



***Veronaea aquatica* sp. nov. (Herpotrichiellaceae, Chaetothyriales, Eurotiomycetes) from submerged bamboo in China**

Sajini K.U. Chandrasiri^{‡§¶¶}, Yu-lin Liu[§], Jun-En Huang[‡], Milan C. Samarakoon[†], Saranyaphat Boonmee^{¶¶}, Mark S. Calabon^{†¶}, Dian-Ming Hu^{‡§#}

‡ College of Bioscience and Bioengineering, Jiangxi Agricultural University, Nanchang 330045, China

§ Jiangxi Environmental Engineering Vocational College, Ganzhou 341002, China

| Center of Excellence in Fungal Research, Mae Fah Luang University, Chiang Rai 57100, Thailand

¶ School of Science, Mae Fah Luang University, Chiang Rai 57100, Thailand

Biotechnology and Technological Research Centre for Edible and Medicinal Fungi, Jiangxi Agricultural University, Nanchang 330045, China

Corresponding author: Dian-Ming Hu (hudianming1@163.com)

Academic editor: Danny Haelewaters

Received: 16 Feb 2021 | Accepted: 26 Aug 2021 | Published: 23 Sep 2021

Citation: Chandrasiri SK.U, Liu Y-I, Huang J-E, Samarakoon MC, Boonmee S, Calabon MS, Hu D-M (2021)

Veronaea aquatica sp. nov. (Herpotrichiellaceae, Chaetothyriales, Eurotiomycetes) from submerged bamboo in China. Biodiversity Data Journal 9: e64505. <https://doi.org/10.3897/BDJ.9.e64505>

Abstract

Background

Freshwater fungi are highly diverse and ecologically important in freshwater systems. In China, more than 1000 species of freshwater fungi are known. Here, we present a brown-spored hyphomycetes that was collected on a submerged decaying bamboo culm in a forest stream in China.

New information

Phylogenetic analyses of combined LSU, ITS and TUB2 sequences confirm the placement of our new strain in *Veronaea* (Herpotrichiellaceae), sister to *V. japonica*. *Veronaea aquatica* sp. nov. differs from related taxa *V. compacta* and *V. japonica* in having longer

conidiophores and cylindrical to pyriform or subclavate conidia with 0–2 septa. *Veronaea aquatica* also has darker brown hyphae compared to *V. japonica*. A morphological description and detailed illustrations of *V. aquatica* are provided.

Keywords

one new taxon, hyphomycetes, molecular phylogeny, saprobe, taxonomy, freshwater fungi

Introduction

Freshwater fungi are those taxa that grow in freshwater bodies for the entirety or only part of their life cycle (Goh and Hyde 1996, Dhanasekaran et al. 2006). They are "recyclers" in that they decompose dead organic matter (Harms et al. 2011, Iskandar et al. 2011, Anastasi et al. 2013, Tsui et al. 2016, Grossart et al. 2019, Gulis et al. 2019). Freshwater fungi can be found in living (plants and animals) and non-living (decaying wood and leaves) substrates (Choi et al. 2019, Grossart et al. 2019, Tsui et al. 2000). They are accommodated in eight phyla: Aphidiomycota, Ascomycota, Basidiomycota, Blastocladiomycota, Chytridiomycota, Monoblepharomycota, Mortierellomycota and Rozellomycota (Zhang et al. 2012, Bao et al. 2019, Calabon et al. 2020, Hyde et al. 2021). The majority of described freshwater fungi are members of Dothideomycetes and Sordariomycetes; however, several taxa have been recorded from Eurotiomycetes (Liu et al. 2015, Luo et al. 2016, Luo et al. 2018b, Luo et al. 2019, Dong et al. 2018, Dong et al. 2020a, Wang et al. 2019).

Coreomyces chinensis and *C. minor* (Laboulbeniaceae, Laboulbeniales, Laboulbeniomycetes) were the first freshwater taxa reported from China (Thaxter 1931, Hu et al. 2013). During the past two decades, studies have used combined morphological and molecular data to describe freshwater taxa from China (Tsui et al. 2000, Li et al. 2017, Luo et al. 2017, Luo et al. 2018a, Luo et al. 2018b, Luo et al. 2019, Su et al. 2018, Bao et al. 2020, Lu et al. 2020). Hu et al. (2013) reviewed the biodiversity of freshwater fungi in China and reported 782 species. Since Hu et al. (2013), this number has increased to more than 1,000 (Luo et al. 2019, Bao et al. 2020, Dong et al. 2020a, Dong et al. 2020b).

Veronaea (Herpotrichiellaceae, Chaetothyriales) was introduced by Cifferi and Montemartini (1958) and is typified by *V. botryosa*, which was isolated from a decomposed rachis of a palm (Arecaceae) in Italy (Arzanlou et al. 2007). Twenty species have been described in *Veronaea*, but sequences are only available for four of them (*V. botryosa*, *V. compacta*, *V. constricta* and *V. japonica*) (Wijayawardene et al. 2020). Only the asexual morphs of *Veronaea* are presently known and they are related to black yeasts (Vicente et al. 2008, Badali et al. 2013, Bonifaz et al. 2013, Dögen et al. 2013).

Species of *Veronaea* are characterised by polyblastic, terminally integrated, cylindrical, solitary, pale brown conidiogenous cells and smooth-walled, septate, cylindrical to pyriform pale brown to brown conidia (Arzanlou et al. 2007, Vicente et al. 2008, Badali et al. 2013,

Dögen et al. 2013). There are three records of *Veronaea* species from freshwater habitats, all on submerged wood. These are *V. botryosa* from Thailand (Dong et al. 2018), *V. coprophila* from the Republic of Seychelles (Hyde and Goh 1998) and *V. oblongispora* from Hong Kong (Tsui 1999). Since most *Veronaea* species lack molecular data, recollecting and sequencing are essential to investigate the phylogenetic relationships amongst species.

In the present study, we introduce *Veronaea aquatica* sp. nov., a freshwater species from submerged decaying bamboo culms collected in a stream in Jiangxi Province, China. A morphological description, illustrations and a multi-loci phylogeny are presented. The new species is compared with related taxa.

Materials and methods

Sample collection and morphological examination

Submerged decaying bamboo culms were collected from a small forest stream in Lushan Mountains, Jiangxi Province, China in December 2017. Samples were incubated at room temperature for two weeks. Microscopic observation was conducted following Hu et al. (2010) and fungal characters were documented using a microscope. The holotype and ex-type living culture were deposited in the Herbarium of Fungi, Jiangxi Agricultural University (HFJAU), Nanchang-China and Jiangxi Agricultural University Culture Collection (JAUCC), respectively.

