



# *Mendogia diffusa* sp. nov. and an updated key to the species of *Mendogia* (Myriangiaceae, Dothideomycetes)

Vinodhini Thiyagaraja<sup>‡,§,¶</sup>, Robert Lücking<sup>#</sup>, Damien Ertz<sup>»,«</sup>, Milan C. Samarakoon<sup>§</sup>,  
Dhanushka N. Wanasinghe<sup>¶,¶</sup>, Samantha C. Karunarathna<sup>¶,¶</sup>, Ratchadawan Cheewangkoon<sup>‡,»</sup>,  
Kevin D. Hyde<sup>§,¶,¶,^,^</sup>

<sup>‡</sup> Department of Entomology and Plant Pathology, Faculty of Agriculture, Chiang Mai University, Chiang Mai 50200, Thailand

<sup>§</sup> Centre of Excellence in Fungal Research, Mae Fah Luang University, Chiang Rai 57100, Thailand

<sup>¶</sup> CAS Key Laboratory for Plant Biodiversity and Biogeography of East Asia (KLPB), Kunming Institute of Botany,

Chinese Academy of Science, Kunming 650201, Yunnan, China

<sup>¶</sup> World Agro forestry Centre East and Central Asia, Kunming 650201, Yunnan, China

<sup>#</sup> Botanischer Garten und Botanisches Museum, Freie Universität Berlin, Berlin, Germany

<sup>»</sup> Research Department, Meise Botanic Garden, Nieuwelaan 38, BE-1860, Meise, Belgium

<sup>«</sup> Fédération Wallonie-Bruxelles, Service Général de l'Enseignement Supérieur et de la Recherche Scientifique, Rue A. Lavallée 1, BE-1080, Bruxelles, Belgium

<sup>»</sup> Innovative Agriculture Research Centre, Faculty of Agriculture, Chiang Mai University, Chiang Mai 50200, Thailand

<sup>^</sup> Department of Biology, Faculty of Science, Chiang Mai University, Chiang Mai 50200, Thailand

<sup>^</sup> Research Center of Microbial Diversity and Sustainable Utilization, Chiang Mai University, Chiang Mai 50200, Thailand

Corresponding author: Kevin D. Hyde ([kdhyde3@gmail.com](mailto:kdhyde3@gmail.com))

Academic editor: Danny Haelewaters

Received: 21 Apr 2021 | Accepted: 05 Aug 2021 | Published: 07 Sep 2021

Citation: Thiyagaraja V, Lücking R, Ertz D, Samarakoon MC, Wanasinghe DN, Karunarathna SC, Cheewangkoon R, Hyde KD (2021) *Mendogia diffusa* sp. nov. and an updated key to the species of *Mendogia* (Myriangiaceae, Dothideomycetes). Biodiversity Data Journal 9: e67705. <https://doi.org/10.3897/BDJ.9.e67705>

## Abstract

## Background

*Mendogia* belongs to Dothideomycetes and its members are epiphytic on living bamboo culms or palms and distributed in tropical regions. Currently, the genus comprises seven species. Another collection resembling *Mendogia* was collected from the leaves of *Fagales* sp. in Thailand. Morphological characteristics and multilocus phylogenetic analyses, using ITS, LSU and SSU sequences, showed that the fungus is new to science, described herein

as *Mendogia diffusa*. *Mendogia diffusa* is characterised by apothecial ascostromata, a carbonised epithecium, dark brown setae on the ascostromatal surface, hyaline paraphysoids, ovoid to clavate asci and oblong to elliptical, muriform ascospores. The fungus has a dark pigmented surface and is occasionally facultatively associated with patches of green algae, but not actually lichenised. Instead, the fungus penetrates the upper leaf surface, forming dark pigmented isodiametric cells below the epidermis.

## New information

Re-examination of specimens of *M. chiangraiensis*, *M. macrostroma* and *M. yunnanensis* revealed the absence of algal associations. The status of *Mendogia philippinensis* (= *M. calami*) and *M. bambusina* (= *Uleopeltis bambusina*) was established, based on morphological comparisons and previous studies. Comprehensive morphological descriptions with phylogenetic analyses support *M. diffusa* as a novel species in *Myriangiaceae*. An updated key to the known species of the genus is also provided.

## Keywords

one new species, morphology, multilocus phylogeny, saprotroph, taxonomy

## Introduction

Dothideomycetes is the largest class in Ascomycota, comprising 19,000 species, including saprotrophs, pathogens, endophytes, epiphytes, fungicolous, lichenised and lichenicolous taxa (Hyde et al. 2013, Hongsanan et al. 2020). *Myriangiales* was introduced by Starbäck (1899), based on species producing crustose ascostromata and muriform ascospores in the Dothideomycetes (Hyde et al. 2013). These species occur as pathogens, saprobes or epiphytes on bark, leaves and branches of plants (Dissanayake et al. 2014, Jayawardena et al. 2014), while some are rock-inhabiting (Ruibal et al. 2009). Kirk et al. (2008) included *Cookellaceae*, *Elsinoaceae* and *Myriangiaceae* in *Myriangiales*. Based on molecular phylogenetic studies, Lumbsch and Huhndorf (2010) accepted only *Elsinoaceae* and *Myriangiaceae* within *Myriangiales*, whereas *Cookellaceae* was treated as Dothideomycetes *incertae sedis*. This classification was accepted in subsequent studies (Hyde et al. 2013, Dissanayake et al. 2014, Jayawardena et al. 2014, Wijayawardene et al. 2014, Dai et al. 2017, Wijayawardene et al. 2017, Wijayawardene et al. 2018, Hongsanan et al. 2020, Jiang et al. 2020, Wijayawardene et al. 2020). *Myriangiaceae* is a poorly known family (Dissanayake et al. 2014) and comprises 11 genera. These are *Anhelliella*, *Ascostratum*, *Butleria*, *Dictyocyclus*, *Eurytheca*, *Hemimyriangium*, *Mendogia*, *Micularia*, *Myriangium*, *Uleomyces* and *Zukaliopsis* (Hongsanan et al. 2020, Wijayawardene et al. 2020). Members in *Myriangiaceae* occur mainly in tropical and sub-tropical areas (Boedijn 1961, Barr 1979).

*Mendogia* was introduced by Raciborski (1900), based on the single species *M. bambusina* collected on bamboo in Indonesia. This genus was, for some time, placed in *Schizothyriaceae* (von Arx and Müller 1975). However, Dai et al. (2017) provided the first molecular data for *M. macrostroma* and transferred this genus to *Myriangiaceae*, based on morphological and phylogenetic analyses. Seven species are currently recognised within this genus (Jiang et al. 2020). They are characterised by small to large, black, flattened, solitary to scattered, superficial ascostromata with a centrally raised area, subglobose to clavate, bitunicate, (6–)8(–10)-spored asci with a distinct ocular chamber and elliptical, muriform, hyaline ascospores (Jiang et al. 2020). The species of *Mendogia*, thus far known, are exclusively epiphytic on living bamboo culms or palms and are found in Brazil, China, Indonesia, Philippines and Thailand (Raciborski 1900, Hennings 1904, von Arx and Müller 1975, Dai et al. 2017). *Mendogia* is distinguished from other genera of this family by its larger ascostromata, thick peridium, carbonaceous outer cells, pseudoparenchymatous inner cells and muriform ascospores (Phookamsak et al. 2016).

