



# *Pseudobactrodesmium* (Dactylosporaceae, Eurotiomycetes, Fungi) a Novel Lignicolous Genus

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During our ongoing surveys of fungi on submerged wood in the Greater Mekong Subregion, we collected two new species similar to *Bactrodesmium longisporum*. *Pseudobactrodesmium* gen. nov. is introduced to accommodate the new species, *P. aquaticum*, *P. chiangmaiensis* and *B. longisporum* is transferred to this genus. Fasciculate conidiophores, enteroblastic conidiogenous cells and subulate to fusiform, phragmoseptate conidia with a tapering apical cell and sheath characterize the genus. *Pseudobactrodesmium aquaticum* has longer conidia than *P. chiangmaiensis*. The placement of *Pseudobactrodesmium* in *Dactylosporaceae* (Eurotiomycetes) is a novel finding based on analyses of combined LSU, SSU, ITS and RPB2 sequence data. Our study reveals that *Pseudobactrodesmium* is likely to be a speciose genus with different species in streams around the world.

**Keywords:** *Bactrodesmium*, multi-gene, sheath, submerged wood, taxonomy

## INTRODUCTION

*Dactylosporaceae* accommodates ecologically and morphologically diverse genera, and was reinstated by Diederich et al. (2018) to replace *Sclerococcaceae* (Réblová et al., 2016). For example, the freshwater genus *Cylindroconidiis* has holoblastic conidiogenous cells (Yu et al., 2018), while the terrestrial genera *Pseudosclerococcum* and *Rhopalophora* are apothecial ascomycetes and dematiaceous phialidic hyphomycetes, respectively (Réblová et al., 2016; Olariaga et al., 2019). The terrestrial and marine genus *Sclerococcum* (= *Dactylospora*) has loose sporodochia with catenate conidia or apothecia-like ascomata often growing on lichens or decaying wood (Hawksworth, 1975; Jones et al., 1999; Pang et al., 2014; Pino-Bodas et al., 2017). Additionally, *Fusichalara minuta*, which is a dematiaceous phialidic hyphomycete, and some beetle-associated strains also cluster in this family (Vargasasensio et al., 2014; Tedersoo et al., 2017).

Aquatic hyphomycetes are a morphologically diverse and polyphyletic group (Shenoy et al., 2006; Baschien et al., 2013; Su et al., 2016). Species with similar morphological characters are difficult to identify without molecular data. Previously, identification was mostly carried out based on morphology and only a few asexual taxa have been subjected to phylogenetic studies (Goh and Hyde, 1996; Cai et al., 2002; Cai and Hyde, 2007). With more molecular data becoming available for phylogenetic analyses, numerous new combinations have been proposed to accommodate poorly documented hyphomycetous species (Lu et al., 2018; Yang et al., 2018a,b). Molecular data also demonstrated that some previously known congeneric species are now distributed in different families, e.g., *Monodictys arctica* in *Leptosphaeriaceae* (Day et al., 2006), *M. capensis* in *Pleomonodictydaceae* (Hernández-Restrepo et al., 2017), and some other *Monodictys* species in *Parabambusicolaceae* (Tanaka et al., 2015). Although the polyphyletic nature of some hyphomycetous genera were partially resolved, e.g., *Dendryphon*, *Sporidesmium* and torula-like species (Su et al., 2016), fresh collections with molecular data are still needed to obtain a natural classification of hyphomycetes.

Invalidly established by Berkeley and Broome (1865) with *Sporidesmium abruptum* as the type, the hyphomycetous genus *Bactrodesmium* was segregated from *Sporidesmium*, with *B. abruptum* as the lectotype (Hughes, 1958). *Bactrodesmium* is distributed worldwide with more than 48 species (Wijayawardene et al., 2017a; Index Fungorum database<sup>1</sup>). It was regarded as a member of Dothideomycetes based on the sexual-aseexual morph connection between *Bactrodesmium obliquum* and *Stuartella suttonii* (Funk and Shoemaker, 1983; Wijayawardene et al., 2017b). However, with molecular evidence, *Bactrodesmium* was shown to be polyphyletic, as *B. gabretae* clustered within Helotiales, Leotiomycetes (Koukol and Kolárová, 2010), *B. cubense* had affinities to *Morosphaeriaceae*, Dothideomycetes (Hernández-Restrepo et al., 2017) and *B. pallidum* clustered in *Savoryellaceae*, Sordariomycetes (Hernández-Restrepo et al., 2017). Recently, *Bactrodesmium fasciculare* was transferred to a newly established genus *Pleotrichocladium* in *Melanommataceae* (Dothideomycetes) based on molecular data and morphology (Hernández-Restrepo et al., 2017). Moreover, the generic type *B. abruptum* was tentatively placed in Dothideomycetes based on morphological evidence but molecular data is still lacking (Pem et al., 2019). The phylogenetic position of other species still needs to be investigated.

We are studying the freshwater fungi on submerged wood along a north–south latitudinal gradient in the Asian/Australian region (Hyde et al., 2016) and have published several papers on the Greater Mekong Subregion (Zhang et al., 2011, 2012, 2013, 2014, 2016, 2017; Dong et al., 2018; Wei et al., 2018; Yu et al., 2018; Wang et al., 2019). In this study, two taxa morphologically similar to *Bactrodesmium longisporum* were collected from submerged wood. To clarify the classification of the two new collections, we analyzed a combined LSU, SSU, ITS and RPB2 sequence dataset and compared their morphological characters. *Pseudobactrodesmium*, a new genus with two new species,

and one new combination are introduced. Morphologically similar genera are compared with *Pseudobactrodesmium* and the taxonomic placements of *Bactrodesmium* species are discussed.

## MATERIALS AND METHODS

### Isolation and Morphology

The decaying wood samples were collected from freshwater streams in Chiang Mai Province, Thailand and Yunnan Province, China. Specimens were placed in zip-lock plastic bags with moist cotton or tissue paper and taken to the laboratory. Morphological observations were carried out after incubation at room temperature for 1–2 weeks. Colonies were examined using a Nikon SMZ-171 dissecting microscope. Photomicrographs were made with a Nikon ECLIPSE Ni compound microscope fitted with a Canon EOS 600D digital camera. Measurements were made with the Tarosoft (R) Image Frame Work program. Images used for figures were processed with Adobe Photoshop CS5 software (Adobe Systems, United States). Single spore isolations were made from conidia onto potato dextrose agar (PDA) at room temperature, as detailed in Chomnunti et al. (2014) and cultured as outlined by Vijaykrishna et al. (2004) and Liu et al. (2010). Herbarium specimens (dry wood with fungal material) were deposited in the herbarium of Mae Fah Luang University (MFLU), Chiang Rai, Thailand and herbarium of Cryptogams, Kunming Institute of Botany Academia Sinica (HKAS), Kunming, China. Living cultures were deposited in Mae Fah Luang University Culture Collection (MFLUCC) and Kunming Institute of Botany Culture Collection (KUMCC). Facesoffungi and Index Fungorum numbers were registered as in Jayasiri et al. (2015) and Index Fungorum (2020), respectively.

