Verrucaria madida (Verrucariaceae, Ascomycota) new to Asia and Russia from the Sakhalin Region

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Abstract. The amphibious freshwater lichen *Verrucaria madida* previously known only from a few scattered, predominantly oceanic localities in Europe, is reported for the first time for Asia and Russia on the basis of morphological, anatomical and molecular data. The species was found on the Crylion Peninsula in southern Sakhalin Island, growing on periodically submerged siliceous rocks in a forest stream. A detailed description of the Russian material is provided, confirming its identity by the unique character of (3)4(5)-spored asci, a green subgelatinous thallus with a characteristic green cortical pigment, prominent perithecia and small ellipsoid ascospores. The characteristics of pycnidia and conidia missing in the protologue are given for the first time. A key morphological finding supporting the phylogenetic relationship with *Wahlenbergiella* is the first documented presence of filiform conidia in *Verrucaria madida*, a trait it shares with *Wahlenbergiella tavaresiae*. The discovery extends the known range of this rare species eastward by over 7000 km and represents a significant range extension from its European localities.

Keywords: *Wahlenbergiella*, aquatic lichens, biogeography, disjunctive distribution, lichenized fungi, new record, pyrenocarpous lichens, range extension, Crylion Peninsula, East Asia.

Verrucaria madida (Verrucariaceae, Ascomycota) — новый для Азии и России вид из Сахалинской области

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Резюме. Впервые для Азии и России на основании морфологических, анатомических и молекулярных данных приводится пресноводный лишайник *Verrucaria madida*, известный ранее лишь по немногим разрозненным, преимущественно океаническим местонахождениям в Европе. Вид был обнаружен на п-ве Крильон на юге о. Сахалин, где произрастал на периодически затопляемых кремнистых скалах в лесном ручье. Приводится подробное описание российского образца, подтверждающее его определение по уникальным признакам: (3)4(5)-споровые сумки, зеленый субжелатинозный таллом с характерным зеленым коровым пигментом, выступающие перитеции и мелкие эллипсоидные аскоспоры. Впервые описаны отсутствующие в протологе характеристики пикнид и конидий. Ключевым морфологическим открытием, подтверждающим филогенетическую связь с *Wahlenbergiella*, является первое документально подтвержденное наличие нитевидных конидий у *Verrucaria madida*, что является общим признаком с *Wahlenbergiella tavaresiae*. Данная находка расширяет известный ареал этого редкого вида к востоку более чем на 7000 км и значительно удалена от его европейских местонахождений.

Ключевые слова: *Wahlenbergiella*, биогеография, водные лишайники, дизъюнктивный ареал, лихенизированные грибы, новая находка, пиренокарповые лишайники, расширение ареала, Восточная Азия, полуостров Крильон.

The genus *Verrucaria* Schrad. (Verrucariaceae) is one of the most diverse and taxonomically challenging groups of lichen-forming fungi, encompassing numerous species specialized for extreme habitats like maritime intertidal zones and freshwater environments (Gueidan *et al*., 2009; Orange, 2013). Among them, freshwater amphibious species colonizing periodically or permanently submerged siliceous rocks in streams represent a highly specialized ecological group, often serving as bioindicators of water purity and hydrological stability (Thüs *et al*., 2014).

Our knowledge of freshwater *Verrucaria* diversity in Sakhalin Island is rather poor since only two *Verrucaria* belonging to the group of terrestrial species occurring on calcareous rocks are known from the Sakhalin Region (Chesnokov, Konoreva, 2022; Kotkova *et al*., 2023).

Verrucaria madida Orange was originally described from France (Orange, 2004). It is

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distinguished by a thin, dark green, subgelatinous thallus, conical involucrellum, small ellipsoid ascospores (9.0–15.0 × 5.5–7.5 μm), and, most notably, (3)4(5)-spored asci, a character considered unique within the genus (Orange, 2004, 2013; Thüs, Schultz, 2009; Krzewicka, 2012). The species has remained to be a rare freshwater lichen in Europe (Orange, 2004, 2013; Krzewicka, Hachułka, 2008; Thüs, Wirth, 2009; Krzewicka, 2012; Tsurykau, 2018). Its populations are known to be sensitive to drought and hydrological changes, leading to its classification as Vulnerable (VU) in Great Britain (Orange *et al.*, 2023) and currently as "R" category (extremely rare species) of the Red list of lichens in Germany (Wirth *et al.*, 2011).

