Acrogenospora (Acrogenosporaceae, Minutisphaerales) Appears to Be a Very Diverse Genus

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During a study of diversity and taxonomy of lignicolous freshwater fungi in China, nine species of Acrogenospora were collected. Seven of these were new species and they are described and illustrated. With morphology, additional evidence to support establishment of new species is provided by phylogeny derived from DNA sequence analyses of a combined LSU, SSU, TEF1α, and RPB2 sequence dataset. Acrogenospora subprolata and A. verrucispora were re-collected and sequenced for the first time. The genus Acrogenospora is far more species rich than originally thought, with nine species found in a small area of Yunnan Province, China.

Keywords: 7 new species, Acrogenosporaceae, molecular analyses, phylogeny, taxonomy

INTRODUCTION

Freshwater fungi are an ecological group that are defined by their presence in freshwater for the whole or part of their life cycle (Thomas, 1996; Wong et al., 1998), and include any species that grow on predominantly aquatic or semi-aquatic substrates (Goh and Hyde, 1996). Freshwater fungi play an important role in nutrient and carbon cycling, biological diversity and ecosystem functioning (Zhang et al., 2008; Swe et al., 2009). There have been many studies of freshwater fungi, especially on diversity, taxonomy and phylogeny (Tsui et al., 2000; Cai et al., 2002; Vijaykrishna et al., 2005; Vijaykrishna and Hyde, 2006; Hirayama et al., 2010; Ferrer et al., 2011; Barbosa et al., 2013; Raja et al., 2013, 2015) and recently from China (Hyde et al., 2016; Yang et al., 2017; Huang et al., 2018a,b; Su et al., 2018; Guo et al., 2019; Luo et al., 2019). In this study, we report nine Acrogenosporaceae species that were collected from freshwater habitats in China. Acrogenosporaceae was established by Jayasiri et al. (2018) to accommodate Acrogenospora within Minutisphaerales, with the latter being a freshwater ascomycetes order, comprising two families, Acrogenosporaceae and Minutisphaeraeaceae (Wijayawardene et al., 2020). Members of these two families are mostly reported from freshwater habitats (Goh et al., 1998; Raja et al., 2015; Bao et al., 2019; Hyde et al., 2019).

Acrogenospora was established by Ellis (1971) with two species, Acrogenospora sphacocephala, and Farlowiella carmichaeliana (asexual morph). Ellis (1972) included two other species A. setiformis and F. australis in this genus. Hughes (1978) accepted the genus and added
two additional species, *A. gigantospora* and *A. novae-zelandiae*. A taxonomic revision was provided by Goh et al. (1998) who accepted eight species, including two new combinations and two new species, and provided descriptions, illustrations and a key to species. Currently, 13 species are included in *Acrogenospora* (Hu et al., 2010; Ma et al., 2012; Hyde et al., 2019). *Acrogenospora* species are characterized by macroeutomatous, mononematous, simple, brown, sometimes percurrently proliferating conidiophores; monoblastic, terminal or intercalary conidiogenous cells; and globose, ellipsoid or obovoid, olivaceous to brown conidia (Hughes, 1978; Goh et al., 1998).

The sexual morph of *Acrogenospora* has been linked with *Farlowiella*. Mason (1941) showed the connection between *A. megalospora* and *Farlowiella armichaeliana* based on cultural studies. Ellis (1971) reported the asexual morph of *F. carmichaeliana* as *A. carmichaeliana*. Ellis (1972) introduced *A. australis* as the asexual morph of *A. australis* based on morphological characters. Goh et al. (1998) accepted these two asexual morphs of *Farlowiella* and synonymized *A. megalospora* under *F. carmichaeliana* and *A. altissima* under *F. australis*. Jayasiri et al. (2018) carried out phylogenetic analyses with seven isolates of *Acrogenospora* and showed that *A. sphaerocephala* clustered with the sexual morph *Farlowiella carmichaeliana*. This confirmed the connection between *Acrogenospora* and *Farlowiella*. Hyde et al. (2019) also supported the asexual-sexual connection between these two genera based on a phylogenetic study. Based on recent nomenclatural changes with regards to one fungus one name, *Acrogenospora* was given priority (Wijayawardene et al., 2014; Rossman et al., 2015).

During our investigation of freshwater fungi on submerged wood along a north/south gradient in the Asian/Australasian region (Hyde et al., 2016), nine isolates of *Acrogenospora* were collected from freshwater habitats in China. Among them, two are identified as existing species, *A. subprolata* and *A. verrucispora*, and another seven are introduced as new species by comparing their morphology with known species of the genus, as well as performing phylogenetic analyses of LSU, SSU, TEF1α, and RPB2 DNA sequence data. The objectives of this study are as follows: (i) describe and illustrate the newly collected *Acrogenospora* spp. from freshwater habitats in China; (ii) provide molecular data for *Acrogenospora* species and understand their phylogenetic relationships.

**MATERIALS AND METHODS**

**Isolation and Morphology**

Samples of submerged wood were collected from Yunnan and Tibet provinces, China and taken to the laboratory in plastic bags. The samples were incubated in plastic boxes lined with moistened tissue paper at room temperature for one week. Specimen observations and morphological studies were conducted following the protocols provided by Luo et al. (2018).

Single spore isolations were carried out following the method described in Chomnunti et al. (2014). Germinating conidia were transferred aseptically to PDA and MEA plates supplemented with 100 mg of streptomycin and grown at room temperature in daylight. Colony color and other characters were observed and measured after 1 week and again after 3 weeks. The specimens were deposited in the Mae Fah Luang University (MFLU) Herbarium, Chiang Rai, Thailand. Living cultures are deposited in the Culture Collection at Mae Fah Luang University (MFLUCC).

**DNA Extraction, PCR Amplification, and Sequencing**

Fungal mycelium was scraped from the surface of colonies grown on potato dextrose agar (PDA) or malt extract agar (MEA) at 25°C for 4 weeks, transferred into a 1.5 mL centrifuge tube and ground using liquid nitrogen. The EZ genoTM fungal gDNA kit (GD2416) was used to extract DNA from the ground mycelium according to the manufacturer’s instructions. Primers for PCR amplification used were LSUrDNA = LR0R/LR7 (Vilgalys and Hester, 1990), SSUrDNA = NS1/NS4 (White et al., 1990), (TEF1-α) = 983F/2218R and (RPB2) = fRPB2-5f/fRPB2-7cR (Liu et al., 1999). The PCR mixture was prepared as follows: 12.5 µl of 2 × Power Taq PCR MasterMix, 20 mM Tris-HCl pH 8.3, 100 Mm KCl, 3 Mm MgCl2, stabilizer, and enhancer), 1 µl of each primer, 1 µl genomic DNA extract and 9.5 µl deionized water. The PCR of LSU, SSU and TEF1α gene was processed as follows: 94°C for 3 min, followed by 35 cycles of denaturation at 94°C for 30 s, annealing at 56°C for 50 s, elongation at 72°C for 1 min and a final extension at 72°C for 10 min, and finally kept at 4°C. The RPB2 gene region was amplified with an initial denaturation of 95°C for 5 min, followed by 40 cycles of denaturation at 95°C for 1 min, annealing at 54°C for 40 s, elongation at 72°C for 90 s, and the final extension at 72°C for 10 min. PCR amplification was confirmed on 1% agarose electrophoresis gels stained with ethidium bromide. Purification and sequencing of PCR products were carried out using the above-mentioned PCR primers at Beijing Tsingke Biological Engineering Technology and Services Co., Ltd. (Beijing, P.R. China).

**Molecular Phylogenetic Analyses**

**Sequencing and Sequence Alignment**

Sequences were assembled with BioEdit and those with high similarity indices were determined from a BLAST search to find the closest matches with taxa in *Acrogenospora* and from recently published data (Jayasiri et al., 2018; Hyde et al., 2019). All consensus sequences and the reference sequences were automatically aligned with MAFFT v. 7 and the strategy was using Auto (Katoh and Standley, 2013). Aligned sequences of each gene region (LSU, SSU, TEF1α and RPB2) were combined and manually improved using BioEdit v. 7.0.5.2 (Hall, 1999). Ambiguous regions were excluded from the analyses and gaps were treated as missing data. Phylogenetic analyses were performed using Maximum Likelihood (ML) and Bayesian tree building criteria.

1http://mafft.cbrc.jp/alignment/server/index.html
Phylogenetic Analyses

Maximum likelihood analysis was performed at the CIPRES Science Gateway v.3.3 (Miller et al., 2010) using RAxML v. 8.2.8 as part of the "RAxML-HPC2 on XSEDE" tool (Stamatakis, 2006; Stamatakis et al., 2008). All model parameters were estimated by RAxML. The final ML search was conducted by using MrModeltest 2.2 (Nylander, 2004), Maximum likelihood bootstrap support was calculated from 1000 bootstrap replicates.