### DNA Extraction, PCR Amplification and Sequencing

Fungi were grown on PDA for 20–30 days at 25°C. A Biospin Fungus Genomic DNA Extraction Kit (Bioer Technology Co., Hangzhou, China) was used to extract total genomic DNA from fresh mycelia according to the manufacturer's instructions. DNA amplification was performed by polymerase chain reaction (PCR). LSU, SSU, ITS and RPB2 gene regions were amplified using the primer pairs LR0R/LR5, NS1/NS4, ITS5/ITS4 and RPB2-5F/RPB2-7cR, respectively (Vilgalys and Hester, 1990; White et al., 1990; Rehner and Samuels, 1994; Liu et al., 1999). The amplifications were carried out in a 25 µL reaction volume containing 9.5 µL ddH<sub>2</sub>O, 12.5 µL 2 × PCR Master Mix, 1 µL DNA template, 1 µL each primer (10 µM). The PCR thermal cycles for the amplification of the gene regions followed the methods in Jeewon et al. (2004); Réblová et al. (2011), and Su et al. (2015). PCR products were checked on 1% agarose electrophoresis gels stained with Gel Red. The sequencing reactions were carried out by Shanghai Sangon Biological Engineering Technology and Services Co., Shanghai, China.

### Phylogenetic Analyses

The qualities of raw sequences generated in this study were checked with Finch TV version 1.4.0. Based on nucleotide

<sup>1</sup><http://www.indexfungorum.org/names/Names.asp>

BLAST<sup>2</sup> and previous publications (Raja et al., 2008; Koukol and Kolárová, 2010; Réblová et al., 2012, 2016; Diederich et al., 2013; Pang et al., 2014; Boonmee et al., 2016; Su et al., 2016; Yang et al., 2016; Hernández-Restrepo et al., 2017; Pino-Bodas et al., 2017; Yu et al., 2018; Dayarathne et al., 2019; Ekanayaka et al., 2019; Olariaga et al., 2019), related sequences together with newly generated ones were selected for constructing a phylogenetic tree. All sequences used in this study are listed in **Table 1**. The individual datasets of LSU, SSU, ITS and RPB2 were aligned using MAFFT v. 7.409 online version (Kazutaka and Standley, 2016) and manually verified with BioEdit v.7.2.5 Biological Sequence Alignment Editor (Ibis BioSciences, CA). Phylogenetic analyses of the combined dataset (LSU, SSU, ITS and RPB2) were inferred with maximum likelihood (ML) and Bayesian inference (BI) analyses.

A ML analysis was performed with RAxML-HPC v.8 on XSEDE in CIPRES Science Gateway (Miller et al., 2010, 2015) with 1000 rapid bootstrap replicates. The model selected for ML was GTRGAMMA. Maximum likelihood bootstrap values equal to or greater than 60% are given above or below the nodes (first value, **Figure 1**). Bayesian inference was conducted with MrBayes v. 3.1.2 (Huelsenbeck and Ronquist, 2001) to evaluate posterior probabilities (BPP) (Rannala and Yang, 1996) by Markov chain Monte Carlo (MCMC) sampling. The best-fit model was GTR + I + G for LSU, SSU and RPB2, and SYM + I + G for ITS. Six simultaneous Markov chains were run for one million generations and trees were sampled every 100 generation (resulting in 10000 trees). The first 2500 trees, representing the burn-in phase of the analyses, were discarded and the remaining 7500 trees were used for calculating posterior probabilities (PP) in the majority rule consensus tree (Larget and Simon, 1999). Bayesian posterior probabilities (BPP) equal to or greater than 0.95 are given above or below the nodes (second value, **Figure 1**).

Phylogenetic trees were viewed with FigTree v1.4.0<sup>3,4</sup> and edited using Microsoft Office PowerPoint 2007 (Microsoft Corporation, WA, United States). The new sequences were deposited in GenBank (**Table 1**).

## RESULTS

### Phylogenetic Analyses

Combined LSU, SSU, ITS, and RPB2 gene regions were employed to explore the taxonomy of new collections. The alignment comprised 79 strains (including two new strains) with an alignment length of 4381 total characters. The RAxML analysis resulted in a best scoring likelihood tree selected with a final value for the combined dataset  $\ln L = -39819.188166$ . The matrix has 2564 distinct alignment patterns, with 62% of undetermined characters or gaps. Estimated base frequencies are as follows: A = 0.256432, C = 0.229269, G = 0.279558, T = 0.234740; substitution rates AC = 1.300864, AG = 2.616909, AT = 1.328213,

CG = 1.028043, CT = 6.168383, GT = 1.000000; gamma distribution shape parameter  $\alpha = 0.360140$ .

In the phylogenetic tree (**Figure 1**), the two new isolates are shown in Eurotiomycetes and distantly related to *Bactrodesmium cubense* (Dothideomycetes), *B. gabretae* (Leotiomycetes), and *B. obovatum* and *B. pallidum* (Sordariomycetes). The morphologically similar genera, e.g., *Bactrodesmiastrum*, *Dictyosporium*, *Digitodesmium*, *Distoseptispora*, and *Sporidesmium*, have phylogenetically unrelated relationships with our new strains (**Figure 1**). *Pseudobactrodesmium aquaticum* and *P. chiangmaiensis* constitute a distinct clade in the family *Dactylosporaceae* (**Figure 1**).

### Taxonomy

***Pseudobactrodesmium*** H. Zhang, W. Dong & K. D. Hyde, **gen. nov.**

*Index Fungorum number:* IF557247; *Facesoffungi number:* FoF07525

*Etymology:* in reference to *bactrodesmium*-like morphology

*Saprobic* on submerged wood in freshwater or decaying wood in terrestrial habitats. **Sexual morph:** Undetermined. **Asexual morph:** Hyphomycetous. *Colonies* sporodochial, superficial, effuse, gregarious or scattered, brown, punctiform. *Mycelium* mostly immersed, composed of septate, branched, hyaline hyphae. *Conidiophores* macronematous, mononematous, fasciculate, compact, erect, subcylindrical, septate, usually unbranched, brown, smooth. *Conidiogenous cells* enteroblastic, with inconspicuous proliferations, integrated, terminal, subcylindrical, pale brown. *Conidia* acrogenous, solitary, dry, thin-walled, smooth-walled, clavate, subcylindrical, narrowly fusiform or subulate, euseptate, phragmoseptate, brown, often enveloped by a hyaline, spherical sheath at the apex. *Apical cells* elongated, tapering gradually toward the apex, with globose tuberculate apex.

