



## Standard Paper

# *Byssoloma orientale* (Pilocarpaceae, Ascomycota), a new species from East Asia

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### Abstract

A new species, *Byssoloma orientale* K. Miyaz. & Y. Ohmura, is described from East Asia. It is characterized by a minutely farinose light green thallus, apothecia with a well-developed byssoid margin that spreads laterally over the thallus surface, a pure black apothecial disc caused by the presence of an aeruginous pigment in the epithecium, (7–)9–12(–17)-septate cylindrical colourless ascospores, and oblong conidia. This species grows on living leaves as well as on tree bark. The molecular phylogenetic position of *B. orientale* within this genus was inferred based on mtSSU sequences, and the species was shown to be closely related to *B. vanderystii*, which has up to 7-septate ascospores and an absence of aeruginous pigment in the epithecium.

**Keywords:** China; conidia; foliicolous lichen; Japan; mtSSU; subtropics

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### Introduction

*Byssoloma* Trevis. is the type genus of the *Pilocarpaceae* (lichenized *Ascomycota*) and is mainly distributed in tropical and subtropical regions worldwide (Lücking 2008). At present, 58 species are recognized worldwide, growing mainly on living leaves and bark, sometimes on rocks and on the thalli of other lichens (Santesson 1952; James 1971; Vězda 1975, 1986, 1987, 1994; Sérusiaux 1978, 1979, 1996, 1998; Kalb & Vězda 1990, 1994; Coppins *et al.* 1992; Sipman & Aptroot 1992; Fárkas & Vězda 1993; Malcolm & Vězda 1995; Ekman 1996; Kondratyuk 1996; Aptroot *et al.* 1997; Lücking *et al.* 1998, 2002; Thor *et al.* 2000; Sérusiaux *et al.* 2002; Schubert *et al.* 2003; Lücking 2006, 2008, 2013, 2014; Cáceres *et al.* 2013; Aptroot 2014; van den Boom 2016; Elix & McCarthy 2018; Wang *et al.* 2020a). The genus *Byssoloma* is characterized by its byssoid apothecial margin (inconspicuous in some species) and I+ dark blue asci with a tubular structure at the apices ('*Byssoloma* type' in Hafellner (1984)), pyriform or oblong conidia, and mainly transversely 1–7-septate ascospores, sometimes up to 19(–23)-septate in some species (Sérusiaux 1993; Lücking 2008).

During the study of *Byssoloma* specimens housed in the herbarium of the National Museum of Nature and Science (TNS), Tsukuba, Japan, several specimens collected in Japan and China were recognized as an undescribed species. The aim of this study is to describe and illustrate the new species *Byssoloma*

*orientale*, and to discuss the variation within the species and the differences with similar taxa.

### Materials and Methods

#### Morphology and chemistry

Morphological observations and photography were performed using a dissecting microscope (SZX16; Olympus, Tokyo, Japan) and a differential interference contrast microscope (BX51; Olympus) equipped with a digital camera (EOS Kiss X10i; Canon, Tokyo, Japan). Anatomical examinations were carried out using hand-cut sections mounted in GAW (glycerin:ethanol:water = 1:1:1) solution (Asahina 1936). The digital images in Fig. 2A & B were prepared using CombineZP image stacking software developed by Alan Hadley (GNU Public License).

Ascus amyloidity was examined using Lugol's solution (I) and K reaction for fungal tissues was tested using 5% KOH solution. Secondary substances were analyzed using high-performance thin-layer chromatography (HPTLC) following Schumm & Elix (2015). The solvent B' (*n*-hexane:methyl tert-butyl ether:formic acid, 140:72:18) (Culbertson & Johnson 1982) was used for HPTLC. The spot colour was checked under 254 and 366 nm wavelength of UV and visible light, before and after spraying with 10% sulphuric acid on the HPTLC plate and charring at 90 °C for 20 min.

#### DNA extraction, PCR amplification and sequencing

DNA extraction for PCR was performed following a modified method of Izumitsu *et al.* (2012) (see Miyazawa *et al.* 2022). Partial sequences of the small subunit of the mitochondrial

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ribosomal RNA gene (mtSSU) were amplified using the primers mrSSU1 and mrSSU3R (Zoller *et al.* 1999) according to the following protocol. PCR was performed in a 15 µl reaction solution containing 2 µl DNA template, 7.5 µl GenRED PCR Mix Plus (Nippon Gene, Tokyo, Japan), 1.5 µl of each primer (2 pmol µl<sup>-1</sup>), and 2.5 µl of distilled water. PCR conditions followed the method of Wang *et al.* (2020b), using a TaKaRa PCR Thermal Cycler Dice® Touch (TaKaRa, Tokyo, Japan). The PCR products were checked by electrophoresis on a 1.5% agarose gel stained with Midori Green Direct DNA Stain (Nippon Genetics, Tokyo, Japan) and visualized using WSE-5200 Printgraph 2M (ATTO Corporation, Tokyo, Japan). PCR products were purified using the ExoSAP-IT™ PCR Product Cleanup Reagent (Thermo Fisher Scientific, Massachusetts, USA). A volume of 13 µl of PCR products with 2 µl of four times diluted ExoSAP-IT™ was incubated at 37 °C for 15 min, then 80 °C for 15 min.