Bayesian analysis was performed using MrBayes v.3.1.2. (Ronquist and Huelsenbeck, 2003). The model of each genes was estimated using MrModeltest 2.2 (Nylander, 2004), Maximum likelihood analysis with 1000 replicates, each with 10 replicates of random stepwise addition and tree bisection reconnection (TBR) branch-swapping. Maxtrees were unlimited, branches of zero length were collapsed and all parsimonious trees were saved. The consistency indices (CI), tree length (TL), homoplasy index (HI), rescaled consistency indices (RC), retention indices (RI) were calculated for each tree. Clade stability was assessed using a bootstrap (BT) analysis with 1000 replicates, each with 10 replicates of random stepwise addition of taxa. Other details are as provided by Jeewon et al. (2002, 2003)

Phylogenetic trees were represented by FigTree v. 1.4.4 (Rambaut, 2014) and edited in Microsoft Office PowerPoint 2016 (Microsoft Inc., United States). Newly generated sequences in this study were deposited in GenBank (Table 1) and the alignment used for the phylogenetic analyses were submitted to TreeBASE with a final likelihood value of -49015.757408 is shown in Figure 1. The matrix had 1149 distinct alignment patterns, with 29.85% undetermined characters or gaps. Estimated base frequencies were: A = 0.253075, C = 0.235518, G = 0.278280, T = 0.194616; substitution rates AC = 1.387195, AG = 3.679854, AT = 1.133462, CG = 0.233127, CT = 7.472473, GT = 1.000000; gamma distribution shape parameter α = 0.303701. Bootstrap support values for RAxML and MP greater than 60% and Bayesian posterior probabilities greater than 0.95 are given at each node (Figure 1).

In the phylogenetic analyses all the new species were included with members of Acrogenospora within Acrogenosporaceae with high support (99% ML and 0.99 BPP). Acrogenospora aquatica, A. guttulatispora, A. submersa, A. yunnanensis grouped together, but separated in different clades. Two isolates of A. aquatica (MFLUCC 16–0949 and MFLUCC 20–0097) formed a distinct clade with high statistical support (95% ML and 1 BPP). Acrogenospora guttulatispora was placed as a sister taxon to A. aquatica and A. submersa. Acrogenospora yunnanensis clustered with A. submersa. Acrogenospora basalcellularispora clustered with A. carchmialiana (CBS 206.36) and sister to A. obovoidispora. Two strains of A. verrucispora (MFLUCC 20–0098 and MFLUCC 18–1617) clustered together with high statistical support (95% ML and 1 BPP), and sister to A. carchmialiana. Acrogenospora olivaceospora and A. subprolata grouped with A. phaerocephala.

Acrogenospora aquatica D.F. Bao, Z.L. Luo, K.D. Hyde & H.Y. Su, sp. nov.

Index Fungorum number: IF 557599; Facesoffungi number: FoF 07984, Figure 2

Holotype—MFLU 20–0291

Etyymology—“Aquatica” in connection with the aquatic habitat from which it was recovered.

Saprobic on submerged decaying wood. Sexual morph: Undetermined. Asexual morph: Colonies effuse on natural substrate, hairy, dark brown. Mycelium mostly immersed, composed of septate, grayish brown, branched, smooth hyphae. Conidiophores 200–250 × 7.5–9.5 μm (x = 226 × 8.6 μm, n = 15), mononematous, macronematous, solitary, erect, straight or slightly flexuous, cylindrical, indeterminate, unbranched, brown to dark brown, paler toward apex, septate, smooth. Conidigenous cells holoblastic, monoblastic, integrated, initially terminal, later becoming intercalary, cylindrical, smooth, pale brown, proliferating percurrently. Conidia 29–34.5 × 24–31 μm (x = 31.8 × 27.7 μm, n = 30), acrogenous, solitary, subprolate to broadly ellipsoidal, base truncate, dark brown to black, asperate, lacking guttules, with a hyaline, globose to subglobose basal cell, smooth.

Material examined: CHINA, Yunnan Province, Dali, Cangshan Mountain, on decaying wood submerged in a stream, January 2016, Q.S. Zhou, S-763 (MFLU 20–0291, holotype), ex-type culture MFLUCC 20–0097. CHINA, Yunnan Province, Dali, Cangshan Mountain, on decaying wood submerged in Qingbixi Stream, March 2016, Z. L. Luo, S-282 (DLU 282, isotype), living culture MFLUCC 16-0949.

Notes: In our study, we found two species, A. basalcellularispora and A. aquatica with a hyaline, globose

RESULTS

Phylogenetic Analyses

The combined LSU, SSU, TEF, and RPB2 sequence dataset included 101 taxa (ingroup) and two outgroup taxa (Diploschistes ocellatus and Stictis radiata) with a total of 3853 characters (LSU: 867 bp; SSU:1020 bp; TEF1α: 915 bp; RPB2: 1051 bp) after alignment including the gaps. The RAxML and Bayesian analyses of the combined dataset resulted in phylogenetic reconstructions with largely similar topologies and the result of ML analysis with a final likelihood value of -49015.757408 is shown in Figure 1. The matrix had 1149 distinct alignment patterns, with 29.85% undetermined characters or gaps. Estimated base frequencies were: A = 0.253075, C = 0.235518, G = 0.278280, T = 0.194616; substitution rates AC = 1.387195, AG = 3.679854, AT = 1.133462, CG = 0.233127, CT = 7.472473, GT = 1.000000; gamma distribution shape parameter α = 0.303701. Bootstrap support values for RAxML and MP greater than 60% and Bayesian posterior probabilities greater than 0.95 are given at each node (Figure 1).

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Notes: In our study, we found two species, A. basalcellularispora and A. aquatica with a hyaline, globose

http://www.phylo.org/portal2/

https://www.treebase.org/
### TABLE 1 | GenBank numbers and culture collection accession numbers of species included in the phylogenetic study.

| Taxa                     | Strain          | GenBank accession no. | References                  |
|--------------------------|-----------------|-----------------------|-----------------------------|
|                          |                 | LSU | SSU | RPB2 | TEF1α                  |
| **Acrogenospora aquatica** | MFLUCC 16–0949  | MT340732 | – | – | MT367152 | This study |
| **Acrogenospora aquatica** | MFLUCC 20–0097  | – | MT340743 | MT367159 | MT367151 | This study |
| **Acrogenospora basicallecularispora** | MFLUCC 16–0992  | MT340729 | – | – | – | This study |
| Acrogenospora carmichaeliana | MFLU 18–1130  | MH606222 | – | – | – | Hyde et al., 2019 |
| Acrogenospora carmichaeliana | CBS 206.36  | MH687287 | – | – | – | Jayasiri et al., 2018 |
| Acrogenospora carmichaeliana | CBS 179.73  | – | GU296148 | – | – | Jayasiri et al., 2018 |
| Acrogenospora carmichaeliana | CBS 164.76  | GU301791 | GU296129 | – | GU349059 | Jayasiri et al., 2018 |
| **Acrogenospora guttulatispora** | MFLUCC 17–1674  | MT340730 | – | MT367157 | – | This study |
| **Acrogenospora obovata** | MFLUCC 18–1622  | MT340736 | MT340747 | MT367163 | MT367155 | This study |
| **Acrogenospora submersa** | MFLUCC 16–0997  | MT340731 | MT340742 | MT367158 | MT367150 | This study |
| Acrogenospora sphaerocephala | MFLUCC 16–0179 | MH606222 | – | MT367164 | – | Hyde et al., 2019 |
| Acrogenospora yunnanensis | MFLUCC 20–0098  | MT340734 | MT340745 | MT367161 | MT367153 | This study |
| Acrospermum adeanum | M 133 | EU940104 | EU940031 | EU940320 | – | Sterrenbos et al., 2010 |
| Acrospermum compressum | M 151 | EU940084 | EU940012 | EU940301 | – | Sterrenbos et al., 2010 |
| Acrospermum graminum | M 152 | EU940085 | EU940013 | EU940302 | – | Sterrenbos et al., 2010 |
| Aigialus grandis | BCC 09270 | GU479782 | GU479747 | – | GU479846 | Giraldo et al., 2014 |
| Aigialus grandis | BCC 18419 | GU479774 | GU479738 | – | GU479838 | Giraldo et al., 2014 |
| Aigialus grandis | BCC 33563 | GU479776 | GU479741 | – | GU479840 | Giraldo et al., 2014 |
| Aliquandostipite khaoyaiensis | CBS 118232 | GU301796 | AF201453 | FJ238360 | GU349048 | Schoch et al., 2009 |
| Aliquandostipite siamensis | SS 81.02 | EF175666 | EF175645 | – | – | Campbell et al., 2007 |
| Amenta zanthoxyli | TH 561 | GU586219 | GU586213 | – | – | Hofmann et al., 2010 |
| Amenta zanthoxyli | TH 592 | GU586218 | GU586212 | – | – | Hofmann et al., 2010 |
| Amenta zanthoxyli | TH 589 | GU586217 | GU586211 | – | – | Hofmann et al., 2010 |
| Asterina cestrica | TH 589 | GU586216 | GU586210 | – | – | Hofmann et al., 2010 |
| Asterina fuchsiae | TH 590 | GU586215 | GU586209 | – | – | Hofmann et al., 2010 |
| Asterina phenacis | TH 589 | GU586217 | GU586211 | – | – | Hofmann et al., 2010 |
| Asterina weinmanniae | TH 592 | GU586218 | GU586212 | – | – | Hofmann et al., 2010 |
| Asterina xanthoxyli | TH 589 | GU586216 | GU586209 | – | – | Hofmann et al., 2010 |
| Asterotexis cucurbitacearum | VIC 24814 | KP143734 | – | – | – | Guatimosim et al., 2015 |
| Asteotaxis cucurbitacearum | PMAM 0141224 | HQ610510 | – | – | – | Guatimosim et al., 2015 |
| Astrospheiria fusispora | MFLUCC 10–0655 | MT340735 | MT340746 | MT367162 | MT367154 | This study |
| **Cladosporium cladosporioides** | CBS 170.54 | AY213694 | DQ678004 | – | – | Rakeman et al., 2005 |
| Cladosporium cladosporioides | CBS 170.54 | AY213694 | DQ678004 | – | – | Rakeman et al., 2005 |
| Diplocystis ocellatus | CBS 225.62 | DQ678026 | DQ677975 | DQ767837 | Phillips et al., 2008 |
| Diplocystis ocellatus | CBS 225.62 | DQ678026 | DQ677975 | DQ767837 | Phillips et al., 2008 |
| Dissoconium aciculare | CBS 208.49 | GU214419 | GU214523 | – | XK288435 | Crous et al., 2009 |

