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The numbers of fungi: contributions from traditional taxonomic studies and challenges of metabarcoding

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Abstract

The global diversity of fungi has been estimated using several different approaches. There is somewhere between 2–11 million estimated species, but the number of formally described taxa is around 150,000, a tiny fraction of the total. In this paper, we examine 12 ascomycete genera as case studies to establish trends in fungal species descriptions, and introduce new species in each genus. To highlight the importance of traditional morpho-molecular methods in publishing new species, we introduce novel taxa in 12 genera that are considered to have low species discovery. We discuss whether the species are likely to be rare or due to a lack of extensive sampling and classification. The genera are *Apiospora*, *Bambusicola*, *Beltrania*, *Capronia*, *Distoseptispora*, *Endocalyx*, *Neocatenulostroma*, *Neodeightonia*, *Paraconiothyrium*, *Peroneutypa*, *Phaeoacremonium* and *Vanakripa*. We discuss host-specificity in selected genera and compare the number of species epithets in each genus with the number of ITS (barcode) sequences deposited in GenBank and UNITE. We furthermore discuss the relationship between the divergence times of these genera with those of their hosts. We hypothesize whether there might be more species in these genera and discuss hosts and habitats that should be investigated for novel species discovery.

Keywords 12 new taxa · *Ascomycota* · Fungal diversity · Fungal numbers · High-throughput sequencing · Host-specificity

The taxonomic novelties introduced in this study are:
Dothideomycetes sensu O.E. Erikss & Winka
Botryosphaeriales C.L. Schoch, Crous & Shoemaker
Botryosphaeriaceae Theiss. & Syd.
Neodeightonia C. Booth
1. ***Neodeightonia pinangae*** Tennakoon, C.H. Kuo & K.D. Hyde, ***sp. nov.***

Mycosphaerellales P.F. Cannon
Teratosphaeriaceae Crous & U. Braun
Neocatenulostroma Quaedvl. & Crous
2. ***Neocatenulostroma castaneae*** Phukhams., Bhunjun & K.D. Hyde, ***sp. nov.***

Pleosporales Luttrell ex M.E. Barr
Bambusicolaceae D.Q. Dai & K.D. Hyde
Bambusicola D.Q. Dai & K.D. Hyde
3. ***Bambusicola nanensis*** Y.R Sun, Yong Wang bis & K.D. Hyde, ***sp. nov.***

Didymosphaeriaceae Munk
Paraconiothyrium Verkley
4. ***Paraconiothyrium fici*** Wijes. & K.D. Hyde, ***sp. nov.***
Eurotiomycetes Tehler ex O.E. Eriksson & K. Winka
Chaetothyriales M.E. Barr
Herpotrichiellaceae Munk
Capronia Sacc.

5. ***Capronia lijian-gensis*** M. Raza & L. Cai, ***sp. nov.***

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Sordariomycetes O.E. Erikss. & Winka
Amphisphaeriales Hawksw. & O.E. Erikss
Apiosporaceae K.D. Hyde, J. Fröhl., J.E. Taylor & M.E. Barr
Apiospora Sacc.
6. *Apiospora tropica* Y.R. Sun, Yong Wang bis & K.D. Hyde, ***sp. nov.***

Conioscyphales Réblová & Seifert
Conioscyphaceae Réblová & Seifert
Vanakripa Bhat, W.B. Kendr. & Nag Raj
7. *Vanakripa chiangmaiense* X.G. Tian & Karun., ***sp. nov.***

Distoseptisporales Z.L. Luo, K.D. Hyde & H.Y. Su
Distoseptisporaceae K.D. Hyde & McKenzie
Distoseptispora K.D. Hyde, McKenzie & Maharachch.
8. *Distoseptispora cylindricospora* D.F. Bao, Z.L. Luo, K.D. Hyde & H.Y. Su, ***sp. nov.***

Sordariales Chad. ex D. Hawksw. & O.E. Erikss.
Beltraniaceae Nann.
Beltrania Penz.
9. *Beltrania aquatica* W. Dong, Doilom & K.D. Hyde, ***sp. nov.***

Togniniales Senan., Maharachch. & K.D. Hyde
Togniniaceae Réblová, L. Mostert, W. Gams & Crous
Phaeoacremonium W. Gams, Crous & M.J. Wingf.
10. *Phaeoacremonium camporesii* Wijes., Camporesi, & K.D. Hyde, ***sp. nov.***

Xylariales Nannf.
Cainiaceae J.C. Krug
Endocalyx Berk. & Broome
11. *Endocalyx ptychospermatis* Y.R. Xiong, Manawas & K.D. Hyde, ***sp. nov.***

Diatrypaceae Nitschke
Peroneutypa Berl.
12. *Peroneutypa kunmingensis* L. Lu, K.D. Hyde & Tibpromma, ***sp. nov.***

Introduction

Fungi thrive in diverse environments and are involved in the decomposition and nutrient cycling of dead plant material in terrestrial and aquatic ecosystems (Wainwright et al. 2003; Bucher et al. 2004; Pointing et al. 2005; Jobard et al. 2010; Nagahama et al. 2011). The diversity in a particular area or ecosystem is usually expressed as the number of species in the system (Bermudez and Lindemann-Matthies 2020), highlighting the fundamental role of taxonomy in biodiversity assessment and biology (Lücking et al. 2021). Some 150,600 fungal species have formally been described (http://www.speciesfungorum.org/; 8 December 2021), but this is only a fraction of the 2 to 11 million estimated species (Hawksworth and Lücking 2017; Lücking et al. 2021; Baldrian et al. 2021). Species estimates from metabarcoding data are highest, such as the 11.7–13.2 million species estimate of Wu et al. (2019). Tropical and warm-temperate areas seem particularly rich in unexplored fungal diversity (Hyde et al. 2018; Menolli and Sanchez-Garcia 2020). However, the most critical aspect of estimating fungal numbers is defining a species accurately (Chethana et al. 2021; Lücking et al. 2021). Thus, global biodiversity needs to be extensively studied to determine the realistic number of fungi (Wu et al. 2019). Several methods have been developed and used to identify and describe fungal species (Taylor et al. 2000; Aime et al. 2021; Bhunjun et al. 2021a; Chethana et al. 2021). Based on the currently accepted classification system, molecular approaches have greatly improved the understanding of evolutionary relationships in fungi (Naranjo-Ortiz and Gabaldón 2020). Evolution refers to the heritable genetic changes that accumulate during the lifetime through environmental adaptations, which result from natural selection, mutation, genetic drift, and migration (gene flow) (Andrews et al. 2012). Therefore, evolutionary studies can help to predict the next trend for fungal discovery.

In this study, we discuss species discovery, the likelihood of new species being discovered, the evolution with plant hosts, and the possibility of the use of metabarcoding for recognizing the "dark taxa" in selected genera (Taberlet et al. 2012; Ryberg and Nilsson 2018). The newly introduced taxa are justified and the potential for discovering additional species is discussed. A comparison of the number of ITS sequences with the number of species epithets listed in Species Fungorum (2021) is appraised. Metabarcoding indicates that fungal diversity is much higher when using a morpho-molecular approach. However, data from high throughput sequencing (HTS) studies cannot be used to describe these species formally as they lack holotypes. High throughput sequencing indicates that many largely unexplored habitats contain large numbers of undescribed taxa (Tedersoo et al. 2021). We also integrate data from different platforms for species introduction and compare the number of species in Species Fungorum with HTS data from UNITE database (Nilsson et al. 2019).

Material and methods

Sample collection, isolation and identification

Fresh specimens were collected from China, Italy, and Thailand. The specimens were maintained in paper bags for transport to the laboratory. Morphological characters were observed using a stereo microscope and a compound microscope as per the guidelines provided in Senanayake et al. (2020). Photomicrographs were processed with Adobe Photoshop version CS6 version 15.0 (Adobe Systems, United States). Representative specimens are deposited in the herbarium of Mae Fah Luang University, Chiang Rai Province, Thailand (MFLU), Cryptogams Kunming Institute of Botany, Academia Sinica, Yunnan Province, China (HKAS), Herbarium Mycologicum Academiae Sinicae, Beijing Province, China (HMAS), Herbaria of Guizhou Academy of Agricultural Sciences, China (GZAAS), the National Chiayi University, Taiwan (NCYU), and Zhongkai University herbarium, Guangzhou Province, China (ZHKU). Representative cultures are deposited at Mae Fah Luang Culture Collection (MFLUCC), Chiang Rai Province, Thailand (MFLU), Dali University Culture Collection, Yunnan Province, China (DLUCC), Kunming Culture Collection, Yunnan Province, China (KUMCC), China General Microbiological Culture Collection Center, Beijing Province, China (CGMCC), and the National Chiayi University Culture Collection, Taiwan (NCYUCC). Faces of fungi numbers and Index Fungorum numbers were obtained as outlined in Jayasiri et al. (2015) and Index Fungorum (2021).

DNA extraction, amplification and sequencing

Total genomic DNA was extracted from fresh mycelium with a Biospin Fungus Genomic DNA Extraction Kit (BioFlux®) (Hangzhou, P.R. China) following the manufacturer's protocol. The nuclear ribosomallarge subunit ribosomal RNA (LSU) gene, the nuclear ribosomal internal transcribed spacer (ITS) region, the nuclear ribosomal small subunit ribosomal RNA (SSU) gene, the translation elongator factor alpha (*tef*1-α) gene, beta-tubulin (*tub*2) gene and the RNA polymerase II second largest subunit (*rpb*2) gene were amplified using primer pairs LR0R/LR5 (Vilgalys and Hester 1990), ITS4/ITS5 (White et al. 1990), NS1/NS4 (White et al. 1990), EF-1/EF-2 (O'Donnell et al. 1998), T1/Bt2b (Glass and Donaldson 1995; O'Donnell and Cigelnik 1997) , ACT-513F and ACT-783R (Carbone and Kohn 1999) and RPB2-5f2/RPB2-7cr (Liu and Hall 1999), respectively. Polymerase chain reaction (PCR) was used to amplify partial genetic regions with primer pairs as described in Tibpromma et al. (2018). The PCR amplification was performed using PCR mixtures containing 5–10 ng DNA, 1X PCR buffer, 0.8 units Taq polymerase, 0.3 µM of each primer, 0.2 mM dNTP and 1.5 mM $MgCl_2$. All the PCR products were visualised on 1% Agarose gels with added 6 µl of 4S green dye, per 100 ml. Successful PCR products were purified and sequenced by Shanghai Sangon Biological Engineering Technology & Services Co. (Shanghai, P.R. China). All sequences generated in this study were submitted to GenBank (Sayers et al. 2021).

Sequence alignment and phylogenetic analyses

Consensus sequences were assembled using Geneious Prime 2021 (Biomatters Ltd., Auckland, New Zealand). Sequences of closely related strains were retrieved using BLASTn searches against GenBank. Sequences were aligned with MAFFT version 7 (Katoh et al. 2019), with minimal adjustment of any ambiguous nucleotides by visual examination and manually corrected in AliView version 1.26 (Larsson 2014). Leading or trailing gaps exceeding the primer binding site were trimmed from the alignments prior to tree building and the gaps in the alignment were treated as missing data. The concatenation of the multimarker datasets was created by using Sequence Matrix version 1.8 (Vaidya et al. 2011).

Individual gene phylogenetic analyses were performed to determine the compatibility and the best marker for species delineation. Phylogenetic analyses of the combined dataset were performed using maximum likelihood, maximum parsimony and Bayesian inference. Maximum likelihood analyses (ML), including 1000 bootstrap pseudoreplicates, were performed at the CIPRES web portal (Miller et al. 2017) using RAxML v. 8.2.12 (Stamatakis 2014). The general time reversible (GTR) model with a discrete gamma distribution plus invariant site (GTR + I + G) was used as the nucleotide substitution model. Maximum parsimony analysis was conducted using PAUP v.4.0b 10 with the heuristic search option and the number of replicates set to 1000 each (Swofford and Swofford 2002). The tree length (TL), composite consistency index (CI), retention index (RI), rescaled consistency index (RC) and homoplasy index (HI) were documented. The best model for each gene was determined in JModelTest version 2.1.10 (Darriba et al. 2012) for the Bayesian analysis. The Bayesian inference posterior probabilities (BPP) distribution (Zhaxybayeva and Gogarten 2002) was estimated by Markov Chain Monte Carlo sampling (MCMC) in MrBayes 3.2.2 on XSEDE (Ronquist and Huelsenbeck 2003). Six simultaneous Markov chains were run for 1,000,000 to 10,000,000 generations, depending on individual settings for the fungal group and trees were sampled at every 100th or 1000th generation. Suitable burn-in thresholds were determined in Tracer version 1.7 (Rambaut et al. 2018). The first 10–25% of generated trees representing the burn-in phase of the analyses were discarded, while the remaining trees were used to calculate

Bayesian posterior probabilities (BPP) in the majority rule consensus tree. The phylograms were visualized in FigTree version 1.4.0 (Rambaut 2014) and edited using Adobe Illustrator CS6 version 15.0 (Adobe Systems, USA).

Genera characteristics and taxonomy of introduced species

In this section, we introduce novel taxa in 12 genera and discuss species discovery and the likelihood of new species being discovered. We did a BLASTn search for the ITS region as it is the primary fungal barcode (Schoch et al. 2012). Taxa with high similarity and query cover (in the range of 90–100%) were considered as close relative to the novel species described in this study. To evaluate the amount of sequence data available in GenBank to the number of species epithets, the number of ITS sequences in each genus was compared with the number of species epithets listed in Species Fungorum (2021) until September 2021 (Table 1). The number of species hypotheses (SH) in UNITE (Nilsson et al. 2019) was also determined using the 98.5% threshold level. The species hypothesis represents the species-level for group of individuals that share a given set of observed characters among their OTUs.

Taxonomy

1. *Neodeightonia* C. Booth

Botryosphaeriaceae was introduced by Theissen and Sydow (1918) to accommodate three genera, *Botryosphaeria*, *Phaeobotryon* and *Dibotryon*. Subsequently, *Neodeightonia* was introduced by Booth and Punithalingam (1969). Phillips et al. (2019) accepted 22 genera in *Botryosphaeriaceae*. *Neodeightonia* is a member of *Botryosphaeriaceae* and is characterized by hyaline, aseptate ascospores with polar apiculi surrounded by a membrane that swells and expands when mounted in water. In the asexual morphs, the conidia are initially hyaline, becoming brown, 1-septate at maturity, with smooth to finely roughened walls, or fine striations (Konta et al. 2016; Wu et al. 2021). This genus was previously considered as a synonym of *Botryosphaeria* (von Arx and Müller 1975). However, *Neodeightonia* is distinguishable from *Botryosphaeria* based on dark, 1-septate ascospores as well as in phylogeny (Phillips et al. 2008). Longitudinal striations on the conidial wall are an additional characteristic feature of this genus (Phillips et al. 2008). *Neodeightonia* differs from *Lasiodipolodia* by the absence of conidiomatal paraphyses, and conidial striations distinguish it from *Diplodia* (Phillips et al. 2008).

There are eight epithets in Species Fungorum (2021), including the recently introduced taxon *N. planchoniae* (Jayasiri et al. 2019, Table 1). All current *Neodeightonia* species have molecular data. There are 171 *Neodeightonia* sequences in GenBank and over 60 are ITS sequences. A BLASTn search of the ITS region of the type species *Neodeightonia subglobosa* strain CBS 448.91 (KF766199) showed a high similarity and query cover (90–100%) to *Diplodia, Neodeightonia* and a few synonymized names such as *Sphaeropsis*. A BLASTn search of the ITS region of *N. subglobosa* also showed high similarity with high query cover (90–100%) to uncultured *Sphaeropsis* sequences. Using the 98.5% threshold level in UNITE, there are 11 species hypotheses (comprising 61 sequences) with high similarity to *Neodeightonia*, which were recovered based on HTS data. *Neodeightonia* species are mainly found on monocotyledons

Table 1 Number of taxa listed under *Apiospora, Bambusicola, Beltrania, Capronia, Distoseptispora, Endocalyx, Neocatenulostroma, Neodeightonia, Paraconiothyrium, Peroneutypa, Phaeoacremonium* and *Vanakripa* in Species Fungorum database from 1870 to 2021

Years (Decade)/Genus	1870	1880	1890	1900	1910	1920	1930	1940	1950	1960	1970	1980	1990*	2000	2010	2020	2021
Apiospora	–	–	1	4	4	1	2	–	6	3	–	1	3	1	–	–	61
Bambusicola	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14	–
Beltrania	–	3	–	–	–	–	1	–	3	1	4	1	2	2	4	5	1
Capronia	–	1	1	–	–	–	–	–	–	–	1	17	33	9	19	–	–
Distoseptispora	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	27	3
Endocalyx	2	–	–	3	–	–	–	–	–	1	–	3	–	1	–	–	1
Neocatenulostroma	–	–	–	–	–	–	–	–	–	–	–	–	–	–	3	–	–
Neodeightonia	–	–	–	–	–	–	–	–	–	–	1	1	–	1	6	–	–
Paraconiothyrium	–	–	–	–	–	–	–	–	–	–	–	–	–	9	15	3	–
Peroneutypa	–	–	–	21	8	4	–	–	4	1	1	2	–	8	8	2	–
Phaeoacremonium	–	–	–	–	–	–	–	–	–	–	–	–	6	29	32	–	1
Vanakripa	–	–	–	–	–	–	–	–	–	–	–	–	2	4	3	–	1

*The introduction of molecular data as an information source in systematic mycology (White et al. 1990)

such as bamboo and palms, except for *N. planchoniae*, which was found on the pericarp of *Planchonia* species (Phillips et al. 2008; Liu et al. 2012; Konta et al. 2016; Jayasiri et al. 2019). As endophytes, some species are host-specific (Rashmi et al. 2019). For example, the endophyte *N. subglobosa* has only been found on *Fragaria*×*ananassa* (Rajamanikyam et al. 2017). Therefore, there is likely to be a large number of species yet to be discovered as some species appear to be host-specific.

Botryosphaeriaceae diverged from other families in *Botryosphaeriales* around 94 MYA in the late Cretaceous period (crown age of 61 MYA in the Paleogene period), in a period dominated by the expansion of angiosperms occupying environments previously dominated by conifers (Phillips et al. 2019; Batista et al. 2021). *Botryosphaeriaceae* are cosmopolitan in distribution, occurring on a wide range of hosts from tropical and temperate regions as, pathogens, endophytes or saprobes (Slippers and Wingfield 2007; Liu et al. 2012; Phillips et al. 2019). Palms (*Arecales*) and bamboo (*Poales*) diverged around 118–116 MYA in the early Cretaceous period and major lineages migrated between Eurasia, the Pacific and the Indian ocean (Baker and Couvreur 2013). Palms and bamboo species further diversified during the plate-driven breakup in the late Cretaceous period which was followed by the Cretaceous extinction event which resulted in the loss of around 70% of species (65.5 MYA, Cretaceous-Tertiary extinction) (Peace et al. 2020). *Neodeightonia* diverged from *Lasiodiplodia* around 19 MYA in the early Neogene period (crown age of 8 MYA in the late Neogene period) (Phillips et al. 2019). Several land-dwelling mammals and plants known today were present during this period (Phillips et al. 2019). *Neodeightonia* species have

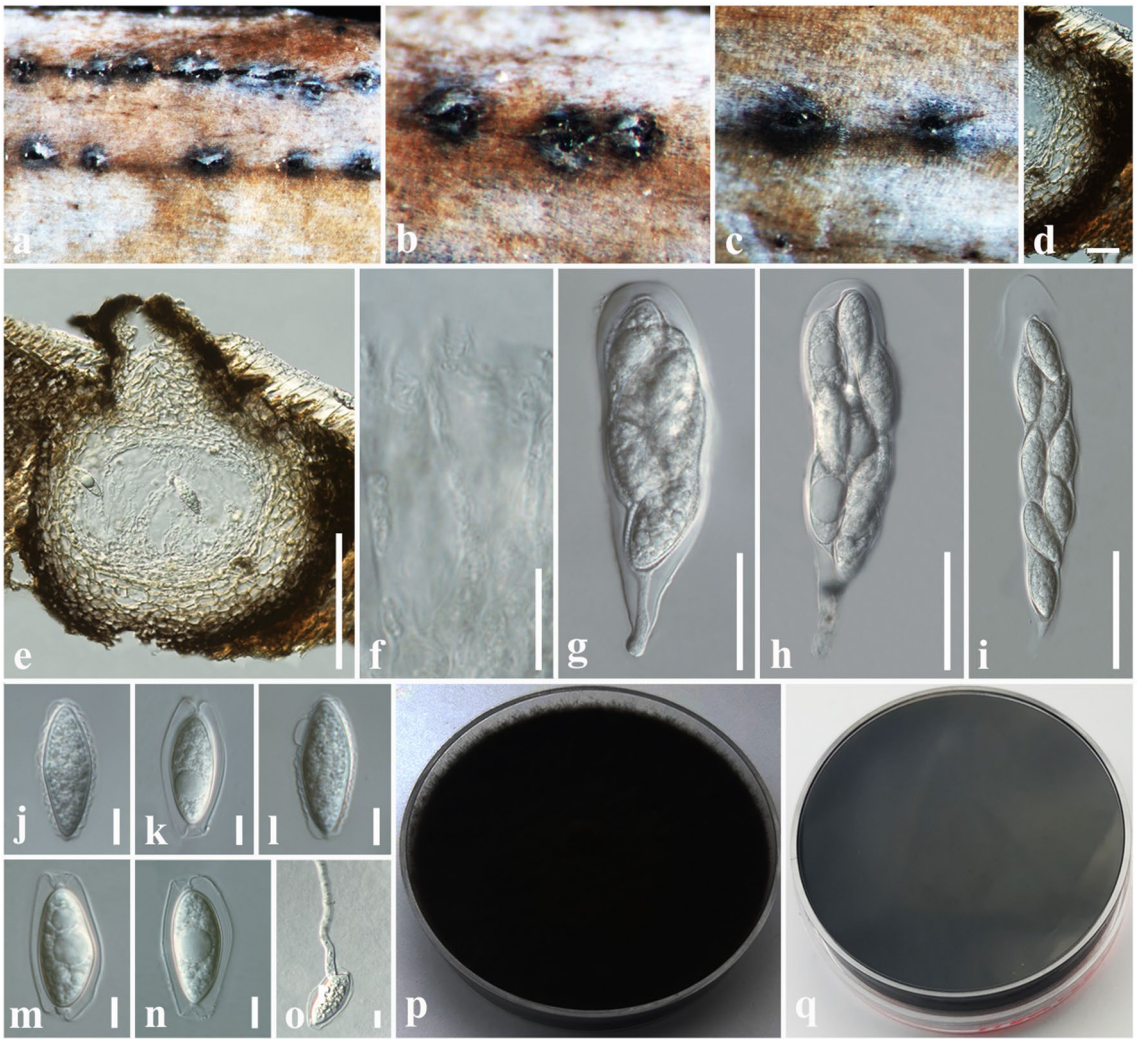


Fig. 1 ***Neodeightonia pinangae*** (MFLU 18–2619, **holotype**). **a** Appearance of ascomata on palm host. **b, c** Close-up of ascomata. **d** Section through peridium. **e** Vertical section of ascoma. **f** Pseudoparaphyses. **g–i** Asci. **j–n** Ascospores mounted in water surrounded by a membrane (**k**, **m**, **n** swelled up ascospores). **o** Germinating ascospore. **p** Colony on PDA from above (2 weeks old). **q** Colony on PDA from below (2 weeks old). Scale bars: **d** = 20 µm, **e** = 100 µm, **f–i** = 40 µm, **j–o** = 5 µm

been found across Eurasia, mostly associated with specific plants such as palms, bamboo and eudicotyledons (*Planchonia*) (Liu et al. 2012; Phillips et al. 2019). The distribution of *Botryosphaeriaceae* began around 94 MYA, which was after the diversification of *Arecales* over several continents (Baker and Couvreur 2013). This might suggest that *Neodeightonia* co-evolved as endophytes with these hosts to adapt to the new environmental conditions.

In this study, we introduce a new species in this genus from dead leaves of *Pinanga tashiroi* collected in Taiwan based on morphology and phylogeny.

Neodeightonia pinangae Tennakoon, C.H. Kuo & K.D. Hyde, ***sp. nov.***

Index Fungorum Number: IF558403; *Facesoffungi number*: FoF09845, Fig. 1

Etymology: Name reflects the host genus *Pinanga*

Holotype: MFLU 18–2619

Saprobic on dead leaves of *Pinanga tashiroi* Hayata. ***Sexual morph***: *Ascomata* 250–330 × 200–250 µm ($\bar{x}$ = 280 × 230 µm, *n* = 10), uni-loculate, immersed to erumpent in host tissue, globose to subglobose, brown to dark brown, rounded at the base. *Ostiole* central, papillate. *Peridium* 30–60 µm wide ($\bar{x}$ = 45 µm, *n* = 20), dark brown, smooth, with two cell layers of *textura angularis*, outer layer comprising thick, dark brown cells, inner layer comprising pale brown to hyaline, thin-walled cells. *Hamathecium* comprising 1.5–2.5 µm wide ($\bar{x}$ = 1.8 µm, *n* = 30), thin-walled, pseudoparaphyses, frequently septate, often constricted at the septa. *Asci* 80–110 × 16–22 µm ($\bar{x}$ = 95 × 19 µm, *n* = 20), 8-spored, bitunicate, fissitunicate, clavate to cylindric-clavate, apically rounded, with a well-developed ocular chamber, pedicel simple. *Ascospores* 25–29 × 10–12 µm ($\bar{x}$ = 28 × 11.5 µm, *n* = 30), biseriate, ellipsoidal-fusiform or fusiform, widest in the middle, both ends obtuse, hyaline, aseptate, with polar apiculi, smooth, thin-walled, surrounded by a membrane that swells and expands when mounted in water. ***Asexual morph***: Undetermined.

Culture characteristics: Colonies on PDA reaching 35 mm diam., after one week at 20–25 °C, colonies medium dense, circular, flat, surface slightly rough in the entire edge, margin well-defined, cottony to fairly fluffy, colony from above black to dark grey; reverse, dark brown to black, not producing pigments in PDA.

Material examined: Taiwan, Chiayi, Fanlu Township area, Dahu forest, dead leaves of *Pinanga tashiroi* (*Arecaceae*), 18 September 2018, D.S. Tennakoon, TAP050A (MFLU 18–2619, **holotype**); ex-type living culture MFLUCC 19–0077; *ibid*. 21 September 2019, D. S Tennakoon, TAP050B (NCYU 19–0223, **paratype**), NCYUCC 19–0144.

GenBank accession numbers: MFLUCC 19–0077: SSU = MZ262519, LSU = MZ262513, ITS = MZ262517, *tef*1-α = MZ268009; NCYUCC 19–0144: SSU = MZ262520, LSU = MZ262514, ITS = MZ262518, *tef*1-α = MZ268010.

Notes: *Neodeightonia pinangae* (MFLUCC 19–0077) fits well with the generic concept of *Neodeightonia* (Liu et al. 2010; Konta et al. 2016; Jayasiri et al. 2019; Wu et al. 2021). The multi-marker phylogeny indicates that our collection constitutes a strongly supported lineage that forms a sister clade to *Neodeightonia planchoniae* and *N. palmicola* with 71% ML and 0.92 BPP support (Fig. 2). *Neodeightonia pinangae* differs from *N. planchoniae* in having larger ascomata (250–330 × 200–250 *vs.* 175–210 × 182–250 µm), asci (80–110 × 16–22 *vs.* 58–70 × 15–21 µm) and ellipsoidal-fusiform or fusiform hyaline ascospores (25–29 × 10–12 *vs.* 18–26 × 7–9 µm) (Jayasiri et al. 2019). A comparison of the 514 nucleotides across the ITS (+ 5.8S) gene region of *Neodeightonia pinangae* with *N. planchoniae* and *N. palmicola* showed 8 (1.5%) and 14 (2.72%) basepair differences, respectively. A synopsis of morphological differences between our species and the sexual morphs of other species is provided in Table 2. We introduce *Neodeightonia pinangae* as a novel taxon based on morphological differences and phylogenetic support.

2. *Neocatenulostroma* Quaedvl. & Crous

Neocatenulostroma was introduced in *Teratosphaeriaceae* by Quaedvlieg et al. (2014), with *N. microsporum* as the type species. The genus includes endophytic, plant pathogenic and saprobic taxa (Markovskaja et al. 2016). *Neocatenulostroma* species have been isolated from a range of substrates, including rocks (Markovskaja et al. 2016). *Neocatenulostroma* species are characterised by globose to slightly subglobose ascomata and chains of longitudinal, cylindrical to Y-shaped or ellipsoidal irregularly branched conidia (Quaedvlieg et al. 2014).