This study introduces a new species of *Mendogia* that appeared unusual due to its growth on leaves and its occasional, facultative association with patches of green algae. We conducted a detailed investigation to resolve the identity of our newly-collected material, including morphological and chemical assessments. The phylogenetic position of the taxon was investigated, based on Maximum Likelihood and Bayesian analyses of combined ITS, LSU and SSU sequences. We further re-examined herbarium collections of *Mendogia chiangraiensis*, *M. macrostroma* and *M. yunnanensis* to test potential associations with algae. Additionally, morphological comparisons between closely-related taxa have led to reclassify several species in *Mendogia* (*M. philippinensis* (= *M. calami*) and *M. bambusina* (= *Uleopeltis bambusina*)). We, therefore, provided an updated key to the genus.

## Materials and methods

### Morphological analysis

The fungal material was collected in Phayao, Thailand. Herbarium specimens of *Mendogia chiangraiensis*, *M. macrostroma* and *M. yunnanensis* were loaned from Mae Fah Luang University Herbarium (MFLU), Chiang Rai, Thailand. Fungal structures on the substrate were observed with a stereomicroscope and micro-morphological features were examined and photographed using a Nikon Eclipse E600 fluorescence microscope with a Canon 750D digital camera. Hand sections of the ascostromata were mounted in water, 5% potassium hydroxide (KOH), 5% Lugol's solution and Trypan blue. All microscopic measurements were measured in water and images were made with Tarosoft Image Frame Work (0.9.0.7) and processed with Adobe Photoshop CS6 Extended 10.0 software (Adobe Systems, San Jose, CA, USA). The newly-proposed synonymies were established, based on revision of available data from previous studies. The holotype specimen of *M. diffusa* was deposited in the Mae Fah Luang University (MFLU) Herbarium, Chiang Rai, Thailand.

## DNA extraction, PCR amplification and sequencing

The E.Z.N.A. Forensic DAT (D3591 – 01, Omega Bio–Tek, Guangzhou, China) kit was used to extract DNA, following the manufacturer's instructions. DNA samples that were intended for use as a template for PCR were stored at 4°C for use in regular work; long-term storage was at -20°C. The small and large subunits (SSU, LSU) of the nuclear ribosomal RNA gene, as well as the internal transcribed spacer (ITS) region were amplified with primer pairs NS1/NS4 (White et al. 1990), LR0R/LR5 (Vilgalys and Hester 1990, Hopple 1994) and ITS5/ITS4 (White et al. 1990), respectively. PCR amplification was performed using a final volume of 25 µl, comprised of 2.0 µl of DNA template, 1 µl of each forward and reverse primer, 12.5 µl of Taq PCR Super Mix and 8.5 µl of sterilised water. Cycling conditions were as follows: initial denaturation at 94°C for 3 min; followed by 40 cycles of denaturation at 94°C for 30 s, annealing at 55°C for 50 s, elongation at 72°C for 1 min; and a final extension at 72°C for 10 min. PCR products were examined on 1% agarose electrophoresis gels and stained with ethidium bromide. Purification and DNA sequencing were performed at Shanghai Sangon Biological Engineering Technology and Services Co. (Shanghai, P.R. China). Forward and reverse sequence reads were assembled and manually edited in Bioedit. Generated sequences were submitted to NCBI GenBank (<https://www.ncbi.nlm.nih.gov/genbank/>). Alignments and phylogenetic trees were submitted to TreeBASE with Submission ID: 28050.

## Phylogenetic analyses and species recognition

The newly-generated sequences were BLAST-searched against the NCBI GenBank standard nr/nt database (<https://blast.ncbi.nlm.nih.gov/BLAST.cgi>). Sequences of closely-related taxa for *Myriangiales* were downloaded from GenBank. We failed to generate sequences for the translation elongation factor 1-alpha (TEF1) using the primer pair EF1-983F/EF1-2218R with the PCR conditions recommended in Jiang et al. (2020). As a result, our phylogenetic analyses were carried out using ITS, LSU and SU sequences (Table 1). *Columnosphaeria fagi* (CBS 171.93), *Dothidea insculpta* (CBS 189.58), *D. sambuci* (DAOM 231303), *Dothiora cannabinae* (CBS 737.71) and *Sydowia polyspora* (CBS 116.290) were used as outgroup taxa (Jiang et al. 2020).

Phylogenetic analyses of both individual and combined aligned data were performed under Maximum Likelihood (ML) and Bayesian Inference (BI) criteria. Multiple alignments were automatically performed for each locus with MAFFT v. 7 (<http://mafft.cbrc.jp/alignment/server/index.html>, Katoh et al. 2017). Terminal ends of sequences and ambiguous regions were trimmed manually using BioEdit v.7.0.5.2 (Hall 2001) and excluded from the analysis. The phylogenetic web tool "ALTER" (Glez-Peña et al. 2010) was used to convert sequence alignment from FASTA to NEXUS format for Bayesian analysis. The estimated model of ML and Bayesian analyses were performed independently for each locus using MrModeltest v. 2.2 (Nylander 2008). ML analysis was performed in IQ-TREE web server under different partitions (Nguyen et al. 2015) for SSU, LSU, ITS1, 5.8S and ITS2 gene regions, with default parameters. MrBayes v. 3.1.2 was used to perform Bayesian analysis (Huelsenbeck and Ronquist 2001). Markov Chain Monte Carlo sampling (MCMC) was run

for 5,000,000 generations and the trees were sampled every 100<sup>th</sup> generation. The first 10% of trees that represented the burn-in phase were discarded and only the remaining 90% of trees were used for calculating posterior probabilities (PP) for the majority rule consensus tree. The resulting trees were visualised in FigTree v.1.4.0 (<http://tree.bio.ed.ac.uk/software/figtree/>), then edited in Microsoft PowerPoint 2013 and converted to a jpeg file using Adobe Photoshop CS6 (Adobe Systems, USA).

Table 1.

Taxa used in this study for the phylogenetic analyses of combined SSU, ITS and LSU sequence data and their GenBank accession numbers. The newly-generated sequences are given in black boldface.