(Continued)
| Taxa | Strain | GenBank accession no. | References |
|------|--------|----------------------|------------|
|      |        | LSU | SSU | RPB2 | TEF1a |
| Dyfroblemices rhizophorae | JK 5349A | GU479799 | GU479766 | – | GU479860 |
| Dyfroblemices sinensis | MFLUCC 17–1344 | MG836699 | MG836700 | – | Hyde et al., 2018 |
| Dyfroblemices tironianensis | NTOU3636 | KC692156 | KC692155 | – | KC692157 |
| Eremomyces bilateralis | CBS 781.70 | HG004545 | – | – | Giraldo et al., 2014 |
| Fissuroma maculans | MFLUCC 10–0866 | JN846724 | JN846734 | – | Liu et al., 2011 |
| Flavobathelium epithyllum | MPN67 | JU327717 | JN887382 | – | Nelsen et al., 2009 |
| Gloiopsis praelonga | CBS 112415 | FJ161173 | FJ161134 | FJ161113 | FJ161090 |
| Gloiumon stellatum | CBS 207.34 | FJ161179 | FJ161140 | – | Boehm et al., 2009 |
| Hysterium angustatum | CBS 236.34 | FJ161180 | GU397359 | FJ161117 | FJ161095 |
| Hysterobrevium smilacis | CBS 114601 | FJ161174 | FJ161135 | FJ161114 | FJ161096 |
| Jahnula aquatica | R 68–1 | EF175665 | EF175633 | – | Campbell et al., 2007 |
| Jahnula seychellensis | SS2113 | EF175665 | EF175644 | – | Campbell et al., 2007 |
| Leptoxyphium cacuminum | MFLUCC 10–0049 | JN832602 | JN832587 | – | Chomnunti et al., 2011 |
| Lophiotrema lignicola | CBS 122364 | GU301836 | GU296166 | – | Schoch et al., 2009 |
| Manglicola guatemalensis | BCC 20156 | FJ743448 | FJ743443 | – | Suetrong et al., 2010 |
| Massaria anomia | CBS 591.78 | FJ161184 | FJ161144 | FJ161119 | FJ161100 |
| Mytilinidion acicola | EB O349 | GU323209 | GU323185 | GU371757 | Schoch et al., 2009 |
| Oedohysterium insidens | CBS 238.34 | FJ161199 | FJ161159 | FJ161125 | FJ161107 |
| Paradictyoarthrinium diffractum | MFLUCC 13–0466 | KP744498 | KP753960 | – | Liu et al., 2015 |
| Phyllosticta capitalensia | CBS 955.73 | FP06289 | FP766300 | – | Guarnaccia et al., 2017 |
| Piedraia hortae | CBS 480.64 | GU214466 | AY016349 | KF902289 | – |
| Pseudorobillarda eucalypti | MFLUCC 11–0025 | JN846729 | JN846739 | – | Liu et al., 2011 |
| Pseudorobillarda phragmitis | CBS 398.61 | EU754203 | EU754104 | – | Gruyter et al., 2009 |
| Pseudovirgaria grisea | CPC 19134 | JF957614 | – | – | Braun et al., 2007 |
| Pseudovirgaria hyperparasitica | CPC 10753 | EU041824 | – | – | Arzanlou et al., 2007 |
| Psiloglonium araucanum | CBS 112412 | FJ161172 | FJ161133 | FJ161112 | FJ161089 |
| Racodium rupestre | L346 | EU048583 | EU048575 | – | Muggiaa et al., 2008 |
| Racodium rupestre | L424 | EU048582 | EU048577 | – | Muggiaa et al., 2008 |
| Rhexothecium globosum | CBS 955.73 | HG004544 | – | – | Giraldo et al., 2014 |
| Saccharata proteae | CBS 115206 | DO377882 | KF766311 | – | Schoch et al., 2009 |
| Salsuginea ramicola | KT 2597.1 | GU479800 | GU479767 | GU479833 | GU479861 |
| Saccharata proteae | CBS 325.33 | FF01821 | KT216542 | – | Quaedvlieg et al., 2014 |
| Sclerotinia spica | AFTOL 398 | AF366666 | U20610 | AY641079 | \* |
| Strigula jamesii | MPN48 | JN887404 | JN887388 | – | Nelsen et al., 2011 |
| Tetraplosphaeria sasicola | MFLUCC 11–0514 | KF301538 | KF301543 | – | KF301557 |
| Thaxteriella inthanonensis | MAFF 239677 | AB524631 | AB524490 | – | Tanaka et al., 2009 |
| Triplonchium griseum | MFLUCC 11–0514 | KF301538 | KF301543 | – | KF301557 |
| Ulospora bilgami | CBS 110020 | DO678076 | DO678025 | DO677974 | DO677921 |

The newly generated sequences are in bold.
Bao et al. Diverse Genus, Acrogenospora (Acrogenosporaceae)

FIGURE 1 | Phylogenetic tree based on RAxML analyses of a combined LSU, SSU, TEF1α and RPB2 dataset. Bootstrap support values for maximum likelihood ≥ 70% and Bayesian posterior probabilities ≥ 0.90 are indicated above the nodes as MLBS/PP. The tree is rooted with Diploschistes ocellatus (AFTOL 958) and Stictis radiata (AFTOL 398). The new isolates are in red.
to subglobose basal cell. *Acrogenospora aquatica* can be distinguished from *A. basalicellularispora* by the size of conidiophores (259–395 × 8–12 vs. 202–250 × 7.8–9.3 µm). In addition, conidia of *A. basalicellularispora* are pale orange-brown to olivaceous-brown, with several small to large guttules, while conidia of *A. aquatica* are dark brown to black and lack guttules.
Acrogenospora aquatica is phylogenetically close to A. guttulatispora. Acrogenospora aquatica similar to A. guttulatispora in having mononematous, macronematous, unbranched conidiophores, holoblastic, monoblastic conidiogenous cells and acrogenous, dark brown to black conidia. However, A. aquatica differs from A. guttulatispora in having subprolate to broadly ellipsoidal conidia with a hyaline, globose to subglobose basal cell, lacking guttules, while conidia of A. guttulatispora are spherical or subspherial, with a large guttule, lacking basal cell.

Acrogenospora basalcellularispora D.F. Bao, Z.L. Luo, K.D. Hyde & H.Y. Su, sp. nov.

Index Fungorum number: IF 557596; Facesoffungi number: FoF 07981, Figure 3

Holotype—MFLU 20–0288

Etymology—Referring to the conidia which have a basal cell.

Saprobic on submerged decaying wood. Sexual morph: Undetermined. Asexual morph: Colonies effuse on natural substrate, hairy, dark brown. Mycelium mostly immersed, composed of grayish brown, septate, branched, smooth hyphae. Conidiophores 260–395 × 8–12 µm (x = 327 × 10 µm, n = 20) wide, mononematous, macronematous, solitary, cylindrical, erect, straight or slightly flexuous, mostly unbranched, septate, brown to dark brown, slightly paler toward apex, smooth. Conidiogenous cells holoblastic, monoblastic, integrated, initially terminal, later becoming intercalary, cylindrical, smooth, pale brown, proliferating percurrently. Conidia 27.5–33.7 × 21.7–25.8 µm (x = 30.6 × 23.7 µm, n = 30) wide, acropleurogenous, solitary, dry, broadly obvoid to spherical, smooth, pale orange-brown to olivaceous brown, aseptate, with several small or large guttules, with a small, hyaline, subcylindrical to subglobose basal cell, germinating from basal cell.

Material examined: CHINA, Yunnan Province, Dali, Gaoligongshan Mountain, on decaying wood submerged in a stream, August 2015, A.L. Shi, S-431 (MFLU 20–0288, holotype); ex-type culture, MFLUCC 16–0992.

Notes: In the phylogenetic analysis, Acrogenospora basalcellularispora clustered with A. sphaerocephala (CBS 206.36) with low support (66% ML and 0.98 BPP). Unfortunately, CBS 206.36 lacks a morphological description and only LSU sequence data is available in GenBank. Morphologically, our new isolate can be distinguished from other Acrogenospora species by its pale orange-brown to olivaceous brown, broadly obvoid to spherical conidia with several small to large guttules and a small, hyaline, subcylindrical to subglobose basal cell. In our study, A. aquatica also has conidia with a basal cell. However, we can distinguish them by the shape (broadly obvoid to spherical vs. subprolate to broadly ellipsoidal) and color (pale orange-brown to olivaceous brown vs dark brown to black) of conidia and size (260–395 × 8–12 vs. 200–250 × 7.5–9.5 µm) of conidiophores.

Acrogenospora guttulatispora D.F. Bao, Z.L. Luo, K.D. Hyde & H.Y. Su, sp. nov.

Index Fungorum number: IF 557597; Facesoffungi number: FoF 07982, Figure 4

Holotype—MFLU 20–0289

Etymology—Referring to the large guttule in the conidia.

Saprobic on submerged decaying wood. Sexual morph: Undetermined. Asexual morph: Colonies effuse on natural substrate, hairy, dark brown. Mycelium mostly immersed, composed of septate, grayish brown, branched, smooth hyphae. Conidiophores 295–330 × 7.5–8.5 µm (x = 312.7 × 8 µm, n = 15), mononematous, macronematous, solitary, erect, straight or slightly flexuous, cylindrical, indeterminate, unbranched, dark brown, paler toward apex, pale brown to hyaline at apex, septate, guttulate, smooth. Conidiogenous cells holoblastic, monoblastic, integrated, initially terminal, later becoming intercalary, cylindrical, smooth, pale brown, proliferating percurrently. Conidia 30–33.5 × 26.5–28 µm (x = 34 × 27 µm, n = 30), acropleurogenous, solitary, spherical or subspherial, truncate at base, hyaline when young, dark brown when mature, aseptate, with a large guttule, smooth.