*Type species:* *Pseudobactrodesmium aquaticum* W. Dong, H. Zhang & K.D. Hyde

*Notes:* *Pseudobactrodesmium* is characterized by enteroblastic conidiogenous cells and subulate or fusiform, evenly pigmented conidia with a tapering apical cell. In contrast, *Bactrodesmium* as typified by *B. abruptum* is quite distinct in producing holoblastic conidiogenous cells and clavate to fusiform, unevenly colored conidia which are mid or dark brown at the upper part and becoming paler toward the basal cell, 3- to multi-transversely septate, with very dark bands at the septa, the upper one thick and black, unequal cells, the penultimate cell much longer than any of the others (Ellis, 1971). *Pseudobactrodesmium* nests well within the family *Dactylosporaceae* in our phylogenetic tree of the combined sequence dataset (**Figure 1**). The unique combination of morphological characters of *Pseudobactrodesmium* stands apart from other existing genera in this family (Hawksworth, 1975; Ellis, 1976; Jones et al., 1999; Réblová et al., 2016; Yu et al., 2018; Olariaga et al., 2019). *Pseudobactrodesmium* is morphologically similar to a few dematiaceous hyphomycetous genera with long or short, septate conidia, e.g., *Bactrodesmiastrum* (Holubová-Jechová, 1984), *Bactrodesmium* (Ellis, 1971, 1976), *Digitodesmium* (Boonmee et al., 2016), *Distoseptispora* (Su et al., 2016), *Scolecotigmina*

<sup>2</sup><http://www.ncbi.nlm.nih.gov/>

<sup>3</sup><http://tree.bio.ed.ac.uk/>

<sup>4</sup><http://jeb1.sourceforge.net/>

**TABLE 1** | Taxa used in the phylogenetic analysis and their corresponding GenBank accession numbers.

| Taxon  | Voucher/Culture        | GenBank accession number |                 |                  |                 |
|--|------------------------|--------------------------|-----------------|------------------|-----------------|
|  |                        | LSU                      | SSU             | ITS              | RPB2            |
| <b><i>Aquapoterium pinicola</i></b>              | <b>ATCC MYA-4213</b>   | <b>NG_056957</b>         | –               | <b>NR_111345</b> | –               |
| <i>Ascotaiwania lignicola</i>                    | NIL00005               | HQ446364                 | HQ446284        | HQ446341         | HQ446419        |
| <i>Ascotaiwania mitriformis</i>                  | HKUCC 3706             | AF132324                 | –               | –                | –               |
| <i>Ascotaiwania sawadae</i>                      | SS00051                | HQ446363                 | HQ446283        | HQ446340         | HQ446418        |
| <b><i>Bactrodesmiastrum monilioides</i></b>      | <b>FMR 10756</b>       | <b>KF771879</b>          | –               | –                | –               |
| <b><i>Bactrodesmiastrum obovatum</i></b>         | <b>FMR 6482</b>        | <b>FR870266</b>          | –               | –                | –               |
| <b><i>Bactrodesmiastrum pyriforme</i></b>        | <b>FMR 10747</b>       | <b>FR870265</b>          | –               | –                | –               |
| <i>Bactrodesmiastrum pyriforme</i>               | FMR 11931              | HE646637                 | –               | –                | –               |
| <i>Bactrodesmium cubense</i>                     | CBS 680.96             | AB807508                 | AB797218        | LC014541         | –               |
| <b><i>Bactrodesmium gabretae</i></b>             | <b>ZK171</b>           | <b>FN561755</b>          | –               | <b>FN561756</b>  | –               |
| <i>Bactrodesmium obovatum</i>                    | CBS 128676             | MH876431                 | –               | MH864978         | –               |
| <i>Bactrodesmium pallidum</i>                    | FMR 11345              | KY853485                 | –               | KY853425         | –               |
| beetle-associated isolate                        | INBio 4503Q            | KM242300                 | –               | –                | –               |
| beetle-associated isolate                        | INBio 4513J            | KM242356                 | –               | –                | –               |
| beetle-associated isolate                        | INBio 4513L            | KM242358                 | –               | –                | –               |
| cf. <i>Sclerococcum montagnei</i>                | Alr 1                  | EF210108                 | –               | –                | –               |
| <i>Cheilymenia stercorea</i>                     | AFTOL 148              | AY544661                 | AY544705        | –                | –               |
| <b><i>Clypeoloculus akitaensis</i></b>           | <b>KT 788</b>          | <b>AB807543</b>          | <b>AB797253</b> | <b>AB809631</b>  | –               |
| <b><i>Cylindroconidiis aquaticus</i></b>         | <b>MFLUCC 11-0294</b>  | <b>MH236579</b>          | <b>MH236580</b> | <b>MH236576</b>  | –               |
| <b><i>Dictyosporium meiosporum</i></b>           | <b>MFLUCC 10-0131</b>  | <b>KP710945</b>          | <b>KP710946</b> | <b>KP710944</b>  | –               |
| <b><i>Dictyosporium olivaceosporum</i></b>       | <b>KH 375</b>          | <b>AB807514</b>          | <b>AB797224</b> | <b>LC014542</b>  | –               |
| <b><i>Dictyosporium thailandicum</i></b>         | <b>MFLUCC 13-0773</b>  | <b>KP716707</b>          | –               | <b>KP716706</b>  | –               |
| <i>Digitodesmium bambusicola</i>                 | CBS 110279             | DQ018103                 | –               | DQ018091         | –               |
| <i>Distoseptispora adscendens</i>                | HKUCC 10820            | DQ408561                 | –               | –                | DQ435092        |
| <i>Distoseptispora leonensis</i>                 | HKUCC 10822            | DQ408566                 | –               | –                | DQ435089        |
| <b><i>Distoseptispora thailandica</i></b>        | <b>MFLUCC 16-0270</b>  | <b>MH260292</b>          | <b>MH260334</b> | <b>MH275060</b>  | –               |
| <b><i>Distoseptispora xishuangbannaensis</i></b> | <b>KUMCC 17-0290</b>   | <b>MH260293</b>          | –               | <b>MH275061</b>  | <b>MH412754</b> |
| <b><i>Fuscosporella pyriformis</i></b>           | <b>MFLUCC 16-0570</b>  | <b>KX550896</b>          | <b>KX550900</b> | –                | –               |
| <i>Fusichalara minuta</i>                        | CBS 709.88             | KX537758                 | KX537773        | KX537754         | KX537770        |
| <i>Loramycetes macrosporus</i>                   | AFTOL-ID 913           | DQ470957                 | DQ471005        | –                | DQ470907        |
| <i>Mollisia cinerea</i>                          | AFTOL-ID 76            | DQ470942                 | DQ470990        | –                | DQ470883        |
| <i>Morosphaeria velatispora</i>                  | KH 218                 | AB807555                 | AB797265        | –                | –               |
| <i>Morosphaeria velatispora</i>                  | KH 221                 | AB807556                 | AB797266        | –                | –               |
| <b><i>Mucispora obscuriseptata</i></b>           | <b>MFLUCC 15-0618</b>  | <b>KX550892</b>          | <b>KX550897</b> | –                | –               |
| <b><i>Parafuscosporella moniliformis</i></b>     | <b>MFLUCC 15-0626</b>  | <b>KX550895</b>          | <b>KX550899</b> | –                | –               |
| <b><i>Pleurotheciella centanaria</i></b>         | <b>DAOM 229631</b>     | <b>JQ429234</b>          | <b>JQ429246</b> | <b>JQ429151</b>  | <b>JQ429265</b> |
| <b><i>Pleurotheciella rivularia</i></b>          | <b>CBS 125238</b>      | <b>JQ429232</b>          | <b>JQ429244</b> | <b>JQ429160</b>  | <b>JQ429263</b> |
| <i>Pleurotheciella rivularia</i>                 | CBS 125237             | JQ429233                 | JQ429245        | JQ429161         | JQ429264        |
| <i>Pleurothecium recurvatum</i>                  | CBS 101580             | GU017318                 | JQ429247        | JQ429147         | –               |
| <i>Pleurothecium recurvatum</i>                  | CBS 101581             | AF261070                 | JQ429248        | JQ429148         | JQ429266        |
| <i>Pseudoascotaiwania persoonii</i>              | A57-14C                | AY590295                 | –               | –                | –               |
| <b><i>Pseudobactrodesmium aquaticum</i></b>      | <b>MFLUCC 18-1015</b>  | <b>MN335230</b>          | <b>MN335226</b> | <b>MN335228</b>  | –               |
| <b><i>Pseudobactrodesmium chiangmaiensis</i></b> | <b>MFLUCC 18-0982</b>  | <b>MN335229</b>          | <b>MN335225</b> | <b>MN335227</b>  | –               |
| <i>Pseudobactrodesmium</i> sp.*                  | NBRC104945             | –                        | –               | –                | –               |
| <b><i>Pseudosclerococcum golindoi</i></b>        | <b>ARAN-Fungi 6619</b> | <b>MK759890</b>          | <b>MK759887</b> | <b>MK759885</b>  | –               |
| <i>Rhopalophora clavisporea</i>                  | CBS 129.74             | KX537755                 | –               | KX537751         | KX537767        |
| <i>Rhopalophora clavisporea</i>                  | CBS 281.75             | KX537756                 | KX537771        | KX537752         | KX537768        |
| <b><i>Rhopalophora clavisporea</i></b>           | <b>CBS 637.73</b>      | <b>KX537757</b>          | <b>KX537772</b> | <b>KX537753</b>  | <b>KX537769</b> |
| <i>Sclerococcum ahtii</i>                        | RP23                   | KY661659                 | –               | KY661686         | –               |
| <b><i>Sclerococcum ahtii</i></b>                 | <b>RP127</b>           | –                        | –               | <b>KY661618</b>  | –               |
| <i>Sclerococcum ahtii</i>                        | RP182                  | –                        | –               | KY661622         | –               |
| <b><i>Sclerococcum chiangraiensis</i></b>        | <b>MFLU 16-0570</b>    | <b>MH718433</b>          | –               | <b>MH718440</b>  | –               |