There are three epithets listed under *Neocatenulostroma* in Species Fungorum (2021) and all species have molecular data (Table 1). Table 1 shows the trend of taxa introduced in *Neocatenulostroma* according to the Species Fungorum (2021). There are 23 ITS sequences of *Neocatenulostroma* in GenBank. A BLASTn search of the ITS region of the type species *Neocatenulostroma microsporum* strain CBS 101951 (NR_145114) showed high similarity (90–100%) to 18 uncultured sequences and 16 unidentified isolates. There are three species hypotheses (comprising 137 sequences) that have high similarity in UNITE. Most *Neocatenulostroma* species are plant pathogens. For example, *N. abietis* causes diseases on a wide range of conifer hosts (firs, pines and junipers) (Markovskaja et al. 2016). *Neocatenulostroma abietis* has also been isolated from a range of substrates, commonly as saprobe or endophyte in pine needles (Quaedvlieg et al. 2014). *Neocatenulostroma microsporum*

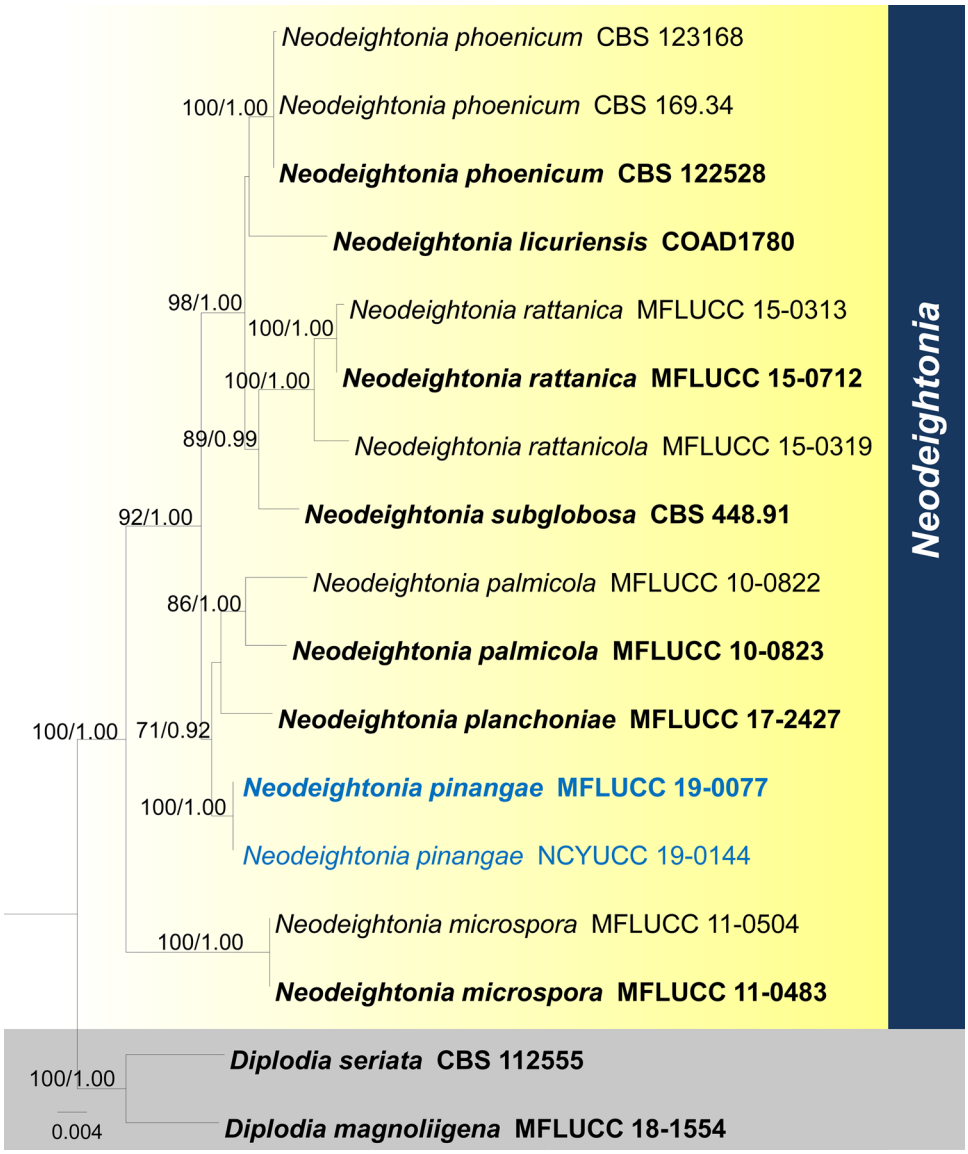


Fig. 2 Phylogram generated from maximum likelihood analysis based on combined LSU, SSU, ITS and *tef*1-α sequence data of *Neodeightonia*. Seventeen taxa were included in the combined analyses, which comprised 2859 characters (LSU = 889 bases, SSU = 1061 bases, ITS = 603 bases, *tef*1-α = 306 bases) after alignment. The best scoring RAxML tree with a final log likelihood score of −5591.196172 is presented. Bootstrap support values for ML equal to or greater than 70% and BPP equal to or greater than 0.90 are given above the nodes. *Diplodia seriata* (CBS 112555) and *D. magnoliigena* (MFLUCC 18–1554) were used as outgroup taxa. The newly generated sequences are indicated in blue. The ex-type strains are indicated in bold

Table 2 Synopsis of the sexual morphs of *Neodeightonia* species

Neodeightonia species	Size (µm)			References
	Ascomata	Asci	Ascospores	
N. microspora MFLU 15–1201	100–150 × 95–150	70–110 × 14–20	10–12 × 4.5–6	Dai et al. (2016)
N. palmicola MFLU 10–0407	180–230 × 270–420	110–210 × 17–22.5	23–31.5 × 8.5–12.5	Liu et al. (2010)
***N. pinangae* MFLU 18–2619**	**250–330 × 200–250**	**80–110 × 16–22**	**25–29 × 10–12**	**This study**
N. planchoniae MFLU 18–2140	175–210 × 182–250	58–70 × 15–21	18–26 × 7–9	Jayasiri et al. (2019)
N. rattanica MFLU 15–1443	222–241 × 246–278	113–141 × 19–25	22–25 × 8–11	Konta et al. (2016)
N. rattanicola MFLU 15–0294	180–215 × 146–168	91–108 × 19–25	22–26 × 8–11	Konta et al. (2016)

causes diseases on leaves of *Protea* and *Encephalartos*, but not conifers (Quaedvlieg et al. 2014). *Neocatenulostroma germanicum* is pathogenic on pine needles and it has also been isolated as a saprobe from rocks and epoxy resin (Pangallo et al. 2015). *Neocatenulostroma abietis* has been associated with different lifestyles in pines. This possibly suggests that *Neocatenulostroma* colonise pines as endophytes, and switch lifestyles at host senescence

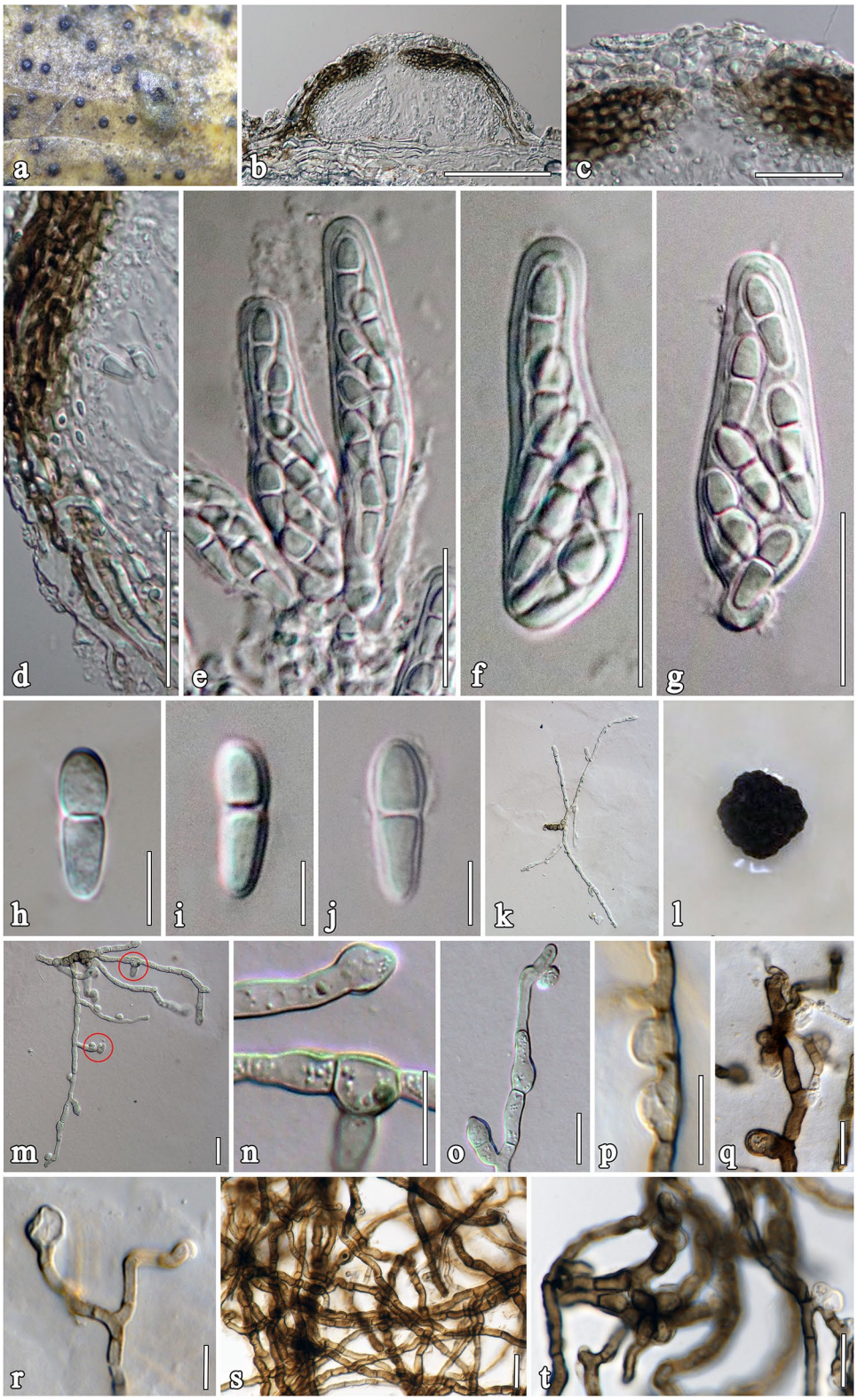


Fig. 3 ***Neocatenulostroma castaneae*** (MFLU 16–1947, **holotype**). **a** Ascomata scattered on the surface of *Castanea sativa*. **b** Section through ascoma. **c** Ostiolar canal. **d** Peridium. **e–g** Asci. **h–j** Ascospores. **k, m** Germinated ascospores (the red circle indicates appressoria produced during the germination stage. **l** Culture characters on PDA. **n–o** Appressorial penetration pegs produced at germination. **p-r** Appressorial pegs produced in culture. **s, t** Mycelia characteristic. Scale bars: **b** = 100 µm. **c–g** = 20 µm. **h–j** = 5 µm, **m–t** = 10 µm

or due to environmental conditions. Studies of hosts with similar or later divergence times as *Pinus* (150 MYA, Keeley 2012) is likely to result in significant novelty as *Neocatenulostroma* species have demonstrated the ability of host-jumping. This is supported by the new species in this study which was isolated from *Fagaceae* which originated around 100 MYA (Manos and Stanford 2001).

We introduce a new species, *Neocatenulostroma castaneae* from dead aerial branches of *Castanea sativa* in Italy based on morphology and phylogeny.

Neocatenulostroma castaneae Phukhams., Bhunjun & K.D. Hyde, ***sp. nov.***

Index Fungorum number: IF558402; *Facesoffungi number*: FoF 09844, Fig. 3

Etymology: Named after the host genus *Castanea.*

Holotype: MFLU 16–1947

Saprobic on *Castanea sativa* Mill. ***Sexual morph*:** *Ascomata* 140 × 176 µm (n = 5) diam., pseudothecial, scattered to gregarious, uniloculate, subepidermal to erumpent, depressed, subglobose in section, dark brown to black, with central apical ostiole. *Peridium* 14–25 µm wide ($\bar{x}$ = 16 µm, n = 8), thick at apex, thin-walled at the lower half, composed of several layers of pale brown to dark brown cells of *textura angularis* at the apex, *textura prismatica* at the sides, inner layer lined with 6–8 layers of subhyaline cells, thin at base. *Hamathecium* aparaphysate. *Asci* 38–60 × 11–15 µm ($\bar{x}$ = 40 × 11 µm, n = 30), 8-spored, bitunicate, subsessile, ovoid to broadly ellipsoid, straight to slightly curved, with short pedicel, apically rounded, ocular chamber clearly visible when immature. *Ascospores* 10–16 × 3–6 µm ($\bar{x}$ = 12 × 4 µm, n = 40), overlapping, biseriate to multiseriate, fusoid-ellipsoidal with obtuse ends, straight or slightly curved, medianly 1-septate, cell above septa larger than those below, thick-walled, hyaline, without persistent mucus sheath. ***Asexual morph*:** Mycelium producing chlamydospores and chlamydospore-like structures after two months, hyaline to dark brown, hyphae, septate, branched, verruculose, thick-walled, transformed into chlamydospores.

Culture characteristics: Ascospores germinating on PDA within 24–48 h. Germinating ascospores become either verruculose, brown and distorted, germ tubes developing from apical and basal cells. Appressorial-like structures are formed at the end of germ hyphae. Colonies on PDA slow-growing, reaching 10 mm in diameter after four weeks of incubation at 25 °C. Colonies black, umbonate at the centre, with circular, friable, black margin; reverse black. Chlamydospore-like structures formed in culture.

Material examined: Italy, Arezzo [AR] Province, Quota – Poppi, on dead aerial branches of *Castanea sativa* Mill. (*Fagaceae*), 3 June 2016, E. Camporesi, IT2990–A (MFLU 16–1947, **holotype**); ex-type living culture, MFLUCC 17–2188.

GenBank accession numbers: LSU = MZ518791, SSU = MZ518821, ITS = MZ519072.

Notes: *Neocatenulostroma castaneae* is phylogenetically distinct but nests with *Austroafricana* and *Neocatenulostroma* in the maximum likelihood, maximum parsimony and Bayesian inference analyses with moderate bootstrap support (Fig. 4). BLASTn results of the LSU sequences showed 97% similarity to *Pseudoteratosphaeria ohnowa* (CBS 112896) across 99% of the query sequence which translates to over 96% similarity, and the ITS region was 93% similar to *Pseudotaeniolina globosa* (CBS 109889) across 99% of the query sequence which translates to over 92% similarity. *Neocatenulostroma castaneae* is distinct from *Austroafricana* and *Neocatenulostroma*, which are saprobes having depressed and subglobose ascomata, with only dark brown chlamydospore-like structures observed in culture (Markovskaja et al. 2016). The sexual morph of *Neocatenulostroma castaneae* is similar to members of *Teratosphaeriaceae* in their aparaphysate, subsessile, ovoid to broadly ellipsoid asci, and fusoid-ellipsoidal ascospores with obtuse ends, such as *Austroafricana, Parateratosphaeria, Teratosphaeria, Teratosphaeriopsis* and *Xenoteratosphaeria* (Quaedvlieg et al. 2012, 2014; Crous et al. 2017; Abdollahzadeh et al. 2020). Chlamydospore-like structures are commonly found in *Teratosphaeriaceae*, as in *Constantinomyces, Incertomyces* and *Monticola* (Ruibal et al. 2018; Crous et al. 2019). *Neocatenulostroma castaneae* is a saprobe on dried branches, but appressorial pegs were noted at the tips or in between the hypha cells in the axenic culture (Fig. 3). This suggests an endophytic or pathogenic life stage (Chethana et al. 2021). *Neocatenulostroma castaneae* is introduced as a new species as it forms a distinct lineage from *Austroafricana* and *Neocatenulostroma* species. The *rpb*2 gene is an important marker for *Teratosphaeriaceae*, therefore, the new taxon is not introduced as a new genus as it lacks the *rpb*2 gene.

3. *Bambusicola* D.Q. Dai & K.D. Hyde

Bambusicola was introduced by Dai et al. (2012) and is typified by *B. massarinia.* It belongs to *Bambusicolaceae, Pleosporales, Dothideomycetes* (Hyde et al. 2013; Dai et al. 2017; Hongsanan et al. 2020). Three genera are accepted in *Bambusicolaceae,* namely *Bambusicola*, *Leucaenicola* and *Palmiascoma* (Dai et al. 2012; Liu et al. 2015; Jayasiri et al. 2019). *Bambusicola* is noticeable as black dots on the host surfaces, and only known from *Bambusoideae* or *Ficus* (Jayasiri et al. 2019). Most *Bambusicola* taxa were isolated from bamboo as pathogen or saprobes, and they can decompose bamboo and woody material (Cai et al. 2006).

Bambusicola originally included four species discovered from bamboo in tropical areas (Dai et al. 2012). There are 14 species listed under *Bambusicola* in Species Fungorum (2021) (Table 1) and 21 species are accepted in

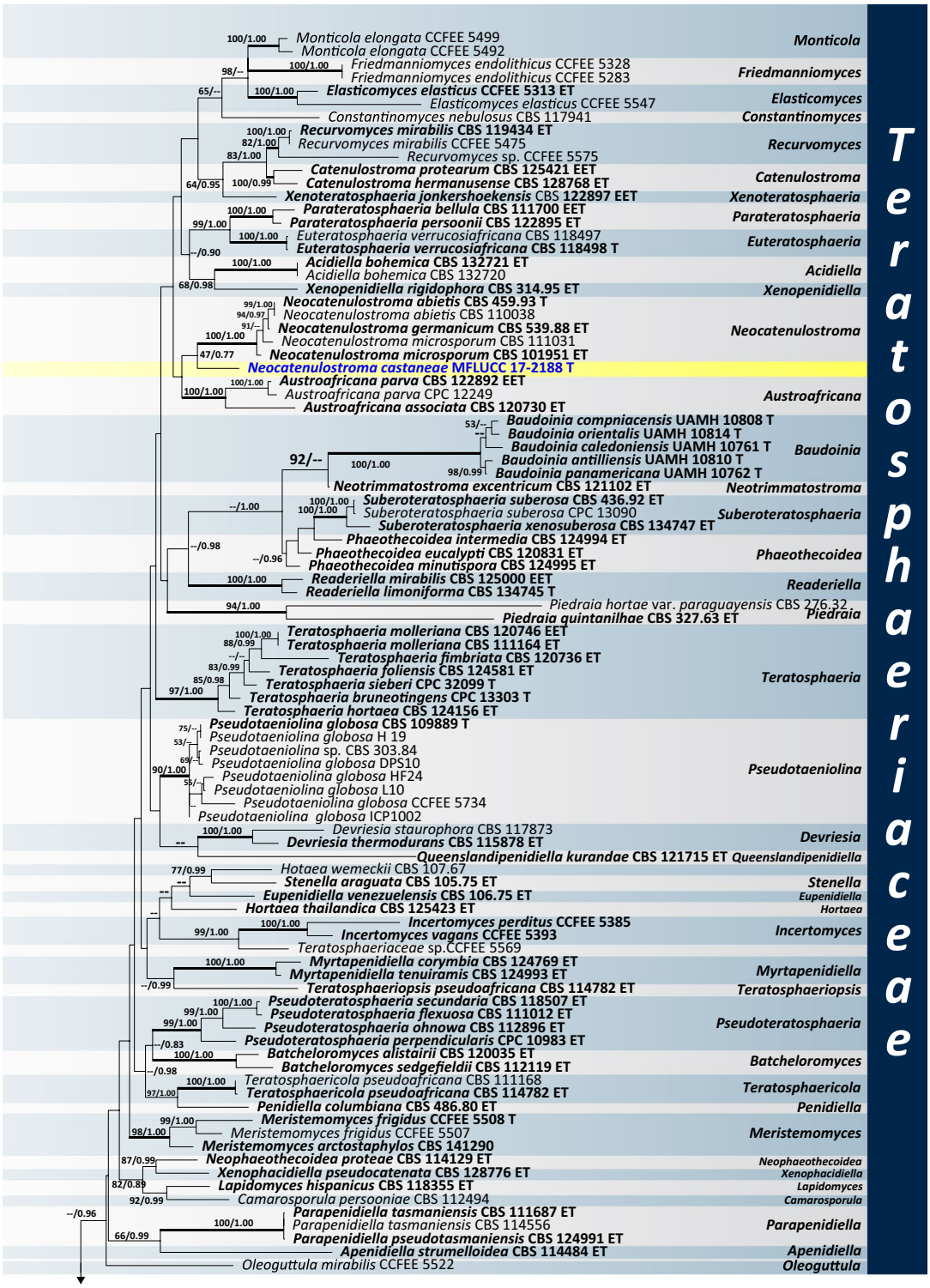


Fig. 4 Phylogram generated from maximum likelihood analysis based on combined LSU, ITS, and *rpb2* sequence data representing the placement of *Mycosphaerellales* taxa. One hundred and thirty-nine taxa were included in the combined analyses, which comprised 1992 characters (LSU = 916 bases, ITS = 736 bases, *rpb2* = 340 bases) after alignment. The best scoring RAxML tree with a final log likelihood score of −39830.487503 is presented. Bootstrap support values for ML equal to or greater than 50% and BPP equal to or greater than 0.70 are given above the nodes. *Capnodium neocoffeicola* (CBS 139614) and *Capnodium paracoartatum* (MFLUCC 14–0282) were used as outgroup taxa. The newly generated sequence is indicated in blue. The type-derived sequences are indicated in bold. Thick branches represent support values equal to or greater than 75% ML and BPP equal to or greater than 0.95

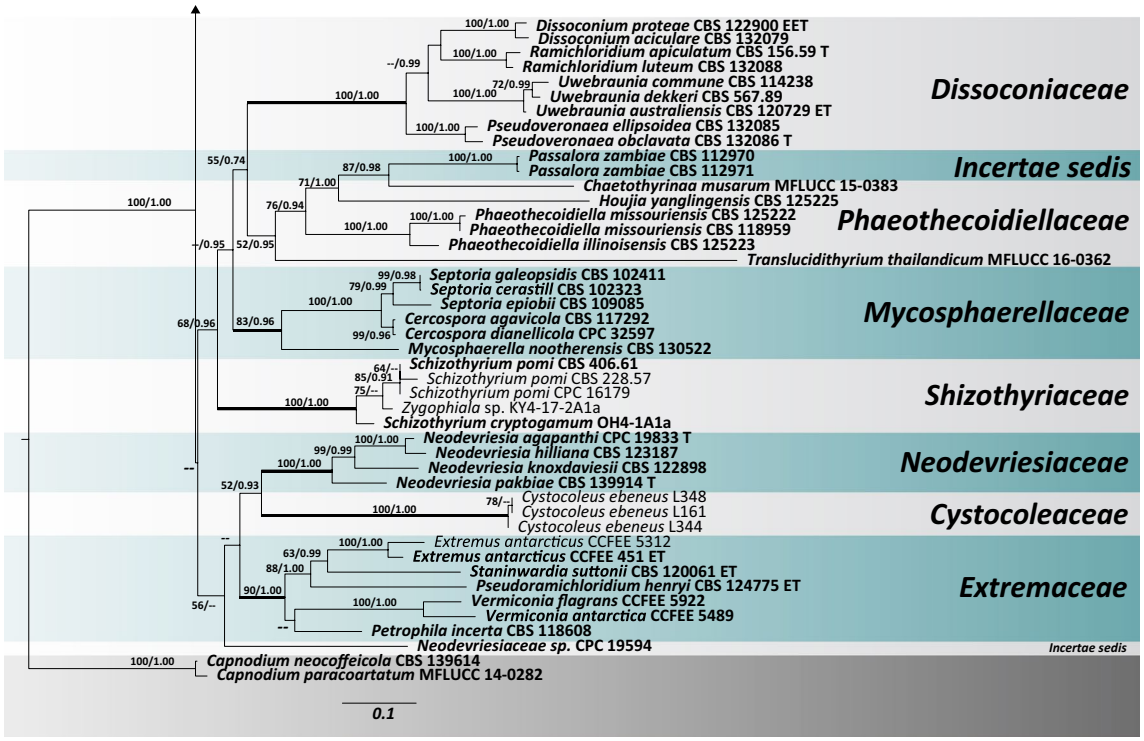


Fig. 4 (continued)

Bambusicolaceae based on morphology and molecular data (Wijesinghe et al. 2021). There are 17 ITS sequences annotated as *Bambusicola* in GenBank. A BLASTn search of the ITS region of the type species *Bambusicola massarinia* strain MFLUCC 11-0389 (NR_121548) showed high similarity and query cover (90–100%) to almost all *Bambusicolaceae* species (one sequence was annotated as *Pleosporales* sp. PSU-ES100 (JN116643) and one unidentified *Phoma* sp. 20_2 (KC354579)). There are ten species hypotheses (comprising 15 sequences) that show high similarity in the UNITE database. Bamboo is mainly distributed in tropical and subtropical areas (Lobovikov et al. 2007). *Bambusicolaceae* diverged around 44 MYA (58–15 MYA), and *Bambusoideae* is thought to have diversified around 42 (44–42) MYA (Guo et al. 2019; Hongsanan et al. 2020; Bhunjun et al. 2021b). It is likely that *Bambusicolaceae* species may have co-evolved with bamboo (Wysocki et al. 2015; Bhunjun et al. 2021b). *Poaceae* became diverse and ubiquitous in the Eocene period and the abundance of grass favoured the evolution of early grazing animals, such as Eohippus (Beaver 2019). This also resulted in the evolution of bamboo-eating mammals such as the red pandas (*Ailurus fulgens*) at around 39.9 MYA (Hu et al. 2017). In addition to *Bambusoideae, Bambusicola* species are also found on *Ficus*. Tree-dwellers such as monkeys, birds, and fruit bats can be hypothesized to have facilitated the diversification of *Bambusicola* species as *Ficus* fruits are an important part of their diet. The majority of studies on *Bambusicola* are confined to China and Thailand, therefore a large number of species is likely to be discovered as other countries are explored for *Bambusicola* diversity. More studies focusing on the endophytic lifestyle of fungi on *Bambusoideae* will advance our understanding of the host-specificity of bambusicolous fungi.

Bambusicola nanensis Y.R Sun, Yong Wang bis & K.D. Hyde, ***sp. nov.***

Index Fungorum number: IF558825; *Facesoffungi number*: FoF 09934, Fig. 5

Etymology: In reference to the location, Nan Province, where the holotype was collected

Holotype: MFLU 21-0090

Saprobic on dead bamboo culms. ***Sexual morph***: Undetermined. ***Asexual morph***: Coelomycetous. *Conidiomata* 140–190 × 200–250 µm, pycnidial, solitary to gregarious, mostly immersed under host tissues, partly erumpent, subglobose, brown. *Conidiomatal wall* 20–55 µm wide, composed of pale brown to brown cells of *textura angularis,* outer layer somewhat partial carbonaceous, inner layer composed of subhyaline gelatinous cells bearing conidiogenous layer. *Conidiogenous cells* holoblastic, phialidic, cylindrical, smooth, hyaline. *Conidia* has two types, macro- and microconidia. *Macroconidia* 32–42 × 1.8–3 µm ($\bar{x}$ = 38 × 2.5 µm,

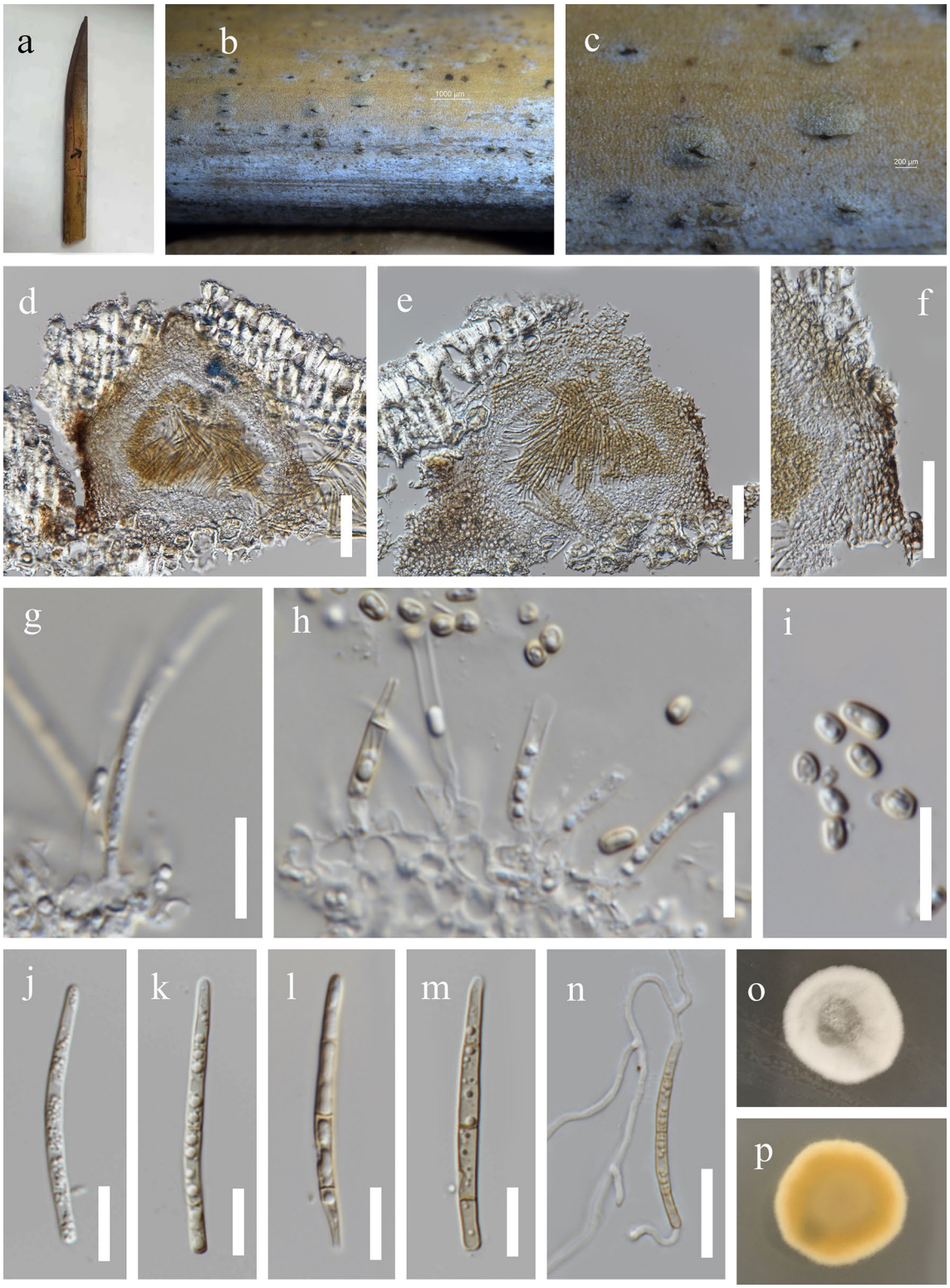


Fig. 5 ***Bambusicola nanensis*** (MFLU 21–0090, **holotype**). **a** Host. **b, c** Fruiting body on bamboo host. **d, e** Section of pycnothyrium. **f** Peridium. **g, h** Conidiogenous cells and developing conidia. **i** Microconidia. **j–m** Macroconidia. **n** Geminating macroconidia. **o, p** Colonies on PDA after 4 weeks. Scale bars: **d–f** = 50 µm, **g–m** = 10 µm, **n** = 20 µm

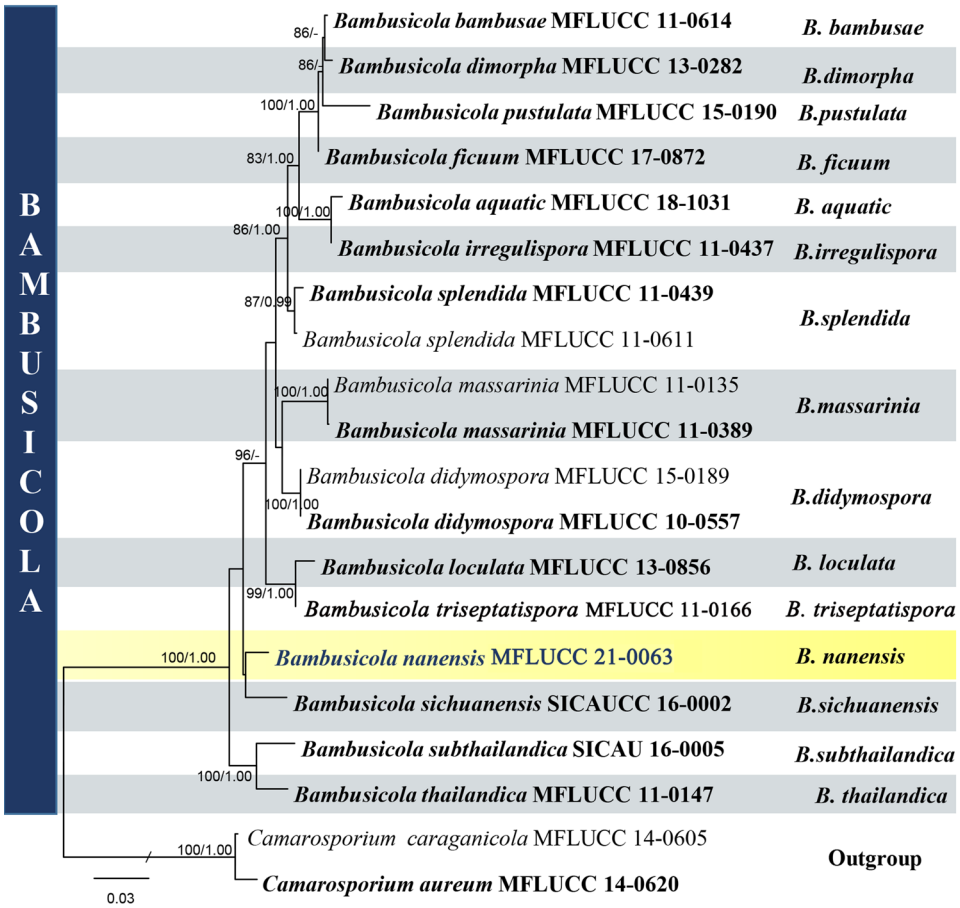


Fig. 6 Phylogram generated from maximum likelihood analysis based on combined LSU, ITS, and SSU sequence data. Related sequences were taken from Genbank and Brahmanage et al. (2020). Twenty taxa were included in the combined analyses, which comprised 2433 characters (LSU = 815 bases, ITS = 819 bases, SSU = 799 bases) after alignment. The best scoring RAxML tree with a final log likelihood score of −7,163.929087 is presented. Maximum likelihood bootstrap support values equal to or greater than 75% and BPP equal to or greater than 0.95 are given above the nodes. *Camarosporium aureum* (MFLUCC 14–0620) and *C. caraganicola* (MFLUCC 14–0605) were used as outgroup taxa. The newly generated sequence is indicated in blue and the type-derived sequences are given in bold

n = 20), vermiform to cylindrical, elongate, rounded at the ends, slightly curved, 2–3-septate, hyaline when young, pale brown to brown when mature, smooth-walled, guttulate. *Microconidia* 2.5–4.5 × 1.2–2.5 µm ($\bar{x}$ = 3 × 2 µm, n = 20), globose or oblong to ellipsoidal, rounded at the ends, aseptate, hyaline to pale brown, guttulates.