Material examined: CHINA, Yunnan Province, Dali, Cangshan Mountain, on decaying wood submerged in Heilongxi stream, June 2013, Z.L. Luo, S-189 (MFLU 20–0289, holotype), ex-type culture, MFLUCC 17–1674 = ICMP 21772.

Notes: Acrogenospora guttulatispora can be distinguished from other species by the large guttule in the conidia. In the phylogenetic analyses, A. guttulatispora is close to A. aquatica. However, the conidia of A. guttulatispora are spherical or subspherical with a large guttule, without a basal cell. While, those A. aquatica are subprolate to broadly ellipsoidal with a hyaline, globose to subglobose basal cell. In addition, there are 22 base pair differences in the RPB2 region between these two species.

Acrogenospora obovoidispora D.F. Bao, Z.L. Luo, K.D. Hyde & H.Y. Su, sp. nov.

Index Fungorum number: IF 557602; Facesoffungi number: FoF 04691, Figure 5

Holotype—MFLU 20–0295

Etymology—Referring to the broadly obvoid conidia of this fungus.

Saprobic on submerged decaying wood. Sexual morph: Undetermined. Asexual morph: Colonies effuse on natural substrate, hairy, dark brown. Mycelium partly immersed, partly superficial, composed of septate, brown to dark brown, branched, smooth hyphae. Conidiophores 209–277 × 7.5–10 µm (x = 243 × 8.8 µm, n = 15), mononematous, macronematous, solitary, erect, straight or slightly flexuous, cylindrical, unbranched, brown to dark brown, paler toward apex, septate, smooth. Conidiogenous cells holoblastic, monoblastic, integrated, initially terminal, later becoming intercalary, cylindrical, smooth, pale brown, proliferating percurrently. Conidia 32.5–37.5 × 27–32 µm (x = 35 × 29.6 µm, n = 30) wide, acropleurogenous, solitary, oval to broadly ellipsoidal, base truncate, aseptate, olivaceous brown to black, thick-walled, smooth.

Material examined: CHINA, Yunnan Province, Dali, Huadianba Mountain, saprobic on decaying wood submerged in a stream, 9 December 2017, Z.L. Luo, S-1614 (MFLU 20–0295, holotype); ex-type culture, MFLUCC 18–1622.

Notes: Acrogenospora obovoidispora is similar to A. gigantospora in having mononematous, macronematous, conidiophores and solitary, aseptate conidia. However, Acrogenospora obovoidispora differs from A. gigantospora in having solitary conidiophores and oval to broadly ellipsoidal,
FIGURE 3 | *Acrogenospora basalicellularispora* (MFLU 20–0288, holotype) (a) Colony on wood. (b) Conidiophores, conidiogenous cells and conidia. (c) Conidiogenous cells and conidia. (d–h) conidia. (j) Germinating conidium. (j,k) Culture on MEA (upper and lower view). Scale bars: (a) 200 μm, (b) 50 μm, (c–i) 20 μm.
olivaceous brown to black conidia, while conidiophores of A. gigantospora are single or in groups of 2–4, and conidia are broadly obovoid to subspherical, dark brown to black (Ma et al., 2012).

**Acrogenospora olivaceospora** D.F. Bao, Z.L. Luo, K.D. Hyde & H.Y. Su, sp. nov.

*Index Fungorum number*: IF 557598; *Facesoffungi number*: FoF 07983, *Figure 6*

*Holotype*—MFLU 20–0290

*Etymology*—Referring to the conidia which are olive-green.

*Saprobic* on submerged decaying wood. **Sexual morph**: Undetermined. **Asexual morph**: Colonies effuse on natural substrate, hairy, dark brown. *Mycelium* mostly immersed, composed of grayish brown, septate, branched, smooth hyphae. *Conidiophores* 100–175 × 6–9 μm (x = 137 × 7.4 μm, n = 20), mononematous, macronematous, solitary, erect, straight or slightly flexuous, cylindrical, indeterminate, unbranched, dark brown to olive, paler toward apex, septate, smooth.
FIGURE 5 | Acrogenospora obovoidispora (MFLU 20–0295, holotype) (a) Colony on wood. (b–e) Conidiophores with conidia. (f–i) Conidiogenous cells with conidia. (j–n) Conidia. Scale bars: (a) 200 μm, (b–e) 50 μm, (f–h) 30 μm, (i–n) 20 μm.
**Conidiogenous cells** holoblastic, monoblastic, integrated, initially terminal, later becoming intercalary, cylindrical, smooth, pale brown, proliferating percurrently. **Conidia** $32-37 \times 28-33 \ \mu m$ ($\bar{x} = 34.5 \times 30.5 \ \mu m \ n = 30$), acropleurogenous, solitary, subprolate to broadly ellipsoidal, base truncate, olive to black, aseptate, thick-walled, lacking guttules, smooth.

**Material examined:** CHINA, Yunnan Province, Dali, Cangshan Mountain, on decaying wood submerged in a stream, March 2016, H.W. Shen, S-715 (MFLU 20-0290, holotype), ex-type culture, MFLUCC 20–0096.

**Notes:** In the phylogenetic analyses, *Acrogenospora olivaceospora* clustered with *A. sphaerocephala* (MFLU 18-1130 and MFLUCC 16-0179). However, *A. olivaceospora* differs from *A. sphaerocephala* by the shape, color and size of conidia (Table 2). *Acrogenospora olivaceospora* has olive to black, subprolate to broadly ellipsoidal conidia, lacking guttules, while conidia of *A. sphaerocephala* are olive-green to brown, spherical or sub spherical and guttulate.

**Acrogenospora olivaceospora** is most similar to *A. subprolata* in having subprolate to broadly ellipsoidal, olive to black, aseptate, thick-walled conidia. However, *A. olivaceospora* has solitary conidiophores whereas those of *A. subprolata* are sometimes in small groups. In addition, the conidiophores of *A. olivaceospora* are shorter (102–172 × 5.8–9 vs. 150–300 × 9–12 \ \mu m) and the conidia are smaller (32–36.9 × 28–32.8 vs. 39–46 × 30–39 \ \mu m).

**Acrogenospora submersa** D.F. Bao, Z.L. Luo, K.D. Hyde & H.Y. Su, sp. nov.

**Index Fungorum number:** IF 557601; **Facesoffungi number:** FoF 07986, **Figure 7**

Holotype—MFLU 20–0294,

Etymology—Referring to the submerged habitat of this fungus.

**Saprobic** on submerged decaying wood. **Sexual morph:** Undetermined. **Asexual morph:** Colonies effuse on natural substrate, hairy, dark brown. **Mycelium** partly immersed, partly superficial, composed of septate, brown
### TABLE 2 | Morphological comparison of *Acrogenospora* species.