(Continued)

TABLE 1 | Continued

| Taxon                                   | Voucher/Culture       | GenBank accession number |                 |                 |                 |
|---|-----------------------|--------------------------|-----------------|-----------------|-----------------|
|   |                       | LSU                      | SSU             | ITS             | RPB2            |
| <i>Sclerococcum deminutum</i>           | RP235                 | –                        | –               | KY661629        | –               |
| <b><i>Sclerococcum fusiformis</i></b>   | <b>MFLU 16-0593</b>   | <b>MH718434</b>          | –               | <b>MH718441</b> | –               |
| <i>Sclerococcum fusiformis</i>          | MFLU 18-0678          | –                        | –               | MH718442        | –               |
| <i>Sclerococcum glaucomarioides</i>     | RP275                 | KY661660                 | –               | KY661632        | –               |
| <i>Sclerococcum haliotrephum</i>        | ATCC:MYA-3590         | FJ176855                 | FJ176802        | –               | FJ238344        |
| <i>Sclerococcum haliotrephum</i>        | J.K. 5129B            | FJ713617                 | –               | –               | FJ713614        |
| <i>Sclerococcum lobariellum</i>         | Diederich 18109       | MH698499                 | –               | –               | –               |
| <i>Sclerococcum lobariellum</i>         | Diederich 17708       | MH698498                 | –               | –               | –               |
| <i>Sclerococcum lobariellum</i>         | ARAN-Fungi 10091      | MK759891                 | –               | –               | –               |
| <i>Sclerococcum mangrovei</i>           | CBS 110444            | FJ176890                 | FJ176836        | –               | FJ238375        |
| <i>Sclerococcum parasiticum</i>         | ARAN-Fungi 2724       | MK759892                 | MK759888        | –               | –               |
| <i>Sclerococcum parasiticum</i>         | RP422                 | KY661666                 | –               | KY661646        | –               |
| <i>Sclerococcum parasiticum</i>         | F283586               | MK759894                 | –               | –               | –               |
| <i>Sclerococcum parasiticum</i>         | F283587               | MK759895                 | –               | –               | –               |
| <i>Sclerococcum parasiticum</i>         | ARAN-Fungi A3044025   | MK759893                 | –               | –               | –               |
| <i>Sclerococcum</i> sp.                 | RP391                 | KY661664                 | –               | –               | –               |
| <i>Sclerococcum sphaerale</i>           | Diederich 17279       | JX081672                 | –               | –               | –               |
| <i>Sclerococcum sphaerale</i>           | Diederich 17283       | JX081673                 | –               | –               | –               |
| <i>Sclerococcum sphaerale</i>           | Ertz 17425            | JX081674                 | –               | –               | –               |
| <i>Sclerococcum stygium</i>             | ARAN-Fungi 3395       | MK759896                 | MK759889        | –               | –               |
| <b><i>Sclerococcum vrijmoediae</i></b>  | <b>NTOU 4002</b>      | <b>KC692153</b>          | <b>KC692152</b> | –               | <b>KC692154</b> |
| <b><i>Sporidesmium aquaticum</i></b>    | <b>MFLUCC 15-0420</b> | <b>KU376273</b>          | –               | –               | –               |
| <i>Sporidesmium bambusicola</i>         | HKUCC 3578            | DQ408562                 | –               | –               | –               |
| <b><i>Sporidesmium fluminicola</i></b>  | <b>MFLUCC 15-0346</b> | <b>KU376271</b>          | –               | –               | –               |
| <b><i>Sporidesmium submersum</i></b>    | <b>MFLUCC 15-0421</b> | <b>KU376272</b>          | –               | –               | –               |
| <b><i>Sporidesmium thailandense</i></b> | <b>MFLUCC 15-0964</b> | <b>MF374370</b>          | –               | <b>MF374361</b> | <b>MF370955</b> |
| <i>Vibrissea truncorum</i>              | CUP-62562             | AY789402                 | AY789401        | AY789403        | –               |

Ex-type strains are in bold; newly generated sequences are highlighted in red. \*The LSU, SSU, and ITS sequences of *Pseudobactrodesmium* sp. NBRC 104945 are available online at <https://www.nite.go.jp/nbrcc/catalogue/NBRCCatalogueDetailServlet?ID=NBRC&CAT=00104945>.