Species	Strain	GenBank Accessions Number		
		ITS	LSU	SSU
<i>Anhelia nectandrae</i>	VIC 31767	<a href="#">NR_111700</a>	<a href="#">NG_042604</a>	-
<i>Columnosphaeria fagi</i>	CBS 171.93	<a href="#">KT693737</a>	<a href="#">AY016359</a>	<a href="#">AY016342</a>
<i>Dothidea insculpta</i>	CBS 189.58	<a href="#">AF027764</a>	<a href="#">NG_027643</a>	<a href="#">DQ247810</a>
<i>Dothidea sambuci</i>	DAOM 231303	<a href="#">NR_111220</a>	<a href="#">NG_027611</a>	<a href="#">NG_012432</a>
<i>Dothiora cannabinae</i>	CBS 737.71	<a href="#">NR_144904</a>	<a href="#">DQ470984</a>	<a href="#">NG_062696</a>
<i>Elsinoe brasiliensis</i>	CPC 18528	<a href="#">NR_148130</a>	<a href="#">JN940394</a>	<a href="#">NG_064989</a>
<i>Elsinoe caleae</i>	CBS 221.50	<a href="#">NR_148131</a>	<a href="#">NG_064001</a>	-
<i>Elsinoe centrolobii</i>	CBS 222.50	<a href="#">NR_148132</a>	<a href="#">KX886969</a>	<a href="#">NG_062717</a>
<i>Elsinoe citricola</i>	CPC 18535	<a href="#">NR_148133</a>	<a href="#">KX886970</a>	<a href="#">JN940559</a>
<i>Elsinoe embeliae</i>	CBS 472.62	<a href="#">NR_148136</a>	<a href="#">KX886974</a>	-
<i>Elsinoe erythrinae</i>	CPC 18542	<a href="#">KX887214</a>	<a href="#">KX886977</a>	<a href="#">JN940550</a>
<i>Elsinoe eucalypticola</i>	CBS 124765	<a href="#">NR_132834</a>	<a href="#">KX886978</a>	-
<i>Elsinoe eucalyptorum</i>	CBS 120084	<a href="#">NR_155080</a>	<a href="#">KX886979</a>	-
<i>Elsinoe euphorbiae</i>	CBS 401.63	<a href="#">NR_148137</a>	<a href="#">KX886980</a>	-
<i>Elsinoe fagarae</i>	CBS 514.50	<a href="#">NR_148138</a>	<a href="#">KX886981</a>	-
<i>Elsinoe fawcettii</i>	CBS 139.25	<a href="#">NR_148139</a>	<a href="#">KX886982</a>	-
<i>Elsinoe krugii</i>	CPC 18531	<a href="#">NR_148150</a>	<a href="#">KX886998</a>	<a href="#">NG_064987</a>
<i>Elsinoe lagoa-santensis</i>	CBS 518.50	<a href="#">NR_148151</a>	<a href="#">KX887002</a>	-
<i>Elsinoe leucopogonis</i>	CPC 32097	<a href="#">NR_159836</a>	<a href="#">NG_064551</a>	-
<i>Elsinoe leucospermi</i>	CBS 111207	<a href="#">NR_148154</a>	<a href="#">KX887005</a>	-
<i>Elsinoe lippiae</i>	CBS 166.40	<a href="#">NR_148155</a>	<a href="#">NG_063985</a>	-

Species	Strain	GenBank Accessions Number		
		ITS	LSU	SSU
<i>Elsinoe mangiferae</i>	CBS 226.50	<a href="#">NR_148156</a>	<a href="#">KX887012</a>	-
<i>Elsinoe perseae</i>	CBS 406.34	<a href="#">NR_148160</a>	<a href="#">NG_063977</a>	-
<i>Elsinoe phaseoli</i>	CBS 165.31	<a href="#">NR_148161</a>	<a href="#">KX887026</a>	<a href="#">NG_062718</a>
<i>Elsinoe quercus-ilicis</i>	CBS 232.61	<a href="#">NR_148164</a>	-	-
<i>Elsinoe sesseae</i>	CPC 18549	<a href="#">KX887288</a>	<a href="#">KX887051</a>	<a href="#">JN940561</a>
<i>Elsinoe sicula</i>	CBS 398.59	<a href="#">NR_148170</a>	<a href="#">KX887052</a>	-
<i>Elsinoe solidaginis</i>	CBS 191.37	<a href="#">NR_148171</a>	<a href="#">KX887053</a>	-
<i>Elsinoe tectiferae</i>	CBS 124777	<a href="#">NR_148172</a>	<a href="#">KX887055</a>	-
<i>Elsinoe terminaliae</i>	CBS 343.39	<a href="#">NR_148173</a>	<a href="#">KX887056</a>	-
<i>Elsinoe terminaliae</i>	CPC 18538	<a href="#">JN943497</a>	<a href="#">JN940371</a>	<a href="#">JN940560</a>
<i>Elsinoe theae</i>	CBS 228.50	<a href="#">NR_148174</a>	<a href="#">KX887058</a>	-
<i>Elsinoe tiliae</i>	CBS 350.73	<a href="#">KX887296</a>	<a href="#">KX887059</a>	-
<i>Elsinoe veneta</i>	CBS 164.29	<a href="#">NR_148175</a>	<a href="#">NG_059194</a>	<a href="#">NG_062714</a>
<i>Elsinoe verbenae</i>	CPC 18561	<a href="#">NR_148176</a>	<a href="#">NG_059208</a>	<a href="#">NG_064988</a>
<i>Endosporium aviarium</i>	UAMH 10530	<a href="#">NR_111286</a>	<a href="#">NG_059195</a>	<a href="#">NG_016524</a>
<i>Endosporium aviarium</i>	UAMH 10531	<a href="#">EU304352</a>	<a href="#">EU304353</a>	-
<i>Endosporium populi-tremuloidis</i>	UAMH 10529	<a href="#">EU304347</a>	<a href="#">EU304348</a>	<a href="#">EU304346</a>
<i>Mendogia diffusa</i>	<b>MFLU 20-0541</b>	<a href="#">MW854639</a>	<a href="#">MW854637</a>	<a href="#">MW854638</a>
<i>Mendogia chiangraiensis</i>	MFLU 19-0005	<a href="#">MK433591</a>	-	<a href="#">MK433594</a>
<i>Mendogia macrostroma</i>	MFLU 13-0642	<a href="#">NR_154192</a>	<a href="#">KU863104</a>	<a href="#">NG_065082</a>
<i>Mendogia yunnanensis</i>	MFLU 19-0006	-	<a href="#">MK433593</a>	<a href="#">MK433601</a>
<i>Myriangium citri</i>	MAaK	<a href="#">KU720544</a>	<a href="#">KU720541</a>	-
<i>Myriangium citri</i>	MASs1	<a href="#">KU720543</a>	<a href="#">KU720539</a>	-
<i>Myriangium citri</i>	MASs2	<a href="#">KU720542</a>	<a href="#">KU720540</a>	-
<i>Myriangium duriaei</i>	CBS 260.36	<a href="#">MH855793</a>	<a href="#">NG_027579</a>	<a href="#">AY016347</a>
<i>Myriangium hispanicum</i>	CBS 300.34	<a href="#">MH855532</a>	<a href="#">MH867034</a>	-
<i>Myriangium haraeenum</i>	CBS 247.33	<a href="#">MH855426</a>	<a href="#">KX887067</a>	-
<i>Myriangium</i> sp.	HK	<a href="#">KR909171</a>	-	-
<i>Sydowia polyspora</i>	CBS 116.29	MH 855019	<a href="#">DQ678058</a>	<a href="#">DQ678005</a>

## Taxon treatments

### *Mendogia diffusa* Thiyagaraja, Ertz, Lücking, Samarak. and K.D. Hyde, sp. nov.

- IndexFungorum [IF 558292](#)
- Facesoffungi number [FoF 09466](#)