During floristic investigation of lichen diversity of Crylion Cape (southern Sakhalin) we have found *Verrucaria madida* which is a new record to Asia and Russia supported by both molecular data and morphology. We provide a morphological description of our specimen including characteristics of pycnidia and conidia missing in the protologue (Orange, 2004) and available descriptions of the species (Krzewicka, Hachułka, 2008; Thüs, Schultz, 2009; Krzewicka, 2012; Orange, 2013; Matura, 2020; Orange *et al.*, 2023). We discuss differences of *V. madida* from morphologically close species and provide illustrations of diagnostic features, ecology and distribution of the species including the list of known localities.

Material and Methods

The material comprises five specimens collected by the first and second authors in 2023–2024 in Crylion Cape (Sakhalin Is.) and deposited in VLA and ALTB. A review of the natural conditions of the Russian Far East and lichenological studies of the region is given in Davydov *et al.* (2021).

Due to the rarity of the species, the habitat conditions at the site of its collection are of particular interest. The Crylion Peninsula is located at the southwestern tip of Sakhalin Is., Russia. The peninsula is characterized by a rugged coastline with cliffs, rocky capes, and numerous small rivers and streams draining forested low mountains and hills. The climate is cold temperate, humid, and strongly influenced by the Sea of Japan, resulting in high precipitation, frequent fog, and cool summers — conditions that can be described as suboceanic. The bedrock is primarily composed of Cretaceous siliceous sedimentary rocks (sandstones and siltstones), providing suitable acidic substrates for siliceous freshwater lichens. The specific locality was the Vodopadnaya River — a small, clear-water forest stream with a stable flow and periodic submersion of rock ca. 2.3 km long flowing to Aniva Bay. A hydrological dam has been installed in the river for the construction of a water pipeline built by the Japanese in the 30–40^{s} of the twentieth century (Gordeev *et al.*, 2024). Therefore, the river is characterized by a stable flow and permanent sinking of stones. It can be assumed that the water quality here has been quite good for many decades, which has been confirmed by recent studies of the composition of drinking water from the river as part of the restoration of the water supply to the Aniva scientific basecamp (Gordeev *et al.*, 2024).

The specimens were examined using a stereomicroscope (Zeiss Stemi 2000-C) and a compound microscope (Zeiss Axio Lab.A1). Cross-sections of perithecia and thalli were made by hand with razor blade and observed after mounting in water. The reaction of cortex was checked using 10% HCl. Measurements of ascospores and perithecia are presented as range including 85% of the variation, bounded by the smallest and largest observed values, following Westberg (2005). Measurements of other parameters are given as minimum–maximum value observed. The measurements of anatomical structures were made to the nearest 0.5 μm. Number of measurements is given for ascospores and perithecia in parentheses (n). The measurements of the distance from localities were made using Google Earth (www.earth.google.com).

To assess the phylogenetic position of the studied specimen within *Verrucaria* s. l., molecular phylogenetic analyses were performed using internal transcribed spacer (ITS) and large subunit (LSU) nrDNA sequences. These included newly generated sequences from fresh material and additional sequences retrieved from the NCBI GenBank database.

Several perithecia were meticulously cleaned of external debris. DNA extraction, PCR amplification, and sequencing followed the protocols of Davydov and Yakovchenko (2017). The primer pairs ITS1F (Gardes, Bruns, 1993) and LR3 (Vilgalys, Hester, 1990) were used. The PCR cycling protocol consisted of an initial denaturation at 94°C for 5 min; 35 cycles of 95°C for 20 s, 52°C for 40 s, and 72°C for 60 s; and a final extension at 72°C for 7 min. Complementary sequence reads were assembled into contigs using Geneious 6.0 (Biomatters Ltd., New Zealand).

The newly obtained sequences of *Verrucaria madida* were combined with relevant sequences of *Verrucaria* s. l. from GenBank to create two separate datasets: one for nrITS (300 sequences, 709 bp

alignment length) and one for nrLSU (161 sequences, 779 bp alignment length). Both datasets were aligned using the MAFFT algorithm (Katoh *et al*., 2005). The ITS dataset (covering ITS1, 5.8S rDNA, and ITS2) was partitioned by locus for subsequent analyses.