Fungal isolation

Single conidia were isolated in the potato dextrose agar (PDA) plate, following the method of Zhang et al. (2013). Germinated conidia were transferred to PDA plates and incubated at 16°C. Colonial characteristics were described after obtaining the pure cultures.

DNA extraction and PCR amplification

Mycelia were scraped off from six week-old colonies grown on PDA and transferred into a 1.5 ml centrifuge tube, followed by grinding in liquid nitrogen. DNA was extracted from the ground mycelium using the EZ gene TM fungal gDNA kit (GD2416) according to the manufacturer's instructions. The partial large subunit rDNA (LSU), internal transcribed spacer (ITS) and partial beta-tubulin (TUB2) were amplified using primer pairs LR0R/LR5, ITS1/ITS4 and T1/Bt2b, respectively (Vilgalys and Hester 1990, White et al. 1990, Hopple 1994, Glass and Donaldson 1995, Rehner and Samuels 1995, O'Donnell and Cigelnik 1997). The amplifications were performed according to Hu et al. (2012) as follows: initial denaturation at 94°C for 3 minutes; followed by 35 cycles of denaturation at 94°C for 30 seconds, annealing at 56°C for 50 seconds, elongation at 72°C for 1 minute; and a final extension at 72°C for 10 minutes. Purification of PCR products and sequencing, using the same primers, were outsourced to Tsingke Biological Technology Company (Beijing, China).

Sequencing and sequence alignment

Consensus sequences were obtained using Lasergene SeqMan Pro v. 7. BLASTn searches were performed to identify highly similar sequences in NCBI GenBank. Other sequences, used in the phylogenetic analyses (Table 1), were downloaded from NCBI GenBank, based on recently-published data (Dong et al. 2018, Wijayawardene et al. 2020). Single-locus alignments were generated with MAFFT v. 7.036 (<http://mafft.cbrc.jp/alignment/server>; Katoh et al. 2019). Alignments were further improved manually when necessary in BioEdit v. 7.0.5.2 (Hall 1999). Ambiguous bases were removed using TrimAI v. 1.3 and the gappyout option (Capella-Gutiérrez et al. 2009).

Table 1.

Table of taxa used in this study and GenBank accession numbers of DNA sequences. The new strain is indicated in bold and type strains are indicated with an asterisk (*).

Name	Strain Number	Gene bank accession number		
		LSU	ITS	TUB2
<i>Aculeata aquatica</i> *	MFLUCC 11–0529	MG922575	MG922571	-
<i>Brycekendrickomyces acaciae</i>	CBS 124104	NG_058633	NR_132828	-
<i>Byssochlamys lagunculariae</i> *	CBS 100.11	NG_058631	NR_144910	AY753354
<i>Capronia pilosella</i>	AFTOL-ID 657	DQ823099	DQ826737	-
<i>Cladophialophora carriponii</i> *	CBS 160.54	NG_055741	NR_121267	EU137201
<i>Exophiala aquamarina</i>	FMR 3998	KU705846	KU705829	-
<i>E. aquamarina</i> *	CBS 119918	-	NR_111626	JN112434
<i>E. brunnea</i>	CBS 587.66	MH870554	MH858890	JN112442
<i>E. equina</i>	CBS 116009	KF928497	KF928433	KF928561
<i>E. equina</i> *	CBS 119.23	-	NR_111627	JN112462
<i>E. jeanselmei</i> *	CBS 507.90	MH873915	MH862234	EF551501
<i>E. nigra</i> *	CBS 535.94	NG_059253	NR_154974	-
<i>E. pisciphila</i>	AFTOL-ID 669	DQ823101	-	-
<i>E. psychrophila</i> *	CBS 191.87	MH873750	MH862061	JN112497
<i>E. salmonis</i> *	CBS 157.67	AY213702	NR_121270	JN112499
<i>E. xenobiotica</i>	CBS 115831	FJ358246	-	-
<i>E. xenobiotica</i> *	CBS 118157	-	NR_111203	DQ182571
<i>Fonsecaea monophora</i>	CBS 102243	FJ358247	EU938579	EU938542
<i>F. pedrosoi</i>	BMU 07690	KJ930165	KJ701014	KM658155

Name	Strain Number	Gene bank accession number		
		LSU	ITS	TUB2
<i>F. pedrosoi</i> *	CBS 271.37	-	NR_130652	-
<i>Marinophialophora garethjonesii</i> *	MFLUCC 16–1449	-	NR_164246	-
<i>Melanoctona tectonae</i> *	MFLUCC 12–0389	KX258779	KX258778	-
<i>Metulocladosporiella musae</i>	CBS 113863	DQ008162	DQ008138	-
<i>Paecilomyces fulvus</i> *	CBS 146.48	NG_063990	NR_103603	FJ389986
<i>Phialophora verrucosa</i>	BMU 07618	KJ930128	KJ700977	KM658080
<i>P. verrucosa</i> *	CBS 140325	-	NR_146242	-
<i>Rhinocladiella atrovirens</i>	CBS 317.33	MH866906	MH855447	-
<i>Thysanorea lotorum</i> *	CBS 235.78	MH872892	MH861130	-
<i>T. papuana</i> *	CBS 212.96	EU041871	EU041814	-
<i>T. rousseliana</i>	CBS 126086	MH875246	MH863784	-
<i>Veronaea aquatica</i>	JAUCC2549	MW046893	MW046892	MW248394
<i>V. botryosa</i>	CBS 102593	KF928493	KF928429	KF928557
<i>V. botryosa</i>	CBS 122236	KF928491	KF928427	KF928555
<i>V. botryosa</i>	MFLUCC 11–0072	MG922574	EU041817	-
<i>V. botryosa</i> *	CBS 254.57	EU041873	EU041816	JN112505
<i>V. compacta</i> *	CBS 268.75	EU041876	EU041818	-
<i>V. constricta</i>	CBS 572.90	MH873920	EU041819	-
<i>V. japonica</i>	CBS 776.84	NG_057789	EU041821	-
<i>V. japonica</i> *	CBS 776.83	EU041875	EU041820	-
Veronaea sp.	DS253	-	MK808629	-
Veronaea sp.	E6917h	-	HM992819	-
Veronaea sp.	HB	-	KR909168	-
Veronaea sp.	NWHC 24266–02–03–03	-	KX148688	-
Veronaea sp.	NWHC 24266–02–04–01	-	KX148689	-

Phylogenetic analysis

Phylogenetic analyses were performed for both individual (LSU, ITS, TUB2) and combined (LSU-ITS-TUB2) datasets. Maximum Likelihood (ML) analyses were performed in the CIPRES Science Gateway v. 3.3 using the RAxML-HPC2 on XSEDE tool (Stamatakis et al. 2008, Miller et al. 2010, Stamatakis 2014). For each single-locus sequence alignment,

GTRGAMMA + I was selected as the best-fit model in MrModeltest 2.3 (Nylander 2004). Bayesian (BYPP) analysis was performed using MrBayes v. 3.1.2. for the combined dataset (Ronquist and Huelsenbeck 2003). Six simultaneous Markov Chains were run for 2,000,000 generations and trees were sampled every 100th generation. The first 2,000 trees were discarded as burn-in; the remaining 18,000 trees were used for calculating posterior probabilities (PP) (Cai et al. 2006). Phylogenograms were visualised using FigTree v. 1.4.0 (<http://tree.bio.ed.ac.uk/software/figtree/>). Modification of the final phylogenetic tree was done in Microsoft PowerPoint.