Culture characteristics: Macroconidia germinated on PDA within 12 h from single spores. Both ends produced germ tubes. Colony diameter reached 15–20 mm after 4 weeks at 26 °C on PDA, circular, with entire margin, flat, cottony, white from above, yellow from below.

Material examined: Thailand, Nan Province, on dead bamboo culms, 15 January 2020, Y.R Sun, NFB5 (MFLU 21–0090, **holotype**); ex-type living culture, MFLUCC 21–0063.

GenBank accession numbers: LSU = OK491652, ITS = OK491656.

Notes: *Bambusicola nanensis* was collected from dead bamboo culms in terrestrial habitats. In the multigene analyses, the new taxon formed a sister clade to *Bambusicola sichuanensis* (SICAUCC 16–0002) (Fig. 6), which was reported from branches of *Phyllostachys heteroclada* in China (Yang et al. 2019). However, *B. nanensis* has smaller conidiomata (140–190 × 200–250 µm *vs.* 422–750 × 420–700 µm) and longer macroconidia (32–42 × 1.8–3 µm *vs.* 16.5–19 × 4 µm) than *B. sichuanensis.* In addition, analysis of nucleotide polymorphism in the ITS region revealed 7.2% (37/515) base differences (without gaps) between these two strains. Therefore, following the guidelines for species delineation described by Jeewon and Hyde (2016), we introduce *B. nanensis* as a novel taxon.

5. *Paraconiothyrium* Verkley

Paraconiothyrium (*Didymosphaeriaceae*) was introduced by Munk (1953), and it is considered one of the most species-rich pleosporalean families (Hyde et al. 2013; Hongsanan et al. 2020; Dissanayake et al. 2021). The sexual morphs of *Didymosphaeriaceae* are characterized by uni-septate ascospores with trabeculate pseudoparaphyses (Wijesinghe et al. 2020), while asexual morphs are fusicladium-like or phoma-like (Hyde et al. 2013; Dissanayake et al. 2021). *Paraconiothyrium* is an asexual genus introduced by Verkley et al. (2004) to accommodate four taxa, *P. brasiliense*, *P. cyclothyrioides*, *P. fungicola*, and *P. estuarinum*

(type species). Members of *Paraconiothyrium* are characterized by eustromatic, pycnidial conidiomata, phialidic or percurrent conidiogenous cells, and aseptate to 1-septate, hyaline to brown conidia (Verkley et al. 2004; Gonçalves et al. 2016). The sexual morph of *Paraconiothyrium* was considered as *Paraphaeosphaeria* (Verkley et al. 2004).

There are 20 epithets listed in Species Fungorum (2021) under *Paraconiothyrium* (Table 1) and over 500 ITS sequences annotated as *Paraconiothyrium* in GenBank. A BLASTn search of the ITS region of the type species *Paraconiothyrium estuarinum* strain CBS 109850 (NR_166007) showed a high similarity and query cover (90–100%) to several *Microsphaeropsis* and *Paraconiothyrium* species as well as one *Fusarium* species which could be a misidentification (MN644543). In 2020, around 100 sequences of *Paraconiothyrium* were deposited, but the phylogenetic placement of some of these taxa are not confirmed. There are 37 species hypotheses (comprising 708 sequences) with high similarity to *Paraconiothyrium* in UNITE. However, as the genus has high diversity, the ITS region alone is not sufficient to demarcate species. Seven taxa were synonymized under this genus. Some *Paraconiothyrium* species were synonymized under *Paraphaeosphaeria* (for example, *Paraconiothyrium minitans* under *Paraphaeosphaeria minitans* and *Paraconiothyrium sporulosum* under *Paraphaeosphaeria sporulosa,* Verkley et al. 2014). *Paracamarosporium* and *Pseudocamarosporium* species have similar morphology, such as pycnidial conidiomata and enteroblastic and phialidic conidiogenesis (percurrent proliferation) with muriform conidia (Wijayawardene et al. 2014). *Pseudocamarosporium* was introduced by Wijayawardene et al. (2014) to accommodate camarosporium-like species. *Pseudocamarosporium* and *Paracamarosporium* show closer affinities, but they differ in morphology by the presence of paraphyses in *Paracamarosporium* (Hongsanan et al. 2020).

Pathogenic, saprobic and endophytic *Paraconiothyrium* species are associated with different plant hosts and substrates (Ariyawansa et al. 2020). Most *Paraconiothyrium* species have been recorded on monocotyledons, such as grasses (Liu et al. 2015), mosses and clubmosses (Budziszewska et al. 2011; de Gruyter et al. 2013), eudicots (Verkley et al. 2004; 2014; Ariyawansa et al. 2014, 2015), soil and estuarine sediments (Verkley et al. 2004) and are also human pathogens (Verkley et al. 2014). A large number of species is likely to be discovered as they can be found on a wide range of hosts.

The crown age of the suborder *Massarineae* is estimated at 130 MYA in the Cretaceous period, and *Didymosphaeriaceae* diverged at around 100–75 MYA in the Cretaceous period (Phukhamsakda et al. 2016). The earliest moss and clubmoss fossils are reported from the Permian period and the crown age was estimated by Wikström and Kenrick (2001) as 298.9–251.9 MYA. Monocotyledons and eudicots (modern seed-bearing plants) diversified in the Cretaceous period (135–130 MYA), while grasses (*Poaceae*) diversified around 65 MYA in the late Cretaceous period (Chen et al. 2017). *Didymosphaeriaceae* diverged before the Cretaceous extinction event. The conditions of high humidity and reduced solar insolation after the extinction event favoured an increase of saprobic fungi that flourished on the detritus (Vajda and McLoughlin 2004). It can be hypothesised that *Didymosphaeriaceae* species diversified to adapt to various hosts that were dominant following the extinction event, such as *Poaceae* (Peace et al. 2020). *Paraconiothyrium* species are widespread and are associated with several lifestyles on a wide range of hosts. We would expect the number of species to increase with the study of hosts which diversified following the extinction event. This is supported by the new species introduced in this study from *Ficus* sp. (eudicots), which has a crown age of around 75–48.5 MYA (Zhang et al. 2019). A new species, *Paraconiothyrium fici,* is introduced based on morphology and multi-marker phylogenetic analyses.

Paraconiothyrium fici Wijes. & K.D. Hyde, ***sp. nov.***

Index Fungorum number: IF559244; *Facesoffungi number*: FoF 10567, Fig. 7

Etymology: Epithet refers to the host genus *Ficus*

Holotype: MFLU 17–0690

Saprobic on dead twigs of *Ficus* sp. ***Sexual morph***: Undetermined. ***Asexual morph***: *Conidiomata* 150–190 × 200–280 µm ($\bar{x}$ = 175 × 235 µm, n = 10) pycnidial, solitary or aggregated, scattered, immersed, uni-loculate, globose to subglobose, black, lacking ostioles. *Conidiomatal wall* 9–17 µm wide, comprising 4–5 cell-layers of thick-walled, hyaline to pale brown cells of *textura angularis*. *Conidiophores* reduced to conidiogenous cells. *Conidiogenous cells* 1.9–4 × 2.2–3 µm ($\bar{x}$ = 2.7 × 2.9 µm, n = 10), enteroblastic, ampulliform to subcylindrical, phialidic with periclinal wall thickening or percurrent proliferations near the apex. *Conidia* 5.5–7.4 × 2.8–3.7 µm ($\bar{x}$ = 6.5 × 3.2 µm, n = 20), globose to cylindrical, initially hyaline, becoming pale to dark brown when mature, thin-walled, smooth, aseptate, with 1–3 small guttules.

Culture characteristics: Conidia germinating on PDA within 24 h, reaching 20–25 mm in 2 weeks at 25 °C. Germ tubes produced from the basal and apical cells of conidia. Mycelia superficial, circular, with entire margin, flat, smooth, from above white; reverse, pale yellow to light brown.

Material examined: Thailand, Chiang Mai Province, Mushroom Research Centre, on a dead twig of *Ficus* sp. (*Moraceae*), 25 January 2017, NI de Silva, NI 145 (MFLU

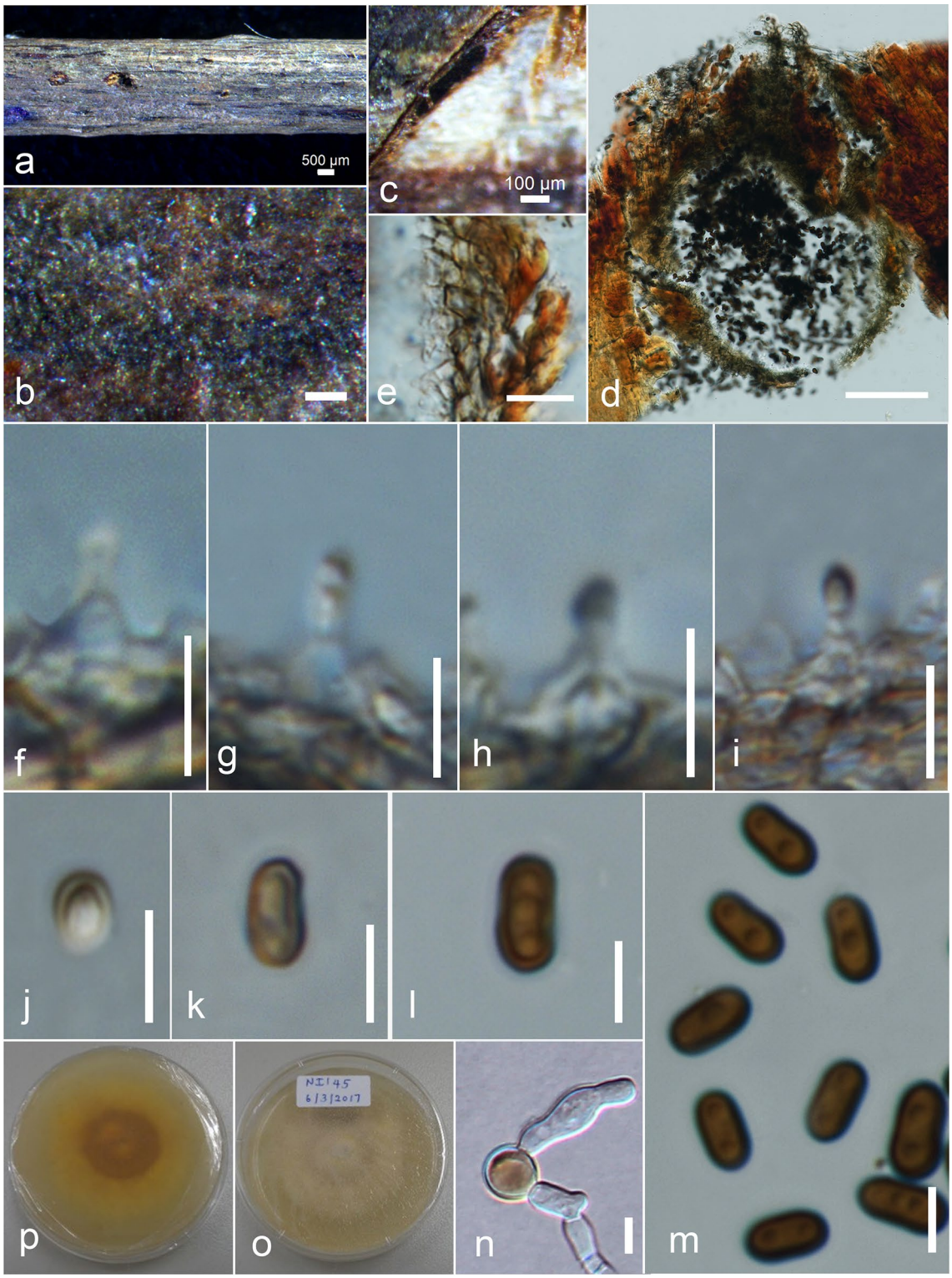
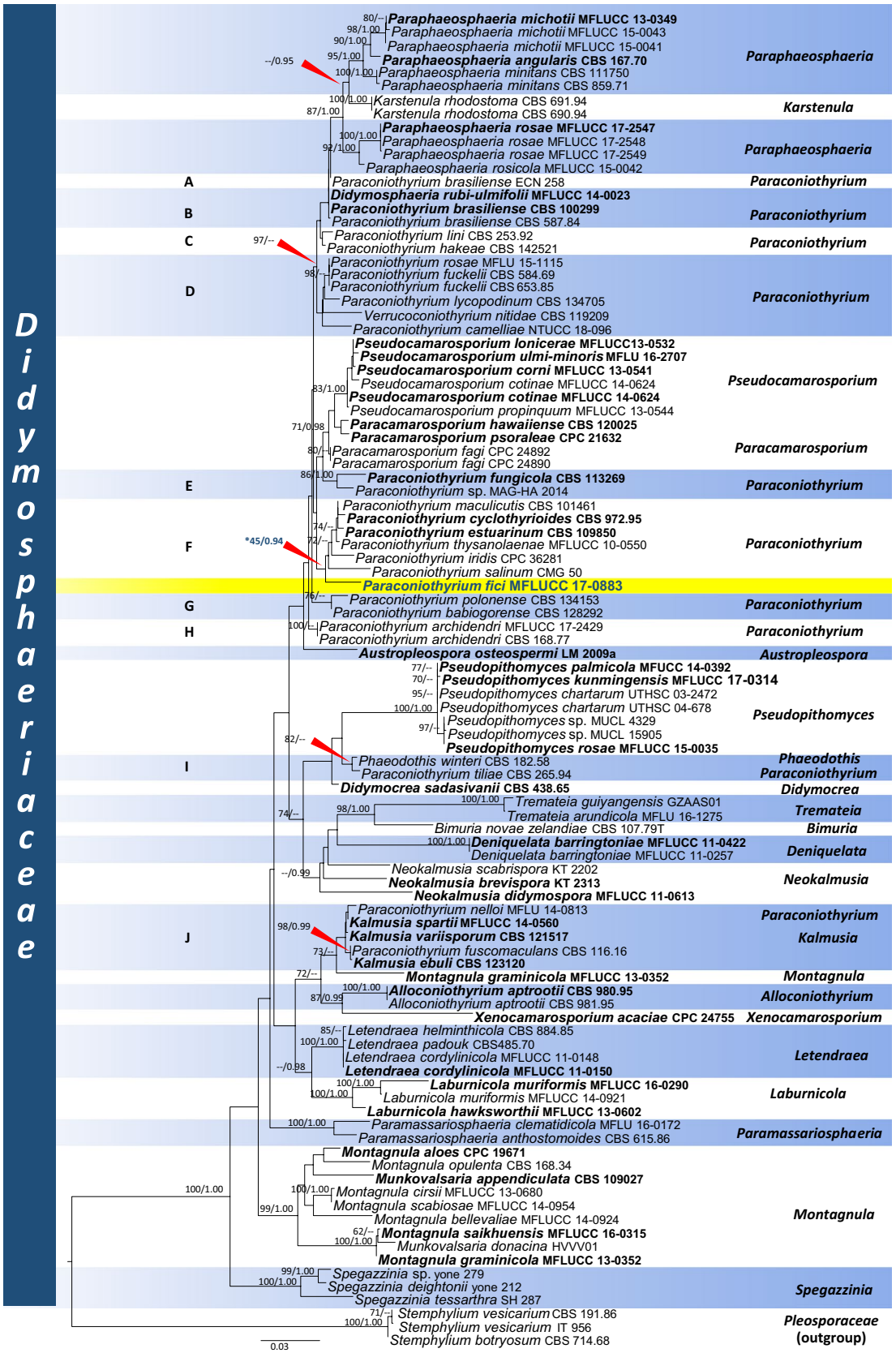


Fig. 7 ***Paraconiothyrium fici*** (MFLU 17–0690, **holotype**). **a** Host. **b** Conidiomata on host surface. **c, d** Longitudinal sections of conidiomata. **e** Conidioma wall. **f–i** Conidiogenous cells. **j–m** Conidia. **n** Germinated conidia**. o–p C**ulture on PDA from surface and reverse. Scale bars: a = 500 µm, **b–c** = 100 µm, **d** = 50 µm, **e** = 10 µm, **f–n** = 5 µm


Didymosphaeriaceae
Paraphaeosphaeria michotii MFLUCC 13-0349
Paraphaeosphaeria michotii MFLUCC 15-0043
Paraphaeosphaeria michotii MFLUCC 15-0041
Paraphaeosphaeria angularis CBS 167.70
Paraphaeosphaeria minitans CBS 111750
Paraphaeosphaeria minitans CBS 859.71
Paraphaeosphaeria
Karstenula rhodostoma CBS 691.94
Karstenula rhodostoma CBS 690.94
Karstenula
Paraphaeosphaeria rosae MFLUCC 17-2547
Paraphaeosphaeria rosae MFLUCC 17-2548
Paraphaeosphaeria rosae MFLUCC 17-2549
Paraphaeosphaeria rosicola MFLUCC 15-0042
Paraphaeosphaeria
A
Paraconiothyrium brasiliense ECN 258
Paraconiothyrium
Didymosphaeria rubi-ulmifolii MFLUCC 14-0023
B
Paraconiothyrium brasiliense CBS 100299
Paraconiothyrium brasiliense CBS 587.84
Paraconiothyrium
C
Paraconiothyrium lini CBS 253.92
Paraconiothyrium hakeae CBS 142521
Paraconiothyrium
Paraconiothyrium rosae MFLU 15-1115
Paraconiothyrium fuckelii CBS 584.69
Paraconiothyrium fuckelii CBS 653.85
D
Paraconiothyrium lycopodinum CBS 134705
Verrucoconiothyrium nitidae CBS 119209
Paraconiothyrium camelliae NTUCC 18-096
Paraconiothyrium
Pseudocamarosporium lonicerae MFLUCC13-0532
Pseudocamarosporium ulmi-minoris MFLU 16-2707
Pseudocamarosporium corni MFLUCC 13-0541
Pseudocamarosporium cotinae MFLUCC 14-0624
Pseudocamarosporium cotinae MFLUCC 14-0624
Pseudocamarosporium propinquum MFLUCC 13-0544
Pseudocamarosporium
Paracamarosporium hawaiiense CBS 120025
Paracamarosporium psoraleae CPC 21632
Paracamarosporium fagi CPC 24892
Paracamarosporium fagi CPC 24890
Paracamarosporium
Paraconiothyrium fungicola CBS 113269
E
Paraconiothyrium sp. MAG-HA 2014
Paraconiothyrium
Paraconiothyrium maculicutis CBS 101461
Paraconiothyrium cyclothyrioides CBS 972.95
Paraconiothyrium estuarinum CBS 109850
F
Paraconiothyrium thysanolaenae MFLUCC 10-0550
Paraconiothyrium iridis CPC 36281
Paraconiothyrium salinum CMG 50
Paraconiothyrium
Paraconiothyrium fici MFLUCC 17-0883
Paraconiothyrium polonense CBS 134153
G
Paraconiothyrium babiogorense CBS 128292
Paraconiothyrium
Paraconiothyrium archidendri MFLUCC 17-2429
H
Paraconiothyrium archidendri CBS 168.77
Paraconiothyrium
Austropleospora osteospermi LM 2009a
Austropleospora
Pseudopithomyces palmicola MFUCC 14-0392
Pseudopithomyces kunmingensis MFLUCC 17-0314
Pseudopithomyces chartarum UTHSC 03-2472
Pseudopithomyces chartarum UTHSC 04-678
Pseudopithomyces sp. MUCL 4329
Pseudopithomyces sp. MUCL 15905
Pseudopithomyces rosae MFLUCC 15-0035
Pseudopithomyces
Phaeodothis winteri CBS 182.58
I
Paraconiothyrium tiliae CBS 265.94
Phaeodothis
Paraconiothyrium
Didymocrea sadasivanii CBS 438.65
Didymocrea
Tremateia guiyangensis GZAAS01
Tremateia arundicola MFLU 16-1275
Tremateia
Bimuria novae zelandiae CBS 107.79T
Bimuria
Deniquelata barringtoniae MFLUCC 11-0422
Deniquelata barringtoniae MFLUCC 11-0257
Deniquelata
Neokalmusia scabrispora KT 2202
Neokalmusia brevispora KT 2313
Neokalmusia didymospora MFLUCC 11-0613
Neokalmusia
Paraconiothyrium nelloi MFLU 14-0813
Paraconiothyrium
Kalmusia spartii MFLUCC 14-0560
J
Kalmusia variisporum CBS 121517
Paraconiothyrium fuscomaculans CBS 116.16
Kalmusia
Kalmusia ebuli CBS 123120
Montagnula graminicola MFLUCC 13-0352
Montagnula
Alloconiothyrium aptrootii CBS 980.95
Alloconiothyrium aptrootii CBS 981.95
Alloconiothyrium
Xenocamarosporium acaciae CPC 24755
Xenocamarosporium
Letendraea helminthicola CBS 884.85
Letendraea padouk CBS485.70
Letendraea cordylinicola MFLUCC 11-0148
Letendraea cordylinicola MFLUCC 11-0150
Letendraea
Laburnicola muriformis MFLUCC 16-0290
Laburnicola muriformis MFLUCC 14-0921
Laburnicola hawksworthii MFLUCC 13-0602
Laburnicola
Paramassariosphaeria clematidicola MFLU 16-0172
Paramassariosphaeria anthostomoides CBS 615.86
Paramassariosphaeria
Montagnula aloes CPC 19671
Montagnula opulenta CBS 168.34
Munkovalsaria appendiculata CBS 109027
Montagnula cirsii MFLUCC 13-0680
Montagnula scabiosae MFLUCC 14-0954
Montagnula bellevaliae MFLUCC 14-0924
Montagnula saikhuensis MFLUCC 16-0315
Munkovalsaria donacina HVVV01
Montagnula graminicola MFLUCC 13-0352
Montagnula
Spegazzinia sp. yone 279
Spegazzinia deightonii yone 212
Spegazzinia tessarthra SH 287
Spegazzinia
Stemphylium vesicarium CBS 191.86
Stemphylium vesicarium IT 956
Stemphylium botryosum CBS 714.68
Pleosporaceae (outgroup)
0.03

◂**Fig. 8** Phylogram generated from maximum likelihood analysis based on combined LSU, SSU, ITS, and *tef*1–α sequence data representing species of *Didymosphaeriaceae* taxa. Sequences were retrieved from GenBank and Ariyawansa et al.(2020). Ninety-nine taxa were included in the combined analyses, which comprised 3217 characters (LSU = 857 bases, SSU = 910 bases, ITS = 527 bases, *tef*1–α = 923 bases) after alignment. The best scoring RAxML tree with a final log likelihood score of −16344.687377 is presented. Bootstrap support values for ML equal to or greater than 40% and BPP equal to or greater than 0.95 are given above the nodes. *Stemphylium vesicarium* (CBS 191.86, IT 956) and *Stemphylium botryosum* (CBS 714.68) were used as outgroup taxa. The newly generated sequence is indicated in bold and blue. The type-derived sequences are indicated in bold and black

17–0690, **holotype**); ex-type living culture, MFLUCC 17–0883.

GenBank accession numbers: LSU = OL770245, SSU = OL770251, ITS = OL770247, *tef*1–α = OL771440

Notes: *Paraconiothyrium fici* forms a separate lineage within clade F as a sister group to a sub-clade of six different *Paraconiothyrium* species, including the type species of the genus (< 45% ML, 0.94 BYPP) (Fig. 8). As presently circumscribed, *Paraconiothyrium* is a paraphyletic genus (Ariyawansa et al. 2020), and in this study, the species of *Paraconiothyrium* are positioned paraphyletically in groups A–J within *Didymosphaeriaceae* (Fig. 8). A detailed morphological comparison was performed among *Paraconiothyrium fici* with *P. cyclothyrioides*, *P. estuarinum, P. maculicutis* and *P. salinum* (Table 3). *Paraconiothyrium fici* could not be compared to *P. thysanolaenae* (MFLUCC 10–0550) and *P. iridis* (CPC 36281) as only their sexual morphs are known. *Paraconiothyrium fici* is similar to species in *Paraconiothyrium* in having pycnidial conidiomata lacking ostioles, ampulliform, phialidic or percurrent conidiogenous cells and hyaline to brown conidia (Verkley et al. 2004). *Paraconiothyrium fici* has slightly larger globose (round) to strong cylindrical conidia (5.5–7.4 × 2.8–3.7), and sometimes it shows 3-guttules when mature as opposed to the 2-polar guttules in the four closely related *Paraconiothyrium* species (Verkley et al. 2004; de Gruyter 2012; Goh et al. 2020; Gonçalves et al. 2020). The nucleotide differences between *P. fici* and related *Paraconiothyrium* species are: *P. cyclothyrioides* (CBS 972.95) LSU: 1.54% (13/844 bases), ITS: 4.65% (21/451 bases); *P. estuarinum* (CBS 109850) LSU: 1.65% (14/844 bases), ITS: 4.42% (20/452 bases); *P. iridis* (CPC 36281) LSU: 1.18% (10/844 bases), ITS: 5.76% (26/451 bases); *P. maculicutis* (CBS 101461) LSU: 1.30% (11/844 bases); *P. salinum* (CMG 50) ITS: 7.03% (32/451 bases), *tef*1–α: 2.57% (22/855 bases) and *P. thysanolaenae* (MFLUCC 10–0550) LSU: 1.30% (11/844 bases), ITS: 4.43% (20/451 bases) excluding gaps. Based on morpho-molecular analyses, *P. fici* is introduced as a novel species.

6. *Capronia* Sacc.

Herpotrichiellaceae was introduced by Munk (1953) and placed in *Chaetothyriales* (Barr 1976; Liu et al. 2015). The family is represented by the sexual morph genus *Capronia* and the asexual genera *Cladophialophora*, *Exophiala*, *Fonsecaea*, *Phialophora*, *Ramichloridium* and *Rhinocladiella* (Hyde et al. 2016; Phookamsak et al. 2019). *Capronia* was introduced by Saccardo (1883) and is typified by *Capronia sexdecimspora*. This genus is characterized by very small, setose ascomata, lacking paraphyses, fissitunicate asci, and septate, or muriform, hyaline or pigmented ascospores (Sánchez et al. 2019).

The family *Herpotrichiellaceae* comprises 16 genera and more than 260 species (Wijayawardene et al. 2020). *Capronia* is the largest genus in *Herpotrichiellaceae* with over 80 extant species classified based on morphology and/or phylogeny (Phookamsak et al. 2019). There are 81 epithets listed in Species Fungorum (2021, Table 1). Species have been investigated through multi-marker phylogenetic analyses based on ITS, *tef*1-α, *tub2* and *act* and occasionally other markers (de Hoog et al. 2011; Untereiner et al. 2011; Teixeira et al. 2017; Phookamsak et al. 2019; Sánchez et al. 2019). The ITS region has proven valuable in delimiting species in *Herpotrichiellaceae* and also used to support sexual-asexual morph connections within *Herpotrichiellaceae* (Uijthof 1996; Uijthof et al. 1998; de Hoog 1999; Rogers et al. 1999). The combined ITS and LSU dataset provides useful resolution within the clades (Untereiner and Naveau 1999; Sánchez et al. 2019; Wan et al. 2021). There are 112 ITS sequences annotated as *Capronia* in GenBank. A BLASTn search of the ITS region of *Capronia lijiangensis* strain CGMCC 3.20501 (as the molecular data of the type species *C. sexdecimspora* is not available) showed a high similarity and query cover (90–100%) to several unidentified names such as *Ascomycete* sp. (ZGZII03175) and one uncultured *Capronia* sp. (MOTU18). There are 52 species hypotheses (comprising 571 sequences) that have high similarity to *Capronia* in UNITE. *Herpotrichiellaceae* harbours a great diversity of polyphyletic asexual morphs, and *Capronia* is a homothallic sexual genus covering all asexual members. Species belonging to this family have different ecological preferences and exhibit highly diversified lifestyles (de Hoog 2011, 2014). Most of them are opportunistic pathogens of human and cool-blooded animals or saprobic on wood, parasitic on fungi or lichens, and also have thermo-tolerance behaviour, but the species are generally not host-specific (Untereiner et al. 1995; Untereiner 2000; Crous et al. 2007; Tsurykau and Etayo 2017; Sánchez et al. 2019). We would expect the number of species to increase as they can be found from a wide range of hosts.

Studies of the major black yeasts and related lineages based on a calibrated phylogenetic tree showed that *Herpotrichiellaceae* emerged around 75–50 MYA, during or after the Cretaceous–Paleogene extinction event. The

Table 3 Synopsis of asexual morph characters of related *Paraconiothyrium* species in clade F based on phylogenetic analyses

Species Name	Conidiomata (µm)	Wall (µm)	Conidiogenous cells (µm)	Conidia (µm)	References
Paraconiothyrium fici (MFLU 17–0690	150–190 diam., × 200–280 high., globose to subglobose	4–5 cell-layers of *textura angularis*	1.9–4.0 × 2.2–3.0, enteroblastic, ampulliform to subcylindrical, phialidic	5.5–7.4 × 2.8–3.7, globose to cylindrical, aseptate, 1–3 small guttules	This study
P. cyclothyrioides (CBS 972.95)	Eustromatic, irregularly globose or flattened, 0.3–1.2(–1.6) mm diam., ostioles absent	30–75, isodiametric and irregular cells, 25–50(–65) (inner layer) cells of *textura angularis*	4.5–8 × 2.5–4, integrated in compact conidiophores, ampulliform to subcylindrical, indeterminate, phialidic,	(2.5–)3–4.8(–6) × (1–)1.2–1.6(–2) (on MEA), short cylindrical, curved, rounded ends, 1–2 small polar guttules, hyaline to yellowish brown	Verkley et al. (2004)
P. estuarinum (CBS 109850)	Eustromatic, globose or flattened, 0.2–0.5(–1) mm diam., ostioles absent	30–45 (outer layer), reddish-brown, isodiametric or flattened cells, 35–60(–75) (inner layer) thick cells of *textura angularis*	4–6.5 × 2.5–3.5(–4), discrete, integrated in compact conidiophores, ampulliform to subcylindrical, indeterminate, percurrent proliferation	2.0–4.9 × 1.3–2.4, ellipsoidal or short-cylindrical, rounded at both ends, hyaline, one-celled	Verkley et al. (2004), Goh et al. (2020)
P. maculicutis (CBS 101461)	50–125 diam., globose to subglobose	5–7 layers of cells arrangement	1.5–3 × 0.5–2.5, indeterminate or ampulliform to filiform	1.5–2.5 × 0.5–1.5, ellipsoidal, hyaline to discolouring or olivaceous	de Gruyter (2012)
P. salinum (CMG 50)	Eustromatic, irregularly globose or flattened	Pseudoparenchymatous, isodiametric cells and irregular cells with yellowish-brown pigmentation	ampulliform to subcylindrical	ellipsoidal or subcylindrical, straight, rounded apices at both ends, aseptate, 1–2 small polar guttules, yellowish-brown	Gonçalves et al. (2020)

ancestor diverged around 130 MYA during the Cretaceous period (Teixeira et al. 2017). The Cretaceous–Paleogene extinction event witnessed the loss of many lineages of animals and plants (Peace et al. 2020). Saprobic fungi such as *Capronia* flourished on the detritus (Vajda and McLoughlin 2004). A new species, *C. lijiangensis*, collected from decaying wood in China is introduced in this study based on morphology and phylogenetic analyses (Fig. 9).