DNA sequencing was performed either on an Applied Biosystems™ 3500xL Genetic Analyzer (Thermo Fisher Scientific) using the BigDye® Terminator v. 3.1 Cycle Sequencing Kit (Thermo Fisher Scientific) following the manufacturer's instructions, or through a DNA sequencing service provided by Eurofins Genomics in Tokyo, Japan.

### Molecular phylogenetic analyses

The five mtSSU sequences of *Byssoloma orientale* from Japanese material were aligned with the 37 registered sequences of selected taxa in GenBank (Table 1) using MAFFT v. 7 (Katoh *et al.* 2019) with default settings. For the outgroup, the sequences of *Byssolecania hymenocarpa* (Vain.) Kalb *et al.* (MK957152 and MK957159) and *Byssolecania* sp. (MK957170) from GenBank were used to enable a comparison with the phylogenetic tree generated by Wang *et al.* (2020a). The final alignment of 631 sites was used for the molecular phylogenetic analyses, after removing sites with gaps and missing data.

The maximum likelihood (ML) phylogenetic tree was generated with the Tamura 3-parameter model (Tamura 1992) plus gamma distribution which was selected as the best-fitting model. Bootstrap values (≥70%) with 1000 replicates for ML and the neighbour-joining method (NJ) are shown on each branch (Fig. 1). A branch with high bootstrap values (≥90%) in both analyses is indicated with a bold black line. All calculations were conducted in MEGA X (Kumar *et al.* 2018).

### Results and Discussion

Within the Japanese material of the new species *Byssoloma orientale*, there are five variable sites and five gap sites in the 825 aligned sites of mtSSU. The identity among five samples was 99.4–99.9%. Since no discernible differences in morphology were observed, these genetic differences were treated as variations within a species.

The ML phylogenetic tree is shown in Fig. 1. The topology of our phylogenetic tree including the sequences of *B. orientale* and other Japanese *Byssoloma* taxa registered in Miyazawa *et al.* (2022) shows no conflict with that of Wang *et al.* (2020a). The samples of *B. orientale* formed a monophyletic clade with high support values (ML/NJ = 100/100) and sister to *B. vanderystii* Sérus. with high support (ML/NJ = 99/99).

### Taxonomic Treatment

#### *Byssoloma orientale* K. Miyaz. & Y. Ohmura sp. nov.

MycoBank No.: MB 849345

Differs from *B. vanderystii* Sérus. by the pure black disc of the epithecium which has a dense accumulation of aeruginous pigment, and by the longer and (7–)9–12(–17)-septate ascospores (18.3–49.2 × 2.0–4.0 µm).

Type: Japan, Ryukyu Islands (Okinawa Pref.), Takae, Higashi-son, Kunigami-gun (26°39'59"N, 128°14'46"E), on leaf of *Arenga engleri* along a stream, 75 m elev., 15 November 2022, K. Miyazawa 1178 (TNS—holotype TNS-L-132526). GenBank Accession no.: LC773156 (mtSSU).

(Fig. 2)

*Thallus* crustose, irregular in shape, continuous, 20–60 mm across, 5–15 µm thick, minutely farinose, light green. *Photobiont* trebouxoid, ellipsoid, (3.6–)4.2–5.3(–5.5) × (2.3–)2.8–3.8(–4.7) µm (*n* = 30).

*Apothecia* sessile, rounded, 0.4–1.2 mm diam., 85–130 µm tall; margin well developed, densely byssoid, persistent, spreading laterally over thallus surface, 50–300 µm wide, white, sometimes brownish white, composed of loosely woven colourless hyphae; *disc* slightly to strongly convex, pure black; *epithecium* with abundant aeruginous pigment, 1.5–4.5 µm tall; *hymenium* 40–65 µm tall, colourless, with or without aeruginous pigment; *hypothecium* 40–65 µm tall, reddish brown, K+ purple; apothecial base brownish black, K–; *paraphyses* branched and sometimes anastomosing, 0.6–1.7 µm wide, often apically thickened (up to 2.2 µm wide). *Asci* clavate, 8-spored, I+ dark blue with the tubular structure at the apices, tholus amyloid ('*Byssoloma*-type' in Hafellner (1984)), 32–60 × 9–13 µm. *Ascospores* cylindrical, (7–)9–12(–17)-septate, with or without slight constriction at septa, colourless, (18.3–)21.0–35.5(–49.2) × (2.0–)2.4–3.3(–4.0) µm (*n* = 30), 6–16.5 times as long as wide.

