINA, Hainan, Ledong Co., Jianfengling, Mingfenggu, 18°44'05"N, 108°52'08"E, 920 m elev., on living leaves, 11 December 2014, J.H. Wang & R.D. Liu HN2014130 [holotype: HMAS, not seen; photos in Jiang *et al.* (2022)!]

Fig. 8D & E

As the Japanese specimens from Okinawa Island agree well with the original description of *S. pseudosubtilissima* from China by Jiang *et al.* (2022), a full description is not repeated here.

Strigula pseudosubtilissima is characterized by the thin, lacinate thallus bordered by a black line (Fig. 8D), the uniseriate, short ascospores (8–12 × 2.5–3 µm) (Fig. 8E), as well as the green thallus color and fully exposed, black perithecia (Fig. 8D) (Jiang *et al.*, 2022). The nuITS



sequences also showed 98–99% identity to those published by Jiang *et al.* (2022; e.g., MW344242, MW344235) (Table S2). *Strigula pseudosubtilissima* is phylogenetically distinct and differs from the typical *S. nitidula* Mont. morphologically by its free, rather long lobes (Jiang *et al.*, 2022). Upon re-examination of all specimens identified as *S. nitidula* housed in TNS which were cited in Thor *et al.* (2000) and Miyazawa *et al.* (2022), it was found that they all possess a laciniae-bearing thallus, consistent with the characteristics of *S. pseudosubtilissima*. Considering the morphological features, the identity in nuITS sequences, and the fact that the type locality of *S. nitidula* is in the Neotropics, we conclude that *S. nitidula* should be excluded from the Japanese mycota.

Strigula pseudosubtilissima was previously reported from only southern China (Jiang *et al.*, 2022). This species is newly reported from Japan. In Japan, this species occurs on Yakushima Island, Amami-Oshima Island, Okinawa Island, and Iriomote Island.

Specimens examined. JAPAN. RYUKYU ISLANDS (Okinawa Pref.): near the Nago Castle Park, Nago, Nago-city, Okinawa Island (26°35'13"N, 127°59'58"E), 140 m elev., on a broad-leaf tree, 28 December 2020, *K. Gibu 40* (TNS); along Hiji River path between Hiji Waterfall Camp site and Hiji Waterfall, Kunigami-son, Kunigami-gun, Okinawa Island (26°43'–44'N, 128°10'–11'E), 20–100 m elev., on *Distylium racemosum*, 13 March 2021, *K. Miyazawa 715*, *K. Gibu*, *K. Watanabe* & *T. Nada* (TNS); around Lake Kuina, Aha, Kunigami-son, Kunigami-gun, Okinawa Island (26°43'17"N, 128°15'55"E), 190 m elev. on *Symplocos stellaris*, 15 November 2022, *K. Miyazawa 1133C* (TNS); *ibid.*, (26°43'13"N, 128°15'55"E), 180 m elev. on *Castanopsis sieboldii* subsp. *lutchuensis*, 15 November 2022, *K. Miyazawa 1136* (TNS); Takazato, Ohgimi-son, Kunigami-gun, Okinawa Island (26°41'28"N, 128°10'42"E), 140 m elev., on a broad-leaf tree along a stream, 16 November 2022, *K. Miyazawa 1211* (TNS).

Additional specimens examined. JAPAN. YAKUSHIMA ISLAND (Kagoshima Pref.): 14 km SW of Anbo, 500 S of Kaminomaki (30°14'N, 130°31'E), 50 m elev., on a broad-leaf tree, 1 November 1994, *G. Thor 12546d pr.p.* (TNS), (in collection of *Strigula nemathora*). RYUKYU ISLANDS (Kagoshima Pref.): 7 km SW of Nishinakama village, ca. 100–200 m N of Yagachi river, near the road, Sumiyo-cho, Oshima-gun, Amami-Oshima Island (24°13'N, 129°21'E), on a broad-leaf tree, 5 February 1995, *G. Thor 12999 pr.p.* (in collection of *Strigula subtilissima*) (TNS). RYUKYU ISLANDS (Okinawa Pref.): along mountain path between Ohtomi-guchi Entrance and Daiichi Yamagoya-ato, Iriomote Island, Yaeyama Islands (24°18'42"N, 123°50'24"E), 220 m elev., on *Cleyera japonica*, 19 November 2019, *K. Miyazawa 384* & *Y. Ohmura* (TNS), *K. Miyazawa 391* & *Y. Ohmura* (TNS); along mountain path between Ohtomi-guchi Entrance and Daiichi Yamagoya-ato, Iriomote Island, Yaeyama Islands (24°19'32"N, 123°50'55"E), 190 m elev., on *Cleyera japonica*, 19 November 2019, *K. Miyazawa 471* & *Y. Ohmura* (TNS); *ibid.*, on *Distylium racemosum*, *K. Miyazawa 477* & *Y. Ohmura* (TNS), *K. Miyazawa 478* & *Y. Ohmura* (TNS); along the trail by Nakama River, ca. 3 km SE from the estuary of Nakara River, Iriomote Island, Yaeyama Islands (24°19'N, 123°46'E), 15 m elev., on Rubiaceae sp., 8 March 2011, *G. Tanaka 335* & *Y. Ohmura* (TNS); along trail in the mountains along Urauchi river from 500 m N of southernmost starting point 6 km NW of Ohara village to small camping site between two streams 2.5 km NNE of starting point (7.5 km NNW of Ohara village), Iriomote Island, Taketomi-cho, Yaeyama-gun (24°18'–20'N, 123°51'E), 160–220 m elev., on *Distylium racemosum*, 10 February 1995, *G. Thor 13138 pr.p.* (in collection of *Mazosia melanophthalma*) (TNS), *G. Thor 13139* (TNS), *G. Thor 13142a pr.p.* (in collection of