| Taxa                | Conidiophores              | Conidia                      | Sequence data | References          |
|---------------------|-----------------------------|------------------------------|---------------|---------------------|
|                     | Color                        | Size (µm)                    | Color         | Shape               | Size (µm)       |                        |                           |
|                     |                              |                              | Dark to blackish brown | Broadly ellipsoidal | 40–60 x 30–36 | Absent                 | Goh et al., 1998         |
| *Acrogenospora altissima* | Blackish brown to black | Up to 800 x 12–20 | Dark brown to black | Subprolate to broadly ellipsoidal, with a basal cell and guttules | 29–34.5 x 24.5–31 | Present                 | This study               |
| *A. aquatica*       | Brown to dark brown, paler toward apex | 202–250 x 7.5–9.5 | Pale orange-brown to olivaceous brown | Broadly obvoid to spherical, with basal cell and guttules | 27.5–33.5 x 21.5–25.5 | Present                 | This study               |
| *A. basaliccellularispora* | Brown to dark brown, paler toward apex | 259–395 x 8–12 | Brown to dark brown | Broadly ellipsoidal to obvoid | 19–32 x 16–23.5 | Present                 | Goh et al., 1998         |
| *A. carmichaeliana* | Brown to dark brown, paler toward apex | Up to 400 x 9–12 | Brown to dark brown | Broadly ellipsoidal to obvoid | 32–41 x 17–24 | Absent                  | Hu et al., 2010          |
| *A. ellipsoidea*    | Pale orange brown to mid brown | 87.5–162.5 x 6.5–7.5 | Dark brown | Ellipsoidal, atrobrunnea, | 30–33.5 x 26.5–28 | Present                 | This study               |
| *A. gigantospora*   | Dark blackish brown          | Up to 700 x 9–14.5            | Dark brown to black | Broadly obvoid to spherical | 25–55 x 21–50 | Absent                  | Hughes, 1978             |
| *A. guttulatispora* | Dark brown, paler toward apex | 294–331 x 7.5–8.6 | Hyaline when young, dark brown at mature, | Spherical or subspherical, with a large guttule | 7.5–9.5 x 7–8.5 | Absent                  | Ma et al., 2012          |
| *A. hainanensis*    | Brown to dark brown, paler toward the apex | 60–80 x 2–3.5 | Brown | Spherical or subspherical | 19–32 x 13–23 | Absent                  | Goh et al., 1998         |
| *A. megalospora*    | Black (opaque), Yellow brown at apex | Up to 400 x 9–12 | Mid to dark brown | Obovoid | 26–54 x 21.5–30.5 | Present                 | Hughes, 1978             |
| *A. novae-zelandiae* | Black (opaque), paler at apex | Up to 720 x 10–16 | Mid to dark brown | Broadly ellipsoidal to oblong | 30–33.5 x 26.5–28 | Present                 | This study               |
| *A. obovoidspora*   | Brown to dark brown, paler toward apex | 209–277 x 7.5–10 | Oliveaceous brown to black | Oval to broadly obvoid | 32.4–37.6 x 27–32 | Present                 | This study               |
| *A. olivaceospora*  | Dark brown to olive, paler toward apex | 102–172 x 5.8–9 | Olive to black | Subprolate to broadly ellipsoidal | 32–36.9 x 28–32.8 | Present                 | This study               |
| *A. ovalia*         | Pale to mid brown           | Up to 240 x 4–4.5            | Mid orange-brown | Oval to oblong or broadly obvoid | 24–33 x 18–22 | Absent                  | Goh et al., 1998         |
| *A. setiformis*     | Dark blackish brown         | Up to 350 x 4–7              | Dark reddish brown | Broadly ellipsoidal | 14.5–24 x 10.5–19 | Absent                  | Ellis, 1972              |
| *A. sphaerocephala* | Mid to dark brown, pale brown at apex | 100–730 x 7.2–10.5 | Pale to mid brown | Subspherical | 17–30 x 15.5–30 | Present                 | Hughes, 1978             |
| *A. submersa*       | Brown to dark brown, paler toward apex | 163–223 x 6.7–10 | Hyaline when young, pale orange-brown to olivaceous brown at mature | Spherical or subspherical | 28–32.5 x 25–28 | Present                 | This study               |
| *A. subprolata*     | Pale to mid brown           | 150–300 x 9–12              | Pale orange-brown to olivaceous brown | Broadly ellipsoidal to subprolate | 39–46 x 30–39 | Present                 | Goh et al., 1998         |
| *A. thailandica*    | Pale to dark brown, paler toward the apex | 850–950 x 3.5–8 | Olive-green to dark brown | Spherical or subspherical | 15.5–24.5 | Present                 | Hyde et al., 2019         |
| *A. verrucispora*   | Brown to dark brown, paler toward apex | 100–230 x 5–6 | Mid to dark brown | Spherical or subspherical | 19–21.5 diam | Present                 | This study               |
| *A. yunnanensis*    | Brown to dark brown, paler toward apex | 260–391 x 8.8–12 | Hyaline when young, dark brown to black at mature | Spherical or subspherical | 23–32.5 x 22–30 | Present                 | This study               |
FIGURE 7 | Acrogenospora submersa (MFLU 20–0294, holotype) (a) Colonies on wood. (b–g) Conidiophores with conidia. (h,l) Conidiogenous cells with conidia. (j,k) Conidia. (i) Germinating conidium. (m,n) Culture on MEA (upper and lower view). Scale bars: (a) 200 µm, (b–g) 50 µm, (h–l) 20 µm.
Bao et al. Diverse Genus, Acrogenospora (Acrogenosporaceae)

**FIGURE 8** Acrogenospora subpulvata (MFLU 20–0293) (a,b) Colonies on wood. (c–e) Conidiophores and conidia. (f–h) Conidiogenous cells with conidia. (i–l) Conidia. Scale bars: (a,b) 200 µm, (c–e) 100 µm, (f,g) 30 µm, (h–l) 20 µm.

to dark brown, branched, smooth hyphae. *Conidiophores* 163–223 × 6.5–10 µm (\( \bar{x} = 193 \times 8.4 \) µm, \( n = 15 \)), mononematous, macronematous, solitary, erect, straight or slightly flexuous, cylindrical, unbranched, brown to dark brown, paler toward apex, septate, smooth. *Conidiogenous cells* holoblastic, monoblastic, integrated, initially terminal, later becoming intercalary, cylindrical, smooth, pale brown, proliferating percurrently. *Conidia* 28–32.5 × 25–28 µm (\( \bar{x} = 30.3 \times 26.5 \) µm, \( n = 30 \)), acropleurogenous, solitary, spherical or subspherical, base truncate, aseptate, hyaline when young, pale orange-brown to olivaceous brown when mature, smooth.

*Material examined:* CHINA, Yunnan Province, saprobic on decaying wood submerged in Lancang River, 9 December 2017,
Notes: *Acrogenospora submersa* is similar to *A. hainanensis* in having mononematous, macronematous, solitary, proliferating percurrently conidiophores, monoblastic, integrated, terminal conidiogenous cells and spherical or subspherical, aseptate conidia. However, *A. submersa* differs from *A. hainanensis* by having longer conidiophores (163–223 × 6.7–10 μm vs. 60–80 × 2–3.5 μm), and much larger conidia (28–32.5 × 25–28 μm vs. 7.5–9.5 × 7–8.5 μm), which are hyaline to pale orange-brown or olivaceous brown rather than brown. Phylogenetically, *A. submersa* is related to *A. guttulatispora* but in a distinct lineage. Therefore, we introduce it as a new species.

*Acrogenospora subprolata* Goh, K.D. Hyde & C.K.M. Tsui, Mycol. Res. 102(11): 1314 (1998) Figure 8

* Saprobic on submerged decaying wood. **Sexual morph:** Undetermined. **Asexual morph:** Colonies effuse on natural substrate, hairy, dark brown. *Mycelium* partly immersed, partly superficial, composed of septate, brown to dark brown, branched, smooth hyphae. *Conidiophores* 212.5–348 × 8–10.5 μm (μ = 280.5 × 9.4 μm, n = 15) wide, mononematous, macronematous, solitary, or in a small group, erect, straight
FIGURE 10 | Acrogenospora yunnanensis (MFLU 20–0292, holotype) (a) Colony on wood. (b–d) Conidiophores, conidiogenous cells and conidia. (e–g) Conidiogenous cells and conidia. (h–k) Conidia. Scale bars: (a) 200 µm, (b–d) 50 µm, (e–g) 30 µm, (h–j) 15 µm.
or slightly flexuous, cylindrical, unbranched, brown to dark brown, paler toward apex, septate, smooth. Conidiogenous cells holoblastic, monoblastic, moniliform, initiated, initially terminal, later becoming intercalary, cylindrical, smooth, pale brown, proliferating percurrently. Conidia 40–51 × 32–40 μm (x = 45 × 31.5 μm, n = 30) wide, acrogenous, solitary, subprolate to broadly ellipsoidal, base truncate, asceptate, hyaline when young, olivaceous brown to black when mature, thick-walled, smooth.

Material examined: CHINA, Tibet Province, saprobic on decaying wood submerged in a stream, 2 May 2017, Z.L. Luo. S-1455 (MFLU 20–0293), living culture, MFLUCC 18–1314.

Notes: Acrogenospora subprolata is characterized by conidiophores that are macronematous, mononematous, solitary or in groups of 2–4 with multiple percurrent proliferations and by acrogenous, subprolate to broadly ellipsoidal, pale orange-brown to olivaceous brown, asceptate, thick-walled conidia. Our isolate fits well with the characters of A. subprolata as described by Goh et al. (1998). Therefore, we identify this collection as A. subprolata.

Acrogenospora verrucispora Hong Zhu, L. Cai & K.Q. Zhang as ‘ verrucospora’, Mycotaxon 92: 384 (2005) Figure 9

Saprobic on submerged decaying wood. Sexual morph: Undetermined. Asexual morph: Colonies effuse on natural substrate, hairy, dark brown. Mycelium partly immersed, partly superficial, composed of septate, brown to dark brown, branched, smooth hyphae. Conidiophores 103–149 × 5.6–7.4 μm (x = 125.8 × 6.5 μm, n = 15) wide, mononematous, macronematous, solitary or sometimes in a small group, erect, straight or slightly flexuous, cylindrical, unbranched, brown to dark brown, paler toward apex, septate, smooth. Conidiogenous cells holoblastic, monoblastic, moniliform, initiated, initially terminal, later becoming intercalary, cylindrical, smooth, pale brown, proliferating percurrently. Conidia 21.3–26.5 × 20.6–25.5 μm (x = 24 × 23 μm, n = 30) wide, acrogenous, solitary, spherical or subpherical, base truncate, asceptate, hyaline when young, orange-brown to olivaceous brown when mature, distinctly verrucose.

Material examined: CHINA, Yunnan Province, Gaoligongsan Mountain, saprobic on decaying wood submerged in a stream, May 2017, H.W. Shen. S-1142 (MFLU 20–0287), living culture, MFLUCC 18–1617.

Notes: Acrogenospora verrucispora was introduced by Zhu et al. (2005) with distinct verrucose conidia, it was collected from bamboo in a stream in Yunnan province, China. A. verrucispora is characterized by mononematous, macronematous, proliferating percurrently conidiophores, monoblastic, integrated conidiogenous cells and acrogenous, solitary, spherical or subpherical, verrucose conidia. Our isolate fits well with the original description of A. verrucispora. As the sequence data of A. verrucispora is not available in GenBank, we identify our isolate as A. verrucispora based on the morphological characters and provide sequence data for this species.

Acrogenospora yunnanensis D.F. Bao, Z.L. Luo, K.D. Hyde & H.Y. Su, sp. nov.

Index Fungorum number: IF 557600; Facesoffungi number: FoF 07985, Figure 10

Holotype—MFLU 20–0292

Etymology—Referring to Yunnan province, China, where the fungus was collected.