Taxon treatment

Veronaea aquatica Chandrasiri, J.E. Huang & D.M. Hu, sp. nov.

- IndexFungorum [IF558295](#)
- Facesoffungi [FoF 05435](#)

Materials

Holotype:

- a. kingdom: Fungi; phylum: Ascomycota; class: Eurotiomycetes; order: Chaetothyriales; family: Herpotrichiellaceae; taxonRank: species; genus: *Veronaea*; specificEpithet: *aquatica*; country: China; stateProvince: Jiangxi Province; locality: Lushan Mountains; verbatimElevation: 675; verbatimLatitude: 29°55'72"N; verbatimLongitude: 115°94'86"E; year: 2017; month: December; day: 31; habitat: stream in small forest, on submerged decaying bamboo culms; fieldNotes: Freshwater; recordedBy: J.E. Huang; identifiedBy: Sajini K. U. Chandrasiri; institutionID: HFJAU 0739; institutionCode: Herbarium of Fungi, Jiangxi Agricultural University; collectionCode: HJ054

Other material:

- a. type: ex-type living culture; collectionID: JAUCC2549; collectionCode: Jiangxi Agricultural University Culture Collection

Description

Saprobic on submerged decaying bamboo (Fig. 2). **Sexual morph:** Undetermined. **Asexual morph:** Hyphomycetous. Colonies effuse, spreading very widely, brown to dark brown, white hairy. Mycelium in the wood immersed or partly superficial, hyphae subhyaline to pale olivaceous, smooth, 1.5–3 µm wide. Conidiophores erect, the lower part is usually straight and the upper half is usually flexuose, usually loosely branched, macronematous, monomenatous, sometimes geniculate, smooth-walled, near the apex pale brown, dark brown at the middle and base, 2.5–4 µm wide and up to 280 µm long. Conidiogenous cells terminally integrated, polyblastic, occasionally intercalary, cylindrical, (3–)10–30 × 2–3.5 µm ($\bar{x} = 16.5 \times 2.5$ µm, n = 30), variable in length, pale brown, later often becoming septate, fertile part subhyaline, wide at the basal part, rachis with crowded, flat to slightly prominent, faintly pigmented; scars flat, slightly pigmented, not thickened, about 0.65 µm diam. Conidia solitary, smooth, cylindrical to subpyriform and some subclavate, 6–11(–12) × 2.5–3.5(–4.0) µm ($\bar{x} = 8.7 \times 3.1$ µm, n =

50), pale brown, most medially 1-spetate, rarely 0 or 2-septate, often constricted at the septum and the colour septum middle brown and the conidia with a round apex and truncate base; with a faintly darkened, unthickened hilum, about 0.5–0.9 µm diam.

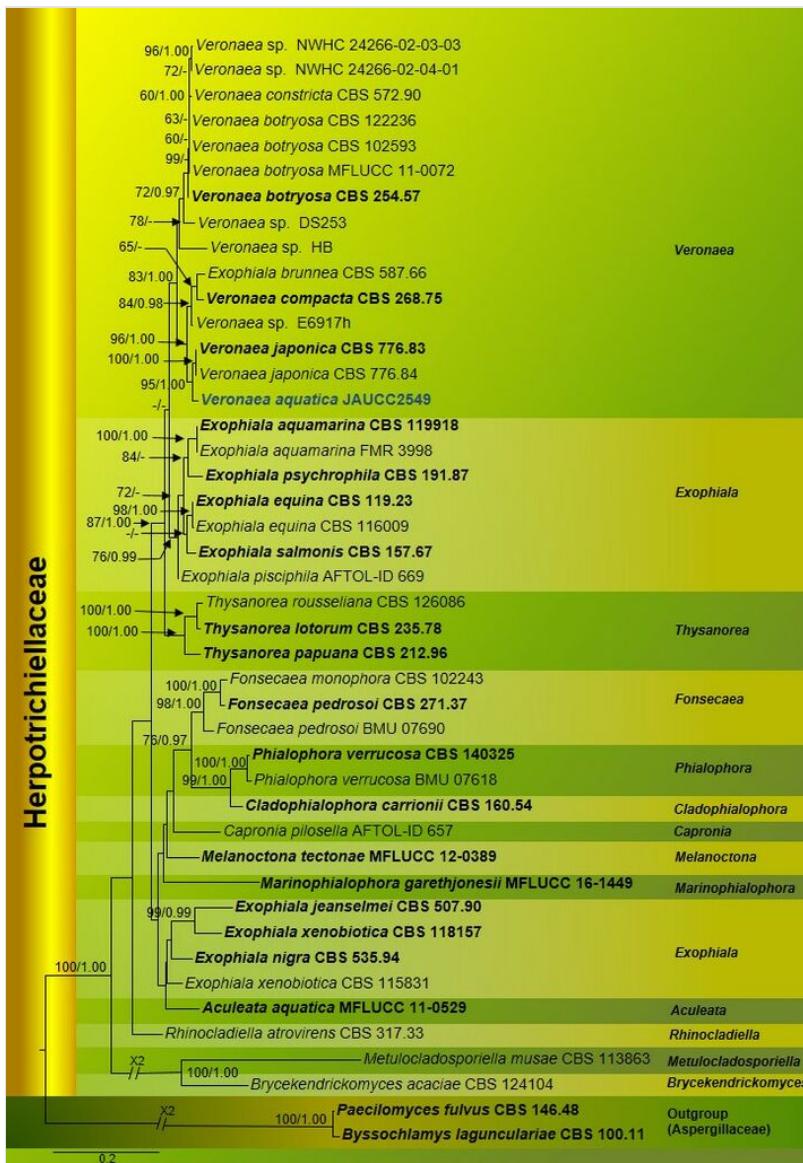


Figure 1. doi:

Phylogenetic tree generated from RAxML analysis of a combined ITS, LSU and TUB2 dataset. ML bootstrap (BS) support values $\geq 60\%$ and Bayesian PP ≥ 0.95 are indicated above branches as MLBS/PP. *Paecilomyces fulvus* (CBS 146.48) and *Byssochlamys lagunculariae* (CBS 100.11) serve as outgroup taxa. Type strains are highlighted in bold; the new species is shown in blue bold.