Racoplaca melanobapha) (TNS), *G. Thor 13152* (TNS); *ibid.*, on *Machilus japonica*, *G. Thor 13148* (TNS); along trail in the mountains along Urauchi river from the camping site between two streams 7.5 km NNW of Ohara village (2.5 km NNE of the southernmost starting point of the trail) and along the trail to ca. 2 km to the NW of the camping site, Taketomi-cho, Iriomote Island, Yaeyama-gun (24°20'N, 123°50'–51'E), 120–160 m elev., on a broad-leaf tree, 11 February 1995, *G. Thor 13276* (TNS), *G. Thor 13284b pr.p.* (in collection of *Eremothecella calamicola*) (TNS); along 1.5 km long trail to Maryudo waterfall from starting point at Urauchi river 5 km SSW of Funaura village, Taketomi-cho, Iriomote Island, Yaeyama-gun (24°21'–22'N, 123°48'E), 5–60 m elev., on a broad-leaf tree, 13 February 1995, *G. Thor 13356 pr.p.* (in collection of *Strigula subtilissima*) (TNS), *G. Thor 13357 pr.p.* (in collection of *Sporopodium lepreurii*) (TNS), *G. Thor 13379 pr.p.* (in collection of *Badimia polilensis*) (TNS); along the trail by Nakara River, ca. 3 km SE from the estuary of Nakara River, Iriomote Island, Yaeyama-gun (24°19'N, 123°46'E), on *Litsea acuminata*, 15 m elev., 8 March 2011, *Y. Ohmura 7916 pr.p.* & *G. Tanaka* (in collection of *Sporocybomyces leucotrichoides*); along mountain path between Ohtomi-guchi Entrance and Daiichi Yamagoya-ato, Iriomote Island, Yaeyama-gun (24°19'01"N, 123°50'32"E), 210 m elev., on a broad-leaf tree, 19 November 2019, *K. Miyazawa 402 pr.p.* & *Y. Ohmura* (in collection of *Arthonia cyanea*) (TNS).

Lichenicolous fungus new to Asia

Hemigrapha strigulae Matzer, Mycol. Pap. 171: 107. 1996. **Type:** COSTA RICA, Puntarenas Prov., near to the Pacific coast, Carara Biological Reservation S of the Río Tárcoles, trail from the entrance of the reservation to the river, ca. 100 m elev., 09°47'N, 84°35'W, moderately moist to moist tropical rain forest, on *Strigula maculata*, 18 August 1991, *M. Matzer 1395* & *B. Pelzmann* (holotype: GZU, not seen). **Fig. 8F–H**

ASCOMATA lichenicolous, thyriothecoid, sessile, superficial, scattered on the host thallus, rarely on perithecia of the host lichen, developing from dark brown to blackish, flat cell-plates, uncovered, elongate, straight or slightly curved, simple or sometimes branched, basally distinctly spreading, black, 250–700(–1150) µm long, 70–115 µm wide, 30–60 µm tall; disc ± slit-like; ascomatal wall in surface view composed of (rect-)angular cells forming a plate, cells arranged in parallel rows, brown; thyriothecia in longitudinal section truncated conical; ascomatal wall at the base of ascomata absent, laterally well-developed, dark brown to blackish; epithecium indistinct, colorless to light brown; hymenium becoming exposed by an apical longitudinal splitting of the ascomatal wall, 20–35 µm tall, hyaline, I–, K/I–; hypothecium 5–10 µm tall, light brown; interascal hyphae absent. ASCI fissitunicate, clavate to ellipsoid, not or shortly stipitate, usually 8-spored, 20–32 × 11–18 µm, I–, K/I–, ocular chamber distinct or not. ASCOSPORES hyaline, smooth, becoming brown when old, obovoid, with rounded ends, 1-septate, septum median or suprmedian, upper cell wider, constricted at the septum, without a gelatinous sheath, (8.4–)9.5–11.4(–12.5) × (3.6–)3.9–4.8(–5.2) µm (n = 30), 2–3 times as long as broad. VEGETATIVE HYPHAE numerous, 2–4 µm wide, smooth, composed of oblong cells, septate,



branched, anastomosing, light brown to brown, attached to basal cells of the ascomata wall.

The lichenicolous fungus growing on the thallus of *Strigula* sp. in Okinawa Island was identified as *Hemigrapha strigulae* based on the presence of thyriothecoid ascomata (Fig. 8F & G), fissitunicate asci exceeding 30 µm in length and 15 µm in width, and 1-septate ascospores with the upper cell being wider (Fig. 8H).

The asci measured 20–30 × 11–18 µm, and the ascospores 8.4–12.5 × 3.6–5.2 µm. These measurements are somewhat smaller than those reported in the protologue by Matzer *et al.* (1996) (asci 25–44 × 12–25 µm; ascospores 9–18 × 4–8 µm), but they largely overlap. Short vertical hyphae connected to appressed vegetative hyphae, described in some specimens by Matzer *et al.* (1996), were not observed in our specimens.

We also obtained mtSSU sequences from our collections. A BLAST search returned no closely matching sequences, with the highest identity (86–87%) to *Melaspilea* sp. (KX244981), which, like *Hemigrapha*, belongs to the order Asterinales (Ertz *et al.*, 2016). The identical sequences from separate collections reduce the likelihood of contamination and support the conclusion that the sequences represent *H. strigulae*, whose DNA has not previously been sequenced and registered in GenBank.

In the phylogenetic tree of Asterinales, *H. strigulae* from Okinawa Island formed a clade distinct from the clade comprising *H. asteriscus* (Müll. Arg.) R. Sant. ex D. Hawksw. and *H. atlantica* Diederich & Wedin, and it did not cluster with any other taxa within Asterinales (Fig. 4). *Hemigrapha asteriscus* and *H. atlantica* are characterized by star-shaped ascomata (Diederich and Wedin, 2000; Dai *et al.*, 2018), whereas the ascomata of *H. strigulae* are generally simple but can occasionally fuse to form a star-like shape (Fig. 8F). Based on our phylogenetic tree of Asterinales inferred based on mtSSU sequences, *H. strigulae* may need to be reassigned to a different genus. However, a more comprehensive molecular phylogenetic analysis, including additional taxa and loci, is necessary to re-evaluate the taxonomical placement of *H. strigulae* in the future. Although we attempted to obtain the nuLSU sequence from the material collected on Okinawa Island, it could not be amplified successfully.