*Pycnidia* flask-shaped, 100–140 µm diam., greyish black, covered by whitish loose hyphal tissue. *Conidia* oblong without constriction, aseptate, colourless, (3.7–)4.4–5.1(–5.6) × (0.9–)1.1–1.3(–1.6) µm (*n* = 100), 2.5–5 times as long as wide.

*Chemistry*. No secondary substance was detected with HPTLC.

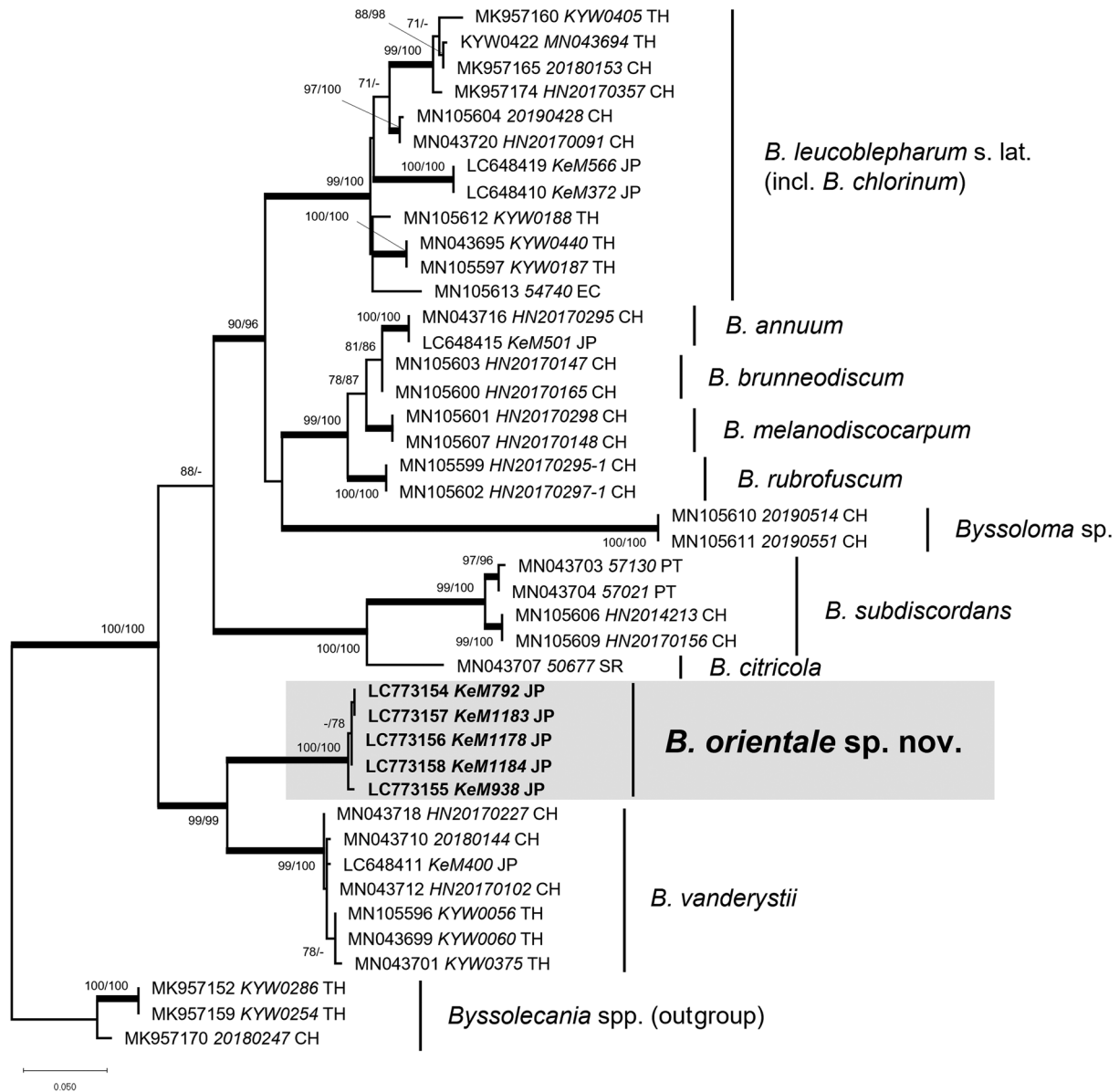
*Etymology*. The epithet '*orientale*' is a Latin adjective that refers to the Far East, where the new species was collected from Japan and China.

*Habitat and distribution*. This species grows on living leaves of *Arenga engleri*, as well as on bark of evergreen broadleaf trees, in conserved rainforests of southern Japan at elevations of 40–300 m and central China at elevations of 400–500 m.