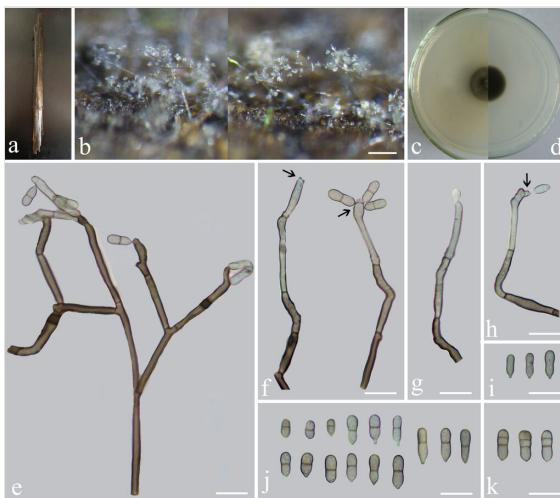


Figure 2. [doi](#)

Veronaea aquatica (HFJAU0739, holotype) **a** Submerged bamboo; **b** Colonies on submerged bamboo culm; **c, d** Colony on PDA from above and below; **e–h** Conidiophores, conidiogenous cells and conidia; note the scars (arrowed in e, d); **i–k** Conidia. Scale bars: **b** = 100 µm, **e–k** = 10 µm.

Culture characteristics: Conidia germinating on PDA within 24 hrs. Colonies growing on PDA, circular, reaching 10–20 mm diam. after 2–3 weeks at 28°C, *from above* flat, dense, olivaceous to medium brown, lightly raised at centre, surface rough; *from below* medium to dark brown.

Etymology: Referring to the aquatic habitat.

Notes

Veronaea aquatica is morphologically most similar to *V. japonica* and *V. botryosa*. However, *V. aquatica* has 0–2-septate conidia, whereas those of *V. japonica* are 0–1-septate. In addition, the conidiophores of both *V. compacta* (up to 50 µm) and *V. japonica* (up to 65 µm) are shorter compared to *V. aquatica* (280 µm). *Veronaea aquatica* has conidiogenous cells that are 10–30 µm in length, while those of *V. botryosa* are 100 µm long. In addition, the conidiophores of *V. aquatica* are 280 µm long; they are shorter in *V. botryosa* (73–124 µm) (Fig. 2).

Veronaea aquatica shares the highest identity with *V. japonica* (CBS 776.83) in its LSU (99.65%) and ITS (98.08%). In its TUB2, it shares 89.61% identity with *Exophiala brunneae* (CBS 587.66). However, not enough TUB2 data are available to make conclusions about relationships, based on this gene region. Our tree topology (Fig. 1) is similar to Wang et al. (2019), although these authors did not include *E. brunneae* (CBS 587.66) in their analysis. In our study, *E. brunneae* (CBS 587.66) is clustered with *V. compacta* (CBS 268.75) with poor support (Fig. 1).

Analysis

Phylogenetic analyses

The final aligned concatenated dataset (LSU, ITS, TUB2) was comprised of 44 strains including two outgroup taxa, *Byssochlamys lagunculariae* (CBS 100.11) and *Paecilomyces fulvus* (CBS 146.48) (Aspergillaceae) and 734 distinct alignment patterns, with 23.30% of undetermined characters or gaps. The best-scoring RAxML tree (-lnL = 12666.921) is shown in Fig. 1. Tree topologies from ML and Bayesian analyses were congruent; no significant differences were observed at the generic level. *Veronaea aquatica* (JAUCC2549) was retrieved as sister to *V. japonica* with high support (MLBS = 95%, PP = 1.00).

Discussion

The family Herpotrichiellaceae (Eurotiomycetes) was introduced by Munk (1953) and currently includes 16 genera (Wijayawardene et al. 2020). The anamorph–teleomorph relationships within Herpotrichiellaceae were described by Müller et al. (1987) and Untereiner et al. (1995). Most anamorphs are dematiaceous and opportunistic fungi (*Capronia*, *Cladophialophora*, *Exophiala*, *Veronaea*) (Untereiner et al. 1995, Crous et al. 2007).

Species of *Veronaea* can be found on wood submerged in freshwater, in soil and on different terrestrial hosts. Fungi in the genus are saprobes (*V. coprophila*, *V. japonica*) or pathogens of plants (*V. ficina*, *V. filicina*) (Kharwar and Singh 2004, Arzanlou et al. 2007, Dong et al. 2018). *Veronaea botryosa* is a human pathogen, which causes phaeohyphomycosis disease (Kondo et al. 2007, Sang et al. 2011, Bonifaz et al. 2013). *Veronaea* is widely distributed across Australia, Brazil, China, Egypt, India, New Zealand, North America, South Africa and the UK (Dingley 1972, Papendrof 1976, Morgan-Jones 1982, Moustafa and Abdul-Wahid 1990, Kharwar and Singh 2004, Soares and Barreto 2008, Pan et al. 2009, Pan et al. 2012, Pan and Zhang 2010).

This paper introduces a new species of *Veronaea*, bringing the number of species to twenty-one, based on morphology and molecular phylogenetic analyses. We compared the new species to the most related species in Table 2. Several unidentified *Veronaea* species have also been isolated, such as *Veronaea* sp. DS253 (from root of *Bouteloua dactyloides*), *Veronaea* sp. E6917h (from *Socratea exorrhiza*), *Veronaea* sp. HB (from grapevine), *Veronaea* sp. [NWHC 24266–02–03–03; NWHC 24266–02–04–01 (from snake)] (Fig. 1). These taxa are needed to be studied and identified in future research. The Kingdom of Fungi is an incredibly diverse group, with many taxa awaiting discoveries—including those from freshwater habitats. Exploring new fungal taxa, understanding their ecology and generating molecular phylogenetic data will promote fungal conservation (Cheek et al. 2020).

Table 2.