This species has been recorded from Africa (Democratic Republic of the Congo) and from Central and South America (Costa Rica and Brazil) (Matzer *et al.*, 1996). In Japan, *Hemigrapha strigulae* was found only on *Strigula* sp. at a single locality on Okinawa Island. This species is new to Asia. Despite examining numerous specimens of *Strigula* s. lat., *H. strigulae* appears to be quite rare in Japan.

Specimens examined. JAPAN. RYUKYU ISLANDS (Okinawa Pref.): Yona Field, University of the Ryukyus, Iji, Kunigami-gun, Okinawa Island (26°45'34"N, 128°13'00"E), 210 m elev., on *Strigula* sp. on *Distylium racemosum*, 10 March 2023, K. Miyazawa 1517B & Y. Ohmura (TNS); *ibid.*, on *Strigula* sp. on

Machilus japonica, K. Miyazawa 1521 *pr.p.* (in collection of *Badimia polillensis*) (TNS), K. Miyazawa 1522 (TNS).

First molecular evidence for the genus

Microtheliopsis uleana Müll. Arg., Flora, Regensburg 73: 195. 1890. **Type:** BRAZIL, Rio de Janeiro, Morro da Nova Cintra, 1887, *Ule* 22 (holotype: G-00292618!).

From material collected on Okinawa Island, representing a new record for the island (Fig. S1, panel AC), we obtained the first DNA sequence data (mtSSU) for *Microtheliopsis uleana*. A BLAST search showed that the closest matches were fungal sequences belonging to the order Chaetothyriales, although the sequence similarity was relatively low (91%; Table S2), leaving its precise phylogenetic placement uncertain. A phylogenetic analysis based on mtSSU placed the Okinawa specimens in a moderately supported clade (NJ/ML = 87/85) together with members of Cyphellophoraceae within Chaetothyriales (Fig. 5).

The family Microtheliopsidaceae, which currently contains only the genus *Microtheliopsis*, is characterized by perithecioid ascomata with an aparaphysate, hemiamyloid hamathecium, fissitunicate asci, and greyish-brown ascospores (Lücking, 2008). Because molecular data have so far been lacking, its systematic placement has been discussed based on morphological and ecological characteristics. Eriksson (1981) regarded the family as closely related to Herpotrichiellaceae, now included in Chaetothyriales, whereas Aptroot (in Eriksson and Reynolds, 1994) suggested an affinity with the Verrucariales. In contrast, Lücking (2008) rejected both views based on morphological and ecological differences, concluding that “the family is monogeneric, containing only the genus *Microtheliopsis*,” and placed it in the Chaetothyriales.

To further evaluate the placement of *Microtheliopsis* within Chaetothyriales, we compared its features with those of Cyphellophoraceae, which showed the closest relationship in our phylogenetic tree (Fig. 5). Most members of Cyphellophoraceae are known only as anamorphic fungi, but some species produce bitunicate asci and perithecioid ascomata with septate ascospores (Yang *et al.*, 2018, 2022), resembling *Microtheliopsis* in these characters. However, they differ in having pseudoparaphyses and hyaline ascospores, whereas *Microtheliopsis* lacks paraphyses and has greyish-brown spores. Ecologically, species of Cyphellophoraceae have been isolated from a wide range of habitats, including living or decaying leaves, wood, resin, domatia, and ant-made carton, as well as human nails and skin, but no lichenized species have been reported (Réblová *et al.*, 2013; Vasse *et al.*, 2017; Yang *et al.*, 2018, 2022; Quan *et al.*, 2020). The genus *Microtheliopsis*, in contrast, is fully lichenized and foliicolous, thus differing both morphologically and ecologically from Cyphellophoraceae.

Taken together, our molecular, morphological, and



ecological data indicate that *Microtheliopsis* belongs to the Chaetothyriales, but represents an independent, monogeneric lineage distinct from other genera within the order. This supports the interpretation of Lücking (2008). Nevertheless, because single-locus (mtSSU) analyses are generally insufficient to infer higher-level relationships, further studies using multilocus loci (e.g., nuLSU, *RPB1*, and *RPB2*) will be required to clarify the phylogenetic relationships of *Microtheliopsis* and to confirm the monogeneric status of Microtheliopsidaceae within the Chaetothyriales.

Specimens examined. JAPAN. RYUKYU ISLANDS (Okinawa Pref.): along Hiji River path between Hiji Waterfall Camp site and Hiji Waterfall, Kunigami-son, Kunigami-gun, Okinawa Island (26°43–44'N, 128°10–11'E), 20–100 m elev., on *Aidia canthioides*, 13 March 2021, *K. Miyazawa 717 pr. p.*, *K. Gibu*, *K. Watanabe* & *T. Nada* (in collection of *Badimia polillensis*) (TNS); Takazato, Ohgimi-son, Kunigami-gun (26°41'25"N, 128°10'41"E), 140 m elev., *Neolitsea sericea* along a stream, 16 November 2022, *K. Miyazawa 1205* (TNS); Takae, Higashi-son, Kunigami-gun (26°40'02"N, 128°14'42"E), 85 m elev., on *Hoya carnosa* along a stream, 15 November 2022, *K. Miyazawa 1153* (TNS); *ibid.*, on a broad-leaf tree, *K. Miyazawa 1156* (TNS), *K. Miyazawa 1157 pr. p.* (in collection of *Badimia polillensis*) (TNS); *ibid.*, (26°39'59"N, 128°14'46"E), 75 m elev., on *Lasianthus fordii* along a stream, *K. Miyazawa 1173 pr. p.* (in collection of *Porina* sp.) (TNS), *K. Miyazawa 1174* (TNS); along Henan River path between parking space and Ta-taki Waterfall, Tsuha, Ohgimi-son, Kunigami-gun (26°37–38'N, 128°05'33–36"E), 20–40 m elev., on *Camellia japonica*, 14 March 2021, *K. Miyazawa 749A*, *K. Gibu* & *T. Nada* (TNS); along Genka river path, Genka, Nago-city (26°36'55–59"N, 128°03'46–49"E), 40 m elev., on *Arenga engleri*, 14 March 2021, *K. Miyazawa 793*, *K. Gibu* & *T. Nada* (TNS).