Maximum likelihood (ML) phylogenetic analyses were conducted with RAxML 8.0.26 (Stamatakis, 2014) via the raxmlGUI v.1.3.1 interface (Silvestro, Michalak, 2012). The GTRGAMMA model of nucleotide substitution was applied to each partition. Branch support was evaluated with 1000 rapid bootstrap replicates, and a majority-rule consensus tree was generated.

Results

Phylogenetic placement and confirmation of identity. In phylogenetic analyses based on both ITS (Fig. 1) and LSU (Fig. 2) loci, the sequence obtained from the studied *Verrucaria madida* specimen (PZ094348) clustered with strong statistical support alongside the reference sequence of *V. madida* from Scotland, United Kingdom (identified by A. Orange, GenBank accession number FJ664868). A pairwise distance matrix indicated minimal sequence divergence between the Sakhalin specimen and the Scottish reference: in the ITS region, they differed by a single nucleotide (500/501 bp, 99.8% similarity), and in the LSU region, by four nucleotides (558/562 bp, 99.3% similarity).

With maximum support values, *Verrucaria madida* formed a sister relationship with *Wahlenbergiella tavaresiae* (R. L. Moe) Gueidan et al. (HQ822056 — ITS; HQ822059 — LSU). Together, these two species constitute a well-defined clade nested within a broader clade that includes *W. mucosa* (Ach.) Gueidan et Thüs, the type species of the genus *Wahlenbergiella* Gueidan et Thüs.

Morphology. The material from Russia fits well the protologue (Orange, 2004) and agrees with the available descriptions of the species (Krzewicka, Hachułka, 2008; Thüs, Schultz, 2009; Krzewicka, 2012; Orange, 2013; Matura, 2020; Orange *et al*., 2023) and color illustrations of the species (Thüs, Schultz, 2009; Krzewicka, 2012; Orange, 2013; Nimis, 2026). Here we provide description of the species based on our material from Asian part of Russia (Fig. 3A–E).

Verrucaria madida Orange, 2004, The Lichenologist 36(6): 349. — Type: France, Cantal, west of Murat, 1.8 km west of Fraisse-Haute, 45°06′N, 2°44′E, alt. ca. 1000 m a. s. l., shallowly submerged on sloping rocks in stream in woodland,

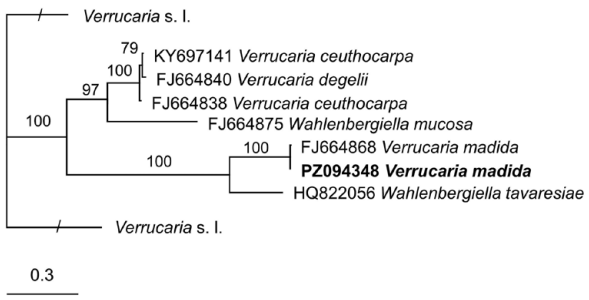

Fig. 1. Phylogenetic placement of the newly sequenced *Verrucaria madida* specimen based on ITS nrDNA analysis. The figure shows a relevant section of the maximum likelihood (RAxML) phylogram of the ITS1-5.8S-ITS2 nrDNA region. Bootstrap support values are shown at nodes. The newly generated sequence is indicated in bold. Branch lengths are proportional to the estimated number of substitutions per site under the GTRGAMMA model. Branches marked with a diagonal line have been shortened to reduce the figure size.

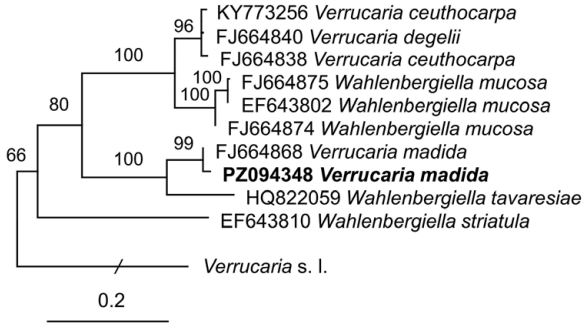

Fig. 2. Phylogenetic placement of the newly sequenced *Verrucaria madida* specimen based on LSU nrDNA analysis. The figure shows a relevant section of the maximum likelihood (RAxML) phylogram of the LSU nrDNA region. Bootstrap support values are shown at nodes. The newly generated sequence is indicated in bold. Branch lengths are proportional to the estimated number of substitutions per site under the GTRGAMMA model. Branches marked with a diagonal line have been shortened to reduce the figure size.

lightly shaded, with *Verrucaria rheitrophila*, 16 V 1990, *A. Orange 7959* (NMW.C90.13.74, holotype; BERN, UPS, isotypes).