Saprobic on submerged decaying wood. Sexual morph: Undetermined. Asexual morph: Colonies effuse on natural substrate, hairy, dark brown. Mycelium partly immersed, partly superficial, composed of septate, brown to dark brown, branched, smooth hyphae. Conidiophores 260–390 × 8.5–12 μm (x = 326 × 10.3 μm, n = 15), mononematous, macronematous, solitary, erect, straight or slightly flexuous, cylindrical, unbranched, brown to dark brown, paler toward apex, septate, smooth. Conidiogenous cells holoblastic, monoblastic, integrated, initially terminal, later becoming intercalary, cylindrical, smooth, pale brown, proliferating percurrently. Conidia 23–32.5 × 22–30 μm (x = 28 × 26 μm, n = 30), acropleurogenous, solitary, spherical or sub spherical, truncate at base, asceptate, hyaline when young, dark brown to black when mature, smooth.

Material examined: CHINA, Yunnan Province, Laojunshan Mountain, on decaying wood submerged in a stream, August 2015, A.L. Shi, S-1114 (MFLU 20–0292, holotype); ex-type culture, MFLUCC 18–1611. CHINA, Gaoligongsan mountain, saprobic on decaying wood submerged in a stream, August 2015, A.L. Shi. S-774 (DLU 774, isotype), living culture, MFLUCC 20–0099.

Notes: In the phylogenetic analysis, Acrogenospora yunnanensis shares a sister relationship to A. submersa. Morphologically, A. yunnanensis can be distinguished from A. submersa by the longer conidiophores (Table 2) and color of conidia. Acrogenospora yunnanensis has dark brown to black conidia with a large guttule, while conidia of A. submersa are pale orange-brown to olivaceous brown at maturity and lack a guttule.

Morphologically, A. yunnanensis is most similar to A. gigantospora and A. subprolata in having similar conidial shape. However, they differ in size of conidiophores and conidia (Table 2).

DISCUSSION

In this study, we provide new descriptions and illustrations for seven new species and two known species of Acrogenospora. This study contributes to a better taxonomic understanding and proposes that there could be a number of additional new species within the genus and its diversity could be much higher than anticipated. Acrogenospora species are cosmopolitan with worldwide distribution, they are mainly found on dead and submerged wood especially in freshwater habitats (Hughes, 1978; Goh et al., 1998; Ma et al., 2012; Hyde et al., 2019). Among the 20 Acrogenospora spp., 15 species were reported from freshwater habitats and only 5 of them were recovered from terrestrial habitats. Our study has shown that in a small area of Yunnan Province there are 14 species of Acrogenospora in streams alone and indicates that the genus is highly diverse, and has been found to occur with other genera in the region (Hyde et al., 2019). Previous studies have also reported that there could be an amazing fungal diversity hidden in the South East Asian region (Hyde et al., 2018).
Acrogenospora species are quite similar to each other, and previous studies suggested to distinguish them based on conidial shape, size, and color and the degree of pigmentation of the conidiophores (Hughes, 1978, Table 2). We found that guttules and basal cells of conidia are also important characters to distinguish species and a morphological comparison of all Acrogenospora species is provided (Table 2).

Previous publications on submerged wood in freshwater have lumped several Acrogenospora collections and identified them based on morphology as A. sphaerocephala (Table 3) perhaps because of the difficulty of using morphs alone to delineate species and due to a lack of DNA sequence data. It is likely that the collections of A. sphaerocephala in older publications (Table 3) are wrongly named and further taxonomic work is necessary.

Before this study, there were 13 species of Acrogenospora but only three of them had sequence data available in GenBank, and there was no data for the ex-type strains. Our phylogenetic sampling included 12 strains of Acrogenospora (Acrogenosporaceae), and all strains grouped with four species of Minutisphaera (Minutisphaeraceae) within Minutisphaerales (99% ML and 0.99 PP, Figure 1). The results were similar to the analyses by Jayasiri et al. (2018). In our analyses, Acrogenospora carmichaeliana (CBS 206.36) did not cluster with other strains of A. carmichaeliana, instead clustered with our new isolate A. basalicellularispora with low statistical support. Unfortunately, there are no morphological descriptions for CBS 206.36, so we are unable to compare its morphology with our new isolate. Further collections and phylogenetic studies of Acrogenospora are needed to better understand the phylogenetic placement of those species which lack sequence data and, undoubtedly, many more novel species can be found.

The phylogenetic analysis provide clear resolution to the taxonomic complexities within this group. Protein-coding genes have been shown to be essential to identify a taxon up to species level (Tang et al., 2007, 2009; Jeewon et al., 2017). In our study, we sequenced the RPB2 and TEF1α sequence data to distinguish Acrogenospora species and the phylogenetic trees are provided in Supplementary Files 1, 2. In our phylogenetic tree (LSU + SSU + TEF1α + RPB2, Figure 1), Acrogenospora aquatica, A. guttulatispora, A. submersa and A. yunnanensis grouped together, but they constitute different clades based on phylogenies derived from the TEF and RPB2 data which clearly support that they are phylogenetically distinct species. Acrogenospora verrucispora clustered with A. carmichaeliana (Figure 1), but there are 9 bp differences in TEF1α gene region. In addition, they can be easily distinguished from each other by the shape, color and wall of conidia, (conidia of A. verrucispora are spherical or subspherical, orange-brown to olivaceous brown, distinctly verrucose-walled, while A. carmichaeliana has broadly ellipsoidal to obvoid, brown to dark brown, smooth-walled conidia). Acrogenospora olivaceospora is close to A. sphaerocephala, however, there are 12.3% nucleotide differences in RPB2 gene region between them. These results support our establishment of the new taxon as recommended by Jeewon and Hyde (2016). As for

| Acrogenospora collections | Location    | Habitat         | Host                          | References                  |
|---------------------------|-------------|-----------------|-------------------------------|-----------------------------|
| A. altissima              | New Zealand | Lake            | Rotten wood of Weinmannia racemosa | Goh et al., 1998            |
| A. aquatica               | China (Yunnan) | Stream         | Submerged wood               | This study                  |
| A. basalicellularispora   | China (Yunnan) | Stream         | Submerged wood               | This study                  |
| A. ellipsidea             | China (Yunnan) | Stream         | Submerged wood               | Hu et al., 2010             |
| A. guttulatispora         | China (Yunnan) | Stream         | Submerged wood               | This study                  |
| A. gigantospora           | New Zealand | Lake            | Rotten wood of Weinmannia racemosa | Hughes, 1978              |
| A. obovoidspora           | China (Yunnan) | Stream         | Submerged wood               | This study                  |
| A. olivaceospora          | China (Yunnan) | Stream         | Submerged wood               | This study                  |
| A. ovala                  | China (Hongkong) | Reservoir     | Submerged wood               | Goh et al., 1998            |
| A. sphaerocephala         | China (Hongkong) | Stream         | Submerged wood               | Tsui et al., 2000           |
| A. sphaerocephala         | Philippines | Stream          | Submerged wood and bamboo     | Cai et al., 2003            |
| A. sphaerocephala         | China (Hongkong) | Stream         | Submerged wood and Pinus baits | Ho et al., 2001             |
| A. sphaerocephala         | Durban, South Africa | River     | Submerged Phragmites        | Hyde et al., 1998           |
| A. sphaerocephala         | Seychelles   | River           | Submerged wood               | Goh et al., 1998            |
| A. sphaerocephala         | China (Hongkong) | Reservoir     | Submerged wood               | Goh and Hyde, 1999          |
| A. sphaerocephala         | Australia    | River           | Submerged wood               | Goh et al., 1998            |
| A. sphaerocephala         | UK           | River           | Submerged wood               | Goh et al., 1998            |
| A. submersa               | China (Yunnan) | River           | Submerged wood               | This study                  |
| A. subprolata             | China (Tibet) | Stream          | Submerged wood               | This study                  |
| A. subprolata             | China (Hongkong) | River         | Submerged wood               | Goh et al., 1998            |
| A. thailandica            | Thailand     | Stream          | Submerged wood               | Hyde et al., 2019           |
| A. verrucispora           | China (Yunnan) | Stream         | Submerged wood              | Zhu et al., 2005             |
| A. verrucispora           | China (Yunnan) | Stream         | Submerged wood               | This study                  |
| A. yunnanensis            | China (Yunnan) | Stream         | Submerged wood               | This study                  |
A. *basalicellularispora* and A. *subprolata* there are no DNA sequences available from protein-coding genes but they can be easily distinguished from other species based on morphological characters (Table 2).

Hyde et al. (2019) discussed whether *Acrogenospora sphaerocephala* was the asexual morph of *Farlowiella carmichaeliana* and whether A. megalospora was wrongly introduced as the asexual morph of *F. carmichaeliana*. In our phylogenetic analyses, *Acrogenospora sphaerocephala* did not cluster with *A. carmichaeliana*, forming different clades within Acrogenosporaceae. DNA sequences of Ex-type strains of both A. megalospora and *Farlowiella carmichaeliana* are not available in GenBank. Therefore, the connection of sexual and asexual morph of *Farlowiella carmichaeliana* is not clear and this needs further morpho-molecular evidence.

**DATA AVAILABILITY STATEMENT**

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/Supplementary Material.