A list of the other foliicolous lichens collected from Okinawa Island

A total of 27 genera and 59 species of foliicolous lichens were found to occur on Okinawa Island based on our field survey (for 26 genera, 51 species, and one subspecies) and previous studies (for eight genera and eight species: Thor *et al.*, 2000; Yamamoto *et al.*, 2021; Miyazawa and Ohmura, 2023, 2024).

In the list mentioned below, the species new to Okinawa Island are marked with asterisk (*) before the taxon name. Following the species name, taxonomic notes when necessary, locality number (see Table S1), and the specimen number are indicated. The abbreviations for collector names are as follows. KG: K. Gibu, KM: K. Miyazawa. Detailed information of collections and the GenBank accession numbers of DNA sequences are shown in Table S2.

**Arthonia accolens* Stirt.

Specimens examined. 12: KM1331. 20a: KG30 *pr. p.* 20b: KG32. 20c: KM1429.

**Arthonia cyanea* Müll. Arg.

Specimens examined. 5: KM1133B. 15a: KM668.

**Arthonia fuscoicyanea* U. Becker & Lücking

Specimen examined. 8: KM1213A.

Additional specimen examined. JAPAN. RYUKYU

ISLANDS (Okinawa Pref.): along mountain path between Chukan-Hiroba and Itachikigawa River Junction, Iriomote Island (24°20'26"N, 123°49'58"E), 160 m elev., on *Areceaceae* sp., 19 November 2019, *K. Miyazawa 582* & *Y. Ohmura* (TNS).

Arthonia trilocularis Müll. Arg.

Specimens examined. 4: KM739B. 11: KM749B *pr. p.* 17: KG43 *pr. p.*

**Asterothyrium sasae* Y. Suto

The specimens from Okinawa Island have apothecia and produce 1-septate ascospores measuring 17.6–30.5 × 6.1–12.8 µm (Fig. S1B). These spore measurements largely overlap with those of *Asterothyrium sasae* Y. Suto, described from Honshu, Japan, by Suto and Ohtani (2018) (16–37 × 5–10 µm), rather than with those of *Asterothyrium decipiens* (Rehm) R. Sant. [35–55 × 9–14 µm (Santesson, 1952; Lücking, 2008)] or *A. microsporum* R. Sant. [8–10 × 2–3 µm (Santesson, 1952; Lücking, 2008)]. In Japan, *Asterothyrium* cf. *decipiens* has been reported from Iriomote Island based solely on specimens with pycnidia (Thor *et al.*, 2000; Miyazawa *et al.*, 2022). The relationship between *A. sasae* and *A. cf. decipiens* from Iriomote Island should be carefully examined with further sampling and molecular phylogenetic analyses.

BLAST results indicated that the mtSSU sequences of the material from Okinawa Island showed 95–100% identity with *Linhartia* sp. and *Asterothyrium* sp., members of the family Gomphillaceae, as published by Lebreton *et al.* (2025) (Table S2). The taxonomy of this material requires further examination.

Specimens examined. 4: KM727B. 11: KM750B.

Bacidina pallidocarnea (Müll. Arg.) Vězda

Specimens examined. 1: KM677A-1, KM677B-1.

**Bysssolecania hymenocarpa* (Vain.) Kalb, Vězda & Lücking

Specimen examined. 11: KM699C.

**Bysssolecania* cf. *variabilis* Vězda, Kalb & Lücking

The morphology of the material from Okinawa Island agrees well with that previously reported from Japan as *Bysssolecania variabilis* by Thor *et al.* (2000). The apothecia show the typical *Bysssolecania* morphology, forming small spot-like discs (Fig. S1E) with a reduced excipulum and thick, straight, unbranched paraphyses (1.5–2.5 µm wide) that are densely arranged in a palisade-like structure and embedded in a gelatinous matrix.

In contrast, BLAST results showed that the mtSSU sequences of the Okinawa material exhibit 97–98% identity with those of *Jejulea byssolomoides* J.P. Halda, J.J. Woo & J.S. Hur, a saxicolous species recently described by Halda *et al.* (2022) (Table S2). In the mtSSU phylogeny, the Okinawa specimens and *J. byssolomoides* form a well-supported clade (NJ/ML = 99/99) (Fig. 6), indicating a close genetic relationship. Conversely, sequence identity with the mtSSU sequence of the



Neotropical *Byssolecania variabilis* (AY567780; Andersen and Ekman 2005) is considerably lower (81–82%), and these taxa are clearly separated in the phylogenetic tree (Fig. 6).

According to Halda *et al.* (2022), *J. byssolomoides* is characterized by sparsely branched and anastomosing paraphyses with lumina 1–2 µm wide. However, in their figures (Fig. 3C in Halda *et al.*, 2022), the paraphyses appear rather straight and unbranched, embedded in a gelatinous matrix, giving an impression more like the *Byssolecania*-type. Moreover, although not statistically supported, our phylogenetic tree places *Jejulea* close to the clade of *Byssolecania* spp. (Fig. 6), the topology that differs from that reported by Halda *et al.* (2022).

In consideration of these results, the generic boundaries between *Byssolecania* and *Jejulea* require re-evaluation using multilocus datasets (e.g., nuLSU, *RPB1*, and *RPB2*). Given that the type locality of *Byssolecania variabilis* is in the Neotropics and that the Japanese material may represent a different taxon, we provisionally treat the Okinawa specimens as *Byssolecania* cf. *variabilis* based on the currently available morphological and molecular evidence.

Specimens examined. 2: KM1513, KM1549, KM1553. 4: KM730C. 20a: KG33. 20b: KG78D, KG81.