Synopsis of related species

Name	Conidiophore	Conidiogenous cell	Conidia	Conidial septation	References
<i>Exophiala brunnea</i>	Branched 8–350 µm long	Occasionally intercalary, variable in shape, flask-shaped, ovoid, oblong, symmetrical or curved, fimbriate	Cylindrical to pyriform, proximally tapered and usually slightly stipitate 4.5–10 × 2–3 µm	aseptate	Papendorf (1969)
<i>Veronaea aquatica</i>	Loosely branched, sometimes geniculate, up to 280 × 2.4–4 µm	Occasionally intercalary, scars flat, rachis with crowded, flat to slightly	Cylindrical to pyriform, some subclavate, rounded at the apex 6.3–11(–11.8) × 2.4–3.7(–4.0) µm	0–1(–2)	This study
<i>Veronaea botryosa</i>	Unbranched 73–124.5 × 2–3 µm	Integrated, occasionally interspersed, flat to slightly prominent denticles, rachis with crowded	Ellipsoidal or fusiform, rounded at the apex (3–)6.5–8.5(–12) × (1.5–)2–2.5(–3) µm	1(–2)	Bonifaz et al. (2013), Dong et al. (2018)
<i>V. compacta</i>	Unbranched or branched at acute angles, rarely exceeding 50 µm	Occasionally intercalary, integrated, hardly prominent denticles, scars flat	Ellipsoidal to ovoid or oblong to subcylindrical, rounded at the apex, acropleurogenous (4–)6–7(–9) × 2–3 µm	0–1(–2)	Papendrof (1976)
<i>V. japonica</i>	Unbranched or occasionally branched 65 × 2–3 µm	Occasionally intercalary, hardly prominent denticles, scars flat, slightly pigmented	Ellipsoidal to ovoid, rounded at the apex (6–)7–8(–10) × 2–2.5(–4) µm	(0–)1	Arzanlou et al. (2007)
<i>V. oblongispora</i>	320 × 3–5 µm	Integrated, polyblastic, bearing thin, flat conidial scars	Oblong, obtuse at the apex 7–8 × 4–5 µm	aseptate	Morgan-Jones 1982

Acknowledgements

We would like to thank the National Natural Science Foundation of China (NSFC 32070023), the Key Project of Jiangxi Provincial Department of Science and Technology Youth Fund (20192ACBL21017), the Key Research and Development Plan of Jiangxi Province (20161BBF60078), the Natural Science Foundation of Education Department of Jiangxi Province (GJJ190168) and Thailand Research Fund (RDG6130001) for financial support. Saranyaphat Boonmee would like to thank the Mae Fah Luang University Fund (No. 631C15001). K.S.U. Chandrasiri would like to express her profound gratitude to S.M.B.C. Samarakoon, N. Wijesinghe and W.A.E. Yasanthika for their valuable support.

MS Calabon is grateful to the Mushroom Research Foundation and Department of Science and Technology - Science Education Institute (Philippines).

References

- Anastasi A, Tigini V, Varese GC (2013) The bioremediation potential of different ecophysiological groups of fungi. *Soil Biology* 32: 29-49. https://doi.org/10.1007/978-3-642-33811-3_2
- Arzanlou M, Groenewald JZ, Gams W, Braun U, Shin H-D, Crous PW (2007) Phylogenetic and morphotaxonomic revision of *Ramichloridium* and allied genera. *Studies in Mycology* 58: 57-93. <https://doi.org/10.3114/sim.2007.58.03>
- Badali H, Yazdanparast SA, Bonifaz A, Mousavi B, De Hoog GS, Klaassen CH, Meis JF (2013) *Veronaea botryosa*: molecular identification with amplified fragment length polymorphism (AFLP) and in vitro antifungal susceptibility. *Mycopathologia* 175: 505-513. <https://doi.org/10.1007/s11046-013-9631-6>
- Bao DF, Wanasinghe DN, Luo ZL, Mortimer PE, Kumar V, Su HY, Hyde KD (2019) *Murispora aquatica* sp. nov. and *Murispora fagicola*, a new record from freshwater habitat in China. *Phytotaxa* 416: 1-13. <https://doi.org/10.11646/phytotaxa.416.1.1>
- Bao DF, Mckenzie EH, Bhat DJ, Hyde KD, Luo ZL, Shen HW, Su HY (2020) *Acrogenospora* (*Acrogenosporaceae*, *Minutisphaerales*) appears to be a very diverse genus. *Frontiers in Microbiology* 11: 1606. <https://doi.org/10.3389/fmicb.2020.01606>
- Bonifaz A, Davoudi MM, De Hoog GS, Padilla-Desgarennes C, Vzquez-Gonzlez D, Navarrete G, Meis JF, Badali H (2013) Severe disseminated phaeohyphomycosis in an immunocompetent patient caused by *Veronaea botryosa*. *Mycopathologia* 175: 497-503. <https://doi.org/10.1007/s11046-013-9632-5>
- Cai L, Jeewon R, Hyde KD (2006) Phylogenetic investigations of Sordariaceae based on multiple gene sequences and morphology. *Mycological Research* 110: 137-150. <https://doi.org/10.1016/j.mycres.2005.09.014>
- Calabon MS, Hyde KD, Jones EB, Chandrasiri S, Dong W, Fryar SC, Yang J, Luo ZL, Lu YZ, Bao DF, Boonmee S (2020) www.freshwaterfungi.org, an online platform for the taxonomic classification of freshwater fungi. *Asian Journal of Mycology* 3 (1): 419-44. <https://doi.org/10.5943/ajom/3/1/14>
- Capella-Gutiérrez S, Silla-Martínez JM, Gabaldón T (2009) TrimAl: a tool for automated alignment trimming in large-scale phylogenetic analyses. *Bioinformatics* 25 (15): 1972-1973. <https://doi.org/10.1093/bioinformatics/btp348>
- Cheek M, Nic Lughadha E, Kirk P, Lindon H, Carretero J, Looney B, Douglas B, Haelewaters D, Gaya E, Llewellyn T, Ainsworth AM (2020) New scientific discoveries: Plants and fungi. *Plants, People, Planet* 2 (5): 371-388. <https://doi.org/10.1002/ppp3.10148>
- Choi YJ, Lee SH, Nguyen TT, Nam B, Lee HB (2019) Characterization of *Achlya americana* and *A. bisexualis* (Saprolegniales, Oomycota) isolated from freshwater environments in Korea. *Mycobiology* 47: 135-142. <https://doi.org/10.1080/12298093.2018.1551855>
- Cifferi R, Montemartini A (1958) Sui generi *Muchmoria* Sacc e *Veronaea* n. gen. *Atti. 1st. Bot. Univ. Lab. Crittogram. Pavia* (15)67-72.