**AUTHOR CONTRIBUTIONS**

D-FB conducted the experiments, analyzed the data, and wrote the manuscript. EM, DB, and KH revised the manuscript. Z-LL planned the experiments and analyzed the data. H-YL planned the experiments and funded the experiments. H-WS conducted the manuscript. EM, DB, and KH revised the manuscript. Z-LL

**REFERENCES**

Arzanlou, M., Groenewald, J. Z., Gams, W., Braun, U., Shin, H. D., and Crous, P. W. (2007). Phylogenetic and morphotaxonomic revision of *Ramichloridium* and allied genera. Stud. Mycol. 58, 57–93. doi: 10.1016/s1322-5118(07)58003-4

Bao, D. F., Hyde, K. D., Luo, Z. L., Su, H. Y., and Nalumpang, S. (2019). *Minutisphaera* aquaticum sp. nov. increases the known diversity of *Minutisphaeraceae*. Asian J. Mycol. 2, 306–314. doi: 10.5945/ajom/2/1/25

Barbosa, F. R., Gusmao, L. F. P., Raja, H. A., and Shearer, C. A. (2013). New species and new records of freshwater ascomycetes from Brazil and Costa Rica. Mycologia 105, 335–343. doi: 10.3852/12-054

Boehm, E. W. A., Schoch, C. L., and Spatafora, J. W. (2009). On the evolution of the Hysteriaceae and *Mytiliniidaceae* (Pleosporomycetidae, Dothideomycetes, Ascomycota) using four nuclear genes. Mycol. Res. 113, 461–479. doi: 10.1016/j.mycres.2008.12.001

Boonmee, S., Rossman, A. Y., Liu, J. K., Li, W. J., Dai, D. Q., Bhat, D. J., et al. (2014). *Tubufusales*, ord. nov., integrating sexual and asexual generic names. Fungal Divers. 68, 239–298. doi: 10.1007/s13225-014-0304-7

Boonmee, S., Zhang, Y., Chomnunti, P., Chukeatirote, E., Tsui, C. K. M., Bahkali, A. H., et al. (2011). Revision of *lignicolous Tubufusaceae* based on morphological reexamination and phylogenetic analysis. Fungal Divers. 51, 63–102. doi: 10.3114/sim.2009.64.02

Braun, U., Crous, P. W., Groenewald, J. Z., Verkley, G. M., Groenewald, J. Z., and Crous, P. W. (2011). *Pseudovirgaria*, a fungicolous hyphomycete genus. *IMA Fungus* 2, 65–69. doi: 10.5598/imafungus.2011.02.01.09

Cai, L., Jeewon, R., and Hyde, K. D. (2006). Phylogenetic investigations of Sordariaceae based on multiple gene sequences and morphology. Mycol. Res. 110, 137–150. doi: 10.1016/j.mycres.2005.09.014

Cai, L., Tsui, C. K. M., Zhang, K. Q., and Hyde, K. D. (2002). Aquatic fungi from Lake Fuxian, Yunnan, China. Fungal Divers. 9, 57–70.

Cai, L., Zhang, K. Q., McKenzie, E. H. C., and Hyde, K. D. (2003). Biodiversity of fungi on submerged wood in a stream and its estuary in the Tai Ho Bay, Hong Kong. Fungal Divers. 13, 205–220.

Campbell, J., Ferrer, A., Raja, H. A., Sivichai, S., and Shearer, C. A. (2007). Phylogenetic relationships among taxa in the Jahnulales inferred from 18S and 28S nuclear ribosomal DNA sequences. Can. J. Bot. 85, 873–882. doi: 10.1139/b07-080

Chomnunti, P., Hongsaensan, S., Aguirre-Hudson, B., Tian, Q., Perisho, D., Dhami, M. K., et al. (2014). The sooty moulds. *Fungal Divers.* 66, 1–36. doi: 10.3114/sim.2009.66.01

Crous, P. W., Schoch, C. L., Hyde, K. D., Wood, R., Gueidan, C., de Hoog, G. S., et al. (2015). Phylogenetic insights resolve *Phoma*–*Didymocyrtis* (Pleosporales, Phaeosphaeriaceae) as polyphyletic: *Didymocyrtis* (Pleosporales, Phaeosphaeriaceae) with *Phoma*-like anamorphs resurrected and segregated from *Polycoccum* (Trypetheliales, Polycoccaceae fam. nov.). *Fungal Divers.* 74, 53–89. doi: 10.1007/s11235-015-0345-6

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**SUPPLEMENTARY MATERIAL**

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmicb.2020.01606/full#supplementary-material

**FILE S1 | Phylogenetic tree based on RAxML analysis of TEF1α sequence data. Bootstrap support values for maximum likelihood and maximum parsimony (MP, red) higher than 75% are indicated above the nodes as MLBS/MPBS. The tree is rooted with *Hysterographium fraxini* (MFLU 15-3035 and MFLU 15-3681).**

**FILE S2 | Phylogenetic tree based on RAxML analysis of RPB2 sequence data. Bootstrap support values for maximum likelihood and maximum parsimony (MP, red) higher than 75% are indicated above the nodes as MLBS/MPBS. The tree is rooted with *Aliquandostipite* khaoayaiensis (AFTOL-ID 1364).**
Ferrer, A., Miller, A. N., and Shearer, C. A. (2011). *Minutisphaera* and *Natipusilla*: two new genera of freshwater Dothideomycetes. *Mycologia* 103, 411–423. doi: 10.3852/10-177

Giraldo, A., Gené, J., Sutton, D. A., Madrid, H., Cano, J., Crous, P. W., et al. (2014). Phylogenetic circumscription of *Artographus* (Eremomycetaceae, Dothideomycetes). *Persoonia* 32, 102–114. doi: 10.3767/003158514X680207

Goh, T. K., and Hyde, K. D. (1996). Biodiversity of freshwater fungi. *J. Ind. Microbiol.* 17, 328–334. doi: 10.1007/BF01574764

Goh, T. K., and Hyde, K. D. (1999). Fungi on submerged wood and bamboo in the Plover Cove Reservoir, Hong Kong. *Fungal Divers.* 3, 57–85.

Goh, T. K., Hyde, K. D., and Tsui, K. M. (1998). The hyphomycete genus *Minutisphaera*. *Mycologia* 90, 530–539. doi: 10.2307/3760087

Guarnaccia, V., Groenewald, J. Z., Li, H., Glienke, C., Carstens, E., Hattingh, V., et al. (2010). Complete phylogenies of Plasmodiophora and allied anamorph genera: towards a reclassification of the Plasmodiophoromycetes. *Mycologia* 103, 508–519. doi: 10.1080/00275514.2009.101002.

Guojing, S., Zhang, Z., Qiao, M., and Yu, Z. F. (2019). *Phalangispora sinensis* sp. nov. from Yunnan, China and two new members of Wiesneriomycetaceae. *Int. J. Syst. Evol. Microbiol.* 69, 3217–3223. doi: 10.1099/ijsem.0.003612

Hall, T. A. (1999). BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symp. Ser.* 31, 95–98.

Hirayama, K., Bahkali, A. H., and Hyde, K. D. (2010). Four new freshwater fungi gen. nov. from Pummam, China and description of two new species, *Pan paracapitales* and *P. paracapitricarpa*, from citrus in Europe. *Stud. Mycol.* 67, 161–185. doi: 10.1016/j.simyco.2017.05.003

Guatimosim, E., Firmino, A. L., Bezerra, J. L., Pereira, O. L., Barreto, R. W., and Crous, P. W. (2015). Towards a phylogenetic reappraisal of *Parmulariaceae* and *Asterinaceae* (Dothideomycetes). *Persoonia* 35, 230–241. doi: 10.3767/003158514X680846

Guo, J. S., Zhang, Z., Qiao, M., and Yu, Z. F. (2019). *Phalangispora sinensis* sp. nov. from Yunnan, China and two new members of Wiesneriomycetaceae. *Int. J. Syst. Evol. Microbiol.* 69, 3217–3223. doi: 10.1099/ijsem.0.003612

Hall, T. A. (1999). BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symp. Ser.* 31, 95–98.

Hirayama, K., Tanaka, K., Raja, H. A., Miller, M. A., Pfeiffer, W., and Schwartz, T. (2010). “Creating the CIPRES Science Gateway.” Proceedings of the 2010 Mycological Institute.

Hu, D. M., Cai, L., Chen, H., Bahkali, A. H., and Hyde, K. D. (2010). Four new freshwater fungi associated with submerged wood from Southwest Asia. *Sydowia* 62, 191–203.

Huang, S. K., Jeewon, R., Hyde, K. D., Bhat, D. J., Wen, T. C., and Dommergues, P. (2018b). *Phalangispora sinensis* sp. nov. from freshwater habitats in China. *Mycotaxon* 99, 451–660. doi: 10.1007/s13225-015-0324-y

Huang, S. K., Jeewon, R., Wanasinghe, D. N., Rampadarath, S., Puchooa, D., Zhou, L. G., Liu, A. R., et al. (2017). Nomenclatural and identification pitfalls of endophytic mycota based on DNA sequence analyses of ribosomal and protein genes phylogenetic markers: a taxonomic dead end? *Mycosphere* 8, 1802–1817. doi: 10.5943/mycosphere/8/10/7

Katoh, K., and Standley, D. M. (2013). MAFFT multiple sequence alignment software version 7: improvements in performance and usability. *Mol. Biol. Evol.* 30, 772–780. doi: 10.1093/molbev/msb010

Luo, Z. L., Hyde, K. D., Liu, J. K., Phookamsak, R., Wikee, S., Li, Y. M., Ariyawansha, H., et al. (2015). Fungal diversity notes 1–110: taxonomic and phylogenetic contributions to fungal species. *Fungal Divers.* 72, 1–197. doi: 10.1007/s13225-015-0324-y

Luo, Z. L., Hyde, K. D., Bhat, D. J., Wang, Y. G., Luo, Z. L., and Hyde, K. D. (2019). Freshwater Sordariomycetes. *Fungal Divers.* 99, 451–660. doi: 10.1007/s13225-019-00438-1