Capronia lijiangensis M. Raza & L. Cai, ***sp. nov.***

Index Fungorum number: IF558077; *Facesoffungi number*: FoF 10531, Fig. 9

Etymology: refers to Lijiang city in China from where it was collected

Holotype: HMAS 350625

Saprobic on wood. ***Sexual morph***: *Ascomata* 105–145 µm high, 110–175 µm diam., stromatic, solitary or scattered in small groups, immersed, uni-loculate, individual or aggregated, black, with globose to subglobose ostiole. *Peridium* 15–40 µm wide, comprising several layers; outer layers of thick-walled, dark brown cells of *textura globulosa*; inner layers of thin-walled cells of *textura prismatica*, lightly pigmented or hyaline. *Ascospores* 9.5–15 × 3.5–5 µm ($\bar{x}$ = 11.97 ± 1.13 × 4.06 ± 0.39 µm, *n* = 40), initially light brown, becoming reddish-brown to brown, oblong to ellipsoidal, or subclavate with truncate base, 3-septate, not constricted at the septa, smooth-walled. ***Asexual morph*:** *Hyphae* 1.5–2.5 µm diam, smooth-walled, hyaline, septate, branched. *Conidiomata* 85–175 µm diam, acervular, erumpent, confluent, subglobose, conidiophores and setae formed on the cushion of rounded to angular brown cells. *Setae* 110–180 µm long, base cylindrical, tip obtuse to acute, pale to dark brown. *Conidiophores* 50–105 × 1.5–2 µm ($\bar{x}$ = 78.87 ± 18.38 × 1.58 ± 0.23 µm, *n* = 15), aggregated, septate, branched, smooth or verruculose. *Conidiogenous cells* 4.5–8.5 × 1.5–2.8 µm ($\bar{x}$ = 7.16 ± 1.44 × 1.87 ± 0.39 µm, *n* = 15), terminal, subcylindrical, determinate, discrete, hyaline, smooth or verruculose. *Conidia* 1.5–3.8 × 1–1.7 µm ($\bar{x}$ = 2.34 ± 0.37 × 1.32 ± 0.14 µm, *n* = 60), one-celled, subhyaline to pale olivaceous, smooth, subglobose to ellipsoidal.

Culture characteristics: Colonies on PDA reaching 40–45 mm diam., after 4 weeks at 25 ± 2 °C, slow growing, colonies circular, umbonate, dull to rough with entire edge, sparse; colony from above: whitish to nyanza; from below, black; not producing pigment in PDA media.

Material examined: China, Yunnan Province, Lijiang City, on dead wood, July 2015, M. Raza (HMAS 350625, **holotype**); ex-type living culture, CGMCC3.20501, LC15700.

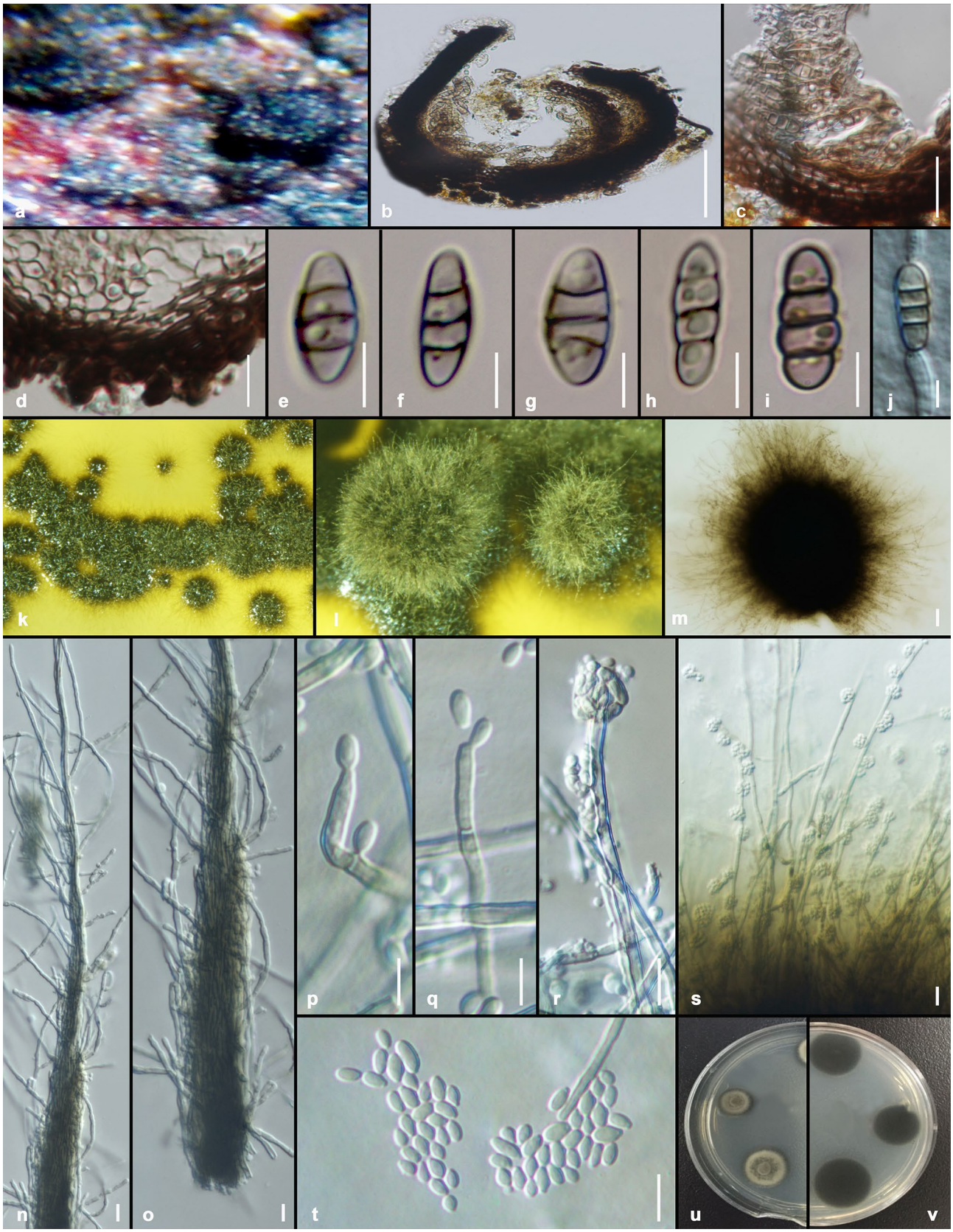
GenBank accession numbers: ITS = OK487581, LSU = OK487580, SSU = OK487582.

Notes: *Capronia lijiangensis* formed a well-supported sister clade to *C. camelliae-yunnanensis* and *C. pilosella* with 78% ML and 1.00 BPP support (Fig. 10). *Capronia lijiangensis* differs by 18 bases in the ITS region, three bases in the LSU gene and two bases in the SSU gene compared to *C. camelliae-yunnanensis. Capronia lijiangensis* differs from *C. pilosella* by eight bases in the ITS region, six bases in the LSU and one base in the SSU genes. *Capronia lijiangensis* produces wider and shorter conidia as compared to those in *C. pilosella* (9.5–15 × 3.5–5 µm *vs*. 7.5–17 × 2.5–4 µm) (Müller et al. 1987) while *C. camelliae-yunnanensis* was described in the asexual state (Phookamsak et al. 2019). *Capronia lijiangensis* is the first species in *Capronia* known to have both sexual and asexual morphs, but asci were not observed due to limited and dried ascomata on the natural substrate.

7. *Apiospora* Sacc.

Apiospora was introduced by Saccardo (1875) and belongs to *Apiosporaceae* (Hyde et al. 2020a; Wijayawardene et al. 2020; Pintos and Alvarado 2021). *Apiosporaceae* was established by Hyde et al. (1998) and is typified by *Apiospora* (Ellis 1971; Senanayake et al. 2015; Feng et al. 2021). The asexual morph *Arthrinium* has been linked to the sexual morph of *Apiospora* (Ellis 1971; Seifert et al. 2011). Crous and Groenewald (2013) synonymized *Apiospora* under *Arthrinium* based on the one fungus-one name principle, but the genera are regarded as distinct based on molecular data (Pintos and Alvarado 2021). Six genera are recognized in *Apiosporaceae*, viz. *Appendicospora*, *Arthrinium*, *Apiospora*, *Dictyoarthrinium*, *Endocalyx* and *Nigrospora* (Hyde et al. 2020a; Wijayawardene et al. 2020; Pintos and Alvarado 2021). The sexual morph of *Apiospora* is similar to *Khuskia* and *Nigrospora* (Pintos and Alvarado 2021). The asexual morphs of *Apiospora* and *Arthrinium sensu stricto* are also similar in having basauxic conidiogenesis cells (Hughes 1953; Pintos and Alvarado 2021). *Apiospora* is a distinct lineage in the phylogenetic analyses and is morphologically distinct from the other genera in *Apiosporaceae*.

There are 85 epithets listed under *Apiospora* in Species Fungorum (2021) with two new species introduced by Crous et al. (2021). Table 1 shows the species discovery trend in *Apiospora* based on Species Fungorum (2021). *Arthrinium* has "*Papularia*"-like asexual morphs with basauxic conidiogenesis cells and "*Apiospora*"-like sexual morphs (Smith et al. 2003; Crous and Groenewald 2013; Jiang et al. 2019; Pintos and Alvarado 2021). *Arthrinium* and *Apiospora* have no clearly defined differences in morphology, although most species of *Arthrinium* are more diverse in the shapes of conidia than those in *Apiospora* (Hawksworth et al. 2011; Crous and Groenewald 2013; Pintos and Alvarado 2021). Most of the species were previously described based on morphology, but DNA sequence analyses have increased the discovery rate of *Apiospora* species. There are 63 ITS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◂**Fig. 9** ***Capronia lijiangensis*** (HMAS 350625, **holotype**). **a** Blackish ascomata on host. **b** Cross section of ascoma. **c-d** Peridium structure. **e–i** Ascospores. **j** Germinating ascospore. **k** Conidiomata on PDA. **l** Mature conidiomata on PDA, top view. **m** Conidioma mounted in lactic acid. **n** Tip of setae. **o** Base of setae. **p–q** Conidiogenous cell and conidia. **r–s** Conidiophores. **t** Conidia. **u–v** Culture characteristics on PDA after 4 weeks (**u** from above, **v** from below). Scale bars: **b** = 50 µm, **c–d** = 10 µm, **e–j, m–t** = 5 µm

sequences annotated as *Apiospora* in GenBank. A BLASTn search of the ITS region of *Apiospora tropica* strain MFLUCC 21–0056 (as the molecular data of the type species *A. montagnei* is not verified) showed a high similarity and query cover (90–100%) to almost all *Apiospora*/*Arthrinium* species. Few of the sequences were annotated as *Pleosporales* sp. (PBC4) or fungal sp. (BMP3011). Thus, we may miss some of the *Apiospora* taxa as we did not include the unidentified sequences in the phylogenetic analysis. There is one UNITE species hypothesis (comprising 12 sequences) that show high similarity to *Apiospora*. *Apiospora* species are saprobes, for example, *A. setostroma* (Jiang et al. 2019; Kwon et al. 2021), and they also act as endophytes, pathogens on invasive plants or opportunistic pathogens on humans, such as, *A. sacchari* and *A. paraphaeosperma* (Ramos et al. 2010; Sharma et al. 2014). *Apiospora* species have been mostly found on *Poaceae*, but also from other host families (Pintos and Alvarado 2021). A large number of species will likely be discovered as some species appear to be host genus or family specific. For example, *A. pterosperma* has only been associated with *Cyperaceae* (Pintos and Alvarado 2021). Fifty-five species of *Arthrinium* were classified as *Apiospora* by Pintos and Alvarado (2021) based on multigene phylogenetic analysis. Sixty-six taxa were validated by morphological characters and molecular data (Pintos and Alvarado 2021). Multi-marker datasets based on LSU, ITS, *tub*2, and *tef*1–α markers are important to separate *Apiospora* and *Arthrinium* as two distinct clades within *Apiosporaceae* (Hyde et al. 1998; Smith et al. 2003; Pintos and Alvarado 2021).

Apiosporaceae taxa have a widespread distribution mainly with terrestrial habitats on a variety of hosts and do not appear to be host-specific (Jiang et al. 2019; Hyde et al. 2020a; Pintos and Alvarado 2021). The species of *Apiosporaceae* are not only found in temperate, cold or alpine regions (Jiang et al. 2019; Feng et al. 2021; Kwon et al. 2021), but have also been reported in tropical or subtropical areas (Senanayake et al. 2015; Tang et al. 2020; Tian et al. 2021). Most *Apiosporaceae* species however, occur on monocotyledons such as *Arecaceae* and *Poaceae*, while some species were found associated with algae, herbaceous dicotyledons and soil (Sharma et al. 2014; Jiang et al. 2019; Kwon et al. 2021). The divergence estimate of *Apiosporaceae* is around 18 MYA, whereas the ancestor lineage evolved around 94 MYA (Hyde et al. 2020a). This was during the Cenomanian–Turonian extinction event (94 MYA) when global warming caused increased temperatures in the oceans and resulted in low plant nutrients (Pearce et al. 2009). There was peak abundances of green algal groups due to an increase in oxygen deficiency and total organic carbon content in the ocean (Pearce et al. 2009). Monocotyledons and eudicots diversified during 135–130 MYA synchronously while *Poales* (grasses) species diversified around 135–110 MYA (Cretaceous–Paleogene). The divergence time estimate of *Poaceae* is around 44 MYA, and *Arecaceae* is thought to have diversified around 66–100 MYA. It seems that *Apiosporaceae* species have co-evolved with *Arecaceae*.

More studies focusing on the endophytic lifestyle of fungi on *Arecaceae* will probably help us understand the host-specificity of *Apiosporaceae* fungi. A new species, *Apiospora tropica* was found on dead bamboo culms in Thailand and is described based on morphology and phylogenetic analyses (Figs. 11, 12).

Apiospora tropica Y.R. Sun, Yong Wang bis & K.D. Hyde, ***sp. nov.***

Index Fungorum number: IF558826; *Facesoffungi number*: FoF 09901, Fig. 11

Etymology: epithet "*tropica*" means humid tropical.

Holotype: MFLU 21–0084

Saprobic on dead bamboo culms. ***Sexual morph****: Ascostromata* raised, immersed to erumpent, raised areas on the host surface, with ascostromata breaking through raised cracks at the black centre, multi-loculate, forming groups in stromata, gregarious, fusiform. *Locules* 136–188 µm diam., 87–103 µm high, immersed in stromata, perithecial, arranged in a row, ampulliform to subglobose, brown to reddish-brown, ostioles with periphyses. *Peridium* comprising 3–5 layers, thick-walled, composed of dark brown cells of *textura angularis*. *Hamathecium* composed of long, 5–6.5 µm wide, septate, unbranched paraphyses, not anastomosing. *Asci* 83–98 × 15–18 µm ($\bar{x}$ = 88.5 × 16.5 µm, n = 15), 8-spored, unitunicate, clavate, apically rounded, sessile to subsessile. *Ascospores* 21–26 × 5.5–10 µm ($\bar{x}$ = 24 × 7 µm, n = 20), biseriate, partly overlapping, reniform, rarely straight, hyaline, septate, slightly constricted at the septum, sometimes with an indistinct septum when mature, usually 2-celled, with a large upper cell and a smaller lower cell, mostly curved at the lower cell, smooth-walled, surrounded by a large entire sheath, becoming shallow when dry. ***Asexual morph*:** Undetermined.

Culture characteristics: Ascospores germinating on WA within 12 h at room temperature. The hyaline germ tube germinates from a point of one cell of the ascospores. Colonies slow-growing on PDA at room temperature, circular, with an irregular edge, cottony, dense at the center, white from above, dark brown to brown in the center from below.

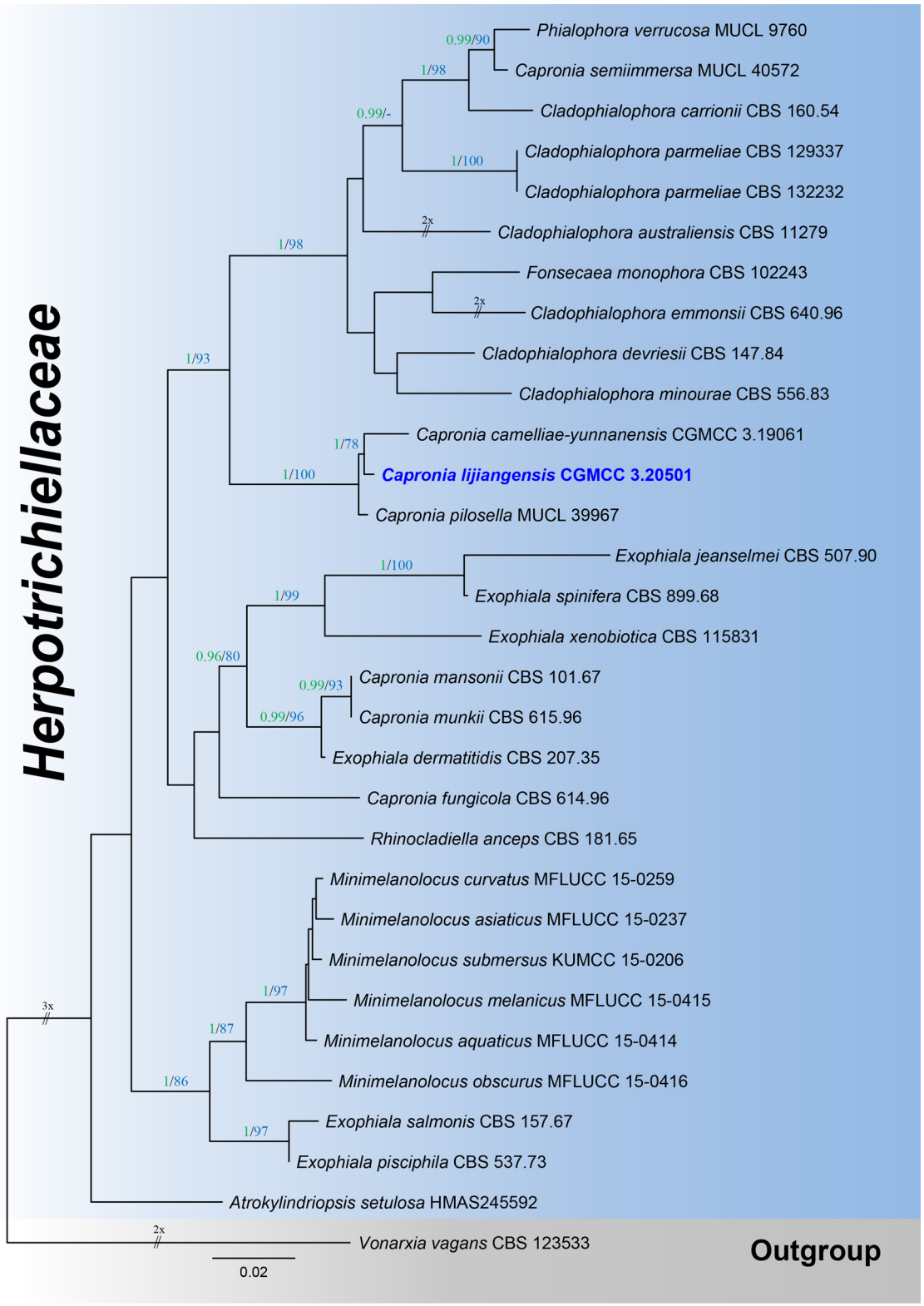


Fig. 10 Phylogenetic tree generated from maximum likelihood analysis based on combined ITS, SSU and LSU sequence data of *Herpotrichiellaceae*. Thirty-one taxa were included in the combined analyses, which comprised 2473 characters (LSU = 892 bases, ITS = 593 bases, SSU = 988 bases) after alignment. The best scoring RAxML tree with a final log likelihood score of -9356.923724 is presented. Bootstrap support values for ML equal to or greater than 75% and BPP equal to or greater than 0.95 are given above the nodes. The new isolate is in blue and bold. The tree is rooted with *Vonarxia vagans* (CBS 123533)

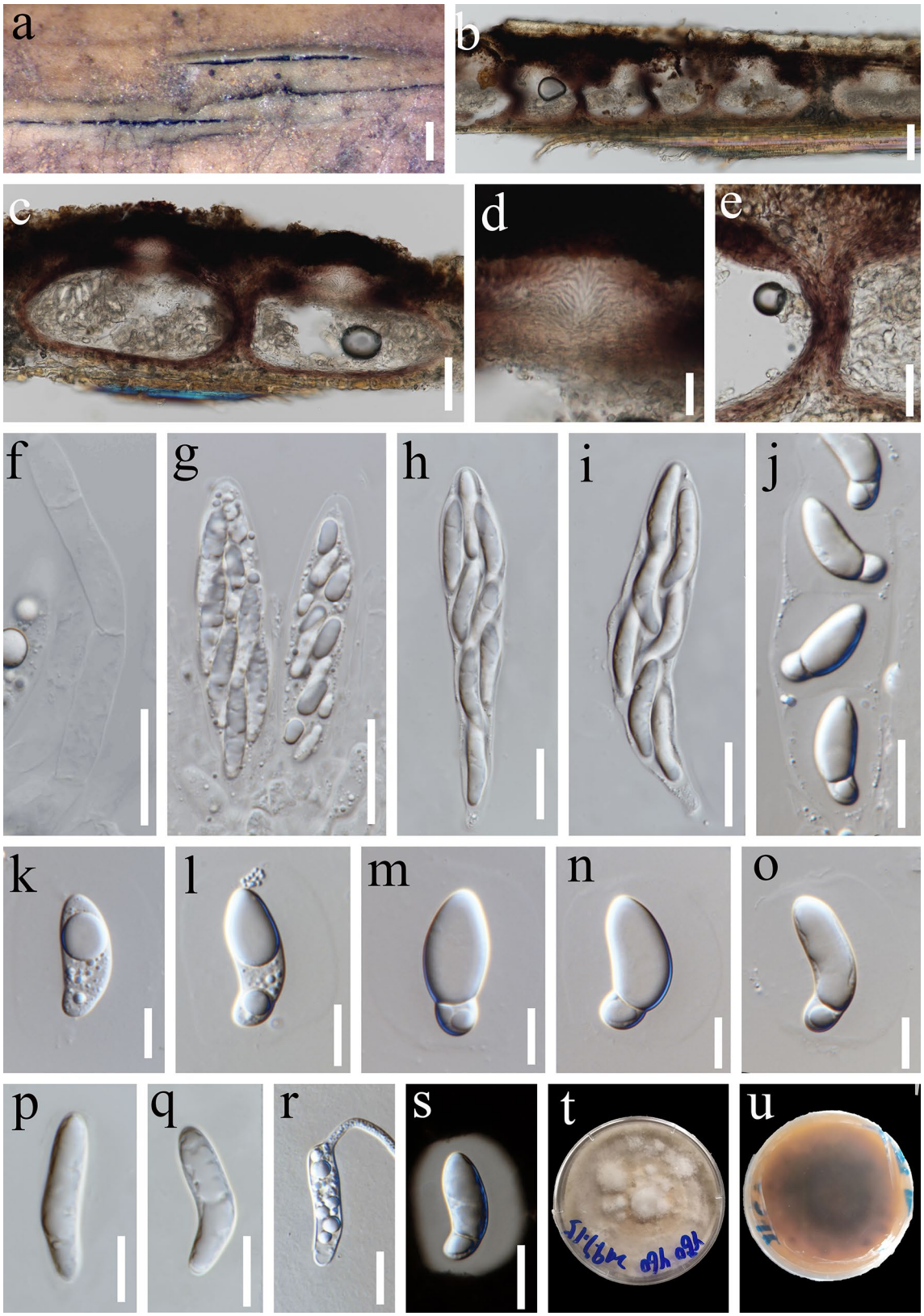
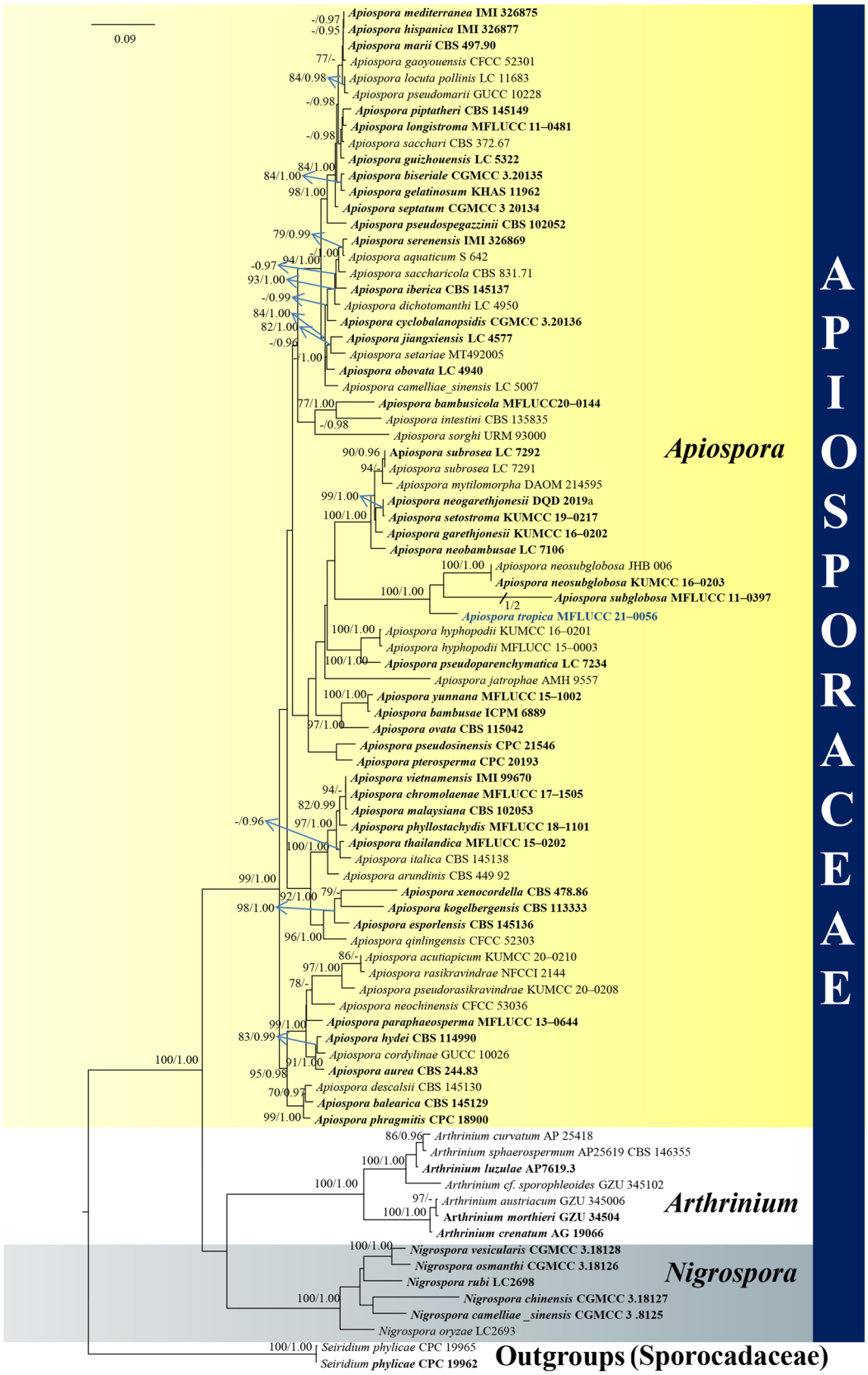


Fig. 11 *Apiospora tropica* (MFLU 21–0084, **holotype**). **a** Stromata on bamboo host. **b, c** Section of an ascostroma. **d** Ostiole with periphyses. **e** Peridium. **f** Paraphyses. **g–j** Asci. **k–q, s** Ascospores. **r** Germinated ascospore (**s** Ascospore stained in Indian ink). **t–u** Culture on PDA. Scale bars: **a** = 300 µm, **b–c** = 50 µm, **d–j** = 20 µm, **k–s** 10 µm


0.09
Apiospora mediterranea IMI 326875
Apiospora hispanica IMI 326877
Apiospora marii CBS 497.90
Apiospora gaoyouensis CFCC 52301
Apiospora locuta pollinis LC 11683
Apiospora pseudomarii GUCC 10228
Apiospora piptatheri CBS 145149
Apiospora longistroma MFLUCC 11–0481
Apiospora sacchari CBS 372.67
Apiospora guizhouensis LC 5322
Apiospora biseriale CGMCC 3.20135
Apiospora gelatinosum KHAS 11962
Apiospora septatum CGMCC 3 20134
Apiospora pseudospegazzinii CBS 102052
Apiospora serenensis IMI 326869
Apiospora aquaticum S 642
Apiospora saccharicola CBS 831.71
Apiospora iberica CBS 145137
Apiospora dichotomanthi LC 4950
Apiospora cyclobalanopsidis CGMCC 3.20136
Apiospora jiangxiensis LC 4577
Apiospora setariae MT492005
Apiospora obovata LC 4940
Apiospora camelliae_sinensis LC 5007
Apiospora bambusicola MFLUCC20–0144
Apiospora intestini CBS 135835
Apiospora sorghi URM 93000
Apiospora subrosea LC 7292
Apiospora subrosea LC 7291
Apiospora mytilomorpha DAOM 214595
Apiospora neogarethjonesii DQD 2019a
Apiospora setostroma KUMCC 19–0217
Apiospora garethjonesii KUMCC 16–0202
Apiospora neobambusae LC 7106
Apiospora neosubglobosa JHB 006
Apiospora neosubglobosa KUMCC 16–0203
Apiospora subglobosa MFLUCC 11–0397
Apiospora tropica MFLUCC 21–0056
Apiospora hyphopodii KUMCC 16–0201
Apiospora hyphopodii MFLUCC 15–0003
Apiospora pseudoparenchymatica LC 7234
Apiospora jatrophae AMH 9557
Apiospora yunnana MFLUCC 15–1002
Apiospora bambusae ICPM 6889
Apiospora ovata CBS 115042
Apiospora pseudosinensis CPC 21546
Apiospora pterosperma CPC 20193
Apiospora vietnamensis IMI 99670
Apiospora chromolaenae MFLUCC 17–1505
Apiospora malaysiana CBS 102053
Apiospora phyllostachydis MFLUCC 18–1101
Apiospora thailandica MFLUCC 15–0202
Apiospora italica CBS 145138
Apiospora arundinis CBS 449 92
Apiospora xenocordella CBS 478.86
Apiospora kogelbergensis CBS 113333
Apiospora esporlensis CBS 145136
Apiospora qinlingensis CFCC 52303
Apiospora acutiapicum KUMCC 20–0210
Apiospora rasikravindrae NFCCI 2144
Apiospora pseudorasikravindrae KUMCC 20–0208
Apiospora neochinensis CFCC 53036
Apiospora paraphaeosperma MFLUCC 13–0644
Apiospora hydei CBS 114990
Apiospora cordylinae GUCC 10026
Apiospora aurea CBS 244.83
Apiospora descalsii CBS 145130
Apiospora balearica CBS 145129
Apiospora phragmitis CPC 18900
Apiospora
Arthrinium curvatum AP 25418
Arthrinium sphaerospermum AP25619 CBS 146355
Arthrinium luzulae AP7619.3
Arthrinium cf. sporophleoides GZU 345102
Arthrinium austriacum GZU 345006
Arthrinium morthieri GZU 34504
Arthrinium crenatum AG 19066
Arthrinium
Nigrospora vesicularis CGMCC 3.18128
Nigrospora osmanthi CGMCC 3.18126
Nigrospora rubi LC2698
Nigrospora chinensis CGMCC 3.18127
Nigrospora camelliae _sinensis CGMCC 3 .8125
Nigrospora oryzae LC2693
Nigrospora
Seiridium phylicae CPC 19965
Seiridium phylicae CPC 19962
Outgroups (Sporocadaceae)
APIOSPORACEAE

◂**Fig. 12** Phylogram generated from maximum likelihood analysis based on combined LSU, ITS, *tef*1–α and *tub*2 sequence data from *Apiosporaceae* and related families in the order *Amphisphaeriales*. Eighty-four taxa were included in the combined analyses which comprised 3500 characters (LSU = 863 bases, ITS = 634 bases, *tef*1–α = 1020 bases, *tub*2 = 983 bases) after alignment. The best scoring RAxML tree with a final log likelihood score of −31266.866896 is presented. Bootstrap support values for ML equal to or greater than 75% and BPP equal to or greater than 0.95 are given at the nodes. *Seiridium phylicae* strains CPC 19962 and CPC 19965 were used as outgroup taxa. The newly generated sequence is indicated in blue. The type-derived sequences are given in bold

Material examined: Thailand, Kanchanaburi Province, Thong Pha Phum District, Pilok Subdistrict, dead bamboo culms, 28 June 2019, Guang-Cong Ren, Y60 (MFLU 21–0084, **holotype**); ex-type living culture, MFLUCC 21–0056.