Thallus crustose, superficial, thin (30.0–62.5 μm thick), continuous, subgelatinous, without prothallus. Upper surface dark green, smooth, matt to somewhat shiny. Photobiont green alga with maximum diam. 15 μm. Medulla not differentiated. Pseudocortex absent or present, with green pigment in well-lit sites turning brown after HCl. Dark basal layer absent. Perithecia numerous (128–260 per 1 cm^2), prominent, forming moderate elevations 180–420 μm in diam., initially fully covered by thallus partially disappearing in older perithecia to expose the black, rounded apex. Ostiole indistinct to visible as delicate papilla with

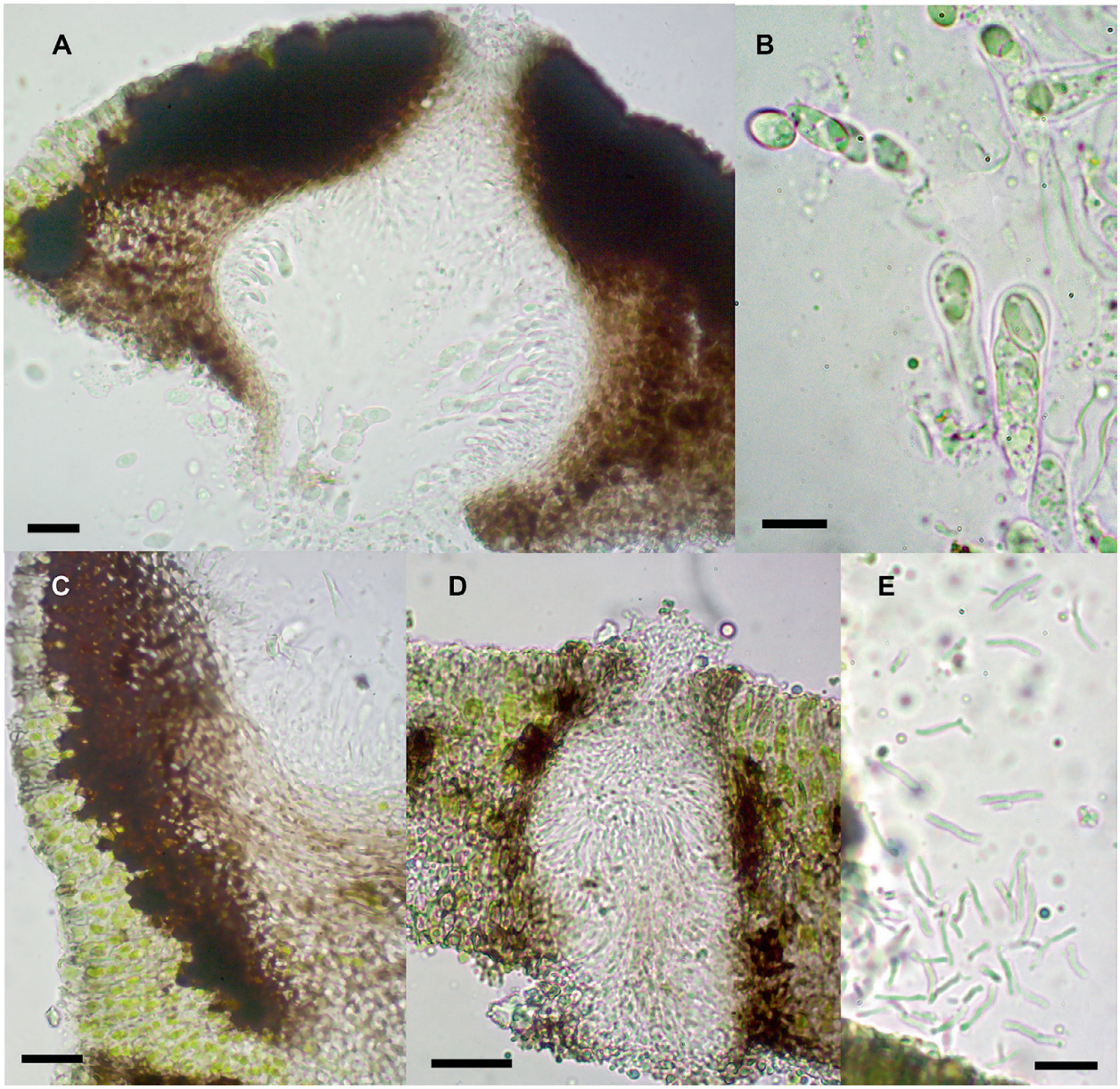

Fig. 3. *Verrucaria madida* (ALTB, *E. Davydov 20219*).
A — section of the perithecium; B — asci with four ascospores; C — uneven upper surface of the involucrellum and green cortical pigment of the thallus; D — section of pycnidia; E — conidia. Scale bars: A, C, D — 20 μm; B, E — 10 μm.