(Braun et al., 1999), and *Sporidesmium* (Su et al., 2016), but they are separated by molecular evidence (Figure 1).

***Pseudobactrodesmium aquaticum*** W. Dong, H. Zhang & K.D. Hyde, sp. nov., Figure 2

*Index Fungorum* number: IF557248; *Facesoffungi* number: FoF07526

*Etymology*: aquaticum in reference to the aquatic habitat

*Holotype*: MFLU 18-1171

*Saprobic* on submerged wood in freshwater. **Sexual morph**: Undetermined. **Asexual morph**: Hyphomycetous. *Colonies* sporodochial, superficial, effuse, gregarious or scattered, brown, punctiform. *Mycelium* mostly immersed, composed of septate, branched, hyaline hyphae. *Conidiophores* 26–38 × 3–4.5 μm ( $\bar{x}$  = 34 × 3.8 μm,  $n$  = 10), macronematous, mononematous, fasciculate, compact, erect, subcylindrical, the apex slightly wider than the base, septate, slightly constricted at septa, usually unbranched, brown, smooth. *Conidiogenous cells* enteroblastic, with inconspicuous proliferations, integrated, terminal, subcylindrical, pale brown. *Conidia* (80–)90–105 × 6–8.5 μm ( $\bar{x}$  = 95 × 7.5 μm,  $n$  = 20), acrogenous, solitary, dry, thin-walled, smooth-walled, clavate when young, subcylindrical to narrowly fusiform, or subulate when mature, straight or

slightly curved, euseptate, (15–)16–19-phragmoseptate, slightly constricted and darker at septa, pale brown to brown, obscurely guttulate, wedge-shaped at basal cell, with tapering apical cells, often enveloped by a hyaline, spherical, thin, gelatinous sheath at the apex, 13–20 μm diam. *Apical cells* elongated, up to 6 μm long, tapering gradually toward the apex, easily becoming senescent, subhyaline, with obscured, subglobose tuberculate ends.

*Culture characteristics*: On PDA, colony circular, slow growing, reaching 10 mm in 50 days at 25°C, gray to brown from above, dark gray from below, surface rough, dry, raised, entire at edge.

*Material examined*: CHINA, Yunnan Province, Pingbian City, on submerged wood in a stream, 20 September 2017, W. Dong, WF-24A-1 (MFLU 18-1171, **holotype**), ex-type living culture MFLUCC 18-1015; *ibid.* WF-24A-2 (HKAS 101707, **isotype**), ex-isotype living culture KUMCC 18-0056.

*Notes*: *Pseudobactrodesmium aquaticum* is introduced as the type species of *Pseudobactrodesmium* having the typical euseptate, phragmoseptate conidia with apical sheath. The enteroblastic conidiogenous cells are particularly obvious in Figure 2e.