#### Material

##### *Holotype*:

- a. kingdom: Fungi; phylum: Ascomycota; class: Dothideomycetes; order: *Myriangiales*; family: *Myriangiaceae*; genus: *Mendogia*; specificEpithet: *diffusa*; scientificNameAuthorship: Thiyagaraja, Ertz, Lücking, Samarak. and K.D. Hyde; continent: Asia; country: Thailand; stateProvince: Phayao; locality: Phu Sang; recordedBy: Milan C. Samarakoon; identificationID: MFLU 20-0541; identifiedBy: Vinodhini Thiyagaraja; dateIdentified: 4 Dec 2018; modified: 4 December 2018; institutionID: MFLU; institutionCode: Mae Fah Luang University; occurrenceID: MFLU 20-0541

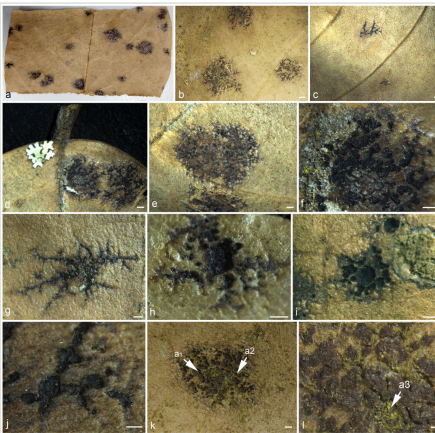


Figure 1. [doi](#)

*Mendogia diffusa* (MFLU 20-0541) a, b, d–l. Ascomata on upper leaf surface; c. Ascomata on lower leaf surface; arrows point the algae. Scale bars: b = 1000  $\mu$ m, g–j = 500  $\mu$ m

#### Description

*Saprotrophic* on dead leaves. *Thallus* absent (Fig. 1 and Fig. 2). **Sexual morph:** *Ascomata* scattered in dense, pseudostromatic, irregularly stellate groups over an effuse, thallus-like, dark structure, with thin covering layer, superficial, solitary or gregarious, easily removed from the host surface, carbonaceous, ovoid to sub-globose, black, abundant, with numerous external dark brown setae on the epithecium, which are branched at the end, individual loci (120-)225–410  $\mu$ m wide, 250–180  $\mu$ m high. *Epithecium* 16–33  $\mu$ m thick, distinct, dark brown. *Hymenium* 40–95  $\mu$ m high, hyaline.

*Hypothecium* 35–75 µm thick, distinct, thicker in the centre, brownish, infrequently with free-living unicellular algae below the hypothecium. *Excipulum* inconspicuous. *Paraphysoids* 1.1–3.3 µm thick, abundant, anastomosing, branched, not or slightly enlarged at the apex. *Asci* 45–70 × 25–35 µm ( $\bar{x}$  = 57.5 × 30 µm, n = 20), 8-spored, bitunicate, fissitunicate, ovoid to clavate, tholus thickened, tip blunted, with poorly developed stipe, ascus wall apically thickened with well-developed ocular chamber, concave. *Ascospores* 15–25 × 6–10 µm ( $\bar{x}$  = 20 × 8 µm, n = 20), irregularly arranged, hyaline, oblong to elliptical, both ends bluntly tapered, muriform, with 5–6 transverse septa, 3–6 longitudinal septa, slightly constricted at each septum, smooth-walled, without gelatinous sheath, occasionally asymmetrical. *Hymenium* I–, KI–, *Asci* I–, KI–. **Asexual morph:** Undetermined.

### Etymology

Referring to the morphology of the fungus with ascostromata that are diffuse and spread extensively on the leaves.



Figure 2. [doi](#)

*Mendogia diffusa* (MFLU 20-0541, holotype) **a–e**. Vertical sections of ascomata in water (upper surface); **f**. Vertical section of an ascoma in water (lower surface); fh, hair-like structure on leaf; **g**. Ascomata in trypan blue; **h, i**. (a1, a2) Algae; **j**. *Paraphysoids* in water; **k–m**. Asci in water; **n**. Asci in 5% KOH stained with Lugol's solution; **o1–o8**. Ascospores in water. Scale bars: (a–g) = 200 µm, (h–j) = 5 µm, (k–n) = 30 µm, (g–j) = 30 µm, (o1–o8) = 10 µm

**Habitats and Distribution:** On dead leaves of *Fagales* sp. Thus far, only known from Thailand, Phayao Province, Phu Sang District.

### Notes

*Mendogia diffusa* is the first reported species in the genus from dead dicotyledonous leaves. Other species were mostly reported from bamboo culms, with the exception of *M. manaosensis* that is reported from palm leaves (Vitória 2012, Dai et al. 2017) and



*M. philippinensis* (= *M. calami*) that is found on living leaves of *Calamus* palms (Jiang et al. 2020). In those species, ascostromata do not penetrate the leaf surface and they also differ from *M. diffusa* in the sharply delimited ascostromata; and *M. philippinensis* further differs in the smaller ascospores. The new taxon shares morphological characteristics with *Mendogia bambusina*: carbonaceous peridium, paraphysoid-like filaments, similar asci and ascospores. However, *M. diffusa* differs in the absence of ascostromata, presence of setae (Dai et al. 2017), the type of habitat (*Fagales* leaves vs. bamboo or palms culms) and its distribution (Thailand vs. Indonesia) (Hyde et al. 2013, Dai et al. 2017).

***Mendogia philippinensis* (Syd. & P. Syd.) Arx & E. Müll., Stud. Mycol. 9: 29 (1975).**

#### Nomenclature

Basionym: *Pleostomella philippinensis* Syd. & P. Syd., Anns mycol. 15(3/4): 221 (1917); Type: The Philippines, Biliran, 1914, RC McGregor 18371 (S-F61491).

Syn. nov.: *Mendogia calami* H.B. Jiang, Phookamsak and K.D. Hyde, in Jiang, Phookamsak, Xu, Karunarathna, Mortimer and Hyde, Mycol. Progr. 19: 47 (2020); Type: The Philippines, Mt. Makiling, S. A. Reyes 3367a, (S-F48343).

#### Notes

*Mendogia calami* was recently introduced from leaves of *Calamus* sp. in the Philippines (Jiang et al. 2020). However, there are no discernible differences between *M. philippinensis* and *M. calami*, neither in phenotype nor in substrate ecology. Jiang et al. (2020) did not discuss *M. philippinensis* when establishing *M. calami* and the difference implied in the table and key (ascostroma size, number of longitudinal septa) are either due to age (ascostroma size) or they are non-existent (the ascospores of *M. calami* have mostly one, rarely two longitudinal septa in the photographs and the protologue of *M. philippinensis* also indicates mostly one longitudinal septum) (Sydow and Sydow 1917). This synonymy needs further testing with molecular data as previous studies on palms have shown that the taxa on different palm species differ (Konta et al. 2016, Konta et al. 2017) as they may have derived from endophytes.

***Mendogia bambusina* Racib., Parasit. Alg. Pilze Java's (Jakarta) 3: 31 (1900)**

#### Nomenclature

Syn. nov.: *Uleopeltis bambusina* Syd. & P. Syd., Anns mycol. 12(6): 565 (1914)

*Ital. 1 (Fasc. 3): 159 (1862)*. Type: The Philippines, Luzon, Bulacan Prov., Angat, 1913, M Ramos, Bur. Sci. 21852 (GZU, S-F5988).