GenBank accession numbers: LSU = OK491653, ITS = OK491657, *tub*2 = OK560922.

Notes: The multi-gene phylogenetic analysis of combined LSU, ITS, *tef*1–α, and *tub*2 sequence data revealed that *Apiospora tropica* forms a sister clade to *A. neosubglobosa* and *A. subglobosum* with strong bootstrap support (MLBS/BPP 100/1.00) (Fig. 12). In a BLASTn search in GenBank, the closest match of the ITS sequence of *Apiospora tropica* (MFLUCC 21–0056) was 86.33% similar across 100% of the query sequence, which translates into 86.33% similarity to *A. pterosperma* (CBS 134000). The closest match of the LSU and *tub*2 sequences of *A. tropica* were 97.51% and 85% similar across 94% and 70% of the query sequence, which translates into 91.66% and 59.5% similarity to *A. neosubglobosa* (GZAAS 20–0099), respectively. *Apiospora tropica* is morphologically similar to *A. gelatinosa* in the shape of ascostromata, asci and ascospores (Feng et al. 2021). However, the locules, asci and ascospores of *A. tropica* are smaller than *A. gelatinosa* (locules 87–103 × 136–188 µm *vs.* 144–199 × 184–214 µm, asci 83–98 × 15–18 µm *vs.* 85–121 × 15–24 µm and ascospores 21–26 × 5.5–10 µm *vs.* 28–31 × 6–8 µm). Therefore, we introduce *A. tropica* as a novel species based on both phylogenetic evidence and morphology.

8. *Vanakripa* Bhat, W.B. Kendr. & Nag Raj

Vanakripa was introduced by Bhat and Kendrick (1993), with *V. gigaspora* as the type species. The genus is considered *incertae sedis* in *Pezizomycotina* (Wijayawardene et al. 2020), and a generic key was provided by Mota et al. (2008). *Vanakripa* has a special clavate to vermiform, hyaline, separating cells attached to the conidia (Bhat and Kendrick 1993).

There are nine epithets listed under *Vanakripa* in Species Fungorum (2021) (Table 1). The latest addition was *V. inexpectata* by Leão-Ferreira et al. (2013) and *V. chinensis* by Zhang et al. (2021), and they are the only two species introduced within the last decade. A BLASTn search of the ITS region of *Vanakripa chiangmaiense* strain MFLUCC 21–0158 (as the molecular data of the type species *V. gigaspora* is not available) showed high similarity and query cover (90–100%) to *Vanakripa minutiellipsoidea* strain CBS 112523. The ITS region also showed high similarity (> 90%) to members of *Conioscyphales*, but the query cover of the results was lower than 50%. There are two species hypotheses (comprising two sequences) that show high similarity to *Vanakripa* in UNITE. There are only four ITS sequences annotated as *Vanakripa* in GenBank as most species were described based only on morphology. *Vanakripa minutiellipsoidea* is the only other *Vanakripa* species with molecular data and was isolated from a submerged dead petiole of *Eleiodoxa conferta* (Pinnoi 2003). Thus, four species were confirmed based on morphology and molecular data. *Vanakripa* species are mostly found on submerged wood in aquatic environments in the tropical zone (Mota et al. 2008). The other species were isolated from undetermined hosts, and their host specificity needs to be further investigated. A new species, *Vanakripa chiangmaiense* is introduced from an undetermined decaying wood in Thailand.

Vanakripa chiangmaiense X.G. Tian & Karun., ***sp. nov.***

Index Fungorum number: 559388; *Facesoffungi number*: 10569, Fig. 13

Etymology: Referring to the province where the fungus was collected

Holotype: HKAS 21–122165

Saprobic on decaying wood. ***Sexual morph*:** Undetermined. ***Asexual morph*:** *Colonies* on the natural substrate, scattered, black sporodochia. *Mycelium* is mostly immersed in substratum, composed of septate, branched, hyaline hyphae. *Conidiophores* micronematous, hypha-like, cylindrical, septate, simple or branched, smooth, hyaline. *Conidiogenous cells* 4.5–6.5 µm wide, monoblastic, holoblastic, terminal, integrated, cylindrical, granules. *Separating cells* (16–)20.5–39(–53.5) × (5–)8–12(–14) µm ($\bar{x}$ = 30 × 10 µm, n = 25), clavate to vermiform, hyaline. *Conidia* (20.5–)22–25.5(–27.5) × (15–)16.5–19.5(–21) µm ($\bar{x}$ = 24 × 18 µm, n = 35), acrogenous, solitary, ellipsoid, dark brown, with a darker colour in the guttulate area, aseptate, smooth or verruculose, thin sheath around spores, one guttulate, usually separating cell attached to the conidia.

Culture characteristics: Conidia germinating on PDA within 24 h. Colonies on PDA floccose, rounded, sallow to yellow, white aerial hyphae at the surface; reverse yellow from the centre with light yellow at the rim.

Material examined: Thailand, Chiang Mai Province, saprobic on decaying wood, 16 December 2020, X.G. Tian, U4–4 (HKAS 21–122165, **holotype**); ex-type living culture, MFLUCC 21–0158.

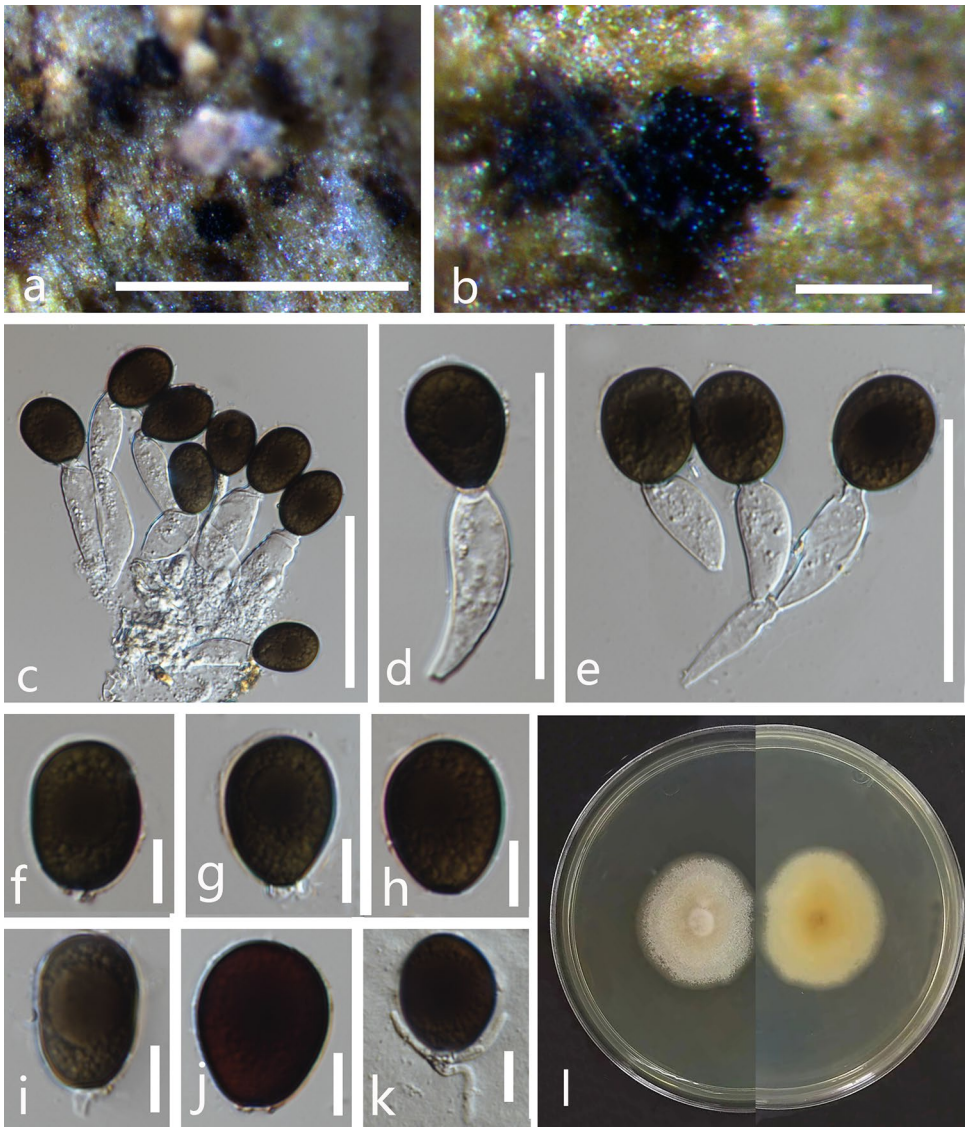


Fig. 13 ***Vanakripa chiangmaiense*** (HKAS 21–122165, **holotype**) **a, b** Colonies on dead wood. **c–e** Conidiophore with conidia. **f–j** Conidia. **k** Germinating conidium. **l** Culture on PDA after two weeks of incubation on PDA. Scale bars: **a** = 500 µm, **b** = 200 µm, **c–e** = 50 µm, **f–k** = 10 µm

GenBank accession numbers: LSU = OL606152, SSU = OL606141, ITS = OL753684.

Notes: *Vanakripa chiangmaiense* is closely related to *V. minutiellipsoidea* (0.99 BPP, Fig. 14), but the classification of *Conioscypha* and *Vanakripa* needs further studies. *Vanakripa chiangmaiense* has ellipsoid, smooth or verruculose conidia, and *V. minutiellipsoidea* has ellipsoid to broadly clavate, smooth conidia (Pinnoi 2003). The closest match of the ITS sequence of *Vanakripa chiangmaiense* was *V. minutiellipsoidea* (CBS 112523) with 88.04% similarity across 80% of the query sequence, which translates into 70.43% similarity based on a BLASTn search. The closest match of the LSU sequence of *V. chiangmaiense* was *V. minutiellipsoidea* (CBS 112523) with 98.10% similarity across 100% of the query sequence, which translates into 98.10% similarity. Therefore, we introduce *V. chiangmaiense* as a new species based on phylogenetic and morphological evidence.

9. *Distoseptispora* K.D. Hyde, McKenzie & Maharachch.

Distoseptispora, the only genus in *Distoseptisporaceae* (*Sordariomycetes*), was introduced by Su et al. (2016a, b) to accommodate several *Sporidesmium* and sporidesmium-like taxa. *Distoseptispora* is quite similar to *Sporidesmium* in having solitary or gregarious conidiophores, monoblastic, determinate or percurrent conidiogenous cells, cylindrical, fusiform, obclavate, obpyriform, sometimes with rostrate conidia (Su et al. 2016a, b; Luo et al. 2018, 2019; Hyde et al. 2020a). However, *Distoseptispora* differs from *Sporidesmium* in having darker conidia with slightly paler, but not hyaline rounded apices, basal cells cut off by cross walls and are of indeterminate length and relatively short conidiophores (Su et al. 2016a, b). *Distoseptispora* formed a distinct

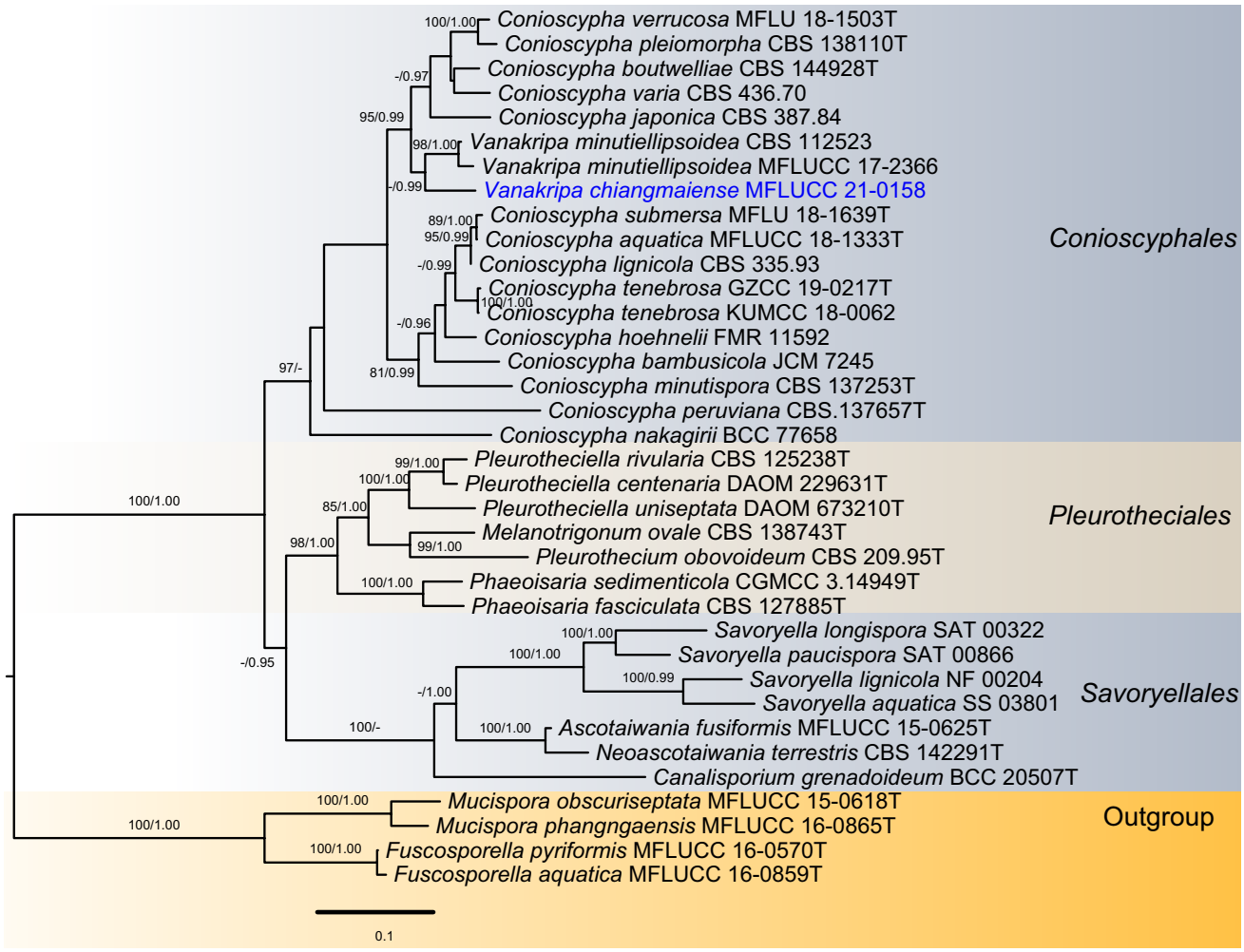


Fig. 14 Phylogenetic tree generated from maximum likelihood (ML) analysis based on combined ITS, LSU, SSU and *rpb*2 sequence data for selected families. Bootstrap support values for maximum likelihood (ML) equal to or greater than 75% and BPP equal to or greater than 0.95 are given above the nodes. *Mucispora obscuriseptata* (MFLUCC 15–0618), *M. phangngaensis* (MFLUCC 16–0865), *Fuscosporella pyriformis* (MFLUCC 16–0570) and *F. aquatica* (MFLUCC 16–0859) were used as outgroup taxa. The new species is indicated in blue. The type-derived sequences are indicated as T

clade, hence, *Distoseptisporaceae* was established to accommodate several sporidesmium-like taxa based on morphology and phylogeny (Su et al. 2016a, b; Luo et al. 2019; Hyde et al. 2021). *Distoseptispora* is typified by *D. fluminicola* and characterized by macronematous, unbranched, septate, brown conidiophores, monoblastic, integrated, determinate conidiogenous cells and acrogenous, solitary, euseptate or distoseptate, cylindrical conidia with a basal cell with cross walls and a basal scar (Su et al. 2016a, b; Yang et al. 2018; Luo et al. 2018, 2019; Hyde et al. 2020a). Based on multigene analyses, Luo et al. (2019) raised *Distoseptisporaceae* to order level as *Distoseptisporales*. *Aquapteridosporaceae* has also been added to *Distoseptisporales* based on morphology, phylogenetic analyses, and divergence time estimates (Hyde et al. 2021).

Distoseptispora is a well-studied genus with 30 species listed in Species Fungorum. Unusually, all species have sequence data available in GenBank (Table 1). There are 74 ITS sequences annotated as *Distoseptispora* in GenBank. A BLASTn search using the ITS region of the type species *Distoseptispora fluminicola* strain MFLUCC 15-0417 (NR_154041) showed high similarity and query cover (90–100%) to *Distoseptispora* and a single uncultured fungus clone C1_AF3. There are 52 species hypotheses (comprising 101 sequences) that have high similarity to *Distoseptispora* in UNITE. There are over 490 species epithets listed as *Sporidesmium* in Index Fungorum but there are only 32 ITS sequences annotated as *Sporidesmium* in GenBank and 12 species hypotheses (comprising 16 sequences) in UNITE. Therefore, some *Sporidesmium* epithets listed in Index Fungorum could represent *Distoseptispora* species

Fig. 15 ***Distoseptispora cylindricospora*** (HKAS 115796, **holotype**). **a, b** Colonies on decaying wood. **c–h** Conidiophores with conidia. **i** Conidiophores. **j, k** Conidia. **l** Colony on MEA. Scale bars: **c–h** = 100 µm, **i–k** = 20 µm

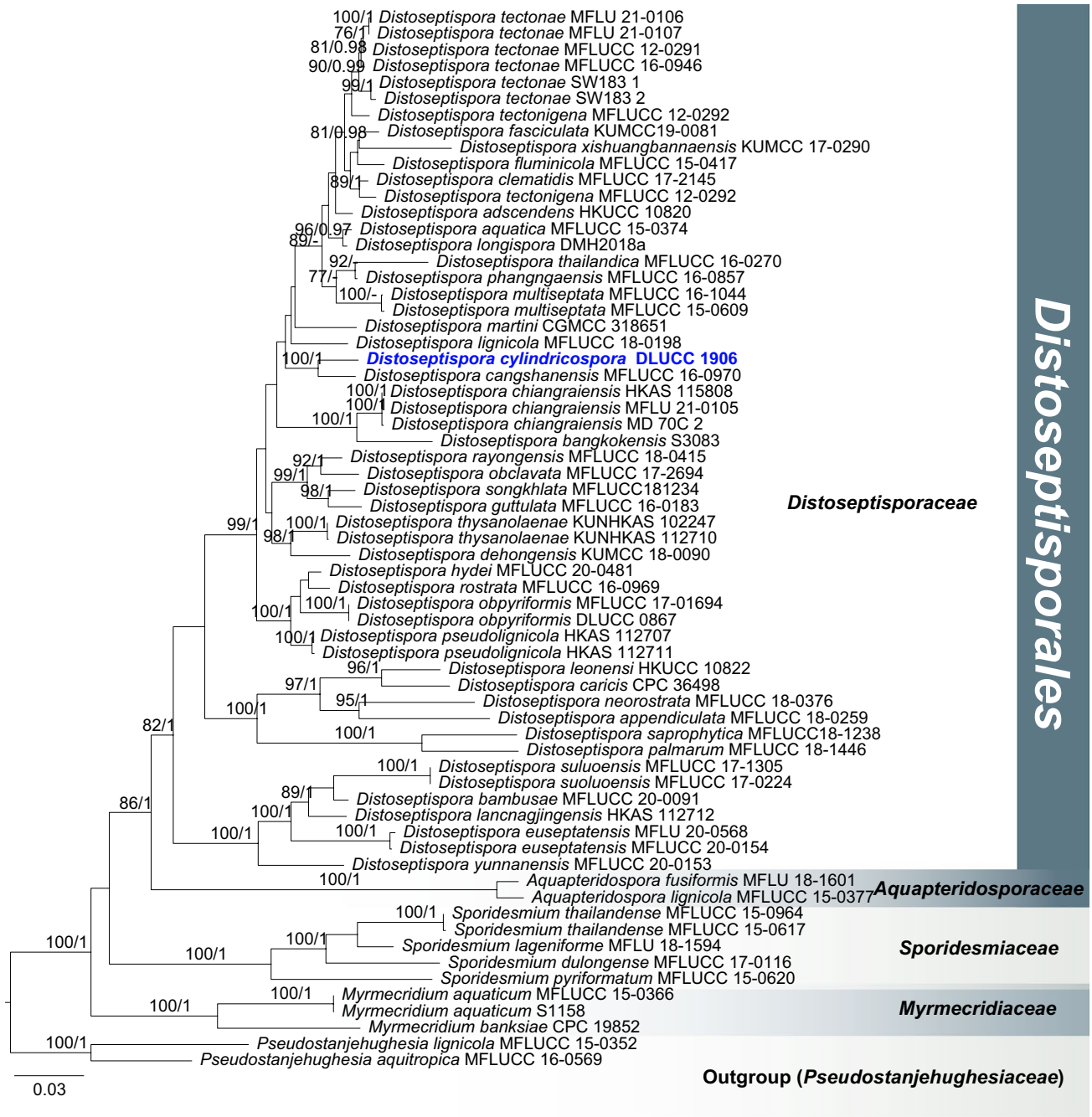


Fig. 16 Phylogram generated from maximum likelihood analysis based on combined LSU, SSU, ITS and *tef*1–α sequence data from *Distoseptisporales* and related families in *Diaporthomycetidae*. Sixty-five taxa were included in the combined analyses, which comprised 3461 characters (LSU = 991 bases, SSU = 939 bases, ITS = 601 bases, *tef*1–α = 930 bases) after alignment. The best scoring RAxML tree with a final log likelihood score of –22818.203442 is presented. Bootstrap support values for ML equal to or greater than 75% and BPP equal to or greater than 0.95 are given above the nodes. *Pseudostanjehughesia lignicola* (MFLUCC 15–0352) and *Pseudostanjehughesia aquitropica* (MFLUCC 16–0569) were used as outgroup taxa. The new species is indicated in blue and bold

and molecular analysis is needed to confirm their taxonomic placement. For example, the morphology of *Sporidesmium tropicale* fits the generic concept of *Distoseptispora*, but its placement remains doubtful due to the lack of molecular data (Kocková-Kratochvílová et al. 1987). *Distoseptispora* species are reported as saprobes on palms (Hyde et al. 2019a), *Pandanus* (Tibpromma et al. 2018), *Tectona* (Hyde et al. 2016) and undetermined submerged wood from

freshwater and terrestrial habitats (Su et al. 2016a, b; Hyde et al. 2016, 2019a, b, 2020a, b, c, d; Yang et al. 2018; Luo et al. 2018, 2019; Sun et al. 2020; Monkai et al. 2020; Song et al. 2020). *Distoseptispora* species can be found in a wide range of habitats, therefore, we would expect the number of species to increase with extensive studies.

Hyde et al. (2020a) estimated the crown age of *Distoseptisporaceae* at around 44.21 MYA, followed by the Cretaceous–Paleogene extinction event (65 MYA). After this extinction event, there was a mass extinction of three-quarters of plant and animal species (Ward et al. 2005). The conditions of high humidity and reduced solar insolation after the extinction event favoured saprobic fungi such as *Distoseptispora* that flourished on the detritus (Vajda and McLoughlin 2004). It can be hypothesised that *Distoseptispora* species diversified to adapt to various hosts, that were prevalent during this period (Peace et al. 2020). The divergence time estimates of palms, *Pandanaceae* and *Tectona* are around 42.14–26.55 MYA, 97.5–41.9 MYA and 33.28–21.45 MYA, respectively (Gallaher et al. 2015; Yasodha et al. 2018; Pichardo-Marcano et al. 2018). This suggests that *Distoseptispora* evolved before palms and *Tectona*. The majority of species have been reported from China and Thailand (Su et al. 2016a, b; Hyde et al. 2016; Yang et al. 2018; Luo et al. 2018, 2019; Monkai et al. 2020; Song et al. 2020) and studies in other countries are likely to yield novel taxa. In this study, we introduce a new species, *D. cylindratispora,* from freshwater habitat in China based on phylogeny and morphology (Figs. 15, 16).

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

Index Fungorum number: IF558840; *Facesoffungi number*: FoF 10532, Fig. 15

Etymology: Referring to the cylindrical conidia of this fungus

Holotype: HKAS 115796

Saprobic on submerged, decaying wood in freshwater. ***Sexual morph*:** Undetermined. ***Asexual morph*:** *Colonies* on the substratum superficial, effuse, scattered, gregarious, hairy, brown to dark brown. *Mycelium* mostly immersed, composed of branched, septate, brown to dark brown, smooth hyphae. *Conidiophores* 105–157 × 6.5–8.5 µm ($\bar{x}$ = 131 × 7.5 µm, n = 25), macronematous, mononematous, erect, cylindrical, mostly in a small group of 2–7, rarely solitary, straight or slightly flexuous, unbranched, 18 to 30-septate, smooth, dark brown. *Conidiogenous cells* 6–8.5 × 5.5–7.5 µm ($\bar{x}$ = 7.3 × 6.7 µm, n = 25), holoblastic, monoblastic, integrated, determinate, terminal, cylindrical, brown to dark brown. *Conidia* 136.5–278 × 8.5–11 µm ($\bar{x}$ = 207 × 9.5 µm, n = 25), acrogenous, solitary, dry, cylindrical to elongated, straight or slightly curved, truncated at the base, rounded at the apex, 20–65-distoseptate, smooth, greenish-brown to dark brown, hyaline at the apex, smooth, thick-walled.

Culture characteristics: Colonies on PDA attaining 3.5 cm diam., after 4 weeks at room temperature, greyish brown to brown at above, circular, smooth, velvety; reverse black, brown to dark brown.

Material examined: China, Yunnan Province, Dali City, on submerged decaying wood, 12 June 2017, Hongwei Shen, S–1906 (HKAS 115796, **holotype**); ex-type living culture, DLUCC 1906.

GenBank accession numbers: ITS = OK491122, LSU = OK513523, SSU = OK513520, *tef*1–α = OK524220.

Notes: *Distoseptispora cylindricospora* can be easily distinguished from other *Distoseptispora* species by its conidiophores. The conidiophores of *D. cylindricospora* mostly occur in small groups and the conidiophores can be up to 20–65-septate. However, the conidiophores of other *Distoseptispora* species are usually solitary and have fewer than 10 septa (Su et al. 2016b; Hyde et al. 2016, 2019a, b; 2020a, b, c, d; Xia et al. 2017; Yang et al. 2018; Luo et al. 2018, 2019; Sun et al. 2020; Monkai et al. 2020; Song et al. 2020).

In the phylogenetic analyses, *Distoseptispora cylindricospora* is sister to *D. cangshanensis* with 100 ML/1.00 BPP bootstrap support (Fig. 16). *Distoseptispora cylindricospora* is similar to *D. cangshanensis* in having macronematous, mononematous, septate, brown conidiophores, monoblastic, integrated, terminal conidiogenous cells and acrogenous, obclavate, multi-distoseptate, brown conidia (Luo et al. 2018). However, the conidiophores of *D. cylindricospora* mostly occur in a small group of 2–7, rarely solitary and the septation of conidiophores are less in *D. cangshanensis* (18–30-septate *vs*. 1–5 septate). The conidia of *D. cylindricospora* are longer than *D. cangshanensis* (136.5–278 × 8.5–11 *vs*. 58–166(–287) × 10–14 µm) (Luo et al. 2018).

10. *Beltrania* Penz.