**Byssoloma annuum* (Vain.) G. Thor, Lücking & Tat. Matsumoto

The BLAST results showed 97–100% identity to *B. annuum* sequences from Japan and China (Hainan), suggesting some intraspecific genetic variation. Despite this, the sequences from Okinawa Island formed a well-supported clade with those from Iriomote Island and Hainan (China) in the mtSSU tree (NJ/ML = 100/99) (Fig. 3).

Specimens examined. 8: KM1210A, KM1214, KM1216. 11: KM776. 15b: KG71.

**Byssoloma chlorinum* (Vain.) Zahlbr.

Specimens examined. 2: KM1550. 8: KM1221. 11: KM781B, KM785A. 20a: KG34. 20b: KG78A, KG80 *pr.p.*, KG81 *pr.p.* 20c: KM1426, KM1430. 22: KM1112.

**Byssoloma leucoblepharum* (Nyl.) Vain.

The material from Okinawa Island is characterized by a greyish light green thallus and apothecia measuring 0.5–1.2 mm diam. including the byssoid margin with strongly convex discs that are dark and slightly bluish in color (Fig. S1H). The white byssoid margin is often well-developed and conspicuous, spreading widely over the thallus (Fig. S1H). As apothecia age, cracks frequently appear at the edge of the disc, which may subsequently become detached from the thallus.

Byssoloma leucoblepharum appears to be a heterogeneous species complex (Lücking, 2008; Wang *et al.*, 2020b). The material from Okinawa Island closely resembles *Patellaria xanthoblephara* Müll. Arg.

(holotype: G-00290909!), which was treated as a synonym of *B. leucoblepharum* by Santesson (1952), particularly in its dark discs and well-developed byssoid apothecial margin. However, *P. xanthoblephara* differs in having a slightly brownish apothecial margin.

Based on our molecular phylogenetic analyses of mtSSU sequences, *B. leucoblepharum* is divided into several clades, consistent with previous studies (Wang *et al.*, 2020b; Miyazawa and Ohmura, 2023). Given its global distribution and numerous synonyms, a careful re-evaluation of *B. leucoblepharum* is necessary.

The mtSSU sequences of the material from Okinawa Island showed 99% identity in BLAST searches with those of ‘*Byssoloma leucoblepharum* subclade 3’ published by Wang *et al.* (2020b) from China. The specimens belonging to the subclade 3 are characterized by relatively large apothecia (up to 0.6 mm diam.), with pale to dark grey-brown, strongly convex discs. Although the apothecial size of the material from Okinawa Island appears to be larger, the strongly convex discs and the presence of cracks around the discs, as observed in the photos (Fig. 2 in Wang *et al.*, 2020b), are similar to those of subclade 3. In the mtSSU phylogenetic tree, the material from Okinawa Island clustered within the subclade 3 (NJ/ML = 100/88) (Fig. 3).

Specimens examined. 4: KM725. 15b: KG72, KM659. 20a: KG37. 20b: KG78B, KG80, KG88. 20c: KM1435. 22: KM1110.

**Byssoloma subleucoblepharum* G. Thor, Lücking & Tat. Matsumoto

Specimen examined. 5: KM1133D.

**Byssoloma vanderystii* Sérus.

Specimens examined. 10: KM1170, KM1175, KM1177, KM1180, KM1173 *pr.p.* 15a: KM654, KM655, KM656B. 17: KG47.

**Calopadia puiggarii* (Müll. Arg.) Vězda

Specimens from Okinawa Island showed disc colors ranging from black (Fig. S1L), resembling *Calopadia subcoerulescens* (Zahlbr.) Vězda, to brown (Fig. S1M), as in *C. fusca* (Müll. Arg.) Vězda. However, since disc coloration varied continuously and no clear morphological or molecular discontinuities were observed, all specimens were identified as *C. puiggarii*. The mtSSU sequences showed 97–99% identity with *C. puiggarii* from Hainan, China (Wang *et al.*, 2020a; MK957172) (Table S2).

Specimens examined. 2: KM1551. 4: KM703. 6: KM1199. 7: KM1407A. 11: KM748F, KM750A, KM753 *pr.p.*, KM759, KM752, KM764, KM766A-1, KM766A-2, KM781A, KM782A, KM784, KM785D, KM786. 12: KM1287. 15a: KM673B. 20c: KM1421, KM1424.

**Coenogonium geralense* (Henn.) Lücking [as *Dimerella flavicans* Vězda & Farkas, in Thor *et al.* (2000)]

Specimens examined. 1: KM686, KM688, KM690. 2: KM1509, KM1520, KM1525, KM1534, KM1539, KM1541, KM1547. 4: KM729, KM732. 5: KM1151. 10: KM1166. 11: KM765, KM775, KM795. 14: KM795. 15a: KM653, KM657, KM661, KM671. 15b:



KG70, KG73, KG76, KG77. 17: KG42, KG45. 20a: KG33 *pr.p.* 20b: KG81 *pr.p.* 22: KM1109.

**Coenogonium subluteum* (Rehm) Kalb & Lücking [as *Dimerella epiphylla* (Müll. Arg.) Malme, in Thor *et al.* (2000)]

The material from Okinawa Island often has apothecia with very minute marginal hairs (Fig. S10), a feature also observed in other Japanese specimens identified as *Coenogonium subluteum* (Thor *et al.*, 2000). In contrast, the apothecial margin of *C. subluteum* s. str. is described as smooth (Lücking, 2008). This variation in the presence of marginal hairs on the apothecia among Japanese specimens may represent intraspecific variability or indicate an undescribed taxon. Further studies using DNA markers are needed to evaluate the taxonomic significance of this morphological variation.

Specimens examined. 7: KM1402, KM1405, KM1409 *pr.p.*, KM1412, KM1414, KM1417, KM1418, KM1419. 23: KM1103, KM1105.