## Notes

*Uleopeltis* was introduced to accommodate *U. manaosensis* and later the second species *U. bambusina* added to this genus (Hennings 1904, Dai et al. 2017). *Uleopeltis manaosensis* was synonymised under *Mendogia*, while *U. bambusina* remained in *Uleopeltis* which was collected from bamboo culms in the Philippines (Hennings 1904, von Arx and Müller 1975, Dai et al. 2017). The species lacks molecular data and shares similar morphological characteristics with the type species of *Mendogia* (von Arx and Müller 1975). Dai et al. (2017) gave spores of the type material of *Mendogia bambusina* as  $13.5\text{--}25 \times 5\text{--}8 \mu\text{m}$ , but mature ascospores in the photographs are  $15\text{--}21 \times 7\text{--}9 \mu\text{m}$ . Raciborski (1900) gave the ascospores as  $17\text{--}19 \times 8 \mu\text{m}$  for *M. bambusina*. This supports the assessment of von Arx and Müller (1975) that *M. bambusina* and *Uleopeltis bambusina* are conspecific. The synonymisation is formalised here. The report of *M. bambusina* from Brazil on palm leaves (Vitória 2012) has been documented with morphological and anatomical photographs and agrees well with the material from the Paleotropics. The African *Pleiostromella halleriae* (Doidge 1921) will also key out close to *M. bambusina* and may represent another synonym. It is the only other species described in *Pleiostromella*, a synonym of *Mendogia*, but has apparently never been dispositioned. Unfortunately, no type was indicated and a total of six collections on two host species (leaves of *Halleria elliptica* and *H. lucida*) were listed. The ascus and ascospore dimensions ( $50\text{--}70 \times 20\text{--}33 \mu\text{m}$ ;  $22\text{--}24 \times 9\text{--}10 \mu\text{m}$ ) partly fit *M. bambusina*, but Doidge described two types of asci, one ovate and ca.  $50 \times 30 \mu\text{m}$  and the other clavate and ca.  $65\text{--}70 \times 20\text{--}25 \mu\text{m}$ . The latter fits *M. bambusina*, whereas the former does not conform to any of the species recognised here. Revision of all paratypes is necessary to assess the taxonomic status of this material (Sydow and Sydow 1917).

## Identification keys

Key to the species of <i>Mendogia</i>		
1	Ascomata scattered in dense, pseudostromatic, irregularly stellate groups over an effuse, thallus-like, dark structure, with thin covering layer, interascal hyphae forming distinct paraphysoids, asci $45\text{--}70 \times 25\text{--}35 \mu\text{m}$ , ascospores $15\text{--}25 \times 6\text{--}10 \mu\text{m}$ , on dead dicotyledonean leaves, Thailand	<i>Mendogia diffusa</i>
–	Ascomata one to many immersed in sharply delimited, rounded ascostromata, without associated thallus-like structure, interascal hyphae, asci and ascospores variable, on living bamboo culms or palm leaves	2

2	Ascospores narrowly oblong, transversely septate, 30–55 × 3.5–4.5 µm, interascal hyphae forming sparsely branched paraphysoids, asci cylindrical-clavate, 85–120 × 10–12 µm, Brazil	<i>Mendogia manaosensis</i> (≡ <i>Uleopeltis manaosensis</i> )
–	Ascospores broadly oblong to somewhat tapering, muriform, interascal hyphae variable, asci broadly oblong to obclavate	3
3	Ascstromata with distinct chambers appearing peritheciiform in cross section, but forming dense, concentric structures, with the asci in a single layer formed at the bottom of the chambers (type II), interascal hyphae forming more or less distinct paraphysoids, asci 45–55 × 16–20 µm, ascospores 14–18 × 5–6.5 µm, on living palm leaves, Philippines	<i>Mendogia philippinensis</i> (≡ <i>Pleiestomella philippinensis</i> ) (≡ <i>Mendogia calami</i> )
–	Ascstromata indistinctly chambered (arthothelioid) or asci in concentric structures mostly towards the periphery, with the asci irregularly dispersed in irregular layers (type I), on bamboo culms (rarely on palm leaves) interascal hyphae forming indistinct paraphysoids or textura angulate	4
4	Interascal hyphae forming indistinct paraphysoids, asci developing in concentric structures mostly towards the periphery, 17–25 µm broad, ascospores 15–28 × 7–11 µm, without gelatinous caps, on bamboo culms or palm leaves, USA, Brazil, Indonesia, Philippines	<i>Mendogia bambusina</i> (≡ <i>Uleopeltis bambusina</i> )
–	Interascal hyphae forming a textura angulata, asci and ascospores variable	5
5	Ascstromata 5–20 mm diam., asci 70–85 × 28–35 µm, ascospores 20–27 × 9–11 µm, without gelatinous sheath or caps, on bamboo culms, Thailand	<i>Mendogia macrostroma</i>
–	Ascstromata 1–5 mm diam., asci and ascospores variable in size, but ascospores with thin gelatinous sheath and distinct gelatinous caps	6
6	Asci 55–75 × 25–30 µm, ascospores 19–23 × 8–11 µm, on bamboo culms, China	<i>Mendogia yunnanensis</i>
–	Asci 75–165 × 30–40 µm, ascospores 25–35 × 12–16 µm, on bamboo culms, Thailand	<i>Mendogia chiangraiensis</i>

## Analysis

### Phylogenetic analyses

The genera of *Myriangiaceae* were well recovered, as studied in Jiang et al. (2020). The final alignment comprised 50 strains including the new strain and 2469 nucleotide positions. The topologies of the single gene markers tree and the tree topology obtained from the combined five-locus (SSU, LSU, ITS1, 5.8S, ITS2) dataset were congruent. Our phylogenetic analyses supported the placement of *Mendogia diffusa* within *Mendogia*. The average standard deviation of split frequencies at the end of total MCMC generations was calculated as 0.0024 in the Bayesian analysis.

### Discussion

*Mendogia* has previously been recorded from monocotyledons, but, in the present case, was collected on a dicotyledon, indicating many more species are likely to be discovered. Other species currently recognised in *Mendogia* (see key above) differ from the new species in the sharply delimited ascostroma (Dai et al. 2017, Jiang et al. 2020), which renders the diffusely delimited ascostroma (Fig. 1) as the most diagnostic feature of *M. diffusa*. In terms of ascospore size, *M. bambusina*, *M. macrostroma* and *M. yunnanensis* are closely related to *M. diffusa*. Apart from the sharply delimited ascostromata and the usually bambusicolous habit of all three species, *M. bambusina* has narrower asci and *M. macrostroma* differs in the much larger ascostromata (Raciborski 1900, Dai et al. 2017, Jiang et al. 2020). The internal anatomy of the ascostroma of *M. diffusa* is also distinctive, with easily discernible paraphysoids (Fig. 2). *Mendogia manaosensis* and *M. philippinensis* (= *M. calami*) also form paraphysoid-like interascal hyphae, whereas in *M. bambusina*, these are less distinctive and, in *M. chiangraiensis*, *M. macrostroma* and *M. yunnanensis*, the interascal hyphae form a *textura angularis* (Raciborski 1900, Hennings 1904, Sydow and Sydow 1917, von Arx and Müller 1975, Dai et al. 2017, Jiang et al. 2020). This variation in morphology and internal anatomy of such closely-related species is remarkable, especially given that, in our phylogenetic analysis, *M. diffusa* and *M. chiangraiensis* formed a sister clade to *M. macrostroma* and *M. yunnanensis* (Fig. 3), although without support. The new taxon shows more than 2% nucleotide differences in the ITS region compared to other *Mendogia* species. This, along with the discussed morphological differences, supports recognition as a new species (Jeewon and Hyde 2016). Unfortunately, DNA sequences are lacking for three of the seven recognised species in the genus: *M. bambusina*, *M. manaosensis* and *M. philippinensis* (= *M. calami*). *Mendogia diffusa* should not be confused with the superficially similar *Diplothecha tunae* in the same family (Dissanayake et al. 2014). The latter also forms ascostroma scattered in dense groups instead of sharply delimited ascostromata, but differs in the broad, globose asci and the much thicker covering layer of the ascostroma.