***Pseudobactrodesmium chiangmaiensis*** X. D. Yu, W. Dong & K. D. Hyde, sp. nov., Figure 3

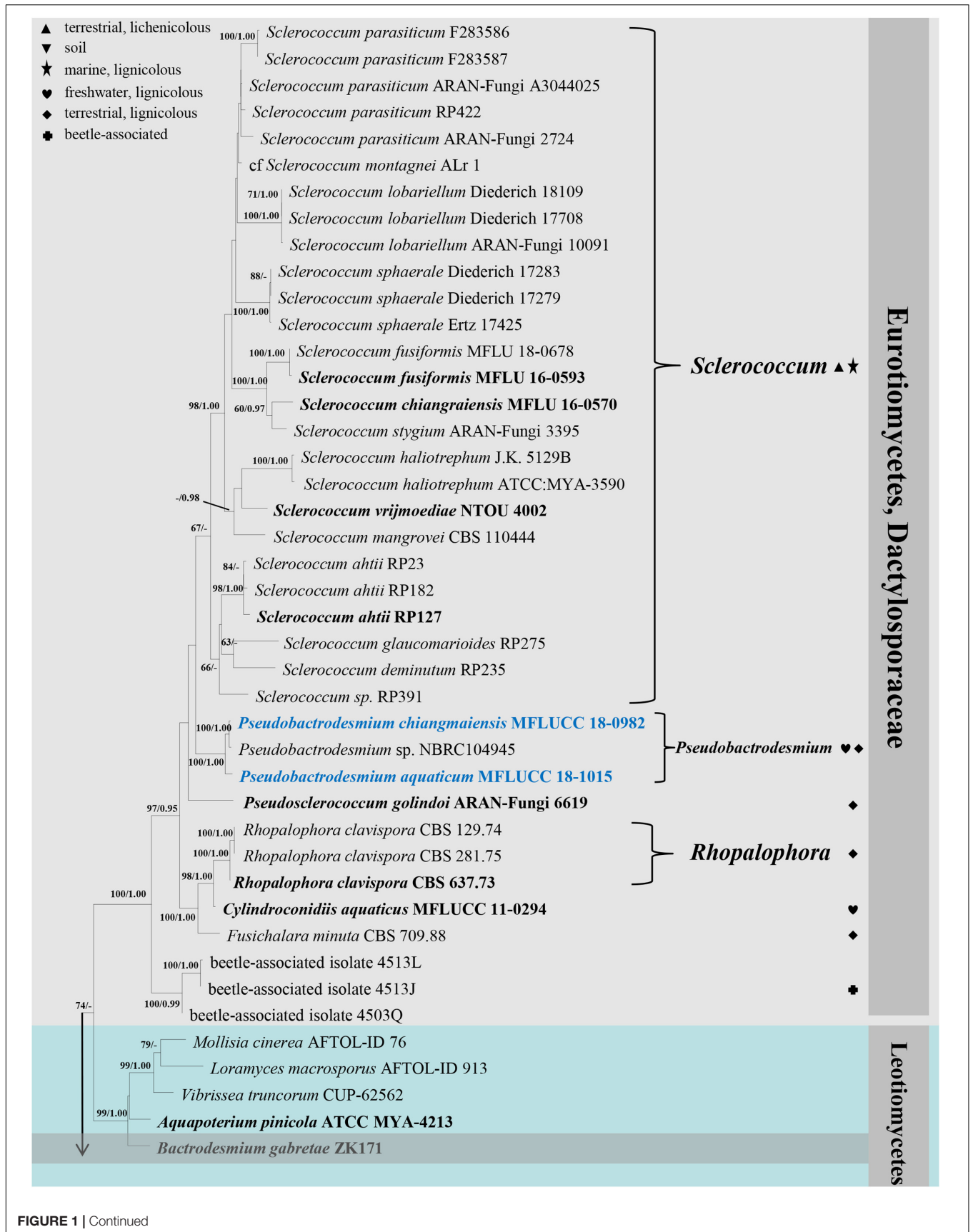
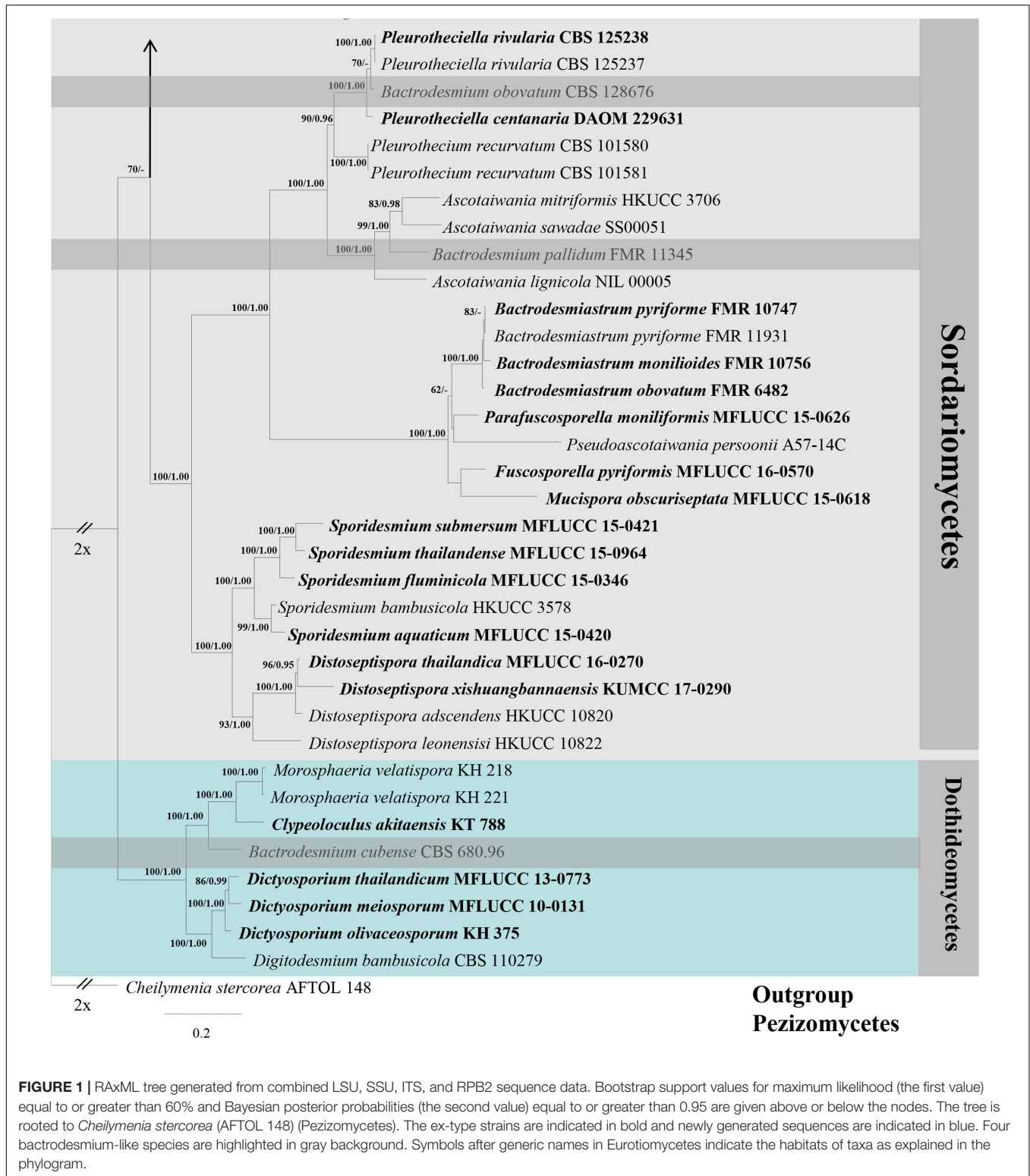
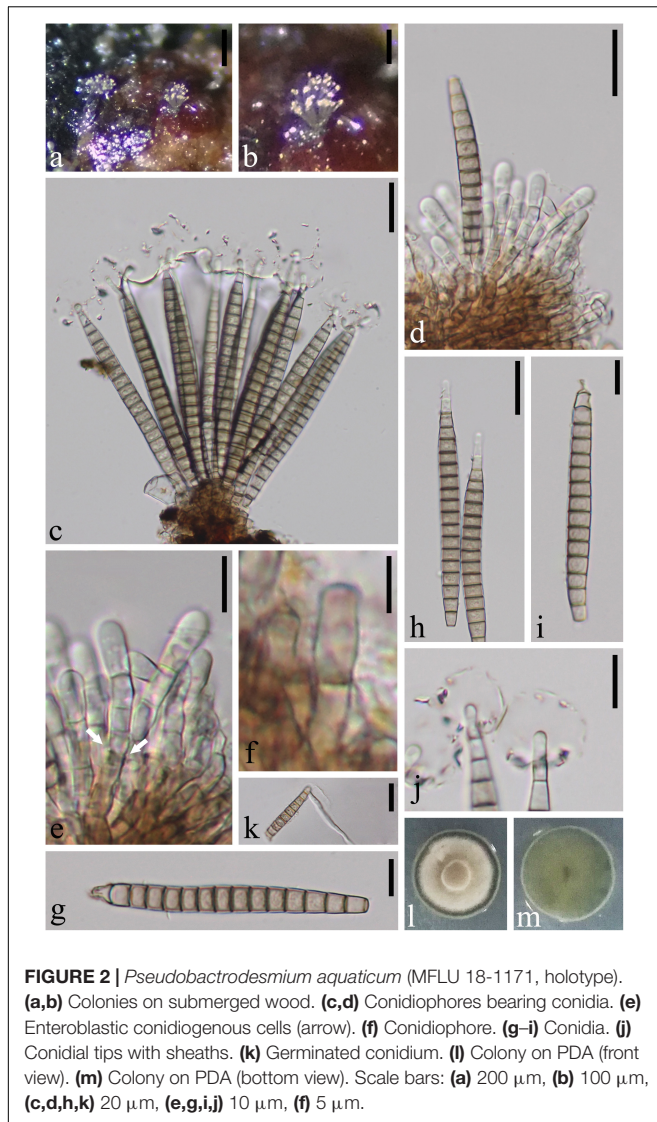