*Notes*. *Byssoloma orientale* is similar to *B. vanderystii* in the byssoid apothecial margin spreading laterally over the thallus surface (Fig. 2A), the 7–17-septate ascospores (Fig. 2G) and the oblong conidia (Fig. 2H), whereas other *Byssoloma* species typically have 3–5-septate ascospores and pyriform conidia. Morphological and molecular phylogenetic analyses in this study show that *B. orientale* is closely related to *B. vanderystii* but that the two species are genetically independent. *Byssoloma*

**Table 1.** Voucher information, GenBank Accession numbers and references for *Byssoloma* and related taxa used in the phylogenetic analysis (Fig. 1). New sequences obtained in this study are in bold.

Taxon	Voucher	GenBank No.	Reference
<i>Byssolecania hymenocarpa</i>	Thailand; W. C. Wang KYW0286 (RAMK-31639)	MK957152	Wang et al. 2020b
	Thailand; W. C. Wang KYW0254 (RAMK-31633)	MK957159	Wang et al. 2020b
<i>Byssolecania</i> sp.	China; W. C. Wang 20180247 (HMAS-L 144266)	MK957170	Wang et al. 2020b
<i>Byssoloma annuum</i>	China; W. C. Wang HN20170295 (HMAS-L 139408)	MN043716	Wang et al. 2020a
	Japan; K. Miyazawa 501 & Y. Ohmura (TNS)	LC648415	Miyazawa et al. 2022
<i>B. brunneodiscum</i>	China; W. C. Wang HN20170147 (HMAS-L 139507)	MN105603	Wang et al. 2020a
	China; W. C. Wang HN20170165 (HMAS-L 139422)	MN105600	Wang et al. 2020a
<i>B. chlorinum</i>	Japan; K. Miyazawa 372 & Y. Ohmura (TNS)	LC648410	Miyazawa et al. 2022
	Japan; K. Miyazawa 566 & Y. Ohmura (TNS)	LC648419	Miyazawa et al. 2022
<i>B. citricola</i>	Suriname; P. v. d. Boom 50677	MN043707	Wang et al. 2020a
<i>B. leucoblepharum</i>	Thailand; W. C. Wang KYW0405 (RAMK-31929)	MK957160	Wang et al. 2020b
	Thailand; W. C. Wang KYW0422 (RAMK-31715)	MN043694	Wang et al. 2020a
	China; W. C. Wang HN20170357 (HMAS-L 139782)	MK957174	Wang et al. 2020a
	China; W. C. Wang 20180153 (HMAS-L 140621)	MK957165	Wang et al. 2020a
	China; W. C. Wang 20190428 (HMAS-L 144223)	MN105604	Wang et al. 2020b
	China; W. C. Wang HN20170091 (HMAS-L 139568)	MN043720	Wang et al. 2020b
	Thailand; W. C. Wang KYW0188 (RAMK-31585)	MN105612	Wang et al. 2020b
	Ecuador; P. v. d. Boom 54740	MN105613	Wang et al. 2020a
	Thailand; W. C. Wang KYW0440 (RAMK-31945)	MN043695	Wang et al. 2020a
	Thailand; W. C. Wang KYW0187 (RAMK-31584)	MN105597	Wang et al. 2020a
<i>B. melanodiscocarpum</i>	China; W. C. Wang HN20170298 (HMAS-L 139744)	MN105601	Wang et al. 2020a
	China; W. C. Wang HN20170148 (HMAS-L 139508)	MN105607	Wang et al. 2020a
<b><i>B. orientale</i></b>	Japan; K. Miyazawa 792, K. Gibu & T. Nada (TNS)	<b>LC773154</b>	<b>This study</b>
	Japan; K. Miyazawa 938, K. Gibu & A. Ohmaki (TNS)	<b>LC773155</b>	<b>This study</b>
	Japan; K. Miyazawa 1178 (TNS-L-132526, holotype)	<b>LC773156</b>	<b>This study</b>
	Japan; K. Miyazawa 1183 (TNS)	<b>LC773157</b>	<b>This study</b>
	Japan; K. Miyazawa 1184 (TNS)	<b>LC773158</b>	<b>This study</b>
<i>B. rubrofuscum</i>	China; W. C. Wang HN20170295-1 (HMAS-L 144214)	MN105599	Wang et al. 2020a
	China; W. C. Wang HN20170297-1 (HMAS-L 144216)	MN105602	Wang et al. 2020a
<i>B. subdiscordans</i>	Portugal; P. v. d. Boom 57130	MN043703	Wang et al. 2020a
	Portugal; P. v. d. Boom 57021	MN043704	Wang et al. 2020a
	China; W. C. Wang HN2014213 (HMAS-L 132508)	MN105606	Wang et al. 2020a
	China; W. C. Wang HN20170156 (HMAS-L 139514)	MN105609	Wang et al. 2020a
<i>B. vanderystii</i>	China; W. C. Wang HN20170227 (HMAS-L 139541)	MN043718	Wang et al. 2020a
	China; W. C. Wang HN20170102 (HMAS-L 139579)	MN043712	Wang et al. 2020a
	Thailand; W. C. Wang KYW0375 (RAMK-31659)	MN043701	Wang et al. 2020a
	Thailand; W. C. Wang KYW0056 (RAMK-31553)	MN105596	Wang et al. 2020a
	Thailand; W. C. Wang KYW0060 (RAMK-31556)	MN043699	Wang et al. 2020a
	China; W. C. Wang 20180144 (HMAS-L 140612)	MN043710	Wang et al. 2020a
	Japan; K. Miyazawa 400 & Y. Ohmura (TNS)	LC648411	Miyazawa et al. 2022
	China; W. C. Wang 20190514 (HMAS-L 144227)	MN105610	Wang et al. 2020a
<i>Byssoloma</i> sp.	China; W. C. Wang 20190551 (HMAS-L 144217)	MN105611	Wang et al. 2020a