*Mendogia diffusa* was found on dead leaves and the fungal structures penetrate the upper epidermis of the leaf surface, turning the epidermal cells into a dark pigmented layer (Fig. 2). Such dark pigmented cells are absent where the ascostroma are not observed.

Some ascostromata observed were found to loosely associate with algal colonies (Fig. 1). The algae are probably trentepohlioid, 3–5  $\mu\text{m}$  thick, rounded to slightly elongate and greenish. However, since these are absent from most of the ascostromata and no closer anatomical associations or penetration structures were detected, we assume that this association is opportunistic, the algae is taking advantage of the microrelief formed by the ascostromata to colonise the otherwise smooth leaf surface. While the ascostromata were detected on dead leaves, it is unclear whether the fungus is also present on living leaves and how common is the observed opportunistic association with algae. It is possible that *M. diffusa* indirectly benefits from the presence of the algae as an additional carbon source, through leaching or by decomposing dead algal cells. Similar cases of loose associations have been reported from saxicolous biocoenoses where rock-inhabiting fungi are often growing together with algae or cyanobacteria (Muggia et al. 2013). Muggia et al. (2016) found alpine rock lichens to be associated with members of *Myriangiales*.

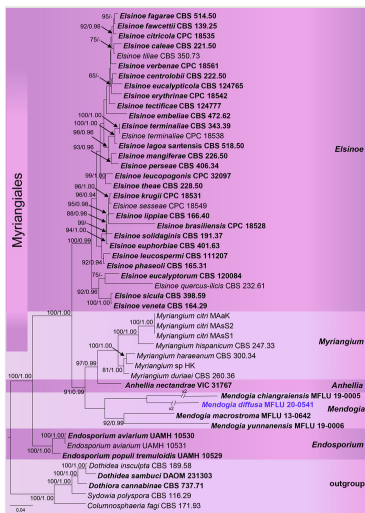


Figure 3. [doi](#)

Phylogeny of Myriangiales reconstructed from a multilocus dataset with SSU, LSU, ITS1, 5.8S and ITS2. The topology is the result of ML inference performed with IQ-TREE. ML bootstrap support values  $\geq 65\%$  and Bayesian posterior probabilities  $\geq 0.95$  are presented above each branch. Ex-type strains are shown in black bold; the new species is highlighted in blue bold font.

## Acknowledgements

We thank the Thailand Research Fund (“The future of specialist fungi in a changing climate: baseline data for generalist and specialist fungi associated with ants, *Rhododendron* species and *Dracaena* species DBG6080013” and “Impact of climate change on fungal diversity and biogeography in the Greater Mekong Sub-region RDG6130001”) and “The 2019 high-end foreign expert introduction plan to Kunming Institute of Botany (granted by the Ministry of Science and Technology of the People’s

Republic of China (Grant Number G20190139006)) for funding this research. Kevin D. Hyde thanks Chiang Mai University for the award of Visiting Professor. S.C. Karunarathna would like to thank the CAS President's International Fellowship Initiative (PIFI) young staff under grant number: 2020FYC0002 and the National Science Foundation of China (NSFC) under the project code 31851110759, the CAS President's International Fellowship Initiative (PIFI) under the following grant: 2018PC0006 and the National Science Foundation of China (NSFC, project code 31851110759). We also thank Udeni Jayalal, Nalin Wijayawardene, Diana Sandamali and Danushka Sandaruwan for their support during this research. We thank Shaun Pennycook, for helping in the nomenclature. Dhanushka Wanasinghe would like to thank CAS President's International Fellowship Initiative (PIFI) for funding his postdoctoral research (number 2021PC0008), the National Science Foundation of China and the Chinese Academy of Sciences for financial support under the following grants: 41761144055, 41771063 and Y4ZK111B01.

## References

- Barr ME (1979) A classification of ascomycetes. *Mycologia* 71 (5): 935-957. <https://doi.org/10.2307/3759283>
- Boedijn KB (1961) *Myriangiales* from Indonesia. *Persoonia-Molecular Phylogeny and Evolution of Fungi* 2 (1): 63-75.
- Dai DQ, Phookamsak R, Wijayawardene NN, Li WJ, Bhat DJ, Xu JC, Taylor JE, Hyde KD, Chukeatirote E (2017) Bambusicolous fungi. *Fungal Diversity* 82 (1): 1-105. <https://doi.org/10.1007/s13225-016-0367-8>
- Dissanayake AJ, Jayawardena RS, Boonmee S, Thambugala KM, Tian Q, Mapook A, Senanayake IC, Yan J, Li YM, Li X, Chukeatirote E, Hyde KD (2014) The status of *Myriangiaceae* (Dothideomycetes). *Phytotaxa* 176 (1): 219-239. <https://doi.org/10.11646/phytotaxa.176.1.22>
- Doidge EM (1921) South African ascomycetes in the National Herbarium I. *Bothalia* 1: 5-32.
- Glez-Peña D, Gómez-Blanco D, Reboiro-Jato M, Fdez-Riverola F, Posada D (2010) ALTER: program-oriented conversion of DNA and protein alignments. *Nucleic Acids Research* 38 (Web Server issue): 14-18. <https://doi.org/10.1093/nar/gkq321>
- Hall T (2001) BioEdit version. 5.0.6. North Carolina State University.
- Hennings P (1904) Fungi Amazonici a cl Ernesto Ule collecti II. *Hedwigia* 43: 242-273.
- Hongsanan S, Hyde KD, Phookamsak R, Wanasinghe DN, McKenzie EH, Sarma VV, Boonmee S, Lücking R, Bhat DJ, Liu NG, Tennakoon DS, Pem D, Karunarathna A, Jiang SH, Jones EB, Phillips AJ, Manawasinghe IS, Tibpromma S, Jayasiri SC, Sandamali DS, Jayawardena RS, Wijayawardene NN, Ekanayaka AH, Jeewon R, Lu YZ, Dissanayake AJ, Zeng XY, Luo ZL, Tian Q, Phukhamsakda C, Thambugala KM, Dai DQ, Chethana KW, Samarakoon MC, Ertz D, Bao DF, Doilom M, Liu JK, Pérez-Ortega S, Suija A, Senwana C, Wijesinghe SN, Konta S, Niranjana M, Zhang SN, Ariyawansa HA, Jiang HB, Zhang JF, Norphanphoun C, de Silva NI, Thiyagaraja V, Zhang H, Bezerra JD, Miranda-González R, Aptroot A, Kashiwadani H, Harishchandra D, Sérusiaux E, Aluthmuhandiram JV, Abeywickrama PD, Devadatha B, Wu HX, Moon KH, Gueidan C, Schumm F, Bundhun D, Mapook A, Monkai J, Chomnunti P, Suetrong S,