FIGURE 1 | Continued

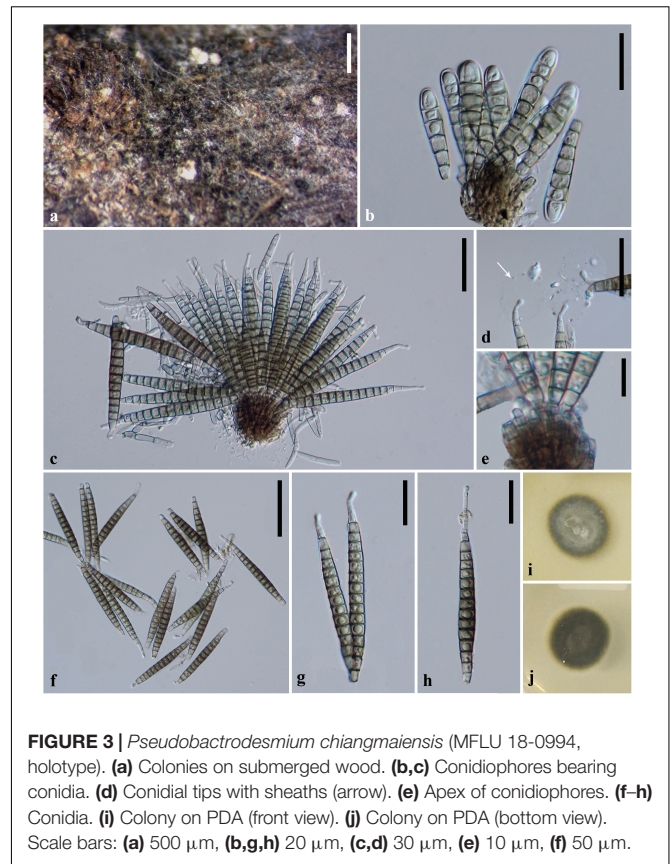


*Index Fungorum* number: IF557249; *Facesoffungi* number: FoF07527  
*Etymology*: name reflects Chiang Mai, from where the species was collected

*Holotype*: MFLU 18-0994  
*Saprobic* on submerged wood in freshwater. **Sexual morph**: Undetermined. **Asexual morph**: Hyphomycetous.  
*Colonies* sporodochial, superficial, effuse, gregarious or



scattered, dark brown to black, punctiform. *Mycelium* mostly immersed, composed of septate, branched, hyaline hyphae. *Conidiophores* 15–23  $\times$  2.5–4  $\mu\text{m}$  ( $\bar{x}$  = 21.5  $\times$  3.5  $\mu\text{m}$ ,  $n$  = 10), macronematous, mononematous, fasciculate, compact, erect, subcylindrical, septate, slightly constricted at the septa, usually unbranched, brown, smooth. *Conidiogenous cells* enteroblastic, with inconspicuous proliferations, integrated, terminal, subcylindrical, pale brown. *Conidia* 40–90  $\times$  5.5–8.5  $\mu\text{m}$  ( $\bar{x}$  = 70  $\times$  7  $\mu\text{m}$ ,  $n$  = 50), acrogenous, solitary, dry, thin-walled, smooth-walled, clavate when young, subcylindrical to narrowly fusiform, or subulate when mature, straight or slightly curved, euseptate, 6–19-phragmoseptate, slightly constricted and darker at septa, pale brown to brown, obscurely guttulate, wedge-shaped at basal cell, with tapering apical cells, often enveloped by a hyaline, spherical, thin, gelatinous sheath at the apex, 17–21  $\mu\text{m}$  diam. *Apical cells* elongated, up to but rarely 16  $\mu\text{m}$  long, tapering gradually toward apex, subhyaline, with subglobose tuberculate ends.



**Culture characteristics:** On PDA, colony circular, reaching 15 mm in 20 days at 25°C, dark gray to dark brown from above, dark gray to black from below, surface rough, dry, raised, margin entire.

**Material examined:** Thailand, Chiang Mai Province, on submerged wood in a stream, 9 February 2018, X.D. Yu, Y11 (MFLU 18-0994, **holotype**), ex-type living culture MFLUCC 18-0982.

**Notes:** *Pseudobactrodesmium chiangmaiensis* differs from *P. aquaticum* in having shorter conidia (40–90  $\times$  5.5–8.5  $\mu\text{m}$  vs. (80–)90–105  $\times$  6–8.5  $\mu\text{m}$ ), longer apical cells (up to 16  $\mu\text{m}$  vs. up to 6  $\mu\text{m}$ ), as well as darker colonies on the host (dark brown to black vs. brown). The conidial sheaths are obscure in *P. chiangmaiensis* when mounted in water, while they are easily observed in *P. aquaticum*. This is probably because the specimens were senescent which led the sheaths to deliquesce. In our phylogenetic tree, *P. chiangmaiensis* groups with *P. aquaticum* with strong bootstrap support (100% MLBS, 1.00 PP, **Figure 1**). However, a comparison of sequence data between *P. chiangmaiensis* and *P. aquaticum* shows a difference of 6, 7, 20, and 32 nucleotides in LSU, SSU, ITS, and TEF gene regions, respectively. This indicates that they are distinct species according to guidelines of Jeewon and Hyde (2016).

***Pseudobactrodesmium longisporum*** (M.B. Ellis) W. Dong & K.D. Hyde, **comb. nov.**

**Index Fungorum number:** IF557250; **Facesoffungi number:** FoF07466



≡ *Bactrodesmium longisporum* M.B. Ellis, More Dematiaceous Hyphomycetes (Kew): 68 (1976)

≡ *Stigmina longispora* (M.B. Ellis) S. Hughes, N. Z. J. Bot. 16(3): 353 (1978)

= *Bactrodesmium stilboideum* R. F. Castañeda & G. R. W. Arnold, Revta Jardín bot. Nac., Univ. Habana 6(1): 48 (1985)

≡ *Stigmina longispora* var. *stilboidea* (R. F. Castañeda & G. R. W. Arnold) J. Mena & Mercado, Reporte de Investigación del Instituto de Ecología y Sistemática, Academia de Ciencias de Cuba, Ser. Bot. 17: 10 (1987)

*Holotype*: On dead wood of *Alnus* sp. in Great Britain (IMI 63746 B)

*Known distribution*: New Zealand (Hughes, 1978), Australia (Vijaykrishna and Hyde, 2006), Brazil (Barbosa and Gusmão, 2011; Barbosa et al., 2013; Santa Izabel and Gusmão, 2016, 2018), Cuba (Castañeda Ruiz and Arnold, 1985), Great Britain (Ellis, 1976), Hong Kong, China (Wong and Hyde, 2001), India (Prabhugaonkar, 2011), Venezuela (Castañeda Ruiz et al., 2009), México (Heredia et al., 2018), Peru (Shearer et al., 2015), Philippines (Cai et al., 2003), South Africa (Hyde et al., 1998), Thailand (Hu et al., 2010; this study), United States (Raja et al., 2007).

*Notes*: *Bactrodesmium longisporum* was described by Ellis (1976) with a line-drawing. It was subsequently synonymized with *Stigmina longispora* by Hughes (1978) who observed percurrently proliferating conidiophores in old specimens from New Zealand. *Bactrodesmium stilboideum* is another synonym listed in Index Fungorum database. However, they can be distinguished by the aggregation of conidiophores (synnematous in *B. stilboideum* vs. mononematous, fasciculate conidiophores in *B. longisporum*) (Ellis, 1976; Castañeda Ruiz and Arnold, 1985).