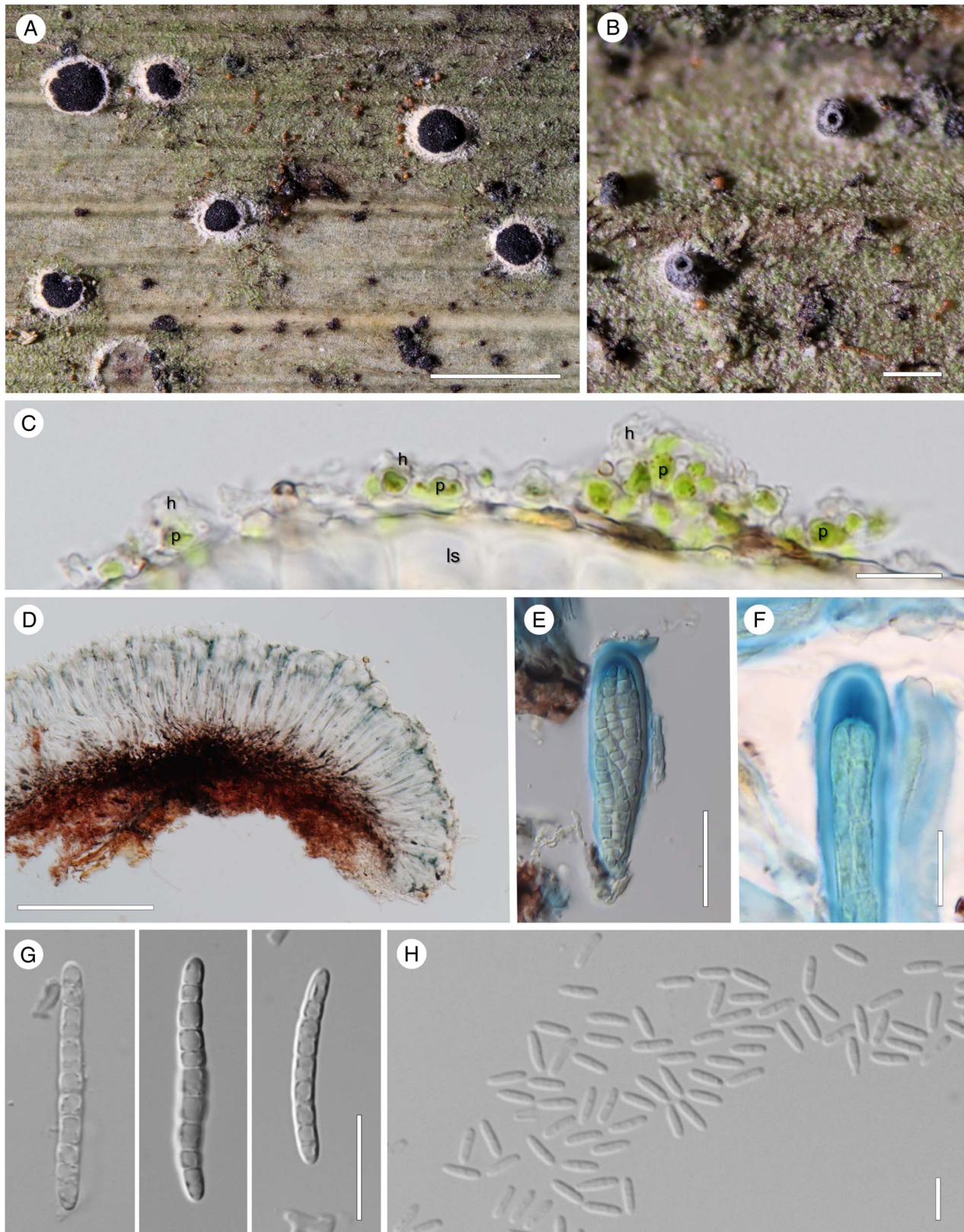
**Figure 1.** Maximum likelihood (ML) tree of mtSSU sequences from selected taxa in *Byssoloma* showing the phylogenetic position of *Byssoloma orientale* collected from Japan (in bold). *Byssolecania* spp. are used as an outgroup. Maximum likelihood and neighbour-joining (NJ) support values ( $\geq 70$ ) are presented for each node (ML/NJ). Branches highly supported ( $\geq 90$ ) by both analyses are indicated with bold black lines. Alphanumeric codes indicate the GenBank number, voucher number and country code (CH = China; EC = Ecuador; JP = Japan; PT = Portugal; SR = Suriname; TH = Thailand).