- Crous PW, Schubert K, Braun U, De Hoog GS, Hocking AD, Shin HD, Groenewald JZ (2007) Opportunistic, human-pathogenic species in the Herpotrichiellaceae are phenotypically similar to saprobic or phytopathogenic species in the Venturiaceae. Studies in Mycology 58: 185-217. <https://doi.org/10.3114/sim.2007.58.07>
- Dhanasekaran V, Jeewon R, Hyde KD (2006) Molecular taxonomy, origins and evolution of freshwater ascomycetes. Fungal Diversity 23: 351-390.
- Dingley JM (1972) Some foliicolous Ascomycetes on ferns in Australia and New Zealand. The genera *Rhagadolobium* P. Henn. & Lind. and *Lauterobachiella* Theiss. & Syd. New Zealand Journal of Botany 10: 74-86. <https://doi.org/10.1080/0028825X.1972.10430213>
- Dögen A, Ilkit M, De Hoog GS (2013) Black yeast habitat choices and species spectrum on high altitude creosote-treated railway ties. Fungal Biology 117: 692-696. <https://doi.org/10.1016/j.funbio.2013.07.006>
- Dong W, Hyde KD, Bhat DJ, Zhang H (2018) Introducing *Aculeata aquatica* gen. et sp. nov., *Minimelanolocus thailandensis* sp. nov. and *Thysanorea aquatica* sp. nov. (Herpotrichiellaceae, Chaetothyriales) from freshwater in northern Thailand. Mycological Progress 17: 617-629. <https://doi.org/10.1007/s11557-018-1389-2>
- Dong W, Hyde KD, Doilom M, Yu XD, Bhat DJ, Jeewon R, Boonmee S, Wang GN, Nalumpang S, Zhang H (2020a) *Pseudobactrodesmium* (Dactylosporaceae, Eurotiomycetes, Fungi) a novel lignicolous genus. Frontiers in Microbiology 11: 456. <https://doi.org/10.3389/fmicb.2020.00456>
- Dong W, Wang B, Hyde KD, McKenzie DJ, Raja HA, Tanaka K, Abdel-Wahab MA, Abdel-Aziz FA, Doilom M, Phookamsak R, Hongsanan S, Wanasinghe DN, Yu XD, Wang GN, Yang H, Yang J, Thambugala AN, Tian Q, Luo ZL, Yang JB, Miller AN, Fournier J, Boonmee S, Hu DM, Nalumpang S, Zhang H (2020b) Freshwater Dothideomycetes. Fungal Diversity 105: 319-575. <https://doi.org/10.1007/s13225-020-00463-5>
- Glass NL, Donaldson GC (1995) Development of primer sets designed for use with the PCR to amplify conserved genes from filamentous ascomycetes. Applied and Environmental Microbiology 61: 1323-1330. <https://doi.org/10.1128/AEM.61.4.1323-1330.1995>
- Goh TK, Hyde KD (1996) Biodiversity of freshwater fungi. Journal of Industrial Microbiology 17: 328-345. <https://doi.org/10.1007/BF01574764>
- Grossart HP, Wyngaert S, Kagami M, Wurzbacher C, Cunliffe M, Rojas-Jimenez K (2019) Fungi in aquatic ecosystems. Nature Reviews Microbiology 17: 339-354. <https://doi.org/10.1038/s41579-019-0175-8>
- Gulis V, Su R, Kuehn KA (2019) Fungal decomposers in freshwater environments. In: Hurst C (Ed.) The Structure and Function of Aquatic Microbial Communities. Advances in Environmental Microbiology. 7. Springer, Cham, 34 pp. [ISBN 978-3-030-16775-2]. https://doi.org/10.1007/978-3-030-16775-2_5
- Hall T (1999) BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. Nucleic Acids Symp. Ser. 41: 95-98.
- Harms H, Schlosser D, Wick LY (2011) Untapped potential: exploiting fungi in bioremediation of hazardous chemicals. Nature Reviews Microbiology 9: 177-192. <https://doi.org/10.1038/nrmicro2519>
- Hopple JS (1994) Phylogenetic investigations in the genus *Coprinus* based on morphological and molecular characters. Duke University, Durham, 417 pp. URL:

- <https://www.proquest.com/dissertations-theses/phylogenetic-investigations-genus-coprinus-based/docview/304128614/se-2?accountid=50161>
- Hu DM, Cai L, Chen H, Bahkali AH, Hyde KD (2010) Four new freshwater fungi associated with submerged wood from Southwest Asia. *Sydowia* 62: 191-203.
 - Hu DM, Chen H, Cai L, Bahkali AH, Hyde KD (2012) *Aquapeziza*: a new genus from freshwater, and its morphological and phylogenetic relationships to Pezizaceae. *Mycologia* 104 (2): 540-546. <https://doi.org/10.3852/11-123>
 - Hu DM, Liu F, Cai L (2013) Biodiversity of aquatic fungi in China. *Mycology* 4: 125-168. <https://doi.org/10.1080/21501203.2013.835752>
 - Hyde KD, Goh TK (1998) Fungi on submerged wood in the Riviere St Marie-Louis, the Seychelles. *South African Journal of Botany* 64: 330-336. [https://doi.org/10.1016/S0254-6299\(15\)30920-0](https://doi.org/10.1016/S0254-6299(15)30920-0)
 - Hyde KD, Bao DF, Hongsanan S, Chethana KW, Yang J, Suwanarach N (2021) Evolution of freshwater Diaporthomycetidae (Sordariomycetes) provides evidence for five new orders and six new families. *Fungal Diversity* <https://doi.org/10.1007/s13225-021-00469-7>
 - Iskandar NL, Zainudin NA, Tan SG (2011) Tolerance and biosorption of copper (Cu) and lead (Pb) by filamentous fungi isolated from a freshwater ecosystem. *Journal of Environmental Sciences* 23: 824-830. [https://doi.org/10.1016/S1001-0742\(10\)60475-5](https://doi.org/10.1016/S1001-0742(10)60475-5)
 - Katoh K, Rozewicki J, Yamada KD (2019) MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics* 20 (4): 1160-1166. <https://doi.org/10.1093/bib/bbx108>
 - Kharwar RN, Singh RK (2004) Additions to the hyphomycete genus *Veronaea* as phytoparasitic species. *Microbiological Research* 159: 103-111. <https://doi.org/10.1016/j.micres.2004.01.012>
 - Kondo Y, Hiruma M, Matsushita A, Matsuba S, Nishimura K, Takamori K (2007) Cutaneous phaeohyphomycosis caused by *Veronaea botryosa* observed as sclerotic cells in tissue. *International Journal of Dermatology* 46: 625-627. <https://doi.org/10.1111/j.1365-4632.2007.02950.x>
 - Liu XY, Udayanga D, Luo ZL, Chen LJ, Zhou DQ, Su HY, Hyde KD (2015) Backbone tree for Chaetothyriales with four new species of *Minimelanolocus* from aquatic habitats. *Fungal Biology* 119: 1046-1062. <https://doi.org/10.1016/j.funbio.2015.08.005>
 - Li WL, Luo ZL, Liu JK, Bhat DJ, Bao DF, Su HY, Hyde KD (2017) Lignicolous freshwater fungi from China I: *Aquadictyospora lignicola* gen. et sp. nov. and new record of *Pseudodictyosporium wauense* from northwestern Yunnan Province. *Mycosphere* 8: 1587-1597. <https://doi.org/10.5943/mycosphere/8/10/1>
 - Luo ZL, Bao DF, Bhat JD, Yang J, Chai HM, Li SH, Bahkali AH, Su HY, Hyde KD (2016) *Sporoschisma* from submerged wood in Yunnan, China. *Mycological Progress* 15: 1145-1155. <https://doi.org/10.1007/s11557-016-1236-2>
 - Luo ZL, Bhat DJ, Jeewon R, Boonmee S, Bao DF, Zhao YC, Chai HM, Su HY, Su XJ, Hyde KD (2017) Molecular phylogeny and morphological characterization of asexual fungi (Tubeufiaceae) from freshwater habitats in Yunnan, China. *Cryptogamie, Mycologie* 38: 27-53. <https://doi.org/10.7872/crym/v38.iss1.2017.27>
 - Luo ZL, Hyde KD, Liu JK, Bhat DJ, Bao DF, Li WL, Su HY (2018a) Lignicolous freshwater fungi from China II: Novel *Distoseptispora* (*Distoseptisporaceae*) species from northwestern Yunnan Province and a suggested unified method for studying