A Thai strain of *B. longisporum* (NBRC 104945) clustered with *Pseudobactrodesmium chiangmaiensis* (MFLUCC 18-0982) in our phylogenetic tree (Figure 1). A comparison of sequence data between NBRC 104945 and MFLUCC 18-0982 shows a difference of 2, 281, 5 nucleotides in LSU, SSU and ITS gene regions, respectively (NBRC 104945 has 3 major insertions spanning over 281 nucleotides in SSU gene). In this study, we name NBRC 104945 as *Pseudobactrodesmium* sp. until its morphological characters are established to formally name this isolate. Five additional strains with only ITS2 sequence data are named as *Bactrodesmium longisporum* in GenBank. However, their status should be treated with caution as they represent OTUS from a metagenomic study of a heap leaching system (Hu et al., 2015) and further evidence of conspecificity is needed.

Unfortunately, the holotype specimen of *B. longisporum* (IMI 63746 B), does not exist in herbarium IMI.<sup>5</sup> According to protologue description of the holotype (Ellis, 1976), *B. longisporum* (IMI 63746 B) has similar conidial size to *P. chiangmaiensis* (MFLU 18-0994) (50–80 × 7–8 μm in former vs. 40–90 × 5.5–8.5 μm in latter). However, *P. chiangmaiensis* has elongated apical cells (up to 16 μm long)

with subglobose tuberculate ends, which were not described and drawn in protologue of *B. longisporum* (Ellis, 1976). The conidiophores of *B. longisporum* are up to 50 μm long, but only 15–23 μm long in *P. chiangmaiensis*. The size of apical sheath of *B. longisporum* is also unclear. Thus, we treat them as different species and synonymize *B. longisporum* under *Pseudobactrodesmium* as the third species in the genus. Epitypification of *Pseudobactrodesmium longisporum* is needed using a collection from its type locality.

## DISCUSSION

*Bactrodesmium longisporum* has been recorded as having a worldwide distribution, however these records have not been verified with molecular data. The type of *B. longisporum* also appears to be lost and therefore its identity cannot be verified. We therefore designate our new species of *Pseudobactrodesmium* from China as the generic type, describe a second species from Thailand and transfer *Bactrodesmium longisporum* to the new genus. However, it is likely that many collections of this species have been misidentified and as more collections are made from different countries, we would expect *Pseudobactrodesmium* to become speciose.

*Bactrodesmium* is a complex genus in need of extensive taxonomic reassessment. Pem et al. (2019) reviewed the holotype material of *Bactrodesmium abruptum* (≡ *Sporidesmium abruptum*) and tentatively placed the generic type in Dothideomycetes *incertae sedis* based on morphology. Both *B. cubense* and *B. obovatum* produce clavate or obovate conidia with darker septa and unequal cells, similar to the type species *B. abruptum* (Ellis, 1971; Zucconi and Lunghini, 1997). However, our phylogenetic study shows that they belong to different classes, Dothideomycetes and Sordariomycetes, respectively (Figure 1). *Bactrodesmium gabretae* differs from *B. abruptum* by its transversely or occasionally oblique, distoseptate conidia, and phylogenetically clustered in Leotiomycetes (Figure 1). *Bactrodesmium pallidum* is different from *B. abruptum* but similar to our new genus *Pseudobactrodesmium* in conidial shape (Ellis, 1959), and phylogeny places this species in Sordariomycetes (Figure 1). Our phylogenetic study is in agreement with the studies of Koukol and Kolárová (2010) and Hernández-Restrepo et al. (2017).

Although molecular data of *B. abruptum* is still missing, the working hypothesis of *Bactrodesmium sensu stricto* in Dothideomycetes provides further evidence for the introduction of *Pseudobactrodesmium*. *Pseudobactrodesmium* shares some morphological characters with *Digitodesmium* in having acrogenous, long, transversely septate conidia with a hyaline sheath at the apex (Kirk, 1981; Boonmee et al., 2016). However, the semi-macronematous, moniliform conidiophores and digitate conidia of *Digitodesmium* are clearly distinguishable from the macronematous, subcylindrical conidiophores and subcylindrical to narrowly fusiform, or subulate conidia of *Pseudobactrodesmium*. Phylogeny also segregates them into different classes, viz. *Pseudobactrodesmium* in Eurotiomycetes,

<sup>5</sup><http://www.herbimi.info/herbimi/results.htm?name=Bactrodesmium%20longisporum>

and *Digitodesmium* in Dothideomycetes (Tsui et al., 2006; Boonmee et al., 2016; this study). The conidia of *Scolecotigmina* are superficially similar to those of *Pseudobactrodesmium*, but the former is characterized by conspicuously annellate conidiogenous cells, thick-walled, smooth to verrucose conidia occasionally with a few longitudinal or oblique septa or a few intermixed distosepta, contrasting with inconspicuously proliferating conidiogenous cells and thin-walled, smooth, transversely phragmoseptate conidia with a hyaline, spherical sheath at the apex in *Pseudobactrodesmium* (Braun et al., 1999; Crous et al., 2013). *Scolecotigmina*, typified by *S. mangiferae*, clustered in Capnodiales (Dothideomycetes) (Crous et al., 2013), while *Pseudobactrodesmium* clustered in *Dactylosporaceae* (Eurotiomycetes). *Pseudobactrodesmium longisporum* is superficially similar to *Gangliostilbe malabarica* in the conidial shape and apical sheath, but the synnemata and apically rounded conidia of the latter can easily be separated from the former (Xia et al., 2015). These characters of *G. malabarica* are also distinguished from those in the collection of Castañeda Ruiz and Arnold (1985) bearing the name *Bactrodesmium stilboideum*.

It is challenging to reconstruct the phylogeny of *Bactrodesmium* considering lack of living cultures of *B. abruptum*. The species having clavate or obovate, long or short, transversely septate conidia with or without apical sheath are common and scattered in different groups (Ellis, 1976; Hughes, 1978; Holubová-Jechová, 1984; Braun et al., 1999; Koukol and Kolárová, 2010; Crous et al., 2013; Xia et al., 2015; Boonmee et al., 2016; Su et al., 2016; Hernández-Restrepo et al., 2017; Videira et al., 2017). These groups of fungi are morphologically similar and therefore molecular characters are of crucial importance to clarify their taxonomy. The sequence data of *B. abruptum* is needed in the future to clarify the natural classification of *Bactrodesmium*.

## DATA AVAILABILITY STATEMENT

The datasets generated for this study can be found in the NCBI GenBank: MN335230, MN335226, MN335228, MN335229, MN335225, and MN335227.

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## AUTHOR CONTRIBUTIONS

WD conducted the experiments, analyzed the data, and wrote the manuscript. KH planned the experiments. MD analyzed the data. X-DY conducted the experiments. DB and RJ revised the manuscript. SB funded the experiments. G-NW conducted the experiments. SN planned the experiments. HZ planned the experiments, analyzed the data, and wrote the manuscript. All authors revised the manuscript.

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**Conflict of Interest:** The 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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