*orientale* differs from *B. vanderystii* in having longer ascospores with more septa ( $18.3\text{--}49.2 \times 2.0\text{--}4.0 \mu\text{m}$ , (7–)9–12(–17) septa vs  $22\text{--}33 \times 2.0\text{--}3.5 \mu\text{m}$ , 7 septa in *B. vanderystii*) (Sérusiaux 1979; Lücking 2008; Miyazawa *et al.* 2022) and in the accumulation of aeruginous pigment in the epithecium resulting in a pure black disc appearance.

*Byssoloma orientale* resembles *B. kakouettae* (Sérus.) Lücking & Sérus. and *B. laurisilvae* Breuss in having ascospores with more than 7 septa. However, *B. kakouettae*, which is reported from Macaronesia and Western Europe, differs from *B. orientale* in having no apothecial margin extending laterally over the thallus surface, an orange to black disc without a pigmented epithecium, larger ascospores ( $40\text{--}67 \times 2.5\text{--}6 \mu\text{m}$ ) with up to 19(–23) septa, no well-branched paraphyses, and narrow and bifusiform to obpyriform conidia (Sérusiaux 1993; Sérusiaux *et al.* 2002; van den

Boom 2021). *Byssoloma laurisilvae*, reported from the Canary Islands, differs from *B. orientale* in having apothecial margins not extending into the thallus surface, a yellowish to ochre disc without a pigmented epithecium, longer ascospores ( $40\text{--}48\text{--}55 \times (3.5\text{--})4\text{--}5 \mu\text{m}$ ) with 11–16 septa, and bifusiform conidia (Breuss 2013; van den Boom 2021).


*Byssoloma orientale* might be confused with *B. chlorinum* (Vain.) Zahlbr. because both have a light green farinose thallus, a pure black disc and a byssoid apothecial margin which spreads laterally over the thallus surface (Fig. 2A). However, *B. chlorinum* differs in having 3-septate ascospores and pycnidia that produce pyriform conidia (Lücking 2008; Miyazawa *et al.* 2022). The differences between the two species are also supported by the results of the molecular phylogenetic analysis in this study (Fig. 1).



**Figure 2.** *Byssoloma orientale* collected from Japan. A, thallus with apothecia (holotype, TNS). B, pycnidia on thallus (holotype, TNS). C, a vertical section of thallus with photobiont cells (holotype, TNS); h = hyphae of mycobiont, p = photobiont cell, ls = leaf surface. D, section of apothecium (*K. Miyazawa et al. 792, TNS*). E, ascus with ascospores stained by Lugol's solution (*K. Miyazawa et al. 792, TNS*). F, apical structure of ascus stained by Lugol's solution (*K. Miyazawa et al. 792, TNS*). G, ascospores with various numbers of septa (*K. Miyazawa et al. 792, TNS*). H, conidia (holotype, TNS). Scales: A = 1 mm; B = 200  $\mu$ m; C = 10  $\mu$ m; D = 50  $\mu$ m; E & F = 20  $\mu$ m; G = 15  $\mu$ m; H = 5  $\mu$ m. In colour online.

**Additional specimens examined.** **China:** Jianxi Sang Province: Yichun Region, Yifeng Co., Mazhishango, Jiulingshan Mts (Guanshan Nature Reserve), on tree bark along river, 400–500 m elev., 1995, *H. Kashiwadani* 41330 (TNS).—**Japan:** Kyushu, Hyuga Prov. (Miyazaki Pref.): Inohae Valley, Kitagawachi, Kitagou-cho, Nichinan-city (31°43'N, 131°22'E), on twig of *Machilus japonica*, c. 100 m elev., 2021, *K. Miyazawa* 938, *K. Gibu* & *A. Ohmaki* (TNS). Ryukyu Islands (Okinawa Pref.): Takae, Higashi-son, Kunigami-gun (26°39'59"N, 128°14'46"E), on leaf of *Arenga engleri* along a stream, 75 m elev., 2022, *K. Miyazawa* 1177 pr. p. (in collection of *Byssoloma vanderystii*) (TNS); *ibid.*, on trunk of broadleaf tree along a stream, *K. Miyazawa* 1183 (TNS), *K. Miyazawa* 1184 (TNS); Genka, Nago-city (26°36'55–59"N, 128°03'46–49"E), on trunk of broadleaf tree along Genka River, 40 m elev., 2021, *K. Miyazawa* 792, *K. Gibu* & *T. Nada* (TNS); along the mountain path, Mt Katsuu, Nago-city (26°37'53"N, 127°56'14"E), on trunk of evergreen broadleaf tree, 300 m elev., 2023, *K. Miyazawa* 1301 (TNS).