Chaiwan N, Dayarathne MC, Yang J, Rathnayaka AR, Bhunjun CS, Xu JC, Zheng JS, Liu G, Feng Y, Xie N (2020) Refined families of Dothideomycetes: Dothideomycetidae and Pleosporomycetidae. *Mycosphere* 11 (1): 1553-2107. <https://doi.org/10.5943/mycosphere/11/1/13>

- Hopple JJ (1994) Phylogenetic investigations in the genus *Coprinus* based on morphological and molecular characters. Duke University
- Huelsenbeck JP, Ronquist F (2001) MRBAYES: Bayesian inference of phylogenetic trees. *Bioinformatics* 17 (8): 754-755. <https://doi.org/10.1093/bioinformatics/17.8.754>
- Hyde KD, Jones EB, Liu JK, Ariyawansa H, Boehm E, Boonmee S, Braun U, Chomnunti P, Crous PW, Dai DQ, Diederich P, Dissanayake A, Doilom M, Doveri F, Hongsanan S, Jayawardena R, Lawrey JD, Li YM, Liu YX, Lücking R, Monkai J, Muggia L, Nelsen MP, Pang KL, Phookamsak R, Senanayake I, Shearer CA, Tanaka K, Thambugala KM, Wijayawardene NN, Wikee S, Wu HX, Zhang Y, Aguirre-Hudson B, Alias SA, Aptroot A, Bahkali AH, Bezerra JL, Bhat DJ, Camporesi E, Chukeatirote E, Gueidan C, Hawksworth DL, Hirayama K, Hoog SD, Kang JC, Knudsen K, Li WJ, Li XH, Liu ZY, Mapook A, McKenzie EH, Miller AN, Mortimer PE, Phillips AJ, Raja HA, Scheuer C, Schumm F, Taylor JE, Tian Q, Tibpromma S, Wanasinghe DN, Wang Y, Xu JC, Yan JY, Yacharoen S, Zhang M (2013) Families of Dothideomycetes. *Fungal Diversity* 63: 1-313. <https://doi.org/10.1007/s13225-013-0263-4>
- Jayawardena RS, Ariyawansa HA, Singtripop C, Mei Y, Yan J, Li X, Nilthong S, Hyde KD (2014) A re-assessment of *Elsinoaceae* (*Myriangiales*, Dothideomycetes). *Phytotaxa* 176 (1). <https://doi.org/10.11646/phytotaxa.176.1.13>
- Jeewon R, Hyde KD (2016) Establishing species boundaries and new taxa among fungi: recommendations to resolve taxonomic ambiguities. *Mycosphere* 7 (11): 1669-1677. <https://doi.org/10.5943/mycosphere/7/11/4>
- Jiang H, Phookamsak R, Xu J, Karunarathna S, Mortimer P, Hyde K (2020) Taxonomic and phylogenetic characterizations reveal three new species of *Mendogia* (*Myriangiaceae*, *Myriangiales*). *Mycological Progress* 19 (1): 41-51. <https://doi.org/10.1007/s11557-019-01540-z>
- Katoh K, Rozewicki J, Yamada KD (2017) MAFFT online service: multiple sequence alignment, interactive sequence choice and visualization. *Briefings in Bioinformatics* 20 (4): 1160-1166. <https://doi.org/10.1093/bib/bbx108>
- Kirk PM, Cannon PF, Minter DW, Stalpers JA (2008) *Dictionary of the fungi*. 10. CAB International, Wallingford, UK, 771 pp.
- Konta S, Hongsanan S, Tibpromma S, Thongbai B, Maharachchikumbura SS, Bahkali AH, Hyde KD, Boonmee S (2016) An advance in the endophyte story: *Oxydothidaceae* fam. nov. with six new species of *Oxydothis*. *Mycosphere* 7 (9): 1425-1446. <https://doi.org/10.5943/mycosphere/7/9/15>
- Konta S, Hongsanan S, Eungwanichayapant PD, Liu JK, Jeewon R, Hyde KD, Maharachchikumbura SS, Boonmee S (2017) *Leptospora* (*Leptosporaceae* fam. nov.) and *Linocarpon* and *Neolinocarpon* (*Linocarpaceae* fam. nov.) are accommodated in *Chaetosphaeriales*. *Mycosphere* 8 (10): 1943-1974. <https://doi.org/10.5943/mycosphere/8/10/16>
- Lumbsch HT, Huhndorf SM (2010) Outline of Ascomycota. *Life and Earth Sciences* 1: 42-64. <https://doi.org/10.3158/1557.1>