Ma, J., Ma, L. G., Zhang, Y. D., Xia, J. W., and Zhang, X. G. (2012). Lignicolous freshwater fungi from China II: novel Distoseptisporaceae species from northwestern Yunnan Province and a suggested unified method for studying lignicolous freshwater fungi. *Mycosphere* 4, 444–461. doi: 10.5943/mycosphere/9/3/2

Mugambi, G. K., and Huhndorf, S. M. (2009b). Parallel evolution of hysterothecial ascomata in ascolocularous fungi (Ascomycota). *Mycotaxon* 105, 1492–1501. doi: 10.1017/S095375620100507X

Mugambi, G. K., and Huhndorf, S. M. (2009b). Parallel evolution of hysterothecial ascomata in ascolocularous fungi (Ascomycota). *Mycotaxon* 105, 1492–1501. doi: 10.1017/S095375620100507X

Njoku, R., Guo, J. S., Zhang, Z., Qiao, M., and Yu, Z. F. (2019). *Phalangispora sinensis* sp. nov. from Yunnan, China and two new members of Wiesneriomycetaceae. *Int. J. Syst. Evol. Microbiol.* 69, 3217–3223. doi: 10.1099/ijsem.0.003612

Njoku, R., Liew, E. C. Y., Simpson, J. A., Hodgkiss, I. J., and Hyde, K. D. (2003). Phylogenetic significance of morphological characters in the taxonomy of Pestalotiopsis species. *Mycotaxon* 87, 161–189. doi: 10.3114/sim.2009.64.05

Njoku, R., Liew, E. C. Y., and Hyde, K. D. (2002). Phylogenetic relationships of *Pestalotiarum* and allied genera inferred from ribosomal DNA sequences and morphological characters. *Mol. Mycol. Evol.* 25, 378–392. doi: 10.1016/S0167-7552(01)00073-8

Pestalotiopsis spp. from Taiwan. *Mycotaxon* 59, 209–215. doi: 10.3767/0003158510680207

Pestalotiopsis spp. from Taiwan. *Mycotaxon* 59, 209–215. doi: 10.3767/0003158510680207

Shearer, C. A., Miller, M. A., Pfeiffer, W., and Schwartz, T. (2010). “Creating the CIPRES Science Gateway.” Proceedings of the 2010 Mycological Institute.

Shearer, C. A., Miller, M. A., Pfeiffer, W., and Schwartz, T. (2010). “Creating the CIPRES Science Gateway.” Proceedings of the 2010 Mycological Institute.
Muggia, L., Hafellnera, J., Wirtzb, N., Hawksworth, D. L., and Grube, M. (2008). The sterile micro filamentous lichenized fungi Cystoecus ebeneus and Racodium rupestre are relatives of plant pathogens and clinically important dothideal fungi. *Mycol. Res.* 112, 50–56. doi: 10.1016/j.mycres.2007.08.025

Nelsen, M. P., Lücking, R., Grube, M., Mbatchou, J. S., Muggia, L., RivasPlata, E., et al. (2009). Unravelling the phylogenetic relationships of lichenised fungi in Dothideomyceta. *Stud. Mycol.* 64, 135–144. doi: 10.3114/sim.2009.64.07

Nelsen, M. P., Lücking, R., Mbatchou, J. S., Andrew, C. J., Spielmann, A. A., and Lumbsch, H. T. (2011). New insights into relationships of lichen-forming Dothideomycetes. *Fungal Divers.* 51, 155–162. doi: 10.1007/s11225-011-0144-7

Nylander, J. A. A. (2004). MrModeltest v2 Program Distributed by the Author. Uppsala: Uppsala University.

Pang, K. L., Hyde, K. D., Alias, S. A., Su etrong, S., Guo, S. Y., I did, R., et al. (2013). Dyfrolomycetae, a new family in the Dothideomycetes, Ascomycota. *Cryptogam. Mycol.* 34, 223–232. doi: 10.7872/crypt.v34.iss3.2013.223

Phillips, A. J. L., Alves, A., Pennycook, S. R., Johnston, P. R., Ramaley, A., Akulov, A., et al. (2008). Resolving the phylogenetic and taxonomic status of dark-spored teleomorph genera in the Botryosphaeriaceae. *Persoonia* 51, 155–162. doi: 10.3767/003158508X340742

Phookamsak, R., Norphanphoun, C., Tanaka, K., Dai, D. Q., Luo, Z. L., Liu, J. K., et al. (2015). Towards a natural classification of Astrosphaeriaceae-like species; introducing Astrosphaeriellaceae and Pseudoastrosphaeriellaceae fam. nov. and Astrosphaeriellopsis, gen. nov. *Fungal Divers.* 74, 143–197. doi: 10.1007/s13225-015-0352-7

Quaedvlieg, W., Binder, M., Groenewald, J. Z., Summerrell, B. A., Carnegie, A. I., Burgess, T. I., et al. (2014). Introducing the Consolidated Species Concept to resolve species in the Teratosphaeriaceae. *Persoonia* 33, 1–40. doi: 10.3767/003158514X681981

Raja, H. A., El-Elum, T., Oberlies, N. H., Shearer, C. A., Miller, A. N., Tanaka, K., et al. (2015). Minutisphaeriales (Dothideomycetes, Ascomycota): a new order of freshwater ascomycetes including a new family, Minutisphaeriaceae, and two new species from North Carolina, USA. *Mycologia* 107, 845–862. doi: 10.3852/15-0313

Raja, H. A., Oberlies, N. H., Figueroa, M., Tanaka, K., Hirayama, K., Hashimoto, A., et al. (2013). Freshwater ascomycetes: Minutisphaera (Dothideomycetes) revisited, including one new species from Japan. *Mycologia* 105, 959–976. doi: 10.3852/12-313

Rakeman, J. L., Lafe, U. B. K., Chen, Y. C., Honeycutt, R. J., and Cookson, B. T. (2005). Multilocus DNA sequence comparisons rapidly identify pathogenic molds. *J. Clin. Microbiol.* 43, 3324–3333. doi: 10.1128/JCM.43.7.3324-3333.2005

Rambaut, A. (2014). FigTree 1.4.2. Availalbe at: http://tree.bio.ed.ac.uk/software/figtree (accessed July 9, 2014).

Rana, B., and Yang, Z. (1996). Probability distribution of molecular evolutionary trees: a new method of phylogenetic inference. *J. Mol. Evol.* 43, 304–311. doi: 10.1007/BF02338839

Ronquist, F., and Huelsenbeck, J. P. (2003). MrBayes3: bayesian phylogenetic inference under mixed models. *Bioinformatics* 19, 1572–1574. doi: 10.1093/bioinformatics/btg170

Rossman, A. Y., Crous, P. W., Hyde, K. D., Hawksworth, D. L., Aptroot, A., Bezerra, J. L., et al. (2015). Recommended names for pleomorphic genera in Dothideomycetes. *IMA Fungus* 6, 507–523. doi: 10.5598/imafungus.2015.06.02.14

Schoch, C. L., Crous, P. W., Groenewald, J. Z., Boehm, E. W. A., Burgess, T. I., de Gruyter, J., et al. (2009). A class wide phylogenetic assessment of Dothideomycota. *Stud. Mycol.* 64, 1–15. doi: 10.3114/sim.2009.64.01

Schoch, C. L., Shoemaker, R. A., Seifert, K. A., Hambleton, S., Spatafora, J. W., and Crous, P. W. (2006). A multigene phylogeny of the Dothideomycetes using four nuclear loci. *Mycologia* 98, 1041–1052. doi: 10.1080/15575236.2006.11832632

Spatafora, J. W., Owensby, C. A., Douhan, G. W., Boehm, E. W. A., and Schoch, C. L. (2012). Phylogenetic placement of the ectomycorrhizal genus *Cenococcum* in Glioniaceae (Dothideomycetes). *Mycologia* 104, 758–765. doi: 10.3852/11-233
Wijayawardene, N. N., Crous, P. W., Kirk, P. M., Hawksworth, D. L., Boonmee, S., Braun, U., et al. (2014). Naming and outline of Dothideomycetes–2014 including proposals for the protection or suppression of generic names. *Fungal Divers.* 69, 1–55. doi: 10.1007/s13225-014-0309-2

Wijayawardene, N. N., Hyde, K. D., Al-Ani, L. K. T., Tedersoo, L., Haelewaters, D., Rajeshkumar, K. C., et al. (2020). Outline of fungi and fungal-like taxa. *Mycosphere* 11, 1060–1456. doi: 10.5943/mycosphere/11/1/8

Wong, K. M. K., Goh, T. K., Hodgkiss, I. J., Hyde, K. D., Ranghoo, V. M., Tsui, C. K. M., et al. (1998). Role of fungi in freshwater ecosystems. *Biodivers Conserv.* 7, 1187–1206. doi: 10.1023/A:1008883716975

Yang, J., Liu, J. K., Hyde, K. D., Jones, E. B. G., and Liu, Z. Y. (2017). Two new species in Fuscosporellaceae from freshwater habitat in Thailand. *Mycosphere* 8, 1893–1903.

Zhang, Y., Jeewon, R., Fournier, J., and Hyde, K. D. (2008). Multi-gene phylogeny and morpho-taxonomy of *Amniculicola lignicola*: novel freshwater fungus from France and its relationships to the Pleosporales. *Fungal Biol.* 112, 1186–1194. doi: 10.1016/j.mycres.2008.04.004

Zhu, H., Cai, L., Hyde, K. D., and Zhang, K. Q. (2005). A new species of *Acrogenospora* from submerged Bamboo in Yunnan, China. *Mycotaxon* 92, 383–386.

**Conflict of Interest:** EM was employed by Manaaki Whenua Landcare Research. The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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