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## References

- Aptroot A** (2014) Two new genera of *Arthoniales* from New Caledonia and the Solomon Islands, with the description of eight further species. *Bryologist* **117**, 282–289.
- Aptroot A, Diederich P, Sérusiaux E and Sipman HJM** (1997) Lichens and lichenicolous fungi from New Guinea. *Bibliotheca Lichenologica* **64**, 1–220.
- Asahina Y** (1936) Mikrochemischer Nachweis der Flechtenstoffe (I). *Journal of Japanese Botany* **12**, 516–525.
- Breuss O** (2013) *Byssoloma laurissilvae* und *Thelotrema lueckingii*, zwei neue Flechtenarten aus Madeira. *Österreichische Zeitschrift für Pilzkunde* **22**, 99–105.
- Breuss O** (2014) Weitere Flechtenfunde aus Madeira. *Stapfia* **101**, 47–51.
- Cáceres MES, Santos MWO, Mendonça CO, Mota DA and Aptroot A** (2013) New lichen species of the genera *Porina* and *Byssoloma* from an urban Atlantic rainforest patch in Sergipe, NE Brazil. *Lichenologist* **45**, 379–382.
- Coppins BJ, James PW and Hawksworth DL** (1992) New species and combinations in the lichen flora of Great Britain and Ireland. *Lichenologist* **24**, 351–369.
- Culberson CF and Johnson A** (1982) Substitution of methyl tert-butyl ether for diethyl ether in the standardized thin-layer chromatographic method for lichen products. *Journal of Chromatography* **238**, 483–487.
- Ekman S** (1996) The corticolous and lignicolous species of *Bacidia* and *Bacidina* in North America. *Opera Botanica* **127**, 1–148.
- Elix JA and McCarthy PM** (2018) Ten new lichen species (*Ascomycota*) from Australia. *Australasian Lichenology* **82**, 20–59.
- Fárkas E and Vězda A** (1993) Five new foliicolous lichen species. *Folia Geobotanica et Phytotaxonomica* **28**, 321–330.
- Hafellner J** (1984) Studien in Richtung einer natürlicheren Gliederung der Sammelfamilien *Lecanoraceae* und *Lecideaceae*. *Beiheft zur Nova Hedwigia* **79**, 241–371.
- Izumitsu K, Hatoh K, Sumita T, Kitade Y, Morita A, Gafur A, Ohta A, Kawai M, Yamanaka T, Neda H, et al.** (2012) Rapid and simple preparation of mushroom DNA directly from colonies and fruiting bodies for PCR. *Mycoscience* **53**, 396–401.
- James PW** (1971) New or interesting British lichens: 1. *Lichenologist* **5**, 114–148.
- Kalb K and Vězda A** (1990) Die Flechtengattung *Byssoloma* in der Neotropis (eine taxonomisch-phytogeographische Studie). *Nova Hedwigia* **51**, 435–451.
- Kalb K and Vězda A** (1994) Beiträge zur Kenntnis der foliicolen Flechten australischer Regenwälder IV. *Bulletin de la Société Linnéenne de Provence* **45**, 235–246.
- Katoh K, Rozwicki J and Yamada KD** (2019) MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics* **20**, 1160–1166.
- Kondratyuk SY** (1996) Four new species of lichenicolous fungi. In Wasser SP (ed.), *Botany and Mycology for the Next Millennium: Collection of Scientific Articles Devoted to the 70th Anniversary of Academician K. M. Sytnik*. Kyiv: M. G. Kholodny Institute of Botany, National Academy of Sciences of Ukraine, pp. 309–315.
- Kumar S, Stecher G, Li M, Knyaz C and Tamura K** (2018) MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Molecular Biology and Evolution* **35**, 1547–1549.
- Lücking R** (2006) Foliicolous lichens from French Guiana (northeastern South America). *Cryptogamie, Mycologie* **27**, 121–147.
- Lücking R** (2008) Foliicolous lichenized fungi. *Flora Neotropica Monograph* **103**, 1–866.
- Lücking R** (2013) *Platygrapha permutans* Nyl. is an earlier name for *Byssoloma rubrireagens* Kalb & Vězda. *Lichenologist* **45**, 579–580.
- Lücking R, Sérusiaux E, Maia LC and Pereira CG** (1998) A revision of the names of foliicolous lichenized fungi published by Batista and co-workers between 1960 and 1975. *Lichenologist* **30**, 121–191.
- Lücking R, Sérusiaux E and Santesson R** (2002) *Ceratopycnidium citricola* is *Byssoloma lueckingii*. *Lichenologist* **34**, 270–272.
- Lumbsch HT, Ahti T, Altermann S, Amo de Paz G, Aptroot A, Arup U, Bárcenas Peña A, Bawingan PA, Benatti MN, Betancourt L, et al.** (2011) One hundred new species of lichenized fungi: a signature of undiscovered global diversity. *Phytotaxa* **18**, 1–127.
- Malcolm WM and Vězda A** (1995) Two new saxicolous species of the lichen genus *Byssoloma* from New Zealand. *Mycotaxon* **55**, 357–362.
- Messuti MI and de la Rosa IN** (2007) *Byssoloma rubromarginatum* (*Pilocarpaceae*: *Ascomycota*), a new corticolous species from *Nothofagus* forests in Argentina. *Mycological Progress* **6**, 235–238.
- Miyazawa K, Ohmura Y and Yamaoka Y** (2022) Noteworthy foliicolous lichens collected from Iriomote Island, southern Japan. *Taiwania* **67**, 155–163.
- Santesson R** (1952) Foliicolous lichens I. A revision of the taxonomy of the obligately foliicolous, lichenized fungi. *Symbolae Botanicae Upsalienses* **12**, 1–590.
- Schubert R, Lücking R, Lumbsch HT** (2003) New species of foliicolous lichens from 'La Amistad' Biosphere Reserve, Costa Rica. *Willdenowia* **33**, 459–465.
- Schumm F and Elix JA** (2015) *Atlas of Images of Thin Layer Chromatograms of Lichen Substances*. Norderstedt: Books on Demand GmbH.
- Sérusiaux E** (1978) Contribution à l'étude des lichens du Kivu (Zaire), du Rwanda et du Burundi. II. Espèces nouvelles de lichens foliicoles. *Lejeunia* **90**, 1–18.
- Sérusiaux E** (1979) Two new foliicolous lichens from tropical Africa. *Lichenologist* **11**, 181–185.
- Sérusiaux E** (1993) New taxa of foliicolous lichens from Western Europe and Macaronesia. *Nordic Journal of Botany* **13**, 447–461.
- Sérusiaux E** (1996) Foliicolous lichens from Madeira, with the description of a new genus and two new species and a world-wide key of foliicolous *Fellhanera*. *Lichenologist* **28**, 197–227.
- Sérusiaux E** (1998) Deux nouvelles espèces de *Byssoloma* Trev. (Lichens, *Pilocarpaceae*) d'Europe occidentale et de Macaronésie. *Cryptogamie, Bryologie, Lichénologie* **19**, 197–209.
- Sérusiaux E, Gómez-Bolea A, Longán A and Lücking R** (2002) *Byssoloma llimonae* sp. nov., from continental Spain, Madeira and the Canary Islands. *Lichenologist* **34**, 183–188.