Beltrania (*Beltraniaceae, Sordariomycetes*) was introduced to accommodate *B. rhombica* which was isolated from leaves of *Citrus limon* in Italy (Penzig 1882). *Beltrania* species generally have unbranched setae with radially lobed basal cells, unbranched conidiophores, denticulate conidiogenous cells and biconic conidia with a separating cell (Hyde et al. 2020a). A sexual morph has not been reported for *Beltrania*. *Beltrania* is similar to *Beltraniella* and *Beltraniopsis* in five aspects (dark setae, conidiophores with radially lobed bases, swollen separating cells, biconic conidia and hyaline equatorial band) as described in Lin et al. (2017a), but molecular evidence supports them as different genera (Crous et al. 2015a, b; Lin et al. 2017a, b; Tibpromma et al. 2018). Many *Beltraniella* and *Beltraniopsis* species lack DNA sequence data. *Beltrania* together with *Beltraniella*, *Beltraniopsis*, *Hemibeltrania*, *Parapleurotheciopsis*, *Porobeltraniella*, *Pseudobeltrania*, *Subramaniomyces*, and

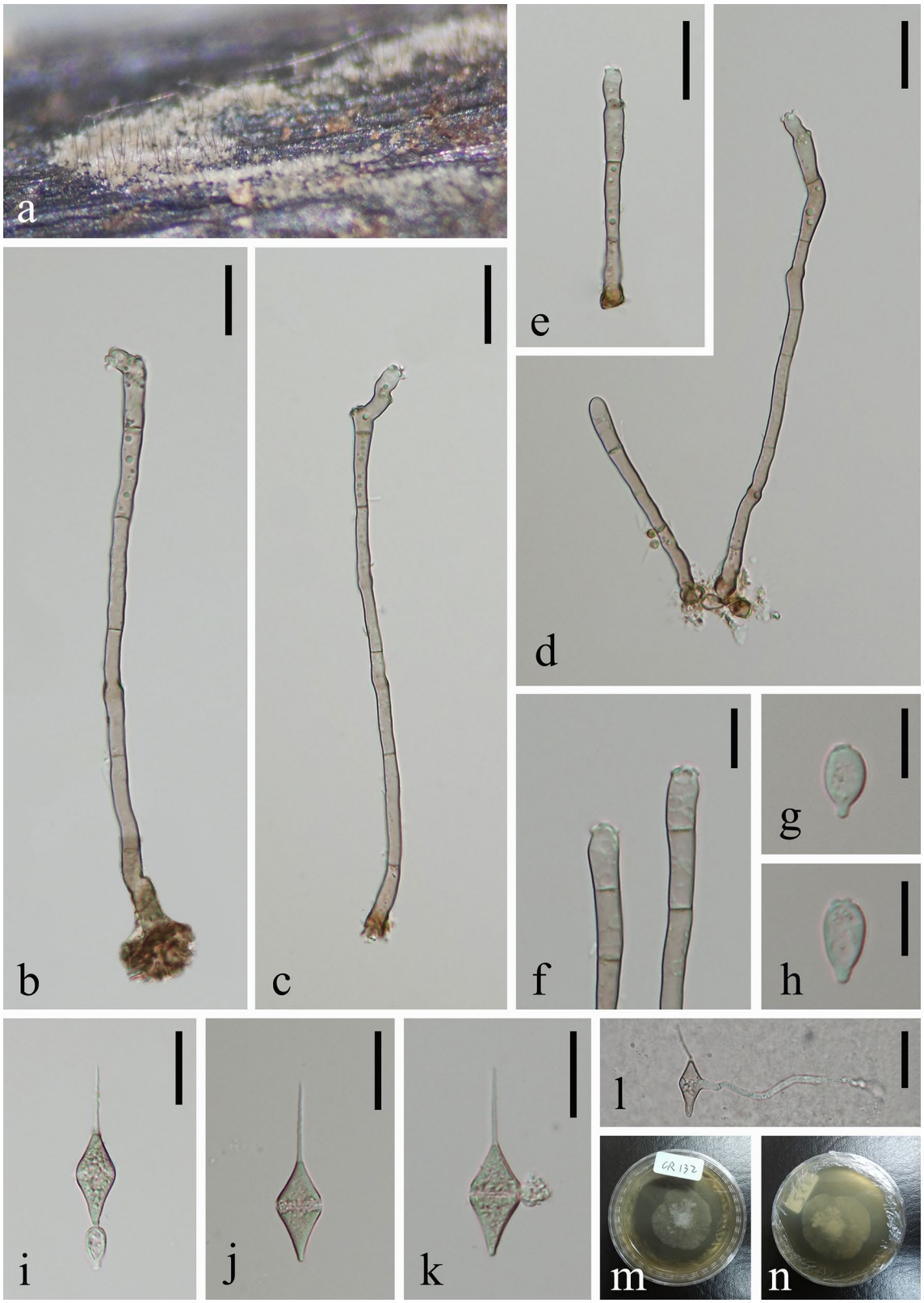


Fig. 17 ***Beltrania aquatica*** (MFLU 18–1703, **holotype**). **a** Colonies on submerged wood. **b–e** Conidiophores. **f** Apex of conidiophores. **g**, **h** Separating cells. **i** Conidium attaching on a separating cell. **j** Conidium. **k** Crushed conidium and parts of its content. **l** Germinating conidium. **m**, **n** Colonies on PDA culture from front and reverse. Scale bars: **b** = 15 µm, **c–e**, **i–k** = 20 µm, **f–h** = 10 µm, **1** = 30 µm

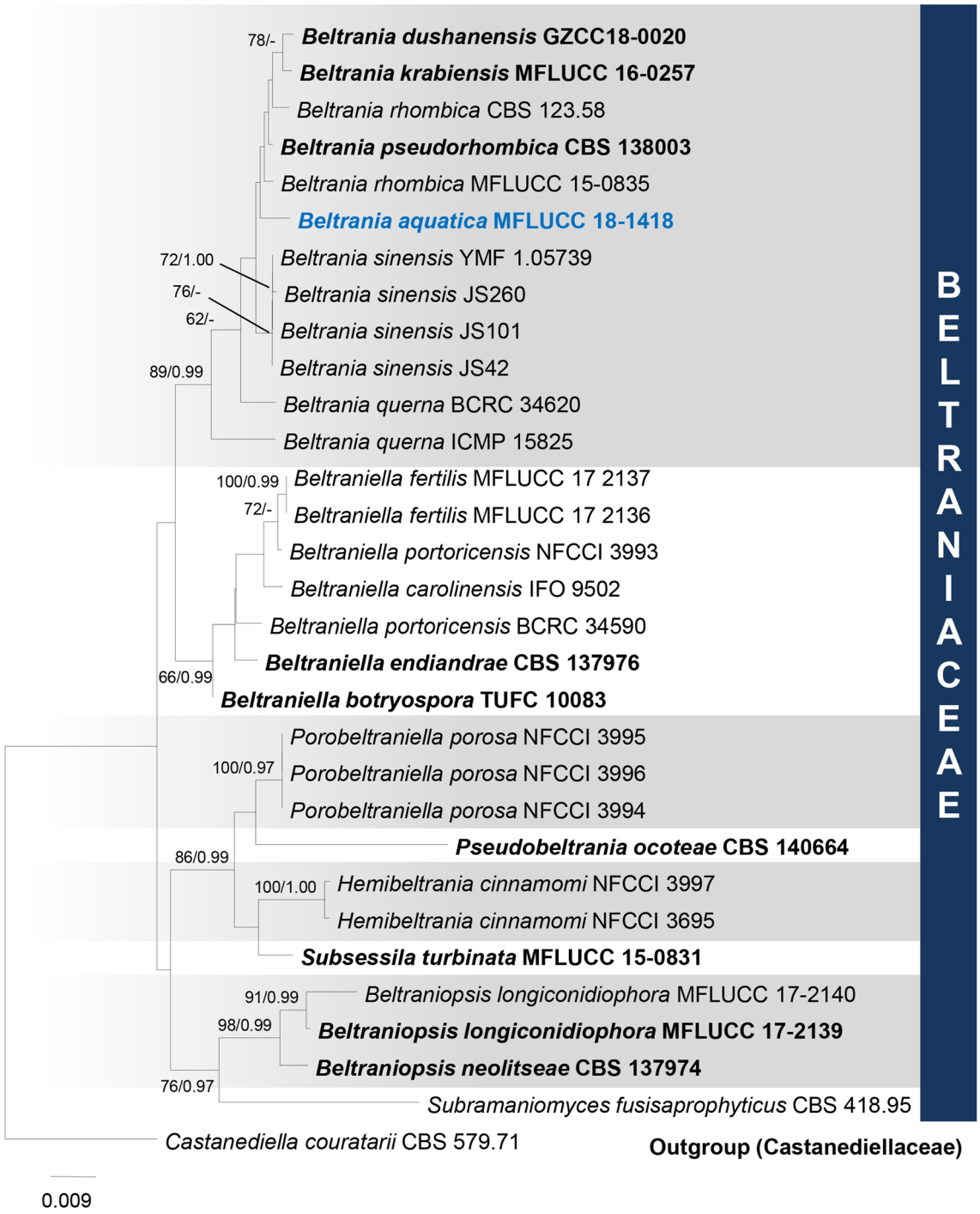


Fig. 18 Phylogram generated from maximum likelihood analysis based on combined LSU and ITS sequence data representing species of *Beltraniaceae*. Related sequences were taken from Hyde et al. (2020a). Thirty-one taxa were included in the combined analyses, which comprised 1452 characters (LSU = 859 bases and ITS = 593 bases) after alignment. The best scoring RAxML tree with a final log likelihood score of −4008.944784 is presented. Bootstrap support values for ML equal to or greater than 60% and BPP equal to or greater than 0.95 are given near the nodes. *Castanediella couratarii* (CBS 579.71) was used as the outgroup taxon. The newly generated sequence is indicated in blue. The type-derived sequences are given in bold

Subsessila are accepted in *Beltraniaceae* based on multi-marker analysis (Crous et al. 2015a, b; Lin et al. 2017a, b; Tibpromma et al. 2018; Wijayawardene et al. 2020).

Beltrania was introduced with a single species, *B. rhombica* in 1882, and *B. querna* was added to the genus after two years (Harkness 1884). Without molecular methods, the identification of new collections was relatively slow, and it took nearly 40 years until another species – *B. malaiensis* was identified in 1931 (Table 1). After 2010, taxonomic studies of *Beltrania* were relatively well-studied because the type species *B. rhombica* was sequenced (Shirouzu et al. 2010; Rajeshkumar et al. 2016; Lin et al. 2017b). Zheng et al. (2020) introduced *B. sinensis* based on morphological and phylogenetic analysis and accepted 16 species in *Beltrania* in their taxonomic key. From 2019 to 2021, another six taxa were introduced, including two varieties of *B. hasaneana* (Bandgar and Patil 2019, 2021; Hyde et al. 2020a; Quevedo et al. 2020; Zheng et al. 2020). Only six species of *Beltrania* (from China, Japan, Malaysia, New Zealand, Thailand) have been sequenced (Shirouzu et al. 2010; Crous et al. 2014, 2015a, b; Lin et al. 2017b; Tibpromma et al. 2018). The phylogeny of *Beltrania* and beltrania-like taxa is not well-resolved.

There are 22 ITS sequences annotated as *Beltrania* in GenBank. A BLASTn search of the ITS region of the representative strain of *Beltrania rhombica* strain CBS 123.58 (MH857718) showed high similarity and query cover (90–100%) to three uncultured fungus clones and five endophytic taxa. These unnamed sequences from uncultured fungal species were derived by Sanger sequencing, therefore, the the estimation based on traditional method still missed some of the *Beltrania* taxa deposited as unidentified sequences and would not be picked up in the phylogenetic analysis. There are four species hypotheses (comprising 47 sequences) that show high similarity with *Beltrania* taxa in UNITE. The divergence time for *Beltraniaceae* has been estimated as 62 MYA which falls in the range of family (Hyde et al. 2017a, b). *Beltraniaceae* species are generally hyphomycetous saprobes, but some are pathogens causing leaf spots (Maharachchikumbura et al. 2016; Hyde et al. 2020a) or endophytes in plant roots (Zheng et al. 2020). *Beltrania* and similar taxa are common in leaf litter (Osono et al. 2009; Shirouzu et al. 2009), however, whether species are host-specific or generalists have not been established. With more sampling and sequencing from unstudied regions and habitats, the fungal number of *Beltrania* is likely to grow significantly. This study introduces a new species, *B. aquatica,* from submerged wood from freshwater habitats in Thailand (Figs. 17, 18).

Beltrania aquatica W. Dong, Doilom & K.D. Hyde, ***sp. nov.***

Index Fungorum number: IF558476; *Facesoffungi number*: FoF 09898, Fig. 17

Etymology: In reference to the aquatic habitat of the fungus

Holotype: MFLU 18–1703

Saprobic on decaying wood submerged in freshwater. ***Sexual morph*:** Undetermined. ***Asexual morph*:** *Colonies* effuse, velutinous, gregarious, brown. *Mycelium* mostly immersed in host substrate, composed of septate, branched, pale brown, thin-walled hyphae. Setae present, numerous, unbranched. *Conidiophores* 65–130 × 4–5.5 µm ($\bar{x}$ = 90 × 4.8 µm, n = 10), macronematous, mononematous, erect, subcylindrical, flexuous, septate, unbranched, pale brown, thin-walled, smooth. *Conidiogenous cells* 9.5–25 × 3.5–6.5 µm ($\bar{x}$ = 16 × 5 µm, n = 10), holoblastic, polyblastic, integrated, terminal, subcylindrical, pale brown, smooth, sympodial proliferations, denticulate, bearing several prominent, rounded, pale brown denticles. *Separating cells* 10–12 × 5.5–6.5 µm ($\bar{x}$ = 11.5 × 6 µm, n = 10), clavate, thin-walled, smooth, pale brown to hyaline, with a tiny, protruding hilum attaching to the denticles of conidiogenous cells, and with 1–2 apical, flat-tipped denticles bearing the conidia. *Conidia* 22–26 × 10–12 µm ($\bar{x}$ = 24 × 11 µm, n = 15), arise from separating cells, acrogenous, solitary, dry, thin-walled, smooth, biconic, straight, one equatorial septate, with a wider transverse band, pale brown, with a subhyaline, persistent, pointed appendage, 13.5–17.5 µm long.

Culture characteristics: Colonies on PDA, colony irregular, reaching 30 mm diam., after 20 days at room temperature (25–30 °C), surface rough, with sparse mycelia, velvety, dry, raised in the middle from the side view, edge entire; from above and below, subhyaline at the margin, white at the middle; not producing pigmentation in culture.

Material examined: Thailand, Chiang Rai Province, on decaying wood submerged in a freshwater stream, 1 July 2018, W. Dong, CR132 (MFLU 18–1703, **holotype**); ex-type living culture, MFLUCC 18–1418; *ibid*., HKAS 105074, isotype, ex-isotype living culture, KUMCC 19–0092.

GenBank accession numbers: LSU = MZ351436, SSU = MZ351439, ITS = MZ351440.

Notes: *Beltrania aquatica* forms a clade with *B. dushanensis*, *B. krabiensis*, *B. pseudorhombica* and *B. rhombica* in our multi-marker analysis (Fig. 18). These species share common morphological characteristics in all aspects but can be distinguished by dimensions of conidiophores, conidia and appendages. *Beltrania aquatica* has similar conidial size to *B. dushanensis* but differs in having longer conidiophores (65–130 µm *vs*. 10–45 µm) and conidial appendages (13.5–17.5 µm *vs*. 6.3–12.1 µm) (Hyde et al. 2020a). *Beltrania aquatica* and *B. krabiensis* are similar in morphology, but the latter has smaller conidia (22–26 × 10–12 µm *vs*. 17–23 × 5–8 µm) and shorter appendages (13.5–17.5 µm *vs*. 4–8 µm) (Tibpromma et al. 2018). *Beltrania pseudorhombica* has shorter conidiophores than *B. aquatica* (30–50 × 4–5 µm *vs*. 65–130 × 4–5.5 µm), and the appendage length of *B. pseudorhombica* is shorter (7–11 µm *vs*. 13.5–17.5 µm) (Crous et al. 2014). The conidia of *B. rhombica* are similar to *B. aquatica* in having a hyaline

to subhyaline, equatorial transverse bands, but the former has shorter conidia (including appendages) (21–32 µm *vs*. 35.5–43.5 µm) (Lin et al. 2017b). *Beltrania aquatica* is herein introduced as a novel species based on its distinct morphology and phylogenetic analysis.

11. *Phaeoacremonium* W. Gams, Crous & M.J. Wingf.

Phaeoacremonium (= *Togninia*) was introduced by Crous et al. (1996) as a hyphomycete genus typified by *P. parasiticum* (Gramaje et al. 2015; Huang et al. 2018; Calabon et al. 2021). *Phaeoacremonium* was previously known to be the asexual morph of *Togninia*, which was introduced by Berlese (1900) with *T. minima* as the type species. Gramaje et al. (2015) proposed to synonymize *Togninia* as *Phaeoacremonium*. Réblová et al. (2004) introduced *Togniniaceae* based on phylogenetic analysis of LSU and SSU markers. *Togniniaceae* comprises both sexual (*Conidiotheca* and *Togninia*) and asexual genera (*Phaeoacremonim*) (Réblová and Mostert 2007). This family has been included in *Calosphaeriales* (Mostert et al. 2003) and *Diaporthales* (Mostert et al. 2006) based on morpho-molecular analysis. Maharachchikumbura et al. (2015) excluded it from *Diaporthales* and introduced it in *Togniniales*. Hyde et al. (2020a), Wijayawardene et al. (2020) and Calabon et al. (2021) accepted *Conidiotheca* and *Phaeoacremonium* in *Togniniaceae*. Members of *Phaeoacremonium* are characterised by black ascomata, asci with hyaline ascospores, and straight or flexuous mononematous conidiophores with oval to reniform phialo-conidia (Huang et al. 2018; Marin-Felix et al. 2018; Spies et al. 2018).

There are 64 species listed in Species Fungorum (2021) under *Phaeoacremonium* (Table 1). Calabon et al. (2021) used morpho-molecular phylogenetic analyses, and Crous et al. (1996) utilized morphology for species identification in *Phaeoacremonium*. Réblová et al. (2004) used SSU and LSU markers, and Maharachchikumbura et al. (2015) used the SSU gene region for taxonomic studies. The majority of species discovered in *Phaeoacremonium* and related taxa were delineated using *act* and *tub*2 genes (e.g., Mostert et al. 2006; Huang et al. 2018; Spies et al. 2018 and Ye et al. 2020), while Calabon et al. (2021) used the LSU, ITS, *tef*1–α, *tub*2, and *act* markers in their study. Over 400 ITS sequences are deposited as *Phaeoacremonium* in GenBank. A BLASTn search of the ITS region of the type species *Phaeoacremonium parasiticum* strain ATCC 26366 (NR_145409) showed high similarity and query cover (90–100%) to eight uncultured fungal sequences. There are 40 species hypotheses (comprising 464 sequences) that show high similarity in UNITE. *Phaeoacremonium* species occur on animals, plants, soil, and also humans as they can be saprobic, parasitic, or hyperparasitic (Mostert et al. 2006; Hyde et al. 2020a). *Phaeoacremonium* species have been recorded on monocotyledonous and dicotyledonous hosts (Réblová et al. 2004; Verkley et al. 2014). Some *Phaeoacremonium* species cause trunk diseases of important forest and ornamental species (Crous et al. 1996; Hashemi and Mohammadi 2016; Kazemzadeh et al. 2017; Hyde et al. 2020a). *Phaeoacremonium minimum* is an important pathogen in young grapevines, and also causes subcutaneous lesions in humans (Gramaje et al. 2009; Choi et al. 2011; Hyde et al. 2020a). It can be hypothesised that *Phaeoacremonium* could occur as opportunistic pathogens and their spores could be transmitted by animals, humans or insects. As the species can be found in a wide range of habitats, we would expect the number of species to increase with extensive studies. Hyde et al. (2020a) estimated the crown age of *Togniniaceae* as 3.04 MYA and a stem age of 137.81 MYA (Cretaceous period). The difference in the crown and stem age of *Togniniaceae* is because crown age is affected by taxon sampling, and a larger sampling is likely to provide a more reliable crown age (Hyde et al. 2017a, b). This study introduces a new species, *P. camporesii,* living as a saprobe on *Corylus* sp. (eudicots) based on morphology and multimarker analyses.

Phaeoacremonium camporesii Wijes., Camporesi, & K.D. Hyde, ***sp. nov.***

Index Fungorum number: IF559245; *Facesoffungi number*: FoF 10568, Fig. 19

Etymology: The epithet honours Mr. Erio Camporesi, who collected the holotype

Holotype: MFLU 19–0506

Saprobic on dead aerial branch of *Corylus avellana* L. ***Sexual morph***: *Stromata* 1–2.2 × 0.8–1.3 mm diam., solitary, scattered, erumpent on the substrate, with numerous ascomata in a single stroma. *Ascomata* 120–300 × 180–260 µm ($\bar{x}$ = 195 × 215 µm, n = 10), perithecial, immersed to semi-immersed, globose to subglobose, sometimes flask-shaped, truncate at the base, black, coriaceous, ostiolate. *Peridium* 15–25 µm thick ($\bar{x}$ = 19 µm, n = 10), membranous, comprising 8–9-layers, outer layer dark brown to brown and inner layer hyaline cells of *textura angularis*. *Paraphyses* comprising numerous, 2–3.5 µm ($\bar{x}$ = 3 µm, n = 10) wide, hyaline, branched, septate, slightly constricted at septa and gradually narrowed towards the apex, longer than asci. *Asci* 17–25 × 4–5 µm ($\bar{x}$ = 22 × 4.5 µm, n = 20), 8-spored, unitunicate, clavate, apex truncate, apedicellate. *Ascogenous hyphae* hyaline, septate, simple, smooth-walled, 2–3 µm at the base. *Ascospores* 4–6 × 1–1.5 µm ($\bar{x}$ = 5.5 × 1.3 µm, n = 30), biseriate, allantoid, reniform with rounded ends, unicellular, hyaline, thin-walled, smooth-walled, often containing small guttules at both ends. ***Asexual morph***: Undetermined.

Culture characteristics: Ascospores germinating on PDA within 24 h. Germ tubes produced from the basal and apical cells of ascospores. Colonies growing on MEA, reaching 20–25 mm in 2 weeks at 16 °C. Mycelia superficial, circular, with entire margin, flat, smooth, from above white; reverse, whitish light brown.

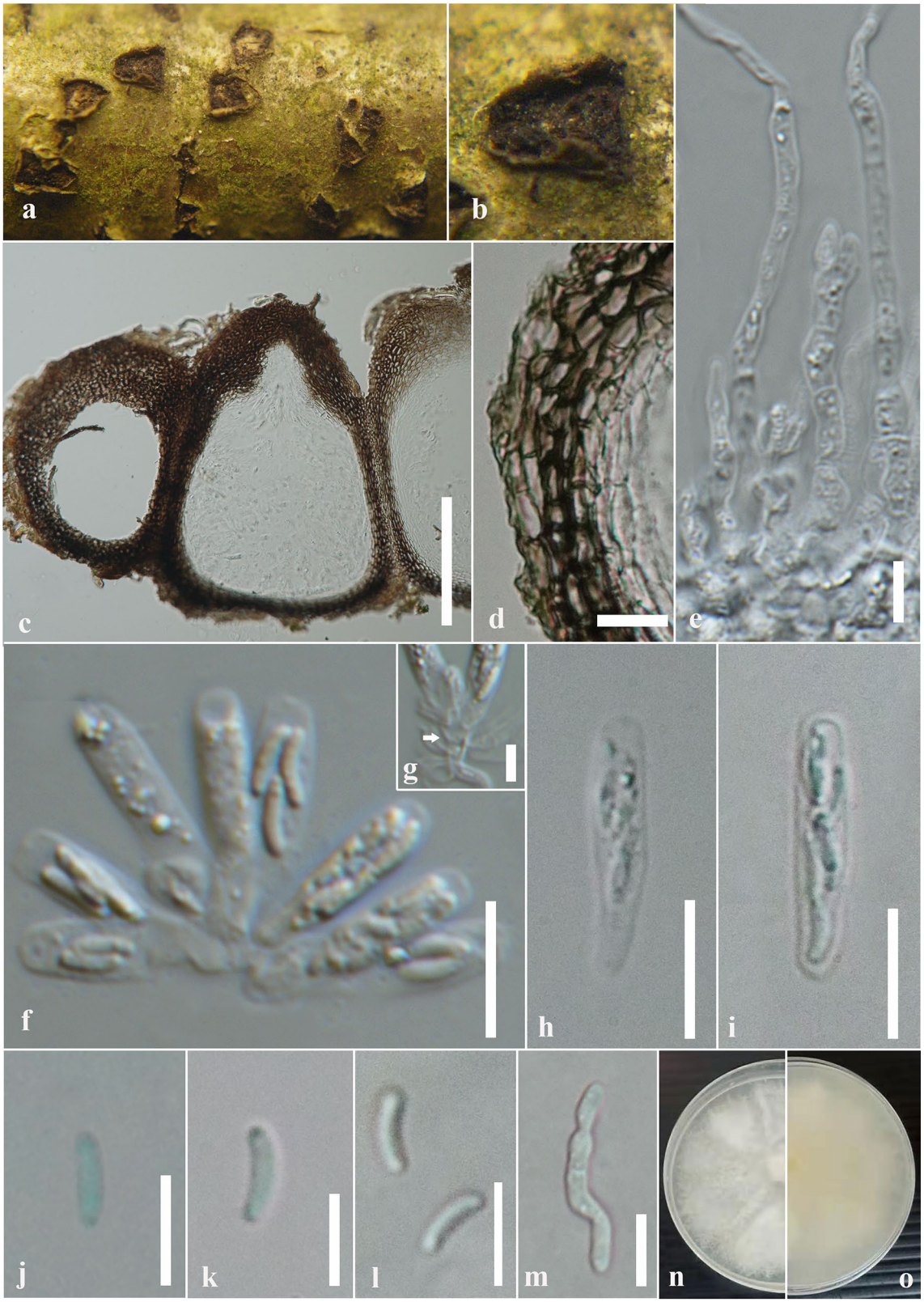


Fig. 19 ***Phaeoacremonium camporesii*** (MFLU 19–0506, **holotype**). **a** Host. **b** Stromata on decaying wood. **c** Longitudinal section of ascomata. **d** Ascomatal wall. **e** Paraphyses. **f–i** Asci and ascogenous hyphae. **j–l** Ascospores. **m** Germinated ascospores. **n, o** Culture on MEA from above and below. Scale bars: **a–c** = 100 µm, **d, f, h–i, m** = 10 µm, **e, g, j–l** = 5 µm

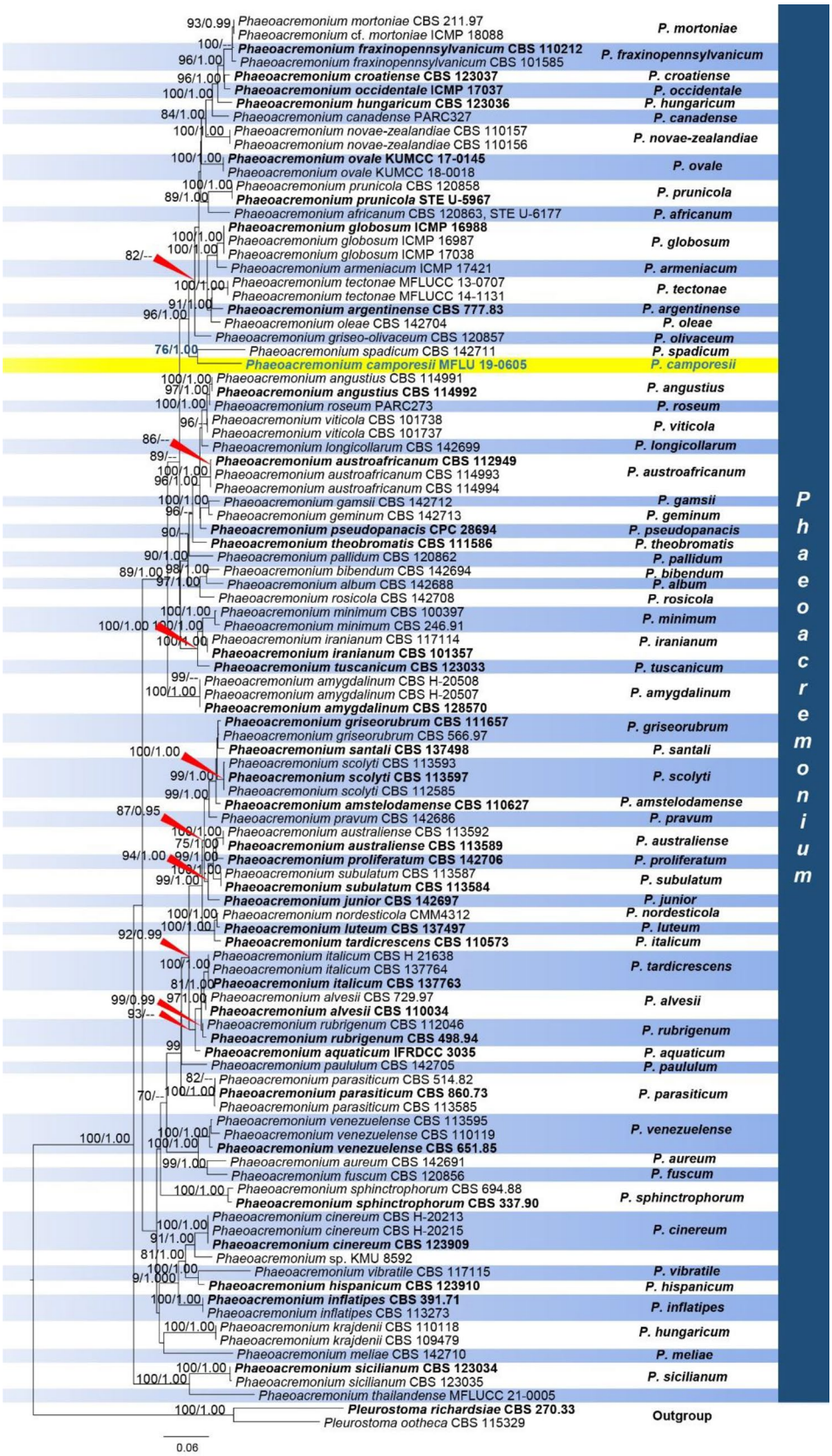


Fig. 20 Phylogram generated from maximum likelihood analysis based on combined LSU, ITS, *tub*2 and *act* sequence data representing species of *Phaeoacremonium*. Sequences were taken from Huang et al. (2018) and Calabon et al. (2021). The combined analyses comprised 103 taxa and 2108 characters (LSU = 892 bases, ITS = 472 bases, *tub*2 = 481 bases, *act* = 263 bases) after alignment. The best scoring RAxML tree with a final log likelihood score of −19257.268076 is presented. Bootstrap support values for ML equal to or greater than 70% and BPP equal to or greater than 0.95 are given at the nodes. *Pleurostoma ootheca* (CBS 115329) and *Pleurostoma richardsiae* (CBS 270.33) were used as outgroup taxa. The newly generated sequence is indicated in blue. The type-derived sequences are given in bold

Material examined: Italy, Forlì-Cesena Province, Tontola—Predappio city, on a dead hanging branch of *Corylus avellana* L. (*Betulaceae*), 30 January 2019, Erio Camporesi, IT4202 (MFLU 19–0506, **holotype**); ex-type living culture, MFLUCC 21–0224.

GenBank accession numbers: ITS = OL770246, *tub*2 = OL771439, *act* = OL771438.

Notes: Most *Phaeoacremonium* species have asexual morphs (Spies et al. 2018; Ye et al. 2020), and the sexual morphs are only known for some taxa (*Phaeoacremonium argentinense*, *P. aquaticum*, *P. austroafricanum*, *P. fraxinopennsylvanicum*, *P. inconspicuum*, *P. krajdenii*, *P. novaezealandiae*, *P. ovale*, *P. parasiticum*, *P. rubrigenum*, *P. thailandense* and *P. viticola*) (Hausner et al. 1992; Mostert et al. 2006; Hu et al. 2012; Huang et al. 2018; Calabon et al. 2021). *Phaeoacremonium camporesii* is similar to other *Phaeoacremonium* species in having acropetal succession in the formation of asci, a thickened ascal apex, hyaline ascogenous hyphae and allantoid, reniform ascospores (Calabon et al. 2021). However, *P. camporesii* differs from other *Phaeoacremonium* species as it lacks a long neck in the ascomata (Mostert et al. 2006; Marin-Felix et al. 2018; Huang et al. 2018). *Phaeoacremonium camporesii* is similar to *P. thailandense* as they lack long ascomatal necks (Calabon et al. 2021). *Phaeoacremonium camporesii* forms a separate lineage with *P. spadicum* (CBS 142711) with 76% ML and 1.00 BPP support (Fig. 20). However, the sexual morph of *P. spadicum* (CBS 142711) is currently undetermined (Spies et al. 2018); therefore, morphological comparison between these taxa was not possible. There were 16.93% (53/313 bases) and 10.68% (28/262 bases) base differences in the *tub*2 and *act* genes of *P. camporesii* (MFLU 19–0506) compared to *P. spadicum* (CBS 142711), excluding gaps. Therefore, we introduce *P. camporesii* as a novel taxon.