**Echinoplaca cf. epiphylla* Fée

The mtSSU sequences of the material from Okinawa Island were identical to each other. These sequences showed approximately 95% identity to *Echinoplaca* aff. *melanothrix* and *Echinoplaca* sp. 'nova-2 EL-2024', published by Lebreton *et al.* (2025) (Table S2), suggesting a possible affinity with these as yet undescribed or re-evaluated taxa. In contrast, they exhibited lower similarity (88–89%) to sequences of *Echinoplaca epiphylla* from Brazil (e.g., MZ827245, MZ827246; Xavier-Leite *et al.*, 2022).

Echinoplaca epiphylla was originally described from French Guiana. Although the material from Okinawa Island shows clear genetic divergence from the South American material identified as *E. epiphylla*, a careful taxonomic re-evaluation, including detailed morphological comparison, is required. Accordingly, our specimens are provisionally referred to as *E. cf. epiphylla*.

Specimens examined. 4: KM701, KM790B, KM791.

**Echinoplaca pellicula* (Müll. Arg.) R. Sant.

Specimens examined. 4: KM727A. 12: KM1322.

**Eremothecella calamicola* Syd.

Specimens examined. 4: KM726D, KM728A.

**Eugeniella micrommata* (Kremp.) Lücking, Sérus. & Kalb [as *Bacidia micrommata* (Kremp.) R. Sant., in Thor *et al.* (2000)]

Specimens examined. 10: KM1161A, KM1181.

**Fellhanera bouteillei* (Desm.) Vězda

Specimens examined. 4: KM709. 6: KM1196. 11: KM750C. 15a: KM664. 15b: KG74. 20b: KG78F. 21: KG68. 22: KM1111, KM1116 *pr.p.* 25: KM1233, KM1240B.

**Fellhanera microdiscus* (Vain.) Vězda

The material from Okinawa Island agrees well morphologically with the description of *Fellhanera microdiscus* provided by Thor *et al.* (2000) (Fig. S20).

However, the BLAST results of the mtSSU sequences showed high identity (99%) with those of *Fellhanera fuscatula* (Müll. Arg.) Vězda from Thailand (Wang *et al.*, 2020a; Table S2). In contrast, the Okinawa sequences showed only 88–89% identity to the sequence published under the name *F. microdiscus* from Hainan, China (MK957175; Wang *et al.*, 2020a), for which no detailed morphological information is available. Given the morphological agreement with *F. microdiscus* sensu Thor *et al.* (2000), the specimens from Okinawa Island are provisionally referred to as *Fellhanera microdiscus*.

Fellhanera microdiscus is generally characterized by 5-septate ascospores, whereas *F. fuscatula* has 7-septate ones (Lücking, 1997, 2000; Thor *et al.*, 2000). However, in Japanese specimens of *F. microdiscus*, irregular septation (1-, 3-, and even 7-septate) has been reported (Thor *et al.*, 2000), suggesting that Wang *et al.* (2020a), who examined Thai material, may have misinterpreted this variation when identifying their specimens.

In addition to ascospore septation, *F. fuscatula* differs from *F. microdiscus* in having a greenish to brownish grey thallus and an ochraceous yellow to (reddish) brown disc with a thin but persistent chamois-colored margin (Lücking, 2008; lectotype: G-00291879!). In contrast, *F. microdiscus* has a dark green thallus and pale brown to blackish-brown discs with a reddish tinge and a distinct whitish margin (Thor *et al.*, 2000; Fig. S1T).

Specimens examined. 2: KM1512, KM1518. 4: KM730A. 8: KM1219.

**Fellhanera rhapsidophylli* (Rehm) Vězda

Specimen examined. 11: KM766C.

**Fellhanera subfuscatula* Lücking

The material from Okinawa Island had predominantly 3-septate ascospores, with 5-septate ones being rare, consistent with the observation by Thor *et al.* (2000) (Fig. S1V).

Specimens examined. 4: KM728B, KM730D. 10: KM1170 *pr.p.*, KM1173 *pr.p.* 11: KM699B. 15a: KM656A, KM660.

**Fouragea viridistellata* (Sérus., Lücking & Sparrius) Ertz & Frisch [as *Opegrapha viridistellata* Sérus., in Thor *et al.* (2000)]

Specimens examined. 7: KM1415. 11: KM740, KM756, KM787. 12: KM1294.

**Gyalectidium radiatum* Lücking, G. Thor & Tat. Matsumoto

Specimens examined. 1: KM684, KM685, KM696. 2: KM1516 *pr.p.*, KM1525, KM1532. 4: KM712, KM726B. 5: KM1141 *pr.p.*, KM1144. 10: KM1188B. 12: KM1300 *pr.p.*, KM1303, KM1304A, KM1314B. 18b: KM1277 *pr.p.*

**Lasioloma arachnoideum* (Kremp.) R. Sant.

The material from Okinawa Island agrees well with the description provided by Santesson (1952) (Fig. S1Y). However, the mtSSU sequences show somewhat low



identity (95–96%) to those of *Lasioloma arachnoideum* from China (OL412922, MK957158; Wang *et al.*, 2023) (Table S2). This moderate level of sequence divergence may reflect intraspecific variation or suggest the presence of a cryptic species. Further phylogenetic and morphological studies are needed to clarify its taxonomic status.

Specimens examined. 8: KM1209. 10: KM1161B, KM1162, KM1163 *pr.p.*

****Mazosia bambusae* (Vain.) R. Sant.**

The mtSSU sequence of the material from Okinawa Island showed a maximum identity of 92% with that of *Mazosia aff. melanophthalma* from Uganda (KJ851009; Frisch *et al.*, 2014) (Table S2), and a lower identity of 90% with the sequence of *M. bambusae* from Guyana (KJ851008; Frisch *et al.*, 2014). The level of genetic divergence suggests the possibility of an overlooked or undescribed taxon. However, given the absence of distinct morphological differences from *M. bambusae*, we provisionally treat the material from Okinawa Island under this name (Fig. S1Z).

Specimens examined. 1: KM683, KM692 *pr.p.*, KM694 *pr.p.*, 12: KM1313.