- Sipman HJM and Aptroot A** (1992) Results of a botanical expedition to Mount Roraima, Guyana. II. Lichens. *Tropical Bryology* **5**, 79–108.
- Tamura K** (1992) Estimation of the number of nucleotide substitutions when there are strong transition-transversion and G + C-content biases. *Molecular Biology and Evolution* **9**, 678–687.
- Thor G, Lücking R and Matsumoto T** (2000) The foliicolous lichens of Japan. *Symbolae Botanicae Upsalienses* **32**, 1–72.
- van den Boom PPG** (2016) Lichens and lichenicolous fungi of the Azores (Portugal), collected on São Miguel and Terceira with the descriptions of seven new species. *Acta Botanica Hungarica* **58**, 199–222.
- van den Boom PPG** (2021) Foliicolous lichens and their lichenicolous fungi in Macaronesia and Atlantic Europe. *Bibliotheca Lichenologica* **111**, 1–197.
- Vězda A** (1975) Foliikole Flechten aus Tanzania (Ost-Afrika). *Folia Geobotanica et Phytotaxonomica* **10**, 383–432.
- Vězda A** (1986) Neue Gattungen der Familie *Lecideaceae* s. lat. (Lichenes). *Folia Geobotanica et Phytotaxonomica* **21**, 199–219.
- Vězda A** (1987) Foliikole Flechten aus Zaire (III). Die Gattung *Byssoloma* Trevisan. *Folia Geobotanica et Phytotaxonomica* **22**, 71–83.
- Vězda A** (1994) Neue foliikole Flechten II. *Nova Hedwigia* **58**, 123–143.
- Wang WC, van den Boom PPG, Sangvichien E and Wei JC** (2020a) A molecular study of the lichen genus *Byssoloma* Trevisan (*Pilocarpaceae*) with descriptions of three new species from China. *Lichenologist* **52**, 387–396.
- Wang WC, Sangvichien E, Wei TZ and Wei JC** (2020b) A molecular phylogeny of *Pilocarpaceae* Zahlbr., including a new species of *Tapellaria* Müll. Arg. and new records of foliicolous lichenized fungi from Thailand. *Lichenologist* **52**, 377–385.
- Zoller S, Scheidegger C and Sperisen C** (1999) PCR primers for the amplification of mitochondrial small subunit ribosomal DNA of lichen-forming ascomycetes. *Lichenologist* **31**, 511–516.