12. *Endocalyx* Berk. & Broome

Petch (1908) introduced *Endocalyx*, typified with *E. thwaitesii* which was assigned to *Apiosporaceae* (*Amphisphaeriales*, *Sordariomycetes*) by Wijayawardene (2020) based on morphology. Konta et al. (2021) transferred *Endocaly*x to *Cainiaceae* (*Xylariales*) based on multigene phylogenetic analyses. Hongsanan et al. (2017) and Wijayawardene et al. (2020) proposed to include *Cainiaceae* in *Xylariomycetidae* and regarded *Cainiaceae* as *incertae sedis*. Samarakoon et al. (2021) accepted 17 families, including *Cainiaceae* in *Xylariales*, *Xylariomycetidae.*

There are eight epithets listed under *Endocalyx* in Species Fungorum (2021), with only two new species introduced since 2000 (Species Fungorum 2021) (Table 1). Molecular data is only available for *E. cinctus* and *E. metroxyli* (from Japan and Thailand; Okada et al. 2017; Konta et al. 2021). Introductions of new species should rely on morphological comparison and molecular data. Only one ITS sequence is annotated as *Endocalyx* in GenBank. A BLASTn search of the ITS region of *Endocalyx ptychospermatis* strain ZHKUCC 21–0008 (as the molecular data of the type species *E. thwaitesii* is not available) showed a high similarity and query cover (90–100%) to two *Xylariales* species. There is only one species hypothesis (comprising one sequence) that has high similarity in UNITE. Most records of *Endocalyx* are saprobes. *Cainiaceae* species are usually found in monocotyledons, mainly grasses (Senanayake et al. 2015). The host-specificity remains to be studied, but most *Endocalyx* species occur on *Arecaceae*, indicating an endophytic lifestyle (Rashmi et al. 2019). Therefore, we would expect the number of species to increase with extensive study of poorly studied hosts.

Samarakoon et al. (2016) reported that *Amphisphaeriales* and *Xylariales* diverged during 252–66 MYA. The stem age of *Cainiaceae* is estimated at around 85.12 MYA, and the crown age is around 48.64 MYA (Samarakoon et al. 2021). *Cainiaceae* diverged before the Cretaceous extinction event. It can be hypothesised that *Cainiaceae* species diversified to adapt to various hosts that were dominant following the extinction event, such as monocotyledons (Peace et al. 2020). The present study introduces *Endocalyx ptychospermatis*, a novel taxon isolated from a palm tree in Guangdong, China.

Endocalyx ptychospermatis YR Xiong, Manawas & KD Hyde, ***sp. nov.***

Index Fungorum number: IF558846; *Facesoffungi number*: FoF 10540, Fig. 21

Etymology: Refers to the name of the host genus, *Ptychosperma macarthurii*

Holotype: ZHKU 21–0001

Saprobic on dead petiole of *Ptychosperma macarthurii*. ***Sexual morph*****:** Undetermined. ***Asexual morph*****:** *Conidiomata* 470–520 µm diam., up to 100 µm high, light yellow to light green, raised, cup-shaped or cylindrical, surrounded by yellow hyphal rings and hyaline conidiophores. *Conidiogenous cells* 4–6 µm long ($\bar{x}$ = 5 µm, n = 20), integrated, unicellular, hyaline, knob-like. *Conidia* 10–20 × 7–15 µm ($\bar{x}$ = 13 × 11 µm, n = 40), unicellular, dark brown, elliptical to closed polygonal with verrucous inclusions.

Culture characteristics: Colonies on PDA reaching 6 cm diam., after seven days at 25 °C, white at first, irregular, raised, undulate, rough, after maturity, smooth at the margin, white from above, pale-brown from below.

Material examined: China, Guangdong Province, on dead petiole of *Ptychosperma macarthurii* (*Arecaceae*). 17 December 2020, YR Xiong (ZHKU 21–0001, **holotype**); ex-type living culture, ZHKUCC 21–0008, ZHKUCC21–0009, ZHKUCC 21–0010.

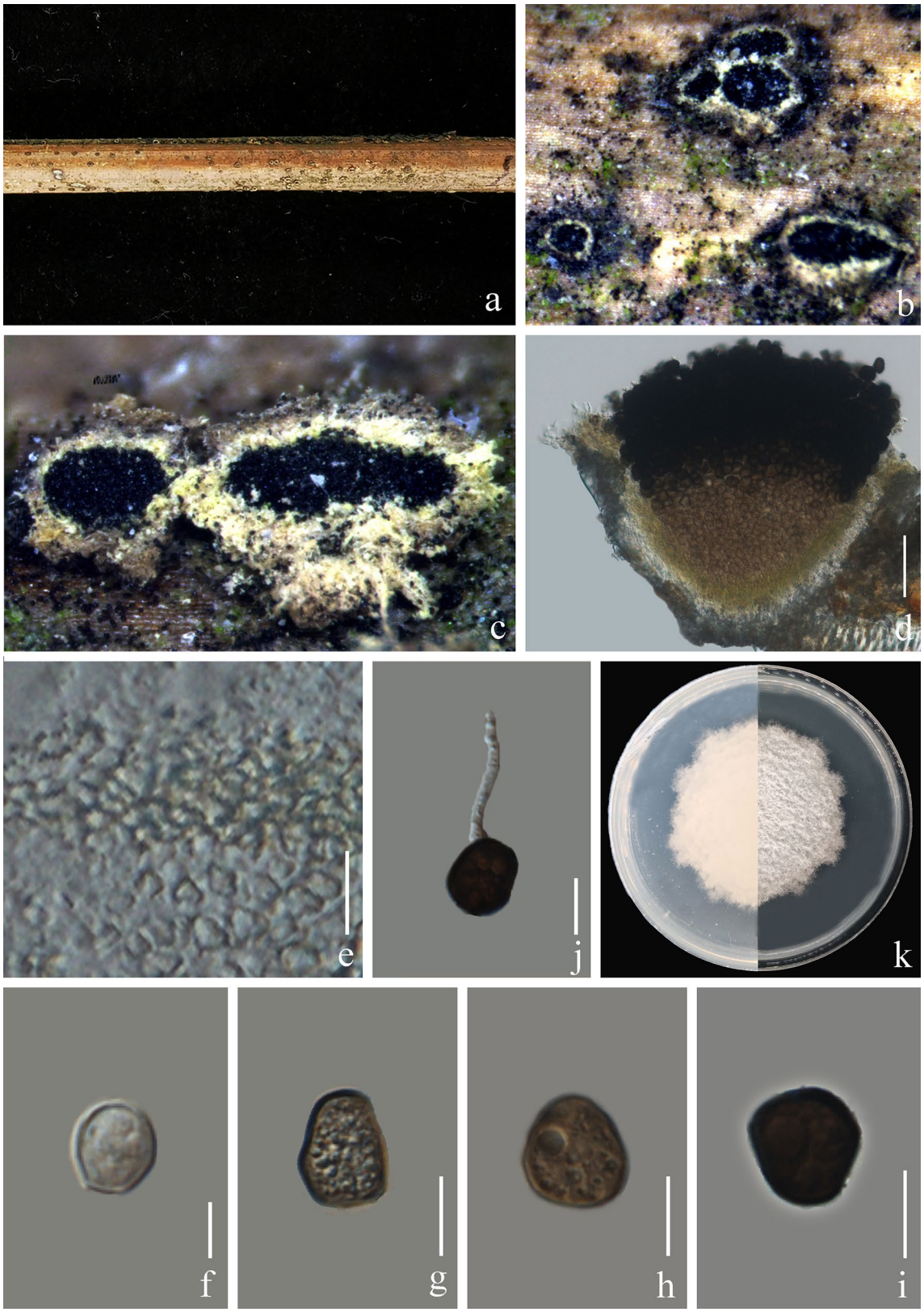


Fig. 21 ***Endocalyx ptychospermatis*** (ZHKU 21–0001, **holotype**). **a–c** Conidiomata on host surface. **d** Section of conidioma. **e** Conidioma wall. **f** Conidia. **g** Culture on PDA. **h–k** Conidia. Scale bars: **d** = 20 µm, **e**, **f**, **i–k** = 10 µm, **h** = 5 µm

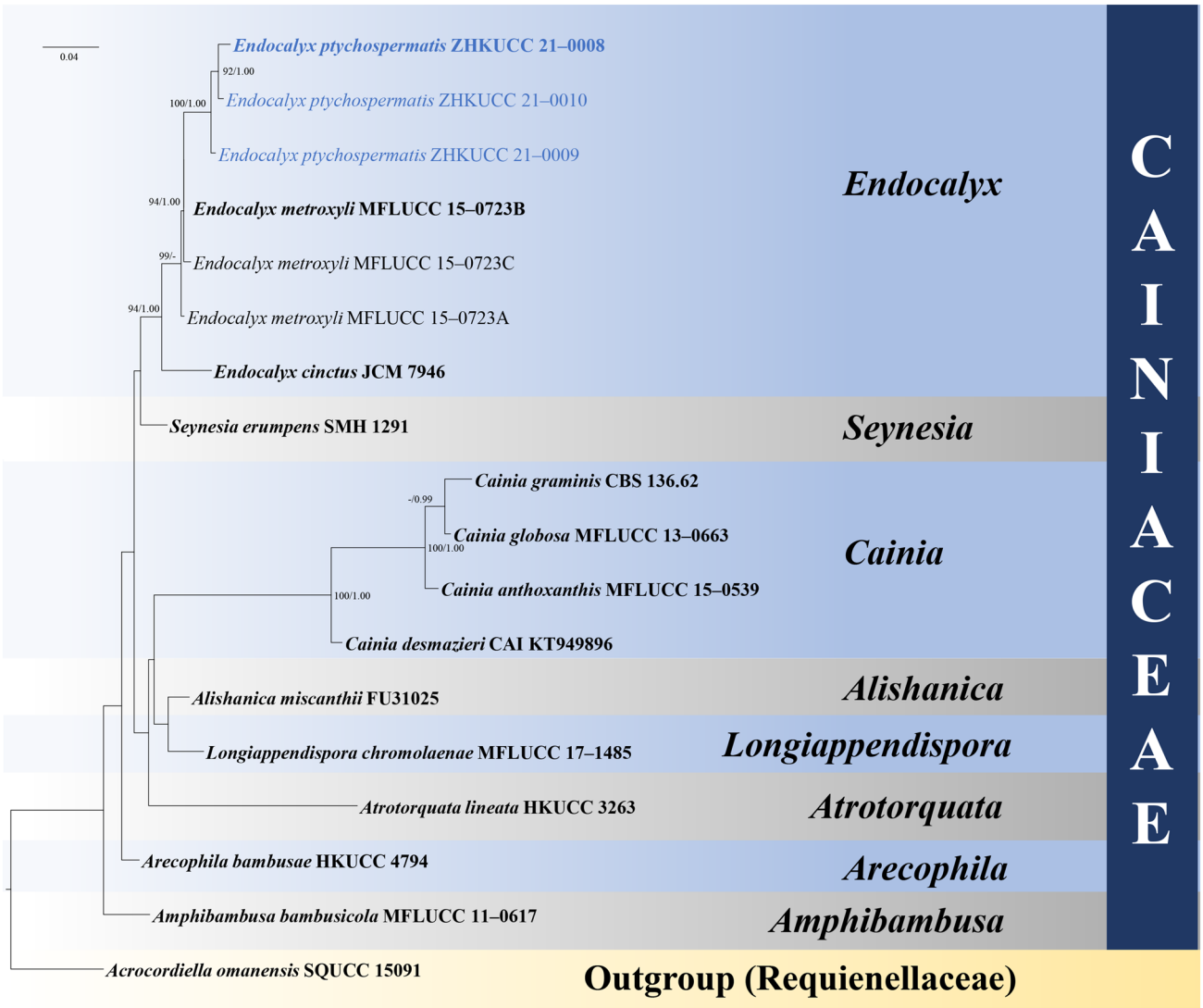


Fig. 22 Phylogram generated from maximum likelihood analysis based on combined LSU, ITS and SSU sequence data from *Cainiaceae* and related families in *Xylariales*. Eighteen taxa were included in the combined analyses, which comprised 2547 characters (LSU = 908 bases, ITS = 571 bases, SSU = 1068 bases) after alignment. The best scoring RAxML tree with a final log likelihood score of −8340.507794 is presented. Bootstrap support values for ML equal to or greater than 75% and BPP equal to or greater than 0.95 are given above the nodes. The tree is rooted with *Acrocordiella omanensis* (SQUCC 15091). The newly generated sequences are indicated in blue and the type-derived sequences are indicated in bold

GenBank accession numbers: ZHKUCC 21–0008; ITS = MZ493352, LSU = OK513439, SSU = OK569894. ZHKUCC 21–0009; ITS = MZ493353, LSU = OK513440, SSU = OK569895. ZHKUCC 21–0010; ITS = MZ493354, LSU = OK513441, SSU = OK569896.

Notes: *Endocalyx ptychospermatis* is related to *E. metroxyli* with 94% ML bootstrap support (Fig. 22). *Endocalyx ptychospermatis* is similar to *E. melanoxanthus* in having unicellular, dark brown conidia (Vitoria et al. 2011). *Endocalyx melanoxanthus* and *E. metroxyli* differ from *E. ptychospermatis* by having conidia with longitudinal germ slits (Vitoria et al. 2011). BLASTn searches of the ITS sequence (525 bases) of *E. ptychospermatis* (ZHKUCC 21–0008) showed 94.85% similarity to *E. metroxyli* (MFLUCC 15–0723B). The LSU sequence (866 bases) showed 99.18% similarity to *E. metroxyli* (MFLUCC 15–0723B). The SSU sequence (1071 bases) showed 99.43% similarity to *E. metroxyli* (MFLUCC 15–0723B). *Endocalyx ptychospermatis* is introduced as a new species based on morphology and phylogenetic analyses.

13. *Peroneutypa* Berl.

Diatrypaceae was proposed by Nitschke (1869) with *Diatrype* as the type genus. *Diatrypaceae* is characterised by

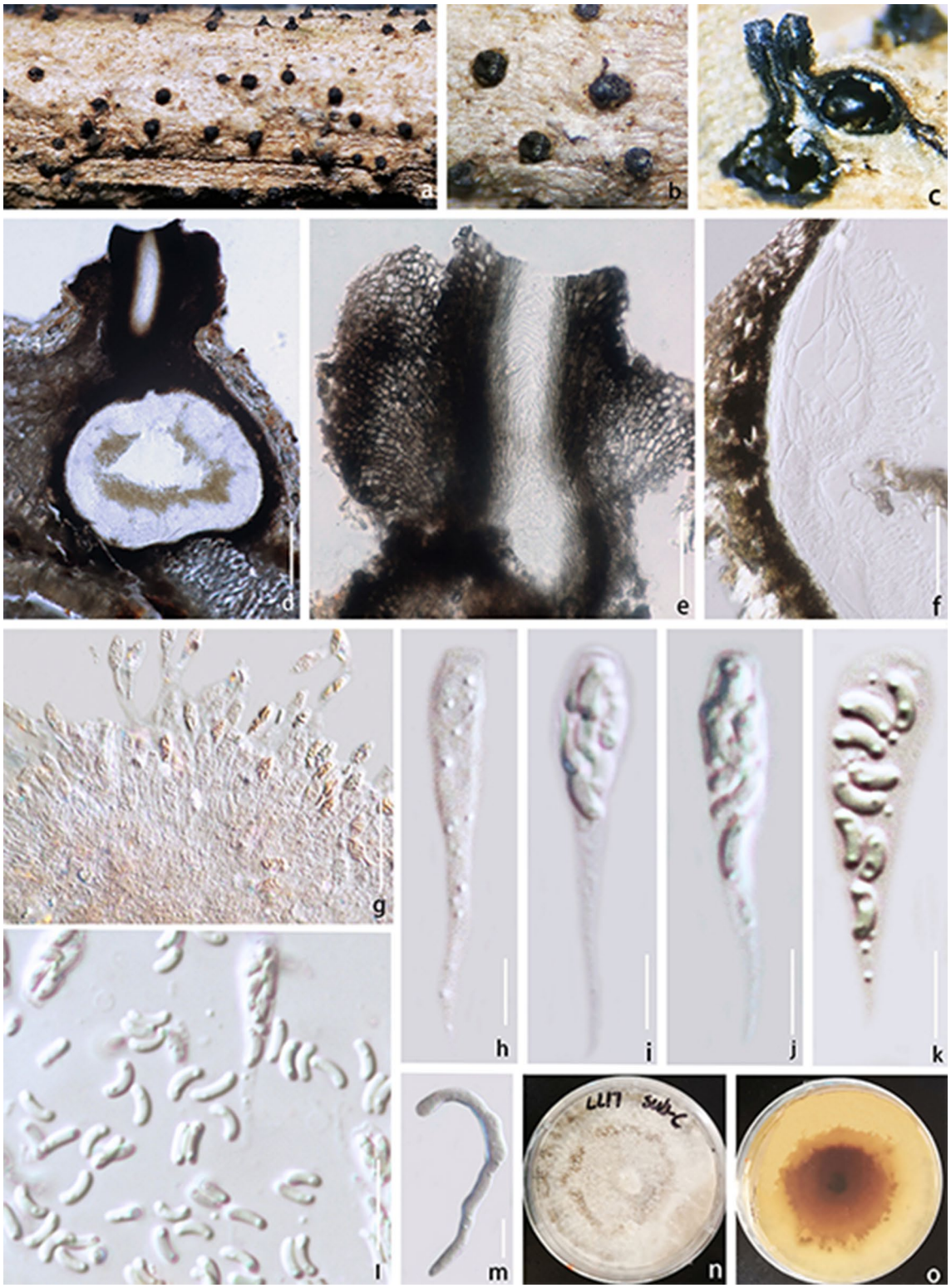


Fig. 23 ***Peroneutypa kunmingensis*** (HKAS 113189, **holotype**). **a** Appearance of stromata on unidentified dead wood. **b** Close-up of erumpent stromata. **c–d** Vertical section of ascomata (including the long neck). **e** Section of the neck. **f** Peridium. **g** Group of asci. **h–k** Individual asci. **l** Ascospores. **m** Germinating ascospore. **n, o** Colonies on PDA after 30 days (n = colony from above, o = colony from below). Scale bars: **d** = 100 μm, **e–f** = 50 μm, **g** = 30 μm, **h–k** = 5 μm, **l–m** = 10 μm

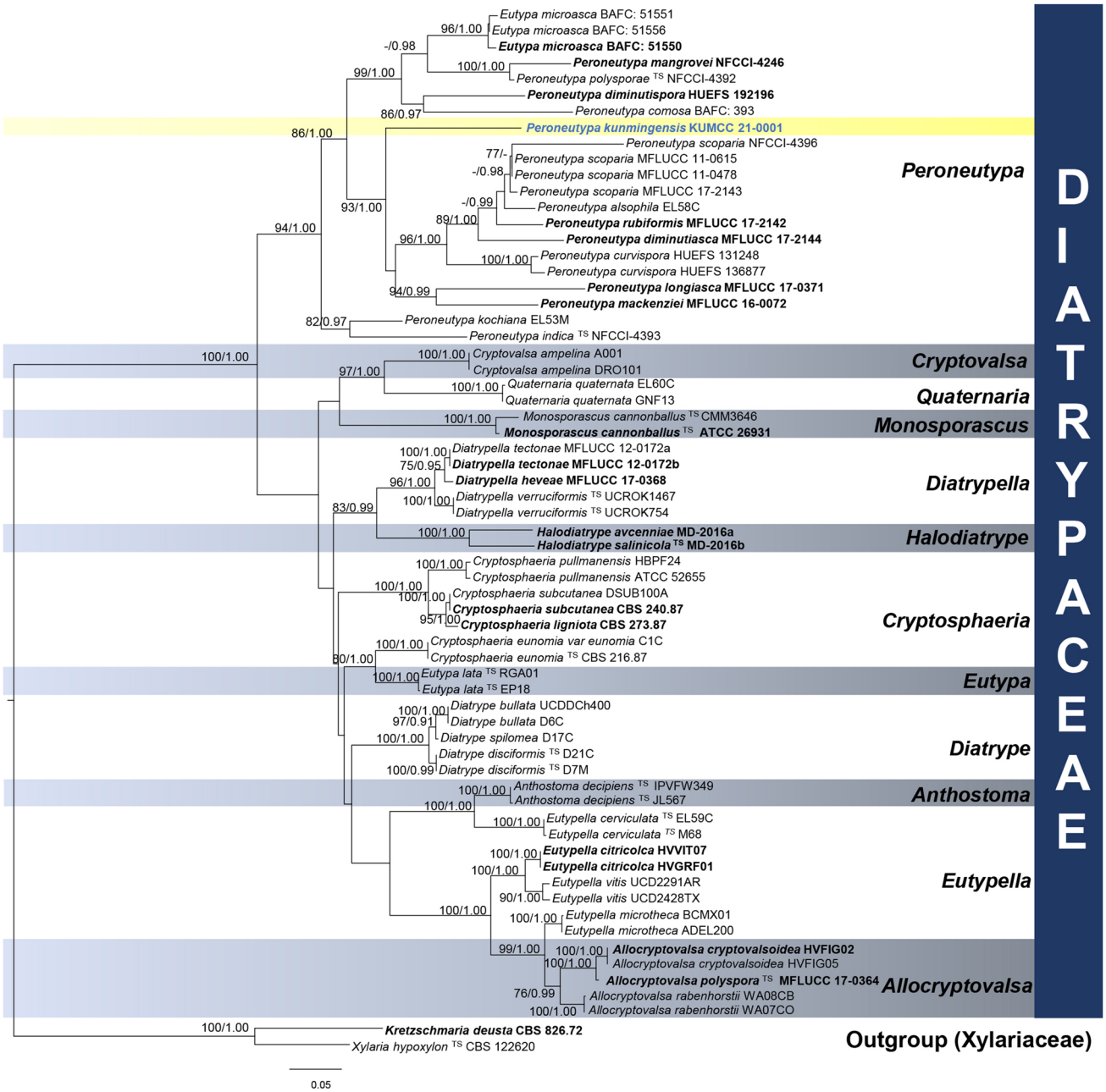


Fig. 24 Phylogram generated from maximum likelihood analysis based on combined ITS and *tub*2 sequence data representing species of *Diatrypaceae*. Related sequences were taken from Dayarathne et al. (2020), Phookamsak et al. (2019) and Shang et al. (2018). Sixty-five taxa were included in the combined analyses, which comprised 1100 characters (ITS = 639 bases, *tub2* = 461 bases) after alignment. The best scoring RAxML tree with a final log likelihood score of −12477.423944 is presented. Bootstrap support values for ML equal to or greater than 75% and BPP equal to or greater than 0.95 are given at the nodes. *Kretzschmaria deusta* (CBS 826.72) and *Xylaria hypoxylon* (CBS 122620) were used as outgroup taxa. The newly generated sequence is indicated in blue. The type-derived sequences are indicated in bold and black; type species are denoted with TS after the species name

perithecial ascomata, usually embedded in a black stroma, cylindric-clavate to clavate with long pedicellate asci and allantoid ascospores (Glawe and Rogers 1984; de Almeida et al. 2016). *Peroneutypa* is a monophyletic genus in *Diatrypaceae* introduced by Berlese (1902) together with the species *P. bellula, P. corniculata* and *P. heteracantha*, but without assigning a type species (Shang et al. 2018; Dayarathne et al. 2020). Rappaz (1987) proposed *P. bellula* as the type species as the herbarium was in good condition. The genus was synonymized under *Eutypella* whereas *Peroneutypa* is characterized by valsoid stroma, long prominent necks, sessile to long stalks, small asci with truncate apices

and allantoid ascospores, but no asexual morph has been reported for this genus (Radu 2013; Raymundo et al. 2014; de Almeida et al. 2016; Shang et al. 2017).

There are 29 epithets listed in Species Fungorum under *Peroneutypa.* Carmarán et al. (2006) resurrected eight species from *Echinomyces* and *Eutypella* and accommodated them under *Peroneutypa.* Shang et al. (2018) revised *Peroneutypa* based on multi-gene analyses with an updated key to *Peroneutypa*. Two new species were also introduced by Dayarathne et al. (2020) and three species were moved to other genera (Table 1). Over 65 ITS sequences are annotated as *Peroneutypa* in GenBank. A BLASTn search of the ITS region showed a high similarity (88.61%) and query cover (> 90%) to *Peroneutypa scoparia* (MG980578). There are 18 species hypotheses (comprising 41 sequences) that have high similarity to *Peroneutypa* in UNITE. Members of this genus are mainly saprobes and pathogens, and they are widely distributed in terrestrial habitats (Lumbsch and Huhndorf 2010; Maharachchikumbura et al. 2015; Shang et al. 2017; Hyde et al. 2019a). As endophytes, some *Peroneutypa* species appear to be host-specific. For example, the endophyte *Peroneutypa scoparia* has only been isolated from *Garcinia sp.* (Phongpaichit et al. 2007), but this could also be due to the lack of sampling. There is likely to be a large number of species that will be discovered as some species appear to be host-specific.

Diatrypaceae includes 21 genera and more than 1500 species (Dissanayake et al. 2021). A higher-level classification with divergence time estimates for *Diatrypaceae* was provided by Hongsanan et al. (2017), and the family was placed in *Xylariales* (*Xylariomycetidae*, *Sordariomycetes*). The stem age of *Diatrypaceae* is estimated at around 82.68 MYA, and the crown age is around 20.51 MYA (Hyde et al. 2020b). *Diatrypaceae* diverged before the Cretaceous extinction event. The conditions of high humidity and reduced solar insolation after the extinction event favoured saprobic fungi such as *Diatrypaceae* that flourished on the detritus (Vajda and McLoughlin 2004). In this study, we introduce a new species of *Peroneutypa* based on morphology and multi-marker phylogenetic data (Figs. 23, 24).

Peroneutypa kunmingensis L. Lu, K.D. Hyde & Tibpromma, ***sp. nov.***

Index Fungorum number: IF558363; *Facesoffungi number*: FoF 09894, Fig. 23

Etymology: In reference to the host location, Kunming, China

Holotype: HKAS 113189

Saprobic on decaying wood. ***Sexual morph***: *Stromata* irregular to pear-shaped, inflated at the apex, scattered or gregarious, visible as black spots on the substrate, absent or with poorly-developed interior, immersed, becoming raised to erumpent by a prolonged ostiolar canal. *Ascomata* (excluding neck) 200–300 × 240–370 µm ($\bar{x}$ = 260 × 317 µm, n = 10), perithecial, fully immersed in a stroma, solitary, dark brown to black, globose to subglobose, glabrous, individual ostiole with a long neck. *Ostioles* 80–200 × 80–120 µm ($\bar{x}$ = 140 × 100 µm, n = 10), cylindrical, sulcate, straight to bent, periphysate, brown to black. *Peridium* 30–60 µm wide, comprising two layers of *textura angularis*, outer section comprising 5–7 layers, thick-walled cells of *textura angularis*, brown to dark cells and darker than inner hyaline cells arranged in a *textura angularis*. *Hamathecium* cylindrical, septate, hyaline, embedded in a mucilaginous matrix. *Asci* 22–30 × 3–5 µm ($\bar{x}$ = 26 × 4.1 µm, n = 20), 8-spored, unitunicate, straight or slight curved, hyaline, long stipe up to 16 µm, with a non-amyloid apical ring. *Ascospores* 3–5.5 × 1–2 µm ($\bar{x}$ = 4.2 × 1.3 µm, n = 30), overlapping 1–2-seriate, oblong to allantoid, hyaline to pale grey, aseptate, smooth-walled, usually with 1–2 oil droplets. ***Asexual morph***: Undetermined.

Culture characteristics: Ascospores germinated within 12 h on PDA, colonies grow rapidly on PDA at room temperature, reaching around 50 mm diam., after 4 weeks. Colonies on medium appear circular to irregular, medium dense, flat or effuse, with fimbriate edge, colonies from above and below white to greyish when immature, slight radish pigments visible from above; reverse pale grey to reddish-brown at maturity. Yellow–brown pigment diffused in PDA.

Material examined: China, Yunnan Province, on dead wood of undetermined host, 4 September 2020, Samantha Karunarathna, LL17 (HKAS 113189, **holotype**); ex-type living culture, KUMCC 21–0001.

GenBank accession numbers: LSU = MZ475069, ITS = MZ475070, *tub*2 = MZ490589.

Notes: The morphology of *Peroneutypa kunmingensis* fits within the generic concept of *Peroneutypa* with its long prominent necks, small asci, and allantoid ascospores (Carmarán et al. 2006). BLASTn results of ITS and *tub*2 sequence data showed similarities to *Peroneutypa scoparia* (MW448609, 88.61% similarity across 95% of the query sequence, which translates into 84.18%) and *P. scoparia* (MG586231, 81.38% similarity across 96% of the query sequence, which translates into 78.12%). *Peroneutypa kunmingensis* differs from *P. scoparia* which has solitary ascomata and small ostioles (Carmarán et al. 2006). Our new species formed a well-separated clade inside *Peroneutypa* with 93% ML and 1.00 BPP support (Fig. 24). We introduce *P. kunmingensis* as a new species based on morphological and phylogenetic support.

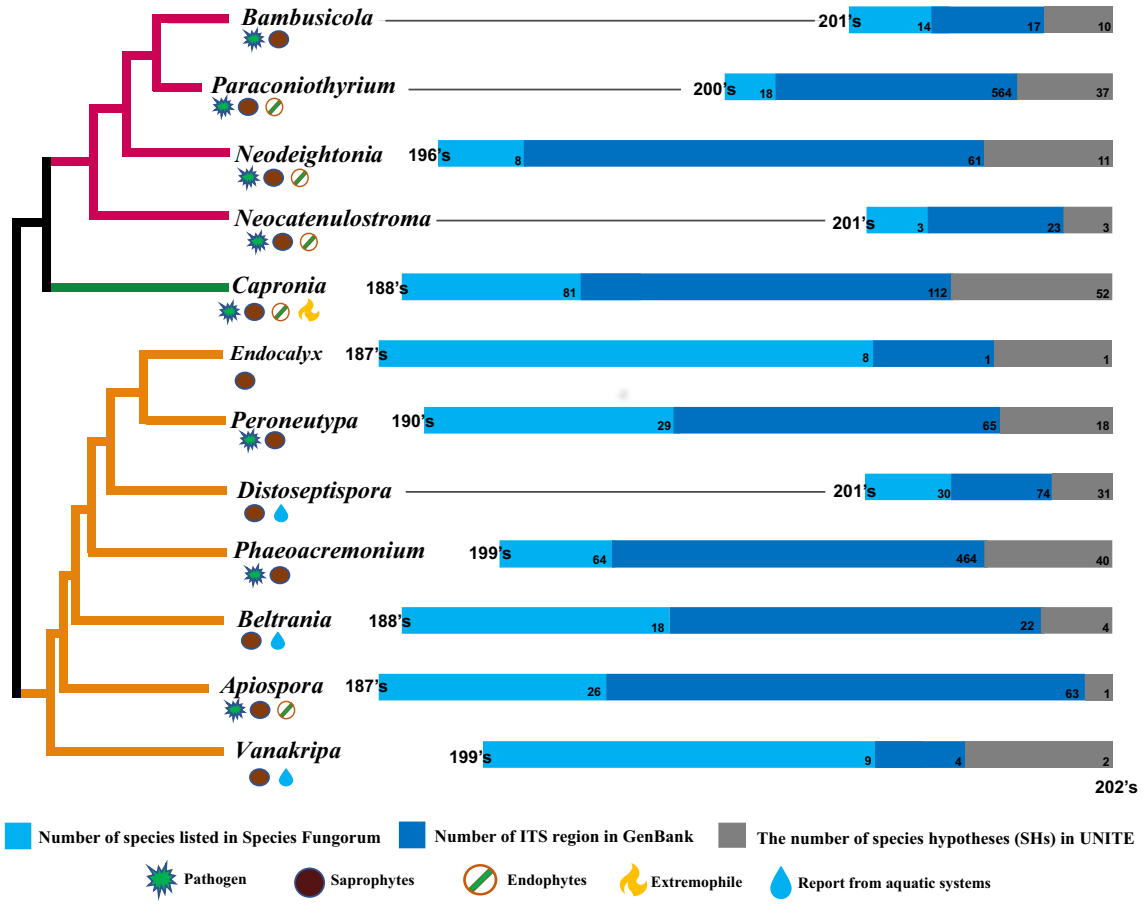


Fig. 25 The estimates of fungal numbers based on taxonomy, the number of ITS region in GenBank (including uncultured fungi with high similarity) and the number of species hypotheses from environmental samples (UNITE) are illustrated for each entry

Discussion

New species introduction versus GenBank depositions

We provide 12 case studies for different ascomycete genera (Fig. 25), with new species introduced in each. In these genera, 288 species have been introduced in the last 25 years while sequence data from 1467 entities (based on ITS sequences) were added during this period. Several studies have shown that the ITS region alone cannot resolve species level relationships, but it does indicate the possible number of species (Lücking et al. 2020; Maharachchikumbura et al. 2021; Pem et al. 2021; Bhunjun et al. 2022).