- Muggia L, Gueidan C, Knudsen K, Perlmutter G, Grube M (2013) The Lichen Connections of Black Fungi. *Mycopathologia* 175: 523-535. <https://doi.org/10.1007/s11046-012-9598-8>
- Muggia L, Fleischhacker A, Kopun T, Grube M (2016) Extremotolerant fungi from alpine rock lichens and their phylogenetic relationships. *Fungal Diversity* 76 (1): 119-142. <https://doi.org/10.1007/s13225-015-0343-8>
- Nguyen LT, Schmidt HA, Von Haeseler A, Minh BQ (2015) IQ-TREE: a fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. *Molecular Biology and Evolution* 32 (1): 268-274. <https://doi.org/10.1093/molbev/msu300>
- Nylander J (2008) MrModeltest2 v. 2.3 (Program for selecting DNA substitution models using PAUP\*). Evolutionary Biology Centre, Uppsala.
- Phookamsak R, Boonmee S, Norphanphoun C, Wanasinghe DN, de Silva NI, Dayarathne MC, Hongsanan S, Bhat DJ, Hyde KD (2016) *Schizothyriaceae*. *Mycosphere* 7 (2): 154-189. <https://doi.org/10.5943/mycosphere/7/2/7>
- Raciborski M (1900) Parasitische Algen und Pilze Java's. 3. Staatsdruckerei, 1–49 pp.
- Ruibal C, Gueidan C, Selbmann L, Gorbushina AA, Crous PW, Groenewald JZ, Muggia L, Grube M, Isola D, Schoch CL, Staley JT, Lutzoni F, de Hoog GS (2009) Phylogeny of rock-inhabiting fungi related to Dothideomycetes. *Studies in Mycology* 64: 123-133. <https://doi.org/10.3114/sim.2009.64.06>
- Starbäck K (1899) Ascomyceten der ersten Regnell'schen Expedition I. Bihang till Kungliga svenska Vetenskaps-Akademiens Handlingar, Afd 3 (25): 1-68.
- Sydow H, Sydow P (1917) Beitrag zur Kenntniss der Pilzflora der Philippinen-Inseln. *Annales Mycologici* 15 (3–4): 165-268.
- Vitória N (2012) Diversidade de Ascomycota em palmeiras nativas e exóticas em áreas de Mata Atlântica nos Estados da Bahia e de Pernambuco. Universidade Federal de Pernambuco, Recife, Brazil.
- von Arx JA, Müller E (1975) A re-evaluation of the bitunicate Ascomycetes with keys to families and genera. *Studies in Mycology* 9: 1-159.
- White TJ, Bruns T, Lee S, Taylor J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. *PCR Protocols* 315-322. <https://doi.org/10.1016/b978-0-12-372180-8.50042-1>
- Wijayawardene NN, Crous PW, Kirk PM, Hawksworth DL, Boonmee S, Braun U, Dai D, D'souza MJ, Diederich P, Dissanayake A, Doilom M, Hongsanan S, Jones EB, Groenewald JZ, Jayawardena R, Lawrey JD, Liu J, Lücking R, Madrid H, Manamgoda DS, Muggia L, Nelsen MP, Phookamsak R, Suetrong S, Tanaka K, Thambugala KM, Wanasinghe DN, Wikee S, Zhang Y, Aptroot A, Ariyawansa HA, Bahkali AH, Bhat DJ, Gueidan C, Chomnunti P, De Hoog GS, Knudsen K, Li W, McKenzie EH, Miller AN, Phillips AJ, Piątek M, Raja HA, Shivas RS, Slippers B, Taylor JE, Tian Q, Wang Y, Woudenberg JH, Cai L, Jaklitsch WM, Hyde KD (2014) Naming and outline of Dothideomycetes–2014 including proposals for the protection or suppression of generic names. *Fungal Diversity* 69 (1): 1-55. <https://doi.org/10.1007/s13225-014-0309-2>
- Wijayawardene NN, Hyde KD, Rajeshkumar KC, Hawksworth DL, Madrid H, Kirk PM, Braun U, Singh RV, Crous PW, Kukwa M, Lücking R, Kurtzman CP, Yurkov A, Haelewaters D, Aptroot A, Lumbsch HT, Timdal E, Ertz D, Etayo J, Phillips AJ, Groenewald JZ, Papizadeh M, Selbmann L, Dayarathne MC, Weerakoon G, Jones EB, Suetrong S, Tian Q, Castañeda-Ruiz RF, Bahkali AH, Pang K, Tanaka K, Dai DQ, Sakayaroj J, Hujslová M, Lombard L, Shenoy BD, Suija A, Maharachchikumbura SS,



Thambugala KM, Wanasinghe DN, Sharma BO, Gaikwad S, Pandit G, Zucconi L, Onofri S, Egidio E, Raja HA, Kodsueb R, Cáceres ME, Pérez-Ortega S, Fiuza PO, Monteiro JS, Vasilyeva LN, Shivas RG, Prieto M, Wedin M, Olariaga I, Lateef AA, Agrawal Y, Fazeli SA, Amoozegar MA, Zhao GZ, Pfliegler WP, Sharma G, Oset M, Abdel-Wahab MA, Takamatsu S, Bensch K, de Silva NI, De Kese A, Karunarathna A, Boonmee S, Pfister DH, Lu Y, Luo Z, Boonyuen N, Daranagama DA, Senanayake IC, Jayasiri SC, Samarakoon MC, Zeng X, Doilom M, Quijada L, Rampadarath S, Heredia G, Dissanayake AJ, Jayawardana RS, Perera RH, Tang LZ, Phukhamsakda C, Hernández-Restrepo M, Ma X, Tibpromma S, Gusmao LF, Weerahewa D, Karunarathna SC (2017) Notes for genera-Ascomycota. *Fungal Diversity* 86: 1-594. <https://doi.org/10.1007/s13225-017-0386-0>

- Wijayawardene NN, Hyde KD, Lumbsch H, Liu JK, Maharachchikumbura SS, Ekanayaka AH, Tian Q, Phookamsak R (2018) Outline of Ascomycota: 2017. *Fungal Diversity* 88: 167-263. <https://doi.org/10.1007/s13225-018-0394-8>
- Wijayawardene NN, Hyde KD, Al-Ani LK, Tedersoo L, Haelewaters D, Rajeshkumar KC, Zhao RL, Aptroot A, Leontyev DV, Saxena RK, Tokarev YS, Dai DQ, Letcher PM, Stephenson SL, Ertz D, Lumbsch HT, Kukwa M, Issi IV, Madrid H, Phillips AJ, Selbmann L, Pfliegler WP, Horváth E, Bensch K, Kirk PM, Kolaříková K, Raja HA, Radek R, Papp V, Dima B, Ma J, Malosso E, Takamatsu S, Rambold G, Gannibal PB, Triebel D, Gautam AK, Avasthi S, Suetrong S, Timdal E, Fryar SC, Delgado G, Réblová M, Doilom M, Dolatabadi S, Pawłowska JZ, Humber RA, Kodsueb R, Sánchez-Castro I, Goto BT, Silva DK, de Souza FA, da Silva GA, Silva IR, Błaszczowski J, Jobim K, Maia LC, Barbosa FR, Fiuza PO, Divakar PK, Shenoy BD, Castañeda-Ruiz RF, Somrithipol S, Lateef AA, Karunarathna SC, Tibpromma S, Mortimer PE, Wanasinghe DN, Phookamsak R, Xu J, Wang Y, Tian F, Alvarado P, Li DW, Kušan I, Matočec N, Mešić A, Tkalčec Z, Maharachchikumbura SS, Papizadeh M, Heredia G, Wartchow F, Bakhshi M, Boehm E, Youssef N, Hustad VP, Lawrey JD, Santiago AL, Bezerra JD, Souza-Motta CM, Firmino AL, Tian Q, Houbraken J, Hongsanan S, Tanaka K, Dissanayake AJ, Monteiro JS, Grossart HP, Suija A, Weerakoon G, Etayo J, Tsurukau A, Vázquez V, Mungai P, Damm U, Li QR, Zhang H, Boonmee S, Lu YZ, Becerra AG, Kendrick B, Brearley FQ, Motiejūnaitė J, Sharma B, Khare R, Gaikwad S, Wijesundara DS, Tang LZ, He MQ, Flakus A, Rodriguez-Flakus P, Zhurbenko MP, McKenzie EH, Stadler M, Bhat DJ, Liu JK, Raza M, Jeewon R, Nassonova ES, Prieto M, Jayalal RG, Erdoğan M, Yurkov A, Schnittler M, Shchepin ON, Novozhilov Y, Silva-Filho AG, Gentekaki E, Liu P, Cavender J, Kang Y, Mohammad S, Zhang LF, Xu RF, Li YM, Dayarathne MC, Ekanayaka AH, Wen TC, Deng CY, Pereira OL, Navathe S, Hawksworth DL, Fan XL, Dissanayake LS, Kuhnert E, Grossart HP, Thines M (2020) Outline of fungi and fungus-like taxa. *Mycosphere* 11 (1): 1060-1456. <https://doi.org/10.5943/mycosphere/11/1/8>