dot at the top. Involucrellum well-developed, conical, reaching to the base and laterally spreading into the thallus, with pale area between involucrellum and lower part of the exciple. Upper surface of involucrellum uneven, serrate due to dark pigmented patches (seen on young ascomata with thalline covering). Exciple brownish at ostiole, sides and more pigmented at the base. Asci 4(5)-spored, clavate, 27–30 × 14–16 μm, ascospores hyaline, ellipsoid to widely-ellipsoid with rounded ends, (9.5)10.0–13.5(15.5) × 5.5–7.0(7.5) μm (n = 53). Pycnidia rarely present, scattered, visible as black dots 40–55 μm wide, conidia filiform, straight or slightly curved, (6.5)9.5–12.0(15.0) × 0.8 μm (n = 25).

Distribution and ecology. Amphibious species occurring on submerged siliceous rocks but also tolerating basic substrates known from Europe and Asia: Great Britain (Wales, Scotland, England), Norway, France, Germany, Belarus, Poland (Orange 2004, 2013; Thüs, Wirth, 2009; Krzewicka, Hachułka, 2008; Krzewicka, 2012; Tsurykau, 2018), and Russia (this paper).

Specimens examined. **Russia, Sakhalin Region:** Sakhalin Is., Anivskii District, Crylion Cape, Aniva Bay, the lower reaches of the Vodopadnaya River, upstream from the old dam surrounded by young alder-spruce forest, mouth of the Vodopadnaya River, rapids on the river, 46°00′45.9″N, 142°09′32.6″E, 25 m a. s. l., siliceous pebble in the water, 20 VIII 2024, *L. Yakovchenko 20236, 20224, 20233, 20524* (GenBank Acc. No. PZ094348), VLA, ALTB;

south of Anastasia Cape near the mouth of the Vodopadnaya River, 46°00′52.9″N, 142°09′37.1″E, 23 m a. s. l., on stones, 22 VIII 2023, *E. Davydov 20219*, ALTB.

Discussion

The Sakhalin specimens match the morphology of the European populations well, though the thallus appears slightly darker, a variation also noted in stressed populations from Germany (Thüs, Wirth, 2009), as well as ascospores insignificantly longer than mentioned in the protologue which is corresponded to the material known from Poland — up to 16 μm long (Krzewicka, Hachułka, 2008).

Verrucaria madida is a unique species within the genus by its (3)4(5)-spored asci (Fig. 3B). However, as they sometimes are difficult to observe the species can be mistaken with morphologically close species. Among the freshwater species the similar *V. capitulata* Harada described from Japan (Harada, 2001, 2012), like *V. madida,* is characterized by green thin continuous gelatinous thalli with perithecia 0.2–0.4 mm diam. with an exposed rounded top and ascospores 9–14 × 5–7 μm, but it is distinguished by perithecia which from the beginning have a more or less thin thalline cover only at the base, by 8-spored asci and by involucrellum that is contiguous with the exciple and the space below the involucrellum and the outer side of the exciple usually obscure. The Japanese freshwater species *V. kiyosumiensis* Harada, known only from *locus classicus* (Harada, 2001, 2012), has similar ascospores (12–16 × 5–7 μm), but differs from *V. madida* by its perithecia which are smaller (0.15–0.25 mm diam.), almost spherical, constricted at base, and lack a thallus cover.

Although morphologically and ecologically somewhat similar, *Verrucaria aquatilis* Mudd is distinguished by its usually darker (black or blackish-green, at least in places with moderate to full sun exposure) thallus, distinctly smaller perithecia (120–240 μm diam.), 8-spored asci, and smaller ascospores, (6.5)7.5–8.2–9.0(10.0) × (4.5)5.5–6.2–6.5(8.0) μm.