****Mazosia melanophthalma* (Müll. Arg.) R. Sant.**

Specimens examined. 1: KM694. 2: KM1505, KM1529, KM1546. 3: KM1194. 4: KM733. 8: KM1206.

***Mazosia phyllosema* (Nyl.) Zahlbr.**

The thallus surface of the material from Okinawa Island is mostly smooth and finely uneven, with irregular warts only rarely observed (Fig. S1, panel AB), which is consistent with the type specimen (holotype: H-NYL 4860!). However, the mtSSU sequences we obtained showed less than 80% identity to those of this species registered in GenBank (MW023084, MW023085; Yao *et al.*, 2021). This indicates that specimens identified as *M. phyllosema* worldwide require careful re-examination based on both detailed morphology and molecular data. In this study, we identify the specimens from Okinawa Island as this species because their morphological characteristics do not conflict with those of the type specimen.

One of the examined specimens, KM1223 (Fig. S1, panel AB), has been distributed as an exsiccata specimen to herbaria B, BG, C, CANB, CANL, DUKE, F, G, GZU, H, KRAM, LIV, M, NY, O, S, UPS, US, W, WIS, and hb. Kalb (Ohmura, 2023). Here, we newly provide the mtSSU sequence derived from this specimen (LC913189; Table S2).

Specimens examined. 8: KM1223. 11: KM770, KM781C, KM785E. 12b: KG23.

****Microxyphiomyces cf. vainioi* (R. Sant.) Xavier-Leite, M. Cáceres & Lücking [as *Tricharia vainioi* R. Sant., in Thor *et al.* (2000)]**

The material from Okinawa Island has long and flexible hairs that occasionally bear double or triple hooks at the tip (Fig. S1, panel AD), which is a characteristic feature of *Microxyphiomyces demoulinii* (Sérus.) Xavier-Leite, M. Cáceres & Lücking (Sérusiaux, 1984). In addition, the mtSSU sequences showed 98–100% identity to *M. demoulinii*, *M. aff. demoulinii*, and *M. aff. vainioi*, as published by Lebreton *et al.* (2025) (Table S2). These results suggest that the material from Okinawa Island may correspond to *M. demoulinii*. However, given the possibility that Japanese specimens previously identified as *Tricharia vainioi* may represent a species complex, a re-examination of all such specimens is necessary before applying a definitive name. We therefore provisionally refer to the material from Okinawa Island as *Microxyphiomyces cf. vainioi*.

Specimens examined. 4: KM698A, KM708, KM791 *pr.p.* 11: KM748C, KM760, KM784 *pr.p.* 13: KG60. 15a: KM664 *pr.p.*, KM665B. 15b: KG75. 18a: KG14. 20a: KG35, KG38. 20b: KG78C.

****Porina kamerunensis* F. Schill. [as *Porina chrysophora* (Stirt.) R. Sant., in Thor *et al.* (2000)]**

Specimens examined. 2: KM1536. 4: KM738, KM739. 9: KM1320, KM1335, KM1336 *pr.p.* 10: KM1171 *pr.p.*, KM1172 *pr.p.* 11: KM751, KM761, KM762, KM769A *pr.p.* 12a: KM1286, KM1287 *pr.p.*, KM1300, KM1307A, KM1308, KM1309, KM1323, KM1327, KM1329. 13: KG57. 15a: KM666, KM667. 19: KG2. 20a: KG30, KG32 *pr.p.* 20b: KG87. 20c: KM1425. 22: KM1108, KM1113. 25: KM1224.

****Porina nitidula* Müll. Arg.**

Three sequences obtained from the material of Okinawa Island showed 92–99% identity to each other. One of them showed 96–99% identity to *Porina subnitidula* (OQ383626; unpublished) (Fig. S1, panel AF), while the other two showed 99% identity to *P. magnoliae* N.I. de Silva, S. Lumyong & K.D. Hyde (PQ202026; Dong *et al.*, 2025) and *Porina* sp. (OM219178, OM219179; unpublished) from China (Fig. S1, panels AG–AH). Although the BLAST identity to *P. nitidula* was low (<92% based on GenBank sequences; Table S2), the morphological features: black subglobose, tomentose perithecia (0.15–0.25 mm diam.) producing 5-septate ascospores (22–27 × 3.5–4.5 µm), overlap with the morphological concept of *P. nitidula* as defined by Lücking (2008). We therefore tentatively treat the Okinawa material under this name, pending further examination.

Porina magnoliae was described by Dong *et al.* (2025) as a saprobic fungus on dead twigs of *Magnolia grandiflora* L. However, based on its phylogenetic position and the algal layer visible in their figures, it is likely lichenized. Some Japanese material might correspond to *P. magnoliae*, but its taxonomic status requires careful reassessment.

Specimens examined. 4: KM790C. 15a: KM662, KM673C, KM676. 18a: KG13. 20c: KM1435 *pr.p.*

****Porina rufula* (Kremp.) Vain.**

Two of the three newly obtained sequences from Okinawa Island showed 99% identity to those of *Porina rufula* from China (OR164482, OR164485; unpublished) (Fig. S1AI). The three sequences from Okinawa Island shared at least 90% identity with each another. This comparatively low similarity indicates that they may represent genetically divergent lineages, making a definitive identification premature at this stage. Additional sampling and further analysis will be required.

Specimens examined. 9: KM1321. 10: KM1163, KM1164, KM1169, KM1172 *pr.p.*, KM1179. 11: KM757C. KM769A. 12a: KM1295, KM1297, KM1298, KM1328, KM1330.

****Porina tetramera* (Malme) R. Sant.**

Specimens examined. 4: KM735. 17: KG46.

****Porina trichothelioides* R. Sant.**

Specimen examined. 4: KM698B.

Additional specimen examined. JAPAN. RYUKYU ISLANDS (Okinawa Pref.): Haemida Beach, Iriomote Island, Yaeyama Islands (24°16'24"N, 123°49'54"E), 10 m elev., on *Arenga engleri*. 21 November 2019, K. Miyazawa 572 & Y. Ohmura (TNS).