Fungi have generally been poorly studied for novel medicinal compounds. Many of the genera discussed in this study produce medicinal compounds, and this aspect has barely been researched. *Beltrania rhombica* has been reported to have antibacterial and antifungal properties against *Staphylococcus aureus* and *Candida albicans*, respectively (Rukachaisirikul et al. 2005). Several antifungal bioactive compounds against pathogenic fungal species (Reátegui et al. 2006; Silva et al. 2017) and other compounds such as naphthalenone and phytotoxins p-hydoxybenzaldehyde (Evidente et al. 2000; Tabacchi et al. 2000; Abou-Mansour et al. 2004) have been identified in *Phaeoacremonium* species. Species of *Apiospora* have also been used as antifungal agents in the pharmaceutical industry (Hyde et al. 2019b). Over 95 novel secondary metabolites have been reported from *Paraconiothyrium* (Wang et al. 2021). *Paraconiothyrium* produces sesquiterpenes, which has several biological activities such as anti-tumour, anti-inflammatory and antibacterial (Wang et al. 2021). *Paraconiothyrium* produces a variety of hydrolytic and oxidative active enzymes, including cellulases, hemicellulases, and lignin-degrading accessory enzymes (Wang et al. 2021).

Apiospora has the largest number of epithets listed in Index Fungorum (2021) among the selected genera in this study. Most *Apiospora* species have been found on monocotyledonous plants from a range of climates (Pintos and Alvarado 2021). The ITS sequence data for about 30 taxa have been deposited each year for the last two years, and the

number of species is likely to increase due to their diverse lifestyles and diverse host range. This is evident in several recent studies (Sharma et al. 2014; Jiang et al. 2019). Most *Bambusicola* species have been collected on *Bambusoideae* which are found mostly in tropical and subtropical areas (Lobovikov et al. 2007). The number of species reported in *Bambusicola* and the number of sequences for taxa deposited in GenBank as *Bambusicola* every year has remained low since the genus was introduced. The number of species is expected to increase as a large number of novel species continue to be introduced every year from *Bambusoideae*. The discovery of new taxa in *Beltrania* was relatively low until the application of molecular data in 1990. This resulted in 13 new species being introduced in 31 years as compared to 13 species in 100 years before that (Index Fungorum 2021). The number of ITS sequences deposited as *Beltrania* in GenBank has also increased every decade, which would suggest an increase in the number of species. Among the selected genera, *Capronia* has the second largest number of epithets listed in Index Fungorum (2021) after *Apiospora,* and none of these genera is host-specific (Sánchez et al. 2019; Pintos and Alvarado 2021). Molecular data has improved species resolution in *Capronia*, which resulted in the discovery of 65 epithets in the 30 years since 1990 compared to 26 species in over 100 years before that (Index Fungorum 2021). The majority of *Capronia* species are saprotrophs on decaying wood, bark and leaves, while some may be fungicolous (Untereiner et al. 2011). Therefore, a large number of species is expected to be introduced in this genus.

Distoseptispora species have mainly been reported as saprobes from a range of hosts, but only from China and Thailand (Song et al. 2020). This could suggest geographic specificity or could be due to the lack of studies from other countries. The genus has over 70 ITS sequences in GenBank. *Endocalyx* and *Vanakripa* are less collected genera as there are less than five species that have been introduced in the last ten years with a small amount of sequence data in GenBank. Host-specificity of taxa remains to be determined, but *Endocalyx* species are usually found on monocotyledons. Of the species introduced in this paper, *Neodeightonia* and

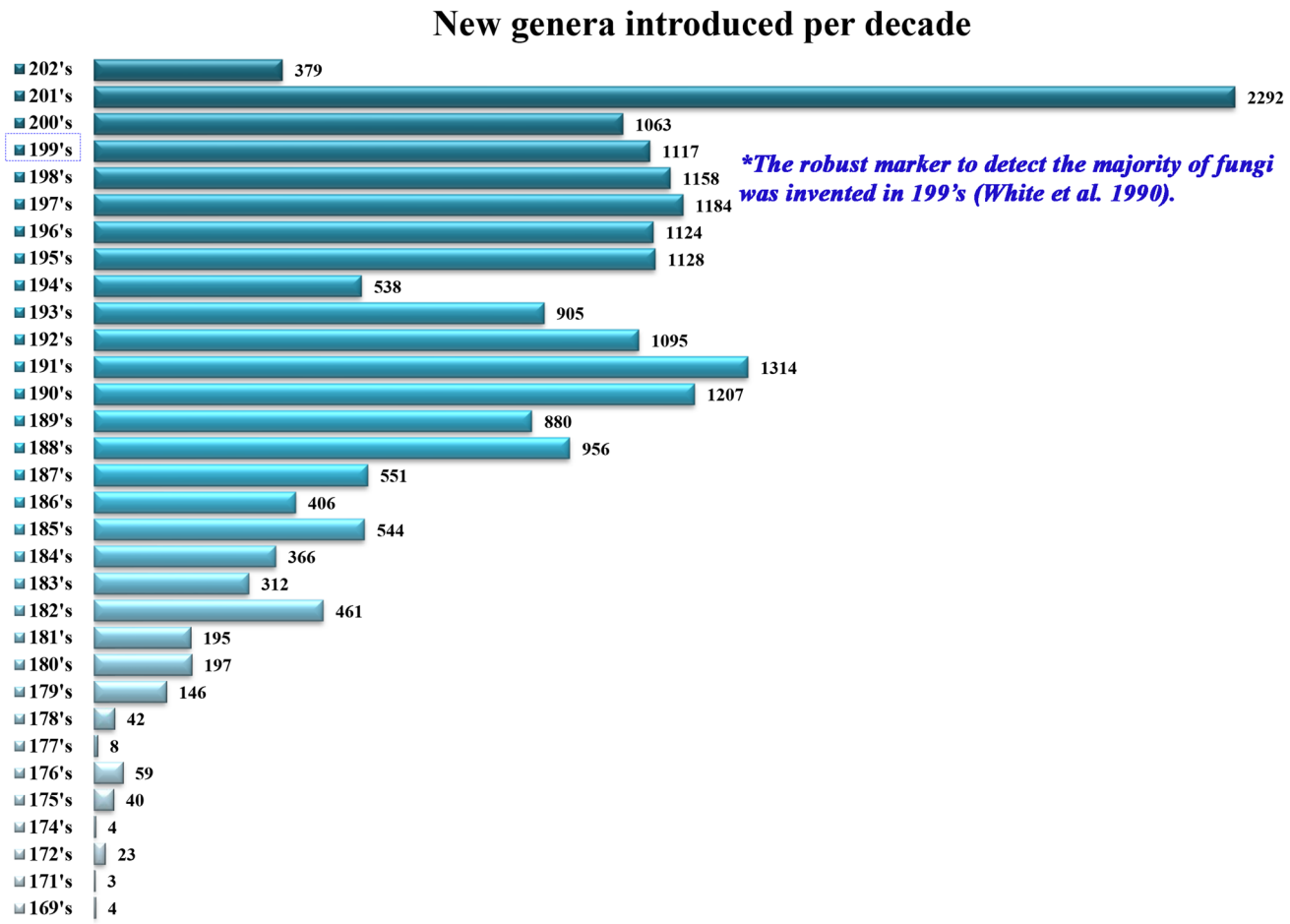


Fig. 26 Trend of new genera introduced every decade from 1690 to 2020 based on data from Index Fungorum (2021). Primers targeting the fungal ITS region were published in 1990. 202's=the decade starting in 2020

Vanakripa have the lowest number of species epithets listed in Index Fungorum (2021). Most *Neodeightonia* species have been recorded recently as saprobes in Thailand (Phillips et al. 2019), and there are over 60 ITS sequences in GenBank. *Paraconiothyrium* has 20 species listed in Species Fungorum (2021), but over 500 ITS sequences are available in GenBank. *Paraconiothyrium* species have a worldwide distribution in diverse habitats (Ariyawansa et al. 2020). We expect that several species remain to be discovered and *Paraconiothyrium* is likely to attract more attention in future studies as it can produce several novel secondary metabolites (Wang et al. 2021). *Peroneutypa* species are associated with various lifestyles and are widely distributed (Hyde et al. 2019a). Eighteen *Peroneutypa* species have been introduced in the last 31 years, and 65 ITS sequences were deposited in GenBank over the same period. There are over 60 epithets of *Phaeoacremonium* listed in Index Fungorum (2021), and there are over 400 ITS sequences in GenBank. *Phaeoacremonium* species have been recorded from a wide range of hosts, including monocotyledons and dicotyledons. They have worldwide distribution with reports from America, Europe, Scandinavia, Ukraine, the Middle East and Africa (Gramaje et al. 2015). Several novel secondary metabolites have been identified from *Phaeoacremonium* species, and are likely to attract several extensive studies in the future. The potential for taxonomic novelties is presumably very large. *Neocatenulostroma* species are associated with various lifestyles such as endophytes, plant pathogens and saprobes (Markovskaja et al. 2016). There are no new species that have been introduced in *Neocatenulostroma* since it was introduced in 2014, but 23 ITS sequences were deposited in GenBank over the same interval. The ITS region has been suggested to represent the universal barcode for fungi (Schoch et al. 2012).

Most species in this study have been found in humid/tropical/subtropical climates such as in Thailand and the southern part of China. Gramineae-inhabiting genera such as *Apiospora* and *Bambusicola* were more frequently discovered from warm climate zones, thus further studies in tropical regions would probably result in the discovery of novel taxa (Dai et al. 2017; Pintos and Alvarado 2021). Although several previous studies have targeted fungal diversity on these hosts, we suspect that a large number of species remain to be discovered.

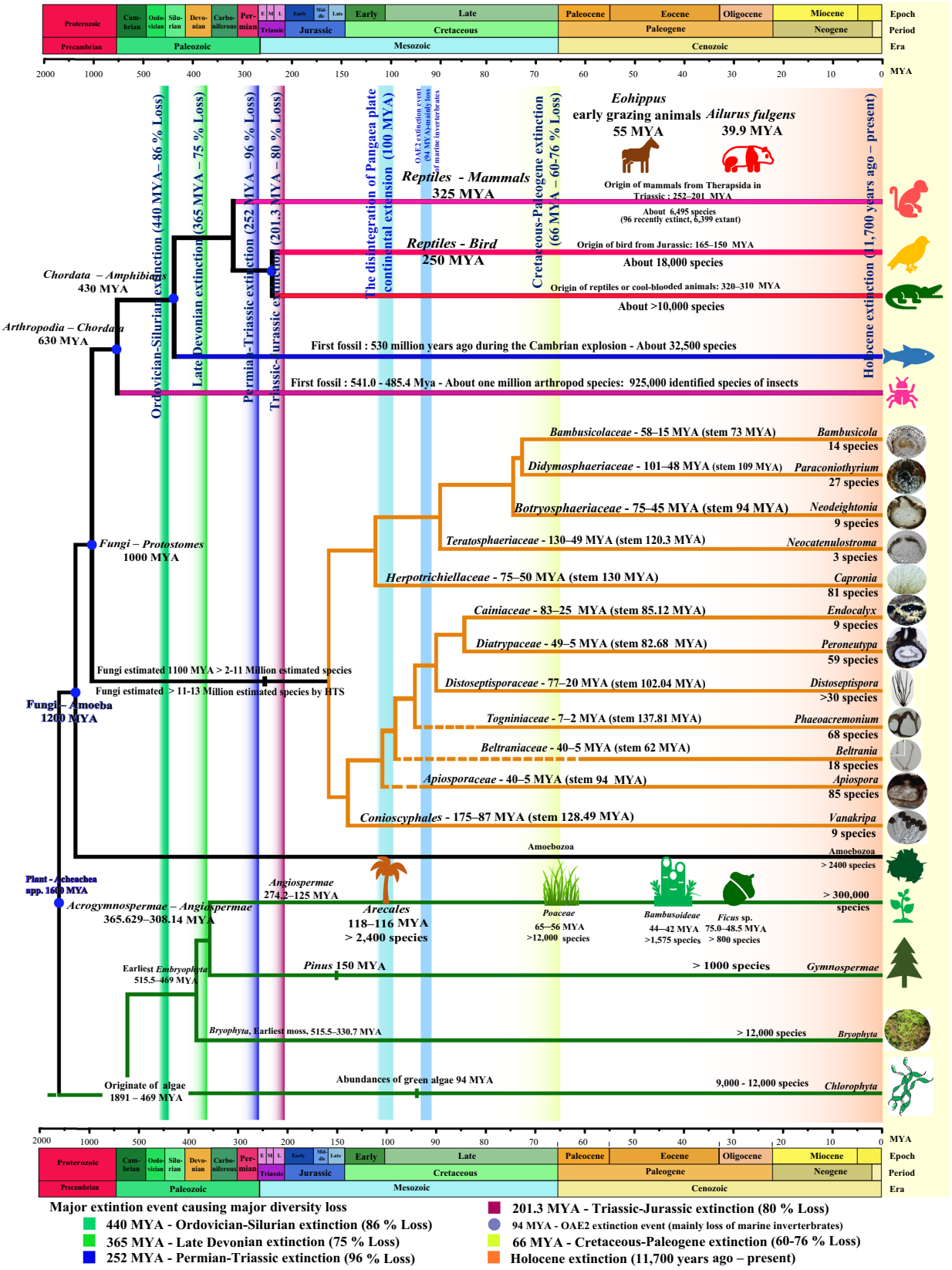
Another way to look at fungal diversity is to examine taxa from a single habitat, host and substrate, for example, studies of Dai et al. (2017), Tibpromma et al. (2018), Mapook et al. (2020) and Phukhamsakda et al. (2020). Overlapping taxa from each host in these studies are low. This indicates that there is some degree of host-specificity among these taxa at host, genus or family levels. Studies will increase the knowledge of taxa on these hosts and help answer how the environment affects the evolutionary development of fungal communities.

Table 4 The number of species hypothesis at 1.5% threshold and the number of sequences recovered from environmental samples (UNITE)

Genus	SH in Unite at 1.5% threshold	Sequences
Apiospora	1	12
Bambusicola	10	15
Beltrania	4	47
Capronia	52	571
Distoseptispora	31	101
Endocalyx	1	1
Neocatenulostroma	3	137
Neodeightonia	11	61
Paraconiothyrium	37	708
Peroneutypa	18	41
Phaeoacremonium	40	464
Vanakripa	2	2

New genus introductions

Approximately 150,000 extant fungi and fungus-like taxa are presently recognized (Wijayawardene et al. 2020), representing 3.5–7% of the 2.2–3.8 million estimated species (Species Fungorum 2021; Hyde et al. 2020a, 2021). The large number of species discovered has also led to the introduction of several new genera every year. Figure 26 shows the trend of new genera introduced every decade from 1690 to 2020 based on data from Index Fungorum (2021). Since the 1900s, over 1000 genera were introduced every decade, except in the 1930s and 1940s as a result of World War II (van Goethem and van Zanden 2021). There was a peak of over 2200 new genera introduced from 2010–2019 (Fig. 26). This is due to a large number of novel taxa being discovered from extensive studies based on a specific location or host (Lücking and Hawksworth 2018), notably Mapook et al. (2020) and Phukhamsakda et al. (2020), each introducing 12 genera, Crous et al. (2020) with six new genera and Yuan et al. (2020) with five new genera. Molecular advancements have increased the rate of species discovery, and they have, furthermore, provided important insights to understand the diversity of fungi, identify rare species and establish conservation goals (Willis 2018). High-throughput sequencing has added a new dimension to the assessment of fungal diversity—one that dramatically increased the estimated number to 11.7–13.2 million species (Wu et al. 2019). It seems clear that Sanger-based molecular mycology and high-throughput sequencing-powered metabarcoding effectively target different species. This paper explores the potential of Sanger-based mycology to unravel new species.


Proterozoic
Cambrian
Ordovician
Silurian
Devonian
Carboniferous
Permian
Triassic
Jurassic
Cretaceous
Paleogene
Neogene
Precambrian
Paleozoic
Mesozoic
Cenozoic
Epoch
Period
Era
MYA
Ordovician-Silurian extinction (440 MYA– 86 % Loss)
Late Devonian extinction (365 MYA – 75 % Loss)
Permian-Triassic extinction (252 MYA – 96 % Loss)
Triassic- Jurassic extinction (201.3 MYA – 80 % Loss)
The disintegration of Pangaea plate continental extension (100 MYA)
OAE2 extinction event (94 MYA)-mainly loss of marine inverterbrates
Cretaceous-Paleogene extinction (66 MYA – 60-76 % Loss)
Holocene extinction (11,700 years ago – present)
Eohippus
early grazing animals
55 MYA
Ailurus fulgens
39.9 MYA
Origin of mammals from Therapsida in Triassic : 252–201 MYA
About 6,495 species
(96 recently extinct, 6,399 extant)
Reptiles - Mammals
325 MYA
Reptiles - Bird
250 MYA
Origin of bird from Jurassic: 165–150 MYA
About 18,000 species
Origin of reptiles or cool-blooded animals: 320–310 MYA
About >10,000 species
Chordata – Amphibians
430 MYA
Arthropodia – Chordata
630 MYA
First fossil : 530 million years ago during the Cambrian explosion - About 32,500 species
First fossil : 541.0 - 485.4 Mya - About one million arthropod species: 925,000 identified species of insects
Bambusicolaceae - 58–15 MYA (stem 73 MYA)
Bambusicola
14 species
Didymosphaeriaceae - 101–48 MYA (stem 109 MYA)
Paraconiothyrium
27 species
Botryosphaeriaceae - 75–45 MYA (stem 94 MYA)
Neodeightonia
9 species
Teratosphaeriaceae - 130–49 MYA (stem 120.3 MYA)
Neocatenulostroma
3 species
Herpotrichiellaceae - 75–50 MYA (stem 130 MYA)
Capronia
81 species
Cainiaceae - 83–25 MYA (stem 85.12 MYA)
Endocalyx
9 species
Diatrypaceae - 49–5 MYA (stem 82.68 MYA)
Peroneutypa
59 species
Distoseptisporaceae - 77–20 MYA (stem 102.04 MYA)
Distoseptispora
>30 species
Togniniaceae - 7–2 MYA (stem 137.81 MYA)
Phaeoacremonium
68 species
Beltraniaceae - 40–5 MYA (stem 62 MYA)
Beltrania
18 species
Apiosporaceae - 40–5 MYA (stem 94 MYA)
Apiospora
85 species
Conioscyphales - 175–87 MYA (stem 128.49 MYA)
Vanakripa
9 species
Fungi – Protostomes
1000 MYA
Fungi estimated 1100 MYA > 2-11 Million estimated species
Fungi estimated > 11-13 Million estimated species by HTS
Fungi – Amoeba
1200 MYA
Amoebozoa
Amoebozoa
> 2400 species
Plant - Acheachea
app. 1600 MYA
Acrogymnospermae – Angiospermae
365.629–308.14 MYA
Angiospermae
274.2–125 MYA
Arecales
118–116 MYA
> 2,400 species
Poaceae
65–56 MYA
>12,000 species
Bambusoideae
44–42 MYA
>1,575 species
Ficus sp.
75.0–48.5 MYA
> 800 species
> 300,000
species
Earliest Embryophyta
515.5–469 MYA
Pinus 150 MYA
> 1000 species
Gymnospermae
Bryophyta, Earliest moss, 515.5–330.7 MYA
> 12,000 species
Bryophyta
Originate of algae
1891 – 469 MYA
Abundances of green algae 94 MYA
9,000 - 12,000 species
Chlorophyta
Major extintion event causing major diversity loss
440 MYA - Ordovician-Silurian extinction (86 % Loss)
365 MYA - Late Devonian extinction (75 % Loss)
252 MYA - Permian-Triassic extinction (96 % Loss)
201.3 MYA - Triassic-Jurassic extinction (80 % Loss)
94 MYA - OAE2 extinction event (mainly loss of marine inverterbrates)
66 MYA - Cretaceous-Paleogene extinction (60-76 % Loss)
Holocene extinction (11,700 years ago – present)

◂**Fig. 27** An overview of fungal diversification. The fungal evolution data were retrieved from Liu et al. (2017), Hongsanan et al. (2020), Hyde et al. (2020a, b, c, d); the Pangaea dispersal data were retrieved from Peace et al. (2020); the relationship of different kingdom and plants were retrieved from Dahlgren et al. (2012), Baker and Couvreur (2013) and Eguchi and Tamura (2016); Insect divergence estimates were retrieved from Condamine et al. (2016), Shin et al. (2021); fish divergence estimates from Nelson et al. (2006) and Long et al. (2014); reptile divergence estimates from Sues (2019); mammal divergence estimates from Senft and Macfalan (2021); timeline for Earth's: Burgess et al. (2014); chronostratigraphic Chart: Cohen et al. (2012, 2013). E = Early, M = Middle, L = Late. The pictures (fungi and moss) were from the authors. The drawings (animal and plants) were retrieved from Microsoft power point graphic and the figure was illustrated with Adobe Illustrator CC 2019 (Adobe Inc.)

Observations on the potential of environmental sequencing for mycology

Sanger sequencing has increased the number of species discovered tremendously, but there is also a large amount of data that have been recovered from metabarcoding efforts (Nilsson et al. 2019). The GlobalFungi database contains over 600 million fungal metabarcoding reads across over 17,000 samples with geographical locations and additional metadata from 178 studies (Větrovský et al. 2020; Tedersoo et al. 2021). It is important to integrate these data into the current taxonomic framework to be able to target the large diversity of hitherto poorly explored taxa, including the so-called dark taxa. These are species and lineages that are known only from sequence data and that at present cannot be linked to any physical specimen, culture, or resolved taxonomic name (Ryberg and Nilsson 2018). The challenge for the future will be to develop specific ways (media, baits) to target these taxa and to consider protocols for naming species known only from DNA sequences. Another challenge is that many environmental sequencing efforts have targeted Europe and North America, which has left many countries in other parts of the world significantly under-sampled in this regard. The majority of the new species in the present study are described from Asia, which offers an outlook on the potential to discover new species from environmental samples from Asia.

Beltrania, *Capronia*, *Distoseptispora*, *Peroneutypa* and *Vanakripa* are expected to have a high diversity in environmental samples as they are commonly found as saprotrophs. This is reflected in the large number of species hypotheses recorded for *Capronia* and *Distoseptispora* with 571 and 101 sequences, respectively in UNITE (Table 4). The highest number of sequences were recorded in *Paraconiothyrium* with over 700 sequences classified as 37 species hypotheses. The lowest number of species hypotheses was recorded in *Endocalyx* (one SH) and *Vanakripa* (two SHs). *Apiospora* was recently synonymised with *Arthrinium*, and there are 72 species hypotheses classified as *Arthrinium* representing some *Apiospora* species. The low number of species hypotheses in some genera could be due to the lack of available ITS sequences in GenBank or because metabarcoding sequences are usually not deposited in GenBank (Hawksworth and Lücking 2017). All in all, it seems reasonable that a considerable number of new species are recoverable through environmental sequencing, and the present study hopes to motivate researchers to look beyond species that form fruiting bodies and those might not be straightforward to raise in culture.

Evolution

Divergence time studies suggest that almost all true fungi have a single common ancestor. It is hypothesised that the earliest fungi may have evolved about 1010–890 MYA (Fig. 27) and lived at the mouth of a river (Loron et al. 2019). They were probably aquatic organisms with a flagellum before integrating into the terrestrial environment (Heckman et al. 2001). The fossil record shows that fungi were abundant, and they may have been the dominant life form on earth about 250 MYA (Loron et al. 2019). Taxa of *Apiosporaceae* diverged around 18 MYA, and the ancestor diverged around 94 MYA, which correlates with the estimated diversification of *Poaceae* in the Cretaceous–Paleogene period (Hyde et al. 2020a). *Apiospora* species are mainly associated with *Poaceae* and also with a variety of other hosts (Sharma et al. 2014; Pintos and Alvarado 2021). *Bambusicolaceae* and the *Bambusoideae* hosts diversified around 44–42 MYA (Hongsanan et al. 2020), which could explain the host-specificity in most *Bambusicolaceae* taxa. *Herpotrichiellaceae* emerged during or after the Cretaceous–Paleogene extinction event at 75–50 MYA (Teixeira et al. 2017). *Herpotrichiellaceae* species have different ecological preferences and exhibit highly diversified lifestyles, which could be the result of adaptation to new or different hosts after the extinction event. *Distoseptisporaceae* diverged around 44.21 MYA, following the Tertiary–Cretaceous extinction event, which resulted in the loss of the majority of plant and animal species (Phillips et al. 2019; Hyde et al. 2020a). This may have favoured the saprotrophic lifestyles of *Distoseptispora* and allowed them to associate with several hosts.

There are approximately 60,000 species of monocotyledons, including the most prominent monocotyledon families *Arecaceae* (palms) and *Poaceae* (true grasses). Numerous fungal species from palms presumably remain to be discovered in *Bartalinia*, *Neodeightonia*, and the lesser-known genus *Endocalyx*. These genera are estimated to have diversified in the Paleogene or late Cretaceous. The evolution and diversification of *Arecaceae* (106.6–89.8MYA) and *Poaceae* (65 MYA) is estimated to have occurred during major diversification events of the monocotyledons, which appeared in

the late Cretaceous (150–140 MYA to late Jurassic–early Cretaceous) (Soltis and Soltis 2004). This was a time of great productivity in the world's oceans and the main diversification of angiosperm plants, and also the time when several continents separated due to plate tectonics (Soltis and Soltis 2004). Therefore, this might suggest that extensive sampling of monocotyledons in different continents is likely to yield a large number of species as they evolved 150–140 MYA. The loss of biodiversity is ongoing due to various factors such as extinction events, loss of natural habitat, the overuse of natural resources, overpopulation, global warming, and human-induced pollution (Dunlap and Jorgenson 2012). The introduction of foreign plants by accident (e.g., weeds) such as trade and animal migration has furthermore led to the loss of species in agriculture, forestry and industry (e.g., eucalyptus and rubber) (Thuiller et al. 2008). The impact of global warming has prolonged the growing season of plants in terrestrial ecosystems (Linderholm 2006). As a result, plants could alter the community composition and deplete soil nutrients, which would make the soil uninhabitable for other plants, animals, insects and micro-organisms (Jobbagy and Jackson 2001; Wagg et al. 2014; Pugnaire et al. 2019).

The climate change effects on biodiversity have resulted in a need for more effective ways to discover species (Volodin et al. 2013). Novel algorithmic approaches for analyzing sequence data combined with rapidly expanding DNA barcode libraries could provide a potential solution (Kokkonen 2015). There is a need to establish how many species are likely to be discovered before some host plants become extinct (Costello et al. 2013). This study suggests that there is some level of host-specificity as a result of the co-evolution of fungal groups and their respective hosts. Therefore, extensive studies of hosts that co-evolved with fungal groups are likely to warrant the discovery of a large diversity of novel fungi. An important factor in predicting fungal numbers is whether species are host-specific or generalists (Zhou and Hyde 2001). Some species in this study are ubiquitous, whereas some show some level of specificity. Determining host-specificity based on the knowledge of 150,000 fungal species is not likely to be reliable as it represents only 10% of the most conservative estimate of 1.5 million species (Species Fungorum 2021). A large diversity of fungi is likely to be discovered in unstudied countries and hosts, even in small genera such as *Atrocalyx*, *Endocalyx Lignosphaeria, Okeanomyces, Rhamphoriopsis* and *Vanakripa.* There is a need for studies in hot and humid climates which could increase the number of species in many genera.

Concluding remarks

Fungi have been found from all habitats, and many new species have been found in historically understudied regions and habitats (Hyde et al. 2020a, b, c, d). A great diversity is likely to be discovered in tropical and warm-temperate areas (Hillebrand 2004). New fungal species are also likely to be found in areas that have been extensively studied. Thailand has been studied extensively, and yet it continues to be one of the top countries for fungal discoveries (Hyde et al. 2018; Index Fungorum 2021). Metabarcoding has revealed a much larger diversity of fungi than traditional methods, which only targets taxa with visible fruiting bodies or species cultured on artificial media (Wu et al. 2019). A large diversity of undescribed species will likely continue to be discovered by metabarcoding, even in environments that have been extensively studied using traditional methods (Martin-Sanchez and Sáiz-Jiménez 2012; Lindahl et al. 2013; Su et al. 2015; Wang et al. 2015; Wu et al. 2019).

Most fungal species evolved following the great extinction events during the Triassic-Jurassic extinction, where 66–80% of biodiversity on earth became extinct. Much of the evolved diversity followed the Pangaea plate disintegration that started in the Middle Jurassic and formed continental amalgamation in the early Cretaceous. The finally shaped supercontinent was detected in the Cretaceous to Cenozoic, and the event resulted in independent speciation of the modern taxa (Peace et al. 2020). The Cretaceous-Paleogene mass extinction resulted in the loss of biodiversity especially in the vertebrate groups and 80% species-level extinctions of land plants (Wilf and Johnson 2004). The surviving mammals, birds, frogs, and fishes rapidly diversified in the early Cenozoic. During this time, other organisms also independently evolved with an estimated 925,000 insect species, 6,495 mammal species, 32,500 fish species and 18,000 bird species (Burgin et al. 2018; Willis 2018; Cheek et al. 2020).

Fungi have the second-largest estimated species numbers after insects (2–11 million estimated species). Known species of fungi are less than plants, yet the estimates are much higher. Due to the lack of studies and few morphological differences, fungi that evolved with their hosts are likely to be many more fungal species than currently known. There is no reason that fungi should not have been subjected to the same evolutionary pressures and that the numbers of fungi that have evolved are greater than the present evidence has revealed. Fungi have limited morphological characters to differentiate them, and thus large numbers of cryptic species are likely to exist in most genera. We can only establish accurate fungal diversity estimates with extensive molecular studies of fungal species.

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Declarations

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.

Consent to participate All authors have agreed to participate in this research.

Consent for publication All authors have read and approved the submitted manuscript.

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