- lignicolous freshwater fungi. *Mycosphere* 9: 444-461. <https://doi.org/10.5943/mycosphere/9/3/2>
- Luo ZL, Hyde KD, Bhat DJ, Jeewon R, Maharachchikumbura SS, Bao DF, Li WL, Su XJ, Yang XY, Su HY (2018b) Morphological and molecular taxonomy of novel species Pleurotheciacaeae from freshwater habitats in Yunnan, China. *Mycological Progress* 17: 511-530. <https://doi.org/10.1007/s11557-018-1377-6>
 - Luo ZL, Hyde KD, Liu JK, Maharachchikumbura SS, Jeewon R, Bao DF, Bhat DJ, Lin CG, Li WL, Yang J, Liu NG, Lu YZ, Jayawardena RS, Li JF, Su HY (2019) Freshwater Sordariomycetes. *Fungal Diversity* 99: 451-660. <https://doi.org/10.1007/s13225-019-00438-1>
 - Lu YZ, Zhang JY, Lin CG, Luo ZL, Liu JK (2020) *Pseudodactylaria fusiformis* sp. nov. from freshwater habitat in China. *Phytotaxa* 446: 95-102. <https://doi.org/10.11646/phytotaxa.446.2.2>
 - Miller MA, Pfeiffer W, Schwartz T (2010) Creating the CIPRES Science Gateway for inference of large phylogenetic trees. In *2010 gateway computing environments workshop (GCE)1-8*. <https://doi.org/10.1109/GCE.2010.5676129>
 - Morgan-Jones G (1982) Notes on hyphomycetes. XL: new species of *Cadinaea* and *Veronaea*. *Mycotaxon* 14: 175-180.
 - Moustafa AF, Abdul-Wahid OA (1990) *Veronaea constricta*, a new hyphomycete from Egyptian soils. *Mycotaxon* 38: 167-171.
 - Müller E, Petrini O, Fisher PJ, Samuels GJ, Rossman AY (1987) Taxonomy and anamorphs of the Herpotrichiellaceae with notes on generic synonymy. *Transactions of the British Mycological Society* 88 (1): 63-74.
 - Munk A (1953) The system of pyrenomycetes. *Dansk Botanisk Arkiv* 15: 1-163.
 - Nylander JA (2004) MrModeltest v.2. Program distributed by the author.
 - O'Donnell K, Cigelnik E (1997) Two divergent intragenomic rDNA ITS2 types within a monophyletic lineage of the fungus *Fusarium* are nonorthologous. *Molecular Phylogenetics and Evolution* 7: 103-116. <https://doi.org/10.1006/mpev.1996.0376>
 - Pan H, Zhang T, Kong J (2009) Notes on soil dematiaceous hyphomycetes from the Yellow River source area, China I. *Mycosistema* 28: 14-19.
 - Pan H, Zhang T (2010) New species of *Monodictys* and *Veronaea* from soil in the Yellow River source area, China. *Mycotaxon* 113: 259-262. <https://doi.org/10.5248/113.259>
 - Pan H, Xia H, Zhang T (2012) Three newly recorded species of *Veronaea* and *Wardomyces* from China. *Mycosistema* 31: 33-135.
 - Papendorf MC (1969) New south african soil fungi. *Transactions of the British Mycological Society* 52 (3): 483-489. [https://doi.org/10.1016/S0007-1536\(69\)80132-4](https://doi.org/10.1016/S0007-1536(69)80132-4)
 - Papendorf MC (1976) Notes on *Veronaea* including *V. compacta* sp. nov. *Bothalia* 12: 119-121. <https://doi.org/10.4102/abc.v12i1.1384>
 - Rehner SA, Samuels GJ (1995) Molecular systematics of the Hypocreales: a teleomorph gene phylogeny and the status of their anamorphs. *Canadian Journal of Botany* 73: 816-823. <https://doi.org/10.1139/b95-327>
 - Ronquist F, Huelsenbeck JP (2003) MrBayes 3: Bayesian phylogenetic inference under mixed models. *Bioinformatics* 19: 1572. <https://doi.org/10.1093/bioinformatics/btg180>
 - Sang H, Zheng XE, Kong QT, Zhou WQ, He W, Lv GX, Shen YN, Liu WD (2011) A rare complication of ear piercing: a case of subcutaneous phaeohyphomycosis caused by