****Racoplaca melanobapha* (Kremp.) S.H. Jiang, Lücking & J.C. Wei [as *Strigula melanobapha* (Kremp.) R. Sant., in Thor *et al.* (2000)]**

Specimens examined. 1: KM680, KM682, KM683 *pr.p.*, KM691, KM692, KM693, KM694 *pr.p.*, KM695. 2: KM1504, KM1506. 3: KM1194 *pr.p.* 4: KM715 *pr.p.* 5: KM1133A, KM1134, KM1135, KM1141, KM1142, KM1148. 17: KG50. 20a: KG24, KG27. 22: KM1115, KM1116.

****Spinomyces albostrigosus* (R.Sant.) Xavier-Leite, Cáceres & Lücking [as *Tricharia albostrigosa* R. Sant., in Thor *et al.* (2000)]**

Specimens examined. 6: KM1195, KM1198. 11: KM748E, KM751 *pr.p.*, KM755, KM760 *pr.p.*, KM763, KM764, KM777 *pr.p.*, KM781D, KM785C. 12a: KM1286 *pr.p.* 15a: KM665. 18b: KM1276, KM1280B.

****Sporocybomyces leucotrichoides* (Vain.) Xavier-Leite, M. Cáceres & Lücking [as *Echinoplaca leucotrichoides* (Vain.) R. Sant., in Thor *et al.* (2000)]**

Specimens examined. 4: KM720, KM730B, KM731. 8: KM1204. 10: KM1162 *pr.p.* 11: KM699A. 14: KM794. 20a: KG28, KG33 *pr.p.*, KG34 *pr.p.* 20b: KG78E, KG79, KG80 *pr.p.* 20c: KM1428, KM1431 *pr.p.*, KM1432, KM1433.

****Sporopodium flavescens* (R. Sant.) Vězda**

The material from Okinawa Island often has minute warts on the thallus (Fig. S1, panels AN–AO), whereas the type specimen bears them only sparsely (holotype: S!). The sequences obtained from the material from Okinawa Island showed 97–98% identity to sequences OL412900 and OL412935, which were referred to as "*Sporopodium asiatica*" by Wang *et al.* (2023) (Table S2). However, "*S. asiatica*" has not yet been validly published, and given the absence of significant morphological differences from the type of *S. flavescens*, we provisionally identify the material from Okinawa Island as *S. flavescens*. The taxonomic significance of the thallus warts remains

unclear and requires further detailed investigation.

Specimens examined. 8: KM1212. 10: KM1155, KM1160. 11: KM766B.

****Sporopodium phyllocharis* (Mont.) A. Massal.**

Specimens examined. 2: KM1531. 4: KM735 *pr.p.* 6: KM1197, KM1200. 7: KM1404, KM1407C. 11: KM745 *pr.p.*, KM746, KM748B, KM784 *pr.p.*, KM786 *pr.p.* 13: KG59. 18b: KM1277.

****Tapellaria nigrata* (Müll. Arg.) R. Sant.**

In the HPTLC analyses (with solvent system B') of the specimens from Okinawa Island and other Japanese specimens reported by Thor *et al.* (2000), several spots at Rf class 4–5 were detected, showing UV+ green or black reactions after spraying with sulfuric acid and heating. Although characteristic secondary metabolites have not been well documented in members of *Tapellaria* (Lücking, 2008), foreign material of *T. epiphylla* and *T. phyllophila* also showed several common UV+ spots, with some variation in the patterns. As UV-fluorescent xanthenes are known from other genera of Pilocarpaceae such as *Bapalmuia*, *Calopadia*, and *Sporopodium* (Kalb *et al.*, 2000; Lücking, 2008), the unidentified substances detected in *Tapellaria* are likely xanthenes, but not identified as lichexanthone.

When illuminated with UV light, the thallus exhibited orange–yellow fluorescence of varying intensity (from strong to weak; Fig. S1, panels AT–AY), and in some specimens it showed vivid yellow fluorescence (e.g., KM789; Fig. S1, panels AV–AY), suggesting quantitative variation in the chemical substances. The taxonomic significance of these unidentified compounds remains uncertain and requires further investigation.

Thalli bearing only campylidia are often co-occurring with *Calopadia puiggarii*, which also has only campylidia, making field identification difficult based on morphology. However, even in such cases, *T. nigrata* can be distinguished from *C. puiggarii* by its thicker, whiter thallus that is UV+ weak orange to vivid yellow (Fig. S1, panels AX–AY). No secondary substances were detected in *C. puiggarii* by HPTLC.

Specimens examined. 4: KM734, KM736, KM789. 11: KM774.

Additional specimens examined. [*Tapellaria nigrata* (Müll. Arg.) R. Sant.] JAPAN. AMAMI ISLANDS (Kagoshima Pref.): 5 km NW of Nishinakama village, steep SW slope up to 300 m from Sumiyo River just N of the road, Yamato-son, Oshima-gun, Amami-Oshima Island (28°18'N, 129°22'E), 150–200 m elev., on *Ilex* sp. in dense old-growth, subtropical deciduous forest, 4 February 1995, G. Thor 12868 (TNS); *ibid.*, on a broad-leaf tree, G. Thor 12914 (TNS). [*Tapellaria epiphylla* (Müll. Arg.) R. Sant.] MADEIRA, Casa das Queimadas, 900 m elev., on living leaves of *Laurus azorica*, 29 January 1969, L. Tibell 3710b (TNS). [*Tapellaria phyllophila* (Stirt.) R. Sant.] BRAZIL, São Paulo, Ilha de São Sebastiao; etwa 130 km östlich von São Paulo, Westhang des Morro das Tacas, auf einem Palmwedel, in einem sehr feuchten, dunklen Regenwald, an einem Fluß., 21 April 1978, K. Kalb & G. Plobst s.n. [Kalb, Lich. Neotrop. 37 (TNS)].

****Trichothelium assurgens* (Cooke) Aptroot & Lücking [as *Trichothelium marianense* H. Harada, in Thor *et al.* (2000)]**

Specimens examined. 11: KM757B, KM766E.



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