An uneven upper surface of involucrellum of *Verrucaria madida* due to the presence of dark pigmented areas (young ascomata) (Fig. 3C) could resemble this in freshwater *Hydropunctaria* species, which differ by the presence of black dots or columns in the thallus and by 8-spored asci, while *V. madida* has no such pigmented inclusions and never has 8-spored asci. *Hydropunctaria rheitrophila* (Zschacke) C. Keller et al. rarely develops thalli without black inclusion (Thüs, in litt.) and can have ascospores of similar size, but differs by its smaller (100–250 μm diam.), more immersed perithecia. *Hydropunctaria scabra* (Vězda) C. Keller et al. has a greenish to blackish thallus, often with a cortex pigment quite similar to this in *V. madida*, but it is distinguished by the presence of a dark basal layer, the absence of a transparent area between exciple and involucrellum, and by its larger, oblong ascospores and shorter conidia (3.5–5.0 × 1.2 μm).

Most of the other freshwater species of *Verrucaria* have larger ascospores (longer than 15 μm) and usually a paler thallus.

The discovery of *Verrucaria madida* on Sakhalin Is. is biogeographically remarkable. It represents a first record of this species in Asia and Russia, extending its known global range eastward by ca. 7000 km from the nearest known locality in East Europe (Belarus). The discovery suggests that *V. madida* may have a circumboreal potential distribution, persisting in rare, ecologically stable habitats that meet its stringent requirements: pure, cold, acidic streams mostly in a humid, suboceanic climate. The discovery of *V. madida* on the Crylion Peninsula marks its first known occurrence in Asia. Its distribution is also remarkably localized; despite searches in nearby streams, including the Anastasia River, which lies only 500 meters distant, the species was found at only one site. This high degree of localization fully corresponds to the known ecology of *V. madida* described in the literature as rare, occurring in more or less fragmented populations often confined to a single stream or a specific reach within it (Orange, 2004; Thüs, Schultz, 2009; Orange *et al*., 2023). Its absence in neighboring, potentially suitable streams may be explained by the species' probable requirement for a very narrow set of microclimatic and hydrological parameters (flow stability, water temperature, light regime, immersion regime) which are met only at few sites and a poor capacity for recolonization of previously occupied sites after extreme conditions (Thüs, Wirth, 2009).

This study contributes to resolving the systematic position of the lichenized fungus described as *Verrucaria madida*. Phylogenetic reconstructions based on analyses of ribosomal nucleotide sequences provide robust evidence that *V. madida* forms a well-supported clade (bootstrap >95%) with members of the marine genus *Wahlenbergiella*, where it is placed as the sister taxon to *W. tavaresiae*. This result offers molecular corroboration for the previously suggested affinity of *V. madida* with the genus *Wahlenbergiella* (Gueidan *et al*., 2011; Orange *et al*., 2023). A key morphological

finding supporting this phylogenetic relationship is the first documented presence of filiform conidia in *V. madida* (Fig. 3D, E), a trait it shares with *W. tavaresiae* and which serves as an independent, diagnostic character aligned with the molecular phylogenetic signal. The resulting phylogram in conjunction with morphological, anatomical, and ecological data raises the question of the optimal delineation of generic boundaries. Three logical taxonomic scenarios can be considered: 1) the inclusion of *V. madida* within the genus *Wahlenbergiella*, necessitating an expansion of its diagnostic characters; 2) the description of a new genus for the clade (*W. tavaresiae* + *V. madida*), united by the synapomorphic presence of filiform conidia; or 3) the segregation of monotypic genera to *W. tavaresiae* and *V. madida* maximally emphasizing their morphological and ecological divergence: for *V. madida* it would be particularly justified by the unique combination of (3)4(5)-spored asci and a freshwater ecology; for *W. tavaresiae* — by its possession of a unique photobiont. In addition, this would result in a more sharply defined diagnosis for *Wahlenbergiella* s. str., effectively reverting it to its original circumscription (Gueidan *et al.*, 2009).

Following the cautious approach advocated by A. Orange (Orange *et al.*, 2023) and the current absence of data for additional marker regions, we refrain from implementing formal nomenclatural changes at this time. Instead, we focus on the continued accumulation of data, particularly molecular sequences, for the *Wahlenbergiella* s. l. group. It is anticipated that a more conclusive taxonomic picture will emerge following a comprehensive revision of this group, especially with the inclusion of material from East Asia and other regions of the world.

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Conflicts of Interest. The authors declare no conflict of interest.

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