- Veronaea botryosa in China. Medical Mycology 49: 296-302. <https://doi.org/10.3109/13693786.2010.513340>
- Soares DJ, Barreto RW (2008) Fungal pathogens of the invasive riparian weed *Hedychium coronarium* from Brazil and their potential for biological control. Fungal Diversity 28: 85-96.
 - Stamatakis A, Hoover P, Rougemont J (2008) A rapid bootstrap algorithm for the RAxML web servers. Systematic Biology 57: 758-771. <https://doi.org/10.1080/10635150802429642>
 - Stamatakis A (2014) RAxML version 8: a tool for phylogenetic analysis and post-analysis of large phylogenies. Bioinformatics 30: 1312-1313. <https://doi.org/10.1093/bioinformatics/btu033>
 - Su XJ, Luo ZL, Jeewon R, Bhat DJ, Bao DF, Li WL, Hao YE, Su HY, Hyde KD (2018) Morphology and multigene phylogeny reveal new genus and species of Torulaceae from freshwater habitats in north western Yunnan, China. Mycological Progress 17: 531-545. <https://doi.org/10.1007/s11557-018-1388-3>
 - Thaxter R (1931) Contribution towards a monograph of the Laboulbeniaceae part V. Memoirs of the American Academy of Arts and Sciences 16: 1-435. <https://doi.org/10.2307/25058136>
 - Tsui CK, Hyde KD, Hodgkiss IJ (2000) Biodiversity of fungi on submerged wood in Hong Kong streams. Aquatic Microbial Ecology 21: 289-298. <https://doi.org/10.3354/ame021289>
 - Tsui CK, Baschien C, Goh TK (2016) Biology and ecology of freshwater fungi. In: Li DW (Ed.) Biology of Microfungi. Springer, Cham, Switzerland. [ISBN 978-3-319-29137-6]. https://doi.org/10.1007/978-3-319-29137-6_13
 - Tsui KM (1999) Biodiversity and longitudinal distribution of fungi on submerged wood, with reference to human disturbance. The University of Hong Kong, Hong Kong:, 1315 pp.
 - Untereiner WA, Straus NA, Malloch D (1995) A molecular-morphotaxonomic approach to the systematics of the Herpotrichiellaceae and allied black yeasts. Mycological Research 99 (8): 897-913. [https://doi.org/10.1016/S0953-7562\(09\)80748-X](https://doi.org/10.1016/S0953-7562(09)80748-X)
 - Vicente VA, Attili-Angelis D, Pie MR, Queiroz-Telles F, Cruz LM, Najafzadeh MJ, De Hoog GS, Zhao J, Pizzirani-Kleiner A (2008) Environmental isolation of black yeast-like fungi involved in human infection. Studies in Mycology 61: 137-144. <https://doi.org/10.3114/sim.2008.61.14>
 - Vilgalys R, Hester M (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several *Cryptococcus* species. Journal of Bacteriology 172: 4238-4246. <https://doi.org/10.1128/jb.172.8.4238-4246.1990>
 - Wang GN, Yu XD, Dong W, Bhat DJ, Boonmee S, Zhang D, Zhang H (2019) Freshwater hyphomycetes in Eurotiomycetes: a new species of *Minimelanolocus* and a new collection of *Thysanorea papuana* (Herpotrichiellaceae). Mycological Progress 18: 511-522. <https://doi.org/10.1007/s11557-019-01473-7>
 - White TJ, Bruns T, Lee S, Taylor JW (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. In: Innis MA, Gelfand DH, Sninsky JJ, White TJ (Eds) PCR protocols: A guide to methods and application. 18. Academic Press, Inc, San Diego, CA, USA, 7 pp. <https://doi.org/10.1016/B978-0-12-372180-8.50042-1>

- Wijayawardene NN, Hyde KD, Al-Ani LK, Tedersoo L, Haelewaters D, Rajeshkumar KC, Zhao RL, Aptroot A, Leontyev DV, Saxena RK, Tokarev YS, Dai DQ, Letcher PM, Stephenson SL, Ertz D, Lumbsch HT, Kukwa M, Issi IV, Madrid H, Phillips AJ, Selbmann L, Pfliegl WP, Horvth E, Bensch K, Kirk PM, Kolaříková K, Raja HA, Radek R, Papp V, Dima V, Ma J, Malosso E, Takamatsu S, Rambold G, Gannibal PB, Triebel D, Gautam AK, Avasthi S, Suetrong S, Timdal E, Fryar SC, Delgado G, Réblová M, Doilom M, Dolatabadi S, Pawowska JZ, Humber RA, Kodsube R, Sánchez-Castro I, Goto BT, Silva DK, Souza FA, Oehl F, Silva GA, Silva IR, Baszkowski J, Jobim K, Maia LC, Barbosa FR, Fiúza PO, Divakar PK, Shenoy BD, Castañeda-Ruiz RF, Somrithipol S, Lateef AA, Karunaratna SC, Tibpromma S, Mortimer PE, Wanasinghe DN, Phookamsak R, Xu J, Wang Y, Tian F, Alvarado P, Li DW, Kušan I, Matočec N, Mešić A, Tkalcic Z, Maharachchikumbura SS, Papizadeh M, Heredia G, Wartchow F, Bakhshi M, Boehm E, Youssef N, Hustad VP, Lawrey JD, Santiago AL, Bezerra JD, Souza-Motta CM, Firmino AL, Tian Q, Houbraken J, Hongsanan S, Tanaka K, Dissanayake AJ, Monteiro JS, Grossart HP, Suija A, Weerakoon G, Etayo J, Tsurykau A, Vázquez V, Mungai P, Damm U, Li QR, Zhang H, Boonmee S, Lu YZ, Becerra AG, Kendrick B, Brearley FQ, Motiejūnaitė J, Sharma B, Khare R, Gaikwad S, Wijesundara DS, Tang LZ, He MQ, Flakus A, Rodriguez-Flakus P, Zhurbenko MP, McKenzie EH, Stadler M, Bhat DJ, Liu JK, Raza M, Jeewon R, Nassanova ES, Prieto M, Jayalai RG, Erdoğdu M, Yurkov A, Schnittler M, Shchepin ON, Novozhilov YK, Silva-Filho AG, Gentekaki E, Liu P, Cavender JC, Kang Y, Mohammad S, Zhang LF, Xu RF, Li YM, Dayarathne MC, Ekanayaka AH, Wen TC, Deng CY, Pereira OL, Navathe S, Hawksworth DL, Fan XL, Dissanayake LS, Kuhnert E, Grossart HP, Thines M (2020) Outline of Fungi and fungus-like taxa. *Mycosphere* 11: 1060-1456. <https://doi.org/10.5943/mycosphere/11/1/8>
- Zhang H, Hyde KD, McKenzie EH, Bahkali AH, Zhou D (2012) Sequence data reveals phylogenetic affinities of *Acrocalymma aquatica* sp. nov., *Aquasubmersa mircensis* gen. et sp. nov. and *Clohesyomyces aquaticus* (freshwater coelomycetes). Cryptogamie, Mycologie 33: 333-346. <https://doi.org/10.7872/crym.v33.iss3.2012.333>
- Zhang K, Su YY, Cai L (2013) An optimized protocol of single spore isolation for fungi. Cryptogamie, Mycologie 34: 349-356. <https://doi.org/10.7872/crym.v34.iss4.2013.349>